



Spatial competition in a global disturbance minimum; the seabed under an Antarctic ice shelf

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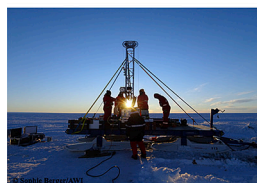
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HIGHLIGHTS

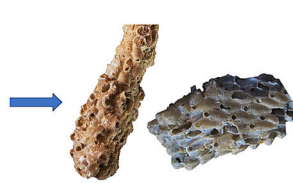
- Life in vast sub-ice-shelf habitats among Earth's least known and least disturbed.
- Boreholes through Ekström Ice Shelf allow unique access to sub-glacial benthos.
- Seabed samples provide first evidence of competition for space under ice shelves.
- Sub-ice-shelf spatial competition complex and globally-high in intensity and severity.
- Implications for ecosystem response to climate-induced environmental change.

GRAPHICAL ABSTRACT

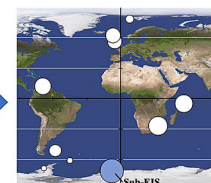
Discovering and characterising interactions between marine life beneath the 1.6 million km² of floating ice shelves overlying Antarctica's continental shelf



Boreholes drilled through an Antarctic ice shelf to collect rare sub-glacial seabed samples 300 m below sea level



Stereo microscopy used to detect and characterise competition for space between lithophiles on biogenic sub-glacial substrata



Sub-ice-shelf competition (Sub-EIS) is strikingly different to other polar areas, and more akin to temperate and tropical areas

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ABSTRACT

The marine habitat beneath Antarctica's ice shelves spans ~1.6 million km², and life in this vast and extreme environment is among Earth's least accessible, least disturbed and least known, yet likely to be impacted by climate-forced warming and environmental change. Although competition among biota is a fundamental structuring force of ecological communities, hence ecosystem functions and services, nothing was known of competition for resources under ice shelves, until this study. Boreholes drilled through a ~200 m thick ice shelf enabled collections of novel sub-ice-shelf seabed sediment which contained fragments of biogenic substrata rich in encrusting (lithophilic) macrobenthos, principally bryozoans – a globally-ubiquitous phylum sensitive to environmental change. Analysis of sub-glacial biogenic substrata, by stereo microscopy, provided first evidence of spatial contest competition, enabling generation of a new range of competition measures for the sub-ice-shelf benthic space. Measures were compared with those of global open-water datasets traversing polar, temperate and tropical latitudes (and encompassing both hemispheres). Spatial competition in sub-ice-shelf samples was found to be higher in intensity and severity than all other global means. The likelihood of sub-ice-shelf competition being intraspecific was three times lower than for open-sea polar continental shelf areas, and competition complexity, in terms of the number of different types of competitor pairings, was two-fold higher. As posited for

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an enduring disturbance minimum, a specific bryozoan clade was especially competitively dominant in sub-ice-shelf samples compared with both contemporary and fossil assemblage records. Overall, spatial competition under an Antarctic ice shelf, as characterised by bryozoan interactions, was strikingly different from that of open-sea polar continental shelf sites, and more closely resembled tropical and temperate latitudes. This study represents the first analysis of sub-ice-shelf macrobenthic spatial competition and provides a new ecological baseline for exploring, monitoring and comparing ecosystem response to environmental change in a warming world.

1. Introduction

With anthropogenic greenhouse gas (GHG) emissions at unprecedented levels and atmospheric carbon dioxide concentrations still rising (Friedlingstein et al., 2022), one of the most significant, and perhaps most conspicuous, changes to a warming world is the shrinking of the cryosphere (icescape) (Turner and Comiso, 2017; IPCC, 2019; Parkinson, 2019; Rogers et al., 2020).

In the southern polar region, ice shelves are the floating extensions of the Antarctic Ice Sheet, dominate most of the Antarctic coastline, fringing ~75 % (Rignot et al., 2013), and overlie one-third of Antarctica's continental shelf (Clarke and Johnstone, 2003). The under-ice-shelf marine environment is aphotic and vast, ~1.6 million km² (Clarke and Johnstone, 2003), and, mainly on account of challenges of access, one of the least known habitats on Earth (Barnes et al., 2021b; Griffiths et al., 2021), as well as one vulnerable to GHG-induced global warming (Miles et al., 2017; Lai et al., 2020; Gilbert and Kittel, 2021). Furthermore, the seabed underneath ice shelves is ostensibly among the least disturbed marine surface habitats on the planet (Barnes, 2017).

In Antarctica, episodic retreats and collapses of ice shelves at their outer marine termini, calving fronts, constitute a major source of icebergs (Bigg, 2015). Such icebergs can cause disturbance by colliding with the seafloor of the open-water polar continental shelf (Gutt, 2001). These collisions, referred to as “ice scours” or “iceberg ploughmarks”, can be ubiquitous across the shallower shelf of the seasonal sea ice zone and occur to maximum depths of 650 m (Dowdeswell and Bamber, 2007), and are considered one of the most catastrophic natural disturbance events to benthic marine systems (Gutt and Starman, 2001). In contrast, the expansive seafloor underneath ice shelves is relatively undisturbed, the presence of (permanent) ice shelf above affording it protection from ice-mediated disturbance, in some instances over millennia timescales. Thus, in terms of natural disturbance, Antarctica's continental shelf comprises some of the most and least disturbed seabed habitats on Earth (Gutt and Starman, 2001; Barnes, 2017), with the under-ice-shelf environment representing a rare example of a disturbance minimum for life.

Sampling the environment under ice shelves is challenging and costly, and thus collections of sub-ice-shelf biological samples, are a rarity, constraining our understanding of this vast space. Boreholes hot-water-drilled through ice shelves, however, are an essential method for accessing and enabling the sampling/surveying of sub-ice-shelf marine ecosystems, and various sampling devices can be passed through them into the water column and to the seafloor below. Such access holes, created through less than ten Antarctic ice shelves to date (see Gong et al., 2019), have facilitated some remarkable ecological discoveries, including those related to the underlying seabed habitat and its biotic components. For example, cameras passed down boreholes in the Ross, Amery and McMurdo Ice Shelves uncovered a surprising abundance and variety of seabed-dwelling life – generally unexpected considering the lack of in situ photo-induced primary production, i.e., potential food sources (Pawlowski et al., 2005; Riddle et al., 2007; Kim, 2019). More recently, borehole cameras through Filchner-Ronne Ice Shelf revealed colonisation of hard substrata (a boulder in the particular example) by primary consumers, including suspension-feeding sponges, is possible hundreds of km from the ice-shelf front, and considerable distances from light and open water (Griffiths et al., 2021). Furthermore, physical seafloor samples obtained via sediment grabber and corers dropped

through boreholes in the Ekström Ice Shelf, eastern Weddell Sea (Kuhn et al., 2019), provided evidence of benthic life spanning circa 5800 years as well as an unprecedented richness in bryozoan species exceeding even that of the open-sea continental shelf (Barnes et al., 2021b), such assemblages and novel observations of interactions between individual biota/colonies being the basis of the current study.

Competition is a fundamental component and structuring force of communities (Dayton, 1971; Turner and Todd, 1994; Lomolino et al., 2004), hence influences associated ecosystem services. However, the nature of any competition under ice shelves was, until the current study, unknown or unreported. Borehole-derived samples of the lithophilic benthos residing under the Ekström Ice Shelf recently revealed that both cheilostome and cyclostome encrusting bryozoans are represented (Barnes et al., 2021b). Hence, the corresponding samples and their colonisers can be harnessed to discern whether competition, particularly spatial competition, actually occurs under Antarctic ice shelves and, if so, evaluate whether it resembles open-sea polar competition, as well as where it may fit in a more global context. This research, therefore, not only helps narrow a significant knowledge gap but also provides new baseline information for future ecological monitoring and projected long-term Antarctic studies (see Gutt et al., 2022; Lowther et al., 2022). Furthermore, a rare and novel opportunity is provided in that polar latitude data can, in this instance, be decoupled from high disturbance. As the study area has been relatively unaffected by climate change thus far (e.g., especially compared to much of the Antarctic Peninsula) (Gutt et al., 2022), gaining knowledge of the interactions between the contemporary assemblage constituents is particularly valuable as future temporal change can be more confidently attributed to climate/environmental change.

Previously, Barnes and Neutel (2016) demonstrated high-latitude (polar) spatial competition to be extremely hierarchical and suggested that without disturbance, superior competitors would monopolise space. Such monopolisation should, therefore, eventually lead to most spatial competition being intraspecific (i.e., between members of the same species), hence more tie/stand-off outcomes between competitors (as competitively matched) rather than more “severe” definitive win-losses. In addition, polar substrata from continental-shelf depths have indicated low colonisation levels (Barnes and Kuklinski, 2010). Thus, it was first hypothesised that the intensity and severity of sub-ice-shelf spatial competition, being of a very high-latitude environment of minimal disturbance, would be globally low and mainly comprise intraspecific encounters between the strongest competitor(s). Hence, the second hypothesis was that the complexity of spatial competition under ice shelves would also be low, with little diversity in pairwise competitive encounters due to the majority of spatial competition involving the most dominant competitor(s). Finally, McKinney et al. (1998) previously showed that during and following a massive disturbance event (i.e., mass extinction), cyclostomes dominated over cheilostomes, but then cheilostomes recovered to dominate over cyclostomes across calmer geological time. Thus, it was also predicted that cheilostomes would be especially competitively dominant under ice shelves, given that the sub-ice-shelf seafloor environment is anticipated to be a long-standing disturbance minimum.

2. Materials and methods

2.1. Study area and sites

In January 2018 (austral summer 2017/18), as part of the Sub-Ekström Ice Shelf-Observations (Sub-EIS-Obs) Project (Kuhn and Gædicke, 2015; Kuhn et al., 2019), seafloor material was collected from two continental shelf sites, EIS-2 and EIS-3, underneath the Ekström Ice Shelf, eastern Weddell Sea, Dronning Maud Land, East Antarctica (Fig. 1, Table S1); the wider environs of particular interest for long-term systematic ecological studies related to the impacts of climate and environmental change (see Gutt et al., 2022; Lowther et al., 2022). Sites EIS-2 and EIS-3 were ~19.6 km apart, the distance determined using Vector Analysis Tools in QGIS v3.22.9. The site closest to the ice-shelf edge/front, EIS-2, was at 250 m water depth in a 58 m high sub-ice-shelf cavity and ~3.4 km from seasonally-open water. The second site, EIS-3, was at 300 m water depth in a 110 m high sub-ice-shelf cavity and ~9.6 km

from seasonally-open water. Both sites, being sub-ice-shelf (and set back from the ice-shelf calving front), are protected from iceberg-mediated disturbance; indeed, seaward of Ekström's ice-shelf front transiting/drifting icebergs scour and rework the sediment of the adjacent open continental shelf (Oetting et al., 2022 and see Fig. 7 within).

2.2. Collection of physical samples (seabed substrata)

The sub-glacial seafloor samples of this study (corresponding to one sample per site) were brought up from a depth of 250–300 m to the ice-shelf surface through hot water drill (bore)holes (the ice shelf being ~190 m thick at each location) and were obtained from the seabed surface sediment layer (up to 5 cm depth) using a Wippermann grabber (Wippermann GmbH, Germany) at EIS-2 and JLU vibrocorer (Justus Liebig University, Germany) at EIS-3 (Kuhn et al., 2019; Gong et al., 2019; Kuhn et al., 2021). Dead bryozoan fragments (skeletons), i.e., the seabed substrata examined in this study, constituted 9.7 and 8.95 % of

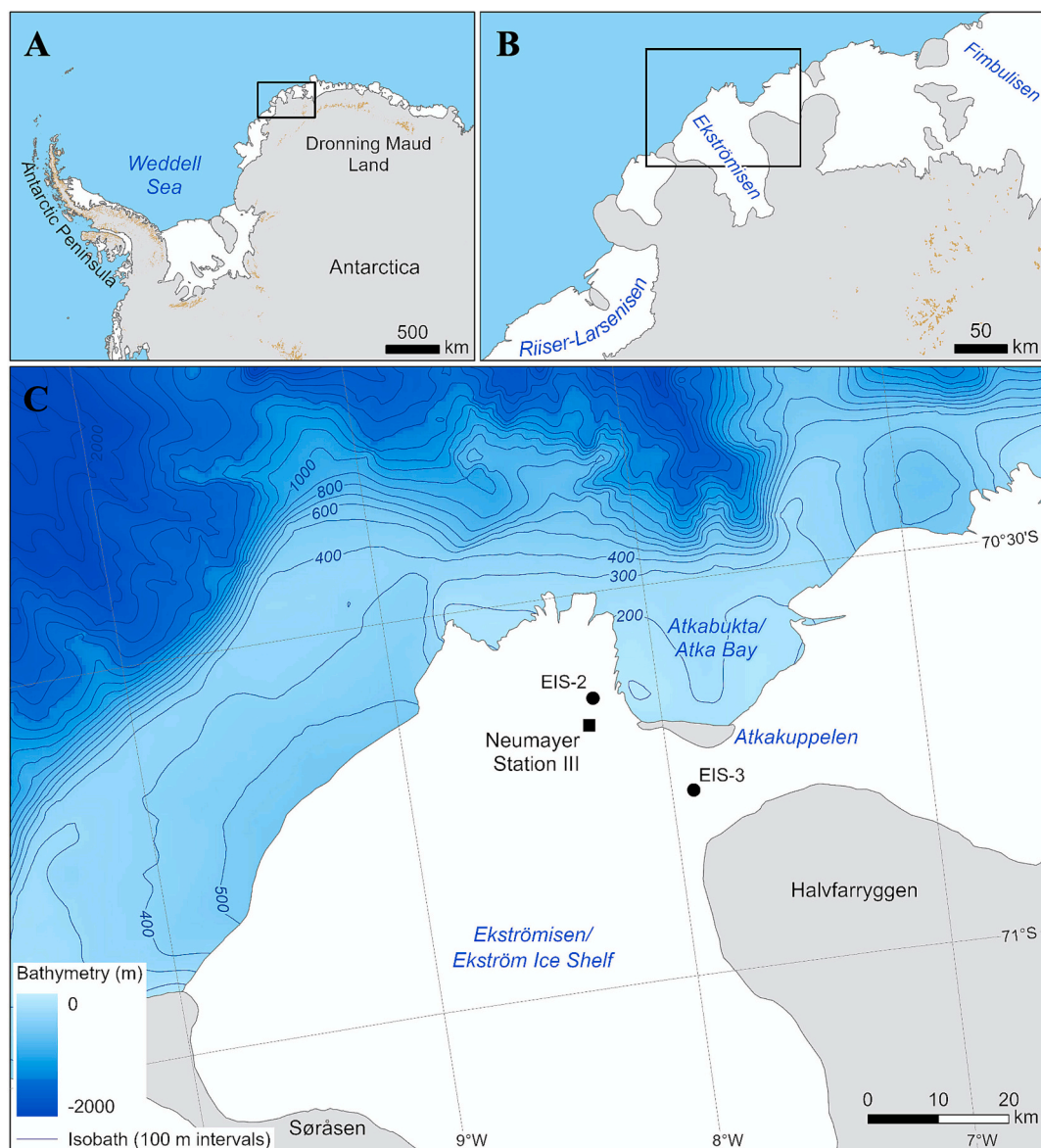


Fig. 1. East Antarctic Southern Ocean study zone and sites. White indicates ice shelves, and grey indicates ice-covered land/grounded ice. (A) Weddell Sea region indicating the Antarctic Peninsula, Dronning Maud Land and general location of Ekström Ice Shelf and environs; (B) Ekström Ice Shelf (Ekstrømissen) and neighbouring ice shelves off Dronning Maud Land with extent of main map indicated; and (C) main map showing locations of borehole study sites, EIS-2 and EIS-3 (black circles), where underlying seafloor substrata, investigated for macrobenthic spatial competition, was collected, and with position of nearby Neumayer III research station shown (black square). Bathymetry is from the International Bathymetry Chart of the Southern Ocean v2 (Dorschel et al., 2022), with 100 m contours.

the seafloor sediment samples of EIS-2 and EIS-3, respectively (see Barnes et al., 2021b).

2.3. Stereo microscopy for analysis of spatial competition

Spatial contest competition between encrusting colonists (predominantly bryozoans) on the isolated bryozoan fragments (158 and 166 for EIS-2 and EIS-3, respectively; 324 total) was examined using stereo microscopes (Leica M165 FC and S8 APO; Leica Microsystems (UK) Ltd., UK), with example images provided in Fig. 2. Each fragment was analysed following the same procedure. For each fragment, the surface area was calculated (cm^2), and all colonies, i.e., potential competitors, residing on the fragment were counted (enabling calculations of colony density, i.e., number of colonies cm^{-2}). Each colony was identified to the highest taxonomic resolution possible, predominantly to species level, using Hayward (1995) and proceeding primary literature. Colonised fragments were further inspected for competitive interactions between colonies, determined whereby the growth boundaries of colonies physically met, with at least 5 % of their perimeter being affected (as per Barnes and Kuklinski, 2004) and signs/indications that both colonies were alive at the time of the interaction, i.e., detection of defensive responses in colony morphology such as the formation of protective spines on newer zooids at the growth edge (e.g., Seroy and Grünbaum, 2018; Liow et al., 2019). Following established criteria, for every competitive encounter, the outcome was classified as either a tie/stand-off or a win-loss; a tie being, for example, where the growth of colonies ceased along the contact margin or reciprocal overgrowth occurred, and a win-loss where a colony overgrew another to cover the apertures of its zooids (Stebbing, 1973; Buss and Jackson, 1979; Barnes and Kuklinski, 2004; Liow et al., 2016). The outcome for each competing colony was also logged (as a tie, win or loss). In addition, for all competitive interactions, the lowest taxonomic divergence point of the competing colonists, i.e., kingdom, phyla, class, family, genus or species, or different colonies of the same species, was also recorded. All data pertaining to microscopy studies were recorded in Microsoft Excel (Microsoft Corp, USA).

2.4. Spatial competition measures explored

Data generated from stereo microscopy analyses were subsequently

used to calculate a series of differing spatial competition measures for both EIS-2 and EIS-3 samples. The measures and their associated calculations (based on literature-derived definitions; see Barnes and Neutel, 2016; Barnes et al., 2021a, and summarised in Table S2) were: Density – the number of competitive encounters divided by the total substratum surface area examined; Intensity – the number of competitive encounters divided by the total number of colonies observed, i.e., the probability of a given colony experiencing competition; Severity – the number of competitive encounters resulting in a definitive (win-loss) outcome divided by the total number of colonies, i.e., the probability of a colony being involved in severe competition; Identity – the number of intraspecific encounters (encounters between colonies/individuals of the same species) divided by the total number of competitive encounters, i.e., the probability of a competitive encounter being intraspecific; Dominance – the number of competitive encounters involving the most frequent competitor divided by the total number of competitive encounters; Complexity – the number of different pairwise competitive encounter types (e.g., Competitor A versus B is one type); and Taxonomic spread – the proportion of competitive encounters falling within each of seven categories based on the lowest taxonomic divergence of the respective combatting competitors. The categories included competitors being of the same species (i.e., the most taxonomically similar category and constituting intraspecific competition) to being from different species, genera, families, classes, phyla and kingdoms (the latter being the most taxonomically divergent category). The taxonomic divergence of competitors provides a further way to examine complexity of competition.

2.5. Global open-sea bryozoan assemblage datasets

To determine where sub-ice-shelf competition fits in a more global context, competition measures for EIS-2 and EIS-3 were compared with those obtained/calculated from available and comparable global open-sea bryozoan assemblage datasets (Barnes and Kuklinski, 2010; Barnes and Neutel, 2016); it is, however, acknowledged that comparisons are constrained in power due to the scarcity of sub-ice-shelf samples necessitating comparisons of single measures with means from elsewhere. The comparison datasets encompassed a latitudinal range of 5 to 78° across the two hemispheres and were classified as either tropical,

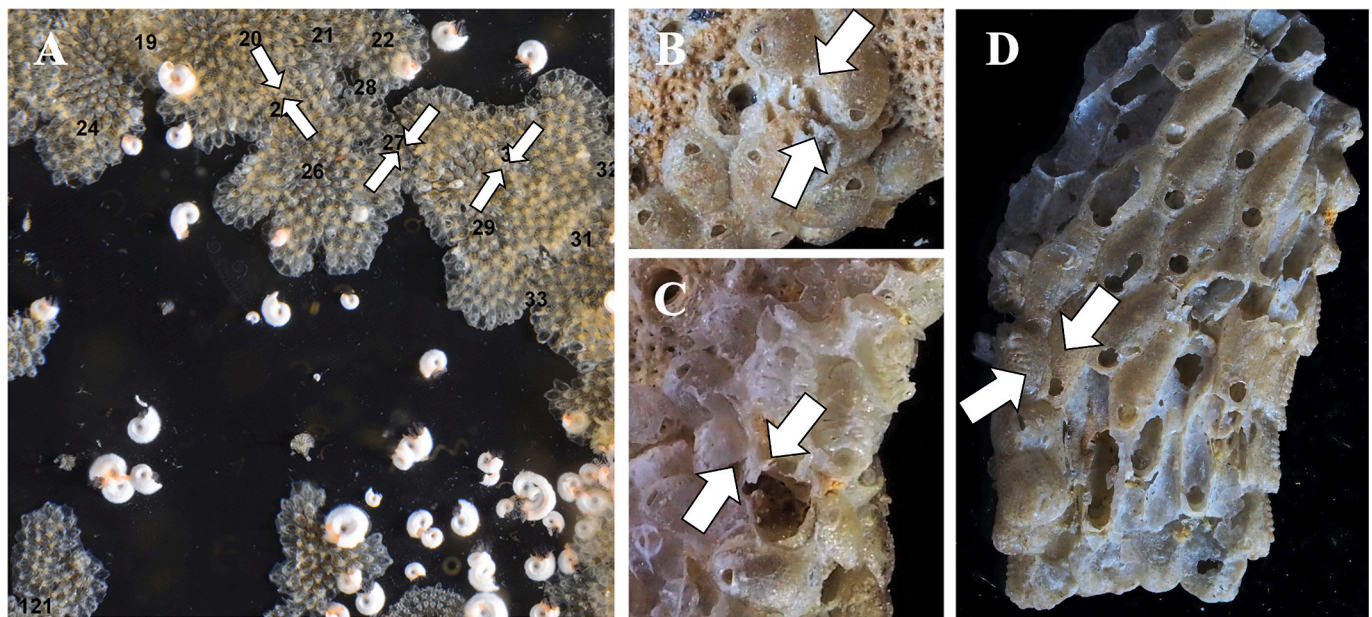


Fig. 2. Example images showing spatial competition between bryozoan colonies (indicated by white arrows): (A) on a settlement panel from Antarctic shallow waters (15 m depth) (Barnes et al., 2021a) and (B-D) on bryozoan fragments of sub-ice-shelf sediment samples (this study), whereby (B) shows colonies of the same species competing for space (intraspecific competition), and (C-D) depict colonies of different species competing for space (interspecific competition).

temperate or polar, defined here as ≤ 30 , >30 to <60 and $\geq 60^\circ\text{N/S}$, respectively. All datasets focused on encrusting bryozoan assemblages of island or continental shelf systems and employed comparable methods for analysing colonisation and competition. Substrata were abiotic, ranged from pebble to boulder grain sizes (with surface areas of ~ 2 to 500 cm^2) and collected via SCUBA, Agassiz trawls or dredging techniques. Datasets were based on multiple samples from multiple locations within a sampling area, the exception being the eastern Weddell Sea dataset (Barnes and Kuklinski, 2010), which comprised four individual samples from four locations (and only used for the competition intensity comparison). For more information regarding comparison datasets, see Barnes and Kuklinski (2010) and Barnes and Neutel (2016).

2.6. Interclade spatial competition

The relative competitive success of the two major bryozoan clades, cheilostomes (Gymnolaemata) and cyclostomes (Stenolaemata), was investigated by determining the percentage win rate of cheilostomes against cyclostomes for EIS-2 and EIS-3 using all competitive encounters in which the two clades met. Sub-ice-shelf win rates were then compared to those of literature data, encompassing fossil and recent assemblages. These assembled data span >100 million years before present and global space, i.e., across varying latitudes. The fossil assemblage data was compiled by McKinney (1995) and those of global living bryozoans by Barnes and Dick (2000). The probability of the sub-ice-shelf cheilostome win-rate observation was also calculated.

3. Results

The surface area of sub-glacial substrata (fragments) ranged from 0.2 to 7.2 cm^2 , with a mean area of 0.8 cm^2 . Of the 158 and 166 fragments microscopically examined from EIS-2 and EIS-3 seafloor sediment samples, 39 and 48 % were found to be colonised by encrusting macrobenthos, respectively. The colonists were identified as predominantly cheilostome, followed by cyclostome bryozoans, with occasional tube-building serpulid polychaetes. Colony density for EIS-2 and EIS-3 substrata was ~ 1.3 and $1.6\text{ colonies cm}^{-2}$, respectively. Spatial contest competition was detected on 47 and 30 % of colonised substrata for EIS-2 and EIS-3, respectively, with up to 21 competitive interactions being observed on a single fragment. Competition density for the EIS-2 and EIS-3 samples was ~ 0.54 and ~ 0.79 competitive encounters cm^{-2} , corresponding to 5443 and 7875 competitive encounters m^{-2} , respectively. Regarding colonists, cheilostomes were the most speciose taxon, the major occupiers of space on fragments, and were involved in most competitive interactions; for EIS-2, cheilostomes were involved in ~ 92 % of all pairwise encounters (>94 % when bryozoan-bryozoan encounters considered exclusively), and for EIS-3, cheilostomes were involved in 100 % of the encounters.

3.1. Intensity, severity and identity of spatial competition

The intensity of competition on sub-ice-shelf samples was ~ 41 and 49 % for EIS-2 and EIS-3, respectively. Sub-ice-shelf intensity values were high relative to global levels (Fig. 3A), and, in particular, very high compared to other polar data from similar depths and region, i.e., the eastern Weddell Sea open-shelf dataset; the mean intensities were 5 % and 15 % for the eastern Weddell Sea shelf and the collective polar region, respectively, therefore sub-ice-shelf competition intensity was nine and three times higher, respectively.

The severity of sub-ice-shelf competition was ~ 31 and 39 % for EIS-2 and EIS-3, respectively. Sub-ice-shelf severity values were also high relative to global levels and outside corresponding 95 % confidence intervals (Fig. 3B). Competition severity under the ice shelf was much higher than that observed for other polar data; the mean severity of polar data being 12.5 %, hence sub-ice-shelf values almost three times higher (similar in difference to competition intensity).

Regarding competition identity, i.e., the proportion of intraspecific encounters, sites EIS-2 and EIS-3 presented very similar values at 19.4 and 18.7 %, respectively. Sub-ice-shelf identity values also markedly differed from that of open-water polar data (Fig. 3C), the mean intraspecificity of competition for other polar data being >45.5 %, equivalent to greater than a twofold difference. Sub-ice-shelf identity values were more similar to those observed for non-polar environments.

3.2. Complexity of spatial competition

Two initial aspects of competition complexity were investigated: the numerical dominance in encounters by the most frequent single competitor, i.e., the proportion of competitive encounters involving the most common competitor, and the number of different pairwise competitor combinations discerned (Fig. 4).

The numerical dominance by a single competitor at EIS-2 and EIS-3 was 26.4 and 42.9 %, respectively (Fig. 4A). Such under-ice-shelf dominance levels were found to be more comparable with that of equivalent competition in tropical and temperate samples (with means of 39.5 and ~ 49 %, respectively), and around or less than half that previously recorded for polar regions, the collective polar mean being ~ 85 %, and the Antarctic specific mean 94 %. The species most frequently involved in competitive interactions were cheilostomes *Microporella stenopora* for EIS-2 and *Lacerna watersi* for EIS-3.

Regarding how many types of competitive encounters were present, sub-ice-shelf samples presented 43 and 31 different types for EIS-2 and EIS-3, respectively (Fig. 4B). The EIS-3 value was more similar to those of lower-latitude and Arctic samples, with the mean number of encounter types for temperate and tropical regions being ~ 30 and for the Arctic 28, whereas EIS-2 exhibited a particularly high diversity in pairwise competitive encounter types compared to anywhere else. Both

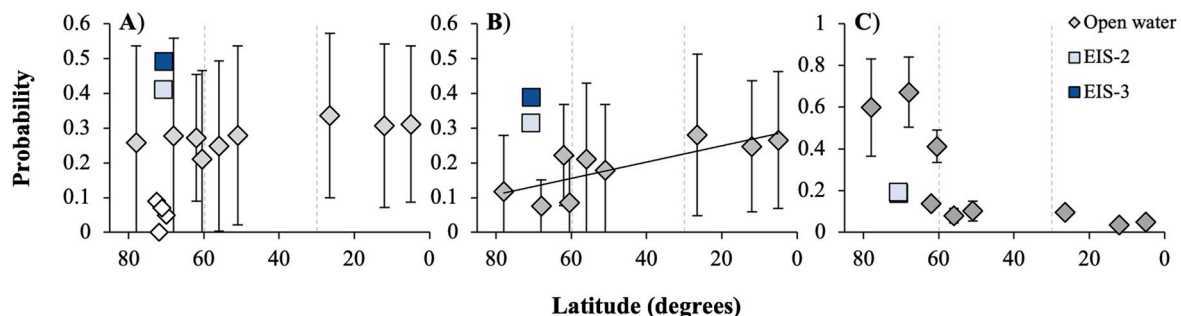


Fig. 3. Spatial competition on marine substrata from under an Antarctic ice shelf and comparison with competition across different latitudes. Including: (A) Intensity; (B) Severity (with regression line); and (C) Identity. Sub-Ekström Ice Shelf (EIS) data are shown as individual samples (with light and dark blue squares for sites EIS-2 and EIS-3, respectively). Open-water data are shown as means with standard deviations for the shallows (grey diamonds, calculated using data from Barnes and Neutel, 2016) and as individual samples for ~ 120 – 650 m shelf depths (white diamonds, computed utilising data from Barnes and Kuklinski, 2010). Regression-associated ANOVA indicated a significant inverse relationship between latitude and competition severity ($R^2 = 0.61$, $F = 10.99$ and $p = 0.01$).

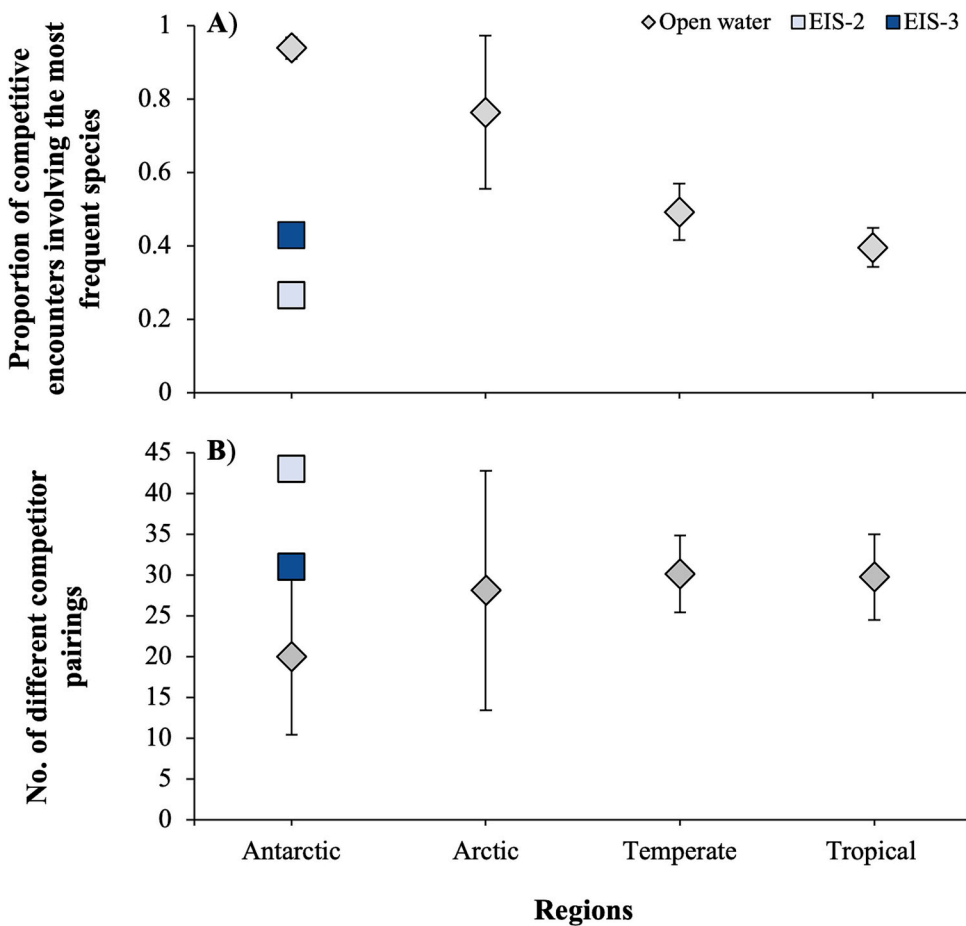


Fig. 4. Complexity of spatial competition on marine substrata from under an Antarctic ice shelf and comparison with competition complexity of Antarctic, Arctic, temperate and tropical regions. Including: (A) Numerical dominance of the most frequent competitor in interactions; and (B) Variety of pairwise competitive encounter types. Sub-Ekström-Ice-Shelf (EIS) data are shown as individual samples (squares – light and dark blue for sites EIS-2 and EIS-3, respectively). Open-water data are shown as means with standard deviations for the shallows (grey diamonds, calculated using datasets from Barnes and Neutel, 2016).

under-ice-shelf samples exhibited a greater variety of encounter types (at least >50 % more) than the open-water Antarctic region, which had a mean of 20 types.

3.3. Taxonomic difference between competitors for space

As a broader way of realising complexity of competition, the frequencies of the taxonomic divergences (taxonomic spread) of competitors were explored for the sub-ice-shelf samples and subsequently compared with those calculated from available global datasets (Fig. 5).

For EIS-2 and EIS-3, the taxonomic difference between competitors varied from within species (intraspecific), e.g., *Lacerna watersi*, to between representatives of different phyla, i.e., Bryozoa and Annelida (Fig. 5A). However, the most common spatial competitive encounters found on sub-Ekström-Ice-Shelf samples (i.e., dead bryozoan fragments) were between competitors belonging to different families (of the same class, phyla and kingdom) at >45 and 55 % of all encounters for EIS-2 and EIS3, respectively. The mean proportions of competition being interfamilial for tropical, temperate and polar regions were 72, 68 and 32.7 %, correspondingly, i.e., the sub-ice-shelf findings sitting between that of lower-latitude and polar regions (Fig. 5A,B). Under-ice-shelf patterns of spatial competition also showed comparatively moderate levels of intraspecific competition with a mean >18.4 % (Fig. 5A), whereas means for tropical, temperate and polar regions were ~4, ~10 and >55 %, respectively, i.e., again, the sub-ice-shelf findings lying between lower latitude and polar, however, in this case, more towards tropical and temperate regions.

3.4. Interclade spatial competition

The win rate between the two most abundant marine bryozoan clades: cheilostomes (all of class Gymnolaemata) and cyclostomes (all of class Stenolaemata), was established for each sub-ice-shelf sample. At both under-Ekström-Ice-Shelf sites, cheilostomes were competitively superior and exhibited very high win rates against cyclostomes, at 92.9 % for EIS-2 and 86.2 % for EIS-3 (Fig. 6).

When comparing sub-ice-shelf cheilostome win rates with those of present-day living assemblages and fossil assemblages, the sub-ice-shelf samples interestingly displayed not only two of the three highest win rates against cyclostomes in present-time but also when the fossil record was considered (Fig. 6); the mean win rate for fossil assemblages being 66.5 % across time. The probability of two of the three highest win rates occurring in the sub-ice-shelf samples (out of all 33 samples) is <0.006 (i.e., <1 %).

4. Discussion

Competition for resources, including space, food and mates, is a common and fundamental component of populations and communities across global ecosystems (Lomolino et al., 2004; Schemske et al., 2009). However, to the authors' knowledge, before this study, competition for any resource had not been described for the vast environment under the Antarctic ice shelves. Indeed, prior to recent discoveries that complex, rich and abundant life can occur on the seabed underlying ice shelves (Kim, 2019; Barnes et al., 2021b), the sheer presence of competition in this permanently dark, historically-assumed food-scarce (Clarke and Johnstone, 2003) habitat may have been a surprise. The results of the current study, however, not only show for the first time that competition

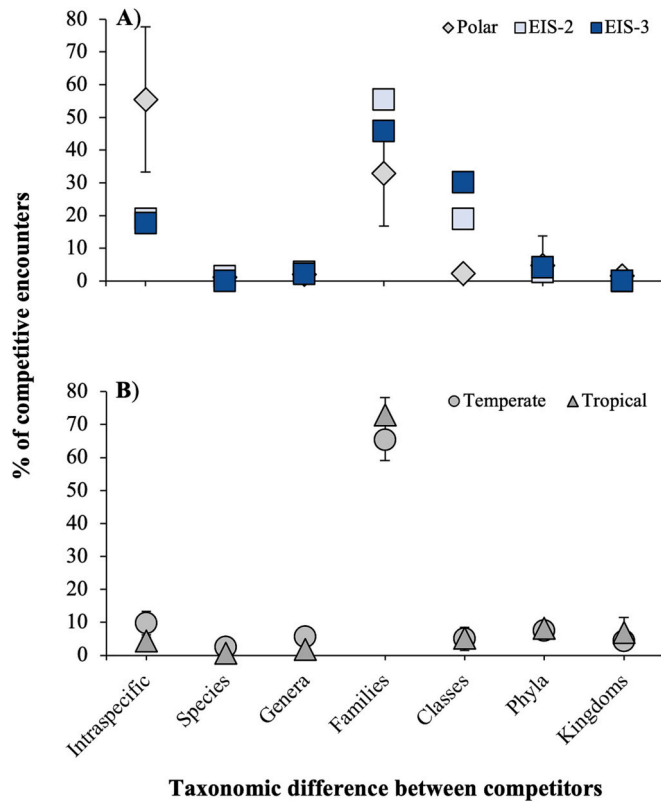


Fig. 5. Taxonomic difference between competitors for space on marine substrata from under an ice shelf and comparison with different regions. Including: (A) polar – sub-ice-shelf and open water; and (B) temperate and tropical. Sub-Ekström Ice Shelf (EIS) data are shown as individual samples (with light and dark blue squares for sites EIS-2 and EIS-3, respectively). Open-water data are shown as means with standard deviations for the shallows (calculated utilising data from Barnes and Neutel, 2016) with symbols for polar, temperate and tropical regions being diamonds, triangles and circles, respectively.

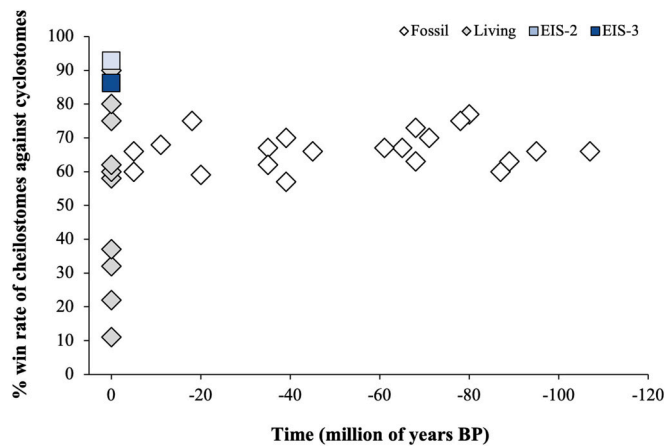


Fig. 6. Outcomes of spatial competition between two major marine bryozoan clades: Cheilostomatida and Cyclostomatida, in terms of cheilostome win rates (%) over cyclostomes, on marine substrata from under an Antarctic ice shelf, Ekström Ice Shelf (EIS), and comparison with win rates of open-water global living and fossil assemblages (i.e., present and before present, BP) (Barnes and Dick, 2000 and references therein).

is present, indeed prevalent below an ice shelf (Ekström Ice Shelf, Dronning Maud Land), but also that the nature of such sub-ice-shelf competition is quite different from any previously reported from open-water polar latitudes.

Sub-ice-shelf spatial competition was not of globally-low intensity or severity as initially hypothesised. Instead, both measures were high under Ekström Ice Shelf relative to those of the global marine data, and particularly compared to other polar data from open-water areas of the seasonal sea ice zone (Fig. 3A,B). If present, under-ice-shelf competition was expected to be principally intraspecific, as observed elsewhere in polar seas; however, this was not supported – just 18–19 % of competitive encounters were intraspecific compared to a non-sub-ice-shelf polar mean of ~46 % (Fig. 3C). The second hypothesis that competition complexity under an ice shelf would be low (as in other polar areas) was also not supported; sub-ice-shelf samples displayed higher complexity levels than all other global datasets (Fig. 4A,B), and the taxonomic divergence of competitors was predominantly at the family (followed by class) level rather than at the intraspecific level (Fig. 5). The expectation, based on McKinney et al. (1998), that cheilostome bryozoans would be extremely competitively dominant over cyclostomes in such a disturbance minimum as under an ice shelf was, however, supported by the results of the study (Fig. 6). Nonetheless, in all the measures of spatial competition explored, sub-ice-shelf competition bore most resemblance to lower-latitude (non-polar) rather than open-sea high-latitude (polar) competition. In respect, the nature of competition for resources in one of Earth’s least known, and perhaps least disturbed habitats appears (according to the current study) to be atypical and has a distinctive mix of attributes compared to similar assemblages elsewhere (e.g., Karlson and Jackson, 1981; Quinn, 1982; Russ, 1982; Chornesky, 1989).

Competition for resources can frequently occur between competitors of differing taxonomic relatedness, as extreme as belonging to different kingdoms (Hochberg and Lawton, 1990) or phyla (Brown and Davidson, 1979). These extremes in competitor relatedness are common in the marine environment and often involve humans as competitors (Diamond, 1987), e.g., for fish stocks (Östman et al., 2013; Hansson et al., 2018) or space via coastal development/re-assignment (Richards and Friess, 2015) – such competition for such resources having considerable ramifications for society and nature’s near future. Taxonomic relatedness of spatial competitors is not randomly spread in terms of frequency, and on the seabed, competition appears to be most commonly interfamilial (between members of different families) for reasons yet to be clarified. However, polar coastal shelf competition is predominantly intraspecific (Barnes et al., 2014; Barnes and Neutel, 2016), except seemingly under ice shelves (this study). The current study explored how competitive encounters were distributed across a competitor-relatedness spectrum in an environment unlike any other investigated to date – the seabed underneath an ice shelf. The spread of competitive encounters for space across the competitor-relatedness spectrum was similar for both sub-ice-shelf sites; however, the overall pattern differed from that of other global data (Fig. 5).

Historically, under-ice-shelf environments were thought to be food-sparse yet space-plentiful, with low densities of a few colonist species (Griffiths et al., 2021). However, it is now known, principally through studies utilising borehole-enabled seafloor imagery and sediment sample collections, that some benthic assemblages under ice shelves can be dense and complex (e.g., Riddle et al., 2007; Kim, 2019). If competition for any resource was anticipated in an environmental setting of seemingly little food and much space, exploitation competition (for scarce food) might have been more expected than contest competition. However, from the limited imagery that has been obtained from sub-ice-shelf seafloor environments and reported on (e.g., Post et al., 2014), it would appear that substrata typically viewed as “hard” and colonisable, such as dropstones (Ziegler et al., 2017) and boulders (Griffiths et al., 2021), also seem rare; thus, space for colonisation by encrusting species (lithophiles) is potentially at a premium in the under-ice-shelf habitat, hence competed for. From the current study on sub-glacial substrata from the eastern Weddell Sea, it is now evident that even when much finer-grained suitable hard substrata are available under ice shelves, such as biologically-generated skeletal fragments (Barnes et al., 2021b; and this

study), encrusting biota can be both abundant and species-rich, and much spatial contest competition can transpire.

In the under-ice-shelf environments investigated in the current study, bryozoans, specifically cheilostomes, were both the major spatial competitors and the main spatial resource (hard substrata) being competed for, i.e., as dead fragments of erect bryozoans – the cheilostomes re-purposed, following death, as platforms for new life. This type of ecosystem structuring, whereby organisms use the skeletal remains of others as living space (i.e., “taphonomic feedback”; Kidwell and Jablonski, 1983), is also reflected in coral reef systems, where coral is the primary substratum and competitor for this space (e.g., Buss and Jackson, 1979); otherwise, coral reefs and under-ice-shelf benthic habitats appear considerably contrasting.

Food availability, and quality, are important to the structuring of marine benthic assemblages (Svensson and Marshall, 2015; Campanyà-Llovet et al., 2017), as is space in all habitats, not least for access to food (Kellner and Asner, 2014). It has been speculated by Barnes et al. (2021b) that food might be so limited under ice shelves that spatial competitors with feeding (planktotrophic) larvae may struggle to survive and colonise space there. Indeed, most of the competitors for space identified in the present study were those with exclusively yolk-feeding (lecithotrophic) larvae. This apparent dominance of larval form could be because lecithotrophic larvae are less sensitive to a potentially food-poor/–inconsistent water column, whereas planktotrophic larvae must feed in the water column to achieve the size and maturity required for settlement (and subsequent metamorphosis to colony development). In addition, lecithotrophic larvae are generally thought to have lower dispersal capabilities than planktotrophic larvae, so presumably would mostly settle closer to their origin, providing appropriate substratum is available, such as the cheilostome bryozoan fragments in this study. Nonetheless, clearly an adequate enough or adequately consistent food supply has been present and/or delivered under Ekström Ice Shelf, at least to the sites sampled, to also support adult planktotrophic life there over thousands of years (Barnes et al., 2021b).

While Antarctica’s open continental shelf hosts some of Earth’s most naturally disturbed environments (Gutt and Starmans, 2001), the seafloor underneath ice shelves comparatively represents a disturbance minimum and a potential refuge from natural (and potentially anthropogenic) disturbance, in part owing to the existence and persistence of the floating ice shelf above, and additionally evidenced by lifespans, under Ekström Ice Shelf, of almost 6000 years (Barnes et al., 2021b). These two systems, either side of the ice-shelf front, therefore, present as profoundly different settings for competitors and competition. McKinney (1995) found that in environmental conditions of strong fossilisation (warm shallow seas), competition for space between the two major bryozoan clades remained relatively constant over a 100 Ma time span, with cheilostomes (consistently) competitively outperforming cyclostomes, with a mean win rate of 66.5 % across time. However, evidence from current habitats across Earth’s wider spectrum of environmental conditions indicates competition between these clades, and the competitive success of one over another, can be much more variable (Barnes and Dick, 2000). If under-ice-shelf environments are as extreme as being long-enduring disturbance minima, hence also potentially echoing conditions of calmer geological time, the expectation was to find extreme interclade results, which is precisely what was found in this study; cheilostomes winning, on average, ~90 % of spatial contests against cyclostomes (Fig. 6).

Marine ice losses are one of the most striking and rapid responses to global climate change (Turner and Comiso, 2017; Parkinson, 2019). Although ice-shelf dynamics have proven complex, and sea ice losses in some regions have been matched by gains in others, it seems reasonable to deduce that marine (and terrestrial) icescapes, and hence associated habitats such as those explored in this study, must be under considerable threat from GHG-emissions-driven global warming (IPCC, 2019; Gilbert and Kittel, 2021). With ice-shelf retreat or collapse, there is a potential for the disturbance regime of the previously overlain continental shelf to

significantly alter – rapidly transitioning from an extremely low- to high-disturbance environment. In response, the nature and dynamics of competition may change, which would have implications for both assemblage structure and broader habitat functions and services that are yet to be fully realised.

5. Conclusions

Rare borehole-derived collections of sub-ice-shelf seabed substrata and stereo microscopy methodologies have provided not just the first evidence of competition from a distinct and mainly unexplored environment, but also from a habitat that has persisted for thousands of years, and, therefore, potentially of exceptionally low disturbance. Due to the ubiquity of bryozoans, sub-ice-shelf findings could be compared with existing global datasets, and although sampling is limited, it appears that spatial competition under Ekström Ice Shelf is not only very different from that of open-water polar areas but also remarkably similar, in several traits, to non-polar marine benthic environments. Whether such findings extend to or are more widely representative of the sub-ice-shelf habitats fringing Dronning Maud Land, East Antarctica, and elsewhere in this vast ecosystem, is yet to be confirmed. Nonetheless, the results of this study further indicate the potential utility of bryozoans as indicators of environmental differences. The findings also offer a precedent that perhaps in a permanently ice-covered and minimally-disturbed seafloor environment, spatial competition among the benthos can be intense and severe, unique in nature, and be dominated by a particular faunal clade.

CRedit authorship contribution statement

Bétina A.V. Frinault: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **David K.A. Barnes:** Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Validation, Writing – review & editing. **Boris K. Biskaborn:** Resources, Writing – review & editing. **Raphael Gromig:** Resources, Writing – review & editing. **Claus-Dieter Hillenbrand:** Resources, Writing – review & editing. **Johann P. Klages:** Resources, Writing – review & editing. **Nikola Koglin:** Resources, Writing – review & editing. **Gerhard Kuhn:** Resources, Writing – review & editing.

Declaration of competing interest

The authors declare no competing interest.

Data availability

Data are available upon reasonable request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.166157>.

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