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Climate change and glacier retreat drive shifts in an Antarctic benthic ecosystem

Ricardo Sahade,^{1*} Cristian Lager,¹ Luciana Torre,¹ Fernando Momo,^{2,3} Patrick Monien,^{4,5} Irene Schloss,⁶ David K. A. Barnes,⁷ Natalia Servetto,¹ Soledad Tarantelli,¹ Marcos Tatián,¹ Nadia Zamboni,¹ Doris Abele⁸

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The Antarctic Peninsula (AP) is one of the three places on Earth that registered the most intense warming in the last 50 years, almost five times the global mean. This warming has strongly affected the cryosphere, causing the largest ice-shelf collapses ever observed and the retreat of 87% of glaciers. Ecosystem responses, although increasingly predicted, have been mainly reported for pelagic systems. However, and despite most Antarctic species being benthic, responses in the Antarctic benthos have been detected in only a few species, and major effects at assemblage level are unknown. This is probably due to the scarcity of baselines against which to assess change. We performed repeat surveys of coastal benthos in 1994, 1998, and 2010, analyzing community structure and environmental variables at King George Island, Antarctica. We report a marked shift in an Antarctic benthic community that can be linked to ongoing climate change. However, rather than temperature as the primary factor, we highlight the resulting increased sediment runoff, triggered by glacier retreat, as the potential causal factor. The sudden shift from a “filter feeders–ascidian domination” to a “mixed assemblage” suggests that thresholds (for example, of tolerable sedimentation) and alternative equilibrium states, depending on the reversibility of the changes, could be possible traits of this ecosystem. Sedimentation processes will be increasing under the current scenario of glacier retreat, and attention needs to be paid to its effects along the AP.

INTRODUCTION

Recent rapid regional warming along the Antarctic Peninsula (AP) has driven massive loss of ice shelves and retreat of tidewater glaciers, together with a reduction of seasonal sea-ice extension (1–3). Surface waters at the Western AP have warmed by almost 1°C in the latter half century and strong surface salinity changes, especially in coastal areas during summer (4, 5). Biological responses are increasingly being predicted from single species to ecosystem levels, including changes in abundance, diversity, and assemblage structure (6–10). However, shifts have been reported particularly in the pelagic system, in phytoplankton with cross-food web links from krill to penguins (11, 12). Although by far most Antarctic species occur in the benthos, to date observed responses from abundant and diverse communities on the seabed have been restricted to only a few species (13, 14). Most of the reported shifts in benthic species were related to catastrophic events, such as ice-shelf collapses, or to the colonization of newly ice-free areas (15–21). Whereas only one taxon, bryozoans, was reported to be affected by the gradual change of a factor driven by climatic change, exhibiting a linear relationship with the increment of ice disturbance (13, 14), major effects at the community level remain unknown (13, 14).

In polar areas, temperature rise is often predicted to be the pervasive factor, for example, the still controversial colonization of spider crabs,

which could severely affect shelf benthic communities by a top-down control that was absent in these ecosystems for millions of years (10, 22, 23). Therefore, most work has been devoted to analyzing temperature effects using physiological and ecological approaches (24). However, in the short term, cascading effects such as ice scouring action and the increased sedimentation caused by glacier retreat seem to be influencing coastal benthos more significantly than temperature directly. Sedimentation effects on community structure or species performance have recently received attention (6, 8, 25–27), which is probably due to the proximity of scientific research stations to glacier termini.

Ecosystem response to climate change is the most pressing issue in future Antarctic research (28), and because of the relative constancy of environmental variables, slow growth rates, and population turnover (9), Antarctic benthic ecosystems can be considered good sentinels for monitoring effects of climate change. The scarce knowledge of most Antarctic areas and especially the present lack of established baselines against which to assess change could be responsible for the paucity of recorded biotic effects of the AP warming. Thus, there is likely an underestimate of current responses in Antarctic benthos.

Here, we carried out a long-term study of a benthic ecosystem in an Antarctic fjord (Potter Cove, King George/25 de Mayo Island, and South Shetland Islands; Fig. 1). We focused on megabenthic assemblage structure and observed major shifts over 15 years. We relate these shifts to factors driven by the recent rapid regional climate change, and the physiological traits of species either particularly sensitive or rather resistant to such changes, by integrating physiological and ecological approaches.

RESULTS

Assemblage structure

The benthic assemblage structure was analyzed at three stations that differed with respect to glacial influence, for example, sediment inputs

¹Instituto de Diversidad y Ecología Animal [Consejo Nacional de Investigaciones Científicas y Técnicas–Universidad Nacional de Córdoba (CONICET-UNC)], Facultad de Ciencias Exactas, Físicas y Naturales, UNC, Avenida Vélez Sarsfield 299, 5000 Córdoba, Argentina.

²Instituto de Ciencias, Universidad Nacional de General Sarmiento, Juan M. Gutiérrez 1150, B1613GSX Los Polvorines, Argentina. ³Instituto de Ecología y Desarrollo Sustentable, Universidad Nacional de Luján, Luján 6700, Argentina. ⁴Institute for Chemistry and Biology of the Marine Environment, Carl-von-Ossietzky Straße 9-11, 26129 Oldenburg, Germany.

⁵Department of Geosciences, University of Bremen, Klagenfurter Straße (GEO), 28359 Bremen, Germany. ⁶Instituto Antártico Argentino, Balcarce 290, Ciudad Autónoma de Buenos Aires C1064AAF, Argentina. ⁷British Antarctic Survey, Natural Environment Research Council, Madingley Road, Cambridge CB3 0ET, UK. ⁸Alfred Wegener Institut for Polar and Marine Research, Columbusstraße, 27568 Bremerhaven, Germany.

*Corresponding author. E-mail: rsahade@efn.uncor.edu

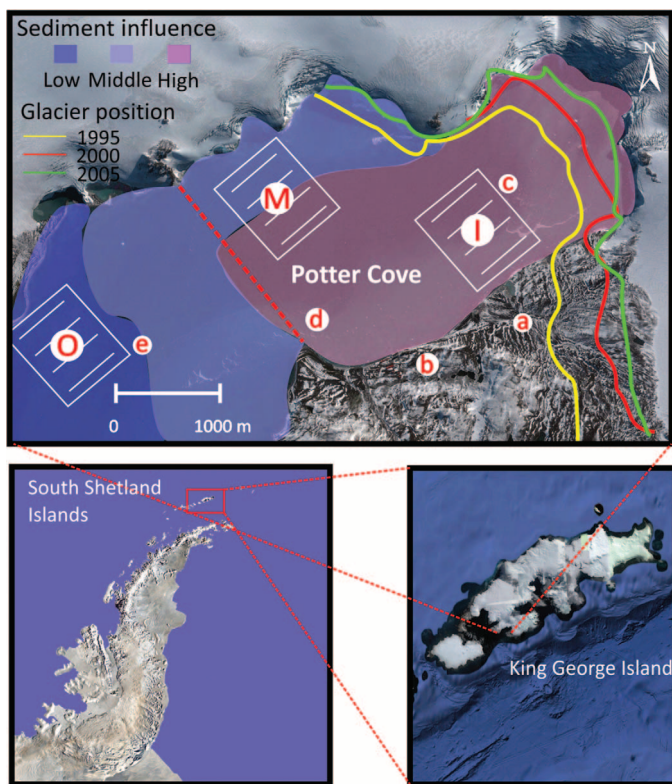


Fig. 1. Map of Potter Cove. Picture of 2010 showing glacier retreat since 1995 and the gradient of sediment influence in different areas of the cove, represented by the color gradient. Rectangles are sampling stations with their depth sampling profiles, 15, 20, 25, and 30 m. The Inner Station (I) is most exposed to sediments carried by (a) Potter and (b) Matias creeks. M, Middle Station; O, Outer Station. Inner and Middle stations are located in the inner cove (c), sheltered from the entrance of big icebergs by a sill at 26- to 28-m depth (d; red dashed line). Outer Station is in the outer cove (e). (c) PO3 sediment core location (bathymetry of Potter Cove shown in fig. S1).

originating from meltwater streams (South Coast creeks, Fig. 1), substratum types, and the hydrographic characteristics of Potter Cove (29, 30). The Inner Station (I; Fig. 1), located at the creeks' debouch, is strongly affected by glacial meltwater and sediment discharge. Silt/clay sediments characterize this station. The Middle Station (M, Fig. 1) is less affected by sediment input than the Inner Station in the shallows (15 to 20 m), but in similar ways between 25 and 30 m (31). In the Middle Station, the substratum is formed by moraine deposits interspersed with fine sediments. The Outer Station (O, Fig. 1) is the least influenced by sedimentation and is typified by hard substrata (Fig. 1) (30, 31). Photographic surveys were undertaken in 1994, 1998, and 2010. Percent cover and densities were estimated for megabenthic taxa (>10 mm) at depths from 15 to 30 m (32). Major shifts were observed in species composition, abundances, and benthic community structure in areas directly exposed to sedimentation, such as the Inner Station and deeper zones of the Middle Station, but not in the Outer Station where the effect of glacial discharge was minimal (Fig. 1) (29–31). The changes in species abundances and community structure are shown in Fig. 2 and by the nonmetric multidimensional scaling (nMDS), analysis of similarity (ANOSIM), and similarity percentage (SIMPER)

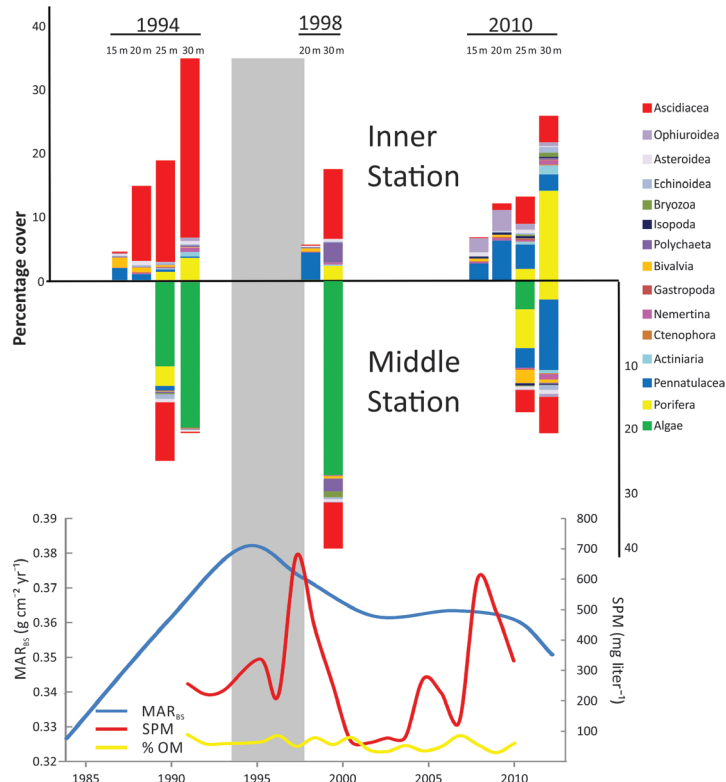


Fig. 2. Species coverage and sediments at Potter Cove. Percentage cover of the different taxa at the Inner Station and at 25- to 30-m depth of the Middle Station, the areas that showed marked shifts in benthic communities at Potter Cove (see details for all the stations and depths in fig. S2). At the Inner Station, trends of decreasing abundance in ascidians and increased pennatulids, sponges, and mobile taxa are visible. Note that at 30-m depth, there are less taxa present in 1998 than in 1994 or 2010. The Middle Station exhibited a shift from macroalgal to zoobenthic dominance, particularly pennatulids, sponges, and ascidians. In 1998, only transects at 20- and 30-m depths were sampled. The lower part of the graph shows mass accumulation rates of bulk sediments (MAR_{BS}), total suspended particulate matter (SPM), and percentage of organic matter (OM) in the time lapse of the benthic surveys. MAR_{BS} and SPM peaked between 1994 and 1998 (gray shadow bar, which could be a threshold for this ecosystem), and the MAR_{BS} values were also the highest registered during the last century (see fig. S3).

analyses (Fig. 3, Table 1, and tables S1 and S2). The nMDS analysis shows that the Outer Station and shallower zones of the Middle Station group together (all depths and sampled years), including the deeper areas of the Middle Station of 1994 and 1998. Whereas the Inner Station and the deeper zones of the Middle Station from 2010 clumped together in three subgroups, the first one grouped samples of 15 and 20 m except the 20-m samples of 1994. These samples were in the second subgroup closer to the deeper areas of the same year and the 30-m samples of 1998. The last subgroup clumped samples of 2010 from 25 and 30 m of the Inner and Middle stations. ANOSIM and SIMPER analyses indicated that these differences were statistically significant, the Inner Station showed a higher overall differentiation, and the pairwise comparison showed that higher dissimilarities were observed at deeper zones of the Inner and Middle stations, and that ascidians, sponges, and pennatulids are the taxa that contributed more to these differences in the Inner Station, whereas algae, ophiuroids,

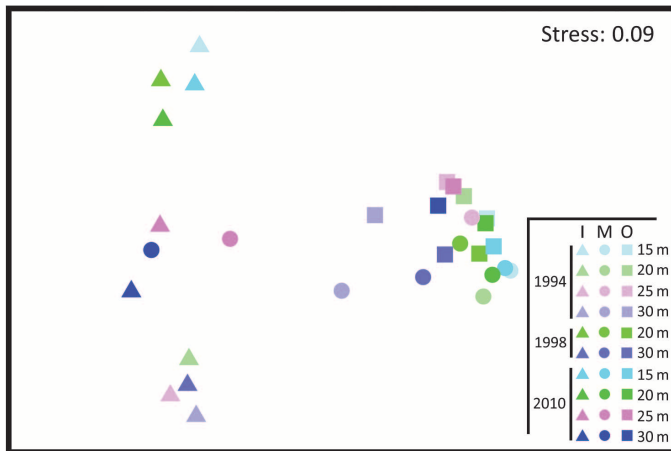


Fig. 3. Shifts of benthic assemblages at Potter Cove between 1994 and 2010. nMDS ordination of relationships among stations, depths, and year, showing high similarity between the Outer Station and the shallower depths (15 to 20 m) of the Middle Station across years. In contrast, the Inner Station and deeper areas of the Middle Station (25 to 30 m) showed a marked change. Analyses were performed using Bray-Curtis similarity index.

ascidians, and pennatulids were responsible for the differences observed in the Middle and Outer stations (Table 1; see tables S1 and S2 for a full pairwise comparison among all sampling dates and stations).

In 1994, the Inner Station was characterized by marked depth zonation, mainly modulated by ice action (32). At 15 m, the bivalve *Laternula elliptica* and the pennatulid *Malacobelemnion daytoni* dominated the benthos. The community was more complex, diverse, and dominated by ascidians with increasing depth. At 30 m, the assemblage was characterized as “sessile suspension feeders with associated fauna, dominated by nonsponges,” in this case, the dominant filter feeders being ascidians [following the ecological classification of Antarctic benthic communities proposed by Gutt (33)]. During this first survey, ascidians occurred at 28.4 ind m^{-2} , occupying 28.1% of cover at 30-m depth. Density of the ascidian *Molgula pedunculata* alone was 16.5 ind m^{-2} , covering 16.5% of space. In 1998, the fauna at the Inner Station was impoverished, with ascidians rare at 20 m, densities had halved, and coverage was reduced to 9.6% at 30-m depth. *M. pedunculata* was the most affected species with just 2.5 ind m^{-2} and 0.5% coverage. The increase in density/percentage cover relationship indicates a decrease in the size of the individuals. In contrast, the sea pen *M. daytoni* increased from 27.1 to 86.8 ind m^{-2} at 20-m depth. In 2010, our third survey of these locations found further shifts: ascidians were even less abundant than in 1998, reduced by a third in density and sixfold in coverage when compared to 1994 (Fig. 2). In contrast, sea pens increased 12-fold in density to 314.2 ind m^{-2} . Furthermore, their depth range was extended. In 1994, they were restricted to 15 to 20 m, but by 2010, they were ubiquitous between 15 and 30 m of the Inner Station, as well as deeper (25 to 30 m) at the Middle Station [that is, areas more affected by sediment input (29–31), Figs. 1 and 2]. Sponges also increased in abundance in 2010 and dominated the Inner Station at 30-m depth. Space occupation by actinians and mobile fauna, such as echinoderms, nemertean, and isopods, increased at the Inner and deeper (25 to 30 m) Middle Stations (Fig. 2). By 2010, the structure first detailed in 1994 had shifted to a “mixed assemblage”

(33), dominated by suspension feeders accompanied by mobile fauna, deposit feeders, scavengers, and predators (Fig. 3 and fig. S4). The major suspension feeders switched from being ascidians to sponges and the pennatulid *M. daytoni*, and echinoderms, isopods, and actinians became more prevalent in the new assemblage. Similarly, in deeper waters (25 to 30 m) at the Middle Station, macroalgae (rather than ascidians) declined from dominance. Between 1998 and 2010, macroalgae were replaced by a fauna similar to that of the Inner Station dominated by *M. daytoni*, ascidians, and sponges (Fig. 3 and fig. S2). This change could be indicative of an extension in the sediment plume darkening the area and thus hindering the establishment and growth of macroalgae in previously suitable areas. In contrast to the changes observed in the Inner and deeper Middle stations, composition, abundances, and benthic community structure changed neither at the Outer Station nor at the Middle station shallows (15 to 20 m) (Fig. 3 and fig. S2).

Environmental factors

In the last two decades, concentrations of SPM increased significantly in the inner Potter Cove (Fig. 1), with mean values increasing from 7.5 mg liter⁻¹ to ca. 15 mg liter⁻¹. In contrast, no significant changes of SPM concentrations were observed at a hydrographic monitoring station close to our outer station (34). Maximum monthly mean values, measured since 1991, peaked in 1997 to 1998, then decreased and peaked again in 2008 to 2009 (Fig. 2). SPM and sediment accumulation at Potter Cove are mainly driven by meltwater runoff from the retreating Fourcade Glacier (35). In the adjacent Maxwell Bay, where Potter Cove is tributary, mass accumulation rates of bulk sediment (MAR_{BS}) have tripled since the 1940s (36). Consistently, MAR_{BS} estimations based on ²¹⁰Pb analyses obtained from a sediment core sample (PO3) in the inner Potter Cove (Fig. 1) indicated a continuous increase of sediment accumulation since 1900, and MAR_{BS} values around 1995 were three times those measured near 1900 and the highest registered so far (Fig. 2 and fig. S3). Both SPM and MAR_{BS} data sets provide evidence for a sedimentation maximum between 1995 and 1998, which was between our first two photographic surveys. However, the second peak in SPM of 2008 to 2009 was not reflected in the MAR_{BS} . These differences can be caused by parameters such as wind speed and wind direction, determining that most of the sediments can be either transported outside the cove or deposited on the bottom. The second SPM peak signal was lacking in the MAR_{BS} data, probably indicating that most of these sediments were carried out from the Inner cove by the prevailing currents and therefore affecting seabed organisms to a lesser extent. Moreover, MAR_{BS} data set integrated the accumulation of sediments on the bottom over longer time periods, offering a closer perspective on benthic fauna than SPM.

Conceptual and mathematical models

Two conceptual models were developed to represent ecosystem responses to environmental changes and processes showing diversity variation with time. A simple simulation of the multispecies spatial competition model under sedimentation, based on Levins competition model, was constructed as well (Fig. 4). In Fig. 4 (A to C), three ecosystem responses to environmental shifts are represented. (A) Linear response to a gradual environmental shift with two different communities at both extremes of environmental conditions. Communities can change between states in a continuous phase shift along with the

Table 1. ANOSIM and SIMPER analyses. (A) ANOSIM pairwise analysis among years within each Station and depth. Note that 15- and 25-m depths of 1998 were compared with 20 m and 20 and 30 m of 1994 and 2010, respectively. (B) SIMPER analysis showing the degree of dissimilarity among years and the relevant taxa. See tables S1 and S2 for overall comparisons of ANOSIM and SIMPER analyses.

A															
Station	Inner				Middle				Outer						
Depth (m)	15	20	25	30	15	20	25	30	15	20	25	30			
1994–1998	0.09	0.24*	0.55*/0.16*	0.15*	0.03	0.05	0.04/0.26*	0.13*	0.10	0.17*	0.17*/0.26*	0.17*			
1994–2010	0.24*	0.41*	0.39*	0.46*	0.07	0.01	0.52*	0.38*	0.07	0.07	0.02	0.08			
1998–2010	0.15*	0.19*	0.31*/0.40*	0.40*	0.10	0.73*	0.39*/0.73*	0.73*	0.08	0.08	0.18*/0.07	0.07			
	Global R: 0.40*				Global R: 0.28*				Global R: 0.21*						
B															
Station	Inner				Middle				Outer						
Depth (m)	15	20	25	30	15	20	25	30	15	20	25	30			
1994–1998	62,78	79,56	89,76	65,7	63,62	75,96	69,61	84,79	82,67	74,32	60,27	65,91	66,41	57,71	61,45
	Pen	Asc	Asc	Asc	Asc	Alg	Alg	Alg	Alg	Alg	Alg	Alg	Alg	Alg	Alg
	Biv	Pen	Pen	Pol	Pol	Ast	Biv	Pol	Asc	Asc	Biv	Biv	Oph	Oph	Asc
	Ast	Biv	Biv	Por	Por	Pol	Asc	Asc	Ast	Pol		Ast	Biv	Asc	Oph
				Pen	Nem	Asc	Ast	Ast		Pen					
								Bivalve		Ech					
1994–2010	63,57	79,46	75,67	78,4	51,98	44,87	93,66		81,53	57,13	58,51	58,78	70,96		
	Oph	Asc	Asc	Asc	Alg	Alg	Alg	Pen	Alg	Alg	Alg	Alg	Alg		
	Pen	Pena	Pen	Por		Ast	Pen	Asc	Ast	Ast	Oph	Asc			
	Biv	Oph	Oph	Pen		Biv	Biv	Alg			Ast	Oph			
	Ast	Biv	Por	Act			Asc	Ech				Oph			
			Biv	Oph			Por	Biv							
								Ech							
1998–2010	66,46	66,61	70,41	85,19	81,86	68,62	70,85	86,08	82,91	92,2	53,73	55,59	61,36	52,79	50,86
	Pen	Pen	Pen	Asc	Por	Alg	Alg	Alg	Alg	Alg	Alg	Alg	Alg	Alg	Alg
	Oph	Oph	Asc	Pen	Asc	Asc	Ast	Pen	Asc	Pen	Biv	Biv	Oph	Oph	Asc
	Biv	Biv	Oph	Pol	Pen	Biv	Biv	Biv	Pen	Asc	Ast	Ast	Biv	Asc	Oph
	Ast	Asc	Biv	Por	Pol		Poli	Asc	Biv	Pol			Ast	Ast	
			Ast	Oph	Act			Por	Pol	Biv					
			Iso		Ech			Ast	Por	Ast					

* Statistical differences of R values.

driving factor. (B) Sudden change between states. Communities can absorb environmental changes until those changes push the system over the threshold limit from one state to the other. States can change according to environmental factors and move forward and backward, so that the threshold for community 1 collapse is the same as the one for its recovery. (C) Thresholds with hysteresis occurring in which different communities can be present under the same environmental conditions, that is, the community has alternative equilibria for a given range of conditions. The thresholds for community 1 collapse and recovery are different, represented by the red dots. Figure 4 (D to F)

shows three possible processes affecting diversity over time: (D) Classical succession. Community 1 is characteristic of early successional stages, and community 2 represents mature stages. In this case, environmental conditions are gradually modified by biological processes and diversity increases gradually. (E) Gradual replacement between communities (for example, in an ecosystem displacement process). Communities 1 and 2 are characteristic of different sets of environmental conditions that gradually change with time. In this case, the intermediate condition shows a higher diversity because there is a mix of both communities. (F) Sudden change between communities due to a nonlinear

response to environmental conditions. Communities 1 and 2 represent two different alternative states. Environmental conditions change gradually with time, but the shift between communities is marked by a tipping point. In this case, the diversity is lower in the intermediate condition. The observed process, especially at 30-m depth at the Inner Station, showed a Shannon diversity index of $H' = 2.24$, $H' = 1.16$, and $H' = 3.11$ in 1994, 1998, and 2010, respectively, suggesting a sudden change between alternative equilibrium states (as shown in Fig. 4, C and F). Finally, Fig. 4G shows a multispecies competition model. The model includes 10 species with similar mortality rates, hierarchical competition, and colonization capacities (which allow stable coexistence). Additionally, a mortality factor (that is, sedimentation) was added to the best competitors. The system was tested using

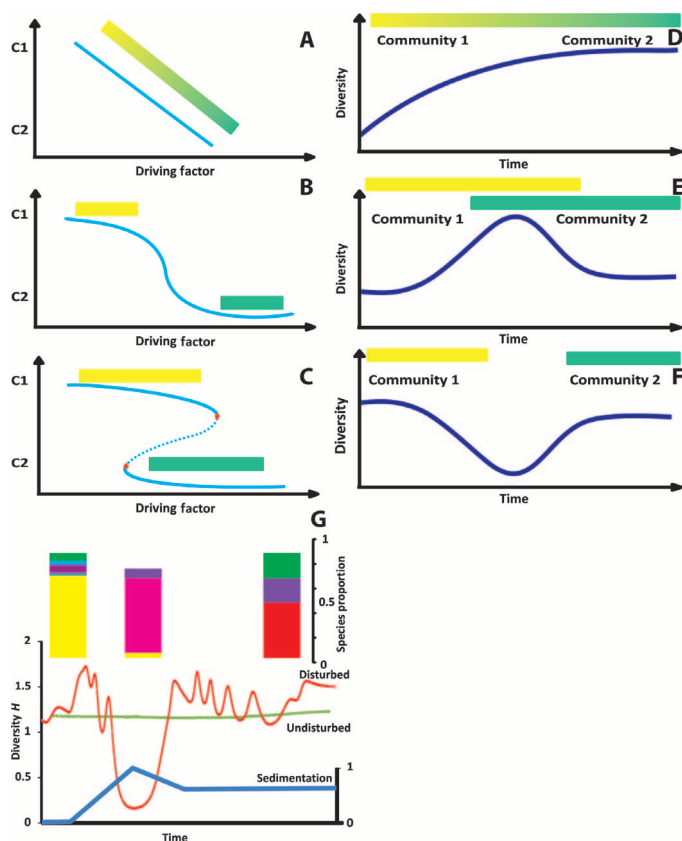


Fig. 4. Community shifts: Conceptual and mathematical models of ecosystem dynamics under environmental changes. (A to C) The plots represent (A) a linear response to a gradual environmental shift with two different communities at both extremes of environmental conditions; (B) a sudden change between states, under which communities can absorb changes in environmental factors until a threshold limit pushes the system from one state to the other; and (C) thresholds with hysteresis occur when different communities can be present under the same environmental conditions. C1, community 1; C2, community 2. (D to F) Benthic shifts and three possible processes showing diversity variation with time. (D) Classical succession: Community 1 is characteristic of early successional stages, and community 2 represents mature stages. (E) Gradual replacement between communities (for example, in an ecosystem displacement process). (F) Sudden change between communities due to a nonlinear response to environmental conditions. (G) A simple simulation of a multispecies spatial competition model under sedimentation based on Levins competition model.

sedimentation that mimics the recorded ones (blue line in a 0 to 1 scale) and without sedimentation (undisturbed system, green line). With sedimentation (red line), diversity diminishes at a critical point, then oscillates and comes back to initial values. However, benthic structure differs from the previous stable state. Bar graphs over the lines show species composition proportion of each state of the disturbed system, and different colors represent different species.

DISCUSSION

Our results clearly show that megabenthic community structures experienced a major shift in the Potter Cove ecosystem. The affected communities were located in areas with higher sediment influence, a factor that also showed a significant increment in the last two decades. Consistently, the more affected and favored groups exhibited different physiological responses to sediment load: ascidians, the most diminished taxon in terms of abundance, showed higher sedimentation sensitivity compared to other nonaffected or boosted species such as *L. elliptica* or *M. daytoni* (25, 26, 31). Therefore, we propose that increased sedimentation could be driving the observed shifts in this benthic ecosystem. However, other factors, such as water temperature, salinity, and chlorophyll a concentrations, were taken into account and have also been monitored at the inner and outer cove sectors continuously for ~20 years (30, 37). Salinity and chlorophyll showed no significant trends during this period, whereas sea surface temperature increased homogeneously across stations in Potter Cove (30, 37). The maintenance of salinity and chlorophyll values and the homogeneity shown by the slight temperature increment is unlikely to explain such different dynamics among the sampled stations. Scouring by large icebergs can be discounted as a possible cause in the deeper areas of the inner Potter Cove, which is separated from the outer cove by a moraine ridge rising to 28 m of water depth (Fig. 1). Changes in scouring by smaller ice fragments would also be unlikely to explain the patterns found, that is, affecting some sessile epifaunal groups greater than others. Traces would also be observable in the photographs. We also exclude top-down or bottom-up regulation as causal processes, because there was neither a significant increment in potential predators (especially for ascidians), for example, asteroids or gastropods, particularly the species *Diplasterias brucei* and *Marseniopsis mollis* (32), nor a change in local primary production (34). Moreover, the Potter Cove benthic ecosystem can be considered as an importing system because the low local primary production (34) is too low to fuel the high secondary production observed in the benthos (32), which is therefore more likely sustained by advection of allochthonous organic matter. Hence, increased sedimentation driven by glacier retreat, caused in turn by the rapid warming of the AP, appears the most likely forcing factor that explains the observed changes in Potter Cove benthic communities between 1994 and the present.

Reported shifts in Antarctic benthos are very scarce, limited to a few species, and associated with acute environmental changes (15–19). Recolonization after the Larsen Ice-Shelf collapse (18–20) and glacial retreat at Potter Cove (21) were also related to rapid environmental changes. However, effects produced by gradual shifts in factors related to the warming of the AP have only been reported for bryozoans. Recordings showed a reduction in abundance that was linearly related to the increment of ice disturbance favored by reduced sea-ice formation (13, 14). In Potter Cove, we have shown a change at the level of

the entire epibenthic community, shifting from “ascidian-dominated filter feeders” to a mixed assemblage, two characteristic defined assemblages that can be found in different Antarctic locations (33).

The sudden shift in the benthic community coincident with peaks in sedimentation may point to the existence of critical thresholds and poses the question of whether these shifts are reversible or not. If not, the shift would represent a transition to an alternative equilibrium state of the ecosystem. Implications of sudden shifts can be of major importance because gradual changes in environmental variables, such as those observed in sedimentation, can have no or negligible effects until a threshold is reached and then rapid ecosystem shifts take place. If thresholds for the collapse and recovery of the system states do not coincide (hysteresis) then these shifts are difficult to reverse (38, 39), (Fig. 4). The nonlinear nature of interspecific relationships, the physiological responses to sediments observed in some of the involved species (25, 26, 31), and the different communities observed in our first (1994) and last (2010) surveys under similar sedimentation conditions (Fig. 2) suggest that hysteresis could be a possible trait of this ecosystem. The observed intermediate state with fewer taxa than at both extremes of the process contrasts with succession or gradual replacement (for example, ecosystem displacement), further supporting this hypothesis (Fig. 4).

Potter Cove is a fjord system historically subjected to high sedimentation, and abundant and diverse epibenthic megafauna have been described there even under these conditions (32). A recent study of macrobenthos structure in three fjords along the Western AP also reported high diversity and abundance patterns in inner fjords and predicted that sedimentation resulting from rapid warming could be an important factor affecting these ecosystems (6). The higher diversity found in Antarctic fjords related to adjacent areas suggests that these systems can be considered important hot spots for Antarctic benthic diversity. In contrast, Arctic counterparts are characterized by strong faunal impoverishment toward the glacier front and the absence of epifaunal suspension feeders (40). Our results suggest that although rich, sediment-tolerant, benthic assemblages can establish in Antarctic fjords, their structure and composition depend on sedimentation thresholds. Once such thresholds are surpassed, the system can suddenly shift to another state. Indeed, in Martel Inlet, a fjord close to Potter Cove, observations show much higher sedimentation rates and an impoverished benthic community with epifaunal suspension feeders almost absent (27), a pattern more closely resembling those assemblages described in Arctic rather than Antarctic fjords. The ongoing glacier retreat suggests that sedimentation is likely to be an important factor in coastal ecosystem dynamics and that conditions at Potter Cove could extend along the Western AP in the near future, representing a major threat for these hot spots of Antarctic diversity.

MATERIALS AND METHODS

Sampling design

Photographic surveys were performed during the summer seasons of 1994, 1998, and 2010. Pictures were taken with a Nikonos V camera, using a 15-mm lens and a Nikonos SB-104 strobe in 1994 and 1998 and a Sony SR12 Digital Camera in 2010. The cameras were mounted on an aluminum frame of 50 × 50 cm, allowing quantitative estimations of densities (ind m²) and coverage of identifiable taxa (>1 cm).

At each station, photographs were taken by SCUBA diving following particular depth profiles of 15, 20, 25, and 30 m. Areas shallower than 15 m were not sampled because they were almost devoid of epifauna due to ice action, and deeper waters were not accessible by SCUBA diving due to dive regulations. For the analyses, at least 50 pictures of each depth and station were processed and the same procedure was used in each survey.

Images were analyzed first by counting all the individuals of the taxa present, except for colonial forms (that is, sponges or bryozoans) and macroalgae, and then the percentage cover of all taxa was estimated, superposing a grid of 100 dots randomly distributed on the image.

Statistical analysis

Raw data of percentage cover obtained from photo-transects were square root-transformed to down-weight the influence of the most dominant taxa, and then a similarity matrix was constructed using the Bray-Curtis similarity distance. Three multivariate procedures were applied on the basis of the similarity matrix. In the first term and to visualize changes in species composition and assemblage structure across stations, depths, and time, an indirect ordination analysis, nMDS, was used. Then, for testing spatial differences and temporal changes in surveyed assemblages, an ANOSIM was used. This analysis provides a test statistic *R* that varies between −1 and 1, the zero value representing the null hypothesis of no differences among a set of samples. Values between 0 and −1 are unlikely as they would indicate higher dissimilarity among replicates within a sample than with replicates from different samples. Generally, *R* lies between zero and 1, representing the magnitude by which samples differ (41, 42). Finally, to identify the taxa responsible for the overall dissimilarity between two groups of samples, the SIMPER procedure was used. Multivariate analyses were performed using the PRIMER and PAST software packages (41, 43).

Equation of the Levins hierarchical multispecies spatial competition model. The equation of the Levins hierarchical multispecies spatial competition model (44) after the modifications of Hastings (45) and Tilman (46) is as follows

$$\frac{dp_i}{dt} = c_i p_i \left(1 - \sum_{j=1}^i p_j \right) - m_i p_i - \left(\sum_{j=1}^{i-1} c_j p_j p_i \right) - s_i p_i S$$

where p_i is the abundance of species i , c_i is the colonization efficiency of species i , m_i is the mortality rate of species i , s_i is the sensitivity to sedimentation of species i , and S is the sedimentation rate.

Then, species i could only colonize the fraction of space that is free, that is, the space fraction that has not already been occupied by that species i or by species that are better competitors than i . Each species i can colonize this fraction as a function of its abundance (p_i) and its own colonization efficiency. The space is never completely full because each species has its own mortality rate that is constantly enhancing space. There is also a competition term that includes the abundance that species i lost as a function of its abundance (p_i) and the abundance (p_j) and colonization efficiency (c_j) of each better competitor species j . For this particular work, a term of mortality due to sedimentation S was included. This mortality is a function of the species abundance (p_i), its sensitivity to sedimentation (s_i), and the sedimentation rate (S).

Sediments and mass accumulation rates. Total SPM was measured gravimetrically after filtering 0.25 to 2 liters of seawater through combusted preweighed 25-mm Whatman GF/F filters. After filtration, filters were rinsed twice with distilled water to remove sea salt, then dried for 24 hours at 60°C, and weighed again. Filters were then burned at 500°C for 4 hours to obtain the ash-free dry mass to estimate the content of organic matter. Samples were taken monthly since 1992 at two stations in Potter Cove [see details by Schloss (34)].

²¹⁰Pb analyses were carried out for five samples obtained from a 34-cm-long sediment core (PC/P03), which was obtained in the inner Potter Cove (Fig. 1). Activities of radionuclides (²¹⁰Pb, ²¹⁴Pb, and ²¹⁴Bi) were measured by γ -spectrometry (Ge-detector, GWC 2522-7500 SL, Canberra Industries Inc.) and processed with Genie 2000 3.0 (Canberra Industries Inc.). Counting statistics showed a lack of precision lower than 5% for the samples except those with very low ²¹⁰Pb activity (<0.08 Bq g⁻¹). The accuracy of this method was tested by using a standard reference material similar in matrix composition to the sediment samples (UREM-11) and was better than 10% for all radioisotope concentrations. To take account of changing sedimentation rates with time, the age of each sediment slice and mass accumulation rates of bulk sediments (MAR_{BS}) were determined according to the constant flux model of Sanchez-Cabeza and Ruiz-Fernández (47), which is based on the constant rate of supply model of Appleby and Oldfield (48). ²¹⁰Pb excess data were calculated by the difference of the total ²¹⁰Pb activity and the supported ²¹⁰Pb flux, which is given by the average of ²¹⁴Pb and ²¹⁴Bi activities. Activities of radionuclides of lacking sediment samples were interpolated at 1-cm steps.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/1/10/e1500050/DC1>

Fig. S1. Bathymetry of Potter Cove.

Fig. S2. Coverage of the different taxa at each of the stations, depths, and dates sampled at Potter Cove.

Fig. S3. ²¹⁰Pb profile and mass accumulation rates of bulk sediments (MAR_{BS}) for Potter Cove.

Fig. S4. Benthic assemblages in 1994 and 2010.

Table S1. Overall pairwise comparison of ANOSIM analyses among stations, depths, and dates.

Table S2. SIMPER analyses among depths and dates within each station.

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