On the origin of Antarctic marine benthic community structure

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Environmental conditions fostering marine communities around Antarctica differ fundamentally from those in the rest of the world's oceans, particularly in terms of pronounced climatic fluctuations and extreme cold. Here, we argue that the rarity of pelagic larval stages in Antarctic marine benthic invertebrate species is a consequence of evolutionary temperature adaptation and that this has greatly contributed to the current structure of the Antarctic benthic community. In arguing this position, we challenge the likelihood of previously suggested survival strategies of benthic communities on the Antarctic continental shelf and slope during Cenozoic glacial periods. By integrating evidence from marine geology and geophysics, we suggest that the Antarctic continental shelf and slope were both unfavourable environments for benthic communities during glacial periods and that community survival was only possible in the deep sea or in shelters on the continental shelf as a result of the diachronism in maximum ice extent.

Introduction

Throughout the evolution of terrestrial and marine ecosystems, physical disturbance has been one of the major factors determining community structure. During glacial–interglacial cycles, most ecosystems experience significant environmental change, although the magnitude of recurrent direct mechanical destruction of environments by ice on the Antarctic continental shelf during the later part of the Cenozoic era (65 million years ago to the present day) is unparalleled anywhere else on Earth. During the present interglacial, iceberg scouring or ploughing, caused by an iceberg running aground on the shelf, is the main physical process affecting the benthic communities (see Glossary) in shallow waters on the Antarctic continental shelf [1,2]. Effects of iceberg scouring vary locally and, on a larger geographical scale, intermediate levels of disturbance by icebergs can even enhance benthic diversity on the Antarctic continental shelf [1,3,4]. Enhanced habitat structuring through local disturbance has been frequently used to explain Antarctic species richness and community structure [2].

Previous attempts to explain Antarctic marine community structure are based mainly on present-day patterns in the recolonization of habitats, following physical destruction

by ice scouring at a relatively minor scale [4–6]. However, we suggest that these patterns cannot be applied to conditions during Cenozoic glaciations. Here, we advocate that, during the glacial periods of the late Cenozoic, the well-documented advance of grounded ice sheets across the Antarctic shelf and associated mass-wasting processes on the continental slope caused a disturbance of an order of magnitude higher than present iceberg ploughing and thus erased whole shelf communities. By considering life-history constraints for marine invertebrates living under polar conditions and integrating recent marine geological and geophysical evidence, we conclude that the continental shelf and slope of Antarctica were unfavourable environments for benthic invertebrates to survive glacial periods. Consequently, we have to revise our idea of entire Antarctic shelf communities surviving glacial periods on the continental shelf and slope of Antarctica; future research, which should be based upon interdisciplinary approaches, should also emphasize deep-sea–shallow-water faunal relationships.

Glossary

Benthic: inhabiting the ocean floor.
Broadcasters: species that distribute their offspring over long geographical distances, usually related to the early life-history adaptations that facilitate this process.
Brooding: developmental mode of benthic, non-feeding (lecithotrophic) larvae protected by parents.
Cenozoic: the latest of the geological eras, extending from 65 million years ago to the present.
Cryptic speciation: hidden diversity resulting from species mistakenly being treated as a single species even though their gene pools are distinct.
Diachronous: time transgressive (e.g. a sediment layer is diachronous if it represents different periods of time).
Eurybathy: a wide range in depth distribution.
Lecithotrophic larvae: non-feeding developmental mode (pelagic and/or benthic), relying on energy sources of maternal origin (e.g. a yolk sac).
Last glacial period: the most recent ice age, when global ice sheets reached their maximum, sea level was at its lowest and global temperatures were at their minimum, corresponding to the time period 24–12 ka.
Milankovitch timescales: timescales of the Milankovitch cycles, which include the variations in the orbit of the Earth (eccentricity; periodicity: 100 kyr), in the tilt of its axis (obliquity; periodicity: 41 kyr), and in the shifting of the wobble of the Earth on its axis (precession; periodicities: 19 kyr and 23 kyr); the Milankovitch cycles are responsible for variations of the exposure of the Earth to insolation and are thought to have controlled the ice ages during the late Cenozoic.
Pelagic: inhabiting the water column.
Planktotrophic larvae: pelagic, actively feeding and free-swimming developmental mode.
Reservoir effect: the shift in apparent radiocarbon age caused by the original carbon having an anomalously low or high ^{14}C content; marine organic specimens draw their carbon from seawater, which is not in equilibrium with the atmosphere and contains variable amounts of 'old', recycled carbon.

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Box 1. Thorson's concept of marine invertebrate reproduction

Developed by Thorson [11,12] and later known as Thorson's rule [8,13,14] is the controversial concept [10,28,56] that there is a global-scale latitudinal gradient in the distribution of planktotrophic larvae (Figure Ia, modified, with permission, from [57]). Thorson concluded that this pattern, together with an increased energy investment in single offspring with increasing latitude (Figure Ib), is an adaptation to the mismatch of prolonged developmental times and short seasons of food availability (i.e. primary production) selecting against feeding pelagic larvae under polar conditions [11,12]. He distinguished between planktotrophic (pelagic) and lecithotrophic larvae, which he considered to be benthic living only [8]. We now know of various intermediate larval feeding modes and drifting stages [7,60], but the total number of larval morphotypes known from Antarctic waters is still <250 [15,16]. Increasing records of pelagic larvae in Antarctic waters have frequently been used to challenge this idea [10,14–16,58,59], but even allowing for missing species identification and unknown energetic conditions in most larval records [15,16], the lack of planktonic larvae is striking compared with the benthic diversity of Antarctic waters [61,62].

However, there are many aspects of our current knowledge, such as density-dependent energy contents in eggs [63] that complicate, for example, simple egg-size comparisons as an energetic measure across latitudes at a global scale. Furthermore, longevity in Antarctic invertebrates might contribute to the total number of pelagic and planktotrophic larvae being underestimated, given that reproductive effort might be directed to periods with more favourable conditions for larvae in species with, for example, a relatively narrow temperature window [64]. Moreover, successful recruitment through pelagic life stages in sessile filter feeders, such as sponges, might only occur less than once a decade [65] owing to physiological constraints in the cold, an important difference compared with life histories of such filter feeders elsewhere in the oceans, which show a more regular recruitment pattern. Such slow recruitment in Antarctic waters affects the ability of such species to respond quickly to local habitat disturbances.

Today, benthic invertebrates with pelagic larval development are the first to recolonize habitats that are physically destroyed by grounded icebergs at small and intermediate geographical scales in Antarctica. During glacial periods, these opportunistic life forms might have been among the few species that were able to survive physical disturbance through advancing grounded ice sheets and iceberg ploughing of a much higher intensity. Either they could have survived diachronous fluctuations in ice extent on the shelf during a glacial period by migrating from one shelter to another, or they could have been quickest to recolonize the continental shelf from the deep sea during the following deglaciation
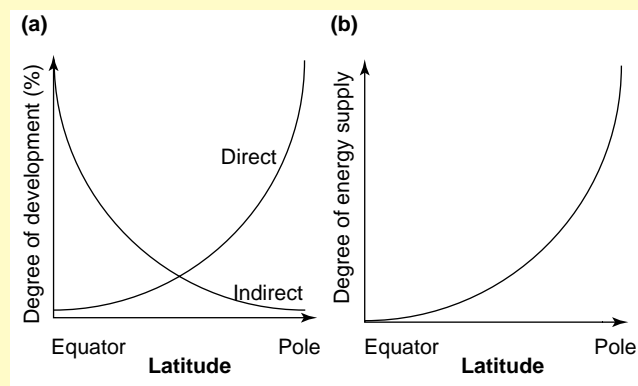

Figure I.

Invertebrate reproduction in the sea

Most marine benthic invertebrates have pelagic developmental stages. Following hatching from the egg on the ocean floor, the larvae are exported into the water column of the open sea, an environment that can differ

significantly (e.g. in terms of temperature, salinity and food availability [7]) from that of the benthic environment that they will occupy as adults. Pelagic larval stages are rare in polar benthic invertebrates [8], a finding that has been attributed predominantly to a failure to synchronize prolonged developmental periods, as a result of a lowered metabolism at low temperatures [9], with the short seasons of food availability at high latitudes [10]. This observation was summarized by Thorson [11,12], and later referred to as Thorson's rule (Box 1) [11,13,14].

With increasing observations of pelagic larval stages in polar regions, especially in shallow-water benthic organisms [10,14–16], numerous reasons to dismiss Thorson's rule have been proposed (Box 1). Here, we present an interdisciplinary view of the factors involved in determining Antarctic benthic community structure during glacial–interglacial cycles. We suggest that the overall scarcity in pelagic early life-history stages in Antarctic marine benthic invertebrates is responsible for the modern Antarctic marine benthic community structure because it controls the rate at which species recolonize benthic habitats through pelagic drifting stages.

Extinction in the sea

The pre-industrial mean global oceanic temperature has been in a general decline over the past 50 million years as a result of plate tectonic reconfigurations, rearrangements of oceanic circulation systems and a decrease in the atmospheric concentration of carbon dioxide [17,18]. These processes led to a dramatic steepening of temperature gradients across latitudes, contributing to the oceanographical and climatic isolation of Antarctica and the Southern Ocean, culminating in the rapid onset of extensive glaciations on the continent ~34 million years ago [5,19,20]. One of the consequences of Antarctic cooling for Southern Ocean marine ecosystems was a dramatic change in their biodiversity, including the loss of major taxonomic groups such as pelagic and benthic top predators (e.g. sharks and crabs), and a reduction in the biodiversity of groups such as bivalve molluscs, teleost fishes and decapods [9,21–23]. Although the long-term impacts of Antarctic cooling on Southern Ocean biodiversity and the consequences of biodiversity loss for Antarctic benthic community structure [17,21,24,25] are well known, our understanding of the effect of glacial–interglacial cycles on Milankovitch timescales on structuring Antarctic marine communities is still far from complete.

Recent work, which suggests that there will be further changes in Antarctic marine biodiversity as a result of recent climate change, has questioned whether Antarctica is isolated biologically. However, this work has addressed different evolutionary timescales when comparing the oceanographical and deep-sea gateways through which marine organisms can colonize the Southern Ocean [23,26–28]. On short timescales, pelagic larvae, including taxa that went extinct during Antarctic cooling, might be at an advantage to successfully (re-)colonize Antarctica following glaciation by crossing the Antarctic Circumpolar Current, compared with species without pelagic life-history forms, which need to conquer Antarctica by migrating through the deep sea, which might take

Box 2. Environmental conditions on the Antarctic continental margin during a late Quaternary glacial–interglacial cycle

Figure Ia details the environmental conditions on the Antarctic continental margin during an interglacial period and their influences on marine benthic communities. The global sea level is at its maximum ('highstand'), sea-ice covers the Antarctic continental margin only seasonally, and ice sheets have retreated to the coast. Some of the icebergs, which calve directly from the ice-sheet margin at the coast or from an ice shelf, run aground on the continental shelf, thereby locally devastating benthic communities. However, on a larger geographical scale, such intermediate levels of disturbance are responsible for high benthic diversity on the shelf. Material that is resuspended by ploughing icebergs serves as an additional food source for benthic filter feeders that are characteristic of modern benthic communities (in Figure I, the morphology of the continental margin is highly exaggerated vertically).

Figure Ib details the environmental conditions on the Antarctic continental margin during a glacial period and their influences on marine benthic communities. Accompanying the global sea-level drop, caused by ice-sheet build up in the northern hemisphere and in Antarctica, grounded ice masses advance across the shelf, thereby erasing the benthic shelf fauna. Outer shelf areas that are unaffected by grounded ice are either covered by ice shelves or heavily scoured by icebergs, making them unsuitable for occupation by benthic animals. At the shelf edge, the grounded ice masses release huge amounts of glaciogenic debris, which is then redeposited down the continental slope by sediment gravity flows, such as slumps, slides, debris flows and turbidity currents. Benthic fauna, which might have emigrated onto the slope, are erased by these processes as a result of enhanced sedimentation rates. Furthermore, benthic animals on the slope suffer from a low food supply, which results from long-term sea-ice coverage above the Antarctic continental margin. Given that the maximum ice extent onto the Antarctic shelf might occur diachronously, benthic organisms, if they are to survive, must either find refuges on the shelf and slope, or migrate further into the deep sea, if they are able to tolerate such conditions.
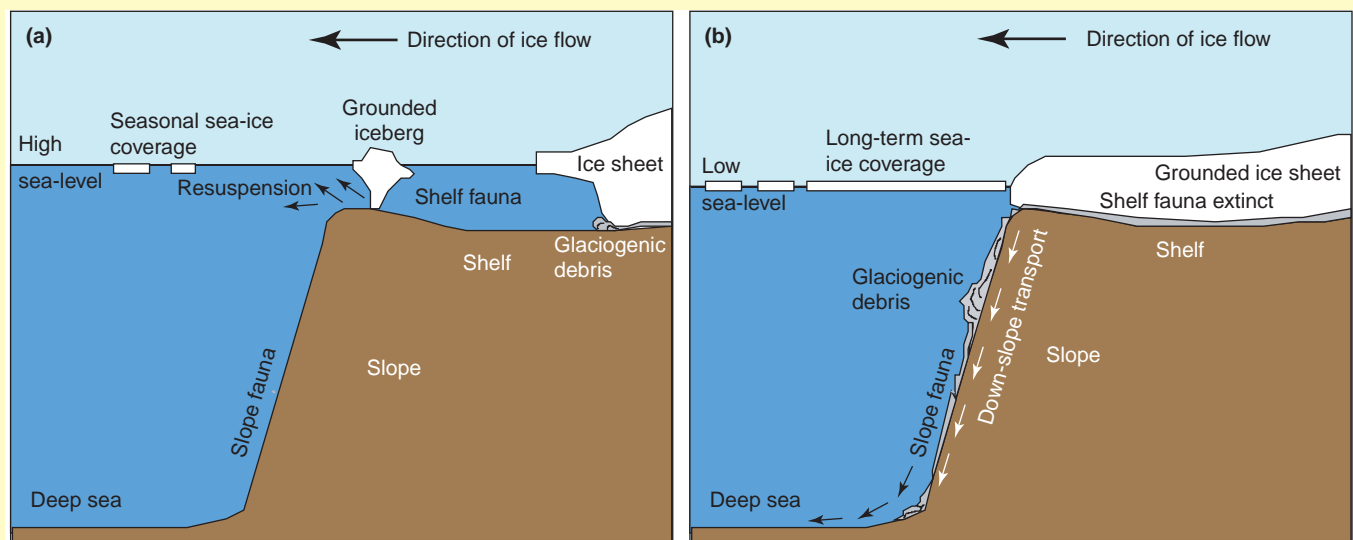
Figure I.

millions of years [23,27,28]. It has been suggested that the pace of such colonization processes following significant environmental change [26], is dependent mainly on life-history strategies that are adapted to the harsh living conditions, mainly low temperatures, at high latitudes [23,26–28].

Antarctica during the last glacial period
Marine geological and geophysical data indicate that, during the last glacial period, grounded ice masses advanced from the present coastline seaward across the continental shelf around Antarctica [29] (Box 2, Figure Ib). This finding is corroborated by results of glaciological modelling that indicate a seaward expansion of the Antarctic ice sheets in response to a fall in global sea-levels, driven mainly by ice-sheet build-up in the northern hemisphere [30] (Figure 1). The modelled West and East Antarctic ice sheets reached their maximum extent around Antarctica ~15 000 years ago (ka) [30]. The advance of grounded ice masses across the shelf would have erased the benthic fauna and is, therefore, considered to be the main limiting factor in the survival of

marine shallow-water benthos [31] (Box 2, Figure Ib). However, marine geological evidence also shows that grounded ice did not advance to the shelf edge on some parts of the East Antarctic shelf, such as the western Ross Sea [32,33], Prydz Bay [34] and George Vth Land [35] (Box 2; Figure 1). Consequently, such shelf areas were assumed to act as shelters, where benthic organisms might have survived during glacial periods [36]. This is, however, unlikely, given that these shelf regions were likely to be either covered by ice shelves [33,34] or subject to intense iceberg scouring [35].

Brey *et al.* [31] interpreted the wide eurybathy of many Antarctic invertebrate taxa compared with those from other continental shelves as evidence that these Antarctic species escaped the inhospitable conditions on the Antarctic shelf during glacial periods by emigrating to greater depths on the upper continental slope. However, numerous results from multibeam echosounding, seismic reflection profiling, acoustic sub-bottom profiling and sediment-coring studies document that, during the last glacial period, submarine mass-wasting processes, such as slides, debris flows and turbidity currents, redeposited
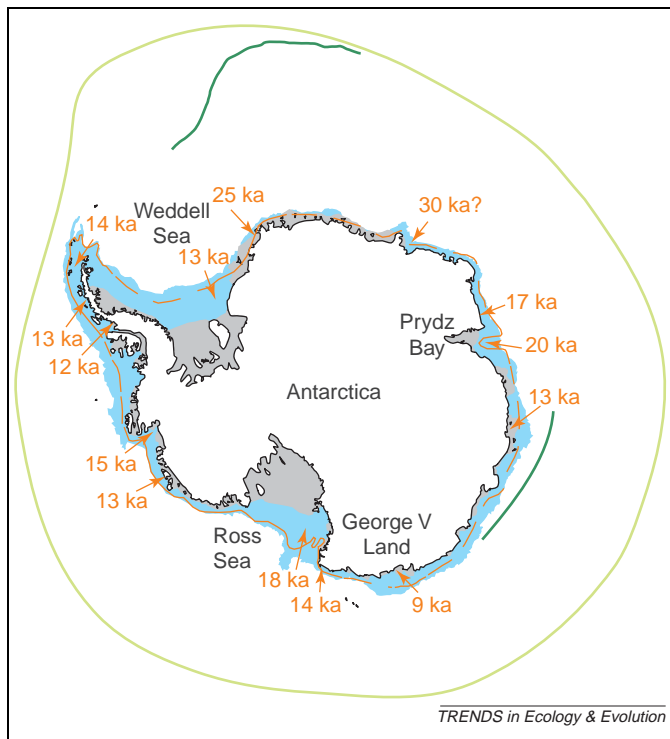
Figure 1. Extent of grounded ice and sea ice around Antarctica during the last glacial period. Grey shaded areas depict the present-day ice shelves. The orange line marks the maximum expansion of grounded ice onto the shelf according to Anderson *et al.* [29]. Orange numbers give the oldest radiocarbon ages of glacial-marine deposits on the shelf, illustrating the minimum age of ice-sheet retreat from the Antarctic shelf during deglaciation [29]. The blue-shaded area represents the depth interval between the present coastline and the 1000-m contour on the continental slope (taken from [66]), corresponding to those areas that were covered by grounded ice and ice shelves, or affected by intense mass wasting, respectively. The bright green line depicts the maximum summer sea-ice extent during the last glacial period according to [47] and the dark green line the extent according to Gersonde *et al.* [48]. The winter sea-ice limit was located even farther to the north according to both reconstructions [47,48] and is not shown.

glaciogenic debris onto the continental slope in many places around Antarctica [33,37–43] (Box 2, Figure Ib). These processes are likely to have had structuring effects of catastrophic dimensions on benthic communities [2].

Although it is suggested, based on present geological evidence, that mass-wasting processes affected the entire continental slope, we still can only guess how often such processes occurred. This is crucial for estimating the timescale of the impact on the benthic communities and the possibility that communities would have been able to recover from such a disturbance. However, Dimakis *et al.* [44] estimated that mass wasting on a glaciated continental slope in the northern hemisphere typically occurred at least once every 95 to 170 years. If this is a reliable estimate, and such conditions are applicable to glaciated continental margins elsewhere, the Antarctic slope fauna would have been severely affected during glacial periods, because it might take one hundred to several hundreds of years for the Antarctic benthos to reach community equilibrium following physical destruction [2,5,45,46]. Although we do not yet have good methods for dating the age of most Antarctic invertebrates, Polar invertebrates are known to have slow growth rates, longevity and delayed age at first maturity, as a consequence of adaptation to cold conditions [9,36]. It is

thus likely that the selective pressure of submarine mass wasting had a major physical impact on the slope fauna. Additionally, benthic organisms on the slope would have been stressed by low food availability [36], caused by a drop in phytoplankton productivity in response to almost permanent sea-ice cover around Antarctica during the last glacial period (Box 2, Figure Ib [47,48]). The combination of these factors might have contributed to the present impoverishment in diversity of some shallow-water taxa, such as decapods [23] and bivalves [17,24], in Antarctic waters.

The origin and fate of the shelf fauna
Given that the continental slope is unlikely to be a refuge for Antarctic benthic invertebrates, how did the benthic fauna survive the last glacial period? It might be that they migrated to the deep sea, recolonizing the Antarctic margin from the deep during the following interglacial. Alternatively, the onset and duration of maximum ice extent around Antarctica might have occurred diachronously, leaving isolated shelters on the shelf that changed location throughout a glacial period so that benthic animals migrated from one shelter to the next. There is now evidence for the diachronous deglaciation of the Antarctic shelf, as indicated by the chronological pattern of ice-sheet retreat from the shelf reconstructed from the oldest radiocarbon ages of glacial-marine deposits [29] (Figure 1). Even if a regionally variable carbon reservoir effect (1300–6000 y) is taken into account, the deglaciation indeed appears to have occurred diachronously. A diachronous timing of the coldest climatic conditions around Antarctica during the last glacial period is also indicated by the timing of maximum cooling and sea-ice expansion in the Southern Ocean, which preceded the global sea-level minimum corresponding to the maximum ice sheet build-up [48]. Diachronous deglaciation is also consistent with recent ice-sheet modelling results, which emphasize the role of physical mechanisms other than global sea-level rise in triggering the retreat of grounded ice [49].

In each case, the resulting shallow-water niches, present locally even during the last glacial period or re-opened during subsequent deglaciation, would have been prone to recolonization by pioneering species with adaptable life cycles that could disperse and radiate around Antarctica during the following interglacial. This scenario explains the characteristic biogeographical pattern of circum-Antarctic distribution of some taxa, such as filter feeders and crustaceans, but could also explain cryptic speciation as a result of isolation in glacial shelf shelters. Such speciation is known in some brooding Antarctic isopods with a limited potential for dispersal. All marine isopods, other than a few parasitic forms, as well as other peracarid crustaceans such as amphipods, produce offspring that resemble miniature copies of their parents, without having drifting stages in pelagic larvae. Such taxa might be particularly subject to cryptic speciation processes that result from isolation in glacial shelters [50,51].

But how likely is a successful circum-Antarctic, post-glacial recolonization of the shelf by refuge fauna that

might have survived a glacial period in locally alternating shelters on the shelf? The scarcity of pelagic larval development of Antarctic invertebrate species is likely to affect directly their ability to spread from one locally restricted shelter to another. Thus, it is likely that only those refuge fauna with planktonic larvae were able to re-establish successfully following deglaciation, whereas the circum-Antarctic deep-sea and deeper slope fauna could have been geographically favoured to occupy the released habitat more quickly [23,52].

It has also been suggested that pelagic larval stages are a key requirement in the evolution of Antarctic intertidal and shallow subtidal benthic communities, which are heavily impacted by grounded ice [6]. We consider that the few broadcasters with pelagic larvae, which have the ecological advantage of a quick recolonization of highly disturbed intertidal or sublittoral habitats [2,45], might be at a disadvantage in the longer term, especially during glacial periods, when intertidal habitats are broadly erased. Again the question arises as to how these inter-tidal communities with a narrow depth distribution range, from the intertidal to shallow subtidal, survived. The few species with pelagic life stages might have found refuges in shallow waters around sub-Antarctic islands, awaiting more favourable conditions to recolonize intertidal habi-tats of the Antarctic continent. This might also explain why many of the albeit few broadcasting benthic inverte-brate species with pelagic larval stages are presently found in the intertidal–shallow subtidal of Antarctica [6] and are characterized by a wide distributional range, including sub-Antarctic islands of the Southern Ocean.

Even if local slope and/or shelf refuges occurred during glacial periods, the impact of submarine mass wasting and ice shelf and permanent sea-ice cover on Antarctic benthic communities must have been significant over evolutionary timescales. In particular, these processes are likely to have been crucial for the survival of sessile filter feeders, such as sponges, which are characteristic of present-day Antarctic benthic communities [2–4,36]. High sedimen-tation rates can have structuring effects on benthic communities, especially on filter feeders [53]; for example, they should particularly select against filter and suspen-sion feeders, such as gorgonians and sponges, which have evolved feeding mechanisms that exploit the supply of only the smallest particles [54]. Dayton and Oliver [36] observed that the benthic community of suspension and filter feeders (i.e. sponges, actinarians, hydroids and many bivalves) underneath the present-day Ross Ice Shelf in the Antarctic Ross Sea resembles that of the deep sea. Filter feeders were found to be even more abundant in oligo-trophic (areas of low primary production) than in eutrophic (areas of high primary production) sub-ice shelf areas, which might be due to their ability to feed on even bacteria and dissolved organic matter [54] (eutrophic conditions in sub-ice shelf areas occur as a result of current transport flow beneath the ice shelf). This finding could also point to a direct evolutionary link between sub-ice shelf and deep-sea benthos. This link is supported by a successful transplant of the deep-sea acorn barnacle *Bathylasma corolliforme* from the shelf into shallow waters [55]. These examples show that utilizing the minimum of food available might have been the key factor in the development of the wide diversity of filter feeders in Antarctic seas that is characteristic of present-day communities.

Conclusions and future challenges

We have a clear understanding of climate-induced long-term biodiversity changes through geological time, which can be explained by distinct ecological and physiological links. However, it is still difficult to interpret the conse-quences of environmental changes caused by climatic oscillations on Milankovitch timescales for marine organ-isms and community structure. Here, we have shown that the magnitude of late Cenozoic fluctuations in ice-sheet extension and resulting mass wasting around Antarctica might have been crucial for the survival of benthic communities on the continental shelf and slope. Whereas most invertebrate species with sufficient depth range might have survived glacial periods in the circum-Antarctic deep sea, only a few species with adaptive early life cycles, mainly through pelagic larvae or drifting stages, might have been able to migrate from one shelf shelter to another during the diachronous onsets and terminations of glaciations in Antarctica. At present, and on a much smaller geographical scale, such species are still among the first to recolonize benthic habitats following erasure by iceberg ploughing. Although we still do not have good constraints on the frequency of mass-wasting events on the continental slope, there is intrigu-ing evidence that the time required for community recovery under polar conditions might exceed the typical interval of ~100 years between mass-wasting events during glacial periods. In addition, sediment gravity flows and resulting high sedimentation and high resuspension rates should have broadly selected against filter feeders that were adapted to cope with a minimum of food supply of the finest particles. The survival of filter feeders that are now characteristic of current communities is thus only likely to have occurred in the oligotrophic environment underneath the ice shelf and/or sea-ice coverage or in the deep sea.

Future studies need to emphasize the use of molecular tools to explain radiation and extinction processes, the age of species, phylogenetic affinities of related species and, in the case of the Southern Ocean in particular, the taxonomic reliability of, for example, the circum-Antarctic distribution of marine benthic invertebrates. Studying communities that are exposed to ecological and physio-logical limits of life might provide important insights into community evolution and resilience through time. Within this perspective, we need to re-emphasize autecological studies of life histories, which resemble the evolutionary history of the organism, especially during their early ontogeny. Such studies will help us increase our under-standing of the past, present and future abilities of organisms, and thus of communities, to respond to environmental change.

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