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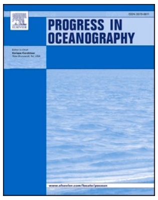

Towards a unifying pan-arctic perspective: A conceptual modelling toolkit[☆]

P. Wassmann[a,*], E.C. Carmack[b], B.A. Bluhm[a], C.M. Duarte[c], J. Berge[a,d,e], K. Brown[b,f], J. M. Grebmeier[g], J. Holding[h,i], K. Kosobokova[j], R. Kwok[k], P. Matrai[l], S. Agusti[c], M. Babin[m], U. Bhatt[n], H. Eicken[n], I. Polyakov[o], S. Rysgaard[h,p], H.P. Huntington[q]

[a] *Department of Arctic and Marine Biology, UiT The Arctic University of Norway, P.O. Box 6050, Langnes, 9037 Tromsø, Norway*
[b] *Fisheries and Oceans Canada, 9860 West Saanich Road, Sidney, BC V8L 4B2, Canada*
[c] *Red Sea Research Center (RSRC), Building 2, Level 3, Room 3219, King Abdullah University of Science and Technology (KAUST), Thuwal 23955-6900, Saudi Arabia*
[d] *University Centre on Svalbard, Dept of Arctic Biology, P.O. Box 156, 9171 Longyearbyen, Norway*
[e] *Centre for Autonomous Marine Operations and Systems, Department of Biology, Norwegian University of Science and Technology, NTNU, Norway*
[f] *Woods Hole Oceanographic Institution, Department of Marine Chemistry and Geochemistry, Woods Hole, MA, 02543 USA*
[g] *Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, P.O. Box 38, 146 Williams Street, Solomons, MD 20688 USA*
[h] *Arctic Research Centre (ARC), Aarhus University, Ny Munkegade, bldg. 1540, 8000 Aarhus C, Denmark*
[i] *Department of Bioscience, Aarhus University, Vejlsøvej 25, 8600, DK-8600 Silkeborg, Denmark*
[j] *Shirshov Institute of Oceanology, Russian Academy of Sciences, Nahimovskiy prospekt 36, Moscow 117997, Russia*
[k] *Jet Propulsion Laboratory, California Institute of Technology, 4800 Oak Grove Dr, Pasadena, CA 91109, USA*
[l] *Bigelow Laboratory for Ocean Sciences, 60 Bigelow Drive, P.O. Box 380, East Boothbay, ME 04544, USA*
[m] *Unité Mixte Internationale Takuvik, CNRS (France) & Université Laval (Canada), Pavillon Alexandre-Vachon, Local 2078, 1045, avenue de la Médecine, Université Laval, Québec (QC) G1V 0A6, Canada*
[n] *International Arctic Research Center, University of Alaska Fairbanks, 2160 Koyukuk Dr, Fairbanks, AK 99775-7340, USA*
[o] *University of Alaska Fairbanks, International Arctic Research Center, College of Natural Science and Mathematics, Department of Atmospheric Science, PO Box 757335, Fairbanks, AK 99775, USA*
[p] *Centre for Earth Observation Science, Department of Geological Sciences, 522 Wallace Building, University of Manitoba, Winnipeg, MB R3T 2N2, Canada*
[q] *Ocean Conservancy, 23834 The Clearing Dr., Eagle River, AK 99577, USA*

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ABSTRACT

The Arctic Ocean is overwhelmingly forced by its lateral boundaries, and interacts with, the global system. For the development of nested conceptual models of the Arctic Ocean ecosystem we here choose the full pan-Arctic as our focal scale. Understanding the pan-Arctic scale, however, requires that we look at the underlying scales of its major components, by considering regionality, connectivity and seasonality. Six regions are identified on the basis of hydro-morphological characteristics, which subsequently reflect ecological function and traits. Regions are static, tied to geography, but are linked by contiguous domains of shared function that facilitate material transports and share key ecological features. The pan-Arctic scale also requires attention to forcing by the seasonal light intensity, wherein the maximum length of a single day varies from near 24 h at the Arctic Circle to about 4400 h (183 days) at the North Pole. The light climate forces a strong phenology in the Arctic, as reflected in the periodic life cycle events of organisms. In addition to light climate, Arctic Ocean ecosystems are dominated by three fundamental variables: ice cover, nutrient/food availability and advection. The conditions under which each of these variables play out in the course of a year are set by the regions and contiguous domains within which they operate and interact. Together, the defined regions and their seasonality, the contiguous domains and their connectivity, and the three fundamental variables allow unambiguous application of scale-nested, parsimonious and adaptive, conceptual models, from which to 1) create testable hypotheses, 2) plan and then modify field campaigns, and 3) communicate essential results to managers and the general public. The development of these nested conceptual pan-Arctic scale models creates a vital step into the future of unifying, integrative oceanographic and ecological work.

[☆] We construct and construct and yet intuition still has its use. Without it we can do a lot, but not everything. When intuition is joined to exact research it speeds up the process of exact research. Paul Klee.

[*] Corresponding author.
E-mail address: paul.wassmann@uit.no (P. Wassmann).

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1. Introduction

The Arctic Ocean (AO; also called the Arctic Mediterranean Sea, classifying it as an estuary of the Atlantic Ocean) is located in the Arctic north polar region. Because of its connections with the Atlantic and Pacific Oceans, the role it plays in the water cycle and large circulation of the ocean and atmosphere, and its disproportionate impact on climate, it can be considered as the functional center of the Northern Hemisphere (Fig. 1; for abbreviations applied throughout the text, see Table 1; for a definition of essential terms and abbreviations in the text, see glossary). Here we take as a working definition of the AO the Arctic north polar region (basins and adjacent shelves) poleward of four gateways (see below), keeping in mind that no strict boundary will satisfy all functional and geopolitical issues. Baffin Bay and the Sea of Okhotsk are separate Arctic oceans with independent boreal and polar outflows. The AO is almost completely surrounded by the vast landmasses of Eurasia and North America and, presently, is almost completely covered by sea ice in winter. The ocean receives freshwater and material supplies from a vast network of rivers that drain these surrounding landmasses. It is connected to the subarctic Pacific Ocean via the Bering Strait and particularly to the Atlantic Ocean by gateways at Davis Strait, Fram Strait and the Barents Sea opening. Easterly winds to the north and westerly winds to the south encircle the central AO and adjacent land masses, completing the Arctic land-sea-air system (Fig. 1). Importantly, this structure of concentric circles means that the AO cannot be understood, predicted and/or managed through traditional sectorial approaches exclusively out of Europe, Asia or North America, but only through integrated, circum-Arctic and tightly interconnected, systemic approaches. Consequently, pan-Arctic integration and international cooperation in research and management are indispensable. It is essential that such cooperation crosses territorial borders, in line with the patterns of ice drift, winds, ocean currents and plankton organisms in the AO (e.g. Wassmann, 2006). For an overview on major AO expeditions over the last 130 years that create a knowledge base for our current understanding, see Appendix 1.

Table 1
Abbreviations.

Water masses	
ACBC	Arctic Circumpolar Boundary Current
AO	Arctic Ocean
ASW	Arctic Surface Waters
AW	Atlantic Water
BSB	Barents Sea Branch
FSB	Fram Strait Branch
NHTC	Northern Hemisphere Thermohaline Circulation
PW	Pacific Water
Domains/Processes	
APHD	Atlantic and Pacific Halocline Domain
CBCD	Circumpolar Boundary Current Domain
DBD	Deep Basins Domain
MIZ	Marginal Ice Zone
SPBC	Sympagic-Pelagic-Benthic Coupling
SIZ	Seasonal Ice Zone
SIZD	Seasonal Ice Zone Domain
RCD	Riverine Coastal Domain
ULAD	Upper Layer Advective Domain
TPD	Transpolar Drift

Despite notable past success involving science-capable icebreakers and ice drift stations, collaborative ventures in the AO region remain few, not least due to major logistic challenges. As a consequence, our basic knowledge of the AO remains patchy. Long time series are lacking from many important regions, and our understanding of the seasonal ice cover and its associated biology is limited and often missing, in particular during winter, spring and early summer. The available literature addressing pan-Arctic integration has been edited and summarized for example in Wassmann (2006, 2011, 2015). One reason that research on the oceanography and ecology of the AO has lagged behind efforts elsewhere is the difficulty and harshness of year-round field sampling; another is that efforts have been insufficient to cover the broad extent of

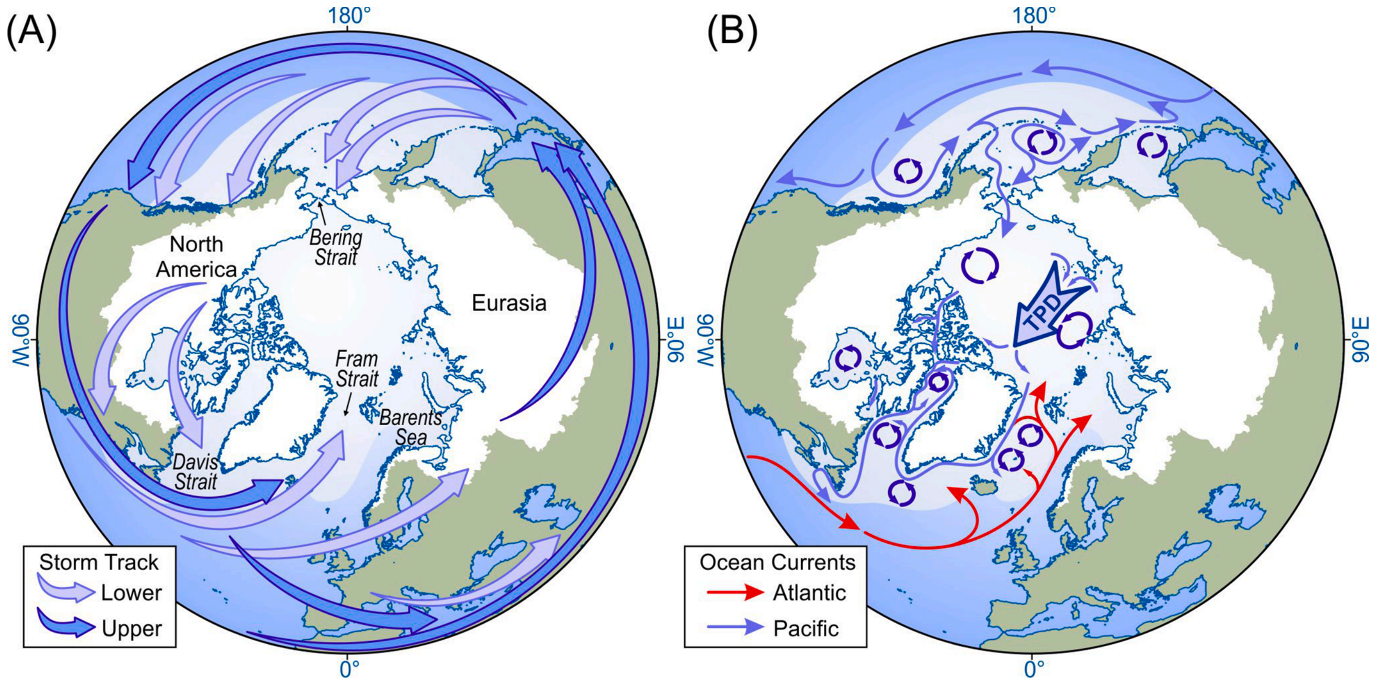

Fig. 1. Two Northern Hemisphere maps showing the encircling of the Arctic Ocean by extensive landmasses, atmospheric transports, watersheds and the connection with the Pacific and Atlantic Oceans. Figures are redrawn from Prowse et al. (2015) and Carmack et al. (2016) illustrating (A) the delivery of moisture and freshwater to the Arctic drainage basins by extra-tropical storm tracks (in the lower and higher atmosphere), and (B) oceanic pathways from the Pacific and Atlantic into and out of the Arctic Ocean and major gyres. In both maps the white shaded area denotes the Arctic drainage basins, as discussed by Prowse et al. (2015). TPD is the Transpolar Drift. The light-blue shaded area depicts surface waters influenced by fresh-water stratification. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

this "ocean opening" owing to a lack of political and Earth ecosystem vision.

Events of recent years (e.g. the International Polar Year, 2007–2009) and the now accepted impact of global climate change have altered this view (Landrum and Holland, 2020). An increased number of nations are becoming interested in conducting Arctic research, more ice-reinforced ships are now available and the amount of research funding that is dedicated to Arctic research is growing (e.g. the largest polar expedition in history, MOSAiC, https://mosaic-expedition.org/). Still, the lack of an adequate basic comprehension of this vast and complex system impedes a knowledge-based understanding of the ecosystem and, consequently, responsible resource management of the AO. In addition to recent and ongoing studies providing 'puzzle pieces', we need emphasis on regions that are not investigated and on syntheses that provide the required high-level understanding. Otherwise, the outcomes of recent and ongoing studies, while possibly scientifically relevant and sound, may fall for responsible policy making and management. Continued lack of integration and conceptualization may leave us simply in a worse position to manage the impacts of economic growth and industry operations in the future Arctic. In recognition of this shortcoming the Arctic Council signed an "Agreement on Enhancing International Arctic Scientific Cooperation" (Arctic Council, 2017), which intends to facilitate and promote pan-Arctic cooperation across the vastness of the AO. This agreement, which now has entered into force (Arctic Council, 2018) creates a mandate for more adequate endeavors to understand the vastness and the mediterranean nature of the AO.

Managing the imminent pressures derived from the forecasted increase in fisheries, petroleum and mineral extraction, other industrial operations and transportation in the AO requires knowledge. The cascade of effects of climate change affecting both Arctic and non-Arctic nations provides even greater challenges for sustainable ecosystem and resource management (Duarte et al., 2012a; Box et al., 2019; Overland et al., 2019; Landrum and Holland, 2020). As a pre-requisite, an elaboration of the major research questions and programs aimed at advancing our understanding of the AO system is essential. Currently, such programs, which involve great efforts and resources, largely lack shared paradigms to help identify the key processes and levers that such programs should aim to elucidate. A need thus exists to develop community-shared theories and conceptual models that help unify our differing or lacking perspectives. Genuinely pan-Arctic perspectives and tools are required to understand, predict and manage a mediterranean-type AO now undergoing major change. One of the greatest unplanned experiments in human history is rapidly taking place before our eyes in the AO: ice-free conditions during late summer, an intensified hydrological cycle, strongly altered stratification and mixing, ocean acidification, an unprecedented change in underwater light climate and rapid warming of surface water. In summary and discussed throughout this publication, the changes in the AO are based upon four fundamentals, but highly consequence-rich and interconnected variables: ice cover (including increased stratification), light climate, nutrient/food availability and advection, each of which will be discussed throughout this publication.

1.1. Why use a conceptual model approach?

Our system-wide perspective is motivated by the observations that: (1) global climate change is real and the Arctic is the most rapidly changing of all Earth systems, with major physical and ecological consequences (McLaughlin et al., 2011; Bhatt et al., 2014; IPCC, 2018); (2) the loss of sea ice is the leading signal of climate change (Kwok and Rothrock, 2009; Kwok et al., 2009; Duarte et al., 2012a; Stroeve et al., 2012; Carmack et al. 2015a), with the role of the ocean in heat exchange gaining disproportionally in importance (Carmack et al., 2015a; Polyakov et al., 2017); (3) the AO is coupled to and forced by the subarctic Pacific and Atlantic Oceans, with large-scale interactions affecting change in all three seas (Carmack et al., 2010; Polyakov et al., 2017; 2018; Lind et al., 2018); (4) the physical, chemical and biological components within the AO are mutually interacting, with cascading consequences throughout the system (Carmack et al., 2012b; Huntington et al., 2014; Grebmeier et al., 2015); (5) the high-latitude hydrological cycle is intensifying, with substantial consequence for terrestrial and marine systems (Prowse et al., 2015; Carmack et al., 2016; Baumann et al., 2018; Landrum and Holland, 2020).

For clarity, we here designate a conceptual model as being a depiction (graphical, verbal or generic mathematical expression) of a process or a system, including its internal dynamics and its external drivers. It is a model constructed of ideas and theories to help the reader understand key processes and structural elements in the system that the model represents. The term conceptual model may be used to refer to models that are formed after a generalization of processes and linkages. Conceptual models are typically the seemingly implementation and abstractions of things in the real world, whether physical, ecological or social, and are typically qualitative and descriptive, without attempting to formulate quantitative predictions. They are constructs. As such, they offer a system-wide perspective and often represent the framework around which quantitative models are built. Conceptual models advance and communicate our understanding by simplifying the complexity of multi-component systems (e.g. ecosystems) and allow us to focus on the salient processes and structural elements of such systems.

A conceptual model should be integrative, adaptive, anticipatory and succinct. Thus, in the evolution of any given scientific investigation, a conceptual model is useful in: A) defining the initial scope of the problem, establishing testable hypotheses and developing experimental design; B) adapting program design during the course of the investigation as new information is acquired; and C) summarizing and communicating final results. Guidance can be applied to the development of field programs, targeted experiments, numerical modelling and outreach. A unified and pan-Arctic conceptual model for the AO, hosting a nested array of additional models addressing specific regions and processes, can thus be instrumental in providing a shared understanding; this will allow improved coordination in research efforts addressing the AO in a time of change, while also minimizing the research gaps. By simplifying complex ecosystems into their core structural elements, linkages and functional processes, conceptual models provide a powerful tool to formulate hypotheses that inform scenarios of future change and evaluate intervention options. For an example of the application of conceptual models, see Appendix 2.

1.2. Approach and goal

What do we wish to achieve here? Step by step, we wish to build up a hierarchy of unifying and comprehensive physical and ecological conceptual models for the AO. We attempt to generate shared, high-level paradigms that synthesize our understanding of the key processes and elements governing the response of the AO ecosystem in relation to current pressures and changes. We aim at doing so by summarizing existing and generating new, interdisciplinary and parsimonious conceptual models of the functioning of the AO.

We try to raise the attention of current and future AO scientists and managers to prepare for a more holistic understanding of the new emerging ocean; an understanding that is required if the goals of sustainability are to be met (cf. Arctic Council, 2016; Auad et al., 2018). The interconnected ecosystem elements and concepts of the AO will then contribute to a generic understanding where new research can be placed into existing conceptual models. We finish by discussing how knowledge-based ecosystem and resource management in today's and the future AO can be shaped out of an adaptive and anticipatory conceptual model approach, how it can support the integration of indigenous and local knowledge and how communication with the general public can be strengthened.

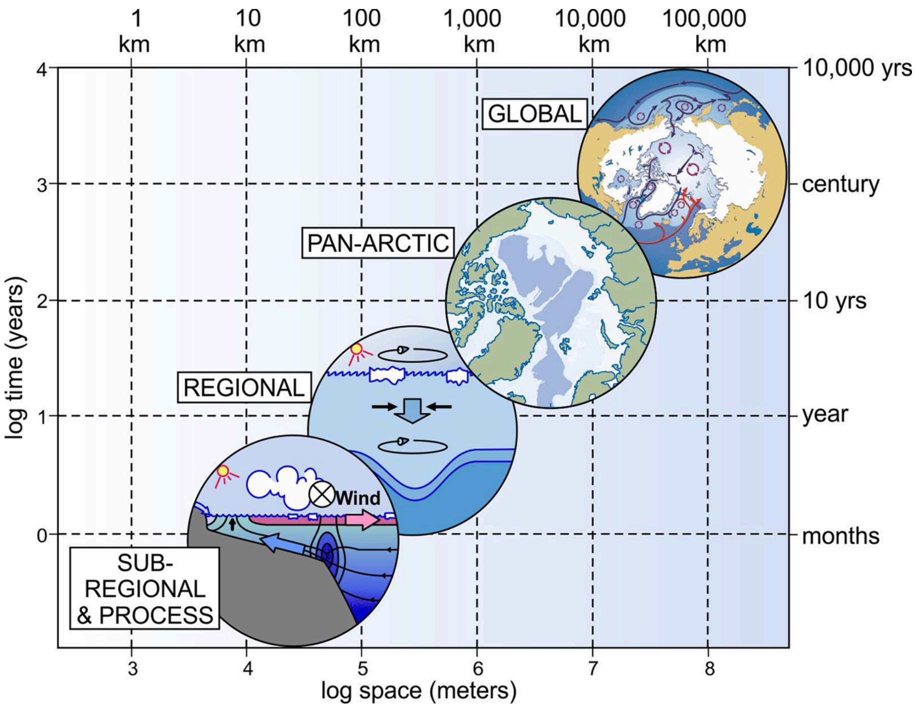

Fig. 2. A highly schematic, Sverdrup-type diagram that shows spatial and temporal scales that couple global, pan-Arctic and regional marine systems in descending log scales of space and time. The global scale recognizes the interactions of global scale processes (thermohaline circulation, hydrological cycle, atmospheric forcing), and is externally forced by even large scales. The pan-Arctic marine system, the focus of this paper, is nested at smaller spatial and temporal space and time scales. It is fully coupled to the global marine system through exchanges of energy, freshwater, water masses and material properties including, for example, the Atlantic and Pacific through-flows and the delivery of freshwater to regional drainage basins by atmospheric transport. The pan-Arctic marine system is, in turn, underlain by regional domains, as discussed in Section 2 including inflow shelves, interior shelves, outflow shelves, the pan-Arctic shelf-break and slope, the Eurasian and Amerasian basins, and major ridge systems (see Carmack and Wassmann (2006) and Bluhm et al. (2015) for discussion). Below are the mesoscale and submesoscale processes that act to regulate biogeochemical processes within specific regions. Forcing is often held to pass top-down from larger to smaller scales, while feedbacks and emergent properties are held to be driven bottom-up.

2. Global and pan-Arctic setting and basic physical function

The changes in the Arctic have already had unprecedented impacts and consequences across a range of economic (Alvarez et al., 2020), environmental (National Academy of Sciences, 2007), societal (Stephen, 2018) and geopolitical (Tingstad, 2018) realities in the lower latitudes, most notably the rising sea level, increases in extreme weather and substantial changes in international geopolitics. The Arctic and the northern oceans thus drive global-scale changes that further accelerate and amplify changes within the Arctic (IPCC, 2018). However, those changes, in turn, drive unprecedented changes affecting the rest of planet Earth, particularly the Northern Hemisphere (AMAP, 2017). A genuine evaluation of the function of the AO demands a global context and a pan-Arctic perspective (Fig. 1).

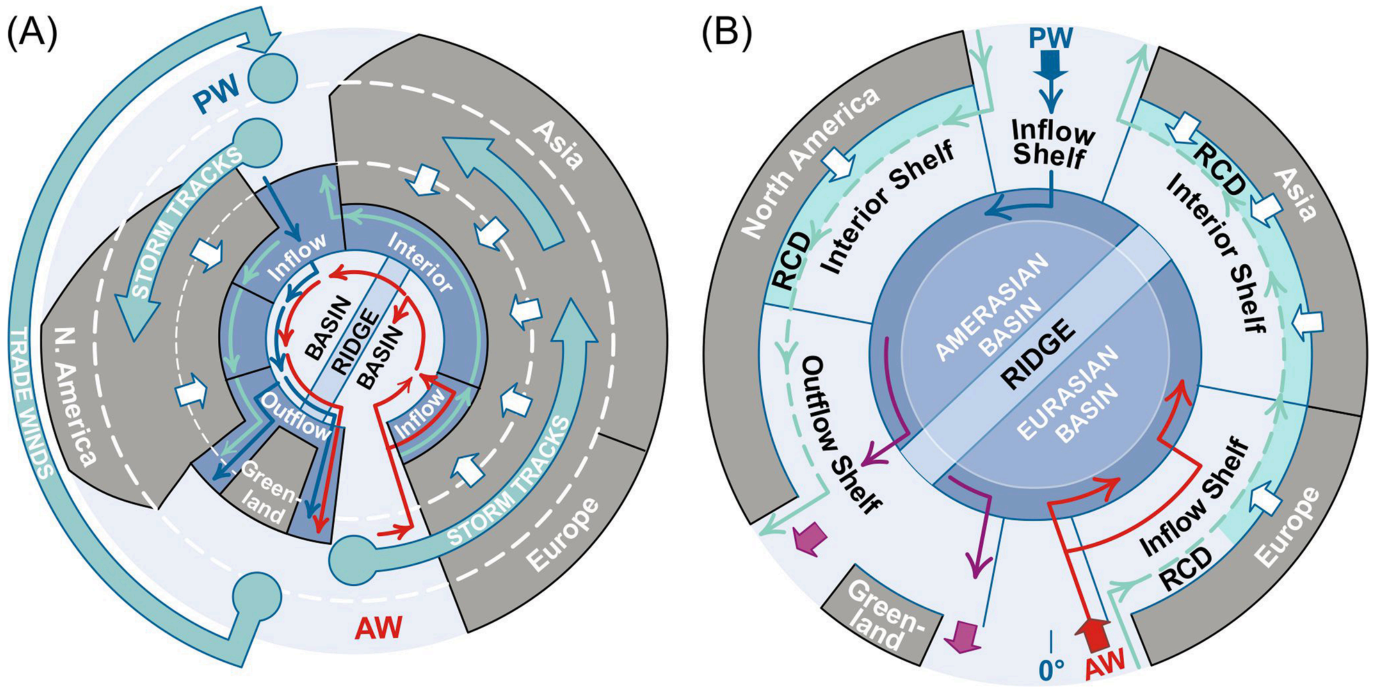

Fig. 3. Functional connection of the Arctic Ocean at the pan-Arctic scale. To the left the figure comprises the entire Northern Hemisphere, including the continents and the transportation of moisture by trade winds to the North Pacific and the westerly storm tracks (A). To the right scheme the focus is upon the functional connections of the Arctic Ocean and adjacent watershed (B). The schematic depicts the currents linking the Pacific, Arctic and Atlantic Oceans, the main pathways of moisture transport to Arctic drainage basins, the northward flow of rivers to the Arctic Ocean, the establishment of low-salinity coastal currents by river inflow, and the primary geographical domains. Redrawn from Bluhm et al. (2015) and Carmack et al. (2016).

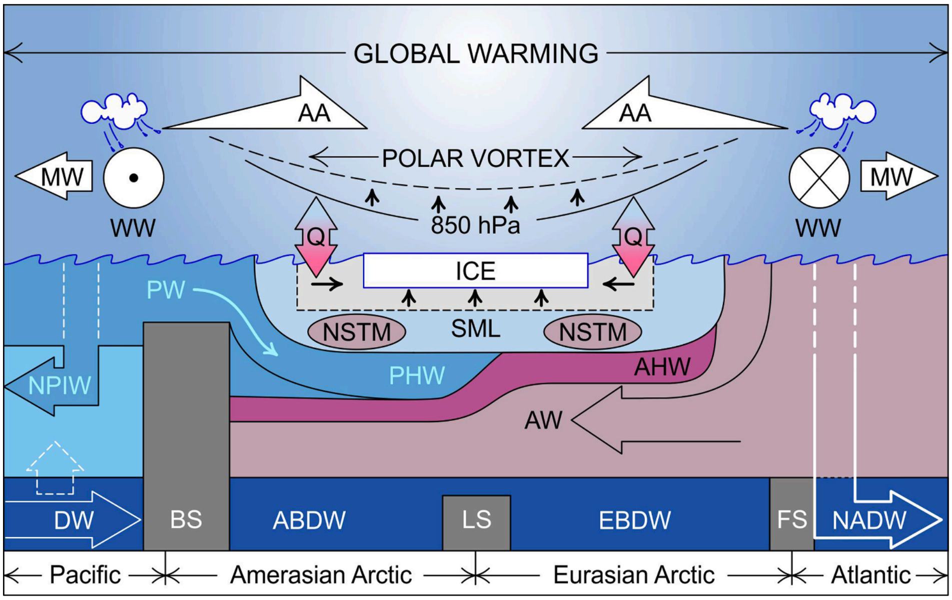

Fig. 4. Schematic representation of the basic structure and hydrological functions of the Arctic Ocean and the coupling of Arctic and subarctic marine and atmospheric systems under Arctic warming. The 850-mbar surface is taken as representative of the Polar Vortex that was previously prominent, but which is now broken up into a multitude of vortecies, allowing in recent years for significant variability in Arctic Ocean weather. Abbreviations are: AA Arctic amplification with tapering indicating increased poleward warming; WW Westerly wind with eddy flux convergence occurring along the Westerly wind maximum; MW meridional winds associated with Jet Stream meanders; Q ocean/atmospheric heat exchange; in the center the sea ice, fresh-water stratification and SML (Surface Mixed Layer); NSTM near surface temperature maximum forming near expanding open water areas; PW low salinity Pacific water inflow; AW high salinity Atlantic water inflow; NPIW North Pacific Intermediate water in the subarctic Pacific; DW is deep water, for which North Pacific, Arctic Ocean and North Atlantic varieties exist; PHW and AHW are Pacific and Atlantic Halocline Water. Take note of the strong stratification by various water bodies in the central Arctic Ocean. See text for changes and feedbacks. Redrawn from Carmack et al. (2012b).

The AO is roughly half continental shelf and half basin and ridge complex. Currently, it is approximately two thirds seasonally and one third perennially ice-covered, that now exposes an increasing portion of basin waters to sunlight and wind (Bluhm et al., 2015; Wadhams, 2017). The necessary starting point in developing a unified perspective is to recognize that the Arctic marine system is strongly coupled to the global system and that this coupling is bi-directional, with the global ocean affecting the Arctic and the Arctic strongly affecting the global ocean. Maintaining this perspective requires an internally consistent and logical use of scale, both spatial and temporal, in the development of nested and adaptive conceptual models. Fig. 2 is a highly schematic, Sverdrup-type illustration grouping the spatial and temporal scales that encompass global, pan-Arctic and regional systems; simply starting with this perspective helps us in setting research goals and efforts. The global marine system scale is represented by large spatial and time scales and is itself externally forced by even larger scales. The pan-Arctic marine system, the focus of this paper, is nested at smaller spatial and temporal scales and is coupled to the global marine system through exchanges of energy, freshwater, water masses and material properties with bordering subarctic oceans and terrestrial land masses (Fig. 1). This system, in turn, is underlain by regional and contiguous domains, as discussed below in Sections 3 and 4. Beneath the regional scale are the various mesoscale and sub-mesoscale processes that advect material properties and act to regulate biogeochemical rates and processes within specific regions. Energy and physical forcing pass top-down from larger to smaller scales (fluid dynamics: from gyres over whirls to viscosity), while feedbacks and emergent properties are driven bottom-up (Easterling and Kok, 2002).

The AO's thermohaline structure and circulation are forced at the global scale with freshwater delivery to the AO by the atmosphere as demanded by the climate system to transport heat (in this case as latent heat) from the low to high latitudes, and by the subsequent need to redress the resulting ocean salt balance through the meridional thermohaline circulation. The transport of heat and moisture begins with the Trade and Westerly winds which carry moisture first from the Atlantic to the Pacific and continues with the Westerly winds which carry moisture to the Arctic drainage basins (Fig. 3A). In contrast to the southern hemisphere, the configuration of continents in the northern hemisphere is such that they effectively capture precipitation from the storm tracks of the Westerlies and redirect in north-flowing rivers disproportionate quantities of freshwater into the mediterranean configuration of the AO (Fig. 1A). The unequal areal coverage of lakes in high-latitude drainage basins further affects freshwater storage, modification and release timing to the ocean (Verspoorter et al., 2014). Hence, while the AO represents only 1% (in terms of volume) and 3% (in terms of surface area) of the global ocean, it collects over 11% of the global river discharge (Dai and Trenberth, 2002; McClelland et al., 2011; Carmack et al., 2016). Briefly, thus, the freshwater budget of the AO (determining stratification and ice-cover) is governed by: the delivery of fresh and low-salinity waters to the AO by river inflow, net precipitation, distillation during the freeze/thaw cycle and Pacific Ocean inflows; the disposition (e.g. sources, pathways and storage) of freshwater components within various domains of the AO (e.g. basins, shelves, coastal zone); and the release and net export of freshwater components into the bordering convective domains of the North Atlantic (Aagaard and Carmack, 1989; Carmack et al., 2016; Brown et al., 2020a).

The AO joins the global ocean through the inflow of both Pacific-origin water (PW) through the shallow (~50 m) Bering Strait into the Canada Basin, and counter-flowing Atlantic-origin water (AW) through the eastern portion of the deep (~2600 m) Fram Strait and across the relatively deep (200–400 m) Barents Sea shelf into the Nansen Basin (Fig. 1B). Depending on pathways and mixing history, the incoming AW exits the AO as either; (a) a lighter (fresher) component by mixing with freshwater or (b) denser (more saline) component than came in by cooling and brine formation. Consequently, at the pan-Arctic scale, the system acts as both a positive and negative estuary (Carmack and Wassmann, 2006; Fig. 4). Modified forms of PW and AW exit through the western Fram Strait and Davis Strait gateways (Fig. 1B). The considerable stratification of the AO is partly shaped, entangled and driven by westerly winds that create the Polar Vortex features (Fig. 4).

3. Regionality: hydro-morphological features and biogeochemical cycling of shelves, the shelf-break and deep basins

While the pan-Arctic system is the focal scale of this work, it is of

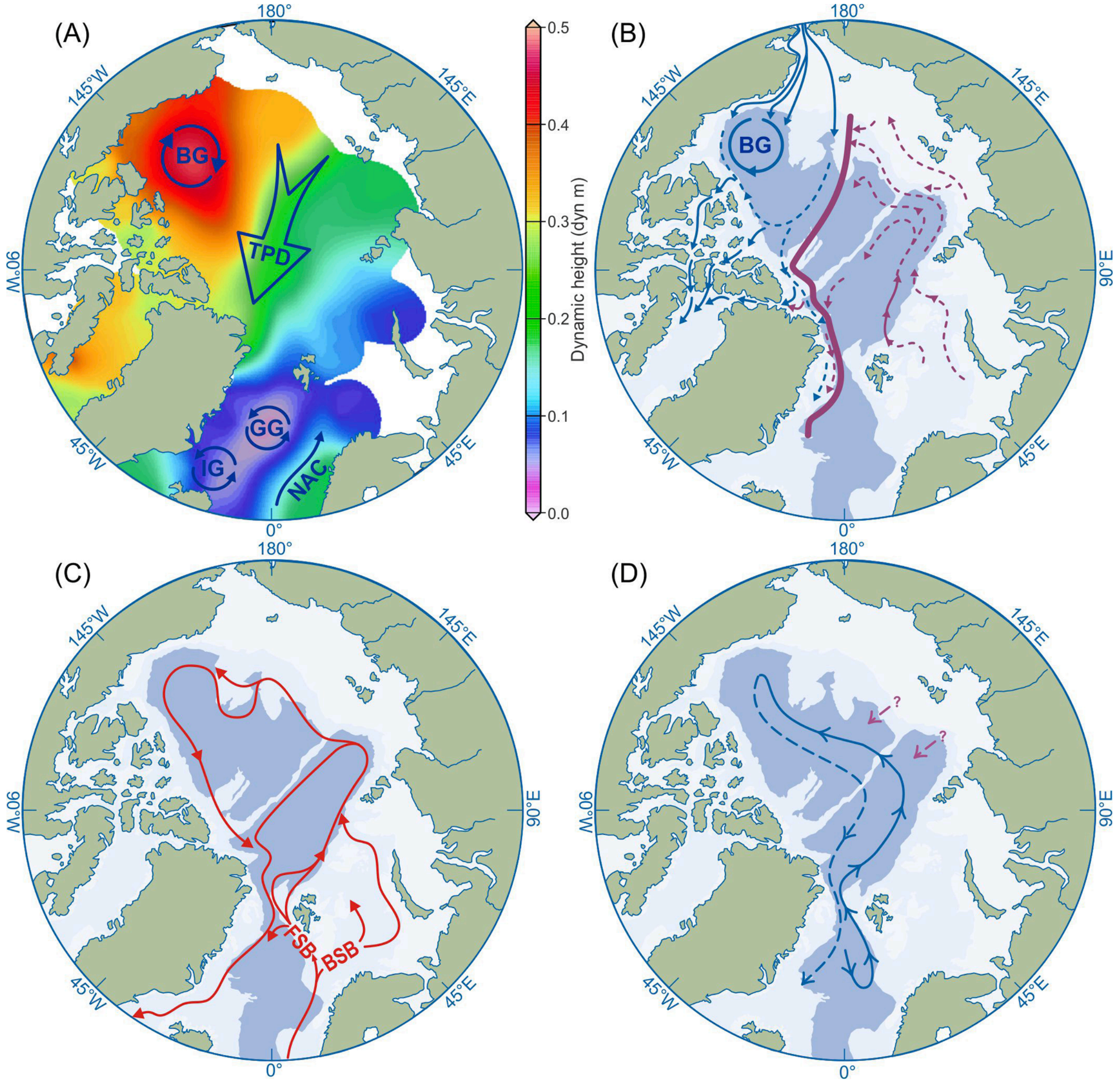

Fig. 5. Schematic representation showing four large-scale circulation systems (with L > 1000 km); these are: (A) the large scale wind-driven circulation which forces the cyclonic Trans-Polar Drift (TPD) from interior shelves of Siberia to the export shelf of the Fram Strait and the anticyclonic Beaufort Gyre in the southern Canada Basin (BG): also shown are the Icelandic and Greenlandic Gyres (IG and GG, respectively) and the North Atlantic Current (NAC); (B) the circulation of waters that comprise the halocline complex, composed largely of waters of Pacific (blue) and Atlantic (red) origin that are modified during passage over the inflow and Siberian interior shelves, respectively (the thick, red line is the P/A front); (C) the topographically-trapped Arctic Circumpolar Boundary Current which carries AW cyclonically around the boundaries of the entire suite of basins (FSB and BSB are the Fram Strait and Barents Sea Branch), and (D) the very slow exchange of Arctic Ocean Deep Waters that enter on the eastern and leave on the western Fram Strait. Redrawn from Bluhm et al. (2015). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

critical significance to recognize the nested, component parts of the system. This is important to guide the selection of appropriate regional-scale applications, and not to overgeneralize findings from a particular region to the entire system (for example, see Polyakov et al., 2018). We thus follow approaches by Carmack and Wassmann (2006) and Bluhm et al. (2015) and distinguish among basic shelf, shelf-break and basin regimes on the basis of topography, hydrography and biogeochemical function.

The shelf, shelf break and basin regimes are an integrated part of the physical oceanography and connected through currents. Four large-scale circulation systems can be distinguished. In the uppermost layers down to about 200 m depth we find the wind-driven circulation that forces the cyclonic Trans-Polar Drift (TPD) from interior shelves of Siberia to Fram Strait and the anticyclonic Beaufort Gyre in the southern Canada Basin (Fig. 5A). Below, we find the circulation of waters that comprise the halocline complex, composed largely of waters of Pacific and Atlantic origin that are modified during passage over the inflow and Siberian interior shelves (Fig. 5B). Under which lies the topographically trapped Arctic Circumpolar Boundary Current that carries AW cyclonically around the boundaries of the entire suite of basins (FSB and BSB are the Fram Strait and Barents Sea Branch) (Fig. 5C). At depth we find the slow exchange of Arctic Ocean Deep Waters that enter on the eastern and leave on the western Fram Strait (Fig. 5D).

3.1. *Shelf types and basic biogeochemical function*

The shelves of the Arctic Mediterranean are strikingly different from those of the remaining World Ocean. No other ocean comprises as much shelf area as the AO: >50% (Jakobsson et al., 2008). Being so dominant and increasingly exposed to sunlight, emphasis on these shallow realms, bounded by a narrow and steep shelf-break and slope, is needed to understand their functional dynamics (Fig. 5). In order to obtain a more adequate perspective of the pan-Arctic shelves we expand on the typology proposed by Carmack and Wassmann (2006). Inflow, interior

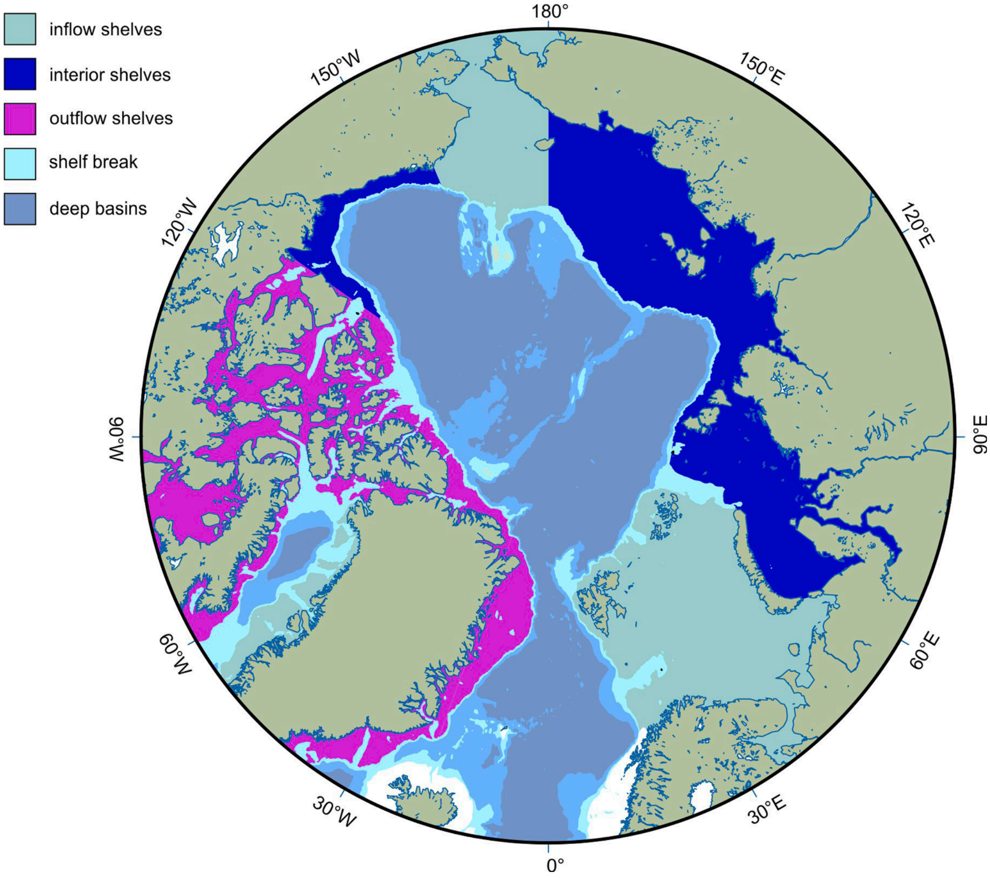

Fig. 6. Three shelf types exist in the Arctic Ocean: inflow (tourquoise-gray), interior (blue) and outflow (pink) shelfs. Also shown (turquoise) is the shelf-break and upper slope region that surrounds the outer shelves and the deep Canadian and Eurasian basins (gray). Redrawn from Carmack and Wassmann (2006). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and outflow shelves are distinguished (Fig. 6), which represent entirely different functional shelf types that shape and are shaped by their biogeochemical roles (Fig. 7). Among the three basic shelf types we further differentiate between the shallow and deep inflow shelves (Northern Bering Sea/Chukchi Sea and Barents Sea, respectively; e.g. Wassmann et al., 2006; Hunt et al., 2013), the narrow and wide interior shelves (Beaufort Sea and Kara/Laptev/East Siberian Seas, respectively; e.g. Williams and Carmack, 2015) and the branching and longitudinal outflow shelves (Canadian Archipelago and east-Greenland shelf, respectively; e.g. Michel et al., 2015; Fig. 7).

3.1.1. *Inflow shelves*

During transit of inflowing subarctic waters along western Spitsbergen and across the Barents, Bering and Chukchi Seas the waters are strongly shaped and altered by biogeochemical and physical processes (Sakshaug et al., 1994; Grebmeier et al., 2015; Vernet et al., 2019; Fig. 7). Transformations during transit depend on the width and depth of the shelves that, in turn, affect the water's residence time, in particular in the biogeochemically active layers (the euphotic zone and the benthic boundary layer). These waters subsequently subduct at fronts (e.g. the Polar Front in the Barents Sea) or along the shelf-break (e.g. north of Svalbard), and thus influence property distributions within the Arctic basin (e.g. Polyakov et al., 2013, 2017). Inflow shelves also play an important role during the advection of pelagic organisms, in particular zooplankton (Kosobokova and Hirche, 2009; Wassmann et al., 2015; Ershova et al., 2015a, Hunt et al., 2016). The direct supply of freshwater from rivers to the southern Barents Sea is relatively low, and consequently stratification of surface waters is weak in the relatively deep southern Barents Sea. In contrast, stratification is relatively strong in the northern Barents Sea, the site of the Seasonal Ice Zone (SIZ) and is enhanced by ice melt and inputs from the massive Siberian rivers (Smedsrud et al., 2013). On the other inflow shelf, the supply of relatively fresh Pacific Water (PW) through the shallow Bering Strait and local ice melt support a much stronger seasonal stratification in the Chukchi Sea (Woodgate et al., 2006, 2015).

Inflow shelves have by far the highest primary production within the AO, comprising about two-thirds of the total (Sakshaug, 2004; Matrai et al., 2013; Varela et al., 2013; Lee et al., 2015). It is for the most carried out by ice-algae and phytoplankton, but benthic microalgal production in the Arctic has not been studied adequately, but estimates have been provided that microalgae play a significant role (Glud et al., 2009). The introduction of nutrients and advection of suspended biomass is an essential feature of inflow shelves and is particularly significant in the shallow Bering Strait and adjacent Chukchi Sea where it directly fuels a biomass-rich benthic community (Grebmeier et al., 2015). Also, advection of larger zooplankton and propagules of benthic biota from sub-Arctic or boreal regions onto and over the inflow shelves is an essential aspect of their specific functionality (Wassmann et al., 2015; Ershova et al., 2015b, 2019; Silberberger et al., 2016) (see Section 4). The resulting biological community structure in both water column and at the seafloor reflects their boreal to Arctic sources (Anisimova, 1989; Hopcroft et al., 2010; Ershova et al., 2015a; Fossheim et al., 2015).

3.1.2. *Interior shelves*

Interior shelves are all shallow and are characterized by the impact of major rivers, such as the Yenisei, Ob, Lena and Mackenzie Rivers, and numerous smaller rivers (Williams and Carmack, 2015). The major distinction between Eurasian and Amerasian interior shelves is that the Eurasian interior shelves are several hundred km wide while those of North America are much narrower (Figs. 6, 7). Interior shelves exhibit a

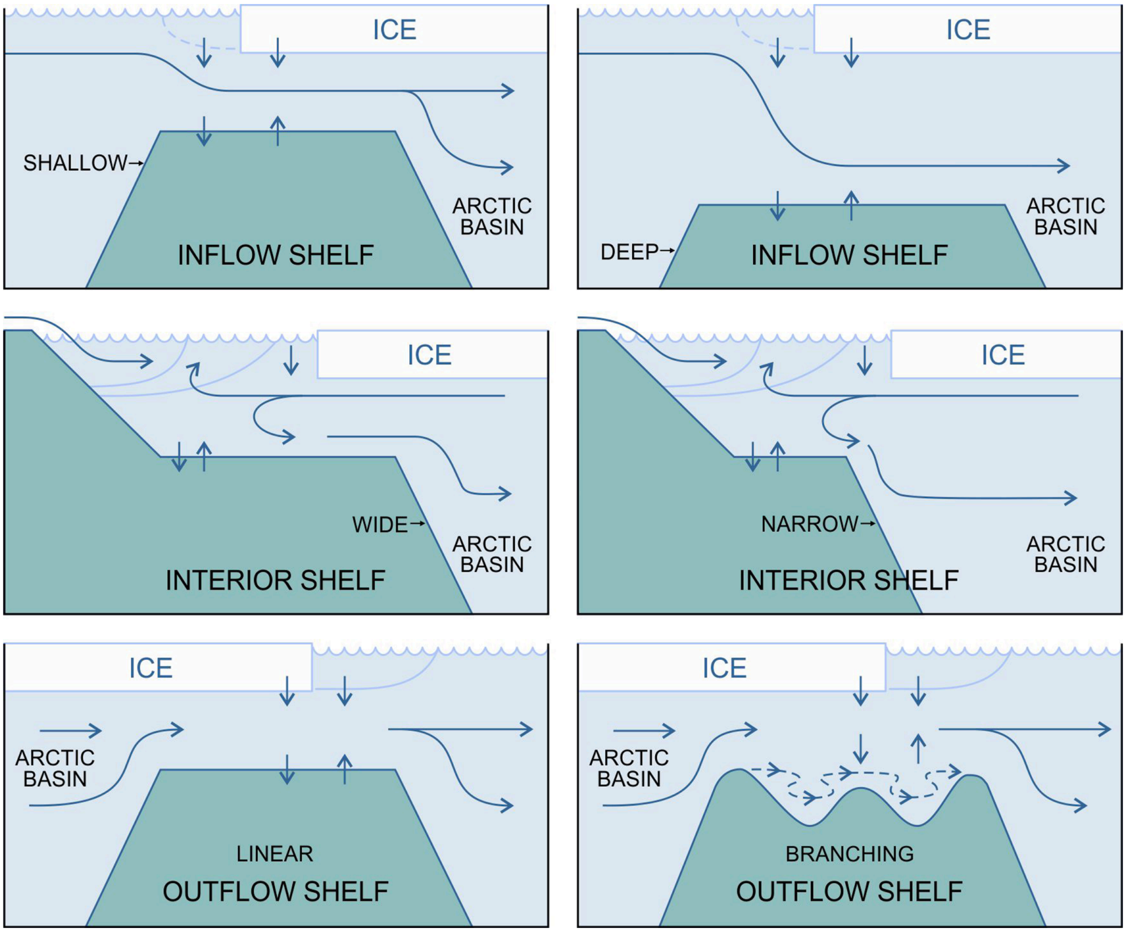

Fig. 7. Typology of distinct shelf types in the Arctic Ocean: inflow (top), interior (middle) and outflow (bottom) shelves. Among these categories one may separate deep (left) and shallow (right) inflow shelves, wide (left) and narrow (right) interior shelves, and linear (left) and branched/topography-rich (right) outflow shelves. Following this, the Barents Sea is a deep and the Chukchi Sea is a shallow inflow shelf. The Kara, Laptev and East Siberian Seas are wide interior shelves, while the Beaufort Sea is a narrow inflow shelf. The East Greenland shelf has banks and troughs but is "linear" while the Canadian Arctic Archipelago has a branched and topographically complex shelf. Redrawn and updated from Carmack and Wassmann (2006).

positive estuarine circulation (river plume spreading) in summer and a negative estuarine circulation (caused by brine drainage during sea ice formation) in winter (Carmack and Wassmann, 2006). During periods of river plume spreading, the nearshore flocculation of estuarine and marine matter (both particulate and dissolved) is high but decreases offshore with distance from the river deltas (e.g. Lasareva et al., 2019). The combined effects of wind and tides on this process can be significant and can thus enhance or reduce the dispersion of plume water towards the sea. Below the freshened surface layer, the estuarine circulation transports seawater towards the littoral zone (McClelland et al., 2011). The horizontal exchange of water masses is thus substantial and sometimes results in the formation of multiple fronts; horizontal variations in salinity are, therefore, large. The load of terrigenous matter from the rivers can be large and, thus, turbidity and light extinction is high (Goñi et al., 2013). The innermost portion of interior shelves is characterized by landfast ice that melts during summer (Mahoney et al., 2014). When pack ice collides against the landfast ice, and between these two ice types, bands of ridges (stamukhi) form under convergent and flaw polynyas under divergence conditions. The presence of this stamukhi zone can also act as an ice dam, impeding the spreading of river water over the shelf in early spring in particular in the Beaufort Sea and possibly other regions (McClelland et al., 2011).

Compared to the inflow shelves, the biogeochemical transformations taking place on interior shelves are different in that they are dominated by processing of terrestrial carbon (Fig. 7). The supply of terrestrial carbon into the interior shelves is transformed into usable food for marine organisms by bacteria and this comprises an increasingly important food source for Arctic biota, as already observed for freshwater systems (Dunton et al., 2012; Taipale et al., 2016). Photosynthetic primary production and the general biological activity are lower than on inflow shelves, and much of the allochthonous matter is of a refractory nature (Divine et al., 2015; Bell et al., 2016). High turbidity and export of surface waters below the ice cover, followed by nutrient limitation due to strong salt stratification are the main causes for the low primary production (Babin et al., 2015). Biomass of planktonic organisms is thus comparatively lower than on inflow shelves although hot spots may occur in certain areas (Smoot and Hopcroft, 2017a); biomass of benthic organisms is equally highly variable but also generally lower than on inflow shelves (Dunton et al., 2006; Ravelo et al., 2015). Some of the food for the benthic organisms is of marine origin and derives from the estuarine circulation bringing deeper waters onshore, some is locally produced, and a significant amount derives from littoral and riverine sources (Dunton et al., 2012; Stasko et al., 2018). Biological community structure in the water column and at the seafloor clearly differ from those in inflow shelves due to both the increased significance of Arctic species, and the importance of freshwater and terrestrial carbon inputs (Deubel et al., 2003; Hirche et al., 2006; Garneau et al., 2009; Ershova and Kosobokova, 2019). Sustained easterly winds promote upwelling over the shelf-break, particularly when ice cover is reduced (Carmack and Chapman, 2003; Williams et al., 2006; Spall et al., 2014; see 3.2). The combined effect results in different nutrient upwelling scenarios on narrow and wide shelves (Fig. 7). For example, upwelling of offshore nutrients may reach the innermost shelf region and strongly stimulating primary production along the narrow shelves of the Beaufort Sea (Tremblay et al., 2011). Whereas on the wide shelves off Siberia upwelled nutrients are presumably limited to the vicinity of the shelf-break.

3.1.3. Outflow shelves

Outflow shelves bring Arctic and Pacific halocline water back into the North Atlantic (i.e. the Nordic and Labrador Seas) via the Canadian Arctic Archipelago and along the east coast of Greenland (Figs. 6, 7). The outflow shelves are not simple gates or channels, rather transit times of out-flow shelves are sufficiently long for thermohaline and biogeochemical changes to occur en route (Michel et al., 2015; Frey et al., 2019). The Canadian Arctic Archipelago in particular has long and highly variable flow-through and residence times (McLaughlin et al., 2004). On the whole, the Archipelago is a complex network of channels, sub-basins and sills, while the east Greenland shelf is less structured but deeper. The Archipelago which can be divided into a) Beaufort-Amundsen, b) High Arctic, c) Baffin - Labrador, d) Kitikmeot and e) Hudson-Foxe regions (Oceans North Conservation Society, World Wildlife Fund Canada, and Ducks Unlimited Canada, 2018) is currently ice-covered during most of the year with extensive, but variable, ice-melt and stratification observed during summer and early autumn. Heavy ice and multiyear ice cover the northern-most portions of outflow shelves and sea ice export strongly contributes to structuring spatially diverse productivity regimes (Michel et al., 2015). However, sea ice conditions demonstrate significant declines in multi- year ice and a redistribution of ice types over the past three decades (Wadhams, 2017).

The average current direction of the longitudinal East Greenland and Baffin Island outflow shelves is basically parallel to the ice edge but is also influenced by a combination of tidal mixing and wind-forced up and downwelling (Rysgaard et al., 2020). Also, the longitudinal outflow shelves of the western Fram Strait are, to various degrees, perpetually covered by pack ice transported from the Transpolar Drift (TPD). Most of the ice produced in the AO melts along these longitudinal outflow shelves. This results in significant stratification and reduced salinity of the East Greenland Current.

Primary production and associated community structure on outflow shelves are spatially variable (Ardyna et al., 2011, 2013; Mayot et al., 2018; Michel et al., 2015). In the southernmost network sections of the Canadian Archipelago outflow shelf, primary production can be significant (Tremblay et al., 2006). Generally, however, low nitrate concentrations in eastern Greenland shelf water (except adjacent to fjords and mixing/upwelling supporting topography; Rysgaard and Gissel Nielsen, 2006; Rysgaard and Glud, 2007) and continuous ice export are thought to be responsible for comparatively low primary production (Michel et al., 2015). The contribution of ice algae production is thought to be high at least in the southern network of the Canadian Arctic outflow shelf (Matrai and Apollonio, 2013). Primary production is highly seasonal, quickly nutrient limited and proves to be highly variable between years. The zooplankton dynamics are even more variable, probably due to irregular advection episodes through the Canadian Archipelago (Hamilton et al., 2009; Apollonio, 2013). Of all Arctic shelves, the outflow shelves have the largest area of coastal hard substrates, most high flow passages, the most abundant proximal glaciers and some of the most prominent polynyas, all resulting in highly variable – yet poorly mapped - benthic communities (Kenchington et al., 2011; Roy et al., 2015). In contrast to most other shelves, the coastal areas of outflow shelves include long stretches and increasing biomass of macroalgae primary producers (Krause-Jensen et al., 2012; Filbee-Dexter et al., 2019). Polynyas of various sizes play a role as local hot spots (Smith and Barber, 2007; Vincent, 2019), with close pelagic-benthic coupling in pockets of high vertical mixing (Ambrose and Renaud, 1995).

3.2. Shelf-break and slope types and basic biogeochemical function

The shelf-break (submerged offshore edge of a shallow continental shelf, where the seafloor transitions to continental slope) and upper slope (seaward border of the continental shelf) form the transition zone between shelves and basins, comprising the approximate depth range of 200–1000 m in most areas (Fig. 6; Jakobsson et al., 2008). The lower slope extends to the transition to the continental rise which in the AO is mostly between 2000 and 3000 m. The shelf-break and upper slope are characterized by strong gradients in physical, chemical and biological properties over a narrow horizontal band (see Section 4.2.2). It encircles the two main Arctic basins and forms a contiguous feature stretching counterclockwise ~8000 km from northwest Svalbard to northeast Greenland (Fig. 6). The belt is influenced by three key physical-ecological processes: i) one that is thermohaline driven and along-slope, ii) one that is wind-forced and cross-slope and iii) one that is tidally-driven and promotes internal wave generation and vertical mixing.

The shelf-break and slopes of the AO play a significant role in its overall physical oceanography and biogeochemical cycling. The topographically-trapped Arctic Circumpolar Boundary Current (ACBC) carries AW, heat, nutrients, organic matter and zooplankton cyclonically along the shelf-break and upper slope around the boundaries of the entire suite of AO basins (Woodgate et al., 2001; see Fig. 5C and Section 4.2). The ACBC along with canyons intersecting the upper slope also maintains fronts that appear to concentrate biological aggregations (Bluhm et al., 2020 and references therein).

The recent decrease in summer ice cover on the shelf edge supports increased upwelling and has fundamentally changed the productivity and stratification along the circum-Arctic shelf-break (Williams and Carmack, 2015; Bluhm et al., 2020; see Section 3.2). Along the Eurasian and western Amerasian shelf-break, nutrient availability has increased, while the accumulation of ice and freshwater along the slopes of northeastern Canada and northern Greenland have contributed to increased stratification, preventing open water and upwelling (Slagstad et al., 2015). Increased solar radiation, coupled with upwelled nutrients have induced a significant increase in new production on the Eurasian and western Amerasian shelf edges to levels similar to those experienced on the adjacent shelves (Tremblay et al., 2011). Cross-slope connectivity also includes shelf-to-basin processes including brine-drainage during sea ice formation, contributing to halocline formation, and transport of riverine and shelf-derived materials down slope.

Stratification along the slope regions north of Svalbard appears to have decreased due to increased influence of AW (Polyakov et al., 2017, 2018; Lind et al., 2018), with an increasing tendency of AW (and decreasing stratification) to spread eastwards towards Siberia. These changes in sea ice, river inflow and ice melt may change future vertical nutrient flux, accordingly, affecting primary production and phytoplankton size distributions (Randelhoff et al. 2015; Randelhoff and Guthrie, 2016). Advection of expatriate Atlantic or Pacific origin mesozooplankton is also characteristic of the slope domain (Kosobokova, 2012; Bluhm et al., 2015, Wassmann et al., 2015; Ershova et al., 2019). Numerical models project a doubling and tripling of primary production along the slopes on the Eurasian side and western Amerasian side, respectively (from north of Svalbard to the western Beaufort Sea) (Slagstad et al., 2015), while production remains low or even declines in the central AO and the north-eastern Canada/northern Greenland shelves.

3.3. Basin types and basic biogeochemical function

Two main basins occupy the deep central AO, i.e. the Eurasian and Amerasian basins, separated by the Lomonosov Ridge between the Greenland and Siberian shelves (Fig. 5D). In turn, the Eurasian Basin is divided into the Nansen and Amundsen basins by the Nansen-Gakkel Ridge, and the Amerasian Basin into the Makarov and Canada basins by the Alpha-Mendeleev Ridge. Deep basin domains are influenced both by their deep connection to the Atlantic (~2600 m) and shallow connection to the Pacific (~50 m), and by the broad shelves around

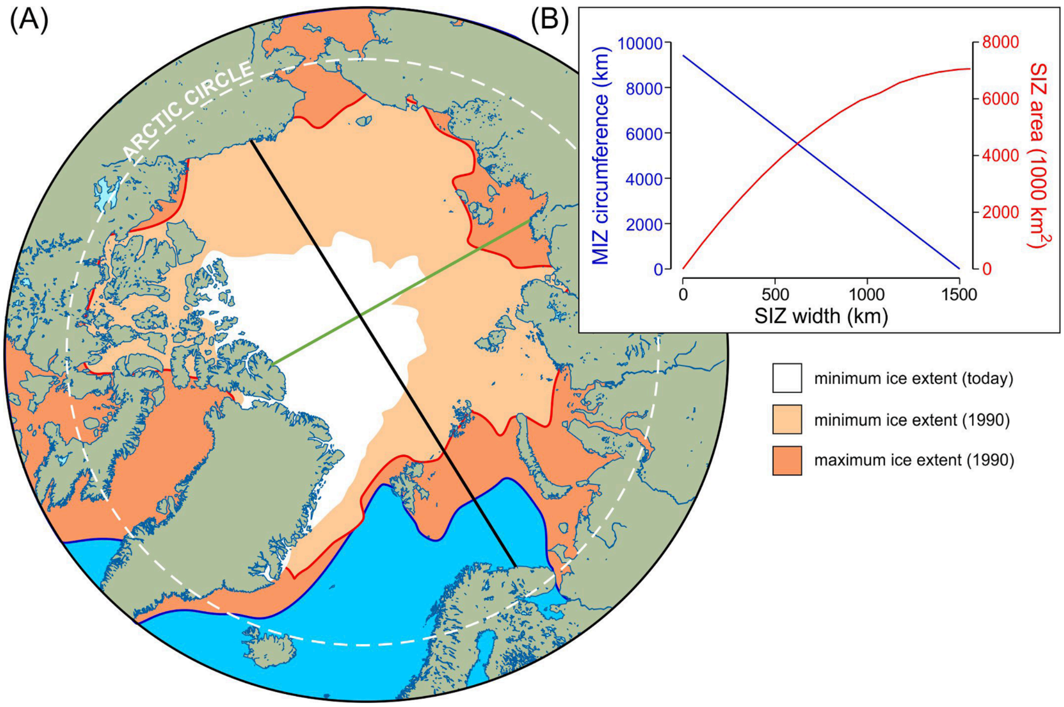

Fig. 8. Seasonal ice zone domain. A) Illustrates the maximum and minimum sea ice extent 30 years ago (dark orange and light orange, respectively). The white area depicts the recent minimum sea ice extent. Also shown are the transect lines illustrated in Fig. 9A (black) and 9B (green). (B) The relationship between the marginal ice zone (MIZ – outer rim of seasonal ice zone) circumference (km) and the seasonal ice zone (SIZ – zone between minimum and maximum ice extent) radii (km) in an assumed circular, ice-covered ocean. While the MIZ length decreases in a linear manner when the SIZ declines, the SIZ area (km^2) increases in curvilinear manner. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

them (Jakobsson et al., 2008). The ridges that separate the deep basins form boundaries for exchange of water masses and steering of deep ocean circulation, but counterintuitively play less of a role as barriers for the dispersal of biota (Kosobokova et al., 2011; Bluhm et al., 2011b; and reviewed by Bluhm et al., 2015).

Only one third of the deep Amerasian and Eurasian basins remain perennially ice-covered, seasonally exposing much of the basin area to sunlight and wind. Two basic water mass assemblies are observed within the basin domain, with the difference between them being the absence or presence of PW sandwiched between the Arctic Surface Waters (ASW) above and the AW complex below. The boundary between these domains is the Atlantic/Pacific halocline front (Figs. 4, 5). Both domains have vertical stratification that constrains (or even prevents) the transfer of nutrients to the euphotic zone, thus leading to their oligotrophic state, particularly in the more strongly stratified Amerasian Basin where, despite high nutrient concentrations in the inflow, a convective reset of surface layer nutrients by haline convection in winter is virtually absent. First and multi-year sea ice drastically alter albedo and insulate the underlying water column from extreme winter heat loss while its mechanical properties (thickness, concentration, roughness, etc.) greatly affect the efficiency of momentum transfer from the wind to the underlying water.

Owing to the mentioned nutrient limitation, coupled with light limitation due to snow and ice cover and extreme sun angle, primary production in the sea ice and the water column of the two basin domains is very low compared to the adjacent shelves (Gosselin et al., 1997). Severe nutrient limitation and complete euphotic-zone drawdown in the Amerasian Basin appear to favor small phytoplankton (Li et al., 2009, 2013), a ubiquitous deep chlorophyll maximum layer (Carmack and McLaughlin, 2011; Ardyna et al., 2013) and a low-energy food web (Iken et al., 2010). In contrast, nutrients persist in the western Eurasian Basin, even in summer, suggesting light limitation, heavy grazing or both as the dominant controls. Further these higher stocks of nutrients in the Eurasian Basin are more conducive to marginal ice zone blooms which are less abundant in the Amerasian Basin. Within the interior basins, the ice is now thinner and less compact, and thus more responsive to wind stress than in the pre-1970s (Gascard et al., 2008). Increased accumulation of freshwater strengthens stratification, particularly in the Amerasian Basin, and further constrains vertical nutrient flux. This affects phytoplankton size distributions, and thus limits primary production in parts of the basins now and likely in the future (Randelhoff and Guthrie, 2016; Randelhoff et al., 2020). The result of low nutrient surface waters is that vertical carbon supplies to the basin seafloor are low (Macdonald and Carmack, 1991; Wiedmann et al., 2020), largely advective (horizontal) and terrestrial in origin (Fahl and Stein, 1999), and generally support low benthic and fish biomass (Bluhm et al., 2011b; Mecklenburg et al., 2018; Zhulay et al., 2019), although localized islands of larger than anticipated biomass are now recognized (Vedenin et al., 2018).

4. Contiguous domains in the Arctic Ocean

The regional domains and their biogeochemical cycles discussed in Section 3 are linked to each other through contiguous domains. A contiguous domain is one whose components i) share a common boundary or set of properties and functions, and ii) are connected, over defined scales, in time and space. In our pan-Arctic scale application, we seek common functional traits or phenomena that appear continuously or at least once during an annual cycle. Contiguous domains may or may not link specifically to geography as they may cross and link regional and biogeographical domains. They may further expand or contract over interannual time scales. These linkages allow material transports and share key ecological functions and causal mechanisms (Carmack and McLaughlin, 2001; Carmack and Wassmann, 2006).

In investigating the AO through the conceptualization of contiguous domains, we take a macroecological view. In this way we examine patterns in water mass and species distribution, and in species abundance to i) determine relationships between abiotic and biotic factors, and further ii) to understand and model climate change impacted ecosystems along space-and-time climate gradients (Li et al., 2013; Fossheim et al., 2015). Macroecology deals with the study of relationships between organisms and their environment at large spatial scales to characterize and explain patterns of abundance, distribution and diversity. The perception gained from this view will prove valuable in the design of synoptic-scale research programs and the management and conservation of marine Arctic resources. It is a key to understand the ecological impacts of climate change that rely on a comprehension of the functions that each domain provides.

When considering conceptual models out of our pan-Arctic perspective, it is important to recognize which biogeographical scales come closest to matching those of the climate system itself (cf. Carmack and McLaughlin, 2001). Functions within a given contiguous domain are thus likely to share broad linkages in response to climate forcing. Conversely, the response of different contiguous domains to climate forcing may likely be qualitatively and quantitatively different, and failure to recognize the interplay of scale, regionality, seasonality and contiguity may lead to a current challenge deriving from our sectorial research approaches: over-extrapolation and misinterpretation. The contiguous nature of significant elements of the AO ecosystems requires thus a distinct pan-Arctic approach.

In defining contiguous domains in the AO, we attempt to lay the foundation for a better interpretation of previous and future investigations by placing the region in a more realistic time/space perspective. The AO is a beta ocean system (stratification permanently set by salt, in contrast to an alpha ocean where stratification is permanently set by heat) which defines hydrographic and ecosystem connections through the underlying cause of permanent stratification similarities; that is, salt (β) or temperature (α) stratification (Carmack, 2007). Within this system, we recognize 6 contiguous domains grouped by their reliance on seasonal (Section 4.1) or advective processes (Section 4.2).

4.1. *Contiguous domains constrained by seasonal processes: Seasonal ice zone domain*

The SIZ is the area of the AO that extends from the permanent ice zone to the boundary where winter sea ice extent is at a maximum (Fig. 8A). The Seasonal Ice Zone Domain (SIZD, see glossary) is mainly shaped through seasonal processes such as radiation and stratification and links shelves and basins i.e it is a pulsating, expanding and shrinking area. It is now the largest contiguous domain in the AO. It comprises the cumulative area that is temporarily ice-covered at any given time within a year, i.e. basically the area between maximum and minimum ice extent in a given year. In the period 1979–2000 the ice extent (area of ocean with at least 15% ice) ranged between 15.5 and 6,5 10^6 km^2 (maximum in March and minimum in September, respectively). Currently, the ice extent ranges between about 14.5 and 4 10^6 km^2. Thus, the maximum extension of the SIZD has decreased by about 1 10^6 km^2, while its current area has increased from about 9 to 10.5 10^6 km^2 (about the territory of the European continent). For details, see https://earth.gsfc.nasa.gov/cryo/data/current-state-sea-ice-cover. In recent decades the SIZD has thus increased by about 15% and will increase significantly more in the near future, when summer ice disappears from the North Pole.

Ice and snow limit the penetration of solar radiation and thus photosynthesis of ice algae and phytoplankton. Ice and stratification by ice melt reduce the impact of wind on vertical mixing and can support an ice edge bloom where and when nutrients are available, especially on the shelves. Thirty years ago, this domain was a narrow rim, limited in areal extent, rarely crossing the shelf-break, but climate warming has greatly decreased the area of summer ice cover (i.e. multi-year ice) while only marginally decreasing winter cover, thus resulting in vast widening of the SIZD (Fig. 8A). Global climate change has and had immense consequences on the SIZD and will continue to exert defining pressures on this domain for decades to come. As the knowledge base for SIZD dynamics – combined physical, biogeochemical and ecological - is limited, and where climate change in this domain is the most pronounced, the lack of key information is particularly discomforting. The number of time-series moorings and research platforms is small, and the expanding cover of the region means the SIZD is not well represented in any conceptual model. The past, present and future highly dynamic nature of the SIZD is exemplified in Figs. 8B and 9. The shrinking and expansion of the SIZD can be compared to the breathing of an organism. In summer, the SIZD breathes in, opens up for primary production and the unfolding of seasonal and perennial Arctic marine life. In autumn and winter, the SIZD breathes out, along with declining radiation, spreads the sea ice cover like a lid over the AO. The seasonal inhalation and exhalation of the SIZD sets the rhythm for the biological carbon pump and export production to the AO benthos (see Section 5.3).

The SIZ is created by annual ice melt and consists of two types of ice: drifting pack ice (that dominates by area) and landfast ice. Land fast ice is attached to the coastline, to the sea floor along above shoals, and to grounded icebergs in summer (Greenland). It is a defining feature of Arctic coasts and can extend hundreds of kilometers offshore (Mahoney et al., 2014; Yu et al., 2014; Dammann et al., 2019). Fast ice may either grow in place from sea water, sometimes with admixtures by river water (Eicken et al., 2005) or by freezing pieces of ice drifting to the shore or other anchor sites. In most regions the pack ice meets the fast ice during maximum ice cover. Here we find ridging, known as stamukhi; a partially grounded accumulation of sea ice rubble that typically develops along the boundary between fast ice and the drifting pack ice, or becomes incorporated into the fast ice. In addition to stamukhi we also find here polynyas, areas of sustained open water surrounded by sea ice (Macdonald and Carmack, 1991; Smith and Barber, 2007; Williams et al., 2007). Polynya is often used as a generic term for an area of unfrozen sea within the ice pack. Rapid ice melt of fast ice is also part of the SIZ, but this melt is much smaller by a factor of 3.3 by area (mean 1.84 million km^2 between 1975 and 2007, Yu et al., 2014) than that of the pack ice zone. Disproportionally high, however, is the use of land fast ice by horizontally or vertically migrating, feeding and/or resting marine life (Gradinger et al., 2009; Hamilton et al., 2017) and by local Arctic human communities for both travel and subsistence hunting (Eicken et al., 2009, 2014; Fox Gearheard et al., 2017).

Outside the land fast ice zone, we find the SIZ of the pack ice that is free-floating, not connected to land. It expands generally north- and inwards with the AO melting season. Before climate warming accelerated in recent decades, the summertime SIZ - assuming it was circular - had a width of ~ 1,500 km. The outer rim or circumference of the SIZ is the marginal ice zone (MIZ, the transition between the open ocean and sea ice, Strong et al., 2017) of>9,000 km (Fig. 8B). Previously the MIZ circumference was too long to be circumnavigated and studied synoptically during a single cruise. In the near future the maximum SIZD width will only be about 500 km and the MIZ circumference less than 6,000 km and could thus be circumnavigated in 2–3 weeks. The area of today's SIZ, at a width of 500 km is > 6 million km^2 (Fig. 8B) that still renders the investigation of the SIZ an enormous challenge for the low number of few available research platforms. The MIZ is biologically important because its stable upper layer of the water is mixed by a combination of ice melting and wind. This leads to a comparatively brief, but intense production of phytoplankton in the water masses near and inside the MIZ itself. Zooplankton, fish, marine mammals and seabirds exploit this and gather at the ice edge. The MIZ is therefore vulnerable to pressures and the biologically most active fringe of the SIZD pack ice. During summer the ice cover of the SIZD gets thinner and the large ice-covered SIZD supports ice algae and later phytoplankton (and ice algae) blooms, both in partially open water and under sea ice (Gradinger et al., 1999; Gradinger, 2009; Ardyna et al., 2014, 2020; Mayot et al., 2018). The majority of the ice algae bloom is not consumed inside the ice brine channel system by sea ice metazoans, but rather sinks out to provide food for pelagic and benthic organisms (Bluhm et al.

2010; Gradinger and Bluhm, 2020).

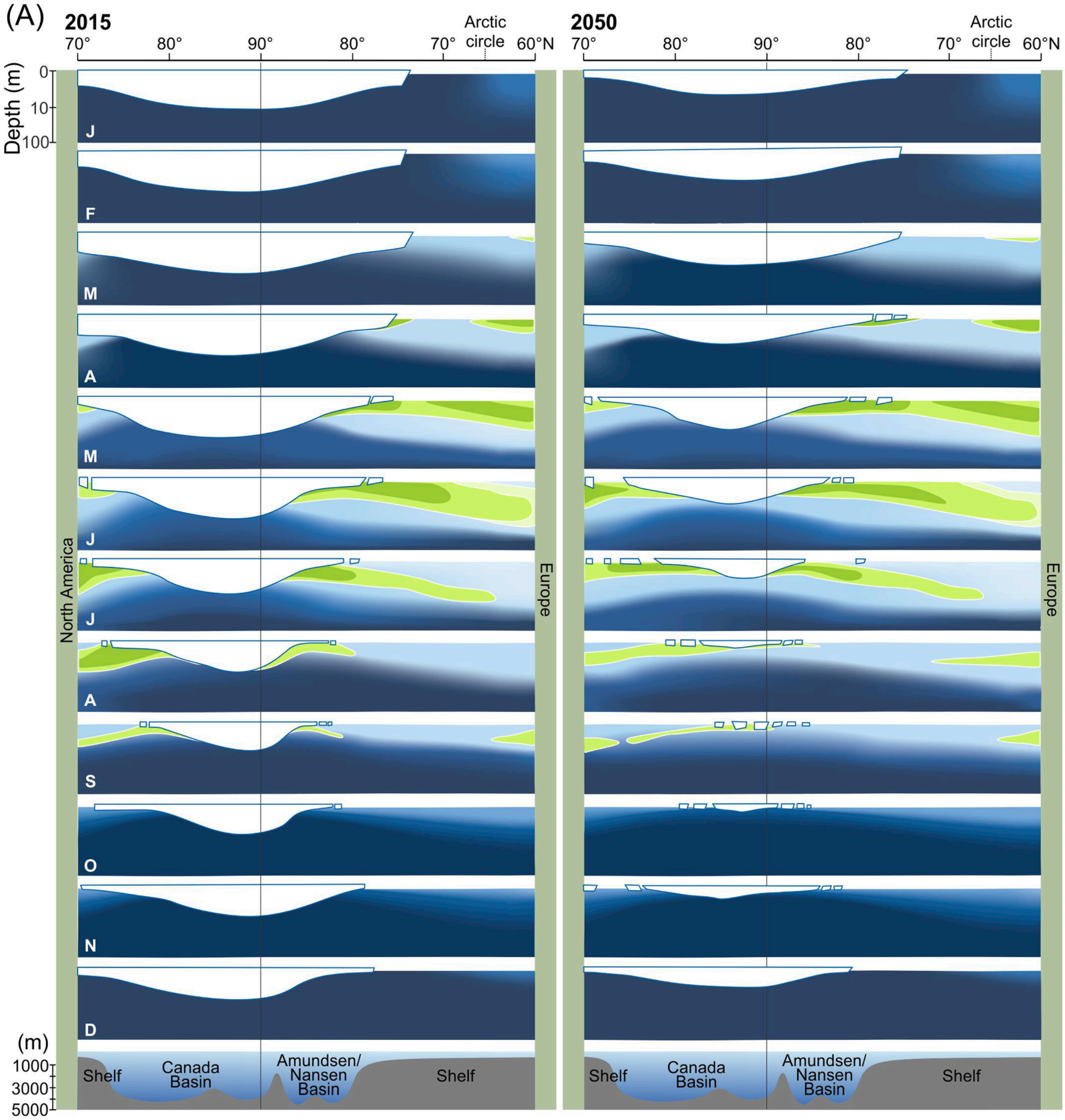

Fig. 9. Hypothetical, annual variability of ice (white), light (blue) and algae blooms (green) across the Arctic Ocean, now (left) and in the future (2050 right). The annual variability of sea ice thickness, light and plankton blooms for every month (Jan to Dec) across the Arctic Ocean are shown: now (to the left) and 2050 (to the right). The figure depicts a transect from the Barents Sea to the Beaufort Sea shelf (A, black line Fig. 8a) while a transect from the north of Greenland to the Laptev Sea shelf is shown in (B, green line Fig. 8a). The figure shows that the algae blooms in the Arctic Ocean are not smooth circles that shrink unevenly from the periphery on the shelf towards the center (basins). The blooms have a variable phenology with regard to timing, strength and width, and biomass may shift in depth location in the water column seasonally. The greatest changes in the future take place in the most productive months. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

To better comprehend the dynamic nature of the SIZD across the AO (the phenology and latitudinal variability are addressed in Section 5.2 and Figs. 16–18), monthly hypothetical transects were developed, reflecting ice over and thickness, light and plankton blooms were developed (Fig. 9). One such transect stretches across the AO from the wide and productive Barents Sea to the narrow Beaufort Sea shelf (Figs. 8A, 9A) while the other transect runs from the wide Laptev Sea shelf to the heavily ice-covered regions north of Greenland (Figs. 8A, 9B. The distribution of SIZD blooms in space and time is very uneven across the AO. The phenology of ice and phytoplankton varies significantly across the AO with the largest blooms and greatest climate-related ice melt on the Eurasian side (Arrigo and van Dijken, 2015; Slagstad et al., 2015). The maximum development of the autotroph bloom is encountered in May through July, dictated by ice cover, light and nutrients. Climate change will influence the time window of the autotroph development since thinner ice and leads already occurring after spring equinox will induce an early onset of thin bloom layers close to the surface after equinox (e.g. Assmy et al., 2017). Most of the thinning and reduction of ice cover takes place towards the end of the early productive season (with high new production) and thus does not immediately influence bloom development. Recently, pelagic autumn blooms, however, have increasingly been encountered (Loeng et al., 2005; Ardyna et al., 2014; Oziel et al., 2017). At high latitudes they become quickly light limited when solar radiation decreases, and they depend upon increased nutrient availability through vertical mixing by winds and

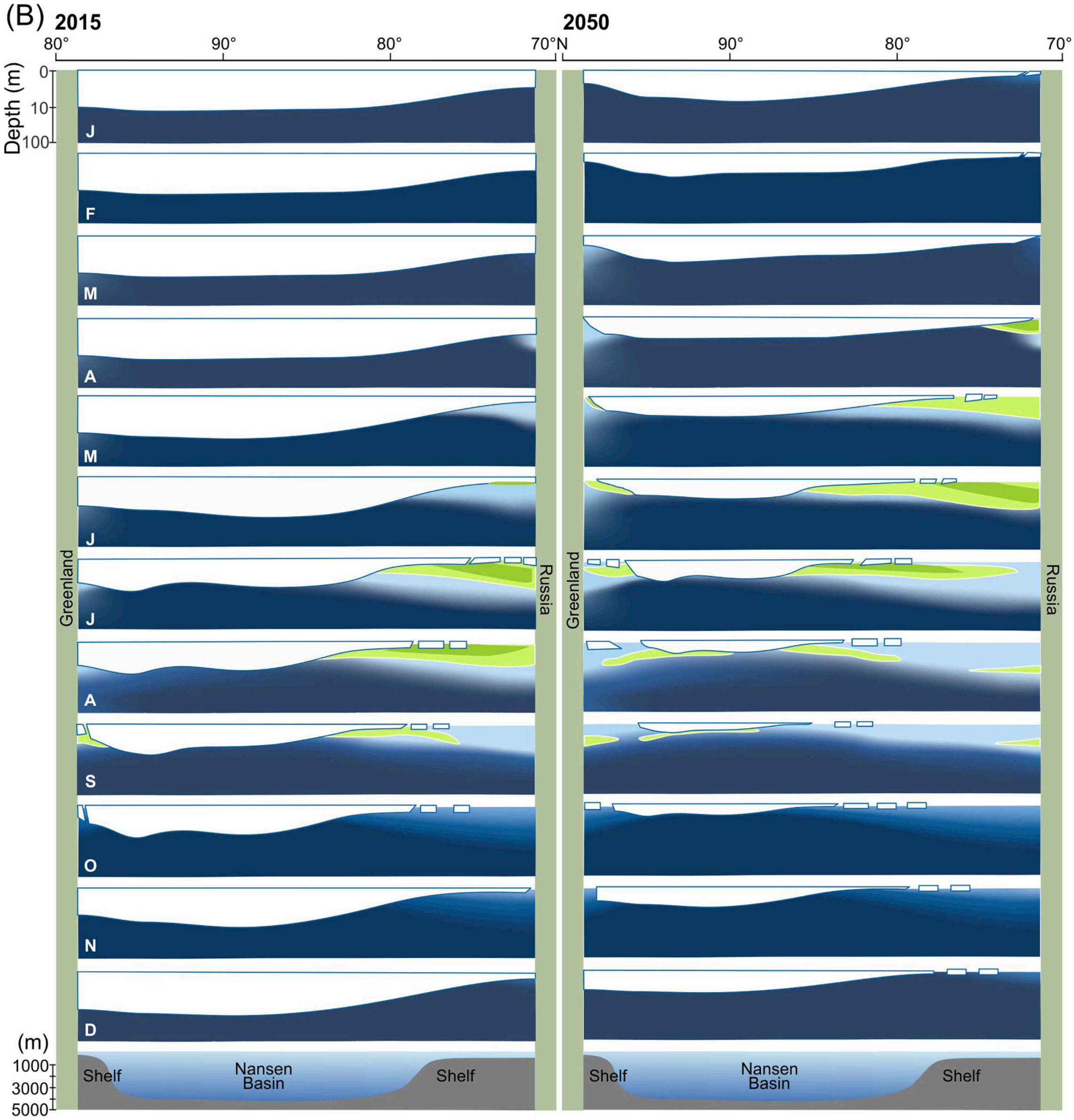

Fig. 9. (*continued*).

tides.

4.2. Contiguous domains constrained by advective processes

Within the AO at least five additional, linked, contiguous domains can be identified which, to a variable degree are impacted by advection and the characteristics of water masses. The ecology of advection thus plays a fundamental role in these domains (c.f. Carmack and Wassmann, 2006; Wassmann et al., 2015). With decreasing significance of advection these contiguous domains are:

- the Riverine Coastal Domain (RCD), which links all shelf typologies with the hinterland
- the Upper Layer Advective Domain (ULAD), which connects the AO with the northern Pacific and Atlantic Oceans and the northern Barents Sea
- the Atlantic and Pacific Halocline Domain (APHD), which recognize the spreading of Pacific halocline above Atlantic halocline waters into the Amerasian and Eurasian basins
- the Circumpolar Boundary Current Domain (CBCD) along the shelf-break, which surrounds the basins and links shelf-basin exchanges
- the Deep Basins Domain (DBD) which is exposed to sluggish advection from the North Atlantic.

4.2.1. Riverine coastal domain

North-flowing Arctic rivers deliver significant quantities of freshwater, nutrients, sediment and other material properties to the coastal ocean (Prowse et al. 2015; Haine et al., 2015; Carmack et al., 2015a,b). Upon exiting an estuary, the buoyant, low-salinity water will be diverted by the Earth's rotation to form a right-directed, buoyancy-driven current along the coast whose width scales with the Rossby radius of deformation (Carmack et al., 2015b; Sharples et al., 2017). The physics governing the fate of such waters beyond estuary mouths is extremely complex, forced by buoyancy, the Coriolis force, winds and tides, and shaped by coastal geometry (cf. Horner-Devine et al., 2015). It thus proves useful to address this problem with a simple, mechanistic model, and define the Riverine Coastal Domain (RCD, see glossary) as a narrow and shallow coastal feature, confined by the buoyancy boundary

Fig. 10. Highly schematic representation of potential buoyancy-boundary flows driven by continental discharge along northern coastlines around North America and Eurasia. The flow is not continuous, and the schematic represents the merging of multiple sources of freshwater discharge from northern North America and northern Eurasia. Hundreds of rivers and glacial ice melt, which have a propensity for the formation of an aggregate or contiguous domain along the coastline are here termed the Riverine Coastal Domain (RCD), shown with a red line. Redrawn from Carmack et al. (2015b). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

current, and linking multiple freshwater sources around the Arctic coastal perimeter. The RCD is made contiguous, with common structure and function, by the aggregate of continental runoff sources, with diverse timing of discharge, and which extends counterclockwise around the perimeter of the coast, broken only by the major gateways at Bering and Fram Straits (Fig. 10; Carmack et al., 2015b; see watershed in Fig. 1B and rivers in Fig. 3B). Though the RCD concept is highly idealized, realizations of the RCD have been described all around the Arctic coasts, specifically for the coasts of the East Siberian Sea (Weingartner et al. 1999), the Canadian Arctic (Carmack et al., 2015a,b), the Kara Sea (Janout et al., 2015), and the Kara, Laptev and East Siberian Seas (Osadchiev et al., 2020). Other examples of the RCD in Arctic waters are listed in Carmack et al. (2015a,b) while Sharples et al. (2017) provide a fully global perspective.

Due to its continental sources, the RCD carries terrestrial signals from surrounding rivers, lakes and watersheds that not only impact light, nutrient and carbon regimes (e.g. Brown et al., 2020b) but also provide a coastal pathway for the dispersal and migration of marine biota such as anadromous fish and Arctic brackish water zooplankton (Craig, 1984). The RCD acts as the initial connection between terrestrial and marine ecosystems, such that physical and biogeochemical variables within the RCD yield a contiguous gradient of environmental conditions along and across the pan-Arctic coastal zone between and among shelf domains. The RCD may become even more prominent as terrestrial runoff, permafrost thaw and local ice melt are assumed to increase in the near future under continued climate warming (for estimates of permafrost carbon input into the Arctic coastal zone, see Lantuit et al., 2012). However, due to the small cross-shelf size of the RCD (~10 km) and its nearshore, shallow location that is outside the operation range of most research vessels, detailed observations of this feature are virtually missing from regions outside fjords, with the exception of a handful of study areas in the vicinity of Arctic field stations.

The seasonally highly dynamic and physically challenging conditions of the coastal zone result in recognizably different biotic communities than are found farther offshore. Arctic nearshore zooplankton communities, for example, are characterized by neritic and euryhaline or brackish taxa – especially near/in river deltas/river estuaries all around the Arctic (Lischka et al., 2001; Deubel et al., 2003; Hirche et al., 2006; Walkusz et al. 2010; Smoot and Hopcroft, 2017b). Benthic nearshore communities, including demersal marine fishes, show generally low diversity, again mostly euryhaline species and often low abundance/biomass, thought to be related to a combination of seasonally low salinity, and mechanical disturbance through ice gouging (though this effect extends beyond the RCD) (Wesławski et al., 1997; Conlan and Kvitek, 2005; Ravelo et al., 2015). Biomass and production can, however, be comparatively higher in lagoons (Dunton et al., 2006, 2012), and in interstitial meiofaunal that is able to recover more quickly from disturbance (Urban-Malinga et al., 2005). Pelagic coastal migratory and forage fishes, however, can be abundant in the coastal domain (Roux et al., 2016). It is this narrow coastal belt where all indigenous subsistence travel and hunting activities in the marine realm take place.

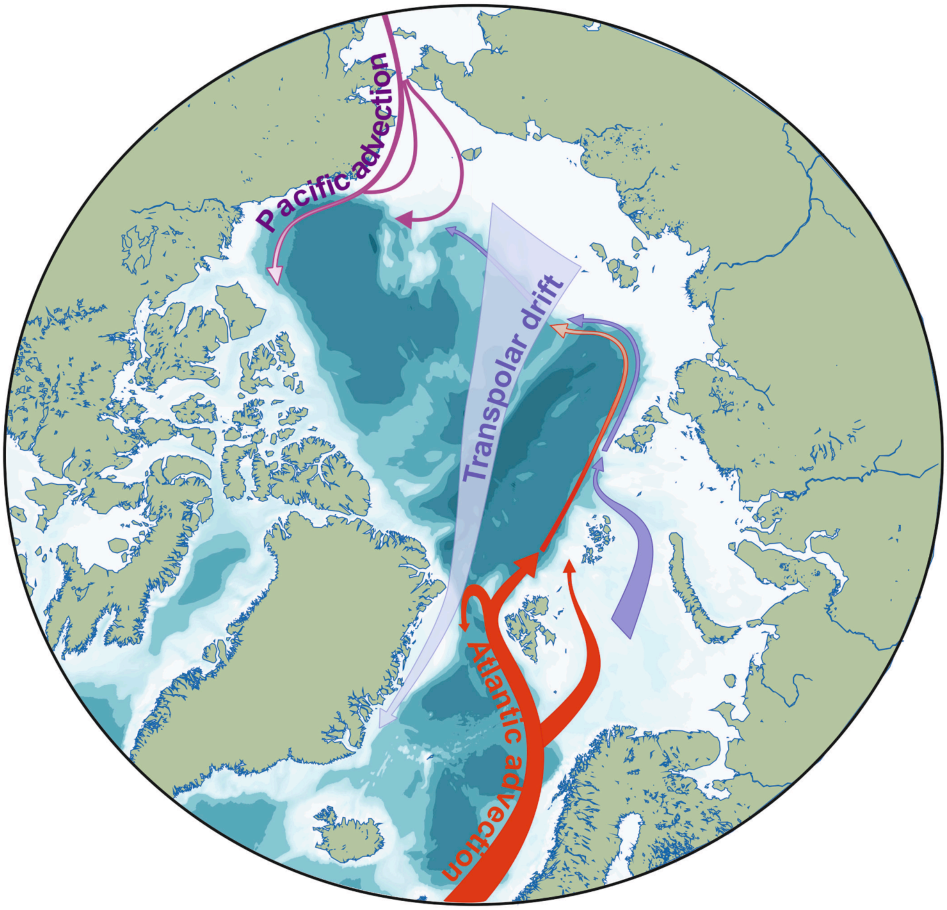

Fig. 11. The Upper Layers Advective Domain of the Arctic Ocean. Within this domain, we distinguish among four sub-domains: the Atlantic (red), the Pacific (pink), the Arctic (light red) and the Transpolar (light purple) advective domains. All have lengths of several thousand km and pass through several biogeographic regions. Redrawn from Wassmann et al. (2015). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

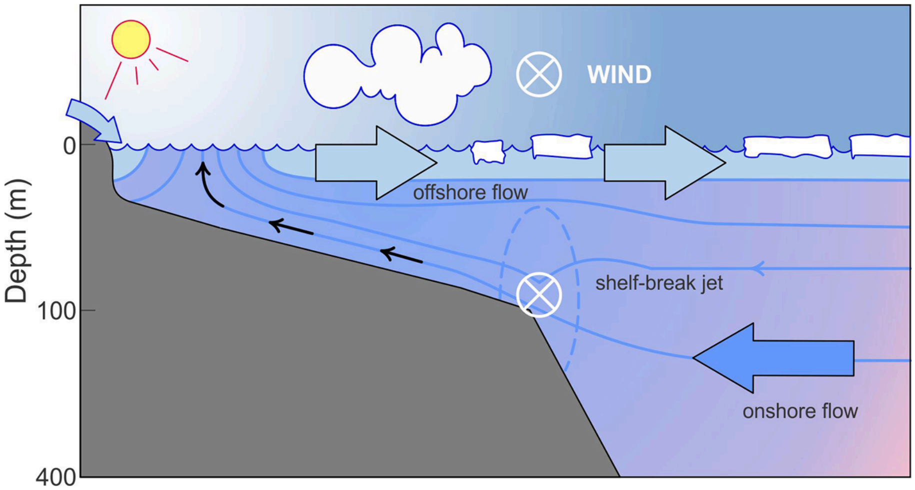

Fig. 12. Cartoon illustrating shelf-break upwelling during times when sea ice cover, to various degrees withdraws beyond the shelf-break into the deep Arctic Ocean basins and is exposed to easterly winds (crossed circle directed into the page). The light blue arrow depicts offshore flow in the surface layer and the dark blue arrow depicts the onshore flow. Upwelling currents across the shelf is shown by small black arrows, while the shelf-break jet is shown by the crossed circle at the shelf-break. Blue lines denote salinity stratification, with salinity increasing downwards. Note that the position where upwelling water reaches the surface will depend on stratification, air sea-ice coupling, and shelf geometry. Upwelling provides the shelves and shelf-breaks with additional nutrients that may reach into the surface waters or flow beneath ice to create subsurface blooms (not shown; e.g. Martin et al., 2010). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.2.2. *Upper layer advective domains*

We define the combined waters above the halocline and advected by the North Pacific, North Atlantic and the Barents Sea or transported through the TPD as the Upper Layer Advective Domain (ULAD, see glossary; Fig. 11). Note that surface waters within the subarctic Atlantic and Pacific subduct upon entering the AO and continue as mid-depth interflows. The advection of nutrient-, detritus- and plankton-rich waters from the Pacific and Atlantic Oceans and the northern Barents Sea into the AO plays a crucial role for the ecology and seasonality of the AO ecosystem (Wassmann et al., 2015; Hunt et al., 2016). In addition, the Siberian shelf is connected to the Fram Strait through TPD advection (Fig. 11). Such flows connect subarctic with Arctic biota, supporting both primary production and higher trophic level consumers (Vernet et al., 2019; Wassmann et al., 2019). By volume of water and biomass inflow, the dominant contribution to ULAD are by the northeastern North Atlantic and the Barents Sea (Fig. 11). ULAD overlaps at the shelf-break and upper slope with the circumpolar boundary current domain (see Section 4.2.3).

While ULAD connects Arctic biota with subarctic inputs, its outflow also influences the physical, chemical and biological oceanography of adjacent subarctic waters through advective outflows, in particular through western Fram Strait, but also through the Canadian Arctic Archipelago. However, exports of biomass out of the AO into the North Atlantic Ocean are thought to be far smaller than the influx from the south (e.g. Wassmann et al., 2015). Thus, AO ecosystems are net beneficiaries of planktonic biomass through northward advection, especially along the relatively narrow advective pathways of ULAD: large amounts of food create the basis for fish and marine mammals feeding at the perimeter of the AO basins. Further, the transport of ice with its associated biota and conspicuous amounts of terrestrial matter that drifts across the AO with the TPD also delivers a supply of DOC and biogenic matter from the Laptev Sea to the western Fram Strait regions (Hop and Pavlova, 2008). The biotic impact of Atlantic-, Pacific- or Arctic origin taxa being transported through ULAD depends on their ability to survive along the transport path (Hirche and Kosobokova, 2007). Thus, advective transport can be thought of as "trail of life and death" in the AO (Wassmann et al., 2015).

We distinguish three specific ULAD based on water mass structures (Fig. 11): the Atlantic-Arctic (including the Barents Sea branch), the Pacific-Arctic, and the Transpolar Advective domains. The Atlantic-Arctic ULAD connects the North Norwegian shelf from the Lofoten Islands to the shelf-break and upper slope domain of the western Eurasian sector of the AO. This ULAD crosses several biogeographic boundaries with impacts on species abundance and life histories. For example, the supply of the Atlantic copepod *Calanus finmarchicus* along the domain is particularly substantial (contributing 30–60% to overall zooplankton biomass north of Svalbard and the Kara Sea, Kosobokova, 2012). The Pacific-Arctic ULAD connects the shelf of the northern Bering Sea to the Chukchi and the western Beaufort Seas and even all the way to northern Greenland, supporting pelagic and benthic biomass hotspots and higher trophic levels along the way, and facilitating biomass-rich eddies north of Point Barrow (Berline et al., 2008; Grebmeier et al., 2015; Moore et al., 2018a). The Barents Sea branch of the Atlantic-Arctic ULAD derives from the cold waters of the northern Barents Sea and connects, through the St. Anna Trough, to the shelf-break and upper slope domain along the Siberian sector of the AO. Similar to the Atlantic-Arctic ULAD, the supply of the Arctic copepod *Calanus glacialis* along this domain is highly significant, but less investigated (Kosobokova, 2012).

The third ULAD is that of the TPD that connects the biota (and suspended biomass) of the Laptev Sea shelf with the western Fram Strait where ice-associated biomass is released to the water column as pack ice melts (Hop and Pavlova, 2008). The recent eastward spread of warm AW (Polyakov et al., 2017, 2020a,b) has resulted in seawater warming which are melting Russia's coastal "ice nurseries" faster than before. Some 80% of nursery ice now melts before it joins the open ocean, compared to 50% before 2000 (Krumpens et al., 2019). The result will be that ice-transported food supplies will be reduced for those animals in the open AO that hitherto relied on food from TPD-transported sea ice. Further, when increased volumes of AW reach the Laptev Sea shelf in the future the biogenic matter of the TPD may cease and disappear. Model investigations suggest that the transport of detrital carbon from the Laptev Sea to the Fram Strait by the TPD ceased already decades ago (D. Slagstad, P. Wassmann, unpubl. res.)

The ULAD is typically characterized by net heterotrophy; i.e. consumption of biomass is greater than local production. Physical and biological forcing is not contained inside conventional latitudinal biogeographic regions and teleconnections are created across biogeographic and production zones. Advected boreal or subarctic water penetrate the circular nature of the AO and make it dependent upon the Pacific and Atlantic Oceans. Changes in advection through the North Atlantic advection (Asbjørnsen et al., 2019), the increasing spread of AW north of Svalbard (Polyakov et al., 2017) and the increasing Bering Strait throughflow driven largely by the increasing Pacific-Arctic pressure gradient (Woodgate, 2013, 2018) result in the ULAD, along with the SIZD, being the fastest changing contiguous domains in the AO (e.g. Vernet et al., 2019; Wassmann et al., 2019).

4.2.3. *Circumpolar boundary current domain*

At the shelf-break, the Circumpolar Boundary Current Domain (CBCD, see glossary) is the dominant thermohaline feature of the AO (Fig. 5C, Aagaard, 1989; Rudels et al., 1994). It is a continuation of the Atlantic-Arctic and Barents Sea ULAD (Fig. 11), but we list it separately because the CBCD transports subducted, modified AW that circumnavigates the entire AO shelf-break and slope. Dickson et al., (2008) and Beszczynska-Möller et al. (2011) estimate that between 8 and 9 Sv enter the Nordic Seas over the Greenland-Scotland Ridge (sill depth ~800 m)

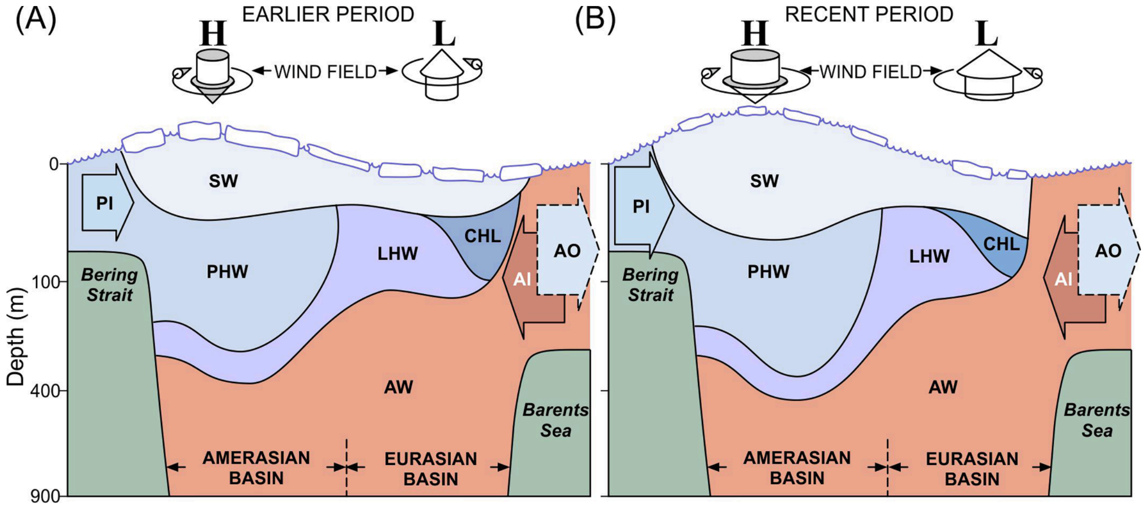

Fig. 13. Changes in the distribution of the Atlantic and Pacific Halocline Domains as related to the predominant wind fields (H and L for atmospheric high and low pressure, respectively). The change from earlier (left) towards recent windfields (right) and increased supply of advected Pacific and Atlantic inflows (PI, AI) result in important changes in the position of the halocline. Take note of the recent increase in sea level height and depth of the surface water (SW), in particular in the Amerasian Basin. Take also note how the dominating Atlantic Water (AW) spreads in recent times further into the Arctic Ocean, in particular in the surface. The Cold Halocline Water (CHL), however decreased in recent years. AO (Atlantic Outflow); PHW (Pacific Halocline Water); LHW (Lower Halocline Water). Redrawn from Polyakov et al. (2018).

and roughly half of this flow continues to the AO; of the AW continuing north, about half enters the AO via Fram Strait as the Fram Strait Branch (FSB) and subducts below Arctic Surface waters (ASW) north of Svalbard (Fig. 5C). The other branch first crosses the Barents and the westernmost Kara Seas, subducts along the Atlantic Polar Front, continues across the eastern Barents Sea, and then drains through the St. Anna Trough as the Barents Sea Branch (BSB) (Dmitrenko et al., 2010; Beszczynska-Möller et al. 2012; Rudels et al., 2012, 2013; Bluhm et al., 2015). Because the BSB water is strongly modified en route by mixing with local Barents Sea waters, it enters the basin with a broader density range than FSB waters. Both water masses interleave laterally and subduct below the continuing FSB. Aagaard and Woodgate (2001) also noted that the high-latitude freezing and melting cycle can supply additional freshwater injection into the interior of the AO, resulting in a secondary salinity minimum at about 800 m depth. A third water mass formed locally on the eastern Barents and western Kara Seas also drains into the basin through St. Anna Trough (Aksenov et al., 2011). Subsequently, the three branches become the ACBC (see Section 3.2) and continue cyclonically around the basin perimeter, with bifurcations occurring where ridge and slope topographies intersect. The transit is marked by slope cutting canyons. Currents tend to be strongest where the slope is steep (Isachsen et al., 2003). Aksenov et al. (2011) modeled the ACBC and demonstrated that transports along the AO margins were forced by the joint effects of buoyancy loss and regional winds, which create high pressure upstream in the Barents Sea. There is still debate as to the volume transports of AW into and out of the AO. What is important is that the ACBC carries a huge and varied mix of water properties and biogenic material as it travels this circuit.

The CBCD can be pictured as a long, narrow band that rapidly transports materials around the ocean perimeter, allows on-slope and off-slope exchange, and radiates mixing energy into the basinś interior (Fig. 5C). For a description of the productivity and in particular the current ecological changes, see Section 3.2. Increases in primary production are expected for the Eurasian but less so in the Amerasian CBCD (Slagstad et al., 2015; Polyakov et al. 2020a,b).

4.2.4. *Atlantic and pacific halocline domains*

The AO halocline is a complex structure below the ULAD and above the AW in which river inflows, ice melt, winter convection, and the insertion of Pacific and Atlantic waters - modified on their respective inflow and interior shelves - all contribute to the vertical salt stratification (Fig. 13). These halocline components have distinct physical, chemical and biological characteristics according to their sources and maintain identifiable structures both horizontally and vertically within the AO interior (Polyakov et al., 2018; Brown et al. 2020a). The Pacific- and slightly denser Atlantic-source halocline components are as different from each other as are their parent oceans. Here, we will describe them as comprising the Atlantic and Pacific Halocline Domain (APHD), i.e. distinct, contiguous halocline domains that together cover the upper 900 m of the entire central AO (cf. Bluhm et al., 2015, Fig. 13).

Waters of Pacific origin enter through Bering Strait, flow northwards across the broad Chukchi Shelf along three major branches, are modified en route on seasonal time scales, and enter the Amerasian Basin though submarine canyons at the shelf-break, where they spread into the basin interior (Pickart, 2004; Weingartner et al., 2005; Shimada et al., 2006; Danielson et al., 2017). Pacific-origin halocline waters arrive as two main varieties, the warmer and fresher summer waters, and the colder and more saline winter waters (Coachman and Barnes, 1961; Shimada et al., 2005; Steele et al., 2004; McLaughlin et al., 2009). These waters are largely confined to the Amerasian Basin owing to the anticyclonic Beaufort High wind field and tend to strongly accumulate within the convergent Beaufort Gyre (Carmack et al., 2008; Proshutinsky et al., 2009). The distinguishing features of the Pacific halocline waters is, that they are higher in nutrients, and fresher and less dense, so that they

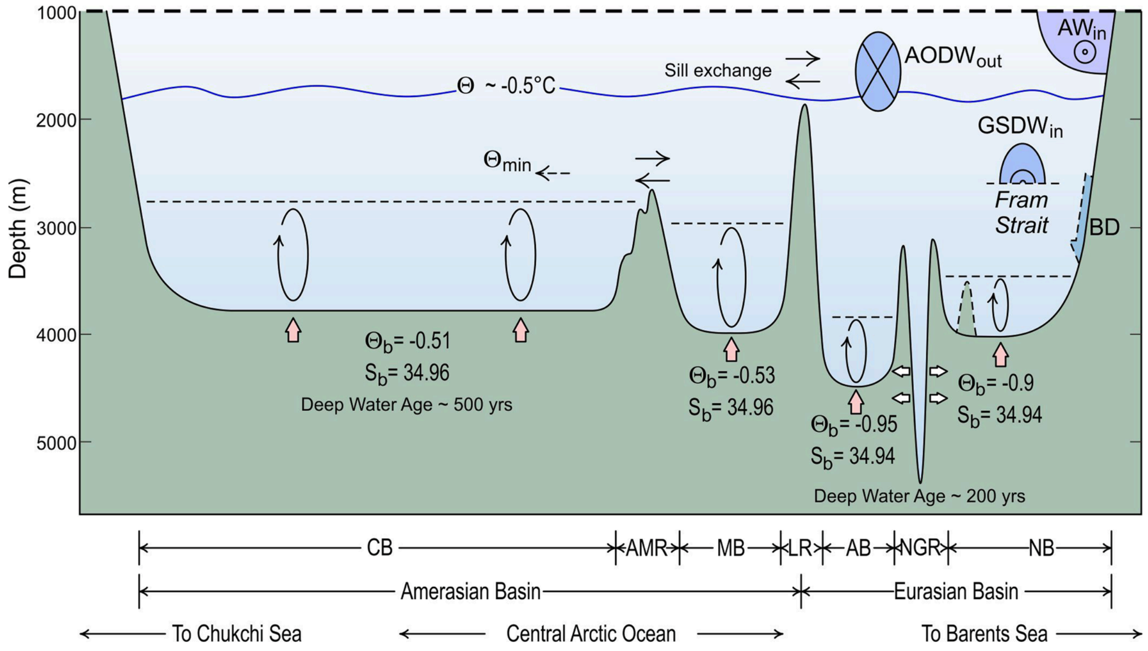

Fig. 14. Deep Basin Domain (DBD). The beginning of the DBD is somewhat arbitrarily defined by the commonly used bounding temperature of Atlantic water at 0 °C. A functionally more meaningful upper boundary for the DBD is at sill depth of the Lomonosov Ridge. This domain is physically characterized by low current flows, water exchange between basins being limited by ridges/sills, old age of the water, low and stable temperature, and high salinity. The age of the deep water is about 200 years in the Nansen and Amundsen basins, but about 500 years in the Canadian Basin (^{14}C ages; other tracers may give differing ages). Biochemically, the DBD receives low vertical carbon inputs while horizontal carbon input may be important. Today's biotic connectivity to the north Atlantic and the global deep-sea is high while that to the Pacific is essentially absent. The DBD is intersected by ridges, with local outflows of chemical-rich fluids and (largely unmapped) seamounts. AWin (Atlantic Water inflow); AODWout (Atlantic Ocean Deep Water outflow); GSDWin (Greenland Sea Deep Water inflow); BD (Brine Drainage); NB (Nansen Basin), NGR (Nansen-Gakkel Ridge); AB (Amundsen Basin); LR (Lomonosov Ridge); MB (Makarov Basin); AMR (Alpha-Mendeleev Ridge); CB (Canada Basin). The dashed vertical lines and circle arrows indicate bottom water mixing. Sb (salinity); Θb (potential temperature).

overlie the Atlantic halocline waters and add to the salt-stratification of the Amerasian AO.

Atlantic-origin halocline waters are largely modified and formed in the Eurasian sector of the AO, either on Siberian shelves (Aagaard et al., 1981; Jones and Anderson, 1986; Aksenov, et al., 2011; Polyakov et al., 2017) or by winter convection in the Nansen Basin (Rudels et al., 1996). Indeed, as early as the mid-1980′s, arguments were presented that Atlantic-origin waters were modified by freeze/thaw processes during passage over the Barents and Siberian shelves, and subsequently entered the deep ocean (Jones and Anderson, 1986); a hypothesis also supported by numerical modelling (Killworth and Smith, 1984; Aksenov et al., 2011). An important feature of the Atlantic-origin halocline water that underlies the Pacific-origin water in the Amerasian Basin is its associated oxygen minimum.

A major front, termed the Atlantic/Pacific Halocline Front, blocks the spreading of Pacific water into the Eurasian Basin and allows only the lower portion of the Atlantic-origin halocline water into the Amerasian Basin (reviewed in Bluhm et al., 2015). There is debate whether this front is stationary and locked to topography, or free to shift from one stable configuration to another under climate forcing (cf. McLaughlin et al., 1996).

An important aspect of the ’halocline complex’ is that it is not “a” single, pan-Arctic structure, but instead it is dependent on region, and there can be an assembly of multiple layers that comprise a staircase of downwards-increasing water density that insulates the warm and nutrient-rich Atlantic layer from the overlying Polar Mixed Layer and ice (McLaughlin et al., 1996). The initial halocline layer forms as incoming AW encounters out-going sea ice in the western Nansen Basin and is capped by the resulting freshened layer (cf. Rudels et al., 1996; Walsh and Carmack, 2003). Then, progressing counterclockwise around the basin, individual ”steps” (or layers) are formed and shaped on the shelves, and are advected into the adjacent basins, or within the basins by the freeze/thaw cycle and net precipitation, where they ‘stack themselves’ according to their densities (cf. Aagaard et al., 1981; Walsh et al. 2007; Aksenov et al., 2011; Polyakov et al. 2012). The Amerasian Basin has more ’steps’ in the staircase than the Eurasian Basin, owing to the input of PW through Bering Strain, and the halocline so formed is distinct from that of the Eurasian Basin (Fig. 13; Bluhm et al., 2015). Between the ’clines’ near-homogenous layers are found, which is why vertical profiles of salinity in this domain actually look like a staircase (see Jackson et al., 2011, their Fig. 2). Therefore, to get from the AW base of the halocline complex to the surface and ice, heat and material properties must progress one step at a time.

Importantly, a marked difference in stratification, as measured by integrated stability (Available Potential Energy) of over an order of magnitude exists across the Arctic basins (Polyakov et al., 2018). The primary control of the APHD on biological production in the AO is that its strong stratification shapes the biogeochemical function of the central AO basins: it effectively prevents the vertical supply of nutrients (Brown et al., 2020a) and thereby hampers primary production, irrespective of increasing light levels in the changed AO (Randelhoff et al., 2019). This effect is stronger on the Amerasian side where the APHD is more strongly stratified than on the Eurasian side. Further, the APHD plays a significant role in the distribution of planktonic species, as reflected in its mesozooplankton inhabitants (e.g. Bluhm et al., 2015).

4.2.5. Deep Basin domains

The Deep Basin Domain (DBD, see glossary) lies below the Atlantic Layer. It is several thousand meters thick and by volume, comprises the largest – yet the least studied – contiguous domain (Fig. 14). It is made up of individual layers, formed and shaped on the shelves, that are advected into the adjacent basins, where they ‘stack themselves’ according to density. The pathways, rates of spreading of AO deep waters and biological communities and processes within it are poorly known (Kosobokova, 2012), but in general there is direct deep-water exchange between the Norwegian and Greenland Seas and the Nansen Basin via Fram Strait (sill depth ~ 2600 m). From there the flow is thought to proceed from the Nansen Basin to the Amundsen Basin to the Makarov Basin and finally to the Canada Basin (MacDonald et al., 1993; Schlosser et al., 1997). From the Amerasian Basin there must be a return flow back to the Eurasian Basins, Nordic Sea and North Atlantic (Aagaard et al., 1985; Rudels et al., 2013). Indirect proof for these water exchanges between basins are (1) deep-water zooplankton communities that have higher community similarity within the DBD horizontal layers than across vertical layers in a given basin (Kosobokova, 2012); (2) generally similar zoogeographic patterns in benthic communities across basins (Bluhm et al., 2005, 2011a); and (3) the high proportion of Arcto-Atlantic affinity biota across the deep-sea floor in the DBD (Mironov et al., 2013; Zhulay et al., 2019). Endemic species, however, do occur also in both the water column and at the seafloor as typical for any deep-sea area.

The overall motion of deep water within the basins below sill depth is sluggish, as clearly reflected at the deep-sea floor where animal traces are well-preserved and abundant despite low faunal densities (Zhulay et al., 2019). Schlosser et al. (1997) calculated the mean isolation age of the Eurasian Basin bottom water >2500 m to be ~250 years while that of the Amerasian Basin >2500 m to be an additional 200 years older. Thus, the Amerasian Basin deep waters are either presently not being ventilated (Macdonald and Carmack, 1991; Macdonald et al., 1993; Aagaard and Carmack, 1994), or are being ventilated much more slowly with continuous renewal by shelf water (by freezing and brine rejection on the shelves) or influxes from the adjacent Eurasian Basins (Aagaard et al., 1985; Östlund et al., 1987; Jones et al., 1995; Rudels et al., 2000). The influxes from the adjacent Eurasian Basins would provide a mechanism to carry organic material and biota to depth. More rapid flows are expected along basin and ridge slopes, and through narrow gaps in the ridges (Bluhm et al., 2015).

Given that the organic matter flux from surface primary production to the DBD is very limited (Wiedmann et al., 2020) and much of the carbon is refractory in nature (Iken et al., 2005). Biotic densities and biomass are generally low (Bluhm et al., 2011a; Kosobokova, 2012). The persistence of the same endemic deep-sea species of zooplankton, even at extremely low densities, throughout the entire DBD, despite the presence of underwater ridges, further emphasizes the contiguous nature of DBD and the exchange of deep waters within it. In the absence of fresh algal food, feeding guilds in deep-dwelling zooplankton are dominated by carnivores, omnivores and deposit feeders (Kosobokova et al., 2002, 2011). However, the supply of biogenic matter through chemoautotrophs, presently not adequately quantified, must also to be considered as a food source (e.g. Griffith et al., 2012; Åström et al., 2017). Benthic macrofaunal communities - often essentially sessile - tend to follow the global trend of diminishing size with increasing depth related to food limitation (Wei et al., 2010), while larger - often mobile - fauna can actively search for food, and can find it surprisingly quickly (Premke et al., 2006; Boetius et al., 2013). Drop stones ubiquitously found across the DBD provide exceptions to both patterns as they consistently house biodiversity islands of hard-bottom fauna (Zhulay et al., 2019), albeit often unknown life cycles and feeding strategies, yet extremely low recruitment rates (Meyer-Kaiser et al., 2019).

5. Major processes forcing the biogeochemical cycles in the Arctic Ocean

Before we reach the last suite of conceptual models, those of food webs, we connect some of the most important processes to regional aspects and the functional domains. We start in the AO surface layer that is dominated by an extreme annual variability of light, freshening, stratification and warming (Agustí et al., 2010). This circumarctic, highly-stratified band of surface water within the MIZ then shapes the development and the pelagic and ice-associated spring blooms. These blooms come seasonally soon to an end because of nutrient depletion, which is one of the most significant characteristics of today’s MIZ. But the AO

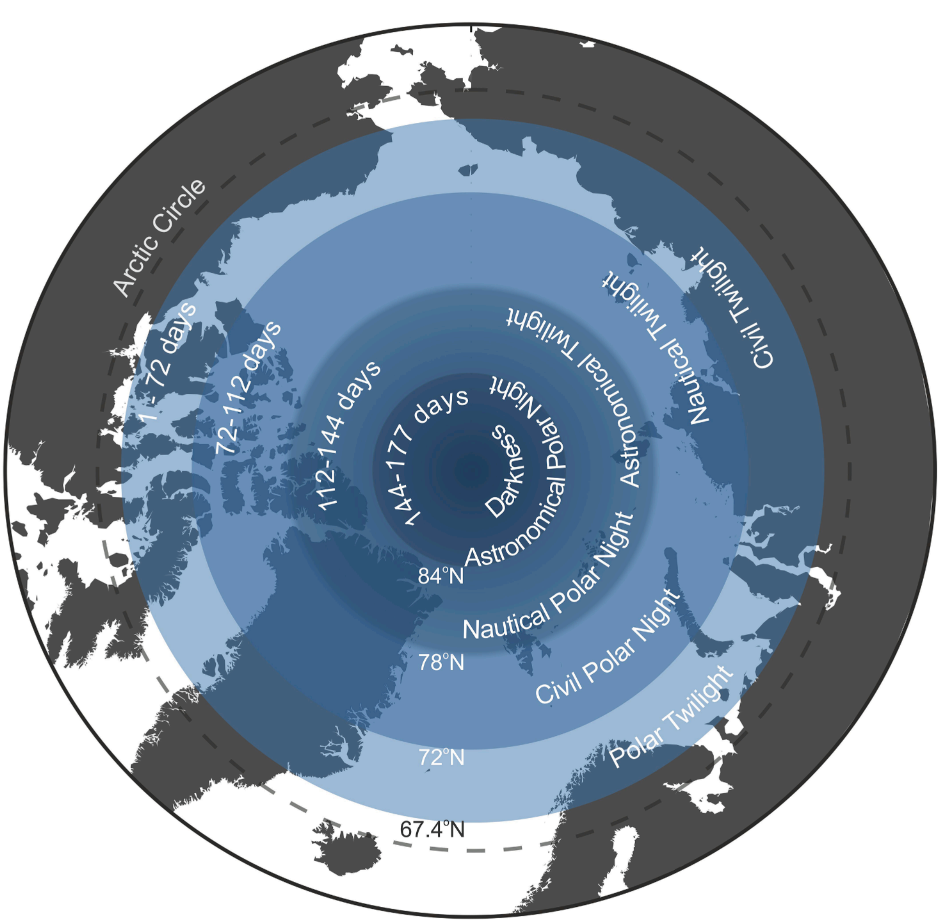

Fig. 15. The Polar Night north of the Arctic Circle. Between 67.4 and 72°N the sun is below the horizon from 1 to 72 days per year. Between 72 and 78°N the sun is below the horizon between 72 and 112 days per year. Between 78 and 84°N the sun is below the horizon for 112–144 days per year. Above 84°N the sun is below the horizon for 144–177 days per year. Take note that the light regimes vary between regions such as north of Svalbard, in the Barents Sea, the Beaufort shelf or the Chukchi Sea take place under widely different light regimes which are thus difficult to compare.

Table 2
Definitions of Polar Night and twilight based on solar elevation. Polar Night definitions are for solar elevation at the winter solstice, while for twilight the definitions apply at any point in the solar day (see Urban and Seidelmann, 2013). Note that "darkness" does not necessarily mean the total absence of light. Relevant latitudes are based on geometric positions of the sun. Note also that the notations of twilight and Polar Night are different from Cohen et al. (2020).

	Polar Night Definition	Twilight Definition	Relevant latitude (N and S) at noon on winter solstice
0 to −6	Polar Twilight	Civil Twilight	66–72°
−6 to −12	Civil Polar Night	Nautical Twilight	72–78°
−12 to −18	Nautical Polar Night	Astronomical Twilight	78–84°
less than −18	Astronomical Polar Night	Darkness	84–90°

will also face increased stratification and nutrient limitation as the MIZ retreats increasingly over the already strongly stratified basins (Tremblay et al., 2015; Assmy et al., 2017; Randelhoff et al., 2020). Together light, freshening, stratification and warming excerpt a strong impact on the highly seasonal productivity of, and the life cycle of organisms, in the AO. In turn, the phenology of autotrophs in sea ice and within the water column is connected to rocky littorals, boulders and the seabed (Carmack et al., 2006).

5.1. Light forcing

Light availability (or lack thereof) is a key determinant for the phenology of autotrophs and heterotrophs in the AO. Light availability is a function of solar radiation at the top of the atmosphere, sun angle, clouds, presence and character of ice, snow cover and shading (by other autotrophs, colored dissolved matter and/or suspended particles). Combined, these factors set up a highly spatially and temporally variable light forcing over the expanse of the AO. For solar radiation during the dark season we distinguish between various types of Polar Night (Fig. 15 and Table 2), where the exact zone and type of Polar Night at a given location depends on a) latitude and b) angle between the horizon and the sun (for details, see Berge et al., 2020). Geometrically, there is one day of Polar Night at the Arctic Circle (66.33°N), while the Polar Night lasts for 183 days at the North Pole. However, due to atmospheric refraction of sunlight, there will appear to be direct sunlight at noon at sea level on the winter solstice up to approximately 67.4°N. For the same reason, the Polar Night lasts "only" 177 days at the North Pole, not 183 days as one would expect from geometry alone.

For the northern hemisphere up to 72.0° N the entire duration of Polar Night is limited to Polar Twilight zone. Further north in a band from 72° to 78° N, Polar Night begins with a period of Polar Twilight which is followed by Civil Polar Night, and then again by Polar Twilight before the sun reappears above the horizon. Still further north in a band from 78° to 84° N, Polar Night consists of Polar Twilight and Civil Polar Night followed by Nautical Polar Night, and then again by Civil Polar Night and Polar Twilight. And finally in a band from 84° to 90° N, the periods of Polar Twilight, Civil Polar Night, and Nautical Polar Night are followed by Astronomical Polar Night when solar elevation remains 18° below the horizon at the winter solstice, and then again by the three lesser periods before the sun returns above the horizon. The Midnight Sun period with similar periods of permanent sun light is a mirror of the Polar Night period.

Solar radiation in the Arctic is thus extremely variable with regard to latitude, ranging from roughly 6 months of direct sunlight at the North Pole to the sun being under the horizon for just minutes at the Arctic

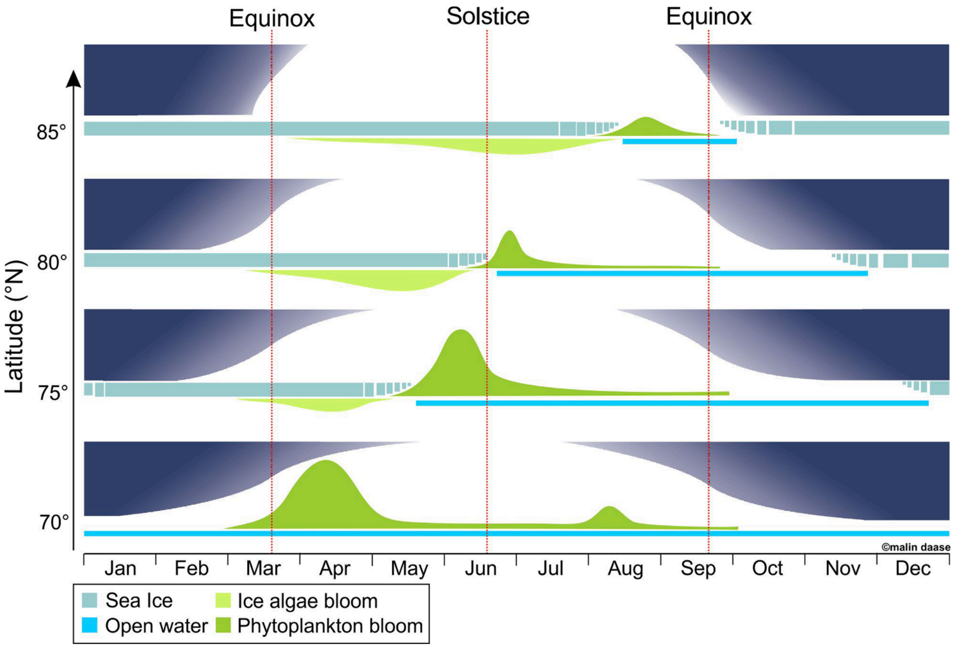

Fig. 16. Hypothetical phenology of ice algae and phytoplankton blooms as a function of latitude. Light, ice and stratification determine the environmental envelope that regulates the timing of ice algae and phytoplankton bloom development along a latitudinal axis of open water-Seasonal Ice Zone Domain (ranging from 75 to 85°N). There are long to short productive periods in open water (70–75°N) and heavily ice-covered regions (>73–75°N) in the European Arctic corridor, respectively. Inside each longitudinal light window with its variable ice cover, the timing and extent of the ice and phytoplankton and ice algae phenology change from April in the south towards late summer at high latitudes. A recent feature is the tendency for autumn blooms that has been observed in the Polar Twilight zone, but these blooms will have no light base in the Nautical Polar Night zone (see Fig. 15). Modified from Leu et al. (2011).

Circle. In addition, ice and snow covers modify the light reaching organisms in the ice and surface ocean. The light regime in the seasonally ice-covered Chukcki Sea is similar to that in northern Norway and the southern Barents Sea, but the latter experiences less or no ice cover. The Bering Strait and Bering Sea, situated outside the main AO region, experience year-round solar radiation, but ice cover can still result in low light conditions for biota. In contrast, the Nautical and Astronomically Polar Night is only experienced in the northernmost regions of the AO. Investigations during the full annual light regime have been carried out in only a few places, e.g. in coastal waters off northern Svalbard, the Canadian Arctic Archipelago, northern Greenland and the White Sea (e.g. Ashjian et al., 2003; Leu et al., 2011; Kosobokova and Pertsova, 2018). Also, some regions encompass Arctic biota but experience a sub-Arctic light regime, and vice versa. For example, northern Norway and the southern Barents Sea experience a Polar Twilight light regime, but the biota is dominated by advected boreal forms that tuned to far greater irradiation and a different phenology. Thus, the ambient light regime sets up important patterns that impact the biota, but do not necessarily determine it. Many studies that seemingly took place in the AO have been carried out in regions that are south of the Arctic circle (66°N), outside the Arctic light/darkness regime defined in Fig. 15 (such as southern Greenland, Hudson Bay and the Bering Sea). Ice cover and temperature are indeed not the only criteria for marine Arctic ecology, yet the annual light cycle has to be clearly defined to allow clear and unambiguous generalizations. Marine ecological investigations in the AO will benefit from being far more rigorous in describing and considering the light climate, for example through applying the present conceptual model.

In addition to incoming irradiance, the variable ice cover across the AO and this has obvious consequences for the phenology of auto- and heterotrophs (Kirchman et al., 2009; Leu et al., 2015; Figs. 9, 16). The thickness of ice cover, the size and variability of leads and snow cover have a significant and highly variable impact upon the underwater light climate (e.g. Pavlov et al., 2019; Tedesco et al., 2019; Randelhoff et al., 2019). At high latitudes low sun angle and seasonal cloudiness are important for underwater light. Sea ice melt is closely connected to salt stratification, another factor dictating the biogeochemical characteristics of the AO euphotic zone. Freshening arises from ice melt which is caused by solar radiation and atmospheric warming from above (Wassmann et al., 2010; Carmack et al., 2016) and by warm water melting from below (in particular AW; see Carmack et al., 2012a; Polyakov et al., 2017). The ice albedo, or reflectivity, also impacts heat absorption by the ice, which is further influenced by materials frozen into ice (so-called dirty ice) and atmospheric deposition of black carbon (Lee et al., 2013; Goelles and Boggild, 2015).

5.2. Phenology and seasonal productivity variation

Within their respective envelops of hydro-morphological characteristics and contiguous domains, the ecology of AO organisms experiences extensive phenological cycles that characterize the ecology of the AO. The study of seasonal cyclic organismal events in algae and animal life, i.e. their phenology, is influenced by seasonal and interannual variations in climate. Phenologies are thus now responding to global warming through the detectable footprints of climate change (Wassmann et al., 2011). For example, changes in autotroph phenologies (e.g. Kahru et al., 2011; Rubao et al., 2012; Tedesco et al., 2019) are now affecting match and mismatch relationships between predator (including grazers) and prey (e.g. Edwards and Richardson, 2004; Post, 2016; Ramírez et al., 2017). Phenological observations provide high temporal resolution of ongoing changes related to climate change. Investigations of phenology are thus instrumental to fully understand the impacts of climate change.

To illustrate this principle and to partly hypothesize patterns of geographic variability of autotrophic phenologies in ice-covered waters, we can use latitudinal scenarios along an imagined transect from the Barents Sea (70°N) to almost the North Pole (85°N) (Fig. 16). At 70°N in the southern Barents Sea, there is some indirect light (Civil Twilight) in the middle of a winter day while there are two months of midnight sun and several months characterized by steeply increasing and decreasing daylight. At this latitude, rates of increase and decrease of daylight are about 12 min per day at equinox. With only open water in this region, we may find a spring bloom as early as April/May. However, the lack of ice-melt may result in weak stratification, hence the buildup of the bloom may be slower, but the bloom may last longer. Towards the end of the midnight sun period, a minor bloom may be possible in late August (e.g. Oziel et al., 2017).

At 75°N in the Civil Polar Night zone, we experience darkness for almost three months and sea ice cover typically between November and May, with an increase and decrease of daylight of about 16 min per day. Light penetration through ice/snow and an ice cover that is actively

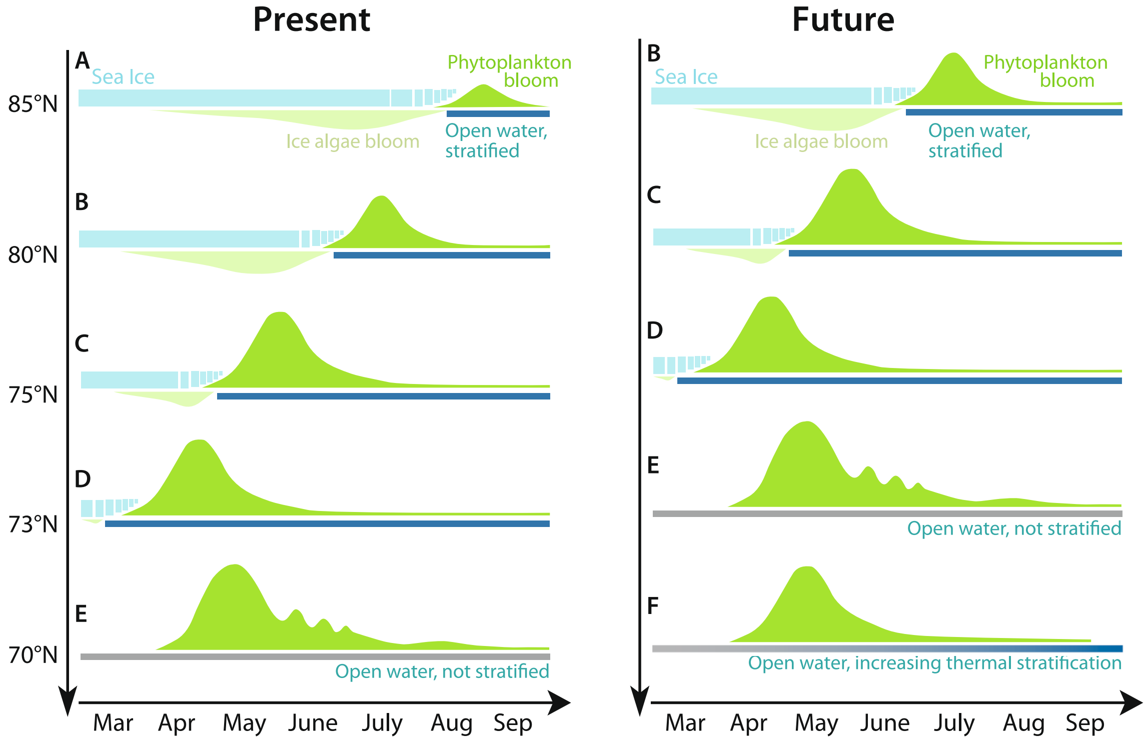

Fig. 17. Climate change alters the phenology of the ice algae and phytoplankton blooms. Present-day scenario (left) and predicted future scenario with a warmer climate (right) along similar latitudes. The hypothetical timing of the ice algae and phytoplankton bloom development in the Eurasian Arctic corridor along a latitudinal axis is indicated: from the open water-seasonal ice zone region (ranging from 75 to 85°N) with long to short productive periods in open water (70–75°N) to heavily ice-covered regions (>73–75°N). Notice how today's bloom development scenario A disappears for good while the new scenario F enters at the southern section of the latitudinal gradient in the future. Panels E and F exemplify the course of primary production in the scenario of continuously open water in the central/southern Barents Sea, characterized by no major freshwater source and weak and slow development of surface water stratification. The variable production in June (panel E) arises through variations in nutrient supply caused by vertical mixing events triggered by low-pressure passage after the end of the spring bloom. Panel F projects future primary production at 70°N after Arctic warming leads to increasing thermal stratification and decreased primary production. Modified from Leu et al. (2011) and Wassmann and Reigstad (2011).

breaking up supports an ice algae bloom in April and an open-water phytoplankton bloom in early June. Here ice returns often as late as December at this latitude. At 80°N and northwards, in the Nautical Polar Night zone darkness lasts for four months and ice cover may last until the end of June. The rates of increase and decrease in daylight are about 25 min per day at equinox. An ice algae bloom may occur in April and May (dependent on ice thickness and snow cover) and use available nutrients, likely resulting in a small phytoplankton bloom based on the leftover nutrients in early July. Sea ice often returns in November. At 85°N the light and dark periods last for more than five months each and the rate of increase and decrease rates of light are about 50 min per day at equinox. Most of the nutrients are used up by sea ice algae through a lengthy growth period lasting from April to August, as determined by ice thickness and snow cover (Fernández-Méndez et al., 2014). Before daylight disappears, a small phytoplankton bloom may occur (see Loeng et al., 2005; Ardyna et al., 2014; Oziel et al., 2017), but one may challenge if such blooms should be called an autumn bloom.

There has been a steady decline in nutrient concentrations in the AO inflow regions of the Northeastern North Atlantic (e.g. Rey, 2012; Hátún et al., 2017), the cause being the effect of climate change on subpolar gyres (e.g. increased thermal stratification). Despite the increase in radiation along the south to north gradient depicted in Fig. 16, increased stratification and reduced vertical mixing and nutrient supply are likely to lead to a decrease in autotrophic new production in the central AO (Ardyna et al., 2014, 2020; Randelhoff et al., 2019). With thinner ice at increasing latitudes stronger and more persistent ice algae blooms that take a greater share of new production can be expected. In contrast and despite longer level periods, phytoplankton blooms will likely decrease with increasing latitude caused by prior ice algae nutrient consumption, especially in the more strongly stratified Amerasian Basin. The post-bloom period with increased stratification and depressed nutrient supply of the post-bloom period will also be marked by a succession of progressively smaller autotrophs throughout summer (Li et al., 2009; Leu et al., 2015) and a prolonged period of post bloom heterotrophy (Vaquer-Sunyer et al., 2012). Also, the timing of the phytoplankton bloom onset is progressively delayed from April in the south to early September in the north. The conceptual model in Fig. 16 is neither intended to reflect the highly interannual dynamic nature of the Barents Sea and adjacent AO nor does it fully match the phenology of bloom cycles along the Pacific Arctic shelf-basin gradient. It merely illustrates the principle patterns that define these seasonal transitions. The principles behind Fig. 16 are also the base for Fig. 9A, B (left column) which depict todays large-scale phenology of autotrophs and their dependence on light and ice-cover across the entire SIZD.

Climate change and the resulting reduction in ice cover will modify the phenology of autotrophs, but biota (as reflected through mesozooplankton grazing, microbial and viral cycling, vertical export) cannot break out of the constraining envelope created by solar radiation and nutrient availability. For example, the bloom development at 70°N in the sector dominated by AW will move progressively northwards to 75°N and 80°N off the shelf, with phytoplankton rather than ice algae able to use up the available nutrients as ice cover is reduced (Fig. 17). Notably, the surface water nutrient concentrations in the Arctic basins are far lower than those of the shelves, let alone those in the advected PW and AW (e.g. Tremblay et al., 2015). Modelling projects that the nutrient concentration in the central AO surface water will in fact continuously decline during this century (Slagstad et al., 2015). Larger blooms of either ice algae or phytoplankton are not expected in the

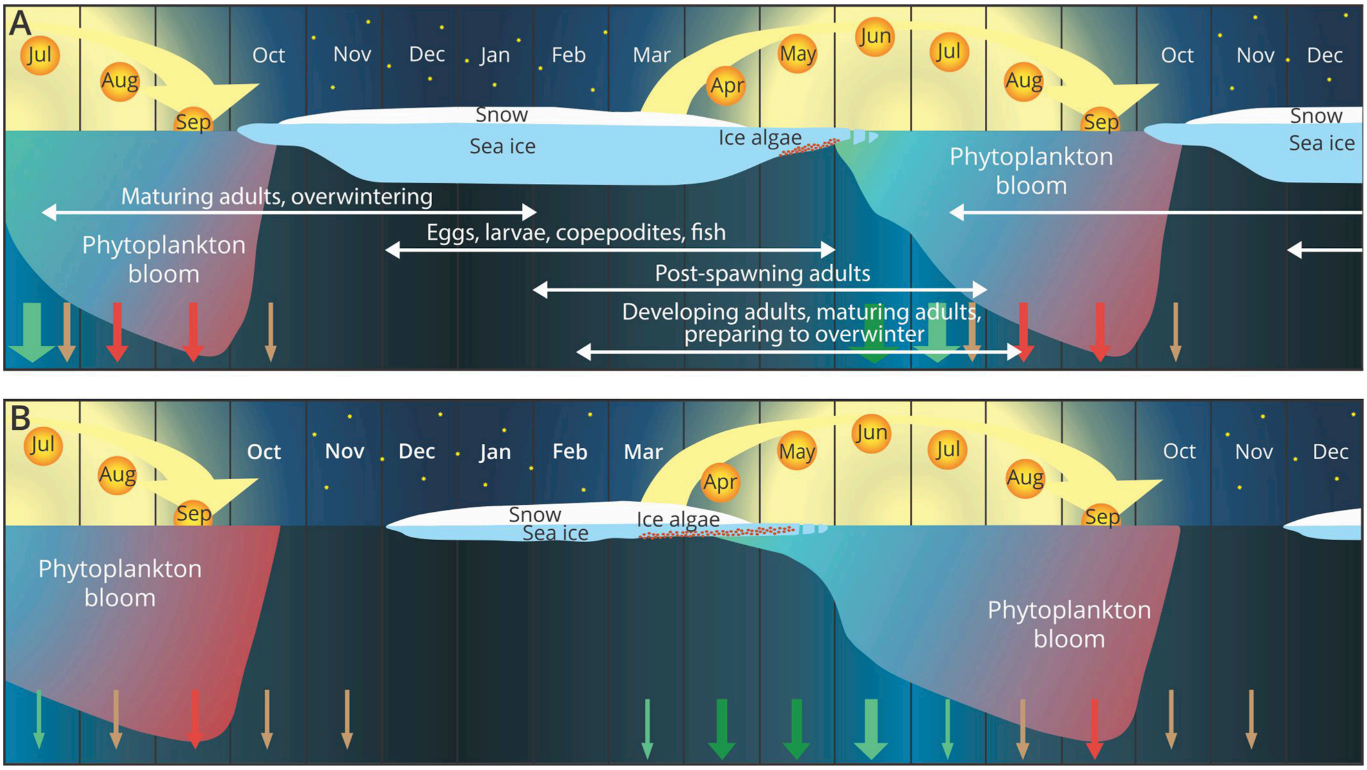

Fig. 18. Phenology of the bloom development and in downward carbon export at about 78°N in the Barents Sea over a two-year period. The present-day climate is depicted in panel A and the consequences of a warmer climate with thinner ice in winter and more melting of summer ice is displayed in panel B. A thinning of sea ice, variable snow cover, supports a) more intense and earlier ice algae blooms and b) a greater annual extent of the seasonal ice zone. The green-to-red gradient indicates the balance of suspended biomass from autotrophic (green) to heterotrophic (red) sources. The annual new and export production in both scenarios is assumed similar because stratification (induced by sea ice melt and increased surface warming) limit nutrient availability. Greater wind stress may though increase the vertical contribution of nutrients. The width and color of the vertical arrows illustrate the semi-quantitative magnitude and composition; autotroph, fecal pellet and detritus (green, red and brown, respectively) of vertical export. In an adaption to the short productive period and cold temperature many organisms at Civil Polar Night and Nautical Polar Night latitudes expand their annual life cycle to more than year. Some of the involved processes that organisms such as polar cod apply during the Polar Night are indicated in panel A (see white vertical bars). To understand the marine ecology at high latitudes in the AO, we must have to change our traditional attention to spring and summer but pay increasingly attention to the a) autumn and overwintering and b) multiannual time spans. Winter seems to play an essential role for the marine ecology of the AO. Redrawn from Wassmann and Reigstad (2011). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

basins because of the limited and decreasing availability of nutrients (Slagstad et al., 2015). This is in contrast to the shelves (in particular the Eurasian ones) where pelagic primary production increases as a function of increased open water area, i.e. higher input of solar radiation (Arrigo and van Dijken, 2015; Slagstad et al., 2015) though still ultimately controlled by nutrient availability (Tremblay et al., 2015). Increased atlantification/borealization (Polyakov et al., 2018; Randelhoff et al., 2018; Oziel et al., 2020) and changes in vertical mixing (Randelhoff and Guthrie, 2016; Randelhoff et al., 2019; Polyakov et al. 2020b) and increased shelf-break upwelling (Carmack and Chapman, 2003) may further influence and increase the future primary production on the shelves and the shelf-break (Fig. 12).

In today's Barents Sea bloom-development encountered in May-June at 70°N (Fig. 17E, left) may in the future be encountered at 73°N (Fig. 17E, right). Similarly, the bloom scenario that today is encountered at 73°N (Fig. 17D, left) may be observed at 75°N in the future (Fig. 17 D, right). Similary to the northward expansion of boreal species into the AO region, the MIZ bloom may shift northwards, at the expense of more Arctic, high-amplitude phenologies. This development resulted from the large-scale reduction of the multiyear sea ice. Fig. 17 depicts the marine analog of borealisation, i.e. the northwards displacement of both sub-Arctic water masses and boreal species. This development from today into the future can also be studied for the large-scale phenology of autotrophs and their dependence on light and ice cover across the entire SIZD (Fig. 9A, B (left column: today; right column: future)).

Fig. 17 E and F illustrate the assumed course of primary production in a scenario of continuously open water, which characterizes the central and southern Barents Sea that has no major freshwater source and a weak and slowly progressing in surface water stratification during summer. In regions where freshwater stratification is prominent such scenarios will not be encountered. The variable production in June (Fig. 17E, 70°N) arises through variations in nutrient supply caused by vertical mixing events triggered by the passage of low-pressure systems after the end of the spring bloom. Fig. 17 F at 70°N projects future primary production to decrease after Arctic warming has resulted in increasing thermal stratification, unless occurring mostly as subsurface blooms (Mayot et al., 2018). However, also late summer surface (Ardyna et al., 2014; Oziel et al., 2017) and subsurface blooms (Martin et al., 2010; Horvath et al., 2017) have recently been detected. These phenomena add new features to the phenology of autotrophs in the ice-free AO.

Previous and future scenarios in the phenology of the MIZ are presented in Fig. 18 A, B, respectively. Progressing from present-day to future climate and ice conditions, the principle seasonality will persist, but the timing will change. Climate warming will also result in a widening of the SIZ (Fig. 9) and a wider time window for primary production (Fig. 18). With greater incident light availability in the euphotic zone and earlier stratification due to melting sea ice, a decrease in the amplitude of the spring bloom may be encountered. Without an ice edge at its current position, the bloom will become less distinct and surface

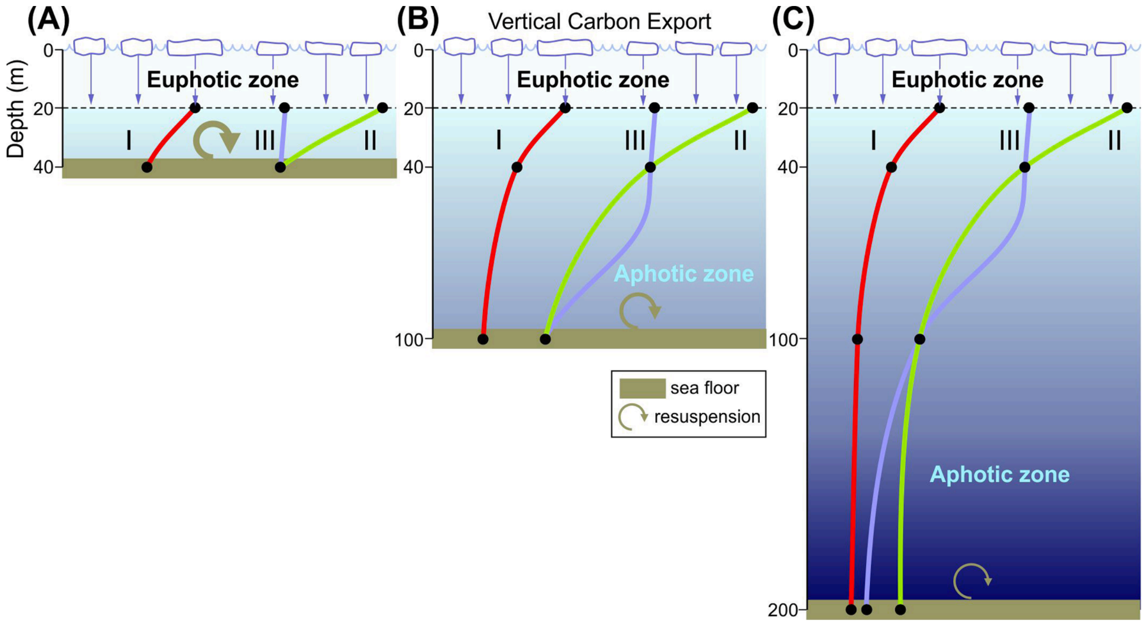

Fig. 19. Hypothetical graph explaining the principles of sympagic-pelagic-benthic coupling (SPBC) for shallow (A), moderately deep (B) and deep ocean (C) regions. The thin vertical lines (grey) illustrate the subsurface contribution of ice-derived biogenic matter. The level of new production (based upon nutrient availability and supply and light availability) increases the amount of the suspended biomass that can sink. Scenario I (red) illustrates the SPBC for less productive regions, whereas scenario II (green) illustrates the highly productive and stratified regions. Depth and the intensity of the pelagic retention, in particular in the upper twilight zone, plays a major role dictating the intensity of SPBC. Benthic organisms in shallow regions, such as the Chukchi Sea (see panel A) enjoy a far higher supply and quality of biogenic matter than deeper shelves (such as the deeper Barents Sea, see panel C). In the AO basins the SPBC is assumed to be weak (not shown). Vertical mixing in non-ice-covered regions which will become more frequent in the future results in a dilution of suspended biomass in the upper layers and a change vertical flux retention (scenario III, blue). Shallow shelves have far greater resuspension and contribute substantially more to remineralization than those in the deeper ones. Resuspension of particulate matter from the sediment surface, being most intensive on shallow shelves, further contributes to the horizontal export of carbon into the deep basins. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

waters will have decreased food concentrations for grazers that have tuned their life cycle to the initiation of this bloom (Daase et al., 2013). The decreased spring bloom concertation may be balanced by longer annual food availability and more detritus that would favor zooplankton species that can sustain themselves on less food and smaller food particles, i.e. smaller species (Svensen et al., 2018). The time window, in which the system is dominated by heterotrophs will increase. This scenario assumes that nutrient supply, will be unchanged (but see Tremblay et al., 2015).

The phenology of zooplankton has to face the seasonality changes in autotroph production, in particular the timing, density and temporal development of the spring bloom, as discussed before. The life cycles of common zooplankton organisms in the Arctic imply that these need more than one year for their development in contrast to boreal congeners. Biomass-dominant copepods in particular start their development during the productive season, but in the AO lower temperatures and reduced metabolism along with low food availability (especially in the central AO) do not permit them to complete their life cycles within the first productive season. Thus, they need to overwinter to complete their development and life cycles.

To highlight the significance the winter period we start with overwintering, not the spring bloom. For many species the winter at high northern latitudes implies dormancy; for others it implies reproduction and/or preparation for a new productive season, including gonad maturation and producing eggs prior to the onset of algae growth (Conover, 1988; Kosobokova, 1999; Hirche and Kosobokova, 2011; Hirche, 2013; Daase et al., 2013; Kosobokova and Hirche, 2016). While several marine mammals migrate out of the Arctic, lipid-rich zooplankton species and Arctic fish stay. For them and some other invertebrates, late summer and autumn comprise the development to juvenile life stages that accumulate energy reserves. Or, by maturation, they develop into lipid-rich adults prepared for overwintering at depth and in darkness (Falk-Petersen et al., 2009; Berge et al., 2015a,b; Daase et al., 2018).

Already in late winter and early spring, still in darkness, some animals commence reproduction relying on internal reserves (e.g. the key Arctic oceanic copepod *Calanus hyperboreus*) or detrital food (e.g. the brackish water copepods *Drepanopus bungei, Pseudocalanus major*) and their early larvae develop (Hirche, 2013; Kosobokova and Hirche, 2016; Nahrgang et al., 2016; Darnis et al., 2017). The spring period of increasing light and the productive and full day light season is then utilized by their early offspring (new generation) for development into juvenile overwintering stages, while the overwintered late juveniles hatched a year ago (old generation) develop to adulthood. Towards the end of the productive season these two generations prepare to overwinter again (e.g. Fig. 18A, horizontal bars). Thus, the winter period is an important segment of the ecology of zooplankton grazers and fish in the AO which connects the preparation for overwintering and active development during spring and summer.

Life cycle studies in the AO thus demand longer time periods than a year, in particular for a multitude of Arctic biota that are much longer-lived than boreal and tropical counterparts. Therefore, conceptual models of seasonality need to cover a minimum 18 months, such as in Fig. 18. Also, many benthic organisms may exceed longevities of decades or centuries (Bluhm et al., 1998; Ravelo et al., 2017). The phenology timeline in the AO is thus strongly multiannual.

5.3. *Sympagic-pelagic-benthic coupling*

Processes involved in the sympagic-pelagic-benthic coupling (SPBC) include those that connect biota in sea ice, water column and benthic habitats (Grebmeier and Barry, 1991; Carroll and Carroll, 2003; Werner, 2006; Forest et al. 2010). Also entailed in SPBC are the phenology and biological life cycles of a wide range of organisms entangled in highly variable spatial and interannual scales (Wassmann et al., 2004; Grebmeier, 2012; Fernández-Méndez et al., 2014). The domain of SPBC action covers the entire AO; in particular, the SPBC connects the SIZD and water column with the sediments of the extensive shelves, which thus comprise major regions of the AO (Figs. 8A, 9). SPBC depends upon the new production and the accumulation of biogenic matter and of both sea ice algae and phytoplankton (Gosselin et al., 1997; Gradinger, 2009; Lalande et al., 2014), melting of sea ice from below (detachment of particulate matter; Tedesco et al., 2019), loss of biogenic matter from sea ice and the upper layers, the retention of nutrients and biogenic matter in the water column (e.g. Olli et al., 2002; Lalande et al., 2007), the aggregation potential of suspended matter (Engel et al., 2004; Rapp et al., 2018), grazing (Wexels Riser et al., 2002; Tamelander et al., 2012), vertical export of biogenic ice-derived and pelagic matter in the Twilight Zone (i.e. the 200–1,000 m deep layer of water that stretches around the globe; Wassmann et al., 2003; Reigstad et al., 2008; Buesseler and Boyd, 2009), as well as processes in the benthic boundary layer (e.g. resuspension and remineralization by benthic organisms; Thomsen, 2002; Stein and MacDonald, 2004; Grebmeier et al., 2015). As a consequence of this multitude of processes, the activity of SPBC is not evenly distributed, but to a first order is depth-dependent (Fig. 19).

Ice- and snow-cover, horizontal advection, stratification/vertical mixing, nutrients and light shape the basic conditions for primary production, the source of ice-attached and suspended biogenic matter accumulation in the upper water layers (Fig. 19). This physical-chemical-biological continuum creates the basis for new production and thus the potential standing stock of autotrophs that can be grazed, recycled, and exported vertically. For simplicity, advective off-set is not considered in Fig. 19. Because of the orders of magnitude difference between the horizontal velocity of water and the sinking speed of particulate matter vertical flux of individual particles is strongly tilted to the horizontal plane. Regionally, and in particular on the shallowest AO shelves, the horizontal distance between the origin of biogenic matter and its deposition is small. In deeper regions, the horizontal distance for the smaller sinking particles may be hundreds of km away and advection will result in extensive differences in the region of primary production and benthic deposition.

The maximum of the vertical organic matter flux is particularly prominent in the lower euphotic zone and the uppermost section of the twilight zone (Wassmann et al., 2003; Buesseler et al., 2007). Below the euphotic zone aggregate, formation and dissolution of particulate organic matter become important constraints for vertical export (Jackson and Burd, 1998; Stemmann and Boss, 2012; Rapp et al., 2018). In addition, top-down regulation through various categories of grazing zooplankton grazing removes biomass, destroys aggregates and produces/degrades fecal pellets (Wexels Riser et al., 2007). These processes are assumed to take the lead role for the fate of suspended and sinking biogenic matter. The heterotrophs in the AO are deprived for authochthonous food because of the significant influx of long-lived zooplankton (Olli et al., 2007; Wassmann et al., 2015, 2019). Grazing and omnivorous zooplankton orient themselves towards the source of algal food, i.e. they direct their feeding attention towards ice-algae or the base of the euphotic zone with its associated subsurface chlorophyll maximum (Fig. 19). Thus, a great amount of zooplankton biomass in the AO is usually encountered just below the euphotic zone (e.g. Olli et al., 2007), regulating partly the vertical export and contributing significantly to the strength of the retention filter in the upper aphotic zone (Wexels Riser et al., 2007).

The strength of grazing, the types of grazers and their grazing efficiency/mode determine the manner by which suspended biogenic matter is consumed, thus affecting both a slowdown (sinking particles removed, reduction in size) and acceleration (fecal pellets produced) of vertical export (e.g. Wassmann et al., 2003; Buesseler and Boyd, 2009). However, fecal pellets still have some nutritious value for some detritivorous grazers, but through processes such as coprophagy and in particular coprorhexy most of the rapidly sinking particles are retained in the upper water layers in most areas (e.g. Wexels Riser et al., 2002; Iversen and Poulsen, 2007; Svensen et al., 2012). Sloppy feeding and microbial remineralization contribute also the retention of sinking organic matter. As a result, 20–70% of the export production leaving the euphotic zone can be recaptured and retained in the upper 100 m of the water column (most intensive in the 20–60 m depth interval), for example in the case of the Barents Sea (e.g. Olli et al., 2002). Increased light, available nutrient and stratification (vertical excursion of phytoplankton) support bottom-up regulation that increases upper layer primary and new production (Fig. 19; compare scenario I with II). At shallow depths such as in the northern Bering and Chukchi and Laptev Seas, SPBC is highly variable (Fig. 19 panel A), but the supply of biogenic matter to the benthic boundary layer and benthos is much stronger than at greater depths (Lalande et al., 2007, 2009a, 2020). With increasing depth, top-down regulation through grazing, mineralization and fragmentation increasingly takes over, forcing vertical export to decrease (Fig. 19). As a result, the benthic biomass in the highly productive, shallow northern Bering Sea and southern Chukchi Sea (Fig. 19A, Carroll et al., 2008; Grebmeier et al., 2015), with substantial nutrient recycling (Devol et al., 1997; Cooper et al., 2009; Hardison et al., 2017), is far higher than on deeper shelves (Fig. 19C; Bluhm et al., 2011b).

The connection between new production and vertical export can be explained in a curvilinear manner (Wassmann et al., 2003) and quantified as vertical flux attenuation efficiency (Olli, 2015). The depth-dependend grazing processes of planktonic heterotrophs impose a degradation efficiency that determines the vertical flux attenuation and the shape of the vertical export profiles (e.g. Wexels Riser et al., 2001). The potential vertical export can be low or high when the upper water column is stratified (Fig. 19, scenario I and II, respectively). It depends first of all upon the rate of new production and the abundance of detached ice or planktonic biogenic matter (e.g. Assmy et al., 2017; Wollenburg et al., 2018). When vertical mixing is prominent, the export of suspended biogenic matter is lower (scenario III).

The biomass of heterotrophs, their feeding mode, their vertical distribution and water depth determine SPBC (Wexels Riser et al., 2002; Svensen et al., 2012), influencing the efficiency of retention filters. These are particularly efficient when new production is strong and the suspended biomass of large autotrophs, such as diatoms, prevail. This weakens the pelagic-benthic coupling (Wassmann et al., 2003, Wexels Riser et al., 2007). However, grazing does not prevent that living autotrophs such as diatoms and *Phaeocystis* reach deeper waters and the sediment (Wassmann et al., 1990; Boetius et al., 2013; Agustí et al., 2019). Although SPBC can be highly variable at shallow depths, a weak water column retention makes coupling much stronger than in deeper regions of greater depths (Fig. 19A), and a much larger part of the production (can reach over 50% in the Pacific inflow shelves) settles to the seafloor either ungrazed or as fecal pellets (Lalande et al., 2007, 2009b).

Climate change will result in continuously open water at the periphery of the AO. This provides possibilities for more primary production between both equinoxes. Sea ice cover may become an exclusively Polar Night phenomenon. Mixing in these open water results in a delay in the spring bloom that cannot occur before mid-April. The SPBC scenarios in the open waters will develop from scenario II into III, with consequences for both plankton as benthos (see scenarios in Fig. 19A–C). The increasing observations of autumn blooms (Ardyna et al., 2014; Oziel et al., 2017) may support increases in the SPBC, but they will probably not result in increased food for benthos.

The phenology of the SPBC is highly variable in the AO. Vertical carbon export is usually elevated with the timing of the spring bloom, in particular when the bloom is intense, e.g. in the MIZ (Fig. 18A). After the export of fresh material in connection with the spring bloom has passed (Wassmann et al., 1990; Boetius et al., 2013; Agustí et al., 2019), degraded matter and fecal pellets take over the vertical flux, while during post bloom and autumn scenarios detritus dominates (Fig. 18A).

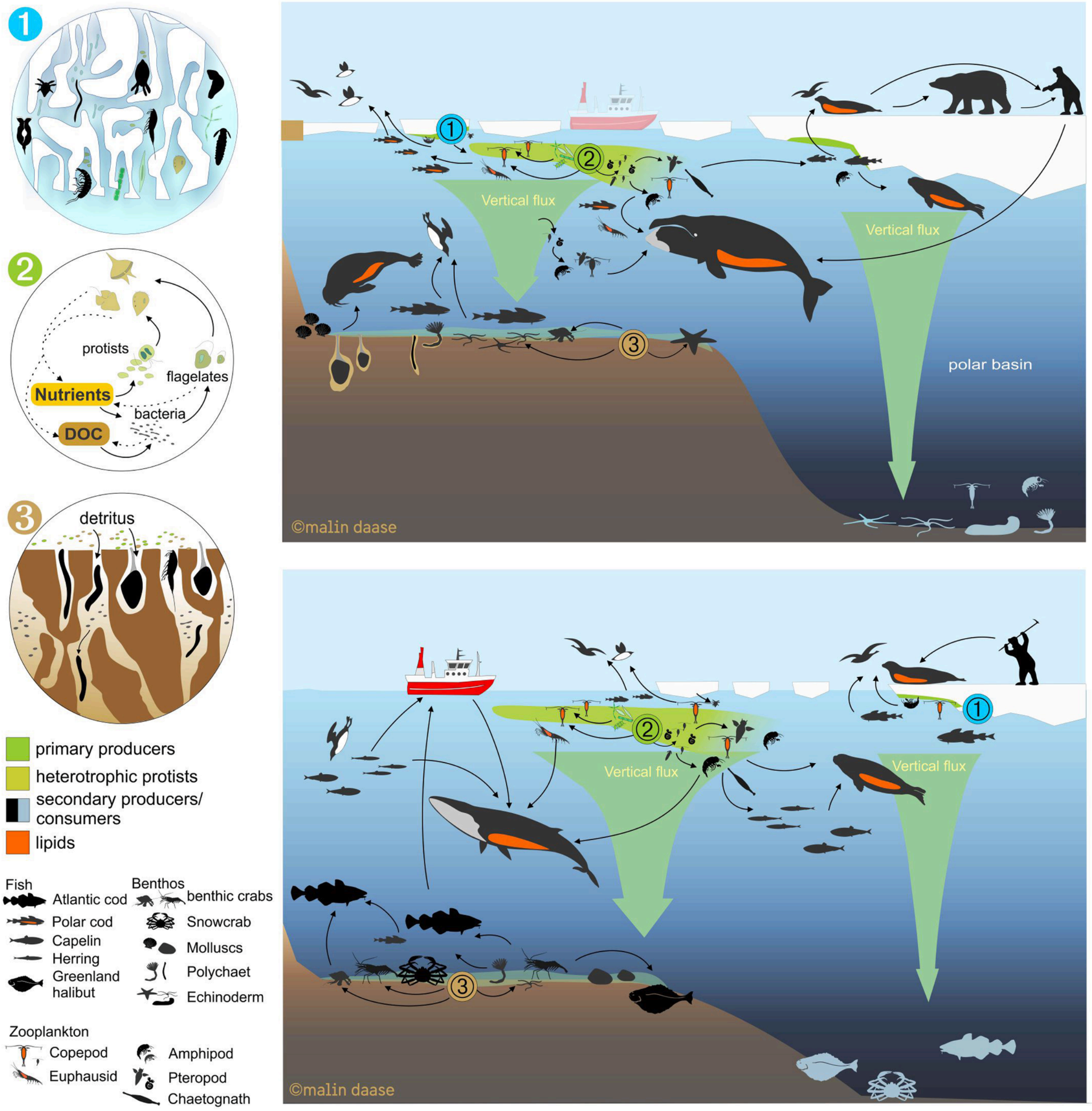

Fig. 20. Conceptual Arctic food web showing dominant taxa and their trophic position and indicating trophic links among species through arrows. This depiction overlays a vertically-structured concept of the Arctic Ocean's compartments including sea ice, water column and seabed. A shallow shelf and more Arctic influence are indicated by characteristic biota, subsistence populations and more sea ice (A, Bering Strait region, Chukchi Sea). The semi-transparent fishing vessel indicates (potential) fisheries moving north. A deep shelf and one with more Atlantic influence are indicated by characteristic biota including commercial species, less sea ice and fishing effort (B). The basin conditions are not shown in detail. Circular insets illustrate the ice brine channel system biota (1), the microbial food web (note archaea, fungi and viruses are also present though not depicted) (2) and the meiofaunal sediment community (3). Primary producers are colored in green, consumers in black (and light blue in deeper waters), and orange indicates particularly lipid-rich biota with high energetic value for their consumers. For more detail, see text Section 6.1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The phenology of vertical flux is strongly regulated by the withdrawal of the ice edge, stratification and the availability of light. Increased vertical export of biogenic matter of increased quality can thus take place throughout the productive season in the AO, but not before April and no later than September (Fig. 18). In the near future, todays scenario of the SIZD illustrated in Fig. 18A may change towards longer periods with ice-free conditions, probably well before 2050 (Overpeck et al., 2005; Notz et al., 2020) (Fig. 18B). That may result in an earlier onset of suspended biogenic matter accumulation. A smoother time development of autotrophs may also result in a decreased amplitude in vertical export (Fig. 18B). The amount of high-quality food reaching the deeper water column and the sediment will decrease and the supply will be more evenly distributed in time.

In summary, the intensity of SPBC is a complex relationship between production, vertical mixing, advective inputs, water depth, the intensity of the retention filter, and benthic remineralization (Dunton et al. 2005; Lalande et al., 2014; Wiedmann et al., 2014; Grebmeier et al., 2015). Sediment community oxygen consumption can used as indication of long-term SPBC, while benthic biomass is typically measured directly, and production often estimated from either respiration or through established P:B relationships. From physical-biological coupled models and remote chlorophyll sensing often new production or bloom intensity are used as proxies in which benthic biomass and production may be high. Neither new production nor pelagic accumulation of biogenic matter solely determine the SPBC. Nor does the supply of biogenic matter to the sediment alone indicate new production and pelagic accumulation of biogenic matter in the upper layers. The connection between primary and benthic production in the AO cannot be established and modelled without a detailed understanding of the curvilinear complexity of the SPBC and the effect of ULADs (Fig. 11).

Table 3
Characteristics of Arctic food webs.

General concept/ focus	Arctic case	Example references
Who eats whom: compartments of a food web	Sea ice as additional realms, housing > 1000 species Dominant grazers: calanoid copepods Large benthic compartments: bivalves, polychaetes, crustaceans, echinoderms Key fish predator: Polar cod Abundant bird and mammal predators: alcids, gulls, ice-associated seals and whales	Planque et al., 2014; Whitehouse et al., 2014
Energy content	High lipid food web, especially in zooplankton, polar (Arctic) cod and capelin, marine mammals; high PUFA content in ice algae	Lee et al., 2006; Leu et al., 2006
Specialization versus generalism	Higher than assumed trophic plasticity, omnivory and mixotrophy; size-structured food webs	Mixotrophy: Sanders and Gast, 2012; Stasko et al., 2018; Harris et al., 2018
Food web length	Typically, 4.5–6 trophic levels: not generally different than in other seas; replacing earlier notion of short food webs	Iken et al., 2005, 2010; Whitehouse et al., 2014; Suprenand et al., 2018
Connectivity	Lower connectivity in Arctic than boreal / sub-Arctic food webs (note only Barents Sea studied); yet typically multiple trophic links per species	De Santana et al., 2013; Kortsch et al., 2015; Planque et al., 2014
Particulate Organic Carbon sources	POC: Phytoplankton, ice algae, carcasses of heterotrophic plankton, terrestrial input from large rivers, tundra and glaciers, macroalgae, microphytobenthos, (locally methane)	Iken et al., 2010; Wang et al., 2016; Renaud et al., 2015; Harris et al., 2018

6. Food web models

Conceptual approaches that aim to investigate organisms and their role in biogeochemical cycling, biodiversity and ecosystem dynamics in the Arctic mediterranean must match the appropriate geography, biophysical and biogeochemical environment, seasonality and light regime, and functionality of contiguous domains (described in Sections 2–5). Within these frameworks, organisms interact in several ways with prominent interactions resulting from trophic relationships and competition for resources. Here we follow the definition of Layman et al. (2015) of a food web as “a network of consumer-resource interactions among a group of organisms, populations, or aggregate trophic units”; an example applicable to the AO is shown in Fig. 20. Climate change and the increasing human use of the Arctic now demand holistic evaluations of the interdependencies of species and their interlinked response to a change or perturbation of their ecosystem. In this section we apply findings from existing regional studies to the typologies proposed in preceding sections to formulate unifying, pan-Arctic conceptualizations based on three critical questions: (1) Who eats whom, (2) How does energy flow across trophic levels, and (3) Which carbon sources are most important to a given taxon or region?

6.1. Food web topology: Who eats whom?

The ‘who eats whom’ question is conceptually depicted through images of species or trophic levels (i.e. species with shared position in the food web, often through similar prey and predators) with arrows connecting each prey to their predator(s) (Fig. 20). The underlying, species-specific trophic information is traditionally derived from stomach content studies, in recent decades complemented by trophic marker studies, and where feasible, complemented by experimental work on predator-prey relationships. Diets and feeding modes are now generally well-documented for common biomass-dominant Arctic species, but poorly characterized for remaining species (Table 3).

We summarize the simplified dominant trophic connections for shallow shelves using the Pacific inflow shelf as an example and for adjacent the basins that currently have no large-scale commercial fisheries (Fig. 20A). Separately we show the simplified food web for deeper shelves with those areas – the Atlantic inflow and parts of the outflow shelves – that house a number of large boreal fish and invertebrates that are regionally commercially harvested (Christiansen et al., 2014) (Fig. 20B). We note that some of these food web connections undergo seasonal variations; the depicted situations focus on productive periods. Moving from the base of the food web to top predators, bacteria take up DOC and support heterotrophic and mixotrophic nanoflagellates, which in turn are prey for other protists (Seuthe et al., 2018; Fig. 20A, microbial inset (2)). These, in addition to larger, phototrophic cells such as diatoms, are then available by grazing, metazoan zooplankton. *Calanus* spp. (e.g. *C. glacialis* and *C. hyperboreus* in Arctic water masses, advected *C. finmarchicus* in inflowing Atlantic water), krill and other zooplankton species capitalize on the spring bloom and provide food for secondary consumer zooplankton such as omnivorous/predatory copepods, arrow worms, jellyfishes, pelagic amphipods and pelagic snails *Clione* as well as for higher trophic level taxa including various fishes, seabirds, seals and whales (Fig. 20).

Examples for abundant planktivores at higher trophic levels include the little auk, some auklets and bowhead whales among Arctic species (Fig. 20A), and minke and fin whales and shearwaters among boreal species (Fig. 20B). During sea ice cover, in particular in the SIZD, primarily herbivorous sympagic (i.e. ice-associated) meiofauna (Fig. 20, brine-channel system, inset 1) and herbivorous, omnivorous and carnivorous amphipods at the under-ice surface make ice-derived carbon, mostly from diatom-dominated blooms (Fig. 20, inset 1), available to young polar cod (*Boreogadus saida*), the dominant truly Arctic fish. Adult polar cod feed primarily on copepods and other crustaceans both in the water column and near bottom and provide prey for many seabirds and mammals, in particular in the areas summarized in Fig. 20A.

Vertical carbon flux (see Section 5.3) fuels detritivores, zooplankton and the microbial loop in mid-water. The material enriches the detritus pool close to and on the seabed. Detritus of diverse sources combined with ungrazed algae in shallow areas support a variety of interstitial meiofauna (Fig. 20A, bottom inset 3), surface and sub-surface deposit-feeding invertebrates such as a suite of polychaetes and other worms, bivalves, and larger epifauna. Near-bottom currents supply a stream of living or resuspended detritus particles to benthic suspension feeders, in particular in high-flow areas or on elevations such as drop stones. All these invertebrates serve as prey for both invertebrate predators such as snails, sea stars, shrimps, crabs, as well as for demersal fishes and benthic-feeding mammals (such as gray whales, bearded seals and walrus) and diving seabirds such as eider ducks (Planque et al., 2014; Whitehouse et al., 2014). The true Arctic fishes, such as sculpins, many snail fishes and eelpouts on the shelves are primarily small-bodied and feed primarily on small demersal invertebrates. In contrast, larger-bodied predators such as Atlantic cod (*Gadus morhua*) and Greenland halibut (*Reinhardtius hippoglossoides*) are found in the waters of the Atlantic inflow and parts of the outflow shelves and adjacent deeper water (Christiansen, 2017; Haug et al. 2017; Fig. 20B), while the cold pool in the Bering Sea has so far largely kept these large predators out of the Pacific inflow shelf (but see recent changes (Grebmeier et al., 2006; Huntington et al., 2020) and interior shelves. The spatial distribution of key players of these food webs and with its spatial characteristics of trophic connections have experienced shifts termed ‘borealization’ in recent decades (e.g. Fossheim et al., 2015; Frainer et al., 2017; Alabia et al., 2018; Polyakov et al. 2020a,b). In the adjacent deep basin, faunal densities are lower because little and low-quality food reaches the deep-sea floor, the proportion of small taxa and detritus feeders increases, yet a number of mobile larger fauna quickly take advantage of food pulses (Fig. 20A).

The conceptualization of Arctic food webs has in the past decades advanced from simple predator-prey interactions and few-species chains towards highly connected webs. The underlying studies acknowledge that: the microbial loop appears to be as active in the Arctic as elsewhere and plays a much larger role in the food webs than previously appreciated (Forest et al., 2011; Seuthe et al., 2018); most species eat multiple other species in the AO (Planque et al., 2014); some species can seasonally or ontogenetically shift diets (Stasko et al., 2018); great trophic diversity is recognized within those higher taxa (e.g. Jumars et al., 2015); substantial regional diet variation exists (Bluhm and Gradinger, 2008); and finally, Arctic food webs are not always short, opposing the previous paradigm (Iken et al., 2005, 2010). Yet, conceptual organismal food webs obviously still need to simplify trophic and taxonomic diversity in some fashion (Fig. 20), depending on a given research question, area or contiguous domain.

Vertical carbon flux fuels detrivorous zooplankton and the microbial loop enriches detritus pools at the seabed, supporting a variety of interstitial meiofauna (Fig. 20A, bottom inset), surface and sub-surface deposit-feeding invertebrates such as polychaetes and other worms, bivalves, and larger epifauna. Near-bottom currents also supply a stream of living or resuspended detritus particles to benthic suspension feeders, in particular in high flow areas or on elevations such as drop stones. In combination with the deposit-feeders, this detritus serves as prey for both invertebrate predators such as snails, sea stars, shrimps, crabs and demersal fishes as well as for benthic-feeding mammals (such as gray whales, bearded seals and walrus) and diving seabirds such as eider ducks (Planque et al., 2014; Whitehouse et al., 2014). The other small-bodied true Arctic fishes feed primarily demersally (Fig. 20A).

At least four features are characteristic of the generalized Arctic predator-prey based food web concept: first, compared to non-polar regions, sea ice provides an additional habitat and related food web for more than 1000 taxa of single- and multi-cellular pro- and eukaryotes. These taxa are partly contained in the size-structured brine channel sea ice matrix (Fig. 20A, top inset (1)) and hence not as freely available as pelagic resources, but rather become available in a seasonal sedimentation pulse and/or channeled through under-ice fauna and are presently mostly a seasonal resource (Bluhm et al., 2017; Hop et al., 2010). Second, characteristic of biomass-dominant Arctic (and a little less so of advected boreal) zooplankton, polar cod and endemic marine mammals have very high lipid (i.e. energy) content (Lee et al., 2006; Fig. 20 A, orange color). This food web of fat is the survival strategy for many species in a cold and highly seasonal habitat where metabolic rates are lower, and life cycles take longer to complete than in the boreal and sub-Arctic habitats (see Section 5.2). Third, a long (albeit highly variable as described earlier) dark season with low levels of primary production often coincides with shifts in habitat ranges and/or trophic habits of organisms: they either migrate out of the Arctic food web for part of the year (e.g. some marine mammals and birds), reduce or completely cease food intake (e.g. as cysts or through diapause), or adopt a mixotrophic or otherwise plastic feeding strategy resulting in overall higher than previously assumed polar night activity (Hirche and Kosobokova, 2011; Berge et al., 2015b; Kosobokova and Hirche, 2016). Fourth, humans in the Arctic food web are a combination of subsistence-harvesting indigenous peoples whose cultures often focus around harvests of marine mammal, birds and migratory fish in the RCD (Suprenand et al., 2018; Fig. 20A), and commercial operators that are currently at the Atlantic-Arctic perimeter focusing on boreal fishes that have expanded their occurrence into Arctic waters (Fig. 20B). In summary, characteristics of Arctic regionality and contiguous domains drive differences in regional food webs through environmental forcing on biotic communities and their trophic interactions.

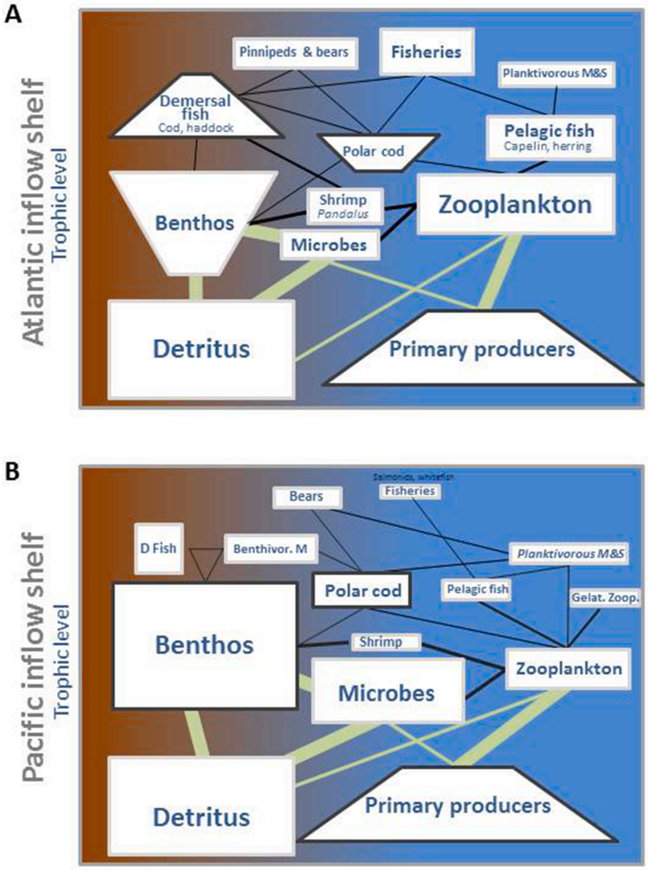

Fig. 21. Conceptual depiction of energy flow in Atlantic (top panel) and Pacific (bottom panel) inflow shelves. Dominant functional and/or taxonomic groups are shown as rectangles and trapezoids and are vertically arranged along a trophic level axis, starting from the base of the food web at the bottom. A given group may extend across several trophic levels; box size indicates the relative biomass of a given group. Trapezoids indicate increasing or decreasing relative importance along a south (lower side)-to-north (upper side) gradient (only shown where very prominent). Brown shades indicate benthic-dominated, blue shades pelagic-dominated flows. Lines between boxes show (only particularly prominent) energy flows with green lines denoting energy transfers from the lowest trophic levels and detritus and black lines denoting energy flow between consumer levels. Dark gray outlines marks groups with particularly many trophic links, of which only some are shown. Modified from Whitehouse et al. (2014) and informed by Carroll and Carroll (2003), Dommasnes et al. (2001), Iken et al. (2010), de Santana et al. (2013), Hunt et al. (2013), Kortsch et al. (2015, 2019), Skaret and Pitcher (2016), Pedersen et al. (2018), Suprenand et al. (2018). D = demersal, gelat. zoop. = gelatinous zooplankton, M = marine mammals, S = seabirds. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

6.2. *Energy flow and connectivity in Arctic food webs*

The food web concept has been expanded to the analysis of structural properties of holistic food webs, and this approach has begun to be applied to the AO. One important metric describes the flow of energy between taxa or functional compartments and across trophic levels. Energy flows have been estimated based on ‘who eats whom and by how much matrices’ in combination with biomass, production, consumption and trophic efficiency rates by using energy mass balance models (e.g. Christensen and Walters, 2004). In addition, ecological network analysis characterizes food web connectivity through, for example, the number and strength of interactions between compartments of the food web using nodes and paths (e.g. Ulanowicz and Wolff, 1991; Dunne et al., 2002, 2004) (Fig. 21). Jointly these analyses show that, while Arctic and high latitude food webs were long thought to be generally short and

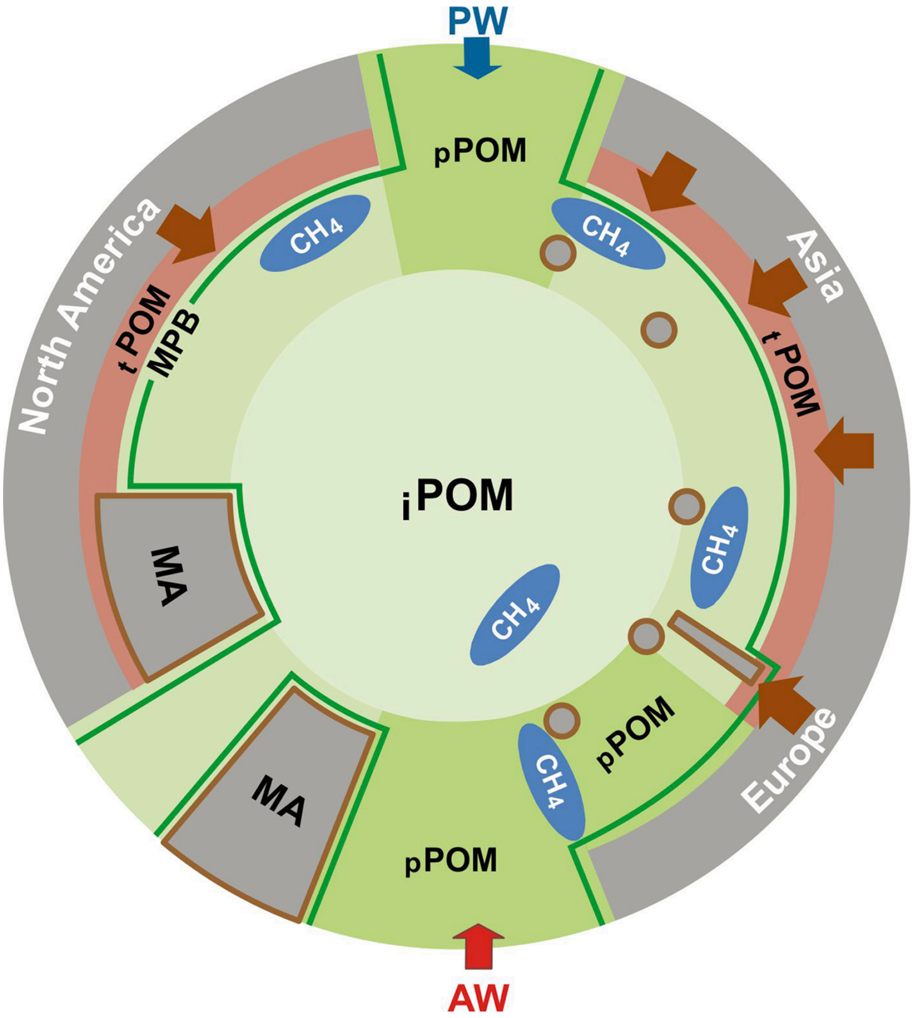

Fig. 22. Particulate carbon sources supporting the (eukaryotic) Arctic food web. Substantial methane sources (blue ovals, CH_4) are documented in sub-sea surface sediments, and early evidence suggests methane uptake into the food web. Carbon sources playing strong roles in a given region of the Arctic Ocean are shown: Pelagic particulate organic matter (pPOM) is the primary (particulate) carbon end member, and overwhelmingly so in the inflow shelves (dark green). In the central basin, ice-derived POM (iPOM, light green) can contribute about half to primary production. Interior shelves in particular receive substantial amounts of terrestrial organic matter (tPOM, light brown) from permafrost and rivers (brown arrows), though glaciers also contribute. Rocky shores of Greenland, the Canadian Arctic Archipelago (gray trapezoids), Svalbard and Russian shelf island groups (gray circles) provide increasing amounts of macroalgae carbon (MA and brown outlines). Notably, dissolved organic carbon (DOC; not shown in this figure) contributes most carbon to the entire carbon pool, but must be taken up through the microbial loop, namely bacteria, before entering the eukaryotic food web. Microphytobenthos (MPB) may exceed phytoplankton production in areas to ca. 30 m depth. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

simple with high trophic efficiency (though they exist under certain conditions and in certain places), longer food webs and complex structure are in fact rather common (e.g., Dunton et al., 2012; Kortsch et al., 2019; Saint-Beat et al., 2020; Table 3); this complexity makes depictions of conceptual models of Arctic foods webs as attempted in Fig. 20 simplistic at best. The linkage of the now more thoroughly established microbial loop to the refined ‘classical’ food web (e.g., Saint-Beat et al., 2018) shows that 4.5–5.5 trophic levels are typical of Arctic food webs (Figs. 20, 21, Table 3). Short Arctic food webs do exist under certain conditions and in certain places. Estimates of the number of trophic levels derived from stomach contents largely agree with those estimated from trophic markers, except that detrital consumers of highly reworked material appear at higher trophic levels when estimated from $\delta^{15}N$ values (e.g. Iken et al., 2010).

Trophic pathway analysis has also documented prominent differences within and among Arctic regions, among Arctic and Antarctic regions, and among Arctic and non-polar regions (de Santana et al., 2013; Whitehouse et al., 2014; Kortsch et al., 2019; Saint-Beat et al., 2020). For example, differences among Arctic food webs include high system production and throughput via benthic compartments on the shallow, productive, and tightly coupled Pacific inflow shelf versus higher retention in the pelagic system on the deeper Atlantic inflow shelf (Whitehouse et al., 2014). Network analysis of food webs in the boreal versus arctic parts of the Atlantic inflow shelf, the Barents Sea, revealed a lower number of links per trophic species and higher compartmentalization through more specialized feeding in Arctic compared to boreal and sub-Arctic food webs. This difference is driven by few biomass dominant omnivorous generalists that are major components of the highly connected food web of boreal character (Kortsch et al., 2015, 2019). As a result, it has been suggested that the boreal-Arctic food web is inverted compared to the classical trophic pyramid, meaning it has a comparably higher proportion of predator biomass (de Santana et al., 2013). The phenomenon of spreading trophic generalists in a changing climate and their effects on food web connections is in fact recognized globally (Bartley et al., 2019). It is argued that predatory species may make the Arctic food web more vulnerable, because of their ability to efficiently spread perturbations in case of the northward spreading generalist predators (Kortsch et al., 2015), and to promote trophic cascade effects in case of the loss of a key predator species (de Santana et al., 2013). A number of key Arctic predator species rely on sea ice as a habitat (Laidre et al., 2008; Wassmann et al., 2011), and it is, hence, not far-fetched to consider the fragility of several key predator species in the Arctic food web and the cascading effects this may have on the whole food web. Energy-flow models and network approaches should be applied to other regions and contiguous domains of the Arctic, however, before they can fully be generalized within our pan-Arctic framework.

6.3. *Carbon sources of the Arctic food web*

A suite of carbon sources drives marine food webs of the AO. On a pan-Arctic level the Arctic food web in open waters is thought to be primarily fueled by highly seasonal phytoplankton blooms (Oziel et al., 2017). These blooms in turn are partly fueled by advective inputs in inflow shelves, and less so in other Arctic areas (Wassmann et al., 2015).

Consequently, phytoplankton are the major carbon end member in Arctic inflow shelves, mediated through a combination of advected and *in situ* production (Wassmann et al., 2015; Vernet et al., 2019). Increasingly, additional particulate carbon sources are recognized as regionally and/or seasonally contributing moderate to large proportions to total diets, especially outside the inflow shelves. These additional sources include ice-algae across the SIZD, terrestrial carbon in the RCD and adjacent areas (down to slope communities), microphytobenthos and macroalgae carbon mostly in shallow areas, and possibly methane seeps on some shelves (Fig. 22). These findings are largely based on trophic markers such as fatty acids biomarkers, bulk carbon and compound-specific stable isotopes, the isoprenoid lipid markers such as IP_{25}, and lignin phenols (e.g. Goñi et al., 2013; Kohlbach et al., 2016) (Fig. 22), as well as combined with mixing models to estimate carbon source partitioning.

These models suggest that ice algae produced in the SIZD may in certain time windows and areas contribute noteworthy or even larger proportions of carbon than phytoplankton to key Arctic organisms across trophic levels (Fig. 22). Biomass-dominant Arctic copepods, pelagic amphipods and krill, for example, were estimated to derive a fifth to the majority of their carbon from ice algae organic matter in the central AO (Kohlbach et al., 2016) and in the Pacific inflow shelf (Wang et al., 2015). Ice-derived carbon also supplies large fractions of carbon to young polar (Arctic) cod in the SIZD of the central AO (Kohlbach et al., 2017), but very little in open-water interior shelf locations (Graham et al., 2014). At yet higher trophic levels, high ice-derived carbon contributions were also estimated for various seals in the Pacific inflow shelves in cold years (Wang et al., 2016). Furthermore, microphytobenthos may play an appreciable role as a carbon source in nearshore shallow shelves and fjords (McTigue et al., 2015, Harris et al. 2018) where their primary production may exceed that of phytoplankton (Glud et al. 2009), and also contribute to the microbial food web (Holding et al., 2017).

The role of terrestrial carbon – once thought to be unusable for marine food webs – has attracted growing attention and is now recognized as a carbon subsidy for the Arctic marine system. Conceptual models of the Arctic hydrological cycle (Vörösmarty et al., 2000) and of carbon pathways (ACIA, 2004) show this material to primarily enter from rivers that drain ponds and lakes, (thawing) permafrost, as well as glacial melt, all sources thought to increase under scenarios of climate warming (McClelland et al., 2004; Agustí et al., 2010; Carmack et al., 2016). It has been recently found that groundwater is also a major source of dissolved organic matter to Arctic coastal waters (Connolly et al., 2020). Tracers such as trophic and lignin markers suggest terrestrial carbon covers vast areas of nearshore and shelf areas in interior shelves, slopes, and also parts of the deep basins, while it is less prominent far away from sedimentary shores and large rivers, such as in parts of the Canadian Arctic Archipelago and on the inflow shelves (Iken et al., 2010; Goñi et al., 2013). Although terrestrial carbon must necessarily undergo bacterial processing before becoming usable for marine consumers and is arguably not a preferred carbon source, it may contribute substantially to diets of coastal fish and subsistence-harvested whales in interior shelf (Beaufort) lagoons (Harris et al., 2018) and slope biota (Bell et al., 2016).

Along Arctic rocky shores and in fjords of primarily outflow shelves but also other Arctic island groups, macroalgae provide an inter- to subtidal carbon belt that adds to the carbon source diversity and amount. Certain benthic taxa were estimated to receive over half of their carbon from macroalgal sources even at depths of several hundred meters in a fjord (Renaud et al., 2015; Gaillard et al., 2017). Given the recent increase in macroalgae biomass along Arctic rocky shores related to ice thinning and declining extent and duration, an increasing role of macroalgae carbon is envisioned for Arctic food webs (Krause-Jensen and Duarte, 2014).

Methane occurs in substantial amounts in Arctic shelf sediments and water – in addition to massive stores on land (Shakhova et al., 2010, 2014; Lorenson et al., 2016). Though there is currently no evidence that the contribution of methane via chemosynthesis is a substantial source to Arctic food webs, locally, however, methane-derived carbon enters consumers as documented in Barents Sea cold seeps (Westbrook et al., 2009; Åström et al., 2016; Sen et al., 2018).

In summary, the proportional roles of different carbon sources that fuel Arctic food webs as well as the taxa involved in these food webs are highly variable, strongly tied to the regionality of the Arctic, and currently changing (Fig. 22). Observed changes suggest that boreal taxa moving into warming seas may in the future play larger roles in future food webs than previously and change food web topology, and terrestrial and macroalgae carbon contributions and/or amounts may be increasing: both of which will contribute to changing food web topology. The conceptual and quantitative models can, for example, help (a) identify taxa / functional groups that may perpetuate food web changes, and estimate the magnitude of change, (b) anticipate which food web compartments benefit or loose under regional carbon source shifts, and (c) guide targeted experiments or monitoring of certain food web compartments that may either be likely to be sensitive to change or increase in subsistence or commercial relevance.

7. Complexity and nesting of conceptual models: Examples combining advection and phenology

After selecting the pan-Arctic as our focal scale, we examined the key regional domains and the functional mechanisms that connect these domains. The same approach can be applied - in a nested, descending scale - to specific regions and contiguous domains.

Moore et al. (2018a) selected the Pacific-Arctic domain as their focal scale, and then examined how phenology affects three contiguous domains within that Pacific-Arctic domain (the SIZ, the shelf-break-slope and the riverine coastal domain), as defined in Carmack and Wassmann (2006), Bluhm et al. (2015) and Carmack et al. (2015b). In doing so, they bring additional detail into a nested model approach. At the pan-Arctic scale, for example, we here combined Pacific inflows into one water mass, which we have called Pacific-origin water (PW), whereas Moore et al. (2018a) recognize that the PW is further comprised of three water masses that are assembled over the Bering/Chukchi shelf: Alaska Coastal Water, Bering Shelf Water and Anadyr Water. In turn, each of these water masses has distinct phenologies for the timing and extent of the spring bloom, vertical mixing of nutrients and biogeochemical attributes. Moore et al. (2018a) further recognize, at the regional scale, the phenology of each contiguous domain; e.g. the seasonal pattern of the SIZD relocating north- and expanding southwards, the brief freshet forcing the RCD, the timing of shelf-break upwelling in relation to SIZD behavior, and the sympagic-pelagic-benthic coupling that is tied to the Pacific through flow. Moore et al. (2018a) term this complex approach the ‘Arctic Pulses’ model and argue that the same logic can be applied to other regions of the AO.

A complementary model by Grebmeier et al. (2015) expanded details of advective processes as the through-flow waters transit across the Chukchi Sea, onto the Beaufort Shelf and then into the Canada Basin. This model examined the various phytoplankton, zooplankton, benthic and upper trophic biomass distributions moving into, through and out of the Chukchi Sea in association with host water masses. In another example Carmack and Melling (2011) divided the Canadian Arctic Archipelago, which we here term an outflow shelf, into five sub-regions based on freshwater supply, ice regime and water mass throughflow (Oceans North Conservation Society, World Wildlife Fund Canada, and Ducks Unlimited Canada, 2018).

There is recent evidence from west Greenland that the relative movement of three water masses, cold Baffin Bay Polar Water, warm Subpolar Mode Water and local Southwest Greenland Coastal Water are positioning to each other, e.g. when one spread out the other shrink (Rysgaard et al., 2020). This seems not only to control the transport of heat to glaciers, but species that are advected with these water masses.

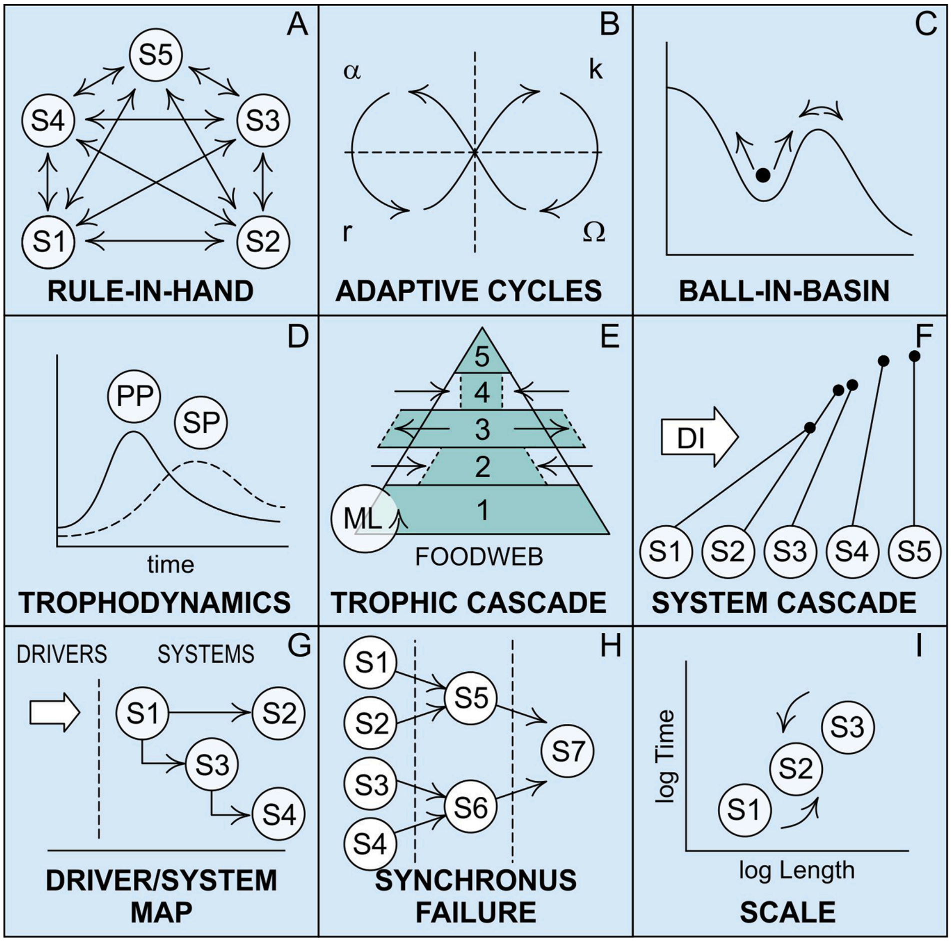

Fig. 23. Icons for established approaches to complex systems level modeling. Panel A: C.S. Holling's so-called *rule of hand* which states that most complex adaptive system will be governed by the interactions among a small number (say 5 ± 2) internal parameters; changes to any of these internal parameters will alter the behavior and equilibrium state of the overall system and its response to external forcing (drivers) (Holling, pers. comm.). Panel B: The *complex adaptive cycle* which states that a given social-ecological system will undergo a natural cycle of 1) growth, 2) collapse, 3) release and 4) reorganization (Gunderson and Holling, 2002). Panel C: The *ball-in-basin* which conveys the ability (resilience) of a system to return to its equilibrium state (K1) when perturbed; As resilience is decreased the K1 basin depth shoals; at some point a given external shock may force the system beyond its threshold (tipping point; Wassmann and Lenton, 2012; Duarte et al., 2012b) into a new stable equilibrium (Walker et al., 2006). Ongoing changes in sea ice dynamics may illustrate this process (Duarte et al., 2012a). Panel D: The concept of *trophodynamics* (e.g. phasing, match-mismatch, etc.) in which the joint phenologies of prey and predator influence the efficiency carbon transfer up a given food web (Parsons, 1988). Typically, a well-matched phase will result in a robust pelagic food web, while mismatched phasing will strengthen pelagic benthic coupling (Wassmann, 1998). Panel E: The concept of *trophic cascade*, a top-down process in which reduction (enhancement) at one trophic level may result in enhancement (reduction) at the underlying level, followed by reverse effects at successive levels (Carpenter and Kitchell, 1993). Examples include removing a planktivorous fish from a system which results in reduced grazing of zooplankton which results in a greater number of phytoplankton, and so on; cascade effects will spill over into nutrient and water quality effect as well. Panel F: The process of *system cascade*, wherein an external driver (e.g. climate warming) may directly affect one system (e.g. sea ice cover) which in turn affects another system (e.g. increased ocean stratification) which affects yet another system (e.g. nutrient availability), and so on through the food web (Carmack et al., 2016). The main feature here is not that the initial driver affects succeeding systems in the chain directly, but rather through the cascade links. In addition, each succeeding system will have different tipping points and feedback processes. Panel G: A mapping approach to following a systeḿs cascade in which links between a given drivers are followed through linked systems. Panel H: The process of *synchronous failure*, a conceptual framework that shows how multiple stresses can interact within a single social-ecological system to cause a shift in that system's behavior based on identified causes for patterns, intermediate processes, and ultimate outcomes (Homer-Dixon et al., 2015). Synchronous failure can often be characterized by a pattern of expanding scale and magnitude. Panel I: The importance of scale, into which each of the above concepts must be mapped (Carmack and McLaughlin, 2001).

Physics may have key control the biology and the complexity of pan-Arctic organism distribution. More synoptic cruses in main regions of the AO are needed to resolve the complexity of water mass distribution, contiguous domains and organisms.

The situation on the Eurasian shelf and slope to the central AO creates similar challenges of comprehension: several contiguous domains overlap in space and time. The ULAD along the Eurasian shelf-break of the central AO is continuous throughout the year, but the advection of zooplankton biomass is highly pulsed, with minima in spring and maxima in August north of Svalbard (Wassmann et al., 2019; Fig. 11). During the maximum advection period of *Calanus finmarchicus,* these copepods are already in overwintering mode and exert only a limited grazing impact upon the rich spring bloom (maximum in June) in this region. Simultaneously the SIZD domain is retreating northwards with high speed (Fig. 9A), exposing the CBCD to light and potential upwelling and shelf-basin exchange (Carmack and Chapman, 2003; Randelhoff and Guthrie, 2016; Fig. 12). Below these domains the Atlantic halocline complex (Fig. 13) is an important feature of the Eurasian basin waters, limiting the vertical supply of nutrients (Fig. 14). Despite of the simplification that any conceptual model presents, the spatial overlapping of contiguous domains (see Section 8) with distinct phenology will obviously create complex scenarios.

Another example of nesting within a regional domain is given by Michel et al. (2015). They noted that within the general classification of outflow shelves, four different conditions of nutrients and stratification exist, creating specific phenologies that planktonic heterotrophs, SPBC and the benthos have to cope with. The first is the condition of high initial nutrient concentrations followed by the development of strong stratification, leading to the spring bloom. These conditions are observed in Barrow Strait within the eastern Canadian Arctic Archipelago and in the MIZ off East Greenland, where new production is determined by the initial inventory since re-supply is constrained by stratification throughout the growing season. The second condition is one of low initial nutrients and strong stratification, which is found in much of the western Canadian Arctic Archipelago and on the East Greenland shelf, and which results in a weak bloom and low annual productivity. The third condition is one of high nutrients and strong mixing found in areas such as the North Water Polynya and in areas of shelf-break upwelling in the Beaufort Sea (e.g. Fig. 12) and along the eastern Greenland shelf (S. Rysgaard, unpubl. res.) where high levels of new production are sustained throughout the growing season. The fourth condition is one of variable nutrient concentrations and low light that occurs where extensive ice cover and/or extremely high latitudes limit light input regardless of nutrient inventories.

Taken together, the 'Arctic Pulses' model of Moore et al. (2018a), the 'Advective' model of Grebmeier et al. (2015), various conceptual models of the Eurasian advective shelf regime (e.g. Wassmann et al., 2019) and the Canadian Arctic Archipelago (Michel et al., 2015) illustrate the validity of the multi-scale nested approach advocated here and serve as examples for application elsewhere. They all indicate how strongly the AO is connected to the subarctic Pacific and Atlantic Oceans and how advection powerfully shapes the function of the entire AO (Frainer et al., 2017; Polyakov et al., 2017; Alabia et al., 2018; Polyakov et al., 2020a). Vice versa, fundamental processes in the Northern Hemisphere, first and foremost sea level rise, deep-water formation, C draw-down and weather variability, are direct consequences of climate warming in the AO region.

8. Understanding and managing Arctic Ocean systems: From "framing" and field observations to modelling, decision making and communication

Rapid decline of sea ice coverage and surface warming propel the AO into a focal point of attention, not only for the Arctic coastal states, but also for the attention of many nations of the Northern Hemisphere (IPCC, 2013; Box et al., 2019). The increment of weather extremes (Waugh et al., 2017; Box et al., 2019) and sea level rise caused by Greenland ice melt (King et al. 2020; Mouginot et al., 2019) embody obvious challenges for the entire Northern Hemisphere. In the forthcoming decade and with increasing accessibility, crucial decisions regarding oil/gas exploitation, fisheries, mining, transport and tourism will have to be accomplished in the AO. However, to evaluate comprehensively the impact of sea ice change and warming on biodiversity and ecosystem sustainability for most of the AO, the knowledge base for sustainable resource- and ecosystem-management is inadequate. Although research efforts have strongly increased in recent years and will continue to do so [e.g. ArcticNet (http://www.arcticnet.ulaval.ca/), N-ICE (https://www.npolar.no/en/projects/n-ice2015), Nansen Legacy (https://arvenetternansen.com/), MOSAIC (https://www.mosaic-expedition.org/)] the pace is not proportional to that of climate change and the knowledge demand to make well-evaluated decisions. Let us recall that the immense size of the SIZD is already about 11 10^6 km^2 where only certain sectors have been investigated (see 4.1). It is thus timely to develop a strategy that provides a solid basis in support of the decision-making needed by Arctic coastal nations and those interested in developing the AO.

Studying poorly known or unknown sea regions often starts with expeditions into the unknown and broad, but uncoordinated investigations of a range of issues, such as circulation, water column structure, chemical properties, species and organism abundance. This strategy is still applied for so far little-investigated AO regions and the expanse of today's SIZD. A few marine AO regions have been or are regularly investigated and adequately presented in the literature (e.g. the Chukchi, Beaufort and Barents Seas, the Bering Strait and sections of the Canadian and Svalbard Archipelagos and recently also the ecosystems along the TPD (e.g. N-ICE, MOSAiC)). They benefit from the strategy of recurrent and regular field observations that give rise to time series, phenologies and a broader understanding of ecosystem function. Regretfully biogeochemical time series are rare in the AO (but see Cottier et al., 2010; Moore et al., 2018b; A-TWAIN, https://www.npolar.no/prosjekter/a-twain). Sooner or later the question arises as to how the system in a particular region, let alone the entire AO, works and how processes or properties within the entire ocean can be understood in a pan-Arctic fashion. To address this next level of understanding one has to develop or assume theoretical approaches of the broader structure, function and population dynamics of the system. The selection of adequate conceptual models becomes now essential.

Ecosystem investigations are an indispensable part of conceptual models of the AO. They can be achieved by adapting a wide range of generic theoretical approaches that are not constrained to a specific ecosystem or a particular regionality (Fig. 23). For example, one may apply the theory of adaptive cycles (Fig. 23B) or apply a system-stability concept (Fig. 23C). One may approach the system by studying its trophodynamics (Fig. 23D) or investigating trophic cascades (Fig. 23E), etc. In order to study a lesser known system inside the frame of a specific theory one has to define what is considered "the system", which is a segment inside a continuity. To accomplish that, one has to apply "framing". Framing is a key component of studying nature or other systems (Trede and Higgs, 2009) and is related to agenda-setting, the process by which problems and alternative solutions gain attention. It is an integral, initial part of conveying and processing data to develop understanding. For example, out of the many functional aspects of the AO one could "place a frame" onto the MIZ or certain water masses and define a SIZ system (such as the SIZD, see Figs. 8, 9). In particular when numerical modelling is applied, framing becomes an important objective: one has to identify the model domain, transport across border, nesting inside the model domain etc. (e.g. Wassmann et al. 2010; Slagstad et al., 2015). Framing is an essential aspect of our scientific endeavors and is well described by Albert Einsteińs quotation that "we cannot solve our problems with the same level of thinking that created them. We have to rise above it to the next level".

In order to understand systems, to study their dynamics and in

Box 1

. Four elements of conceptual models that will guide the design, implementation and interpretation of field experiments and monitoring.

Scale: Scale recognizes that processes occur over wide-ranging dimensions of space and time, and often there exists an empirical relationship between space and time scales, frequently expressed in so-called Sverdrup diagrams. *A priori* recognition of scale, such as first identifying the focal scale together with its interacting larger and smaller scales, is useful in the design of multidisciplinary field experiments.

Pattern: Pattern can be defined, simply, as any non-random structure or process and – generally – an emergent property (bottom-up) of a complex adaptive system (i.e. rules at a lesser scale give rise to structure at a greater scale).

Seasonality: Seasonality is one of many key times scales inherent in Arctic marine systems but, owing to the phenology of biotic components, is also a critical starting point in experimental design. Seasonality in temperature, light, sea ice and the hydrological cycle all constrains the Arctic marine ecosystems.

Regionality: Regionality recognizes spatial variability (non-homogeneity) within a system and is often viewed in terms of descending dimension. At the global scale, the Arctic marine system has general features such as extremes of temperature and light availability, seasonal ice cover, salt stratification, etc. But different components of this system have distinct characteristics that strongly influence internal dynamics and response to forcing, and these differences must be recognized in responsible management policy and implementation.

addition to framing activities, conceptual models play an important role for both scientists and managers. A model has to be simple, but not too simple, says Einstein. Conceptual models have thus to be simple, but not too simple, and the distinction between the two options depends upon the insight and capacity of the researcher, manager or decision maker. A wide range of preferentially multidisciplinary knowledge and the involved scales, patterns, seasonalizes and regionalities are thus indispensable (see the essential four elements of conceptual models, Box 1). In Fig. 24A, we show a highly simplified conceptual model of the continental proportions, topography, river run-off, and currents of the AO. In all its details this depiction is probably the simplest manner to illustrate the AO that also presents salient features, without getting too simple. Despite of the oversimplification this conceptual model will be considered complex by many. In Fig. 24B, we show, schematically, the spatial distribution of five upper water column contiguous domains throughout the AO. Again, the level of complexity is conspicuous despite the extreme simplification. Any region in the AO will thus be impacted by a range of functional and topographic features, currents and a multitude of vertically overlapping contiguous domains. However, in a simplified, two-dimensional manner Fig. 24B illustrates the contiguous domains that researchers have to have in mind when doing field investigations in the AO. Fig. 24 omits an additional, serious challenge: time. Even under an extreme reduction of reality several contiguous domains will act in concert simultaneously at various depth intervals. This knowledge has serious implications how an investigation of nay water column in the AO. The various layers may be part different contiguous domains and thus reveal different spatial temporal processes. Are the conceptual models presented in Fig. 24 as simple as possible, or too simple?

To communicate well the above implications to those involved in AO science, management and decision-making it is beneficial to grasp the complexity behind basic conceptual models. Conceptualization of reality is thus the essential *modus operandi* that addresses problem definition, selection of investigation programs and decisions that have to be made, let alone the indispensable communication of results to management authorities and the general public. Conceptual models comprise a strategy to define, solve and communicate challenges, which combines routinely separated activities and skills into an “interdisciplinary” cooperation. Also, a good conceptual model should dare escape from earlier and more constraint concepts, but address the challenge in a more holistic, integrative manner.

An important fact when dealing with ecosystems, frequently forgotten by decision-makers and managers, is that we cannot manage what we do not know. For managing an ecosystem we need to know the basics players and ecological characteristics. Regretfully many ecosystems are being managed through assumptions and extrapolations from adjacent, better-known regions without evaluating id the conditions for doing so are in place. The precautionary principle is often not applied, and ecosystem management can, thus, imply a high degree of risk. Sustainable ecosystem and resource management must be 1) multidisciplinary, 2) systemic and 3) knowledge based. For the inadequately investigated and poorly understood regions of the AO this creates a major challenge. How can, for example, ecosystem management of the industrial use of resources and ship traffic in the central AO be administered in a sustainable manner before sufficient knowledge of the affected system and key species has been accumulated? In support of an adequate system-based understanding of Arctic marine ecosystems the tool kit for conceptual models presented here may help build investigation programs that addresses management needs. An important aspect of these endeavors is pan-Arctic science publications that inform the scientific community at large of what is known from the pan-Arctic expanse (e.g. Wassmann 2006, 2011, 2015; CAFF, 2017; Wassmann et al. 2020).

After many decades when research in the AO was carried out in a few shelf regions, along restricted transects, at seasonally skewed (late summer/early autumn) and variable times, with a limited set of scientific methods and most often in a nation’s territorial waters, it has dawned on scientists that the AO is *one,* not a fractionated ocean. It is the ocean where the effects of climate warming are strongest and where a mediterranean nature prevails, despite extensive functional regionality. The current circumstances in the AO prompt us to consider the region as a *mare nostrum.*[1] The AO is one of the world’s 5 mediterranean[2] seas, that have limited exchange of water with outer oceans and water circulation dominated by salinity and temperature differences rather than winds (Günther, 1980; see Fig. 1). The geographic nature of mediterranen seas implies that they can only be adequately managed through international cooperation by their coastal states (e.g. The Council of the Baltic Sea States (CBSS); CIESM - The Mediterranean Science Commission). This is also the vision of the Arctic Council, but, so far, international cooperation has been most strongly advocated by scientists (see the volumes edited by Wassmann, 2006, 2011, 2015; Spiridinov et al., 2011; various CAFF, PAME and AMAP reports). A recent step towards a wise management of the AO is the legally binding *Agreement on Enhancing International Arctic Scientific Cooperation*, initiated by the Arctic Council (Showstack, 2018). It promises “to increase effectiveness and efficiency in the development of scientific knowledge about the Arctic”. The agreement focuses on facilitating access to research areas, research infrastructure and facilities, and data. Lately an *Agreement to*

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[1] Mare Nostrum (our sea) was a Roman name for the Mediterranean Sea.

[2] Medius = middle + terra = land, earth.

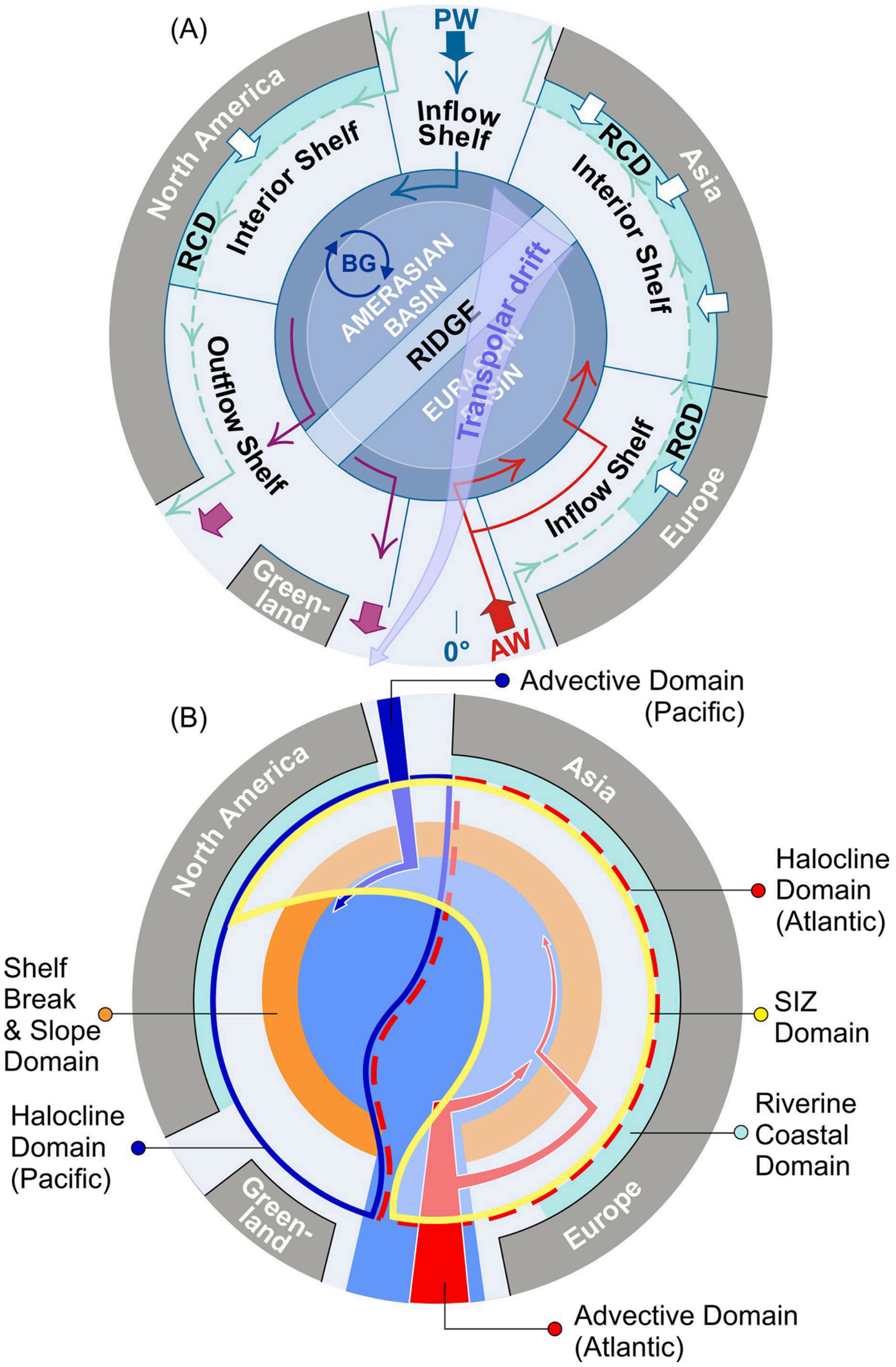

Fig. 24. Two hypothetical figures that illustrate how one may move from observations over abstraction to the ultimate simplified "template"-type conceptual model. A) illustrates continents, shelfs and basins, major currents freshwater run-off and connectivity to the Atlantic- and Pacific Oceans. B) illustrates all of the contiguous domains that are plotted into this hypothetical depiction of the Arctic Ocean. For each region in the Arctic Ocean, researchers need to have the basic knowledge, illustrated in A and B, in mind.

Prevent Unregulated High Seas Fisheries in the Central Arctic Ocean was signed. It prevents fisheries in the central AO, and is based, inter alia, upon cooperation in science and research and the establishment of appropriate conservation and management measures. The agreement commits the five Arctic coastal states of Norway, Russia, the United States, Canada, and Denmark/Greenland/the Faroe Islands as well as Japan, South Korea, Iceland and the EU – which have large fishing fleets – to abstain from any future unregulated fishing in the international waters of the AO for the foreseeable future. Thus along with the scientific endeavors to comprehend the AO in a holistic manner, now also the political and management aspects of the AO are approached with increasing dedication.

Our endeavors to plan the work, an appropriate conceptual model should be developed. The perspectives should neither be *circum*- (Latin prefix with the meaning "roundabout, around") nor *trans*- (Latin "on the other side of"), but *pan-Arctic* [(based upon the Greek term pan (all, every, throughout)]. At the end attempts should end up in a *syn-Arctic* comprehension (syn = acting or considered together; united) that translates into a comprehensive, wider-ranging and encompassing strategy. The local, indigenous and scientific knowledge should be implemented into a pan-Arctic mental picture. In general terms, a sequence of methods, activities and institutions should be applied to the pan-AO, assuring adaptive decision making (Fig. 25).

The approximately 4 million non-indigenous and indigenous people (as defined by AMAP) that are and have been living in the Arctic for centuries and millennia, accumulating knowledge and experience,

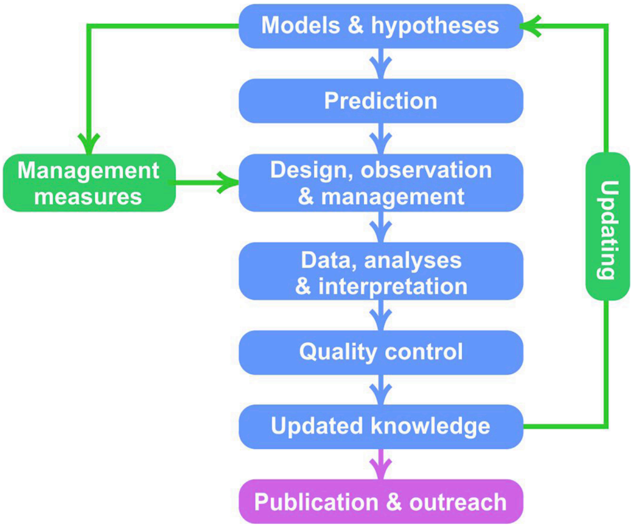

Fig. 25. Schematic sequence of methods, activities and institutions that assure adaptive decision making. Starting with a hypothesis that results in predictions observations and a sampling design are formed. After quality control of the data the updated knowledge gives rise to an revise of the hypothesis (prediction) and eventually to the formulation of a model that then provides the base for a new round of investigations. Also, the needs of the management come into play here. They use the model results and contribute to management measures that become part of the new observation regime, the research design and management features. For every sequence of activities result are published scientifically while communication with decisions makers, politicians and the general public (consisting in our case first of all the people living in the Arctic) is mandatory. In concert this creates the strategy for adaptive decision making which ultimately also improves the conceptual model of the Arctic Ocean.

should continue to have an impact upon knowledge-based resource- and ecosystem-management. In most Arctic nations, locals have only recently been involved in AO management decisions. The knowledge of all Arctic people is clearly of interest and relevance for a sustainable, knowledge-based resource and ecosystem management of the future (Fig. 26). To create scenarios that safeguard the inclusion of local ecological knowledge (tied to place through experience and observation over a single lifetime or over many generations) and traditional ecological knowledge (indigenous knowledge, e.g. Berkes et al., 2000; Huntington, 2000; Drew, 2005) regarding the AO (e.g. Nichols et al., 2004; Eicken et al., 2014) is a challenge that scientist, managers and politicians need to pay attention to (Nuttal, 1998; Carmack and MacDonald, 2008; Fox Gearheard et al., 2017). The selection and definition of core values has to be discussed along our pathway into our climate change- and economic opportunity-impacted future in the AO (Fig. 26). Our journey must be based upon knowledge brought about by research and careful evaluations of the effects of transport, fisheries and industrial activities. The hackneyed phrase that the AO ecosystem management must remain ecologically sustainable or even resilient (Carson and Peterson, 2016; Overland, 2020), i.e. take place in manners that, over time, do not alter the ecosystem carrying capacity, is still not rigorously applied. Whether it will be and whether it bears fruits throughout the AO of the future remains to be seen.

9. Outlook

Alarmed by John Maynard Keynes's (1937) citation that «the difficulty lies not so much in developing new ideas as in escaping from old ones», we argue that to understand the AO in a fully pan-Arctic manner we have to challenge which of the older confined and sectorial ideas have to be revised and changed. To obtain a more balanced, pan-Arctic perspective, in favor of interaction and cooperation we unified older concepts and ideas, revised them and added new ones. To provide significant elements for shared, high-level paradigm synthesis of our understanding of the key processes and elements governing the response of the Arctic ecosystem of today and the future, we thus presented a hierarchy of known and new conceptual models. We urge AO scientists and managers to co-operate and undertake a holistic comprehension of a new emerging ocean which expanse, so far, has been inadequately investigated. This dearth now challenges our ability to adequately evaluate climate change and the associated meteorological and ecological responses in the Northern Hemisphere. The current advancement in knowledge is already too slow to address today's change in climate and sustainable use of the transformed AO.

The conceptual modelling toolkit we portray will not only support the basic understanding and management challenges of those directly working in the Arctic, but the various elements can also serve as tools to communicate insight, understanding and support among politicians, decision makers and the general public. The latter aspect is imperative. The people of the Northern Hemisphere and their political leadership need to understand that the local challenges they face [e.g. sea-level rise (Dahl-Jensen, 2000; Mouginot et al., 2019) and weather extremes (Waugh et al., 2017; Box et al., 2019)] may demand research in remote, Arctic regions where "nobody lives" (the population in the Arctic regions comprises only 0.05% of human population). Some principal AO climate change research of generic interest is already carried out [e.g. the invasion of boreal species (Frainer et al., 2017; Alabia et al., 2018) and changes in biodiversity (Spiridinov et al., 2011; CAFF, 2017)]. Ongoing systemic research (e.g. the Nansen Legacy and MOSAiC projects) will pave the road for improvements of future AO management in specified regions. However, resource-hungry nations, representing 99.95% of

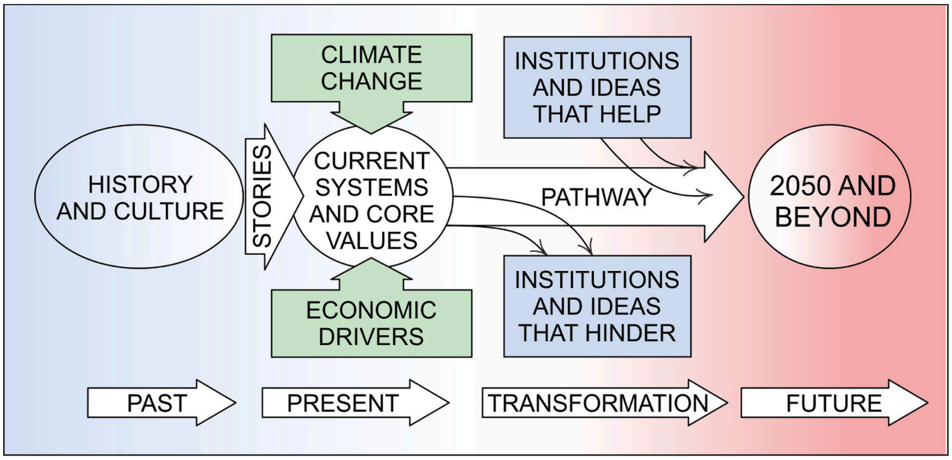

Fig. 26. A schematic that illustrates how knowledge (our history and culture) is transferred, created and shaped (current system and core values), transformed and impacted (pathway) to create the base for our future. In our present, humanitýs core values (here summarized in the term sustainability without which there will be no justifiable future) play a crucial role. We are forced by climate change and economic drivers. During the time between now and the future (pathway) discussions and debates are indispensable and the public has to distinguish between the institutions and ideas that block or hinder a sustainable future (also see Falardeau et al., 2019).

humanity plan to exploit the rich resource of the entire, hitherto ice-covered ocean. They may be less concerned with the ecological consequences, the requirements of the local population and the demands of long-term sustainability (Alvarez et al., 2020). It is essential to get all stakeholders and the human population at large involved in a sustainable future for the AO. To achieve this goal, communicating results, narratives, pictures and iconic graphics are essential.

Conceptual models can strongly facilitate interdisciplinarity by providing a shared understanding of the system. Developing them involves an element of intuition which, joined to research, speeds up the process of exact science (see citation of P. Klee at the start). Once established, such models often have inertia that profoundly influence the interpretation of data. They can shape common directions for years to come, thereby becoming essential underpinnings of new paradigms. Conceptual models have to accommodate transience as they do not represent a final product.

Having in mind the transient nature of conceptual models for the AO, we wish to end with a citation from Aagaard and Carmack (1989), a visionary document that already 30 years ago encompassed many of the changes currently experienced in and adjacent to the AO. “While our scenario is highly conjectural, it is quite in keeping with the message of change that Fridjof Nansen himself preached on numerous occasions. For example, in a lecture on the Fram drift delivered in 1897 he ended with these words: *Everything is drifting, the whole ocean moves ceaselessly, a link in Nature’s never-ending cycle, just as shifting and transitory as the human theories*“.

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. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2020.102455.

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Glossary of terms and definitions of the domains applied in this publication

Term: Definition

Arctic Ocean (AO): Here generally the Arctic north polar region (basins and adjacent shelves) poleward of the four gateways Bering Strait, Davis Strait, Fram Strait and the Barents Sea Opening

Atlantic/Pacific halocline: The halocline front that separates the Amerasian and Eurasian halocline systems

Contiguous domain: Connected regions of shared physical, chemical and ecological properties and functions

Seasonal Ice Zone Domain (SIZD): Area of the AO that extends from the permanent ice zone (autumn minimum) to the boundary where winter sea ice extent is at a maximum

Riverine Coastal domain (RCD): A narrow (5–15 km wide), shallow (~10 m deep) contiguous feature that is confined by the spreading of river and glacial water discharge

Upper Layer Advective domain (ULAD): The combined waters above the halocline and advected by the North Pacific, North Atlantic and the Barents Sea or transported through the Transpolar Drift

Circumpolar Boundary Current domain (CBCD): The dominant thermohaline feature of the AO shelf-break

Atlantic and Pacific Halocline Domain (APHD): Halocline domain that cover the upper 900 m of the entire central AO

Deep Basin Domain (DBD): Below the Atlantic Layer of the AO, i.e. the water between 0°C and sill depth