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Oceanography, biogeochemical cycles, and biodiversity in the Central Arctic Ocean: current state of knowledge and directions for future

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1 **Oceanography, biogeochemical cycles, and biodiversity in the Central Arctic Ocean:**
2 **current state of knowledge and directions for future research as part of the Tara Polaris**
3 **expeditions**

4
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83 Abstract

84 Climatic changes in the physical environment modulate biogeochemical cycles, biodiversity, and
85 trophic interactions in the Central Arctic Ocean (CAO). Physical processes and sea-ice
86 conditions are highly seasonal in the CAO and dependent on interactions that occur throughout
87 the evolution of the upper ocean–sea ice–lower atmosphere system. Understanding these
88 seasonal interactions is critical to comprehending and predicting the long-term trends as the
89 CAO moves towards ice-free summers and to informing future policy decisions at the core of
90 ongoing discussions concerning the CAO Fisheries agreement, e.g., at the Arctic Council and
91 International Council for Exploration of the Sea working group on the CAO. Here, we review
92 current knowledge of the physical environment, biogeochemical cycles, and biodiversity in the
93 waters of the CAO, identify emerging research questions, and introduce the science plan for the
94 first Tara Polaris drift onboard the *Tara Polar Station* to advance knowledge and address these
95 questions. Despite increased observational programs in the CAO over the past years, e.g., the
96 Nansen and Amundsen Basin Observational System (NABOS) and Multidisciplinary drifting
97 Observatory for the Study of Arctic Climate (MOSAIC), extensive knowledge gaps remain in
98 relation to ocean stratification, sea ice and lightscape, nitrogen fixation and nutrient fluxes,
99 carbon export and transfer, sympagic-pelagic coupling, aerosol production, contaminant
100 transport and transformation, chronobiology, and fish distribution. Further knowledge on overall
101 CAO biodiversity, ecosystem functionality and interannual variability is also critically needed.
102 We describe a way forward to address these knowledge gaps using ice-tethered and profiling
103 instruments coupled with multi-omics, culturing, and imagery approaches deployed from *Tara*
104 *Polar Station* during the first of ten Tara Polaris drifts designed to facilitate detection of
105 interannual variability and change over time.

106 1. Introduction and state of the art

107 Water mass properties, currents, and sea ice shape habitats in the Central Arctic Ocean (CAO).
108 Environmental drivers govern the functioning of the entire ecosystem, including biogeochemical
109 cycles, biodiversity, and transport of matter and energy across trophic networks. The physical
110 environment also drives the capacity for adaptation or replacement of organisms living in the
111 water column (pelagic) or at the ice-water interface (sympagic; Galand et al., 2009; Salazar et al.,
112 2019). A better understanding of the interactions between ocean physical conditions,
113 biogeochemical cycles, and biology is thus essential to model and forecast the future CAO.
114 Physical processes and sea-ice conditions are highly seasonal and dependent on upper ocean–sea
115 ice–lower atmosphere interactions that occur during ice formation, thinning, and ice melt
116 (Brandon et al., 2010; Sumata et al., 2023). Increased sea-ice fragmentation and open leads in
117 winter can increase heat loss and CO₂ exchange compared to previous conditions when the sea-
118 ice lid better insulated the water underneath (Ericson et al., 2023; Boutin et al., 2024).
119 Understanding the time scales and full range of physical and environmental interactions is
120 particularly critical to comprehending and predicting long-term trends as the CAO moves
121 towards ice-free summers and shorter winters with more dynamic sea-ice conditions (Jahn et al.,
122 2024).

123
124 Knowledge about the pelagic ecosystem of the CAO remains scarce. In the context of rapid
125 climate change and loss of habitats, there is a pressing need for coordinated interdisciplinary and
126 comprehensive data collections collated over complete annual cycles (Pelt et al., 2017; Rabe et
127 al., 2022). Several large programs, including the Nansen and Amundsen Basin Observational
128 System (NABOS), the Norwegian N-ICE2015 and Nansen Legacy expeditions, and the

129 Multidisciplinary drifting Observatory for the Study of Arctic Climate (MOSAiC) (Granskog et
130 al., 2018; Pnyushkov and Polyakov, 2022; Kohlbach et al., 2025), have increased knowledge on
131 the Eurasian side of the CAO. However, the high regional and natural variability combined with
132 ongoing climate change calls for continued observations, especially outside the better observed
133 summer seasons. Here, we review our current understanding of the pelagic ecosystem of the
134 CAO. We further introduce novel research questions to be addressed in future programs, which
135 include the Tara Polaris I expedition, the first of ten planned consecutive transarctic drifts over
136 the coming 20 years (Babin et al., n.d.). We focus on how physical oceanic conditions and sea
137 ice affect biogeochemical cycles and pelagic ecosystems in the CAO, and vice versa. While
138 essential sampling activities required to monitor marine ecosystems at high latitudes are
139 described briefly, we emphasise novel approaches and questions that remain mostly unexplored
140 yet are likely to advance our understanding of the pelagic ecosystem in the region.

141 1.1. Physical environment

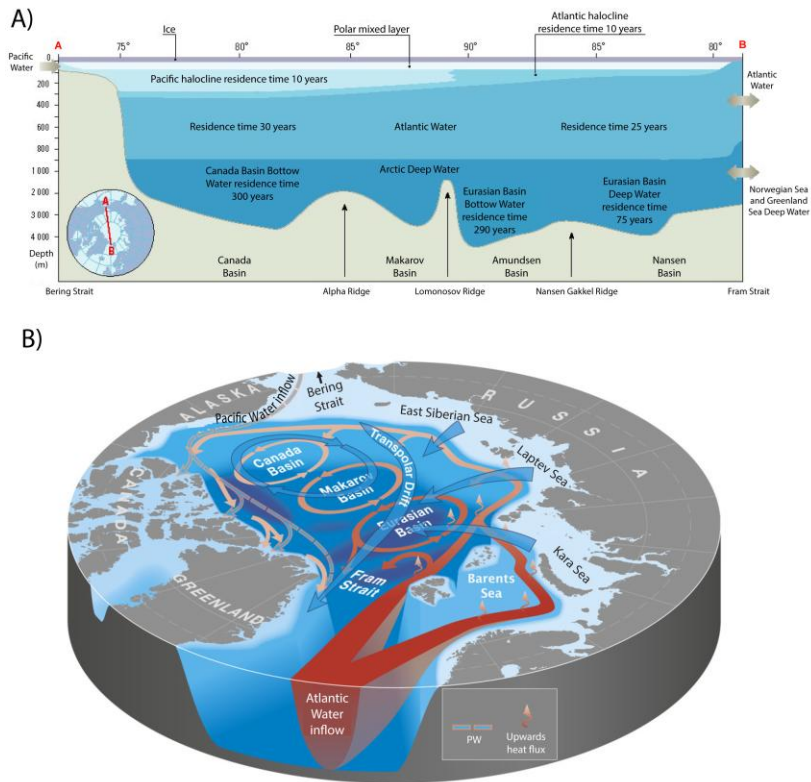
142 1.1.1 Water masses and circulation

143 The CAO comprises the deep Amerasian (Canada and Makarov) and Eurasian (Nansen and
144 Amundsen) basins. Being surrounded by continents, the CAO has limited connectivity with
145 subarctic basins and the world ocean. Still, the inflow of saltier Atlantic deepwater and fresher
146 Pacific surface waters through the gateways on the Atlantic and Pacific side are important drivers
147 of deep-water circulation and characteristic layering in the Arctic Ocean (Polyakov et al., 2024).
148 The Arctic Ocean receives more than 10% of the global freshwater runoff and, consequently, is
149 the world's freshest ocean, although a large portion of the freshwater is retained on the shelves
150 (Aagaard and Carmack, 1989; McClelland et al., 2012). In polar regions, salinity is the primary

151 source of stratification and the depth of the brackish surface mixed layer (SML) varies seasonally
152 and regionally, with the Eurasian Basin having a deeper SML (approximately 20 m in summer
153 and 70 m to >100 m in winter) than the Amerasian Basin (approximately 8 m in summer and 30
154 m in winter; Peralta-Ferriz and Woodgate, 2015). The uniformly cold layer below the Eurasian
155 Basin SML increases in salinity with depth, forming a halocline atop the warmer and saltier
156 Atlantic Water (Figure 1A). In the Amerasian Basin, Pacific Waters entering via the Bering
157 Strait form an intermediate layer between the Arctic SML and the warmer deep Atlantic Water
158 layer (Figure 1A, B). In summer, solar radiation warms the SML to above-freezing temperatures
159 leading to sea-ice melt which, together with river runoff, freshens the SML, enhances surface
160 stratification and restricts vertical mixing across the SML (Maykut and McPhee, 1995; Jackson
161 et al., 2010; Smith et al., 2023). As a result, the Arctic SML serves as a heat reservoir, with its
162 dynamics controlling heat distribution and exchanges between the ocean, sea ice, and atmosphere
163 (Maykut and McPhee, 1995; McPhee et al., 2003; Perovich et al., 2014). Yet, there are
164 uncertainties related to the direction and magnitude of air–sea exchange along the transpolar drift
165 (Loose et al., 2024).

166

167 The upper ocean stratification is dynamic and continuously changing across seasons (e.g.,
168 Solomon et al., 2021). Over the past decade, the positioning of the Atlantic Water layer has
169 become shallower and the heat exchange with the SML has increased, resulting in regionally
170 warmer surface waters and increased sea-ice melt (Polyakov et al., 2012; Ingvaldsen et al., 2021;
171 Schultz et al., 2024). This feature was first observed along the Eurasian slopes but was also
172 recently detected in the Amerasian Basin (Polyakov et al., 2025a).



173

174 **Figure 1. Water masses and major currents in the Central Arctic Ocean.** A) Stratification of

175 water masses across the basins (reproduced from the Arctic Monitoring and Assessment

176 Programme; AMAP, 1998); residence times are approximate. B) Circulation of the surface water

177 (blue), intermediate Pacific Water (PW, dashed pink/blue arrows), and warmer Atlantic Water

178 (AW, red and solid orange, where the transition from red to orange indicates upward heat flux;

179 reproduced from Carmack et al., 2015).

180

181 The first evidence of strong Atlantic Water warming — up to 1°C — was observed in 1990 when

182 a warm pulse entered the Nansen Basin (Quadfasel et al., 1991). This pulse travelled through the

183 ocean interior, reaching the Makarov Basin by 1993 and the Canada Basin by 2000 (Carmack et

184 al., 1995; Morison et al., 1998; Shimada et al., 2004). A second, even warmer pulse

185 (approximately 0.2°C warmer) entered through Fram Strait in 1999 (Schauer et al., 2004) and
186 reached the eastern Eurasian Basin by 2004 (e.g., Polyakov et al., 2005). Since 2007–2008, the
187 thermodynamic state of the ocean interior has remained relatively stable, with no significant
188 changes over the following decade (Polyakov et al., 2020a).

189 During the 2010s–2020s, observations revealed unprecedented yet contrasting changes in
190 stratification across the two major Arctic Ocean basins. On the Amerasian side, enhanced
191 freshening and deepening of the surface freshwater layer, driven by sea-ice melt, redirection of
192 Siberian river runoff into the Beaufort Gyre, and the intensification of the Arctic High and
193 associated wind-driven upper ocean convergence, have strengthened stratification. This
194 strengthening has led to a more pronounced separation between surface and deep ocean layers
195 (e.g., Yamamoto-Kawai et al., 2009; Proshutinsky et al., 2009; Morison et al., 2012; Polyakov et
196 al., 2017).

197 In contrast, in the Eurasian Basin, increased air–sea interactions and weakened stratification have
198 resulted in the shoaling of the Atlantic Water layer and intensified current shear, altering the
199 seasonal cycle of Atlantic Water temperature and vertical heat flux (e.g., Polyakov et al., 2020b).
200 Specifically, the seasonal temperature range of the Atlantic Water layer in the eastern Eurasian
201 Basin increased from 0.2–0.3°C in 2004–2007 to over 1°C in 2013–2015 (Polyakov et al., 2017).
202 Significant shoaling of the Atlantic Water upper boundary, from depths greater than 160 m in
203 2002 to about 65 m in 2023, along with the loss of the permanent halocline layer, has enhanced
204 upper ocean ventilation and wintertime entrainment of oceanic heat toward the sea ice. For
205 instance, inferred divergent Atlantic Water heat fluxes of approximately 18 W m⁻² during 2021–
206 2023 exceeded those recorded by moorings in the 2010s. As a result, the equivalent losses in sea-

207 ice thickness due to reduced winter ice formation increased from approximately 0.4 m in the
208 early 2010s to 0.7–1.0 m in recent years (Polyakov et al., 2025a).

209 A significant portion of these changes is attributed to anomalous inflows from the Nordic seas,
210 which is commonly referred to as Atlantification (Polyakov et al., 2017; 2020a; Ingvaldsen et al.,
211 2021). This process, occurring in the Eurasian Basin of the Arctic Ocean, has led to weakened
212 upper ocean stratification and enhanced release of Atlantic Water heat, accelerating sea-ice loss
213 in the region (Polyakov et al., 2017; 2020b). The continued eastward progression of
214 Atlantification into the Amerasian Basin is now having substantial impacts on the upper ocean,
215 sea ice, and ecological components of the Arctic climate system (Polyakov et al., 2025a), with
216 uncertain consequences for the broader marine food web.

217

218 1.1.2 Sea ice

219 Sea ice plays a critical role in the Arctic environment, acting as a regulator of air–ocean heat
220 exchange and freshwater balance in the polar basins (e.g., Aagaard and Carmack, 1989). It
221 reaches its maximum extent of approximately 14–15 million km² in March and declines to
222 around 4–6 million km² by September. Sea-ice thickness varies significantly depending on
223 location, season, and age, but historically it has ranged from 2 m to 3 m, with a substantial
224 portion composed of multi-year ice that has survived at least one melt season (Janh et al., 2024).
225 Sea-ice concentration remains high in the CAO, while it is more variable in the marginal ice
226 zone. Due to its high reflectivity, sea ice exhibits a high albedo (approximately 0.6–0.8), playing
227 a key role in the global energy balance and climate system through the sea ice–albedo feedback
228 mechanism (Manabe and Stouffer, 1980). Major circulation patterns in the Arctic include the
229 Beaufort Gyre and the Transpolar Drift (Figure 1B).

230

231 The rapid decline in the extent and volume of Arctic sea ice has become a prominent signal of
232 global climate change. The extent of Arctic summer sea ice has decreased by nearly half
233 compared to the 1970s. Since 2007, the annual minimum of sea-ice extent in September has been
234 lower than in any previous year during the era of satellites (Stroeve and Notz, 2018). The ice
235 cover is becoming thinner (Lindsay and Schweiger, 2015), younger (Kwok, 2018), and more
236 mobile (Rampal et al., 2011). Results from the MOSAiC transpolar drift in 2019/20 confirmed a
237 thinner sea-ice cover that grew faster, drifted faster, and melted faster compared to historical
238 observations (Raphael et al., 2024). Such significant changes have not been observed since at
239 least the Last Interglacial at around 130,000 years ago (Vermassen et al., 2023), and the
240 likelihood of ice-free Septembers in the Arctic Ocean before 2050 is now high (Jahn et al.,
241 2024), though daily ice-free conditions may occur before 2030 (Heuzé and Jahn, 2024).
242 According to projections from intercomparisons of coupled models, the Arctic will likely
243 become ice-free in summer by 2035 (Wang and Overland, 2012; Notz and Stroeve, 2016;
244 Sigmond et al., 2018; Rantanen et al., 2022; AMAP, 2024). In addition to impacting habitats and
245 ecosystems, sea-ice reduction favours anthropogenic activity in the high Arctic (Melia et al.,
246 2016).

247

248 1.1.3 Seasonal cycle

249 Over the past decade, the seasonal cycles of sea ice concentration, shear, and current speed in the
250 upper Arctic Ocean have also changed markedly. In particular, longer summers have led to
251 earlier surface melt and later freeze-up. This has amplified the seasonal cycle of current speed
252 and shear and produced a close coupling between upper ocean dynamics and sea ice conditions

253 in the Siberian sector of the Arctic Ocean, as reflected by a strong negative correlation ($R = -$
254 0.94) between the seasonal cycles of sea ice concentration and current shear from 2013 to 2023
255 (Polyakov et al., 2025b).

256 Currents in the Arctic halocline and SML are impacted significantly by the seasonal evolution of
257 stratification. In the shallow (<20–30 m) summer SML, currents increase because strong
258 stratification constrains wind energy from propagating into the deeper layers. Strong near-inertial
259 currents that are generated when sea ice is reduced account for more than half of the summertime
260 current speed and shear (e.g., Brenner et al., 2023; Polyakov et al., 2025b). In the winter, a
261 thicker surface layer is created by deep upper ocean ventilation associated with Atlantification in
262 the Siberian Arctic, which distributes wind energy to far deeper (>100 m) layers. Polyakov et al.
263 (2025b) provided evidence of winter amplification in the average currents across the 100 m
264 upper ocean layer in response to higher wintertime forcing. This winter amplification of currents
265 and shear at depths is highly consistent with increasing seasonality and a general loss of double-
266 diffusive staircases in the region over the 2004 to 2023 period (Lundberg and Polyakov, 2025).
267 Consequently, stratification represents a physically significant link in the strong connection
268 between the seasonal evolution of currents and sea-ice concentration.

269

270 1.1.4 Optics and light field

271 The marine lightscape of the CAO is unique for two reasons: 1) seasonal variations in incident
272 irradiance are extreme; and 2) the majority of incident photons do not reach the epipelagic zone
273 (0–200 m) because sea ice and overlying snow are ubiquitous for most of the year. While
274 variation in day length is constant from year to year at any latitude (Lund-Hansen et al., 2020),
275 the effect of clouds, ice and snow is highly variable in space at scales of metres to tens of

276 kilometres at any time of the year, as well as inter-annually (Katlein et al., 2019). Compared with
277 other oceanic basins, the epipelagic zone of the CAO is thus often characterised by continuous
278 darkness or twilight during the polar night, continuous illumination during the midnight sun
279 period, and variable irradiance at small scales due to heterogeneous ice cover. Sea-ice features,
280 such as leads and melt ponds, result in abrupt variations in submarine irradiance over as many as
281 four orders of magnitude (Lei et al., 2010; Nicolaus et al., 2012; Arrigo et al., 2014). The optical
282 properties in the water column are also influenced by coloured dissolved organic material from
283 large rivers, mainly in Russia, and transported with the Transpolar Drift, which is reflected by a
284 stronger impact in the Eastern Eurasian part of the CAO (Schulz et al., 2024, and references
285 therein).

286

287 1.2 Biogeochemical fluxes

288 1.2.1 Nutrients and nitrogen

289 In addition to light, the nutrients nitrogen, phosphorus, iron, and silicon predominantly control
290 primary production in the CAO, with nitrogen generally being the most limiting among the
291 nutrients (e.g., Tremblay et al., 2015; von Friesen and Riemann, 2020). Primary production and
292 upward vertical fluxes of nutrients and organic matter are more constrained in the CAO than in
293 other sectors of the Arctic due to the strong water column stratification (e.g., Bluhm et al., 2015;
294 Fernández-Méndez et al., 2015), which also impacts vertical carbon export (Randelhoff et al.,
295 2020). In winter, as seawater freezes, salt is rejected and reduces stratification in the SML and
296 the halocline (e.g., Rudels, 1989). While lateral nutrient input from rivers is high on Arctic
297 shelves, entrainment of saline and nutrient-rich deeper waters plays a crucial role in nutrient

298 supply to the surface in the highly stratified basins of the CAO, where winter mixing is absent, to
299 sustain production when light becomes available in spring (Fernández-Méndez et al., 2015;
300 Tremblay et al., 2015; Randelhoff et al., 2020). The increased contact between the deeper
301 nutrient-rich Atlantic water and the surface layers in the regions impacted by Atlantification is
302 known to facilitate increased nutrient supply in periods of increased mixing (Randelhoff et al.,
303 2018; Schultz et al., 2024). A longer ice-free period also increases the possibility for wind
304 mixing and resupply of nutrients at the surface (Randelhoff and Sundfjord, 2018). However, how
305 the ongoing changes in CAO sea-ice cover will impact stratification and, ultimately, nutrient
306 replenishment, still remains poorly understood.

307

308 In nitrogen-limited systems, nitrogen fixation by microorganisms results in the conversion of N₂
309 to ammonia and nitrate, which is then available to algae and can contribute significantly to
310 nitrogen supply (e.g., von Friesen and Riemann, 2020). This process was assumed to be rare in
311 the Arctic Ocean due to the absence of cyanobacteria; however, non-cyanobacterial diazotrophs
312 are present in the Arctic. Nitrogen fixation by free-living bacteria or bacteria-microalgae
313 symbiosis has been documented and quantified for Arctic shelves (Sipler et al., 2017; Harding et
314 al., 2018), but rarely for the deeper basins of the CAO. There, the first studies suggest that this
315 process is an underestimated contribution to nutrient supply for primary production, especially in
316 actively melting sea-ice regions, and supported by dissolved organic carbon from phytoplankton
317 as carbon source for the arctic diazotrophs (von Friesen and Riemann, 2020; von Friesen et al.,
318 2025). River water transported with the Transpolar Drift can maintain relatively elevated
319 concentrations of other nutrients, such as dissolved iron, in the Amundsen and Markov basins,
320 and hence support nitrogen fixation (Klunder et al., 2012). In general, a trend toward less sea ice

321 and a longer productive season could increase the importance of nutrient-regenerative microbial
322 food webs in a stratified Arctic Ocean (Ardyna et al., 2011; Kohlbach et al., 2023).

323

324 1.2.2 Carbon

325 As in other oceans, the estimates of vertical fluxes in the basins of the CAO reveal a deficit in the
326 quantified organic carbon production and export compared to benthic needs (Wiedmann et al.,
327 2020) and call for improved insight into the different steps involved in carbon cycling. In
328 general, the processes behind the sources and formation of particulate and dissolved organic
329 carbon as well as retention and export of biogenic matter need to be studied in far greater detail
330 across the CAO, especially during the winter (Roca-Martí et al., 2016; Rapp et al., 2018; Toullec
331 et al., 2021). Specifically, while several global ocean studies have assessed planktonic
332 interactions, including among bacteria and viruses, in the carbon cycle (Guidi et al., 2016),
333 similar studies are lacking in the Arctic and during the polar night (Guidi et al., 2016; Gregory et
334 al., 2019; Salazar et al., 2019).

335

336 The main source of organic carbon in the photic zone of the CAO is the photosynthetic fixation
337 of inorganic carbon (primary production) by phytoplankton (Ardyna et al., 2024) and ice algae
338 (Gradinger et al., 2024), and by chemolithoautotrophic archaea and bacteria during the arctic
339 winter and in the deeper ocean layers (Alonso-Sáez et al., 2010; Royo-Llonch et al., 2021).
340 Organic carbon supply and its partitioning between particulate and dissolved organic carbon is
341 driven by changes in ice extent and conditions, and associated changes in productivity (Thomas
342 et al., 1995; Jørgensen et al., 2015). For example, on Arctic shelves the input of sympagic
343 biogenic matter to benthos is strongly correlated with the duration of the sea-ice period (Cautain

344 et al., 2022). Particulate carbon export to depth in the deeper basins of the CAO, however, is less
345 studied. Yet, studies from the Nansen Basin and along the shelf breaks showed that grazers
346 significantly impact phytoplankton and the carbon flux composition, which is reflected in the
347 high abundance of faecal pellets (Dybwad et al., 2021; 2022; Bodur et al., 2023).

348

349 Other carbon sources to the CAO include the cross-slope transport from adjacent seas and
350 contribution of atmospheric carbon deposition (black carbon and organic carbon), which is still
351 unquantified for the CAO (Schmale et al., 2025). Cross-slope transport not only impacts the
352 transport of sediments, but also the export of particulate and dissolved organic carbon (Shen and
353 Brenner, 2018; Krumpen et al., 2019). However, little is known about this carbon transport to the
354 CAO in contrast to information available from the Chukchi Sea (Grebmeier and Harvey, 2005)
355 and the Barents Sea (Lantuit et al., 2013; Rogge et al., 2023). The increased advection of
356 Atlantic and Pacific water and organisms is expected to induce strong changes in the carbon flux
357 dynamics of the CAO. Cross-slope and along-slope transports of organic matter may also be
358 sensitive to changes in shelf-based dense water formation and stratification (Rogge et al., 2023).
359 With thinner sea ice and faster sea-ice transport and melt, the deposition of ice-rafted sediment
360 occurs closer to the shelves than in the past. In general, ice melting and potentially temperature
361 changes are hypothesised to reduce the efficiency of the biological carbon pump in the CAO
362 (von Appen et al., 2021; Bienhold et al., 2022). In addition to particulate organic carbon, changes
363 in water column stratification and water masses impact the fluxes of dissolved organic carbon
364 through modifications to the mixed layer and subduction pumps (Boyd et al., 2019).

365

366 The composition of the phytoplankton and ice algal community also plays a role in carbon export
367 via aggregation, remineralization, and ballasting, altering carbon sequestration and the biological
368 carbon pump (Lalande et al., 2014; Fadeev et al., 2021; Lalande and Dezutter, 2024). For
369 instance, with climate change, small *Phaeocystis* algae are becoming increasingly abundant at
370 the expense of larger diatoms (Assmy et al., 2017; Ardyna and Arrigo, 2020). This shift alters
371 chemical composition of metabolites from phytoplankton blooms, subsequent particle
372 composition, and thus export, because *Phaeocystis* can produce large mucilaginous aggregated
373 colonies with sinking velocities that differ from dense packages of diatoms (Engel et al., 2017;
374 Trudnowska et al., 2021). The export of *Phaeocystis* cells and derived material, however, may be
375 less efficient and more dependent on downwelling or ballasting than diatoms, leading to reduced
376 vertical carbon export (Reigstad and Wassmann, 2007; Wollenburg et al., 2018).

377

378 Ongoing changes in the composition of the organic carbon pool impact its quality as a substrate
379 for heterotrophic and mixotrophic microbial communities, which in turn might determine its fate
380 in the water column (exported versus remineralized). For instance, substantial amounts of
381 extracellular polysaccharides (Krembs et al., 2011) and proteins (Brogi et al., 2018) are produced
382 in situ in sea ice and may be released to the seawater during ice melt. The fate of carbon in the
383 system will depend not only on dissolved and particulate organic matter composition, but also on
384 the metabolic potential of the producing and degrading microorganisms (Digernes et al., 2025).
385 Environmental forcing by temperature and nitrate availability, and the multiple interactions
386 between the different microbial compartments, influence net fluxes. For example, viruses are
387 predictive of ocean carbon fluxes (Guidi et al., 2016; Kaneko et al., 2021) and can influence
388 dissolved (Kuhlisch et al., 2021) and particulate organic matter composition. Yet, how viruses

389 influence recycling versus export of organic matter — the “shunt versus shuttle” paradigms
390 (Wilhelm and Suttle, 1999; Sullivan et al., 2017; Vincent et al., 2021) — remains poorly
391 quantified. This situation is partially due to our inability to quantify the fraction of cells that are
392 actively being infected (Mruwat et al., 2020; Vincent and Vardi, 2023) and to correctly trace the
393 fate of carbon into either dissolved or particulate pools.

394

395 At higher trophic levels, carbon and lipid transfer by zooplankton and fish relies on sources of
396 carbon-dense fatty acids supplied by phytoplankton (Falk-Petersen et al., 2009). This often-
397 overlooked biochemical link needs to be understood because it is tuned by water temperature,
398 photosynthesis, and availability of nitrogen and phosphorus (Pittera et al., 2018; Holm et al.,
399 2022). Ongoing increases in water temperature are assumed to activate the catabolism of these
400 metabolites in phytoplankton early during the polar night, which may disrupt this key trophic
401 resource (Schaub et al., 2017). Increased temperature is also expected to alter fatty acid quality,
402 which is essential for the health of fish and mammals (Holm et al., 2022). Moreover, increased
403 temperature may affect plankton community composition and therefore contribute to the
404 modification of available metabolites across the food chain. Meta-lipidomic profiling allowing
405 an evaluation of carbon fluxes through lipids from primary to secondary producers is therefore
406 critically needed.

407

408 Ongoing changes in the CAO will affect not only the cycling of organic carbon. Rising
409 atmospheric CO₂ concentrations and increased carbon uptake by the oceans lower calcium
410 carbonate saturation states (mainly aragonite and calcite) and pH, with detrimental consequences
411 for shell-forming marine organisms (Doney et al., 2009). Because of low saturation states of

412 aragonite and calcite, the Arctic Ocean is considered the region most susceptible to acidification
413 and associated ecosystem impacts (Fabry et al., 2009; Terhaar et al., 2020), including carbon
414 export (Anglada-Ortiz et al., 2023). Observational studies have shown an increase in
415 anthropogenic carbon and acidification in the Eurasian Basin (Ulfsbo et al., 2018; Ericson et al.,
416 2023), and modelling studies have suggested that the mesopelagic CAO could store more
417 anthropogenic carbon than anticipated (Terhaar et al., 2020). More accurate knowledge on both
418 the physical oceanography and carbon uptake and export across the annual cycle is required to
419 better forecast the levels and effects of acidification in the CAO.

420

421 1.2.3 Sea spray aerosols

422 Sea spray aerosols consisting of sea salt, dissolved and particulate organic matter, and
423 microorganisms are produced by bubbles bursting on the sea surface due to wind stress
424 (Monahan et al., 1986). The production of sea spray aerosols has been studied in coastal Arctic
425 seas during summer, but production was assumed minimal in winter due to sea ice. However,
426 recent studies have demonstrated that sea spray aerosol is also emitted from open leads (e.g.,
427 Kirpres et al., 2019) and from blowing snow in winter (e.g., Heutte et al., 2024). In addition to
428 sea spray, trace gases like dimethylsulfide (DMS), methanethiol, and isoprene are released from
429 the ocean to the atmosphere, with constant fluxes between the atmosphere and ocean. In
430 particular, DMS production, a biogenic trace gas contributing to aerosol formation, is produced
431 by microbial degradation of dimethylsulfoniopropionate (DMSP), an abundant metabolite in
432 phytoplankton and sea-ice algae that is thought to play important roles in osmoregulation and
433 cryoprotection. Its production is related to nitrogen availability (Bullock et al., 2017). Elevated
434 concentrations of DMSP and DMS are associated with ponded first-year ice where the

435 freshwater lens beneath the melting ice acts as a physical concentrating mechanism and could
436 promote biological production in response to osmotic stress. In contrast, regions with multi-year
437 ice, characterized by low phytoplankton biomass and small flagellates, are not associated with
438 elevated concentrations of DMSP and DMS (Lizotte et al., 2020). How DMS/DMSP production
439 in the CAO will vary as it transitions from an ecosystem dominated by multi-year ice to first-
440 year ice remains an open question.

441
442 Recent studies from the *Tara* Oceans project revealed that multiple DMS/DMSP cycling genes
443 co-occurred in the same bacterial genome in metagenome-assembled genomes from polar
444 oceans. The microbial assemblages from the polar oceans correlated significantly with water
445 depth rather than geographic distance, suggesting that the differences in habitats between surface
446 and deep waters rather than dispersal limitation are the key factors shaping microbial
447 assemblages involved in DMS/DMSP cycling in the CAO (Teng et al., 2021).

448

449 1.2.4 Contaminants

450 Increasingly, contaminants are recognized as integral components of Arctic Ocean
451 biogeochemical cycles, responding sensitively to physical and ecological changes across the
452 atmosphere–sea ice–ocean system. The central Arctic atmosphere, cryosphere, hydrosphere, and
453 biosphere are heavily influenced by anthropogenic activities, with contaminants originating both
454 locally and from long-range transport via rivers, ocean currents, and atmospheric pathways. The
455 loss and thinning of sea ice, enhanced stratification, and shifts in primary productivity modify the
456 transport, transformation, and bioavailability of both legacy and emerging contaminants (Hung et
457 al., 2022; Ghiglione et al., n.d.). Processes such as ice melt, permafrost thaw, and coastal erosion

458 remobilize mercury (Hg), lead (Pb), and persistent organic pollutants (POPs) previously
459 sequestered in frozen reservoirs, increasing their fluxes to the ocean (Schaefer et al., 2020;
460 Rogalla et al., 2025). Seasonal stratification regulates contaminant exchange between surface and
461 deeper waters, while the unique vertical structure of the Arctic Ocean leads to elevated
462 methylmercury concentrations at shallower depths compared to other oceans, enhancing uptake
463 by phytoplankton and subsequent biomagnification (Heimbürger et al., 2015; Schartup et al.,
464 2020).

465
466 Microbial communities, which are key drivers of nutrient and carbon cycling, also mediate
467 contaminant transformations, including Hg methylation and the degradation of organic
468 pollutants, processes that are being reshaped by warming (Villar et al., 2020; Ghiglione et al.,
469 n.d.). The increasing burden of chemicals of emerging Arctic concern, such as per- and
470 polyfluoroalkyl substances (PFAS) and micro- and nanoplastics, adds further complexity. These
471 substances can act as contaminant carriers, alter microbial activities, and influence
472 biogeochemical feedbacks (Kettner et al., 2019; Materic et al., 2022; Ghiglione et al., n.d.).
473 Atmospheric pathways remain a key driver of long-range contaminant delivery and cycling,
474 linking emissions at lower latitudes with Arctic deposition (Dastoor et al., 2022). Similarly, snow
475 and sea-ice processes govern contaminant retention and release, affecting both oceanic inputs
476 and ecosystem exposure (Huang et al., 2023; Vancoppenolle et al., n.d.). Collectively, these
477 interactions highlight the need to integrate contaminant dynamics within the broader framework
478 of Arctic Ocean stratification, sea-ice evolution, and ecosystem function. Future surveys need to
479 generate high-resolution, year-round observational data to refine our understanding of

480 contaminant sources, transport, and fate, and to assess the ecological and human health risks
481 posed by continued emissions and climate change.

482

483 1.3 Biodiversity and trophic interactions

484 Fundamental knowledge gaps in biodiversity and connectivity of communities, from ecosystem
485 to individual species levels, persist in the CAO. There are compelling examples of ecosystem
486 perturbations under climate change, such as the northward expansion of temperate species (from
487 microalgae to marine mammals) with increased Atlantic water transport (Fossheim et al., 2015;
488 Paulsen et al., 2016; Neukermans et al., 2018; Oziel et al., 2020; Husson et al., 2024). In
489 addition, many arctic organisms are highly vulnerable to warmer temperatures (Deb and Bailey,
490 2023), which are expected to continue to increase in the coming decades (Post et al., 2019).
491 However, most ecological studies have focused on Arctic shelves and did not include the deep
492 basins of the CAO. A first pelagic trawling study in the Nansen and Amundsen Basins, however,
493 revealed the presence of sub-Arctic and Atlantic-derived species all the way to 87.5°N
494 (Ingvaldsen et al., 2023). Documenting biodiversity and connectivity in the CAO, using both
495 multi-omics and functional trait perspectives, is thus critical, especially during the transition
496 periods in spring and fall, for predicting the impacts of climate change on the CAO pelagic
497 ecosystem functioning.

498

499 1.3.1 Microbiomes

500 Photosynthetic primary producers in the Arctic comprise sympagic ice algae and drifting pelagic
501 phytoplankton. Both microalgal communities are taxonomically diverse, but pelagic diatoms

502 generally dominate both abundance and species richness in spring (Poulin et al., 2011; Crawford
503 et al., 2018). Commonly observed bloom species are pennate diatoms in the genera
504 *Fragilariopsis* and *Nitzschia* and centric diatoms in the genera *Chaetoceros* and *Thalassiosira*, as
505 well as the large colony-forming centric diatom *Melosira arctica*. Blooms of the prymnesiophyte
506 *Phaeocystis pouchetii* have also been observed, while the endemic alga *Micromonas polaris* is a
507 common species following blooms and in oligotrophic open water regions (Smith et al., 1991;
508 Ardyna and Arrigo, 2020; Hop et al., 2020; Lovejoy et al., 2007). With a longer open water
509 season in some regions, a second phytoplankton bloom likely dominated by dinoflagellates
510 (Freyria et al., 2021) can also occur in early autumn (Ardyna et al., 2014). However, models
511 suggest that enhanced stratification in the deeper basins result in the suppression of the nitracline
512 and deepening of the subsurface chlorophyll maximum (Steiner et al., 2016).

513 While some species appear to be constrained to either sympagic or pelagic life, the distinction
514 between communities is not strict. Pelagic phytoplankton can be incorporated into sea ice and ice
515 algae can contribute to the early summer phytoplankton bloom once released from the ice (see
516 other articles in this special collection). Molecular and community studies on algal adaptation
517 and survival in sea ice are needed (Freyria et al., 2024).

518 Polar microbial communities consist of distinct microbiomes, which differ from tropical and
519 equatorial regions (Ibarbalz et al., 2019; Boulton et al., 2025). In general, species and gene
520 richness decrease towards polar regions (Fuhrman et al., 2008; Salazar et al., 2019). The most
521 drastic difference between the Arctic, including the CAO, and other oceans is that
522 photoautotrophy is dominated by picoeukaryotes. Also, *Prochlorococcus* and *Synechococcus*,
523 which dominate the smallest phytoplankton size class in most of the World Ocean, are absent

524 from the CAO (Lovejoy et al., 2007; Li et al., 2009; Duncan et al., 2022). The extent of
525 prokaryotic diversity is difficult to assess as drastic shifts in bacterial and archaeal communities
526 have been described from low to high latitudes, with entire clades endemic to polar regions
527 (Galand et al., 2010; Salazar et al., 2019; Priest et al., 2023), displaying up to 83% of
528 unclassified prokaryotic genomes at the species level (Royo-Llonch et al., 2021). As for most
529 high Arctic studies, knowledge of microbial communities mainly originates from surveys
530 conducted over Arctic shelves during the ice-free season. How microbial communities change
531 through the entire seasonal cycle in the CAO remains poorly studied (Wietz et al., 2021; 2024),
532 but the contribution to the pelagic microbiome originating from sea ice could increase during the
533 transitional periods in spring and fall (Priest et al., 2023). A late summer transect across the
534 Nansen and Amundsen basins indicated regional differences in protist and plankton communities
535 related to regionality in stratification, nutrients, and light conditions (Kohlbach et al., 2025).
536 Models can also help forecasting how arctic microorganisms may react to environmental changes
537 (Lennon et al., 2024).

538

539 Interestingly, the Arctic Ocean community interactome has shown the highest connectivity
540 compared to other biomes, perhaps explained by a potentially higher prevalence of mixotrophic
541 microbial eukaryotic plankton in the Arctic (e.g., mixotrophic flagellates and ciliates), or by
542 more complex food web structures, albeit characterised by specific energy flow pathways
543 dominated by a small number of species (Chaffron et al., 2021). For viruses in the Arctic Ocean,
544 community diversity differs drastically from other biomes and is elevated for both DNA viruses
545 (largely infecting prokaryotes; Gregory et al., 2019) and RNA viruses (largely infecting
546 microbial eukaryotes; Dominguez-Huerta et al., 2022; Zayed et al., 2022). These findings

547 suggest that the virus community structure follows that of their microbial hosts and that the polar
548 regions represent biological hotspots for viral diversity. These global patterns of marine
549 microbial diversity, together with the high impact of climate warming in the Arctic Ocean, make
550 the region a reservoir of microbial diversity of planetary importance that faces an uncertain
551 future.

552

553 Microbial eukaryotic species do not live in isolation but rather establish numerous cell-cell
554 interactions that can significantly impact their fate and therefore role in the ecosystem (Vincent
555 et al., 2021). For instance, symbiotic relationships between eukaryotic microalgae and closely
556 associated bacteria within their ‘phycosphere’ expand the host’s metabolism (Amin et al., 2012)
557 or ice-binding properties (Guo et al., 2017). Such associations thus likely play an important role
558 in the CAO (Duncan et al., 2022), including for eukaryotic cell evolution (Coale et al., 2024) and
559 global biogeochemical cycling (Tschitschko et al., 2024). Symbiotic relationships are of
560 particular relevance for abundant phytoplankton in the Arctic, such as diatoms that interact with
561 viruses, bacteria, chytrids (Kilias et al., 2020), or ciliates, but little has been reported on such
562 relationships in polar environments.

563

564 Only recently, genome-resolved analyses based on metagenomes and metatranscriptomes have
565 been able to explore the metabolic capabilities of specific bacterial and archaeal taxa (Royo-
566 Llonch et al., 2021). Such analyses highlighted the prevalence of mixotrophy within bacteria and
567 archaea and identified the active members of arctic microbial communities, facilitating the
568 characterization of arctic sentinel bacterial and archaeal taxa. Mixotrophy in prokaryotes can

569 take the form of photoheterotrophy in bacteria or archaea containing proteorhodopsin (Béjà et
570 al., 2000), harbouring bacteriochlorophyll *a* (aerobic anoxygenic phototrophic; Kolber et al.,
571 2000), or carrying out chemolithoautotrophic inorganic carbon fixation and heterotrophy
572 (Alonso-Sáez et al., 2010).

573

574 1.3.2 Higher trophic levels

575 Mesopelagic sound scattering layers from zooplankton and fish have been observed across the
576 CAO (Snoeijs-Leijonmalm et al., 2021). Four large species of copepods, *Calanus hyperboreus*,
577 *C. glacialis*, *C. finmarchicus* and *Metridia longa*, represent 70–90% of the mesozooplankton
578 abundance (Thibault et al., 1999 and references therein; Wold et al., 2025) and ensure secondary
579 production, which makes them crucial mediators between primary production and higher trophic
580 levels. In addition to ice amphipods, such as *Apherusa glacialis* (Kohlbach et al., 2016),
581 armhook squid (Snoeijs-Leijonmalm et al., 2022), euphausiids, pelagic amphipods, and
582 gelatinous zooplankton dominate the macrozooplankton assemblage in the Nansen Basin, while
583 copepods, amphipods, euphausiids, chaetognaths and gelatinous zooplankton dominate in the
584 Amundsen Basin (Ingvaldsen et al., 2023; Wold et al., 2025). In a future CAO, the abundance of
585 gelatinous zooplankton could increase with climate change (Geoffroy et al., 2019; Lombard et
586 al., 2024), which could redirect the carbon flows towards different links of the food web.
587 However, more baseline data on the current assemblages and trophic interactions are required to
588 assess impacts of future changes.

589

590 The abundance and diversity of fish is relatively low in the CAO but could increase with ongoing
591 sea-ice reduction and increased advection of boreal species northward. As a precautionary

592 measure, a 16-year moratorium on commercial fisheries, The International Agreement to Prevent
593 Unregulated Fishing in the High Seas of the Central Arctic Ocean, has been ratified by the
594 European Union and nine other countries in 2021 (Vylegzhanin et al., 2020). This agreement
595 aims to further our understanding of an ecosystem that is emerging below a retreating sea-ice
596 cover before evaluating the possibility for sustainable commercial fisheries. At present, Arctic
597 cod (*Boreogadus saida*) and, to a lesser extent, its close relative ice cod (*Arctogadus saida*)
598 strongly dominate the pelagic fish assemblage, both near the ice interface (David et al., 2016)
599 and at mesopelagic depths (Ingvaldsen et al., 2023). However, whether the *Boreogadus* and
600 *Arctogadus* stocks from the CAO reproduce locally or are advected from shelf areas is not
601 known (David et al., 2016). The importance of sea ice for early life stages of the key forage
602 species Arctic cod is also debated (Geoffroy et al., 2023), with contradictory information that
603 they are ice-associated (David et al., 2016) or can benefit from a shorter ice season (Bouchard et
604 al., 2017). Other pelagic fish captured in the CAO include Atlantic cod (*Gadus morhua*), Glacier
605 lanternfish (*Benthosema glaciale*), Greenland halibut (*Reinhardtius hippoglossoides*), haddock
606 (*Macrocephalus aeglefinus*), black seasnail (*Paraliparis bathybius*), and redfish (*Sebastes*
607 *mentella*) (Snoeijs-Leijonmalm et al., 2022; Ingvaldsen et al., 2023).

608

609 For many animals, the Arctic is a well-stocked larder. They migrate long distances to take
610 advantage of the high biomass and lipid-rich diet that originate from energy transferred through
611 lipid-rich copepods that graze on algae (Falk-Petersen et al., 2009). Yet, most marine mammals
612 observed in the CAO remain at the periphery, close to the ice edge (e.g., Lowry et al., 2019),
613 where they feed on pelagic fish or benthic organisms on the shelf and slope (Bluhm and

614 Gradinger, 2008). In general, the effect of climate change and reduced sea-ice extent on Arctic
615 and ice-associated mammals and birds is predominantly negative (Steiner et al., 2021).

616

617 1.3.3 Chronobiology

618 Chronobiology is the study of periodic phenomena in living organisms. Biological rhythms are
619 found in almost all species and are believed to be evolutionary adaptations to cyclical variations
620 of the environment. Thus, chronobiology examines the mechanisms of the biological clocks and
621 their interactions with other physiological systems (Canadian Society for Chronobiology, 2025).
622 At temperate latitudes, biological rhythms are highly attuned to circadian day-night cycles. In the
623 CAO, the extreme light regime resulting from both the alternation of polar night and midnight
624 sun periods and the heterogeneous sea-ice cover push the limits of how biological clocks interact
625 with the environment (Cohen et al., 2020).

626

627 Oceanographic and biological observations show that phytoplankton adopt various strategies to
628 adapt to changes in light throughout the day and seasons. Microalgae, namely diatoms, survive
629 periods of darkness of up to 6 months (Kvernvik et al., 2018; Lacour et al., 2019; Morin et al.,
630 2020; Sciandra et al., 2022; Joli et al., 2023), while preserving the ability to rapidly return to
631 photosynthetic growth on exposure to even minimal light. During the polar night, when
632 irradiance levels do not allow autotrophy, normally phototrophic prokaryotes and protists have
633 been assumed to switch to heterotrophy to grow (i.e. mixotrophy), but with lower net
634 productivity (Bruhn et al., 2024). Phytoplankton growth under sea ice after the polar night can
635 start as early as February in Baffin Bay (Randelhoff et al., 2020), which is consistent with the
636 lowest light requirements for photosynthesis calculated by Raven et al. (2010) and reported for

637 ice algae by Hancke et al. (2018). More recently, improved sensors detected photosynthesis in
638 the CAO as early as March and at lower light requirements than reported by Hancke et al. (2018)
639 and Hoppe et al. (2024). Adaptation to different photoperiods could then contribute to
640 community renewal and species succession along the seasons, as suggested by observations in
641 temperate regions (Longobardi et al., 2022). Different photoacclimation strategies were
642 documented on polar species depending on whether day length is shorter or longer (Guérin et al.,
643 2024). Most archaea, bacteria and eukaryotes are strongly affected by high latitude seasonality,
644 with evidence from cell counts, biomass distribution and community composition (Iversen and
645 Seuthe, 2011; Ladau et al., 2013; Onda et al., 2017). Gene expression patterns are also affected.
646 Notably, photosynthesis and light-harvesting functions show high seasonal variation in their
647 expression (Wutkowska et al., 2023), from nearly undetectable in January to highly expressed in
648 July.

649
650 Pelagic zooplankton and fish in the CAO conduct seasonal vertical migrations but, in contrast to
651 temperate regions, high-amplitude diel vertical migrations are limited to short periods in spring
652 and fall (Gjørseter et al., 2017; Geoffroy et al., 2019; Bandara et al., 2021; Priou et al., 2021;
653 Snoeijs-Leijonmalm et al., 2022). Diel vertical migration of zooplankton can also be driven by
654 the moonlight cycle during the polar night (Last et al., 2016). Through vertical migrations, both
655 zooplankton and fish contribute to carbon export through faecal pellets and respiration, with
656 seasonal changes in their vertical distribution directly impacting the biological carbon pump.
657 Increased under-ice irradiance in spring and fall due to less sea-ice and snow attenuation could
658 impact the vertical distribution of pelagic organisms and keep them deeper for longer (Flores et
659 al., 2023).

660

661 The mechanisms by which polar species adapt to different photoperiods are still poorly
662 understood. However, understanding these processes is essential for accurately evaluating the
663 effects of changes in snow and sea ice, which could alter the light environment and influence the
664 entire photosynthetic community. In terrestrial organisms, circadian clocks and photoreceptors
665 are at the heart of photoperiodic regulation (Song et al., 2014). The circadian clock components
666 have been elucidated so far only in a few marine animals and microalgae (Häfker et al., 2022),
667 but remain uncharacterized in polar species. Reports on terrestrial organisms emphasize the
668 importance of natural genetic variation in circadian clocks and photoreceptors for adaptation
669 over large areas (Millar, 2016). Recent metagenomic and metatranscriptomic studies in
670 picoeukaryote green algae showed unexpected circadian component diversity across latitudes
671 and a lack of functional clocks in tropical strains, underscoring the diversity of photoperiod
672 adaptations in marine phytoplankton (Rigonato et al., 2025).

673

674 A diverse range of signaling photoreceptors, which detect light intensity and wavelength to
675 control biological functions, have been found in the genomes of marine organisms and
676 environmental genomic datasets (Jaubert et al., 2017; Coesel et al., 2021). These include blue
677 light photoreceptors such as Cryptochrome photoreceptor, Aureochromes, Light-Oxygen-
678 Voltage histidine kinase families, and Phytochrome photoreceptors, which are known for
679 integrating light and temperature signals in plants. The diatom phytochrome, found at high
680 latitudes but absent from equatorial regions (Duchêne et al., 2025), may play a role in adapting to
681 different photoperiods. Marine algae and bacteria also contain green-absorbing rhodopsins,
682 highly diverse light sensors with a retinal chromophore, involved in various light-driven energy
683 and sensory processes (Rozenberg et al., 2021). Originally discovered in bacteria, light-driven
684 proton pump rhodopsins, which are considered major contributors to solar energy capture in the
685 sea, are also found in the genomes and transcriptomes of various marine microbes (Koh et al.,
686 2010), including some *Polaribacter* lineages (González et al., 2008; Royo-Llonch et al., 2021)
687 and Arctic native eukaryotes like dinoflagellates, stramenopiles, haptophytes, and cryptophytes
688 (Vader et al., 2018). The xanthorhodopsin variant from the polar diatom *F. cylindrus* has been
689 shown to influence biomass productivity under iron-limiting conditions (Strauss et al., 2023).
690 The role of proteorhodopsin-based photoheterotrophy in the CAO remains unclear, but it is

691 believed to be crucial for enhancing light absorption and supporting photoheterotrophy in low-
692 light environments. More broadly, photoreceptors are expected to play an important role in
693 restoring photosynthesis and growth capacity when returning to light and in entraining the
694 circadian clock to daily and seasonal cycles.

695

696 1.3.4 Sea ice-pelagic interactions

697 The cryo-pelagic coupling is generally less studied than pelagic ecosystems because logistical
698 difficulties prevent detailed and undisturbed sampling under the ice. However, sympagic fauna
699 play a crucial role in transmitting carbon energy and high-quality organic material from the ice-
700 water interface to the pelagic and benthic food webs (Amiriaux et al., 2021; 2023). Sea-ice algae
701 are key contributors to net primary production and could contribute up to 57% of total primary
702 production in the Arctic (Gosselin et al., 1997). Ultimately, ice algae significantly support the
703 entire marine food web, including marine mammals, providing over 50% of total carbon
704 requirements throughout the year and across all Arctic Ocean regions (Kohlbach et al., 2016;
705 Kunish et al., 2021; Koch et al., 2023). However, uncertainty in estimates of productivity by sea-
706 ice algae are extremely high, due to their patchy distribution, technological challenges in
707 sampling, and difficulties in obtaining in situ productivity estimates (Fernández- Méndez et al.,
708 2014; Katlein et al., 2015). Modelling tools can provide insight into ice algal growth and
709 distribution (Hayashida et al., 2021; Haddon et al., 2024). However, to date there are no methods
710 comparable to remote sensing to monitor the large-scale occurrence of ice algal production,
711 limiting our ability to quantify their contribution and understand their regulation.

712

713 On Arctic shelves, sea-ice reduction generally diminishes sympagic-benthic coupling due to the
714 reduction of large aggregates sinking from the sea ice to the benthos. The longer open water
715 season rather benefits pelagic organisms and promotes remineralization in the water column
716 (Grebmeier et al., 2006; Zhulay et al., 2023). In the deep basins of the CAO, organic material can
717 sink to depth and sequester carbon over long time scales. However, Lalande et al. (2014)
718 compiled under-ice carbon flux measurements and suggested that, in the CAO, nutrient
719 limitation would constrain carbon export in the deep basins despite reduced sea ice and increased
720 light, in contrast to the more productive shelves. Additionally, new physico-chemical conditions
721 in the sea ice and underlying water are expected to alter algal biomass and succession, export
722 pathways, and degradation processes (Rontani et al., 2018; 2021; Burot et al., 2021), including
723 both biotic (bacterial and zooplankton degradation) and abiotic mechanisms (photo-oxidation
724 and autoxidation). Important questions thus remain for the CAO, including whether ice algal
725 production increases with thinning sea ice, how its nutritional quality and role in ecosystem
726 functioning might change, and whether there are sufficient nutrients to support increased pelagic
727 phytoplankton production with the combined effect of sea-ice retreat and increased wind-driven
728 mixing (e.g., Lincoln et al., 2016; Lund-Hansen et al., 2020).

729

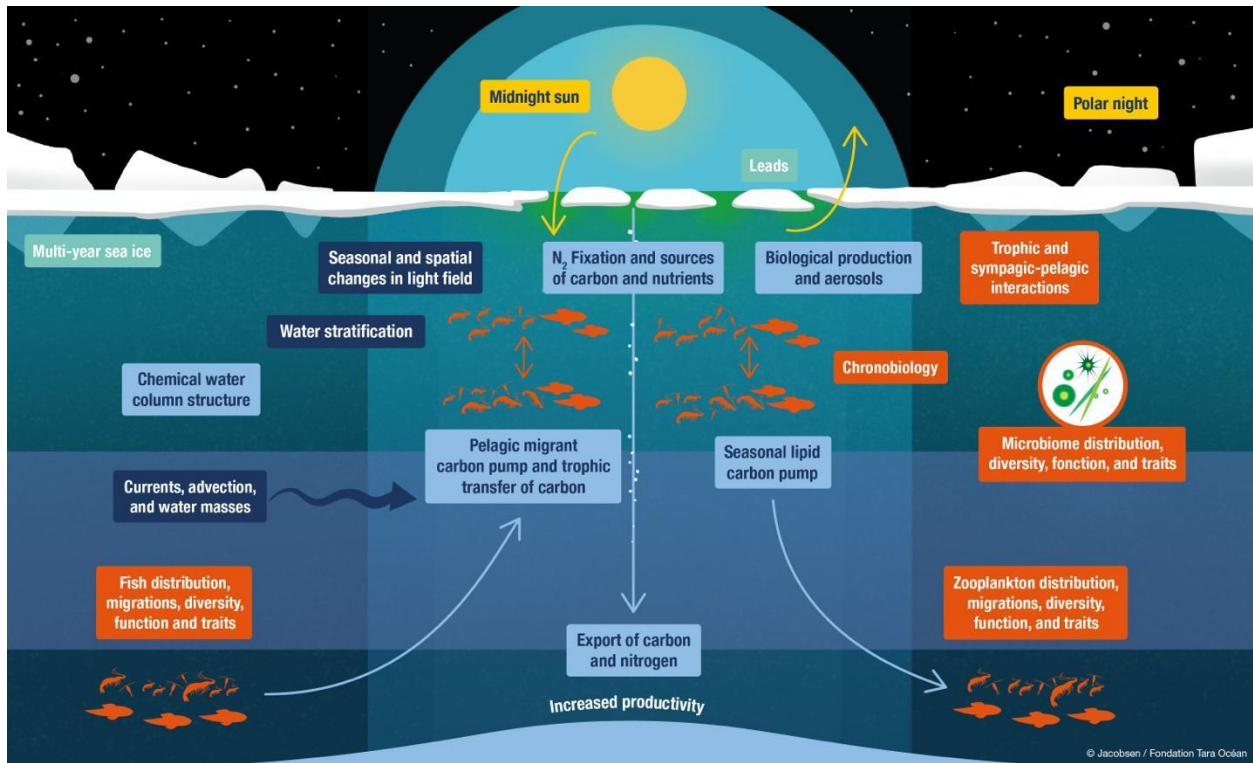
730 The mobile heterogeneous sea ice of the CAO contributes to the dispersion of pelagic organisms.
731 Ice cover contributes to the exporting of microbial clades from the surface to the deep sea in the
732 Arctic and provides strong vertical microbial connectivity (Fadeev et al., 2021). Quiescent
733 diatoms in older sea ice contribute to the algal community in leads and young Arctic sea ice
734 (Kauko et al., 2018). Sea ice also transports early life stages of pelagic and benthic organisms,
735 including ciliates, foraminifera, rotifers, platyhelminthes, harpacticoid copepods and nematodes

736 (Kiko et al., 2017, Marquardt et al., 2023), in addition to ice amphipods (Gulliksen and Lønne,
737 1991) and fish (David et al., 2016). Therefore, continuous sea-ice loss may decrease the
738 horizontal and vertical export efficiency, with potential negative repercussions for Arctic deep-
739 sea ecosystems and pelagic biodiversity (Fadeev et al., 2021), particularly for species with low
740 dispersal capacities (Kiko et al., 2017).

741

742 2. Future research directions: scientific scope

743 Building on the literature review provided in Section 1, we here introduce a strategy to increase
744 our understanding of the pelagic communities and processes in the CAO. We identify specific
745 research questions and hypotheses from which to develop future scientific studies in the CAO.
746 Specifically, utilising *Tara Polar Station*, we suggest an approach to address knowledge gaps
747 related to seasonality in ocean physical conditions, biogeochemical fluxes, and biodiversity and
748 trophic interactions across a complete 16-month transpolar drift during the first Tara Polaris
749 expedition (Figure 2). Long-term research questions (>5 years) are addressed in another article of
750 this special collection (Ardyna et al., n.d.).



751

752 **Figure 2. Pelagic processes in the Central Arctic Ocean for which knowledge gaps persist.**

753 Ocean physical conditions (dark blue), biogeochemical fluxes (light blue), and biodiversity and
 754 trophic interactions (orange). All processes listed here will be addressed during the Tara Polaris I
 755 expedition.

756

757 The overarching objective of the pelagic studies to be conducted during the Tara Polaris I
 758 expedition is to *assess how hydrographic and sea-ice conditions drive pelagic biogeochemical*
 759 *and ecological functioning in the CAO*. Specific research questions and hypotheses related to
 760 each pelagic component have been identified (Tables 1 and 2).

761

762 **Table 1.** Research questions and hypotheses related to the physical environment and
763 biogeochemical fluxes in the Central Arctic Ocean (CAO).

764

How are changes in upper ocean stratification, meltwater layers, and sea ice influencing pelagic habitats in the CAO?

Hypothesis

Increased advection of Atlantic and Pacific waters contributes to sea-ice reduction and modifies all pelagic habitats.

How important are sea-ice coverage and N₂ fixation in driving nutrient fluxes in the CAO?

- How are changes in timing and intensity of sea-ice formation impacting nutrient fluxes?
- How are microorganisms driving N₂ fixation related to sea ice?

Hypotheses

- A reduced ice cover and longer productive season increase the role of regenerative and microbial food webs, reducing the role of N₂ fixation.
- Despite sea-ice reduction, stratification maintains low vertical fluxes of nutrients compared to other oceans.

How are water mass distribution, upper ocean stratification, sea ice, lightscape, and biological community compositions impacting carbon export to depth and transfer across trophic levels?

- What are the seasonal characteristics of the vertical matter flux, and how do they link to the physical environment, primary production, and the plankton communities?
- Which plankton are the most important carbon flux-predicting taxa, and how do they change seasonally?
- What is the role of carbon-dense fatty acids and glycerolipids in trophic networks?

Hypotheses

- Advection of warmer Atlantic water will have cascading impacts on the timing, quantity, and composition of the sinking organic matter from upper ocean layers.
- Viruses are as predictive of carbon flux in the CAO as they are for the global oceans.

- Temperature increase can lead to exhaustion of lipid storage earlier during the polar night and interrupt lipid-dependent trophic interactions in food webs.

What are the roles of sea ice, pelagic-sympagic coupling, and biological production on sea spray aerosols in the CAO?

- What climate-active molecules are produced biogenically?
- What are the origins and concentrations of marine organic aerosols in winter?
- What are the main sources of DMS, methanethiol, and DMSP, and how, when, and how much are transferred to the atmosphere?
- Which genes are expressed in relation to DMSP production?

Hypotheses

- Newly open water and lead formation in winter contribute significantly to aerosol production.
- Differences in habitats between surface and deep waters rather than dispersal limitation are the key factors shaping microbial assemblages involved in DMS/DMSP cycling.

765

766 **Table 2.** Research questions and hypotheses related to trophic interactions in the Central Arctic
767 Ocean (CAO)

How are biodiversity, functions, and traits of pelagic communities linked to physical oceanography and sea ice?

- What are the seasonal shifts in community composition and function (from microbiome to fish)?
- What is the role of sea ice in maintaining biodiversity and connectivity?
- Is there more symbiosis in the CAO than elsewhere?
- How are symbiotic relationships changing over the seasons?
- Is advection of boreal species modifying energy pathways and trophic networks?
- Are local and advected populations competing?
- Are metazoans more vulnerable to virus and pathogen infections under warmer conditions?

- To what extent do viruses alter the microbiome via lysis, horizontal gene transfer, and metabolic reprogramming?
- How are metabolic interactions within microbial communities reacting to changes in salinity during formation and melting of sea ice?

Hypotheses

- Sea ice is a vector that contributes to increase significantly the diversity and abundance of the pelagic microbiome in spring and fall.
- Longer productive seasons do not mean more efficient energy transfer to the food webs.
- Local and advected populations coexist, with niche partitioning and distinct spatio-temporal distribution patterns.

How do seasonal changes in sea ice and lightscape impact chronobiology?

- How are local sea ice and lightscape conditions modifying the timing of the ice algal and phytoplankton blooms?
- Which components of the microbial communities are active during each season?
- What are the responses of polar organisms during different light and photoperiodic conditions- across seasons?
- What is the role of photoreceptors and endogenous clocks during extreme and variable light conditions?
- How do gene flows impact chronobiology and ontogeny across seasons?
- What is the lower light limit for autotrophic activity and what is the role of mixotrophy?
- How ubiquitous is photosynthetic biomass (pelagic and sympagic) during polar night and to what extent is the photosynthetic capacity down-regulated?
- Are changes in the timing of the blooms resulting in more mismatch events for zooplankton?

Hypotheses

- Changes in the photoperiod is a critical environmental cue that, thanks to photosensing and endogenous timekeepers, drives phenology and species succession of Arctic populations.
- Photoreceptors and circadian clock components establish biological rhythms across seasons and are targets of adaptation to different sea-ice and lightscape conditions.
- Weak-light photosensing and rhodopsin-based photoheterotrophy are implicated in restoring photosynthesis and growth at the end of the polar night.
- Mixotrophy is more prevalent in protists than prokaryotes.

- Seasonal gene flow between species and ecotypes via migration, horizontal gene transfer, or viral-mediated transfer shape circadian clock adaptation and regulation, thereby modulating seasonal responses in growth, development, and reproduction.
- The timing of Arctic copepodite production is tightly tied to the ice-algal bloom, while boreal copepodite species are synchronized with the phytoplankton bloom.
- Advected zooplankton from the south (e.g., *Calanus finmarchicus*) take advantage of the new phytoplankton blooms in the late productive season.
- Interactomes increase through metabolic exchanges during the polar night.

Do fish reproduce in the Central Arctic Ocean, and how do they occupy the under-ice habitat?

- Are fish laying eggs and hatching in the basins?
- Is the abundance of pelagic fish sufficient for sustainable commercial fisheries?
- How do fish and their zooplankton prey occupy the sympagic and pelagic habitats across seasons?

Hypotheses

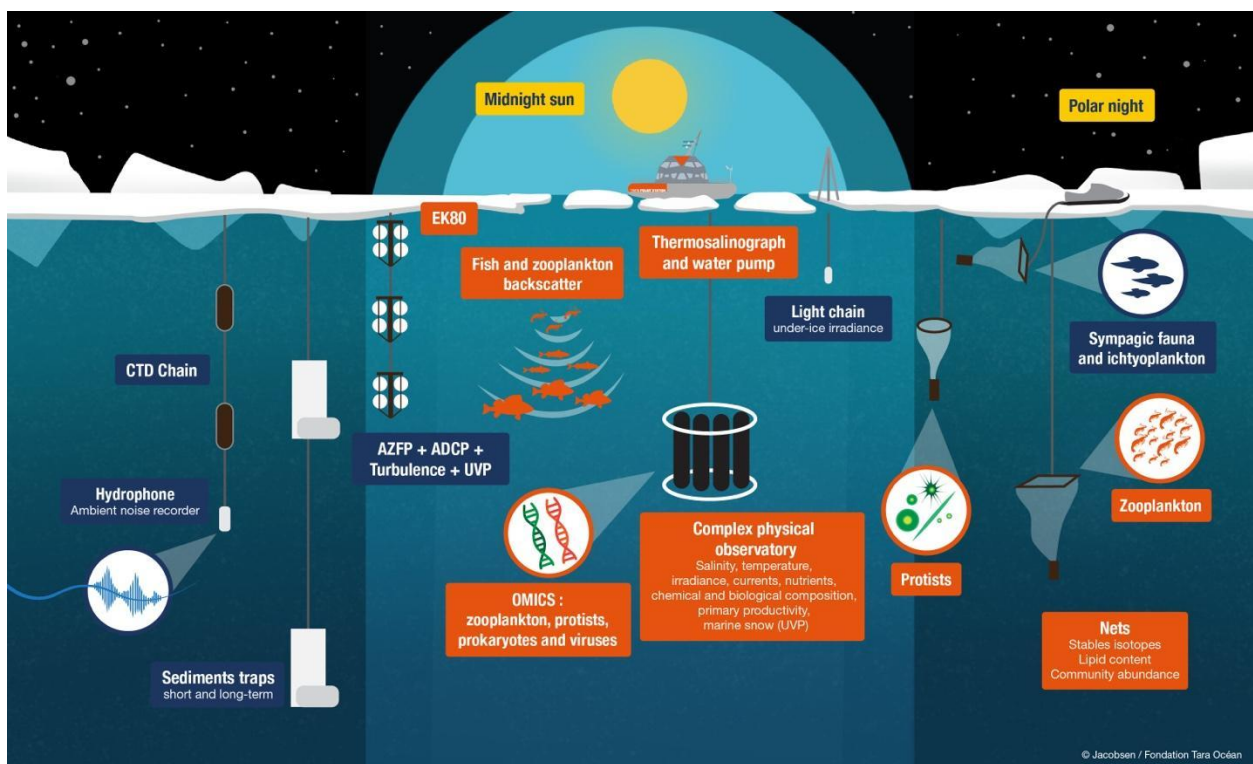
- Fish, including Arctic cod, do not reproduce in the Central Arctic Ocean and are only advected from shelf areas.
- Fish abundance is too low for sustainable commercial fisheries.
- Only early life stages of fish occupy the sympagic zone.

768

769 **3. Approach**

770 Measurements and sampling will be partly conducted from the moonpool of *Tara Polar Station*
 771 and from instruments deployed from the ice (Figure 3). Observations from the moonpool will be
 772 concentrated on the hull-mounted thermosalinograph and echosounder, as well as sensors
 773 mounted on the conductivity-temperature-depth (CTD) rosette. Water samples will be collected
 774 with the rosette, and plankton samples will be collected with nets deployed from the moonpool.

775 Sampling from the ice outside the footprint of *Tara Polar Station* will include CTD sensors with
 776 acoustic Doppler current profilers and turbulence sensors, short- and long-term sediment trap
 777 deployments with underwater vision profilers, a self-contained high-frequency echosounder
 778 (acoustic zooplankton and fish profiler), and under-ice ichthyoplankton net deployments.
 779 Sampling frequency will vary from daily to weekly. Additional sampling with higher resolution
 780 will be conducted with an extended team during the crucial transition periods in spring and early
 781 fall (Tables S1–S3).



782
 783 **Figure 3. Pelagic deployments from and around *Tara Polar Station* planned for the *Tara***
 784 ***Polaris I* expedition.** Deployments from (orange) *Tara Polar Station* include the hull-mounted
 785 echosounder (EK80) and the rosette with conductivity-temperature-depth (CTD) sensors,
 786 underwater vision profiler (UVP), nets, and more. Surrounding deployments (blue) include an
 787 acoustic zooplankton and fish profiler (AZFP), acoustic Doppler current profilers (ADCPs), and
 788 more.

789

790 Our approach will combine direct measurements with laboratory analyses. Using state-of-the-art
791 omics, culturing and imagery approaches, including long read sequencing metagenomics (Oxford
792 Nanopore) and single cell genomics, will be strongly emphasized. An exploration of global
793 community multi-omics (i.e., barcodes, genomics, transcriptomics, proteomics, and
794 metabolomics) for pelagic plankton communities in the CAO will benefit from the integrative
795 approach in microbial oceanography that was spearheaded by *Tara Oceans* (Alberti et al., 2017).
796 Specific focuses will be on i) coupling single cell imaging and isolation with omics and ii) taking
797 advantage of the possibility to monitor real-time changes in community composition via portable
798 long read sequencing of specific genetic markers (e.g., 16S, 18S, cytochrome *c* oxidase subunit
799 I) to monitor ecosystem responses in real time and to adapt analyses accordingly.

800

801 Ultimately, environmental measurements, biological observations and experiments need to be
802 integrated to understand the functioning of the ecosystem and test future scenarios. We will
803 synthesize and integrate observations and laboratory analyses using an ecosystem modelling
804 approach to quantify the flow of energy through the CAO ecosystem (Eddy et al., 2021). At
805 present, an ecosystem model for the CAO that integrates either the midnight sun or the polar
806 night period has not been developed. We will use the Ecopath with Ecosim ecosystem modelling
807 approach to represent energy flow from primary producers through the food web (Christensen
808 and Walters, 2004). Ecopath with Ecosim is a mechanistic model based on mass balance of
809 carbon or wet mass that has been applied to answer questions about ecosystem structure and
810 function, fisheries impacts on ecosystems, and climate change impacts on ecosystems (Worm et
811 al., 2009; Tittensor et al., 2018). Building on this framework, we will examine contaminant

812 dynamics, focusing on mercury and its transformation into methylmercury, which biomagnifies
813 in Arctic food webs (Gillies et al., 2024). Development of an ecosystem model for the CAO will
814 allow for hypothesis testing about ecosystem structure and function. After model development,
815 simulations can be run of scenarios of changing sea ice and primary production, with potential
816 impacts on fisheries. The model can also help to prioritize future sampling efforts to address
817 critical data gaps that may emerge or energy pathways and/or mechanisms that are highly
818 uncertain or sensitive.

819

820 4. Connectivity with other themes

821 Undeniably, pelagic processes in the CAO relate directly to the atmosphere and sea-ice
822 environment. Pelagic contaminants (Ghiglione et al., n.d.) are delivered via similar pathways as
823 carbon and nutrients, including atmospheric deposition, sea-ice melt, and lateral transport
824 (Schmale et al., 2025). The exchanges are reciprocal, with sea spray aerosols and biogenic trace
825 gases transferred to the atmosphere from bubble bursting and outgassing, respectively, at sea
826 surface. Atmospheric nitrogen can also be deposited in the form of nitrogen oxides, ammonia,
827 and ammonium (Reay et al., 2008). Snow and ice thickness, including melt ponds, directly
828 influence primary production, diel vertical migrations of pelagic organisms, and the retention or
829 release of contaminants by modifying the underwater lightscape and ice–ocean interface.
830 Colonisation from sea ice and interaction between the pelagic and sympagic ecosystems,
831 including the contribution of ice algae to carbon export, further demonstrate the clear links
832 between sympagic and pelagic habitats (Vancoppenolle et al., n.d.). Dust and other aerosols
833 transported in the atmosphere to the Arctic from lower latitudes, e.g., from wildfires, can amplify

834 phytoplankton blooms (Ardyna et al., 2022), ballast marine snow, and carry associated
835 contaminants. Finally, pelagic studies to be conducted during Polaris I in 2026–2027 will
836 provide baseline information on oceanography, biodiversity, carbon export, and contaminant
837 distributions against which long-term changes can be assessed over the next 20 years (Ardyna et
838 al., n.d.).

839

840 5. Foreseen outcomes

841 Using a combination of both traditional sampling methods and state-of-the-art omic and imagery
842 approaches, the Tara Polaris expeditions provide an opportunity to understand seasonal changes
843 in traits, functional roles, and trophic interaction of key species across multiple trophic levels,
844 especially during the polar night, which remains poorly documented in the CAO. The drifts will
845 also open a window on the transition periods between seasons, as their timing influences many
846 pelagic processes that are difficult to catch by ship-based sampling. Participation in the Tara
847 Polaris program will foster a truly interdisciplinary approach for pelagic studies during which a
848 multitude of measurements are synchronised in space and time. In addition to providing new
849 information on the physical environment, biogeochemical flux processes, biodiversity and active
850 traits of all trophic levels across different basins of the CAO, this research program will
851 ultimately allow for a better understanding of the role of the CAO in the global carbon and
852 nutrient cycles. Finally, through new observations and modelling (e.g., Steiner et al., 2019), the
853 Tara Polaris expeditions will provide new insights to inform the working group on commercial
854 fisheries in the Arctic, especially regarding pelagic fish distribution and the occurrence, or
855 absence, of fish reproducing and hatching in the CAO. They will also enhance a global

856 understanding on the very unique biodiversity and processes at play in the CAO to support both
857 the ambition of the actual implementation of the CAO Fisheries agreement and the future
858 mitigation of broader impacts that could arise in a melted CAO.

859

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886 Geoffroy, Reigstad and Polyakov wrote the initial outline of the manuscript. Babin, Bowler,
887 Karp-Boss, and Troublé defined the project and structure of the article. All authors contributed to
888 the writing of at least one section, reviewed the final manuscript, and approved its submission.

889

890 Competing interests

891 The authors declare no competing interests.

892

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894

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