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Heikkilä, Maija

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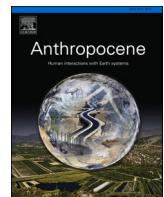
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Invited Review Article

Predicting the future of coastal marine ecosystems in the rapidly changing Arctic: The potential of palaeoenvironmental records

Maija Heikkilä ^{a,b,*}, Sofia Ribeiro ^c, Kaarina Weckström ^{a,b,c}, Anna J. Pieńkowski ^{d,e}^a Environmental Change Research Unit, Ecosystems and Environment Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, P.O. Box 65, 00014, Finland^b Helsinki Institute of Sustainability Science (HELSUS), University of Helsinki, Finland^c Department of Glaciology and Climate, Geological Survey of Denmark and Greenland (GEUS), Øster Voldgade 10, 1350 Copenhagen K, Denmark^d Department of Arctic Geology, The University Centre in Svalbard (UNIS), Longyearbyen, N-9171 Svalbard, Norway^e Institute of Geology, Adam Mickiewicz University, Maków Polnych 16, 61-606 Poznań, Poland

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ABSTRACT

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Frozen components on land and in the ocean (sea ice, ice sheets, glaciers and permafrost) form the cryosphere, which, together with the ocean, moderates the physical and chemical habitat for life in the Arctic and beyond. Changes in these components, as a response to rapidly warming climate in the Arctic, are intensely expressed in the coastal zone. These areas receive increased terrestrial runoff while subject to a changing sea-ice and ocean environment. Proxies derived from marine sediment archives provide long-term data that extend beyond instrumental measurements. They are therefore fundamental in disentangling human-driven versus natural processes, changes and responses. This paper (1) provides an overview of current Arctic cryosphere change, (2) reviews state-of-the-art palaeoecological approaches, (3) identifies methodological and knowledge gaps, and (4) discusses the strengths and future potential of palaeoecology and palaeoceanography to respond to societally-relevant coastal marine ecosystem challenges. We utilise responses to an open survey conducted by the Future Earth Past Global Changes (PAGES) working group Arctic Cryosphere Change and Coastal Marine Ecosystems (ACME). Significant research advancements have taken place in recent decades, including the increasingly common use of multi-proxy (multiple lines of evidence) studies, improved understanding of species-environment relationships, and development of novel proxies. Significant gaps remain, however, in the understanding of proxy sources and behaviour, the use of quantitative techniques, and the availability of reference data from coastal environments. We highlight the need for critical methodological refinement, interdisciplinary collaboration on research approaches, and enhanced communication across the scientific community.

1. Introduction

Climate warming and associated degradation of the cryosphere on land and in the sea are rapidly transforming coastal marine ecosystems in the Arctic. Thinning and seasonal loss of sea ice (Stroeve and Notz, 2018), increased delivery of freshwater from river runoff (Bring et al., 2016), thawing permafrost (Biskaborn et al., 2019) and melting ice sheets, ice caps and glaciers (Bamber et al., 2018) all have profound and interacting impacts on Arctic coastal waters. Greater freshwater inputs from land together with coastal erosion increase the amount of sediment, organic matter and nutrients delivered into coastal waters, which has poorly known consequences for marine ecosystems and large-scale

climate (Francis et al., 2009; Box et al., 2019; Klein et al., 2019). The impacts of a changing cryosphere on marine ecosystems have direct and profound consequences for human systems, being expressed at multiple spatial scales, from local and indigenous residents to global socio-economies (Larsen and Fondahl, 2015; Meredith et al., 2019). Thinning sea ice and changing land-derived inputs threaten the safety and the sustainability of subsistence hunting and fishing (Brinkman et al., 2016; Lovvold et al., 2016). At the same time, ocean productivity, large-scale commercial fish catches, and the number of harvestable fish and mammal species in the Arctic are predicted to increase (Barange et al., 2014; Haug et al., 2017; Ardyna and Arrigo, 2020). Sea-ice decline promotes marine transportation and tourism potential, which have

* Corresponding author at: Environmental Change Research Unit, Ecosystems and Environment Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, P.O. Box 65, 00014, Finland.

E-mail address: maija.heikkila@helsinki.fi (M. Heikkilä).

socio-economic benefits, but also threaten coastal marine ecosystems, wildlife, and subsistence livelihoods (Miller and Ruiz, 2014; Ng et al., 2018).

A major challenge for understanding and adapting to Arctic marine ecosystem change is the paucity of baseline data. Crucial data on recent changes are derived from satellite (Comiso et al., 2017; Klein et al., 2019) and historical (Walsh et al., 2017) records, traditional knowledge (Aporta et al., 2020), and ecological monitoring programmes providing indispensable in situ measurements (e.g. Soltwedel et al., 2013; Christensen et al., 2017; Grebmeier et al., 2019; AMAP, 2021). These data sources are, however, temporally restricted to recent decades, or in a few exceptional cases (and in lesser detail) to recent centuries. Hence, examination of underlying longer-term processes and coastal ecosystem responses to cryosphere change over past warmer periods is generally not possible from observational data alone. Marine sediments – debris delivered from weathering continents and ice rafting, biogenic remains of terrestrial, marine and sea-ice organisms, and minerals precipitated from seawater – accumulate on the seafloor. Seafloor sediments can provide continuous and versatile records of past marine ecosystem responses over thousands to millions of years. Physical, chemical and biological characteristics, such as grain size, microscopic fossil spectra, chemical and biochemical marker molecules and more recently, ancient DNA, have been used to reconstruct past Arctic environments, providing both qualitative and quantitative time-series of changes in e.g. sea-surface temperatures, sea-ice cover, and primary production (Hillaire et al., 2007; Belt, 2018; Ellegaard et al., 2020). Traditionally, the use of these sediment indicators, commonly termed *proxies*, has focused on their relations to a single physical variable, such as sea-surface temperature. There is a pressing need to critically evaluate and refine existing methods and records, and to develop new approaches that enable better responses to the questions relevant to the rapidly changing Arctic coastal zone.

Here, we review state-of-the-art palaeoecological methods and their use in the study of long-term Arctic marine ecosystem change, and identify knowledge and methodology gaps with a particular focus on societally relevant research in the coastal zone, i.e. the interface between land and sea. We concentrate on proxies used to decipher palaeoenvironmental changes over centennial and millennial time scales, where recent warm periods (e.g. Holocene Thermal Maximum, Roman Warm Period, Medieval Climate Anomaly; all within the current Holocene epoch) can serve as analogues for current climate warming and its consequences. We asked Arctic palaeoecologists/palaeoceanographers and marine ecosystem monitoring community members to provide their views on the state-of-the-art methodology and research gaps via a questionnaire. The survey was openly accessible online (Oct 16–Nov 23, 2019) as an activity of the Future Earth Past Global Changes (PAGES) working group Arctic Cryosphere Change and Coastal Marine Ecosystems (ACME; <http://pastglobalchanges.org/acme>). Here, we utilise the input from respondents in assessing the status of the research field and identifying future priority areas for research directions. While the sample of respondents is not extensive ($n = 29$), and is based on two continents (North America $n = 10$, Europe $n = 19$), the representation of various career stages (13 early career researchers, 16 mid to late career researchers) and the full array of specialties (most relevant biological and biogeochemical proxies, numerical methodology and ecosystem monitoring community) enable us to deliver important community viewpoints on the current status of, and future demands for, long-term records of Arctic coastal ecosystem changes.

2. Cryosphere: change and impacts

The Arctic cryosphere provides some of the most visible signs of recent, human-driven climate change. Most of its components, from permafrost to snow cover, over glaciers and ice sheets to sea ice, have undergone reduction and degradation over the past few decades (AMAP, 2017; Box et al., 2019). For example, sea-ice in the Northern hemisphere

has approximately halved in terms of area, decreasing by $515,000 \text{ km}^2 \text{ decade}^{-1}$ over the period 1979–2016 (Comiso et al., 2017), whereas mean annual temperatures of both continuous and discontinuous permafrost have increased ($+0.39 \pm 0.15^\circ$ and $+0.20 \pm 0.10^\circ \text{ C}$, respectively) from 2007 to 2016, hand-in-hand with rising air temperatures (Biskaborn et al., 2019). These cryospheric changes have the potential to cascade through the Earth System, affecting both its physical and biological components (Fig. 1). They may cross thresholds and tipping points, resulting in synergistic and occasionally irreversible consequences for ecosystems (Duarte et al., 2012), particularly in the Arctic where climatic changes are augmented by Polar Amplification (Screen and Simmonds, 2010).

One of the most visible consequences of Arctic climate change is the dramatic decrease in sea-ice cover, with projections forecasting a summertime ice-free Arctic Ocean by 2035–2050 (Guarino et al., 2020; Notz and SIMIP Community, 2020). Sea-ice loss has important ramifications for the physical system, including increased surface ocean warming, heightened ocean-atmosphere heat and gas exchange, and enhanced coastal erosion (Screen and Simmonds, 2010; Overeem et al., 2011; Vancoppenolle et al., 2013; Barnhart et al., 2014; Vihma, 2014). For ecosystems (Fig. 1), one of the most obvious implications of sea-ice decline is the loss of ice-dwelling (sympagic) and ice-dependent life, such as the poorly studied ice-associated algae and their accompanying food web, which encompasses both ice fauna and zooplankton (Lønne and Gulliksen, 1989; Søreide et al., 2010; Poulin et al., 2011; van Leeuwe et al., 2018). Disappearing sea ice also impacts organisms at higher trophic levels that rely on it as a substrate for reproduction, nutrition, and life histories, including polar bears (*Ursus maritimus*), walrus (*Odobenus rosmarus*), and ringed seals (*Pusa hispida*). The shift to increasingly later freeze-up and earlier breakup of sea ice (Barnhart et al., 2016) has particularly negative impacts on the apex predator *U. maritimus* (Laidre et al., 2020). Together with decreasing sea ice, elevated surface water temperatures as a result of Atlantification (Polyakov et al., 2020) can affect all trophic levels and thereby the overall food web. For Arctic species, negative consequences of such temperature-driven ecosystem shifts range from the decline of cold-adapted microbes, which play a key role in biogeochemical cycles (Deming, 2002), to shifting reproduction regimes of keystone species including the copepod *Calanus glacialis* (Søreide et al., 2010) and polar cod (*Boreogadus saida*) (Nahrgang et al., 2014).

Rising net precipitation, permafrost thaw and melting of glaciers and ice sheets are increasing river discharge and freshwater inputs to the Arctic seas (Rawlins et al., 2010; Carmack et al., 2016). Recent work indicates increased transfer of material from the coastal zone to the Arctic Ocean via the Transpolar Drift (Charette et al., 2020). Terrestrial inputs are the dominant source of new organic matter (carbon and nutrients) to Arctic coastal and shelf waters (Fig. 1), especially in areas with major river influence, such as in the Kara and Laptev Seas and on the Beaufort Shelf (Stein et al., 2004b). In the Kara Sea, for example, more than 70% of the organic carbon (OC) preserved in shelf sediments is of terrigenous origin (Fernandes and Sicre, 2000); similarly high values (> 50%) are found on the Beaufort Shelf (MacDonald et al., 2004). A recent modelling study estimated that land-derived nutrients fuel 28–51% of the current annual Arctic Ocean new primary production (Terhaar et al., 2021). While the fluxes of macronutrients primarily support primary production in the receiving coastal waters, OC fuels heterotrophic bacterial activity and decreases light attenuation. Enhanced freshwater inputs into the Arctic marine environment can thus lead to hydrographic shifts counteracting biological productivity, including stronger salinity-driven stratification preventing vertical nutrient flux (Carmack and McLaughlin, 2011; Fu et al., 2020; Randalhoff et al., 2020), and increased sediment load and particulate matter decreasing light availability for primary producers (Murray et al., 2015). Due to the particularly strong chemical and physical gradients in fjords, they exhibit a clear seasonality in organic matter (and nutrient) source and cycling. There, marine organic matter can dominate the

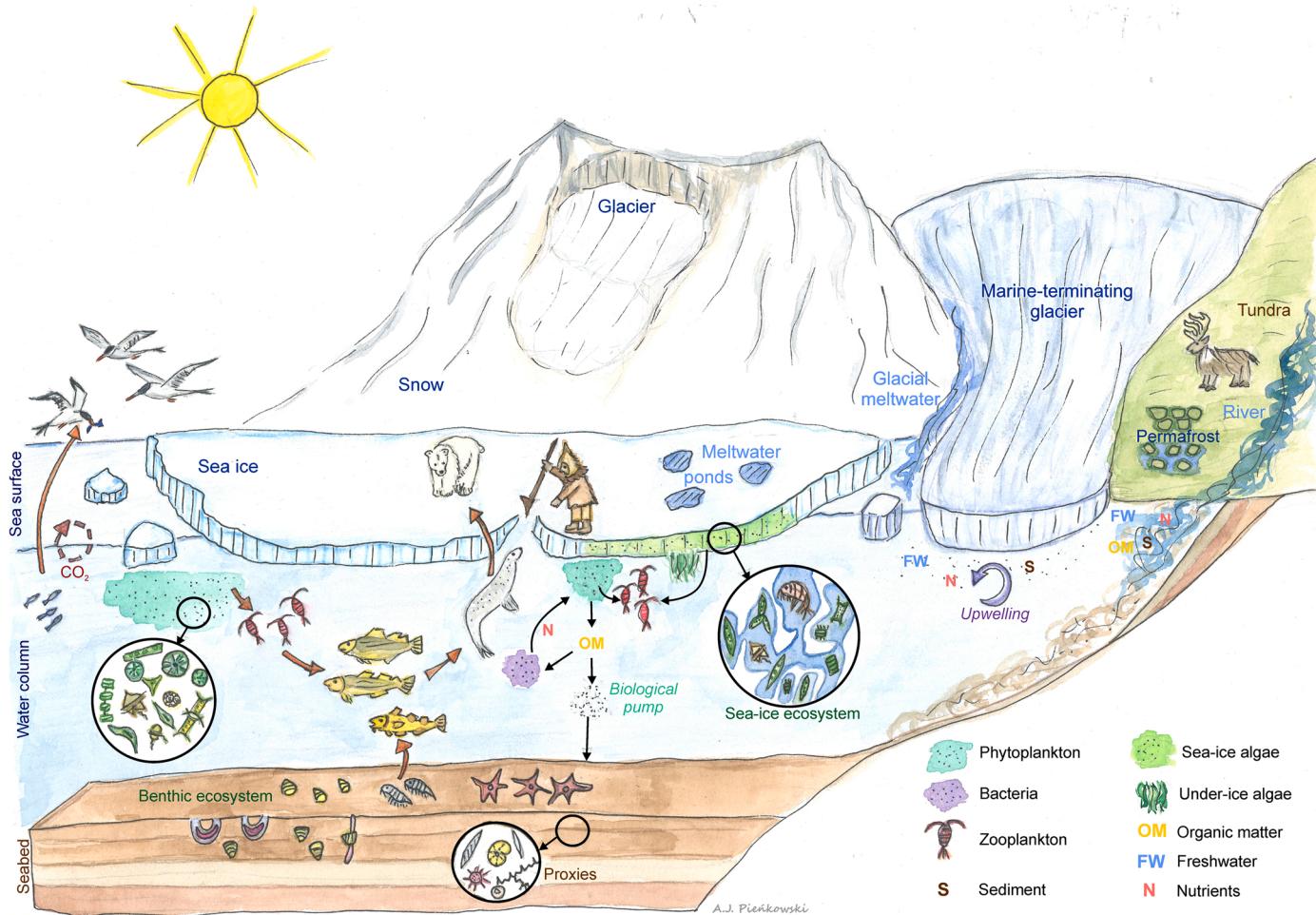


Fig. 1. Overview of key cryosphere processes and ecosystem interactions in the coastal zone, including deposition and preservation of proxies (paleo-records).

water-column OC pool during the spring bloom, while later in the summer terrestrial OC becomes more important (McGovern et al., 2020). Hence, the balance between the inputs of sediment, organic C and nutrients has a strong impact on the primary producers and on the net carbon dioxide (CO_2) flux of the ecosystem (Hessen et al., 2010).

Marine-terminating glaciers and ice shelves, particularly in the fjords of Greenland and Svalbard, are frequently associated with high marine primary productivity; in fjords with low primary productivity, high secondary (zooplankton) productivity has been observed close to the ice front. Both phenomena support higher organisms, such as seabirds and marine mammals (Lydersen et al., 2014; Laidre et al., 2016). The marine termini of ice sheets and glaciers deliver nutrients and OC to the marine environment via surface runoff and subglacial meltwater discharge (Fig. 1). Glacier meltwater is especially important in terms of providing micronutrients, such as iron, which are largely circulated locally (Hopwood et al., 2016). Recent studies have shown, however, that macronutrients, such as nitrate are replenished by a different mechanism: upwelling of bottom waters entrained in subglacial meltwater plumes (Meire et al., 2017; Hopwood et al., 2018; Vonnahme et al., 2020). Consequently, the retreat of glaciers onto land from the marine environment, as widely observed in settings, such as Svalbard (Nuth et al., 2013) or Greenland (Howat and Eddy, 2011), can curb fjord-scale productivity by restricting nutrient delivery to the marine environment, with potential negative socio-economic impacts, such as declines in harvestable resources (Meire et al., 2017). Nevertheless, nutrient delivery to the marine environment may continue after glacial retreat, as newly exposed postglacial sediments both on land (via surface runoff) and the seabed can contribute to the marine nutrient pool (Wehrmann

et al., 2014; see also Monien et al. (2017)), though not necessarily to the same degree as via sub-glacial processes. Overall, it is thought that glacier retreat will reduce biological productivity in the Arctic marine coastal ecosystem, especially in fjord settings (Meire et al., 2017; Hopwood et al., 2018).

3. Overview of palaeoceanographic/palaeoecological proxies and their use in the Arctic

Despite their potentially dramatic consequences, climatic shifts have only been directly observed and systematically recorded for a relatively short period of time. For example, the majority of (above ocean) air and sea-surface temperature recordings extend back to the mid 19th century (Parker et al., 2000), whereas satellite-based sea-ice observations cover just over four decades (Stroeve et al., 2012). These are relatively short time spans considering climate is, in the strictest sense, defined as the longer (~30-year) average of weather variables (IPCC et al., 2013). Data that extend beyond the observational and instrumental periods (pre-1850) are therefore needed to disentangle the effects of human-driven versus natural climate change, contextualise recent and ongoing shifts, and test and improve numerical models, including those concerned with future climate projections (Masson-Delmotte et al., 2013). Such longer-term information is provided by the physical, biological, and chemical proxies preserved in various natural archives, including peat and aquatic sediments, glacial ice, and tree rings (Gornitz, 2009). The seabed, with its underlying sediments in particular (Fig. 1), has significantly advanced our understanding of the Earth's climate history over the last ~170 million years (e.g., Zachos et al.,

2001; Westerhold et al., 2020).

Although proxy indicators of past environmental change are readily found in natural archives, their deposition, preservation, and retainment are affected by numerous factors. In the marine environment, much of the organic matter produced in the water column is recycled by microbial activity, so that only a small fraction of material (e.g., micro-organisms, particulate matter) reaches the seabed (Ragueneau et al., 2000; Passow and Carlson, 2012). The deposition of material on the seabed does not necessarily guarantee preservation, however, as various biogeochemical processes, such as microbially-driven reduction and oxidation of OC (Zonneveld et al., 2019), the dissolution of biogenic silica (BSi) in silica-undersaturated and aluminium-poor conditions (Van Cappellen et al., 2002) and calcite (CaCO_3) by CO_2 -supersaturated bottom waters below ~ 3000 m (Dittert and Henrich, 2000) may further alter or degrade material after deposition. Additionally, seafloor activity by organisms, such as polychaete worms can disturb and mix material on and within seabed sediment layers, especially in highly-productive coastal areas (Mermilliod-Blondin and Rosenberg, 2006). Fast burial of material promotes preservation but factors, such as rate of production, subsequent influx of particles to the seabed, and oxygen levels at the water-sediment interface also play important roles. Typically, coastal and shallow marine areas have much higher rates of sedimentation compared to deep ocean basins, as reflected in the level of resolvable temporal detail (i.e., decadal/centennial vs. millennial resolution) within these records (Ruddiman, 2014).

Palaeoceanographic and palaeoecological proxies are generally subdivided according to their origin and nature (Gornitz, 2009; Gregory et al., 2006). Physical proxies include physical characteristics, such as sediment grain size, mineralogy, and colour. For example, the presence of coarse mineral grains within usually fine-textured deep ocean sediments can denote large influxes of icebergs carrying and depositing terrestrial sediments whose mineralogy may be traced back to their source (Broecker, 1994; Andrews, 2000; St. John, 2008). Biogenic proxies are remains of organisms, such as nanno- and microfossils, and specific biogeochemical remains or biomarkers. Biogenic proxies that commonly underlie marine-based climate and ecosystem reconstructions are mainly produced by planktic, benthic and sympagic primary producers and heterotrophic protists. These include planktic and benthic foraminifera (Jorissen et al., 2007; Kucera, 2007; Aagaard-Sørensen et al., 2010), coccolithophores (Gard, 1989; Giraudieu and Beaufort, 2007), diatoms (Miettinen et al., 2015; Krawczyk et al., 2017; Oksman et al., 2017), radiolarians (Lazarus, 2005; Matul and Mohan, 2017) and dinoflagellate cysts (Dale, 1983; de Vernal and Marret, 2007; Ellegaard et al., 2017).

The main prerequisite for the incorporation of nanno- and microfossils into the sedimentary record is that they have a preservable hard part, such as a shell of calcite (planktic foraminifera, most benthic foraminifera, coccolithophores), opaline silica (diatoms, radiolarians), or organic refractory material (dinoflagellate cysts, other non-pollen palynomorphs). Since protists are universally abundant, small-sized (typically < 1 mm), and contain species whose distribution follow distinct environmental gradients (e.g. sea-surface temperature), their fossil records are particularly valuable and practical for reconstructing past environments and climate (e.g. Gregory et al., 2006). Aside from their fossil record (skeletal remnants), marine micro-organisms also yield biogeochemical proxies. These derive either from the chemical composition of microfossil hard parts, which preserve in the sedimentary record, or biomarkers that may preserve in the absence of skeletal remains. Besides protists (mostly unicellular eukaryotes), some bacteria and archaea also produce source-specific molecules that are valuable proxies.

Examples of biogeochemical proxies include the stable isotopic composition of oxygen ($^{18}\text{O}/^{16}\text{O}$, or $\delta^{18}\text{O}$) and carbon ($^{13}\text{C}/^{12}\text{C}$, or $\delta^{13}\text{C}$) incorporated from seawater into foraminiferal shells. Oxygen isotopes can shed light on past water temperature, salinity, and within a longer timeframe, provide information on global ice sheet extent and sea level

(Pearson, 2012). Carbon isotopes can elucidate biological productivity, water circulation, and carbon cycling (Rohling and Cooke, 1999). The ratio between various elements incorporated into foraminiferal shells, such as Mg/Ca, can also give insights into variables, such as water temperature (e.g. Skirbekk et al., 2016). Two common biomarker-based palaeothermometers are the indices TEX₈₆, and U^{K}_{37} . TEX₈₆ (TetraEther indeX of tetraethers consisting of 86 carbon atoms) is based on the distribution of archaeal isoprenoid glycerol dialkyl glycerol tetraethers (GDGTs) (Ho et al., 2014), while U^{K}_{37} represents the relative unsaturation of three different long-chain ketone lipids, or alkenones, synthesised by coccolithophores and other haptophytes (Prahl and Wakeham, 1987; Tierney and Tingley, 2018). Terrigenous leaf waxes and sterols, and their isotopic composition, on the other hand, can be useful in tracing land-derived sources of organic matter (Volkman, 1986; Pancost and Boot, 2004; Eglinton and Eglinton, 2008). More recently, highly-branched isoprenoids (HBIs) synthesised by some obligate sea-ice diatoms (IP₂₅, IPSO₂₅) and open-water phytoplankton (HBI III, HBI IV) have been used to reconstruct seasonal sea ice and phytoplankton blooms along the sea-ice edge (Belt et al., 2007, 2019; Belt, 2018). Lastly, emerging approaches in palaeoceanography include ancient DNA preserved in sediments, either via a full assessment of major organism groups, such as diatoms or dinoflagellates (De Schepper et al., 2019; Zimmermann et al., 2020), or alternatively targeting a specific organism of interest, such as the sea-ice-affiliated dinoflagellate *Polella glacialis* (De Schepper et al., 2019; Ribeiro et al., 2020).

Proxy indicators generally provide indirect measures of past conditions, yet they can be used both qualitatively and quantitatively, describing e.g., colder or warmer water or exact sea surface temperature (SST) in degrees Celsius, respectively. Knowledge of the relationship of a proxy to one or more environmental variable underpins its use in palaeoclimatology, whether the reconstructions are qualitative or quantitative (Fig. 2). For example, the use of biomarker indices or microfossil assemblages to reconstruct past SSTs requires knowledge of the relationship of current SSTs to the ketone lipid ratios or microfossil species abundances, respectively (e.g. Tierney and Tingley, 2018; de Vernal et al., 2020).

Despite the importance of the Arctic in the global climate system, data available from this region are still far from complete, largely due to its remoteness and challenging conditions for data acquisition. Palaeoceanographic studies in the Arctic have predominantly focused on the reconstruction of past climate and ecosystem evolution, including studies on sediment transport, sea surface temperature and salinity, ocean circulation, sea-ice cover, productivity, ice sheet and ice shelf activity, and the description and biogeography of biota (Schröder-Adams et al., 1990; Koç and Jansen, 1994; Bauch et al., 2001; Nørgaard-Pedersen et al., 2003; Stein et al., 2004a; Ottesen et al., 2005; Cronin and Cronin, 2015 and references therein). Over recent decades, quantitative reconstructions, particularly of SSTs, have been frequently published (e.g. Rueda et al., 2013; Rasmussen et al., 2014; Sicre et al., 2014; Miettinen et al., 2015; Caron et al., 2019), alongside a growing body of studies focusing on the development of tools for describing and quantifying past sea-ice variability (e.g. Müller et al., 2009; Belt, 2018 and references therein; Wang et al., 2021). This trend is likely driven by the well-documented and marked decline of Arctic sea ice alongside increasing global temperatures (Notz and Stroeve, 2018).

Of particular relevance to these recently observed cryosphere changes are those palaeoecological studies that focus on Holocene variability in sea ice, terrestrial runoff and their effects on physical and chemical water column properties defining primary productivity. Sea-ice variability in Arctic coastal and shelf areas has been reconstructed on Holocene time scales using both biogenic and physical proxies, qualitatively, semi-quantitatively and quantitatively (e.g. Stein et al., 2012; de Vernal et al., 2013a). Certain ice-associated indicator species preserved in sediments, and species assemblage changes in dinoflagellate cysts and diatoms are widely used, as are quantitative inference models (transfer functions, modern analogue technique) based on these

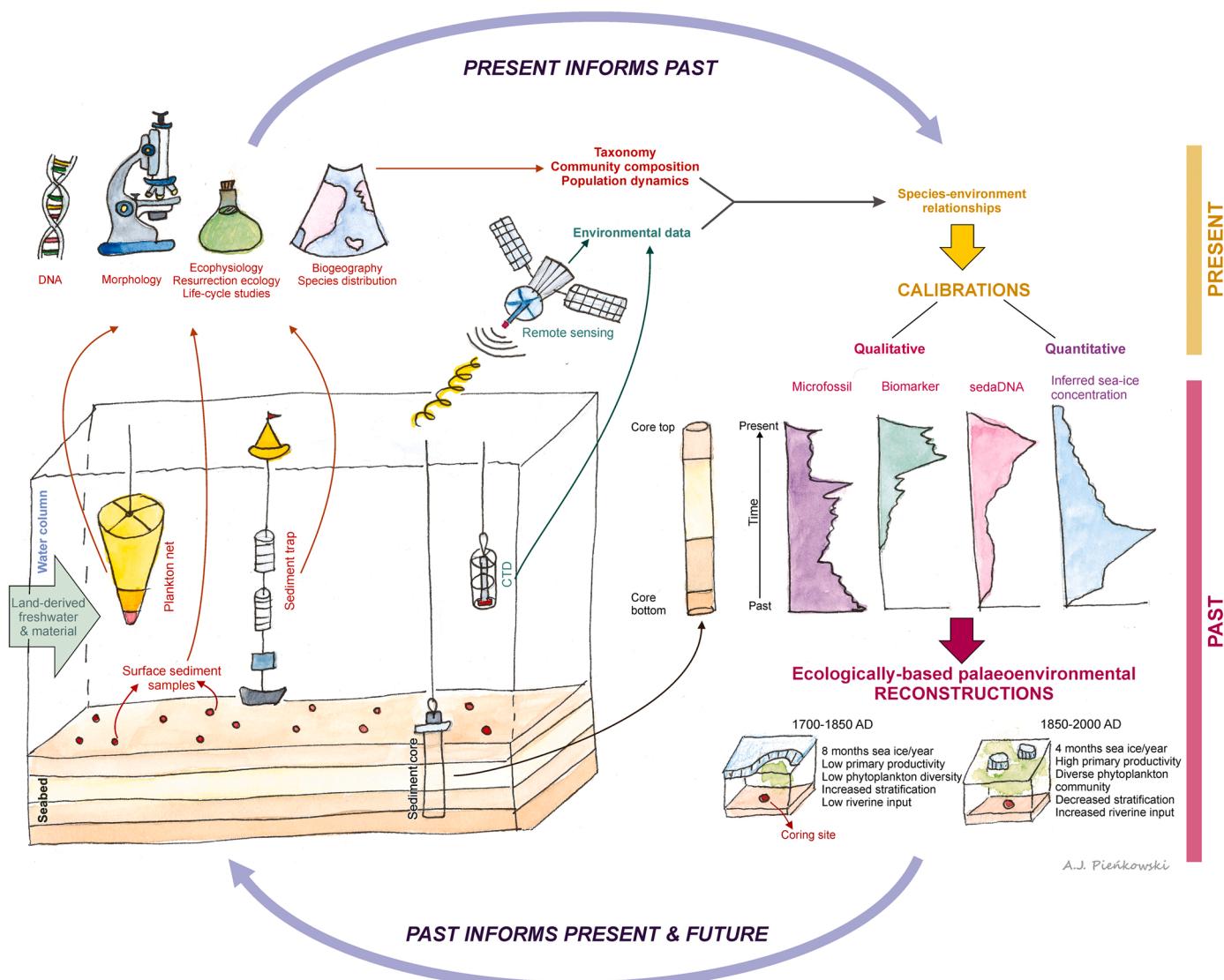


Fig. 2. A conceptual illustration of the premise of collecting, calibrating and using palaeoecological data and ecological understanding to provide records of long-term Arctic change.

proxies. Such species-environment inference models are built using modern reference/calibration data sets, which consist of surface sediment dinoflagellate cyst/diatom assemblages (marine datasets contain approximately 40–90 species) and accompanying environmental data from spatially distributed sampling sites (the unified reference database for Northern Hemisphere dinoflagellate cyst assemblages includes 1968 sites, while several diatom reference databases exist with typically >50 sites). The resulting inference model is subsequently applied to down-core fossil assemblages, providing quantitative reconstructions of environmental parameters back in time (e.g. Koç et al., 1993; de Vernal et al., 2001; Ledu et al., 2010; Miettinen et al., 2015; Sha et al., 2016; Krawczyk et al., 2017; Falardeau et al., 2018) (Fig. 2). A rapid rise of sea-ice reconstructions based on HBI biomarkers has followed the introduction of IP₂₅ (Belt et al., 2007), to date the most well-known and most widely used of the HBIs (e.g. Massé et al., 2008; Vare et al., 2010; Müller et al., 2012; Cabedo-Sanz et al., 2013; Méheust et al., 2016; Detlef et al., 2018), which is produced by certain sea-ice dwelling diatom species (Brown et al., 2014; Limoges et al., 2018a). For a detailed recent review on their development, strengths and constraints, see Belt (2018), who also discusses ratio-based semi-quantitative sea-ice indices using HBIs and phytoplankton markers (e.g. PIP₂₅, P_{III}P₂₅).

Sea-ice studies based on sedimentological ice-rafter debris (IRD) and

its mineralogical composition, foraminifera assemblages, and ostracod indicator species have often focused on longer time scales (the Cenozoic, Quaternary glacial-interglacial ice-rafting variability) and/or offshore locations (e.g. central Arctic Ocean, Fram Strait, continental slope regions; Hebbeln, 2000; Stickley et al., 2009; Cronin et al., 2010; Stein et al., 2012 and references therein; Polyak et al., 2013). Examples of coastal and shelf sea-ice reconstructions using foraminifera (together with other proxies) are given in Seidenkrantz (2013) who reviews the potential of foraminifera as sea-ice proxies. Past sea-ice variability has also been studied using driftwood (Funder et al., 2011; Nixon et al., 2016) and bowhead whale remains on glacio-isostatically raised beaches (e.g., Dyke et al., 2006), particularly in areas that are undersampled in marine sediment records, such as the Canadian Arctic. Furthermore, sea-ice histories have been inferred from methane sulphonic acid, bromine and sea salt in ice cores (Criscitiello et al., 2013; Spolaor et al., 2016; Rhodes et al., 2018).

Due to the projected dramatic increase in terrestrial inputs (freshwater, OC and nutrients) to Arctic coastal areas (Haine et al., 2015; Fritz et al., 2017; Nielsen et al., 2021), these inputs and their potential ecosystem effects have been topical in recent oceanographic studies (McClelland et al., 2011; Tank et al., 2012; Hopwood et al., 2020; Terhaar et al., 2021). To date, however, long-term palaeoceanographic

reconstructions on the variability of terrestrial inputs, in particular their covariance with cryosphere changes and their influence on the marine ecosystem, remain sparse (Wegner et al., 2015, see however Faux et al. (2011) and Hörner et al. (2016)). The same is generally true for studies focusing on the links between cryosphere changes and primary productivity over centennial to millennial time scales. There are, however, recent studies exploring Holocene interplay between sea ice and primary productivity off west and northwest Greenland and on the shelves of the Chukchi and East Siberian seas (e.g. Stein et al., 2017; Limoges et al., 2020; Saini et al., 2020; Krawczyk et al., 2021; Ribeiro et al., 2021). In addition, several recent studies provide important insight into the past impact of meltwater and glacier runoff on primary productivity in coastal settings (Kumar et al., 2018; Syring et al., 2020a; Allan et al., 2021).

4. Knowledge gaps and methodological challenges

Research efforts, and thus the understanding of proxy behaviour in various settings, are unevenly distributed across the marine Arctic. Most research efforts have focused on the European and Canadian Arctic shelves, whereas the Russian Arctic and central Arctic Ocean remain poorly studied. This was reflected in the answers obtained by the community survey (Supplement 1). It must be pointed out that the number of respondents to the community survey was not extensive ($n = 29$) and that participants were based in either North America or Europe. Consequently, obtained responses may be skewed towards these numerical and spatial factors. Nevertheless, the survey offers an important glimpse into community perspectives on the state of the discipline and potential future research directions of palaeoenvironmental research.

When asked to identify geographical areas with major data gaps, questionnaire participants pointed to the Russian Arctic, as expected: East Siberian Sea (45%) and Laptev Sea (28%). There are, however, recent studies from these seas that reconstruct Holocene variability in sea-ice cover, riverine inputs and primary production based mainly on HBI and sterol and organic matter isotopic biomarkers (Hörner et al., 2016; Stein et al., 2017; Thibodeau et al., 2018). The Lincoln Sea was also highlighted by the survey as an area with major data gaps (41% of respondents). The area encompassing the Lincoln Sea, the northern coast of Greenland and the Canadian Arctic Archipelago are expected to be the last refuge for perennial sea ice in the Arctic – the so-called ‘Last Ice Area’. Therefore, the importance of this region cannot be overstated. This area may be crucial for the survival of key Arctic species, and sea ice here is the last stronghold against accelerated mass loss from the northwest Greenland Ice Sheet. The knock-on effects of declining sea ice will also have profound consequences for the high-Arctic Inuit communities of Greenland and Canada (Egeesiaq et al., 2017; Ribeiro et al., 2021).

After the Russian Arctic and the Lincoln Sea, the Greenland Sea was identified by survey respondents as understudied (28%). The present-day marine environment off East Greenland is dominated by the southward flowing East Greenland Current transporting cold and fresh surface polar water and sea ice from the Arctic Ocean. In fact, the East Greenland Current is responsible for roughly 85% of the sea-ice export from the Arctic Ocean and for nearly 50% of liquid freshwater export (Haine et al., 2015). Meltwater from the Greenland Ice Sheet affects northeast Greenland marine ecosystems in various ways, including alterations in nutrient and light availability, and food web structure. Together with changes in sea-ice cover, ocean warming and acidification, freshening is an important driver for ecosystem change (Sejr et al., 2017) that remains poorly quantified for this area on longer time-scales. The generally low productivity and low sedimentation rates on the northeast Greenland shelf make it very challenging to obtain and interpret records at high resolution. While new Holocene records are available from this region (Syring et al., 2020b; Zehnich et al., 2020), there remain outstanding issues with microfossil preservation, particularly regarding diatoms – although sedimentary ancient DNA methods

may offer a promising alternative (Zimmermann et al., 2020). More importantly, only a few high-resolution records exist that cover recent centuries. These are mainly from fjords located farther south, on the southeast Greenland coast, and under the influence of the warm Irminger Current (Holland et al., 2008; Andresen et al., 2012; Mouginot et al., 2015). From the northeast Greenland shelf, Ribeiro et al. (2017), Limoges et al. (2018a, 2018b), and Luostarinen et al. (2020) provide much needed modern reference data by analysing not only the spatial distribution, but also seasonal production and vertical coupling of biological proxies from the high-arctic fjord systems of Tyrolerfjord-Young Sound and Independence Fjord. These data can provide a baseline for comparisons in future palaeoceanographic studies in these locations. Such data are, however, needed from various coastal areas of interest, and should ideally be more tightly connected with existing and developing ecological monitoring series in the future. For example, bio-mooring arrays and long-term sediment traps have been deployed in the Arctic Ocean and its marginal shelves for a few decades. Since these samplers operate continuously and throughout the year, their generated data are important in detecting long-term shifts in the marine ecosystem (Forest et al., 2013; Lalande et al., 2019 and references therein) while also contributing to proxy understanding (Heikkilä et al., 2016; Luostarinen et al., 2020; Pospelova et al., 2020) (Fig. 2).

While nearshore environments are often excellent for obtaining high-resolution records due to higher sedimentation rates, existing data are largely biased towards Arctic offshore environments. This is partly due to the fact that offshore waters are considerably easier to access and navigate with oceanographic vessels, while nearshore sampling typically involves greater risk due to e.g. icebergs, prolonged land-fast ice cover, and lack of bathymetric data. Accordingly, the majority of survey participants disagreed or strongly disagreed with the statement “our knowledge of past changes in Arctic nearshore environments is comparable with our knowledge of past changes in Arctic offshore environments” (Fig. 3). This knowledge bias is also reflected in existing modern reference databases used for proxy calibration (Belt, 2018; Oksman et al., 2019 and references therein; de Vernal et al., 2020), and difficulties in linking the proxy calibration data with satellite observations due to complications deriving from e.g., grid resolution, coastal outline delimitation and cloud coverage (Politi et al., 2019). As a result, existing proxy databases focus on data points farther away from coasts and are inadequate in fully capturing the impacts of land-derived inputs on proxy distribution. The survey participants identified a range of parameters related to land-ocean linkages, for which new and more reliable proxies are required: nutrient fluxes (13%), freshwater runoff (12%), and glacial runoff (10%), alongside a need for better proxies for sea-ice concentration (17%), and primary production (12%). The perceived need for improvements across multiple fronts, and the lack of clear community consensus, likely reflects the challenge of understanding how inherently indirect and complex biological proxies are coupled with recent, equally multifaceted, cryosphere change. Recent monitoring efforts of land-ocean inputs via glaciers and rivers in the Arctic (e.g. McClelland et al., 2015; Hopwood et al., 2020), are helpful for proxy calibration in coastal areas. Such data are still, however, spatially and temporally fragmented, and the challenge of modelling the spatial and temporal scales calls for coordinated and sustained observation programmes (Straneo et al., 2019).

The community survey included several questions on methodological standards and limitations. The participants were overall satisfied with the field sampling, storage and instrumentation used to collect sediment samples, but gaps were identified in the data analytical techniques and mechanistic understanding of proxies (Fig. 3).

The majority of survey participants (79%) declared that prior to statistical analyses they “use exploratory data analyses and data visualisation techniques to make sure the datasets meet the general principles, requirements and assumptions of the approach”. However, nearly 45% consider that we do not, as yet, have adequate methods for the quantitative determination of widely reconstructed environmental

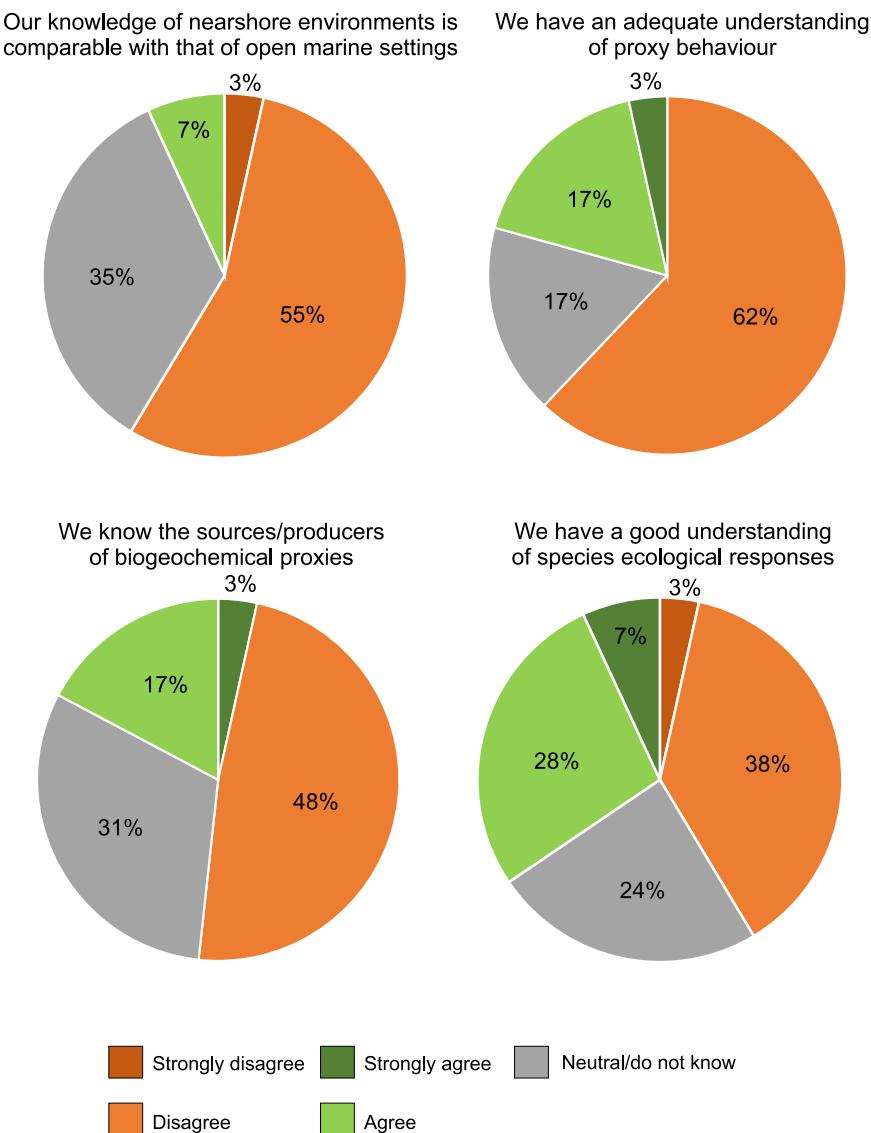


Fig. 3. Major knowledge gaps identified by the respondents to the PAGES ACME community survey (2019); see all survey results in [Supplement 1](#).

parameters, such as SST and sea ice, and more than 65% consider that we do not currently have an adequate understanding of proxy behaviour. Problems with reference datasets for quantitative reconstruction include poor or non-existent age control on the surface sediments used in modern reference sets, and varying taxonomy of older vs. newer reference set entries. In terms of statistical inference methods applied in quantitative reconstructions, a misalignment between the statistical knowledge of method users and method developers often precludes a more critical evaluation and use of mathematical approaches by the community. For example, spatial autocorrelation and the environmental range of reference datasets are often overlooked, as is the reconstruction of non-causal variables and the influence of secondary environmental variables (Telford and Birks, 2005; Birks et al., 2010; Juggins, 2013; Turner et al., 2021). Furthermore, there appear to be limited statistical expertise within the palaeoceanographic and palaeoecological fields to fully evaluate the validity and robustness of quantitative reconstructions.

Another important shortcoming identified by the community is the lack of adequate knowledge of species ecologies and source producers of biogeochemical proxies, such as lipid biomarkers (according to 52% of survey respondents). While the knowledge of marine proxies applied at high latitudes has rapidly evolved in the past decades (de Vernal et al.,

2013a; Goñi et al., 2013; Belt, 2018), we still do not know the habitat characteristics, seasonal bloom windows, preservation through the sea-ice–water column–sediment continuum, or even biomarker and resting stage producers for many biogenic proxies we readily apply in reconstructions. Investigating the responses of species and biomarker production to environmental variables (Ribeiro et al., 2017; Limoges et al., 2018a; Oksman et al., 2019; Brown et al., 2020; Weckström et al., 2020), as well as seasonal and population dynamics (Pospelova et al., 2010; Fahl and Stein, 2012; Heikkilä et al., 2016; Limoges et al., 2018a; Bai et al., 2019; Park et al., 2019; Luostarinen et al., 2020) is key to improving the interpretation of proxy records. For a more in-depth understanding of how species and populations may respond to environmental change, laboratory experiments and resurrection ecology approaches based on e.g. resting stages and DNA preserved in sediment records can offer useful insights (Ribeiro et al., 2013; Ellegaard et al., 2020).

Knowledge of proxy-environment relationships in nearshore areas is particularly deficient. Owing to marked terrestrial influences, it is likely that proxy controls here differ from those established based on open ocean calibrations. For lipid biomarker records, there remains significant work before the effects of coastal processes, such as nutrient fluxes and salinity shifts, and their impact on proxy-based reconstructions are

fully understood. It is known that sea-ice biomarker IP₂₅ is produced by sympagic diatoms (Brown et al., 2014; Limoges et al., 2018a), while alkenones used to calculate the SST proxy U^K₃₇ are produced by coccolithophores (Volkman et al., 1980, 1995). There is mounting evidence, however, that biomarker production by both groups is affected by oxygen and nutrient availability and salinity-driven shifts in the structure and abundance of source populations (Versteegh et al., 2001; Kim et al., 2009; Brown et al., 2020). To describe and better compare regional sea-ice conditions from HBIs, an index (PIP₂₅) using sterols (such as brassicasterol) produced by pelagic phytoplankton has been suggested (Müller et al., 2011). It is reasonable to assume that in offshore settings brassicasterol is largely produced by pelagic organisms (but see Belt et al. (2013)). In nearshore sites, however, the influence of land-derived brassicasterol, which is also produced by terrestrial plants and fungi (Volkman, 1986; Yunker et al., 2005), cannot easily be disregarded. While more recent developments of sea-ice biomarker indices have concentrated on other HBIs instead of sterols (Köseoglu et al., 2018; Belt et al., 2019), calibrations in nearshore environments are still required. On the other hand, lowered salinity also influences alkenone production, which may be dominated by coastal Group 2 haptophytes of the genera *Isochrysis*, *Ruttnera*, and *Tisochrysis*, as opposed to coccolithophore-producing Group 3 species *Emiliania huxleyi* and *Gephyrocapsa oceanica* (Theroux et al., 2010; Salacup et al., 2019). Recently, Wang et al. (2021) found a separate lineage of low-salinity Group 2 haptophytes whose occurrence in sea water and sediments was linked to extended sea-ice cover. Failing to carefully consider mixed sources of alkenone producers in a sample will lead to spurious SST reconstructions and thus interpretations.

5. The ability of existing palaeoenvironmental approaches to address pressing Arctic challenges

The broad array of proxies and notable methodological developments in recent decades have primed the palaeoenvironmental research community to respond to the pressing need for a baseline understanding of Arctic coastal ecosystems. Above, we have outlined the growing knowledge of geographic distribution and ecological niches of microfossil proxies; the rapid growth in the use and understanding of chemical biomarkers; the development of training sets for quantitative reconstructions; and the potential of sedimentary DNA techniques in deciphering past nearshore ecosystems. Similarly, we have identified important methodological gaps that hinder the generation of societally-relevant long-term records from the coastal Arctic zone.

The need for a more elaborate understanding of ecological and environmental proxy controls is widely acknowledged (Fig. 2), given that 65% of the survey respondents identified a lack of understanding in proxy behaviour in their fields of expertise. This has serious consequences for the use of quantitative reconstruction techniques and provides a prominent signal from the community for future action. Crucially, while the development of individual proxies and approaches remain essential, the need for co-generation of methods and records will become a necessity if we are to understand Arctic coastal systems under multiple environmental pressures from the atmosphere, the land, and the sea. In the survey, 86% of the respondents agreed with the need to move away from single-proxy, single-site reconstructions, and instead supported collaborative efforts to answer important research questions. Indeed, one of the most notable advances in Arctic palaeoceanography is the increasingly frequent use of several lines of proxy evidence—the multi-proxy approach (Kucera et al., 2005; Weckström et al., 2013; Moros et al., 2016; Pieńkowski et al., 2017; Harning et al., 2021)—together with a growing body of large regional or proxy-specific reconstruction compilations (de Vernal et al., 2013b; Moffa-Sánchez et al., 2019; Miles et al., 2020). Notably, every proxy has its limitations such that the application of multiple tools, along with proxy testing and comparison, is often the optimal reconstruction strategy. This is especially relevant in dynamic regions, such as the Arctic coastal zone, which

receives variable inputs via rivers and glacial ice, and whose sedimentary record will reflect a mixture of *in situ* and marine vs. terrestrial influences, as well as potential anthropogenic fingerprints (Crossland et al., 2005).

Although the multi-proxy approach is becoming more widespread, many palaeoceanographic studies on Arctic coastal and shelf regions are still relying on a single-proxy approach to reconstruct the variable of interest, e.g. sea ice or SST, using either a particular microfossil group (dinoflagellate cysts, diatoms, foraminifera, ostracods), quantitative microfossil-based inference models, isotope geochemistry of specific microfossil remains, or variable-specific biomarkers (e.g. HBIs for sea ice, alkenones and GDGTs for temperature). These single-proxy reconstructions are then complemented with rapid and less specific complimentary proxy analyses, such as grain size, bulk sediment chemistry (e.g. carbon, nitrogen), and X-Ray fluorescence (XRF). In the case of quantitative inference models, the resulting reconstructions are often not combined with more nuanced information that could be derived from species assemblage data via individual species' ecologies. The consideration of such contextual assemblage information is essential, since the quantitative reconstruction is reduced to a single variable, which, although of interest, is importantly based on a species matrix driven by multiple simultaneous environmental variables.

The benefit of the multi-proxy approach stems from the often indirect relationship between the individual proxies and their environment. As an example, the most commonly used sea-ice indicator diatom species reflect the marginal ice zone environment where they bloom as the ice melts (Oksman et al., 2019; Weckström et al., 2020). These marginal ice zone or MIZ conditions, defined by a strongly stratified water column due to a cold and fresh meltwater layer on top of ambient seawater, can also occur under different settings, such as when cold glacial meltwater enters an Arctic fjord (Oksman et al., 2017; Weckström et al., 2020). Here, combining the diatom record with e.g. HBI group biomarkers would help decipher the particular environmental setting. Vice versa, production of IP₂₅ in the sea-ice matrix can be affected by salinity changes and nutrient availability (Limoges et al., 2018a). In such cases, microfossil assemblages may be of valuable help in accurately interpreting the HBI record (Limoges et al., 2020; Saini et al., 2020). Additionally, proxies have different distributions and their preservation may vary in time and space.

Most of the proxy methods require expertise gained from years of training as well as specialised laboratory infrastructure. Hence, it is often not feasible for a single research group to produce records with more than a couple of lines of evidence. This leads, on the one hand, to highly specific expertise and standards. On the other hand, however, this poses an elevated risk of 'jigsaw' multi-proxy studies where individual approaches and records are used to form a final story, but suffer from poor integration and coherence. In order to develop long-term records that can disentangle multiple terrestrial and marine impacts and their interactions in a warmer coastal Arctic, both in-depth understanding of proxy behaviour and concurrent methodological development are essential. Nonetheless, without interdisciplinary collaboration on research approaches, proxy-specific developments will not live up to their full potential. Most respondents (76%) to the community questionnaire would rather focus efforts on more time-consuming but larger studies, including several lines of evidence, instead of fast publication. Almost all respondents expressed the need for more efficient channels for within-community communication (93%) and a preference for focused research community workshops over conventional conferences (83%).

The existing large suite of proxies has much potential for assessing interlinked changes in ice, ocean, and terrestrial domains. For example, microfossils reflect group- and species-specific niches related to sea ice, stratification, nutrients, salinity and light availability that can be further elaborated by modern monitoring, experimental and molecular studies. Lipid biomarkers and elemental and isotopic ratios, in turn, provide signatures of various aspects of ice, ocean, and terrestrial origins

(Pancost and Boot, 2004; Theroux et al., 2010; Diefendorf and Freimuth, 2017; Belt, 2018). At the same time, the size and quality of ecological descriptions based on spatial datasets have improved (Oksman et al., 2019; Van Nieuwenhove et al., 2020), understanding of proxy sources and dynamics are developing (Bai et al., 2019; Luostarinen et al., 2020; Wang et al., 2021), and published records apply increasingly highly resolved sediment archives (e.g. Ribeiro et al., 2012; Müller and Stein, 2014; Limoges et al., 2020; Wu et al., 2020). These trends in research progress, together with the community ambition towards more integrated and open research approaches, have improved the availability of, and potential for, multifaceted records elaborating long-term drivers of change along Arctic coasts.

6. Outlook

- Palaeoenvironmental records provide long-term insights that are crucial for understanding and predicting the future of Arctic ecosystems that support indigenous, local and global human livelihoods. Recent rapid warming in the Arctic is coupled with sea-ice loss and increased terrestrial runoff from melting glaciers, ice sheets, and thawing permafrost, placing coastal ecosystems under multifaceted environmental pressures. There is, thus, a pressing need to critically evaluate and enhance palaeoecological and palaeoceanographic methods, datasets and approaches so that these are better suited for answering the questions relevant to the transforming Arctic coastal zone.
- There is a general lack of palaeoecological and modern calibration data from nearshore areas compared to the open ocean, also identified by respondents to the research community survey. In addition, the survey answers pointed to the lack of palaeo proxy data from the Russian Arctic, the Lincoln Sea, and the Greenland Sea.
- The wide and increasing array of existing proxies, the growing trend in multi-proxy studies, the constant development of spatial datasets, the enhanced understanding of microfossil species' ecologies and population dynamics, and the advancement of methods, have provided essential steps forward. Significant knowledge gaps remain, however, with respect to proxy behaviour, sources and producers of biogeochemical proxies, species ecological responses and quantitative reconstruction approaches, as identified in the survey. In particular, the development of multifaceted coastal reference datasets would crucially improve our understanding of biogenic proxy responses to environmental pressures across land-sea boundaries, and the predictive value of past reconstructions from the Arctic coastal zone.
- Filling knowledge and methodological gaps necessitates more emphasis on interdisciplinary collaboration (i.e. collaborative design and development) on research questions and approaches across the field. Present progress and future outlook highlight the outstanding potential of palaeo-records for better predicting future changes and supporting local and global decision-making in the Arctic coastal zone.

Author contributions

The four authors designed the article, implemented the community questionnaire and wrote the manuscript together. M.H. served as the coordinating author. A.J.P. designed and drew the illustrations (Figs. 1 and 2), with contributions to the design from all other authors.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:[10.1016/j.ancene.2021.100319](https://doi.org/10.1016/j.ancene.2021.100319).

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