
Influence of sea-ice dynamics on coastal Antarctic benthos: A case study on lantern clams (*Laternula elliptica*) in Adélie Land

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Abstract :

Polar regions are warming faster than the world average and are profoundly affected by changes in the spatio-temporal dynamics of sea ice, with largely unknown repercussions on the functioning of marine ecosystems. Here, we investigated the impacts of interannual sea-ice variability on coastal benthic communities in Antarctica, focusing on a close-to-pristine area (Adélie Land). We investigated shell growth of the circum-Antarctic bivalve *Laternula elliptica*, considered a key species in these soft bottom benthic communities. Chondrophores of live-collected clams were prepared using standard sclerochronological methods to study the interannual variability of shell growth from 1996 to 2015. Our results show that the master chronology varied with sea-ice dynamics. When sea ice breaks up too early, sympagic algae do not have time to accumulate sufficiently high biomass, thus strongly limiting the energy input to the benthos. This negatively affects the physiological performance of *L. elliptica*, thereby altering their population dynamics and hence the functioning of these soft-bottom ecosystems.

Highlights

► *Laternula elliptica* shell growth was studied in Adélie Land using sclerochronology. ► Lantern clam growth increments can be measured with accuracy in shell chondrophores ► A 20-year long chronology highlighted strong growth synchrony between individuals. ► Interannual variation in the chronology was mostly attributed to sea-ice phenology. ► Clam shells can serve as archives of the zoobenthic response to climate change.

Keywords : Benthic-pelagic coupling, Clams, East Antarctica, Food source, Growth, Ice, *Laternula elliptica*, Master chronology, Sclerochronology, Sympagic algae

1. Introduction

Polar regions are witnessing some of the world's most pronounced and accelerated impacts of climate change (Constable et al., 2022). These changes are vividly reflected in Antarctica's cryosphere dynamics, which has undergone dramatic shifts in the past decade. While there was a modest overall increase in sea-ice extent from the advent of the satellite era until 2014 (Parkinson, 2019), recent observations have unveiled a substantial and rapid decline, marked by two consecutive summers with record-breaking low sea ice levels in 2022 and 2023 (Turner et al., 2022; Purich and Doddridge, 2023). Changes in primary and secondary productivity, in food-web structure and geographical shifts in species distributions are among the main expected consequences of climate change on Antarctic marine communities (Constable et al., 2022). Among these, shallow-water and coastal benthic communities have a higher vulnerability to impacts of climate change (Rogers et al., 2020). Unfortunately, the critical questions regarding pelagic-benthic coupling and its responses to climate change have been inadequately explored, primarily because of the scarcity of long-term monitoring of both oceanography and benthic communities (Dayton et al., 2016). From that prospect, biological archives have the capacity to document the nature and rate of past ecological change, elucidate the driving environmental forces, and refine current ecosystem and climate models (Strugnell et al., 2022).

Here, we focused on a circumpolar bivalve, the Antarctic lantern clam *Laternula elliptica* (Fig. 1). With a maximum shell length of >100 mm, it is the largest bivalve species in Antarctic waters together with the Antarctic scallop *Adamussium colbecki* (Ralph & Maxwell, 1977). Several studies have reported a maximum longevity of 33 to 36 years in the King George Island population, West

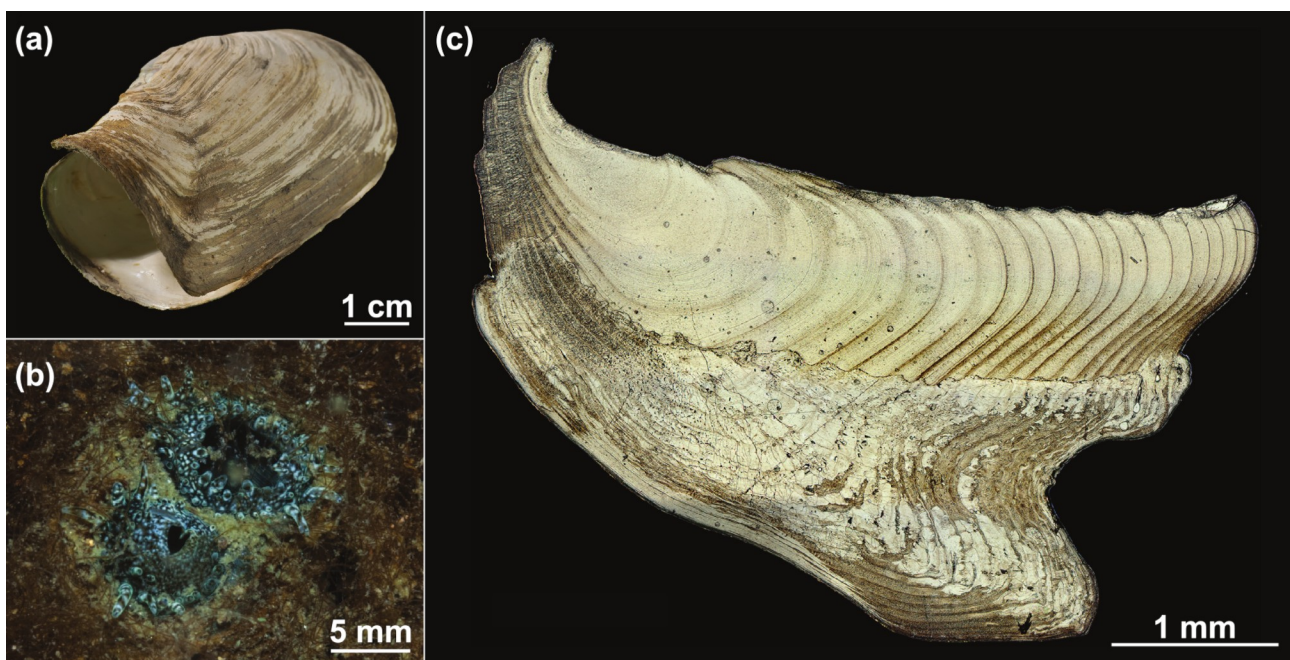


Figure 1: (a) Overview of the shell of a specimen of *Laternula elliptica* collected in January 2016 near the Dumont d'Urville research station – © Sébastien Hervé (UBO). The wide opening at the posterior edge is used for extension/retraction of the siphons. (b) Picture of the inhalant and exhalant siphons of a buried specimen of *L. elliptica*. Note that the sediment around the siphons is covered with biofilm (microphytobenthos and filamentous algae). (c) Acetate peel replica of a *L. elliptica* cross-section cut along the chondrophore (hinge) of the right valve.

Antarctic Peninsula (Philipp et al., 2005; Román-González et al., 2017). This clam is a suspension feeder that lives burrowed in soft subtidal sediments down to 700 m water depth. It is often considered a key species in Antarctic shallow soft-bottom communities because it plays a major role in the pelagic-benthic coupling (Momo et al., 2002). Its filtration capacities enhance the vertical carbon flux between the water column and the seafloor and, through biodeposition of faeces and pseudo-faeces, this species possibly sustains other benthic fauna (Ahn, 1993). For this reason, physiological rates and population dynamics of *L. elliptica* are likely to affect the entire ecosystem functioning (Agüera et al., 2017).

Most studies on the Antarctic lantern clam address physiology, energy flow or metabolism and have been conducted in the West Antarctic Peninsula, mainly in localities close to King George Island and the Rothera research station (Ahn et al., 2003; Peck et al., 2004; Morley et al., 2012). Conversely, a very limited number of studies have focused on *L. elliptica* specimens collected in East Antarctica, and even fewer have addressed research questions related to the shell matrix (see Román-González (2021) for a review on sclerochronological studies on *L. elliptica*). However, sclerochronology can undoubtedly provide priceless ecological information contained in bivalve shells (Peharda et al., 2021). As noticed by Clarke et al. (2007), “*studies of long-lived organisms that leave a record of aspects of their population dynamics in their skeletons will be an important means of documenting the response of benthic organisms to past climate change*”. Based on stable oxygen isotope records, Brey & Mackensen (1997) demonstrated that lines and increments observed in shells are formed annually and that most of *L. elliptica* shell growth occurs during the austral summer. Nonetheless, analysing annual growth increments in the chondrophore (a large spoon-shaped form projecting from the hinge plate) may be more appropriate than focusing on growth lines visible on the external shell surface. This is because the latter is more susceptible to degradation when compared to the inner shell surface housing the chondrophore (Sato-Okoshi & Okoshi, 2008). Some studies have highlighted that variations in isotopic and elemental composition of *L. elliptica* shells reflect changes in the cryosphere dynamics (e.g. Wing et al., 2020), but very few have attempted to use the interannual differences in growth increment width as a proxy for environmental variability. Combining growth increment width chronologies from different specimens allows for the creation of longer, multi-decadal, time-series referred to as composite or master chronologies. To the best of our knowledge, there is only one published study on the master chronology of shell growth in lantern clams (Brey et al., 2011).

In this study, we focused on lantern clams collected in shallow waters off the coast of Adélie Land, East Antarctica (Fig. 2a,b). This area, referred to as the Dumont d’Urville Sea, includes one of the largest polynyas in Antarctica (Mertz Glacier Polynya). The presence of this large area of ice-free water is important for the entire trophic web because it promotes phytoplankton growth and, therefore, high energy flow between trophic levels (Arrigo & van Dijken, 2003).

The primary goal of this paper is to describe *L. elliptica* shell growth dynamics with respect to environmental variability. To do so, we analysed annual growth patterns in chondrophores of 27 live-collected specimens and built a 20-year long master chronology that was subsequently compared with environmental variability over the 1995–2015 period. Our ultimate goal was to assess the potential of these shells as archives of the zoobenthic response to climate change.

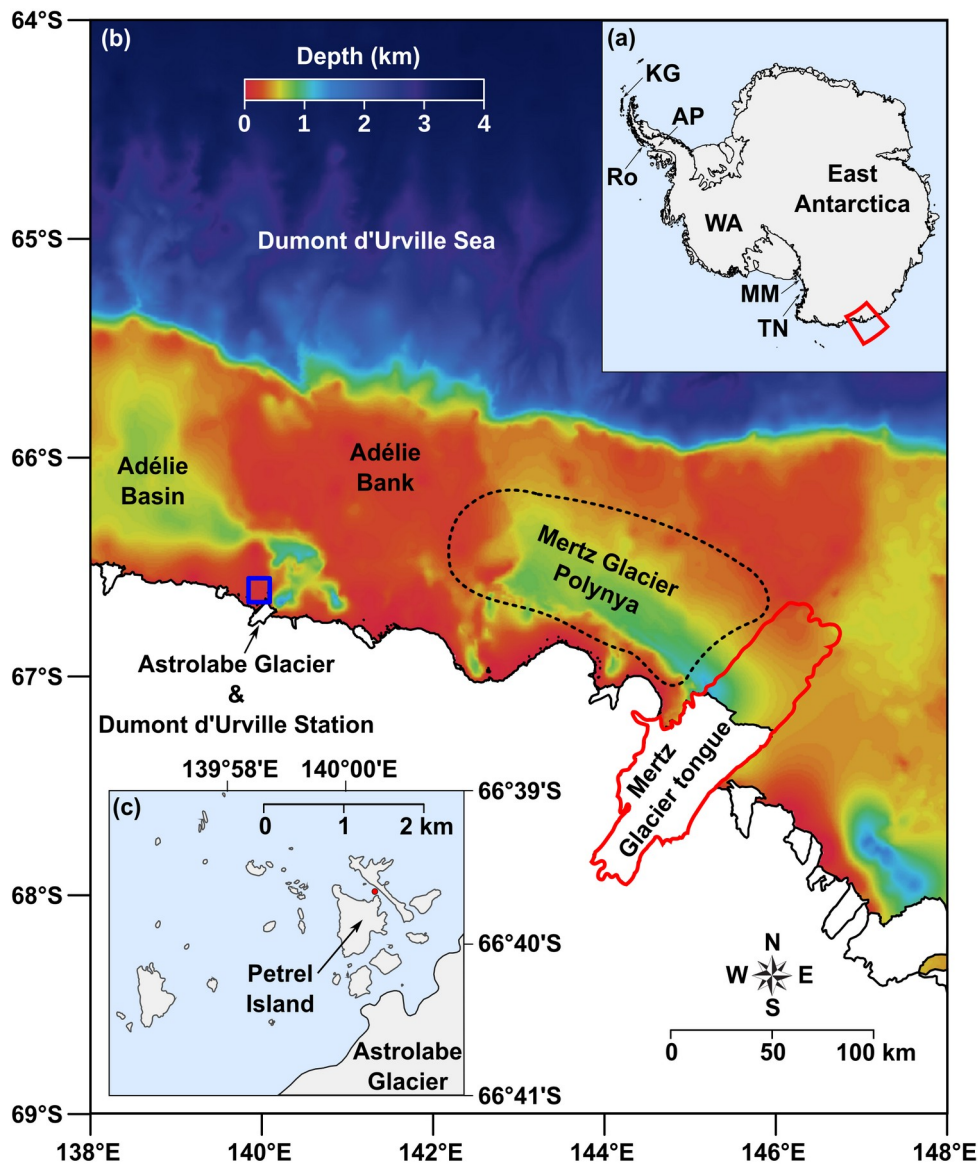


Figure 2: (a) Polar stereographic map of Antarctica. AP = Antarctic Peninsula; KG = King George Island; MM = McMurdo Sound; Ro = Rothera Research Station; TN = Terra Nova Bay; WA = West Antarctica. Red boxed area is shown in panel b. (b) Bathymetric map of Dumont d'Urville Sea. High resolution bathymetric data come from the MEAsURES BedMachine Antarctica dataset (Morlighem, 2019). The red line delimits the position and extent of the Mertz Glacier tongue before its calving in February 2010. The dotted black line roughly delimits the Mertz Glacier Polynya. The blue box off the Astrolabe Glacier represents the area over which satellite data were averaged. (c) Map of the Cape Geology Archipelago. The red dot shows the exact location (Chenal du Lion) where live specimens of *Laternula elliptica* were collected in January 2016.

2. Materials and Methods

2.1. Shell sampling and growth measurements

Laternula elliptica specimens were collected near the French scientific station, the Dumont d'Urville Station, which lies on Petrel Island in the Cape Geology Archipelago (Fig. 2c). A total of 27 live lantern clams were harvested by SCUBA diving at 21 m depth in the Chenal du Lion (66°39'41"S; 140°00'36"E; Fig. 2c) on Jan 11, 2016 and Jan 14, 2016. Upon collection, soft tissues were carefully removed from the valves. Shells were washed in water, gently brushed to remove mud and left to air dry. Shell lengths were measured using a vernier calliper (range: 69-101 mm, mean = 88.8 mm, s.d. = 8.4 mm). Chondrophores of right valves were embedded in epoxy resin. Epoxy blocks were ground along the axis of maximum shell growth and polished, and acetate peels were prepared following etching in 0.1 M HCl for 1 min 40 s. Acetate peel images were prepared using an Axio Lab A1 microscope equipped with a Zeiss AxioCam ERc 5s camera and obtained photographs were stitched in Image-Pro Premier software to measure annual growth increment widths. A calendar year was assigned to each growth increment by visual cross-dating backward from the sampling year. Growth increment widths were measured from the last deposited growth increment (margin) towards preceding years using Image-Pro Premier software.

Qualitative verification of cross-dating and chronology construction were conducted using R 4.2.1 (R Core Team, 2022) and the package dplR (Bunn, 2008). Each original measurement time series was first power-transformed to stabilise variance throughout the growth series (Cook & Peters, 1997). It was then detrended by calculating the ratio (also referred to as "growth index") for each year between each set of power-transformed measurements and its best-fit negative exponential function in order to remove the ontogenetic growth trend present within the series. The dplR package was also used for calculating series intercorrelation, the overall average comparison between each individual time series and the average of all others.

A standard chronology was built by averaging each year's growth indices using Tukey's biweight robust mean which minimises the effects of outliers. In addition, a residual chronology was constructed where autocorrelation was removed from each series before averaging. To this end, each power-transformed, detrended, individual time series was prewhitened by fitting an autoregressive model. Then all prewhitened time series were averaged using the Tukey's biweight robust mean.

Expressed population signal (EPS) was used for assessing the reliability of chronology and an arbitrary EPS value of 0.85 was considered as the threshold at which the sample set adequately reflects the theoretical population from which it was drawn (Wigley et al., 1984). EPS was calculated with dplR over a running window of 8 years with 4 years overlap.

2.2. Environmental data

Several environmental variables may influence the physiology and therefore growth of secondary producers inhabiting Antarctic coastal ecosystems: sea-ice dynamics, water temperature and the amount of food. Unfortunately, no continuous measurements of these parameters are available for waters near the Petrel Island. Therefore, we used satellite data to obtain information on sea-ice concentration (SIC), sea surface temperature (SST) and chlorophyll *a* concentration (Chl-*a*). All files were downloaded in NetCDF4 format and were processed using R 4.2.1 (R Core Team, 2022).

NOAA/NSIDC Climate Data Record of Passive Microwave Sea Ice Concentration provided SIC values on a 25×25 km grid at daily and monthly resolutions, over the 1995–2015 period (Meier et al., 2017). For each 12-month period, three main parameters describing sea-ice dynamics were calculated (see Peng et al., 2018). As per convention, the first and last days of a given 12-month period were set to September 1st (year *y*) and August 31st (year *y*+1), respectively, because these dates include the growth period of *L. elliptica*. The day of retreat corresponds to the last day SIC dropped below 15 %, i.e. the end of the seasonal ice loss period. The day of advance is the beginning of the seasonal ice gain period and is defined as the first day SIC increases to more than 15 %. The number of days between these two dates is defined as the inner ice-free period and it captures the period of open ocean with an ice fraction of less than 15 %.

The NOAA Optimum Interpolation Sea Surface Temperature (OI SST V2) dataset was used to obtain time series between 1995 and 2015 with two different resolutions: (1) daily, high-resolution (0.25×0.25°) data and (2) monthly, low-resolution (1×1°) data. Both datasets were provided by the NOAA PSL, Boulder, Colorado, USA, from their website at <https://psl.noaa.gov>.

An estimation of the monthly concentration of Chl-*a* was obtained between 1997 and 2015 from GlobColour, by averaging data from different sensors (SeaWiFS, MERIS, MODIS Aqua, and VIIRS). Chl-*a* concentration was estimated from the OC5 algorithm (Gohin et al., 2002), with a spatial resolution of 4×4 km, in areas with open water. It must be kept in mind that satellite Chl-*a* data provide only a biased view of reality, not least because they give no hint of what is going on beneath the sea surface. Therefore, the actual Chl-*a* concentration in the entire water column is certainly higher than our estimates. Moreover, satellite data do not discriminate the size spectrum of phytoplankton species. Yet, many suspension feeders select for particle size when feeding.

2.3. Data treatment and statistical analyses

Time series of environmental variables were obtained by calculating daily (SST, SIC) or monthly (Chl-*a*) averages of all cells (size and number depending on the sensor resolution) contained within a 66 km² polygon (dark blue rectangle off Astrolabe Glacier on Fig. 2b: 66°35'–66°40'S; 139°55'–140°05'E). Then, for each growth season (September 1st to August 31st), we calculated the day of retreat, the day of advance, the length of the inner ice-free period, and the monthly averages of SST and Chl-*a* concentration in December, January, February and March. The

relationship between the residual chronology indices and environmental variable time series was assessed by calculating the Spearman's rank correlation coefficient, because most data were not normally distributed.

To gain insight on possible correlations between the residual chronology and environmental parameters at a much wider scale, spatial correlation maps (Spearman's ρ) were computed over a ca. 3 million km² ocean area (60°–75°S; 105°–175°E). For each cell of the gridded environmental datasets, pairwise Spearman's correlations were computed between the residual chronology indices and SIC (resolution 25 km), SST (1°) and Chl-*a* (4 km) average values for the months of November, December, January, February and March. Only correlations at a 90 % significance level (or higher) are displayed on these maps.

For the above-described statistical analyses, we did not consider data after 2012, due to the calving of the Mertz Glacier tongue in February 2010. Before this event, the tongue extended approx. 145 km from the grounding line and protruded approx. 100 km out to sea from the coastline (Fig. 2b; Giles, 2017). In mid-February 2010, the massive iceberg B-9B collided with the tongue, precipitating its calving. Previous studies have shown that this sudden change to the regional icescape resulted in an increase in SIC west of the Mertz Glacier (Campagne et al., 2015) along with changes in the dynamics and distribution of primary production (Shadwick et al., 2013). Around Petrel Island, major changes were observed after the calving, with the almost total lack of sea-ice melt from winter 2012 to spring 2015/2016 which led to the formation of multi-year ice reaching a significant thickness (Michel et al., 2019). Our observations around Petrel Island in summer 2015/2016 revealed places where the fast ice thickness reached 5 m. These atypical years had negative impacts on many seabirds. Barreau et al. (2019) show that unusually high summer SIC (e.g. in 2016) impaired the breeding success of Adélie penguins. Similarly, Barbraud et al. (2015) highlight the negative impact of multi-year sea ice accumulation in 2013/2014 on the breeding success of many seabird species, including Adélie penguins (not a single chick raised in 2014), emperor penguins, south polar skuas, southern fulmars, Cape petrels and Wilson's storm petrels. These environmental conditions were considered as abnormal and were not included in the statistical analyses of long-term data.

3. Results

3.1. Variability of environmental parameters

Over the 1995–2015 period, SIC usually varied seasonally from 0 % in summer to approx. 100 % in winter (Fig. 3). However, SIC did not drop to 0 % in 2011/2012 (minimum SIC = 5 %), in 2012/2013 (38 %), in 2013/2014 (69 %) or in 2014/2015 (13 %). This is reflected in the duration of the inner ice-free period which varied between 26 and 93 days between 1995/1996 and 2011/2012, and dropped down to less than 1 week thereafter (0 days in 2012/2013 and 2013/2014, 3 days in 2014/2015). Annual minimum SST ranged between -1.8 °C and -1.6 °C (monthly averages), with low interannual variability (Fig. 3). On the other hand, annual maxima

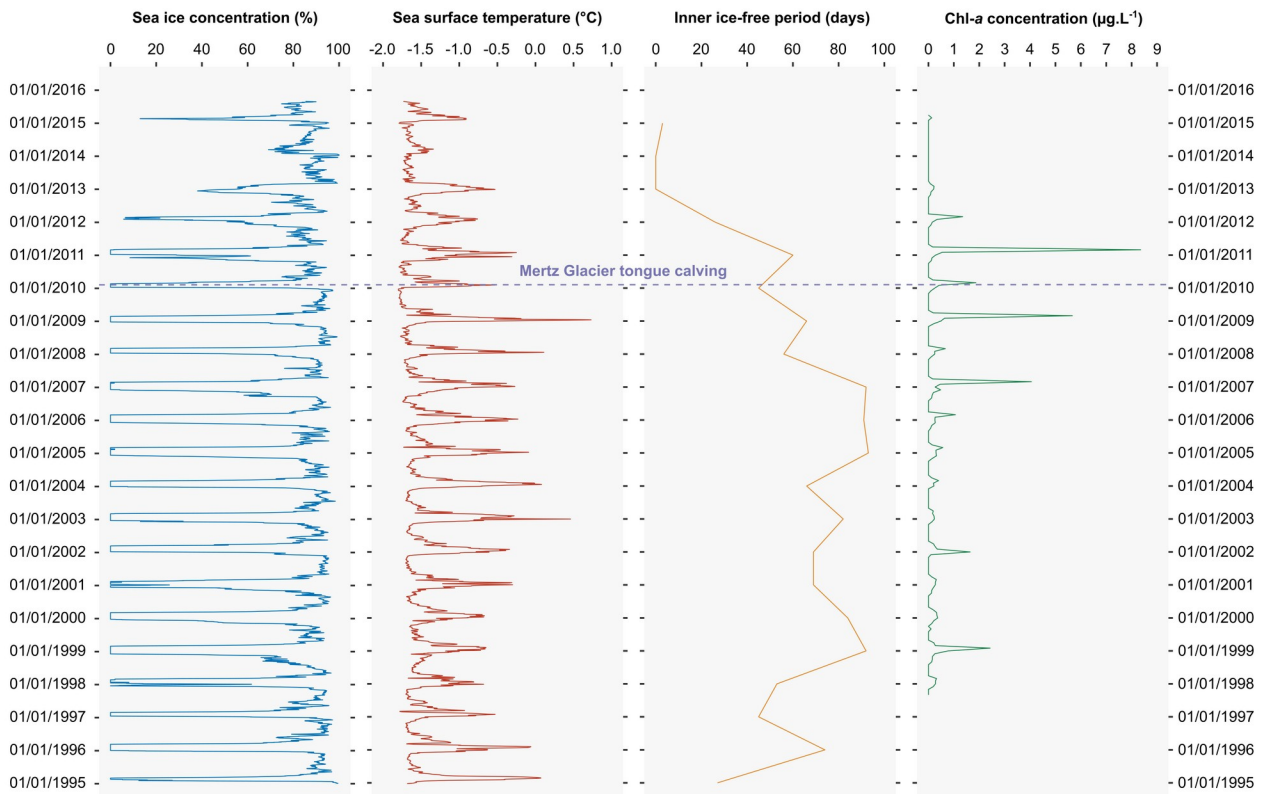


Figure 3: Time series of sea-ice concentration, sea surface temperature, duration of the inner ice-free period and Chl-*a* concentration. The dashed line indicates the date the Mertz Glacier tongue calving occurred.

showed year-to-year variations. Monthly average SST values reached a maximum of 0.0 °C in summer 2008/2009, but never increased beyond -1.4 °C in summer 2013/2014. Remotely sensed Chl-*a* monthly data (only measured from September 1997 on; Fig. 3), used as a proxy for phytoplankton biomass dynamics, showed high interannual variation with annual maxima ranging from almost 0 µg.L⁻¹ in 2013/2014 to 8.4 µg.L⁻¹ (2010/2011). On average, the maximum annual Chl-*a* concentration was 1.65 µg.L⁻¹ (s.d. = 2.25). Overall, Chl-*a* concentration tended to be higher between 2006 and 2012 compared with the 1997–2006 and 2012–2015 periods. Of note, the low levels between years 2012 and 2015 were synchronous with a long period of summer sea-ice cover in the area.

3.2. Master chronology

The majority of annual growth increments had clear boundaries (Fig. 1c). However, the limits of the first 3 to 4 annual increments (those formed during early ontogeny) were often hardly discernible (at least for accurate increment width measurements) due to very faint annual lines. We estimated that accurate measurements of increment width began when the individuals were aged 3.7 years old (± 1.7). Similarly, the last increments (1 or 2) were too narrow to be measured with accuracy on some specimens. Overall, the number of clearly discernible annual increments in the analysed shells ranged from 16 to 23 (mean = 19.3; s.d. = 1.8). Considering our estimation of the number of unclear, ontogenetically youngest increments, the maximum age of the shells was

likely close to 30 years. There was a strong ontogenetic decrease in shell growth during the first 10 years of life. Shells had a strong synchronous growth signal (Fig. 4): series intercorrelation was 0.768. The oldest measured growth increment corresponds to the year 1993 (i.e. the 1992/1993 growth season). Shell chronologies were represented by more than 10 individuals from year 1996 onward. According to the EPS, the residual chronology was robust (EPS > 0.85) after year 1996. The highest and lowest growth indices corresponded to the 2007/2008 and 2014/2015 growth seasons, respectively (Fig. 4). Overall, the residual chronology was characterised by a decrease in growth indices from 1997/1998 to 2002/2003, an increase until 2007/2008, then a plateau until 2011/2012 and finally a decrease until collection.

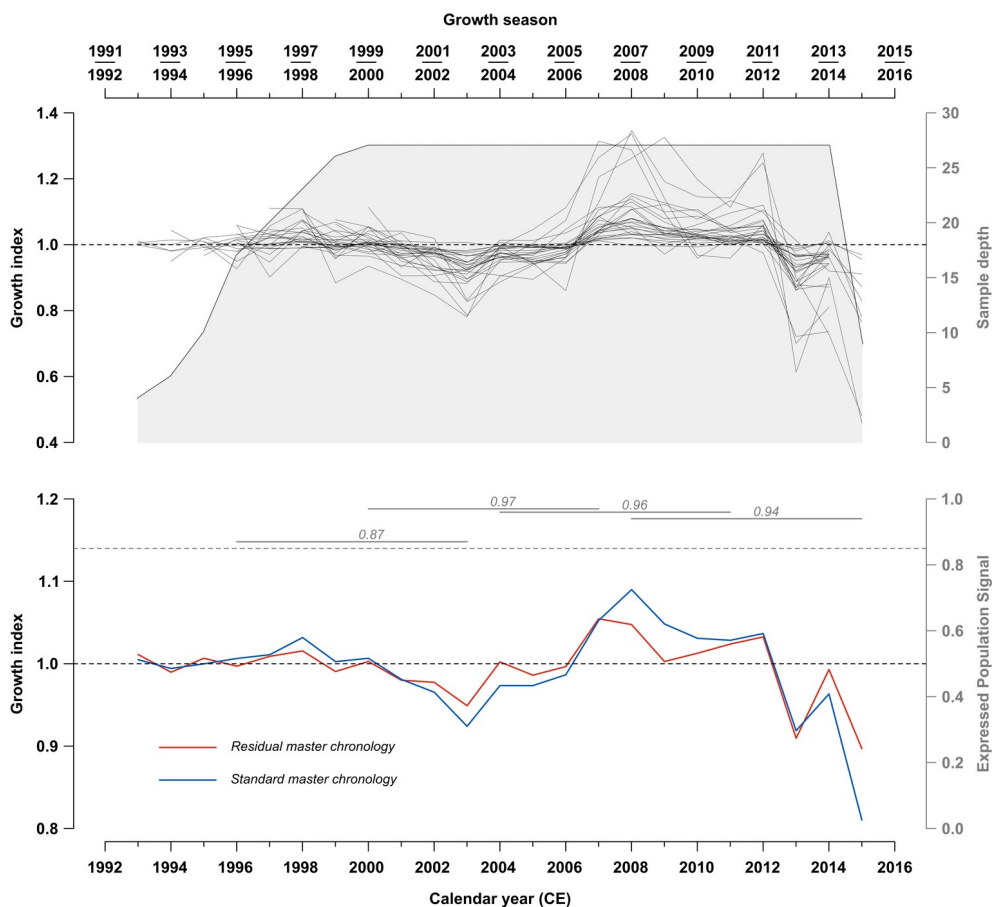


Figure 4: Upper panel: Individual power-transformed, detrended, growth time series. Lower panel: Standard and residual master chronologies of *Laternula elliptica* shell growth. The EPS statistics is indicated in italics and was calculated over a running window of 8 years with 4 years overlap.

3.3. Correlation with environmental parameters

Spearman's rank correlations were computed between the residual chronology indices and environmental variable time series (significance level = 0.10). At a local scale (Fig. 5), shell growth was significantly correlated with Chl-*a* concentration in March ($S = 164$; $n = 15$; $\rho = 0.707$; $P = 0.003$), the average SST in December ($S = 1204$; $n = 17$; $\rho = -0.476$; $P = 0.053$), the length of the inner ice-free period ($S = 1220$; $n = 17$; $\rho = -0.495$; $P = 0.043$) and the date of retreat ($S = 459$; $n = 17$; $\rho = 0.438$; $P = 0.079$). These last three variables were also significantly correlated with each other. When the day of retreat occurred early in the season, it led to an increase in SST in December ($S = 1240$; $n = 17$; $\rho = -0.518$; $P = 0.033$) and to a longer inner ice-free period ($S = 1573$; $n = 17$; $\rho = -0.927$; $P < 0.005$). As a result, average SST in December and inner ice-free period were positively correlated ($S = 346$; $n = 17$; $\rho = 0.576$; $P = 0.016$).

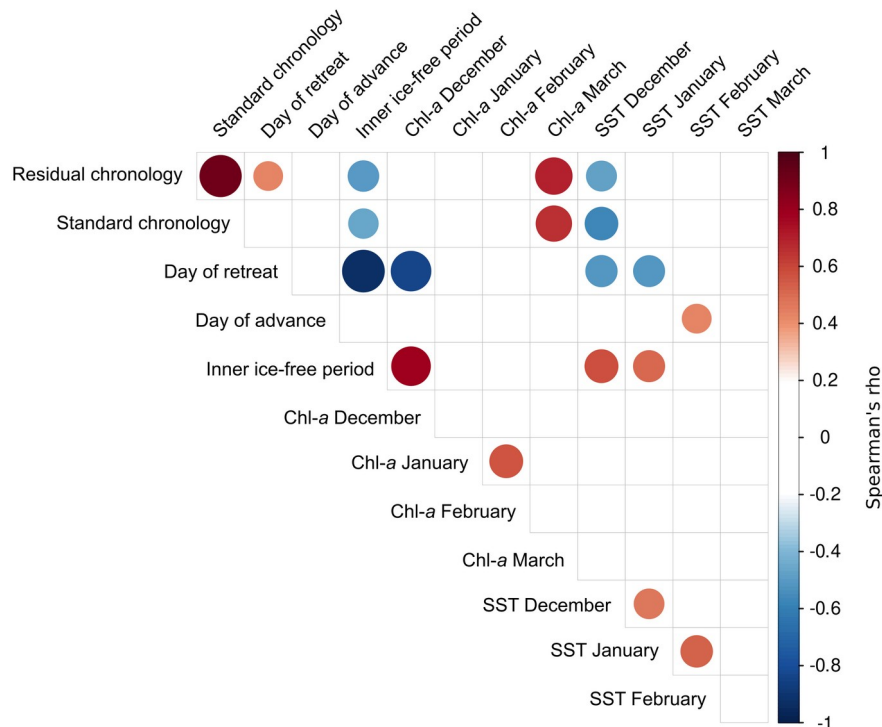


Figure 5: Spearman's rank correlation matrix between *Laternula elliptica* master chronologies (standard and residual) and environmental variables. Only pairwise correlations with a P -value < 0.10 are shown as red or blue circles.

At a much wider scale (Australian sector of the Southern Ocean), some significant correlations were found between shell growth and SIC, SST and Chl-*a*, for the November-March period (Fig. 6). The amount of sea ice present in November-December east and northeast of Petrel Island was positively correlated with lantern clam shell growth (Fig. 6a). This relationship probably explains the negative correlation found between residual chronology indices and SST for the same months, in the same area (Fig. 6b). Contrary to the correlation with SIC, which only involved a few patches along the coast from January to March, the correlation between shell growth and SST

covered a large area until the end of summer. For these two environmental variables, the statistical tests highlighted a one-way correlation with the residual chronology indices: either positive for SIC (with only a few patches displaying a negative correlation), or negative for SST (a few spots were characterised by a positive correlation between SST and shell growth).

The relationship between shell growth and Chl-*a* concentration was slightly more equivocal. East of 150°E, there were almost no significant correlations or some patches with a significantly negative correlation (purple areas on Fig. 6c). On the other hand, large areas located between 61 and 64°S, and between 120 and 150°E, had December-to-March Chl-*a* concentrations that were

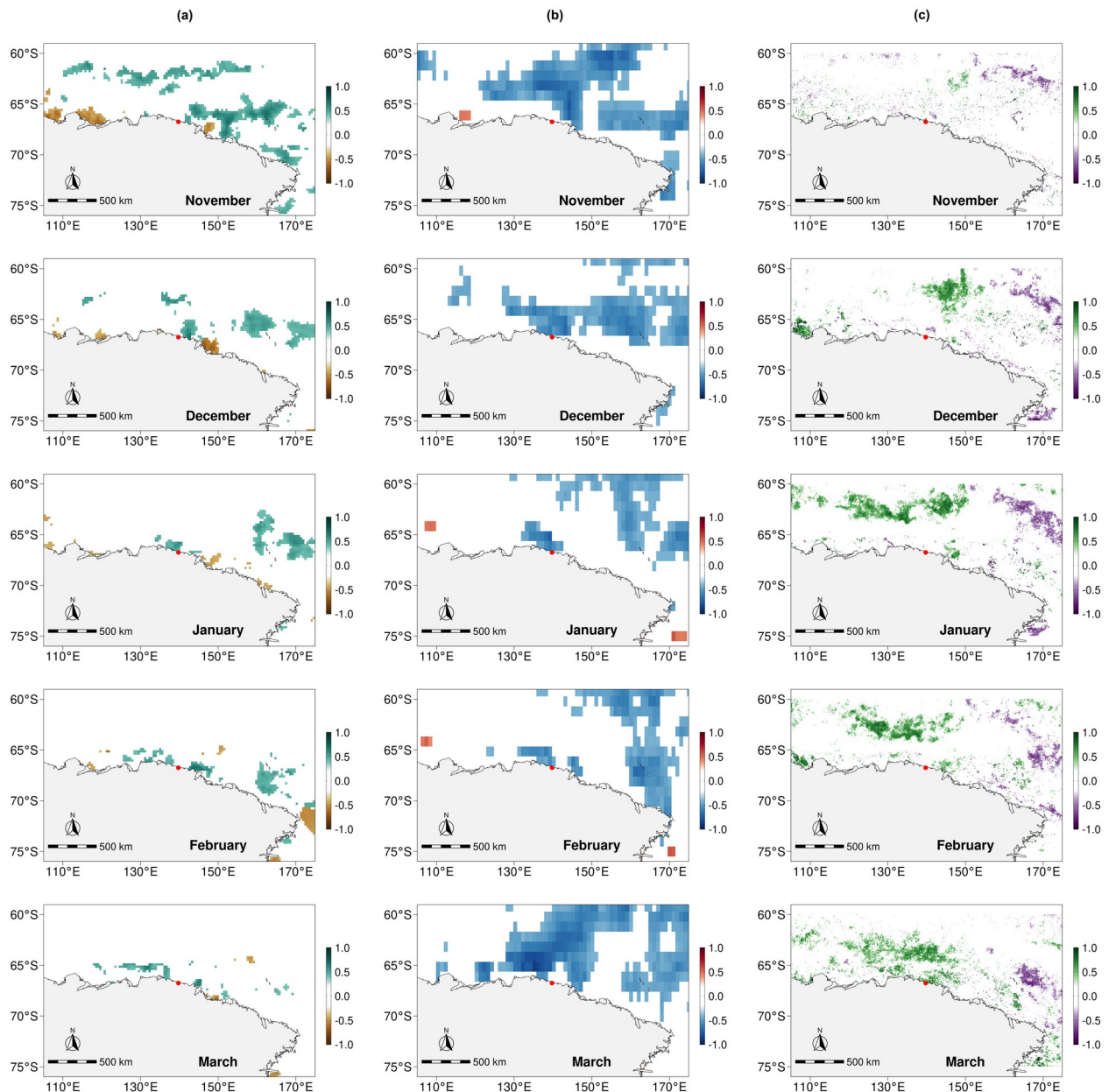


Figure 6: Spatial correlation maps between the *Laternula elliptica* residual master chronology and environmental variables, computed for five different months between November and March. Only statistically significant Spearman's rank correlations (P -value < 0.10) are displayed. (a) Correlations with sea-ice concentration. (b) Correlations with sea surface temperature. (c) Correlations with Chl-*a* concentration. The red dot shows the location of the Dumont d'Urville station.

positively correlated with shell growth (green areas on Fig. 6c). These green patches tended to be closer to the coast in March than during the preceding months. For all the spatial correlation maps focusing on Chl-*a*, it must be kept in mind that white areas indicate either (1) a lack of statistically significant correlation with shell growth or (2) gaps in satellite data, which occurred due to cloud or sea-ice cover.

4. Discussion

4.1. Shell growth synchrony

The maximum longevity of lantern clams from Petrel Island is estimated at about 30 years, in agreement with lifespan in the King George Island population (Philipp et al., 2005; Román-González et al., 2017). The oldest specimens were > 100 mm in shell length, indicating a relatively high growth rate in such a cold environment. Most of *L. elliptica* shell growth occurs during summer (Brey & Mackensen, 1997), which corresponds to a very short time window (December to March) at Petrel Island. Summer environmental conditions are therefore ecological factors that may exert control on annual increment width. Small interannual environmental differences may result in large changes in growth performance (Brey et al., 2011). All lantern clams from a given population should respond similarly to environmental variability.

Our 20-year long master chronology indeed highlights very strong growth synchrony between individuals (Fig. 4), as demonstrated by the very high series intercorrelation (0.768). This intercorrelation echoes that reported from a 49-year long master chronology built from King George Island specimens (Brey et al., 2011). These similar patterns strongly suggest that the interannual variability in shell growth is controlled by one or several environmental drivers affecting the whole population in the same way, rather than by biotic interactions such as predation which randomly affect only a given proportion of these individuals.

4.2. Drivers of interannual shell growth dynamics

Statistical comparisons between our master chronology and time series of environmental parameters highlighted that annual increments were wider when the inner ice-free period is short (which correlates with a later day of retreat), when the December SST was relatively low and when the March Chl-*a* concentration was relatively high (Fig. 5). In addition, spatial correlation maps clearly highlighted that shell growth is not solely influenced by local environmental variability, but also by SIC, SST and primary production features at a much wider scale (Fig. 6). An increase in the length of the inner ice-free period could possibly affect shell growth in several different ways: (1) warming of the water column, (2) higher probability of iceberg scouring, and (3) modifications in the relative contributions of primary producers on *L. elliptica* diet.

4.2.1. Water temperature

At first glance, a significant negative correlation between master chronology and water temperature, highlighted both at a local scale (Fig. 5) and at the wider scale of the Dumont d'Urville Sea (Fig. 6b), may seem incongruent. Given that *Laternula elliptica* shells grow mainly during austral summer, it seems unlikely that the small difference in SST of only ~1.5 °C between the coldest and warmest summers (Fig. 3) explains this statistical correlation. However, Antarctic marine species are essentially stenothermic due to the extreme stability of their thermal environment and have a low tolerance for variation in temperature (Peck et al., 2014). Thus, even small increases in water temperature can have physiological repercussions (Morley et al., 2012). In a study on the influence of temperature on the physiology of Antarctic ectothermic organisms, Peck et al. (2014) showed that *L. elliptica* biological activities, including burrowing, are negatively affected at temperatures of 2-3 °C. This finding supports the existence of a negative relationship between shell growth and SST.

However, this relationship may also be a side effect of the negative correlation between shell growth and inner ice-free period duration, that is also correlated with SST (Fig. 5). When the duration of the inner ice-free period is extended, solar radiation can warm the surface waters longer, thus increasing the summer SST maxima. Therefore, we cannot rule out the possibility that it is the length of the open water period that affects shell growth, rather than SST.

4.2.2. Iceberg scouring

At a local scale, we found a negative correlation between inner ice-free period duration and *L. elliptica* shell growth. A long inner ice-free period may increase the likelihood of an iceberg drifting into the area and scouring the seafloor, thus negatively affecting benthic communities. Indeed, iceberg scour has previously been shown to damage *L. elliptica* shells at many locations around Antarctica (Ahn et al., 2003), including Petrel Island (Harper et al., 2012). However, our specimens were sampled in a deep (20-25 m) and narrow (60 m) channel, which makes it very virtually impossible for large icebergs to pass through and scour the seabed. Moreover, none of the shells analysed in this study showed obvious breakage or recalcification scars, ruling out contact with icebergs at our study site. Therefore, it could be that the inner ice-free period duration acts on shell growth, not through SST or iceberg scouring, but rather through other processes such as primary producer dynamics.

4.2.3. Phytoplankton and microphytobenthos

Using Dynamic Energy Budget modelling, Agüera et al. (2017) demonstrated that the relatively fast growth rate of lantern clams, even at low temperature, is related to low maintenance costs and to their capacity for building energy reserves. Irrespective of water temperature, lantern clams can grow fast by taking advantage of any ephemeral food supply, stored as proteins in their muscle tissues (Ahn et al., 2003). This efficient energy storage strategy makes them able to thrive even in periods of food shortage. Although their study focused on

variations in soft tissue mass (and not on shell growth rate), [Ahn et al. \(2003\)](#) highlighted that *L. elliptica* growth rate at King George Island is positively correlated with Chl-*a* concentration, but not with water temperature, thus demonstrating that food is the main factor governing growth.

Indeed, Chl-*a* concentrations measured before freeze onset (March) at both local ([Fig. 5](#)) and wider scales ([Fig. 6c](#)), are positively correlated with shell growth at Petrel Island. However, quite surprisingly, no significant correlation was found between shell growth and Chl-*a* concentrations around Petrel Island in December, January and February ([Fig. 5](#)). Actually, over the period 1997-2011, the monthly Chl-*a* concentration was significantly higher in March (mean_{March} = 1.71 $\mu\text{g}\cdot\text{L}^{-1}$) than in the preceding months (mean_{December-February} = 0.19 to 0.48 $\mu\text{g}\cdot\text{L}^{-1}$), as was the interannual variability (s.d._{March} = 2.43 $\mu\text{g}\cdot\text{L}^{-1}$; s.d._{December-February} = 0.11 to 0.55 $\mu\text{g}\cdot\text{L}^{-1}$). Although an earlier day of retreat (= longer inner ice-free period) significantly stimulates local phytoplankton production in December ([Fig. 5](#)), early summer Chl-*a* concentration never reached the levels recorded in March. Therefore, the relatively low phytoplankton amounts and limited year-to-year variability in summer have virtually no influence on the interannual variability in shell growth. On the contrary, phytoplankton production in early autumn acts as a crucial energy supply for *L. elliptica*. When limited, it impairs the clam metabolism, which translates into a narrow annual growth increment.

Additional evidences of the importance of phytoplankton for *L. elliptica* shell growth are the correlations found at a wider scale from December to March ([Fig. 6c](#)). They suggest that the remote, offshore, phytoplankton production may be partly advected in from ice-free areas to the coast by Circumpolar Deep Water that intrudes onto the plateau during summer ([Campagne et al., 2016](#)), and then benefits the shallow benthic communities. The importance of phytoplankton advected under sea ice was already highlighted by [Dayton et al. \(1986\)](#) in their study on benthic communities in the east side of the McMurdo Sound.

[Dayton et al. \(1986\)](#) also strengthened the importance of benthic primary production for soft-bottom invertebrate communities at McMurdo Sound. Similarly, in a study carried out at Petrel Island in 2014/2015, [Michel et al. \(2019\)](#) concluded that benthic biofilm (which was extremely abundant at that time) accounted for >90% of *L. elliptica*'s diet. Although microphytobenthos covered large areas in shallow waters (< 10 m water depth; see [Fig. 1b](#)) during our study, we did not observe such benthic biofilm at our sampling site. We hypothesise that it was likely too deep (20-25 m), without sufficient irradiance, for benthic microalgae to develop.



Figure 7: Picture of falling sympagic algae (vertical export to the benthos) under unusually thick (3 m) fast ice off Petrel Island (picture taken on Jan 07, 2016) – © Erwan Amice (CNRS).

4.2.4. *Sympagic algae*

Based on our diving experience in this ecosystem, we postulate that sympagic algae (Fig. 7) are other important sources of energy for *L. elliptica*. Sympagic algae grow under sea ice in spring and summer and therefore need a late day of retreat (i.e. short inner ice-free period) to accumulate high biomass. When sympagic algal filaments are long/heavy enough, they ultimately fall through the water column and reach the sediment within a few hours or days (Fig. 7). When sea ice melts and breaks up early, this energy supply to the benthos is limited, which possibly explains why *L. elliptica* shell growth is impaired under longer inner ice-free periods. This hypothesis is strengthened by the positive correlation between shell growth and SIC in November-December, east/northeast of Petrel Island (Fig. 6a). The area where this correlation is significant has been identified as a region of drifting sea ice (Massom & Stammerjohn, 2010). Pack ice forms hundreds of kilometres east of the Mertz Glacier, and drifts westwards with the Antarctic Coastal Current. When this pack-ice river approaches the Mertz Glacier, it is deflected northwards by fast ice and grounded icebergs that have accumulated against the eastern side of the glacial tongue. It then forms a mid-pack stream along the shelf break, thus protecting fast ice off Petrel Island from the destructive action of ocean swell coming from the open ocean (Massom & Stammerjohn, 2010). When this mid-pack stream is absent, fast ice is destroyed earlier in spring, which does not allow sufficient time for sympagic algae to accumulate under sea ice, thus negatively affecting *L. elliptica* shell growth.

Therefore, we suggest that sympagic algae are an important, albeit ephemeral, organic matter supply, and may constitute a valuable energy source for benthic primary consumers at Petrel Island. Two stable isotope studies of *L. elliptica* tissues in the Ross Sea (Norkko et al., 2007;

Wing et al., 2012) highlighted large dietary plasticity, related to sea-ice conditions. In the vicinity of the Terra Nova Bay polynya, *L. elliptica* mainly feeds upon organic matter contained in the sediment (microphytobenthos, bacteria, detritus); at New Harbour (in the McMurdo Sound), which experiences cold stenothermal conditions, prolonged darkness and persistent sea-ice coverage, its diet is dominated by sympagic algae and, to a lesser extent, sediment (Norkko et al., 2007). Our study site more closely resembles New Harbour than the open water conditions of the Terra Nova Bay polynya, suggesting that the contribution of sympagic material to the *L. elliptica* diet is likely quite high off Petrel Island. Similarly, Wing et al. (2012) concluded that sympagic material is a core component of the coupling between sea-ice dynamics and secondary production in coastal trophic webs where sea-ice cover is high.

On the other hand, a recent study carried out at Petrel Island found contradictory results. Using an isotope approach based on a Bayesian mixing model, Michel et al. (2019) suggest that lantern clams rely almost exclusively on benthic production at Petrel Island, with virtually no contribution from sympagic algae. However, they analysed benthic invertebrates collected during summers 2013/2014 and 2014/2015. Shell growth dynamics during these two seasons were not included in our statistical analysis because sea ice did not go out during those years, which is not representative of a "normal" state. The relative availabilities of *L. elliptica* food sources (benthic, sympagic, pelagic) were possibly different during these times in comparison with "normal" years. Moreover, Antarctic benthic invertebrates may have a slow isotope turnover rate (Wing et al., 2012). Therefore, clams analysed in Michel et al. (2019) may not have reached isotopic equilibrium with their food at the time of sampling.

Some studies also reported high densities (up to 25 m⁻¹) of *L. elliptica* at localities (e.g. New Harbour) where sympagic production is negligible because of very thick sea-ice that rarely goes out to sea (Dayton et al., 2019). Those observations suggest that *L. elliptica* does not absolutely require sympagic algae to grow fast, and that its diet (and relative contributions of benthic, pelagic and sympagic food sources) is highly flexible and can differ both temporally and spatially.

5. Conclusions

Year-to-year *Laternula elliptica* variability in shell growth can be explained by environmental drivers. Intuitively, reduced sea ice would appear to be advantageous for bivalve shell growth because it can enhance phytoplankton growth. But the situation seems more complicated than this straightforward explanation as a longer inner ice-free period also decreases the time required to accumulate high biomass of sea-ice algae. We propose that around Petrel Island, an Antarctic coastal ecosystem with an extended sea-ice cover period, both phytoplankton and sympagic algae are important sources of energy for *L. elliptica*. This means that if the inner ice-free period was to increase at that location in the next decades because of global warming, the growth dynamics of *L. elliptica* could be severely impaired unless the lower contribution of sympagic algae to its diet could be compensated by a higher phytoplankton or microphytobenthic production. If not, it would severely affect benthic food webs because *L. elliptica* is a key species in Antarctic shallow soft bottom communities (Ahn, 1993; Momo et al., 2002). Due to (i) their large geographical

(circumpolar distribution, extending north to the sub-Antarctic islands) and temporal distributions (abundant remains in raised beach Quaternary deposits; [Berkman et al., 1998](#)), (ii) the strong synchrony in interannual shell growth variation between specimens and (iii) the sensitivity of shell growth to sea-ice dynamics, we conclude that *L. elliptica* shells are highly relevant and outstanding sclerochronological archives for the reconstruction of past and present Antarctic environmental variability.

Acknowledgements

JT, EA and LC were supported by the Institut Polaire Français Paul Émile Victor (IPEV) and the Antarctic programme IPEV 1124 REVOLTA (“Ecological Resources and Valorisation using a Long-Term Observatory in Adélie Land”). HU and MP were funded by the Croatian Science Foundation project BivACME (IP-04-2019-8542). GlobColour data (<http://globcolour.info>) used in this study were developed, validated, and distributed by ACRI-ST, France. This manuscript received meticulous attention and expert handling from Associate Editor Luigi Musco. It also greatly benefited from critical reviews and very helpful comments by Paul K. Dayton and two anonymous reviewers.

CRedit author statement

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Declaration of competing interest

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

Data availability statement

Data available in the SEANOE (SEA scientific Open data Edition) repository: <https://doi.org/10.17882/89420> (Thébault & Peharda, 2022).

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