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The Changing Arctic Ocean: consequences for biological communities, biogeochemical processes and ecosystem functioning

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1. Introduction

The Arctic region is undergoing some of the most rapid rates of climate change in the world [1], with dramatic transformations underway in terrestrial, coastal and offshore environments that have immediate and long-term consequences for socio-ecological systems [e.g. 2-5]. Significant changes in the type, extent and thickness of ice cover [6], meltwater input [7], and water mass dynamics [8], coupled with warming and ocean acidification [9], have already begun to impact ecosystem processes and the flora and fauna that inhabit a range of Arctic habitats [10]. The pace of change is such that our understanding of the way in which Arctic systems are structured and function is outdated, and insufficient to inform management, mitigation and adaptation efforts across the region [11,12]. Projections indicate that, even if global stabilisation of temperature below 1.5°C is realised, changes will continue to manifest over an extended period, perhaps even millennial timescales [13], and may include unprecedented shifts in structure [14]. Changes to key components of Arctic ecosystems are already occurring, yet the collated evidence of how changes to baseline conditions are proceeding across the Arctic Ocean is still poorly constrained [15], focused on a limited number of exemplar areas [16], and seldom adopts a holistic view that begins to provide a nuanced understanding of the *modus operandi* of the Arctic [17]. This is concerning because informed decision- and policy-making benefits from a broad understanding of system dynamics, including feedbacks and the likelihood of ecological surprises [18], yet the focus of study is already shifting from the natural sciences to social sciences and humanities to meet legislative and policy demands [19]. Now more than ever, foundational concepts and evidence are needed to support sustainable management and policy, preferentially with a focus on continually acquiring, interpreting, and applying new interdisciplinary knowledge to enhance understanding [20].

2. New evidence and emerging themes

With the recognition of the complexity of system dynamics comes a need to synthesise evidence on how climatic forcing is changing the fundamentals of the system. It was within this spirit that this thematic section was commissioned, with interdisciplinary contributions from a range of active national and international research programmes. In doing so, we did not seek to represent all active areas of Arctic science, nor was it the intention to produce a comprehensive overview of specific topics of interest, rather our motivation was to highlight some of the emerging themes and evidence, stimulate discussion and expedite insight. The contributions received consider the mechanistic basis and consequences of change over a variety of spatio-temporal scales and for a number of different Arctic regions for three research clusters: the water column, seasonality and benthic-pelagic coupling. Here, we briefly introduce the contributed papers within the context of the wider literature before offering some observations on the salient research deficiencies, challenges and opportunities that show promise in establishing a practical research agenda.

The water column

The waters of the Arctic Ocean respond quickly and in multiple ways to changing forcing parameters, including changes in freshwater input from land, modulations of ocean currents and water mass distribution, and shorter and more dispersed sea ice cover [8]. Of particular interest are processes in the shallowest part of the Arctic Ocean, the photic zone, where changes in primary productivity and ecosystem dynamics are expected to have significant effects on carbon sequestration from the atmosphere. The photic zone is affected most directly by changing sea ice conditions, increasing light availability, as well as stratification and nutrient limitation. A better understanding of plankton ecology and biogeochemical processes in the photic zone is therefore of critical importance to understand the role of a future Arctic Ocean as a potential atmospheric carbon sink. In this respect, the extent to which under-ice algal blooms contribute to primary production in the Arctic Ocean has become a highly topical (e.g. [21,22]) issue. Bouman et al. [23] use a spectrally-resolved model of primary production to identify the set of conditions under which subsurface chlorophyll maxima contribute to water-column productivity, a key feature that escapes detection by satellites. They conclude that the uneven distribution and sparsity of chlorophyll measurements in the Arctic Ocean means that the common practice of spatial and temporal averaging of profile data underestimates the importance of subsurface chlorophyll maxima. Next, Kostakis et al. [24] study a multitude of biogeochemical parameters in the Barents Sea water column under different ice conditions using a glider system, a technology capable of covering wide areas of the ocean autonomously and complementary to satellite-derived data. Using these data, they develop and test a bio-optical model that links commonly measured parameters from glider-mounted sensors with satellite derived measurements of bulk optical properties. Combining satellite data with discrete shipboard measurements, Orkney et al. [25] adopt a similar philosophy to highlight the northward migration of certain phytoplanktonic groups (especially *Phaeocystis* algae) in the Barents Sea. They confirm previous suggestions of a north-eastward expansion in coccolithophore blooms, and suggest that observations of increased levels of chlorophyll *a* in the region may, at least in part, be explained by increasing frequencies of *Phaeocystis* blooms. Finally, Noethig et al. [26] use sediment traps to quantify the export of different biogenic particles from the photic zone into the deeper waters of the Arctic Ocean, a crucial aspect of pelagic-benthic coupling needed to move fixed carbon from shallow into deep waters and, ultimately, to the seafloor – and a process that is both currently impossible to resolve using remote sensing technology, and poorly constrained by most models. They observe negligible export fluxes of

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2 85 particulate matter and biomarkers during the Polar night, but an increase in export fluxes under reduced sea
3 86 ice cover during the summer reflecting enhanced primary production. However, export fluxes of particulate
4 87 matter in the Nansen and Amundsen basins decrease with depth, indicating a strong degradation of organic
5 88 matter in Arctic surface waters.
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9 90 **Seasonality**

10 91 Perhaps the most characteristic feature of the Arctic region is the intense seasonality in physical, chemical,
11 92 and biological features, both on land and in the sea. This seasonality results in pulses of primary productivity
12 93 that largely sustain ecosystems for the entire year. Warmer air and water temperatures, however, affect
13 94 timing of ecological processes via changing phenologies of plants and animals, migration/advection patterns
14 95 of predators and prey, and community composition as Arctic species are replaced by advancing southern
15 96 taxa [27-30]. These changes can have substantial implications for ecosystem functioning by altering carbon
16 97 drawdown and storage, trophic interactions, nutrient cycling, and the integrity of Arctic assemblages. Here,
17 98 [Henley et al. \[31\]](#) document seasonal availability of nitrate in the surface ocean on the northern Barents Sea
18 99 shelf. They show that, whilst availability varies little between ice-covered and ice-free locations, the
19 100 productivity season in ice-free waters is extended by advection of nutrients in Atlantic waters. Increased
20 101 Atlantification in the region could contribute to prolonged uptake of atmospheric carbon in a warming Arctic.
21 102 [Von Jackowski et al. \[32\]](#) investigate bacterioplankton dynamics that are affected by changes in the organic
22 103 matter pool. They show that seasonal patterns in pelagic primary production affect availability of dissolved
23 104 organic matter (DOM), and the availability of substrate has greater impact on bacterial activity than
24 105 increasing temperature. Further, as [Tisserand et al. \[33\]](#) show, algal community composition determines the
25 106 lability of DOM available for bacterial growth, and the bacterial strains that are most effective at its cycling.
26 107 Thus, complex relationships within the microbial community and at the base of the food web may be
27 108 profoundly altered by changes in seasonality of nutrient supply and algal community structure. The fate of
28 109 fixed carbon is tightly linked to climate feedback mechanisms via sedimentary processes, such as
29 110 bioturbation. [Solan et al. \[34\]](#) examine how invertebrate faunal activity and associated ecosystem functioning
30 111 is influenced by seasonal ice-cover that affects food supply to the seafloor, and by mesoscale oceanographic
31 112 features that influence benthic community structure. Their experiments, conducted over two consecutive
32 113 years along a transect intersecting the Barents Sea Polar Front, reveal that whilst faunal composition reflects
33 114 proximity to Arctic versus boreal conditions, faunal activity is moderated by seasonal variations in sea ice
34 115 extent that influence food supply to the benthos. In a recently ice-free Arctic fjord, however, [Morata et al. \[35\]](#)
35 116 document a reduction in seasonality in bioturbation and benthic carbon cycling, although nutrient fluxes
36 117 retain a strong seasonal signal. These authors suggest that increased detrital carbon dampens the seasonal
37 118 carbon signal from pelagic phytoplankton. In the only time-series study in this themed section capable of
38 119 detecting climate-related changes, [Al-Habahbeh et al. \[36\]](#) report slow recovery times from disturbance and
39 120 abrupt shifts in community structure for two shallow hard-bottom communities and conclude, based on trait
40 121 analyses, that Arctic systems may be particularly vulnerable to climate-related perturbations. Food-web
41 122 interactions in the Arctic are highly influenced by seasonal migrations of both predators and prey. [Hutchison](#)
42 123 [et al. \[37\]](#) incorporate migration into a food-web model and find better approximation of predator-prey cycles
43 124 than when a static model is used. Seasonal and interannual variability, therefore, modifies processes at the
44 125 base of the food chain, with consequent effects through microbial and faunal processing, up to trophic
45 126 interactions reaching top predators. Recent studies have indicated that seasonal paradigms of the Arctic are

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2 127 not so straightforward as once thought [e.g. 38], and climate change is likely to further alter perspectives as
3 128 communities and their functioning respond to multiple changing drivers.
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6 130 **Benthic-pelagic coupling**

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8 131 Benthic–pelagic coupling plays a major role in determining the production, biological structure and food web
9 132 stability of both systems [39]. This coupling is often stronger in shallower areas compared to deeper areas,
10 133 due to the shorter distance between the productive, euphotic zone and the benthic realm [40]. However, in
11 134 northern Baffin Bay, [Olivier et al. \[41\]](#), using a bivalve, provide evidence of a strong benthic-pelagic coupling
12 134 to 600 m depths. They identify a clear shift in bivalve growth variation since the late 1970s related to food
13 135 supply. Over the last half-century, a more regular export of diatoms from the euphotic zone may have
14 136 increased food supply to the benthos. Two hypotheses are possible to explain a more regular export of food
15 136 supply: the potential temporal or spatial mismatch between the phytoplankton bloom and its pelagic
16 137 consumers, and/or local changes in sea-ice dynamics that moderate phytoplankton production. Climate
17 138 change leading to ice loss could result in major gains in stored (probably sequestered) carbon at the shelf
18 138 seafloor adjacent to parts of Antarctica [42]. Here, [Souster et al. \[43\]](#) compare the stocks of zoobenthic blue
19 139 carbon between the Barents Sea and shelf seas of the Western Antarctic Peninsula. They find that the blue
20 140 carbon stock of the Barents Sea is twice that of the Antarctic soft sediment shelf and could have great
21 140 potential for increased carbon drawdown. Their results highlight the need to investigate zoobenthic blue
22 141 carbon in the Arctic to better inform global estimates of carbon budgets and climate feedbacks. Along these
23 142 lines, [Faust et al. \[44\]](#) explore how ongoing changes in the Barents Sea will change the organic and
24 142 inorganic sediment composition in the future. Their results, based on comparisons between the seasonally
25 143 ice-covered north and permanently ice-free south Barents Sea, imply that continuing sea-ice reduction and
26 144 the associated modification of vertical carbon fluxes might create shifts in surface sedimentary organic
27 144 carbon content which, in turn, may result in overall reduced carbon sequestration. As the sea ice reduction
28 145 will continue northward and modify the ocean primary production, patterns of the benthic-pelagic phosphorus
29 146 cycle are also likely to change. By comparing sediments and porewaters from the Barents Sea slope and the
30 147 Yermak Plateau, [Tessin et al \[45\]](#) conclude that increased delivery of labile organic matter in response to
31 147 elevated surface productivity will increase the oxidant demand and Fe remobilization within sediments and
32 148 cause the Yermak Plateau to shift towards the conditions observed in the Barents Sea slope. Increased
33 149 organic carbon fluxes on the Barents Sea slope may result in large fluxes of P from sediments to bottom
34 149 waters, as a large stock of P has been accumulated in surface sediments. [Stevenson et al. \[46\]](#) demonstrate
35 150 mechanistic links between microbial processing and changes in organic and inorganic parameters that are
36 151 coupled to biological mixing and the reactivity of organic material. They find direct links between aerobic
37 152 processes, reactive organic carbon and highest abundances of bacteria and archaea in the uppermost
38 152 sediment layer followed by dominance of microbes involved in nitrate/nitrite and iron/manganese reduction
39 153 across the oxic-anoxic redox boundary and sulphate reducers at depth. Using an original approach, [Freitas
40 154 et al. \[47\]](#) combine field observations from the Barents Sea with a Reaction-Transport model to quantify
41 154 organic matter processing and its drivers. Their results indicate that, at sites influenced by Atlantic Water,
42 155 there is a clear burial of highly reactive marine derived organic matter. This allows them to establish a
43 156 baseline systematic understanding of seafloor geochemistry, helping to anticipate likely modifications linked
44 156 to future climatic scenarios in the Arctic. From all these studies it is clear that ice reduction, alongside other
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2 168 components of climate change, affects the underlying seafloor without significant delay and plays a central
3 169 role in moderating and redefining benthic-pelagic coupling processes.
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6 171 **3. Research priorities**

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8 172 By focusing on distinguishing natural variation and/or localized responses from long term regional climatic
9 173 forcing, the contributions in this thematic issue provide a sensible focus for new innovative science in the
10 174 immediate future. Whilst we acknowledge that the conclusions drawn here are not based on a
11 175 comprehensive review and gap analysis of the wider literature, it is clear that contrasting regional responses
12 176 to climate change across multiple seasons and locations are informative and, when taken together, can
13 177 hasten understanding. Based on this overview, and in no particular order of importance, we offer the
14 178 following observations in the hope they will stimulate debate and novel lines of inquiry:
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- 17 180 1. *Value basic discovery and observational science, museum collections and historical archives and*
18 181 *use this repository of information and perspectives to inform hypothesis driven investigation.*

19 182 A cursory look at the literature cited by the contributors to this theme reveals that phenomenological
20 183 observations are common and well-articulated, reflecting major investments in the recent past that
21 184 stimulated much effort in establishing the basic science of the Arctic region. Emphasis is now
22 185 needed to move beyond confirmatory observation and towards interrogation of system complexities,
23 186 including unambiguous experimental demonstration of key mechanisms in the absence of
24 187 confounding or collinear factors.

- 25 188 2. *Undertake diversification in the gathering of knowledge and evidence whilst adopting a holistic pan-*
26 189 *Arctic view.*

27 190 The major geographical and seasonal bias in knowledge needs to be addressed by diverting effort
28 191 away from regionally and/or temporally constrained study and focusing on testing the generality of
29 192 observations, theory and/or conceptual advances. Historical compartmentalization of disciplines [48]
30 193 has compounded this problem as there are large gaps in understanding about the extent to which
31 194 different landscapes are interconnected [49].

- 32 195 3. *Remove over-reliance on infrequent occupancy by embracing new technology, including cultural*
33 196 *knowledge, satellite derived information and autonomous systems, whilst extending ground-truthing*
34 197 *and calibration efforts.*

35 198 Synoptic efforts are required to routinely gather information at large scales and across all seasons,
36 199 with a view to understanding system generalities and localized exceptions. Effort will be needed to
37 200 expand capability beyond the current subset of variables, and to employ novel complex system
38 201 approaches to identify inter-linkages and distinguish natural variability from directional change. Such
39 202 efforts will need thorough interrogation, even relatively well-established parameters like chlorophyll
40 203 concentrations in relatively accessible marginal parts of the Arctic Ocean require a more detailed
41 204 deconvolution.

- 42 205 4. *Establish detailed unambiguous understanding of the vulnerability and/or resilience of Arctic species*
43 206 *and ecosystems to the type, timing, sequence and combination of multiple drivers of change.*

44 207 Most projections of the fate of Arctic species, ecosystems and associated levels of ecosystem
45 208 functioning are based on assumed or extrapolated responses to change. There is little empirical
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backing for assumptions made, and little attention has been devoted to establishing the relative importance of the different components, or properties, of directional forcing [e.g. 40,50,51].

5. *Divert effort from using bulk or integrative indicators of ecosystem response towards establishing specific mechanistic understanding of how and when specific drivers of change operate.*

Whilst various of measures of ecosystem response are accepted and routinely used, the relative roles of specific pathways or components that underpin the bulk signal are less known, but have been summarised [52]. For carbon, for example, which degradation pathways are important, what type of carbon matters, and what are the relative roles of deposition versus burial? [53] Further, the adequacy and utility of methods for measuring and assessing the stocks and flows of various aspects of ecosystem responses have received little attention [54-56].

6. *Transition from documenting negative impacts of change to formulating a socio-ecological, solutions-based narrative that will be effective in providing evidence to support decision and policy making across the Arctic.*

Very little attention has been devoted to formulating an integrated sustainable management plan for the Arctic, or in determining which evidence is needed to support decision and policy making.

Indeed, a solutions-based narrative is not well-developed for the marine benthos [57], and there are virtually no socio-economic studies for the Arctic [58,59]. Approaches involving multiple disciplines that mobilise and build on indigenous and local knowledge are urgently required [16,60], but need to be supplemented by socio-ecological contributions to aid understanding of system dynamics.

4. Conclusion

Understanding the consequences of climate change and anthropogenic activity in the Arctic requires a multi-faceted approach and, as the contributions in this themed issue indicate, there has been significant progression in a number of areas. However, it is clear that Arctic science is undergoing a transition from observational and phenomenological documentation to interrogative empirical research aimed at developing theory and mechanistic understanding. Recent availability of international funding has fueled this evolution, and the extensive use of observing technology, coupled with the extended occupancy time of field researchers within the Arctic, is allowing new insights about seasonal dynamics and processes that occur over larger spatial scales. Nevertheless, investigations remain regionally constrained and compartmentalized within disciplines or domains, although an integrative comprehension is beginning to materialize. Our brief analysis here, albeit limited in scope, suggests a developing directional change in research foci towards an interdisciplinary research agenda focused on understanding how whole system changes lead to alternative outcomes. Achieving this research agenda will require the merger of perspectives, scaling up of data acquisition and analysis, and pooled initiatives that pursue the mechanistic basis of consequential change for biological communities, biogeochemical processes and ecosystems. For the moment, as this themed section illustrates, compiling new and existing data, and taking advantage of a state-of-the-art models and adopting upscaling approaches, allows generalities to be established about how Arctic systems respond to perturbation. As new data become available, model-data comparisons will highlight areas of divergence, allowing refinement of hypotheses and data needs, whilst field data and experiments will provide mechanistic information to enable the re-parameterisation of models to reflect new understanding of system complexity. It will be important to implement this knowledge to identify thresholds and feedbacks, minimise uncertainty and

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2 250 provide evidence/advice for prioritizing mitigation and/or adaptation needs as the expression of climate
3 251 change intensifies.
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8 254 **Author contributions**

9 255 All authors contributed equally to the manuscript.
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12 257 **Competing interests**

13 258 The authors declare that they have no competing interests.
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