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REVIEW ARTICLE

Biological response to climate change in the Arctic Ocean: the view from the past

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Abstract The Arctic Ocean is undergoing rapid climatic changes including higher ocean temperatures, reduced sea ice, glacier and Greenland Ice Sheet melting, greater marine productivity, and altered carbon cycling. Until recently, the relationship between climate and Arctic biological systems was poorly known, but this has changed substantially as advances in paleoclimatology, micropaleontology, vertebrate paleontology, and molecular genetics show that Arctic ecosystem history reflects global and regional climatic changes over all timescales and climate states (10^3–10^7 years). Arctic climatic extremes include 25 °C hyperthermal periods during the Paleocene-Eocene (56–46 million years ago, Ma), Quaternary glacial periods when thick ice shelves and sea ice cover rendered the Arctic Ocean nearly uninhabitable, seasonally sea-ice-free interglacials and abrupt climate reversals. Climate-driven biological impacts included large changes in species diversity, primary productivity, species' geographic range shifts into and out of the Arctic, community restructuring, and possible hybridization, but evidence is not sufficient to determine whether or when major episodes of extinction occurred.

Introduction

Today's Arctic climate is warming faster than most other regions and losing summer sea-ice cover at historically unprecedented rates [27, 186]. This pattern of "Arctic amplification" is due to the changes in albedo [145], heat exchange between the atmosphere and ocean and other processes [146, 172] that are consistent with paleoclimate evidence for elevated polar temperatures during past warm periods [21, 126]. In addition to sea-ice decline, concerns exist about other climate-related processes that affect Arctic Ocean environments, such as submarine methane release [166], glacier melting [70], greater riverine discharge [147], marine ecosystem shifts [75], changes in biological productivity [9, 198], habitat loss and extinction [163], and carbon cycling [5, 180].

Instrumental and observational records are too short to fully evaluate the long-term effects of climate change on Arctic ecosystems, but two disparate fields—paleoclimatology and molecular genetics—now provide a unique context for assessment of climate change in the Arctic. In contrast to model simulations of future climatic and ecosystem change, paleoclimatology and genetics look back in time, using geochronology, physical, geochemical and paleoecological proxy methods, and DNA-based molecular clock analyses. Here we assess marine ecosystem response to past climate changes using an integrated approach based on Arctic sediment records of past intervals

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of warmth, orbital-scale glacial-interglacial cycles, and abrupt climate transitions coupled with DNA-based phylogenetic reconstructions and fossil records of polar vertebrate lineages. Although all parts of Arctic marine ecosystems cannot be studied, our study involves a wide variety of taxonomic groups and several key biological metrics of Arctic ecosystems including biodiversity, primary productivity, biogeography (range expansion and contraction) and hybridization. We address the fundamental question: does climate change cause large-scale loss of biodiversity through species' extinctions (α diversity) or rearrangement of species abundances within local communities, geographic range shifts (β diversity) [52, 65], or ecosystem restructuring [28, 76].

Advances in Arctic paleoclimatology

Most early studies of the Arctic Ocean sedimentary record were based on cores taken from research stations floating on sea ice in the 1960s and 1970s, which provided important discoveries but were geographically limited and lacked sufficient stratigraphic and age control [183]. Since the early 1990s, cruises led by German, Swedish, Canadian, Russian, and US researchers expanded the spatial and temporal coverage of Arctic sediment cores used for paleoceanography [135] (Fig. 1, Supplementary Table 1). In addition, greatly improved age control now allows a more complete reconstruction of Arctic Cenozoic climate history that, with exceptions, allows correlations with paleoclimate records from extra-Arctic regions.

Rapid advances have also come from the development of sediment proxy methods used to reconstruct environmental conditions and biological, chemical and physical processes influenced by climate (Supplementary Table 2). Examples used in the following discussion of Arctic climate and ecosystem evolution include micropaleontological records of benthic and pelagic communities, proxies of sea-ice cover, sediment transport, marine biological productivity, ocean temperature, salinity, dissolved oxygen and circulation, and ice sheet and ice shelf activity.

Cenozoic climate in the Arctic

In 2004, the Arctic Coring Expedition (ACEX), part of the Integrated Ocean Drilling Program (IODP Expedition 302), recovered 428 m of sediment from the central Arctic Lomonosov Ridge dating back to 56 million years (Ma) [10, 129, 182]. For the first time, a unique, though incomplete record of Arctic climatic and faunal evolution can be compared to the Cenozoic greenhouse-to-icehouse climate transition established on the basis of deep-sea foraminiferal $\delta^{18}O$ records of sea level and temperature and ice core records of atmospheric CO_2 concentrations and

temperature (Fig. 2). Initial study of ACEX Paleocene-Eocene micropaleontological records Expedition 302 [59] identified numerous diatoms ($\sim$40 taxa), silicoflagellates and ebridians ($\sim$40), palynomorphs ($\sim$58), agglutinated benthic foraminifera ($\sim$40) and, due to poor pre-Miocene preservation of calcareous shells, lesser numbers of calcareous nannoplankton, calcareous benthic and planktic foraminifers, and ostracode taxa.

ACEX researchers also investigated key climatic and ecosystem events including the Paleocene-Eocene Thermal Maximum (PETM), an $\sim$170,000-year long warm period about 56 Ma when sea-surface temperatures in the Arctic (SST) reached 22 °C [174]. In addition, ACEX recovered sediment from two younger hyperthermal periods—the Eocene Thermal Maximum 2 (ETM2) at 53.5 Ma [175] and the *Azolla* horizon $\sim$48.5 Ma [22]. During ETM2 TEX_{86}-derived SST estimates indicate Arctic temperatures reached 25 °C, dinoflagellate cysts document freshwater influx and eutrophication, and palm pollen suggests winter temperatures on adjacent continents exceeded 8 °C. The dominance of the genus *Azolla*, a free-floating, freshwater fern, and associated microfossils, characterized an $\sim$800,000-year long interval of episodic fresh surface water, a stratified ocean, endemism in silicoflagellates and ebridians [134], SSTs of 10–14 °C [22], and intermittent oxygen depletion [181] (Fig. 2d, f). During Paleocene-Eocene hyperthermal events, marine primary productivity in the central Arctic varied greatly with maximum values reaching 50–100 C g m^{-2} year^{-1} [106, 181]. These values are comparable to those from today's highly productive Arctic marginal ice zones [138] and higher than estimates for the central Arctic Ocean over the last 18 Ma, including today (Fig. 2c).

During the interval 48–45 Ma, Arctic SSTs fell by as much as 5–10 °C depending on which proxy method is used [182, 200]. This cooling is coincident with the inception of a winter sea-ice regime seen in ice-rafted debris (IRD) [179] and sea-ice diatom records [184] (Fig. 2a). There is also lithological evidence for ephemeral perennial sea ice at times between 47 and 44 Ma [42] (Fig. 2b). Climate history of the late Eocene, Oligocene and early Miocene is poorly known because one age model calls for a major sedimentary unconformity from 44 to 18 Ma [11], and another for a condensed zone representing the interval from 36 to 12 Ma [149]. This introduces uncertainty in identifying key Cenozoic cooling events, such as the Eocene/Oligocene transition $\sim$34 Ma, and their biological impacts. There is, nonetheless, evidence for stepwise cooling during the last 18 Ma of the Cenozoic greenhouse-icehouse transition. For example, IRD, mineral, and radiogenic proxies record a shift from a mid-Miocene climatic optimum ($\sim$15 Ma) toward a colder climate since about 13 Ma [41, 66, 79, 179].

Fig. 1 Map of selected sediment core sites used for paleoceanographic reconstruction. The *key symbols* designate the age of the record. The *black triangle* is the Cenozoic record from IODP ACEX Project [10, 129]. "Orbital" cores record multiple glacial interglacial cycles. "Orbital, MIS 11" cores are orbital records that include warm interglacial Marine Isotope Stage 11 ∼400 ka. "Holocene, Late Holocene" cores contain the last 1000–2000 years. Core sites keyed as "Productivity" were used in Arctic productivity studies. *Red lines* show the approximate margins of ice sheets. The Laurentide-Innuitian, Greenland and Eurasian ice sheet margins are maximum extent during the Quaternary [97, 188]. The Iceland ice sheet extent is the LGM [89]. Following [97], *red* crosshatched areas may or may not have been covered by ice sheets. *NWR* Northwind Ridge. Supplementary Table 1 provides information about core sites. Basemap is International Bathymetric Chart of the Arctic Ocean (IBCAO) [96]. See O'Regan [135] and Stein et al. [182] for additional core records
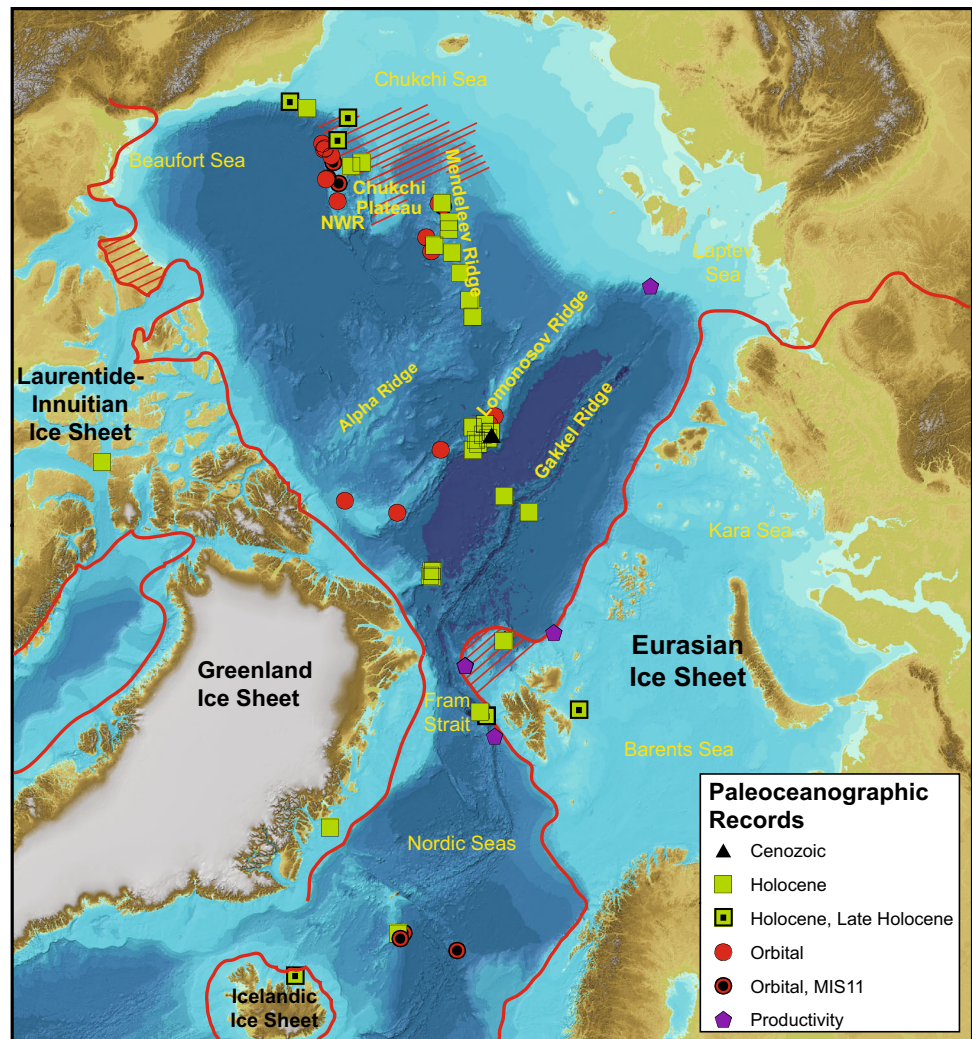
Early- to mid-Pliocene global climate (5–3 Ma) serves as an important benchmark for understanding modern climate because Pliocene atmospheric CO_2 concentrations were near today's level (400 ppmv, [139, 171]), but global mean annual temperature (MAT) was about 2.5–3 °C higher [53] and peak sea level ∼22 m higher [127]. Pliocene Arctic Ocean summer SSTs were appreciably warmer than modern and seasonally sea-ice-free conditions existed in some regions [108, 121]. Non-marine proxy records from continental sections also point to a warm Pliocene climate in the high latitudes of the northern hemisphere. At Lake El'gygytgyn (Lake "E") in Siberia summer temperatures were 8 °C warmer than modern [21] and at Ellesmere Island, Canada, summer and MAT were 11.8 and 18.3 °C higher than today [13]. In addition to periods of warmth, the Pliocene saw continued intensification of Northern Hemisphere glaciations and crossing of climate thresholds at 4 and 2.75 Ma as ice sheets reached Arctic coastlines

[107]. Such warm Pliocene conditions allowed a major trans-Arctic migration of mollusks [58, 195], ostracodes [37], and other groups ∼4.5–3.8 Ma when the Bering Strait opened [71, 194]. The direction of this migration was mainly from Pacific-to-Atlantic and probably led to the evolution of some of today's endemic Arctic species.

Quaternary glacial-interglacial cycles

Climatic cycles driven by changes in earth's orbital geometry (eccentricity, tilt and precession) are known throughout the geological record. Orbital cycles have been recognized in early to mid Eocene Arctic sediments from the ACEX core site [141, 167], but they are much better known from Quaternary sediments deposited during the last 600 ka across the entire Arctic Ocean. Quaternary glacial-interglacial cycles (here we use marine oxygen isotopic stage (MIS) terminology, [115]) signify changes in global ice volume and ocean temperature inferred from
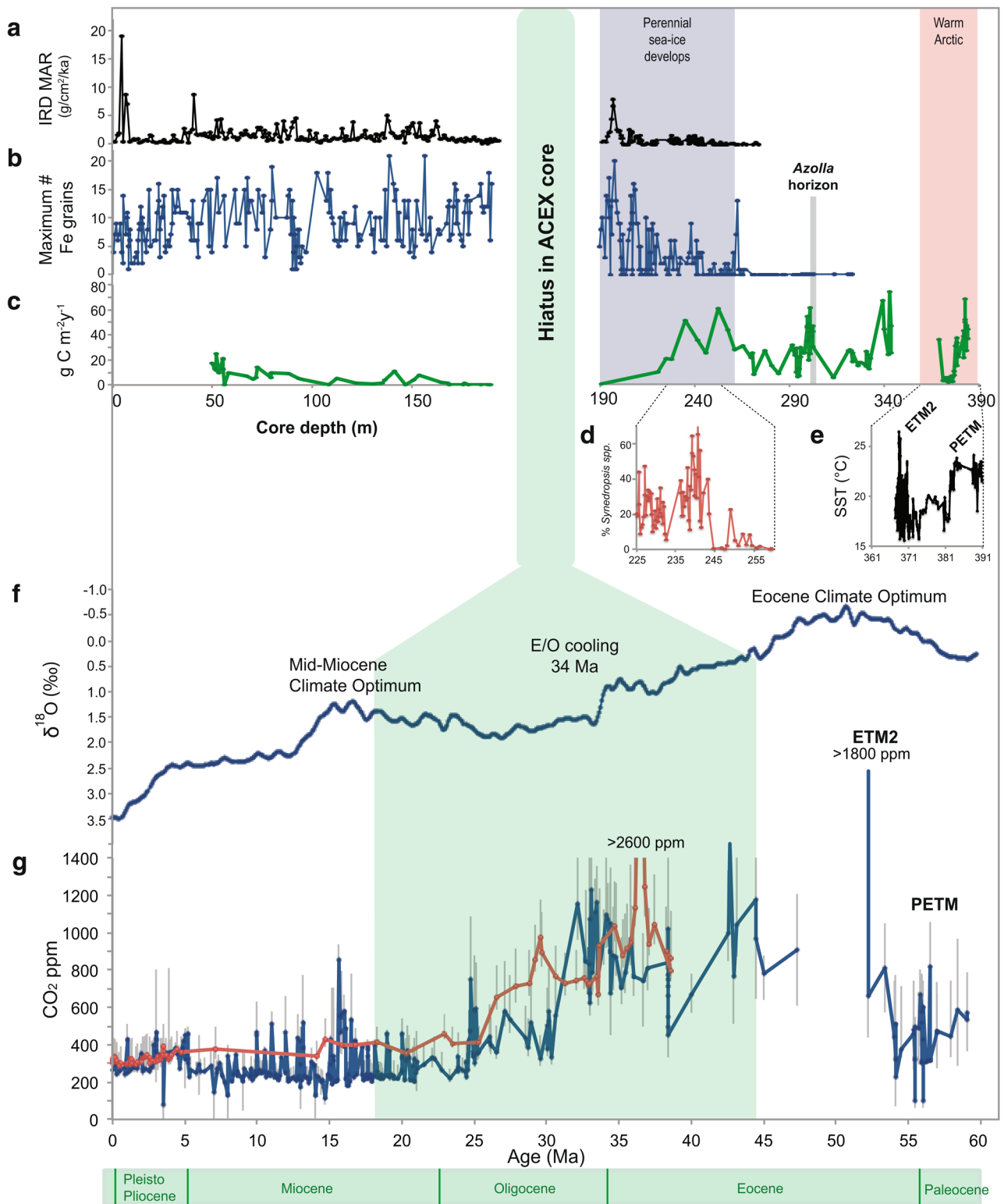
◄**Fig. 2** Cenozoic climate history from central Arctic ACEX core (**a–e**) compared with global ice volume and temperature (**f**, [30] and atmospheric CO_2 concentrations (**g** compilation from [17] (*blue curve*) and alkenone-based pCO_2 (*red*) from [208]. Major steps in Cenozoic climate events are labeled (Paleocene-Eocene Thermal Maximum (PETM), Eocene Climate Optimum, Eocene Thermal Maximum 2 (ETM2), Eocene/Oligocene (E/O) cooling, mid-Miocene Climate Optimum). **a** Cenozoic IRD, a sea ice proxy, based on terrigenous coarse sand fraction [179]. **b** Iron-oxide grain record of first perennial sea ice ∼44 Ma (260 m core depth) and subsequent sea-ice variability [42]. **c** Paleoproductivity reconstruction from nitrogen fraction showing low productivity (<20 g C m^{-2} a^{-1}) during the ice-covered Miocene and high productivity (∼50–100 g C m^{-2} a^{-1}) during warm, ice-free, and biologically productive Paleocene-early Eocene [106]. **d** Sea-ice diatom *Synedropsis* spp. abundance [184]. **e** TEX_{86}- derived SST showing the PETM [174]

deep-sea foraminiferal oxygen isotopes (Fig. 3a). These are accompanied by changes in atmospheric temperature and CO_2 concentrations known from Antarctic ice cores and other proxy records (Fig. 3b, c). In the Arctic Ocean, glacial-interglacial cycles are seen in a variety of proxies: manganese concentrations [92, 118, 148, 155, 156], sediment physical properties (grain size, bulk density) [136], mineral assemblages and trace elements [61], organic biomarkers [204], and stable isotopes [1, 153, 176] (Fig. 3d–f). Variability in these proxies reflects massive changes in ice cover, river runoff, and ocean circulation during opposing extremes of interglacial warmth with summer sea-ice-free conditions and glacial-age ice cover.

Although not gaining as much attention as past warm periods, glacial periods in the Arctic and adjacent subarctic deserve special attention because they provide a stark environmental contrast with interglacials and concrete evidence for the resiliency of marine ecosystems in the face of large-scale climate oscillations. Records of the Last Glacial Maximum (LGM, MIS 2, ∼24–19 ka) and the penultimate glacial MIS 6 (∼150 ka) have excellent age control [150], broad spatial sediment core coverage, extensive submarine geophysical surveys, and onshore glacial geological mapping. At these times, the Arctic Ocean was reduced to ∼50 % of its current area due to the combined effects of a 125 m fall in global sea level (increased ice-sheet volume), which exposed the vast Arctic continental shelves, and the expansion of ice sheets and ice shelves bordering the Arctic Ocean [43, 90, 91, 93, 94]. During glacial maxima, the cryosphere, including ice sheets, ice shelves, glaciers and sea ice, was substantially more extensive than what we see today (Fig. 1). The Laurentide, Innuitian, Eurasian, Barents Sea-Svalbard, and Icelandic Ice Sheets covered large parts of continental regions adjacent to the Arctic Ocean [56, 188], but perhaps as important, extensive ice shelves as thick as 1 km have

been identified from submarine glacial landforms mapped using geophysical methods on the Chukchi margin and Yermak Plateau [97, 98, 131, 196], the Lomonosov Ridge and Chukchi Plateau [151], the Lomonosov Ridge [110], and the Morris Jesup Rise [95]. During peak glacial conditions, sea ice was so thick during glacial maxima that little or no IRD could be transported to the central basin from continental margins leaving a sediment-starved central Arctic Ocean [150, 153]. Although the thickness of glacial-age sea ice is not known precisely, multiyear sea ice, called paleocrystic ice, thicker than today's >40 m-thick ice shelves off Ellesmere Island, may have dominated the glacial Arctic Ocean before the main phase of deglaciation began at 15 ka [20].

At the same time that the LGM Arctic Ocean proper was dominated by thick sea ice and ice shelves, sea ice extended far southward into subarctic regions of the Nordic Seas, the northern North Atlantic and the Bering Sea. Using dinoflagellate cyst assemblages from more than 50 core sites, de Vernal et al. [48] reconstructed spatial patterns of LGM sea ice, SST and sea-surface salinity from mid-to-high latitudes across the Northern Hemisphere. Among their findings were the presence of mid-latitude sea ice, stronger seasonality, nearshore to offshore SST gradients, and reduced surface salinities. Planktic foraminiferal assemblages and stable isotope values [132], and epipelagic ostracodes [38] also indicate southward migration of sea ice into the Nordic Seas and North Atlantic during glacial periods MIS 2, 4, and 6. Similarly, in the southern Bering Sea, LGM sea ice is evident from diatom assemblages [24].

Biological response to glacial-interglacial cycles

Perhaps the most striking biological manifestations of orbital cycles in the Arctic Ocean and surrounding seas are patterns of microfossil density, species diversity, and assemblage composition, which, when combined with physical and geochemical proxies, provide compelling evidence for ecosystem response to climate change. In contrast to the pre-Miocene sediments in the Arctic, which lack calcareous microfossils [see above], commonly preserved microfossil groups in the Quaternary include benthic and planktic [153, 201]) foraminifera, calcareous nannofossils [12], and ostracodes [39]. Along Arctic margins and in the Nordic Seas, diatoms [16], tintinnids (planktic ciliates, [169]), and dinoflagellates [120] also occur. In addition to faunal and floral remains, there are indirect proxies of oscillating biological activity, notably organic biomarkers of sea-ice diatoms and phytoplankton [60] and sediment manganese oxyhydroxide content related to terrestrial input, ice cover, and bioturbation [117, 118].
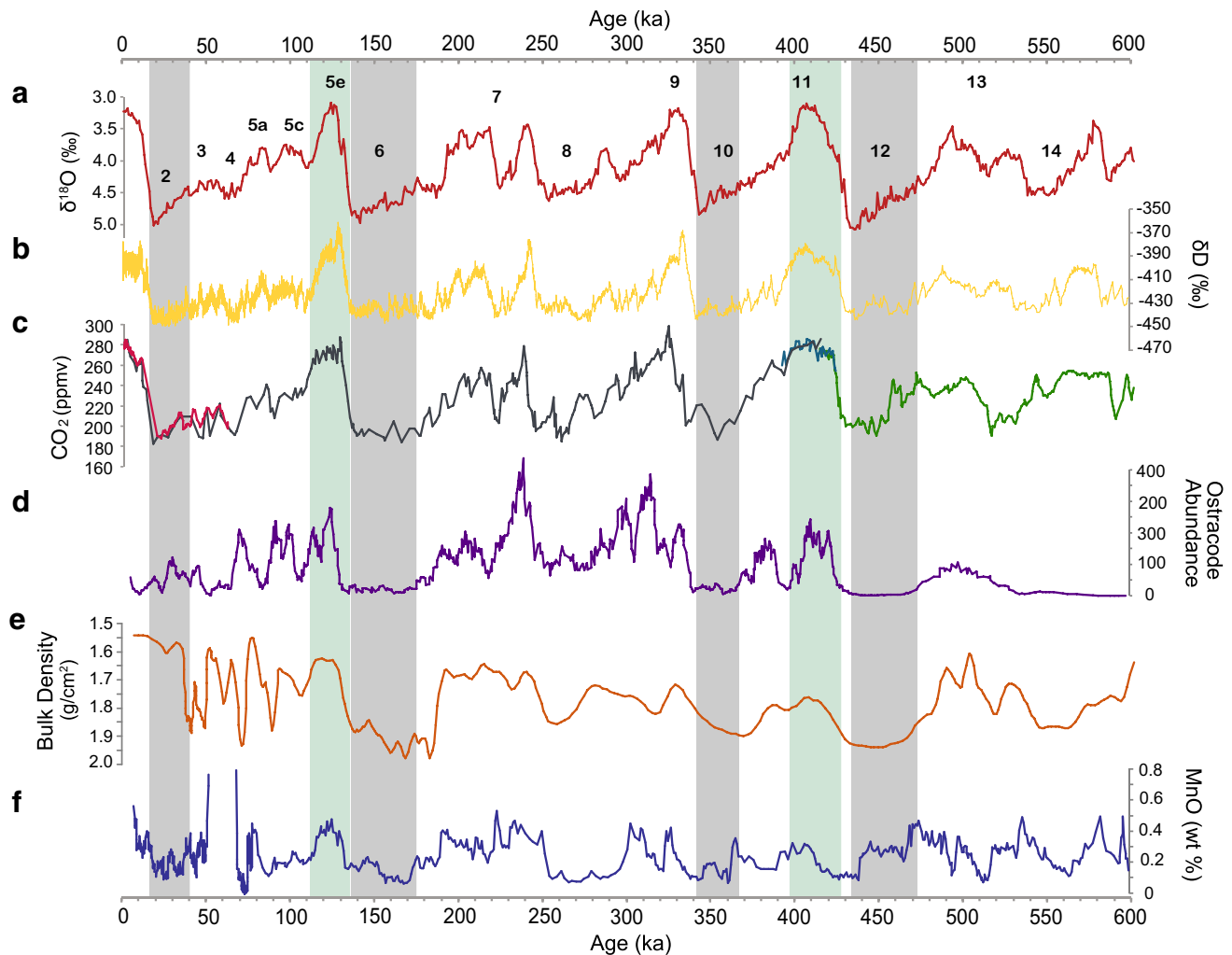
Fig. 3 Quaternary Climate. Global (*top panels* **a–c**) and Arctic (*bottom panels* **d–f**) climate proxies for the last 600,000 years. **a** Benthic oxygen isotope curve reflects global ice volume and temperature, marine isotope stages are numbered [115], **b** EPICA dome C deuterium, a temperature proxy [99], **c** EPICA dome C CO_2 curves [measured at Bern (*green*), Grenoble (*blue*), Taylor Dome (*gray*) and Vostok (*red*)] [173]. Deuterium and CO_2 values are on EDC3 gas age scale, **d** Arctic ostracode density composite from five western Arctic cores (Cronin et al. 2013), **e** Manganese content in sediments from Oden 96-12 core [Lomonosov Ridge [92], **f** Sediment density (Lomonosov Ridge IODP 302 ACEX core [136]). *Green bars* show periods that, based on Arctic proxies, were likely seasonally sea-ice free. These correspond to particularly warm marine isotope stages 5e and 11. *Gray bars* denote glacial stages with thick Arctic sea ice inferred from proxies corresponding to marine isotope stages 2, 6, 10, and 12

The density of calcareous microfossils in sediments from central Arctic ridges is directly linked to interglacial and glacial climate regimes and changes in sea-ice cover, surface productivity, sedimentation, and post-depositional processes [12, 119]. It is well established that foraminifera (benthic and planktic) and ostracodes are major components of the sand-sized fraction in interglacial sediments in contrast to near absence in glacial-age sediments [1, 80] (Fig. 3d). In addition to density, microfossil biodiversity is extremely variable in the eastern Arctic, where benthic foraminiferal diversity measured by the Fisher α and Shannon Wiener indices varied several-fold during the last glacial cycle [203], and in the western Arctic over the last few glacial-interglacial cycles [154]. Mechanisms driving species diversity patterns within the Arctic include the strength of inflowing warm Atlantic water, ice cover and surface productivity.

Microfossil assemblage composition (e.g. β diversity), measured by the relative abundances of environmentally sensitive species and genera, is also a useful measure of ecosystem dynamics. One striking example of climate-driven migration is the Pacific diatom *Neodenticula seminae,* a species that sediment records show disappeared in the North Atlantic Ocean ∼800 ka. It has recently been discovered that this species has migrated back into the North Atlantic and Nordic Seas during the last 2 decades

almost certainly in response to higher ocean temperatures allowing inter-oceanic migration [125, 161]. In Arctic cores, biogeographic range shifts occur frequently due to changes in climate and ocean circulation over various timescales. One widely used benthic foraminifera, *Epistominella exigua*, is a phytodetritus-eating, opportunistic species that dominates modern oceanic frontal zones [73]. Microfossil assemblages with dominant *E. exigua* indicate seasonally sea-ice-free and/or marginal ice zone conditions that characterized the early-mid Quaternary ($\sim$1.5 Ma–300 ka) prior to the development of perennial sea ice. This species is common during warm interglacials MIS 5 (125 ka, the Eemian Interglacial) and MIS 11 (400 ka) but absent during glacial periods [154].

As discussed above, ice shelves and thick sea ice covered the glacial Arctic Ocean, and, as a consequence, species were forced to migrate southward into extra-Arctic regions on a large scale. We can track the range expansion and contraction of sea-ice and marginal ice zone species because the ecology of several groups is well known from large, pan-Arctic surface sediment databases. In the case of dinoflagellates, fossil assemblages are used to estimate months of sea ice cover in subarctic seas [48, 49]. The epipelagic ostracode species *Acetabulastoma arcticum*, which today lives as a parasite on sea-ice dwelling species of the amphipod *Gammarus,* is also a useful sea-ice proxy in the Arctic and adjacent seas [38]. As expected from its ecology, this species occurs only in glacial age sediments (MIS 2, 4 and 6) in cores from the Nordic Seas and North Atlantic.

There is also evidence in the Arctic for two well-known global climate transitions involving changes in the pattern of orbital glacial-interglacial cycles—the Mid-Pleistocene Transition between 1.2 Ma and 700 ka [26], and the mid-Brunhes Event $\sim$450–400 ka [205]. Importantly, both climate transitions involved changes in Arctic sea-ice ecosystems. For example, the mid-Pleistocene transition, a shift from 41 to 100-kyr glacial-interglacial cycles, is characterized by faunal turnover (including regional extinctions) in Arctic foraminifera and ostracodes and reduced marine productivity. These signal a change from a seasonally ice-free to mostly perennial sea-ice cover during interglacial periods [154]. Globally, the mid-Brunhes Event coincides with the glacial termination between MIS 12 and MIS 11 ($\sim$450–400 ka) after which interglacial periods had smaller continental ice sheets, higher sea level, warmer temperatures, and higher atmospheric CO_2 concentrations. MIS 11 was an exceptionally warm interglacial, notable because, whereas atmospheric CO_2 concentrations ($\sim$280 ppmv) and orbital insolation were similar to those of the Holocene interglacial, global sea level was higher than today, perhaps due to the collapse of parts of the Antarctic Ice Sheet [84, 160, 165]. Arctic

sediments from the Northwind, Mendeleev, and Lomonosov Ridges show that during MIS 11, there was no summer sea ice and SSTs reached 8–10 °C [39]. Warm Arctic Ocean summers during MIS 11 are also evident in the Nordic seas and the subpolar North Atlantic [15, 100], in Lake "E" sediments [123] and from terrestrial pollen in cores off southern Greenland [50]. Subsequent interglacial and interstadial periods (MIS 9, 7, 5 and 3) also experienced, at least at times, summer sea-ice-free conditions [133, 137].

In sum, the contrast between glacial and interglacial oceanic environmental conditions in the Arctic and subarctic reflects frequent biogeographic marine ecosystem shifts of several thousand kilometers supporting the view that climate change alters β diversity but does not cause the systematic loss of species.

Abrupt, suborbital climate transitions

One pressing question is whether climate has reached a "tipping point" such that we are witnessing an abrupt climate reversal (over a century or less) [25]. The last deglacial period ($\sim$19–11.7 ka) included several well-known millennial climate events whose onsets and terminations were abrupt transitions. These include stadial periods called Heinrich Event 1 (H1, 17–15 ka), the Younger Dryas climate reversal (YD, 13–11.7 ka) and interstadials called the Bølling-Allerød (B/A, 14.6–13 ka), and the Preboreal period (PB, 11.7–9 ka) (Fig. 4). Importantly, past abrupt climate reversals had major impacts on Arctic marine ecosystems over timescales much shorter than orbital cycles and they provide a unique context for today's changing Arctic. The last glacial period from 60 to 15 ka included multiple Heinrich Events, identified by ice-rafted sediment and sea-surface cooling in the North Atlantic Ocean, and Dansgaard-Oeschger (DO) cycles identified in Greenland ice core oxygen isotopes and extra-Arctic proxy records.

Changes in the dominant species in benthic foraminifer assemblages occurred on the Yermak Plateau and Barents Sea slope during stadial-interstadial events. These changes suggest a more than twofold change in marine productivity (from 30 to >60 g C m^{-2} year^{-1}) (Fig. 4a) [202]. On the Laptev Sea margin, changes in dominant benthic foraminiferal species occur over a century or less at the onset and termination of H1 and the YD. Decreases in planktic foraminiferal stable isotope values during the YD up to 1 per mil are known from the Beaufort and Laptev Seas and the Mendeleev Ridge [6, 157, 177]. Faunal and isotopic proxies signify complex hydrological changes in the surface and subsurface Arctic Ocean caused by freshwater influx probably from multiple catastrophic glacial lake drainage episodes [192] and changes in the strength of inflowing Atlantic water. It is worth noting that other types of catastrophic events disrupted Arctic marine
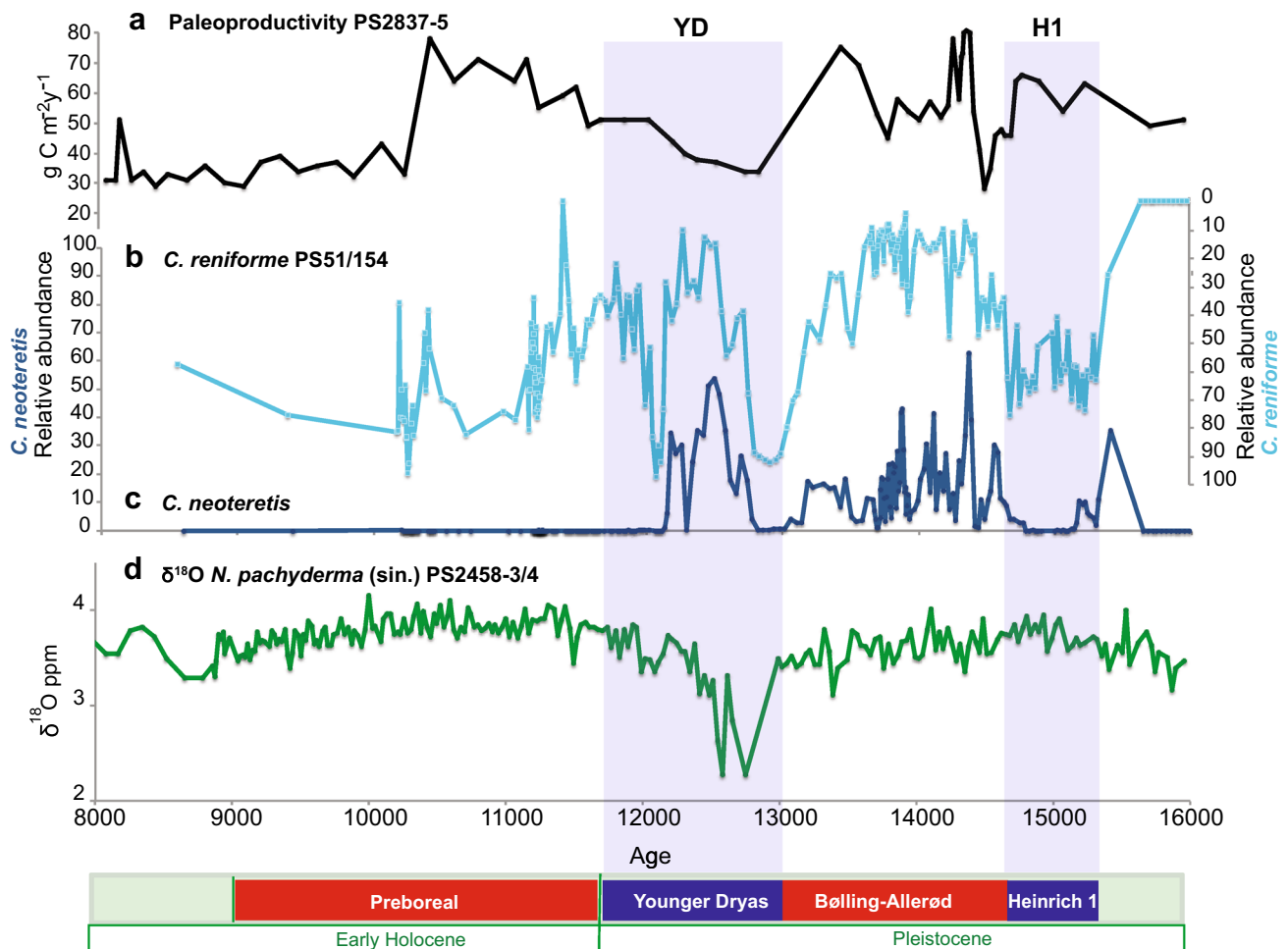
Fig. 4 Abrupt climate change in the Arctic during the last deglacial period including Bølling-Allerød and Preboreal interstadials and Heinrich 1 (H1, 17–15 ka) and Younger Dryas (YD, 13–11.7 ka) stadials. **a** Benthic foraminiferal record of marine productivity from core PS2837-5 (1023 m water depth), Yermak Plateau, showing high interstadial and low stadial (YD) productivity [202]. **b–c.** Two species of benthic foraminifera from core PS51/154 (270 m water depth) highlight ecosystem changes during abrupt stadial-interstadial oscillations [190]. Absence of *C. neoteretis* (*dark blue*) and dominance of *C. reniforme* (*light blue*, *y* axis reversed) at 15 and 13 ka signify ocean circulation changes related to freshwater influx at the end of H1 and the YD. **d** Oxygen isotope values of planktic foraminifer *Neogloboquadrina pachyderma* (sin) in core PS2458 from Laptev Sea continental margin (983 m water depth) show abrupt decline at 13 ka due to fresh water influx during YD [177]. Higher $\delta^{18}O$ values reflect ice sheet retreat during Preboreal and Bølling-Allerød

ecosystems, such as mega-iceberg discharges caused by Eurasian Ice Sheet surge and collapse, which scoured the seafloor in the Kara-Barents Seas [95, 131, 152] and central Arctic as far back as 500,000 ka [110]. Space limits our discussion to the Arctic Ocean proper, but suborbital millennial-scale events also caused frequent marine ecosystem reorganizations in the Nordic Seas during the last glacial-interglacial cycle [14, 78].

Holocene climate oscillations

Although smaller in scale than glacial-interglacial cycles, climate variability during the Holocene interglacial period had significant impacts on polar biological systems. There is extensive evidence for an Early Holocene Thermal Maximum (EHTM) ~ 11–7 ka with regionally variable seasonally sea-ice-free conditions based on circum-Arctic lake and ice core records [101, 187], glacial geology [122], ocean temperatures [62], IRD [44], dinoflagellate assemblages [112], and sea-ice biomarkers [130]. The EHTM was followed by Neoglacial cooling, which witnessed the development of what we know as the preindustrial, perennial sea-ice-covered Arctic, culminating in the Little Ice Age (LIA, 1400–1900 C.E.). Temporally and spatially variable sea-ice cover throughout the Holocene is among the most notable discoveries of the last decade [170, 193] because it reflects an Arctic Ocean highly sensitive to insolation and unforced climate variability.

Similarly, high-resolution late Holocene records covering the last 1000–2000 years are particularly important because they provide baseline variability to interpret recent trends in sea ice and temperature. Terrestrial [40, 102], marine SST [178], and sea ice [104] proxies show natural climate variability during the late Holocene, including the Medieval Climate Anomaly (600–1400 C.E.) and the LIA, as well as anomalous 20th century patterns.

Arctic Ocean marine mammals

Marine mammals are a major component of modern Arctic sea-ice ecosystems [74, 105] and their molecular genetics and paleontology provide insights about past climate changes in the Arctic. The use of molecular sequences of DNA and proteins to infer species' phylogeny and divergence times (i.e., a molecular clock) is an important aspect of phylogenetics [191]. These analyses, combined with vertebrate fossil evidence, can provide information about the temporal distribution of species, which can be used with paleoclimate data to better understand the Arctic climate-biological relationships, especially for vertebrate lineages (Supplementary Table 3). As we see below, molecular methods are increasingly applied to integrated paleoclimatic-ecosystem studies in the Arctic, so it is important to briefly consider the strengths and limitations.

The molecular approach involves comparison of the amino acid sequences of proteins or nucleic acid sequences (DNA or RNA) in different species [158, 191, 197, 209]. Molecular sequences will diverge by mutation from a common ancestral sequence at some rate, which is the time component of the "clock". If the rate of sequence divergence is constant, then its extent will be a function of time and the phylogenetic relationships and time of divergence of the sequences can be estimated. If the time of divergence of the sequences is assumed to be equal to the time of divergence of the species, then an estimate of species' divergence time is obtained. The assumptions of a constant rate of sequence divergence (depending on mutation rate and population genetic factors of selection, population size, migration) and that a sequence divergence reflects the species divergence are key factors affecting the accuracy of molecular clocks. Single gene sequences often do not reflect the species phylogeny so multiple genes or entire genome sequences are needed for robust analyses (e.g., [142]). DNA from extant animals is typically used to quantify sequence divergence, but ancient DNA (aDNA) from fossil material as old as 0.7 ma can also be used and provide valuable insights [168].

The accuracy of molecular clocks also depends on the accuracy of a fossil calibration date to identify the divergence time for at least one node of the phylogenetic tree of the taxa considered [7, 87, 124, 143]. Divergence time estimates can be controversial because of potential discrepancies of molecular clocks depending on the genes, calibration points, and models of molecular evolution considered [69, 158, 191, 197].

Case studies of vertebrate phylogeny with fossils and DNA sequences

In the case of Arctic climate change, the divergence time of polar bears (*Ursus maritimus*) and its sister species, brown bears (*U. arctos*), is especially relevant because there is concern about reduced summer sea ice habitat, especially for some geographic populations [3, 4, 54, 185]. Polar bears and brown bears are thought to have evolved from a common ancestor during the Pleistocene [111], and a polar bear fossil from the last interglacial (Eemian) period ~125 ka established this age as their minimum time of divergence [2, 88, 114].

Molecular clock estimates of the divergence time of polar bears and brown bears vary widely depending on the genes used. These include divergence times of 2–3 Ma using proteins [72], 110–130 ka with mitochondrial DNA (mtDNA, [8, 19, 46, 57, 109, 114, 189, 206, 207]), 0.43–1.12 Ma with Y-chromosome DNA sequences [18] and 0.34–2.0 Ma with nuclear DNA sequences [57, 77, 206]. The most recent analyses of genome sequences estimated the polar bear-brown bear divergence at 340–480 ka [116], 1.2 Ma [23, 36], and 4–5 Ma [128].

Due to the inherent uncertainty of molecular clocks, some authors have refrained from applying them to these species [32, 67, 140, 199]. Cahill et al. [23] note that the molecular divergence times for bear species are relative, not absolute dates because of the uncertainty of the fossil record regarding bear species' divergences. However, it is reasonable to infer the minimum age of *U. maritimus* is about 125 ka and more likely somewhat older, between 300 ka and 2 Ma. As discussed above, major climate transitions including the mid-Pleistocene Transition and mid-Brunhes Event occurred during this time frame.

Given the dynamic nature of climate-driven habitat changes outlined above, it is important to note that speciation may be accompanied by interbreeding between populations until there is permanent reproductive isolation. Extant populations of polar bears and brown bears have separate gene pools with minimal interbreeding [34–36, 77, 144], but future interbreeding (i.e., hybridization) is hypothesized if sea-ice declines and polar bears spend more time on land [103]. Past interbreeding in these species is suggested by paraphyletic mtDNA phylogeny in which polar bears and brown bears from Admiralty, Baranof, and Chichagof islands (ABC) in southeast Alaska have haplotypes in a clade separate from other brown bears [32, 35]. In addition, polar bears and ABC brown bears

share nuclear alleles [77, 116, 128], including <1 % of the autosomal genome and 6.5 % of the X-chromosome loci [23], but none of the Y-chromosome [18]. The pattern of genes shared by polar bears and ABC brown bears—maternally inherited mtDNA > X chromosome > autosomes > Y-chromosomes—is consistent with introgressive hybridization of male brown bears mating with female polar bears. This is hypothesized to have occurred about 12 ka when brown bears replaced polar bears during post-glacial colonization of the ABC islands [23].

Pinniped phylogenies also shed light on the development of the Arctic marine ecosystem. The pinnipeds, which include seals (Phocidae), sea lions (Otariidae), and walruses (Odobenidae), live in Arctic and subarctic seas with seasonal or perennial ice. Seals of the subfamily Phocinae (tribe Phocini) include three closely related genera in the northern hemisphere whose divergence has been estimated with fossil and molecular data relevant to our discussion. This includes the ringed seal (*Pusa hispida*), a primary prey of polar bears. The genus *Pusa* has a circumpolar Arctic distribution that in addition to *P. hispida* in the central Arctic includes Caspian seals (*P. caspica*) in the Caspian Sea, and Baikal seals (*P. sibirica*) in (freshwater) Lake Baikal, Siberia. *Phoca* includes the harbor seal (*P. vitulina*) in the temperate and subarctic northern hemisphere, and the spotted seal (*P. largha*) in the subarctic North Pacific Ocean. The gray seal (*Halichoerus grypus*) occurs in the North Atlantic Ocean.

However, seal classification is not definitive because of close relationships among various groups. For example, harbor seals and spotted seals are sometimes considered conspecific, and some taxonomists suggest that *Pusa* and *Halichoerus* could be reclassified as *Phoca* [45, 86]. This is reflected in equivalent mtDNA divergence (mean sequence divergence 3.36 %) of ringed seals, harbor seals, and gray seals, which has been used as a standard to calibrate a molecular clock for other taxa [7].

The fossil record shows that ringed seals occurred in the Arctic region during Quaternary interglacial and interstadial periods, including the eastern Beaufort Sea (∼42 ka), Greenland (130 ka), and the Chukchi Sea (130 ka, [81, 162]). *Phoca* (harbor seal or spotted seal) fossils also occur in the Chukchi Sea (115–130 ka, [162]). This indicates that the oldest fossils of ringed seals and spotted/harbor seals in the Arctic are the same age as the oldest polar bear fossil from the Eemian (MIS 5) interglacial. Even though molecular clock estimates suggest a much older origin of polar bears, the fossil data provide a minimum estimate of their origin and that of ringed and harbor/spotted seals. This confirms that the bears and seals co-existed in the Arctic during MIS 5 and persisted until the present.

Molecular genetic data indicate that the Phocini radiated during the last 1–2 Ma. Analysis of 8935 bp of 16 nuclear genes and mtDNA indicates that *Pusa* and *Phoca* split 1.58 Ma; and within *Phoca* harbor seals and spotted seals split 0.4–1.3 Ma, and within *Pusa* ringed, Caspian, and Baikal seals split 0.7–1.8 Ma [68]. Analysis of 26,818 bp of 52 nuclear and mtDNA genes indicate *Pusa* and *Phoca* split 2.1 Ma; and within *Phoca* harbor seals and spotted seals split 1.1 Ma, and within *Pusa* ringed, Baikal, and Caspian seals split 2.0 Ma [86]. The differences in these estimates reflect the different genes and models used, but they also indicate that seal species, including ringed seals, probably existed over much of the Pleistocene and Holocene along with polar bears.

The walrus (*Odobenus rosmarus*) also lives in Arctic and subarctic sea-ice-covered regions. Two subspecies are generally recognized, the Atlantic walrus (*O. r. rosmarus*) in the central Canadian Arctic east to the Kara Sea and the Pacific walrus (*O. r. divergens*) in the Bering and Chukchi Seas. A population in the Laptev Sea is related to the Pacific walrus [63, 113]. The fossil record shows that the Odobenidae evolved in the mid-Miocene ∼16–21 Ma [47] and *O. rosmarus* is the only extant species, although up to 14 genera and 20 species lived in the past [47, 81]. *Odobenus rosmarus* is thought to have migrated from the Atlantic to the Pacific about 600 ka [81]; walrus fossils in the Bering and Chukchi Seas date to about 130 ka, on Vancouver Island, British Columbia 70 ka Ma, and as far south as California ∼270 ka [82].

Molecular clock estimates suggest the walrus family diverged from the sea lion family (Otariidae) about 15.1–18 Ma [68, 86]. There are no extant taxa for molecular clock comparison of walruses with other Odobenidae, but an estimate of divergence of the Atlantic and Pacific walrus can be made considering their mtDNA divergence of 1–1.6 % [33] and a rate of pinniped mtDNA evolution of 1.2 %/Ma [7]. These data suggest the Atlantic and Pacific subspecies split sometime between 83 and 133 ka, although there may have been gene flow between the oceans over this time considering the changes in sea-ice conditions described above.

Vertebrate range expansion and contraction during climate changes

Vertebrate paleontology often combined with paleoclimatic and/or molecular genetics provides key information about Arctic mammalian response to climate change. For example, Cooper et al. [29] recently analyzed genetic (13 events) and paleontological (18 events) megafaunal "transition events" for terrestrial taxa within the context of abrupt climate transitions including Dansgaard-Oeschger events identified in Greenland ice cores and Cariaco Basin sediments. They defined faunal transitions as geographically widespread or global extinctions, or invasions, of species or major clades.

The bulk of the evidence indicated terrestrial vertebrates are affected by abrupt climate transitions.

In addition, there have been several studies in which polar bear evolution has been assessed in the context of orbital paleoclimate cycles over the past few million years [23, 46, 57, 77, 128]. If, as DNA and fossil evidence suggests, polar bears and their primary prey, ringed seals and other prey such as walruses, have existed for at least 125 ka and likely hundreds of thousands of years, then they experienced extreme climate conditions of glacial periods as well as partially or completely summer sea-ice-free interglacial periods (MIS 11, MIS 5 and the early Holocene). Microfossil proxy evidence for southward expansion of sea ice during glacial periods implies that vertebrate species that are dependent on sea ice habitat might have also migrated southward into the Nordic and Bering Sea-North Pacific regions.

Several lines of evidence support this idea of frequent geographically extensive range shifts, not only in terrestrial vertebrates [29], but sea ice based marine mammals as well. First, the close genetic relationships among bear species and among seal species discussed above, including evidence for hybridization, suggests dynamic population shifts. Moreover, large-scale range expansion during glacial periods is evident in the fossil record of vertebrates in extra-Arctic regions [81]. For example, the post-glacial Champlain Sea (13–9 ka, [159]) of New York, Vermont, and Canada has well-studied Arctic vertebrate faunas that include whales, walruses, brown bears and seals [64, 83]. Likewise, in coastal regions around Alaska, fossil records [31, 85] support molecular genetic data [23] showing that during the LGM, polar bears and ringed seals ranged as far south as the Gulf of Alaska, considerably south of their current Arctic ranges. In the case of summer sea-ice-free interglacial periods, the presence of winter sea ice habitat, polar bears' ability to fast during summer [164], seals ability to use land areas in the absence of sea ice, and the availability of new prey species shifting ranges into the Arctic may have allowed survival during warm periods. Walrus also have an extensive glacial and post-glacial fossil record [55] including specimens from the paleo-Hudson River Valley on the New York and New Jersey continental shelf dated at ∼10.6–11.2 ka [51].

Discussion

The Cenozoic ecosystem changes in the Arctic described above are summarized in Figs. 5 and 6 within the context of climate changes over different timescales. Several conclusions can be made. First, a seasonally ice-free marginal and central Arctic Ocean was common not only during Greenhouse worlds of PETM and Early Eocene, but also during the Pliocene, the early Quaternary before the Mid-Pleistocene Transition, during MIS 11, MIS 5 and regionally during the early Holocene. During orbital climatic cycles of the last few hundred thousand years, interglacial periods were characterized by perennial and at times seasonal sea ice cover and inhabited by marine ecosystems similar to those of the pre-industrial Holocene. Some species thought to be dependent on summer sea ice (e.g., polar bears) survived through these periods. In contrast, during glacial periods the much smaller Arctic Ocean and much of the adjacent continents were covered with massive ice sheets, thick ice shelves, and sea ice making large regions virtually uninhabitable to most species that inhabit today's Arctic. Despite the scale, frequency and
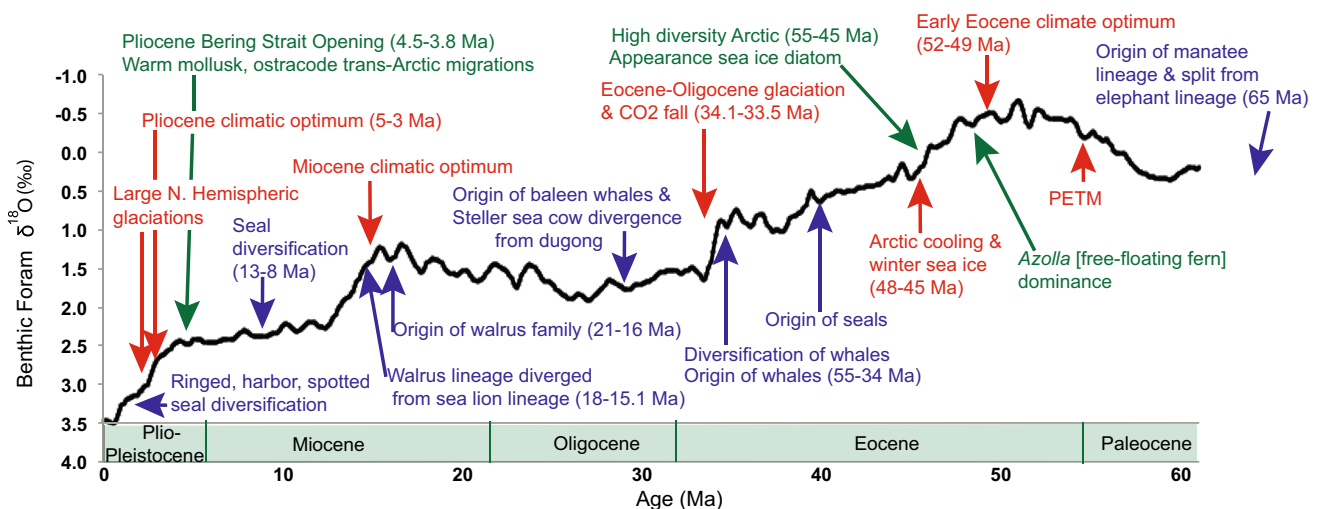
Fig. 5 Summary of Arctic Ocean biological and climatic events during the Cenozoic. *Blue letters* are marine mammal events, *red* are climatic events, *green* are biological events. See text and Supplementary Tables 1–3 and Supplementary references for sources
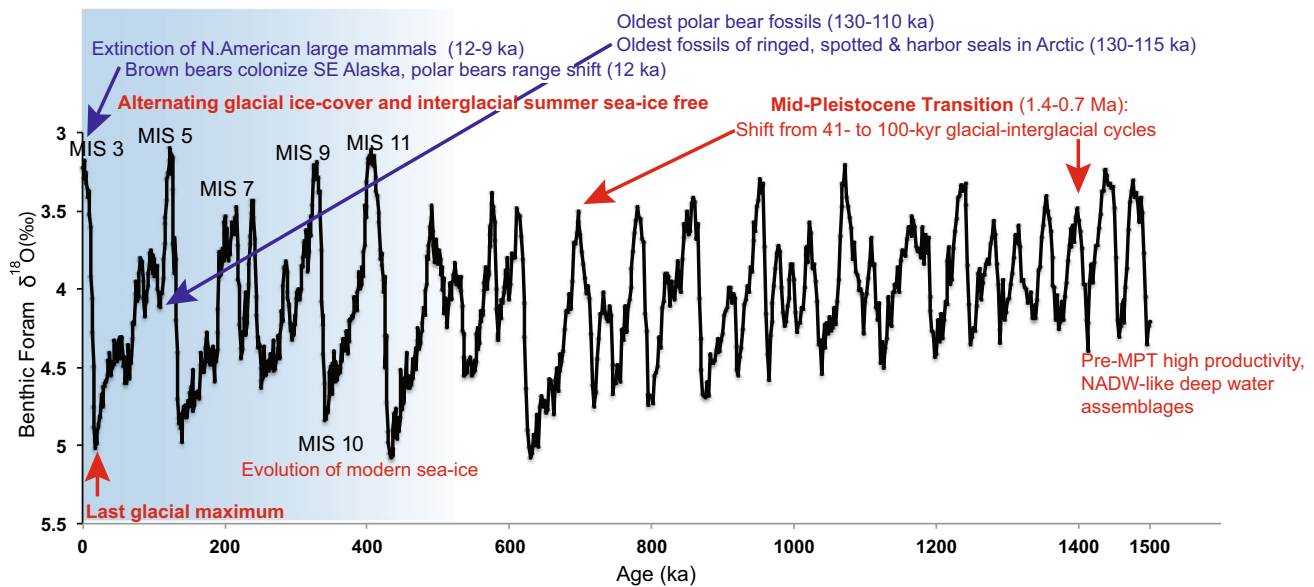
Fig. 6 Summary of Arctic Ocean biological and climatic events during mid-to-late Quaternary orbital glacial-interglacial cycles. *Blue letters* are marine mammal events, *red* are climatic events, *green* are biological events. See text and Supplementary Tables 1–3 and Supplementary references for sources

rapidity of Quaternary climate changes, Arctic marine ecosystems associated with sea-ice habitats were extremely resilient, adapting through geographic range expansion into the Arctic during warm periods, and south into extra-Arctic regions during glacial periods. The stratigraphic record of the last 1.5 Ma indicates that no marine species' extinction events occurred despite major climate oscillations. The Cenozoic sedimentary record is too incomplete to conclude that large climate transitions caused extinction of Arctic species, but hopefully future IODP coring will recover more complete records [182]. More generally, future cross-discipline studies of Arctic species and ecosystems combining molecular methods and paleoclimate reconstructions will result in a better understanding of how biological systems respond to climate changes.

References

1. Adler RE, Polyak L, Crawford KA, Grottoli AG, Ortiz JD, Kaufman DS, Channell JET, Xuan C, Sellén E (2009) Sediment record from the western Arctic Ocean with an improved Late Quaternary age resolution: HOTRAX core HLY0503-8JPC, Mendeleev Ridge. Glob Planet Change 68:18–29

2. Alexanderson H, Ingólfsson Ó, Murray AS, Dudek J (2013) An interglacial polar bear and an early Weichselian glaciation at Poolepynten, western Svalbard. Boreas 42:532–543

3. Amstrup SC, Marcot BG, Douglas DC (2007) Forecasting the range-wide status of polar bears at selected times in the 21st century, administrative report, 123 pp, U.S. Geol. Surv., Alaska Sci. Cent., Anchorage, Alaska. Available at http://www.usgs.gov/newsroom/special/polar_bears/

4. Amstrup SC, Marcot BG, Douglas DC (2008) A Bayesian network modeling approach to forecasting the 21st century worldwide status of polar bears. In: DeWeaver ET, Bitz CM, Tremblay LB (eds) Arctic sea ice decline: observations, projections, mechanisms, and implications. Geophysical Monograph Series vol 180. AGU, Washington, pp 213–268

5. Anderson LG, Tanhua T, Björk G, Hjalmarsson S, Jones EP, Jutterström S, Rudels B, Swift JH, Wåhlström I (2010) Arctic ocean shelf–basin interaction: an active continental shelf CO_2 pump and its impact on the degree of calcium carbonate solubility. Deep Sea Res Part I Oceanogr Res Pap 57:869–879

6. Andrews JT, Dunhill G (2004) Early to mid-Holocene Atlantic water influx and deglacial meltwater events, Beaufort Sea slope, Arctic Ocean. Quat Res 61:14–21

7. Arnason U, Xu X, Gullberg A, Graur D (1996) The ''phoca standard'': an external molecular reference for calibrating recent evolutionary divergences. J Mol Evol 43:41–45

8. Arnason U, Gullberg A, Janke A, Kullberg M (2007) Mitogenomic analyses of caniform relationships. Mol Phylogenet Evol 45:863–874

9. Arrigo KR, van Dijken GL (2011) Secular trends in Arctic Ocean net primary production. J Geophys Res Oceans. doi:10.1029/2011JC007151

10. Backman J, Moran K, McInroy DB, Mayer LA (2006) Arctic coring expedition. In: Proceedings of the integrated ocean drilling program 302. doi:10.2204/iodp.proc.302.2006

11. Backman J, Jakobsson M, Frank M, Sangiorgi F, Brinkhuis H, Stickley C, O'Regan M, Løvlie R, Pälike H, Spofforth D, Gattacecca J, Moran K, King J, Heil C (2008) Age model and core-seismic integration for the Cenozoic Arctic Coring Expedition

sediments from the Lomonosov Ridge. Paleoceanography. doi:10.1029/2007PA001476

12. Backman J, Fornaciari E, Rio D (2009) Biochronology and paleoceanography of the late pleistocene and holocene calcareous nannofossil abundances across the Arctic Basin. Mar Micropaleontol 72:86–98

13. Ballantyne AP, Greenwood DR, Sinninghe Damsé JS, Csank AZ, Eberle JJ, Rybczynski N (2010) Significantly warmer Arctic surface temperatures during the Pliocene indicated by multiple independent proxies. Geology 38:603–606

14. Bauch HA (2013) Interglacial climates and the Atlantic meridional overturning circulation: is there an Arctic controversy. Quat Sci Rev 63:1–22

15. Bauch HA, Erlenkeuser H, Helmke JP, Struck U (2000) A paleoclimatic evaluation of marine oxygen isotope stage 11 in the high northern Atlantic (Nordic seas). Glob Planet Change 24(1):27–39

16. Bauch HA, Polyakova YI (2003) Diatom-inferred salinity records from the Arctic Siberian Margin: implications for fluvial runoff patterns during the Holocene. Paleoceanography. doi:10.1029/2002PA000847

17. Beerling DJ, Royer DL (2011) Convergent cenozoic CO2 history. Nat Geosci 4:418–420

18. Bidon T, Janke A, Fain SR, Eiken HG, Hagen SB, Saarma U, Hallstrom BM, Lecomte N, Hailer F (2014) Brown and polar bear Y chromosomes reveal extensive male-biased gene flow within brother lineages. Mol Biol Evol 31(6):1353–1363. doi:10.1093/molbev/msu109

19. Bon C, Caudy N, de Dieuleveult M, Fosse P, Philippe M, Maksud F, Beraud-Colomb E, Bouzaid E, Kefi R, Laugier C et al (2008) Deciphering the complete mitochondrial genome and phylogeny of the extinct cave bear in the Paleolithic painted cave of Chauvet. Proc Natl Acad Sci USA 105:17447–17452

20. Bradley RS, England JH (2008) The Younger Dryas and the sea of ancient ice. Quat Res 70:1–10

21. Brigham-Grette J, Melles M, Minyuk P, Andreev A, Tarasov P, DeConto R, Koenig S, Nowaczyk N, Wennrich V, Rosén P, Haltia E, Cook T, Gebhardt C, Meyer-Jacob C, Snyder J, Herzschuh U (2013) Pliocene warmth, polar amplification and stepped Pleistocene cooling recorded in NE Arctic Russia. Science 340:1421–1427

22. Brinkhuis H, Schouten S, Collinson ME, Sluijs A, Sinninghe Damsté JS, Dickens GR, Huber M, Cronin TM, Onodera J, Takahashi K, Bujak JP, Stein R, van der Burgh J, Eldrett JS, Harding IC, Lotter AF, Sangiorgi F, van Konijnenburg-van Cittert H, de Leeuw JW, Matthiessen J, Backman J, Moran K, The Expedition 302 Scientists (2006) Episodic fresh surface waters in the Eocene Arctic Ocean. Nature 441:606–609

23. Cahill JA, Green RE, Fulton TL, Stiller M, Jay F, Ovsyanikov N, Salamzade R, St John J, Stirling I, Slatkin M, Shapiro B (2013) Genomic evidence for island population conversion resolves conflicting theories of polar bear evolution. PLoS Genet 9:e1003345. doi:10.1371/journal.pgen.1003345

24. Caissie BE, Brigham-Grette J, Lawrence KT, Herbert TD, Cook MS (2010) Last glacial maximum to Holocene sea surface conditions at Umnak Plateau, Bering Sea, as inferred from diatom, alkenone, and stable isotope records. Paleoceanography. doi:10.1029/2008PA001671

25. CCSP (2008) Abrupt Climate Change. A report by the US Climate Change Science Program and the Subcommittee on Global Change Research [Clark, P.U., A.J. Weaver (coordinating lead authors), E. Brook, E.R. Cook, T.L. Delworth, and K. Steffen (chapter lead authors)]. US Geological Survey, Reston, VA, p 459

26. Clark PU, Archer D, Pollard D, Blum JD, Rial JA, Brovkin V, Mix AC, Pisias NG, Roy M (2006) The middle Pleistocene transition: characteristics, mechanisms, and implications for long-term changes in atmospheric pCO$_2$. Quat Sci Rev 25:3150–3184

27. Comiso JC (2012) Large decadal decline of the arctic multiyear ice cover. J Clim 25:1176–1193

28. Conversi A, Dakos V, Grådmark A, Ling S, Folke C, Mumby PJ, Greene C, Edwards M, Blenckner T, Casini M, Pershing A, Möllmann C (2014) A holistic view of marine regime shifts. Philos Trans R Soc B 370:20130279. doi:10.1098/rstb.2013.0279

29. Cooper A, Turney C, Hughen KA, Brook BW, McDonald HG, Bradshaw CJ (2015) Abrupt warming events drove late pleistocene holarctic megafaunal turnover. Science 349:602–606. doi:10.1126/science.aac4315

30. Cramer BS, Toggweiler JR, Wright JD, Katz ME, Miller KG (2009) Ocean overturning since the Late Cretaceous: inferences from a new benthic foraminiferal isotope compilation. Paleoceanography. doi:10.1029/2008PA001683

31. Crockford S, Frederick G (2007) Sea ice expansion in the Bering Sea during the Neoglacial: evidence from archaeozoology. Holocene 17:699–706

32. Cronin MA, Amstrup SC, Garner GW, Vyse ER (1991) Interspecific and intraspecific mitochondrial DNA variation in North American bears (*Ursus*). Can J Zool 69:2985–2992

33. Cronin MA, Hills S, Born EW, Patton JC (1994) Mitochondrial DNA variation in Atlantic and Pacific walruses. Can J Zool 72:1035–1043

34. Cronin MA, MacNeil MD (2012) Genetic relationships of extant North American brown bears (*Ursus arctos*) and polar bears (*U. maritimus*). J Hered 103:873–881

35. Cronin MA, McDonough MM, Huynh HM, Baker RJ (2013) Genetic relationships of North American bears (*Ursus*) inferred from amplified fragment length polymorphisms and mitochondrial DNA sequences. Can J Zool 91:626–634

36. Cronin MA, Rincon G, Meredith RW, MacNeil MD, Islas-Trejo A, Canovas A, Medrano JF (2014) Molecular phylogeny and SNP variation of polar bears (*Ursus maritimus*), brown bears (*U. arctos*) and black bears (*U. americanus*) derived from genome sequences. J Hered 105:312–323

37. Cronin TM (1991) Late Neogene marine ostracoda from Tjörnes, Iceland. J Paleontol 65(5):767–794

38. Cronin TM, Gemery L, Briggs WM Jr, Jakobsson M, Polyak L, Brouwers EM (2010) Quaternary sea-ice history in the Arctic Ocean based on a new Ostracode sea-ice proxy. Quat Sci Rev 29:3415–3429

39. Cronin TM, Polyak L, Reed D, Kandiano ES, Marzen RE, Council EA (2013) A 600-ka Arctic sea-ice record from Mendeleev Ridge based on ostracodes. Quat Sci Rev 79:157–167

40. D'Andrea WJ, Vaillencourt DA, Balascio NL, Werner A, Roof SR, Retelle M, Bradley RS (2012) Mild Little Ice Age and unprecedented recent warmth in an 1800 year lake sediment record from Svalbard. Geology 40:1007–1010

41. Darby DA (2008) Arctic perennial ice cover over the last 14 million years. Paleoceanography. doi:10.1029/2007PA001479

42. Darby DA (2014) Ephemeral formation of perennial sea ice in the Arctic Ocean during the middle Eocene. Nat Geosci 7:210–213

43. Darby DA, Polyak L, Bauch HA (2006) Past glacial and interglacial conditions in the Arctic Ocean and marginal seas—a review. Prog Oceanogr 71:129–144

44. Darby DA, Ortiz J, Polyak L, Lund S, Jakobsson M, Woodgate RA (2009) The role of currents and sea ice in both slowly deposited central Arctic and rapidly deposited Chukchi–Alaskan margin sediments. Global Planet Change 68:58–72

45. Davis CS, Delisle I, Stirling I, Siniff DB, Strobeck C (2004) A phylogeny of the extant Phocidae inferred from complete

mitochondrial DNA coding regions. Mol Phylogenet Evol 33:363–377

46. Davison J, Ho SYW, Brayk SC, Korsten M, Tammeleht E, Hindrikson M, Østbye K, Østbye E, Lauritzen S-E, Austin J et al (2011) Late-quaternary biogeographic scenarios for the brown bear (*Ursus arctos*), a wild mammal model species. Quat Sci Rev 30:418–430

47. Deméré TA, Berta A, Adam PJ (2003) Pinnipedimorph evolutionary biogeography. Bull Am Mus Nat History 279:32–76

48. de Vernal A, Hillaire-Marcel C, Darby DA (2005a) Variability of sea ice cover in the Chukchi Sea (western Arctic Ocean) during the Holocene. Paleoceanography, 20, PA4018. doi:10.1029/2005PA001157

49. de Vernal A, Eynaud F, Henry M, Hillaire-Marcel C, Londeix L, Mangin S, Matthiessen J, Marret F, Radi T, Rochon A, Solignac S, Turon J-L (2005) Reconstruction of sea-surface conditions at middle to high latitudes of the Northern Hemisphere during the Last Glacial Maximum (LGM) based on dinoflagellate cyst assemblages. Quat Sci Rev 24:897–924

50. de Vernal A, Hillaire-Marcel C (2008) Natural variability of Greenland climate, vegetation, and ice volume during the past million years. Science 320:1622–1625

51. Donnelly JP, Driscoll N, Uchupi E, Keigwin L, Schwab W, Thieler ER, Swift S (2005) Catastrophic meltwater discharge down the Hudson River Valley: a potential trigger for the Intra-AllerØd cold period. Geology 33:89–92

52. Dornelas M, Gotelli NJ, McGill B, Shimadzu H, Moyes F, Sievers C, Magurran AE (2014) Assemblage time series reveal biodiversity change but not systematic loss. Science 344:296–299

53. Dowsett HJ, Robinson MM, Haywood AM, Hill DJ, Dolan AM, Stoll DK, Chan W-L, Abe-Ouchi A, Chandler MA, Rosenbloom NA, Otto-Bliesner BL, Bragg FJ, Lunt DJ, Foley KM, Riesselman CR (2012) Assessing confidence in Pliocene sea surface temperatures to evaluate predictive models. Nat Clim Change 2:365–371

54. Durner GM, Douglas DC, Nielson RM, Amstrup S, McDonald TL, Stirling I, Mauritzen M, Born EW, Wiig Ø, DeWeaver E et al (2009) Predicting 21st-century polar bear habitat distribution from global climate models. Ecol Monogr 79:25–58

55. Dyke AS, Hooper J, Harington CR, Savelle JM (1999) The Late Wisconsinan and Holocene record of walrus (*Odobenus rosmarus*) from North America: a review with new data from Arctic and Atlantic Canada. Arctic 52:160–181

56. Dyke AS, Andrews JT, Clark PU, England JH, Miller GH, Shaw J, Veillette JJ (2002) The Laurentide and Innuitian ice sheets during the last glacial maximum. Quat Sci Rev 21:9–31

57. Edwards CJ, Suchard MA, Lemey P, Welch JJ, Barnes I, Fulton TL, Barnett R, O'Connell TC, Coxon P, Monaghan N et al (2011) Ancient hybridization and an Irish origin for the modern polar bear matriline. Curr Biol 21:1251–1258

58. Einarsson T, Hopkins DM, Doell RD (1967) The stratigraphy of Tjörnes, Northern Iceland, and the history of the Bering Land Bridge. In: Hopkins DM (ed) The bering land bridge. Stanford University Press, Stanford, pp 312–325

59. Expedition 302 Scientists (2006) Sites M0001–M0004. In: Backman J, Moran K, McInroy DB, Mayer LA (eds), and the Expedition 302 Scientists, Proceedings of IODP, 302: Edinburgh (Integrated Ocean Drilling Program Management International, Inc.). doi:10.2204/iodp.proc.302.104.2006

60. Fahl K, Stein R (2012) Modern seasonal variability and deglacial/Holocene change of central Arctic Ocean sea-ice cover: new insights from biomarker proxy records. Earth Planet Sci Lett 351–352:123–133

61. Fagel N, Not C, Gueibe J, Mattielli N, Bazhenova E (2014) Late quaternary evolution of sediment provenances in the Central Arctic Ocean: mineral assemblage, trace element composition and Nd and Pb isotope fingerprints of detrital fraction from the Northern Mendeleev Ridge. Quat Sci Rev 92:140–154

62. Farmer JR, Cronin TM, de Vernal A, Dwyer GS, Keigwin LD, Thunell RC (2011) Western Arctic Ocean temperature variability during the last 8000 years. Geophys Res Lett 38:L24602

63. Fay FH (1982) Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. US Department of the Interior, Fish and Wildlife Service. North American Fauna 74:1–279

64. Feranec RS, Franzi DA, Kozlowski AL (2014) A new record of ringed seal (*Pusa hispida*) from the late Pleistocene Champlain Sea and comments on its age and paleoenvironment. J Vertebr Paleontol 34(1):230–235. doi:10.1080/02724634.2013.784706

65. Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov AV (2015) Recent warming leads to a rapid borealization of fish communities in the Arctic. Nat Clim Change 5:673–678. doi:10.1038/NCLIMATE2647

66. Frank M, Backman J, Jakobsson M, Moran K, O'Regan M, King J, Haley BA, Kubik PW, Garbe-Schönberg D (2008) Beryllium isotopes in central Arctic Ocean sediments over the past 2.3 million years: stratigraphic and paleoclimatic implications. Paleoceanography. doi:10.1029/2007PA001478

67. Fulton TL, Strobeck C (2006) Molecular phylogeny of the Arctoidea (Carnivora): effect of missing data on supertree and supermatrix analyses of multiple gene data sets. Mol Phylogenet Evol 41:165–181

68. Fulton TL, Strobeck C (2010) Multiple fossil calibrations, nuclear loci and mitochondrial genomes provide new insight into biogeography and divergence timing for true seals (Phocidae, Pinnipedia). J Biogeogr 37:814–829

69. Galtier N, Nabholz B, Glémin S, Hurst GDD (2009) Mitochondrial DNA as a marker of molecular diversity: a reappraisal. Mol Ecol 18:4541–4550

70. Gardner AS, Moholdt G, Cogley JG, Wouters B, Arendt AA, Wahr J, Berthier E, Hock R, Pfeffer WT, Kaser G, Ligtenberg SRM, Bolch T, Sharp MJ, Hagen JO, van den Broeke MR, Paul F (2013) A reconciled estimate of glacier contributions to sea level rise: 2003–2009. Science 340:852–857

71. Gladenkov AYu, Oleinik AE, Marincovich L Jr, Barinov KB (2002) A refined age for the earliest opening of Bering Strait. Palaeogeogr Palaeoclimatol Palaeoecol 183:321–328

72. Goldman D, Giri PR, O'Brien SJ (1989) Molecular genetic-distance estimates among the Ursidae as indicated by one and two-dimensional protein electrophoresis. Evolution 43:282–295

73. Gooday AJ (1988) A response by benthic foraminifera to the deposition of phytodetritus in the deep sea. Nature 332:70–73

74. Grebmeier JM, Cooper LW, Feder HM, Sirenko BI (2006) Pelagic-benthic coupling and ecology dynamics in the Pacific-influenced Amerasian Arctic. Prog Oceanogr 71:331–361

75. Grebmeier JM (2012) Shifting patterns of life in the pacific arctic and sub-arctic seas. Annu Rev Mar Sci 4:63–78

76. Grebmeier JM, Bluhm BA, Cooper LW, Danielson S, Arrigo KR, Blanchard AL, Clarke JT, Day RH, Frey KE, Gradinger RR, Kedra M, Konar B, Kuletz KJ, Lee SH, Lovvorn JR, Norcross BL, Okkonen SR (2015) Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. Prog Oceanogr. doi:10.1016/j.pocean.2015.05.006

77. Hailer F, Kutschera VE, Hallstrom BM, Klassert D, Fain SR, Leonard JA, Arnason U, Janke A (2012) Nuclear genomic sequences reveal that polar bears are an old and distinct bear lineage. Science 336:344–347

78. Hald M, Dokken T, Mikalsen G (2001) Abrupt climatic change during the last interglacial-glacial cycle in the polar North Atlantic. Mar Geol 176:121–137

79. Haley BA, Frank M, Spielhagen RF, Eisenhauer A (2008) Influence of brine formation on Arctic Ocean circulation over the past 15 million years. Nat Geosci 1:68–72

80. Hanslik D, Löwemark L, Jakobsson M (2013) Biogenic and detrital-rich intervals in central Arctic Ocean cores identified using X-ray fluorescence scanning. Polar Res 32:18386. doi:10.3402/polar.v32i0.18386

81. Harington CR (2008) The evolution of Arctic marine mammals. Ecol Appl 18(Suppl.):S23–S40

82. Harington CR, Beard G (1992) The Qualicum walrus: a Late Pleistocene walrus (Odobenus rosmarus) skeleton from Vancouver Island, British Columbia, Canada. Ann Zool Fennici 28:311–319

83. Harington CR, Cournoyer M, Chartier M, Fulton TL, Shapiro B (2014) Brown bear (Ursus arctos) (9880 ± 35 BP) from late-glacial Champlain Sea deposits at Saint-Nicolas, Quebec, Canada, and the dispersal history of brown bears. Can J Earth Sci 51:527–535. doi:10.1139/cjes-2013-0220

84. Hay C, Mitrovica JX, Gomez N, Creveling JR, Austermann J, Kopp RE (2014) The sea-level fingerprints of ice-sheet collapse during interglacial periods. Quat Sci Rev 87:60–69

85. Heaton TH, Grady F (2009) The fossil bears of Southeast Alaska. In: Proceedings of the 15th international congress of speleology 1(1):I-N

86. Higdon JW, Bininda-Emonds ORP, Beck RMD, Ferguson SH (2007) Phylogeny and divergence of the pinnipeds (Carnivora:Mammalia) assessed using a multigene dataset. Biomed Central Evol Biol 7:216. doi:10.1186/1471-2148-7-216

87. Hipsley CA, Müller J (2014) Beyond fossil calibrations: realities of molecular clock practices in evolutionary biology. Front Genet 5(138):1–11

88. Ingólfsson Ó, Wiig Ø (2008) Late Pleistocene fossil find in Svalbard: the oldest remains of a polar bear (Ursus maritimus Phipps, 1744) ever discovered. Polar Res 28:455–462

89. Ingólfsson Ó, Norodahl H, Schomacker A (2010) Deglaciation and Holocene glacial history of Iceland. Dev Quat Sci 13:51–68

90. Jakobsson M (2000) Mapping the Arctic Ocean: bathymetry and pleistocene paleoceanography. Stockholm University, Stockholm

91. Jakobsson M (2002) Hypsometry and volume of the Arctic Ocean and its constituent seas. Geochem Geophys Geosyst 3(5):1–18

92. Jakobsson M, Løvlie R, Al-Hanbali H, Arnold E, Backman J, Mörth M (2000) Manganese and color cycles in Arctic Ocean sediments constrain Pleistocene chronology. Geology 28:23–26

93. Jakobsson M, Grantz A, Kristoffersen Y, Macnab R (2003) Physiographic provinces of the Arctic Ocean seafloor. Geol Sci Am Bull 115:1443–1455

94. Jakobsson M, Løvlie R, Arnold EM, Backman J, Polyak L, Knutsen JO, Musatov E (2001) Pleistocene stratigraphy and paleoenvironmental variation from Lomonosov Ridge sediments, central Arctic Ocean. Glob Planet Change 31(1–4):1–22

95. Jakobsson M, Nilsson J, O'Regan M, Backman J, Löwemark L, Dowdeswell JA, Mayer L, Polyak L, Colleoni F, Anderson LG, Björk G, Darby D, Eriksson B, Hanslik D, Hell B, Marcussen C, Sellén E, Wallin Å (2010) An Arctic Ocean ice shelf during MIS 6 constrained by new geophysical and geological data. Quat Sci Rev 29:3505–3517. doi:10.1016/j.quascirev.2010.03.015

96. Jakobsson M, Mayer L, Coakley B, Dowdeswell JA, Forbes S, Fridman B, Hodnesdal H, Noormets R, Pedersen R, Rebesco M, Schenke HW, Zarayskaya Y, Accettella D, Armstrong A, Anderson RM, Bienhoff P, Camerlenghi A, Church I, Edwards M, Gardner JV, Hall JK, Hell B, Hestvik O, Kristoffersen Y, Marcussen C, Mohammad R, Mosher D, Nghiem SV, Pedrosa MT, Travaglini PG, Weatherall P (2012) The international bathymetric chart of the Arctic Ocean (IBCAO) version 3.0. Geophys Res Lett 39:L12609. doi:10.1029/2012gl052219

97. Jakobsson M, Ingólfsson Ó, Long AJ, Spielhagen RF (2014) The dynamic Arctic. Quat Sci Rev 92:1–8

98. Jakobsson M, Nilsson J, Anderson L, Backman J, Björk G, Cronin TM, Kirchner N, Koshurnikov A, Mayer L, Noormets R, O'Regan M, Stranne C, SWERUS-C3 Scientific Team (in press) An ice shelf covering the entire central Arctic Ocean during the penultimate glaciation. Nat Commun

99. Jouzel J, Masson-Delmotte V, Cattani O, Dreyfus G, Falourd S, Hoffmann G, Minster B, Nouet J, Barnola JM, Chappellaz J, Fischer H, Gallet JC, Johnsen S, Leuenberger M, Loulergue L, Luethi D, Oerter H, Parrenin F, Raisbeck G, Raynaud D, Schilt A, Schwander J, Selmo E, Souchez R, Spahni R, Stauffer B, Steffensen JP, Stenni B, Stocker TF, Tison JL, Werner M, Wolff EW (2007) Orbital and millennial Antarctic climate variability over the past 800,000 years. Science 317:793–796

100. Kandiano ES, Bauch HA, Fahl K, Helmke JP, Röhl U, Pérez-Folgado M, Cacho I (2012) The meridional temperature gradient in the eastern North Atlantic during MIS 11 and its link to the ocean–atmosphere system. Palaeogeogr Palaeoclimatol Palaeoecol 333–334:24–39

101. Kaufman DS, Ager TA, Anderson NJ, Anderson PM, Andrews JT, Bartlein PJ, Brubaker LB, Coats LL, Cwynar LC, Duvall ML, Dyke AS, Edwards ME, Eisner WR, Gajewski K, Geirsdóttir A, Hu FS, Jennings AE, Kaplan MR, Kerwin MW, Lozhkin AV, MacDonald GM, Miller GH, Mock CJ, Oswald WW, Otto-Bliesner BL, Porinchu DF, Rühland K, Smol JP, Steig EJ, Wolfe BB (2004) Holocene thermal maximum in the western Arctic (0–180 W). Quat Sci Rev 23:529–560

102. Kaufman DS, Schneider DP, McKay NP, Ammann CM, Bradley RS, Briffa KR, Miller GH, Otto-Bliesner BL, Overpeck JT, Vinther BM, Arctic Lakes 2 k Project Members (2009) Recent warming reverses long-term Arctic cooling. Science 325: 1236–1239

103. Kelly BP, Whitely A, Tallmon D (2010) The Arctic melting pot. Nature 468:891

104. Kinnard C, Zdanowic CM, Fisher DA, Isaksson E, de Vernal A, Thompson LG (2011) Reconstructed changes in Arctic sea ice over the past 1450 years. Nature 479:509–512

105. Kovacs KM, Lydersen C, Overland JE, Moore SE (2011) Impacts of changing sea-ice conditions on Arctic marine mammals. Mar Biodivers 41:181–194

106. Knies J, Mann U, Popp BN, Stein R, Brumsack H-J (2008) Surface water productivity and paleoceanographic implications in the Cenozoic Arctic Ocean. Paleoceanography. doi:10.1029/2007PA001455

107. Knies J, Mattingsdal R, Fabian K, Grøsfjeld K, Baranwal S, Husum K, De Schepper S, Vogt C, Andersen N, Matthiessen J, Andreassen K, Jokat W, Nam S-I, Gaina C (2014) Earth and Planetary Science Letters 387: 132–144

108. Koenig S, DeConto RM, Pollard D (2014) Impact of reduced Arctic sea ice on Greenland ice sheet variability in a warmer than present climate. Geophys Res Lett 41:3934–3943. doi:10.1002/2014GL059770

109. Krause J, Unger T, Noçon A, Malaspinas A-S, Kolokotronis S-O, Stiller M, Soibelzon L, Spriggs H, Dear PH, Briggs AW et al (2008) Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene-Pliocene boundary. Biomed Central Evol Biol 8:220. doi:10.1186/1471-2148-8-220

110. Kristoffersen Y, Coakley B, Jokat W, Edwards M, Brekke H, Gjengedal J (2004) Seabed erosion on the Lomonosov Ridge, central Arctic Ocean: a tale of deep draft icebergs in the Eurasia Basin and the influence of Atlantic water inflow on iceberg motion. Paleoceanography. doi:10.1029/2003PA000985

111. Kurtén B (1964) The evolution of the polar bear, *Ursus maritimus* (Phipps). Acta Zool Fenn 108:1–30

112. Ledu D, Rochon A, de Vernal A, Barletta F, St-Onge G (2010) Holocene sea ice history and climate variability along the main axis of the Northwest Passage, Canadian Arctic. Paleoceanography. doi:10.1029/2009PA001817

113. Lindqvist C, Bachmann L, Andersen LW, Born EW, Arnason U, Kovacs KM, Lydersen C, Abramov AV, Wiig Ø (2009) The Laptev Sea walrus *Odobenus rosmarus laptevi*: an enigma revisited. Zool Scr 38(2):113–127

114. Lindqvist C, Schuster SC, Sun Y, Talbot SL, Qi J, Ratan A, Tomsho LP, Kasson L, Zeyl E, Aars J, Miller W, Ingólfsson Ó, Bachmann L, Wiig Ø (2010) Complete mitochondrial genome of a Pleistocene jawbone unveils the origin of polar bear. Proc Natl Acad Sci USA 107:5053–5057

115. Lisiecki LE, Raymo ME (2005) A Pliocene-Pleistocene stack of 57 globally distributed benthic δ^{18}O records. Paleoceanography. doi:10.1029/2004PA001071

116. Liu S et al (2014) Population genomics reveal recent speciation and rapid evolutionary adaptation in polar bears. Cell 157:785–794

117. Löwemark L, O'Regan M, Hanebuth T, Jakobsson M (2012) Late Quaternary spatial and temporal variability in Arctic deep-sea bioturbation and its relation to Mn-cycles. Palaeogeogr Palaeoclimatol Palaeoecol 365–366:192–208

118. Löwemark L, März C, O'Regan M, Gyllencreutz R (2014) Arctic Ocean Mn-stratigraphy: genesis, synthesis and inter-basin correlation. Quat Sci Rev 92:97–111

119. Marzen R, DeNinno L, Cronin TM. Arctic Ocean calcareous microfossil and productivity cycles over orbital timescales (submitted)

120. Matthiessen J, de Vernal A, Head M, Okolodkov Y, Zonneveld K, Harland R (2005) Modern organic-walled dinoflagellate cysts in Arctic marine environments and their (paleo-) environmental significance. Paläontologische Zeitschrift 79:3–51

121. Matthiessen J, Knies J, Vogt C, Stein R (2009) Pliocene palaeoceanography of the Arctic Ocean and subarctic seas. Philos Trans R Soc A 367:21–48

122. Mayewski PA, Rohling EE, Stager JC, Karlén W, Maasch KA, Meeker LD, Meyerson EA, Gasse F, van Kreveld S, Holmgren K, Lee-Thorp J, Rosqvist G, Rack F, Staubwasser M, Schneider RR, Steig EJ (2004) Quat Res 62:243–255

123. Melles M, Brigham-Grette J, Minyuk PS, Nowaczyk NR, Wennrich V, DeConto RM, Anderson PM, Andreev AA, Coletti A, Cook TL, Haltia-Hovi EA, Kukkonen M, Lozhkin AV, Rosén P, Tarasov P, Vogel H, Wagner B (2012) 2.8 million years of Arctic climate change from Lake El'gygytgyn NE Russia. Science 337:315–320

124. Meredith RW, Janečka JE, Gatesy J, Ryder OA et al (2011) Impacts of the cretaceous terrestrial revolution and KPg extinction on mammal diversification. Science 334:52–524. doi:10.1126/science.1211028

125. Miettinen A, Koç N, Husum K (2013) Appearance of the Pacific diatom *Neodenticula seminae* in the northern Nordic Seas—an indication of changes in Arctic sea ice and ocean circulation. Mar Micropaleontol 99:2–7

126. Miller GH, Alley RB, Brigham-Grette J, Fitzpatrick JJ, Polyak L, Serreze MC, White JWC (2010) Arctic amplification: can the past constrain the future? Quat Sci Rev 29:1779–1790

127. Miller KG, Wright JD, Browning JV, Kulpecz A, Kominz M, Naish TR, Cramer BS, Rosenthal Y, Peltier WR, Sosdian S (2012) High tide of the warm Pliocene: implications of global sea level for Antarctic deglaciation. Geology 40:407–410

128. Miller W, Schuster SC, Welch AJ, Ratan A, Bedoya-Reina OC, Zhao FQ, Kim HL, Burhans RC, Drautz DI, Wittekindt NE et al (2012) Polar and brown bear genomes reveal ancient admixture and demographic footprints of past climate change. Proc Natl Acad Sci USA 109:E2382–E2390

129. Moran K, Backman J, Brinkhuis H, Clemens SC, Cronin T, Dickens GR, Eynaud F, Gattacceca J, Jakobsson M, Jordan RW, Kaminski M, King J, Koc N, Krylov A, Martinez N, Matthiessen J, McInroy D, Moore TC, Onodera J, O'Regan M, Pälike H, Rea B, Rio D, Sakamoto T, Smith DC, Stein R, St John K, Suto I, Suzuki N, Takahashi K, Watanabe M, Yamamoto M, Farrel J, Frank M, Kubik P, Jokat W, Kristoffersen Y (2006) The Cenozoic palaeoenvironment of the Arctic Ocean. Nature 441:601–605

130. Müller J, Werner K, Stein R, Fahl K, Moros M, Jansen E (2012) Holocene cooling culminates in sea ice oscillations in Fram Strait. Quat Sci Rev 47:1–14

131. Niessen F, Hong JK, Hegewald A, Matthiessen J, Stein R, Kim H, Kim S, Jensen L, Jokat W, Nam S-I, Kang S-H (2013) Repeated Pleistocene glaciation of the East Siberian continental margin. Nat Geosci 6:842–846

132. Nørgaard-Pedersen N, Spielhagen RF, Erlenkeuser H, Grootes PM, Heinemeier J, Knies J (2003) Arctic Ocean during the Last Glacial Maximum: Atlantic and polar domains of surface water mass distribution and ice cover. Paleoceanography. doi:10.1029/2002PA000781

133. Nørgaard-Pedersen N, Mikkelsen N, Lassen SJ, Kristoffersen Y, Sheldon E (2007) Reduced sea ice concentrations in the Arctic Ocean during the last interglacial period revealed by sediment cores off northern Greenland. Paleoceanography 22: PA1218. doi:10.1029/2006PA001283

134. Onodera J, Takahashi K, Jordan RW (2008) Eocene silicoflagellate and ebridian paleoceanography in the central Arctic Ocean. Paleoceanography. doi:10.1029/2007PA001474

135. O'Regan M (2011) Late Cenozoic Paleoceanography of the Central Arctic Ocean. IOP Conference Series: *Earth and Environmental Science* 14. doi:10.1088/1755-1315/14/1/012002

136. O'Regan M, King J, Backman J, Joakobsson M, Pälike H, Moran K, Heil C, Sakamoto T, Cronin TM, Jordan RW (2008) Constraints on the Pleistocene chronology of sediments from the Lomonosov Ridge. Paleoceanography. doi:10.1029/2007PA001551

137. Otto-Bliesner BL, Marshall SJ, Overpeck JT, Miller GH, Hu A, CAPE Last Interglacial Project members (2006) Simulating Arctic climate warmth and icefield retreat in the last inter-glaciations. Science 311: 1751–1753

138. Pabi S, van Djiken GL, Arrigo KR (2008) Primary production in the Arctic Ocean, 1998–2006. J Geophys Res. doi:10.1029/2007JC004578

139. Pagani M, Liu Z, LaRiviere J, Ravelo AC (2009) High Earths-system climate sensitivity determined from Pliocene carbon dioxide concentrations. Nat Geosci 3:27–30

140. Pagès M, Calvignac S, Klein C, Paris M, Hughes S, Hänni C (2008) Combined analysis of fourteen nuclear genes refines the Ursidae phylogeny. Mol Phylogenet Evol 47:73–83

141. Pälike H, Spofforth DJA, O'Regan M, Gattacceca J (2008) Orbital scale variations and timescales from the Arctic Ocean. Paleoceanography. doi:10.1029/2007PA001490

142. Pamillo P, Nei M (1988) Relationships between gene trees and species trees. Mol Biol Evol 5:568–583

143. Parham JF, Donoghue PCJ, Bell CJ, Calway TD, Head JJ, Holroyd PA et al (2012) Best practices for justifying fossil calibrations. Syst Biol 61:346–359. doi:10.1093/sysbio/syr107

144. Peacock E, Sonsthagen SA, Obbard ME, Boltunov A, Regehr EV et al (2015) Implications of the circumpolar genetic structure of polar bears for their conservation in a rapidly warming Arctic. PLoS ONE 10(1):e112021. doi:10.1371/journal.pone.0112021

145. Perovich DK, Polashenski C (2012) Albedo evolution of seasonal Arctic sea ice. Geophys Res Lett 39:L08501. doi:10.1029/2012GL051432

146. Perovich D, Richter-Menge J, Polashenksi C, Elder B, Arbetter T, Brennick O (2014) Sea ice mass balance observations from the North Pole Environmental Observatory. Geophys Res Lett 41:2019–2025. doi:10.1002/2014GL059356

147. Peterson BJ, McClelland J, Curry R, Holmes RM, Walsh JE, Aagaard K (2006) Trajectory shifts in the Arctic and subarctic freshwater cycle. Science 313:1061–1066

148. Phillips RL, Grantz A (1997) Quaternary history of sea ice and paleoclimate in the Amerasia basin, Arctic Ocean, as recorded in the cyclical strata of Northwind Ridge. Geol Soc Am Bull 109:1101–1115

149. Poirier A, Hillaire-Marcel C (2011) Improved Os-isotope stratigraphy of the Arctic Ocean. Geophys Res Lett. doi:10.1029/2011GL047953

150. Poirier RK, Cronin TM, Briggs WM Jr, Lockwood R (2012) Central Arctic paleoceanography for the last 50 kyr based on ostracode faunal assemblages. Mar Micropaleontol 88–89:65–76

151. Polyak L, Edwards MH, Coakley BJ, Jakobsson M (2001) Ice shelves in the Pleistocene Arctic Ocean inferred from glacio-genic deep-sea bedforms. Nature 410(6827):453–459

152. Polyak L, Levitan M, Khusid T, Merklin L, Mukhina V (2002) Variations in the influence of riverine discharge on the Kara Sea during the last deglaciation and the Holocene. Glob Planet Change 32:291–309

153. Polyak L, Curry WB, Darby DA, Bischof JF, Cronin TM (2004) Contrasting glacial/interglacial regimes in the western Arctic Ocean as exemplified by a sedimentary record from the Mendeleev Ridge. Palaeogeogr Palaeoclimatol Palaeoecol 203:73–93

154. Polyak L, Best KM, Crawford KA, Council EA, St-Onge G (2013) Quaternary history of sea ice in the western Arctic Ocean based on foraminifera. Quat Sci Rev 79:145–156

155. Poore RZ, Phillips RL, Rieck HJ (1993) Paleoclimate record for Northwind Ridge, western Arctic Ocean. Paleoceanography 8:149–159

156. Poore RZ, Ishman SE, Phillips RL, McNeil DH (1994) Quaternary stratigraphy and paleoceanography of the Canada basin, Western Arctic Ocean. US Geological Survey Bulletin 2080

157. Poore RZ, Osterman L, Curry WB, Phillips RL (1999) Late Pleistocene and Holocene meltwater events in the western Arctic Ocean. Geology 27:759–762

158. Pulquério MJF, Nichols RA (2006) Dates from the molecular clock: how wrong can we be? Trends Ecol Evol 22:180–184

159. Rayburn JA, Cronin TM, Franzi DA, Knuepfer PLK, Willard DA (2011) Timing and duration of glacial lake discharges and the Younger Dryas climate reversal. Quat Res 75:541–551

160. Raymo ME, Mitrovica JX (2012) Collapse of polar ice sheets during the stage 11 interglacial. Nature 483:453–456

161. Reid PC, Johns DG, Edwards M, Starr M, Poulin M, Snoeijs P (2007) A biological consequence of reducing Arctic ice cover: arrival of the Pacific diatom *Neodenticula seminae* in the North Atlantic for the first time in 800,000 years. Glob Change Biol 13:1910–1921

162. Repenning CA (1983) New evidence for the age of the Gubik Formation. Quat Res 19:356–372

163. Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP, Schmitz OJ, Smith DW, Wallach AD, Wirsing AJ (2014) Status and ecological effects of the World's largest carnivores. Science. doi:10.1126/science.1241484

164. Robbins CT, Lopez-Alfaro C, Rode KD, Tøien Ø, Nelson OL (2012) Hibernation and seasonal fasting in bears: the energetic costs and consequences for polar bears. J Mammal 93(6):1493–1503. doi:10.1644/11-MAMM-A-406.1

165. Rohling EJ, Grant K, Bolshaw M, Roberts AP, Siddall M, Hemleben Ch, Kucera M (2009) Antarctic temperature and global sea level closely coupled over the past five glacial cycles. Nat Geosci 2:500–504

166. Ruppel C (2011) Methane hydrates and contemporary climate change. Nat Knowl 2(12):12 **(online only)**

167. Sangiorgi F, van Soelen EE, Spofforth DJA, Pälike H, Stickley CE, St. John K, Koç N, Schouten S, Damsté S, Brinkhuis H (2008) Cyclicity in the middle Eocene central Arctic Ocean sediment record: orbital forcing and environmental response. Paleoceanography 23. doi:10.1029/2007PA001487

168. Sarkissian C et al (2015) Ancient genomics. Philos Trans R Soc B 370:2013087

169. Scott DB, Schell T, St-Onge G, Rochon A, Blasco S (2009) Foraminiferal assemblage changes over the last 15,000 years on the Mackenzie/Beaufort sea slope and Amundsen Gulf, Canada: implications for past sea-ice conditions. *Paleoceanography* 24, PA2219. doi:10.1029/2007PA001575

170. Seidenkrantz M-S et al (2014) Northern Hemisphere sea-ice cover during the Holocene—proxy data reconstruction and Modeling. AGU Abstract Dec. 2014 Annual Mtg

171. Seki O, Foster GL, Schmidt DN, Mackensen A, Kawamura K, Pancost RD (2010) Alkenone and boron-based Pliocene pCO2 records. Earth Planet Sci Lett 292:201–211

172. Serreze MC, Barry RG (2011) Processes and impacts of Arctic amplification: a research synthesis. Glob Planet Change 77:85–96

173. Siegenthaler U, Stocker TF, Monnin E, Lüthi D, Schwander J, Stauffer B, Raynaud D, Barnola J-M, Fischer H, Mason-Delmotte V, Jouzel J (2005) Stable carbon cycle–climate relationship during the late Pleistocene. Science 310:1313–1317

174. Sluijs A, Schouten S, Pagani M, Woltering M, Brinkhuis H, Sinninghe Damsté JP, Dickens GR, Huber M, Reichart G-J, Stein R, Matthiessen J, Lourens LJ, Pedentchouk N, Backman J, Moran K, the Expedition 302 Scientists (2006) Subtropical Arctic Ocean temperatures during the Palaeocene/Eocene thermal maximum. Nature 441: 610–613

175. Sluijs A, Schouten S, Donders TH, Schoon PL, Röhl U, Reichart G-J, Sangiorgi F, Kim J-H, Sinninghe Damsté JS, Brinkhuis H (2009) Warm and wet conditions in the Arctic region during the Eocene Thermal Maximum 2. Nat Geosci 2:777–780

176. Spielhagen RF, Baumann KH, Erlenkeuser H, Nowaczyk NR, Nørgaard-Pedersen N, Vogt C, Weiel D (2004) Arctic Ocean deep-sea record of northern Eurasian ice sheet history. Quat Sci Rev 23:1455–1483

177. Spielhagen RF, Erlenkeuser H, Siegert C (2005) History of freshwater runoff across the Laptev Sea (Arctic) during the last deglaciation. Glob Planet Change 2005:187–207

178. Spielhagen RF, Werner K, Sørensen SA, Zamelczyk K, Kandiano E, Budeus G, Husum K, Marchitto TM, Hald M (2011) Enhanced modern heat transfer to the arctic by warm Atlantic water. Science 331:450–453

179. St. John K (2008) Cenozoic ice-rafting history of the central Arctic Ocean: terrigenous sands on the Lomonosov Ridge. Paleoceanography. doi:10.1029/2007PA001483

180. Stein R, MacDonald RW (eds) (2004) The organic carbon cycle in the Arctic Ocean. Springer, Berlin

181. Stein R, Boucsein B, Meyer H (2006) Anoxia and high primary production in the Paleogene central Arctic Ocean: first detailed records from Lomonosov Ridge. Geophys Res Lett. doi:10.1029/2006GL026776

182. Stein R, Weller P, Backman J, Brinkhuis H, Moran K, Pälike H (2014) Cenozoic Arctic Ocean climate history: some highlights from the IODP Arctic coring expedition (ACEX). Dev Mar Geol 7:259–293

183. Stein R, Fahl K, Müller J (2012) Proxy reconstruction of Cenozoic Arctic Ocean Sea-Ice History—from IRD to IP25. Polarforschung, 82(1):37–71. hdl:10013/epic.40432.d001

184. Stickley CE, St. John K, Koç N, Jordan RW, Passchier S, Pearce RB, Kearns LE (2009) Evidence for middle Eocene Arctic sea ice from diatoms and ice-rafted debris. Nature 460:376–379

185. Stirling I (2011) Polar bears: the natural history of a threatened species. Fitzhenry & Whiteside, Brighton

186. Stroeve JC, Markus T, Boisvert L, Miller J, Barrett A (2014) Changes in Arctic melt season and implications of sea ice loss. Geophys Res Lett 41:1216–1225

187. Sundqvist HS, Kaufman DS, McKay NP, Balascio NL, Briner JP, Cwynar LC, Sejrup HP, Seppä H, Subetto DA, Andrews JT, Axford Y, Bakke J, Birks HJB, Brooks SJ, de Vernal A, Jennings AE, Ljungqvist FC, Rühland KM, Saenger C, Smol JP, Viau AE (2014) Arctic Holocene proxy climate database—new approaches to assessing geochronological accuracy and encoding climate variables. Clim Past 10:1–63

188. Svendsen JI, Alexanderson H, Astakhov VI, Demidov I, Dowdeswell JA, Funder S, Gataullin V, Henriksen M, Hjort C, Houmark-Nielsen M, Hubberten HW, Ingólfsson Ó, Jakobsson M, Kjaer KH, Larsen El, Lokrantz H, Lunkka JP, Lyså A, Mangerud J, Matiouchkov A, Murray A, Möller P, Niessen F, Nikolskaya O, Polyak L, Saarnisto M, Siegert C, Siegert MJ, Spielhagen RF, Stein R (2004) Late quaternary ice sheet history of northern Eurasia. Quat Sci Rev 23:1229–1271

189. Talbot SL, Shields GF (1996) A phylogeny of the bears (Ursidae) inferred from complete sequences of three mitochondrial DNA genes. Mol Phylogenet Evol 5:567–575

190. Taldenkova EE, Bauch HA, Stepanova A, Ovsepyan Y, Pogodina I, Klyuvitkina T, Nikolaev S (2013) Benthic and planktic community changes at the North Siberian margin in response to Atlantic water mass variability since last deglacial times. Mar Micropaleontol 99:29–44

191. Tamura K, Battistuzzi FU, Billing-Ross P, Murillo O, Filipski A, Kumar S (2012) Estimating divergence times in large molecular phylogenies. Proc Natl Acad Sci USA. doi:10.1073/pnas.1213199109

192. Tarasov L, Peltier WR (2005) Arctic freshwater forcing of the Younger Dryas cold reversal. Nature 435:662–665

193. Vare LL, Massé G, Gregory TR, Smart CW, Belt ST (2009) Sea ice variations in the central Canadian Arctic Archipelago during the Holocene. Quat Sci Rev 28:1354–1366

194. Verhoeven K, Louwye S, Eiríksson J, De Schepper S (2011) A new age model for the Pliocene-Pleistocene Tjörnes section on Iceland: its implication for the timing of North Atlantic-Pacific palaeoceanographic pathways. Palaeogeogr Palaeoclimatol Palaeoecol 309:33–52

195. Vermeij GJ (1991) Anatomy of invasion: the trans-Arctic interchange. Paleobiology 17:281–307

196. Vogt PR, Crane K, Sundvor E (1994) Deep Pleistocene iceberg plowmarks on the Yermak Plateau: sidescan and 3.5 kHz evidence for thick calving ice fronts and a possible marine ice sheet in the Arctic Ocean. Geology 22:403–406

197. Warnock RCM, Yang Z, Donoghue PCJ (2012) Exploring uncertainty in the calibration of the molecular clock. Biol Lett 8:156–159

198. Wassman P (2011) Arctic marine ecosystems in an era of rapid climate change. Prog Oceanogr 90:1–17

199. Wayne RK, Van Valkenburgh B, O'Brien SJ (1991) Molecular distance and divergence time in carnivores and primates. Mol Biol Evol 8:297–319

200. Weller P, Stein R (2008) Paleogene biomarker records from the central Arctic Ocean (Integrated Ocean Drilling Program Expedition 302): organic carbon sources, anoxia, and sea surface temperature. Paleoceanography. doi:10.1029/2007PA001472

201. Wollenburg JE, Kuhnt W (2000) The response of benthic foraminifers to carbon flux and primary production in the Arctic Ocean. Mar Micropaleontol 40:189–231

202. Wollenburg JE, Knies J, Mackensen A (2004) High-resolution paleoproductivity fluctuations during the past 24 kyr as indicated by benthic foraminifera in the marginal Arctic Ocean. Palaeogeogr Palaeoclimatol Palaeoecol 204:209–238

203. Wollenburg JE, Mackensen A, Kuhnt W (2007) Benthic foraminiferal biodiversity response to a changing Arctic palaeoclimate in the last 24,000 years. Palaeogeogr Palaeoclimatol Palaeoecol 255:195–222

204. Yamamoto M, Polyak L (2009) Changes in terrestrial organic matter input to the Mendeleev Ridge, western Arctic Ocean, during the Late Quaternary. Glob Planet Change 68:30–37

205. Yin QZ, Berger A (2010) Insolation and CO_2 contribution to the interglacial climate before and after the Mid-Brunhes Event. Nat Geosci 3:243–246

206. Yu L, Li Q-W, Ryder OA, Zhang Y-P (2004) Phylogeny of the bears (Ursidae) based on nuclear and mitochondrial genes. Mol Phylogenet Evol 32:480–494

207. Yu L, Li Y-W, Ryder OA, Zhang Y-P (2007) Analysis of complete mitochondrial genome sequences increases phylogenetic resolution of bears (Ursidae), a mammalian family that experienced rapid speciation. BMC Evol Biol 7:198–209

208. Zhang YG, Pagani M, Liu Z, Bohaty SM, DeConto R (2013) A 40-million-year history of atmospheric CO_2. Philos Trans R Soc A. doi:10.1098/rsta.2013.0096

209. Zuckerkandl E, Pauling L (1965) Evolutionary divergence and convergence in proteins. In: Bryson V, Vogel HJ (eds) Evolving genes and proteins. Academic Press, pp 97–166