



**HAL**  
open science

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

Maxime Geoffroy, Igor Polyakov, Marit Reigstad, Silvia G Acinas, Rémi Amiraux, Hélène Angot, Mathieu Ardyna, Marcel Babin, Chris Bowler, Douglas Couet, et al.

### **► To cite this version:**

Maxime Geoffroy, Igor Polyakov, Marit Reigstad, Silvia G Acinas, Rémi Amiraux, et al.. Oceanography, biogeochemical cycles, and biodiversity in the Central Arctic Ocean: current state of knowledge and directions for future. *Elementa: Science of the Anthropocene*, inPress. <hal-05480562>

**HAL Id: hal-05480562**

**<https://hal.science/hal-05480562v1>**

Submitted on 27 Jan 2026

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire HAL, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HAL Authorization

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  
5 Maxime Geoffroy (maxime.geoffroy@mi.mun.ca)<sup>1,2</sup> Orcid: 0000-0003-2633-5565

6 Igor Polyakov (ivpolyakov@alaska.edu)<sup>3</sup>

7 Marit Reigstad (marit.reigstad@uit.no)<sup>2</sup> Orcid: 0000-0002-8592-7192

8 Silvia G. Acinas (sacinas@icm.csic.es)<sup>4</sup>

9 Rémi Amiraux (remi.amiraux@takuvik.ulaval.ca)<sup>5,6</sup> Orcid: 0000-0002-1369-3614

10 Hélène Angot (helene.angot@univ-grenoble-alpes.fr)<sup>7</sup> Orcid: 00000000-0003-4673-8249

11 Mathieu Ardyna (Mathieu.Ardyna@takuvik.ulaval.ca)<sup>5,6</sup> Orcid: 0000-0002-4703-6655

12 Marcel Babin (marcel.babin@takuvik.ulaval.ca)<sup>5,6</sup>

13 Chris Bowler (cbowler@biologie.ens.fr)<sup>8</sup>

14 Douglas Couet (douglas.couet@sb-roscoff.fr)<sup>9</sup>

15 Tyler D. Eddy (tyler.eddy@mi.mun.ca)<sup>1</sup> Orcid: 0000-0002-2833-9407

16 Angela Falciatore (angela.falciatore@ibpc.fr)<sup>10</sup>, Orcid: 0000-0003-3318-9578

17 Lionel Guidi (lionel.guidi@imev-mer.fr)<sup>11,12</sup>

18 Mario Hoppmann (Mario.Hoppmann@awi.de)<sup>13</sup> Orcid: 0000-0003-1294-9531

19 Marie-Noëlle Houssais (marie-noelle.houssais@locean.ipsl.fr)<sup>14</sup>

20 Lee Karp-Boss (lee.karp-boss@maine.edu)<sup>15</sup> Orcid: 0000-0003-2851-1921

21 Connie Lovejoy (connie.lovejoy@bio.ulaval.ca)<sup>16</sup> Orcid: 000-0001-8027-2281

22 Eric Marechal (eric.marechal@cea.fr)<sup>17</sup>

23 Eric Pelletier (eric.pelletier@genoscope.fr)<sup>18,19</sup> Orcid: 0000-0003-4228-1712

- 24 Eva Ortega-Retuerta (ortegaretuerta@obs-banyuls.fr)<sup>20</sup>
- 25 Jean-François Ghiglione (ghiglione@obs-banyuls.fr)<sup>21</sup> ORCID: 0000-0001-7475-2262
- 26 Georg Pohnert (georg.pohnert@uni-jena.de)<sup>21</sup> Orcid: 0000-0003-2351-6336
- 27 Benjamin Rabe (benjamin.rabe@awi.de)<sup>13</sup> Orcid: 0000-0001-5794-9856
- 28 Guillem Salazar (guillem.salazar@csic.es)<sup>22</sup>
- 29 Julia Schmale (julia.schmale@epfl.ch)<sup>23</sup>
- 30 Nina Schuback (nina.schuback@swisspolar.ch)<sup>24</sup>
- 31 Matt Sullivan (sullivan.948@osu.edu)<sup>25</sup>
- 32 Sandra Tippenhauer (sandra.tippenhauer@awi.de)<sup>13</sup> Orcid: 0000-0003-3405-6275
- 33 Romain Troublé (romain@fondationtaraocean.org)<sup>26</sup> Orcid: 0000-0002-8304-808X
- 34 Emilia Trudnowska (emilia@iopan.pl)<sup>27</sup> Orcid: 0000-0003-3471-6632
- 35 Assaf Vardi (assaf.vardi@weizmann.ac.il)<sup>28</sup>
- 36 Flora Vincent (Flora.vincent@embl.de)<sup>29</sup> Orcid: 0000000169763004

37

### 38 **Affiliations**

39 <sup>1</sup>Centre for Fisheries Ecosystems Research, Fisheries and Marine Institute of Memorial  
40 University of Newfoundland and Labrador, St. John's, Newfoundland and Labrador, Canada

41 <sup>2</sup>Department of Arctic and Marine Biology, UiT The Arctic University of Norway, Tromsø,  
42 Norway

43 <sup>3</sup>University of Alaska Fairbanks, Fairbanks, USA

44 <sup>4</sup>Institut de Ciències del Mar, CSIC, Barcelona, Spain

45 <sup>5</sup>Takuvik Joint International Laboratory, CNRS (France) — Laval University, Canada

46 <sup>6</sup>Département de biologie et Québec-Océan, Université Laval, Québec, QC, Canada

47 <sup>7</sup> Univ. Grenoble Alpes, CNRS, INRAE, IRD, Grenoble INP, IGE, Grenoble, France

48 <sup>8</sup>ENS - CNRS, Paris, France

49 <sup>9</sup>CNRS/ Station Biologique de Roscoff, Roscoff, France

50 <sup>10</sup>Laboratoire de Photobiologie et Physiologie des Plastides et des Microalgues, UMR7141,  
51 CNRS, Sorbonne Université, Institut de Biologie Physico-Chimique, Paris, France

52 <sup>11</sup>Sorbonne Université, CNRS, Laboratoire d'Océanographie de Villefranche, LOV, F-06230  
53 Villefranche-sur-Mer, France

54 <sup>12</sup>Research Federation for the Study of Global Ocean Systems Ecology and Evolution,  
55 FR2022/Tara Oceans GOSEE, Paris, France

56 <sup>13</sup>Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven,  
57 Germany

58 <sup>14</sup>Laboratoire d'Océanographie et du Climat: Expérimentations et Approches Numériques  
59 (LOCEAN), Sorbonne Université, CNRS, IRD, MNHN, Paris, France

60 <sup>15</sup>School of Marine Sciences and Climate Change Institute, University of Maine, Orono, Maine,  
61 USA

62 <sup>16</sup>Département biologie, Québec Océan, Institut de Biologie Intégrative et des Systèmes,  
63 Université Laval, Québec QC, Canada

64 <sup>17</sup>Laboratoire de Physiologie Cellulaire et Végétale, UMR5168 CEA - CNRS - INRAE -  
65 Université Grenoble Alpes, IRIG, CEA-Grenoble, Grenoble, France

66 <sup>18</sup>Metabolic Genomics, Genoscope, Institut de Biologie François-Jacob, CEA - CNRS -  
67 Université Paris Saclay, Evry, France

68 <sup>19</sup>Research Federation for the study of Global Ocean System Ecology and Evolution, CNRS,  
69 Paris, France

- 70 <sup>20</sup>UMR7621 Laboratoire d'océanographie microbienne - CNRS - Sorbonne Univ., France
- 71 <sup>21</sup>Balance of the Microverse Cluster of Excellence, Friedrich Schiller University Jena, 07743
- 72 Jena, Germany
- 73 <sup>22</sup>Institute for Integrative Systems Biology (I2SysBio), University of Valencia-CSIC, Valencia,
- 74 Spain
- 75 <sup>23</sup>Extreme Environments Research Laboratory, École Polytechnique Fédérale de Lausanne,
- 76 EPFL Valais Wallis, Sion, Switzerland
- 77 <sup>24</sup>Swiss Polar Institute, Switzerland
- 78 <sup>25</sup>Ohio State University, USA
- 79 <sup>26</sup>Tara Ocean Foundation, Paris, France
- 80 <sup>27</sup>Institute of Oceanology Polish Academy of Sciences, Poland
- 81 <sup>28</sup>The Weizmann Institute of Science, Israel
- 82 <sup>29</sup>Developmental Biology Unit, EMBL, Heidelberg, Germany

## 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 CO<sub>2</sub> 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

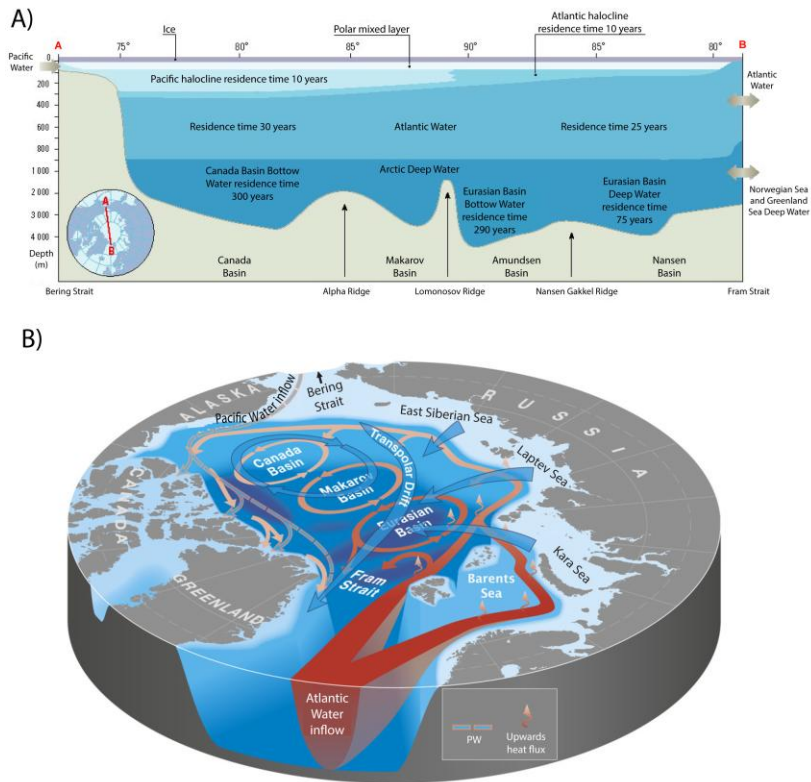
### 142 1.1.1 Water masses and circulation

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<sup>-2</sup> 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 km<sup>2</sup> in March and declines to  
222 around 4–6 million km<sup>2</sup> 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 N<sub>2</sub>  
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 CO<sub>2</sub> 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 Snoeijjs-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

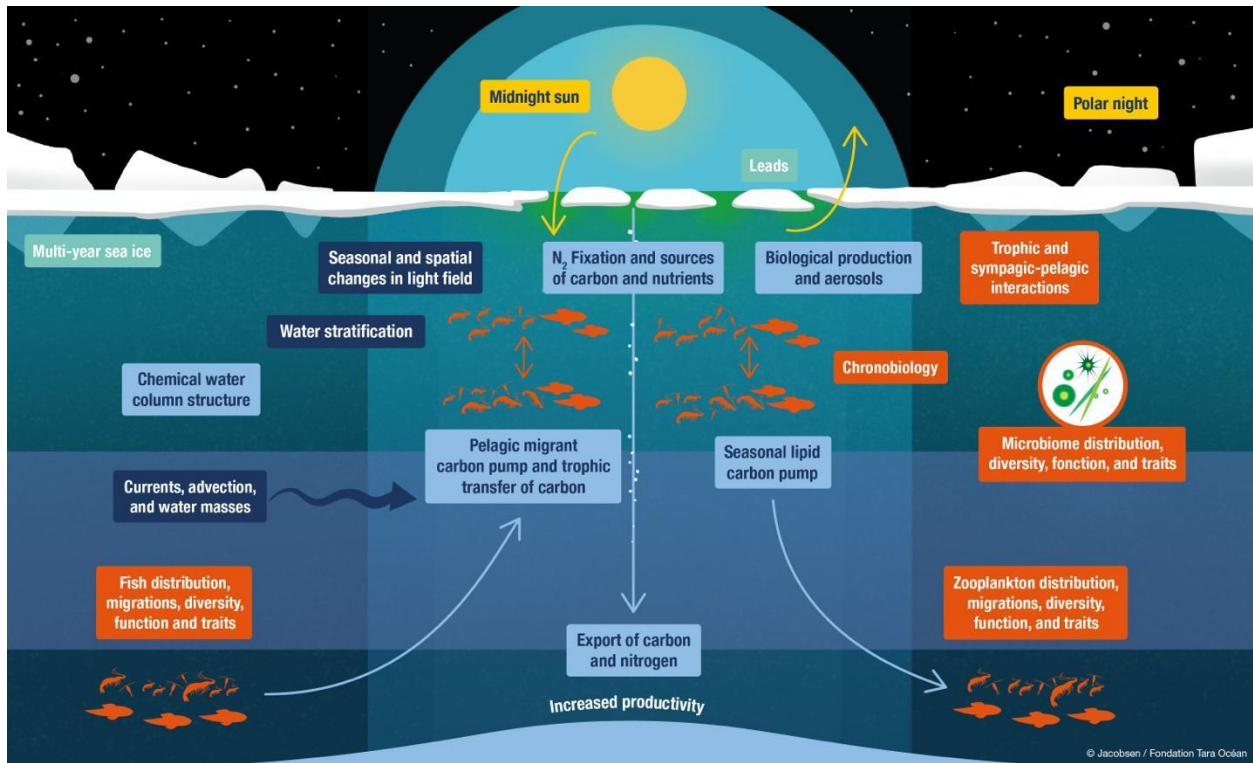
730 The mobile heterogeneous sea ice of the CAO contributes to the dispersion of pelagic organisms.  
731 Ice cover contributes to the exporting of microbial clades from the surface to the deep sea in the  
732 Arctic and provides strong vertical microbial connectivity (Fadeev et al., 2021). Quiescent  
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 N<sub>2</sub> 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 N<sub>2</sub> 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 N<sub>2</sub> 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*

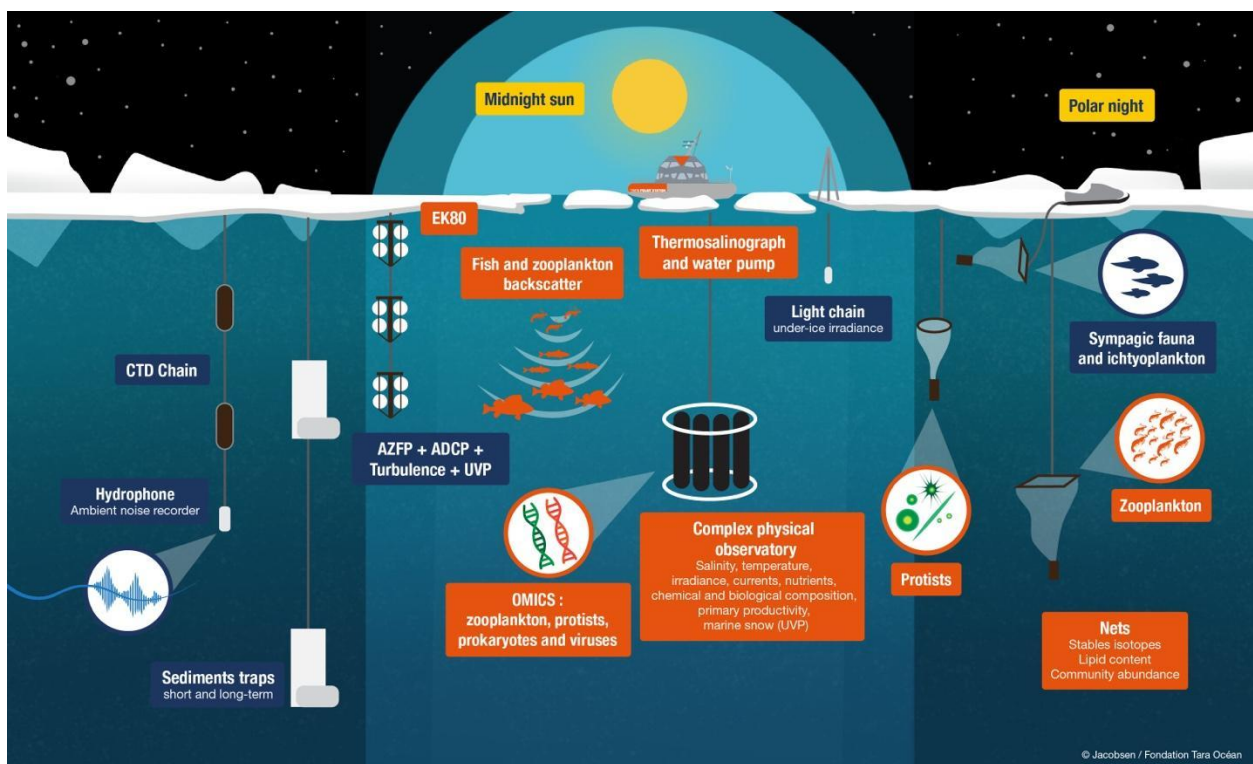
- Fish, including Arctic cod, do not reproduce in the Central Arctic Ocean and are only advected from shelf areas.
- Fish abundance is too low for sustainable commercial fisheries.
- Only early life stages of fish occupy the sympagic zone.

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

## 860 Acknowledgements

861 Paul Wassmann contributed to the initial version of the manuscript. We thank Eugenie Jacobsen  
862 for the design of the first versions of Figures 2 and 3. These new perspectives to address Central  
863 Arctic Ocean knowledge gaps could not be foreseen without the vision and support of the Tara  
864 Ocean Foundation and its multiple public, corporate and private funders such as France 2030,  
865 Capgemini, the Prince Albert II de Monaco Foundation, Monaco Explorations, BNP Paribas,  
866 AXA, CMN, Fondation Didier et Martine Primat, agnès b., Bic, Fondation Albedo pour la  
867 Cryosphere, Fondation Veolia, and CNES et Bureau Veritas Marine.

868

## 869 Funding information

870 CL, MG, MA and MB are financially supported by the Natural Sciences and Engineering  
871 Research Council (NSERC) through the Discovery Grant program. CL, MA and MB are  
872 supported by Sentinelle Nord. IP is supported by the National Science Foundation award  
873 #1724523 and Office of Naval Research award #N00014-21-1-2577. SGA is supported by Polar  
874 EcoGen, Plan Nacional I+D+I 2020 (PID2020-116489RBI00) and PolarOMICS, Plan Nacional  
875 I+D+I 2023 (PID2023-146919NB-C21). EM is supported by the French National Research  
876 Agency (GRAL Labex ANR-10-LABEX-04, EUR CBS ANR-17-EURE-0003, ANR DIM ANR-

877 21-CE02-0021, ANR AlpAlga ANR-20-CE02-0020, PEPR Algadvance A-22-PEBB-0002). HA  
878 is supported by the French National Research Agency (ANR ATOX ANR-24-CE01-7616). This  
879 work benefited from the institutional support of the ‘Severo Ochoa Centre of Excellence’  
880 accreditation (CEX2019-000928-S). JS holds the Ingvar Kamprad Chair, sponsored by Ferring  
881 Pharmaceuticals, for extreme environments research, and was supported by the Swiss National  
882 Science Foundation project grant no. 212101. This is a contribution to the SEDNA project  
883 funded by the Norwegian Research Council (Grant #352539).

884

## 885 Author contributions

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

## 893 References

894

895 Aagaard, K, Carmack, EC. 1989. The role of sea ice and other fresh water in the Arctic  
896 circulation. *Journal of Geophysical Research: Oceans* 94(C10): 14485–14498. doi:  
897 10.1029/jc094ic10p14485.

898 Amin, SA, Parker, MS, Armbrust, EV. 2012. Interactions between diatoms and bacteria.  
899 *Microbiology and Molecular Biology Reviews* 76(3): 667–684. doi:  
900 10.1128/membr.00007-12.

901 Amiraux, R, Archambault, P, Moriceau, B, Lemire, M, Babin, M, Memery, L, Massé, G,  
902 Tremblay, J-É. 2021. Efficiency of sympagic-benthic coupling revealed by analyses  
903 of n-3 fatty acids, IP25 and other highly branched isoprenoids in two filter-feeding  
904 Arctic benthic molluscs: *Mya truncata* and *Serripes groenlandicus*. *Organic*  
905 *Geochemistry* 151: 104160. doi: 10.1016/j.orggeochem.2020.104160v.

906 Amiraux, R, Mundy, CJ, Pierrejean, M, Niemi, A, Hedges, KJ, Brown, TA, Ehn, JK,  
907 Elliott, KH, Ferguson, SH, Fisk, AT, Fisk, AT, Gilchrist, G, Harris, LN, Iken, K,  
908 Jacobs, KB, Johnson, KF, Kuzyk, ZA, Limoges, A, Loewen, TN, Love, OP,  
909 Matthews, CJD, Ogloff, WR, Rosenberg, B, Søreide, JE, Watt, CA, Yurkowski DJ.  
910 2023. Tracing carbon flow and trophic structure of a coastal Arctic marine food web  
911 using highly branched isoprenoids and carbon, nitrogen and sulfur stable isotopes.  
912 *Ecological Indicators* 147: 109938. doi: 10.1016/j.ecolind.2023.109938.

913 Alberti, A, Poulain, J, Engelen, S, Labadie, K, Romac, S, Ferrera, I, Albini, G, Aury, J-M,  
914 Belser, C, Bertrand, A, Cruaud, C, Silva, CD, Dossat, C, Gavory, F, Gas, S, Guy, J,  
915 Haquelle, M, Jacoby, E, Jaillon, O, Lemainque, A, Pelletier, E, Samson, G, Wessner,  
916 Genoscope Technical Team, Acinas, SG, Royo-Llonch, M, Cornejo-Castillo, FM,  
917 Logares, R, Fernández-Gómez, B, Bowler, C, Cochrane, G, Amid, C, Hoopen, PT,

918 Vargas, CD, Grimsley, N, Desgranges, E, Kandels-Lewis, S, Ogata, H, Poulton, N,  
919 Sieracki, ME, Stepanauskas, R, Sullivan, MB, Brum, JR, Duhaime, MB, Poulos, BT,  
920 Hurwitz, BL, Coordinators, TO, Pesant, S, Karsenti, E, Wincker, P. 2017. Viral to  
921 metazoan marine plankton nucleotide sequences from the *Tara* Oceans expedition.  
922 *Scientific Data* 4(1): 170093. doi: 10.1038/sdata.2017.93.

923 Alonso-Sáez, L, Galand, PE, Casamayor, EO, Pedrós-Alió, C, Bertilsson, S. 2010. High  
924 bicarbonate assimilation in the dark by Arctic bacteria. *ISME Journal* 4(12): 1581–  
925 1590. doi: 10.1038/ismej.2010.69.

926 AMAP. 1998. AMAP Assessment Report: Arctic Pollution Issues. *Arctic Monitoring and*  
927 *Assessment Programme (AMAP)*, Oslo, Norway. xii+859 pp.

928 AMAP. 2024. AMAP Arctic Climate Change Update 2024: Key Trends and Impacts.  
929 *Arctic Monitoring and Assessment Programme (AMAP)*, Tromsø, Norway. x+122pp.

930 Ardyna, M, Gosselin, M, Michel, C, Poulin, M, Tremblay, J-É. 2011. Environmental  
931 forcing of phytoplankton community structure and function in the Canadian High  
932 Arctic: contrasting oligotrophic and eutrophic regions. *Marine Ecology Progress*  
933 *Series* 442: 37–57. doi: 10.3354/meps09378.

934 Ardyna, M, Babin, M, Gosselin, M, Devred, E, Rainville, L, Tremblay, J-É. 2014. Recent  
935 Arctic Ocean sea ice loss triggers novel fall phytoplankton blooms. *Geophysical*  
936 *Research Letters* 41(17): 6207–6212. doi: 10.1002/2014gl061047.

937 Ardyna, M, Arrigo, KR. 2020. Phytoplankton dynamics in a changing Arctic Ocean.  
938 *Nature Climate Change* 10(10): 892–903. doi: 10.1038/s41558-020-0905-y.

939 Ardyna, M, Hamilton, DS, Harmel, T, Lacour, L, Bernstein, DN, Laliberté, J, Horvat, C,  
940 Laxenaire, R, Mills, MM, Dijken, G van, Polyakov, I, Claustre, H, Mahowald, N,

941 Arrigo, KR. 2022. Wildfire aerosol deposition likely amplified a summertime Arctic  
942 phytoplankton bloom. *Communications Earth & Environment* 3(1): 201. doi:  
943 10.1038/s43247-022-00511-9.

944 Ardyna, M, Leu, E, Mundy, CJ. 2024. Phytoplankton production in the Arctic Ocean and  
945 its environmental drivers, in Wassmann, P, eds. *Elements of a pan-Arctic Ocean*  
946 *ecology*. Orkana Press.

947 Ardyna, M, Nicolaus, M, Houssain, M-N, Raut, J-C, Angot, H, Bisson, K; Flores, JM,  
948 Galand, PE, Ghiglione, J-F, Geoffroy, M, Heimbürger-Boavida, L-E, Law, KS,  
949 Lovejoy, C, Ravetta, F, Rysgaard, S, Schmale, J, Schuback, N, Sonke, JE,  
950 Vancollenolle, M, Tremblay, J-É, Babin, M, Bowler, C, Karp-Boss, L, Troublé, R.  
951 n.d. Tara Polaris expeditions: Sustained decadal observations of the coupled Arctic  
952 system in rapid transition. *Elementa: Science of the Anthropocene*, in review.

953 Arrigo, KR, Perovich, DK, Pickart, RS, Brown, ZW, Dijken, GL van, Lowry, KE, Mills,  
954 MM, Palmer, MA, Balch, WM, Bates, NR, Benitez-Nelson, CR, Brownlee, E, Frey,  
955 KE, Laney, SR, Mathis, J, Matsuoka, A, Mitchell, BG, Moore, GWK, Reynolds, RA,  
956 Sosik, HM, Swift, JH. 2014. Phytoplankton blooms beneath the sea ice in the  
957 Chukchi sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 105: 1–  
958 16. doi: 10.1016/j.dsr2.2014.03.018.

959 Assmy, P, Fernández-Méndez, M, Duarte, P, Meyer, A, Randelhoff, A, Mundy, CJ, Olsen,  
960 LM, Kauko, HM, Bailey, A, Chierici, M, Cohen, L, Doulgeris, AP, Ehn, JK,  
961 Fransson, A, Gerland, S, Hop, H, Hudson, SR, Hughes, N, Itkin, P, Johnsen, G,  
962 King, JA, Koch, BP, Koenig, Z, Kwasniewski, S, Laney, SR, Nicolaus, M, Pavlov,  
963 AK, Polashenski, CM, Provost, C, Rösel, A, Sandbu, M, Spreen, G, Smedsrud, LH,

964 Sundfjord, A, Taskjelle, T, Tatarek, A, Wiktor, J, Wagner, PM, Wold, A, Steen, H,  
965 Granskog, MA. 2017. Leads in Arctic pack ice enable early phytoplankton blooms  
966 below snow-covered sea ice. *Scientific Reports* 7(1): 40850. doi: 10.1038/srep40850.

967 Babin, M, Karp-Boss, L, Bowler, C, Ardyna, M, Flores, JM, Geoffroy, M, Ghiglione, JF,  
968 Law, KS, Nicolaus, M, Rabe, B, Schmale, J, Gonzales Arcinas, S, Deming, JW,  
969 Galand, P, Linnkowski, T, Moulin, C, Pelletier, E, Polyakov, I, Raut, JC, Rysgaard,  
970 S, Vancoppenolle, M, Troublé, R. n.d. The Tara Polaris scientific vision: Advancing  
971 our understanding of the central Arctic Ocean to better address life in Earth System.  
972 *Elementa Science of the Anthropocene*, in review.

973 Bandara, K, Varpe, Ø, Wijewardene, L, Tverberg, V, Eiane, K. 2021. Two hundred years  
974 of zooplankton vertical migration research. *Biological Reviews* 96(4): 1547–1589.  
975 doi: 10.1111/brv.12715.

976 Béjà, O, Aravind, L, Koonin, EV, Suzuki, MT, Hadd, A, Nguyen, LP, Jovanovich, SB,  
977 Gates, CM, Feldman, RA, Spudich, JL, Spudich, EN, DeLong, EF. 2000. Bacterial  
978 rhodopsin: evidence for a new type of phototrophy in the sea. *Science* 289(5486):  
979 1902–1906. doi: 10.1126/science.289.5486.1902.

980 Bienhold, C, Schourup-Kristensen, V, Krumpen, T, Nöthig, E-M, Wenzhöfer, F,  
981 Korhonen, M, Vredenburg, M, Hehemann, L, Boetius, A. 2022. Effects of sea ice  
982 retreat and ocean warming on the Laptev Sea continental slope ecosystem (1993 vs  
983 2012). *Frontiers in Marine Sciences* 9: 1004959. doi: 10.3389/fmars.2022.1004959.

984 Bodur, YV, Renaud, PE, Goraguer, L, Amargant-Arumí, M, Assmy, P, Dąbrowska, AM,  
985 Marquardt, M, Renner, AHH, Tatarek, A, Reigstad, M. 2023. Seasonal patterns of  
986 vertical flux in the northwestern Barents Sea under Atlantic Water influence and sea-

987 ice decline. *Progress in Oceanography* 219: 103132. doi:  
988 10.1016/j.pocean.2023.103132.

989 Boulton, W, Salamov, A, Grigoriev, IV, Calhoun, S, LaButti, K, Riley, R, Barry, K, Fong,  
990 AA, Hoppe, CJM, Metfies, K, Oetjen, K, Eggers, SL, Müller, O, Gardner, J,  
991 Granskog, MA, Torstensson, A, Oggier, M, Larsen, A, Bratbak, G, Toseland, A,  
992 Leggett, RM, Moulton, V, Mock, T. 2025. Metagenome-assembled-genomes  
993 recovered from the Arctic drift expedition MOSAiC. *Scientific Data* 12(1): 204. doi:  
994 10.1038/s41597-025-04525-8.

995 Bluhm, BA, Gradinger, R. 2008. Regional variability in food availability for Arctic marine  
996 mammals. *Ecological Applications* 18(2): S77–S96. doi: 10.1890/06-0562.1.

997 Bluhm, BA, Kosobokova, KN, Carmack, EC. 2015. A tale of two basins: An integrated  
998 physical and biological perspective of the deep Arctic Ocean. *Progress in*  
999 *Oceanography* 139: 89–121. doi: 10.1016/j.pocean.2015.07.011.

1000 Bodur, YV, Renaud, PE, Goraguer, L, Amargant-Arumí, M, Assmy, P, Dąbrowska, AM,  
1001 Marquardt, M, Renner, AHH, Tatarek, A, Reigstad, M. 2023. Seasonal patterns of  
1002 vertical flux in the northwestern Barents Sea under Atlantic Water influence and sea-  
1003 ice decline. *Progress in Oceanography* 219: 103132. doi:  
1004 10.1016/j.pocean.2023.103132.

1005 Bouchard, C, Geoffroy, M, LeBlanc, M, Majewski, A, Gauthier, S, Walkusz, W, Reist, JD,  
1006 Fortier, L. 2017. Climate warming enhances polar cod recruitment, at least  
1007 transiently. *Progress in Oceanography* 156: 121–129. doi:  
1008 10.1016/j.pocean.2017.06.008.

1009 **Boutin, G**, Ólason, E, Rampal, P, Regan, H, Lique, C, Talandier, C, Brodeau, L, Ricker, R.  
1010 2023. Arctic sea ice mass balance in a new coupled ice–ocean model using a brittle  
1011 rheology framework. *The Cryosphere* 17: 617–638. doi.org/10.5194/tc-17-617-2023

1012 **Boyd, PW**, Claustre, H, Levy, M, Siegel, DA, Weber, T. 2019. Multi-faceted particle  
1013 pumps drive carbon sequestration in the ocean. *Nature* 568(7752): 327–335. doi:  
1014 10.1038/s41586-019-1098-2.

1015 **Brandon, MA**, Cottier, FR, Nilsen, F. 2010. Sea ice and oceanography. *Sea Ice*: 79–111.  
1016 doi: 10.1002/9781444317145.ch3.

1017 **Brenner, S**, Thomson, J, Rainville, L, Crews, L, Lee, CM. 2023. Wind-driven motions of  
1018 the ocean surface mixed layer in the Western Arctic. *Journal of Physical*  
1019 *Oceanography* 53(7): 1787–1804. doi: 10.1175/jpo-d-22-0112.1.

1020 **Brogi, SR**, Ha, S-Y, Kim, K, Derrien, M, Lee, YK, Hur, J. 2018. Optical and molecular  
1021 characterization of dissolved organic matter (DOM) in the Arctic ice core and the  
1022 underlying seawater (Cambridge Bay, Canada): Implication for increased  
1023 autochthonous DOM during ice melting. *Science of the Total Environment* 627: 802–  
1024 811. doi: 10.1016/j.scitotenv.2018.01.251.

1025 Bruhn, CS, Lundholm, N, Hansen, PJ, Wohlrab, S, John, U. 2024. Transition from a  
1026 mixotrophic/heterotrophic protist community during the dark winter to a  
1027 photoautotrophic spring community in surface waters of Disko Bay, Greenland.  
1028 *Frontiers in Microbiology* 15: 1407888. doi: /10.3389/fmicb.2024.1407888.

1029 **Bullock, HA**, Luo, H, Whitman, WB. 2017. Evolution of dimethylsulfoniopropionate  
1030 metabolism in marine phytoplankton and bacteria. *Frontiers in Microbiology* 8: 637.  
1031 doi: 10.3389/fmicb.2017.00637.

1032 Burot, C, Amiraux, R, Bonin, P, Guasco, S, Babin, M, Joux, F, Marie, D, Vilgrain, L,  
1033 Heipieper, HJ, Rontani, J-F. 2021. Viability and stress state of bacteria associated  
1034 with primary production or zooplankton-derived suspended particulate matter in  
1035 summer along a transect in Baffin Bay (Arctic Ocean). *Science of the Total  
1036 Environment* 770: 145252. doi: 10.1016/j.scitotenv.2021.145252.

1037 Canadian Society for Chronobiology. 2025. What is chronobiology? Available at  
1038 <http://www.chronobiocanada.com/>.

1039 Carmack, EC, Macdonald, RW, Perkin, RG, McLaughlin, FA, Pearson, RJ. 1995.  
1040 Evidence for warming of Atlantic water in the Southern Canadian Basin of the  
1041 Arctic Ocean: Results from the Larsen-93 Expedition. *Geophysical Research Letters*  
1042 22(9): 1061–1064. doi: 10.1029/95gl00808.

1043 Carmack, E, Polyakov, I, Padman, L, Fer, I, Hunke, E, Hutchings, J, Jackson, J, Kelley, D,  
1044 Kwok, R, Layton, C, Melling, H, Perovich, D, Persson, O, Ruddick, B,  
1045 Timmermans, ML, Toole, J, Ross, T, Vavrus, S, Winsor, P. 2015. Toward  
1046 quantifying the increasing role of oceanic heat in sea ice loss in the new Arctic.  
1047 *Bulletin of the American Meteorological Society* 96(12): 2079–2105. doi:  
1048 10.1175/bams-d-13-00177.1.

1049 Cautain, IJ, Last, KS, McKee, D, Bluhm, BA, Renaud, PE, Ziegler, AF, Narayanaswamy,  
1050 BE. 2022. Uptake of sympagic organic carbon by the Barents Sea benthos linked to  
1051 sea ice seasonality. *Frontiers in Marine Science* 9: 1009303. doi:  
1052 10.3389/fmars.2022.1009303.

1053 Chaffron, S, Delage, E, Budinich, M, Vintache, D, Henry, N, Nef, C, Ardyna, M, Zayed,  
1054 AA, Junger, PC, Galand, PE, Lovejoy, C, Murray, AE, Sarmento, H, Tara Oceans

1055 Coordinators, Acinas, SG, Babin, M, Iudicone, D, Jaillon, O, Karsenti, E, Wincker,  
1056 P, Karp-Boss, L, Sullivan, MB, Bowler, C, de Vargas, C, Eveillard, D. 2021.  
1057 Environmental vulnerability of the global ocean epipelagic plankton community  
1058 interactome. *Science Advances* 7(35): eabg1921. doi: 10.1126/sciadv.abg1921.

1059 Christensen, V, Walters, CJ. 2004. Ecopath with Ecosim: methods, capabilities and  
1060 limitations. *Ecological Modelling* 172(2–4): 109–139. doi:  
1061 10.1016/j.ecolmodel.2003.09.003.

1062 Coale, TH, Loconte, V, Turk-Kubo, KA, Vanslebrouck, B, Mak, WKE, Cheung, S,  
1063 Ekman, A, Chen, J-H, Hagino, K, Takano, Y, Nishimura, T, Adachi, M, Gros, ML,  
1064 Larabell, C, Zehr, JP. 2024. Nitrogen-fixing organelle in a marine alga. *Science*  
1065 384(6692): 217–222. doi: 10.1126/science.adk1075.

1066 Coesel, SN, Durham, BP, Groussman, RD, Hu, SK, Caron, DA, Morales, RL, Ribalet, F,  
1067 Armbrust, EV. 2021. Diel transcriptional oscillations of light-sensitive regulatory  
1068 elements in open-ocean eukaryotic plankton communities. *Proceedings of the*  
1069 *National Academy of Sciences*, 118(6): p.e2011038118.  
1070 <https://doi.org/10.1073/pnas.2011038118>.

1071 Cohen, JH, Berge, J, Moline, MA, Johnsen, G, Zolich, AP. 2020. Light in the Polar Night.  
1072 In: Berge, J, Johnsen, G, Cohen, JH. Polar night marine ecology - life and light in the  
1073 dead of night. Springer: 37-66.

1074 Crawford, DW, Cefarelli, AO, Wrohan, IA, Wyatt, SN, Varela, DE. 2018. Spatial patterns  
1075 in abundance, taxonomic composition and carbon biomass of nano- and  
1076 microphytoplankton in Subarctic and Arctic Seas. *Progress in Oceanography* 162:  
1077 132–159. doi: 10.1016/j.pocean.2018.01.006.

1078 Dastoor, A, Angot, H, Bieser, J, Christensen, JH, Douglas, TA, Heimbürger-Boavida, LE,  
1079 Jiskra, M, Mason, RP, McLagan, DS, Obrist, D, Outridge, PM. 2022. Arctic mercury  
1080 cycling. *Nature Reviews Earth & Environment* 3(4): 270-286. doi: 1038/s43017-022-  
1081 00269-w.

1082 David, C, Lange, B, Krumpen, T, Schaafsma, F, Franeker, JA van, Flores, H. 2016. Under-  
1083 ice distribution of polar cod *Boreogadus saida* in the central Arctic Ocean and their  
1084 association with sea-ice habitat properties. *Polar Biology* 39(6): 981–994. doi:  
1085 10.1007/s00300-015-1774-0.

1086 Deb, JC, Bailey, SA. 2023. Arctic marine ecosystems face increasing climate stress.  
1087 *Environmental Reviews* 31(3): 403–451. doi: 10.1139/er-2022-0101.

1088 Digernes, MG, Bodur, YV, Amargant-Arumí, M, Müller, O, Hawkes, JA, Kohler, SG,  
1089 Dietrich, U, Reigstad, M, Paulsen, ML. 2025. Contrasting seasonal patterns in  
1090 particle aggregation and dissolved organic matter transformation in a sub-Arctic  
1091 fjord. *Biogeosciences* 22: 601–623. doi: 10.5194/bg-22-601-2025.

1092 Dominguez-Huerta, G, Zayed, AA, Wainaina, JM, Guo, J, Tian, F, Pratama, AA, Bolduc,  
1093 B, Mohssen, M, Zablocki, O, Pelletier, E, Delage, E, Alberti, A, Aury, JM, Carradec,  
1094 Q, Silva, C da, Labadie, K, Poulain, J, Coordinators, TO, Bowler, C, Eveillard, D,  
1095 Guidi, L, Karsenti, E, Kuhn, JH, Ogata, H, Wincker, P, Culley, A, Chaffron, S,  
1096 Sullivan, MB. 2022. Diversity and ecological footprint of Global Ocean RNA  
1097 viruses. *Science* 376(6598): 1202–1208. doi: 10.1126/science.abn6358.

1098 Doney, SC, Fabry, VJ, Feely, RA, Kleypas, JA. 2009. Ocean acidification: the other CO<sub>2</sub>  
1099 problem. *Annual Review of Marine Science* 1(1): 169–192. doi:  
1100 10.1146/annurev.marine.010908.163834.

1101 Duchêne, C, Bouly, JP, Pierella Karlusich, JJ, Vernay, E, Sellés, J, Bailleul, B, Bowler, C,  
1102 Ribera d'Alcalà, M, Falciatore, A, Jaubert, M. 2025. Diatom phytochromes integrate  
1103 the underwater light spectrum to sense depth. *Nature*, 637(8046): 691-697.  
1104 <https://doi.org/10.1038/s41586-024-08301-3>.

1105 **Duncan, A**, Barry, K, Daum, C, Eloë-Fadrosh, E, Roux, S, Schmidt, K, Tringe, SG,  
1106 Valentin, KU, Varghese, N, Salamov, A, Grigoriev, IV, Leggett, RM, Moulton, V,  
1107 Mock, T. 2022. Metagenome-assembled genomes of phytoplankton microbiomes  
1108 from the Arctic and Atlantic Oceans. *Microbiome* 10(1): 67. doi: 10.1186/s40168-  
1109 022-01254-7.

1110 **Dybwad, C**, Assmy, P, Olsen, LM, Peeken, I, Nikolopoulos, A, Krumpen, T, Randelhoff,  
1111 A, Tatarek, A, Wiktor, JM, Reigstad, M. 2021. Carbon export in the seasonal sea ice  
1112 zone north of Svalbard from winter to late summer. *Frontiers in Marine Science* 7:  
1113 525800. doi: 10.3389/fmars.2020.525800.

1114 **Dybwad, C**, Lalande, C, Bodur, YV, Henley, SF, Cottier, F, Ershova, EA, Hobbs, L, Last,  
1115 KS, Dąbrowska, AM, Reigstad, M. 2022. The influence of sea ice cover and Atlantic  
1116 water advection on annual particle export north of Svalbard. *Journal of Geophysical*  
1117 *Research: Oceans* 127(10). doi: 10.1029/2022jc018897.

1118 **Eddy, TD**, Bernhardt, JR, Blanchard, JL, Cheung, WWL, Colléter, M, Pontavice, H du,  
1119 Fulton, EA, Gascuel, D, Kearney, KA, Petrik, CM, Roy, T. 2021. Energy flow  
1120 through marine ecosystems: confronting transfer efficiency. *Trends in Ecology &*  
1121 *Evolution* 36(1): 76–86. doi: 10.1016/j.tree.2020.09.006.

1122 **Engel, A**, Bange, HW, Cunliffe, M, Burrows, SM, Friedrichs, G, Galgani, L, Herrmann, H,  
1123 Hertkorn, N, Johnson, M, Liss, PS, Quinn, PK, Schartau, M, Soloviev, A, Stolle, C,

1124 Upstill-Goddard, RC, Pinxteren, M van, Zäncker, B. 2017. The ocean's vital skin:  
1125 toward an integrated understanding of the sea surface microlayer. *Frontiers in*  
1126 *Marine Science* 4: 165. doi: 10.3389/fmars.2017.00165.

1127 Ericson, Y, Fransson, A, Chierici, M, Jones, EM, Skjelvan, I, Omar, A, Olsen, A, Becker,  
1128 M. 2023. Rapid fCO<sub>2</sub> rise in the northern Barents Sea and Nansen Basin. *Progress in*  
1129 *Oceanography* 217: 103079 doi.org/10.1016/j.pocean.2023.103079.

1130 Fabry, V, McClintock, J, Mathis, J, Grebmeier, J. 2009. Ocean acidification at high  
1131 latitudes: the bellwether. *Oceanography* 22(4): 160–171. doi:  
1132 10.5670/oceanog.2009.105.

1133 Fadeev, E, Rogge, A, Ramondenc, S, Nöthig, E-M, Wekerle, C, Bienhold, C, Salter, I,  
1134 Waite, AM, Hehemann, L, Boetius, A, Iversen, MH. 2021. Sea ice presence is linked  
1135 to higher carbon export and vertical microbial connectivity in the Eurasian Arctic  
1136 Ocean. *Communications Biology* 4(1): 1255. doi: 10.1038/s42003-021-02776-w

1137 Falk-Petersen, S, Mayzaud, P, Kattner, G, Sargent, JR. 2009. Lipids and life strategy of  
1138 Arctic *Calanus*. *Marine Biology Research* 5(1): 18–39. doi:  
1139 10.1080/17451000802512267.

1140 Fernández-Méndez, M, Katlein, C, Rabe, B, Nicolaus, M, Peeken, I, Bakker, K, Flores, H,  
1141 Boetius, A. 2015. Photosynthetic production in the central Arctic Ocean during the  
1142 record sea-ice minimum in 2012. *Biogeosciences* 12(11): 3525–3549. doi:  
1143 10.5194/bg-12-3525-2015.

1144 Fernández-Méndez, M, Wenzhöfer, F, Peeken, I, Sørensen, HL, Glud, RN, Boetius, A.  
1145 2014. Composition, buoyancy regulation and fate of ice algal aggregates in the  
1146 central Arctic Ocean. *PLoS ONE* 9(9): e107452. doi: 10.1371/journal.pone.0107452.

1147 Flores, H, Veyssière, G, Castellani, G, Wilkinson, J, Hoppmann, M, Karcher, M, Valcic, L,  
1148 Cornils, A, Geoffroy, M, Nicolaus, M, Niehoff, B, Priou, P, Schmidt, K, Stroeve, J.  
1149 2023. Sea-ice decline could keep zooplankton deeper for longer. *Nature Climate*  
1150 *Change*: 1–9. doi: 10.1038/s41558-023-01779-1.

1151 Fossheim, M, Primicerio, R, Johannesen, E, Ingvaldsen, RB, Aschan, MM, Dolgov, AV.  
1152 2015. Recent warming leads to a rapid borealization of fish communities in the  
1153 Arctic. *Nature Climate Change* 5(7): 673–677. doi: 10.1038/nclimate2647

1154 Freyria, NJ, Joli, N, Lovejoy, C. 2021. A decadal perspective on north water microbial  
1155 eukaryotes as Arctic Ocean sentinels. *Scientific Reports* 11(1): 8413. doi:  
1156 10.1038/s41598-021-87906-4.

1157 Freyria, NJ, Oliveira, TC de, Chovatia, M, Johnson, J, Kuo, A, Lipzen, A, Barry, KW,  
1158 Grigoriev, IV, Lovejoy, C. 2024. Stress responses in an Arctic microalga  
1159 (*Pelagophyceae*) following sudden salinity change revealed by gene expression  
1160 analysis. *Communications Biology* 7(1): 1084. doi: 10.1038/s42003-024-06765-7.

1161 Friesen, LW von, Riemann, L. 2020. Nitrogen fixation in a changing Arctic Ocean: an  
1162 overlooked source of nitrogen? *Frontiers in Microbiology* 11: 596426. doi:  
1163 10.3389/fmicb.2020.596426.

1164 Friesen, LW von, Farnelid, H, von Appen, W-, Benavides, M, Grosso, O, Laber, CP,  
1165 Schüttler, J, Sundbom, M, Torres-Valdés, S, Bertilsson, S, Peeken, I, Snoeijts-  
1166 Leijonmalm, P, Riemann, L. 2025. Nitrogen fixation under declining Arctic sea ice.  
1167 *Communications Earth & Environment* 6(1): 811. doi: 10.1038/s43247-025-02782-4.

1168 Fuhrman, JA, Steele, JA, Hewson, I, Schwalbach, MS, Brown, MV, Green, JL, Brown, JH.  
1169 2008. A latitudinal diversity gradient in planktonic marine bacteria. *Proceedings of*

1170 *the National Academy of Sciences* 105(22): 7774–7778. doi:  
1171 10.1073/pnas.0803070105.

1172 Galand, PE, Casamayor, EO, Kirchman, DL, Lovejoy, C. 2009. Ecology of the rare  
1173 microbial biosphere of the Arctic Ocean. *Proceedings of the National Academy of*  
1174 *Sciences* 106(52): 22427–22432. doi: 10.1073/pnas.0908284106.

1175 Galand, PE, Potvin, M, Casamayor, EO, Lovejoy, C. 2010. Hydrography shapes bacterial  
1176 biogeography of the deep Arctic Ocean. *ISME Journal* 4(4): 564–576. doi:  
1177 10.1038/ismej.2009.134.

1178 Geoffroy, M, Daase, M, Cusa, M, Darnis, G, Graeve, M, Hernández, NS, Berge, J,  
1179 Renaud, PE, Cottier, F, Falk-Petersen, S. 2019. Mesopelagic sound scattering layers  
1180 of the High Arctic: seasonal variations in biomass, species assemblage, and trophic  
1181 relationships. *Frontiers in Marine Science* 6: 364. doi: 10.3389/fmars.2019.00364.

1182 Geoffroy, M, Bouchard, C, Flores, H, Robert, D, Gjørseter, H, Hoover, C, Hop, H, Hussey,  
1183 NE, Nahrgang, J, Steiner, N, Bender, M, Berge, J, Castellani, G, Chernova, N,  
1184 Copeman, L, David, CL, Deary, A, Divoky, G, Dolgov, AV, Duffy-Anderson, J,  
1185 Dupont, N, Durant, JM, Elliott, K, Gauthier, S, Goldstein, ED, Gradinger, R,  
1186 Hedges, K, Herbig, J, Laurel, B, Loseto, L, Maes, S, Mark, FC, Mosbech, A, Pedro,  
1187 S, Pettitt-Wade, H, Prokopchuk, I, Renaud, PE, Schembri, S, Vestfals, C, Walkusz,  
1188 W. 2023. The circumpolar impacts of climate change and anthropogenic stressors on  
1189 Arctic cod (*Boreogadus saida*) and its ecosystem. *Elementa: Science of the*  
1190 *Anthropocene* 11(1). doi: 10.1525/elementa.2022.00097.

1191 Ghiglione JF, Heimbürger-Boavida L, Fourquez M, Hough I, Sonke JE, ter Halle A, Law  
1192 KS, Schmale J, Flores JM, Gigault J, Ardyna M, Kohler SG, Xie Z, Cullen JT,

1193 Geoffroy M, Moulin C, Troublé R, Karp-Boss L, Bowler C, Babin M, Angot H. n.d.  
1194 Tara Polaris expeditions: seasonal and long-term contaminant monitoring in the  
1195 changing central Arctic. *Elementa: Science of the Anthropocene*, in review.

1196 Gillies, EJ, Li, ML, Christensen, V, Hoover, C, Sora, KJ, Loseto, LL, Cheung, WW,  
1197 Angot, H, Giang, A. 2024. Exploring drivers of historic mercury trends in Beluga  
1198 whales using an ecosystem modeling approach. *ACS Environmental Au* 4(5) : 219-  
1199 235. doi : 10.1021/acsenvironau.3c00072.

1200 Gjørseter, H, Wiebe, PH, Knutsen, T, Ingvaldsen, RB. 2017. Evidence of diel vertical  
1201 migration of mesopelagic sound-scattering organisms in the Arctic. *Frontiers in*  
1202 *Marine Science* 4: 332. doi: 10.3389/fmars.2017.00332.

1203 Gosselin, M, Levasseur, M, Wheeler, PA, Horner, RA, Booth, BC. 1997. New  
1204 measurements of phytoplankton and ice algal production in the Arctic Ocean. *Deep*  
1205 *Sea Research Part II: Topical Studies in Oceanography* 44(8): 1623–1644. doi:  
1206 10.1016/s0967-0645(97)00054-4.

1207 González, JM, Fernández-Gómez, B, Fernández-Guerra, A, Gómez-Consarnau, L,  
1208 Sánchez, O, Coll-Lladó, M, Campo, J del, Escudero, L, Rodríguez-Martínez, R,  
1209 Alonso-Sáez, L, Latasa M, Paulsen, I, Nedashkovskaya, O, Lekunberri, I, Pinhassi, J,  
1210 Pedrós-Alió, C. 2008. Genome analysis of the proteorhodopsin-containing marine  
1211 bacterium *Polaribacter* sp. MED152 (*Flavobacteria*). *Proceedings of the National*  
1212 *Academy of Sciences* 105(25): 8724–8729. doi: 10.1073/pnas.0712027105.

1213 Gradinger, R, Campbell, K, Leu, E. 2024. Ice flora in a pan-arctic scenario, in Wassmann  
1214 P eds. *Elements of a pan-Arctic Ocean ecology*. Orkana Press.

1215 Granskog, MA, Fer, I, Rinke, A, Steen, H. 2018. Atmosphere-ice-ocean-ecosystem  
1216 processes in a thinner Arctic sea ice regime: the Norwegian Young Sea ICE (N-  
1217 ICE2015) Expedition. *Journal of Geophysical Research: Oceans* 123(3): 1586–  
1218 1594. doi: 10.1002/2017jc013328

1219 Grebmeier, JM, Harvey, HR. 2005. The Western Arctic Shelf–Basin Interactions (SBI)  
1220 project: An overview. *Deep Sea Research Part II: Topical Studies in Oceanography*  
1221 52(24–26): 3109–3115. doi: 10.1016/j.dsr2.2005.10.004.

1222 Grebmeier, JM, Overland, JE, Moore, SE, Farley, EV, Carmack, EC, Cooper, LW, Frey,  
1223 KE, Helle, JH, McLaughlin, FA, McNutt, SL. 2006. A major ecosystem shift in the  
1224 northern Bering Sea. *Science* 311(5766): 1461–1464. doi: 10.1126/science.1121365.

1225 Gregory, AC, Zayed, AA, Conceição-Neto, N, Temperton, B, Bolduc, B, Alberti, A,  
1226 Ardyna, M, Arkhipova, K, Carmichael, M, Cruaud, C, Dimier, C, Domínguez-  
1227 Huerta, G, Ferland, J, Kandels, S, Liu, Y, Marec, C, Pesant, S, Picheral, M, Pisarev,  
1228 S, Poulain, J, Tremblay, J-É, Vik, D, Coordinators, TO, Babin, M, Bowler, C,  
1229 Culley, AI, Vargas, C de, Dutilh, BE, Iudicone, D, Karp-Boss, L, Roux, S,  
1230 Sunagawa, S, Wincker, P, Sullivan, MB. 2019. Marine DNA viral macro- and  
1231 microdiversity from pole to pole. *Cell* 177(5): 1109-1123.e14. doi:  
1232 10.1016/j.cell.2019.03.040.

1233 Guérin, S, Bruyant, F, Gosselin, M, Babin, M, Lavaud, J. 2024. Photoperiodic dependent  
1234 regulation of photosynthesis in the polar diatom *Fragilariopsis cylindrus*. *Frontiers*  
1235 *in Photobiology*, 2, p.1387119. <https://doi.org/10.3389/fphbi.2024.1387119>.

1236 Guidi, L, Chaffron, S, Bittner, L, Eveillard, D, Larhlimi, A, Roux, S, Darzi, Y, Audic, S,  
1237 Berline, L, Brum, JR, Coelho, LP, Espinoza, JCI, Malviya, S, Sunagawa, S, Dimier,

1238 C, Kandels-Lewis, S, Picheral, M, Poulain, J, Searson, S, Tara Oceans Coordinators,  
1239 Stemmann, L, Not, F, Hingamp, P, Speich, S, Follows, M, Karp-Boss, L, Boss, E,  
1240 Ogata, H, Pesant, S, Weissenbach, J, Wincker, P, Acinas, SG, Bork, P, de Vargas,  
1241 C, Iudicone, D, Sullivan, MB, Raes, J, Karsenti, E, Bowler, C, Gorsky, G. 2016.  
1242 Plankton networks driving carbon export in the oligotrophic ocean. *Nature*  
1243 532(7600): 465–470. doi: 10.1038/nature16942.

1244 Gulliksen, B, Lønne, OJ. 1991. Sea ice macrofauna in the Antarctic and the Arctic. *Journal*  
1245 *of Marine Systems* 2(1–2): 53–61. doi: 10.1016/0924-7963(91)90013-k.

1246 Guo, S, Stevens, CA, Vance, TDR, Olijve, LLC, Graham, LA, Campbell, RL, Yazdi, SR,  
1247 Escobedo, C, Bar-Dolev, M, Yashunsky, V, Braslavsky, I, Langelaan, DN, Smith,  
1248 SP, Allingham, JS, Voets, IK, Davies, PL. 2017. Structure of a 1.5-MDa adhesin that  
1249 binds its Antarctic bacterium to diatoms and ice. *Science Advances* 3(8): e1701440.  
1250 doi: 10.1126/sciadv.1701440.

1251 Haddon, A, Farnole, P, Monahan, AH, Sou, T, Steiner, N. 2024. Environmental controls  
1252 and phenology of sea ice algal growth in a future Arctic. *Elementa: Science of the*  
1253 *Anthropocene* 12(1): 00129. doi: 10.1525/elementa.2023.00129.

1254 Häfker, NS, Andreatta, G, Manzotti, A, Falciatore, A, Raible, F, Tessmar-Raible, K. 2023.  
1255 Rhythms and clocks in marine organisms. *Annual Review of Marine Science*, 15(1):  
1256 509-538. <https://doi.org/10.1146/annurev-marine-030422-113038>.

1257 Hancke, K, Lund-Hansen, LC, Lamare, ML, Pedersen, SH, King, MD, Andersen, P,  
1258 Sorrell BK. 2018. Extreme low light requirement for algae growth underneath sea  
1259 ice: a case study from Station Nord, NE Greenland. *Journal of Geophysical*  
1260 *Research: Oceans* 123(2): 985–1000. doi: 10.1002/2017jc013263.

1261 **Harding, K**, Turk-Kubo, KA, Sipler, RE, Mills, MM, Bronk, DA, Zehr, JP. 2018.  
1262 Symbiotic unicellular cyanobacteria fix nitrogen in the Arctic Ocean. *Proceedings of*  
1263 *the National Academy of Sciences*: 201813658. doi: 10.1073/pnas.1813658115.

1264 **Hayashida, H**, Jin, M, Steiner, NS, Swart, NC, Watanabe, E, Fiedler, R, Hogg, AM, Kiss,  
1265 AE, Matear, RJ, Strutton, PG. 2021. Ice Algae model intercomparison project phase  
1266 2 (IAMIP2). *Geoscientific Model Development* 14(11): 6847-6861. doi:  
1267 10.5194/gmd-14-6847-2021.

1268 Heimbürger, LE, Sonke, JE, Cossa, D, Point, D, Lagane, C, Laffont, L, Galfond, BT,  
1269 Nicolaus, M, Rabe, B, van Der Loeff, MR. 2015. Shallow methylmercury production  
1270 in the marginal sea ice zone of the central Arctic Ocean. *Scientific Reports* 5(1):  
1271 p.10318. doi: 10.1038/srep10318.

1272 **Heutte, B**, Bergner, N, Beck, I, Angot, H, Dada, L, Quéléver, LLJ, Laurila, T, Boyer, M,  
1273 Brasseur, Z, Daellenbach, KR, Henning, S, Kuang, C, Kulmala, M, Lampilahti, J,  
1274 Lampimäki, M, Petäjä, T, Shupe, MD, Sipilä, M, Uin, J, Jokinen, T, Schmale, J.  
1275 2023. Measurements of aerosol microphysical and chemical properties in the central  
1276 Arctic atmosphere during MOSAiC. *Scientific Data* 10(1): 690. doi:  
1277 10.1038/s41597-023-02586-1.

1278 **Heuzé, C**, Jahn, A. 2024. The first ice-free day in the Arctic Ocean could occur before  
1279 2030. *Nature Communications* 15(1): 10101. doi: 10.1038/s41467-024-54508-3.

1280 **Holm, HC**, Fredricks, HF, Bent, SM, Lowenstein, DP, Ossolinski, JE, Becker, KW,  
1281 Johnson, WM, Schrage, K, Mooy BASV. 2022. Global ocean lipidomes show a  
1282 universal relationship between temperature and lipid unsaturation. *Science*  
1283 376(6600): 1487–1491. doi: 10.1126/science.abn7455.

1284 Hop, H, Vihtakari, M, Bluhm, BA, Assmy, P, Poulin, M, Gradinger, R, Peeken, I,  
1285 Quillfeldt, C von, Olsen, LM, Zhitina, L, Melnikov, IA. 2020. Changes in sea-ice  
1286 protist diversity with declining sea ice in the Arctic Ocean from the 1980s to 2010s.  
1287 *Frontiers in Marine Science* 7: 243. doi: 10.3389/fmars.2020.00243.

1288 Hoppe, CJM, Fuchs, N, Notz, D, Anderson, P, Assmy, P, Berge, J, Bratbak, G, Guillou, G,  
1289 Kraberg, A, Larsen, A, Lebreton, B, Leu, E, Lucassen, M, Müller, O, Oziel, L, Rost,  
1290 B, Schartmüller, B, Torstensson, A, Wloka, J. 2024. Photosynthetic light  
1291 requirement near the theoretical minimum detected in Arctic microalgae. *Nature*  
1292 *Communications* 15: 7385. doi : 10.1038/s41467-024-51636-8.

1293 Huang, S, Wang, F, Yuan, T, Song, Z, Wu, P, Zhang, Y. 2023. Modeling the mercury  
1294 cycle in the sea ice environment: a buffer between the polar atmosphere and ocean.  
1295 *Environmental Science & Technology* 57(39): 14589–14601. doi:  
1296 10.1021/acs.est.3c05080.

1297 Hung, H, Halsall, C, Ball, H, Bidleman, T, Dachs, J, De Silva, A, Hermanson, M,  
1298 Kallenborn, R, Muir, D, Sühling, R, Wang, X. 2022. Climate change influence on  
1299 the levels and trends of persistent organic pollutants (POPs) and chemicals of  
1300 emerging Arctic concern (CEACs) in the Arctic physical environment—a review.  
1301 *Environmental Science: Processes & Impacts* 24(10): 1577–1615. doi:  
1302 10.1039/D1EM00485A.

1303 Husson, B, Bluhm, BA, Cyr, F, Danielson, SL, Eriksen, E, Fossheim, M, Geoffroy, M,  
1304 Hopcroft, RR, Ingvaldsen, RB, Jørgensen, LL, Lovejoy, C, Meire, L, Mueter, F,  
1305 Primicerio, R, Winding, M. 2024. Borealization impacts shelf ecosystems across the

1306 Arctic. *Frontiers in Environmental Science* 12: 1481420. doi:  
1307 10.3389/fenvs.2024.1481420.

1308 Ibarbalz, FM, Henry, N, Brandão, MC, Martini, S, Busseni, G, Byrne, H, Coelho, LP,  
1309 Endo, H, Gasol, JM, Gregory, AC, Mahé, F, Rigonato, J, Royo-Llonch, M, Salazar,  
1310 G, Sanz-Sáez, I, Scalco, E, Soviadan, D, Zayed, AA, Zingone, A, Labadie, K,  
1311 Ferland, J, Marec, C, Kandels, S, Picheral, M, Dimier, C, Poulain, J, Pisarev, S,  
1312 Carmichael, M, Pesant, S, Coordinators, TO, Babin M, Boss, E, Iudicone, D, Jaillon,  
1313 O, Acinas, SG, Ogata, H, Pelletier, E, Stemmann, L, Sullivan, MB, Sunagawa, S,  
1314 Bopp, L, Vargas, C de, Karp-Boss, L, Wincker, P, Lombard, F, Bowler, C, Zinger,  
1315 L. 2019. Global trends in marine plankton diversity across kingdoms of life. *Cell*  
1316 179(5): 1084-1097.e21. doi: 10.1016/j.cell.2019.10.008.

1317 Ingvaldsen, RB, Assmann, KM, Primicerio, R, Fossheim, M, Polyakov, IV, Dolgov, AV.  
1318 2021. Physical manifestations and ecological implications of Arctic Atlantification.  
1319 *Nature Reviews Earth & Environment* 2(12): 874–889. doi: 10.1038/s43017-021-  
1320 00228-x.

1321 Ingvaldsen, RB, Eriksen, E, Gjørseter, H, Engås, A, Schuppe, BK, Assmann, KM,  
1322 Cannaby, H, Dalpadado, P, Bluhm, BA. 2023. Under-ice observations by trawls and  
1323 multi-frequency acoustics in the Central Arctic Ocean reveals abundance and  
1324 composition of pelagic fauna. *Scientific Reports* 13(1): 1000. doi: 10.1038/s41598-  
1325 023-27957-x.

1326 Iversen, KR, Seuthe, L. 2011. Seasonal microbial processes in a high-latitude fjord  
1327 (Kongsfjorden, Svalbard): I. Heterotrophic bacteria, picoplankton and  
1328 nanoflagellates. *Polar Biology* 34(5): 731–749. doi: 10.1007/s00300-010-0929-2.

1329 Jackson, JM, Carmack, EC, McLaughlin, FA, Allen, SE, Ingram, RG. 2010. Identification,  
1330 characterization, and change of the near-surface temperature maximum in the  
1331 Canada Basin, 1993–2008. *Journal of Geophysical Research: Oceans* 115(C5). doi:  
1332 10.1029/2009jc005265.

1333 Jahn, A, Holland, MM, Kay, JE. 2024. Projections of an ice-free Arctic Ocean. *Nature*  
1334 *Reviews Earth & Environment* 5(3): 164–176. doi: 10.1038/s43017-023-00515-9.

1335 Jaubert, M, Bouly, JP, d’Alcalà, MR, Falciatore, A. 2017. Light sensing and responses in  
1336 marine microalgae. *Current Opinion in Plant Biology*, 37: 70-77.  
1337 <https://doi.org/10.1016/j.pbi.2017.03.005>.

1338 Joli, N, Concia, L, Mocaer, K, Guterman, J, Laude, J, Guerin, S, Sciandra, T, Bruyant, F,  
1339 Ait-Mohamed, O, Beguin, M, Forget, M, Bourbousse, C, Lacour, T, Bailleul, B, Nef,  
1340 C, Savoie, M, Tremblay, J-É, Campbell, DA, Lavaud, J, Schwab, Y, Babin, M,  
1341 Bowler, C. 2023. Hypometabolism to survive the long polar night and subsequent  
1342 successful return to light in the diatom *Fragilariopsis cylindrus*. *New Phytologist*  
1343 241(5): 2193-2208. doi: 10.1111/nph.19387.

1344 Jørgensen, L, Stedmon, CA, Kaartokallio, H, Middelboe, M, Thomas, DN. 2015. Changes  
1345 in the composition and bioavailability of dissolved organic matter during sea ice  
1346 formation. *Limnology and Oceanography* 60(3): 817–830. doi: 10.1002/lno.10058.

1347 Kaneko, H, Blanc-Mathieu, R, Endo, H, Chaffron, S, Delmont, TO, Gaia, M, Henry, N,  
1348 Hernández-Velázquez, R, Nguyen, CH, Mamitsuka, H, Forterre, P, Jaillon, O,  
1349 Vargas, C de, Sullivan, MB, Suttle, CA, Guidi, L, Ogata, H. 2021. Eukaryotic virus  
1350 composition can predict the efficiency of carbon export in the global ocean. *Science*  
1351 24(1): 102002. doi: 10.1016/j.isci.2020.102002.

1352 **Katlein, C**, Fernández-Méndez, M, Wenzhöfer, F, Nicolaus, M. 2015. Distribution of algal  
1353 aggregates under summer sea ice in the Central Arctic. *Polar Biology* 38(5): 719–  
1354 731. doi: 10.1007/s00300-014-1634-3.

1355 **Katlein, C**, Arndt, S, Belter, HJ, Castellani, G, Nicolaus, M. 2019. Seasonal evolution of  
1356 light transmission distributions through Arctic sea ice. *Journal of Geophysical*  
1357 *Research: Oceans* 124(8): 5418–5435. doi: 10.1029/2018jc014833.

1358 **Kauko, HM**, Olsen, LM, Duarte, P, Peeken, I, Granskog, MA, Johnsen, G, Fernández-  
1359 Méndez, M, Pavlov, AK, Mundy, CJ, Assmy, P. 2018. Algal colonization of young  
1360 Arctic sea ice in spring. *Frontiers in Marine Science* 5: 199. doi:  
1361 10.3389/fmars.2018.00199.

1362 Kettner, MT, Oberbeckmann, S, Labrenz, M, Grossart, HP. 2019. The eukaryotic life on  
1363 microplastics in brackish ecosystems. *Frontiers in Microbiology* 10: 538. doi:  
1364 10.3389/fmicb.2019.00538.

1365 **Kiko, R**, Kern, S, Kramer, M, Mütze, H. 2017. Colonization of newly forming Arctic sea  
1366 ice by meiofauna: a case study for the future Arctic? *Polar Biology* 40(6): 1277–  
1367 1288. doi: 10.1007/s00300-016-2052-5.

1368 **Kilias, ES**, Junges, L, Šupraha, L, Leonard, G, Metfies, K, Richards, TA. 2020. Chytrid  
1369 fungi distribution and co-occurrence with diatoms correlate with sea ice melt in the  
1370 Arctic Ocean. *Communications Biology* 3(1): 183. doi: 10.1038/s42003-020-0891-7.

1371 **Kirpes, RM**, Bonanno, D, May, NW, Fraund, M, Barget, AJ, Moffet, RC, Ault, AP, Pratt,  
1372 KA. 2019. Wintertime Arctic sea spray aerosol composition controlled by sea ice  
1373 lead microbiology. *ACS Central Sciences* 5(11): 1760–1767. doi:  
1374 10.1021/acscentsci.9b00541.

1375 Klunder, MB, Bauch, D, Laan, P, De Baar, HJ, van Heuven, SMAC, Ober, S. 2012.  
1376 Dissolved iron in the Arctic shelf seas and surface waters of the central Arctic  
1377 Ocean: Impact of Arctic river water and ice-melt. *Journal of Geophysical Research:*  
1378 *Oceans* 117(C1). doi: 10.1029/2011JC007133.

1379 Koh, EY, Atamna-Ismaeel, N, Martin, A, Cowie, ROM, Beja, O, Davy, SK, Maas, EW,  
1380 Ryan, KG. 2010. Proteorhodopsin-bearing bacteria in Antarctic sea ice. *Applied*  
1381 *Environmental Microbiology* 76(17): 5918–5925. doi: 10.1128/aem.00562-10.

1382 Kohlbach, D, Graeve, M, Lange, BA, David, C, Peeken, I, Flores, H. 2016. The  
1383 importance of ice algae-produced carbon in the central Arctic Ocean ecosystem:  
1384 Food web relationships revealed by lipid and stable isotope analyses. *Limnology and*  
1385 *Oceanography* 61(6): 2027–2044. doi: 10.1002/lno.10351.

1386 Kohlbach, D, Goraguer, L, Bodur, YV, Müller, O, Amargant-Arumí, M, Blix, K, Bratbak,  
1387 G, Chierici, M, Dąbrowska, AM, Dietrich, U, Edvardsen, B, García, LM, Gradinger,  
1388 R, Hop, H, Jones, E, Lundesgaard, Ø, Olsen, LM, Reigstad, M, Saubrekka, K,  
1389 Tatarek, A, Wiktor, JM, Wold, A, Assmy, P. 2023. Earlier sea-ice melt extends the  
1390 oligotrophic summer period in the Barents Sea with low algal biomass and  
1391 associated low vertical flux. *Progress in Oceanography* 213: 103018. doi:  
1392 10.1016/j.pocean.2023.103018.

1393 Kohlbach, D, Fransson, A, Amargant-Arumi, M, Assmann, KM, Assmy, P, Bratbak, G,  
1394 Chierici, M, Cristea, A, Divine, DV, Down, E, Eikrem, W, Foss, Ø, Gardner, J,  
1395 Gradinger, RR, Granskog, MA, Hess, S, Ingvaldsen, RB, Koenig, Z, Kwaśniewski,  
1396 S, Majaneva, S, Marquardt, M, Müller, O, Ntniou, IV, Ormańczyk, M, Raffel, B,  
1397 Renaud, P, Renner, AHH, Freitas, TR de, Sen, A, Smoła, Z, Svensen, C, Vader, A,

1398 Våge, S, Wiktor, J, Wold, A, Zabłocka, M, Ziegler, A, Bluhm, BA. 2025. Nansen  
1399 and Amundsen basins: Gradients of physico-chemical properties and biota  
1400 composition with implications for future resource management of the central Arctic  
1401 Ocean. *Elementa: Science of the Anthropocene* 13(1): 00016. doi:  
1402 10.1525/elementa.2024.00016.

1403 **Kolber, ZS**, Dover, CLV, Niederman, RA, Falkowski, PG. 2000. Bacterial photosynthesis  
1404 in surface waters of the open ocean. *Nature* 407(6801): 177–179. doi:  
1405 10.1038/35025044.

1406 **Koch, CW**, Brown, TA, Amiriaux, R, Ruiz-Gonzalez, C, MacCorquodale, M, Yunda-  
1407 Guarin, GA, Kohlbach, D, Loseto, LL, Rosenberg, B, Hussey, NE, Ferguson, SH,  
1408 Yurkowski, DJ. 2023. Year-round utilization of sea ice-associated carbon in Arctic  
1409 ecosystems. *Nature Communications* 14(1): 1964. doi: 10.1038/s41467-023-37612-  
1410 8.

1411 **Krembs, C**, Eicken, H, Deming, JW. 2011. Exopolymer alteration of physical properties of  
1412 sea ice and implications for ice habitability and biogeochemistry in a warmer Arctic.  
1413 *Proceedings of the National Academy of Sciences* 108(9): 3653–3658. doi:  
1414 10.1073/pnas.1100701108.

1415 **Krumpen, T**, Belter, HJ, Boetius, A, Damm, E, Haas, C, Hendricks, S, Nicolaus, M,  
1416 Nöthig, E-M, Paul, S, Peeken, I, Ricker, R, Stein, R. 2019. Arctic warming interrupts  
1417 the Transpolar Drift and affects long-range transport of sea ice and ice-rafted matter.  
1418 *Scientific Reports* 9(1): 5459. doi: 10.1038/s41598-019-41456-y.

1419 **Kuhlisch, C**, Schleyer, G, Shahaf, N, Vincent, F, Schatz, D, Vardi, A. 2021. Viral infection  
1420 of algal blooms leaves a unique metabolic footprint on the dissolved organic matter  
1421 in the ocean. *Science Advances* 7(25): eabf4680. doi: 10.1126/sciadv.abf4680.

1422 **Kunisch, E**, Graeve, M, Gradinger, R, Haug, T, Kovacs, K, Lydersen, C, Varpe, Ø, Bluhm,  
1423 B. 2021. Ice-algal carbon supports harp and ringed seal diets in the European Arctic:  
1424 evidence from fatty acid and stable isotope markers. *Marine Ecology Progress Series*  
1425 675: 181–197. doi: 10.3354/meps13834.

1426 **Kvernvik, AC**, Hoppe, CJM, Lawrenz, E, Prášil, O, Greenacre, M, Wiktor, JM, Leu, E.  
1427 2018. Fast reactivation of photosynthesis in arctic phytoplankton during the polar  
1428 night. *Journal of Phycology* 54(4): 461-470. doi: 10.1111/jpy.12750.

1429 **Kwok, R**. 2018. Arctic sea ice thickness, volume, and multiyear ice coverage: losses and  
1430 coupled variability (1958–2018). *Environmental Research Letters* 13(10): 105005.  
1431 doi: 10.1088/1748-9326/aae3ec.

1432 **Ladau, J**, Sharpton, TJ, Finucane, MM, Jospin, G, Kembel, SW, O’Dwyer, J, Koeppel, AF,  
1433 Green, JL, Pollard, KS. 2013. Global marine bacterial diversity peaks at high  
1434 latitudes in winter. *ISME Journal* 7(9): 1669–1677. doi: 10.1038/ismej.2013.37.

1435 **Lacour, T**, Morin, P-I, Sciandra, T, Donaher, N, Campbell, DA, Ferland, J, Babin, M.  
1436 2019. Decoupling light harvesting, electron transport and carbon fixation during  
1437 prolonged darkness supports rapid recovery upon re-illumination in the Arctic  
1438 diatom *Chaetoceros neogracilis*. *Polar Biology*: 1–13. doi: 10.1007/s00300-019-  
1439 02507-2.

1440 Lalande, C, Nöthig, E, Somavilla, R, Bauerfeind, E, Shevchenko, V, Okolodkov, Y. 2014.  
1441 Variability in under-ice export fluxes of biogenic matter in the Arctic Ocean. *Global*  
1442 *Biogeochemical Cycles* 28(5): 571–583. doi: 10.1002/2013gb004735.

1443 Lalande, C, Dezutter, T. 2024. Pan-Arctic downward export fluxes, in Wassmann P eds.  
1444 *Elements of a pan-Arctic Ocean ecology*. Orkana Press.

1445 Lantuit, H, Overduin, PP, Wetterich, S. 2013. Recent progress regarding permafrost coasts.  
1446 *Permafrost and Periglacial Processes* 24(2): 120–130. doi: 10.1002/ppp.1777.

1447 Last, KS, Hobbs, L, Berge, J, Brierley, AS, Cottier, F. 2016. Moonlight drives ocean-scale  
1448 mass vertical migration of zooplankton during the Arctic winter. *Current Biology*  
1449 26(2): 244–251. doi: 10.1016/j.cub.2015.11.038.

1450 Lei, R, Zhang, Z, Matero, I, Cheng, B, Li, Q, Huang, W. 2012. Reflection and transmission  
1451 of irradiance by snow and sea ice in the central Arctic Ocean in summer 2010. *Polar*  
1452 *Research* 31(0): 17325. doi: 10.3402/polar.v31i0.17325.

1453 Lennon, JT, Abramoff, RZ, Allison, SD, Burckhardt, RM, DeAngelis, KM, Dunne, JP,  
1454 Frey, SD, Friedlingstein, P, Hawkes, CV, Hungate, BA, Khurana, S, Kivlin, SN,  
1455 Levine, NM, Manzoni, S, Martiny, AC, Martiny, JBH, Nguyen, NK, Rawat, M,  
1456 Talmy, D, Todd-Brown, K, Vogt, M, Wieder, WR, Zakem, EJ. 2024. Priorities,  
1457 opportunities, and challenges for integrating microorganisms into Earth system  
1458 models for climate change prediction. *mBio* 15(5): e00455-24. doi:  
1459 10.1128/mbio.00455-24.

1460 Li, WKW, McLaughlin, FA, Lovejoy, C, Carmack, EC. 2009. Smallest algae thrive as the  
1461 Arctic Ocean freshens. *Science* 326(5952): 539–539. doi: 10.1126/science.1179798.

1462 **Lincoln, BJ**, Rippeth, TP, Lenn, Y, Timmermans, ML, Williams, WJ, Bacon, S. 2016.  
1463 Wind-driven mixing at intermediate depths in an ice-free Arctic Ocean. *Geophysical*  
1464 *Research Letters* 43(18): 9749–9756. doi: 10.1002/2016gl070454.

1465 **Lindsay, R**, Schweiger, A. 2015. Arctic sea ice thickness loss determined using subsurface,  
1466 aircraft, and satellite observations. *Cryosphere* 9(1): 269–283. doi: 10.5194/tc-9-269-  
1467 2015.

1468 **Lizotte, M**, Levasseur, M, Galindo, V, Gourdal, M, Gosselin, M, Tremblay, J-É, Blais, M,  
1469 Charette, J, Husserr, R. 2020. Phytoplankton and dimethylsulfide dynamics at two  
1470 contrasting Arctic ice edges. *Biogeosciences* 17(6): 1557–1581. doi: 10.5194/bg-17-  
1471 1557-2020.

1472 Lombard, F, Guidi, L, Manoela C, B, Coelho, LP, et al. 2024. Ubiquity of inverted  
1473 'gelatinous' ecosystem pyramids in the global ocean. *bioRxiv*. doi:  
1474 <https://doi.org/10.1101/2024.02.09.579612>.

1475 Longobardi, L, Dubroca, L, Margiotta, F, Sarno, D, Zingone, A. 2022. Photoperiod-driven  
1476 rhythms reveal multi-decadal stability of phytoplankton communities in a highly  
1477 fluctuating coastal environment. *Scientific reports* 12(1), p.3908.  
1478 <https://doi.org/10.1038/s41598-022-07009-6>

1479 **Loose, B**, Fer, I, Ulfso, A, Chierici, M, Droste, ES, Nomura, D, Fransson, A, Hoppema,  
1480 M, Torres-Valdés, S. 2024. An analysis of air-sea gas exchange for the entire  
1481 MOSAiC Arctic drift. *Elementa: Science of the Anthropocene* 12(1). doi:  
1482 10.1525/elementa.2023.00128.

1483 **Lovejoy, C**, Vincent, WF, Bonilla, S, Roy, S, Martineau, M, Terrado, R, Potvin, M,  
1484 Massana, R, Pedrós-Alió, C. 2007. Distribution, phylogeny, and growth of cold-

1485 adapted picoprasinophytes in Arctic Seas. *Journal of Phycology* 43(1): 78–89. doi:  
1486 10.1111/j.1529-8817.2006.00310.x.

1487 **Lowry, LF**, Citta, JJ, O’Corry-Crowe, G, Quakenbush, LT, Frost, KJ, Suydam, R, Hobbs,  
1488 RC, Gray, T. 2019. Distribution, abundance, harvest, and status of western Alaska  
1489 beluga whale, *Delphinapterus leucas*, stocks. *Marine Fisheries Review* 81(3–4). doi:  
1490 10.7755/mfr.81.3-4.2.

1491 **Lundberg**, M, Polyakov, IV. 2025. Climate change drives evolution of thermohaline  
1492 staircases in the Arctic Ocean. *Journal of Geophysical Research: Oceans* 130(1).  
1493 doi: 10.1029/2024jc021538.

1494 **Lund-Hansen**, L, Hawes, I, Hancke, K, Salmansen, N, Nielsen, J, Balslev, L, Sorrell, B.  
1495 2020. Effects of increased irradiance on biomass, photobiology, nutritional quality,  
1496 and pigment composition of Arctic sea ice algae. *Marine Ecology Progress Series*  
1497 648: 95–110. doi: 10.3354/meps13411.

1498 **Manabe, S**, Stouffer, RJ. 1980. Sensitivity of a global climate model to an increase of CO<sub>2</sub>  
1499 concentration in the atmosphere. *Journal of Geophysical Research: Ocean* 85(C10):  
1500 5529–5554. doi: 10.1029/jc085ic10p05529.

1501 **Marquardt, M**, Goragner, L, Assmy, P, Bluhm, BA, Aaboe, S, Down, E, Patrohay, E,  
1502 Edvardsen, B, Tatarek, A, Smoła, Z, Wiktor, J, Gradinger, R. 2023. Seasonal  
1503 dynamics of sea-ice protist and meiofauna in the northwestern Barents Sea. *Progress*  
1504 *in Oceanography* 218: 103128. doi: 10.1016/j.pocean.2023.103128.

1505 Materić, D, Kjær, HA, Vallelonga, P, Tison, JL, Röckmann, T, Holzinger, R. 2022.  
1506 Nanoplastics measurements in Northern and Southern polar ice. *Environmental*  
1507 *research* 208: 112741. doi: 10.1016/j.envres.2022.112741.

1508 Maykut, GA, McPhee, MG. 1995. Solar heating of the Arctic mixed layer. *Journal of*  
1509 *Geophysical Research: Oceans* 100(C12): 24691–24703. doi: 10.1029/95jc02554.

1510 McClelland, JW, Holmes, RM, Dunton, KH, Macdonald, RW. 2012. The Arctic Ocean  
1511 estuary. *Estuaries and Coasts* 35(2): 353–368. doi: 10.1007/s12237-010-9357-3.

1512 McPhee, MG, Kikuchi, T, Morison, JH, Stanton, TP. 2003. Ocean-to-ice heat flux at the  
1513 North Pole environmental observatory. *Geophysical Research Letters* 30(24). doi:  
1514 10.1029/2003gl018580.

1515 Melia, N, Haines, K, Hawkins, E. 2016. Sea ice decline and 21st century trans-Arctic  
1516 shipping routes. *Geophysical Research Letters* 43(18): 9720–9728. doi:  
1517 10.1002/2016gl069315.

1518 Millar, AJ. 2016. The intracellular dynamics of circadian clocks reach for the light of  
1519 ecology and evolution. *Annual review of plant biology*, 67(1): 595-618.  
1520 <https://doi.org/10.1146/annurev-arplant-043014-115619>.

1521 Monahan, EC, Spiel, DE, Davidson, KL. 1986. Oceanic whitecaps, and their role in air-sea  
1522 exchange processes. *Oceanography Science Library*: 167–174. doi: 10.1007/978-94-  
1523 009-4668-2\_16.

1524 Morin, P, Lacour, T, Grondin, P, Bruyant, F, Ferland, J, Forget, M, Massicotte, P,  
1525 Donaher, N, Campbell, DA, Lavaud, J, Babin, M. 2020. Response of the sea-ice  
1526 diatom *Fragilariopsis cylindrus* to simulated polar night darkness and return to light.  
1527 *Limnology and Oceanography* 65(5): 1041–1060. doi: 10.1002/lno.11368.

1528 Morison, J, Steele, M, Andersen, R. 1998. Hydrography of the upper Arctic Ocean  
1529 measured from the nuclear submarine U.S.S. *Pargo*. *Deep Sea Res Part I*:

1530 *Oceanographic Research Papers* 45(1): 15–38. doi: 10.1016/s0967-0637(97)00025-  
1531 3.

1532 **Morison, J**, Kwok, R, Peralta-Ferriz, C, Alkire, M, Rigor, I, Andersen, R, Steele, M. 2012.  
1533 Changing Arctic Ocean freshwater pathways. *Nature* 481(7379): 66–70. doi:  
1534 10.1038/nature10705.

1535 MOSAiC. 2016. MOSAiC-Multidisciplinary drifting Observatory for the Study of Arctic  
1536 Climate Science Plan. Available at [https://mosaic-expedition.org/wp-](https://mosaic-expedition.org/wp-content/uploads/2020/12/mosaic_scienceplan.pdf)  
1537 [content/uploads/2020/12/mosaic\\_scienceplan.pdf](https://mosaic-expedition.org/wp-content/uploads/2020/12/mosaic_scienceplan.pdf).

1538 **Mruwat, N**, Carlson, MCG, Goldin, S, Ribalet, F, Kirzner, S, Hulata, Y, Beckett, SJ,  
1539 Shitrit, D, Weitz, JS, Armbrust, EV, Lindell, D. 2020. A single-cell polony method  
1540 reveals low levels of infected *Prochlorococcus* in oligotrophic waters despite high  
1541 cyanophage abundances. *ISME Journal* 15(1): 41–54. doi: 10.1038/s41396-020-  
1542 00752-6.

1543 **Neukermans, G**, Oziel, L, Babin, M. 2018. Increased intrusion of warming Atlantic water  
1544 leads to rapid expansion of temperate phytoplankton in the Arctic. *Global Change*  
1545 *Biology* 24(6): 2545–2553. doi: 10.1111/gcb.14075.

1546 **Nicolaus, M**, Katlein, C, Maslanik, J, Hendricks, S. 2012. Changes in Arctic sea ice result  
1547 in increasing light transmittance and absorption. *Geophysical Research Letters*  
1548 39(24). doi: 10.1029/2012gl053738.

1549 **Notz, D**, Stroeve, J. 2016. Observed Arctic sea-ice loss directly follows anthropogenic CO<sub>2</sub>  
1550 emission. *Science* 354(6313): 747–750. doi: 10.1126/science.aag2345.

1551 **Onda, DFL**, Medrinal, E, Comeau, AM, Thaler, M, Babin, M, Lovejoy, C. 2017. Seasonal  
1552 and interannual changes in ciliate and dinoflagellate species assemblages in the

1553 Arctic Ocean (Amundsen Gulf, Beaufort Sea, Canada). *Frontiers in Marine Science*  
1554 4: 16. doi: 10.3389/fmars.2017.00016.

1555 **Oziel, L**, Baudena, A, Ardyna, M, Massicotte, P, Randelhoff, A, Sallée, J-B, Ingvaldsen,  
1556 RB, Devred, E, Babin, M. 2020. Faster Atlantic currents drive poleward expansion  
1557 of temperate phytoplankton in the Arctic Ocean. *Nature Communications* 11(1):  
1558 1705. doi: 10.1038/s41467-020-15485-5.

1559 **Paulsen, ML**, Doré, H, Garczarek, L, Seuthe, L, Müller, O, Sandaa, R-A, Bratbak, G,  
1560 Larsen, A. 2016. *Synechococcus* in the Atlantic Gateway to the Arctic Ocean.  
1561 *Frontiers in Marine Science* 3: 191. doi: 10.3389/fmars.2016.00191.

1562 **Pelt, TI van**, Huntington, HP, Romanenko, OV, Mueter, FJ. 2017. The missing middle:  
1563 Central Arctic Ocean gaps in fishery research and science coordination. *Marine*  
1564 *Policy* 85: 79–86. doi: 10.1016/j.marpol.2017.08.008.

1565 **Peralta-Ferriz, C**, Woodgate, RA. 2015. Seasonal and interannual variability of pan-Arctic  
1566 surface mixed layer properties from 1979 to 2012 from hydrographic data, and the  
1567 dominance of stratification for multiyear mixed layer depth shoaling. *Progress in*  
1568 *Oceanography* 134: 19–53. doi: 10.1016/j.pocean.2014.12.005.

1569 **Perovich, D**, Richter-Menge, J, Polashenski, C, Elder, B, Arbetter, T, Brennick, O. 2014.  
1570 Sea ice mass balance observations from the North Pole Environmental Observatory.  
1571 *Geophysical Research Letters* 41(6): 2019–2025. doi: 10.1002/2014gl059356.

1572 **Pittera, J**, Jouhet, J, Breton, S, Garczarek, L, Partensky, F, Maréchal, É, Nguyen, NA,  
1573 Doré, H, Ratin, M, Pitt, FD, Scanlan, DJ, Six, C. 2018. Thermoacclimation and  
1574 genome adaptation of the membrane lipidome in marine *Synechococcus*.  
1575 *Environmental Microbiology* 20(2): 612–631. doi: 10.1111/1462-2920.13985

1576 Pnyushkov, A, Fairbanks, U of A, Polyakov, I. 2022. Nansen and Amundsen Basins  
1577 Observational System (NABOS): Contributing to understanding changes in the  
1578 Arctic. *Oceanography* 35(3–4): 90–93. doi: 10.5670/oceanog.2022.104.

1579 Polyakov, IV, Beszczynska, A, Carmack, EC, Dmitrenko, IA, Fahrbach, E, Frolov, IE,  
1580 Gerdes, R, Hansen, E, Holfort, J, Ivanov, VV, Johnson, MA, Karcher, M, Kauker,  
1581 F, Morison, J, Orvik, KA, Schauer, U, Simmons, HL, Skagseth, Ø, Sokolov, VT,  
1582 Steele, M, Timokhov, LA, Walsh, D, Walsh, JE. 2005. One more step toward a  
1583 warmer Arctic. *Geophysical Research. Letters* 32(17). doi:10.1029/2005GL023740

1584 Polyakov, IV, Pnyushkov, AV, Timokhov, LA. 2012. Warming of the Intermediate  
1585 Atlantic Water of the Arctic Ocean in the 2000s. *Journal of Climate* 25(23): 8362–  
1586 8370. doi: 10.1175/jcli-d-12-00266.1.

1587 Polyakov, IV, Pnyushkov, AV, Alkire, M, Ashik, IM, Baumann, T, Carmack, EC,  
1588 Goszczko, I, Ivanov, V, Kanzow, T, Krieshfield, R, Kwok, R, Sundfjord, A,  
1589 Morison, J, Rember, R, Yulin, A. 2017. Greater role for Atlantic inflows on sea-ice  
1590 loss in the Eurasian Basin of the Arctic Ocean. *Science* 356(6335): 285–291. doi:  
1591 10.1126/science.aai8204.

1592 Polyakov, IV, Alkire, MB, Bluhm, BA, Brown, K, Carmack, EC, Chierici, M, Danielson,  
1593 S, Ellingsen, I, Ershova, EA, Gårdfeldt, K, Ingvaldsen, RB, Pnyushkov, AV,  
1594 Slagstad, D, Wassman, P. 2020a. Borealization of the Arctic Ocean in response to  
1595 anomalous advection from sub-arctic seas. *Frontiers in Marine Sciences* 7: 491. doi:  
1596 10.3389/fmars.2020.00491.

1597 Polyakov, IV, Rippeth, TP, Fer, I, Alkire, MB, Baumann, TM, Carmack, EC, Ingvaldsen,  
1598 R, Ivanov, VV, Janout, M, Lind, S, Padman, L, Pnyushkov, AV, Rember, R. 2020b.

1599 Weakening of cold halocline layer exposes sea ice to oceanic heat in the eastern  
1600 Arctic Ocean. *Journal of Climate* 33(18): 8107–8123. doi: 10.1175/jcli-d-19-0976.1

1601 Polyakov, I, Carmack, E, Rudels, B. 2024. Physical Oceanography, in Wassmann P eds.,  
1602 *Elements of a pan-Arctic Ocean ecology*. Orkana.

1603 Polyakov, IV, Pnyushkov, AV, Charette, M, Cho, K-H, Jung, J, Kipp, L, Muilwijk, M,  
1604 Whitmore, L, Yang, EJ, Yoo, J. 2025a. Atlantification advances into the Amerasian  
1605 Basin of the Arctic Ocean. *Science Advances* 11(8): eadq7580. doi:  
1606 10.1126/sciadv.adq7580.

1607 Polyakov, IV, Pnyushkov, AV, Carmack, EC, Charette, M, Cho, K-H, Dykstra, S,  
1608 Haapala, J, Jung, J, Kipp, L, Yang, EJ. 2025b. Role of sea ice, stratification, and  
1609 near-inertial oscillations in shaping the upper Siberian Arctic Ocean currents.  
1610 *EGUsphere* 2025: 1–27. doi: 10.5194/egusphere-2025-2316.

1611 Post, E, Alley, RB, Christensen, TR, Macias-Fauria, M, Forbes, BC, Gooseff, MN, Iler, A,  
1612 Kerby, JT, Laidre, KL, Mann, ME, Olofsson, J, Stroeve, JC, Ulmer, F, Virginia, RA,  
1613 Wang, M. 2019. The polar regions in a 2°C warmer world. *Science Advances* 5(12):  
1614 eaaw9883. doi: 10.1126/sciadv.aaw9883.

1615 Priest, T, von Appen, W-J, Oldenburg, E, Popa, O, Torres-Valdés, S, Bienhold, C, Metfies,  
1616 K, Boulton, W, Mock, T, Fuchs, BM, Amann, R, Boetius, A, Wietz, M. 2023.  
1617 Atlantic water influx and sea-ice cover drive taxonomic and functional shifts in  
1618 Arctic marine bacterial communities. *ISME Journal* 17(10): 1612–1625. doi:  
1619 10.1038/s41396-023-01461-6.

1620 Poulin, M, Daugbjerg, N, Gradinger, R, Ilyash, L, Ratkova, T, Quillfeldt, C von. 2011. The  
1621 pan-Arctic biodiversity of marine pelagic and sea-ice unicellular eukaryotes: a first-

1622 attempt assessment. *Marine Biodiversity* 41(1): 13–28. doi: 10.1007/s12526-010-  
1623 0058-8.

1624 Priou, P, Nikolopoulos, A, Flores, H, Gradinger, R, Kunisch, E, Katlein, C, Castellani, G,  
1625 Linders, T, Berge, J, Fisher, JAD, Geoffroy, M. 2021. Dense mesopelagic sound  
1626 scattering layer and vertical segregation of pelagic organisms at the Arctic-Atlantic  
1627 gateway during the midnight sun. *Progress in Oceanography* 196: 102611. doi:  
1628 10.1016/j.pocean.2021.102611.

1629 Proshutinsky, A, Krishfield, R, Timmermans, M, Toole, J, Carmack, E, McLaughlin, F,  
1630 Williams, WJ, Zimmermann, S, Itoh, M, Shimada, K. 2009. Beaufort Gyre  
1631 freshwater reservoir: state and variability from observations. *Journal of Geophysical*  
1632 *Research: Oceans* 114(C1). doi: 10.1029/2008jc005104.

1633 Quadfasel, D, Sy, A, Wells, D, Tunik, A. 1991. Warming in the Arctic. *Nature* 350(6317):  
1634 385–385. doi: 10.1038/350385a0.

1635 Rabe, B, Heuzé, C, Regnery, J, Aksenov, Y, Allerholt, J, Athanase, M, Bai, Y, Basque, C,  
1636 Bauch, D, Baumann, TM, Chen, D, Cole, ST, Craw, L, Davies, A, Damm, E,  
1637 Dethloff, K, Divine, DV, Doglioni, F, Ebert, F, Fang, YC, Fer, I, Fong, AA,  
1638 Gradinger, R, Granskog, MA, Graupner, R, Haas, C, He, H, He, Y, Hoppmann, M,  
1639 Janout, M, Kadko, D, Kanzow, T, Karam, S, Kawaguchi, Y, Koenig, Z, Kong, B,  
1640 Krishfield, RA, Krumpen, T, Kuhlmeier, D, Kuznetsov, I, Lan, M, Laukert, G, Lei, R,  
1641 Li, T, Torres-Valdés, S, Lin, L, Lin, L, Liu, H, Liu, N, Loose, B, Ma, X, McKay, R,  
1642 Mallet, M, Mallett, RDC, Maslowski, W, Mertens, C, Mohrholz, V, Muilwijk, M,  
1643 Nicolaus, M, O'Brien, JK, Perovich, D, Ren, J, Rex, M, Ribeiro, N, Rinke, A,  
1644 Schaffer, J, Schuffenhauer, I, Schulz, K, Shupe, MD, Shaw, W, Sokolov, V,

1645 Sommerfeld, A, Spreen, G, Stanton, T, Stephens, M, Su, J, Sukhikh, N, Sundfjord,  
1646 A, Thomisch, K, Tippenhauer, S, Toole, JM, Vredenburg, M, Walter, M, Wang, H,  
1647 Wang, L, Wang, Y, Wendisch, M, Zhao, J, Zhou, M, Zhu, J. 2022. Overview of the  
1648 MOSAiC expedition: Physical oceanography. *Elementa: Science of the*  
1649 *Anthropocene* 10(1). doi: 10.1525/elementa.2021.00062.

1650 Rampal, P, Weiss, J, Dubois, C, Campin, J -M. 2011. IPCC climate models do not capture  
1651 Arctic sea ice drift acceleration: Consequences in terms of projected sea ice thinning  
1652 and decline. *Journal of Geophysical Research: Oceans* 116(C8). doi:  
1653 10.1029/2011jc007110.

1654 Randelhoff, A, Sundfjord, A. 2018. Short commentary on marine productivity at Arctic  
1655 shelf breaks: upwelling, advection and vertical mixing. *Ocean Sciences* 14(2): 293–  
1656 300. doi: 10.5194/os-14-293-2018.

1657 Randelhoff, A, Reigstad, M, Chierici, M, Sundfjord, A, Ivanov, V, Cape, M, Vernet, M,  
1658 Tremblay, J-É, Bratbak, G, Kristiansen, S. 2018. Seasonality of the physical and  
1659 biogeochemical hydrography in the inflow to the Arctic Ocean through Fram Strait.  
1660 *Frontiers in Marine Sciences* 5: 224. doi: 10.3389/fmars.2018.00224.

1661 Randelhoff, A, Holding, J, Janout, M, Sejr, MK, Babin, M, Tremblay, J-É, Alkire, MB.  
1662 2020. Pan-Arctic Ocean primary production constrained by turbulent nitrate fluxes.  
1663 *Frontiers in Marine Sciences* 7: 150. doi: 10.3389/fmars.2020.00150.

1664 Rantanen, M, Karpechko, AYu, Lipponen, A, Nordling, K, Hyvärinen, O, Ruosteenoja, K,  
1665 Vihma, T, Laaksonen, A. 2022. The Arctic has warmed nearly four times faster than  
1666 the globe since 1979. *Communications Earth & Environment* 3(1): 168. doi:  
1667 10.1038/s43247-022-00498-3.

1668 Raphael, IA, Perovich, DK, Polashenski, CM, Clemens-Sewall, D, Itkin, P, Lei, R,  
1669 Nicolaus, M, Regnery, J, Smith, MM, Webster, M, Jaggi, M. 2024. Sea ice mass  
1670 balance during the MOSAiC drift experiment: Results from manual ice and snow  
1671 thickness gauges. *Elementa: Science of the Anthropocene* 12(1): 0040. doi:  
1672 10.1525/elementa.2023.00040.

1673 Rapp, JZ, Fernández-Méndez, M, Bienhold, C, Boetius, A. 2018. Effects of ice-algal  
1674 aggregate export on the connectivity of bacterial communities in the central Arctic  
1675 Ocean. *Frontiers in Microbiology* 9: 1035. doi: 10.3389/fmicb.2018.01035

1676 Raven, JA, Kübler, JE, Beardall, J. 2000. Put out the light, and then put out the light.  
1677 *Journal of the Marine Biological Association of the United Kingdom* 80(1): 1–25.  
1678 doi: 10.1017/s0025315499001526.

1679 Reay, DS, Dentener, F, Smith, P, Grace, J, Feely, RA. 2008. Global nitrogen deposition  
1680 and carbon sinks. *Nature Geoscience* 1(7): 430–437. doi: 10.1038/ngeo230

1681 Reigstad, M, Wassmann, P. 2007. Does *Phaeocystis* spp. contribute significantly to  
1682 vertical export of organic carbon? *Biogeochemistry* 83: 217–234. doi:  
1683 10.1007/s10533-007-9093-3.

1684 Rigonato, J, Lozano, JC, Vergé, V, Jaillon, O, Bouget, FY. 2025. Latitudinal diversity in  
1685 circadian and light-sensing genes in an ecologically vital group of marine  
1686 picoeukaryote algae. *The ISME Journal*, 19(1): p.wraf263.  
1687 <https://doi.org/10.1093/ismejo/wraf263>.

1688 Roca- Martí, M, Puigcorbé, V, Rutgers van der Loeff, MM, Katlein, C,  
1689 Fernández- Méndez, M, Peeken, I, Masqué, P. 2016. Carbon export fluxes and  
1690 export efficiency in the central Arctic during the record sea- ice minimum in 2012:

1691 A joint  $^{234}\text{Th}/^{238}\text{U}$  and  $^{210}\text{Po}/^{210}\text{Pb}$  study. *Journal of Geophysical Research: Oceans*  
1692 121(7): 5030–5049. doi: 10.1002/2016JC011816.

1693 Rogalla, B, Allen, SE, Colombo, M, Myers, PG, Orians, KJ. 2025. Modeling dissolved Pb  
1694 concentrations in the western Arctic Ocean: the continued legacy of anthropogenic  
1695 pollution. *Journal of Geophysical Research: Oceans* 130(4): p.e2025JC022415.  
1696 doi:10.1029/2025JC022415.

1697 Rogge, A, Janout, M, Loginova, N, Trudnowska, E, Hörstmann, C, Wekerle, C, Oziel, L,  
1698 Schourup-Kristensen, V, Ruiz-Castillo, E, Schulz, K, Povazhnyy, VV, Iversen, MH,  
1699 Waite, AM. 2023. Carbon dioxide sink in the Arctic Ocean from cross-shelf  
1700 transport of dense Barents Sea water. *Nature Geoscience* 16(1): 82–88. doi:  
1701 10.1038/s41561-022-01069-z.

1702 Rontani, J-F, Amiraux, R, Lalande, C, Babin, M, Kim, H-R, Belt, ST. 2018. Use of  
1703 palmitoleic acid and its oxidation products for monitoring the degradation of ice  
1704 algae in Arctic waters and bottom sediments. *Organic Geochemistry* 124: 88–102.  
1705 doi: 10.1016/j.orggeochem.2018.06.002.

1706 Rontani, J-F, Amiraux, R, Smilk, L, Wakeham, SG, Paulmier, A, Vaultier, F, Sun-Yong,  
1707 Ha, Jun-oh, M, Belt, ST. 2021. Type II photosensitized oxidation in senescent  
1708 microalgal cells at different latitudes: does low under-ice irradiance in polar regions  
1709 enhance efficiency? *Science of the Total Environment* 779: 146363. doi:  
1710 10.1016/j.scitotenv.2021.146363.

1711 Royo-Llonch, M, Sánchez, P, Ruiz-González, C, Salazar, G, Pedrós-Alió, C, Sebastián, M,  
1712 Labadie, K, Paoli, L, Ibarbalz, FM, Zinger, L, Churchward, B, Coordinators, TO,  
1713 Babin, M, Bork P, Boss, E, Cochrane, G, Vargas, C de, Gorsky, G, Grimsley, N,

1714 Guidi, L, Hingamp, P, Iudicone, D, Jaillon, O, Kandels, S, Not, F, Ogata, H, Pesant,  
1715 S, Poulton, N, Raes, J, Sardet, C, Speich, S, Settmann, L, Sullivan, MB, Chaffron,  
1716 S, Eveillard, D, Karsenti, E, Sunagawa, S, Wincker, P, Karp-Boss, L, Bowler, C,  
1717 Acinas, SG. 2021. Compendium of 530 metagenome-assembled bacterial and  
1718 archaeal genomes from the polar Arctic Ocean. *Nature Microbiology* 6(12): 1561–  
1719 1574. doi: 10.1038/s41564-021-00979-9.

1720 Rozenberg, A, Inoue, K, Kandori, H, Béjà, O. 2021. Microbial rhodopsins: the last two  
1721 decades. *Annual review of microbiology*, 75(1): 427-447.  
1722 <https://doi.org/10.1146/annurev-micro-031721-020452>.

1723 Rudels, B. 1989. The formation of polar surface water, the ice export and the exchanges  
1724 through the Fram Strait. *Progress in Oceanography* 22(3): 205–248. doi:  
1725 10.1016/0079-6611(89)90013-x.

1726 Salazar, G, Paoli, L, Alberti, A, Huerta-Cepas, J, Ruscheweyh, H-J, Cuenca, M, Field, CM,  
1727 Coelho, LP, Cruaud, C, Engelen, S, Gregory, AC, Labadie, K, Marec, C, Pelletier, E,  
1728 Royo-Llonch, M, Roux, S, Sánchez, P, Uehara, H, Zayed, AA, Zeller, G,  
1729 Carmichael, M, Dimier, C, Ferland, J, Kandels, S, Picheral, M, Pisarev, S, Poulain, J,  
1730 Coordinators, TO, Acinas, SG, Babin, M, Bork, P, Bowler, C, Vargas, C de, Guidi,  
1731 L, Hingamp, P, Iudicone, D, Karp-Boss, L, Karsenti, E, Ogata, H, Pesant, S, Speich,  
1732 S, Sullivan, MB, Wincker, P, Sunagawa, S. 2019. Gene expression changes and  
1733 community turnover differentially shape the global ocean metatranscriptome. *Cell*  
1734 179(5): 1068-1083.e21. doi: 10.1016/j.cell.2019.10.014.

1735 Schaefer, K, Elshorbany, Y, Jafarov, E, Schuster, PF, Striegl, RG, Wickland, KP,  
1736 Sunderland, EM. 2020. Potential impacts of mercury released from thawing  
1737 permafrost. *Nature Communications* 11(1): 4650. doi: 10.1038/s41467-020-18398-5.

1738 Schartup, AT, Soerensen, AL, Heimbürger-Boavida, LE. 2020. Influence of the arctic sea-  
1739 ice regime shift on sea-ice methylated mercury trends. *Environmental Science &*  
1740 *Technology Letters* 7(10): 708–713. doi: 10.1021/acs.estlett.0c00465.

1741 Schaub, I, Wagner, H, Graeve, M, Karsten, U. 2017. Effects of prolonged darkness and  
1742 temperature on the lipid metabolism in the benthic diatom *Navicula perminuta* from  
1743 the Arctic Adventfjorden, Svalbard. *Polar Biology* 40(7): 1425–1439. doi:  
1744 0.1007/s00300-016-2067-y.

1745 Schauer, U, Fahrbach, E, Osterhus, S, Rohardt, G. 2004. Arctic warming through the Fram  
1746 Strait: Oceanic heat transport from 3 years of measurements. *Journal of Geophysical*  
1747 *Research: Oceans* 109(C6). doi: 10.1029/2003jc001823.

1748 Schmale, J, Flores, JM, Law, KS, Raut, J-C, O'Brien, J, Vardi, A, Koren, I, Ravetta, F,  
1749 Bekki, S, Pazmino, A, Ardyna, M, Geoffroy, M, Lovejoy, C, Nicolaus, M, Babin, M,  
1750 Bowler, C, Karp-Boss, L 2025. Tara Polaris: Shedding light on microbial and  
1751 climate feedback processes in the Arctic atmosphere. *Elementa: Science of the*  
1752 *Anthropocene* 13(1): 00030.

1753 Schulz, K, Koenig, Z, Muilwijk, M, Bauch, D, Hoppe, CJM, Droste, ES, Hoppmann, M,  
1754 Chamberlain, EJ, Laukert, G, Stanton, T, Quintanilla-Zurita, A, Fer, I, Heuzé, C,  
1755 Karam, S, Mieruch-Schnülle, S, Baumann, TM, Vredenburg, M, Tippenhauer, S,  
1756 Granskog, MA. 2024. The Eurasian Arctic Ocean along the MOSAiC drift in 2019–  
1757 2020: An interdisciplinary perspective on physical properties and processes.

1758 *Elementa: Science of the Anthropocene* 12(1): 00114. doi:  
1759 10.1525/elementa.2023.00114.

1760 **Sciandra, T**, Forget, M, Bruyant, F, Béguin, M, Lacour, T, Bowler, C, Babin, M. 2022. The  
1761 possible fates of *Fragilariopsis cylindrus* (polar diatom) cells exposed to prolonged  
1762 darkness. *Journal of Phycology* 58(2): 281–296. doi: 10.1111/jpy.13232.

1763 **Shen, Y**, Benner, R. 2018. Mixing it up in the ocean carbon cycle and the removal of  
1764 refractory dissolved organic carbon. *Scientific Reports* 8(1): 2542. doi:  
1765 10.1038/s41598-018-20857-5.

1766 **Shimada, K**, McLaughlin, F, Carmack, E, Proshutinsky, A, Nishino, S, Itoh, M. 2004.  
1767 Penetration of the 1990s warm temperature anomaly of Atlantic Water in the Canada  
1768 Basin. *Geophysical Research Letters* 31(20). doi: 10.1029/2004gl020860.

1769 **Sigmond, M**, Fyfe, JC, Swart, NC. 2018. Ice-free Arctic projections under the Paris  
1770 Agreement. *Nature Climate Change* 8(5): 404–408. doi: 10.1038/s41558-018-0124-y

1771 **Sipler, RE**, Gong, D, Baer, SE, Sanderson, MP, Roberts, QN, Mulholland, MR, Bronk,  
1772 DA. 2017. Preliminary estimates of the contribution of Arctic nitrogen fixation to the  
1773 global nitrogen budget. *Limnology and Oceanography Letters* 2(5): 159–166. doi:  
1774 10.1002/lol2.10046.

1775 **Smith, MM**, Angot, H, Chamberlain, EJ, Droste, ES, Karam, S, Muilwijk, M, Webb, AL,  
1776 Archer, SD, Beck, I, Blomquist, BW, Bowman, J, Boyer, M, Bozzato, D, Chierici,  
1777 M, Creamean, J, D’Angelo, A, Delille, B, Fer, I, Fong, AA, Fransson, A, Fuchs, N,  
1778 Gardner, J, Granskog, MA, Hoppe, CJM, Hoppema, M, Hoppmann, M, Mock, T,  
1779 Muller, S, Müller, O, Nicolaus, M, Nomura, D, Petäjä, T, Salganik, E, Schmale, J,  
1780 Schmidt, K, Schulz, KM, Shupe, MD, Stefels, J, Thielke, L, Tippenhauer, S, Ulfsbo,

1781 A, Leeuwe, M van, Webster, M, Yoshimura, M, Zhan, L. 2023. Thin and transient  
1782 meltwater layers and false bottoms in the Arctic sea ice pack—recent insights on  
1783 these historically overlooked features. *Elementa: Science of the Anthropocene* 11(1).  
1784 doi: 10.1525/elementa.2023.00025.

1785 **Smith, WO**, Codispoti, LA, Nelson, DM, Manley, T, Buskey, EJ, Niebauer, HJ, Cota, GF.  
1786 1991. Importance of *Phaeocystis* blooms in the high-latitude ocean carbon cycle.  
1787 *Nature* 352(6335): 514–516. doi: 10.1038/352514a0.

1788 **Snoeijs-Leijonmalm, P**, Gjørseter, H, Ingvaldsen, RB, Knutsen, T, Korneliussen, R, Ona,  
1789 E, Skjoldal, HR, Stranne, C, Mayer, L, Jakobsson, M, Gårdfeldt, K. 2021. A deep  
1790 scattering layer under the North Pole pack ice. *Progress in Oceanography* 194:  
1791 102560. doi: 10.1016/j.pocean.2021.102560.

1792 **Snoeijs-Leijonmalm, P**, Flores, H, Sakinan, S, Hildebrandt, N, Svenson, A, Castellani, G,  
1793 Vane, K, Mark, FC, Heuzé, C, Tippenhauer, S, Niehoff, B, Hjelm, J, Sundberg, JH,  
1794 Schaafsma, FL, Engelmann, R, Team TEMosa. 2022. Unexpected fish and squid in  
1795 the central Arctic deep scattering layer. *Science Advances* 8(7): eabj7536. doi:  
1796 10.1126/sciadv.abj7536.

1797 **Solomon, A**, Heuzé, C, Rabe, B, Bacon, S, Bertino, L, Heimbach, P, Inoue, J, Iovino, D,  
1798 Mottram, R, Zhang, X, Aksenov, Y, McAdam, R, Nguyen, A, Raj, RP, Tang, H.  
1799 2021. Freshwater in the Arctic Ocean 2010–2019. *Ocean Sciences* 17(4): 1081–  
1800 1102. doi: 10.5194/os-17-1081-2021.

1801 Song, YH, Shim, JS, Kinmonth-Schultz, HA, Imaizumi, T. 2015. Photoperiodic flowering:  
1802 time measurement mechanisms in leaves. *Annual review of plant biology*, 66(1):  
1803 441-464. <https://doi.org/10.1146/annurev-arplant-043014-115555>

1804 Steiner, NS, Sou, T, Deal, C, Jackson, JM, Jin, M, Popova, E, Williams, W, Yool, A. 2016.  
1805 The future of the subsurface chlorophyll-a maximum in the Canada Basin—A model  
1806 intercomparison. *Journal of Geophysical Research: Oceans* 121(1): 387–409. doi:  
1807 10.1002/2015jc011232.

1808 Steiner, NS, Cheung, WW, Cisneros-Montemayor, AM, Drost, H, Hayashida, H, Hoover,  
1809 C, Lam, J, Sou, T, Sumaila, UR, Suprenand, P, Tai, TC. 2019. Impacts of the  
1810 changing ocean-sea ice system on the key forage fish Arctic cod (*Boreogadus saida*)  
1811 and subsistence fisheries in the western Canadian Arctic—evaluating linked climate,  
1812 ecosystem and economic (CEE) models. *Frontiers in Marine Science* 6: 179. doi:  
1813 10.3389/fmars.2019.00179.

1814 Steiner, NS, Bowman, J, Campbell, K, Chierici, M, Eronen-Rasimus, E, Falardeau, M,  
1815 Flores, H, Fransson, A, Herr, H, Insley, SJ, Kauko, HM, Lannuzel, D, Loseto, L,  
1816 Lynnes, A, Majewski, A, Meiners, KM, Miller, LA, Michel, LN, Moreau, S, Nacke,  
1817 M, Nomura, D, Tedesco, L, Franeker, JA van, Leeuwe, MA van, Wongpan, P. 2021.  
1818 Climate change impacts on sea-ice ecosystems and associated ecosystem services.  
1819 *Elementa: Science of the Anthropocene* 9(1). doi: 10.1525/elementa.2021.00007

1820 Strauss, J, Deng, L, Gao, S, Toseland, A, Bachy, C, Zhang, C, Kirkham, A, Hopes, A,  
1821 Utting, R, Joest, EF, Tagliabue, A. 2023. Plastid-localized xanthorhodopsin increases  
1822 diatom biomass and ecosystem productivity in iron-limited surface oceans. *Nature*  
1823 *microbiology*, 8(11): 2050-2066. <https://doi.org/10.1038/s41564-023-01498-5>.

1824 Stroeve, J, Notz, D. 2018. Changing state of Arctic sea ice across all seasons.  
1825 *Environmental Research Letters* 13(10): 103001. doi: 10.1088/1748-9326/aade56.

1826 Sullivan, MB, Weitz, JS, Wilhelm, S. 2017. Viral ecology comes of age. *Environmental*  
1827 *Microbiology Reports* 9(1): 33–35. doi: 10.1111/1758-2229.12504.

1828 Sumata, H, Steur, L de, Divine, DV, Granskog, MA, Gerland, S. 2023. Regime shift in  
1829 Arctic Ocean sea ice thickness. *Nature* 615(7952): 443–449. doi: 10.1038/s41586-  
1830 022-05686-x.

1831 Teng, Z-J, Qin, Q-L, Zhang, W, Li, J, Fu, H-H, Wang, P, Lan, M, Luo, G, He, J, McMinn,  
1832 A, Wang, M, Chen, XL, Zhang, YZ, Chen, Y, Li, CY. 2021. Biogeographic traits of  
1833 dimethyl sulfide and dimethylsulfoniopropionate cycling in polar oceans.  
1834 *Microbiome* 9(1): 207. doi: 10.1186/s40168-021-01153-3.

1835 Terhaar, J, Tanhua, T, Stöven, T, Orr, JC, Bopp, L. 2020. Evaluation of data-based  
1836 estimates of anthropogenic carbon in the Arctic Ocean. *Journal of Geophysical*  
1837 *Research: Oceans* 125(6): e2020JC016124. doi: 10.1029/2020jc016124.

1838 Thibault, D, Head, EJH, Wheeler, PA. 1999. Mesozooplankton in the Arctic Ocean in  
1839 summer. *Deep Sea Research Part II: Topical Studies in Oceanography* 46(8): 1391–  
1840 1415. doi: 10.1016/s0967-0637(99)00009-6.

1841 Thomas, DN, Lara, RJ, Eicken, H, Kattner, G, Skoog, A. 1995. Dissolved organic matter  
1842 in Arctic multi-year sea ice during winter: major components and relationship to ice  
1843 characteristics. *Polar Biology* 15(7): 477–483. doi: 10.1007/bf00237461.

1844 Tittensor, DP, Eddy, TD, Lotze, HK, Galbraith, ED, Cheung, W, Barange, M, Blanchard,  
1845 JL, Bopp, L, Bryndum-Buchholz, A, Büchner, M, Bulman, C, Carozza, DA,  
1846 Christensen, V, Coll, M, Dunne, JP, Fernandes, JA, Fulton, EA, Hobday, AJ, Huber,  
1847 V, Jennings, S, Jones, M, Lehodey, P, Link, JS, Mackinson, S, Maury, O, Niiranen,  
1848 S, Oliveros-Ramos, R, Roy, T, Schewe, J, Shin, YJ, Silva, T, Stock, CA, Steenbeek,

1849 J, Underwood, PJ, Volkholz, J, Watson, JR, Walker, ND. 2018. A protocol for the  
1850 intercomparison of marine fishery and ecosystem models: Fish-MIP v1.0.  
1851 *Geoscientific Model Development* 11(4): 1421–1442. doi: 10.5194/gmd-11-1421-  
1852 2018.

1853 **Toullec, J**, Moriceau, B, Vincent, D, Guidi, L, Lafond, A, Babin, M. 2021. Processes  
1854 controlling aggregate formation and distribution during the Arctic phytoplankton  
1855 spring bloom in Baffin Bay. *Elementa: Science of the Anthropocene* 9(1). doi:  
1856 10.1525/elementa.2021.00001.

1857 **Tremblay, J-É**, Anderson, LG, Matrai, P, Coupel, P, Bélanger, S, Michel, C, Reigstad, M.  
1858 2015. Global and regional drivers of nutrient supply, primary production and CO<sub>2</sub>  
1859 drawdown in the changing Arctic Ocean. *Progress in Oceanography* 139: 171–196.  
1860 doi: 10.1016/j.pocean.2015.08.009.

1861 **Trudnowska, E**, Lacour, L, Ardyna, M, Rogge, A, Irisson, JO, Waite, AM, Babin, M,  
1862 Stemmann, L. 2021. Marine snow morphology illuminates the evolution of  
1863 phytoplankton blooms and determines their subsequent vertical export. *Nature*  
1864 *Communications* 12(1): 2816. doi: 10.1038/s41467-021-22994-4.

1865 **Tschitschko, B**, Esti, M, Philippi, M, Kidane, AT, Littmann, S, Kitzinger, K, Speth, DR,  
1866 Li, S, Kraberg, A, Tienken, D, Marchant, HK, Kartal, B, Milucka, J, Mohr, W,  
1867 Kuypers, MMM. 2024. Rhizobia–diatom symbiosis fixes missing nitrogen in the  
1868 ocean. *Nature* 609: 100–105. doi: 10.1038/s41586-024-03900-0 .

1869 **Ulfso, A**, Jones, EM, Casacuberta, N, Korhonen, M, Rabe, B, Karcher, M, Heuven,  
1870 SMAC van. 2018. Rapid changes in anthropogenic carbon storage and ocean

1871 acidification in the intermediate layers of the Eurasian Arctic Ocean: 1996–2015.  
1872 *Global Biogeochemical Cycles* 32(9): 1254–1275. doi: 10.1029/2017gb005738.

1873 Vader, A, Laughinghouse, HD, Griffiths, C, Jakobsen, KS, Gabrielsen, TM. 2018. Proton-  
1874 pumping rhodopsins are abundantly expressed by microbial eukaryotes in a high-  
1875 Arctic fjord. *Environmental Microbiology* 20(2): 890–902. doi: 10.1111/1462-  
1876 2920.14035.

1877 Vancoppenolle, M, Deming, JW, Rysgaard, S, Fripiat, F, Acinas, SG, Babin, M, Ehn, J,  
1878 Haapala, J, Marechal, E, Mundy, CJ, Nicolaus, M, Tedesco, L, Vincent, F. n.d.  
1879 Microbial life in Arctic pack ice: prospects from the Tara Polaris Expeditions.  
1880 *Elementa Science of the Anthropocene*, in review.

1881 Vermassen, F, O'Regan, M, de Boer, AM, Schenk, F, Razmjooei, M, West, G, Cronin,  
1882 TM, Jakobsson, M, Coxall, HK. 2023. A seasonally ice-free Arctic Ocean during the  
1883 Last Interglacial. *Nature Geoscience* 16(8): 723–729. doi: 10.1038/s41561-023-  
1884 01227.

1885 Villar, E, Cabrol, L, Heimbürger- Boavida, LE. 2020. Widespread microbial mercury  
1886 methylation genes in the global ocean. *Environmental Microbiology Reports* 12(3):  
1887 277-287. doi: 10.1111/1758-2229.12829.

1888 Vincent, F, Sheyn, U, Porat, Z, Schatz, D, Vardi, A. 2021. Visualizing active viral  
1889 infection reveals diverse cell fates in synchronized algal bloom demise. *Proceedings*  
1890 *of the National Academy of Sciences* 118(11): e2021586118. doi:  
1891 10.1073/pnas.2021586118.

1892 Vincent, F, Vardi, A. 2023. Viral infection in the ocean—a journey across scales. *PLOS*  
1893 *Biology* 21(1): e3001966. doi: 10.1371/journal.pbio.3001966.

1894 von Appen W-J, Waite, AM, Bergmann, M, Bienhold, C, Boebel, O, Bracher, A, Cisewski,  
1895 B, Hagemann, J, Hoppema, M, Iversen, MH, Konrad, C, Krumpen, T, Lochthofen,  
1896 N, Metfies, K, Niehoff, B, Nöthig, EM, Purser, A, Salter, I, Schaber, M, Scholz, D,  
1897 Soltwedel, T, Torres-Valdes, S, Wekerle, C, Wenzhöfer, F, Wietz, M, Boetius A.  
1898 2021. Sea-ice derived meltwater stratification slows the biological carbon pump:  
1899 results from continuous observations. *Nature Communications* 12(1): 7309. doi:  
1900 10.1038/s41467-021-26943-z.

1901 Vylegzhanin, AN, Young, OR, Berkman, PA. 2020. The Central Arctic Ocean Fisheries  
1902 Agreement as an element in the evolving Arctic Ocean governance complex. *Marine*  
1903 *Policy* 118: 104001. doi: 10.1016/j.marpol.2020.104001.

1904 Wang, M, Overland, JE. 2012. A sea ice free summer Arctic within 30 years: An update  
1905 from CMIP5 models. *Geophysical Research Letters* 39(18). doi:  
1906 10.1029/2012gl052868.

1907 Wiedmann, I, Ershova, E, Bluhm, BA, Nöthig, E-M, Gradinger, RR, Kosobokova, K,  
1908 Boetius, A. 2020. What feeds the benthos in the Arctic basins? Assembling a carbon  
1909 budget for the deep Arctic Ocean. *Frontiers in Marine Sciences* 7: 224. doi:  
1910 10.3389/fmars.2020.00224.

1911 Wietz, M, Bienhold, C, Metfies, K, Torres-Valdés, S, von Appen, W-J, Salter, I, Boetius,  
1912 A. 2021. The polar night shift: seasonal dynamics and drivers of Arctic Ocean  
1913 microbiomes revealed by autonomous sampling. *ISME Communications* 1(1): 76.  
1914 doi: 10.1038/s43705-021-00074-4.

1915 Wietz, M, Engel, A, Ramondenc, S, Niwano, M, von Appen, W-J, Priest, T, Jackowski, A  
1916 von, Metfies, K, Bienhold, C, Boetius, A. 2024. The Arctic summer microbiome

1917 across Fram Strait: Depth, longitude, and substrate concentrations structure  
1918 microbial diversity in the euphotic zone. *Environmental Microbiology* 26(2):  
1919 e16568. doi: 10.1111/1462-2920.16568.

1920 **Wilhelm, SW**, Suttle, CA. 1999. Viruses and nutrient cycles in the sea: viruses play critical  
1921 roles in the structure and function of aquatic food webs. *Biosciences* 49(10): 781–  
1922 788. doi : 10.2307/1313569.

1923 Wold, A, Hop, H, Svensen, C, Søreide, JE, Majaneva, S, Koenig, Z, Ormanczyk, M,  
1924 Kwasniewski, S. 2025. Zooplankton communities across the Nansen and Amundsen  
1925 Basins of the Arctic Ocean. *ICES Journal of Marine Science* 82(10): fsaf184. doi:  
1926 10.1093/icesjms/fsaf184.

1927 **Wollenburg, JE**, Katlein, C, Nehrke, G, Nöthig, E-M, Matthiessen, J, Gladrow, DAW,  
1928 Nikolopoulos, A, Gázquez-Sanchez, F, Rossmann, L, Assmy, P, Babin, M, Bruyant,  
1929 F, Beaulieu, M, Dybwad, C, Peeken, I. 2018. Ballasting by cryogenic gypsum  
1930 enhances carbon export in a *Phaeocystis* under-ice bloom. *Scientific Reports* 8(1):  
1931 7703. doi: 10.1038/s41598-018-26016-0.

1932 **Worm, B**, Hilborn, R, Baum, JK, Branch, TA, Collie, JS, Costello, C, Fogarty, MJ, Fulton,  
1933 EA, Hutchings, JA, Jennings, S, Jensen, OP. 2009. Rebuilding global fisheries.  
1934 *Science* 325(5940): 578–585. doi: 10.1126/science.1173146.

1935 **Wutkowska, M**, Vader, A, Logares, R, Pelletier, E, Gabrielsen, TM. 2023. Linking  
1936 extreme seasonality and gene expression in Arctic marine protists. *Scientific Reports*  
1937 13(1): 14627. doi: 10.1038/s41598-023-41204-3.

1938 Yamamoto-Kawai, M, McLaughlin, FA, Carmack, EC, Nishino, S, Shimada, K. 2009.  
1939 Aragonite undersaturation in the Arctic Ocean: effects of ocean acidification and sea  
1940 ice melt. *Science* 326(5956): 1098–1100. doi: 10.1126/science.1174190.

1941 Zayed, AA, Wainaina, JM, Dominguez-Huerta, G, Pelletier, E, Guo, J, Mohssen, M, Tian,  
1942 F, Pratama, AA, Bolduc, B, Zablocki, O, Cronin, D, Solden, L, Delage, E, Alberti,  
1943 A, Aury, JM, Carradec, Q, Silva, C da, Labadie, K, Poulain, J, Ruscheweyh, HJ,  
1944 Salazar, G, Shatoff, E, Coordinators, TO, Bundschuh, R, Fredrick, K, Kubatko, LS,  
1945 Chaffron, S, Culley, AI, Sunagawa, S, Kuhn, JH, Wincker, P, Sullivan, MB, Acinas,  
1946 SG, Babin, M, Bork, P, Boss, E, Bowler, C, Cochrane, G, Vargas, C de, Gorsky, G,  
1947 Guidi, L, Grimsley, N, Hingamp, P, Iudicone, D, Jaillon, O, Kandels, S, Karp-Boss,  
1948 L, Karsenti, E, Not, F, Ogata, H, Poulton, N, Pesant, S, Sardet, C, Speich, S,  
1949 Stemmann, L, Sullivan, MB, Sungawa, S, Wincker, P. 2022. Cryptic and abundant  
1950 marine viruses at the evolutionary origins of Earth’s RNA virome. *Science*  
1951 376(6589): 156–162. doi: 10.1126/science.abm5847.

1952 Zhulay, I, Iken, K, Renaud, PE, Kosobokova, K, Bluhm, BA. 2023. Reduced efficiency of  
1953 pelagic–benthic coupling in the Arctic deep sea during lower ice cover. *Scientific*  
1954 *Reports* 13(1): 6739. doi: 10.1038/s41598-023-33854-0