

1 **Towards a unifying pan-Arctic perspective: A conceptual modelling toolkit¹**

2
3 Wassmann¹, P., Carmack², E.C., Bluhm¹, B., Duarte³, Berge, J.^{1,4,5}, Brown^{2,6}, K.,
4 Grebmeier⁷, J.M., Holding^{8,9}, J., Kosobokova¹⁰, K., Kwok¹¹, R., Matrai¹², P., Agusti³,
5 S.R., Babin¹³, M., Bhatt¹⁴, U., Eicken¹⁴, H., Polyakov¹⁵, I., Rysgaard¹⁶, S. and
6 Huntington¹⁷, H.

7
8 ¹ Department of Arctic and Marine Biology
9 UiT - The Arctic University of Norway
10 P. O. Box 6050 Langnes, 9037 Tromsø, Norway

11
12 ² Fisheries and Oceans Canada,
13 9860 West Saanich Road,
14 Sidney, BC, V8L 4B2, Canada,

15
16 ³ Red Sea Research Center (RSRC)
17 Building 2, Level 3, Room 3219
18 King Abdullah University of Science and Technology (KAUST)
19 Thuwal 23955-6900, Kingdom of Saudi Arabia

20
21 ⁴ University Centre on Svalbard
22 Dept of Arctic Biology
23 Pb 156, 9171 Longyearbyen, Norway

24
25 ⁵ Centre for Autonomous Marine Operations and Systems
26 Department of Biology
27 Norwegian University of Science and Technology, NTNU, Norway

28
29 ⁶ Woods Hole Oceanographic Institution
30 Department of Marine Chemistry and Geochemistry
31 Woods Hole, MA, 02543 USA

32
33 ⁷ Chesapeake Biological Laboratory
34 University of Maryland Center for Environmental Science
35 PO Box 38, 146 Williams Street
36 Solomons, Maryland 20688 USA

37
38 ⁸ Arctic Research Centre (ARC)
39 Aarhus University
40 Ny Munkegade, bldg. 1540
41 DK-8000 Aarhus C, Denmark

42
43 ⁹ Department of Bioscience
44 Aarhus University
45 Vejlsøvej 25, 8600,

¹ 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

46 DK-8600 Silkeborg, Denmark
47
48 ¹⁰ Shirshov Institute of Oceanology,
49 Russian Academy of Sciences,
50 Nahimovskiy prospekt 36,
51 Moscow 117997, Russia
52
53 ¹¹ Jet Propulsion Laboratory
54 California Institute of Technology
55 4800 Oak Grove Dr
56 Pasadena, CA 91109, USA
57
58 ¹² Bigelow Laboratory for Ocean Sciences
59 Research Faculty, Colby College
60 60 Bigelow Drive, PO Box 380
61 East Boothbay, ME 04544, USA
62
63 ¹³ Unité Mixte Internationale Takuvik
64 CNRS (France) & Université Laval (Canada)
65 Pavillon Alexandre-Vachon, Local 2078
66 1045, avenue de la Médecine
67 Université Laval, Québec (QC) G1V 0A6, Canada
68
69 ¹⁴ Dept. of Atmospheric Sciences & Geophysical Institute
70 University of Alaska Fairbanks
71 903 Koyukuk Dr
72 Fairbanks, Alaska 99775-7320, USA
73
74 ¹⁵ University of Alaska Fairbanks
75 International Arctic Research Center,
76 College of Natural Science and Mathematics,
77 Department of Atmospheric Science
78 PO Box 757335, Fairbanks AK 99775, USA
79
80 ¹⁶ Centre for Earth Observation Science
81 Department of Geological Sciences
82 522 Wallace Building
83 University of Manitoba
84 Winnipeg, MB, R3T 2N2, Canada
85
86 ¹⁷ Ocean Conservancy
87 23834 The Clearing Dr.
88 Eagle River, AK 99577 USA
89
90
91

92 **0. Abstract**

93 The Arctic Ocean is forced by and interacts with the global system, and we here
94 choose the full pan-Arctic as our focal scale for development of nested conceptual
95 models of the Arctic Ocean ecosystem. To understand the pan-Arctic scale,
96 however, requires that we look at the underlying scales of its major components,
97 by considering regionality, connectivity and seasonality. Six regions are identified
98 on the basis of hydro-morphological characteristics, which subsequently reflect
99 ecological function and traits. Regions are static, tied to geography, but are linked
100 by contiguous domains of shared function that facilitate material transports and
101 share key ecological features. The pan-Arctic scale also requires attention to
102 forcing by the seasonal light climate, wherein the maximum length of a single day
103 varies from near 24 hours at the Arctic Circle to about 4400 hours at the North
104 Pole. The light climate in turn forces a strong phenology in the Arctic, as reflected
105 by periodic life cycle events of organisms and how these biotic cycles are
106 influenced by seasonal and interannual variations in climate. Arctic Ocean
107 ecosystems are dominated by four fundamental variables: ice cover, light climate,
108 nutrient/food availability and advection. The conditions under which each of
109 these variables play out in the course of a year are set by the regions and
110 contiguous domains within which they operate and interact. In concert, the
111 defined regions and their seasonality, the contiguous domains and their
112 connectivity, and the four fundamental variables allow unambiguous application
113 of scale-nested, parsimonious and adaptive, conceptual models, from which to 1)
114 create testable hypotheses, 2) plan and then modify field campaigns, and 3)
115 communicate essential results to managers and the general public. The

116 development of these nested conceptual pan-Arctic scale models creates a vital
117 step into the future of unifying, integrative oceanographic and ecological work.
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167 **1. Introduction**

168 The Arctic Ocean (AO; also called the Arctic Mediterranean Sea, classifying it as an
169 estuary of the Atlantic Ocean) is located in the Arctic north polar region and
170 operates as the functional center of the Northern Hemisphere (**Fig.1**) (for
171 abbreviations applied throughout the text, see Table 1). It is almost completely
172 surrounded by the vast landmasses of Eurasia and North America and almost
173 completely covered by sea ice in winter. The ocean receives freshwater and
174 material supplies from a vast network of rivers that drain these surrounding
175 landmasses. It is connected to the subarctic Pacific Ocean via the Bering Strait and
176 particularly the Atlantic Ocean by gateways at Davis Strait, Fram Strait and the
177 Barents Sea opening. Easterly winds to the north and westerly winds to the south
178 encircle the central AO and adjacent land masses, completing the Arctic land-sea-
179 air system (**Fig. 1**). Thus, and importantly, the AO cannot be understood, predicted
180 and/or managed through traditional sectorial approaches out of Europe, Asia or
181 North America, but only through integrated, circum-Arctic and tightly
182 interconnected, systemic approaches. Consequently, pan-Arctic integration and
183 international cooperation in research and management are indispensable. It is
184 essential that such cooperation crosses territorial borders, in line with the
185 patterns of ice drift, winds, ocean currents and plankton organisms in the AO (e.g.
186 Wassmann, 2006). Here we take as a working definition of the AO the Arctic north
187 polar region (basins and adjacent shelves) poleward of the four gateways noted
188 above, keeping in mind that no strict boundary will satisfy all functional and
189 geopolitical issues.

190 A range of national investigations have been carried out in the AO since
191 those of the early Arctic explorers (e.g. Nansen, 1897). Significant marine

192 ecological work was carried out on the Siberian shelf and adjacent seas of the
193 Sovjet Union before WWII, summarized by Zenkevich (1963). From 1937 and
194 onwards the Soviet Union/Russia sustained an extensive sequence of ice drift
195 stations (Ugryumov et al., 2005; Romanov et al., 2007; Belkin and Kessel, 2017)
196 that carried out oceanographic work (for the most part physical oceanography).
197 This work has continued up to recent times (e.g. Barneo ice camp,
198 <http://campbarneo.com/>), now in a more interdisciplinary manner. Important
199 early investigations of the AO included the US Arctic Drifting Stations in the 1950s-
200 1960s (e.g. Cabaniss et al., 1965). Some of the large continental shelf programs in
201 North America were carried out in the 1970s (e.g. WEBSEC, NOGAP, OCSEAP)
202 related to the oil exploration and discovery. Already in the 1980's Norway
203 invested heavily in a large-scale and multi-discipline investigation of the
204 Norwegian sector of the Barents Sea (Pro Mare; e.g. Sakshaug et al., 1991). This
205 work continues in the ice-covered northern Barents Sea and adjacent Nansen
206 Basin through the Nansen Legacy project (<https://arvenetternansen.com/>). In
207 the eastern Bering Strait and Chuckie Sea the multidisciplinary "The Western
208 Arctic Shelf – Basin Interactions project" (SBI) started in the late 1990's (e.g.
209 Grebmeier et al., 2009), followed by the «Russian-American Long-term Census of
210 the Arctic program" (RUSALCA) between 2004 and 2015 (e.g. Hopcroft et al.,
211 2010). Polynyas, such as the Northeast Water Polynya, the North Water
212 Polynya/Nares Strait system and the Laptev Sea Polynya were also the subject of
213 intensive studies (e.g. Hirche and Kwasniewski, 1997; Tremblay et al., 2006;
214 Dimitrenko et al., 2010). The Canadian ArcticNet initiative carried out a range of
215 overwintering expeditions to the Canadian sector of the AO
216 (<http://www.arcticnet.ulaval.ca/media/publications.php>). The coastal marine

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217 diversity and ecosystems along the Siberian coast have been investigated and
218 summarized by Spiridonov et al. (2011). Throughout the last decade major annual
219 marine ecological expeditions to the Kara, Laptev and East Siberian Seas have
220 been carried out, but little has so far been published in English (but see e.g.
221 Arashkevich et al., 2010; Flint et al., 2015; Drits et al., 2017; Sukhanova et al.,
222 2017).

223 Rather long-standing traditions are established for international
224 cooperation in Arctic science. The first International Polar Year, for example, took
225 place in 1882-83 and involved scientists from many countries. Subsequent
226 International Polar Years were held in 1932-33, 1957-58 (as part of the
227 International Geophysical Year) and 2007-2008 (Barr and Lüdeke, 2010).
228 Interdisciplinary studies in the AO started with the Swedish icebreaker R/V
229 Ymir's attempt to reach the North Pole. Repetitive expeditions by R/V Polarstern
230 of the Alfred Wegener Institute followed from 1989 and onwards, continued by
231 R/V Oden 1991 and Arctic Ocean Section in 1994. However, the AO was excluded
232 from the World Ocean Circulation Experiment WOCE in 1990-1998. The dominant
233 view then was that the AO played an insignificant role for the World Ocean and
234 was insignificant for the global climate.

235 In light of what is today's accepted truth the evaluation of just 30 years ago
236 is difficult to understand. There are four reasons, all well-known decades ago, why
237 the AO is distinct from other oceans and critical to our planet's survival (World
238 Economic Forum, 2019). First, its impact on the global climate system is
239 disproportionately large. Second, despite its small area it collects up over 10% of
240 global river runoff. Third, owing to its complex and irregular coastline the Arctic
241 marine domain comprises about a third of the world's coastline. And fourth, the

242 AO contains one-quarter of the world's continental shelf, regions of immense
243 socio-ecological importance. On all counts, the little AO holds a pivotal place on
244 the global stage.

245 Despite notable past success involving science capable icebreakers and ice
246 drift stations, a true collaborative spirit in the AO region remains restricted. As a
247 consequence, our basic knowledge of the AO remains patchy. Long time series are
248 lacking from many important regions, and our understanding of the seasonal ice
249 cover and its associated biology is limited and often missing, in particular during
250 winter, spring and early summer. The available literature addressing pan-Arctic
251 integration has been edited and summarized in Wassmann (2006, 2011, 2015).
252 One reason that research on the oceanography and ecology of the AO has lagged
253 behind efforts elsewhere is the difficulty and harshness of year-round field
254 sampling and that the efforts have been insufficient to cover the extent of this
255 opening-up ocean owing to a lack of political and Earth ecosystem vision.

256 Events of recent years (e.g. the International Polar Year, 2007-2009) and
257 the now accepted impact of global climate change has altered this view. An
258 increased number of nations are becoming interested in conducting Arctic
259 research, more ice-reinforced ships are now available and the amount of research
260 funding that is dedicated to Arctic research is growing (e.g. the largest polar
261 expedition in history, MOSAiC, <https://mosaic-expedition.org/>). Still, the lack of
262 an adequate basic comprehension of this vast and complex system risks failing to
263 achieve a knowledge-based understanding of the ecosystem and, consequently, a
264 responsible resource management of the Arctic Mediterranean Sea. In addition to
265 recent and ongoing studies providing 'puzzle pieces', we need emphasis on
266 regions that are not investigated and on syntheses that provide the required high-

267 level understanding. Otherwise, the outcomes of recent and ongoing studies, while
268 possibly scientifically relevant and sound, may fall short of providing the high-
269 level understanding required for responsible policy making and management.
270 Continued lack of integration and conceptualization may leave us simply in worse
271 position to manage the impacts of economic growth and industry operations in
272 the future Arctic. In recognition of this shortcoming the Arctic Council signed an
273 “Agreement on Enhancing International Arctic Scientific Cooperation” (Arctic
274 Council, 2017), which intends to facilitate and promote pan-Arctic cooperation
275 across the vastness of the AO. This agreement, which now has entered into force
276 (Arctic Council, 2018) creates a mandate for more adequate endeavors to
277 understand the vastness and the mediterranean nature of the AO.

278 Managing the imminent pressures derived from the forecasted increase in
279 fisheries, petroleum and mineral extraction, other industrial operations and
280 transportation in the AO requires knowledge. The cascade of effects of climate
281 change affecting both Arctic and non-Arctic nations provides even greater
282 challenges for sustainable ecosystem and resource management (Duarte et al.,
283 2012; Box et al., 2019; Overland et al., 2019). As a pre-requisite an elaboration of
284 the major research questions and programs aimed at advancing our
285 understanding of the AO system is essential. Currently, such programs, which
286 involve great efforts and resources, largely lack shared paradigms to help identify
287 the key processes and levers that such programs should aim to elucidate. A need
288 thus exists to develop community-shared theories and conceptual models that
289 help unify our differing or lacking perspectives. Genuinely pan-Arctic perspectives
290 and tools are required to understand, predict and manage a mediterranean-type
291 AO now undergoing major change. One of the greatest unplanned experiments in

292 human history is rapidly taking place before our eyes in the AO: ice-free condition
293 during late summer, an accelerated hydrological cycle, strongly altered
294 stratification and mixing, ocean acidification, an unprecedented change in
295 underwater light climate and rapid warming of surface water. In summary and
296 discussed throughout this publication the changes in the AO are based upon 4
297 fundamental, but highly consequence-rich and interconnected variables: ice cover
298 (including increased stratification), light climate, nutrient/food availability and
299 advection.

300

301 1.1. Why use a conceptual model approach?

302 We are motivated to begin with a system-wide perspective by the observations
303 that: (1) global climate change is real and the Arctic is the most rapidly changing
304 of all Earth systems, with major physical and ecological consequences
305 (McLaughlin et al., 2011; Bhatt et al., 2014; IPCC, 2018); (2) the loss of sea-ice is
306 the leading signal of climate change (Kwok et al., 2009; Duarte et al., 2012; Stroeve
307 et al., 2012), with the role of the ocean in heat exchange gaining disproportionately
308 in importance (Carmack et al., 2015; Polyakov et al., 2017); (3) the AO is coupled
309 to and forced by the subarctic Pacific and Atlantic Oceans, with large-scale
310 interactions affecting change in all three seas (Carmack et al., 2010; Polyakov et
311 al., 2017; 2018; Lind et al., 2018); (4) the physical, chemical and biological
312 components within the AO are mutually interacting, with cascading consequences
313 throughout the system (Carmack et al., 2012; Huntington et al., 2014; Grebmeier
314 et al., 2015); (5) the high-latitude hydrological cycle is accelerating, with
315 substantial consequence for terrestrial and marine systems (Prowse et al., 2015;
316 Carmack et al., 2016).

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

331 A conceptual model should be integrative, adaptive, anticipatory and
332 succinct. Thus, in the evolution of any given scientific investigation a conceptual
333 model is useful in: A) defining the initial scope of the problem, establishing
334 testable hypotheses and developing experimental design; B) adapting program
335 design during the course of the investigation as new information is acquired; and
336 C) summarizing and communicating final results. Guidance can be applied to
337 development of field programs, targeted experiments, numerical modelling and
338 outreach. Such models may also be used to create scenarios to explore future
339 consequences of management and change. A unified and pan-Arctic conceptual
340 model for the AO, hosting a nested array of additional models addressing specific
341 regions and processes, can thus be instrumental in providing a shared

342 understanding that will allow improved coordination in research efforts
343 addressing the AO in a time of change, while also minimizing the research gaps. By
344 simplifying complex ecosystems into their core structural elements, linkages and
345 functional processes, conceptual models provide a powerful tool to formulate
346 hypotheses that inform scenarios of future change and evaluate intervention
347 options.

348 Examples of these applications of conceptual models may illustrate why
349 such models are, if not necessary, useful. A conceptual model forces us to identify
350 essential features of a system with respect to a particular issue or geographic
351 region. For example, which aspects of the ecosystem are going to affect and be
352 affected by commercial shipping, in light of continuing climate change? A good
353 conceptual model can help develop testable hypotheses, for example, “Shifts in the
354 large-scale distribution of marine mammals will be affected by environmental
355 change more than by ship traffic.” The conceptual model can then help in
356 designing, carrying out, and as needed modifying field research to address the
357 hypothesis (A). For example, a comparison of two areas would need to consider
358 the characteristics of both areas to make sure the comparison was valid, and to
359 gather additional data as needed to verify that this is indeed the case (B). In this
360 shipping example, it is not sufficient that both areas have marine mammals. They
361 must also be susceptible to similar influences of climate change, so that the
362 presence of ship traffic in one region can be usefully compared with the absence
363 of ship traffic in the other. Or that differences between the regions can be factored
364 into the analysis of the observations from each region. On the basis of the results
365 of the fieldwork, a new model of ship traffic can be developed, perhaps to identify
366 times and routes that have greater or lesser effects on marine mammal

367 distribution and behavior. The new model, of course, can be further tested and
368 refined over time. When it comes to applying the new knowledge to the
369 management of shipping, the conceptual model can help explain what matters and
370 why, to help build a persuasive case for any management actions and to help show
371 why other potential management actions are not necessary or may even be
372 counterproductive (C). The conceptual model in this case serves as a device to
373 focus attention and to provide a common basis for discussion and understanding,
374 among all participants in all stages of the continuum from research to analysis to
375 management.

376

377 1.2 Approach and goal

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

385 We try to raise the attention of today's and the future's AO scientists and
386 managers to prepare for a more holistic understanding of the new emerging
387 ocean; an understanding that is required if the goals of sustainability are to be met
388 (cf. Arctic Resilience Report, 2016; Auad et al., 2018). The interconnected
389 ecosystem elements and concepts of the AO will then contribute to a generic
390 understanding where new research can be placed into existing conceptual models.
391 We finish by discussing how knowledge-based ecosystem and resource

392 management in today's and the future's AO can be shaped out of an adaptive and
393 anticipatory conceptual model approach, how it can support the integration of
394 indigenous and local knowledge and how communication with the general public
395 can be strengthened.

396

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

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

409 The AO, itself, is a mediterranean sea that is roughly half continental shelf
410 and half basin and ridge complex. Currently, it is roughly two thirds seasonally
411 and one third perennially ice-covered, thus now exposing an increasing portion of
412 basin waters to sunlight and wind (Bluhm et al., 2015; Wadhams, 2017). The
413 necessary starting point in developing a unified perspective is to recognize that
414 the Arctic marine system is strongly coupled to the global system and that this
415 coupling is bi-directional, with the global ocean affecting the Arctic and the Arctic
416 strongly affecting the global ocean. Maintaining this perspective requires an
417 internally consistent and logical use of scale, both spatial and temporal, in the
418 development of nested and adaptive conceptual models. **Fig. 2** is a highly
419 schematic, Sverdrup-type illustration grouping the spatial and temporal scales
420 that encompass global, pan-Arctic and regional systems; simply starting with this
421 perspective helps us setting research goals and efforts. The global marine scale

422 system is represented by large spatial and time scales and is itself externally
423 forced by even larger scales. The pan-Arctic marine system, the focus of this paper,
424 is nested at smaller spatial and temporal scales and is coupled to the global marine
425 system through exchanges of energy, freshwater, water masses and material
426 properties with bordering subarctic oceans and terrestrial land masses. This
427 system, in turn, is underlain by regional and contiguous domains, as discussed
428 below in sections 3 and 4. Beneath the regional scale are the various mesoscale
429 and sub-mesoscale processes that advect material properties and act to regulate
430 biogeochemical rates and processes within specific regions. Energy and physical
431 forcing pass from top-down from larger to smaller scales, while feedbacks and
432 emergent properties are driven bottom-up.

433 The AO's thermohaline structure and circulation are forced at the global
434 scale with freshwater delivery to the AO by the atmosphere as demanded by the
435 climate system to transport heat (in this case as latent heat) from the low to high
436 latitudes, and by the subsequent need to redress the resulting ocean salt balance
437 through the meridional thermohaline circulation. The transport of heat and
438 moisture begins with the Trade and Westerly winds which carry moisture first
439 from the Atlantic to the Pacific and continues with the Westerly winds which carry
440 moisture to the Arctic drainage basins (**Fig. 3A**). In contrast to the southern
441 hemisphere, the configuration of continents in the northern hemisphere is such
442 that they effectively capture precipitation from the storm tracks of the Westerlies
443 and redirect in north-flowing rivers disproportionate quantities of freshwater in
444 north-flowing rivers into the mediterranean configuration of the AO (**Fig. 1A**). The
445 disproportionate areal coverage of lakes in high-latitude drainage basins further
446 affects freshwater storage, modification and release timing to the ocean

447 (Verspoorter et al., 2014). Hence, while the AO represents only 1% (in terms of
448 volume) and 3% (in terms of surface area) of the global ocean, it collects over 11%
449 of the global river discharge (Dai and Tenberth, 2002; McClelland et al., 2011;
450 Carmack et al., 2016). The freshwater budget of the AO is governed by: the delivery
451 of fresh and low-salinity waters to the AO by river inflow, net precipitation,
452 distillation during the freeze/thaw cycle and Pacific Ocean inflows; the disposition
453 (e.g. sources, pathways and storage) of freshwater components within various
454 domains of the AO (e.g. basins, shelves, coastal zone); and the release and net
455 export of freshwater components into the bordering convective domains of the
456 North Atlantic (Aagaard and Carmack, 1989; Carmack et al., 2016; Brown et al.,
457 2020a).

458 The AO joins the global ocean through the inflow of both Pacific-origin
459 water (PW) through the shallow (~50 m) Bering Strait into the Canada Basin, and
460 counter-flowing Atlantic-origin water (AW) through eastern portion of the deep
461 (~2600 m) Fram Strait and across the relatively deep (200-400 m) Barents Sea
462 shelf into the Nansen Basin (**Figs. 1B, 4**). Depending on pathways and mixing
463 history the incoming AW exits the AO as a lighter (fresher) component than when
464 it came in by mixing with freshwater than when it came in or a denser (more
465 saline) component than when it came in by cooling and brine formation.
466 Consequently, at the pan-Arctic scale, the system acts as both a positive and
467 negative estuary (Carmack and Wassmann, 2006; **Fig. 4**). Modified forms of PW
468 and AW exit through the western Fram Strait and Davis Strait gateways (**Fig. 1B**).
469 The considerable stratification of the AO is partly shaped, entangled and driven by
470 westerly winds that create the Polar Vortex features (**Fig. 4**).

471

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

474 While the pan-Arctic system is the focal scale of this work, it is of critical
475 significance to recognize the nested, component parts of the system. This is
476 important to guide the selection of appropriate regional-scale applications, and
477 not to overgeneralize findings from a particular region to the entire system (for
478 example, see Polyakov et al., 2018). For this we follow approaches by Carmack and
479 Wassmann (2006) and Bluhm et al. (2015) and distinguish among basic shelf, shelf
480 break and basin regimes on the basis of topography, hydrography and
481 biogeochemical function.

482 The shelf, shelf break and basin regimes are an integrated part of the
483 physical oceanography and connected through currents. Four large-scale
484 circulation systems can be distinguished. In the uppermost layers down to about
485 200 depth we find the wind-driven circulation which forces the cyclonic Trans-
486 Polar Drift (TPD) from interior shelves of Siberia to the export shelf of the Fram
487 Strait and the anticyclonic Beaufort Gyre in the southern Canada Basin (**Fig. 5A**).
488 Below there we find the circulation of waters that comprise the halocline
489 complex, composed largely of waters of Pacific and Atlantic origin that are
490 modified during passage over the inflow and Siberian interior shelves (**Fig. 5B**).
491 The topographically-trapped Arctic Circumpolar Boundary Current which carries
492 AW cyclonically around the boundaries of the entire suite of basins (FSB and BSB
493 are the Fram Strait and Barents Sea Branch) (**Fig. 5C**). At depth we find the slow
494 exchange of Arctic Ocean Deep Waters that enter on the eastern and leave on the
495 western Fram Strait (**Fig. 5D**).

496

497 3.1 Shelf types and basic biogeochemical function
498 The shelves of the Arctic Mediterranean are strikingly different from those of the
499 remaining World Ocean. No other ocean comprises as much shelf area as the AO:
500 > 50 % (Jakobsson et al., 2008). Being so dominant and increasingly exposed to
501 sunlight, emphasis on these shallow realms, bounded by a narrow and steep shelf
502 break and slope, is needed to understand their functional dynamics (**Fig. 5**). In
503 order to obtain a more adequate perspective of the pan-Arctic shelves we expand
504 on the typology proposed by Carmack & Wassmann (2006). Inflow, interior and
505 outflow shelves are distinguished (**Fig. 6**), which represent entirely different
506 functional types that shape and are shaped by their biogeochemical roles (**Fig. 7**).
507 Among the three basic shelf types we further differentiate between the shallow
508 and deep inflow shelves (Northern Bering Sea/Chukchi Sea and Barents Sea,
509 respectively; e.g. Hunt et al. 2013), the narrow and wide interior shelves (Beaufort
510 Sea and Kara/Laptev/East Siberian Seas, respectively; e.g. Williams and Carmack,
511 2015) and the branching and longitudinal outflow shelves (Canadian Archipelago
512 and east-Greenland shelf, respectively; e.g. Michel et al., 2015; **Fig. 7**).

513

514 *3.1.1 Inflow shelves*

515 During transit of inflowing subarctic waters along western Spitsbergen and across
516 the Barents, Bering and Chukchi Seas the waters are strongly shaped and altered
517 by biogeochemical and physical processes (Grebmeier et al., 2015; Vernet et al.
518 2019; **Fig. 7**). Transformations during transit depend on the width and depth of
519 the shelves that, in turn, affect the water's residence times, in particular in the
520 biogeochemically active layers (the euphotic zone and the benthic boundary
521 layer). These waters subsequently subduct at fronts (e.g. the Polar Front in the

522 Barents Sea) or along the shelf break (e.g. north of Svalbard), and thus influence
523 property distributions within the Arctic basin (e.g. Polyakov et al. 2013, 2017).
524 Inflow shelves also play an important role during the advection of pelagic
525 organisms, in particular zooplankton (Kosobokova and Hirche, 2009; Wassmann
526 et al., 2015; Ershova et al., 2015a, Hunt et al., 2016). The direct supply of
527 freshwater from rivers to the southern Barents Sea is relatively low, and
528 consequently stratification of surface waters is weak in the relatively deep
529 southern Barents Sea, but relatively strong in the SIZ of the northern Barents Sea
530 where stratification is enhanced by ice melt and inputs from the massive Siberian
531 rivers (Smetsrud et al., 2013). The supply of relatively fresh Pacific water through
532 the shallow Bering Strait and local ice melt support a much stronger seasonal
533 stratification in the Chukchi Sea (Woodgate et al. 2006, 2015).

534 Inflow shelves have by far the highest primary production within the AO,
535 comprising about two-thirds of the total (Sakshaug, 2004; Matrai et al., 2013). The
536 introduction of nutrients and advection of suspended biomass is an essential
537 feature of inflow shelves and is particularly significant in the shallow Bering Strait
538 and adjacent Chukchi Sea where it directly fuels a biomass-rich benthic
539 community (Grebmeier et al., 2015). Also, advection of larger zooplankton and
540 propagules of benthic biota from sub-Arctic or boreal regions onto and over the
541 inflow shelves is an essential aspect of their specific functionality (Wassmann et
542 al., 2015; Ershova et al., 2015b, 2019b; Silberberger et al., 2016) (see section 4
543 Contiguous domains). The resulting biological community structure in both water
544 column and at the seafloor, reflects their boreal to arctic sources (Aninisimova,
545 1989; Hopcroft et al., 2010; Ershova et al., 2015a; Fossheim et al., 2015).

546

547 3.1.2. *Interior shelves*

548 Interior shelves are all shallow and are characterized by the impact of major
549 rivers, such as the Yenisei, Ob, Lena and Mackenzie Rivers, and numerous smaller
550 rivers (Williams and Carmack, 2015). The major distinction between Eurasian and
551 Amerasian interior shelves is that the Eurasian interior shelves are several
552 hundred km wide while those of North America are much narrower (**Figs. 6, 7**).
553 Interior shelves exhibit a positive estuarine circulation (river plume spreading) in
554 summer and a negative estuarine circulation (caused by brine drainage during sea
555 ice formation) in winter. During periods of river plume spreading the nearshore
556 flocculation of estuarine and marine matter (both particulate and dissolved) is
557 high but decreases offshore with distance from the river deltas. The combined
558 effects of wind and tides can be significant and can thus enhance or reduce the
559 dispersion of plume water towards the sea. Below the freshened surface layer, the
560 estuarine circulation transports seawater towards the littoral zone (McClelland et
561 al., 2011). The horizontal exchange of water masses is thus substantial and
562 sometimes results in the formation of multiple fronts; horizontal variations in
563 salinity are large. The load of terrigenous matter from the rivers can be large and
564 thus turbidity and light extinction is high (Goñi et al., 2013). The innermost
565 portion of interior shelves is characterized by land fast ice that melts during
566 summer (Mahoney et al., 2014). Here pack ice collides against the land fast ice, and
567 between these two ice types, bands of ridges (stamukhi) form under convergence
568 and flaw polynyas form under divergence conditions. The presence of this
569 stamukhi zone in the early season can also act as an ice dam, impeding the
570 spreading of river water over the shelf in early spring (McClelland et al., 2011).

571 Compared to the inflow shelves, the biogeochemical transformations
572 taking place on interior shelves are different in that they are dominated by
573 processing of terrestrial carbon (**Fig. 7**). The supply of terrestrial carbon into the
574 interior shelves is transformed into usable food for marine organisms by bacteria
575 and this comprises an increasingly important food source for Arctic biota, as
576 already observed for freshwater systems (Dunton et al., 2012; Taipale et al., 2016).
577 Photosynthetic primary production and the general biological activity are lower
578 than on inflow shelves, and much of the allochthonous matter is of a refractory
579 nature (Divine et al., 2015; Bell et al., 2016). High turbidity and export of surface
580 waters below the ice cover, followed by nutrient limitation due to strong salt
581 stratification are the main causes for the low primary production (Babin et al.,
582 2015). Biomass of planktonic organisms is thus comparatively lower than on
583 inflow shelves although hot spots may occur in certain areas (Smoot et al., 2017);
584 biomass of benthic organisms is equally highly variable but also generally lower
585 than on inflow shelves (Dunton et al., 2006; Ravelo et al., 2015). Some of the food
586 for the benthic organisms is of marine origin and derives from the estuarine
587 circulation bringing deeper waters onshore, some is locally produced, and a
588 significant amount derives from littoral and riverine sources (Dunton et al., 2012;
589 Stasko et al., 2018). Biological community structures in the water column and at
590 the seafloor clearly differ from those in inflow shelves due to both the increasing
591 influence of Arctic species and freshwater and terrestrial carbon inputs (Deubel
592 et al., 2003; Hirche et al., 2006; Garneau et al., 2009; Ershova et al., 2019a).
593 Sustained easterly winds promote upwelling over the shelf break, particularly
594 when ice cover is reduced (Carmack and Chapman, 2003; Williams and Carmack,
595 2015; **Fig. 12**). This results in rather different nutrient upwelling scenarios on

596 narrow and wide shelves (**Fig. 7**). For example, along the narrow shelves of the
597 Beaufort Sea primary production can be strongly stimulated and upwelling of off-
598 shore nutrients may reach the innermost shelf region (Tremblay et al., 2011). On
599 the wide shelves off Siberia upwelled nutrients are presumably limited to the
600 vicinity of the shelf break.

601

602 *3.1.3. Outflow shelves*

603 Outflow shelves allow Arctic and Pacific halocline water back into the North
604 Atlantic (i.e. the Nordic and Labrador Seas) via the Canadian Arctic Archipelago
605 and along the east coast of Greenland (**Figs. 6, 7**). The outflow shelves are not
606 simple gates or channels, but transit times of out-flow shelves are sufficiently long
607 for thermohaline and biogeochemical changes to occur en route (Michel et al.,
608 2015). The Canadian Arctic Archipelago in particular has long and highly variable
609 flow-through and residence times (McLaughlin et al., 2005). On the whole, the
610 Archipelago is a complex network of channels, sub-basins and sills, while the east
611 Greenland shelf is less structured but deeper. The archipelago (which can be
612 divided into a) Beaufort-Amundsen, High Arctic, c) Baffin - Labrador, d) Kitikmeot
613 and e) Hudson-Foxe regions (Oceans North Conservation Society, World Wildlife
614 Fund Canada, and Ducks Unlimited Canada, 2018) is currently ice-covered during
615 most of the year with extensive, but variable, ice-melt and stratification observed
616 during summer and early autumn. Heavy ice and pack ice cover the northern-most
617 portions of outflow shelves. Sea ice conditions demonstrate significant declines in
618 multi- year ice and a redistribution of ice types over the past 3 decades (Wadhams,
619 2018). Sea ice export strongly contributes to structuring spatially diverse
620 productivity regimes (Michel et al., 2015).

621 The average current direction of the longitudinal East Greenland and Baffin
622 Island outflow shelves is basically parallel to the ice edge, but is also influenced by
623 a combination of tidal mixing and wind-forced up and downwelling. Also, the
624 longitudinal outflow shelves of the western Fram Strait and eastern Greenland
625 are, to various degrees, perpetually ice-covered by pack ice transported from the
626 Transpolar Drift. Most of the ice produced in the AO melts along the longitudinal
627 outflow shelves. This results in significant stratification and reduced salinity of the
628 East Greenland Current. Primary production and associated community structure
629 on outflow shelves are spatially variable (Ardyna et al., 2011, 2013; Mayot et al.,
630 2018; Michel et al., 2015). In the southernmost network sections of the outflow
631 shelf primary production can be significant (Tremblay et al., 2006). Generally,
632 however, low nitrate concentrations in eastern Greenland and continuous ice
633 export are thought to be responsible for comparatively low primary production
634 (Michel et al. 2015). The contribution of ice algal production is thought to be high
635 at least in the southern network of the outflow shelf (Matrai and Apollonio, 2013).
636 It is highly seasonal, quickly nutrient limited and proves to be highly variable
637 between years. The zooplankton dynamics are even more variable, probably due
638 to irregular advection episodes through the Archipelago (Hamilton et al., 2009;
639 Apollonio, 2013). Of all Arctic shelves, the outflow shelves have the largest area of
640 coastal hard substrates, most high flow passages, the most abundant proximal
641 glaciers and some of the most prominent polynyas, all resulting in – yet poorly
642 mapped - highly variable benthic communities (Kenchinton et al., 2011; Roy et al.,
643 2015). In contrast to most other shelves, the coastal areas include long stretches
644 of, and increasing biomass of macroalgal primary producers (Krause-Jensen et al.,
645 2012; Filbee-Dexter et al., 2019). Polynyas of various sizes play a role as local hot

646 spots, with close pelagic-benthic coupling in pockets of high vertical mixing
647 (Ambrose and Renaud, 1995; Smith and Barber, 2007).

648

649 3.2. Shelf break and slope types and basic biogeochemical function

650 The shelf break (submerged offshore edge of a shallow continental shelf, where
651 the seafloor transitions to continental slope) and upper slope (seaward border of
652 the continental shelf) form the transition zone between shelf and basins,
653 comprising the approximate depth range of 80-1000 m in most areas (**Fig. 6**;
654 Jakobsson et al. 2008). It is characterized by strong gradients in physical, chemical
655 and biological properties over a narrow horizontal band (see 4.2.2). It encircles
656 the two main basins and forms a contiguous feature stretching counter-clockwise
657 ~ 8000 km from northwest Svalbard to northeast Greenland (**Fig. 6**). The belt is
658 influenced by three key physical-ecological processes: i) one that is thermohaline
659 driven and along-slope, ii) one that is wind forced and cross-slope, and iii) one that
660 is tidally driven and promotes internal wave generation and vertical mixing.

661 The shelf break and slopes of the AO play a significant role for its overall
662 physical oceanography and biogeochemical cycling. The topographically-trapped
663 Arctic Circumpolar Boundary Current (ACBC) carries AW cyclonically along the
664 shelf break and upper slope around the boundaries of the entire suite of AO basins
665 (see **Fig. 5B** and section 4.2).

666 The recent decrease in summer ice cover on the shelf edge supports
667 increased up-welling and has fundamentally changed the productivity and
668 stratification along the circum-Arctic shelf break (**Fig. 12**, Williams and Carmack,
669 2017). Along the Eurasian and western Amerasian shelf edge, nutrient availability
670 has increased, while the accumulation of ice and freshwater along the slopes of

671 northeastern Canada and northern Greenland have contributed to increased
672 stratification, preventing open water and upwelling (Slagstad et al., 2015).
673 Increased solar radiation, coupled with upwelled nutrients has induced a
674 significant increase in new production on the Eurasian and western Amerasian
675 shelf edges to levels similar to those experienced on the adjacent shelves
676 (Tremblay et al., 2011).

677 Stratification along the slope regions north of Svalbard appears to have
678 decreased due to increased influence of AW (Polyakov et al., 2017, 2018; Lind et
679 al., 2018), with an increasing tendency of AW (and decreasing stratification) to
680 spread eastwards towards Siberia. These changes in ice, river inflow and ice melt
681 may change the vertical nutrient flux may change accordingly, affecting primary
682 production and phytoplankton size distributions (Randelhoff and Guthrie, 2017).
683 Advection of expatriate Atlantic or Pacific origin mesozooplankton is also
684 characteristic of the slope domain (Kosobokova, 2012; Bluhm et al., 2015,
685 Wassmann et al., 2015; Ershova et al. 2019b).

686 As such, the shelf break and adjacent slopes are currently experiencing
687 some of the greatest ecological changes in the AO. Numerical models project a
688 doubling and tripling of primary production along the slopes on the Eurasian side
689 and western Amerasian side (from north of Svalbard to the Beaufort Sea)
690 (Slagstad et al., 2015), while production remains low or even declines in the
691 central AO and the north-eastern Canada/northern Greenland shelves. While the
692 shelf break and slope band that stretches from north of Svalbard to the Beaufort
693 Sea has seen primary production increase; whereas it has decreased along the CAA
694 and northern Greenland shelves.

695

696 3.3. Basin types and basic biogeochemical function

697 Two main basins occupy the deep central AO, the Eurasian and Amerasian basins,
698 separated by the Lomonosov Ridge between the Greenland and Siberian shelves
699 (**Fig. 5D**). In turn, the Eurasian Basin is divided into the Nansen and Amundsen
700 basins by the Nansen-Gakkel Ridge, and the Amerasian Basin into the Makarov
701 and Canada basins by the Alpha-Mendeleev Ridge. Deep basin domains are
702 influenced both by their deep connection to the Atlantic (~ 2600 m) and shallow
703 connection to the Pacific (~ 50 m), and by the broad shelves around them
704 (Jakobsson et al., 2008). The ridges that separate the deep basins form boundaries
705 for exchange of water masses and steering of deep ocean circulation, but
706 counterintuitively play less of a role as barriers for the dispersal of biota
707 (Kosobokova et al., 2011; Bluhm et al., 2011; and reviewed by Bluhm et al. 2015).

708 Only one third of the Amerasian and Eurasian basins of the deep AO are
709 currently perennially ice-covered, so that much of the basin area is now seasonally
710 exposed to sunlight and wind. Within the basin domain two basic water mass
711 assemblies are observed, the difference between them being the absence or
712 presence of PW sandwiched between Arctic Surface Waters (ASW) above and the
713 AW complex below; the boundary between these domains is the Atlantic/Pacific
714 halocline front (**Figs. 4, 5**). Both domains have vertical stratification that
715 constrains the transfer of nutrients to the surface layer (euphotic zone), thus
716 leading to their oligotrophic state, particularly in the more strongly stratified
717 Pacific Arctic where, despite high nutrient concentrations in the inflow, convective
718 reset of surface layer nutrients by haline convection in winter is virtually absent.
719 First and multi-year sea ice drastically alters albedo and insulates the underlying
720 water column from extreme winter heat loss while its mechanical properties

721 (thickness, concentration, roughness, etc.) greatly affect the efficiency of
722 momentum transfer from the wind to the underlying water.

723 Owing to the mentioned nutrient limitation, coupled with light limitation
724 due to snow and ice cover and extreme sun angle, primary production in sea ice
725 and water column of the two basin domains is very low compared to the adjacent
726 shelves (Gosselin et al., 1997). Severe nutrient limitation and complete euphotic
727 zone drawdown in the Amerasian Basin appears to favor small phytoplankton (Li
728 et al., 2009), a ubiquitous deep chlorophyll maximum layer (Carmack et al., 2011;
729 Ardyna et al. 2013) and a low energy food web (Iken et al., 2010). In contrast,
730 nutrients persist in the western Eurasian Basin, even in summer, suggesting light
731 limitation, heavy grazing or both as the dominant controls. Further these higher
732 stocks of nutrients in the Eurasian Basin are more conducive to marginal ice
733 blooms which are less abundant in the Amerasian Basin. Within the basin interior
734 the ice is now thinner and less compact, and thus more responsive to wind stress
735 than in the pre-1970s (Gascard et al., 2008). Increased accumulation of fresh
736 water and stratification, particularly in the Amerasian Basin constrains vertical
737 nutrient flux and affects phytoplankton size distributions, thus limiting primary
738 production in parts of the basins now and likely in the future (Randelhoff and
739 Guthrie, 2017). The result of low nutrient surface waters is that vertical carbon
740 supplies to the basin seafloor are low (Macdonald and Carmack, 1991), largely
741 advective (horizontal) and terrestrial in origin (Fahl and Stein, 1999), and
742 generally support low benthic and fish biomass (Bluhm et al., 2011; Mecklenburg
743 et al., 2018; Zhulay et al., 2019), though localized islands of larger than anticipated
744 biomass are now recognized (Vedenin et al., 2018).

745

746 **4. Contiguous domains in the Arctic Ocean**

747 The regional domains and their biogeochemical cycles discussed in section 3 are
748 linked to each other through contiguous domains. A contiguous domain is one
749 whose components i) share a common boundary or set of properties and
750 functions, and ii) are connected, over defined scales, in time and space. In our pan-
751 Arctic scale application, we seek common functional traits or phenomena that
752 appear continuously or at least once during an annual cycle. Contiguous domains
753 may or may not link specifically to geography as they may cross and link regional
754 and biogeographical domains. They may further expand or contract over
755 interannual time scales. These linkages allow material transports and share key
756 ecological functions and causal mechanisms (Carmack and McLaughlin, 2000;
757 Carmack and Wassmann, 2006).

758 In investigating the AO through the conceptualization of contiguous
759 domains, we take a macroecological view. In this way we examine patterns in
760 water mass and species distribution, and in species abundance to determine
761 relationships between abiotic and biotic factors, and further to understand and
762 model climate change impacted ecosystems along space-and-time climate
763 gradients (Li, 2002, 2009; Fossheim et al. 2015). Macroecology deals with the
764 study of relationships between organisms and their environment at large spatial
765 scales to characterize and explain patterns of abundance, distribution and
766 diversity. The perception gained from this view will prove valuable in the design
767 of synoptic scale research programs and the management and conservation of
768 marine arctic resources, it is a key to understanding the ecological impacts of
769 climate change that rely in in understanding the functions each domain provides.

770 When considering conceptual models for the AO it is important to
771 recognize which biogeographical scales come closest to matching those of the
772 climate system itself (cf. Carmack and McLaughlin, 2001). In this context it is again
773 useful to think in terms of contiguous domains. Functions within a given
774 contiguous domain are thus likely to share broad linkages also in response to
775 climate forcing. Conversely, the response of different contiguous domains to
776 climate forcing may likely be different in qualitatively and quantitatively different,
777 and failure to recognize the interplay of scale, regionality, seasonality and
778 contiguity may lead to over-extrapolation and misinterpretation. The contiguous
779 nature of significant elements of the AO ecosystems implies thus a distinct pan-
780 Arctic approach.

781 In defining contiguous domains, we attempt to lay the foundation for a
782 better interpretation of previous and future investigations by placing the AO in a
783 more realistic time/space perspective. Thereby a full set of scales linking climate
784 to biota along entire contiguous domains may be accommodated in the future,
785 with improved understanding of domain-wide responses to variance in climate.
786 The AO is a beta ocean system (defined by temperature and salinity, in contrast to
787 an alpha ocean) which defines hydrographic and ecosystem connections through
788 the underlying cause of permanent stratification similarities; that is, salt (β) or
789 temperature (α) stratification (Carmack, 2007). Within this system, we recognize
790 6 contiguous domains grouped by their reliance on seasonal processes (section
791 4.1) or advective processes (section 4.2). The AO is decisively connected to and
792 forced by Pacific and Atlantic water that enter perpendicular to the AO
793 Mediterranean through the Bering and Fram straights and the St. Anna Trough.
794 Advection from outside, but also inside the AO is thus an overruling process that

795 shapes all contiguous domains of the AO (section 4.2). An exception is the Seasonal
796 Ice Zone Domain (SIZD, see 4.1) which is mainly shaped through seasonal
797 processes, including radiation and stratification and links shelves and basins
798 through a pulsating, expanding and shrinking area (however, in recent years
799 incoming AW is playing an ever increasing role in the retreat of sea ice north of
800 Svalbard and probably in the northern Kara Sea in the near future; see Polyalov
801 et al 2017). With increasing thinning of the ice cover, the outer part of the central
802 AO experiences ever more open water and greater fetch that may open up for
803 increased vertical mixing of nutrients (Randelhoff et al. 2015; Randelhoff and
804 Guthrie, 2016). The exact position/shape/coverage of the SIZD at any given time
805 may also be subject to advection by wind and currents, and is thus a spatially and
806 temporally dynamic contiguous domain.

807

808 4.1 Seasonal Ice Zone Domain

809 The seasonal ice zone is the area of the AO that extends from the permanent ice
810 zone to the boundary where winter sea ice extent is at a maximum. The Seasonal
811 Ice Zone Domain (SIZD) is now the largest contiguous domain in the AO. It
812 comprises the cumulative area that is temporarily ice-covered at any given time
813 within a year, i.e. basically the area between maximum and minimum ice extent
814 in a given year. Ice and snow limit the penetration of solar radiation and thus
815 photosynthesis of ice algae and phytoplankton. Ice and stratification by ice melt
816 reduce the impact of wind on vertical mixing and can support an ice edge bloom
817 where and when nutrients are available, especially on the shelves. Thirty years
818 ago, this domain was limited in areal extent, rarely crossing the shelf break, but
819 climate warming has greatly decreased the area of summer ice cover while only

820 marginally decreasing winter cover, thus resulting in vast widening of the SIZD
821 (**Fig. 8A**); it now comprises about 2/3 of the total area of the AO (similar to the
822 size of the territory of Europe). Global climate change has and will have in decades
823 to come have immense consequences in the SIZD. As the knowledge base for SIZD
824 dynamics - physical and biogeochemical- - is limited, and climate change is
825 greatest, the lack of key information is particularly discomfoting. The number of
826 time-series moorings and research platforms is small and the expanding cover of
827 the region means the SIZD is not well represented in any conceptual mode. The
828 past, present and future highly dynamic nature of the SIZD is exemplified in **Fig.**
829 **8B**. The shrinking and expansion of the SIZ can be compared to with the breathing
830 of an organism. In summer the SIZD breathes in and opens up for primary
831 production and the unfolding of seasonal and perennial Arctic life. In autumn and
832 winter the SIZD breathes out and, along with declining radiation, spreads the sea
833 ice cover like a lid over the AO. The seasonal exhalation and inhalation of the
834 domain sets the rhythm for the biological carbon pump and export production to
835 the AO benthos (see 5.3).

836 The seasonal ice zone is created by annual ice melt and consists of two
837 types of ice: pack ice (that dominates by area) and land fast ice. Land fast ice
838 attached to the coastline, to the sea floor along shoals, and to grounded icebergs
839 in summer (Greenland) is a defining feature of Arctic coasts and can extend
840 hundreds of kilometers offshore (Mahoney et al., 2014; Yu et al., 2014). Fast ice
841 may either grow in place from the sea water with admixtures by river water
842 (Eicken et al., 2005) or by freezing pieces of ice drifting to the shore or other
843 anchor sites. In most regions the pack ice meets the fast ice during maximum ice
844 cover. Here we find ridging, known as stamukhi; a partially-grounded

845 accumulation of sea ice rubble that typically develops along the boundary
846 between fast ice and the drifting pack ice, or becomes incorporated into the fast
847 ice. In addition to stamuki we also find here polynyas, areas of open water
848 surrounded by sea ice (Macdonald and Carmack, 1991). It is often used as a
849 generic term for an area of unfrozen sea within the ice pack. Rapid ice melt of fast
850 ice is also part of the seasonal ice zone, but this melt is much smaller by a factor of
851 3.3 by area (mean 1.84 million km² between 1975-2007, Yu et al., 2014) than that
852 of the pack ice zone. Disproportionally high, however, is the use of land fast ice by
853 horizontally or vertically migrating, feeding and/or resting marine life (Gradinger
854 et al., 2009; Hamilton et al., 2017) and by local Arctic human communities for both
855 travel and subsistence hunting (Eicken et al., 2009, 2014; Fox Gearheard et al.,
856 2017).

857 Outside the land fast ice zone we find the SIZ of the pack ice that is free-
858 floating, not connected to land. It expands generally north- and inwards with the
859 AO melting season. Before climate warming accelerated in recent decades, the SIZ
860 - assuming it was circular - had a radius of ~1,500 km in summertime. The outer
861 rim of the SIZ is the marginal ice zone (MIZ) of more than 9,000 km (**Fig. 8B**).
862 Previously the MIZ circumference was too long to be circumnavigated and studied
863 synoptically during a single cruise. Soon the maximum SIZD width will only be
864 about 500 km and the MIZ circumference less than 6,000 km, and could thus be
865 circumnavigated in 2-3 weeks. The area of today's SIZ at a width of 500 km is > 6
866 million km² (**Fig. 8B**) renders the investigation of the SIZ an enormous challenge
867 for the low number of available research platforms. The MIZ forms the biologically
868 most active fringe of the pack ice SIZD. During summer the ice cover of the SIZD
869 gets thinner and the large ice-covered SIZD supports ice algal and later

870 phytoplankton blooms (Gradinger et al., 1999; Gradinger, 2009; Ardyna et al.,
871 2014; Mayot et al., 2018).

872 To better comprehend the dynamic nature of the SIZD across the AO (the
873 phenology and latitudinal variability is addressed in section 5.2 and **Figs. 16-18**),
874 monthly hypothetical transects, reflecting ice over and thickness, light and
875 plankton blooms were developed (**Fig. 9**). One such transect stretches across the
876 AO from the wide and productive Barents Sea to the narrow Beaufort Sea shelf
877 (**Figs. 8B, 9A**) while the other transect runs from the wide Laptev Sea shelf to the
878 heavily ice-covered regions north of Greenland (**Figs. (B, 9B)**). The distribution of
879 SIZD phytoplankton blooms in space and time is very uneven across the AO. The
880 phenology of ice and phytoplankton varies significantly across the AO with the
881 largest blooms and greatest ice-melt on the Eurasian side (Arrigo and van Dijken,
882 2015; Slagstad et al., 2015). The maximum development of the phytoplankton
883 bloom is encountered May through July, dictated by ice cover, light and nutrients.
884 Climate change will influence the time window of the phytoplankton development
885 since thinner ice and leads already after equinox will induce an early onset of thin
886 bloom layers close to the surface (e.g. Assmy et al., 2017). Most of the thinning and
887 reduction of ice cover takes place towards the end of the early productive season
888 (with high new production) and thus does not immediately influence the bloom
889 development. Recently pelagic autumn blooms, however, have increasingly been
890 encountered (Loeng et al., 2005; Ardyna et al., 2014; Oziel et al., 2017). At high
891 latitudes they become quickly light limited when solar radiation decreases and
892 they depend upon increased nutrient availability through vertical mixing by winds
893 and tides.

894

895 4.2 Contiguous domains constrained by advective processes

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

- 901 • the Riverine Coastal Domain (RCD), which links all shelf typologies with
902 hinterland
- 903 • the upper layer advective domains (ULAD), which connects the AO with the
904 northern Pacific and Atlantic Oceans and the northern Barents Sea
- 905 • the Atlantic and Pacific Halocline domains (APHD), which recognize the
906 spreading of Pacific halocline waters into the Amerasian and Eurasian
907 basins
- 908 • the Circumpolar Boundary Current Domain (CBCD) along the shelf-break,
909 which surrounds the basins and links shelf-basin exchanges
- 910 • the Deep Basins Domain (DBD) which is exposed to sluggish advection
911 from the North Atlantic.

912

913 4.2.1 Riverine Coastal Domain

914 The riverine coastal domain (RCD) is a narrow (5-15 km wide), shallow (~10 m
915 deep) contiguous feature that is confined by the spreading of river and glacial
916 water discharge (**Fig. 10**). It is forced by an aggregate of continental runoff sources
917 (**Fig. 1A**), with diverse timing of discharge, and which extends counterclockwise
918 around the perimeter of the coast, broken only by the major gateways at Bering
919 and Fram straits (Carmack et al., 2015) (**Figs. 1B, 3**). Due to its riverine sources,

920 the RCD carries a terrestrial signal from surrounding rivers, lakes and watersheds
921 that affects light, nutrient and carbon regimes, and provides a coastal pathway for
922 the dispersal and migration of marine biota such as anadromous fish and arctic
923 brackish water zooplankton. The RCD acts as the initial connector between
924 terrestrial and marine ecosystems such that physical and biogeochemical
925 variables within the RCD yield a contiguous gradient of environmental conditions
926 along and across the pan-Arctic coastal zone between and among shelf domains.
927 The RCD may become even more prominent as terrestrial runoff, permafrost thaw
928 and local ice melt are assumed to increase in the near-future climate (for estimates
929 of permafrost carbon input into the Arctic coastal zone, see Lantuit et al., 2013).
930 However, due to the small cross-shelf size of the RCD (~10 km) and its nearshore,
931 shallow location that is outside the operation range of most research vessels,
932 detailed observations of this feature are virtually missing, with probably the
933 exception of the the Alaskan nearshore shelf and estuarine lagoons of the Beaufort
934 Sea (e.g. Dunton et al., 2006, 2012).

935 The seasonally highly dynamic and physically challenging conditions of the
936 coastal zone result in recognizably different biotic communities than are found
937 farther offshore. Zooplankton communities are characterized by neritic and
938 brackish taxa – especially near/in river deltas/river estuaries (Lischka et al.
939 (2001) for the Laptev and Deubel et al. (2003) and Hirche et al. (2006) for the Kara
940 Seas, respectively). Benthic communities including demersal marine fishes show
941 low diversity and biomass thought to be related to a combination of seasonally
942 low salinity, and mechanical disturbance through ice gouging (though this effect
943 extends beyond the RCD) (Ravelo et al., 2015). Coastal migratory and forage
944 fishes, however, can be abundant in this domain (Roux et al., 2016), and it is this

945 narrow coastal belt where all indigenous subsistence travel and hunting activities
946 in the marine realm take place.

947

948 *4.2.2 Upper Layer Advective domains*

949 We define the combined waters above the halocline and advected by the North
950 Pacific, North Atlantic and the Barents Sea or transported through the Transpolar
951 Drift as the Upper Layer Advective Domains (ULAD) (**Fig. 11**). Note that surface
952 waters within the subarctic Atlantic and Pacific subduct upon entering the AO
953 continue as mid-depth interflows. The advection of nutrient-, detritus- and
954 plankton-rich waters from the Pacific and Atlantic Oceans and the northern
955 Barents Sea into the AO plays a crucial role for the ecology and seasonality of the
956 AO ecosystem (Wassmann et al., 2015; Hunt et al., 2016). In addition, the Siberian
957 shelf is connected to the Fram Strait through the Transpolar Drift advection (**Fig.**
958 **11**). Such flows connect subarctic with arctic biota, supporting both primary
959 production and higher trophic level consumers (Vernet et al 2019; Wassmann et
960 al. 2019). By volume of water and biomass inflow, the dominant contribution to
961 the ULAD is by the northeastern North Atlantic and the Barents Sea (**Fig. 11**).
962 ULAD overlaps at the shelf break and upper slope with the circumpolar boundary
963 current domain (see 4.2.3).

964 While the ULAD connects Arctic biota with subarctic inputs, its outflow also
965 influences the physical, chemical and biological oceanography of adjacent
966 subarctic waters through advective outflows, in particular through western Fram
967 Strait, but also through the Canadian Arctic Archipelago. However, exports of
968 biomass out of the AO into the North Atlantic Ocean are thought to be far smaller
969 than the influx from the south (e.g. Wassmann et al., 2015). Thus, AO ecosystems

970 are net planktonic biomass beneficiaries through advection, especially along the
971 relatively narrow advective pathways of the ULADs: large amounts of food create
972 the basis for fish and marine mammals feeding at the perimeter of the AO basins.
973 Further, the transport of ice with its associated biota and conspicuous amounts of
974 terrestrial matter that drifts across the AO with the Transpolar Drift also delivers
975 a supply of DOC and biogenic matter from the Laptev Sea to the western Fram
976 Strait regions (Hop and Pavlova, 2011). The biotic impact of Atlantic-, Pacific- or
977 Arctic origin taxa being transported in the ULAD depends on their ability to
978 survive along the transport path (Hirche and Kosobokova, 2007). Thus, advective
979 transport can be thought of as “trail of life and death” in the AO (Wassmann et al.,
980 2015).

981 We distinguish three specific ULADs based on water mass structures (**Fig.**
982 **11**): the Atlantic-Arctic (including the Barents Sea branch), the Pacific-Arctic, and
983 the Transpolar Advective domains. The Atlantic-Arctic ULAD connects the North
984 Norwegian shelf from the Lofoten Islands to the shelf break and upper slope
985 domain of the western Eurasian sector of the AO. This ULAD crosses several
986 biogeographic boundaries with impacts on species abundance and life histories.
987 For example, the supply of the Atlantic copepod *Calanus finmarchicus* along the
988 domain is particularly substantial (contributing 30-60% to overall zooplankton
989 biomass, Kosobokova, 2012). The Pacific-Arctic ULAD connects the shelf of the
990 northern Bering Sea to the Chukchi and, in particular, the western Beaufort Seas
991 (all the way to northern Greenland), supporting pelagic and benthic biomass
992 hotspots and higher trophic levels along the way, and facilitating biomass rich
993 eddies beyond Point Barrow (Berline et al., 2008; Grebmeier et al., 2015; Moore et
994 al., 2018a). The Barents Sea branch of the Atlantic-Arctic ULAD derives from the

995 cold waters of the northern Barents Sea and connects, through the upper third of
996 the St. Anna Trough, to the shelf break and upper slope domain along the Siberian
997 sector of the AO. Similar to the Atlantic-Arcitic ULAD, the supply of the Arctic
998 copepod *Calanus glacialis* along this domain is highly significant, but less
999 investigated (Kosobokova, 2012).

1000 The third ULAD is that of the Transpolar Drift that connects the biota (and
1001 suspended biomass) of the Laptev Sea shelf with the western Fram Strait where
1002 ice-associated biomass is released to the water column during as pack ice melts
1003 (Hop and Pavlova, 2011). The recent eastward spread of warm AW (Polyakov et
1004 al., 2017) has resulted in warming temperatures which are melting Russia's
1005 coastal "ice nurseries" faster than before. Some 80% of nursery ice now melts
1006 before it joins the open ocean, compared to 50% before 2000 (Krumpal et al.,
1007 2019). The result will be that food supplies will be reduced for those animals in in
1008 the open AO that rely on the food from sea ice will receive reduced food from TPD-
1009 transported sea ice. Further, if AW reaches the Laptev Sea in the future the
1010 Transpolar Drift may cease and disappear. Model investigations suggest that the
1011 transport of detrital carbon from the Laptev Sea to the Fram Strait by the
1012 Transpolar Drift ceased already decades ago (D. Slagstad, P. Wassmann, unpubl.
1013 res.)

1014 The ULADs are typically characterized by net heterotrophy; i.e.
1015 consumption of biomass is greater than local production. Physical and biological
1016 forcing inside the conventional latitudinal biogeographic regions is minimized and
1017 teleconnections are created across biogeographic and production zones. They
1018 penetrate the circular nature of the AO and make them dependent upon the Pacific
1019 and Atlantic Oceans. Changes in advection through the North Atlantic (Asbjørnsen

1020 et al., 2019), the increasing spread of AW north of Svalbard (Polyakov et al., 2017)
1021 and the increasing Bering Strait throughflow driven largely by the increasing
1022 Pacific-Arctic pressure gradient (Woodgate et al., 2013) result in the ULADs, along
1023 with the SIZD, being the fastest changing contiguous domains in the AO (e.g.
1024 Vernet et al., 2019; Wassmann et al., 2019).

1025

1026 *4.2.3 Circumpolar Boundary Current domains*

1027 At the shelf break, the Circumpolar Boundary Current Domain (CBCD) is the
1028 dominant thermohaline feature of the AO (**Fig. 5b, c**, Aagaard, 1989; Rudels et al.,
1029 1994). It is a continuation of the Atlantic-Arctic and Barents Sea ULAD (**Fig. 11**),
1030 but we list it separately because the CBC transports subducted, modified AW, that
1031 circumnavigates the entire AO shelf break and slope. Beszczynska-Möller et al.
1032 (2011) estimate that between 8 and 9 Sv ($1 \text{ Sv} = 10^6 \text{ m}^3 \text{ s}^{-1}$) enter the Nordic Seas
1033 over the Greenland Scotland Ridge (sill depth $\sim 800 \text{ m}$) and roughly half of this
1034 flow continues on to the AO; of the AW continuing north, about half enters the AO
1035 via Fram Strait as the Fram Strait Branch (FSB) and subducts below Arctic Surface
1036 waters (ASW) north of Svalbard (**Fig. 5C**). The other branch first crosses the
1037 Barents and the westernmost Kara Seas, subducts along the Atlantic Polar Front,
1038 continues across the eastern Barents Sea, and then drains through the St. Anna
1039 Trough as the Barents Sea Branch (BSB) (Rudels et al., 2012, 2013; Dmitrenko et
1040 al., 2014; Bluhm et al., 2015). Because the BSB water is strongly modified *en route*
1041 by mixing with local Barents Sea waters, it enters the basin with a broader density
1042 range than FSB waters and both interleaves laterally and subducts below the
1043 continuing FSB. Aagaard and Woodgate (2001) also noted that the high-latitude
1044 freezing and melting cycle can supply additional freshwater injection into the

1045 interior of the AO, resulting in a secondary salinity minimum at about 800m depth.
1046 A third water mass, formed locally on the eastern Barents and western Kara Seas
1047 also drains into the basin through St. Anna Trough (Aksenov et al., 2011).
1048 Subsequently, the three branches become the ACBC and continue cyclonically
1049 around the basin perimeter, with bifurcations occurring where ridge and slope
1050 topographies intersect. The transit is marked by slope cutting canyons and
1051 currents tend to be strongest where the slope is steep (Isachsen et al., 2003).
1052 Aksenov et al. (2011) modeled the ACBC and demonstrated that transports along
1053 the AO margins were forced by the joint effects of buoyancy loss and non-local
1054 winds which created high pressure upstream in the Barents Sea. There is still
1055 debate as to the volume transports of AW into and out of the AO, with a total
1056 amount of 4–8 Sv being generally accepted (cf. Dickson et al., 2008). What is
1057 important is that the ACBC carries a huge and varied mix of water properties and
1058 biogenic material as it travels this circuit.

1059 The CBCD can be pictured as a long, narrow band that rapidly transports
1060 materials around the ocean perimeter, allows on slope and off slope exchange, and
1061 radiates mixing energy into the interior (**Fig. 5a, b, c**). For a description of the
1062 productivity and in particular the current ecological changes, see 3.2. Increases in
1063 primary production are expected for the Eurasian but less so in the Amerasian
1064 CBCD (Slagstad et al., 2015).

1065

1066 *4.2.4 Atlantic and Pacific Halocline Domains*

1067 The AO halocline is a complex structure below the ULAD in which river inflows,
1068 ice melt, winter convection, and the insertion of Pacific and Atlantic waters -
1069 modified on their respective inflow and interior shelves - all contribute to the

1070 vertical salt stratification (**Fig. 13**). These halocline components have distinct
1071 physical, chemical and biological characteristics according to their sources, and
1072 maintain identifiable structures both horizontally and vertically within the AO
1073 interior (Polyakov et al., 2018). The Pacific and slightly denser Atlantic
1074 components are as different from each other as are their parent oceans. Here we
1075 will describe them as the Atlantic and Pacific Halocline Domains (APHD), i. e.
1076 distinct, contiguous halocline domains that cover the entire central AO (cf. Bluhm
1077 et al., 2015, **Fig. 13**).

1078 Waters of Pacific origin enter through Bering Strait, flow northwards
1079 across the broad Chukchi Shelf along three major branches, are modified en route
1080 on seasonal time scales, and enter the Amerasian Basin through submarine
1081 canyons at the shelf break, where they spread into the basin interior (Pickart,
1082 2004; Weingartner, 2005; Shimada et al., 2006; Danielson et al., 2017). Pacific-
1083 origin halocline waters arrive as two main varieties, the warmer and fresher
1084 summer waters, and the colder and more saline winter waters (Coachman and
1085 Barnes, 1961; Shimada et al., 2001; Steele, 2004; McLaughlin et al., 2009). These
1086 waters are largely confined to the Canada Basin owing to the anticyclonic Beaufort
1087 High wind field, and tend to accumulate within the convergent Beaufort Gyre. The
1088 key distinction of the Pacific halocline water is that they are higher in nutrients
1089 and fresher, so that they overlie the Atlantic variety and add to the salt-
1090 stratification of the Amerasian AO.

1091 Atlantic-origin halocline waters are largely modified and formed on
1092 Siberian shelves (Aagaard et al., 1981; Aksenov, et al., 2011; Polyakov et al., 2017).
1093 Still, as early as the mid-1980's, arguments were presented that Atlantic-origin
1094 waters were modified by freeze/thaw processes during passage over the Barents

1095 and Siberian shelves, and subsequently entered the deep ocean (Jones and
1096 Anderson, 1986); a hypothesis also supported by numerical modelling (Killworth
1097 and Smith, 1984; Aksenov et al., 2011). An important feature of the Atlantic-origin
1098 halocline water that underlies the Pacific-origin water in the Amerasian Basin is
1099 its associated oxygen minimum.

1100 A major front, termed the Atlantic/Pacific Halocline front blocks the
1101 spreading of Pacific water into the Eurasian Basin and allows only the lower
1102 portion of the Atlantic-origin halocline water into the Amerasian Basin (reviewed
1103 in Bluhm et al., 2015). There is debate whether this front is stationary and locked
1104 to topography, or free to shift from one stable configuration to another under
1105 climate forcing (cf. McLaughlin et al., 1996; Carmack et al., 1996).

1106 An important aspect of the 'halocline complex' is that there is no such thing
1107 as 'a' halocline but instead there are multiple layers that comprise a staircase of
1108 increasing water density with depth that insulates the warm Atlantic layer in the
1109 basement from the Polar Mixed Layer and ice. The individual "steps" (or layers)
1110 are formed and shaped on the shelves, and are advected into the adjacent basins,
1111 where they 'stack themselves' according to density. Therefore, to get from the base
1112 to the surface one has to take one step at a time. Between the 'clines' near-
1113 homogenous layers are found which is why vertical profiles of salinity in this
1114 domain actually look like a staircase. The Amerasian Basin has more 'steps' in the
1115 staircase than the Eurasian Basin (**Fig. 13**). The primary control of the APHD on
1116 biological production in the AO is its strong stratification that shapes the
1117 biogeochemical function of the central AO basins: it effectively prevents the
1118 vertical supply of nutrients and thereby hampers primary production,
1119 irrespective of increasing light levels in the changed AO. This effect is stronger in

1120 the Amerasian side where the APHD is more strongly stratified than on the
1121 Eurasian side. Further, the APHD plays a significant role in the distribution of
1122 planktonic species, as reflected in its mesozooplankton inhabitants (e.g. Bluhm et
1123 al., 2015). The domain is made up of individual layers, formed and shaped on the
1124 shelves, that are advected into the adjacent basins, where they ‘stack themselves’
1125 according to density.

1126

1127 *4.2.5 Deep Basin Domains*

1128 The Deep Basin Domain (DBD) lies below the Atlantic Layer. It is several thousand
1129 meters thick and by volume, comprises the largest – yet the least studied –
1130 contiguous domain (**Fig. 14**). The pathways, rates of spreading of AO deep waters
1131 and biological communities and processes within it are poorly known
1132 (Kosobokova, 2012), but in general there is direct deep-water exchange between
1133 the Norwegian and Greenland Seas and the Nansen Basin via Fram Strait (sill
1134 depth ~ 2600 m). From there the flow is thought to proceed from the Nansen
1135 Basin to the Amundsen Basin to the Makarov Basin and finally to the Canada Basin
1136 (MacDonald et al., 1993; Schlosser et al., 1997). From the Amundsen Basin there
1137 must be a return flow back to the Eurasian Basins, Nordic Sea and North Atlantic
1138 (Aagaard et al., 1985; Rudels et al., 2013). Indirect proof for these water exchanges
1139 between basins are (1) deep-water zooplankton communities that have higher
1140 community similarity within the DBD horizontal layers than across vertical layers
1141 in a given basin (Kosobokova, 2012); (2) generally similar zoogeographic patterns
1142 in benthic communities across basins (Bluhm et al., 2011); and (3) and the high
1143 proportion of Arcto-Atlantic affinity biota across the deep-sea floor in the DBD
1144 (Mironov et al., 2013; Zhulay et al., 2019).

1145 The overall motion of deep water within the basins below sill depth is
1146 sluggish as clearly reflected at the deep-sea floor where animal traces are well-
1147 preserved and abundant despite low faunal densities (Zhulay et al., 2019).
1148 Schlosser et al. (1997) calculated the mean isolation age of the Eurasian Basin
1149 bottom water >2500 m to be ~250 years while that of the Amerasian Basin > 2500
1150 m to be an additional 200 years older. Thus, the Amerasian Basin deep waters are
1151 either presently not being ventilated (Macdonald and Carmack, 1991; Macdonald
1152 et al., 1993; Aagaard and Carmack, 1994), or are being ventilated much more
1153 slowly with continuous renewal by shelf water (by freezing and brine rejection on
1154 the shelves) or influxes from the adjacent Eurasian Basins (Aagaard et al., 1985;
1155 Östlund et al., 1987; Jones et al., 1995; Rudels et al., 2000). The influxes from the
1156 adjacent Eurasian Basins would provide a mechanism to carry organic material
1157 and biota to depth. More rapid flows are expected along basin and ridge slopes,
1158 and through narrow gaps in the ridges (Bluhm et al., 2015).

1159 Given that the organic matter flux from surface primary production to the
1160 DBD is very limited and much of the carbon is refractory in nature (Iken et al.,
1161 2005), biotic densities and biomass are generally low (Bluhm et al., 2011;
1162 Kosobokova, 2012). Extremely low concentrations, but the persistent presence of
1163 rare endemic deep-sea species of zooplankton throughout the DBD despite the
1164 presence of underwater ridges once again emphasizes the contiguous nature of
1165 DBD and the exchange of deep waters within it. In the absence of fresh algal food,
1166 feeding guilds in deep-dwelling zooplankton are dominated by carnivores,
1167 omnivores and deposit feeders (Kosobokova et al., 2002, 2011). However, the
1168 supply of biogenic matter through chemolithotrophs in the DBD, presently not
1169 adequately quantified, has also to be considered as a food source (e.g. Griffith et

1170 al., 2012; Åström et al., 2017). Benthic macrofaunal (often essentially sessile)
1171 communities tend to follow the global trend of diminishing size with increasing
1172 depth related to food limitation (Wei et al., 2010), while larger - often mobile -
1173 fauna can actively search for and surprisingly quickly find food (Premke et al.,
1174 2006; Boetius et al., 2015). Exceptions to both patterns are drop stones
1175 ubiquitously found across the DBD which consistently house biodiversity islands
1176 of hard-bottom fauna (Zhulay et al., 2019) with often unknown life cycle and
1177 feeding strategies, yet extremely low recruitment rates (Meyer-Kaiser et al.,
1178 2019).
1179
1180

1181 **5. Major processes forcing the biogeochemical cycles in the Arctic Ocean**

1182 Before we reach the last suite of conceptual models, those of food webs, we
1183 connect some of the most important processes to regional aspects and the
1184 functional domains. We start in the AO surface layer that is dominated by an
1185 extreme annual variability of light, freshening, stratification and warming (Agustí
1186 et al. 2010). Together both processes exert a strong impact on the highly
1187 seasonal productivity of and the life cycle of organisms in the AO. In turn, the
1188 phenology of autotrophs in sea- ice, the water column is connected to rocks and
1189 the seabed.

1190

1191 5.1 Light forcing

1192 Light availability (or lack thereof) is a key determinant for the phenology of
1193 autotrophs and heterotrophs in the AO. Light availability is a function of available
1194 solar radiation, sun angle, presence and the character of ice, snow cover and
1195 shading (by autotrophs, colored dissolved matter and/or suspended particles).
1196 Combined, these factors set up a highly spatially and temporally variable light
1197 forcing over the expanse of the AO. For ~~astronomical~~ solar radiation during the
1198 dark season we distinguish between various types of Polar Night (**Fig. 15**), where
1199 the exact zone and type of Polar Night at a given location depends on a) latitude
1200 and b) angle between the horizon and the sun. For details, see Berge et al. 2020).
1201 Geometrically, there is one day of Polar Night at the Arctic circle (66.33°N), and
1202 the Polar Night lasts for 183 days at the North Pole. However, due to atmospheric
1203 refraction of sunlight, at sea level there will appear to be direct sunlight at noon
1204 on winter solstice up to approximately 67.4°N. For the same reason, the Polar

1205 Night lasts “only” 177 days at the North Pole, not 183 as one would expect from
1206 geometry alone.

1207 For the northern hemisphere, the brightest level of Polar Night is Polar
1208 Twilight which occurs ~~from 67.4° up~~ to 72° N when solar elevation remains
1209 between 0° and 6° below the horizon at the winter solstice. The entire duration of
1210 Polar Night at these latitudes is limited to Polar twilight zone. Further north in a
1211 band from 72° to 78° N, Polar Night begins with a period of Polar Twilight which
1212 is followed by Civil Polar Night when solar elevation remains between 6° and 12°
1213 below the horizon at winter solstice, and then again by Polar Twilight. Still further
1214 north in a band from 78° to 84° N, Polar Night consists of Polar Twilight and Civil
1215 Polar Night followed by Nautical Polar Night when solar elevation remains
1216 between 12° and 18° below the horizon at the winter solstice, and then again by
1217 Civil Polar Night and Polar Twilight. And finally in a band from 84° to 90° N, the
1218 periods of Polar twilight, Civil Polar Night, and Nautical Polar Night are followed
1219 by Astronomical Polar Night when solar elevation remains 18° below the horizon
1220 at the winter solstice, and then again by the three lesser periods before the sun
1221 returns above the horizon. The Midnight Sun period with similar periods of
1222 permanent sun light is a mirror of the Polar Night.

1223 Solar radiation in the Arctic is thus extremely variable with regard to
1224 latitude, ranging from roughly 6 months of direct sunlight at the North Pole to the
1225 sun being under the horizon for just minutes at the Arctic Circle. In addition, ice
1226 and snow covers modify the light reaching organisms in the ice and surface ocean.
1227 The light regime in the seasonally ice-covered Chuckie Sea is similar to that in
1228 northern Norway and the southern Barents Sea, but the latter experiences less or
1229 no ice-cover. The Bering Strait and Bering Sea, situated outside the main AO

1230 region, experience solar radiation year-round, but ice cover can still result in low
1231 light conditions for the biota. In contrast, the Nautical and Astronomically Polar
1232 Night is only experienced in the northernmost regions of the AO. Investigations
1233 during the full annual light regime have been carried out only a few places, e. g. in
1234 coastal waters off northern Svalbard, the Canadian Arctic Archipelago, northern
1235 Greenland and the White Sea (e.g. Ashjian et al., 2003; Kosobokova and Pertsova,
1236 2018). Also, some regions encompass Arctic biota but experience a sub-Arctic light
1237 regime, and vice versa. For example, northern Norway and the southern Barents
1238 Sea experience a Polar Twilight light regime, but the biota is dominated by
1239 advected boreal forms from the south. Thus, the ~~astronomical-ambient~~ light
1240 regime sets up important patterns that impact the biota, but do not necessarily
1241 determine it. Many “typical” studies in the AO have been carried out in regions that
1242 are south of the Arctic circle (66°N), outside the Arctic light/darkness regime
1243 defined in **Fig. 15** (such as southern Greenland, Hudson Bay and the Bering Sea).
1244 Ice cover and temperature are indeed not the only criteria for marine Arctic
1245 ecology, yet the annual light cycle has to be clearly defined to allow clear and
1246 unambiguous generalizations. Marine ecological investigations in the AO have to
1247 be far more rigorous in describing and considering the light climate.

1248 In addition to light availability, ice cover is highly variable across the AO
1249 and this has obvious consequences for the phenology of auto- and heterotrophs
1250 (Kirchman et al., 2009; Leu et al., 2015; **Figs. 9, 16**). Sea ice melt is also closely
1251 connected to salt stratification, another factor dictating the biogeochemical
1252 characteristics of the AO euphotic zone. Freshening arises from ice melt which is
1253 caused by solar radiation and atmospheric warming from above (Wassmann et al.,
1254 2010; Carmack et al., 2016) and by warm water melting from below (in particular

1255 AW; see Carmack et al., 2012a; Polyakov et al., 2017). The ice albedo, or
1256 reflectivity, also impacts heat absorption by the ice, which is further influenced by
1257 dirty ice and atmospheric deposition of black carbon (Lee et al., 2013; Goelles and
1258 Boggild 2015). The circumarctic, highly stratified band of surface water within
1259 the MIZ then shapes the development and of both the pelagic and ice associated
1260 spring blooms. These blooms, consisting of both sea ice algae and phytoplankton,
1261 come seasonally soon to an end because of nutrient depletion which is one of the
1262 most significant characteristics of today's MIZ. But the AO will also face increased
1263 stratification and nutrient limitation as the MIZ retreats increasingly to positions
1264 that are positioned over the already strongly stratified basins (Tremblay et al.,
1265 2015; Assmy et al., 2017).

1266

1267 5.2 Phenology and seasonal productivity variation

1268 Within their respective envelopes of hydro-morphological characteristics and
1269 contiguous domains the ecology of AO organisms appears extensive phenological
1270 cycles. The study of seasonal cyclic organismal events in algae and periodic plant
1271 ~~and~~ animal life, i.e. their phenology, is influenced by seasonal and interannual
1272 variations in climate. Phenologies are thus ~~are~~ now responding to global warming
1273 through detectable food prints of climate change (Wassmann et al., 2011). For
1274 example, changes in autotroph phenologies (e.g. Kahru et al., 2011; Rubao et al.,
1275 2012; Tedesco et al., 2019) are now affecting match and mismatch relationships
1276 between predator (including grazers) and prey (e.g. Edwards and Richardson,
1277 2004; Post, 2016; Ramírez et al. 2017). In addition to providing a longer historical
1278 baseline than instrumental measurements, phenological observations provide
1279 high temporal resolution of ongoing changes related to climate change.

Commented [JB1]: Ikke helt sikker på om jeg skjønner dette uttrykket?

1280 ~~Investigations~~Investigations of phenology are thus instrumental to understand
1281 climate change.

1282 To illustrate the principle ~~-~~and partly hypothesize patterns of geographic
1283 variability of autotrophic phenologies in ice-covered water we can use latitudinal
1284 scenarios along an imagined transect from the Barents Sea (70°N) to the North
1285 Pole (85°N) (**Fig.16**). At 70°N in the southern Barents Sea there is some indirect
1286 light (Civil Twilight) in the middle of a winter day while there are two months of
1287 Midnight sun and several months characterized by steeply increasing and
1288 decreasing daylight. At this latitude, rates of increase and decrease of daylight are
1289 about 12 minutes a day. ~~As there is~~With only open water in this region, we and we
1290 may find a spring bloom as early as April/May. However, the lack of ice-melt may
1291 result in weak stratification, hence the buildup of the bloom may be slower but the
1292 bloom may last longer. ~~Towards the beginning of the Polar Twilight Night a~~
1293 minor bloom may be possible in late August (e.g. Oziel et al., 2017). At 75°N and
1294 the Civil Polar Night zone we experience darkness for almost 3 months and ice
1295 cover between November and May, with an increase and decrease of daylight of
1296 about 16 minutes per day. Light penetration through ice/snow and an ice cover
1297 that is actively breaking up supports an ice algae bloom in April and a
1298 phytoplankton bloom in early June. Here ice returns often as late as December. At
1299 80°N and northward, the Nautical Polar Night ~~zone and northward darkness~~ lasts
1300 for 4 months and ice cover may last until the end of June. The rates of increase and
1301 decrease in daylight are about 25 minutes per day. An ice algae bloom may occur
1302 in April and May (dependent on ice thickness and snow cover) and uses available
1303 nutrients, resulting in a small phytoplankton bloom based on the leftover
1304 nutrients in early July. Sea-ice often returns in November. At 85°N the light and

Commented [JB2]: Denne sliter jeg med å forstå... kan den slettes?

1305 dark periods last for more than 5 months each and increase and decrease rates in
1306 light are about 50 minutes per day. Most of the nutrients are used up by sea ice
1307 algae through a lengthy growth period lasting from April to August, as determined
1308 by ice thickness and snow cover (Fernández-Méndez et al., 2014). Before daylight
1309 disappears, a small phytoplankton bloom may occur (see Loeng et al., 2005;
1310 Ardyna et al., 2014; Oziel et al., 2017), but one may discuss if can be entitled an
1311 autumn bloom.

1312 Climate change has resulted in a steady decline of nutrient concentrations
1313 in the AO inflow regions of the Northeastern North Atlantic (e.g. Rey et al., 2012;
1314 Hátún et al., 2017), the cause being the effect of climate change on subpolar gyres.
1315 Along the South to North gradient depicted in **Fig. 16** and despite of the increase
1316 in future radiation a decrease of autotrophic new production is likely in the central
1317 AO-, caused by increased stratification and reduced vertical mixing and nutrient
1318 supply (Ardyna et al., 2014; Randelhoff et al. 2019). With thinner ice at increasing
1319 latitudes stronger and more persistent ice algae blooms can be expected. In
1320 contrast and despite longer ice-free periods, phytoplankton blooms will decrease
1321 with increasing latitude caused by ice algae nutrient consumption. The post-
1322 bloom period with increased stratification and depressed nutrient supply will also
1323 be marked by a succession throughout summer of progressively smaller
1324 autotrophs (Li et al., 2009; Leu et al., 2015) and a prolonged period post bloom
1325 heterotrophy (Vaquer-Sunyer et al., 2012). Also, the timing of the phytoplankton
1326 bloom is progressively delayed from April in the south to early September in the
1327 north. The conceptual model in **Fig. 16** is neither intended to reflect the highly
1328 interannual dynamic nature of the Barents Sea and adjacent AO nor does it fully
1329 match the phenology of bloom cycles along the Pacific Arctic shelf-basin gradient.

1330 It merely illustrates the principle patterns that define these seasonal transitions.
1331 The principles behind **Fig. 16** are also the base for **Fig. 9A, B** (left column) which
1332 depicts today's large-scale phenology of autotrophs and their dependence on light
1333 and ice-cover across the entire SIZD.

1334 Climate change and the resulting reduction in ice cover will modify the
1335 phenology of autotrophs, but the biota cannot break out of the constraining
1336 envelope created by solar radiation and nutrient availability. For example, the
1337 bloom development at 70°N in the sector dominated by AW will move
1338 progressively northwards to 75°N and 80°N off the shelf, with phytoplankton
1339 rather than ice algae to use up the available nutrients as ice cover is reduced (**Fig.**
1340 **17**). Notably, the surface water nutrient concentrations in the Arctic basins are far
1341 lower than those of the shelves, let alone those in the advected PW and AW (e.g.
1342 Tremblay et al., 2015). Modelling projects that the nutrient concentration in the
1343 central AO surface water will in fact continuously decline during this century
1344 (Slagstad et al., 2015). Larger blooms are not expected from either ice algae or
1345 phytoplankton are expected in the basins because of the limited and decreasing
1346 availability of nutrients (Slagstad et al., 2015). This is in contrast to the Eurasian
1347 shelves where pelagic primary production increases as a function of increased
1348 open water area, i.e. higher input of solar radiation (Arrigo and van Dijken, 2015;
1349 Slagstad et al., 2015) though still ultimately controlled by nutrient availability
1350 (Tremblay et al., 2015). Increased Atlantification (Polyakov et al., 2018;
1351 Randelhoff et al., 2018) and changes in vertical mixing (Randelhoff and Guthrie,
1352 2016; Randelhoff et al., 2019) may further influence and increase the future
1353 primary production on the shelves and the shelf break.

1354 In the Barents Sea today's bloom development in May-June at 70°N (**Fig.**
1355 **17 F, left**) may be in the future be encountered at 73°N (**Fig. 17 F, right**).
1356 Similarly, the bloom scenario that today is encountered at 73°N (**Fig. 17 E, left**)
1357 may in the future be observed at 75°N (**Fig. 17 E, right**). Similarly to the northward
1358 expansion of boreal species into the AO region the MIZ bloom may shift
1359 northwards, at the expense of more Arctic phenologies. This development has
1360 already resulted in the large-scale reduction of the multi year sea ice. **Fig. 17**
1361 depicts a similar process than the borealisation, i.e. the northwards displacement
1362 of both sub-Arctic water masses and boreal species. This development from today
1363 into the future can also be studied for the large-scale phenology of autotrophs and
1364 their dependence on light and ice-cover across the entire SIZD (**Fig. 9A, B** (left
1365 column: today; right column: future).

1366 **Fig. 17 E** and **F** illustrate the assumed course of primary production in a
1367 scenario of continuously open water, characterized in the central and southern
1368 Barents Sea that has no major freshwater source and a weak and slow progress in
1369 surface water stratification during summer. In regions where freshwater
1370 stratification is prominent such scenarios will not be encountered. The variable
1371 production in June (**Fig. 17E**, 70°N) arises through variations in nutrient supply
1372 caused by vertical mixing events triggered by the passage of low-pressure systems
1373 after the end of the spring bloom. **Fig. 17 F** at 70°N projects future primary
1374 production after Arctic warming has resulted in increasing thermal stratification
1375 and decreased primary production, unless occurring mostly as subsurface blooms
1376 (Mayot et al., 2018). However, also late summer surface (Ardyna et al., 2014; Oziel
1377 et al. 2017) and subsurface blooms (Horvath et al., 2017) have recently been

1378 detected. These phenomena add new features to the phenology of autotrophs in
1379 the ice-free AO.

1380 Previous and future scenarios in the phenology of the marginal ice zone are
1381 presented in **Fig. 18 A, B**, respectively. Progressing from present-day to future
1382 climate and ice conditions the principle seasonality will persist, but the timing will
1383 change. Climate warming will also result in a widening of the seasonal ice zone
1384 (**Fig. 9**) and a wider time window for primary production (**Fig. 18**). With greater
1385 incident light availability in the euphotic zone and earlier stratification a decrease
1386 in the amplitude of the spring bloom may be encountered. Without an ice edge at
1387 its current position the bloom will become less distinct and surface waters will
1388 have decreased food concentrations for grazers that have tuned their life cycle to
1389 the initiation of this bloom (Daase et al., 2013). The decreased spring bloom
1390 strength may be balanced by longer annual food availability and more detritus
1391 that would favor zooplankton species that can sustain themselves on less food and
1392 smaller food particles, i.e. smaller species (Svensen et al., 2018). The time window
1393 in which the system is dominated by heterotrophs will increase. This scenario
1394 assumes that nutrient supply will be unchanged.

1395 The phenology of zooplankton has to face the seasonality changes in
1396 autotroph production, in particular the timing, density and time development of
1397 the spring bloom. The life cycles of common zooplankton organisms in the Arctic
1398 imply that these need more than one year for their development in contrast to
1399 boreal congeners. Biomass-dominant copepods in particular start their
1400 development during the productive season, but in the AO lower temperatures and
1401 reduced metabolism along with low food availability (in the central AO) do not
1402 permit them to complete their life cycles within the first productive season. Thus

1403 they need to overwinter to continue their development. For many species the
1404 winter at high northern latitudes implies dormancy, for others it implies
1405 reproduction and/or preparation for a new productive season, including gonad
1406 maturation and producing eggs prior to the onset of algal growth (Conover, 1988;
1407 Kosobokova, 1999; Hirche and Kosobokova, 2011; Hirche, 2013; Kosobokova and
1408 Hirche, 2016; Daase et al., 2013). For several marine mammals, the winter implies
1409 migration out of the Arctic. For lipid rich zooplankton species, for Arctic fish, and
1410 for some other invertebrates late summer and autumn are not characterized by
1411 hibernation, but by development to juvenile life stages that accumulate energy
1412 reserves, or by maturation into lipid-rich adults and preparation for
1413 overwintering at depth and in darkness (Falk-Petersen et al., 2013; Berge et al.,
1414 2015 a, b; Daase et al., 2018). In late winter and early spring, still in darkness, some
1415 commence reproduction relying on internal reserves (e.g. the key arctic oceanic
1416 copepod *Calanus hyperboreus*) or detrital food (e.g. the brackish water copepods
1417 *Drepanopus bungei*, *Pseudocalanus major*) and their early larvae develop (Hirche,
1418 2013; Kosobokova and Hirche, 2016; Nahrgang et al., 2016; Darnis et al., 2017).
1419 The spring period of increasing light and the productive and full day light season
1420 is then utilized by their early offspring (new generation) for development into
1421 juvenile overwintering stages, while the overwintered late juveniles born a year
1422 ago (old generation) develop to adulthood. Towards the end of the productive
1423 season these two generations prepare to overwinter again (e.g. Fig. 18A,
1424 horizontal bars). Thus, the winter period is an important segment of the ecology
1425 of zooplankton grazers and fish in the AO which connects the preparation for
1426 overwintering and active development during spring and summer. Life cycle
1427 studies in the AO do thus demand longer time cycles than a year, in particular for

1428 a multitude of Arctic biota that are much longer-lived than boreal and tropical
1429 counterparts. Therefore, conceptual models of seasonality need to cover a
1430 minimum 18 months, such as in Fig. 18. Also, many organisms may exceed
1431 longevities of decades or centuries (Bluhm et al., 1998; Ravelo et al., 2017). The
1432 phenology timeline in the AO is thus multiannual or longer.

1433

1434 5.3 Cryo-pelagic-benthic coupling

1435 Processes of cryo-pelagic-benthic coupling (CPBC) include those that connect
1436 biota in sea ice, water column and benthic habitats (Grebmeier and Barry, 1991;
1437 Carroll and Carroll, 2003; Werner, 2006). Essential processes involved in CPBC
1438 are primary production of both sea ice algae and phytoplankton, vertical export of
1439 biogenic ice-derived and pelagic matter and regeneration of deposited matter at
1440 the seafloor. Also entailed are the phenology and biological life cycles of a wide
1441 range of organism entangled in involved in CPBC which all are highly variable on
1442 both spatial and interannual scales (Wassmann et al., 2004; Grebmeier et al., 2012;
1443 Fernández-Méndez et al., 2014). The domain of CPBC action covers the entire AO
1444 where it regulates the loss of biogenic matter from sea ice and the upper layers,
1445 the retention of nutrients and biogenic matter in the water column, the supply of
1446 food to the benthos, and the regeneration of nutrients and matter at the seafloor.
1447 In particular, the CPBC connects the SIZD with the sediments of the extensive
1448 shelves, comprises thus major parts of the AO (**Figs. 8A, 9**). CPBC depends upon
1449 the new production, the accumulation and biomass of both sea ice algae and
1450 phytoplankton (Gosselin et al., 1997; Gradinger, 2009; Lalande et al., 2014),
1451 melting of sea ice from below (detachment of particulate matter; Tedesco et al.,
1452 2019), the aggregation potential of suspended matter (Engel et al., 2004; Rapp et

1453 al., 2018), grazing (Wexels Riser et al., 2002; Tamelander et al., 2012), vertical flux
1454 attenuation in the the twilight zone (Wassmann et al., 2003; Reigstad et al. 2008;
1455 Buesseler and Boyd, 2009), processes in the benthic boundary layer and benthic
1456 suspension feeding (Thomsen, 2002; Stein et al., 2004). As a consequence of this
1457 multitude of processes, the activity of CPBC is not evenly distributed, but first of
1458 all depth-dependent (**Fig. 19**).

1459 A continuum of physical and chemical forcing (ice- and snow-cover,
1460 horizontal advection, stratification/vertical mixing, nutrients, light) shapes the
1461 basic conditions for primary production, ice-attached biogenic and suspended
1462 matter accumulation in the upper layers (**Fig. 19**). This physical-chemical-
1463 biological continuum creates the base for new production and the potential
1464 standing stock of autotrophs that can be grazed, recycled, and exported vertically
1465 (advective off-set is not considered in this depiction). Because of the orders of
1466 magnitude differences between the horizontal velocity of water and the sinking
1467 speed of particulate matter vertical flux of individual particles is basically tilted to
1468 the horizontal plane. Regionally, and in particular on the shallowest AO shelves,
1469 the distance between the origin of biogenic matter and its deposition is small. In
1470 deeper regions the horizontal distance for the smaller sinking particles may be
1471 hundreds of km and advection will thus play a key role.

1472 The maximum of the vertical organic matter flux is particularly prominent
1473 in the lower euphotic zone and the uppermost section of the twilight zone
1474 (Wassmann et al., 2003; Buesseler et al., 2007). Below the euphotic zone aggregate
1475 formation and dissolution of particulate organic matter become important
1476 constraints for vertical export (Jackson and Burd, 1998; Stemmann et al., 2012)
1477 and top-down regulation through various categories of grazing zooplankton

1478 removes biomass, destroys aggregates and produces fecal pellets (Wexels Riser et
1479 al. 2007). Along the physical-chemical-biological continuum, these processes are
1480 assumed to take the lead role for the fate of suspended and sinking biogenic
1481 matter. Food-deprived communities of heterotrophs are common in the AO
1482 because of the significant influx of long-lived zooplankton (Olli et al. 2007;
1483 Wassmann et al., 2015, 2019). Zooplankton orient themselves towards the source
1484 of food, i.e. they move upwards towards the ice-algae or the base of the euphotic
1485 zone with its associated subsurface chlorophyll maximum (**Fig. 19**). Thus, a great
1486 amount of zooplankton biomass is usually encountered just below the euphotic
1487 zone (e.g. Olli et al., 2007), regulating partly the vertical export and contributing
1488 significantly to the strength of the retention filter in the upper aphotic zone
1489 (Wexels Riser et al., 2007).

1490 The strength of grazing, the types of grazers and the grazing efficiency
1491 determine the mode by which suspended biogenic matter is consumed, thus
1492 effecting both a slowdown (sinking particles removed) and acceleration (fecal
1493 pellets produced) of vertical export (e.g. Wassmann et al., 2003). However, fecal
1494 pellets still have some nutritious value for a number of grazers and through
1495 processes such as coprophagy and particular coprorhexy most of the rapidly
1496 sinking particles are retained in the upper layers in most areas (e.g. Wexels Riser
1497 et al., 2002; Iversen and Poulsen, 2007; Svensen et al., 2012). Sloppy feeding and
1498 microbial remineralization contribute also the retention of sinking organic matter.
1499 As a result, 20-70 % of the export production leaving the euphotic zone can be
1500 recaptured and retained in the upper 100 m (for the most in the 20-60 m depth
1501 interval) in the case of the Barents Sea (e.g. Olli et al., 2002). Hence export
1502 production is far higher on shallower (mostly <50 m) AO shelves, such as the

1503 northern Bering and Chukchi and Laptev Seas (Lalande et al., 2007, 2009a). The
1504 physical-chemical-biological continuum forces the primary production and new
1505 production in the upper layers towards greater production (**Fig. 19**; bottom-up
1506 regulation, compare scenario I with II). At shallow depths (**Fig. 19** panel **A**), CPBC
1507 is highly variable, but the supply of biogenic matter is much stronger than at
1508 greater depths. With increasing depth, the physical-chemical-biological
1509 continuum (top-down regulation through grazing, mineralization and
1510 fragmentation) increasingly takes over, forcing vertical export into the opposite
1511 direction (**Fig. 19**). For example, the benthic biomass in the highly productive,
1512 shallow northern Bering Sea and southern Chukchi Sea (**Fig. 19A**, Grebmeier et al.
1513 2015) is far higher than on deeper shelves (**Fig. 19C**; Bluhm et al. 2011b). As a
1514 consequence, the connection between new production and vertical export can be
1515 explained in a curvilinear manner (Wassmann et al., 2003) quantified as a vertical
1516 flux attenuation efficiency (Olli, 2015). In addition, planktonic heterotrophs also
1517 impose a depth-varying grazing pressure on export production by collectively
1518 developing a retention filter (Wexels Riser et al., 2001) whose vertical extent and
1519 degradation efficiency determines the vertical flux attenuation and the shape of
1520 the vertical export profiles. The potential vertical export can be low or high when
1521 the upper water column is stratified (**Fig. 19**, scenario I and II, respectively). It
1522 depends first of all upon the rate of new production and the abundance of
1523 detached ice or planktonic biogenic matter (e.g. Assmy et al., 2017; Wollenburg et
1524 al., 2018). When vertical mixing is prominent the export of suspended biogenic
1525 matter is lower (scenario III). A strong cryo-pelagic coupling and the strength of
1526 new production will move the vertical export of biogenic matter to the right
1527 (scenario I turns into scenario II, **Fig. 19**).

1528 Grazing in the pelagic decreases the amount of vertical export and can
1529 result in strong vertical flux attenuation (Olli, 2015), which varies with the
1530 intensity and the biomass of heterotrophs and their vertical distribution and
1531 water depth (Wexels Riser et al., 2002; Svensen et al. 2012). Efficient retention
1532 filters may exist, in particular when new production is strong and the suspended
1533 biomass of large autotrophs, such as diatoms, prevail, weakening and determining
1534 pelagic-benthic coupling (Wassmann et al. 2003, Wexels Riser et al., 2007). How
1535 strong CPBC is depends not only on new production and stratification, but to a
1536 high degree on water depth and the intensity of the retention filter (Wexels Riser
1537 et al., 2007; Wiedmann et al. 2014). Grazing does not prevent that living
1538 autotrophs such as diatoms and *Phaeocystis* reach deeper water and the sediment
1539 (Wassmann et al., 1990; Boetius et al. 2013; Augustí et al., 2019). At shallow
1540 depths CPBC is highly variable, but the lack of strong retention makes it much
1541 stronger than in regions of greater depths (**Fig. 19A**). As a result, the benthic
1542 biomass in the highly productive, shallow northern Bering Sea and southern
1543 Chuckie Sea is far higher than on deeper shelves (Carroll et al., 2008; Grebmeier
1544 et al., 2015). Tightly linked to the SIZD, the CPBC is mainly a surface-driven
1545 process in areas wherein the majority of the exported biogenic matter, though
1546 depth-dependent, is retained in the upper water column. On shallow shelves such
1547 as the Pacific inflow shelves, however, a much larger part of the production (can
1548 reach over 50%) settles to the seafloor either ungrazed or as fecal pellets (Lalande
1549 et al., 2007, 2009b), supporting high benthic biomass and substantial nutrient
1550 recycling (Devol et al., 1997; Cooper et al., 2009; Hardison et al., 2017).
1551 Continuously open water at the periphery of the AO (at present for the most on
1552 the North Atlantic side of the AO but permanent open water scenarios will become

1553 more prominent due to climate change) provides possibilities for primary
1554 production between both equinoxes. Sea ice cover may become a Polar Night
1555 phenomenon. Mixing in these open water results in a delay in the spring bloom
1556 which usually does not occur before mid-April. This timing also corresponds to
1557 when ice algae start to grow in those sections of the SIZD where snow cover allows
1558 light penetration. In these regions a strong CPBC can be expected already in April
1559 (**Fig. 18**). Later in the season (after August), primary production is low, mainly
1560 due to nutrient limitation (with indications that increasingly minor autumn
1561 blooms take place Oziel et al., 2017). For the rest of the productive season both ice
1562 algae and phytoplankton will support primary production, forced by light,
1563 stratification and available nutrients. In regions of the AO that are heavily covered
1564 by sea ice the spring bloom will take place later, associated with a strong CPBC in
1565 May/June/July (**Fig. 18**). If the increasing observations of autumn blooms
1566 (Ardyna et al., 2014; Oziel et al., 2017) supports increased CPBC remains to be
1567 seen. It also results in the the principle vertical flux attenuation changes (see
1568 scenario III in Fig. 19A-C).

1569 The timing of the cryo-pelagic-benthic coupling is highly variable in the
1570 AO. The vertical export is usually high with the timing of the spring bloom, in
1571 particular when the bloom is tense, e.g. in the MIZ (**Fig. 18A**). After the export of
1572 fresh material in connection with the spring bloom (Wassmann et al., 1990;
1573 Boetius et al. 2013; Agustí et al., 2019), degraded matter and fecal pellets take over
1574 while during post bloom and autumn scenarios detritus dominates (**Fig. 18A**).
1575 The timing of vertical flux is strongly regulated by the withdrawal of the ice edge,
1576 stratification and the availability of light. Increased vertical export of biogenic
1577 matter of variable quality can thus take place throughout the productive season in

1578 the AO, but not before April and no later than September (**Fig. 18**). In the near
1579 future today's scenario of the SIZD illustrated in **Fig. 18A** may change into longer
1580 periods with ice-free conditions (**Fig. 18B**). That will result in that vertical export
1581 of biogenic matter starts earlier, the dampened time development of autotrophs
1582 will also result in a decreased amplitude in vertical export (**Fig. 18B**). The quality
1583 food reaching the deeper layers and the sediment will decrease and the supply
1584 will be more even.

1585 In summary, the intensity of CPBC is a complex relationship between
1586 production, vertical mixing, advective inputs, water depth, the intensity of the
1587 retention filter, and benthic remineralization (Lalande et al., 2014; Wiedmann et
1588 al., 2014; Grebmeier et al., 2015). Often new production or biogenic matter
1589 accumulation are used as proxies for benthic biomass and production. Neither
1590 new production nor pelagic accumulation of biogenic matter solely determine the
1591 CPBC. Nor does the supply of biogenic matter to the sediment alone indicate new
1592 production and pelagic accumulation of biogenic matter. The connection between
1593 primary and benthic production in the AO cannot be established and modelled
1594 without an detailed understanding of the complexity of the CPBC.

1595
1596

1597 **6. Food web models**

1598 Conceptual approaches that aim to investigate organisms and their role in
1599 biogeochemical cycling, biodiversity and ecosystem dynamics in the Arctic
1600 mediterranean must match the appropriate geography, biophysical and
1601 biogeochemical environment, seasonality and light regime, and functionality of
1602 contiguous domains (described in sections 2 to 5). Within these frameworks,
1603 organisms interact in several ways with the most prominent interaction across
1604 trophic levels. Here we follow the definition of Layman et al. (2015) of a food web
1605 as “a network of consumer-resource interactions among a group of organisms,
1606 populations, or aggregate trophic units”; an example applicable to the AO is shown
1607 in **Fig. 20**. Climate change and the increasing human use of the Arctic now demand
1608 holistic evaluations of the interdependencies of species and their interlinked
1609 response to a change or perturbation of their ecosystem. In this section we apply
1610 findings from existing regional studies to the typologies proposed in preceding
1611 sections to formulate unifying, pan-Arctic conceptualizations based on three
1612 critical questions: (1) Who eats whom, (2) how does energy flow across trophic
1613 levels, and (3) which carbon sources are most important to a given taxon or
1614 region?

1615

1616 **6.1 Food Web Topology: Who eats whom?**

1617 The ‘who eats whom’ question is conceptually depicted through images of species
1618 or trophic levels (i.e. species with shared prey and predators) with arrows
1619 connecting each prey to their predator(s) (**Fig. 20**). The underlying, species-
1620 specific trophic information is traditionally derived from stomach contents
1621 studies and stable isotope studies, and where feasible, complemented by

1622 experimental work on predator-prey relationships. Diets are now generally well-
1623 documented for common, biomass-dominant Arctic species, but poorly for
1624 remaining species (**Fig. 20**, Table 2). We summarize the dominant trophic
1625 connections jointly for – simplified - shallow shelves, the Pacific inflow shelf and
1626 the basins that currently have no large-scale commercial fisheries (**Fig. 20A**), and
1627 separately for deeper shelves and those areas – the Atlantic inflow and parts of
1628 the outflow shelves - that have substantial commercial fisheries, albeit primarily
1629 on boreal species (Christiansen, 2017) (**Fig. 20B**). Moving from the base of the
1630 food web to top predators, bacteria take up DOC and support heterotrophic and
1631 mixotrophic nanoflagellates, which in turn are prey for protists (Seuthe et al.,
1632 2018; **Fig. 20A**, microbial inset (2)). These, in addition to larger, phototrophic cells
1633 such as diatoms, are then available for grazing multi-cellular zooplankton. *Calanus*
1634 spp. (e.g. *C. glacialis* and *C. hyperboreus* in Arctic water masses, advected *C.*
1635 *finmarchicus* in Atlantic water), krill and other zooplankton species capitalize on
1636 the spring bloom and provide food for zooplankton such as
1637 omnivorous/predatory copepods, arrow worms, jellyfishes, pelagic amphipods
1638 and pelagic snails *Clione* as well as higher trophic level taxa including various fish,
1639 seabirds, seals and whales (**Fig. 20**). Examples for dominant planktivorous at
1640 higher trophic levels include the little Auk, auklets and shearwaters, as well as
1641 bowhead whales for Arctic species (**Fig. 20A**), and minke and fin whales as boreal
1642 species (**Fig. 20B**). During ice-cover, primarily herbivorous sympagic meiofauna
1643 and herbivorous, omnivorous and carnivorous amphipods at the under-ice
1644 surface make ice-derived carbon available to young polar cod, the dominant truly
1645 Arctic fish. Adult polar cod feed primarily on copepods and other crustaceans both

1646 in the water column and near bottom and provide prey for many seabird and
1647 mammals, in particular in the areas summarized in **Fig. 20A**.

1648 Vertical carbon flux fuels detritivorous zooplankton and the microbial loop
1649 enriches detritus pools at the seabed, supporting a variety of interstitial
1650 meiofauna (**Fig. 20A**, bottom inset), surface and sub-surface deposit-feeding
1651 invertebrates such as polychaetes and other worms, bivalves, and larger epifauna.
1652 Near-bottom currents also supply a stream of living or resuspended detritus
1653 particles to benthic suspension feeders, in particular in high flow areas or on
1654 elevations such as drop stones. In combination with the deposit-feeders, this
1655 detritus serves as prey for both invertebrate predators such as snails, sea stars,
1656 shrimps, crabs and demersal fishes as well as for benthic-feeding mammals (such
1657 as gray whales, bearded seals and walrus) and diving seabirds such as eider ducks
1658 (Planque et al., 2014; Whitehouse et al., 2014). The other small-bodied true Arctic
1659 fishes such as sculpins, and eelpouts feed primarily demersally (**Fig. 20A**). Large-
1660 bodied predators such as Atlantic cod and Greenland halibut are found in the
1661 waters of Atlantic inflow and parts of the outflow shelves (Christiansen, 2017; **Fig.**
1662 **20B**), while the cold pool in the Bering Sea has so far largely kept these large
1663 predators out of the Pacific inflow shelf (but see changes in 2018, Cornwall, 2019).
1664 The spatial distribution of key players of these food webs, and with its spatial
1665 characteristics of trophic connections, has experienced shifts termed
1666 'borealization' in recent decades (e.g., Fossheim et al., 2015; Frainer et al., 2018;
1667 Alabia et al., 2018; Ellingsen et al., 2020).

1668 The conceptualization of Arctic food webs has advanced from simple
1669 predator-prey interactions and few-species chains towards highly connected
1670 webs. A formal analysis of several extensive Arctic food webs has shown that it

1671 has an unusually high number of predator species compared to basal species (de
1672 Santana et al., 2013). So instead of being represented by the classical pyramid
1673 shape, the Arctic food web is characterized rather by an inverted pyramid which
1674 is more typical of open ocean food webs (de Santana et al., 2013). However, this
1675 makes the Arctic food web more vulnerable to trophic cascade effects given the
1676 loss of a key predator species (de Santana et al., 2013). And given that many of the
1677 key predator species rely on sea ice as a habitat (Wassmann et al., 2011), it is not
1678 far-fetched to consider the fragility of several key predator species in the Arctic
1679 food web and the cascade effects this may have on the whole food web.
1680 Furthermore, the underlying studies acknowledge that: the microbial loop
1681 appears to be as active in the Arctic as elsewhere (Seuthe et al., 2018); most
1682 species eat multiple other species in the AO (Planque et al., 2014); some species
1683 can seasonally or ontogenetically shift diets (Stasko et al., 2018); great trophic
1684 diversity is recognized within most higher taxa (e.g. Jumars et al., 2015);
1685 substantial regional diet variation exists (Bluhm and Gradinger, 2008); and finally
1686 Arctic food webs are not always short, opposing the previous paradigm (Iken et
1687 al., 2005, 2010). Yet, conceptual organismal food webs obviously still need to
1688 simplify trophic and taxonomic diversity in some fashion (**Fig. 20**), depending on
1689 a given research question, area or contiguous domain.

1690 At least four features are characteristic of the generalized Arctic predator-
1691 prey based food web concept: first, sea ice provides an additional – compared to
1692 non-polar regions - habitat and related food web for > 1000 taxa of single- and
1693 multi-cellular pro- and eukaryotes. These taxa are partly contained in the size-
1694 structured brine channel sea ice matrix (**Fig. 20A**, top inset (1)) and hence not as
1695 freely available as pelagic resources, and in addition a (now) mostly seasonal

1696 resource (Bluhm et al., 2017). Second, characteristic of biomass-dominant Arctic
1697 (but little less so of advected boreal)) zooplankton, polar cod and endemic marine
1698 mammals is their very high lipid (i.e. energy) content (Lee et al., 2006) (**Fig. 20 A**,
1699 orange color). This food web of fat is the survival strategy for many in a cold and
1700 highly seasonal habitat where metabolic rates are lower, and life cycles take
1701 longer to complete than in the boreal and sub-Arctic habitats. Third, a long dark
1702 season with low levels of primary production coincides with the habitat ranges of
1703 organisms: either migrating out of the Arctic food web for part of the year (e.g.
1704 some marine mammals), reducing or completely ceasing food intake (e.g. as cysts
1705 or through diapause), or adopting a mixotrophic or otherwise plastic feeding
1706 strategy resulting in overall higher than previously assumed polar night activity
1707 (Hirche and Kosobokova, 2011; Berge et al., 2015b; Kosobokova and Hirche,
1708 2016). Fourth, humans in the Arctic food web are a combination of subsistence-
1709 harvesting indigenous peoples whose cultures often focus around marine
1710 mammal and migratory nearshore fish harvests (Suprenand et al., 2018, **Fig. 20A**),
1711 and commercial operators currently at the Atlantic-Arctic perimeter focusing on
1712 boreal fishes that have expanded their occurrence into Arctic waters (**Fig. 20B**).
1713 Characteristics of the Arctic regionality and contiguous domains drive differences
1714 in regional food webs through environmental forcing on biotic communities and
1715 their trophic interactions.

1716

1717 6.2 Energy flow and connectance in Arctic food webs

1718 The Arctic food web concept has been expanded to depict holistic food web
1719 structural properties. One important metric describes the number and strength of
1720 interactions between compartments of the food web through the flow of energy

1721 between compartments and across trophic levels. Energy flows have been
1722 estimated based on 'who eats who and by how much-matrices' in combination
1723 with biomass, production, consumption and trophic efficiency rates through
1724 either energy mass balance models (e.g. Christensen and Walters, 2004) or
1725 ecological network analysis (e.g. Dunne et al., 2002) (**Fig. 21**). While Arctic and
1726 high latitude food webs in general were initially thought to be short and simple
1727 with high trophic efficiency, longer food webs and complex structure are now
1728 recognized and enter conceptual models of Arctic foods webs (e.g. Kortsch et al.,
1729 2019; Dunton et al., 2012). The linkage of the now-established microbial loop to
1730 the refined 'classical' food web shows that 4.5-6 trophic levels are characteristic
1731 of Arctic food webs (**Figs. 20, 21**, Table 2). Short Arctic food webs are now
1732 recognized as mostly a myth, though they exist under certain conditions and in
1733 certain places. Estimates of the number of trophic levels derived from stomach
1734 contents largely agree with those estimated from trophic markers, except detrital
1735 consumers of highly reworked material appear at higher trophic levels when
1736 estimated from $\delta^{15}\text{N}$ values (e.g. Iken et al., 2010).

1737 Trophic pathway analysis has documented prominent differences among
1738 Arctic regions, among Arctic and Antarctic regions, and among Arctic and non-
1739 polar regions (de Santana et al., 2013; Whitehouse et al., 2014; Kortsch et al.,
1740 2019). Differences in Arctic food webs found or confirmed by energy flow models
1741 include high system production and throughput via benthic compartments on the
1742 shallow, productive, and tightly coupled Pacific inflow shelf versus higher
1743 retention in the (deeper) pelagic system on the Atlantic inflow shelf (Whitehouse
1744 et al., 2014). Network analysis in boreal versus arctic (Barents Sea case) food webs
1745 revealed lower connectance (number of links per trophic species) and higher

1746 modularity (compartmentalization) through more specialized feeding in Arctic
1747 compared to boreal and sub-Arctic food webs. This is driven by the few biomass
1748 dominant omnivorous generalists that are major components of these highly
1749 connected the food web (Kortsch et al., 2015, 2019), a phenomenon recognized
1750 globally (Bartley et al., 2019). Such approaches should be applied to other regions
1751 of the Arctic before they can fully be generalized our pan-Arctic framework.

1752

1753 6.3 Carbon sources of the Arctic food web

1754 A suite of carbon sources drives marine food webs of the AO on a pan-Arctic level
1755 thought to be primarily fueled by highly seasonal phytoplankton blooms (Oziel et
1756 al., 2017), while in coastal regions additional sources come into play (Rysgaard
1757 and Gissel Nielsen, 2006). These blooms in turn are largely fueled by advective
1758 inputs in inflow shelves, and less so in other Arctic areas (Wassmann et al., 2015).
1759 Consequently, phytoplankton is the major carbon end member in Arctic inflow
1760 shelves, mediated through a combination of advected and *in situ* production
1761 (Wassmann et al., 2015; Vernet et al., 2019). Increasingly, additional particulate
1762 carbon sources are recognized as regionally and/or seasonally contributing
1763 moderate to large proportions to total diets, especially outside the inflow shelves
1764 such as ice-algae across the basins, terrestrial carbon in the RCD, and macroalgal
1765 carbon and possibly methane seeps on the shelves (**Fig. 22**). These findings are
1766 largely based on trophic markers such as marker fatty acids biomarkers, bulk
1767 carbon and compound specific stable isotopes, the isoprenoid lipid markers such
1768 as IP₂₅, and lignin phenols (Goñi et al., 2013; Kohlbach et al., 2016) (**Fig. 22**) and
1769 mixing models estimating carbon source partitioning.

1770 These models suggest ice algae produced in the SIZD may in certain time
1771 windows and areas contribute noteworthy or even larger proportions of carbon
1772 than phytoplankton to key Arctic organisms across trophic levels (**Fig. 22**).
1773 Biomass-dominant Arctic copepods, pelagic amphipods and krill, for example,
1774 were estimated to derive 20->90% of their carbon from ice algal organic matter
1775 in the central AO (Kohlbach et al., 2016) and in the Pacific inflow shelf (Wang et
1776 al., 2015). Ice-derived carbon supplied 30-90% of carbon to young polar (Arctic)
1777 cod, *Boreogadus saida*, in the SIZD of the central AO (Kohlbach et al., 2017) but as
1778 little as <5% in open-water interior shelf locations (Graham et al., 2014). At yet
1779 higher trophic levels, high ice-derived carbon contributions were also estimated
1780 for various seals in the Pacific inflow shelves in cold years (Wang et al., 2016).
1781 Furthermore, microphytobenthos may play an appreciable role as a carbon source
1782 in nearshore shallow shelves (McTigue et al., 2015) and also contribute to the
1783 microbial food web (Holding et al., 2017).

1784 The role of terrestrial carbon – once thought to be unusable for marine food
1785 webs – has attracted growing attention and is now recognized as a carbon subsidy
1786 for the Arctic marine system. Conceptual models of the Arctic hydrological cycle
1787 (Vörösmarty et al., 2000) and of carbon pathways (ACIA, 2004) show this material
1788 to primarily enter from rivers that drain ponds and lakes, (thawing) permafrost,
1789 as well as glacial melt, all sources thought to increase under scenarios of climate
1790 warming (McClelland et al., 2004; Agustí et al., 2010; Carmack et al., 2016). Tracers
1791 such as trophic and lignin markers suggest terrestrial carbon covers vast areas of
1792 nearshore and shelf areas in interior shelves, slopes, and also parts of the deep
1793 basins, while it is less prominent far away from sedimentary shores and large
1794 rivers, such as in parts of the Canadian Arctic Archipelago and on the inflow

1795 shelves (Iken et al., 2010; Goñi et al., 2013). Although terrestrial carbon must
1796 necessarily undergo bacterial processing before becoming usable for marine
1797 consumers, it may contribute substantially to diets of coastal fish and subsistence-
1798 harvested whales in interior shelf (Beaufort) lagoons (Harris et al., 2018) and
1799 slope biota (Bell et al., 2016).

1800 Along Arctic rocky shores and in fjords of primarily outflow shelves but
1801 also other arctic island groups, macroalgae provide an inter- to subtidal carbon
1802 belt that adds to the carbon source diversity and amount. Certain benthic taxa
1803 were estimated to receive over half of their carbon from macroalgal sources even
1804 at depths of several hundred meters in a fjord (Renaud et al., 2015). Given the
1805 recent increase in macroalgal biomass along Arctic rocky shores related to ice
1806 thinning and declining extent and duration, an increasing role of macroalgal
1807 carbon is envisioned for Arctic food webs (Krause-Jensen and Duarte, 2014).

1808 Methane occurs in substantial amounts in arctic shelf sediments and water
1809 – in addition to massive stores on land (Shakova et al., 2010, 2014; Lorenson et al.,
1810 2016). Though it is open at this point whether the contribution of methane via
1811 chemosynthesis is a substantial source to Arctic food web. Locally, however,
1812 methane-derived carbon enters consumers as documented in Barents Sea cold
1813 seeps (Åström et al., 2016; Sen et al., 2018).

1814 In summary, the proportional roles of different carbon sources that fuel
1815 Arctic food webs as well as the taxa involved in these food webs are regionally
1816 variable, strongly tied to the regionality of the Arctic, and currently changing (**Fig.**
1817 **22**). Observed changes suggest that boreal taxa moving into warming seas may in
1818 the future play larger roles in the food webs than previously and change food web
1819 topology, and terrestrial and macroalgal carbon contributions and/or amounts

1820 may be increasing. And something about conceptual modelling? What role will
1821 food web models play in conceptual model development and application?
1822

1823 **7. Complexity and nesting of conceptual models: examples combining**
1824 **advection and phenology**

1825 We selected the pan-Arctic as our focal scale, and then examined the key regional
1826 domains of that system and the functional mechanisms that connect these
1827 domains. The same approach can be applied - in a nested, descending scale - to
1828 specific regions and contiguous domains.

1829 Moore et al. (2018a) selected the Pacific-Arctic domain as their focal scale,
1830 and then examined how phenology affects three contiguous domains within that
1831 Pacific-Arctic domain (the seasonal ice zone, the shelf break-slope and the riverine
1832 coastal domain), as defined earlier in Carmack and Wassmann (2006), Bluhm et
1833 al. (2015) and Carmack et al. (2015). In doing so, they bring additional detail into
1834 a nested model approach. At the pan-Arctic scale, for example, we here combined
1835 Pacific inflows into one water mass, which we have called Pacific-origin water
1836 (PW), whereas Moore et al. (2018a) recognize that the PW is further comprised of
1837 three water masses that are assembled over the Bering/Chukchi shelf: Alaska
1838 Coastal Water, Bering Shelf Water and Anadyr Water. In turn, each of these water
1839 masses has distinct phenologies for the timing and extent of the spring bloom,
1840 vertical mixing of nutrients and biogeochemical attributes. Moore et al. (2018a)
1841 further recognize, at the regional scale, the phenology of each contiguous domain;
1842 e.g. the seasonal pattern of the SIZD moving north and south, the brief freshet
1843 forcing the RCD, the timing of shelf-break upwelling in relation to SIZD behavior,
1844 and the cryo-pelagic-benthic coupling that is tied to the Pacific through flow.
1845 Moore et al. (2018a) term this complex approach the 'Arctic Pulses' model and
1846 argue that the same logic can be applied to other regions of the AO.

1847 A complementary model by Grebmeier et al. (2015) expanded details of
1848 advective processes as the through flowing waters transit across the Chukchi Sea,
1849 onto the Beaufort Shelf and then into the Canada Basin. This model examined in
1850 particular the various phytoplankton, zooplankton, benthic and upper trophic
1851 biomass distributions moving into, through and out of the Chukchi Sea in
1852 association to host water masses. In another example Carmack and Melling (2011)
1853 divided the Canadian Arctic Archipelago, which we here term an outflow shelf, in
1854 five sub-regions based on freshwater supply, ice regime and water mass
1855 throughflow (Oceans North Conservation Society, World Wildlife Fund Canada,
1856 and Ducks Unlimited Canada 2018).

1857 The situation on the Eurasian shelf and slope to the central AO creates
1858 similar challenges of comprehension: several contiguous domains overlap in
1859 space and time. The advection of AW along the Eurasian shelf break of the central
1860 AO is continuous throughout the year, but the advection of zooplankton biomass
1861 is highly pulsed, with minima in spring and maxima in August north of Svalbard
1862 (Wassmann et al., 2017). During the maximum advection period of *Calanus*
1863 *finmarchicus*, these copepods are already in overwintering mode and this results
1864 in a limited grazing impact upon the rich spring bloom (maximum in June) in this
1865 region. Simultaneously the SIZ domain is retreating northwards with high speed,
1866 exposing the shelf break and upper slope domain to light and potential upwelling
1867 and shelf-basin exchange (Carmack and Chapman, 2003; Randelhoff and Guthrie,
1868 2016). Below these domains the Atlantic halocline complex is an important
1869 feature of the Eurasian basin waters, limiting the vertical supply of nutrients.
1870 Despite of the simplification that any conceptual model presents, the spatial
1871 overlapping of contiguous domains (see chapter 8 and **Fig. 24**) with distinct

1872 phenology will create a complex scenario.

1873 Another example of nesting within a regional domain is given by Michel et
1874 al. (2015). They noted that within the general classification of outflow shelves four
1875 different conditions of nutrients and stratification exist. These specific
1876 phenologies that planktonic heterotrophs, CPBC and the benthos have to cope
1877 with. The first is the condition of high initial nutrient concentrations followed by
1878 development of strong stratification, leading to the spring bloom. These
1879 conditions are observed in Barrow Strait within the eastern Canadian Arctic
1880 Archipelago and in the MIZ off East Greenland. Here new production is determined
1881 by the initial inventory since re-supply is constrained by stratification throughout
1882 the growing season. The second condition is one of low initial nutrients and strong
1883 stratification which is found in much of the western Canadian Arctic Archipelago
1884 and on the East Greenland shelf, and which results in a weak bloom and low annual
1885 productivity. The third condition is one of high nutrients and strong mixing found
1886 in areas such as the North Water Polynya and in areas of shelf break upwelling in
1887 the Beaufort Sea where high levels of new production are sustained throughout
1888 the growing season. The fourth condition is one of variable nutrient
1889 concentrations and low light that occurs where extensive ice cover and/or
1890 extremely high latitudes limit light input regardless of nutrient inventories.

1891 Taken together, the 'Arctic Pulses' model of Moore et al. (2018a), the
1892 'Advective' model of Grebmeier et al. (2015), various conceptual models of the
1893 Eurasian advective shelf regime (e.g. Wassmann et al., 2019) and the Canadian
1894 Arctic Archipelago (Michel et al., 2015) illustrate the validity of the multi-scale
1895 nested approach advocated here and serve as examples for application elsewhere.
1896 They all indicate how strongly the AO is connected to the sub-arctic Pacific and

1897 Atlantic Oceans and how powerful advection shapes the function of the entire AO
1898 (Frainer et al. 2017; Polyakov et al., 2017; Alabia et al., 2018; Ellingsen et al.,
1899 2020). Vice versa, fundamental processes in the Northern Hemisphere, first and
1900 foremost sea level rise and weather variability, are a direct consequence of climate
1901 warming in the AO region.
1902

1903 **8. Understanding and managing Arctic Ocean systems: from “framing” and**
1904 **field observations to modelling, decision making and communication**

1905 Rapid decline of sea ice coverage and surface warming propels the AO into a focal
1906 point of attention, not only that of the Arctic coastal states, but the attention of
1907 many nations of the Northern Hemisphere (IPCC, 2013; Box et al., 2019). In the
1908 forthcoming decade crucial decisions regarding oil/gas exploitation, fisheries,
1909 mining, transport and tourism have to be accomplished in the AO. For most of the
1910 AO the knowledge base for sustainable resource- and ecosystem-management is
1911 inadequate to evaluate the impact on biodiversity and ecosystem sustainability.
1912 Although research efforts have strongly increased in recent years and will in times
1913 to come [e.g. ArcticNet (<http://www.arcticnet.ulaval.ca/>), Nansen Legacy
1914 (<https://arvenetternansen.com/>), MOSAIC ([https://www.mosaic-](https://www.mosaic-expedition.org/)
1915 [expedition.org/](https://www.mosaic-expedition.org/))] the pace is not proportional with that of climate change and the
1916 knowledge demand to make well-evaluated decisions. It is thus timely to develop
1917 a strategy that provides a solid base in support of decision making that Arctic
1918 coastal nations and those interested in using the AO need to make.

1919 Studying poorly known or unknown sea regions often starts with
1920 expeditions into the unknown and broad, but uncoordinated investigations of a
1921 range of issues, such as circulation, water column structure, chemical properties,
1922 species and organism abundance. For several, so far little investigated AO regions
1923 and the expanse of today's SIZD this strategy is still applied. A few marine AO
1924 regions have been or are regularly investigated and adequately presented in the
1925 literature (e.g. the Chuckie, Beaufort and Barents Seas, the Bering Strait and the
1926 Canadian and Svalbard Archipelagos). They benefit from the strategy of recurrent
1927 and regular field observations that give rise to time series and a broader

1928 understanding of ecosystem function. Regretfully time series are rare in the AO
1929 (but see Cottier et al., 2010; Moore et al. 2018b). Sooner or later the question
1930 arises as to how the system in a particular region, let alone the entire AO, works
1931 and how processes or qualities within it can be understood in a pan-Arctic fashion.
1932 To address this next level of understanding one has to develop or assume
1933 theoretical approaches of the border, structure, function and population dynamics
1934 of the system. The selection of adequate conceptual models becomes now
1935 essential.

1936 Ecosystem investigations are an essential part of conceptual models. They
1937 could be achieved by adapting a wide range of generic theoretical approaches that
1938 are not constrained to a specific ecosystem or particular regionality (**Fig. 23**). For
1939 example, one may apply the theory of adaptive cycles (**Fig. 23B**) or apply a system
1940 stability concept (**Fig. 23B**). One may approach the system by studying its
1941 trophodynamics (**Fig. 23D**) or investigate trophic cascades (**Fig. 23E**), etc. In
1942 order to study a less known system inside the frame of a specific theory one has
1943 to define what is considered “the system”, which is a segment inside a continuity.
1944 For that, one has to apply “framing”. Framing is a key component of studying
1945 nature or other systems (Trede and Higgs, 2009) and is related to agenda-setting,
1946 the process by which problems and alternative solutions gain attention. It is an
1947 integral, initial part of conveying and processing data to develop understanding.
1948 For example, out of the many functional aspects of the AO one could “place a
1949 frame” onto the marginal or seasonal ice zone and define a seasonal ice zone
1950 system (such as the SIZD, see **Figs. 8, 9**). In particular when numerical modelling
1951 is applied framing becomes an important objective: one has to identify the model
1952 domain, transport across border, nesting inside the model domain etc. Framing is

1953 an essential aspect of our scientific endeavors and is well described by Albert
1954 Einstein's quotation that "we cannot solve our problems with the same level of
1955 thinking that created them. We have to rise above it to the next level".

1956 In order to understand systems and to study their dynamics in addition to
1957 framing conceptual models play an important role, for both scientists and
1958 managers. "Who are the essential players, how is the energy flow regulated and
1959 what are the feed-backs of the system"? are some of the essential questions to ask.
1960 A model has to be simple, but not too simple, says Einstein, but even simple models
1961 that only comprise selected elements can be too complex to grasp, in all their
1962 simplification. Conceptual models have thus to be simple, but not too simple, and
1963 the distinction between the two options depends upon the insight and capacity of
1964 the researcher, manager or decision maker. A wide range of preferentially
1965 multidisciplinary knowledge is thus indispensable. In **Fig. 24A**, we show a highly
1966 simplified conceptual model of the topography, river run-off, and currents of the
1967 AO. This depiction is probably the simplest manner to illustrate the AO that also
1968 presents salient features, without getting too simple. Despite of the
1969 oversimplification this conceptual model will be considered complex by many. In
1970 **Fig. 24B**, we show the principle distribution of 5 upper water column contiguous
1971 domains throughout the AO. Again, the level of complexity is conspicuous despite
1972 the extreme simplification in the model. Any area in the AO will thus be impacted
1973 by a range of functional and topographic features, currents and a multitude of
1974 vertically overlapping contiguous domains. However, **Fig. 24B** illustrates what
1975 every researcher has to have in mind when doing field investigations in the AO.
1976 Which are the dominating contiguous domains at the investigation spot? And how
1977 many contiguous domains will a vertical profile involve? How is the geography of

1978 the investigation site linked to various regional and biogeographical domains, for
1979 example those from the Pacific and Atlantic Oceans? Even under extreme
1980 reduction of reality several processes will take place simultaneously that connect
1981 the investigated region in space and time to AO regions and the adjacent oceans of
1982 the Northern Hemisphere. Are conceptual models presented in **Fig. 24** as simple
1983 as possible, or too simple?

1984 To communicate and understand the implications to all involved in AO
1985 science, management and decision making it is beneficial if we are able to grasp
1986 the complexity behind basic conceptual models. Conceptualization of reality is
1987 thus the essential *modus operandi* that addresses problem definition, selection of
1988 investigation programs and decisions that have to be made, let alone the
1989 indispensable communication of results to management authorities and the
1990 general public. As such, conceptual models represent much more than one of many
1991 facets of scientific investigations. They comprise a strategy to define, solve and
1992 communicate challenges, which combines routinely separated activities and skills
1993 into an “interdisciplinary” cooperation. Also, a good conceptual model should dare
1994 escape from earlier and more narrow concepts, but address the challenge in a
1995 more holistic, integrative manner.

1996 An important fact, frequently forgotten by decision-makers and managers,
1997 is that we cannot manage what we do not know. It is only possible to manage an
1998 ecosystem from which we know the basics players and ecological characteristics.
1999 Regretfully many ecosystems are being managed through assumptions and
2000 extrapolations from better known regions. The precautionary principle is often
2001 not applied, and ecosystem management can, thus, imply a high degree of risk.
2002 Sustainable ecosystem and resource management must be 1) multidisciplinary, 2)

2003 systemic and 3) knowledge based. For the inadequately investigated and poorly
2004 understood regions of the AO this creates a major challenge. How can, for example,
2005 ecosystem management of the industrial use of resources and ship traffic in the
2006 central AO be administered in a sustainable manner before sufficient knowledge
2007 of the affected system and key species has accumulated? In support of an adequate
2008 system-based understanding of Arctic marine ecosystems the tool kit for
2009 conceptual models presented here may help build investigation programs that
2010 will be adapted to progress towards improved understanding and addresses
2011 management needs. An important aspect of these endeavors is pan-Arctic science
2012 publications that inform the scientific community at large of what is known from
2013 the pan-Arctic expanse (e.g. Wassmann 2006, 2011, 2015; CAFF, 2017). Further,
2014 and with similar intensity, general publications, exhibitions and videos need to be
2015 produced to inform, educate and enlighten the general public and politicians.

2016 After many decades when research in the AO was carried out in a few shelf
2017 regions, along restricted transects, at seasonally skewed and variable times, with
2018 a limited set of scientific methods and most often in a nation's territorial waters,
2019 it has dawned on scientists that the AO is *one*, not a fractionated ocean. It is the
2020 ocean where the effects of climate warming are strongest and where despite
2021 extensive functional regionality a mediterranean nature prevails. The AO
2022 demands to be considered as a *mare nostrum*². The AO is one of the world's 5
2023 mediterranean³ seas, mostly enclosed seas that have limited exchange of water
2024 with outer oceans and with water circulation dominated by salinity and

² Mare Nostrum (our sea) was a Roman name for the Mediterranean Sea

³ Medius = middle + terra = land, earth

2025 temperature differences rather than winds (Günther, 1980; (see **Fig. 1**). The
2026 geographic nature of mediterranean seas implies that they can only be adequately
2027 managed through international cooperation by their coastal states (e.g. the Baltic
2028 Sea, the Mediterranean Sea). This is also the vision of the Arctic Council, but, so
2029 far, it has been most strongly advocated by scientists, resulting in attempts to
2030 contribute to a more adequate understanding of the AO as a whole (see the
2031 volumes edited by Wassmann, 2006, 2011 2015; Spiridinov et al., 2011; various
2032 CAFF, PAME and AMAP reports). A recent step towards a wise management of the
2033 AO is the legally binding *Agreement on Enhancing International Arctic Scientific*
2034 *Cooperation*, initiated by the Arctic Council (Showstack, 2018). It promises “to
2035 increase effectiveness and efficiency in the development of scientific knowledge
2036 about the Arctic.” The agreement focuses on facilitating access to research areas,
2037 research infrastructure and facilities, and data. Lately an *Agreement to Prevent*
2038 *Unregulated High Seas Fisheries in the Central Arctic Ocean* was signed. It prevents
2039 fisheries in the central AO, which is based, inter alia, upon cooperation in science and
2040 research and the establishment of appropriate conservation and management measures.
2041 The agreement commits the five Arctic coastal states of Norway, Russia, the United
2042 States, Canada, and Denmark/Greenland/the Faroe Islands as well as Japan, South
2043 Korea, Iceland and the EU – which also have large fishing fleets – to abstain from
2044 any future unregulated fishing in the international waters of the AO for the
2045 foreseeable future. After the scientific endeavors to look at the AO in a holistic
2046 manner, also the political and management aspects of the AO are now beginning
2047 to be approached with increasing intensity and dedication. To achieve these goals
2048 and to plan the work an appropriate conceptual model should be developed.

2049 Our endeavors should aim to be neither circum- (Latin prefix with the
2050 meaning “roundabout, around”) nor trans- (Latin “on the other side of”), but *pan-*
2051 *Arctic* [(based upon the Greek term pan (all, every, throughout)]. Such attempts
2052 should end up in a syn-Arctic comprehension (syn = acting or considered together;
2053 united) that translates into a comprehensive, wider-ranging and encompassing
2054 strategy, shaping local, indigenous and scientific knowledge into a pan-Arctic
2055 mental picture which unites the comprehension of the arctic coastal states. In
2056 general terms a sequence of methods, activities and institutions should be applied
2057 to the pan-AO, assuring adaptive decision making (**Fig. 25**).

2058 In order to reach the pan-Arctic integration goal some preconditions are
2059 necessary. Despite of the progress made to establish such a unifying model, care
2060 has to be taken to omit captivating and glossy oversimplifications. *The conceptual*
2061 *model* of the AO does not exist and may never become a reality but may be
2062 approximated in the future through infinitesimal adaptations of existing models
2063 and the iteration of and improvement of the conceptual model of the AO (**Fig. 25**).
2064 While focusing upon our ultimate goal, an adaptive pathway has to be trodden.
2065 Our comprehension of Arctic ecosystems depends on continuous efforts to
2066 understand better and to shape the understanding inside the regionality that
2067 creates the foundation of most scientific endeavors.

2068 The about 4 million non-indigenous and indigenous people (as defined by
2069 AMAP) that are and have been living in the Arctic for centuries and millennia,
2070 accumulating knowledge and experience, should continue to have an impact upon
2071 knowledge-based resource- and ecosystem-management. In most Arctic nations,
2072 locals have only recently been involved in AO management decisions. The
2073 knowledge of all Arctic people is clearly of interest and relevance for a sustainable,

2074 knowledge-based resource and ecosystem management of the future (**Fig. 26**). To
2075 create scenarios to safeguard the inclusion of local ecological knowledge (tied to
2076 place through experience and observation over a single lifetime or over many
2077 generations) and traditional ecological knowledge (indigenous knowledge, e.g.
2078 Berkes et al., 2000; Huntington, 2000; Drews, 2005) regarding the AO (e.g. Nichols
2079 et al., 2004; Eicken et al., 2014) is a challenge that scientist, managers and
2080 politicians need to pay attention to (Fox Gearheard et al., 2017). The selection and
2081 definition of core values has to be discussed along our pathway into our climate
2082 change- and economic opportunity-impacted future in the AO (**Fig. 26**). The
2083 journey into the future must be based upon knowledge that research and careful
2084 evaluations of the effects that transport, fisheries and industrial activities bring
2085 about. The hackneyed phrase that the AO ecosystem management must remain
2086 ecologically sustainable, i.e. take place in manners that, over time, do not alter the
2087 ecosystem carrying capacity, is still not rigorously applied. If it will be and bears
2088 fruits throughout the AO of the future remains to be seen.

2089
2090

2091 **9. Outlook**

2092 Alarmed by John Maynard Keynes's (1936) citation that «the difficulty lies not so
2093 much in developing new ideas as in escaping from old ones», we argue that to
2094 understand the AO in a fully pan-Arctic manner we have to consider which of the
2095 older confined and sectorial ideas have to be revised and changed. To obtain a
2096 more balanced, pan-Arctic perspective, in favor of interaction and cooperation we
2097 unified older concepts and ideas, revised them and added new ones. To provide
2098 significant elements for shared, high-level paradigm synthesis of our
2099 understanding of the key processes and elements governing the response of the
2100 Arctic ecosystem of today and the future, we thus presented a hierarchy of known
2101 and new conceptual models. We urge AO scientists and managers to undertake a
2102 holistic comprehension of a new emerging ocean that has, so far, been
2103 inadequately investigated and which now challenges our ability to understand
2104 climate change and associated the ecological response in the Northern
2105 Hemisphere. The current advancement in knowledge is already conducted at too
2106 slow a pace to address today's climate and human usage of the transformed AO.
2107 Scientist rather run after the development experienced by the AO than be the
2108 forerunner in planning how to investigate and project the future. Here we take
2109 some first steps in this direction.

2110 The conceptual models we describe will not only support the basic
2111 understanding and management challenges of those directly working in the Arctic,
2112 but they can also serve as tools to communicate insight, understanding and
2113 support among politicians, decision makers and the general public. The latter
2114 aspect is imperative. The people of the Northern Hemisphere need to understand
2115 that the local challenges they face [e.g. sea-level rise (Dahl-Jensen, 2000; Moginot

2116 et al. 2019), weather extremes (Box et al., 2017; Waugh et al., 2017)] may need
2117 research in remote, Arctic regions where “nobody lives” (the population in the
2118 Arctic regions comprises only 0.05% of the human population). Some principal
2119 AO climate change research of generic interest is already carried out [invasion of
2120 boreal species (Frainer et al., 2018; Alabia et al., 2018), changes in biodiversity
2121 (Spiridonov et al., 2011; CAFF, 2017)] and ongoing research will pave the ground
2122 for future AO management (e.g., the Nansen Legacy project). Resource hungry
2123 nations, representing 99.95 % of humanity appear to wish to exploit the rich
2124 resource of the remote regions of the AO but may be less concerned with the
2125 ecological consequences, the requirements of the local population and the
2126 demands of long-term sustainability (Alvarez et al. 2020). It is essential to get the
2127 Global community (stakeholders, the human population at large) of the Northern
2128 Hemisphere involved in planning for a sustainable AO by communicating and
2129 communicate results, narratives, pictures and iconic graphics.

2130 Conceptual models can strongly facilitate interdisciplinarity by providing
2131 a shared understanding of the system. Developing them involves an element of
2132 intuition which, joined to research, speeds up the process of exact science (see
2133 citation of P. Klee at the start). Working with the development of conceptual
2134 models also involves approaches relating to, involving or dealing with abstract,
2135 general or universal concepts. Once established, such models often have inertia,
2136 that can exert a profound influence on the interpretation of data and on shaping
2137 common directions, for years to come, thereby becoming essential underpinnings
2138 of new paradigms. The communities of Arctic scientists, managers, politicians and
2139 peoples of the Arctic need interdisciplinarity and shared understanding.
2140 Currently none can perceive conceptual models without taking note and reacting

2141 to the concept of climate change. Conceptual models have three basic functions:
2142 create testable hypotheses, plan and then modify field campaigns, and
2143 communicate essential results to managers and the general public. They have
2144 thus to be able to accommodate transience as they are not permanent and
2145 represent rather an activity than a final product.

2146 Having in mind the transientness of all models for the AO, we wish to end
2147 with a citation from Aargaard and Carmack (1989), a visionary document that
2148 already 30 years ago encompassed many of the changes currently experienced in
2149 and adjacent to the AO. "While our scenario is highly conjectural, it is quite in
2150 keeping with the message of change that Fridjof Nansen himself preached on
2151 numerous occasions. For example, in a lecture on the Fram drift delivered in 1897
2152 he ended with these words: *Everything is drifting, the whole ocean moves*
2153 *ceaselessly, a link in Nature's never-ending cycle, just as shifting and transitory as*
2154 *the human theories".*

2155

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2176 research group Arctic SIZE (<http://site.uit.no/arcticsize/>).

2177

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2178 Box 1. Four elements of conceptual models that will guide the design,
2179 implementation and interpretation of field experiments and monitoring.

2180

2181 *Scale:* Scale recognizes that processes occur over wide-ranging dimensions of
2182 space and time, and often there exists an empirical relationship between space
2183 and time scales, often expressed in so-called Sverdrup diagrams. *A priori*
2184 recognition of scale, such as first identifying the focal scale together with its
2185 interacting larger and smaller scales, is useful in the design of multidisciplinary
2186 field experiments.

2187

2188 *Pattern:* Pattern can be defined, simply, as any non-random structure or process
2189 and – generally – an emergent property (bottom-up) of a complex adaptive system
2190 (i.e. rules at a lesser scale give rise to structure at a greater scale).

2191

2192 *Seasonality:* Seasonality is one of many key times scales inherent in Arctic marine
2193 systems but, owing to the phenology of biotic components, is also a critical starting
2194 point in experimental design. Seasonality in temperature, light, sea ice and the
2195 hydrological cycle all constrain the Arctic marine ecosystems.

2196

2197 *Regionality:* Regionality recognizes spatial variability (non-homogeneity) within a
2198 system and is often viewed in terms of descending dimension. At the global scale
2199 the Arctic marine system has general features such as extremes of temperature
2200 and light availability, seasonal ice cover, salt stratification, etc. But different
2201 components of this system have distinct characteristics that strongly influence
2202 internal dynamics and response to forcing, and these differences must be
2203 recognized in responsible management policy and implementation.

2204

2205

2206 Table 1. Abbreviations

2207

2208 **Water masses**

2209 ACBC Arctic Circumpolar Boundary Current

2210 AO Arctic Ocean

2211 ASW Arctic Surface Waters

2212 AW Atlantic Water

2213 NHTC Northern Hemisphere Thermohaline Circulation

2214 PW Pacific Water

2215

2216 **Domains/Processes**

2217 APH Atlantic and Pacific Halocline domains

2218 CBCD Circumpolar Boundary Current Domains

2219 CPB Cryo-pelagic-benthic coupling

2220 DBD Deep Basins Domains

2221 SIZD Seasonal ice zone domain

2222 RCD Riverine Coastal Domain

2223 ULAD Upper layer advective domains

2224

2225 Table 2. Characteristics of Arctic food webs.
 2226

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	deSantana 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

2227
 2228

2229 **List of figures**

2230

2231 Fig. 1. Two Northern Hemisphere maps showing the encircling of the Arctic Ocean
2232 by extensive landmasses, atmospheric transports, watersheds and the connection
2233 with the Pacific and Atlantic Oceans. Figures are redrawn from Prowse et al.
2234 (2015) and Carmack et al. (2016) illustrating (A) the delivery of moisture and
2235 freshwater to the Arctic drainage basins by extra-tropical storm tracks (in the
2236 lower and higher atmosphere), and (B) oceanic pathways from the Pacific and
2237 Atlantic into and out of the Arctic Ocean and major gyres. In both maps the white
2238 shaded area denotes the Arctic drainage basins, as discussed by Prowse et al.
2239 (2015). TPD is the Transpolar Drift. The light-blue shaded area depicts surface
2240 waters influenced by fresh-water stratification.

2241

2242 Fig. 2. A highly schematic, Sverdrup-type diagram that shows spatial and temporal
2243 scales that couple global, pan-Arctic and regional marine systems in descending
2244 log scales of space and time. The global scale recognizes the interactions of global
2245 scale processes (thermohaline circulation, hydrological cycle, atmospheric
2246 forcing), and is externally forced by even large scales. The pan-Arctic marine
2247 system, the focus of this paper, is nested at smaller spatial and temporal space and
2248 time scales. It is fully coupled to the global marine system through exchanges of
2249 energy, freshwater, water masses and material properties including, for example,
2250 the Atlantic and Pacific through-flows and the delivery of freshwater to regional
2251 drainage basins by atmospheric transport. The pan-Arctic marine system is, in
2252 turn, underlain by regional domains, as discussed in Section 2 including inflow
2253 shelves, interior shelves, outflow shelves, the pan-Arctic shelf-break and slope, the
2254 Eurasian and Amerasian basins, and major ridge systems (see Carmack and
2255 Wassmann (2006) and Bluhm et al. (2015) for discussion). Below are the
2256 mesoscale and sub-mesoscale processes that act to regulate biogeochemical
2257 processes within specific regions. Forcing is often held to pass top-down from
2258 larger to smaller scales, while feedbacks and emergent properties are held to be
2259 driven bottom-up.

2260

2261 Fig. 3. Functional connection of the Arctic Ocean at the pan-Arctic scale. To the left
2262 the figure comprises the entire Northern Hemisphere, including the continents
2263 and the transportation of moisture by trade winds to the North Pacific and the
2264 westerly storm tracks (A). To the right scheme the focus is upon the functional
2265 connections of the Arctic Ocean and adjacent watershed (B). The schematic
2266 depicts the currents linking the Pacific, Arctic and Atlantic Oceans, the main
2267 pathways of moisture transport to Arctic drainage basins, the northward flow of
2268 rivers to the Arctic Ocean, the establishment of low-salinity coastal currents by
2269 river inflow, and the primary geographical domains. Redrawn from Bluhm et al.
2270 (2015) and Carmack et al. (2016).

2271

2272 Fig. 4. Schematic representation of the basic structure and hydrological functions
2273 of the Arctic Ocean and the coupling of Arctic and subarctic marine and
2274 atmospheric systems under Arctic warming. The 850-mbar surface is taken as
2275 representative of the Polar Vortex that was previously prominent, but which is
2276 now broken up into a multitude of vortecies, allowing in recent years for
2277 significant variability in Arctic Ocean weather. Abbreviations are: AA Arctic

2278 amplification with tapering indicating increased poleward warming; WW
2279 Westerly wind with eddy flux convergence occurring along the Westerly wind
2280 maximum; MW meridional winds associated with Jet Stream meanders; Q
2281 ocean/atmospheric heat exchange; in the center the sea ice, fresh-water
2282 stratification and SML (Surface Mixed Layer); NSTM near surface temperature
2283 maximum forming near expanding open water areas; PW low salinity Pacific
2284 water inflow; AW high salinity Atlantic water inflow; NPIW North Pacific
2285 Intermediate water in the subarctic Pacific; DW is deep water, for which North
2286 Pacific, Arctic Ocean and North Atlantic varieties exist. Take note of the strong
2287 stratification by various water bodies in the central Arctic Ocean. See text for
2288 changes and feedbacks. Redrawn from Carmack et al. (2012).
2289

2290 Fig. 5. Schematic showing four large-scale circulation systems (with $L > 1000$ km);
2291 these are: (A) the large scale wind-driven circulation which forces the cyclonic
2292 Trans-Polar Drift (TPD) from interior shelves of Siberia to the export shelf of the
2293 Fram Strait and the anticyclonic Beaufort Gyre in the southern Canada Basin (BG):
2294 also shown are the Icelandic and Greenlandic Gyres (IG and GG, respectively) and
2295 the North Atlantic Current (NAC); (B) the circulation of waters that comprise the
2296 halocline complex, composed largely of waters of Pacific (blue) and Atlantic (red)
2297 origin that are modified during passage over the inflow and Siberian interior
2298 shelves, respectively; (C) the topographically-trapped Arctic Circumpolar
2299 Boundary Current which carries AW cyclonically around the boundaries of the
2300 entire suite of basins (FSB and BSB are the Fram Strait and Barents Sea Branch),
2301 and (D) the very slow exchange of Arctic Ocean Deep Waters that enter on the
2302 eastern and leave on the western Fram Strait. Redrawn from Bluhm et al. (2015).
2303

2304 Fig. 6. Three shelf types exist in the Arctic Ocean: inflow (tourquoise-gray),
2305 interior (blue) and outflow (pink) shelves. Also shown (turquoise) is the shelf break
2306 and upper slope region that surrounds the outer shelves and the deep Canadian
2307 and Eurasian basins (gray). Redrawn from Carmack and Wassmann (2006).
2308

2309 Fig. 7. Typology of distinct shelf types in the Arctic Ocean: inflow (top), interior
2310 (middle) and outflow (bottom) shelves. Among these categories one may separate
2311 deep (left) and shallow (right) inflow shelves, wide (left) and narrow (right)
2312 interior shelves, and linear (left) and branched/topography-rich (right) outflow
2313 shelves. Following this, the Barents Sea is a deep and the Chukchi Sea is a shallow
2314 inflow shelf. The Kara, Laptev and East Siberian Seas are wide interior shelves,
2315 while the Beaufort Sea is a narrow inflow shelf. The East Greenland shelf has banks
2316 and troughs but is a "linear" while the Canadian Arctic Archipelago has a branched
2317 and topographically complex shelf. The basic biogeochemical cycling features of
2318 the three shelf types are presented to the right. Redrawn and updated from
2319 Carmack and Wassmann (2006).
2320

2321 Fig. 8. Seasonal ice zone domain. A) Illustrates the maximum sea ice extent 30
2322 years ago (dark orange) and at present (light orange). The white area depicts
2323 today's minimum ice extent. Also shown are the transect lines illustrated in Figs.
2324 9A (black) and 9B (green). (B) The relationship between the marginal ice zone
2325 (MIZ – outer rim of seasonal ice zone) circumference (km) and the seasonal ice
2326 zone (SIZ – zone between minimum and maximum ice extent) radii (km) in an

2327 assumed circular, ice-covered ocean. While the MIZ length decreases in a linear
2328 manner when the SIZ declines, the SIZ area (km²) increases in curvilinear manner.

2329

2330 Fig. 9. Hypothetical, annual variability of ice (white), light (blue) and plankton and
2331 ice algae blooms (green) across the Arctic Ocean, now (left) and in the future
2332 (2050 right). The annual variability of sea ice thickness, light and plankton blooms
2333 for every month (Jan to Dec) across the Arctic Ocean are shown: now (to the left)
2334 and 2050 (to the right). The figure depicts a transect from the Barents Sea to the
2335 Beaufort Sea shelf (A) while a transect from the north of Greenland to the Laptev
2336 Sea shelf is shown in (B). The figure shows that the phytoplankton blooms in the
2337 Arctic Ocean are not smooth circles that shrink unevenly from the periphery on
2338 the shelf towards the center (basins). The blooms have a variable phenology with
2339 regard to timing, strength and width, and biomass may shift in depth location in
2340 the water column seasonally. The greatest changes in the future take place in the
2341 most productive months.

2342

2343 Fig. 10. Highly schematic representation of potential buoyancy-boundary flows
2344 driven by continental discharge along northern coastlines around North America
2345 and Eurasia. The flow is not continuous, and the schematic represents the merging
2346 of multiple sources of freshwater discharge from northern North America and
2347 northern Eurasia. Hundreds of rivers and glacial ice melt, which have a propensity
2348 for the formation of an aggregate or contiguous domain along the coastline are
2349 here termed the Riverine Coastal Domain (RCD), shown with a red line. Redrawn
2350 from Carmack et al. (2015).

2351

2352 Fig. 11. The Upper Layers Advective Domain of the Arctic Ocean. Within this
2353 domain, we distinguish among 4 sub-domains: the Atlantic (red), the Pacific
2354 (pink), the Arctic (light red) and the Transpolar (light purple) advective domains.
2355 All have lengths of several thousand km and pass through several biogeographic
2356 regions. Redrawn from Wassmann et al. (2015).

2357

2358 Fig. 12. Circumpolar Boundary Current Domains during times when sea ice cover
2359 withdraws, to various degrees withdraws from the shelf into the deep Arctic
2360 Ocean basins and thus is exposed to easterly winds. The cartoon depicts the two-
2361 dimensional upwelling circulation, when ice is leaving the shelf break, (A), and
2362 when the ice has left the shelf break a shelf-break jet can develop that can give rise
2363 to upwelling (B). Upwelling provides the exposed shelves and shelf breaks with
2364 additional nutrients that may reach into the surface waters. If stratification is
2365 strong upwelling may cause subsurface blooms (e.g. Martin et al., 2010).

2366

2367 Fig. 13. Changes in the distribution of the Atlantic and Pacific Halocline Domains
2368 as related to the predominant wind fields (H and L for atmospheric high and low
2369 pressure, respectively). The change from earlier (left) towards recent windfields
2370 (right) and increased supply of advected Pacific and Atlantic inflows (PI, AI) result
2371 in important changes in the position of the halocline. Take note of the recent
2372 increase in sea level height and depth of the surface water (SW), in particular in
2373 the Amerasian Basin. Take also note how the dominating Atlantic Water (AW)
2374 spreads in recent times further into the Arctic Ocean, in particular in the surface.
2375 The Cold Halocline Water (CHL), however decreased in recent years. AO (Atlantic

2376 Outflow); PHW (Pacific Halocline Water); LHW (Lower Halocline Water).
2377 Redrawn from Polyakov et al. (2018).

2378
2379 Fig. 14. Deep Basin Domain (DBD, deeper than 1000 m). This domain is physically
2380 characterized by low current flows, water exchange between basins being limited
2381 by ridges/sills, old age of the water, low and stable temperature, and high salinity.
2382 The age of the deep water is about 200 years in the Nansen and Amundsen basins,
2383 but about 500 years in the Canadian Basin. Biochemically, the DBD receives highly
2384 diminished vertical carbon input, but horizontal carbon input can be important.
2385 This results in low biotic densities and biomass, dominance of soft sediments
2386 dotted with glacial drop stones. The DBD is intersected by ridges, with local
2387 outflows of chemical-rich fluids and (largely unmapped) seamounts. Today's
2388 biotic connectivity to the north Atlantic and the global deep-sea is high while that
2389 to the Pacific is essentially absent. AWin (Atlantic Water inflow); AODWout
2390 (Atlantic Ocean Deep Water outflow); GSDWin (Greenland Sea Deep Water
2391 inflow); BD (Brine Drainage); NB (Nansen Basin), NGR (Nansen-Gakkel Ridge); AB
2392 (Amundsen Basin); LR (Lomonosov Ridge); MB (Makarov Basin); AMR (Alpha-
2393 Mendeleev Ridge); CB (Canada Basin). The dashed vertical lines and circle arrows
2394 indicate bottom water mixing. Sb (salinity); θ_b (potential temperature)

2395
2396 Fig. 15. The Polar Night north of the Arctic Circle. Between 67.4 and 72°N the sun
2397 is below the horizon from 1-72 days per year. Between 72 to 78°N the sun is below
2398 the horizon between 72-112 days per year. Between 78 to 84°N the sun is below
2399 the horizon for 112-144 days per year. Above 84°N the sun is below the horizon
2400 for 144-177 days per year. The period of midnight sun is a geometrically mirror
2401 of the polar night, but due to atmospheric refraction of the sun, the period of
2402 midnight sun is up to 14 days longer than the Polar Night. Take note how the light
2403 regimes vary between regions where marine Arctic research has been and is
2404 carried out (not shown). Investigations north of Svalbard, in the Barents Sea, the
2405 Beaufort shelf or the Chukchi Sea take place under widely different light regimes
2406 and are thus difficult to compare.

2407
2408 Fig. 16. Hypothetical phenology of ice algae and phytoplankton blooms as a
2409 function of latitude. Light, ice and stratification determine the environmental
2410 envelope that regulates the timing of ice algae and phytoplankton bloom
2411 development along a latitudinal axis of open water-Seasonal Ice Zone Domain
2412 (ranging from 75–85°N). There are long to short productive periods in open water
2413 (70–75°N) and heavily ice-covered regions (> 73–75°N) in the European Arctic
2414 corridor, respectively. Inside each longitudinal light window with its variable ice
2415 cover the timing and extent of the ice and phytoplankton and ice algae phenology
2416 changes from April in the south towards late summer at high latitudes. A recent
2417 feature is the tendency for autumn blooms that has been observed in the Polar
2418 Twilight zone, but these blooms will have no light base in the Nautical Polar Night
2419 zone (see Fig. 15).

2420
2421 Fig. 17. Climate change alters the phenology of the ice algae and phytoplankton
2422 blooms. Present-day scenario (left) and predicted future scenario with a warmer
2423 climate (right) along similar latitudes. The hypothetical timing of the ice algae and
2424 phytoplankton bloom development in the Eurasian Arctic corridor along a

2425 latitudinal axis is indicated: from the open water-seasonal ice zone region
2426 (ranging from 75–85°N) with long to short productive periods in open water (70–
2427 75°N) to heavily ice-covered regions (> 73–75°N). Notice how today's bloom
2428 development scenario A disappears for good while the new scenario F enters at
2429 the southern section of the latitudinal gradient in the future. Panels E and F
2430 exemplify the course of primary production in the scenario of continuously open
2431 water in the central/southern Barents Sea, characterized by no major freshwater
2432 source and weak and slow development of surface water stratification. The
2433 variable production in June (panel E) arises through variations in nutrient supply
2434 caused by vertical mixing events triggered by low-pressure passage after the end
2435 of the spring bloom. Panel F projects future primary production at 70°N after
2436 Arctic warming leads to increasing thermal stratification and decreased primary
2437 production. Modified from Leu et al. (2011) and Wassmann and Reigstad (2012).
2438

2439 Fig. 18. Phenology of the bloom development and in downward carbon export at
2440 about 78°N in the Barents Sea over a two-year period. The present-day climate is
2441 depicted in panel A and the consequences of a warmer climate with thinner ice in
2442 winter and more melting of summer ice is displayed in panel B. A thinning of sea
2443 ice, variable snow cover, supports a) more intense and earlier ice algae blooms
2444 and b) a greater annual extent of the seasonal ice zone. The green-to-red gradient
2445 indicates the balance of suspended biomass from autotrophic (green) to
2446 heterotrophic (red) sources. The annual new and export production in both
2447 scenarios is assumed similar because stratification (induced by sea-ice melt and
2448 increased surface warming) limit nutrient availability. Greater wind stress may
2449 though increase the vertical contribution of nutrients. The width and color of the
2450 vertical arrows illustrate the semi-quantitative magnitude and composition
2451 (autotroph, fecal pellet and detritus (green, red, brown, respectively) of vertical
2452 export.

2453 In an adaption to the short productive period and cold temperature many
2454 organisms at Civil Polar Night and Nautical Polar Night latitudes expand their
2455 annual life cycle to more than year. Some of the involved processes that organisms
2456 such as Polar cod apply during the Polar Night are indicated in panel A (see white
2457 vertical bars). To understand the marine ecology at high latitudes in the AO we
2458 must have to change our traditional attention to spring and summer, but pay
2459 increasingly attention to the a) autumn and overwintering and b) multiannual
2460 time spans. Winter seems to play an essential role for the marine ecology of the
2461 AO. Redrawn from Wassmann and Reigstad (2011).
2462

2463 Fig. 19. Hypothetical graph explaining the principles of cryo-pelagic-benthic
2464 coupling (CPBD) for shallow (A), moderate (B) and deep ocean (C) regions. The
2465 thin vertical lines (grey) illustrate the subsurface contribution of ice-derived
2466 biogenic matter. The level of new production (based upon nutrient availability
2467 and supply) and light availability increases amount of the suspended biomass that
2468 can sink. Scenario I (red) illustrates the CPBD for less productive, scenario II
2469 (green) the high productive and stratified regions. Depth and the intensity of the
2470 of the pelagic retention, in particular in the upper twilight zone, plays a major role
2471 for the intensity of cryo- pelagic-benthic coupling. Benthic organisms in shallow
2472 regions, such as the Chukchi Sea (see panel A) enjoy a far higher supply and quality
2473 of biogenic matter than deeper shelves (such as the deeper Barents Sea, see panel

2474 C)). In the AO basins the CPBD is assumed to be weak (not shown). Vertical mixing
2475 in non-ice-covered regions that will become more frequent in the future results in
2476 a dilution of suspended biomass in the upper layers and a change vertical flux
2477 retention (scenario III, blue). Shallow shelves have far greater resuspension and
2478 contribute substantially more to remineralization than those in the deeper ones.
2479 Resuspension of particulate matter from the sediment surface, being most
2480 intensive on shallow shelves, contributes to the horizontal export of carbon into
2481 the deep basins.

2482
2483 Fig. 20. Conceptual Arctic food web showing dominant taxa and their trophic
2484 position and indicating trophic links among species through arrows. This
2485 depiction overlays a vertically structured concept of the Arctic Ocean's
2486 compartments including sea ice, water column and seabed. A shallow shelf and
2487 more Arctic influence is indicated by characteristic biota, subsistence populations
2488 and more sea ice (A, Bering Strait region, Chukchi Sea). The semi-transparent
2489 fishing vessel indicates (potential) fisheries moving north. A deep shelf and one
2490 with more Atlantic influence is indicated by characteristic biota including
2491 commercial species, less sea ice and fishing effort (B). The basin conditions are not
2492 shown in detail. Circular insets illustrate the ice brine channel system biota (1),
2493 the microbial food web (2) and the meiofaunal sediment community (3). Primary
2494 producers are colored in green, consumers in black (and light blue in deeper
2495 waters), and orange indicates particularly lipid-rich biota with high energetic
2496 value for their consumers. For more detail, see text section 6.1.

2497
2498 Fig. 21. Conceptual depiction of energy flow in Atlantic (A) and Pacific (B) inflow
2499 shelves. Dominant functional and/or taxonomic groups are shown as rectangles
2500 and trapezoids and are vertically arranged along a trophic level axis, starting from
2501 the base of the food web at the bottom. A given group may extend across several
2502 trophic levels; box size indicates the relative biomass of a given group. Trapezoids
2503 indicate increasing or decreasing relative importance along a south (lower side)-
2504 to-north (upper side) gradient (only shown where very prominent). Brown
2505 shades indicate benthic-dominated, blue shades pelagic-dominated flows. Lines
2506 between boxes show (only particularly prominent) energy flows with green lines
2507 denoting energy transfers from the lowest trophic levels and detritus and black
2508 lines denoting energy flow between consumer levels. Dark gray outlines marks
2509 groups with particularly high connectance (i.e. many trophic links). Modified from
2510 Whitehouse et al. (2014) and informed by Carroll and Carroll (2003), Dommasnes
2511 et al. (2010), Iken et al. (2010), de Santana et al. (2013), Hunt et al. (2013),
2512 Kortsch et al. (2015, 2019), Skaret and Pitcher (2016), Pedersen et al. (2018),
2513 Suprenand et al. (2018). D = demersal, gelat. zoop. = gelatinous zooplankton, M =
2514 marine mammals, S = seabirds.

2515
2516 Fig. 22. Particulate carbon sources supporting the (eukaryotic) Arctic food web.
2517 Substantial methane sources (blue ovals, CH₄) are documented in sub-sea surface
2518 sediments, and early evidence suggests methane uptake into the food web.
2519 Carbon sources playing strong roles in a given region of the Arctic Ocean are
2520 shown: Pelagic particulate organic matter (pPOM) is the primary (particulate)
2521 carbon end member, and overwhelmingly so in the inflow shelves (dark green). In
2522 the central basin, ice-derived POM (iPOM, light green) can contribute about half to

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2523 primary production. Interior shelves in particular receive substantial amounts of
2524 terrestrial organic matter (tPOM, light brown) from permafrost and rivers (brown
2525 arrows), though glaciers also contribute. Rocky shores of Greenland, the Canadian
2526 Arctic Archipelago (gray trapezoids), Svalbard and Russian shelf island groups
2527 (gray circles) provide increasing amounts of macroalgal carbon (MA and brown
2528 outlines). Notably, dissolved organic carbon (DOC; not shown in this figure)
2529 contributes most carbon to the entire carbon pool, but must be taken up through
2530 the microbial loop, namely bacteria, before entering the eukaryotic food web.
2531 Fig. 23. The figure illustrates icons for established approaches to complex systems
2532 level modeling. Panel A illustrates C.S. Holling's so-called *rule of hand* which states
2533 that most complex adaptive system will be governed by the interactions among a
2534 small number (say 5 ± 2) internal parameters; changes to any of these internal
2535 parameters will alter the behavior and equilibrium state of the overall system and
2536 its response to external forcing (drivers) (Holling, Pers. Comm.). Panel B
2537 illustrates the *complex adaptive cycle* which states that a given social-ecological
2538 system will undergo a natural cycle of 1) growth, 2) collapse, 3) release and 4)
2539 reorganization (Gunderson and Holling, 2002). Panel C illustrates the *ball-in-basin*
2540 which conveys the ability (resilience) of a system to return to its equilibrium state
2541 (K1) when perturbed; As resilience is decreased the K1 basin depth shoals; at
2542 some point a given external shock may force the system beyond its threshold
2543 (tipping point; Wassmann and Lenton, 2012; Duarte et al., 2012) into a new stable
2544 equilibrium (Walker and Salt, 2006). Ongoing changes in sea ice dynamics may
2545 illustrate this process (Duarte et al., 2012). Panel D illustrates the concept of
2546 *trophodynamics* (e.g. phasing, match-mismatch, etc.) in which the joint
2547 phenologies of prey and predator influence the efficiency carbon transfer up a
2548 given food web (Parsons, 1988). Typically, a well-matched phase will result in a
2549 robust pelagic food web, while mismatched phasing will strengthen pelagic
2550 benthic coupling (Wassmann, 1998). Panel E illustrates the concept of *trophic*
2551 *cascade*, a top-down process in which reduction (enhancement) at one trophic
2552 level may result in enhancement (reduction) at the underlying level, followed by
2553 reverse effects at successive levels (Carpenter and Kitchell, 1993). Examples
2554 include removing a planktivorous fish from a system which results in reduced
2555 grazing of zooplankton which results in a greater number of phytoplankton, and
2556 so on; cascade effects will spill over into nutrient and water quality effect as well.
2557 Panel F illustrates the process of *system cascade*, wherein an external driver (e.g.
2558 climate warming) may directly affect one system (e.g. sea ice cover) which in turn
2559 affects another system (e.g. increased ocean stratification) which affects yet
2560 another system (e.g. nutrient availability), and so on through the food web
2561 (Carmack et al., 2014). The main feature here is not that the initial driver affects
2562 succeeding systems in the chain directly, but rather through the cascade links. In
2563 addition, each succeeding system will have different tipping points and feedback
2564 processes. Panel G illustrates a mapping approach to following a system's cascade
2565 in which links between a given drivers are followed through linked systems. Panel
2566 H illustrates the process of *synchronous failure*, a conceptual framework that
2567 shows how multiple stresses can interact within a single social-ecological system
2568 to cause a shift in that system's behavior based on identifies the pattern's causes,
2569 intermediate processes, and ultimate outcomes (Homer-Dixon et al., 2015).
2570 Synchronous failure can often be characterized by a pattern of expanding scale

2571 and magnitude. Panel I illustrates the importance of scale, into which each of the
2572 above concepts must be mapped (Carmack and McLaughlin, 2000).

2573
2574 Fig. 24. Two hypothetical figures that illustrate how one may move from
2575 observations over abstraction to the ultimate simplified “template”-type
2576 conceptual model. A) illustrates continents, shelves and basins, major currents
2577 freshwater run-off and connectivity to the Atlantic- and Pacific Oceans. B)
2578 illustrates all of the contiguous domains that are plotted into this hypothetical
2579 depiction of the Arctic Ocean. For each region in the Arctic Ocean researchers need
2580 to have the basic knowledge, illustrated in A and B, in mind.

2581
2582 Fig. 25. Schematic sequence of methods, activities and institutions that assure
2583 adaptive decision making. Starting with a hypothesis that results in predictions
2584 observations and a sampling design are formed. After quality control of the data
2585 the updated knowledge gives rise to an update of the hypothesis (prediction) and
2586 eventually to the formulation of a model that then provides the base for a new
2587 round of investigations. Also, the needs of the management come into play here.
2588 They use the model results and contribute to management measures that become
2589 part of the new observation regime, the research design and management
2590 features. For every sequence of activities result are published scientifically while
2591 communication with decisions makers, politicians and the general public
2592 (consisting in our case first of all the people living in the Arctic) is mandatory. In
2593 concert this creates the strategy for adaptive decision making which ultimately
2594 also improves the conceptual model of the Arctic Ocean.

2595
2596 Fig. 26. A schematic that illustrates how knowledge (our history and culture) is
2597 transferred, created and shaped (current system and core values), transformed
2598 and impacted (pathway) to create the base for our future. In our present,
2599 humanity’s core values (here summarized in the term sustainability without
2600 which there will be no justifiable future) play a crucial role. We are forced by
2601 climate change and economic drivers. During the time between now and the future
2602 (pathway) discussions and debates are indispensable and the public has to
2603 distinguish between the institutions and ideas that block or hinder a sustainable
2604 future.

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