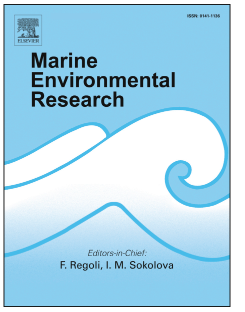
Journal Pre-proof



Antarctic ascidians under increasing sedimentation: physiological thresholds and ecosystem hysteresis

L. Torre, G. Alurralde, C. Lagger, D. Abele, I.R. Schloss, R. Sahade

PII: S0141-1136(21)00033-7

DOI: https://doi.org/10.1016/j.marenvres.2021.105284

Reference: MERE 105284

To appear in: *Marine Environmental Research*

Received Date: 5 December 2020

Revised Date: 11 February 2021

Accepted Date: 15 February 2021

Please cite this article as: Torre, L., Alurralde, G., Lagger, C., Abele, D., Schloss, I.R., Sahade, R., Antarctic ascidians under increasing sedimentation: physiological thresholds and ecosystem hysteresis, *Marine Environmental Research*, https://doi.org/10.1016/j.marenvres.2021.105284.

Title: Antarctic ascidians under increasing sedimentation: physiological thresholds and ecosystem hysteresis.

Authors:

Torre, L.[a,b] ; Alurralde, G.[a,b]; Lagger, C.[a,b]; Abele, D.[c]; Schloss, I.R.[d,e,f] Sahade, R.[a,b]

Affiliations:

[a] Universidad Nacional de Córdoba, Facultad de Ciencias Exactas, Físicas y Naturales, Av. Vélez Sarsfield 299, 5000, Córdoba, Argentina
[b] Instituto de Diversidad y Ecología Animal (Consejo Nacional de Investigaciones Científicas y Técnicas), Córdoba, Argentina.
[c] Alfred Wegener Institute (AWI), Helmholtz Centre for Polar and Marine Research. Bremerhaven, Germany

[d] Instituto Antártico Argentino, San Martín, Provincia de Buenos Aires, Argentina
[e] Centro Austral de Investigaciones Científicas, CONICET, Ushuaia, Argentina
[f] Universidad Nacional de Tierra del Fuego, Ushuaia, Argentina

CRediT author statement: LT, RS and DA conceived the ideas and designed methodology; LT performed samples and data analysed and led the writing of the manuscript; GA: performed sampling and collaborated in data analysis, RS and CL collected and analysed population data.; IS: collected and analysed environmental data; All authors participated in discussion and writing and gave final approval for publication.

Title: Antarctic ascidians under increasing sedimentation: physiological thresholds and ecosystem hysteresis.

Authors:

Torre, L.[a,b*]; Alurralde, G.[a,b]; Lagger, C.[a,b]; Abele, D.[c]; Schloss, I.R.[d,e,f]; Sahade, R.[a,b*]

Affiliations:

[a] Universidad Nacional de Córdoba, Facultad de Ciencias Exactas, Físicas y Naturales, Av. Vélez Sarsfield 299, 5000, Córdoba, Argentina

[b] Instituto de Diversidad y Ecología Animal (Consejo Nacional de Investigaciones Científicas y Técnicas), Córdoba, Argentina.

[c] Alfred Wegener Institute (AWI), Helmholtz Centre for Polar and Marine Research. Bremerhaven, Germany

[d] Instituto Antártico Argentino, San Martín, Provincia de Buenos Aires, Argentina

[e] Centro Austral de Investigaciones Científicas, CONICET, Ushuaia, Argentina

[f] Universidad Nacional de Tierra del Fuego, Ushuaia, Argentina

[*] **Corresponding Authors**

Instituto de Diversidad y Ecología Animal (Consejo Nacional de Investigaciones Científicas y Técnicas) - Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Av. Vélez Sarsfield 299 (5000), Córdoba, Argentina.

torreluciana@gmail.com

rsahade@unc.edu.ar

Research data for this article

All raw data generated in this study is deposited and accessible at PANGEA, https://doi.org/10.1594/PANGAEA.925354 (Torre et al., 2020a). Abundance and densities of benthic organisms close to the Fourcade glacier front at Potter Cove, South Shetland Islands, Antarctica, from December 2009 to February 2010 were taken from PANGAEA, https://doi.org/10.1594/PANGAEA.879315 (Laggert et al., 2017b). Suspended particulate matter measured on water samples of two stations at Potter Cove, King George Island, Western Antarctic Peninsula (1992-2010) were downloaded from PANGAEA, https://doi.org/10.1594/PANGAEA.745596 (Schloss, 2010). Ascidians respiration rate under different TSPM concentration were extracted from PANGEA, https://doi.org/10.1594/PANGAEA.925202 https://doi.pangaea.de/10.1594/PANGAEA.925202 (Torre et al., 2020b). The rest of the data that support the findings of this study are available from the corresponding author upon reasonable request.

Highlights

- Ascidians gut content amount and quality correlates with TSPM gradient and glacier distance.
- SFG indicates currently suitable growth conditions in spite of high TSPM.
- SFG_{TSPM} allowed us to identify environmental thresholds and explain community changes.

Abstract

Glacier melting sediment inputs affect coastal ecosystems on the Antarctic Peninsula. In Potter Cove (South Shetland Islands, Antarctica), the shift from an “ascidian dominated” to a “mixed” assemblage has been linked to sedimentation. However, in recently described newly ice-free areas ascidians became dominant in spite of total suspended particulate matter (TSPM) concentrations, which are the highest measured in Potter Cove. Here, we compared the gut content and energy reserve of three ascidian species at three stations under different TSPM regimes. All analyzed species had a higher gut content with lower %OM at these newly areas. A theoretical relationship between the scope for growth for the targeted ascidians and TSPM explained assemblages' recorded change but failed to explain current ascidians distribution. The results may indicate the existence of a TSPM threshold that allows the spatial coexistence of alternative stable states at benthic Potter Cove system.

Keywords: alternative stable states, Antarctica, ascidians, glacier retreat, hysteresis, scope for growth, sedimentation, suspension feeders.

1. Introduction

Along the Western Antarctic Peninsula (WAP), glacier retreat associated with climate change is opening newly ice-free areas, available to enhanced primary production and new benthic colonisation (Campana et al., 2018; Lagger et al., 2018; Peck et al., 2010; Quartino et al., 2013). These newly ice-free areas in nearshore regions are strongly influenced by the seasonal discharge of inorganic particles washed from land (Dierssen et al., 2002; Gutt et al., 2015; Kim et al., 2018; Moon et al., 2015), affecting shallow-water ecosystems functioning (Clark et al., 2017; Kim et al., 2021; Thrush et al., 2004), from population down to the level of gene expression (Abele et al., 2017; Torre et al., 2017). Key planktonic and benthic suspension feeders are massively constrained in respiration and growth and even suffer massive die outs and biomass loss as c consequence of sedimentary coverage of respiratory organs and body surfaces, and the ingestion of lithogenic particles (Dayton et al., 2016; Fuentes et al., 2016; Pakhomov et al., 2003; Philipp et al., 2011; Slattery and Bockus, 1997). The inability to move and avoid local stress conditions in space and time renders sessile Antarctic organisms particularly vulnerable to the ongoing rapid Antarctic environmental changes. In this sense, it has also been hypothesised that sedimentation of TSPM per se could act as a community shaping factor based on differential sensitivities of each species present. The most tolerant species would stand better, changing competitive relationships, shaping the resulting community even from the earlier recruitment stages (Clark et al., 2017a; Kim et al., 2021; Krzeminska and Kuklinski, 2018; Torre et al. 2017). Understanding the extent to which coastal total suspended particulate matter (TSPM) dynamics affects vital functions and survival of benthic key species will help to predict future Antarctic benthic community composition, and to elucidate ecosystem thresholds (Clark et al., 2017b; Gardner, 2000; Jansenet al., 2018a; 2018b). An ecological threshold is defined by a rapid non-linear change in ecosystem structure and functioning connected with changes in the environmental conditions. Sudden ecosystem shifts are used to determine “threshold values” for environmental parameters, and to define eventual tipping points, leading to switching between alternative stable ecosystem states (Andersen et al., 2009; Folke et al., 2004; Shelkoe et al. 2015; Scheffer and Carpenter, 2003). Rapid climate-related ecological changes of West Antarctic coastal ecosystems offer ideal scenarios to get further insights into ecological concepts such as stability, resilience and sudden shifts (Barnes and Souster, 2011; Dayton et al., 2019; Fillinger et al., 2013; Gutt et al., 2011; Sahade et al., 2015).

Potter Cove on South Shetland Island is one of the best investigated glacial coves of the WAP concerning both the environmental and ecological changes resulting from glacier retreat (Falk et al., 2018; Rückamp et al., 2010; Sahade et al., 2015; Schloss et al., 2012). As a consequence of summer glacier melting and discharge on proglacial rivers that transport lithogenic particles from coastal erosion, forming a shallow sediment admixed freshwater plume of approximately 5m depth extension flows toward Maxwell Bay (Meredith et al., 2018) (see Fig. 1). The intensity with which these sediments are deposited within the cove differs spatially across different sections. Because internal cyclonic surface current extends residence time of the water mass (Lim et al., 2013), major deposition of fine particles occurs in the inner cove area, next to the glacier (Wölfl et al., 2014).

Between 1994 and 1998, a remarkable reduction in the abundance of some ascidians and the expansion of an assemblage dominated by pennatulids, bivalves and some Porifera was observed in sediment covered areas of the cove (Sahade et al., 2015). This sudden shift from an “ascidian dominated assemblage” to a “mixed assemblage” was associated with an increase in the concentration of TSPM (Bers et al., 2013; Schloss et al., 2012) and coincided with the rates of sediment mass accumulation in Maxwell Bay (Monien et al., 2011). These two assemblages were hypothesised to represent alternative stable ecosystem states, as the sudden shift in the benthic community coincided with a massive sedimentation event in 1995 after which the ascidian populations did not recover (Sahade et al., 2015). This interpretation was further supported by experimental evidence showing that for the same TSPM concentration, ascidians' energy demand is higher than other tested suspension feeders (*Laternula elliptica*, *Malacobelemnon daytoni*), and are therefore considered more sensitive to this factor (Philipp et al., 2011; Torre et al., 2012). Moreover, under high TSPM concentrations carbon uptake efficiency is constrained in ascidians, leading to an energetic deficit that compromises their growth and reproduction (Alurralde et al., 2019; Armsworthy et al., 2001; Torre et al., 2014). Additionally, ecological modelled predictions strongly suggest that TSPM is a key factor influencing ascidian capacity to colonise and survive, jeopardising long-term population success (Momo et al., 2008; Torre et al., 2017). Interestingly, the most TSPM sensitive ascidians (Torre et al., 2012; 2014) were able to abundantly colonise a small rocky island (<80 m long and ~30 m depth) which emerged under the retreating glacier around the early 2000s, although they were directly and massively exposed to glacier sediment discharge. Indeed, solitary ascidians were the dominant macrobenthic group (with 47.1 (±1.7 s.e.) % of coverage and a density of 308.6 (±51.1 s.e.) individuals m^{-2}) on the steep rocky walls of this island (Lagger et al., 2018). It is therefore essential to understand the actual sensitivity/vulnerability of these species and the community tipping points to effectively contribute to a broader ecological debate in the context of fast and pressing Antarctic environmental changes (Gutt et al., 2013).

In such challenging environmental conditions, growing on a nearly vertical wall of a recently ice-free rocky island, could be beneficial for benthic suspension feeders i) because sediment coverage on the organisms may be less detrimental than in horizontally positioned specimens (Lagger et al., 2018), ii) the current system in the water column may be more effective in surface cleaning, iii) resuspension of deposited sediments may not reach up to the midwater position of these animals.

Nevertheless, this failed to explain the dominance of ascidians on the horizontal substrate provided by the new areas next to the glacier (Lagger et al., 2017a). Similarly, in highly impacted new ice-free areas within the adjacent Marian Cove (25 de mayo/King George Island, Antarctica), ascidians of very low sizes reach high abundances as in Potter Cove (Kim et al., 2021). Such growth arrestment could be due to the scarce organic material they receive and the energy investment on processing inorganic matter. Therefore, in such a contradictory context, we aim to understand how the ascidian species are able not only to survive at high TSPM concentrations (with low orgánic matter content) but to dominate pioneering communities in glacial sedimentation areas. Another question relates to how they can maintain a positive growth under such intense inorganic sedimentation pressure. Here we propose the following hypotheses

- Ascidian populations are subjected to different sedimentation pressures along the main axis of the cove, which are configured by glacier discharge.
- Ascidians are in their tolerance range of TSPM concentrations. Therefore, they are still not constrained by the current environmental conditions.
- TSPM concentrations are currently in the environmental range of ecological hysteresis, allowing the spatial coexistence of both described assemblages.

The aim of this work was first, to determine to what extent the described summer sediment inputs from glacier discharge, and consequently the increase of TSPM, is affecting the most conspicuous ascidians species of Potter Cove, and secondly, how historical TSPM records could have shaped the ascidian populations within the cove. To do so, we analysed bulk gut content and energy reserve of collected specimens of the most conspicuous ascidians species from three sites in Potter Cove with different estimated sedimentation impact. Additionally, we estimated the scope for growth (SFG, i.e., the remaining of the energy available for growth beyond that required for maintenance) under different TSPM scenarios. Furthermore, we tested SFG under TSPM historical data and contrasted it with ascidians biomass data, and discussed the implications of energy limitation on species abundance and distribution in different areas of Potter Cove. Our results are discussed in the frame of the potential existence of alternative states of the benthic assemblage system.

2. Materials and Methods

2.1. Study area and animal sampling

Sampling was carried out in Potter Cove, Isla 25 de Mayo/King George Island, South Shetland Archipelago (S 62º14’, W 58º40’) during February 2011, using the facilities of the Argentine-German Dallmann laboratory on the Argentinean Carlini station. Three sampling areas, known to differ in the intensity of glacial sediment deposition (Jerosch et al., 2018; Monien et al., 2017), were chosen: two related to the Long-Term Ice-Free Areas (LTIFA) historically monitored stations (Sahade et al., 2015) and one corresponding to the New Ice-Free Areas (NIFA) recently described (Lagger et al., 2017a; Wölfl et al., 2016) (Fig 1). Specifically, the Outer sampling site that corresponds to the LTIFA Outer Station (62° 14′ 10″ S; 58° 42′ 48″ W) is situated in the Northern part of the opening toward Maxwell Bay and is characterised by the presence of a hard-bottom substrate and very low TSPM as it receives the inflowing water from Maxwell Bay. This station has only low glacial influence, being considered a meltwater unaffected marine habitat (Jerosch et al., 2018). The Middle Station correspond to the LTIFA Inner Station (62° 13′ 54″ S; 58° 40′ 06″ W) is characterised by soft-bottom substrate and an intermediate sedimentation influence, and it is currently considered a typical Fjord habitat (Jerosch et al., 2018). Finally, the Inner station corresponding to the NIFA Station (62° 13′ 23,6″ S, 58° 38′ 41,0″ W) comprises the rocky island mentioned above, directly in front of the glacier. It has the highest sedimentation influence being considered a meltwater affected Fjord habitat (Jerosch et al., 2018). Detailed information of station characteristics is summarised in table 1.

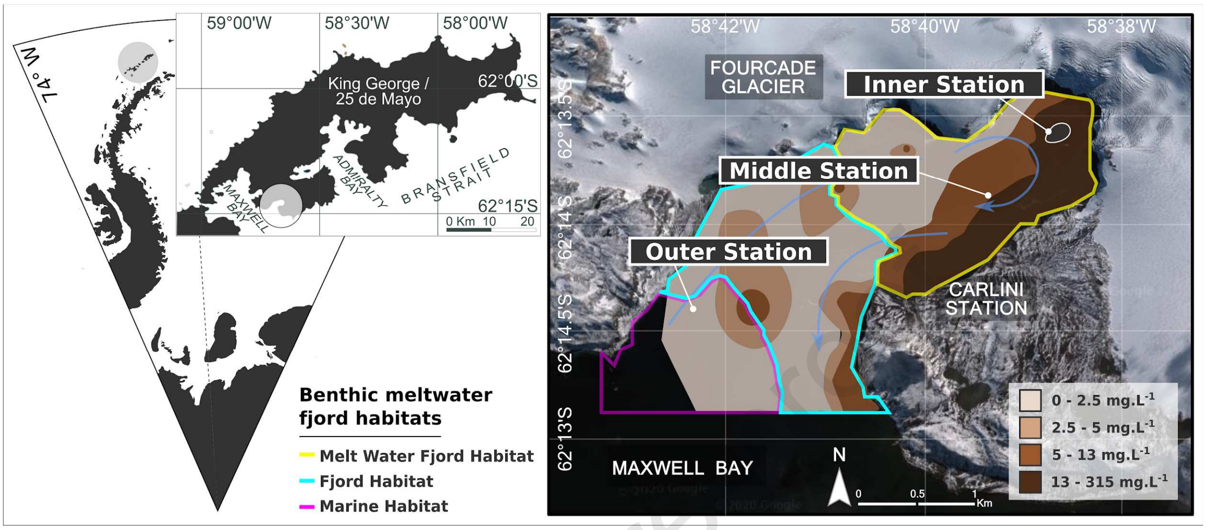


Figure 1: Potter Cove location on Isla 25 de Mayo/King George Island, in the northern Antarctic Peninsula. Sampling station locations are indicated as Outer, Middle and Inner Stations. The black area on Potter Cove map corresponds to the Fourcade Glacier. The white rectangle in the grey area represents Carlini station location. Colour lines mark the boundaries of benthic meltwater fjord habitats in Potter Cove: meltwater fjord habitat (yellow), fjord (light blue) and maritime (pink) habitats (less influenced by meltwater streams) according to Jerosch et al. (2018). Average spatial distribution of TSPM concentration in the surface waters of Potter Cove during summer 2010/2011 (from Monien et al., 2017) is indicated in a brown colour scale.

Table 1: Summary characteristic of sampling stations at Potter Cove (South Shetland Islands, Antarctica)

Station	Inner	Middle	Outer	Source
Distance from glacier front (km)	0.24	1.27	4.14	
Georeference	62º13’23.6’’S 58º38’41’’W	62º13’54’’S 58º40’06’’W	62º14’10’’S 58º42’48’’W	
Substrate type	Rocky island surrounded by medium silt	Fine and very fine sandt	Stone	Wölfl et al. (2014)
Age (ice-free exposure)	~15 years	> 60 years	> 60 years	Wölfl et al. (2016)
Sediment Accumulation Rate (SAR); g cm^{-2} y^{-1}	1.14	0.55	0.0855	Monien et al. (2017)
Nomenclatures used by other authors	-	E1	E2	Schloss et al. (2012)
	IZ	-	OZ	García et al. (2016)
	-	Inner Station	Outer Station	Sahade et al. (2015)
	New Ice-Free Areas	Long-Term Ice-Free Areas	Long-Term Ice-Free Areas	Lagger et al. (2017a)
Habitat type	Melt Water Fjord	Fjord	Marine	Jerosch et al. (2018)
TSPM concentration*	13-315 mg L^{-1}	5-13 mg L^{-1}	0-2.5 mg L^{-1}	Monien et al. (2017)
Solitary ascidians dominance relationship	Cv>Mp>>Ca>Ac**	Mp>>>Ac>Ca>Cv**	Mp>Cv>>Ca>Ac**	Sahade et al. (2015) Lagger et al. (2017a)

*Total suspended particulate matter (TSPM) concentration in the surface waters of Potter Cove during summer 2010/2011.

**Solitary ascidians species considered: *Cnemidocarpa verrucosa* (Cv), *Molgula pedunculata* (Mp), *Ascidia challengeri* (Ac) and *Corella antarctica* (Ca).

Between ten and fifteen specimens of the most conspicuous solitary ascidians species were carefully taken by SCUBA divers from each station at 20 m depth. As many other epibenthic groups in Antarctica, they can inhabit either hard and soft-bottoms. In Potter Cove soft bottoms, these species' larvae can attach themselves to shells, pebble, stones and even sand aggregations (Tatián et al., 1998).

Specimens of *Molgula pedunculata* of 52.2±8.29 grams of fresh mass (g fm) (mean±SE) *Cnemidocarpa verrucosa* of 121.06±10.55 g fm, and *Corella antarctica* of 152.28±17.09 g fm were collected. The chosen species represent erect and flat-form body shapes that respond differently to sedimentation. Not enough specimens of *Ascidia challengeri* were found in the Outer station (even when they have been thereafter recorded (Sahade et al., 2015)), so we excluded this species from this part of the analysis. Characteristics of these species are summarised in Table 2.

Immediately after collection, each specimen was dissected. Note that before dissection the intestinal tract (stomach and intestine portion) was clamped at both ends with surgical clamping forceps to recover its complete content. The total gut content was retrieved by opening one of the extremes of the digestive tract inside a tube and leaving the content to fall into it. Finally, the inner walls of the digestive tract were rinsed off by running Mili-Q water and collected into the same sample tube. Tissue and gut content samples (tunic, mantle, branchial sac, and emptied intestinal tract) were immediately frozen in liquid nitrogen and stored at −80 °C after dissection.

210 **Table 2:** Summarized characteristic of more conspicuous solitary ascidian species of Potter Cove

Species	*Molgula pedunculata*	*Cnemidocarpav errucosa*	*Ascidia challengeri*	*Corella antarctica*	Source
Order / Family	Stolidobranchia / Molgulidae	Stolidobranchia / Styelidae	Phlebobranchia / Ascidiidae	Phlebobranchia / Corellidae	Tatián et al. (1998); Alurralde et al. (2013)
Body shape	Cylindrical	Pedunculated	Laterally flattened	Laterally flattened	Kott (1969); Moniot et al. (2011)
Muscular development	Scarce development	Well developed	Developed mostly around syphons	Developed mostly around syphons	Kott (1969); Moniot et al. (2011)
Feeding behavior	Active filter-feeder	Active filter-feeder	Active filter-feeder	Active filter-feeder	Kott (1969); Moniot et al. (2011)
Pumping rate (L d^{-1} g dm)*	4.8	6.24	4.58	3.55	Kowalke (1998);
Squirting behavior	nd**	TSPM dependent	nd	nd	Kowalke et al., (2001); Torre et al. (2014)
Standard Metabolic rate (mg O_2 $gdrm^{-1}$ d^{-1}) (mean ± standard error)	3.47 ±0.92	5.46 ±1.54	2.47 ±0.12	nd	Torre et al. (2012)
Standard Metabolic rate (ml O_2 g $afdrm^{-1}$ h^{-1})	0.057	0.023	nd	nd	Kowalke et al. (2001)
Respiration under TSPM	available	available	available	nd	Torre et al. (2012)
Absorption efficiency	nd	86.05 ± 0.07%	nd	nd	Alurralde et al. (2019)
Sediment sensitivity	++++	+++	++	nd	Torre et al. (2012)

Reproduction period	Summer	Winter	Summer	nd	Sahade et al. (2004); Sahade (1999)
Maximal mass (KJ)	110.7	227.3 (KJ)	41.4 (KJ)	108.7 (KJ)	Kowalke et al. (2001)
Maximal age	3.1(y)	3.4 (y)	10.6 (y)	3.5 (y)	Kowalke et al. (2001)
Individual Growth performance	1.55	1.83	0.59	1.3	Kowalke et al. (2001)

*Liters per day per gram of dry mass (L d^{-1} g dm)

**Not available data (nd)

2.2. Total gut content analysis

Each gut content sample was dried at 60 ºC until constant weight (~24-48 hours) and dry weight was determined in a 0.1-mg precision degree balance (Sartorius AG LA230S, Göttingen, Germany). OM content of each sample was determined following combustion at 450 ºC for 5 h to obtain the ash weight, which was subtracted from dry weight. To determine %OM, the OM content was divided by the total dry weight and multiplied it by 100.

2.3. Glycogen measurements

Glycogen concentration in the mantle tissue of each individual was determined following Kunst et al. (1984) and Keppler and Decker (1984). Mantle tissue samples (100-200 mg fm) were ground to a powder in liquid nitrogen. 0.5 mL of ice-cold Milli-Q water was added to each sample, and they were homogenised manually for 30 seconds on ice using a small glass homogeniser. The homogenate was heated to 95°C for 10 min to achieve protein denaturation using a water bath. For the hydrolysis of glycogen to glucose, 250µL of the homogenate was mixed with 500µL acetate buffer (0.1 mol, pH 4.8) and 20µL amyloglucosidase (Roche, Mannheim, Germany), and incubated for 2 h at 40°C in a water bath. The rest of the homogenate was kept on ice for later determination of the free glucose concentration. After incubation, samples were centrifuged at 15.000 g for 10 min at 4 °C in a refrigerated centrifuge (Eppendorf AG 5417R, Hamburg, Germany). The supernatant was collected, and glucose concentration was determined using the glucose determination kit (D-glucose UV test, R-Biopharm, Darmstadt, Germany), following the manufacturer's instructions. The glycogen content was calculated as the difference between the hydrolysed and the non-hydrolysed subsamples. Glycogen content is expressed in µg of glycogen per g of fresh mass (µg g fm^{-1}).

2.4. Scope for Growth (SFG)

The scope for growth (SFG) reflects the overall energy balance of an individual. It was estimated as the difference between the energy absorbed from the food and the energy expenditure or consumed due to respiration. A positive SFG reflects the available energy for biomass production (somatic and reproductive tissue growth) after reaching routine metabolic demands, whereas a negative SFG reflects an overall loss of energy by the individual (Gardner, 2000; Navarro et al., 1991). Considering the available data (Alurralde et al., 2019; Kowalke, 1999; Torre et al.,2012; see Table 2), ascidians' SFG under different TSPM concentration (SFG_{TSPM}) was estimated for *M. pedunculata*, *C. verrucosa* and *A. challengeri*. As no respiration data under different TSPM concentration for *C. antarctica* was available, we assumed *A. challengeri* respiration rate to be representative of *C. antarctica,* since both are similar in terms of body shape, standard metabolic rate, pumping rate and growth performance (Kowalke, 1999; Kowalke et al., 2001), much more than to *M. pedunculata* or *C. verrucosa* (see summary data in Table 3).

SFG_{TSPM} was estimated as the difference between assimilation (A) and respiration (R) at different TSPM concentrations (A_{TSPM} and $R_{TSPM,}$ respectively):

$SFG_{TSPM} = A_{TSPM} - R_{TSPM}$

Calculation of SFG_{TSPM}, A_{TSPM} and R_{TSPM} (all in J gms^{-1} d^{-1}) follows Widdows and Johnson (1988) as cited by Gardner (2000):

$I_{TSPM} = PR_{TSPM} \times POM \times 23$ J mg^{-1} AFDW

$A_{TSPM} = I_{TSPM} \times AE_{TSPM}$

$R_{TSPM} = VO_2 \times 20.33$ J mL^{-1} O_2

R_{TSPM} data of *M. pedunculata, C. verrucosa* and *A. challengeri* individuals was measured at different concentrations of TSPM (Torre et al., 2020b; https://doi.org/10.1594/PANGAEA.925202). A_{TSPM} calculation was estimated from Ingestion rate (I) and Absorption efficiency (AE). I and AE depend on particle concentration. In the absence of specific data, AE_{TSPM} of *C. verrucosa* under different TSPM concentrations estimated from Alurralde et al. (2019) was assumed for the three species, as no differences in AE for natural seston are observed for different ascidians species in Potter Cove (Tatián et al. 2004). Considering that filtration is the most energy-consuming activity for these species under increasing TSPM concentration, specific pumping rate (PR) recorded by Kowalke (1999) was corrected from respiration data under different sediment concentration (Torre et al., 2020b). In this way we obtain the specific PR_{TSPM} for each species in order to assess the I_{TSPM}. The calculation of each parameter and their sources are summarised in Table 3.

To estimate the possibility of growth and reproduction for these ascidians at low and high sediment impact in Potter Cove, SFG_{TSPM} was estimated for each species with the maximal summer TSPM recorded at 20 m water depth from published data since 1992 in the middle station (Schloss, 2010; https://doi.org/10.1594/PANGAEA.745596) and since 2009 at the Inner station (García et al., 2016).

Summer values were chosen because they were more abundant, frequent and representative of TSPM concentrations (Neder et al., 2020) and also because glacier inorganic sediment discharge occurs in this warmer period (Shcloss et al., 2012). Additionally, most of the biological parameters considered for SFG estimation were also evaluated during the summer season. On the other hand, maximum recorded values were chosen instead of means as they better represent the most prevalent conditions at Potter Cove. Bad weather conditions with strong winds are a common summer feature (Ruiz Barlet et al., 2021), which constrain sampling opportunities. Thus, it is logical to assume that part of the story is missing, and mean TSPM records would not accurately represent the most typical conditions in Potter Cove.

Table 3: Calculation of each SFG_{TSPM} parameter

Parameter	Calculation	Data Source
SFG_{TSPM} (J gms^{-1} d^{-1})	A_{TSPM} - R_{TSPM}	This work
A_{TSPM} (J gms^{-1} d^{-1})	I_{TSPM} • AE	This work
I_{TSPM} (L g^{-1} h^{-1})	PR_{TSPM} (L g^{-1} h^{-1}) • POM^b (mg L^{-1}) • 23 J mg^{-1} AFDW	This work
AE	-0.27•LN (TSPM (mg L^{-1})) + 1,1124 R^2 = 0.9885	Alurralde et al. (2019)
PR_{TSPM} (L g^{-1} h^{-1})	PR•(R_{TSPM}/$R_s{}^a$)	Kowalke (1999); Torre et al. (2012); Torre et al. (2020b)
POM^b (mg L^{-1})	1.8191•LN (TSPM (mg L^{-1})) - 0.383 R^2 = 0.8658	Alurralde et al. (2019)
R_{TSPM} (J gms^{-1} d^{-1})	$VO_2{}^c$ (mL O_2 g^{-1} d^{-1}) • 20.33 J mL^{-1} O_2	Torre et al. (2012); Torre et al. (2020b)

[a] R_s means respiration rate at natural seston levels (without added sediment).

[b] POM means particulate organic matter.

[c] VO_2 means oxygen consumption rate.

2.5. Data analysis

Gut content between species and stations was analysed with ANCOVA (Analysis of covariance) with total gut content as dependent variable and station and species as independent variables. Individual size (fresh weight) was considered as a covariable due to its strong correlation with gut content (*R^2 = 0.69, $p<0.0001$* for *M. pedunculata*, *R^2= 0.73, p= 0.012* for *C. verrucosa* and *R^2= 0.72, p= 0.014* for *C. antarctica*). %OM of total gut content and mantle glycogen content between species and stations were analysed with ANOVA with %OM and glycogen content as dependent variables and station and species as independent variables. In the absence of normality, data of glycogen content was Log_{10} (x+1) transformed prior to analysis. Finally, we also performed an ANOVA to compare SFG_{TSPM} of all the species between periods at which major changes have been recorded (pre and post-1995 TSPM peak) in the Middle and Inner stations. In all cases, significant differences ($p<0.05$) were estimated with the Bonferroni *post-hoc* test. All statistical analyses were performed with Infostat 2016 (Di Rienzo et al., 2016)

3. Results

3.1. Bulk gut content and energy reserve

Size-dependent total gut content showed differences between stations for the three species. The major significant difference was observed between samples from the Inner and the other two stations for each of the investigated species. At Inner and Middle stations, *M. pedunculata* had significantly lower size-dependent gut content than the other two species (Fig. 2a). The %OM had a clear pattern, increasing with the distance to the glacier in all three species. Furthermore, %OM of gut content was significantly higher in *M. pedunculata* compared with the other two species at all stations (Fig. 2b). Mantle glycogen content of *M. pedunculata* was significantly lower than in the other two species at each station. A significant difference of mantle glycogen between stations was found only for *C. antarctica* where the glycogen content increased with the distance to the glacier (outer > middle> inner cove, Fig. 2c). F and *p* values from ANCOVA and ANOVA analysis are summarized on Table 4.

Table 4: ANCOVA and ANOVA results of total gut content, %OM, glycogen content differences between species and Station.

ANCOVA Total gut content Between stations	**F**	***p***	**n**
M. pedunculata	17.79	*<0.0001*	29
C. verrucosa	23.72	*<0.0001*	30
C. antarctica	21.53	*<0.0001*	29
Size (fresh body mass)		*<0.05*	
Between species	***F***	***p***	***n***
Inner Station	33.09	*<0.0001*	30
Middle Station	16.77	*<0.0001*	31
Outer Station	7.87	*ns**	27
Size (fresh body mass)		*<0.05*	
ANOVA %OM Between stations	**F**	***p***	***n***
M. pedunculata	87.82	*<0.0001*	29
C. verrucosa	12.85	*<0.0001*	30
C. antarctica	10.97	*<0.0004*	29
Between species	**F**	***p***	**n**
Inner Station	11.52	*<0.0001*	30
Middle Station	18.3	*<0.0001*	31
Outer Station	40.35	*<0.0001*	27
ANOVA Mantle glycogen content Between stations	**F**	***p***	**n**
M. pedunculata	2.67	*ns*	26
C. verrucosa	1.85	*ns*	27
C. antarctica	4.286	*0.0235*	32
Between species	**F**	***p***	**n**

Inner Station	9.4	*0.0008*	30
Middle Station	26.89	*<0.0001*	31
Outer Station	21.32	*<0.0001*	27

*ns means no significant differences

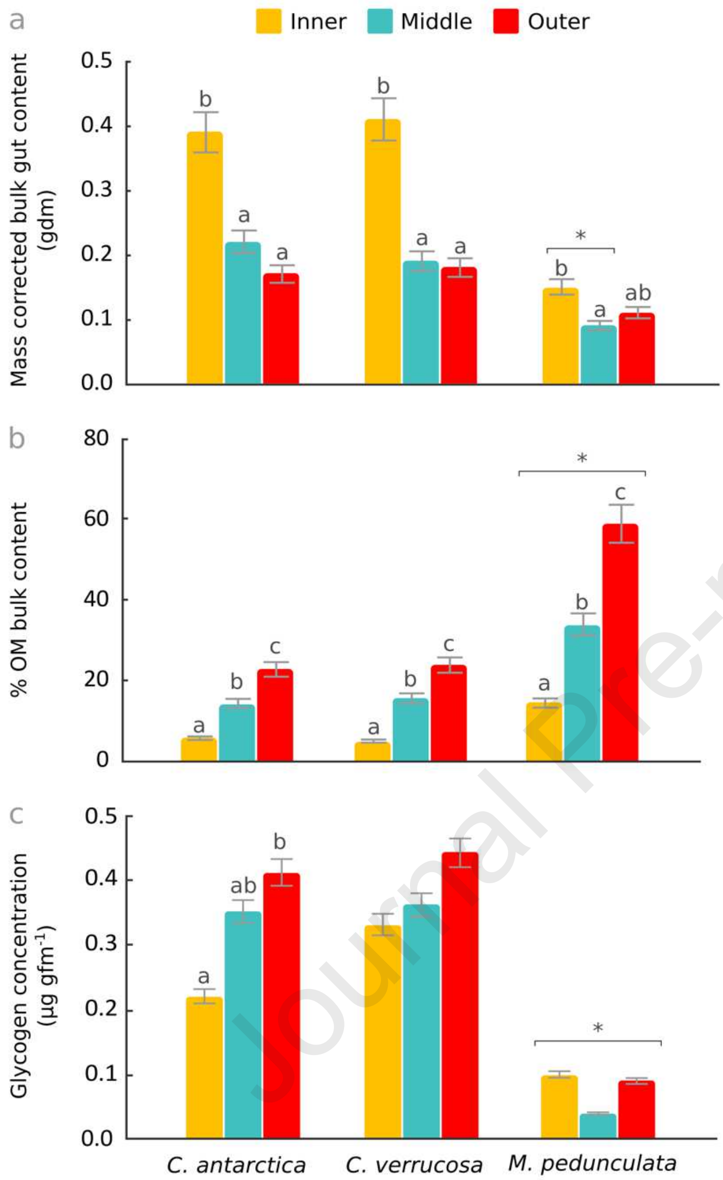


Figure 2: a) Mass corrected total gut content (g dry mass), b) %OM of total gut content and c) Log_{10} transformed Glycogen mantle content (µg g fm^{-1}) of *C. antarctica*, *C. verrucosa* and *M. pedunculata* at each sampling station in Potter Cove. Different letters show significant differences between stations by species with the Bonferroni test (*p<0.05*). Error bars indicate standard error. * Show significant differences (*p<0.001*) between species at all stations. *gdm*: grams of dry mass.

3.2. Scope for Growth under increasing TSPM

The estimated SFG_{TSPM} for the three ascidians showed an increase at lower TSPM concentrations up to a maximum value at around 10 mg L^{-1} beyond which SFG_{TSPM} decreased at higher concentrations and became negative between 40 and 60 mg L^{-1} TSPM. *M. pedunculata* showed a higher SFG at lower and intermediate TSPM concentrations, probably due to its higher filtration rate (Kowalke 1999). Additionally, it represents together with *C. verrucosa* the most sensitive species as its SFG_{TSPM} becomes negative at lower TSPM (~45±15 mg L^{-1}) concentrations than *A. challengeri* (~55±5 mg L^{-1}) (see Fig. 3). *A. challengeri* has a higher SFG_{TSPM} than the other two species only under higher TSPM concentrations, and its SFG_{TSPM} also becomes negative at higher TSPM (Fig. 3).

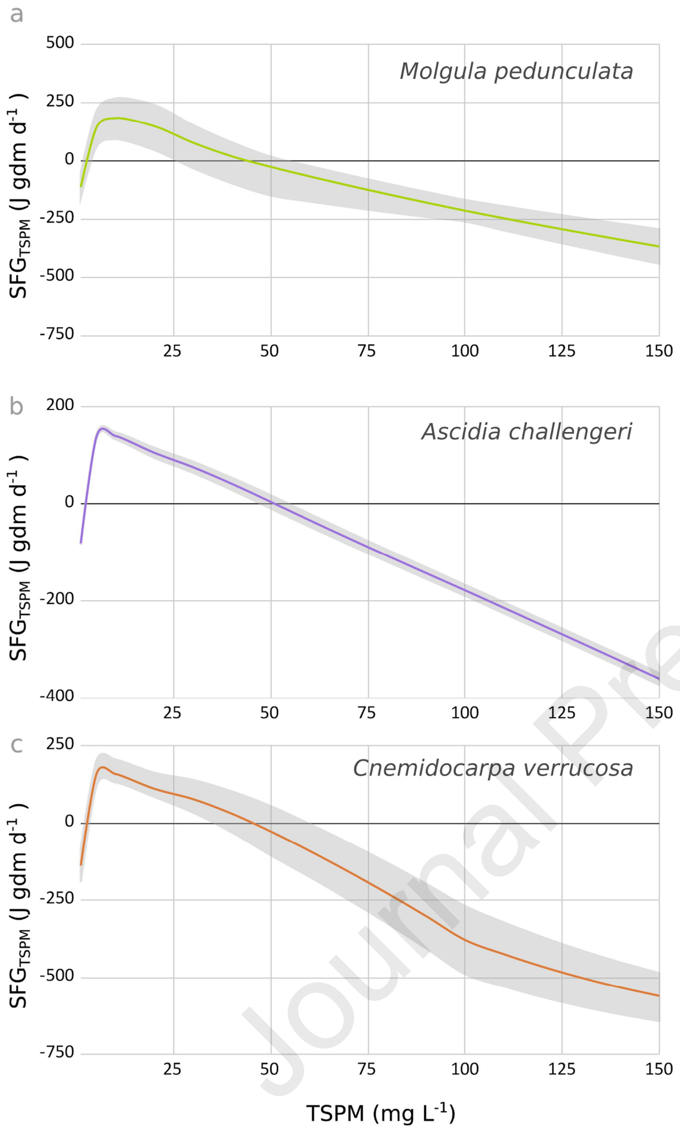


Figure 3: Scope for Growth (SFG_{TSPM}) in J g dm^{-1} d^{-1} under increasing TSPM concentrations (mg L^{-1}) of a) *M. pedunculata*, b) *A. challengeri* and c) *C. verrucosa*. Grey areas represent estimated standard deviation.

SFG_{TSPM} estimation with real TSPM data showed that, at maximum TSPM recorded in the Inner and Middle station, the SFG of the three species is positive for most of the measured maximal summer concentrations from 1993 to 2011 at the Middle station and between 2009 and 2011 at the Inner station (Fig. 4 a, b). For 1995, the SFG_{TSPM} reached a very high negative value for the three species when the recorded maximal TSPM was as high as 162 mg L^{-1}. It also became slightly negative for *M. pedunculata* and *C. verrucosa* in 2000 and 2006 at the Middle station when recorded TSPM was as high as 48 and 46.2 mg L^{-1} respectively. Comparison of pre and post-1995 TSPM peak at the Middle station was only significantly lower after the peak for *A. challengeri* (*ANOVA;* $F=4.62$, $p=0.03$) and *C. verrucosa* (*ANOVA;* $F=5.16$, $p=0.02$). At both considered periods (1992-1994 vs 1996-2011), SFG_{TSPM} means are positive for the three species. Leaving out the 1995 event and despite the observed year-to-year variability, the ascidian SFG_{TSPM} did not differ significantly between the Middle and Inner stations.

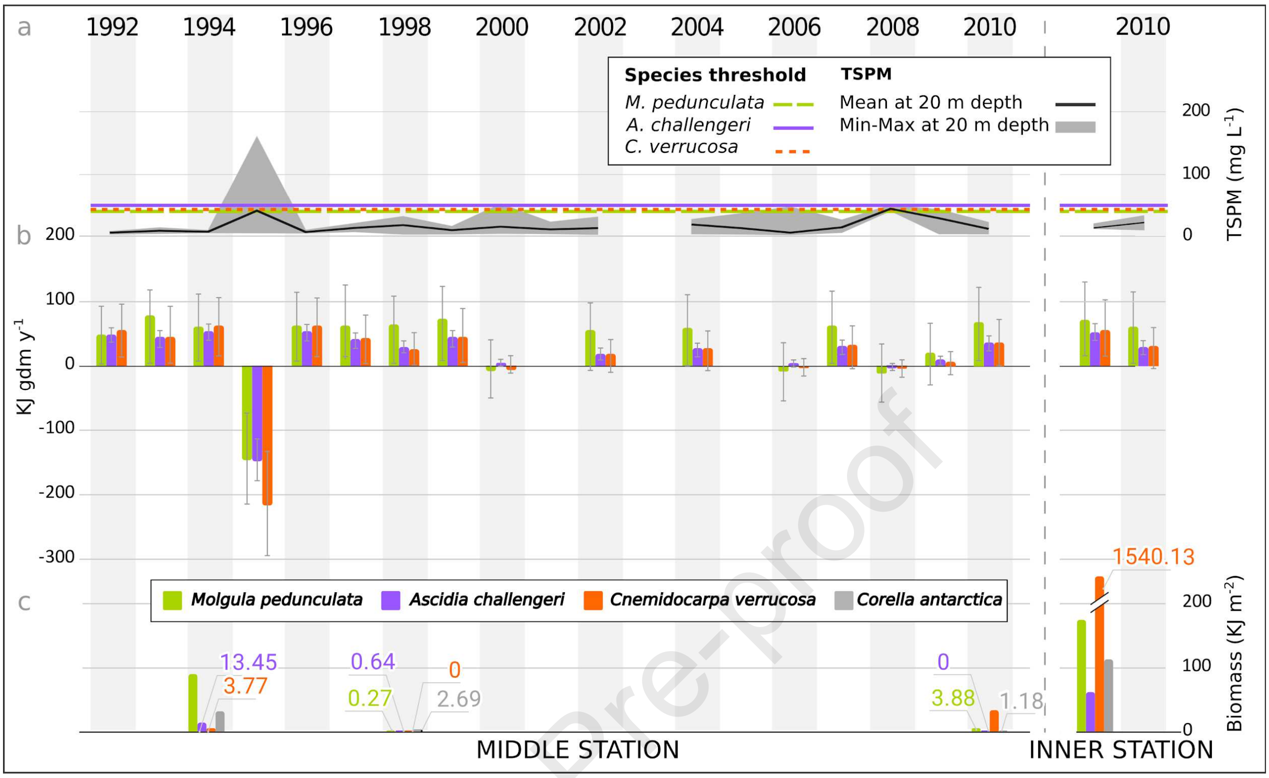


Figure 4: a) TSPM (mg L^{-1}) recorded in the Middle and Inner stations at 20 m depth form Schloss (2010) and García et al. (2016) respectively. The solid black line indicates average summer values, while the grey shaded area represents the minimum and maximum values recorded. Overlapping coloured lines indicate *M. pedunculata*, *A. challengeri* and *C. verrucosa* TSPM thresholds (concentration at which SFG_{TSPM} became negative). b) Estimated SFG_{TSPM} (KJ gdm y^{-1}) for *M. pedunculata*, *A. challengeri* and *C. verrucosa* considering maximal summer TSPM concentration in the Inner and Middle stations. Error bars indicate standard error. c) Biomass (KJ m^{-2}) of *M. pedunculata*, *C. verrucosa*, *A. challengeri* and *C. antarctica* recorded at the Middle station in 1994, 1995 and 2010 from Sahade et al. (2015) and at the Inner station in 2010 from Lagger et al. (2018). *gdm*: grams of dry mass.

4. Discussion

Our study supported the hypothesis that the magnitude of pressure exerted on ascidians by glacier sediment discharge, agrees with sedimentation gradient from the head fjord toward the mouth described by Monien et al. (2017). The negative effect is higher at the Inner station and decreases towards the middle and outer stations. The sedimentation pattern is reflected in the ascidians bulk gut contents and its quality, being highest at the Inner Station with a lower OM fraction and lowest at the Outer one with the highest OM fraction. Like the canary in the coal mine, ascidians may act as sentinels of sedimentation conditions and living ‘sediment traps’ since their gut contents provide relevant insights on the sedimentation process, witnessing what is reaching the bottom in Potter Cove (Tatián et al., 2002; Tatián et al., 2004). As sessile suspension-feeders and primary consumers, ascidians serve as indicators of different aspects of ecosystem functioning and spatial heterogeneity of food sources due to local environment and hydrology (Alurralde et al., 2020; Kim et al., 2021; Lefebvre et al., 2009). Spring/summer glacier discharge and wind stress set local differences between the inner and outer part of Potter Cove, as well as between surface and deeper waters (Ruiz Barlett et al., 2021; Schloss et al., 2012). In addition, variable water retention times and stratification due to meltwater inflows may dilute food sources or patchly distribute them within the fjord (Alurralde et al., 2020). On the other hand, the observed differences among the species provide insights on species-specific trophic traits that could determine to some extent the interplay between energy intake and population abundances. Under increasing TSPM concentrations, ascidians increased their respiration rate (and probably their pumping activity) up to a certain concentration after which ascidians down-regulated their metabolism. Their sensitivity to TSPM was then inversely related to the concentration they react to, being *M. pedunculata* more sensitive than *C. verrucosa* and *A. challengeri* (Torre et al. 2012, 2014). There has been some controversy elucidating the relevance of particle concentration in regulating ascidians´ ingestion rate (Armsworthy et al., 2001; Klumpp, 1984; Petersen and Riisgård, 1992; Petersen et al., 1995). Nevertheless the evidence summarised by Petersen (2007) have demonstrated that gut fullness reduces ascidians ingestion rate. The gut contents of *M. pedunculata* were always less than the other species, especially at the Inner station (with the highest TSPM). This indicates that ingestion is downregulated at lower TSPM concentration in this species. In a turbid environment as Potter Cove, the ability to regulate ingestion rate would therefore be an advantageous trait since it could prevent *M. pedunculata* from overloading their digestive system. This could enable a more efficient food intake strategy, limiting filtration rates at high TSPM concentrations and more importantly, avoids branchial clogging. Here is where sensitivity probably masks a strategy that allows *M. pedunculata* to survive and dominate even in areas subjected to intense sediment regimes (Kim et al., 2021; Lagger et al., 2017a; 2018).

Just like total gut content reflects the TSPM regimes at each station (Fig.1), the gut content OM fraction also coincides with the OM distribution along Potter Cove bottom (Monien et al., 2014). The observed interspecific differences may have resulted from specific branchial sac morphology and pumping rates, which are thought to determine retention efficiency and ingestion rate in ascidians (Kowalke, 1999; Petersen and Svane, 2002; Riisgård and Larsen, 2010). Schloss et al. (1999) postulated that at the bottom-water interface *M. pedunculata* gets better quality food because its siphons are located some centimeters higher than *C. antarctica* and *C. verrucosa*, where TSPM has a higher OM fraction. Nevertheless, the differences in siphon heights between *M. pedunculata* and *C. verrucosa* are markedly lower. *C. verrucosa* is the only one of the studied ascidians that performs squirting, i.e., a rejection reflex happening under high TSPM concentrations (Torre et al., 2014). We believe, therefore, that this particular reflex leads to the difference observed between species since it increases with increasing TSPM concentration, limiting ingestion rate because of the loss of particles rejected before the gut passage (Armsworthy et al., 2001). Not only the amount and quality of available food, but also the rates of its incorporation and utilisation in different processes such as growth, reproduction or environmental stress, would determine an animal's net energy balance (Sokolova, 2013; Sokolova et al., 2012). Glycogen is one of the primary energy sources described for ascidians (Ermak, 1977; Gaill, 1980; Torre et al., 2014) and its accumulation is tightly related to the energy balance of each species (Kang et al. 2011; Torre et al., 2014). As expected, the glycogen levels measured for *C. antarctica* and *C. verrucosa* are coincident with %OM of gut contents, reflecting the significant impact that quality food intake has on the energy storage capacity of these species. However, this was not possible to corroborate on *M. pedunculata* as glycogen was too scarce for comparison, probably because it is mostly stored in muscles, and mantle muscular fibres which are poorly developed in this species (Torre et al., 2014; Monniot et al., 2011; Kott, 1969).

Placing this snapshot of what summer sedimentation represents for antarctic ascidians, and what happened at the population level in a historical context, leads us to the second main finding of our study. After linking sharp changes in megabenthic assemblages' structure with sediment dynamics in Potter Cove, Sahade et al. (2015) suggested this could be a case of a sudden shift with ecosystem hysteresis. The TSPM peak in 1995 was interpreted as a critical threshold, but still, uncertainties remain whether these shifts are reversible or not. Our estimates confirm that TSPM level in 1995 far exceeded the ascidians threshold from the energetic perspective, and represented a breakpoint in the structuring of benthic assemblages occurring in the Middle Station which corresponds to older areas within Potter Cove (referred as Inner by Sahade et al., 2015). The SFG, represents the animal net energy balance and provides an integrative and quantitative assessment of the animal's energy status under a particular food regime (Gardner, 2000). A negative SFG like the one described for the 1995's TSPM peak would have limited ascidians' survival because of high respiratory expenditure and low energy absorption (Alurralde et al., 2019; Torre et al., 2012). Since a positive SFG is a good predictor of growth potential, the estimation of SFG for a particular species allows assessing its potential presence, abundance, survival, and reproduction in a given place. Despite TSPM concentrations remaining higher than before the perturbation, they did not exceed ascidians TSPM threshold (concentration from which each species SFG becomes negative) demonstrating that energy provision is still suitable for ascidians to thrive. Even so, ascidians were unable to restore their dominance in older areas but, paradoxically, they dominated the new ice-free areas. These newer areas in the Inner Station were uncovered many years after the 1995 sedimentation peak, but have been permanently subjected to the highest sediment pressure registered within the cove. At the last benthic photographic survey in Potter Cove in 2010, both states coexisted (Lagger et al., 2017a; 2018; Sahade et al., 2015) between Inner and Middle stations. This suggests that the benthic system in the cove could present alternative equilibrium states for similar values of the environmental condition. Spatial coexistence of alternative stable states when a system is in the environmental condition range that allows hysteresis, are generally described as the result of spatial or temporal heterogeneity (Shurin et al., 2004). Therefore, the current coexistence of both states may be the result of spatial and temporal heterogeneity in TSPM dynamics detailed above (Fig. 5).

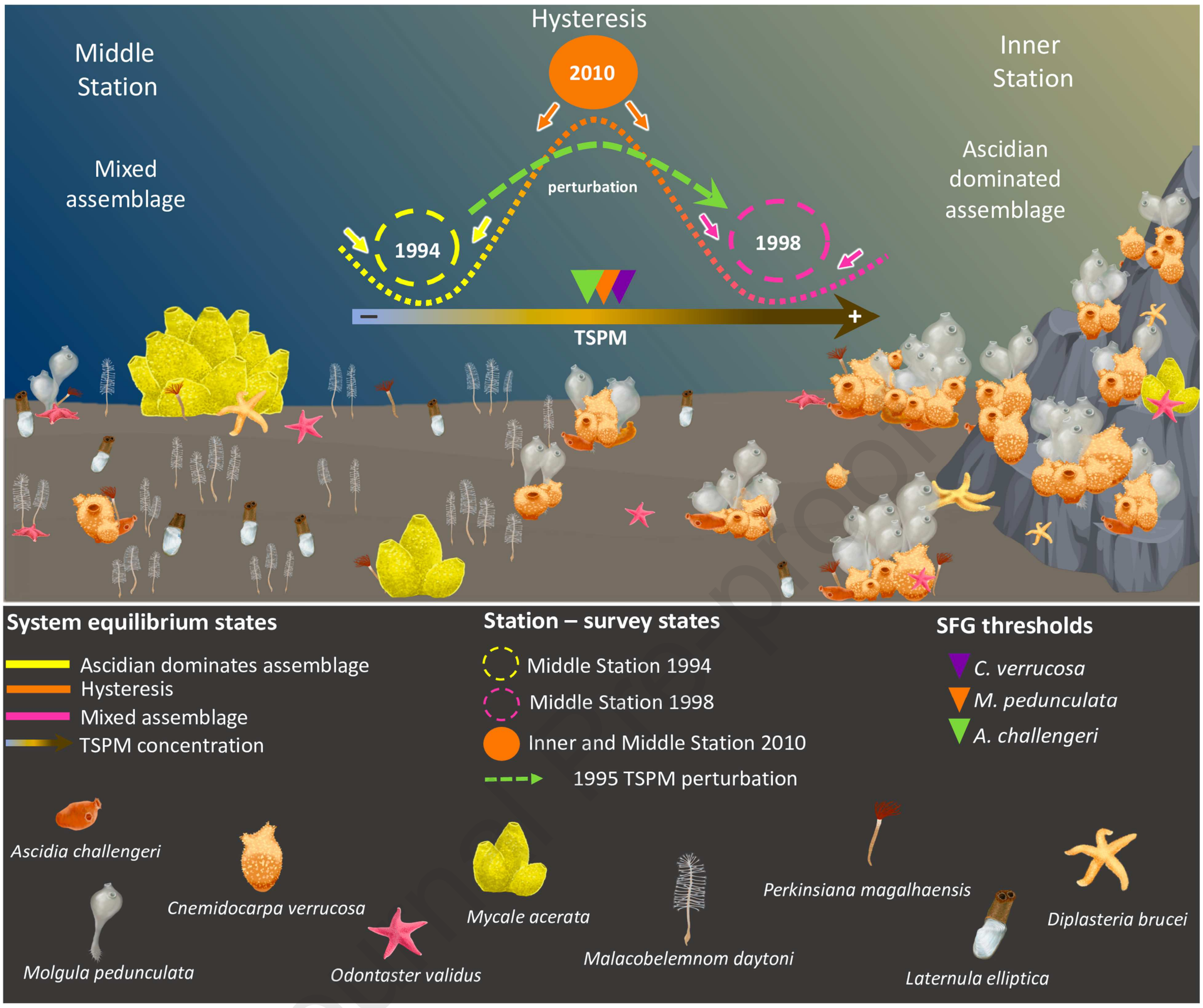


Figure 5: Schematic representation of Potter Cove assemblage composition at the Middle and Inner station since 2010. Equilibrium and hysteresis model (based on Scheffer 2001) is shown by a dotted line and circles indicating states of the Potter Cove system at different surveys under increasing total suspended particulate matter (TSPM) concentration. Two stable states are identified: the "ascidian dominated assemblage" and the "mixed assemblage" and in-between the unstable hysteresis state where the system could turn to any of the other two states. The directions of the system change as a function of TSPM concentration (increasing from left [-] to right [+]) is indicated with small arrows. Ascidian specific scope for growth (SFG) thresholds related to TSPM are indicated. The Middle station composition in the 1994 survey corresponded to an "Ascidian dominated assemblage". After the 1995 TSPM peak (system perturbation), where ascidians SFG thresholds were exceeded, the Middle station assemblage turned into a "mixed assemblage". In the last survey, ascidian dominated assemblage dominated the Inner station while the mixed assemblage dominated the older Middle station. The irreversibility to the ascidian dominated assemblage at the Middle station even when TSPM has been predominantly lower, and coexistence of both states is a clear indication of current system hysteresis.

Assemblage composition often depends on environmental conditions, but also on colonisation or settlement history (Chase, 2003), as early settling species can favour the settlement of a particular assemblage by facilitation process (Kéfi et al., 2016; Urban and De Meester, 2009). In this sense, the rocky substrate provided by the island in the new ice-free area at the Inner Station represents a perfect refuge that may allow constant ascidian recolonisation to the soft-bottoms around it. Species success is usually assumed to be density-dependent, being enhanced at certain population densities via the Allee effect, but under some circumstances, high-density aggregations can also favour population success via protection, predation dissolution, food intake facilitation or self-recruitment (i.e. recruitment of progeny to the parental population or patch) (Bruno et al., 2003; Rius et al., 2017). Density-dependent facilitation processes could, therefore generate positive feedback for a specific assemblage. Several biological processes are inherently species-specific and contribute to shaping ecosystem functioning (Barnes and Sands, 2017), especially when suspension-feeder species dominate in abundance (Mermillon-Blondin, 2011; Schenone and Thrush, 2020). For instance, the fine (muddy) sediment substrate prevailing in the inner Potter Cove may not be suitable for sessile epibenthic organisms' settlement. However, ascidians and other suspension-feeders, act as ecosystem engineers developing complex three-dimensional biogenic structures (Gili et al., 2001; Rossi et al., 2015; Tatián et al., 1998), providing living habitat for epibionts, including organisms from their own species (Rimondino et al., 2015). In this way, the development of clumped patches increases biodiversity by increasing substrate for colonisation. It also favours reproduction, settlement and survival, generating a positive feedback to the "ascidian dominated assemblage" state (Monteiro et al., 2002). In dense populations, the active feeding behaviour allows ascidians to reach high filtration rates (Riisgård et al., 1995) that, along with a remarkable retention efficiency, may limit food availability for other co-occurring animals (Kowalke, 1998; 1999; 2000). On the contrary, once a "mixed assemblage" dominated by epi-infaunal species (e.g. *Malacobelemnom daytoni*) is settled, the colonisation area for ascidian gets compromised. The infaunal species modify bottom sediment, altering water-sediment layer dynamics and geochemistry, increasing bioturbation and sediment accumulation rate favouring their own aggregation (Coco et al., 2006; Mermillod-Blondin, 2011; Tait et al., 2020). Nevertheless, further investigations are necessary to detect and evaluate multiple feedbacks and interactions that may be stabilising these alternative states.

By austral summer 2020, the current assemblage state at Potter Cove remained the same described for 2010 sampling survey (Alurralde, G. *personal communication*). In the light of the results obtained here, it could be possible that just a warmer summer event could trigger higher glacier wash out of terrigenous material. This will increase TSPM to the point that surpasses the tolerance threshold of ascidian assemblages at the Inner station, making the system collapse to the other equilibrium state of a mixed assemblage. This prognosis is not trivial if the warming of the WAP resumes from the current hiatus (Etourneau et al., 2019), as it appears to be the case after the extreme temperatures measured in austral summer 2020 (Robinson et al., 2020). Extensive fjordic areas may follow the same trend observed in Potter Cove, i.e. retreating landward (Meredith et al., 2018). Furthermore, the new ice-free areas are currently getting more relevance on Antarctic blue carbon estimations, because of their high potential for new benthic carbon accumulation and immobilisation, mainly based on functional groups composition (Barnes et al., 2020). Therefore, to assess the possible presence of thresholds, alternative equilibrium states and hysteresis in coastal Antarctic ecosystems is becoming crucial to evaluate responses and potential negative or positive feedback to the ongoing Global Environmental Change.

Conclusions

Ascidians bulk gut contents reflected the sedimentation pattern described in the study area. They can in fact be considered living ‘sediment traps’ since their gut contents provide relevant insights on the sedimentation process, witnessing what is reaching the bottom. The use of SFG allowed us to detect the energy thresholds for each analysed species. Its estimation corroborated a great energetic deficit under the historical sedimentation peak, which could explain the recorded assemblage change in the cove after 1995.

SFG_{TSPM} estimation indicates suitable environmental conditions supporting current ascidians dominance in the new ice-free areas, but it fails to explain why under the current scenario, the ascidian assemblage at the cove has not been restored. These results may indicate the existence of a TSPM threshold that allows the spatial coexistence of alternative stable assemblage states at the benthic Potter Cove system.

Acknowledgements

We thank the Carlini–Dallmann staff for their logistic support. We also thank logistic and financial support by Instituto Antártico Argentino (IAA), Consejo Nacional de Investigaciones Científicas y Técnicas CONICET, FONCyT (Fondo para la Investigación Científica y Tecnológica), SECyT-UNC (Secretaría de Ciencia y Tecnología–UNC), DFG (Deutsche Forschungsgemeinschaft), and EU (European Union) via grants PICTO-DNA N° 2010/119, PICT2017 Nº 2394, IMCONet [FP7 IRSES (International Research Staff Exchange Scheme), action #318718], and PADI Foundation Grant #11234 and #32774. The authors have no conflicts of interest to declare.

References

Abele, D., Vazquez, S., Buma, A. G., Hernandez, E., Quiroga, C., Held, C., Frickenhausa, S., Harms, L., Lopez, J.L., Helmke, E. and Mac Cormack, W. P. 2017. Pelagic and benthic communities of the Antarctic ecosystem of Potter Cove: Genomics and ecological implications. Marine genomics, 33, 1-11. https://doi.org/10.1016/j.margen.2017.05.001

Alurralde, G., Torre, L., Schwindt, E., Castilla, J. C., and Tatián, M. 2013. A re-evaluation of morphological characters of the invasive ascidian *Corella eumyota* reveals two different species at the tip of South America and in the South Shetland Islands, Antarctica. Polar Biology, 36(7), 957-968. https://doi.org/10.1007/s00300-013-1319-3

Alurralde, G., Fuentes, V. L., De Troch, M., and Tatián, M. 2020. Suspension feeders as natural sentinels of the spatial variability in food sources in an Antarctic fjord: A stable isotope approach. Ecological Indicators, 115, 106378. https://doi.org/10.1016/j.ecolind.2020.106378

Alurralde, G., Fuentes, V. L., Maggioni, T., Movilla, J., Olariaga, A., Orejas, C., Schloss, I.R., and Tatián, M. 2019. Role of suspension feeders in antarctic pelagic-benthic coupling: Trophic ecology and potential carbon sinks under climate change. Marine Environmental Research, 152, 104790. https://doi.org/10.1016/j.marenvres.2019.104790

Andersen, T., Carstensen, J., Hernandez-Garcia, E., and Duarte, C. M. 2009. Ecological thresholds and regime shifts: approaches to identification. Trends in Ecology and Evolution, 24(1), 49-57. https://doi.org/10.1016/j.tree.2008.07.014

Armsworthy, S. L., MacDonald, B. A., and Ward, J. E. 2001. Feeding activity, absorption efficiency and suspension feeding processes in the ascidian, *Halocynthia pyriformis* (Stolidobranchia: Ascidiacea): responses to variations in diet quantity and quality. Journal of experimental marine biology and ecology, 260(1), 41-69. https://doi.org/10.1016/S0022-0981(01)00238-6

Barnes, D. K., and Sands, C. J. 2017. Functional group diversity is key to Southern Ocean benthic carbon pathways. PLoS One, 12(6), e0179735. https://doi.org/10.1371/journal.pone.0179735

Barnes, D. K., Sands, C. J., Cook, A., Howard, F., Roman Gonzalez, A., Muñoz–Ramirez, C., ... and Zwerschke, N. 2020. Blue carbon gains from glacial retreat along Antarctic fjords: What should we expect? Global Change Biology, 26(5), 2750-2755. https://doi.org/10.1111/gcb.15055

Barnes, D.K.A., and Souster, T. 2011. Reduced survival of Antarctic benthos linked to climate-induced iceberg scouring. Nature Climate Change, 1(7), 365-368. https://doi.org/10.1038/nclimate1232

Bers, A. V., Momo, F., Schloss, I. R., and Abele, D. 2013. Analysis of trends and sudden changes in long-term environmental data from King George Island (Antarctica): relationships between global climatic oscillations and local system response. Climatic Change, 116(3-4), 789-803. https://doi.org/10.1007/s10584-012-0523-4

Bruno, J. F., Stachowicz, J. J., and Bertness, M. D. 2003. Inclusion of facilitation into ecological theory. Trends in ecology and evolution, 18(3), 119-125. https://doi.org/10.1016/S0169-5347(02)00045-9

Campana, G. L., Zacher, K., Deregibus, D., Momo, F. R., Wiencke, C., and Quartino, M. L. 2018. Succession of Antarctic benthic algae (Potter Cove, South Shetland Islands): structural patterns and glacial impact over a four-year period. Polar Biology, 41(2), 377-396. https://doi.org/10.1007/s00300-017-2197-x

Chase, J. M. 2003. Community assembly: when should history matter? Oecologia, 136(4), 489-498. https://doi.org/10.1007/s00442-003-1311-7

Clark, G. F., Stark, J. S., and Johnston, E. L. 2017a. Tolerance rather than competition leads to spatial dominance of an Antarctic bryozoan. Journal of Experimental Marine Biology and Ecology, 486, 222-229. https://doi.org/10.1016/j.jembe.2016.10.008

Clark, G. F., Stark, J. S., Palmer, A. S., Riddle, M. J., and Johnston, E. L. 2017b. The roles of sea-ice, light and sedimentation in structuring shallow Antarctic benthic communities. PLoS One, 12(1), e0168391. https://doi.org/10.1371/journal.pone.0168391

Coco, G., Thrush, S. F., Green, M. O., and Hewitt, J. E. 2006. Feedbacks between bivalve density, flow, and suspended sediment concentration on patch stable states. Ecology, 87(11), 2862-2870. https://doi.org/10.1890/0012-9658(2006)87[2862:FBBDFA]2.0.CO;2

Dayton, P. K., Hammerstrom, K., Jarrell, S. C., Kim, S., Nordhausen, W., Osborne, D. J., and Thrush, S. F. 2016. Unusual coastal flood impacts in Salmon Valley, McMurdo Sound, Antarctica. Antarctic Science, 28(4), 269-275. https://doi.org/10.1017/S0954102016000171

Dayton, P. K., Jarrell, S. C., Kim, S., Ed Parnell, P., Thrush, S. F., Hammerstrom, K., and Leichter, J. J. 2019. Benthic responses to an Antarctic regime shift: food particle size and recruitment biology. Ecological Applications, 29(1), e01823. https://doi.org/10.1002/eap.1823

Dierssen, H. M., Smith, R. C., and Vernet, M. 2002. Glacial meltwater dynamics in coastal waters west of the Antarctic peninsula. Proceedings of the National Academy of Sciences, 99(4), 1790-1795. https://doi.org/10.1073/pnas.032206999

Di Rienzo, J.A., Casanoves, F., Balzarini, M.G., Gonzalez, L., Tablada, M., and Robledo, C.W. 2016. InfoStat: software estadístico. Córdoba: Universidad Nacional de Córdoba. InfoStat versión 2016.

Etourneau, J., Sgubin, G., Crosta, X., Swingedouw, D., Willmott, V., Barbara, L., ... and Escutia, C. 2019. Ocean temperature impact on ice shelf extent in the eastern Antarctic Peninsula. Nature Communications, 10(1), 1-8. https://doi.org/10.1038/s41467-018-08195-6

Ermak, T. H. 1977. Glycogen deposits in the pyloric gland of the ascidian *Styela clava* (Urochordata). Cell and Tissue Research, 176(1), 47-55. https://doi.org/10.1007/BF00220343

Falk, U., López, D. A., and Silva-Busso, A. 2018. Multi-year analysis of distributed glacier mass balance modelling and equilibrium line altitude on King George Island, Antarctic Peninsula. The

Cryosphere, 12(4), 1211-1232. https://doi.org/10.5194/tc-12-1211-2018

Fillinger, L., Janussen, D., Lundälv, T., and Richter, C. 2013. Rapid glass sponge expansion after climate-induced Antarctic ice shelf collapse. Current Biology, 23(14), 1330-1334. https://doi.org/10.1016/j.cub.2013.05.051

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., and Holling, C. S. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual review of ecology, evolution, and systematics, 35. https://doi.org/10.1146/annurev.ecolsys.35.021103.105711

Fuentes, V., Alurralde, G., Meyer, B., Aguirre, G. E., Canepa, A., Wölfl, A. C., Hass, H.C., Williams, G.N. and Schloss, I. R. 2016. Glacial melting: an overlooked threat to Antarctic krill. Scientific reports, 6, 27234. https://doi.org/10.1038/srep27234

Gaill, F. 1980. Glycogen and degeneration in the pyloric gland of *Dendrodoa grossularia* (Ascidiacea, Tunicata). Cell and Tissue Research, 208(2), 197-206. https://doi.org/10.1007/BF00234870

Garcia, M. D., Hoffmeyer, M. S., Abbate, M. C. L., de Cao, M. S. B., Pettigrosso, R. E., Almandoz, G. O., Hernando, M.P, and Schloss, I. R. (2016). Micro-and mesozooplankton responses during two contrasting summers in a coastal Antarctic environment. Polar Biology, 39(1), 123-137. https://doi.org/10.1007/s00300-015-1678-z

Gardner, J. P. 2000. Where are the mussels on Cook Strait (New Zealand) shores? Low seston quality as a possible factor limiting multi-species distributions. Marine Ecology Progress Series, 194, 123-132. https://doi.org/10.3354/meps194123

Gili, J. M., Coma, R., Orejas, C., López-González, P. J., and Zabala, M. 2001. Are Antarctic suspension-feeding communities different from those elsewhere in the world? Polar Biology, 24(7), 473-485. https://doi.org/10.1007/s003000100257

Gutt, J., Adams, B., Bracegirdle, T., Cowan, D., Cummings, V., di Prisco, G., ... and Peck, L. 2013. Antarctic thresholds-ecosystem resilience and adaptation a new SCAR-biology programme. Polarforschung, 82(2), 147-150. https://epic.awi.de/id/eprint/36131/

Gutt, J., Barratt, I., Domack, E., d'Acoz, C. D. U., Dimmler, W., Grémare, A., et al. 2011. Biodiversity change after climate-induced ice-shelf collapse in the Antarctic. Deep Sea Research Part II: Topical Studies in Oceanography, 58(1-2), 74-83. https://doi.org/10.1016/j.dsr2.2010.05.024

Gutt, J., Bertler, N., Bracegirdle, T.J., Buschmann, A., Comiso, J., Hosie, G., Isla, E., Schloss, I.R., Smith, C.R., Tournadre, J. and Xavier, J.C. 2015. The Southern Ocean ecosystem under multiple climate change stresses an integrated circumpolar assessment. Global Change Biology, 21: 1434-1453. https://doi.org/10.1111/gcb.12794

Jansen, J., Hill, N. A., Dunstan, P. K., Cougnon, E. A., Galton-Fenzi, B. K., and Johnson, C. R. 2018a. Mapping Antarctic suspension feeder abundances and seafloor food-availability, and modeling their change after a major glacier calving. Frontiers in Ecology and Evolution, 6, 94. https://doi.org/10.3389/fevo.2018.00094

Jansen, J., Hill, N. A., Dunstan, P. K., McKinlay, J., Sumner, M. D., Post, A. L., Eléaume, M.P, Armand, L.K., Warnock, J.P., Galton-Fenzi, B.K. and Johnson, C. R. 2018b. Abundance and richness of key Antarctic seafloor fauna correlates with modelled food availability. Nature Ecology and Evolution, 2(1), 71-80. https://doi.org/10.1038/s41559-017-0392-3

Jerosch, K., Pehlke, H., Monien, P., Scharf, F., Weber, L., Kuhn, G., Braun, M.H., and Abele, D. 2018. Benthic meltwater fjord habitats formed by rapid glacier recession on King George Island, Antarctica. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences, 376(2122), 20170178. https://doi.org/10.1098/rsta.2017.0178

Kang, C. K., Choy, E. J., Lee, W. C., Kim, N. J., Park, H. J., and Choi, K. S. 2011. Physiological energetics and gross biochemical composition of the ascidian *Styela clava* cultured in suspension in a temperate bay of Korea. Aquaculture, 319(1-2), 168-177. https://doi.org/10.1016/j.aquaculture.2011.06.016

Kéfi, S., Holmgren, M., and Scheffer, M. 2016. When can positive interactions cause alternative stable states in ecosystems? Functional Ecology, 30(1), 88-97. https://doi.org/10.1111/1365-2435.12601

Keppler, D., and Decker, K. 1984. Glycogen. In: Bergmeyer HU, editor. Methods of enzymatic analysis. Weinheim, Germany: Verlag Chemie p. 11-17

Kim, D. U., Khim, J.S., Ahn, I. Y. 2021. Patterns, drivers and implications of ascidian distributions in a rapidly deglaciating fjord, King George Island, West Antarctic Peninsula. Ecological Indicators, 125 107467. https://doi.org/10.1016/j.ecolind.2021.107467

Kim, H., Ducklow, H. W., Abele, D., Ruiz Barlett, E. M., Buma, A. G., Meredith, M. P., Rozema, P.D., Schofield, O.M., Venables, H.J. and Schloss, I. R. 2018. Inter-decadal variability of phytoplankton biomass along the coastal West Antarctic Peninsula. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences, 376(2122), 20170174. https://doi.org/10.1098/rsta.2017.0174

Klumpp, D. W. 1984. Nutritional ecology of the ascidian *Pyura stolonifera*: Influence of body size, food quantity and quality on filter-feeding, respiration, assimilation efficiency and energy balance. Marine ecology progress series. Oldendorf, 19(3), 269-284. https://www.jstor.org/stable/24816043

Kott, P. 1969. Antarctic Ascidiacea. Antarct Res Ser Washington, 13, 1-239.

Kowalke, J. 1998. Energieumsätze benthischer Filtrierer der Potter Cove (King George Island, Antarktis) = Energy budgets of benthic suspension feeding animals of the Potter Cove (King George Island, Antarctica). Berichte zur Polarforschung (Reports on Polar Research), 286. https://epic.awi.de/id/eprint/26466/1/BerPolarforsch1998286.pdf

Kowalke, J. 1999. Filtration in antarctic ascidians–striking a balance. Journal of Experimental Marine

Biology and Ecology, 242(2), 233-244. https://doi.org/10.1016/S0022-0981(99)00108-2

Kowalke, J. 2000. Ecology and energetics of two Antarctic sponges. Journal of Experimental Marine Biology and Ecology, 247(1), 85-97. https://doi.org/10.1016/S0022-0981(00)00141-6

Kowalke, J., Arntz, W., Tatián, M., and Sahade, R. 2001. Production and respiration of Antarctic ascidians. Polar Biology 24, 663–669. https://doi.org/10.1007/s003000100266

Kunst, A., Draeger, B., and Ziegenhorn, J. 1984. D-Glucose: UV-methods with hexokinase and glucose-6-phosphate dehydrogenase In Bergmeyer HU, editor. Methods of Enzymatic Analysis.

Krzeminska, M., and Kuklinski, P. 2018. Biodiversity patterns of rock encrusting fauna from the shallow sublittoral of the Admiralty Bay. Marine environmental research, 139, 169-181. https://doi.org/10.1016/j.marenvres.2018.03.016

Lagger, C., Nime, M., Torre, L., Servetto, N., Tatián, M., and Sahade, R. 2018. Climate change, glacier retreat and a new ice□free island offer new insights on Antarctic benthic responses. Ecography, 41(4), 579-591. https://doi.org/10.1111/ecog.03018

Lagger, C., Servetto, N., Torre, L., and Sahade, R. 2017a. Benthic colonisation in newly ice-free soft-bottom areas in an Antarctic fjord. PLoS One, 12(11), e0186756. https://doi.org/10.1371/journal.pone.0186756

Lagger, C., Servetto, N., Torre, L., and Sahade, R. 2017b. Abundance and densities of benthic organisms close to the Fourcade glacier front at Potter Cove, South Shetland Islands, Antarctica, from December 2009 to February 2010. PANGAEA, https://doi.org/10.1594/PANGAEA.879315

Lefebvre, S., Harma, C., and Blin, J. L. 2009. Trophic typology of coastal ecosystems based on $\delta^{13}C$ and $\delta^{15}N$ ratios in an opportunistic suspension feeder. Marine Ecology Progress Series, 390, 27-37. https://doi.org/10.3354/meps08187

Lim, C. H., Lettmann, K., and Wolff, J. O. 2013. Numerical study on wave dynamics and wave-induced bed erosion characteristics in Potter Cove, Antarctica. Ocean Dynamics, 63(11-12), 1151-1174. https://doi.org/10.1007/s10236-013-0651-z

Mermillod-Blondin, F. 2011. The functional significance of bioturbation and biodeposition on biogeochemical processes at the water–sediment interface in freshwater and marine ecosystems. Journal of the North American Benthological Society, 30(3), 770-778. https://doi.org/10.1899/10-121.1

Meredith, M. P., Falk, U., Bers, A. V., Mackensen, A., Schloss, I. R., Ruiz Barlett, E., Jerosch, K., Silva Busso, A. and Abele, D. 2018. Anatomy of a glacial meltwater discharge event in an Antarctic cove. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences, 376(2122), 20170163. https://doi.org/10.1098/rsta.2017.0163

Momo, F.R., Sahade, R., and Tatián, M. 2008. Benthic animal communities of Potter Cove (King

George Island, Antarctica): Observed patterns and explanatory models. Reports on Polar and Marine Research 571, 162-167. https://epic.awi.de/id/eprint/28602/1/Wie2008b.pdf#page=166

Monien, D., Monien, P., Brünjes, R., Widmer, T., Kappenberg, A., Busso, A.A.S., Schnetger, B., and Brumsack, H. J. 2017. Meltwater as a source of potentially bioavailable iron to Antarctica waters. Antarctic Science, 29(3), 277. https://doi.org/10.1017/S095410201600064X

Monien, P., Lettmann, K. A., Monien, D., Asendorf, S., Wölfl, A. C., Lim, C. H., Thal, J., Schnetger, B., and Brumsack, H. J. 2014. Redox conditions and trace metal cycling in coastal sediments from the maritime Antarctic. Geochimica et Cosmochimica Acta, 141, 26-44. https://doi.org/10.1016/j.gca.2014.06.003

Monien, P., Schnetger, B., Brumsack, H. J., Hass, H. C., and Kuhn, G. 2011. A geochemical record of late Holocene palaeoenvironmental changes at King George Island (maritime Antarctica). Antarctic Science, 23(3), 255. https://doi.org/10.1017/S095410201100006X

Monniot, F., Dettai, A., Eleaume, M., Cruaud, C., and Ameziane, N. 2011. Antarctic Ascidians (Tunicata) of the French-Australian survey CEAMARC in Terre Adélie. Zootaxa, 2817(1), 1-54. https://doi.org/10.11646/zootaxa.2817.1.1

Monteiro, S. M., Chapman, M. G., and Underwood, A. J. 2002. Patches of the ascidian *Pyura stolonifera* (Heller, 1878): structure of habitat and associated intertidal assemblages. Journal of Experimental Marine Biology and Ecology, 270(2), 171-189. https://doi.org/10.1016/S0022-

0981(02)00020-5

Moon, H. W., Hussin, WMRW, Kim, H. C., and Ahn, I. Y. 2015. The impacts of climate change on Antarctic nearshore mega-epifaunal benthic assemblages in a glacial fjord on King George Island: responses and implications. Ecological Indicators, 57, 280-292. https://doi.org/10.1016/j.ecolind.2015.04.031

Navarro, E., Iglesias, J. I. P., Camacho, A. P., Labarta, U., and Beiras, R. 1991. The physiological energetics of mussels (*Mytilus galloprovincialis* Lmk) from different cultivation rafts in the Ria de Arosa (Galicia, NW Spain). Aquaculture, 94(2-3), 197-212. https://doi.org/10.1016/0044-8486(91)90118-Q

Neder, C., Sahade, R., Abele, D., Pesch, R., and Jerosch, K. 2020. Default versus Configured-Geostatistical Modeling of Suspended Particulate Matter in Potter Cove, West Antarctic Peninsula. Fluids, 5(4), 235. https://doi.org/10.3390/fluids5040235

Pakhomov, E. A., Fuentes, V., Schloss, I., Atencio, A., and Esnal, G. B. 2003. Beaching of the tunicate *Salpa thompsoni* at high levels of suspended particulate matter in the Southern Ocean. Polar Biology, 26(7), 427-431. https://doi.org/10.1007/s00300-003-0494-z

Peck, L. S., Barnes, D. K., Cook, A. J., Fleming, A. H., and Clarke, A. 2010. Negative feedback in the cold: ice retreat produces new carbon sinks in Antarctica. Global Change Biology, 16(9), 2614-2623. https://doi.org/10.1111/j.1365-2486.2009.02071.x

Petersen, J. K. 2007. Ascidian suspension feeding. Journal of Experimental Marine Biology and Ecology, 342(1), 127-137. https://doi.org/10.1016/j.jembe.2006.10.023

Petersen, J. K., Mayer, S., and Knudsen, M. Å. 1999. Beat frequency of cilia in the branchial basket of the ascidian *Ciona intestinalis* in relation to temperature and algal cell concentration. Marine Biology, 133(2), 185-192. https://doi.org/10.1007/s002270050457

Petersen, J. K., and Riisgård, H. U. 1992. Filtration capacity of the ascidian *Ciona intestinalis* and its grazing impact in a shallow fjord. Marine Ecology Progress Series, 9-17. https://www.jstor.org/stable/24831637

Petersen, J. K., Schou, O., and Thor, P. 1995. Growth and energetics in the ascidian *Ciona intestinalis*. Marine Ecology Progress Series 120, 175-184. doi:10.3354/meps120175

Petersen, J., and Svane, I. 2002. Filtration rate in seven Scandinavian ascidians: implications of the morphology of the gill sac. Marine Biology, 140(2), 397-402. https://doi.org/10.1007/s002270100706

Philipp, E. E., Husmann, G., and Abele, D. 2011. The impact of sediment deposition and iceberg scour on the Antarctic soft shell clam *Laternula elliptica* at King George Island, Antarctica. Antarctic Science, 23(2), 127. https://doi.org/10.1017/S0954102010000970

Quartino, M. L., Deregibus, D., Campana, G. L., Latorre, G. E. J., and Momo, F. R. 2013. Evidence of macroalgal colonisation on newly ice-free areas following glacial retreat in Potter Cove (South Shetland Islands), Antarctica. PLoS One, 8(3), e58223. https://doi.org/10.1371/journal.pone.0058223

Riisgård, H. U., Bondo Christensen, P., Olesen, N. J., Petersen, J. K., Møller, M. M., and Andersen, P. 1995. Biological structure in a shallow cove (Kertinge Nor, Denmark)—Control by benthic nutrient fluxes and suspension-feeding ascidians and jellyfish. Ophelia, 41(1), 329-344. https://doi.org/10.1080/00785236.1995.10422051

Riisgård, H. U., and Larsen, P. S. 2010. Particle capture mechanisms in suspension-feeding invertebrates. Marine Ecology Progress Series, 418, 255-293.https://doi.org/10.3354/meps08755

Rimondino, C., Torre, L., Sahade, R., and Tatian, M. 2015. Sessile macro-epibiotic community of solitary ascidians, ecosystem engineers in soft substrates of Potter Cove, Antarctica. Polar Research, 34(1), 24338. https://doi.org/10.3402/polar.v34.24338

Rius, M., Teske, P. R., Manriquez, P. H., Suarez-Jimenez, R., McQuaid, C. D. and Castilla, J. C. 2017. Ecological dominance along rocky shores, with a focus on intertidal ascidians. In, Hawkins, S.J., Evans, A.J., Dale, A.C., Firth, L.B., Hughes, D.J. and Smith, I.P. (eds.) Oceanography and Marine Biology: An Annual Review. Boca Raton FL. CRC Press, pp. 55-84. https://doi.org/10.1201/b21944.

Robinson, S. A., Klekociuk, A. R., King, D. H., Pizarro Rojas, M., Zúñiga, G. E., and Bergstrom, D. M. 2020. The 2019/2020 summer of Antarctic heatwaves. Global Change Biology.

https://doi.org/10.1111/gcb.15083

Rossi, S., Coppari, M., and Viladrich, N. 2015. Benthic-pelagic coupling: new perspectives in the animal forests. Marine animal forests. In: Marine Animal Forests: the Ecology of Benthic Biodiversity Hotspots, vol. 1. Springer, pp. 1–31. https://doi.org/10.1007/978-3-319-17001-5_23-1

Ruiz Barlett E, Sierra M, Costa A, Tosonotto G 2021. Interannual variability of hydrographic properties in Potter Cove during summers between 2010 and 2017. Antarctic Science, 1-20. https://doi.org/10.1017/S0954102020000668

Rückamp, M., Blindow, N., Suckro, S., Braun, M., and Humbert, A. 2010. Dynamics of the ice cap on King George Island, Antarctica: field measurements and numerical simulations. Annals of Glaciology, 51(55), 80-90. https://doi.org/10.3189/172756410791392817

Sahade, R. 1999. Patrones y Procesos en una Comunidad Epi-Bentónica Antártica: el Ejemplo de Caleta Potter.: el ejemplo de Caleta Potter. Doctoral dissertation, Universidad Nacional de Córdoba.

Sahade, R., Lagger, C., Torre, L., Momo, F., Monien, P., Schloss, I., Barnes, D.K.A., Servetto, N., Tarantelli, S. Tatián, M., Zamboni, N., and Abele, D. 2015. Climate change and glacier retreat drive shifts in an Antarctic benthic ecosystem. Science Advances, 1(10), e1500050. https://doi.org/10.1126/sciadv.1500050

Sahade, R., Tatián, M., and Esnal, G. B. 2004. Reproductive ecology of the ascidian *Cnemidocarpa* *verrucosa* at Potter Cove, South Shetland Islands, Antarctica. Marine Ecology Progress Series, 272, 131-140. https://doi.org/10.3354/meps272131

Selkoe, K.A., Blenckner, T., Caldwell, M.R. et al. 2015. Principles for managing marine ecosystems prone to tipping points. Ecosystem Health and Sustainability 1(5),17. http://dx.doi.org/10.1890/EHS14-0024.1

Scheffer, M., and Carpenter, S. R. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology and Evolution, 18(12), 648-656. https://doi.org/10.1016/j.tree.2003.09.002

Schenone, S., and Thrush, S. F. 2020. Unraveling ecosystem functioning in intertidal soft sediments: the role of density-driven interactions. Scientific Reports, 10(1), 1-8. https://doi.org/10.1038/s41598-020-68869-4

Schloss, I.R. 2010. Suspended particulate matter measured on water samples of two stations at Potter Cove, King George Island, Western Antarctic Peninsula (1992-2010). PANGAEA, https://doi.org/10.1594/PANGAEA.745596

Schloss, I. R., Abele, D., Moreau, S., Demers, S., Bers, A. V., González, O., and Ferreyra, G. A. 2012. Response of phytoplankton dynamics to 19-year (1991–2009) climate trends in Potter Cove (Antarctica). Journal of Marine systems, 92(1), 53-66. https://doi.org/10.1016/j.jmarsys.2011.10.006

Schloss, I. R., Ferreyra, G. A., Mercuri, G., and Kowalke, J. 1999. Particle flux in an Antarctic shallow coastal environment: a sediment trap study. Scientia Marina, 63(S1), 99-111. https://doi.org/10.3989/scimar.1999.63s199

Shurin, J. B., Amarasekare, P., Chase, J. M., Holt, R. D., Hoopes, M. F., and Leibold, M. A. 2004. Alternative stable states and regional community structure. Journal of Theoretical Biology, 227(3), 359-368. https://doi.org/10.1016/j.jtbi.2003.11.013

Slattery, M. and Bockus, D. 1997. Sedimentation in McMurdo Sound, Antarctica: a disturbance mechanism for benthic invertebrates. Polar Biology, 18(3), 172-179. https://doi.org/10.1007/s003000050174

Sokolova, I. M. 2013. Energy-limited tolerance to stress as a conceptual framework to integrate the effects of multiple stressors. Integrative and comparative biology, 53(4), 597-608. https://doi.org/10.1093/icb/ict028

Sokolova, I. M., Frederich, M., Bagwe, R., Lannig, G., and Sukhotin, A. A. 2012. Energy homeostasis as an integrative tool for assessing limits of environmental stress tolerance in aquatic invertebrates. Marine Environmental Research, 79, 1-15. https://doi.org/10.1016/j.marenvres.2012.04.003

Tait, L. W., Lohrer, A. M., Townsend, M., Atalah, J., Floerl, O. and Inglis, G. J. 2020. Invasive ecosystem engineers threaten benthic nitrogen cycling by altering native infaunal and biofouling communities. Scientific reports, 10(1), 1-11. https://doi.org/10.1038/s41598-020-58557-8

Tatián, M., Sahade, R. J., Doucet, M. E., and Esnal, G. B. 1998. Ascidians (Tunicata, Ascidiacea) of Potter Cove, South Shetland Islands, Antarctica. Antarctic Science, 10(2), 147-152. https://doi.org/10.1017/S0954102098000194

Tatian, M., Sahade, R., and Esnal, G. B. 2004. Diet components in the food of Antarctic ascidians living at low levels of primary production. Antarctic Science, 16(2), 123-128. https://doi.org/10.1017/S0954102004001890

Tatián, M., Sahade, R., Kowalke, J., Kivatinitz, S. C., and Esnal, G. B. 2002. Food availability and gut contents in the ascidian *Cnemidocarpa verrucosa* at Potter Cove, Antarctica. Polar Biology, 25(1), 58-64. https://doi.org/10.1007/s003000100311

Thrush, S. F., Hewitt, J. E., Cummings, V. J., Ellis, J. I., Hatton, C., Lohrer, A., and Norkko, A. J. F. I. E. 2004. Muddy waters: elevating sediment input to coastal and estuarine habitats. Frontiers in Ecology and the Environment, 2(6), 299-306. https://doi.org/10.1890/1540-9295(2004)002[0299:MWESIT]2.0.CO;2

Torre, L., Abele, D., Lagger, C., Momo, F., and Sahade, R. 2014. When shape matters: Strategies of different Antarctic ascidians morphotypes to deal with sedimentation. Marine environmental research, 99, 179-187. https://doi.org/10.1016/j.marenvres.2014.05.014

Torre, L., Servetto, N., Eöry, M. L., Momo, F., Tatián, M., Abele, D., and Sahade, R. 2012.

Respiratory responses of three Antarctic ascidians and a sea pen to increased sediment concentrations. Polar Biology, 35(11), 1743-1748. https://doi.org/10.1007/s00300-012-1208-1

Torre, L., Tabares, P. C. C., Momo, F., Meyer, J. F., and Sahade, R. 2017. Climate change effects on Antarctic benthos: a spatially explicit model approach. Climatic change, 141(4), 733-746. https://doi.org/10.1007/s10584-017-1915-2

Torre, L., Tatián, M., Momo, F., and Sahade, R. 2020. Antarctic ascidians respiration rate under increasing sedimentation. PANGAEA. https://doi.org/10.1594/PANGAEA.925202

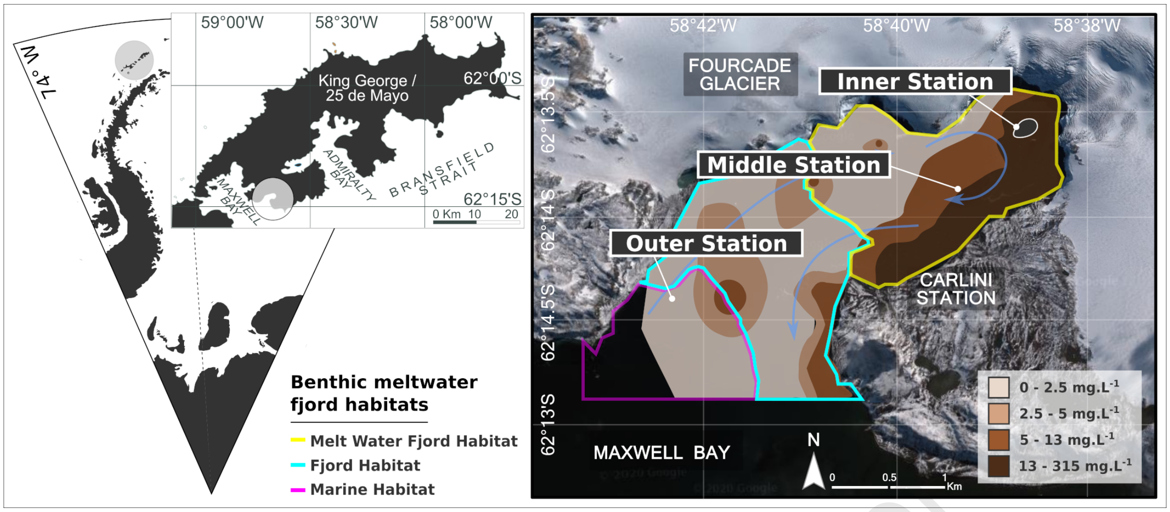
Torre, L; Alurralde, G; Abele, D et al. 2020: Bulk gut content and mantle glycogen content of antarctic ascidians from different stations inside Potter Cove. PANGEA. https://doi.org/10.1594/PANGAEA.925354

Urban, M. C., and De Meester, L. 2009. Community monopolisation: local adaptation enhances priority effects in an evolving metacommunity. Proceedings of the Royal Society B: Biological Sciences, 276(1676), 4129-4138. https://doi.org/10.1098/rspb.2009.1382

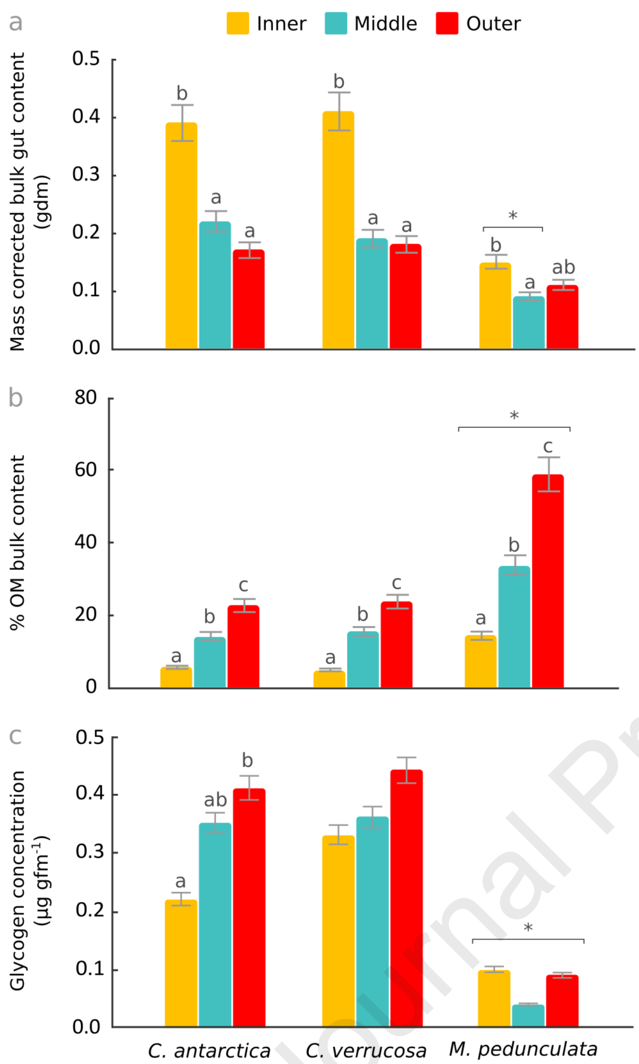
Widdows, J., and Johnson, D. 1988. Physiological energetics of *Mytilus edulis*: Scope for growth. Marine Ecology Progress Series, 113-121. https://www.jstor.org/stable/24827572

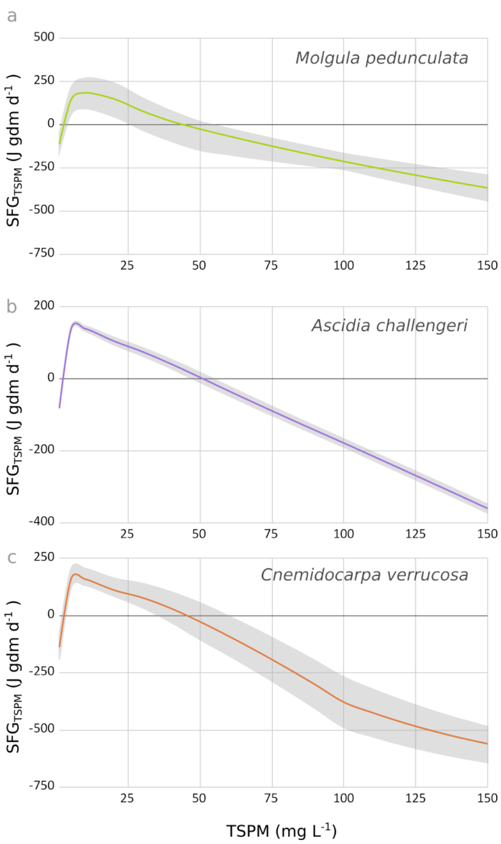
Wölfl, A. C., Lim, C. H., Hass, H. C., Lindhorst, S., Tosonotto, G., Lettmann, K. A., Kuhn, G., Wolff, J., and Abele, D. 2014. Distribution and characteristics of marine habitats in a subpolar bay based on hydroacoustics and bed shear stress estimates—Potter Cove, King George Island, Antarctica. Geo-Marine Letters, 34(5), 435-446. https://doi.org/10.1007/s00367-014-0375-1

Wölfl, A. C., Wittenberg, N., Feldens, P., Hass, H. C., Betzler, C., and Kuhn, G. 2016. Submarine landforms related to glacier retreat in a shallow Antarctic fjord. Antarctic Science, 28(6), 475-486. https://doi.org/10.1017/S0954102016000262

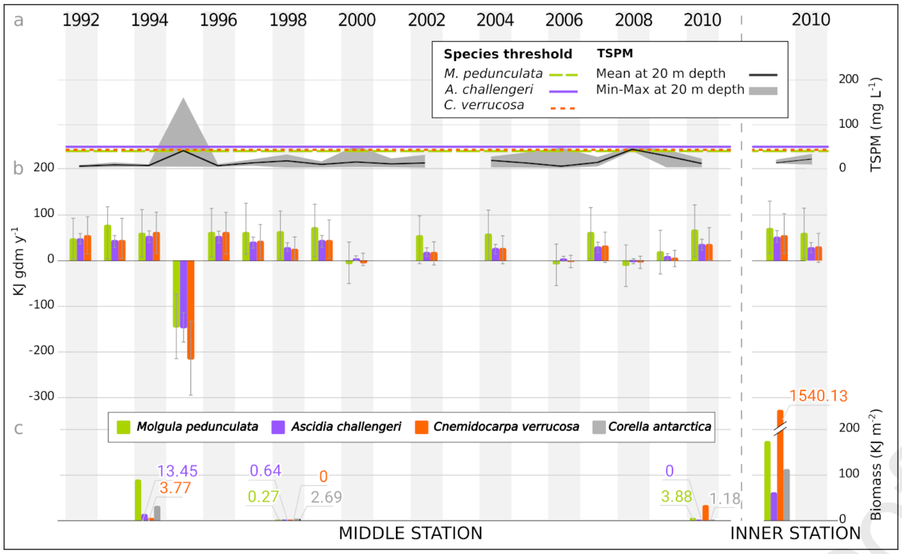


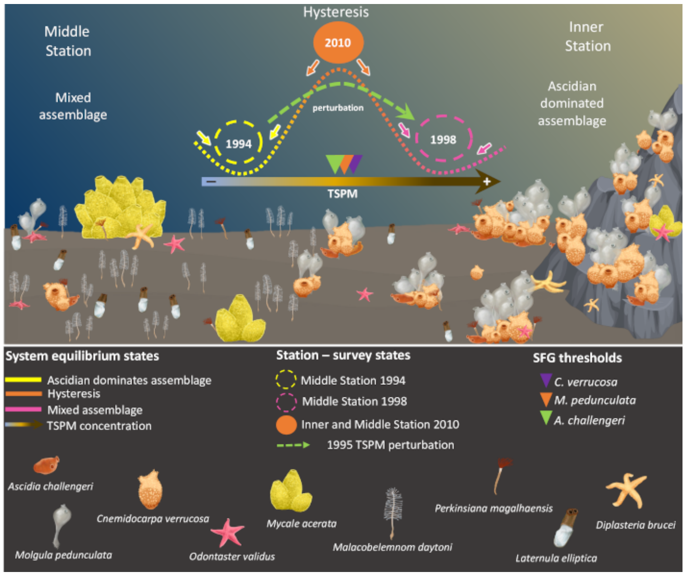
74°W
59°00'W
58°30'W
58°00'W
King George / 25 de Mayo
62°00'S
ADMIRALTY BAY
BRANSFIELD STRAIT
MAXWELL BAY
62°15'S
0 Km 10 20
Benthic meltwater fjord habitats
Melt Water Fjord Habitat
Fjord Habitat
Marine Habitat
58°42'W
58°40'W
58°38'W
FOURCADE GLACIER
Inner Station
Middle Station
Outer Station
CARLINI STATION
62°13.5'S
62°14'S
62°14.5'S
62°13'S
MAXWELL BAY
N
0 0.5 1 Km
0 - 2.5 mg.L-1
2.5 - 5 mg.L-1
5 - 13 mg.L-1
13 - 315 mg.L-1


a
Inner
Middle
Outer
Mass corrected bulk gut content (gdm)
0.5
0.4
0.3
0.2
0.1
0.0
b
a
a
b
a
a
*
b
a
ab
b
% OM bulk content
80
60
40
20
0
*
c
b
a
a
b
c
a
b
c
c
Glycogen concentration (µg gfm^{-1})
0.5
0.4
0.3
0.2
0.1
0.0
b
ab
a
*
C. antarctica
C. verrucosa
M. pedunculata



a
Molgula pedunculata
b
Ascidia challengeri
c
Cnemidocarpa verrucosa
SFGTSPM (J gdm d-1)
TSPM (mg L-1)
500
250
0
-250
-500
-750
200
-200
-400
25
50
75
100
125
150


a
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2010
Species threshold
M. pedunculata
A. challengeri
C. verrucosa
TSPM
Mean at 20 m depth
Min-Max at 20 m depth
200
100
0
TSPM (mg L-1)
b
200
100
0
-100
-200
-300
KJ gdm y-1
c
Molgula pedunculata
Ascidia challengeri
Cnemidocarpa verrucosa
Corella antarctica
13.45
3.77
0.64
0.27
0
2.69
0
3.88
1.18
1540.13
200
100
0
Biomass (KJ m-2)
MIDDLE STATION
INNER STATION


Middle Station
Mixed assemblage
Hysteresis
2010
perturbation
1994
1998
Inner Station
Ascidian dominated assemblage
TSPM
System equilibrium states
Ascidian dominates assemblage
Hysteresis
Mixed assemblage
TSPM concentration
Station – survey states
Middle Station 1994
Middle Station 1998
Inner and Middle Station 2010
1995 TSPM perturbation
SFG thresholds
C. verrucosa
M. pedunculata
A. challengeri
Ascidia challengeri
Cnemidocarpa verrucosa
Mycale acerata
Perkinsiana magalhaensis
Diplasteria brucei
Molgula pedunculata
Odontaster validus
Malacobelemnom daytoni
Laternula elliptica

Title: Antarctic ascidians under increasing sedimentation: physiological thresholds and ecosystem hysteresis.

Authors:

Torre, L.[a,b]□; Alurralde, G.[a,b]; Lagger, C.[a,b]; Abele, D.[c]; Schloss, I.R.[d,e,f] ; Sahade, R. [a,b]□

Affiliations:

[a] Universidad Nacional de Córdoba, Facultad de Ciencias Exactas, Físicas y Naturales, Av. Vélez Sarsfield 299, 5000, Córdoba, Argentina
[b] Instituto de Diversidad y Ecología Animal (Consejo Nacional de Investigaciones Científicas y Técnicas), Córdoba, Argentina.
[c] Alfred Wegener Institute (AWI), Helmholtz Centre for Polar and Marine Research. Bremerhaven, Germany

[d] Instituto Antártico Argentino, San Martín, Provincia de Buenos Aires, Argentina
[e] Centro Austral de Investigaciones Científicas, CONICET, Ushuaia, Argentina
[f] Universidad Nacional de Tierra del Fuego, Ushuaia, Argentina

Highlights

- Ascidians gut content amount and quality correlates with TSPM gradient and glacier distance.
- SFG indicates currently suitable growth conditions in spite of high TSPM.
- SFG_{TSPM} allowed us to identify environmental thresholds and explain community changes.

Declaration of interests

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

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: