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Microbial life in Arctic pack ice:

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Prospects for the *Tara Polaris Expeditions*

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60 **Abstract**

61 Sea ice, unlike freshwater ice, hosts abundant microbial life, thanks to the presence of
62 liquid water inclusions encased within the ice matrix. The forthcoming Tara Polaris
63 Expeditions (TPE), which will document drifting Arctic pack ice repeatedly over multiple
64 years, together offer an unprecedented opportunity to advance understanding of the
65 sea-ice microbiome – its diversity, variations, and ecological roles. In this contribution, we
66 consider the current state of knowledge, identify key research gaps, and outline the
67 potential for progress enabled by TPE. We envision the emergence of new insights into the
68 seasonal evolution of microbial life, resolved at the floe (kilometric) scale, in relation to the
69 evolution of the sea-ice environment – its morphology, light, temperature, and liquid water
70 distribution and properties. Large potential lies in the characterization of diverse
71 microhabitats across the central Arctic Ocean, associated with brine inclusions, pressure
72 ridge cavities, and melt ponds. A major goal will be to document biological processes that
73 remain poorly understood – colonization, diversity, functioning, interactions, and
74 evolutionary dynamics – and that could benefit from the application of newly developed
75 techniques. We argue that TPE is particularly timely, as the loss of multi-year ice may soon
76 constrain opportunities to study life in this rapidly changing habitat.

77 **Keywords**

78 Arctic Ocean, sea ice, ice algae, microbial life, Tara Polar Station

79 **Outline**

80 This outline is here to help readers to appreciate the structure of the manuscript and
81 facilitate browsing it. It will be removed at publication stage.

82 [Abstract](#)

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106 **1. Arctic sea ice loss affects and threatens life in sea ice**

107 Unlike freshwater ice, sea ice hosts abundant microbial life due to the presence of encased
108 liquid water that forms various microbial habitats (Horner, 1985; Thomas and Dieckmann,
109 2002; Boetius et al., 2015; Campbell et al., 2022a). These habitats encompass
110 sub-millimeter, hypersaline brine inclusions (Krembs et al., 2002), slush at the base of the
111 overlying snow (Ewert et al., 2013; Fernández-Méndez et al., 2018), surface melt ponds
112 (Brinkmeyer et al., 2004; Lee et al., 2012; Akino et al., 2025), and voids in pressure ridges
113 (Salganik et al., 2023). Until the end of the 20th century, Arctic sea ice covered much of the
114 Arctic Ocean yearlong and its peripheral seas seasonally, covering approximately 15 million
115 km² in March and 7–8 million km² in September (Parkinson, 2014). Over the last four
116 decades, however, the Arctic sea-ice coverage has decreased, particularly in September, by
117 >10% per decade (Meier and Stroeve, 2022). The vast Arctic sea-ice habitat is thus in rapid
118 decline, with large and highly uncertain implications for microbial life within the ice (Tedesco
119 et al., 2019; Lannuzel et al., 2020; Lim et al., 2022).

120 Microbial life in Arctic sea ice is adapted to unique, extreme conditions (Lund-Hansen et al.,
121 2024) with temperatures as low as –30°C, salinities from 0 g kg⁻¹ in melt ponds to up to 250
122 g kg⁻¹ in brine (Vancoppenolle et al., 2019; Zampieri et al., 2024), and large seasonal
123 variations in light, from the dark polar night to the bright polar day (Nicolaus et al., 2010;
124 Lebrun et al., 2023). Photosynthetic ice algae are adapted to extremely low light levels
125 (Hoppe et al., 2024) and co-habit with other microbes. These algae thrive mostly near the
126 ice-water interface (Arrigo, 2014; Leu et al., 2015; van Leeuwe et al., 2018; Lim et al., 2025),
127 where temperatures and salinities are relatively mild and stable. Heterotrophic bacteria,
128 involved in various biogeochemical cycles, and archaea of largely unknown function, along
129 with abundant viruses, inhabit brines throughout the ice and across the seasons (Deming
130 and Collins, 2017).

131 Microbial life in sea ice is deemed a key feature of the Arctic marine system from ecological
132 and biogeochemical standpoints (Horner, 1985; Vancoppenolle et al., 2013; Mundy and
133 Meiners, 2021). Arctic sea-ice algae produce 2.5–73 Tg organic carbon per year (Legendre
134 et al., 1992; Lim et al., 2025), representing 0.1–21% of pelagic production in Arctic waters,
135 depending on calculation methods and sources. Sea-ice algae can account for as much as
136 50% of the pelagic production in some regions and seasons (Fernández-Méndez et al.,
137 2015). They also provide a rare carbon source during late winter and early spring (Søreide et
138 al., 2010). Upon melting, ice algae and associated organic matter are released into the
139 ocean, where they may seed phytoplankton communities, sustain grazers or export to the
140 seafloor. Sea ice therefore affects underlying pelagic and benthic trophic networks that
141 sustain fish, birds, and mammals (Post et al., 2013; Boetius et al., 2015). In this context,
142 shifts in Arctic sea-ice microbial life could lead to significant changes in crucial ecosystem
143 services, with cascading effects on the biodiversity of the Arctic Ocean (Post et al., 2013;
144 Steiner et al., 2021).

145 The study of life in sea ice can also offer insights into the evolution of life on Earth (Trinks et
146 al., 2005), especially during episodes of near-global ice coverage (Hoffman et al., 2017).
147 Limited space for production, subzero temperatures and hypersalinities of brine place limits
148 on microbial processes and rates within the ice. Yet the concentrating effect of the freezing
149 process may have also provided unique opportunities for life, including lateral gene
150 transfers (via viruses, other nucleic acid-containing particles or free DNA) to facilitate
151 adaptation and evolution (Raymond and Kim, 2012). At times omnipresent across all
152 latitudes during Earth's history, sea ice may well have been a relative hotspot for microbial
153 evolution. Sea ice also inspires the search for microbial life on frozen planetary bodies, as
154 many ocean worlds in our Solar System are salty and largely frozen. This abundance of
155 extraterrestrial salty ice makes Earth's sea ice a prime habitat analog for investigating how
156 life may have evolved beyond Earth and where it may be detectable (Deming and Eicken,
157 2007; Martin and McMinn, 2018; Wolfenbarger et al., 2022).

158 Microbial life in Arctic sea ice is thus well recognized for its exceptional value and
159 importance. However, studying sea ice, especially its microbiology, is hampered by
160 numerous difficulties. The Arctic is cold, remote, and costly to access, yet beyond these
161 logistical challenges, more fundamental issues arise. Accessing the brine-filled pore spaces
162 inhabited by microbes without altering their micrometer-scale habitat structure, or losing
163 material, is a major sampling challenge (Junge et al., 2001; Eicken et al., 2010; Miller et al.,
164 2015). Sea ice is very heterogeneous, and the large horizontal and vertical variations in
165 sea-ice properties at subcentimeter-to-meter scales are amplified for biological activities
166 (Rysgaard et al., 2001; Mikkelsen et al., 2008; Roukaerts et al., 2021), hindering efforts to
167 characterize temporal changes and further complicating sampling. Unlike in the open
168 ocean, ocean color remote sensing cannot detect sea-ice algae, limiting knowledge of
169 large-scale production and variability. Under-ice optical methods provide valuable insights
170 into sea-ice biology (Lange et al., 2017; Hill et al., 2022). Modeling offers further potential,
171 but current efforts are at an early stage, constrained by limited knowledge (e.g., microbial
172 diversity) and scarce observational data, which models often fail to reproduce (e.g.,
173 Castellani et al., 2025).

174 These difficulties help explain why many key steps and fundamental processes involved in
175 the development of microbial life in sea ice remain poorly understood, and why most of
176 what we do know comes from more readily accessible coastal, immobile, landfast ice. In
177 particular, we lack the capacity to fully describe and explain the seasonal cycle, even in
178 coastal sea ice, but especially in pack ice (i.e. ice that drifts), and from the high Arctic (e.g.,
179 Fong et al., 2024). In addition, micro-habitats within the ice and their properties are neither
180 well characterized nor accounted for in primary production estimates (Arrigo, 2017;
181 Campbell et al., 2022a; García et al., 2023). Adaptive strategies are well described from
182 experimental work with cultured sea-ice microbes (Rapp et al., 2025), but less well
183 understood at the community level in their micro-habitats. Precisely how microbes — the
184 unicellular photosynthetic, mixotrophic and heterotrophic eukaryotes and prokaryotes, as
185 well as their viruses — interact with each other, achieving high levels of primary production
186 and subsequent nutrient regeneration, remains to be explored. The door to understanding

187 evolutionary processes, in particular the role of lateral gene transfer, has been opened
188 (Raymond and Kim, 2012; Mock et al., 2017; Zhong et al., 2020), but much remains to be
189 learned genetically and epigenetically. Additionally, understanding the role symbioses play
190 between sea-ice microbes is essential for understanding this unique ecosystem.

191 The relatively slow pace of scientific progress on sea-ice microbiology poses a significant
192 problem in light of the rapid pace of Arctic sea-ice loss. Arctic sea-ice loss stems from
193 anthropogenic carbon emissions, with the decline rate relating directly to cumulative carbon
194 emissions: for each ton of CO₂ released into the atmosphere, we lose about 3 m² of
195 summer sea ice (Notz and Stroeve, 2016). At current carbon emission levels, multi-year ice
196 — the oldest type of sea ice, which is also biologically unique — is projected to disappear,
197 resulting in a summer ice-free Arctic between 2030 and 2050 (SIMIP Community, 2020;
198 Jahn et al., 2024; see **Figure 1**). This loss in the coming decades means that Arctic sea ice
199 will become the first entire biome to be impacted severely by climate change, yet there is
200 still so much to be learned about this critical environment and habitat. As other
201 anthropogenic impacts increase, including import of atmospheric and riverine pollution,
202 resource exploitation, and increased shipping and tourism, the pristine nature of the sea-ice
203 habitat faces significant threats. This vulnerability is illustrated by the high concentrations of
204 microplastics already detected in sea ice (Peeken et al., 2018) and by the release of
205 persistent organic pollutants (POPs) and mercury (Hg) back into the atmosphere from Arctic
206 ice and snow as a result of climate warming (Ma et al., 2011; DiMento et al., 2019). The
207 consequences for the sea-ice microbiome and Arctic ecosystems remain largely unknown.
208 The need for targeted and sustained research to understand what we are losing and what
209 will remain is urgent.

210 Observational monitoring programs are needed to advance understanding of high-latitude
211 marine environments (Willis et al., 2023), and particularly Arctic sea ice. In this paper, we
212 briefly introduce how the Tara Polar Station (Babin et al., in revision), set to deploy in the fall
213 of 2026, will provide a unique long-term platform to study life in sea ice. Over the next
214 quarter century, Tara Polaris Expeditions (TPE) — repeated drifts of the Tara Polar Station
215 (TPS) within the pack ice — will provide unique opportunities to investigate the high Arctic
216 sea-ice environment. Prior drifts across the high Arctic using other platforms to study sea
217 ice have not had biology as a top priority. Here, we review the current state of knowledge of
218 life in Arctic sea ice, including its links to the sea-ice environment, biogeochemistry, and
219 biodiversity, and highlight the main knowledge gaps that the Tara Polaris Expeditions can
220 help to address. Based on considerations of the opportunities and challenges associated
221 with the set up of the station, we make practical recommendations for sea-ice activities,
222 with a particular focus on biological sampling.

223 **2. Life in Arctic pack ice is microbial**

224 Many questions about microbial life in sea ice remain open, particularly regarding how
225 bio-physical interactions at scales ranging from the microscale to the local scale
226 (approximately 1 km) shape sea-ice communities. How has life adapted to the physical and
227 chemical constraints within the sea-ice microstructure? Conversely, how do microbes
228 modify this habitat? How diverse are the strategies that enable survival and growth in this
229 environment, and what can they teach us about evolutionary processes? How are microbial
230 communities in sea ice structured and organized (e.g., spatial distributions, interactions),
231 and what roles do biological interactions play in shaping them? A primary goal of research
232 on board the TPS, closely coupled in time to shore-based analyses, is to address these
233 questions, as discussed below.

234 **2.1 Microbial life in Arctic Pack Ice: highly seasonal and spatially variable**

235 Sea ice is a key component of the Arctic marine ecosystem, serving as a habitat for a
236 diverse array of microorganisms, including bacteria, archaea, protists (notably ice algae),
237 fungi, small invertebrates, and fish larvae. Remarkably, these communities persist despite
238 extreme and highly variable environmental conditions — fluctuations in temperature,
239 salinity, and pH, among others. These conditions raise an important question: where, when,
240 and how do these microbes develop within Arctic sea ice?

241 **For sea-ice algae**, seasonality and spatial variations are closely intertwined. The Arctic is
242 characterized by extreme seasonal variations, which drive major changes in the morphology
243 and properties of the pack-ice habitat (Perovich et al., 2001) and impose strong constraints
244 on primary producers. In landfast ice, algal communities are found preferentially near the ice
245 bottom where their activity is highly seasonal (Smith et al., 1993; Leu et al., 2015; Galindo et
246 al., 2017; Olsen et al., 2017). From the first stages of sea-ice growth, ice algae colonize the
247 ice, providing the initial seed bank for future biomass accumulation (Mundy and Meiners,
248 2021). Winter is characterized by low activity or dormancy of microalgae, resulting in a net
249 heterotrophic phase (although heterotrophic conditions can occur at all seasons and
250 depths; Rysgaard and Glud, 2004; Søgaard et al., 2013; Campbell et al., 2022a).
251 Photosynthetic activity begins with the return of the sun, the timing of which depends on
252 latitude, with snow depth strongly influencing spring bloom onset (Mikkelsen et al., 2008).
253 Ice algal blooms, dominated by a specific sub-group of ice algal taxa – the diatoms, usually
254 develop at the ice-ocean interface, extending into the interior of the ice once permeability
255 increases with warmer conditions. Ice algal activity slows with bottom melt onset and
256 ceases upon complete ice decay.

257 **For bacteria, archaea, and their viruses**, spatial variability and seasonal data — especially
258 in pack ice — remain sparse, limiting our understanding of where and when these microbes
259 contribute to biogeochemical processes across the annual cycle (Lund-Hansen et al.,
260 2020). Much of our knowledge on the localization and seasonality of microbes in Arctic sea
261 ice comes from studies of immobile, landfast Arctic sea ice (Ewert et al., 2013; Leu et al.,

262 2015). Yet, approximately 90% of Arctic sea ice is pack ice (Yu et al., 2013), which, unlike
263 landfast ice, is mobile, drifting under the action of winds and currents (see **Figure 2** for a
264 map of landfast and pack ice distributions and a schematic of their differences). Because
265 pack ice drifts, it is morphologically more diverse than landfast ice, harder to access and
266 more complex to study. Indeed, while pack ice includes a flat, level-ice component similar
267 to that of landfast ice, it is far more heterogeneous in the horizontal dimension due to
268 opening, fracturing, and pressure-ridge formation, processes that are associated with a
269 non-uniform velocity field (Perovich et al., 2003; Nicolaus et al., 2022). These processes
270 result in substantial horizontal variations in sea ice at meter scales (Thorndike et al., 1975;
271 von Albedyll et al., 2024). Another cause of heterogeneity in the properties of pack ice, and
272 the life it contains, is the redistribution of snow due to interacting wind and topography, with
273 snow erosion occurring in areas of level ice and accumulation occurring near pressure
274 ridges (Déry and Yau, 2002; Moon et al., 2019; Nandan et al., 2023).

275 **Large horizontal variations** in snow depth and ice thickness in pack ice, compared with
276 landfast ice, have major implications for microbial life. These variations drastically affect
277 light availability, temperature and brine physico-chemical properties, causing
278 order-of-magnitude shifts in ice algal biomass over just a few meters of horizontal distance
279 (Rysgaard et al., 2001). Deep snow can also foster surface infiltration communities through
280 seawater flooding of the snow base (Horner, 1985; Fernández-Méndez et al., 2018). Thick
281 pressure ridges trap large amounts of seawater upon formation (Leppäranta et al., 1995),
282 contribute 30–50% of the Arctic sea-ice volume (Flato and Hibler, 1995; Mårtensson et al.,
283 2012) and hence are biological hotspots of primary importance (Fernández-Méndez et al.,
284 2018; Lange et al., 2024). Under-ice highly porous platelet ice, possibly more prevalent than
285 initially expected (Katlein et al., 2020), and summer melt ponds also host distinct microbial
286 communities (Brinkmeyer et al., 2004; Mundy et al., 2011; Lee et al., 2012), as do direct
287 under-ice meltwater lenses in the summer (Smith et al., 2023). Overall, pack ice offers more
288 diverse habitats than landfast ice, with poorly understood implications for primary
289 production and for polar marine ecology.

290 **The spatial and temporal distribution** of microbial life in Arctic pack ice remains
291 insufficiently observed, particularly its full diversity beyond ice algae, and it may differ
292 substantially from that in landfast ice. In particular, the seasonal evolution of microbial life
293 across micro-environments has been documented over a quasi-entire ice year only during
294 the recent MOSAiC program (Fong et al., 2024). TPS, an observatory that can be anchored
295 to drifting pack ice and will be deployed multiple years into the future, with a focus on the
296 biological and physical conditions of the ice, thus appears well suited to address all phases
297 of the seasonal cycle of pack ice, across micro-environments and across larger horizontal
298 scales.

299 **2.2 How the Arctic pack ice habitat constrains microbial life**

300 Under what conditions, and at what times and locations, does the Arctic pack-ice
301 environment support microbial life, and by what mechanisms? Observations suggest that

302 microbial life, especially ice algal life, thrives in specific niches and at certain times of the
303 year. As organisms respond physiologically to light, temperature, and chemical properties of
304 the sea-ice medium (Søgaard et al., 2011; Arrigo, 2017; Lund-Hansen et al., 2020), a
305 common perception is that seasonal and spatial variations in sea-ice conditions highly
306 influence biological activity (Cota et al., 1991). However, Arctic pack ice remains
307 incompletely characterized, especially as a microbial habitat. Seasonal studies are limited,
308 rarely span an entire year, and often lack data on ecologically critical parameters.

309 **Light** availability is essential for photosynthesis, and its large temporal and spatial
310 variations in the Arctic strongly affect sea-ice algae. The surface of Arctic pack ice
311 undergoes extreme seasonal changes in solar radiation from polar night to polar day
312 (Lindsay, 1998; Persson et al., 2002; Shupe et al., 2022), with effects reaching the ice base
313 (Katlein et al., 2019; Lebrun et al., 2023). Surface conditions — particularly snow, its
314 humidity, and the presence of melt ponds — strongly modulate surface albedo, amplifying
315 seasonal variations in light intensity within sea ice (Perovich et al., 2002; Light et al., 2022).
316 Light attenuates rapidly with depth in ice, and even more in snow (Untersteiner, 1961; Ehn
317 et al., 2008; Katlein et al., 2021; Fuchs et al., 2024). Spatial variations in snow and sea-ice
318 thickness cause strong horizontal heterogeneity in the light field within sea ice (Katlein et al.,
319 2015; 2019; 2021; Matthes et al., 2020). Sea-ice algae are adapted to photosynthesize at
320 very low light levels, down to $0.01 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (Hoppe et al., 2024) but can be
321 inhibited at high light (Lund-Hansen et al., 2020). Light variations are considered to govern
322 the growth onset (Leu et al., 2015), development (Hancke et al., 2018) and patchiness of ice
323 algae (Rysgaard et al., 2001). Characterizing the light field remains challenging due to snow
324 variability and the macro-porosity of pack ice (Ehn and Mundy, 2013; Matthes et al., 2019;
325 Katlein et al., 2021), but advances during MOSAiC (Nicolaus et al., 2022) — including ROVs
326 that document horizontal variations and autonomous sensors that resolve vertical optical
327 structure (Katlein et al., 2021; Perron et al., 2021; Fuchs et al., 2024) — offer new
328 opportunities.

329 **Temperature** has many direct and indirect effects on microbial life. Ice temperature
330 variations thus play a key, possibly underestimated role, in shaping sea-ice microbial
331 ecosystems. Seasonal and vertical ice temperature variations are well documented from
332 several seasonal field programs, such as IPY-58 (Untersteiner, 1961), SHEBA (Perovich and
333 Elder, 2001), CASES (Miller et al., 2011), TARA (Nicolaus et al., 2010), and MOSAIC (Lei et
334 al., 2022). By contrast horizontal variations are known but remain less well characterized
335 (Sturm et al., 2002; Zampieri et al., 2024), especially in terms of micro-environments.
336 Temperature not only affects ice algal physiology (Arrigo et al., 1993; Mundy and Meiners,
337 2021), but also directly influences brine volume and chemistry, particularly salinity, liquid
338 fraction and fluid transport, all essential to nutrient supply (Assur, 1958; Miller et al., 2015;
339 Vancoppenolle et al., 2019). Better characterizing temperature variations is deemed a key
340 challenge.

341 **Liquid water** within sea ice offers critical habitats for the development of life, with their size,
342 geometry, and properties influencing which inhabitants dominate and by what biological

343 processes, and whether microbial interactions can occur. Liquid water is typically found as
344 inclusions within the ice and in pressure ridge voids, surface melt ponds, underlying platelet
345 ice, and warm snow, each of which presents very different microbial habitats. Liquid
346 inclusions within the ice, for example, shrink during winter, becoming hypersaline and losing
347 connectivity with the ocean, yet expand and freshen in later seasons when the temperature
348 warms, creating fluctuations in opportunities for microbial interactions and nutrient (and
349 gene) exchanges. In this context the spatio-temporal variations of liquid water and their
350 properties are central to biodiversity and the patchiness of microbial life in sea-ice
351 environments. However, significant gaps remain in our understanding of the amount,
352 geometry, and chemical properties of liquid water, not only salinity but also pH, at both the
353 micro-scale (e.g., brine) and macro-scale (e.g., ridge voids). TPS provides a unique
354 opportunity to make progress in characterizing the temporal-spatial fluctuations in the liquid
355 water habitats of sea ice.

356 **Nutrients** are incorporated into Arctic sea ice during ice formation, as evidenced by many
357 nutrients scaling to salinity. Consequently, the nutrient composition of sea ice is largely
358 inherited from that of the underlying seawater, which in turn depends on factors such as
359 location, water depth, and proximity to the coast or a river mouth. Fluid (brine) transport,
360 flushing and biogeochemical transformations, also play important roles (Fripiat et al., 2017;
361 Meiners and Michel, 2017). To sustain the biomass accumulation observed in sea ice,
362 nutrients must be resupplied from the underlying seawater through convection and/or
363 diffusion. These exchanges occur via natural convection during ice growth (Wells et al.,
364 2011; Thomas et al., 2020), but also through less well-constrained mechanisms such as
365 bottom-ice turbulent exchange (Cota et al., 1987; Dalman et al., 2019; Duarte et al., 2022).
366 Biogeochemical processes regulating nutrient availability in sea ice are closely linked to ice
367 algae, which actively take up and store nutrients, often maintaining intracellular
368 concentrations well above ambient levels (Mundy et al., 2025). At the same time, nutrient
369 regeneration within sea ice must rely on an efficient microbial loop, enabling the
370 accumulation of remineralization products (including nutrients and dissolved inorganic
371 carbon) near the ice algal community (Fripiat et al., 2017; Meiners and Michel, 2017;
372 Lannuzel et al., 2020; Roukaerts et al., 2021). Significant uncertainties remain as to which
373 nutrients (nitrogen, phosphorus, silicon, or micronutrients such as iron) constitute the
374 principal (co-)limiting factors for primary production in sea ice, and particularly in pack ice.
375 The Tara Polaris Expeditions, focused on the biology of mobile pack ice, present valuable
376 opportunities to advance our understanding of nutrient dynamics in sea ice.

377 In summary, the sea-ice environment, especially in biologically relevant terms, remains
378 incompletely characterized. TPS offers the means to document variations in Arctic sea ice
379 over time and space, year after year, and to advance our understanding of how the physical
380 sea-ice environment generates and conditions the liquid habitats for life in sea ice.

381 2.3 Colonizing and adapting to Arctic pack ice

382 We know that sea ice supports individual organisms and microbial ecosystems, and which
383 physical-chemical parameters determine that support, even if temporal and spatial
384 variability leaves much to be understood, but how do microorganisms initially colonize the
385 ice? Once within the ice, and particularly within mobile Arctic pack ice, how do they adapt
386 to the more extreme conditions encountered there? Current answers to these questions rely
387 heavily on lab studies, yet understanding what happens in situ is the critical need. Two
388 figures schematize current understanding of the different processes at stake, regarding
389 colonization and adaptation to the sea ice environment (**Figure 3**), and the different
390 microbial groups present in sea ice and their seasonal evolution (**Figure 4**), seasonally, in
391 connection to the sea ice environment.

392 **Colonizing** sea ice in its early stages of formation may be the least understood process
393 across the seasonal sea-ice cycle, despite its primary importance. Indeed, how
394 microorganisms colonize sea ice remains hypothetical (Mundy and Meiners, 2021; Babin et
395 al., 2025). The initial stage of ice formation is characterized by the supercooling of seawater
396 which causes the nucleation of frazil ice crystals free-drifting within the water column.
397 Observed in the upper decimeters of the water column, frazil ice crystals quickly rise (at
398 velocities of a few cm s^{-1}) to the surface where they merge into so-called grease ice before
399 solidifying into an ice sheet (Smedsrud and Skogseth, 2006). Microorganisms, like other
400 particles, are easily scavenged by rising frazil crystals; they can also serve as ice
401 nucleators, in an interactive process known as suspension freezing (D'souza et al., 2013; Ito
402 et al., 2019; Eickhoff et al., 2023; Lund-Hansen et al. 2025).

403 A continuous ice cover, once formed, is subjected to under-ice ocean processes associated
404 with currents, waves, turbulence, and eventually brine convection within bottom sea ice,
405 fostering ice-ocean water and material exchange (Reeburgh, 1984; Cota et al., 1990;
406 Vancoppenolle et al., 2010; Dalman et al., 2019). These processes can further enmesh algal
407 cells within the liquid brine between ice crystals. Smaller bacteria and archaea are thought
408 to colonize newly formed ice by attaching to algal cell surfaces and aggregates, and
409 possibly to the ice itself. As freezing progresses, the entrained microorganisms experience
410 a drastic phase shift from relatively well-buffered open waters to a semi- or completely
411 enclosed ice lattice enclosing higher salinity water. Model sea-ice bacteria engage in
412 chemohalotaxis — swimming up a thermal/saline gradient (Showalter and Deming, 2018),
413 while sea-ice diatoms can glide along ice surfaces (Zhang et al., 2025), possibly enhancing
414 sea-ice colonization. With sparse direct observations, however, our knowledge of physical,
415 biological and chemical colonization mechanisms remains indirect and largely speculative.
416 Yet, as sea ice solidifies and thickens, growing under increasingly cold atmospheric
417 conditions, the organisms colonizing it face increasingly severe conditions, especially those
418 that do not remain near the growing ice-water interface always moderated by the ocean
419 below.

420 **Adapting** to sea-ice conditions thus becomes essential for microorganisms to thrive, or
421 survive, within the ice matrix. Given the large vertical temperature and salinity variations of
422 the brine inclusions within that matrix, microorganisms have evolved a wide range of
423 physiological adaptations to inhabit these inclusions and sustain their cellular functions,
424 including at the levels of membrane fluidity, enzymatic activity, and essential processes
425 such as replication, transcription, and translation (De Maayer et al., 2014; Deming and
426 Collins, 2017). A critical area of interest is the biogenic production of micro-habitat
427 ice-active modifiers, like extracellular polymeric substances (EPS) and ice-binding proteins
428 (IBPs). EPS are believed to aid in the entrapment, retention, and survival of microorganisms
429 within the ice, including the production of biofilms (Krembs et al., 2002; Janech et al., 2006;
430 Krembs and Deming, 2008; Ewert et al., 2013). IBPs, which may be associated with EPS,
431 play multiple roles in cold adaptation: they help prevent freezing, provide cryoprotection,
432 enhance ice adherence, and facilitate ice nucleation (Janesch et al., 2006; Bar Dolev et al.,
433 2016; Białkowska et al., 2020). Furthermore, both IBPs and EPS may contribute to the
434 structural integrity of the ice habitat by stabilizing the brine network during freezing, thereby
435 influencing sea-ice microstructures and desalination processes (Krembs et al., 2011).
436 Despite this general depiction, the specifics of in situ production and functionality of
437 ice-active modifiers, which give an adaptive advantage to microorganisms entrained within
438 sea ice, remain largely unknown.

439 Under favourable growing conditions, the microbial-algal biomass in sea ice can increase
440 rapidly, as the ice environment is stable and, unlike open waters, not prone to mixing. As a
441 result, chlorophyll-a concentrations may reach levels an order of magnitude higher than
442 those typically found in pelagic marine ecosystems. The sea-ice biomass, however, is
443 typically confined to the bottommost centimeters of the ice (Smith et al., 1990; Gradinger,
444 1999) within the tortuosity of the brine network, which represents only a small fraction of the
445 ice volume. This high level of locally concentrated biomass, coupled with significant
446 sub-centimeter variations in the availability of light, nutrients, organic matter, and dissolved
447 O₂, creates microenvironments with distinct biogeochemical properties and likely different
448 strategies for microorganisms to adapt to the ice by interacting with each other, e.g.,
449 polymicrobial biofilm, symbiosis, predation, quorum sensing, chemical and electrical
450 signaling, horizontal gene transfer, etc. (Krembs et al., 2002; Rapp et al., 2021; Roukaerts et
451 al., 2021). For example, anoxic microenvironments have been hypothesized in bottom
452 Arctic sea ice, as denitrification rates — a strictly anaerobic process — along with relevant
453 gene expressions have been measured in melted sea ice (Rysgaard et al., 2004).
454 Traditionally, sea-ice ecological studies have relied on methods and concepts from
455 planktonic research, which involve analyzing bulk-melted samples and thereby eliminating
456 any spatial distribution. However, for understanding organism distribution or microhabitat
457 specificity, fluid and solute transport, and wide-ranging microbial interactions, the seawater
458 model may be less applicable to conceptualizing the sympagic community than models
459 from soils or sediments. Methodological advances are necessary to account for the spatial
460 distribution of biogeochemical properties at sub-centimeter scales in the porous sea-ice
461 matrix, and to study the spatial configuration and related activities of the sea-ice
462 microbiome.

463 Work aboard TPS can help us to make progress on the longstanding issue of colonization:
464 the platform will be present for witnessing and sampling the critical early stages of ice
465 formation, and for documenting later under-ice colonization processes through its moon
466 pool and remotely operated vehicles (ROVs). As a stable platform on the solidified ice,
467 innovative subcellular imaging and preservation methods developed in shore-based labs
468 can be tested and applied on the spot. TPS access to winter sea ice, over repeated annual
469 deployments, can provide exciting opportunities to record and validate both expected and
470 potentially unexpected microbial adaptations to the extreme conditions of temperature,
471 salinity, light and nutrient availability.

472 **2.4 Diversity and functioning of microbial life – the Arctic sea ice** 473 **microbiome**

474 Historically, biodiversity in sea ice was expected to be low due to extreme conditions that
475 must be tolerated in the sea-ice habitat. Cross-study syntheses of taxa detected in sea ice
476 (Arrigo, 2014; van Leeuwe et al., 2018) and first applications of DNA-sequencing
477 technologies to the pack ice microbiome (Bowman et al., 2012) dispelled this perception.
478 Piecing together available short-term studies has indicated that seasonal succession
479 occurs within the ice, but differently in different layers and micro-habitats (van Leeuwe et
480 al., 2018). What appears well-known in landfast ice only sometimes overlaps with drifting
481 pack ice, leaving much to be learned, and biogeochemical and ecosystem consequences in
482 question.

483 **Biodiversity** of microalgae in the sea-ice environment is rich, with hundreds of taxa
484 detected (Arrigo, 2014) representing the functional groups of autotrophs, as the primary
485 producers for the ecosystem, and mixotrophic and heterotrophic flagellates, some of which
486 may produce climatically active gases (e.g., dimethyl sulphide). Diatoms, particularly
487 pennate diatoms (with elongated silicate frustules), tend to dominate in bottom sea ice
488 during springtime, while flagellates thrive in summer surface habitats (melt ponds) of Arctic
489 sea ice. Although data are limited for comparisons, pack ice may be better characterized by
490 mixtures of diatoms and flagellates than by dominant diatoms as in landfast ice (van
491 Leeuwe et al., 2018). What environmental conditions, physiological adaptations, refugia
492 from predators, and associations with ever-present bacteria may lead to mixed versus
493 dominant microalgae is not clear. The application of DNA sequencing technologies,
494 specifically to prokaryotic components of the sea ice microbiome, indicate surprisingly high
495 bacterial diversity (Bowman et al., 2012; Rapp et al., 2021), which may be attributable to the
496 ability of most seawater bacteria entrained during ice formation to persist through winter,
497 even in coldest upper layers of the ice (Collins et al., 2010). Archaea are also entrained into
498 newly forming sea ice and persist through winter, but as a small percentage of the sea-ice
499 microbiome, low in taxonomic diversity and of unknown function. Currently published
500 diversity assessments of the sea-ice microbiome are based on short-term studies that
501 encompass widely varying methods and conditions. A more long-term approach on
502 diversity in drifting pack ice would represent a major advance.

503 **Succession** of microalgae and bacteria in sea ice has been inferred from short-term
504 studies, even while recognizing that data are scattered in time and space and dependent on
505 specific conditions (van Leeuwe et al., 2018). The few studies addressing a full season
506 indicate, for example, micro-algal succession in bottom sea ice from pennate to centric
507 diatoms, likely linked to changes in the light field (e.g., Campbell et al., 2017). Bacterial
508 succession, pieced together from individual studies (Deming and Collins, 2017), begins in
509 autumn when diverse seawater bacteria, including *Pelagibacter* spp., entrain into the
510 growing ice. Limited data on an autumn postbloom have pointed to Coscinodiscophyceae,
511 *Amylibacter* and the SAR116 clade as predominant taxa (Wietz et al., 2021). Winter
512 communities appear dominated by ammonia-oxidizing archaea, such as *Candidatus*
513 *Nitrosopumilus*, while spring and summer transitions favor ice-adapted heterotrophic
514 bacteria, like the gammaproteobacteria *Polaribacter*, *Colwellia*, *Formosa* and uncultured
515 lineages, driven by fresh algal-derived carbon inputs (Rapp et al., 2021; Wietz et al., 2021;
516 Thiele et al., 2022). Evidence exists that the abundant viruses in sea ice, most being novel
517 compared to existing databases, may regulate seasonal microbial population dynamics and
518 facilitate horizontal gene transfer (Zhong et al., 2020), influencing ecosystem resilience.
519 Changing environmental conditions in the sea ice as seasons progress can thus account for
520 differences in microbial diversity and attendant function observed in snapshot studies, yet
521 microhabitats at different locations within Arctic pack ice change differently with the
522 seasons, adding to the challenge of deducing microbial succession.

523 Our knowledge of biodiversity in Arctic sea ice is impressive given logistical constraints and
524 snapshot sampling, but direct links between diversity, succession and environmental
525 conditions over time are missing. The many microhabitats formed by Arctic pack ice are the
526 least evaluated, and most threatened, of sea-ice environments. TPS offers a means to
527 document a full annual cycle of diversity measurements in different spatial settings within
528 Arctic pack ice, coupled to key environmental conditions. DNA sequencing technologies
529 provide the promise of success, both for the deep information they reveal and the
530 avoidance of complex manipulations and incubations in the field.

531 **2.5 Microbial interactions in the sea ice**

532 Microbial species do not live in isolation, and instead engage in a diverse suite of
533 associations at the microscale, ranging from mutualistic to parasitic, as illustrated by
534 cross-domain predator-prey interactions, competition, infection and symbioses between
535 eukaryotes, bacteria, archaea and viruses. In planktonic ecosystems, microbial interactions
536 clearly impact species evolution (Rao et al., 2025), adaptation to changing environments
537 (Xie et al., 2013), succession (Vincent et al., 2023) and ecosystem functioning (Tschitschko
538 et al., 2024); however, much remains to be understood in the sea-ice ecosystem. In
539 particular, the spatial structure of pack ice coupled to seasonality creates a dynamic
540 environment likely to impact encounter rates between species and thus frequency and type
541 of interactions (Campbell et al., 2022b). While intra-domain microbial interactions also play
542 an important role (diatom-diatom nutrient competition, bacteria-bacteria syntrophy), we
543 focus below on cross-domain associations.

544 **Food web** studies examining ice-pelagic-benthic coupling and the particular role of ice
545 algae as a critical and defining food source for the Arctic marine ecosystem are relatively
546 common (e.g., Kohlbach et al., 2022; Amiraux et al., 2023; Koch et al., 2023). This research
547 is typically bolstered by sea-ice biomarkers including the highly-branched isoprenoid, IP25,
548 for which specific, but not bloom-dominating, ice algae species are the sole producers
549 (Brown et al., 2014). However, little is known of the sea ice sub-web (Gradinger and Bluhm,
550 2020) and its importance to the pelagic and benthic sub-webs. Heterotrophic protists and
551 meiofauna have been estimated to consume only 1–10% of ice algal biomass, with no
552 substantial top-down influence on the ice algal bloom (Bluhm et al., 2018; Mundy and
553 Meiners, 2021). However, their abundance can reach >200,000 individuals m⁻²,
554 concentrated towards the bottom 10 cm of the sea ice (Bluhm et al., 2018). These
555 observations make their contribution to the pelagic sub-web a non-negligible, yet
556 undocumented, source of cryo-pelagic coupling. Furthermore, sympagic nematodes appear
557 to have the capacity to directly absorb dissolved organic matter in the sea-ice environment
558 (Tchesunov and Riemann, 1995), identifying the exciting possibility of a “meiofauna loop”
559 that redirects carbon back into the particulate food web. Little is known on trophic
560 interactions within the sea ice, particularly for the central Arctic Ocean, or on the
561 contribution of meiofauna to ice-pelagic coupling. TPS will provide the opportunity to
562 observe the sea-ice food web and trophic interactions alongside the seasonal ice algal and
563 microbial growth progressions.

564

565 **Predator-prey interactions.** Given the importance of food-webs for ecosystem functioning,
566 predator-prey interactions have been relatively well studied in Arctic seas, but far less so in
567 the sea ice itself. The constricted space of the sea-ice brine environment nevertheless
568 provides habitat and food sources for heterotrophic protists, such as ciliates, flagellates,
569 and amoeba, and for the meiofauna (metazoa) able to enter brine channels of the ice. These
570 groups are often over-looked, likely due to low consumption rates of ice algae (Leasi et al.,
571 2021). However, meiofaunal concentrations can be particularly high in the bottom
572 decimeters of sea ice, potentially related to a lack of natural predators – the ice serves as a
573 refuge from predation, making them an important food source for the pelagic web when the
574 sea ice begins to melt (CAFF, 2017). As for many other ice observations, much of our
575 knowledge of these sea-ice heterotrophs comes from shallow coastal seas and landfast ice.
576 However, community composition in these accessible ice formations can differ greatly from
577 that of the central Arctic, e.g., meroplankton taxa are restricted to nearshore sea ice (Bluhm
578 et al., 2018). Furthermore, seasonality and ice thickness are strong predictors of meiofauna
579 composition and abundance, making them particularly susceptible to climate change and
580 thus a potentially valuable indicator of change (Bluhm et al., 2018; Leasi et al., 2021).

581 **Algal-bacterial interactions** are well known in many terrestrial and marine environments,
582 but vastly understudied in sea ice. Comprehensive reviews do not mention sea ice (e.g.,
583 Burgunter-Delamare et al., 2024), despite algal-bacterial interactions being identified as a
584 determinant of the sea-ice microbiome years ago (Stewart and Fritsen, 2004). Both

585 mutualistic and antagonistic, algal-bacteria interactions are often based on exchanges of
586 primary and secondary metabolites from one or the other partner. For instance, diatoms
587 release extracellular polymeric substances (EPS) and DMSP that can be metabolized by
588 bacteria which often live epiphytically on algal surfaces - such as Flavobacteria and
589 Rhodobacterales - forming tight metabolic partnerships (Bowman, 2015; Bellas et al.,
590 2023). As particle-associated bacteria are metabolically more active than free-living ones in
591 winter sea ice (Junge et al., 2004), the presence of algal residues in pack ice may further
592 influence bacterial metabolism. Interestingly, algal-bacteria interactions can also serve as a
593 major tool for survival: some (non-Arctic) algae harbor cyanobacteria that fix nitrogen
594 (Foster et al., 2011), a potentially crucial, but unexplored, adaptation in nutrient-limited polar
595 environments and particularly inside the ice matrix. Another recent example reveals how the
596 Antarctic bacterium *Marinomonas primoryensis* uses a massive adhesin protein (1.5 MDa)
597 with multiple domains to bind specifically to ice and also to Antarctic diatoms (Guo et al.,
598 2017). The adhesin contains regions that mediate both peptide and sugar binding, tethering
599 bacteria to the diatom surface and enabling the bacteria to secure the algae to ice surfaces,
600 facilitating symbiotic microbial interactions in sea-ice environments. Such a mechanism
601 could also be at play in the Arctic pack ice, but observing it would require innovative
602 methods, which repeated TPS deployments could facilitate.

603 **Eukaryotic parasites in the sea ice: fungi and oomycetes.** Fungal (particularly chytrid)
604 and oomycete parasites are widespread in Arctic sea-ice microbial communities (Hassett
605 and Gradinger, 2016; Hassett et al., 2019). While many studies in this area are based on the
606 analysis of co-occurrence networks between putative host and parasite (Kiliyas et al., 2020;
607 Dilliplaine et al., 2025) or provide limited visual evidence for infection (Ilicic et al., 2024),
608 chytrids and oomycetes are notoriously known to infect diatoms (Garvetto et al., 2018;
609 Danz and Quandt, 2023). In planktonic systems, such interactions exert strong influence on
610 primary producers, seasonal microbial succession, and biogeochemical cycles as
611 demonstrated by the “fungal shunt” (Klawonn et al., 2021). Through this process, chytrid
612 fungal parasites infect diatoms (and other microalgae), causing host cell lysis. This releases
613 algal organic matter directly into the environment, fueling bacterial growth and activity,
614 rather than transferring energy up the food chain via grazers. To what extent analogies can
615 be drawn in the winter pack ice remains unknown, but could represent a source of
616 dissolved organic matter during an otherwise nutritiously impoverished period.

617 **Viruses.** Viruses infect virtually every living cell on Earth, with important consequences to
618 biogeochemical cycles (Suttle, 2007); microbes in sea ice are no exception. Viruses are
619 present in high concentrations in sea-ice brines (Collins and Deming, 2011a; Collins and
620 Deming, 2011b), leading to high contact rates with microbial inhabitants (Wells and Deming,
621 2006). Multiple sequencing studies highlight the diversity of phages and potential bacterial
622 hosts in Arctic samples (Zhong et al., 2020; Calayag et al., 2025). A recent review provides
623 extensive coverage of what is known about phages in Arctic sea ice (Heinrichs et al., 2024).
624 Similarly to the study of planktonic systems, research on Arctic eukaryotic viruses lags
625 behind prokaryotic viruses, yet they may be more prevalent than previously thought (Xia et
626 al., 2022).

627 **Conclusion.** Studying microbial interactions in the pack ice from TPS can be expected to
628 follow a stepwise approach, akin to how interactions in planktonic systems were revealed.
629 Moving from mapping the diversity of species to mapping the diversity of cross-domain
630 interactions will be a first key step. As microbial interactions impact the metabolism,
631 adaptation, and evolution of individual species, and ultimately ecosystem function, new
632 questions can then be asked. Can bacteria help microalgae cope with sharp gradients in
633 temperature, salinity, increasing acidification (McMinn et al., 2014) and episodes of brine
634 flushing? Does the sea-ice microbe-concentrating effect lead to new symbiotic associations
635 between algae and prokaryotes, potentially increasing horizontal gene transfer or
636 kleptoplastidy and thus accelerating the rate of evolution? What is the larger
637 biogeochemical impact of microscale interactions occurring in the sea ice?

638 **Needs that the TPS can meet.** To answer these questions, many approaches will be
639 required, in particular in the fields of “omics” and imaging. Though mainly applied to liquid
640 marine samples, well established technologies such as metagenomics and transcriptomics
641 can be used, and possibly metabolomics to decipher chemical signals exchanged between
642 species. Single-cell sequencing approaches are gaining popularity in marine microbiology,
643 as they may reveal new host-virus pairs (Fromm et al., 2024) and plasticity of
644 host-associated microbiomes (Priest et al., 2025). Given the spatial component of the pack
645 ice, inspiration from other fields of molecular biology or terrestrial science may help
646 establish spatial transcriptomics coupled to FISH technology or X-ray imaging of microbial
647 life, thus preserving the essential dimension of species position in the ice, rather than
648 melting of the samples. The latter, however, will require major methodological development,
649 in particular in the area of sample preservation, with broader applications. Indeed, improved
650 subcellular imaging techniques may provide invaluable insights into microbial interactions,
651 but they often require tailored fixation methods, as was recently demonstrated using
652 expansion microscopy on fixed environmental samples of diatom-bacteria interactions (Flori
653 et al., 2025), 3D FIB-SEM to study kleptoplastidy in polar planktonic hosts (Rao et al.,
654 2025), and activity measurements of viral infection using BONCAT-FACS (Couradeau et al.,
655 2019) or single cell mRNA-FISH (Vincent et al., 2021). Breakthroughs in the study of such
656 interactions often require mechanistic work in laboratory culture-based systems, but with its
657 advanced infrastructure and molecular laboratories, the TPS represents a unique
658 opportunity to move our understanding of microbial interactions in sea ice forward on all
659 fronts.

660 **2.6 Evolutionary dynamics of the Arctic sea ice microbiome**

661 Extreme conditions presented by Arctic pack ice are understood to slow the growth rate of
662 its inhabitants, even though photosynthesis in the ice (not necessarily coupled to growth)
663 yields enough organic carbon to contribute substantially to the larger Arctic ecosystem.
664 Microbial evolution through vertically inherited traits and natural selection, however,
665 depends on organism reproduction – the passage of geological time since Earth’s first ice
666 age has allowed for ice-adapted microbes to evolve in this way. Sea ice, by concentrating
667 dissolved and particulate material into its pore spaces – including microbes, viruses and

668 extracellular DNA – also offers the potential for horizontal gene transfer (HGT), which can
669 accelerate the acquisition of ice-adapted traits. HGT in sea ice is in its infancy, as is
670 exploration of possible epigenetic mechanisms for rapid acclimation to sea ice.

671 **Evolution** based on reproduction and natural selection can be expected to occur optimally
672 in the springtime biofilms at the bottom of Arctic sea ice. There, conditions promote
673 biomass production of both eukaryotic and prokaryotic microbes and thus their
674 co-evolution. Based on what little we know about microbe-microbe interactions in sea ice,
675 this co-evolution likely has led to mutualistic behaviors that enable current levels of biomass
676 production and biogeochemical cycling. Understanding how these behaviors may be
677 interrupted in the future represents a serious challenge.

678 **Horizontal gene transfer** has been hypothesized as a means to explain escalated
679 evolutionary adaptations in cold environments (e.g., Deming, 2002), with evidence building
680 for its occurrence in sea ice. Genomic analyses of ice-adapted model organisms have
681 revealed HGT between bacterial orders (genes involved in compatible solute pathways for
682 osmotolerance; Collins and Deming, 2013) and between the domains of bacteria and ice
683 diatoms (genes for ice-binding proteins; Raymond and Kim, 2012). Viromic analyses of
684 sea-ice brines support viruses as key agents of HGT (carrying bacterial genes for
685 membrane fluidity; Zhong et al., 2020). Sea ice, with its freeze-concentrating effects that
686 bring microbes, viruses and DNA into immediate and seasonally prolonged contact, may be
687 serving as an ongoing evolutionary crucible. The potential for HGT in Arctic pack ice
688 habitats warrants focused study.

689 **Epigenetics** can provide means to acclimate rapidly (minutes to hours) to a change in
690 environmental conditions. Rapid changes impacting microbial life are inherent to Arctic
691 sea-ice formation and growth (Ewert et al., 2013). Are there epigenetic mechanisms at work
692 to enable such acclimation to sea-ice conditions, whether following initial entrainment into
693 the ice or longer-term exposure to more severe and fluctuating conditions through winter?
694 DNA methylation is an epigenetic mechanism well-known in model microorganisms to
695 regulate which genes are expressed and to defend against viral infection, all on short
696 notice. The first study of microbial methylomes of sea ice, now readily obtained using
697 Nanopore technology, indicates that DNA methylation functions beyond traditional
698 restriction-modification systems that protect against foreign DNA, instead favoring
699 regulatory functions (Kanaan and Deming, 2025). Other epigenetic mechanisms remain
700 unexplored in this ecosystem. For example, RNA modifications, of which over 100 different
701 types have been identified across all domains of life, represent an additional unexplored
702 layer of epigenetic regulation that could facilitate rapid microbial adaptation to sea-ice
703 conditions.

704 To answer evolutionary questions about the sea-ice microbiome requires more than
705 laboratory studies of model organisms and genomic snapshots of a selected type and
706 season of sea ice. New, simpler and more affordable sequencing technologies with
707 bioinformatics software have removed methodological bottlenecks of past field studies. The

708 TPS itself can provide the seasonal continuity needed to identify when and where Arctic sea
709 ice may be functioning as an evolutionary hotspot.

710 **3. Opportunities, challenges and recommendations**

711 **3.1 TPS provides new opportunities**

712 **Science.** The Tara Polar Station (TPS) offers a unique opportunity to design innovative
713 sampling strategies that capture the full seasonal cycle and transitions between seasons in
714 the central Arctic Ocean. Its drifting capability enables high-resolution, long-term
715 observations across a broad range of ice and ocean conditions — from the high Arctic near
716 the North Pole to the subarctic boundary regions — allowing investigations of
717 environmental gradients and temporal variability at multiple scales. TPS is particularly
718 well-suited to studying the phenology and ecology of ice algae, enabling detailed
719 assessments of how shifting ice regimes and environmental variability affect primary
720 production, species composition, and ecological interactions at the base of the food web.
721 This approach can help address key gaps in current understanding — such as the
722 nutrient-biomass paradox (Vancoppenolle and Tedesco, 2017) and floe-scale productivity
723 variability (Campbell et al., 2022a) — by informing process models and enabling more
724 robust upscaling and assessment of sea-ice primary production. By integrating
725 atmospheric and oceanic observations, and linking physical conditions with
726 biogeochemical processes and biological responses, TPS supports a holistic understanding
727 of feedback mechanisms in the coupled Arctic system and provides critical insight into
728 long-term changes driven by climate forcing.

729 **Technology.** TPS work will be constrained by limited manpower but will benefit from
730 high-bandwidth communications. In this context, autonomous measurement platforms and
731 shore-based operations will be privileged — much like the model of space stations (Babin
732 et al., 2025). Having a stronger focus on ecological questions, advanced molecular and
733 genomic approaches can be coupled with shore-based analyses in real time, enabling an
734 adaptive sampling plan to capture an ecosystem shift in progress. The privileging of
735 autonomous platforms and shore-based operations will force the testing of innovative
736 sampling and measurement methods that require minimal human effort. Building on the
737 legacy of the MOSAiC expedition, environmental monitoring is likely to incorporate a range
738 of autonomous technologies, including under-ice vehicles, drones, and stationary platforms
739 (Nicolaus et al., 2022). High-resolution imagery above and below the sea ice, using ROVs
740 and embedded cameras, will be employed to enhance observational capabilities and
741 provide new knowledge on life in sea ice. Flow cytometry and emerging methods like
742 endoscopic sampling, X-ray imaging, MR scanning and ridge sampling tools offer promising
743 avenues for minimally invasive investigation. Moreover, progressing non-destructive
744 techniques such as optical imaging, salinity and light harps will be developed further,
745 enabling long-term monitoring of polar environments without disrupting fragile ecosystems.

746 **3.2 TPS constraints provide new challenges**

747 Sea ice presents significant challenges for sampling and measurement due to its complex,
748 dynamic, cold and chemically specific nature. Many research programs have aimed to
749 optimize sampling across all habitats, depths, and seasons to capture its full variability –
750 from microscale to floe scale. However, this ideal is hindered by numerous practical
751 constraints (reviewed by Miller et al., 2015). The number of samples that can be collected is
752 limited by logistics, the volume required for various analyses, time-intensive processing
753 steps (such as core extraction, melting, filtration, and subsequent analyses), and restrictions
754 related to onboard storage and laboratory space. Moreover, sampling itself can disturb –
755 and often destroys – the fragile sea-ice environment, with cumulative impacts over the
756 course of a season. Measurement techniques borrowed from oceanography are often
757 ill-suited to sea ice, where extreme cold and high brine salinity introduce additional
758 challenges. The strong spatial heterogeneity of sea ice further complicates interpretation,
759 often scrambling time series and reinforcing the need to capture its diverse habitats. Even
760 within level ice, commonly used methods such as ice coring and brine sackhole sampling
761 each come with specific advantages and limitations, underscoring the need for
762 methodological refinement tailored to the unique conditions of the sea-ice system.

763 **3.3 Recommendations for monitoring / sampling plan**

764 The sampling program for the Tara Polaris Expeditions should be designed to monitor the
765 evolution of snow and sea-ice environments over daily, weekly, seasonal, and interannual
766 timescales by assessing their physical, chemical, and biological properties. Characterizing
767 living conditions in sea ice – particularly for the microbial communities that inhabit the ice
768 and its interface with the ocean – requires monitoring a broad range of physical, chemical,
769 and biological parameters. To this end, we recommend using classical, well-established
770 approaches for routine monitoring, while also testing new methods. The sea-ice sampling
771 program should be closely linked to its oceanic and atmospheric counterparts (Schmale et
772 al., 2025; Geoffroy et al., in revision), both because sea ice is strongly influenced by these
773 media and because similar laboratory analyses will be applied to samples from different
774 origins.

775 The sampling program for the Tara Polaris Expeditions should combine classical,
776 well-established approaches for routine monitoring, while also testing new methods (see
777 **Figure 5** for examples). Characterizing sea-ice habitats, particularly the microbial
778 communities inhabiting the ice and its ocean interface, requires monitoring a broad range of
779 parameters. More precisely, the physical, chemical, and biological properties of snow and
780 sea-ice environments over daily, weekly, seasonal, and interannual timescales. The sea-ice
781 sampling program should also be closely linked to its oceanic and atmospheric
782 counterparts (Schmale et al., 2025; Geoffroy et al., in revision), both because sea ice is
783 strongly influenced by these media and because similar laboratory analyses will be applied
784 to samples from different origins.

785 As the targeted measurements describe the habitat quality, resource availability, and
786 organism viability within and beneath the sea ice, the **impacts of the station** itself on the
787 sampled sea-ice environment need to be minimized and monitored. For example, even low
788 levels of light or nutrient pollution may affect overwintering communities in the sea ice over
789 longer time scales (Fong et al., 2024), requiring careful selection of coring spots outside of
790 the platform's influence despite associated logistical challenges.

791 Preferred sampling methods for sea-ice biological and chemical parameters are
792 parameter-dependent, and trade between accuracy, practicality, and preservation of in situ
793 conditions. **Ice cores** currently remain the preferred method for studies focused on physical
794 and biogeochemical properties, as they allow for vertical resolution and budget analyses
795 (Fripiat et al., 2017; Meiners et al., 2018). Ice core extraction, however, is a destructive
796 technique that requires new sites to be selected each time. The process can also alter
797 surface conditions; especially during the early melt season, it may affect the optical
798 properties and surface meltwater drainage patterns on the ice floe. Furthermore, core
799 extraction leads to brine loss (Notz et al., 2005), and the subsequent melting process —
800 though necessary for most analyses — introduces biological artifacts such as osmotic
801 shocks due to salinity changes and temperature-driven metabolic shifts which will differ
802 strongly in intensity and impact between warmer and colder seasons. Long-term cold
803 storage largely alters the temperature-dependent microstructure and biochemical integrity
804 of the samples.

805 By contrast, for certain biological applications, especially those involving microbial or
806 genomic analyses, brine collected from **sackholes** is often favored. This method helps
807 preserve solute concentrations, reduces osmotic stress, and avoids the contamination risks
808 associated with melting sea ice using external solutions that may contain DNA or viruses.
809 Nevertheless, sackholes come with limitations: brine collection is time-consuming and
810 limited in volume in winter ice, the depth of origin of the sampled brine is often uncertain,
811 seawater intrusions may compromise deeper samples, and the method does not capture
812 material embedded in the ice matrix or at the ice–ocean interface.

813 The **representativeness** of samples is a determining aspect on which the progress enabled
814 by TPS operations will largely depend. Manpower, storage space and melting time, provide
815 primary constraints on the total volume of samples that can be extracted for a given station.
816 Trade-offs between sampling frequency, vertical resolution, and the sampling of the different
817 ice types (multi-year ice, first-year ice) and habitats (level ice, ridges, ponds) will be
818 necessary. We envision that sea-ice samples will provide, first, the most representative and,
819 second, the most precise characterization of the pack-ice environment at the scale of a
820 sea-ice floe (1 km). There will be a need to establish consensus on how best to sample
821 complex and underexplored ice habitats such as ridges, melt ponds, or platelet ice. Finally,
822 avoiding overload of the TPS crew is important, particularly given the concomitant goal of a
823 sustainable long-term (20-year) program — key to bridging in-situ observations with
824 pan-Arctic primary production estimates derived from satellite imagery and large-scale
825 model simulations.

826 As we aim to resolve the seasonal cycle for an entire sea ice floe, we recommend
827 characterizing the sea-ice environment and microbiome at the floe scale (~1 km) on daily to
828 weekly time scales.

829 Physical parameters include :

- 830 ● Sea ice morphology — the floe-scale distributions of ice thickness, snow depth,
831 freeboard, fractures and ridges via images and radar scans. Morphology determines
832 the total habitable volume, and influences light transmission, temperature, and liquid
833 phase properties.
- 834 ● Temperature field — vertical profiles and transects. Temperature influences all
835 biological activities and, together with salinity, controls liquid phase salinity and
836 volume fraction, and therefore habitable space.
- 837 ● Light field (PAR) — vertical profiles and under-ice horizontal transects. Light controls
838 photosynthesis and photochemistry in general.
- 839 ● Liquid fraction — vertical profiles, horizontal surveys and microstructure imaging.
840 Brine inclusions and liquid water provide habitable space for the microbiome.
- 841 ● Under-ice free-floating frazil crystal abundance and distributions — ADCP and
842 imagery. Influences harvesting of water column material and sea ice colonization.
- 843 ● Ice type — first-year versus multi-year surface fraction. First-year and multi-year ice
844 have different vertical salinity profiles, brine network characteristics and optical
845 properties, leading to different biological communities.
- 846 ● Oceanic and atmospheric properties near the sea ice as they affect air-ice and
847 ice-ocean heat, matter and momentum exchanges.

848 Chemical parameters include :

- 849 ● Salinity — of both sea ice and liquid water (brine, ridged ice cavities and melt
850 ponds). Ice salinity, together with temperature, sets liquid fraction and habitable
851 space. Salinity of the liquid can widely vary and largely influence biological
852 processes, in particular via osmotic stress.
- 853 ● Nutrient concentrations — of both sea ice and liquid water; nitrate, ammonium,
854 nitrite, phosphate, silicate. Nutrients limit growth of primary producers.
- 855 ● Organic matter concentrations — of both sea ice and liquid water, particulate and
856 dissolved. Organic matter serves as a substrate and energy source for microbes.
- 857 ● Gas concentrations — in particular oxygen, as it traces photosynthesis and
858 respiration.

- 859 ● pH, dissolved inorganic carbon and alkalinity — of both sea ice and liquid water. pH
860 characterizes the chemistry of brine and influences biology, whereas DIC and
861 alkalinity trace inorganic carbon cycle processes.

862 Biological parameters include:

- 863 ● Sea-ice algal biomass and community composition (via genomics and imaging –
864 base of the ice-associated food web)
- 865 ● Chlorophyll-a concentration (proxy for algal biomass)
- 866 ● Primary production (direct measure of ecosystem functioning and carbon fixation)
- 867 ● Bacterial and archaeal communities (via genomics and imaging – important for
868 deducing biogeochemical cycling, organic matter degradation, microbial
869 interactions)
- 870 ● Gene expression (via transcriptomics and proteomics – important for identifying
871 adaptations, functions, and microbial interactions)
- 872 ● Viruses (via viromics – influence microbial dynamics, biogeochemical cycling,
873 adaptive gene exchange)
- 874 ● Zooplankton and protists (key consumers of ice algae and microbes)
- 875 ● Meiofauna and the sea-ice food web (broadens the scope to higher trophic levels)

876 Together, these parameters can provide insights into the habitability of sea-ice
877 environments, the functioning of microbial food webs, and the impacts of climate-driven
878 change on sea-ice ecosystems. Effective monitoring includes combining field sampling,
879 autonomous sensors, and remote sensing, providing links with modeling for scaling up and
880 forecasting ecosystem responses.

881 **4. Expected outcomes and ways forward**

882 The TPS and its dedicated Tara Polaris Expeditions offer unique, timely and long-term
883 opportunities to advance our understanding of Arctic sea ice, its ecosystems, and their
884 response to rapid environmental change (Ardyna et al., in revision). Building on decades of
885 international sea-ice research, TPS will generate an unprecedented, long-term,
886 high-resolution dataset capturing the seasonal and spatial dynamics of the sea-ice
887 microbiome. This effort will help close key knowledge gaps about the sea-ice ecosystem
888 structure, function, and its role in polar biogeochemical transformations and support of the
889 larger ecosystem. The logistical challenges of operating in the central Arctic from Tara's new
890 drifting platform will drive innovation in autonomous observation systems, minimally
891 invasive sampling, and remote molecular tools, enabling more sustainable and systematic

892 sea-ice research over the 20-year mission. TPS will train a new generation of polar
893 scientists through interdisciplinary research that bridges oceanography, microbiology, and
894 environmental science, developing expertise essential for understanding sea ice as a
895 dynamic habitat for life. Beyond its scientific reach, TPS will also serve as a platform for
896 public engagement, communicating the urgency and wonder of the sea-ice environment
897 and its inhabitants to global audiences. Through open data sharing and international
898 collaboration, TPS will amplify the impact of sea-ice research, shaping the future of Arctic
899 science and deepening global understanding of this fragile and rapidly transforming biome.

900 **Contributions**

901 Coordination and scoping of the manuscript: MV, JD, SR, FF, SA, CJM

902 Figure preparation: MV, FF, SA, CJM, SR.

903 Writing : all authors edited and wrote sections

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912 **AI disclosure statement**

913 ChatGPT was used to edit the style of individual sentences, in some places of the text.

914 **Data accessibility statement**

915 Passive microwave sea ice concentrations data used in Figure 1 are from the Sea Ice
916 Concentration Climate Data Record Release 3.1 - Multimission
917 https://doi.org/10.15770/EUM_SAF_OSI_0023.

918 CMIP6 Climate model outputs shown in Figure 1 were extracted from the IPSL ESGF node
919 <https://esgf-node.ipsl.upmc.fr/projects/cmip6-ipsl/>.

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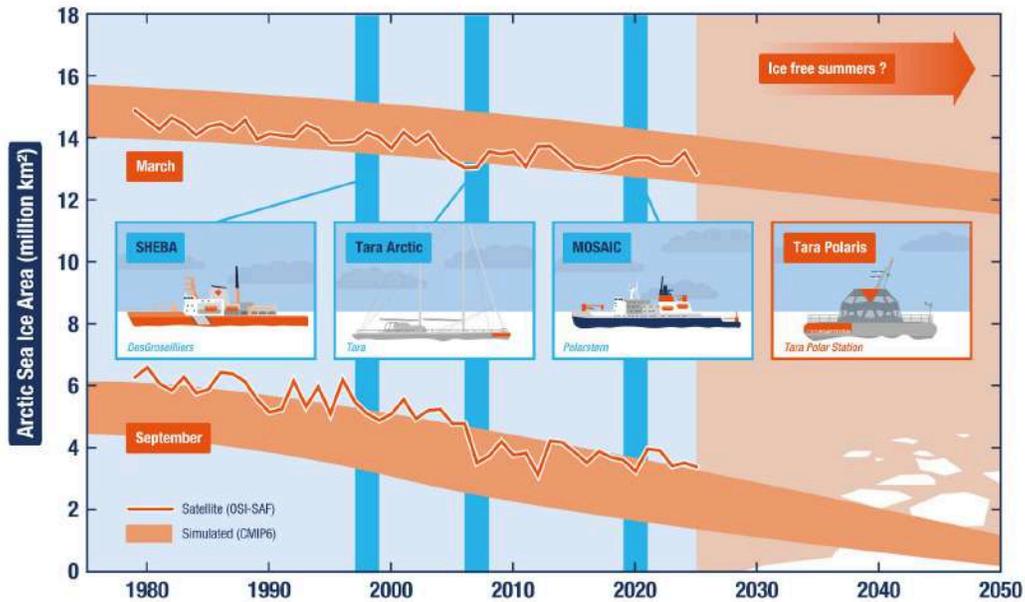
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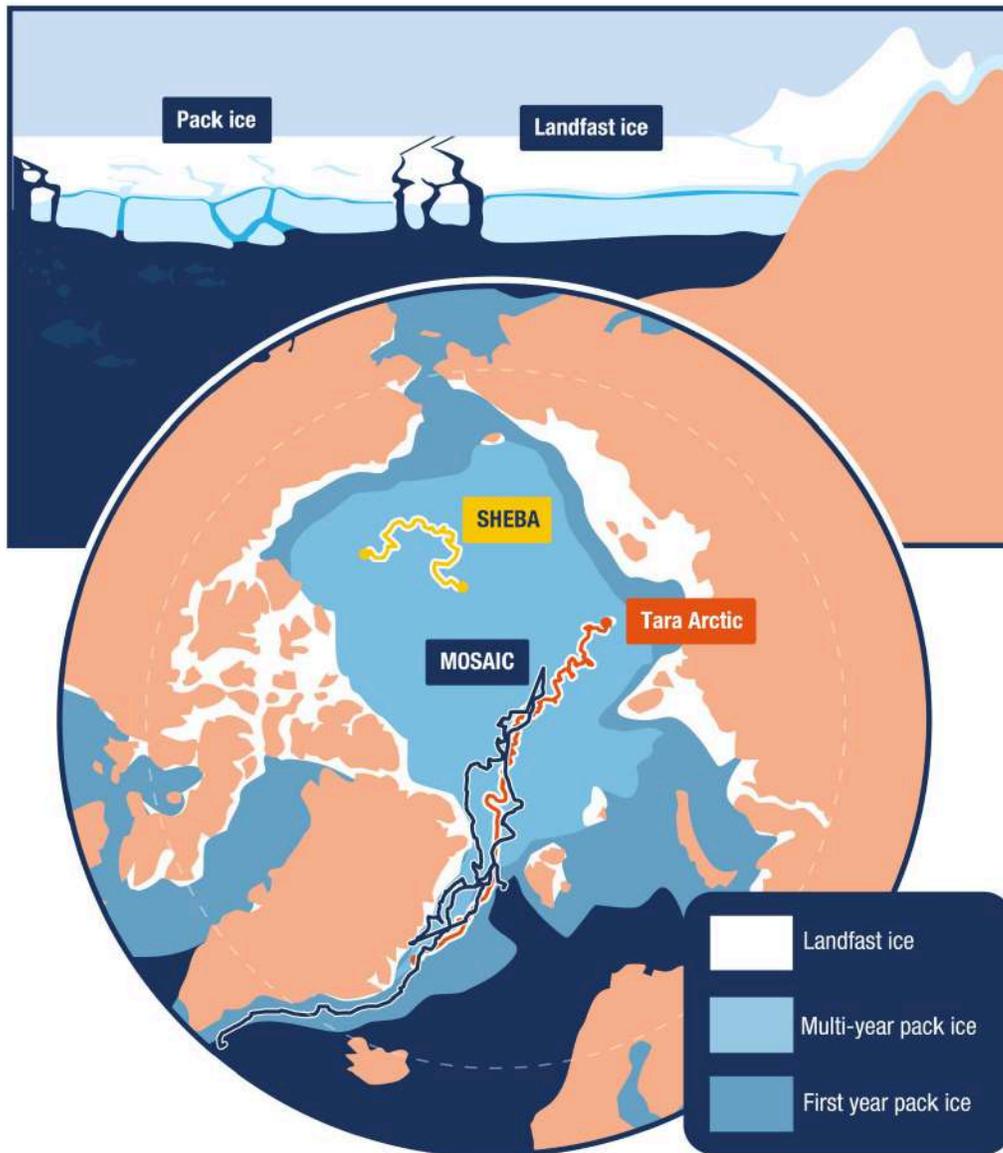
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1563 **Figures**



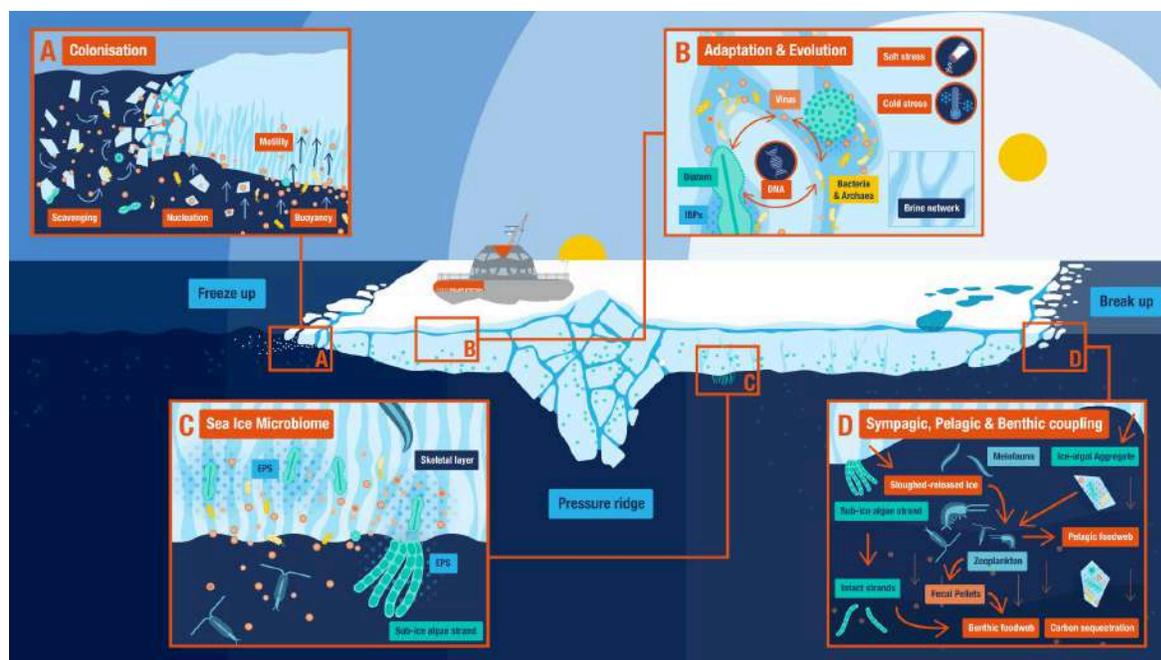
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1565 **Figure 1. Tara Polaris Expeditions, contextualized with projections of Arctic sea-ice**
 1566 **area and recent year-long observational programs.** Projections of sea-ice area from
 1567 satellite passive microwave data are from the OSI-450a1 / OSI-430a Climate Data Record
 1568 (OSI SAF and EUMETSAT SAF On Ocean And Sea Ice, 2025), whereas model simulations
 1569 are from CMIP6 historical and ssp585 simulations (Eyring et al., 2016; SIMIP Community,
 1570 2020).



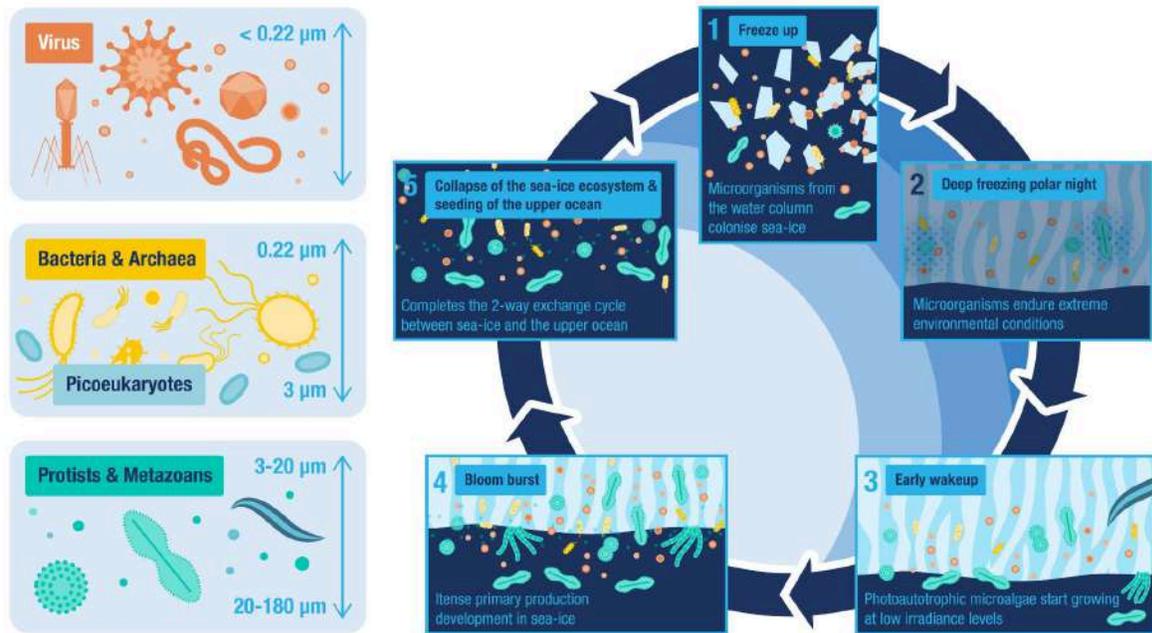
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1572 **Figure 2. Different sea ice types across the Arctic.** (top) Conceptual sketch of pack ice
 1573 against landfast ice. Drifting pack ice is characterized by greater environmental diversity
 1574 than landfast ice, which is immobile and typically flat. (bottom) Climatological map showing
 1575 the distribution of landfast ice and pack ice (first-year and multi-year) along the drift
 1576 trajectories of recent Arctic expeditions mentioned in the text. Landfast-ice climatology is
 1577 based on National Ice Center charts (Yu et al., 2013), whereas pack ice data are derived
 1578 from satellite-based passive microwave retrievals of sea ice concentration using the
 1579 OSI-450a1 / OSI-430a Climate Data Record (OSI SAF and EUMETSAT SAF On Ocean And
 1580 Sea Ice, 2025).



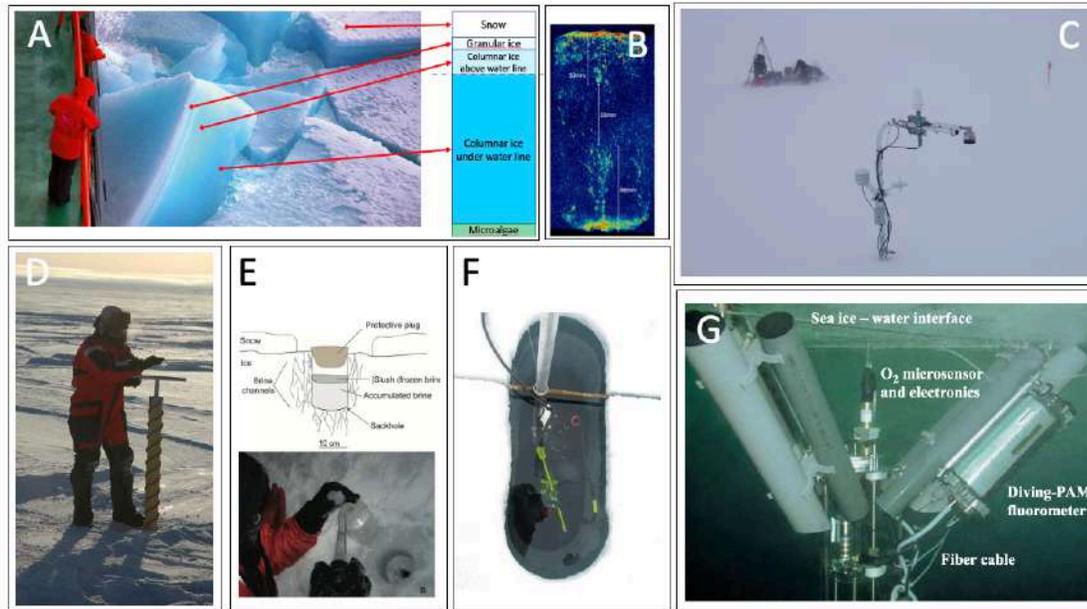
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1582 **Figure 3. Microbial life processes.** The sea ice environment and its connection to the
 1583 processes involved in the development of sea ice microbial life (see Section 2 for details).



1584

1585 **Figure 4.** Microbial targets and processes for “omics” sampling of sea ice and
1586 waters. Size fractionation (left panel) enables both specific group analyses and an
1587 integrated view, from viruses to protists and (not shown) metazoans. Different points in the
1588 sea-ice cycle (right panel), fully and repeatedly sampled by the Tara Polaris Expeditions,
1589 allow investigations to address both longstanding and emerging questions about the
1590 sea-ice microbiome.



1591

1592 **Figure 5.** Examples of observing and sampling sea ice for various physical, chemical and
 1593 biological measurements. (A) Sea ice breaking up and revealing its structurally different
 1594 layers. (B) The microbially inhabited brine network within sea ice (image from Galley et al.,
 1595 2015). (C) Deploying a weather station and thermistor string. (D) Sea-ice coring. (E)
 1596 Sackhole sampling. (F) Measuring oxygen fluxes at the ice–ocean interface with an eddy
 1597 covariance instrument. (G) Microsensor profiling and pulse-amplified modulation (PAM) in
 1598 the sea-ice algal bottom layer (image from Rysgaard et al., 2001).