1 Overview of the MOSAiC expedition: Ecosystem

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33 ABSTRACT

34 An international and interdisciplinary sea ice drift expedition, the 'The Multidisciplinary drifting Observatory for the Study of Arctic Climate' (MOSAiC), was 35 conducted from October 2019 to September 2020. The aim of MOSAiC was to study 36 37 the interconnected physical, chemical and biological characteristics and processes 38 from the atmosphere to the deep sea of the central Arctic system. The ecosystem 39 team addressed current knowledge gaps and explored unknown biological properties 40 over a complete seasonal cycle focusing on three major research areas: biodiversity, 41 biogeochemical cycles and linkages to the environment. In addition to the coverage 42 of core properties along a complete seasonal cycle, dedicated projects covered specific processes and habitats, or organisms on higher taxonomic or temporal 43 44 resolution. A wide range of sampling approaches from sampling, sea ice coring, lead 45 sampling to CTD rosette-based water sampling, plankton nets, ROVs and acoustic 46 buoys was applied to address the science objectives. Further, a wide range of 47 process-related measurements to address e.g. productivity patterns, seasonal migrations and diversity shifts were conducted both in situ and onboard RV 48 49 *Polarstern*. This paper provides a detailed overview of the sampling approaches 50 used to address the three main science objectives. It highlights the core sampling 51 program and provides examples of two habitat- or process-specific projects. First 52 results presented include high biological activities in winter time and the discovery of 53 biological hotspots in underexplored habitats. The unique interconnectivity of the coordinated sampling efforts also revealed insights into cross-disciplinary 54 55 interactions like the impact of biota on Arctic cloud formation. This overview further 56 presents both lessons learned from conducting such a demanding field campaign 57 and an outlook on spin-off projects to be conducted over the next years.

58 **1. INTRODUCTION**

59

60 **1.1. Motivation**

The Multidisciplinary drifting Observatory for the Study of Arctic Climate (MOSAiC) 61 expedition provides unique scientific opportunities to fundamentally understand the 62 63 interlinked physical, chemical, and biological systems in the central Arctic Ocean. 64 The science program was shaped over nearly a decade and provides a foundation to 65 create new and important knowledge regarding the functioning of the Arctic ecosystem within the context of the coupled Arctic climate system. Five closely 66 67 cooperating science teams were formed to develop and execute the integrated 68 science plan, focusing on atmosphere, sea ice, ocean, ecosystem and 69 biogeochemistry. This paper provides an overview of the multiple facets of 70 ecosystem-related research to highlight the interlinked research activities at multiple 71 trophic levels in relation to the environment. Within the MOSAiC ecosystem team 72 (termed ECO team in the following), a total of 25 institutions across 15 nations 73 contributed to generating the field observations and measurements as part of the 74 research program. Similar overviews are available for other MOSAiC research 75 topics, currently for sea ice physics, physical oceanography, and various aspects of 76 the atmosphere (Nicolaus et al., 2022b; Rabe et al., 2022; Shupe et al., 2022), while 77 an overview on biogeochemical research not covered in this article is forthcoming. 78 The integrated ecological observations and knowledge generated by the ECO 79 team was specifically aimed at understanding seasonally-resolved processes on 80 different scales. These are critical for future predictions related to climate change 81 impacts on the Arctic system, including alterations to ecosystem structure and 82 functioning (Intergovernmental Panel on Climate Change (IPCC), 2023). While the 83 research is ongoing, new projects are emerging based on insights, data and 84 collaborations. 85 Section 1 of this paper outlines the main ecological research objectives addressed via the MOSAiC ecosystem research, followed in the second section by a 86 87 more detailed description of the scientific approaches and methods being used. The 88 coordinated ecological research also included biogeochemical variables (e.g. 89 macronutrient concentrations, seawater and ice carbonate chemistry, dissolved

organic carbon) due to their close links to ecosystem processes. Example data sets
 provided in section 3 demonstrate what to expect in the forthcoming peer-reviewed

92 publications. Lastly, section 4 provides insights into "lessons learned" and challenges

93 when planning such a yearlong expedition and point towards some of the expected

⁹⁴ impacts that could arise from the compiled knowledge over the years to come.

95 **1.2.** The Central Arctic Ecosystem and its links to the environment

96 The Arctic Ocean harbors unique and diverse biological communities in all available 97 habitats: sea ice, snow, seawater, atmosphere, and sediments. Although the Arctic 98 Ocean was once considered a relatively species-poor region with limited biological 99 activity, research in recent decades has revised this paradigm (Bluhm et al., 2011). 100 For example, it is now known that there is high biodiversity in all habitats and high 101 biological activity year-round, including in the winter season (Berge et al., 2015; 102 Hobbs et al., 2020). Furthermore, the Arctic ecosystem is not easily generalized due to the particularly high spatio-temporal variability in biological, chemical, and physical 103 104 processes (Bluhm et al., 2015). Arctic marine ecosystems have regionally varying 105 complex community structures and activity patterns, largely driven by differences in abiotic factors like water temperature, depth, salinity, light, inorganic nutrients, and 106 sea ice properties (Balmonte et al., 2018; Bluhm et al., 2018, 2015; Clement Kinney 107 108 et al., 2023; Ershova et al., 2021; Polyakov et al., 2020). Other efforts to explore 109 ecosystem-level research in the central Arctic include SHEBA (e.g., Ashijan et al., 2003; Sherr et al., 2003), the Circumpolar Flaw Lead study (Barber et al., 2015), N-110 ICE2015 (Assmy et al., 2017; Granskog et al., 2018), the Synoptic Arctic Survey 111 112 (Snoeijs-Leijonmalm et al., 2022), Tara Arctic (Ibarbalz et al., 2023; Royo-Llonch et al., 2021), and the Russian ice drift studies (Melnikov, 1980). Yet, despite these 113 114 valuable efforts, the seasonal cycle in the central Arctic remains understudied 115 because the region is difficult to access in winter with thick and extensive sea ice cover and harsh conditions for work in the field. Remote sensing of biological 116 117 properties is also limited by the ice-covered, seasonally dark and often cloud-118 covered Arctic (Babin et al., 2015). New comprehensive time series data are further 119 needed to construct numerical models and test mechanistic hypotheses within the 120 context of Earth System Models (e.g., CMIP5 and CMIP6 for the IPCC AR5 and 6, 121 respectively; IPCC, 2023). Representations of the marine ecosystem are lacking or 122 less advanced than other components of the Earth system within large-scale models. 123 Therefore, MOSAiC research is a critically needed evaluation of the current state of 124 the Arctic marine ecosystem, required to adjust our understanding to new ecosystem 125 components, and improve our understanding of basic biological processes to 126 enhance predictions of future system status.

The central deep Arctic Ocean is divided into four abyssal plains separated by 127 128 the Lomonosov, Gakkel, and Alpha ridges. Even so, the upper water column (~ 1000 129 m) is contiguous with two major ice drift and ocean circulation patterns: the 130 Transpolar Drift (TPD) System and the Beaufort Gyre. The MOSAiC field campaign 131 was established on a sea-ice floe at the Siberian edge of the Amundsen Basin 132 (Figure 1), close to the origin of the TPD. During the campaign, the floe drifted in the 133 TPD across the central Arctic towards Fram Strait. Details regarding the sea ice 134 conditions during MOSAiC are provided by Krumpen et al. (2020) and Nicolaus et al. (2022b). The hydrography in the central Arctic Ocean is characterized by a strong, 135 136 permanent vertical salinity gradient (halocline). The upper surface mixed layer in the Amundsen Basin is characterized by low salinity and largely cold waters, being 137 138 affected by river discharge, ice melt / freeze processes and Pacific inflow inside the

139 TPD (Rabe et al., 2022; Rudels and Carmack, 2022; Schulz et al., 2023a). South of 140 the Amundsen Basin, as separated by the Gakkel ridge, surface waters of the 141 Nansen Basin (Figure 1) are less influenced by the TPD. Here surface waters carry a stronger signal of Atlantic sourced water masses (Schulz et al., 2023b). Below the 142 143 surface mixed layer lay warmer and more saline waters of Atlantic origin. The core of 144 the Atlantic Water is warmest and saltiest north of Svalbard and close to the Barents-145 Kara Sea slope. In addition, modelling studies suggest that Atlantic water can advect 146 biomass from phytoplankton blooms developed in open waters upstream under the sea ice into the eastern Arctic (In addition, modelling studies suggest that Atlantic 147 water can advect biomass from phytoplankton blooms developed in open waters 148 149 upstream under the sea ice into the eastern Arctic (Clement Kinney et al., 2023). It is modified once it enters the basins and circulates around the Arctic, mainly along the 150 151 shelf slopes as a deep circulation loop (Rudels and Carmack, 2022), and over time, becomes colder, fresher, and is subducted deeper in the water column. The 152 influence of these major water sources (i.e. TPD- vs Atlantic-influenced) on the 153 central Arctic Ocean depends on circulation dynamics, which control the proportion, 154 155 layering, and mixing of different source waters and their respective nutrient 156 inventories. In surface waters of the central Arctic, nutrient concentrations are 157 variable, but low relative to the Arctic shelf regions and deeper water masses (Bluhm 158 et al., 2015; Randelhoff et al., 2020).

159 The strong vertical gradients in nutrient concentrations, and factors such as 160 irradiance and other ocean physico-chemical parameters, structure the pelagic realm. Highly diverse communities of phytoplankton and sea ice algae (Poulin et al., 161 162 2011) contribute to the primary production in the central Arctic (Gosselin et al., 1997; Wiedmann et al., 2020). Both ice and pelagic algae have developed several 163 164 successful strategies to overcome months without sufficient light for photosynthesis 165 (Johnsen et al., 2020) and rapidly utilize the light returning after the Polar night 166 (Hoppe, 2022; Kvernvik et al., 2018). Still, the overwintering strategies and modes of 167 nutrition of several key groups and species remain poorly understood. Also, lower trophic herbivores and omnivores, like sea ice meiofauna (Ehrlich et al., 2020; 168 169 Patrohay et al., 2022) or pelagic zooplankton (Ershova et al., 2021; Hop et al., 2021), 170 have evolved life cycles and physiological adaptations that allow them to survive and successfully compete under these extreme conditions in the ice-covered central 171 172 Arctic Ocean. The microbial network, involving diverse bacterial and archaeal 173 communities (Boetius et al., 2015), drives the remineralization of organic matter in 174 ice and water (Balmonte et al., 2018; Laurion et al., 1995; Wietz et al., 2021), which 175 is a key process for supplying nutrients for algal growth. However, heterotrophic 176 bacteria and algae can also compete for inorganic nitrogen resources (Fouilland et 177 al., 2007).

178 Sea ice provides a unique habitat for diverse biota ranging from viruses to 179 marine mammals and birds. It sustains its own food web driven by the productivity of 180 sea ice algae, which has been reported to contribute up to 55% of total primary 181 production in ice covered areas (Gosselin et al., 1997; Wiedmann et al., 2020). This 182 production is channeled through ice-associated herbivores including copepods and 183 amphipods, and fish (specifically Arctic/polar cod, Boreogadus saida). In fact, trophic 184 marker studies have demonstrated that a substantial part of the organic matter from 185 sea ice algae culminates in apex species like ringed and bearded seals, or Arctic birds (e.g. Carlyle et al., 2022; Kohlbach et al., 2016; Kunisch et al., 2021). Diversity 186 187 in sea ice systems is high, including viruses, bacteria, over 1000 species of 188 unicellular algae and protozoa (Poulin et al., 2011), and about 100 associated 189 metazoan taxa living in the ice brine channel system or the bottom of the ice (Bluhm 190 et al., 2018 and references within). Summer melt ponds and low-salinity meltwater accumulated in leads and under the ice are examples of unique habitats that can 191 192 form, disappear, and be replenished again multiple times over relatively short time 193 scales during parts of a seasonal cycle (Smith et al., 2023). Similarly, also under ice 194 productivity can be high in ice covered regions: a recent high resolution biophysical 195 modeling study has found that 63% of the total primary production in the central 196 Arctic occurs in waters with \geq 50% sea ice cover, and 41% of the total primary 197 production in areas with ≥85% cover (Clement Kinney et al., 2020). While 198 considerable information exists for some regions, seasons, and taxa, the majority of 199 biological components in the ice and ocean have not been identified and quantified 200 through a complete annual cycle, particularly in the high Arctic. Filling this knowledge 201 gap by investigating the full range of trophic components from bacteria to metazoans 202 and exploring their unknown connections has been an ambitious and challenging 203 goal of MOSAiC ecosystem research.

204 The activities of and interactions between different taxonomic, functional, and 205 trophic groups change in space and time. In the Arctic, the strong seasonality and 206 high interannual variability in environmental conditions such as temperature, nutrient 207 availability, and irradiance drive the ecosystem state, phenology, and functions 208 (Ardyna and Arrigo, 2020; Kosobokova and Hirche, 2000; Leu et al., 2015). Climate 209 change has already substantially altered the Arctic marine system through increased 210 fractions of first-year ice, stronger and warmer inflow from the Atlantic and Pacific 211 Oceans, freshening of the surface waters, later sea ice formation and earlier onset of 212 melt (Ingvaldsen et al., 2021; Polyakov et al., 2020) with associated biological 213 system responses. For instance, under-ice phytoplankton blooms, algal infiltration 214 communities at the snow-ice interface, and shifts in biodiversity due to borealization 215 are increasingly observed (Ardyna et al., 2020; Fernández-Méndez et al., 2018; 216 Ingvaldsen et al., 2021). Different sensitivities to climate change drivers by various 217 ecosystem components may cause mismatches between trophic levels, such as 218 algae blooms occurring earlier than the zooplankton life stages depending on them 219 as food (Søreide et al., 2010). Also, the shift from a dominance of a multi-year ice 220 (MYI) or second-year ice (SYI) to a first-year ice (FYI) regime will likely impact sea 221 ice biota; however, evidence for change is patchy due to the limited availability of 222 sufficiently long time-series data (Campbell et al., 2022). Comparisons between FYI 223 and MYI diversity of sea ice protists indicate substantially lower (by 39%) diversity in 224 FYI compared to MYI (Hop et al., 2020). The diversity and presence of sea ice 225 meiofauna taxa has also decreased, including the nearly complete absence of 226 flatworms and nematodes in recent studies (Ehrlich et al., 2020). MYI might also act

227 as a seed bank for sea ice algae and fauna for adjacent newly forming and growing 228 FYI (Olsen et al., 2017). Sea ice biogeochemical cycles could be impacted, as FYI is 229 typically saltier, with higher brine volume fractions creating more habitable space, 230 and permeability resulting in higher fluxes within the ice, and increased nutrient 231 supply (Tedesco et al., 2019). Beyond these structural and functional changes in the 232 sea ice ecosystem itself, an alteration of the relative contribution of sea ice algae 233 versus phytoplankton to overall annual primary production also has consequences 234 for other ecosystem components, including through the often tight sympagic-pelagic 235 and sympagic-benthic coupling processes (Rybakova et al., 2019; Wang et al., 2015; 236 Wiedmann et al., 2020).

237 Biological processes in ice and seawater are not only relevant for the marine 238 ecosystem, but impact the entire Arctic System. These processes are linked to 239 physical processes in the atmosphere, ice, and ocean through various coupled 240 processes and feedback mechanisms (Figure 2). Whereas the strong 241 interdependence between the seasonally changing sea ice properties and ocean-242 atmosphere physics is widely recognized (Shupe et al., 2022), the tightly coupled interaction between the sea ice and the biology and chemistry of the ocean 243 244 underneath is not well understood and, as a consequence, often neglected in 245 numerical models. Biological activity affects the cycling and transformation of 246 inorganic molecules and organic matter, and exerts strong controls on the cycling of 247 climate-active gases such as carbon dioxide (CO₂), methane (CH₄), nitrous oxide 248 (N₂O), and dimethyl sulfide (DMS) in the ocean and ice, as well as across the 249 atmosphere-ice-ocean interfaces (Falkowski et al., 1998). For example, CO₂ 250 concentrations are controlled by a range of chemical and biological processes 251 including organic production, remineralization, gas exchange, and inorganic calcium 252 carbonate precipitation within sea ice and dissolution in sea ice meltwater 253 (Angelopoulos et al., 2022; Fransson et al., 2011; Miller et al., 2011; Nomura et al., 254 2018; Rysgaard et al., 2012, 2007) leading to seasonally varying air-sea-ice CO₂ 255 exchange (e.g., Fransson et al., 2013; Mo et al., 2022). Seasonal sea ice melt decreases the partial pressure of CO₂ (pCO₂) of the stratified Arctic surface waters 256 257 through dilution, ikaite dissolution, and supporting phytoplankton blooms near the 258 surface (Fransson et al., 2017). In recent years, enhanced sea ice melt has exposed 259 these low pCO₂ surface waters to high atmospheric pCO₂ levels, thereby promoting 260 CO₂ uptake from the atmosphere (Qi et al., 2022). Over longer periods of time, the enhanced CO₂ uptake decreases the surface waters' pH buffering capacity and 261 262 promoting vulnerability to ocean acidification (Qi et al., 2022). At the same time, the 263 associated decreased buffer capacity for CO₂ promotes ocean acidification. Storm events in different seasons can impact air-sea CO₂ exchange by altering the surface 264 265 layer pCO₂ through wind-induced mixing with subsurface water and by creating 266 leads where direct air-sea gas exchange can occur (Fransson et al., 2017). For sea ice itself, rising temperatures and younger sea ice promote an increase in the brine 267 volume fraction, which in turn enhances the transfer of gases and substances across 268 269 gas-water interfaces within sea ice and between the sea ice and atmosphere 270 (Nomura et al., 2018).

271 Marine biological processes can impact climate relevant processes through 272 linkages beyond production cycles of climate-relevant gases. Biogenic compounds 273 that become aerosol particles can become airborne through the air-water interfaces 274 of the Arctic and serve as cloud condensation nuclei (CCN) and ice nucleating 275 particles (INPs) in the atmosphere, affecting clouds and the radiative balance of the 276 system (Creamean et al., 2022). This, in turn, may feedback on productivity through 277 modulation of the light available to fuel primary production (Kauko et al., 2017). High 278 standing stocks of organisms in the sea ice and water column also change the 279 energy budget and heat uptake of these components as they increase the absorption 280 of shortwave radiation, thereby affecting the freeze and melt cycles of their own 281 habitat (Taskielle et al., 2017; Zeebe et al., 1996). Also, sea ice microstructural 282 properties relevant for gas exchange can be modified through ice algal production of 283 extracellular polymeric substances (Krembs et al., 2011).

284

285 **1.3.** The mission of MOSAiC ecosystem studies

286 The MOSAiC sampling program used existing knowledge on ecosystem-relevant processes and components to fill major gaps in current knowledge and explore so far 287 288 unknown links. The integrated MOSAiC ecosystem research program combined 289 year-round consistent measurements of specific core properties (Table 1) with 290 embedded individual research projects (supplementary Table S1) and opportunistic 291 sampling. The core program included an extensive suite of biological and chemical 292 components sampled from the water column, and undeformed level FYI and SYI. 293 The aim of the core measurement program was to provide a consistent and 294 continuous backbone of key measurements over the drift period, which would allow 295 to link different integrative and complementary process studies. The project-specific 296 measurements either provided higher temporal or spatial resolution beyond the 297 weekly sampling program, or focused on processes or habitats that were not part of 298 the core parameter time-series. Our investigations relied on a combination of 299 traditional tools and more recently developed technologies and cross-cutting approaches. This combined approach facilitated linkages to previous studies, while 300 301 providing new knowledge into the seasonality of high Arctic biological and 302 biogeochemical processes at unprecedented temporal resolution. The work of the 303 ECO team is focused on three fundamental and essential research questions: 1) 304 Which species are present in the Arctic Ocean (WHO, i.e. Biodiversity)? 2) How do 305 fluxes of energy and matter flow through food webs and habitats (HOW, i.e. 306 Ecosystem functioning)? And 3) Why do physical and chemical parameters exert 307 control on species distribution and activities and vice versa (WHY, i.e. linkages with 308 the environment)? 309 *Biodiversity:* The program was designed to capture a full seasonal sampling of 310 ice and seawater habitats, including the dark season, with a wide range of established and innovative tools to achieve the most complete species inventory for 311 312 ice and pelagic biota of the Central Arctic.

313 *Ecosystem functioning*: The flow of matter and energy in ice and seawater 314 substantially changes with time, driven by the strong seasonality of environmental 315 variables (e.g., light and ice freeze-melt cycles) and organism life cycles. Therefore,

- it was essential to systematically determine organism abundances, biomass, and
- 317 activity rates throughout the MOSAiC drift. The program aimed to quantify the
- 318 seasonal fluctuations in algal and bacterial productivity, organismal physiologies
- 319 (including metatranscriptomes) and life cycles, as well as grazing by micro- and
- 320 mesozooplankton, diets of key species, and vertical particle fluxes.

321 Linkages with environment: The combined analysis of ecosystem 322 characteristics with all available MOSAiC environmental data allows us to assess the 323 importance of bottom-up (e.g., light, nutrients, sea ice characteristics) versus top-324 down (e.g., grazing, predation) controls on biological standing stocks and activities 325 over a complete seasonal cycle. The program aimed to assess the contributions of ecosystem processes to the Arctic climate system, e.g., by driving gas fluxes across 326 327 ice-ocean-atmosphere interfaces, or by affecting the heat budget of sea ice directly 328 or through interactions with clouds.

329 These three major focal science areas were approached by considering both 330 their interconnection as well as their relation to the overall MOSAiC science 331 objectives. Therefore, a consistent, coordinated, and methodological framework 332 linking individual measurements within the ECO team was developed. This included 333 strong interdisciplinary partnership with the other MOSAiC teams, like co-located 334 measurements of sea ice and water column properties to identify biologically-335 relevant linkages between the two habitats. The unique year-round access to the 336 high Arctic environment was used to investigate poorly understood and 337 undersampled habitats and seasons. For example, high heterotrophic biological 338 activities and unique biodiversity patterns in winter were expected to precondition the 339 biological response to the return of the light in spring. We furthermore expected that 340 meta-genomic and -transcriptomic data can be used to identify unique physiological 341 mechanisms that sustain survival of organisms and ecosystem services under polar 342 seasonality. The program aimed to provide information relevant for understanding a 343 wider Arctic system by determining the fluxes of climate-relevant compounds like 344 CO₂.

345

346 2. APPROACH AND METHODS

The MOSAiC expedition (PS122) onboard the German research icebreaker RV 347 348 Polarstern (Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und 349 Meeresforschung, 2017) was organized into 5 cruise legs (Figure 1). The field 350 campaign began in late September 2019, and north of the Laptev Sea (Krumpen et 351 al., 2020; Nicolaus et al., 2022b) the first Central Observatory ice camp was 352 established, which was used on cruise legs 1-3 until May 11, 2020 (Figure 3). Team 353 ECO observations began on 15 October 2019, and the full regular weekly sampling 354 by Team ECO started 31 October 2019, which involved measurements and sampling from the ship and ice floe. Leg 1 ended in mid-December and Leg 2 continued on 355 356 until the end of February 2020. Leg 3 extended beyond its originally planned date 357 due to logistical constraints caused by the global COVID-19 pandemic, and ended in 358 mid-May 2020, when RV Polarstern had to leave the first Central Observatory.

359 Following a logistically necessary break, leg 4 re-established and occupied a new 360 Central Observatory (Figure 4) at a different location on the same ice floe from 20 361 June 2020 until the floe disintegrated in the Fram Strait on 31 July 2020. Continued observations were made during leg 5, which involved establishing a new ice camp 362 363 (Figure 5) located on a new ice floe near the North Pole in the second half of August. 364 The MOSAiC ice drift study ended 20 September 2020, with ECO science operations 365 continuing in the marginal ice zone during the transit back to shore. More details on 366 the MOSAiC campaign, can be found in Nicolaus et al. (2022b), Rabe et al. (2022) 367 and Shupe et al. (2022).

368

369 2.1 Water column work program

370 Sampling and measurements in the water column occurred at frequencies from daily, 371 to weekly, with opportunistic, intensive observation sampling occurring a few times over the duration of the expedition, which involved sampling at hourly time scales for 372 373 20-30 hr periods. Sampling frequency was partially based on feasibility and cost-374 benefit evaluation. For most ECO properties, the primary sampling mode was weekly sampling, matching the anticipated rates of change in ecological properties relative 375 376 to anticipated achievability of the sampling program by a small onboard team. The 377 daily sampling for chlorophyll a (Chl-a) and microbial community structure resolved 378 day-to-day changes in fundamental microbial properties, which would be missed with 379 only once-weekly sampling. Herein, major operations executed by Team ECO 380 organized by sampling frequency are briefly described, while detailed method 381 descriptions will be provided in later, targeted publications.

382 383

2.1.1. Continuous measurements and daily sampling approaches

384 A Membrane-Inlet Mass Spectrometer (MIMS) connected to the ship's flow-385 through seawater system allowed the continuous measurement of dissolved O₂ 386 and Ar concentrations to calculate O₂/Ar ratios and infer net community 387 production (NCP) (Tortell, 2005; Ulfsbo et al., 2014), Rokitta et al. unpublished results). The depth of the seawater intake port was 11 m below sea level at the 388 389 keel of the ship. Continuous measurements of these properties were only 390 interrupted during 1) routine maintenance procedures by instrument operators, 2) 391 ship maintenance of flow-through systems, and 3) when discrete bottle sample 392 measurements were performed. Therefore, gaps in continuous data mostly 393 collected during March to October 2020 are approximately 1) once daily for 1-2 394 hrs, 2) 1-2 times monthly for 3-6 hrs, 3) 3-4 hrs weekly. Onboard, routine 395 calibration with reference gasses allowed for tracking of instrument drift over the 396 course of the expedition.

397The AUTOmated FIltration for marine Microbes (AUTOFIM) instrument398(iSiTEC GmbH, Bremerhaven, Germany) automatically collected, filtered, and399preserved water samples for molecular genetic analyses (Metfies et al., 2016)400from December 2019 to October 2020. It is permanently installed on RV401Polarstern a few meters from the flow-through seawater intake system at 11 m at402the bow of the ship. AUTOFIM collected samples on a daily basis, and in some

instances at even higher temporal resolution to resolve spatial changes along the
drift path. Samples were analyzed for microbial community structure using 16S
and 18S rRNA amplicon sequence-based approaches.

406 The fishcam, an in situ video system (FishCam, MacArtney Germany GmbH, 407 Kiel, Germany), was deployed on average at 375 m water depth (range 369 - 376 408 m) from 23 October to 7 November 2019 and at 213 m depth (range 194 - 215 m) 409 from 12 December 2019 to 11 March 2020 through a hole in the ice, approximately 500 m away from the ship (see Snoeijs-Leijonmalm et al. (2022) 410 for details). The system included two HD Internet Protocol cameras, one looking 411 412 sideward and one looking downward, two Luxus High-Power LED light sources of 413 6000 Im each, and a mini-CTD. The system was connected to a personal 414 computer onboard, running PortVis (Serial Port and Video Stream Visualizer) 415 software, version 2.1. Camera images were recorded in LED on:off cycles of 416 5:55, 15:15, or 55:5 min. Fish were also caught via long lines and fishing rods 417 deployed through the moon pool or holes in the ice (Snoeijs-Leijonmalm et al., 418 2022).

Further, a number of discrete water samples were manually collected at a daily or near-daily frequency over the duration of the expedition from a single tap of the ship's flow-through seawater system, which was also used for the MIMS measurements. This included separate samples for 1) Chl-a (except from mid-December to end of February), 2) 16S and 18S rRNA amplicon-based microbial community analyses (except from mid-December to end of February), and 3) ice nucleating particles (INPs, full timeseries).

426 To investigate downward flux, a long-term ice-tethered time-series sediment 427 trap (McLane PARFLUX Mark 78H-21) with 21 sampling cups was deployed at 428 200 m water depth, and tethered to SYI, located ~1000 m away from the ship 429 (Figure 3). Sinking particles were automatically collected for two week intervals 430 (15 or 16 days) from March to November and every month (29-31 days) from 431 December to February. The sampling cups were filled with salt-saturated artificial seawater and HgCl₂ prior to deployment. The sediment trap was operational from 432 433 26 October 2019 to 31 July 2020.

434

435 2.1.2. Discrete sampling

436 The primary sampling approach for the weekly ECO time-series of water column 437 biological and chemical properties relied on the ship CTD rosette, a suite of 438 plankton nets, and a number of small animal- and particle-imaging instruments 439 with deployments over three consecutive days per calendar week. The CTD 440 sensor packages, calibration methods, and post-processing are described in 441 Rabe et al. (2022) and Tippenhauer et al. (2023a, 2023b). In brief, discrete 442 biological samples were collected from 12-liter OTD bottles attached to the 443 shipboard 24-bottle CTD rosette (PS-CTD). From November 2019 to May 2020, 444 additional water column sampling was conducted via a 5-liter 12-Niskin bottle 445 CTD rosette from Ocean City (OC-CTD; via a sheltered in-ice hole located 300 446 meters from RV Polarstern; see Figure 3). In the period between mid-March and

447 mid-May, the PS-CTD was not operational due to the loss of the ice hole 448 alongside the ship (see Rabe et al., 2022), so all water column ECO samples 449 were collected at Ocean City. During this period, use of the OC-CTD led to a 450 lower vertical depth resolution as the total water volume collectable in one cast was substantially less with the OC-CTD (60 L) versus the PS-CTD (288 L). All 451 452 sampling events are listed in Table S4. Sampling order from the individual rosette 453 bottles primarily followed WOCE procedures (Woods 1985), which prioritizes sampling of tracers, gases, and nutrients in time before the sampling of other 454 455 properties. The sequence prioritized sampling of time-sensitive properties and 456 limited contamination between parameters. Co-location of many properties 457 across a smaller number of depth horizons was prioritized over higher vertical 458 resolution of a few properties (Figure 6). Additionally, upper 200 m water column 459 sampling was prioritized over full water column profiling to better resolve upper 460 ocean interactions with sea ice and the atmosphere. Sample types requiring large 461 volumes (e.g. POC/N, DNA and RNA) made it necessary to collect samples in additional casts following a primary full water column cast used to collect small 462 463 volume ECO samples. Standard water depth horizons for biological properties 464 were 2 m, 10 m, Chl-a fluorescence maximum (if present based on CTD 465 fluorescence sensor profile) or 20 m, 50 m, 100 m, and the Atlantic Water core 466 depth. The depth of the Atlantic Water core, detected as the local temperature 467 maximum in each profile, varied significantly along the drift path, from approximately 100 m close to Fram Strait up to 400 m in the Amundsen Basin 468 469 (Rabe et al., 2022; Schulz et al., 2023b). The depth-resolved sampling for Chl-a, nutrients, and total DNA collected from the PS-CTD and OC-CTD rosettes over 470 471 the drift duration relative to a reference depth (400 m) and bottom depth highlight 472 the focus of sample collections in the upper water column (Figure 7).

473 Samples collected by team ECO during the routine CTD rosette-based water 474 column sampling included a wide range of standard variables such as inorganic 475 nutrients (nitrate+nitrite, nitrite, silicic acid, phosphate and ammonium) as well as total dissolved nitrogen and total dissolved phosphorus, total dissolved inorganic 476 477 carbon (DIC) and total alkalinity (TA), dissolved organic carbon (DOC), colored dissolved organic matter (CDOM), Chl-a, algal pigments, POC and PON 478 479 concentrations as well as their isotopic composition, biogenic silica (bSi), total deoxyribonucleic acid (DNA) and ribonucleic acid (RNA) for sequencing, 480 481 taxonomic cell counts (via light microscopy), as well as cell abundance (via flow 482 cytometry). Samples for primary and bacterial production, dissolved oxygen, 483 DOM characterization after solid-phase extraction, and ¹⁴C-DIC were collected at 484 a lower temporal frequency and with larger gaps due to instrumentation failures. 485 Additionally, several complementary samples were collected on a routine basis, 486 such as those for measurements of O₂/Ar ratios in discrete samples, INPs, 487 neutral sugars, and ¹⁵N-nitrate isotopes. Processing of preserved water or filters mainly occurred at the shore-based laboratories, with exceptions of onboard 488 489 measurements of nutrients (Nov 2019 to May 2020), dissolved oxygen (March to 490 Oct 2020), primary and bacterial production (Dec 2019 to May 2020), and a

491 subset of Chl-a samples (March to May 2020). Details on sample processing492 methods can be found in supplementary Table S2.

We aimed for all analyses for each variable to be done in the same laboratory 493 494 and/or using the same instrument to decrease uncertainty due to laboratory or 495 instrument calibration (see supplementary Table S2 for details). In cases where 496 this was not possible (DIC/TA, DNA, RNA, POC/N), interlaboratory calibration 497 samples were collected. In the case of nucleic acid samples, aliguots from the 498 same extracted samples of the core time series were used for specific 499 sequencing approaches in specialized labs (e.g. metabarcoding, genomics, 500 sequencing of specific metazoan or functional primers). Details on the ECO multi-501 omics sampling program are given in Mock et al. (2022).

502 The seasonal life cycles and vertical distribution of zooplankton abundance 503 and biomass were studied using imaging tools and plankton nets, deployed on 504 the same or on two consecutive days during a calendar week. From November to 505 March, a multinet midi (Hydrobios), three ring nets, the Underwater Vision Profiler (UVP) and the Light-frame On-sight Key Species Investigation system (LOKI) 506 507 were deployed through a large hole in the ice alongside the RV Polarstern 508 yielding an almost weekly resolution for many targeted parameters (Tables S4 509 and S5). The multinet was equipped with five nets of 150 µm mesh size to 510 sample five discrete depth intervals between 2000 m and the ocean surface. 511 Those samples were processed for zooplankton identification, abundance, and 512 biomass at shore-based laboratories. The LOKI was deployed approximately 513 weekly from 1000 m to the surface. In addition to high resolution images, the 514 instrument obtained hydrographical parameters, e.g. depth, temperature, salinity, 515 oxygen concentration and fluorescence. The UVP was mounted on the PS-CTD 516 rosette and casts were conducted from various depths to the surface. Ring nets 517 of 1 m² area (150- and 1000-µm mesh) and 0.28 m² area (53-µm mesh) were deployed to varying depths up to 2000 m, to collect zooplankton for analysis of 518 taxonomy, energy content, biomarkers and gut DNA (Table S4). However, the 519 hole next to the vessel could not be maintained in April and May due to strong ice 520 521 dynamics. During that period, only a 150-µm mesh Nansen net and the 53-µm 522 mesh ring net could be deployed at the ice hole at OC. The Nansen net was 523 equipped with an opening/closing device and was deployed in a series of single 524 casts to the same depth intervals as sampled by the Multinet down to a maximum 525 depth of 800 m. Additional ring net tows were conducted over the same depth 526 intervals as used for the Multinet to collect animals for biochemical and genetic 527 analyses and physiological rate measurements. In addition, during all seasons, a 528 net was attached to the under-ice Remotely Operated Vehicle (ROV) 'Beast' 529 (Katlein et al., 2017) for sampling 2-3 depth horizons: the ice-ocean interface, 10 530 m, and 50 m under the ice.

531To determine zooplankton abundance and biodiversity, usually complete532samples from Multi-, Nansen-, and ROV net casts, as well as samples taken with533the small ring net, were preserved with hexamethylenetetramine-buffered 4%534formaldehyde, stored at room temperature and subsequently processed in

535 laboratories in Germany (AWI) and the US (University of Rhode Island). Live 536 specimens for biochemical analyses and physiological rate measurements were 537 sorted from ring net samples under a stereomicroscope onboard and determined 538 to the lowest possible taxonomic level. Only when abundances were low, large 539 organisms were also sorted from Multi- and ROV net samples allocated for 540 taxonomic analyses to obtain sufficient individuals. Most of the live specimens 541 (>10,000 individuals during the entire expedition) were deep-frozen, either 542 individually or pooled in groups depending on size, for biochemical 543 measurements (e.g., total lipid content, C/N ratio, energy content, lipid class 544 composition, omega-3 fatty acids and level of animal sterols such as cholesterol 545 and desmosterol, δ^{13} C and δ^{15} N values), as well as for molecular studies of gut 546 contents (copepods, amphipods) and for biodiversity (gelatinous zooplankton). 547 Key mesozooplankton species (e.g., Calanus glacialis, C. hyperboreus, Metridia 548 longa, Themisto spp.) were photographed prior to freezing to digitally measure 549 certain characteristics, e.g., prosome length (copepods) and oil sac volume (Calanus spp.). For experimental work, individuals of key species were incubated 550 551 for at least 24 h to determine egg production, grazing and respiration rates, and 552 thereafter, deep-frozen to measure organic carbon and nitrogen contents to 553 calculate biomass specific rates (eee details in Case Study 1 below).

554

555 2.2. Sea ice coring and processing

556 The coordinated sea ice sampling by the MOSAiC teams ICE, ECO, and BGC was 557 designed to study the seasonal changes of physical, biological, and geochemical 558 properties of FYI and SYI in an interdisciplinary context (see also Angelopoulos et 559 al., 2022; Nicolaus et al., 2022b; Evgenii Salganik et al., 2023a). During fall 2020, 560 ice areas of undeformed FYI and SYI were identified that were safely accessible by 561 snow machine, relatively homogeneous, and large enough to accommodate repeat 562 visits, potentially for the entire drift. Most importantly, sites had to be located away 563 from RV Polarstern to avoid and minimize the impacts of 1) artificial light pollution, 2) regular on-ice foot traffic, 3) fumes and particulate material from the ship's 564 565 exhaust system and snow machines, and 4) 'technically clean water' discharges 566 from the ship.

567 Tents were set up at each ice coring site to protect newly extracted ice cores 568 from adverse environmental conditions during sectioning, which could quickly alter 569 ice and its physical, biological, and chemical properties. Cores for biological 570 properties were collected using a 9-cm diameter KOVACS Mark II coring system. 571 All coring events are summarized in supplementary Table S6. Most cores were 572 sectioned and parsed into sterile Whirlpak bags directly inside the tent under low 573 and/or red-light conditions to minimize artifacts. In some instances, complete cores 574 were bagged directly in the field and processed on the ship, but in-field sectioning 575 was prioritized when conditions were amenable. Ice core properties were derived 576 from individual core sections or pooled core sections (Figure 8) depending on 577 individual property requirements. Core section pools provided larger melt volumes 578 and sub-sampling for multiple properties from single horizons. Small-scale

horizontal variability was reduced by pooling core sections, creating a morehomogeneous master sample from which to derive related properties.

581 Six to eight full-length ice cores designated for ecological and biological 582 properties were sectioned using similar sectioning schemes and parsed into new, 583 sterile Whirlpak bags in the field. Cores were sectioned from the bottom into two 5 584 cm sections, and then subsequently at 10 cm intervals from top and bottom, 585 leaving a variable length middle section. Middle sections varied by several cms 586 across 3-4 cores. Two pools (termed ECO1 and ECO2) using this procedure were 587 generated and sub-sampled for a majority of biological properties from these two 588 sets (Figure 8). In addition, the bottom 0-3 cm or 0-5 cm of sea ice from 3-4 cores 589 were collected, sectioned, and pooled for individual sets of measurements of net 590 primary productivity (NPP pool) and occasionally bacterial production (from NPP 591 pool), as well as a pool for metatranscriptomes (RNA pool) in the field. 592 Occasionally, full profiles of BP were measured from ECO1 pools.

593 A single core was collected for bulk salinity, oxygen isotopic composition, and 594 inorganic nutrients. This core was sectioned in the field at 5 cm intervals from the 595 top and bottom, leaving a variable-length middle section (Nicolaus et al., 2022b; 596 Evgenii Salganik et al., 2023a). Individual cores were collected for DIC/TA and 597 gypsum. These cores were bagged completely in the field and either sectioned and 598 processed onboard, or stored frozen for future processing onshore.

599 Ice cores and sections were transported back to the ship in coolers, protecting cores from fluctuations in light and temperature. All ECO pool samples were melted 600 601 after the addition of 0.2 µm filtered surface seawater (typically 50 ml per 1 cm of 602 core section) to reduce the impact of osmotic stress and cell loss (Campbell et al., 603 2019; Chamberlain et al., 2022; Garrison and Buck, 1986). Ice core sections in 604 bags were melted in the dark at room temperature (18-22°C) and checked every 4-605 6 hours. Upon completed melt, which took 12 to 40 hours, bags were transferred 606 into dark, temperature-controlled laboratory containers, and parsed for sub-607 sampling of biological properties under red light to minimize artificial light 608 stimulation of biological activities. Samples for Chl-a, algal pigments (HPLC 609 analyses), particulate organic carbon and nitrogen (POC/N), biogenic silica (BSi), taxonomic counts (light microscopy) and cell abundances (flow cytometry), INPs, 610 611 and neutral sugars were typically collected from ECO1 pool (Figure 8). DNA 612 samples were filtered through 0.2 µm filters from ECO2 pool, and the filtrate was 613 reserved for DOC and CDOM determinations. For each melted core section, melt 614 volume factors were derived from added meltwater volume, which were used to 615 derive to calculate melted ice volumes. Data are reported as per unit volume 616 melted ice core as no correction for differences in density of ice and melt water 617 were available.

Core sections for measurements of inorganic nutrients and nitrate isotopic
 composition were directly melted in the dark. Samples were pre-filtered through a
 0.45 μm filter membrane and either analyzed directly onboard, or frozen for
 analysis onshore.

622 DIC/TA cores were sectioned onboard in a freezer laboratory (-15°C) at 10 cm 623 intervals from top and bottom, with a variable length middle section. Sections were 624 placed inside gas-tight bags and air was removed using a vacuum pump to avoid 625 CO₂ exchange. These core sections were directly melted in the dark at 4°C, without 626 addition of buffer or conservational solution. Melted samples were transferred into 627 250 ml borosilicate bottles, augmented with 60 µL of saturated mercuric chloride 628 (HgCl₂) solution, and sealed with a septum cap to prevent CO₂ exchange with the 629 atmosphere, then stored cool until post-cruise analyses in Japan (Nomura et al., 630 2020).

631

632 2.3. Event- and process-driven sampling

In addition to the time-series sampling of water column and sea ice, additional
samples were collected either on an opportunistic or event- and process-driven
basis (see supplementary Table S7 for an overview on all sampling events). For
many of these sampling events, a smaller subset of parameters was sampled, with
Chl-a and nutrients being the most regularly sampled properties.

638 Water samples for biological properties were collected from leads from the 639 upper 1.5 m of water directly below newly forming ice or within the sea surface 640 using peristaltic or hand pumps, from October thru early March, and again from 641 early July till the end of the drift in September 2020. Newly-forming ice was 642 collected by sieves, saws, buckets, and/or ice corers throughout the drift period, 643 except during the continuous melt period between June and end of July 2020. 644 Ecological properties of the seasonally occurring melt ponds were sampled only 645 during August and September 2020. Similar to leads, both ice and water from 646 within and under melt ponds were sampled. Ice from leads and melt ponds was 647 processed without filtered seawater addition on most sampling instances, while 648 filtered seawater was added to ice collected between March and May 2020, similar 649 to the handling of time-series samples of sea ice. Sampling of various stages of ice 650 formation and consolidation was conducted in the marginal ice zone (MIZ) during 651 the transit back to shore at the end of the field campaign (September 2020). Here, 652 a small number of biological properties from sea ice, direct under-ice waters, and 653 the water column was collected from 3 stations. Ice types collected from these transit stations were primarily from ice floe edges, and were not consolidated. The 654 655 distribution of biological properties in pressure ridges (deformed sea ice) was 656 studied using ice coring of keel blocks and collecting water from ridge keel voids 657 (seawater-filled voids between ice blocks in the ridge keel) and below ridges (see 658 case study 1 for details).

659 Water directly from the ice-water interface below level ice was collected 660 except for August to October 2020 for project-specific experimental work by 661 deploying a hand pump through a borehole in the ice. Similarly, under-ice water 662 from the upper 2 m of the water column was occasionally sampled via hand pumps 663 in connection to the time-series common coring activities.

664 In addition to these more opportunistic sampling events, intensive observation 665 periods (IOPs) were included to address research questions on timescales shorter 666 than the one-week interval of the time-series. For example, higher frequency 667 temporal sampling (i.e., 4-10 time points in 20 - 30 hr periods) was conducted to 668 observe potential diurnal dynamics as well as biological changes as a result of 669 important events such as high wind periods, or the onset of freeze. In the beginning 670 of December, a 24-hr IOP with zooplankton collections via both ROV nets and 671 LOKI was conducted. In July, two 24 hr IOPs were conducted. The first one in the 672 beginning of July consisted of 3 LOKI casts and six CTD rosette casts from the 673 ship to cover diurnal patterns in the water column. A second IOP was conducted 674 one week later during rapid melt to also investigate diurnal patterns in the direct 675 under-ice habitat. In September 2020, two IOPs were conducted. In the beginning 676 of September, a 36 hr intensive observation period in collaboration with team 677 OCEAN was conducted to investigate the effects of a high wind event. Collections 678 of under-ice waters occurred within a temporary on-ice laboratory, termed 679 'EcoLodge,' established during the summer period. From June to mid-August 2020, 680 EcoLodge1 was situated approximately 110 m from the ship on level ice, i.e. closer than other major sites but with an under-ice environment that was comparable in 681 682 terms of ice thickness to the FYI coring site, and with surface waters less affected 683 by disturbance from the ship compared to the PS-CTD rosette system. Here, 684 under-ice water with brackish salinity (10-15) was sampled using a peristaltic 685 pump, and filtered directly for Chl-a, POC/N, and microbial community structure 686 analyses. Samples for inorganic nutrients and cell abundance were also collected. 687 During August and September, the re-established EcoLodge2 was located 688 approximately 300 m from the ship on level ice and approximately 15 m from a small, dynamic lead. Here, ice thickness was 125-130 cm. EcoLodge2 served as a 689 690 hub for under-ice water sampling via a peristaltic pump at 14 timepoints over 36 691 hrs. One week later a similar IOP at EcoLodge2 with 12 time points over 24 hrs 692 was conducted to assess the impacts of the onset of freeze up.

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2.4. Modifications to ship-based and on-ice routine operations for ecosystem sampling

696 A number of regular ship operations were considered as potential sources of 697 contamination, for which we took precautions to limit their potential impact. For 698 example, prior to MOSAiC, the ship would regularly release gray water 699 continuously from an outlet located starboard side at 5 m depth. The location and 700 constant release of gray water posed a potential risk to our sampling efforts as this 701 location was within meters of the main PS-CTD sampling. While gray water is 702 technically clean enough to drink, it could carry residual microbial, DOM and 703 nutrient contamination. Also, there was a chance that the gray water, being less 704 saline than ambient seawater, would float towards the surface and interact with the 705 underside of the ice floe, potentially altering important characteristics of the ice and 706 its development. Therefore, during MOSAiC, gray water was retained in the ship's 707 hold for 2-3 days, had salt added back into the solution to increase its salinity, and 708 pumped to 150 m depth from the ship's moon pool. Gray water pumping was 709 conducted on days when no active water column sampling was conducted.

A monthly cleaning routine of the engine's boiler systems was one aspect of normal ship operations, which we had not been aware of in advance, that may have had an impact on our sampling efforts around the ship. Unlike gray water handling, this operation was not possible to adapt. While the dates of the monthly release and of measurements on and around those dates can be reviewed to identify any abnormalities, no direct measurements on possible contamination were done.

717 The ship also emitted continuous artificial light during the drift. Due to safety 718 regulations, the use of light near the ship during our water column sampling could 719 not be significantly reduced. When sampling of the PS-CTD rosette during times of 720 natural darkness (i.e., the Polar night), we reduced the light contamination during 721 sampling by combination of room shading and shaded containers for sample 722 collections (Marangoni et al., 2022). Since the floe drifted in different directions and 723 speeds compared to the water column below, the effects of light pollution on water 724 column-based time series sampling of biogeochemical and many biological 725 parameters can be expected to be minimal. However, e.g. physiological rates of sampled organisms as well as diel vertical migration pattern may have been 726 727 impacted (Ludvigsen et al., 2018). Comparing migration patterns from different 728 devices and locations (e.g., Acoustic Zooplankton Fish Profilers (AZFPs) located at 729 different distances from the ship; Berge et al unpubl. results) may help to evaluate 730 potential impacts. For sea ice, potential impacts of artificial light pollution on 731 photosynthetic biomass and physiology are much larger, as small effects may 732 accumulate over time. To account for this, the long-term sea ice time-series sites 733 were established >1 km from the ship, where light pollution was not detectable. In 734 the field, shaded tents were used for ice processing to reduce the effect of strong 735 ambient light and temperature increases on ice samples during summertime. In the 736 ship-board labs, samples were processed in temperature-controlled, red- and/or 737 low-light conditions.

In addition to reducing artificial light pollution, we also aimed to reduce the 738 739 introduction of nutrients and dissolved carbon to our sea ice samples through our 740 melt process. For most ecological properties collected from sea ice, buffering the 741 melt process with a known volume of saline solution can reduce the impact of 742 osmotic stress and cell loss (Garrison and Buck, 1986). Therefore, we planned to 743 make and add an artificial saline solution, consisting of distilled water and analytical 744 grade sodium chloride, to our sea ice core sections. However, the onboard nutrient 745 analyzer showed that the artificial saline solution contained about 1 µmol kg⁻¹ nitrate+nitrite, which, at the start of the drift, was more than 10 times the ambient 746 747 sea surface water nitrate+nitrite concentration. Therefore, despite our preparations, 748 filtered surface seawater additions were used in the ice core melting process, 749 which impacts some of our parameters such as DOC or INP.

750

2.5. Integrative approaches across the Team ECO work program

In the following sections, some of the approaches that were employed to gain a

holistic understanding of seasonal variations in species composition and food web

- dynamics are highlighted. Further, pathways are identified towards synthesizing
 different data sets to address overarching questions in how organisms, and
 physical properties and processes, control the flow of material and energy. In
 addition, the integrated multi-omics approaches are detailed in Mock et al. (2022).
- 759 2.5.1. Imaging

758

760 Imaging has become an essential tool in zooplankton studies in the last two decades (Giering et al., 2022; Lombard et al., 2019). The in situ cameras LOKI 761 762 and UVP resolve plankton distributions at high vertical resolution (Kiko et al., 763 2017; Schulz et al., 2015). The main strength of the UVP is detecting marine 764 snow, large-sized single-cell organisms (e.g., Rhizaria; Biard et al., 2016), and 765 gelatinous zooplankton (Stemmann et al., 2008). The resolution of the images (1.5 megapixel, picture size depend on organisms size), however, is relatively low 766 767 and often does not allow for species identification, especially of the dominant 768 zooplankton group Copepoda. The LOKI concentrates the organisms with a net, 769 leading to a flow-through chamber (Schulz et al., 2010). Jellyfish are often 770 destroyed by the net, but LOKI captures Copepoda and other abundant taxa 771 (e.g., Ostracoda, Chaetognatha) in high quality images, allowing the 772 determination of copepod genera, species, and often developmental stages 773 (Schmid et al., 2016). In addition to in situ imaging, preserved net samples 774 collected during MOSAiC have been scanned using the laboratory on-desk 775 system ZooScan and single object images have been extracted with the software 776 application ZooProcess (Gorsky et al., 2010). To classify plankton organisms and 777 share images among experts worldwide, all images taken by LOKI, UVP, and 778 ZooScan have been uploaded to EcoTaxa. This is a web-based platform that is 779 an established tool in classifying zooplankton organisms (Picheral et al., 2017) by applying simple machine learning techniques to predict taxonomic categories 780 781 from image parameters. ZooProcess automatically provides size-related 782 parameters of each object, and in combination with the taxonomic classification 783 allows for estimating the zooplankton biomass from preserved net samples 784 (Cornils et al., 2022) from the ice-ocean interface to the deep ocean (max. 2000 785 m).

786 To study the occurrence of squid and fish in the CAO (Snoeijs-Leijonmalm et 787 al., 2022), a continuously recording deep-sea video system (FishCam, MacArtney 788 Germany GmbH, Kiel, Germany) was deployed at 200-400 m water depth. Part of 789 the videos (180 hrs) were studied in real-time mode (Snoeijs-Leijonmalm et al., 790 2022) while an automated procedure for identifying periods of interest (i.e., 791 appearance of large organisms) in the extensive remainder of the video material 792 is currently being developed. The combination of visual techniques, machine 793 learning, and discrete sampling of animals and particulate matter can work 794 together to address long-standing questions on the distributions and controls on 795 these ecosystem components, where few such data are available.

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798 2.5.2. Biomarkers and carbon transformations

799 Biomarkers are molecules (e.g., fatty acids, amino acids, sterols) or isotopic 800 compositions of elements (e.g., carbon) that are somewhat source-specific to 801 primary producers and are incorporated mostly unchanged into the tissue of their 802 consumers. Tracing these biomarkers within the zooplankton and fish community 803 is an essential tool in food web studies that address the relative importance of 804 different sources of organic matter, the role of key Arctic primary producers, and 805 the nutritional status of higher trophic levels (Kohlbach et al., 2022; Kunisch EH 806 et al., 2021; Leu et al., 2020). Compared to previous studies, trophic marker 807 analyses of the MOSAiC samples are improvements in two major aspects. First, 808 a very broad range of trophic markers is being explored including fatty acids. 809 sterols, highly-branched isoprenoids, bulk stable isotope compositions, fatty acidspecific stable isotope compositions, and essential amino acid specific stable 810 811 isotope compositions (eAA-SIA) to balance the strengths and shortcomings of the 812 individual approaches. Second, all the different trophic markers are measured 813 from the same parent samples of homogenized animal tissue to allow a direct 814 comparison of the results and to link the nutritional status of the animals to their 815 food resources. Alongside the trophic marker approaches, animals were also 816 collected for DNA sequencing of gut content. This approach provides a high 817 taxonomic resolution of the ingested species and will further support the 818 interpretation of the trophic marker data (Cleary, 2015).

One key guestion for studying Arctic marine food webs is to elucidate the role 819 820 of ice algae as a source of organic matter. Trophic biomarkers determined across 821 the food web including the particulate organic matter in surface waters and ice 822 cores, as well as zooplankton, will help to identify seasonally varying food web 823 interactions from primary producers to individual zooplankton species. These 824 food web interactions will be linked to primary and bacterial production rates as 825 well as vertical flux studies to enable more complete insights into the Arctic 826 biological system.

827

828 2.5.3. Ecological modeling

829 A variety of bioinformatic and statistical modeling techniques aim at elucidating 830 changes in composition and metabolic potential of Arctic marine microbial 831 communities to improve our understanding of their influence on global 832 biogeochemical cycles. The mechanistic understanding of ecological patterns is 833 initially based on information from gene sequences combined with a descriptive 834 approach of community members using co-occurrence networks that illustrate the 835 occurrence of species at the same place and time (Popa et al., 2020). This graph 836 approach, in which nodes are species and edges represent the correlation 837 strength of their seasonality patterns, enables identification of i) central species (node hubs) and ii) species communities (network clusters) that are defined by 838 839 several populations which are abundant in the same time period (Berry and Widder, 2014). The outcome of such studies allows us to investigate the 840 841 seasonality of microbial community composition, activities, and functions. Further, 842 it enables the identification and definition of yet unknown ecological processes. 843 These processes include the interaction of present species with each other and 844 the environment. To understand this interaction in detail and especially to identify 845 key parameters with strong impact on the Arctic ecology, it is necessary to 846 combine all measured data into a modeling framework (Faust and Raes, 2012). 847 For example, the co-occurrence information of photoautotrophic species with 848 grazers isolated from the ice and water column combined with environmental parameters like water depth, temperature, daylight, etc., can be modeled using a 849 850 Lotka-Volterra (LV) framework (Lotka, 1920; Volterra, 1927) with seasonal forcing 851 approach (Sauve et al., 2020; Vandermeer, 1996). As a result, these models can 852 be used to test several species interaction scenarios after varying the 853 environmental parameters (Succurro and Ebenhöh, 2018). Furthermore, 854 extending the LV by the dynamics of the available resources within the 855 ecosystem (MacArthur consumer-resource models; Goldford et al., 2018; 856 MacArthur, 1970) permits the development of a powerful, theoretical tool to 857 explain the formation and occupation of ecological niches in dependence on 858 external parameters with predictive capabilities for several future scenarios. 859 Microbial community structure and metabolic potential data are also being 860 leveraged for biogeochemical predictions using machine learning. These 861 techniques are well suited to complex, high dimensional, community structure 862 data and can be used to extract patterns of succession and biogeochemical 863 signatures from sequence information (Bowman, 2021). For example, the Random Forest (RF) regression model is effective at predicting biogeochemical 864 865 signatures from amplicon sequence data, providing the potential for extending the data coverage of less frequently sampled key biogeochemical variables (Dutta et 866 867 al., 2022). Additionally, potential microbial drivers for these processes can be 868 identified by applying permutation to the RF models to assess the contributions of 869 specific community members to model performance (DiMucci et al., 2018). Self-870 organizing maps (SOMs) are used to partition the microbial community into functionally distinct modes that can be applied as discrete variables in a variety of 871 872 statistical (Bowman et al., 2017) and mechanistic (Kim et al., 2022) models. This 873 discrete variable reflects key genetic traits of the microbial community, provides 874 reasonable estimates of physiology, and allows for correlation between variability 875 in taxonomic structure and function. Eco-physiological information can then be 876 used to modify and better parameterize data-assimilative marine biogeochemical 877 models for hypothesis testing and *in silico* experimentation – such as quantifying 878 previously identified questions regarding microbial controls on ecological 879 processes and assessing the sensitivity of carbon flow through the microbial food 880 web to climate change scenarios.

881 882

883 **3. RESULTS**

884 The MOSAiC Ecosystem work program generated > 50,000 unique samples and 885 activity measurements characterizing organisms and processes from viruses to fish. 886 We sampled 195 CTD rosette casts, 44 multi-nets, and 21 FYI and 20 SYI common 887 ice coring events. We also collected samples from > 40 time points and sites during 888 events and IOPs covering a complete Arctic seasonal cycle. A majority of sampling 889 events were co-located in time and space or spanned long periods of continuous 890 measurement and/or sample collection (Figure 6). Vertical distributions of most 891 properties in the upper 400 m of the water column were resolved over the drift, but, 892 when possible, also full water column depth profiles of core properties at once-893 weekly intervals were collected (Figures 7). The resolution of the year-long 894 observations to map essential ecosystem properties differed depending on 895 complexity of sampling and needed volumes, e.g. nutrient sampling could be 896 executed more frequently and with greater vertical resolution (Figures 7A, B) than 897 Chl-a (Figures 7C, D) and total DNA sampling (Figures 7E, F).

898

899 3.1. Environmental controls over the drift period

900 The MOSAiC expedition provided a wealth of environmental observations from ice. 901 ocean, and atmosphere. These data provide a critical context to interpret the 902 biological observations during the drift period. An evaluation of the meteorological 903 conditions during the MOSAiC drift indicates that unusually cold temperatures 904 relative to decades-long climatology occurred in November 2019 and March 2020 905 (Rinke et al., 2021). Additionally, Rinke et al. (2021) also identified that the 2019-906 2020 drift year had more frequent storm events in spring, and that summer had a 907 longer sea ice melt season, from late May to early September, approximately a 908 month longer than the median from 1979 - 2019. Also, relative to climatology, the 909 July and August 2020 period was the all-time warmest.

910 Throughout winter, RV Polarstern drifted in northerly directions, with the 911 northernmost location at 88.6°N reached at the end of February 2020. Throughout 912 spring and summer, the floe drifted in southerly directions, with periods of faster 913 (mid-March to mid-April) and slower (mid-April to mid-July) drift speeds. The annual 914 changes in air and water temperature, surface ocean salinity, incoming PAR 915 (photosynthetically active radiation), and surface ocean nutrient concentrations along 916 the drift track are illustrated in Figure 9. These properties are relevant examples of 917 environmental changes over the annual cycle, which potentially influence ecosystem 918 processes. Air temperatures at 2 m (Figure 9B) varied between values as low as -919 40°C in March and up to 6°C during the summer months (Cox et al., 2023; Shupe et 920 al., 2022), driving sea ice freeze-up and melt (Nicolaus et al., 2022b; Evgenii 921 Salganik et al., 2023a). Upper water column (10 m depth) temperatures (Figure 9C) 922 were much less variable, with average daily temperatures near the freezing point 923 during most of the year. Except for the transit periods, maximal temperatures of 924 about -1.3°C were reached at the end of July. Surface ocean salinity (Figure 9C) 925 reflected drift location (Rabe et al., 2022; Schulz et al., 2023b), with rather low levels 926 during drift in the TPD in winter 2019/20. In February and March, TPD influence was 927 gradually replaced by an increasing contribution of more saline Atlantic-influenced 928 waters. After crossing the Gakkel Ridge in late March, average daily surface salinity 929 remained high until reaching the ice edge in Fram Strait with stronger influence of

930 lower salinity waters from the polar waters of the East Greenland Current during July931 2020 (Schulz et al., 2023b).

Solar incoming irradiance (Figure 9D), shown as PAR, at the surface of the sea ice decreased quickly in fall and was below the detection limit from 8th of October until March 13th, marking the period of the polar night. Surface PAR increased as the solar elevation increased, and reached maximal values of >1300 μ mol photons m⁻² s⁻¹ from May to July (note the data gap between mid-July and mid-August). Thereafter, PAR decreased again, with daily maximum values below 200 μ mol photons m⁻² s⁻¹ at the end of the drift.

939 Nutrient concentrations in surface waters (upper 30 m) varied with water 940 masses and through the seasons as the floe drifted (Figure 9E). As the floe drifted 941 northwards, silicic acid and phosphate concentrations increased from November to January, from 1.5 to 4.7 µmol kg⁻¹ and 0.19 to 0.52 µmol kg⁻¹, respectively. Nitrate 942 943 remained mostly constant until February at 1.05±0.37 µmol kg⁻¹. Silicic acid was 944 nearly constant until early February, but phosphate concentrations dropped to 0.35 µmol kg⁻¹ after early January. Trends diverged further thereafter as the drifted further 945 946 southward, with nitrate and phosphate increasing to 4.7 and 0.42 µmol kg⁻¹, 947 respectively, in May, but with silicic acid decreasing to 2.5 µmol kg⁻¹. These opposing 948 trends for the different nutrients likely reflect characteristics of the different water 949 masses as distinguished using the temperature and salinity observations, with 950 increasing influence of Atlantic waters containing relatively more nitrate and 951 phosphate, and less silicic acid. When sampling at the floe resumed in the second 952 half of June, maximum sea water nitrate, silicic acid, and phosphate concentrations 953 of 6.0, 7.5, and 0.66 µmol kg⁻¹, respectively, were measured. Towards the end of 954 August though, as the drift continued southwestward, nitrate levels quickly 955 decreased to <0.5 μ mol kg⁻¹, but phosphate (~0.58 μ mol kg⁻¹) and silicic acid (7.8 956 µmol kg⁻¹) remained comparably high. This is consistent with polar waters of the East 957 Greenland Current in Fram Strait, with more influence of silicic acid rich Pacific-958 derived waters and/or the Transpolar Drift. Thereafter, nutrient concentrations were 959 variable between $\sim 0.5 - 2 \mu mol kg^{-1}$ nitrate, 1-9 $\mu mol kg^{-1}$ silicic acid, and 0.2-0.7 µmol kg⁻¹ phosphate over the summer and fall, as RV *Polarstern* repositioned on a 960 961 new floe close to the North Pole.

962

963 3.2. Observed organisms and biodiversity

964 Despite the extreme seasonal variations in irradiance and other environmental 965 drivers (Figure 9), the same functional and taxonomic groups (flagellates, 966 dinoflagellates, and diatoms) were the major contributors to the sea ice protist assemblages in the different seasons (Figure 10), although there were seasonal 967 968 changes in their relative and absolute abundances. Ongoing analyses based on 969 taxonomic counts via light microscopy, cell abundances via flow cytometry, 18S-970 metabarcoding, and metagenomics (e.g., metagenome-assembled genomes of 971 protists) (Table S2) will elucidate seasonal trends in ice and water column protists in unprecedented detail. Interestingly, the same groups and genera (e.g., 972 973 Gymnodinium spp., Pseudo-nitzschia spp., unidentified flagellates) contributed

- 974 significantly to the protist communities in both habitats over the fully annual cycle
- 975 despite strong variations in environmental conditions (Figure 9). Importantly,
- 976 significant contributions of both in-ice microalgae (e.g., *Nitzschia frigida*) as well as
 977 under-ice-attached microalgae such as *Melosira arctica* to the protist assemblages
 978 were observed. The latter species was so abundant in certain under-ice habitats that
 979 it formed its own microhabitat, which team ECO sampled in more detail.
- A diverse and abundant zooplankton community (Figure 11) was observed over the entire MOSAiC campaign. Ongoing analyses focus on the interplay between seasonal (Figure 9) as well as regional patterns to decipher their seasonally resolved biogeography. The different methods employed to assess fish (Table S2) show that their stocks in the Central Arctic Ocean were very low. Still, Atlantic cod was found unexpectedly as far north as 85.9°N, along with lanternfish, armhook squid, and the Arctic endemic polar cod *Boreogadus saida* (Snoeijs-Leijonmalm et al., 2022).
- 987 Consequences of different community structures for food web dynamics and 988 biogeochemistry are being addressed at each trophic level by different methods along the drift track and over the annual cycle. Initial analyses indicate active fecal 989 990 pellet production and sinking in both winter and summer season (Figure 12). 991 Analyses of carbon, nitrogen, algal pigments, and material types from sinking 992 particulate organic matter collected in short-term and long-term sediment traps will 993 enable estimates of time-integrated fluxes of material over specific periods of the 994 winter and summer seasons below level- and ridged sea ice, and from along the drift 995 track at 200 m depth. Additionally, ongoing analyses of particle size spectra from the 996 LISST and UVP will allow higher resolution estimates of POM fluxes. Profiles from 997 the UVP also generated images of particles > 100 micron in size and based on 998 machine learning techniques, these images can be cataloged into particle-specific 999 types, further informing changes in particle size abundances and distributions along 1000 the drift.
- 1001

1002 3.3. Potential impacts of diverse and ephemeral habitats on ecosystem processes 1003 Consistent with previous research, our initial observations suggest that the presence 1004 of meltwater layers represents a drastic change in the environmental and chemical 1005 nature of the upper ocean, and elicit changes in biological properties and activities 1006 (Smith et al., 2022). Stratification in the upper 1-2 m of the ocean creates a strong 1007 gradient and boundaries which most organisms are unable to cross, thus creating 1008 small microhabitats within each of these layers. These adjacent layers may support 1009 potentially disparate activity rates, standing stocks, and biogeochemical fluxes 1010 despite their close spatial relation. As such, meltwater layers may introduce habitat 1011 structuring which greatly impacts ecosystem functioning. Furthermore, meltwater 1012 layer formation affects the gas exchange process with the atmosphere, such that a 1013 meltwater layer at the surface may lead to the equilibrium of gases with the 1014 atmosphere, thereby reducing the gradient of concentration with the atmosphere and 1015 the flux (Smith et al., 2023; von Appen et al., 2021). The mixing of meltwater and the 1016 underlying seawater during summertime potentially produces water with low CO₂ 1017 concentration.

1018 Based on opportunistic sampling, we could observe ecosystem processes in 1019 various other sea ice types, resulting from different formation processes (Figure 13). 1020 Summer season sampling in leads (Figure 13 A, B) and water close to the bottom of 1021 the ice provided further insight into how ice dynamics and ephemeral phenomena 1022 may alter biological responses over time-scales missed by our regular weekly 1023 sampling. It indicated the formation of extremely high biomass layers on the 1024 boundary between meltwater and seawater, with distinct composition and 1025 biogeochemical characteristics (Smith et al., 2023).New ice formations, typically 1026 ranging from 1 to 10 cm in thickness, and from loosely-formed crystals to 1027 consolidated nilas ice, were sampled periodically throughout the drift, primarily from 1028 leads near or across the central floe (Figure 13 C, D), with preliminary data indicating 1029 higher organismal abundances and Chl-a concentrations than the surrounding 1030 seawater (data not shown). Our series of samples of newly formed ice at different 1031 time periods over the annual cycle will provide us with complementary data on how 1032 environmental conditions (Figure 9) influence biological and ecological processes 1033 during initial thermodynamic ice formation. Sea-ice ridges (Figure 13 G, H) were also 1034 sampled periodically for biological properties and vertical export of material during 1035 MOSAiC. This habitat featured seawater-filled voids with an accumulation and high 1036 activity of microbial biota (see 3.5.1. for details).

1037

1038 3.4. Gaps in time-series measurements

1039 Overall, the MOSAiC ecological field program captured a large number of co-located 1040 properties at a regular frequency. However, with differing competencies across each 1041 field team, and despite efforts to cross-train and build redundancy in skill sets, there 1042 are some gaps in the ecosystem time-series measurements. While risk assessments 1043 and prioritization schemes were devised, execution in the field was determined by 1044 what could be achieved by the field team, and different factors at different times 1045 contributed to variations in the continuity of specific data sets. Here, we outline the 1046 key gaps in measurements, so that future users of MOSAiC ECO data sets can 1047 easily identify when in the annual cycle certain measurements are not available. 1048 Activity rate measurements, such as primary and bacterial production, only began in 1049 January and late December 2019, respectively. Samples for water column DOM 1050 characterization after solid-phase extraction are only available from April, May, August and September 2020. ¹⁵N-nitrate isotopes from sea ice were collected from 1051 1052 December 2019 onwards. RNA samples from bottom portions of sea ice are only 1053 available from April 2020 onwards. There were no daily discrete sample collections 1054 for Chl-a and microbial community structure from December 2019 to end of February 1055 2020. Likewise, MIMS data from December 2019 to the beginning of March 2020 is 1056 of substantially lower reliability compared to the rest of the drift.

1058 **3.5.** Case Studies

1057

1059 In the following, two selected case studies are presented to illustrate the kinds of 1060 results the ECO team is working on to address specific scientific questions. These 1061 examples have been chosen because they demonstrate the interdisciplinary connections within MOSAiC, specifically regarding the role the geophysical
restructuring of ice had on habitat and with respect to how biological processes
contributed to elemental transformations and influenced central Arctic
biogeochemistry.

1066

1067 3.5.1. Pressure ridges, unique habitats for ice-associated biota? 1068 Level, undeformed sea ice provides a wide range of niches for ice-related 1069 organisms, ranging from biota living in the brine channel systems within the ice to 1070 under-ice flora and fauna living at the ice-water interface (Lund-Hansen et al., 2020). 1071 These level sea-ice systems are studied in detail using the ICE and ECO time-series 1072 (see also Nicolaus et al., 2022b). However, deformed sea ice in pressure ridges 1073 adds substantial three-dimensional diversity in the available habitat space through 1074 macroporosity (voids filled with seawater between ice blocks, often referred to as 1075 rubble) in the ridge keels (Fig. 14). Ridge keels in the Arctic can reach substantial ice 1076 drafts exceeding 20 m keel depth (Wadhams and Toberg, 2012), making ridge coring or observations of voids within ridges exceptionally challenging. Sporadic 1077 1078 observations from previous Arctic studies suggested unique biological hotspots 1079 associated with the water filled voids in unconsolidated keel rubble and ice block 1080 surfaces within the pressure ridges (Fernández-Méndez et al., 2018; Gradinger et 1081 al., 2010; Syvertsen, 1991). Truly understanding the ecological processes 1082 associated to pressure ridges was the core of one dedicated research project (Safe 1083 HAVens for ice-associated flora and fauna in a seasonally ice-covered Arctic Ocean 1084 (HAVOC)), that across several MOSAiC teams performed detailed and 1085 interdisciplinary observations of ridges (Figure 14) in the MOSAiC Central 1086 Observatories (CO1 and CO2), with the aim to study the year-round physical and 1087 biological characteristics of sea ice ridges.

1088 Relocations of Polarstern and sea-ice deformation events in the CO caused 1089 disruptions in the time-series, resulting in four different pressure ridge sites being 1090 studied during December 2019 and August 2020, with most HAVOC data being 1091 collected between January and July 2020. Sampling included ice drilling, coring, and 1092 ridge ice and void water sampling to study the temporal evolution of physical 1093 characteristics of pressure ridges such as consolidation and melting (Lange et al., 1094 2023; E. Salganik et al., 2023; Evgenii Salganik et al., 2023b). Further, the ridges 1095 were studied as habitats by examining the relationship between ridge structure and 1096 biological properties (e.g., algal and microbial diversity in ice and void water), under-1097 ice hyperspectral imaging of algal biomass distribution along the pressure ridge 1098 keels (Figure 15), and vertical particle flux in the proximity of the ridges using 1099 sediment traps. The essential comparative measurements of level first-year and 1100 second-year sea ice properties were provided by the ICE and ECO time-series data. 1101 Ongoing interdisciplinary discussions within the HAVOC team already showcased 1102 significant science gains.

Ridge consolidation: Freeze and melt cycles within ridge rubble are more
 complex than for level sea ice and significantly impact biological habitat
 diversity and availability. For example, refreezing of snow-slush transported to

ridge keel during dynamic event in early spring and surface meltwater in
summer led to rapid ridge consolidation with implications on the structure and
functioning of the microbial community and habitat loss for larger fauna in
ridge keels (Salganik et al., 2023ab, Lange et al., 2023).

- Hyperspectral imaging of the bottom of level and ridged sea ice indicates higher fractions of ice surfaces inhabited by algae in the ridged ice (Figure 16). For this purpose, a new Relative ice algal Biomass Index (RBI) was developed (Lange et al., submitted).
- Ice surfaces and water-filled voids within ridges contained distinct microalgal
 and bacterial communities in contrast to level sea ice and seawater.
- Changes in ice structure due to ridge formation, consolidation, and melting have consequences on biological processes reaching beyond the physical location of ridges, as frozen organic material can be released during ridge formation in winter, and melt water can accumulate under level ice next to ridges during summer, both affecting food availability and habitat for under-ice fauna and flora, respectively.
- A new sediment trap deployment methodology under the ridge revealed unique ice-associated particle dynamics and vertical flux measurements,
 Upcoming analyses will focus on comprehensive characterizations of ridge properties (e.g., using time-series data) and will be compared to those from level ice and under-ice seawater samples. This will help to assess how ridge biodiversity and ecosystem functioning are driven by this specific physical habitat (i.e. find answers to
- the who, how and why?). In addition to the knowledge gain, the field experience with
- sampling ridges provides an additional legacy product by HAVOC and MOSAiC
- 1130 through methodological recommendations for future ridge studies.
- 1131

1132 3.3.2. Effects of seasonally changing mesozooplankton grazing on carbon and

- 1133 nitrogen cycling in the central Arctic
- 1134 Mesozooplankton are important transformers of organic carbon (C) and nitrogen (N), 1135 converting phytoplankton and microzooplankton into larger-sized biomass (Figure 17). Mesozooplankton feeding activity and fecal pellet production regulates the 1136 1137 retention of organic C and N in the upper ocean mixed layer versus their transfer to 1138 deeper waters. The Arctic mesozooplankton community is often dominated by 1139 copepods of the genus Calanus, including two high-Arctic species (C. hyperboreus 1140 and C. glacialis) as well as the advected North Atlantic indicator species C. 1141 finmarchicus (Ershova et al., 2021). These species' life cycles differ in their adaptations to Arctic seasonality. Until MOSAiC, there had been no year-round direct 1142 1143 measurements of Calanus-related food web dynamics in the Central Arctic. This is a 1144 complex and challenging task, as evaluating the importance of mesozooplankton-1145 mediated transformations and fluxes requires quantification both of standing stocks 1146 and of rate processes as well as understanding of zooplankton diet in relation to food abundance. It was achievable within the MOSAiC framework only through the tight 1147 1148 collaboration of several science teams providing time series data of ocean and sea

1149 ice physical properties, food availability (microalgae and microzooplankton 1150 abundances and standing stocks), as well as guantification of mesozooplankton 1151 standing stocks and distributions. These time series data provide the necessary context for a research project (Collaborative Research: The role of planktonic lower 1152 1153 trophic levels in carbon and nitrogen transformations in the Central Arctic, a MOSAiC 1154 proposal) focused on direct measurements of the transformations of C and N by the 1155 zooplankton using rate process measurements. The key overarching questions are: 1156 How closely aligned are the life histories and productivity cycles of the 1157 dominant secondary producers to the ice algal and/or phytoplankton blooms? 1158 • What are the transformations that occur (e.g., respiration, feeding, 1159 growth/reproduction, fecal pellet export) and how do these vary throughout 1160 the year? 1161 How do food webs change seasonally? What is the importance of ice vs. • 1162 water column production to spring zooplankton productivity and how important is the microbial food web during summer to growth and overwintering survival 1163 1164 of mesozooplankton? 1165 To answer these questions, project members participated in the MOSAiC cruise from December 2019 to October 2020, with supportive measurements 1166 1167 provided by Team ECO before that period. The experimental studies included 1168 measurements of respiration, egg production timing and rates, egg hatching success 1169 of two dominant copepods (C. glacialis and C. hyperboreus), and grazing rates on 1170 both phytoplankton and microzooplankton of dominant copepods (C. glacialis, C. 1171 hyperboreus, Metridia longa). These experiments were augmented by DNA gut 1172 content analyses. In spring and early summer, when the ice floe had drifted across 1173 the Gakkel Ridge into the more Atlantic-influenced Nansen Basin, the Atlantic 1174 indicator species C. finmarchicus also was included. Individual copepods were 1175 photographed for identification and used for determination of carbon and nitrogen 1176 content, and trophic marker characteristics. 1177 The final detailed analyses of the data sets will relate the experimental rate measurements to their distribution as estimated from nets and the LOKI, prev type 1178 1179 and food concentrations will be augmented by gut DNA contents. The outcomes of 1180 will provide critical data to all three ECO science questions ('who', 'how', and 'why'), 1181 help determine the C and N flow through the planktonic ecosystem (Figure 17) 1182 during different seasons over the course of the drift (Figure 9), and provide critical 1183 information for integrative ecosystem modeling during the ECO synthesis phase. 1184 1185 1186 4. STATUS, LINKAGES, PERSPECTIVES, AND SCIENTIFIC IMPACTS 1187 1188 4.1. Current status and major achievements 1189 MOSAIC ECO sample and data analyses are still ongoing, and new and exciting 1190 data and scientific findings will continue to emerge over the next decade.

1191 Nevertheless, some major achievements can already be identified, some of which

1192 will lead to a step-change in understanding of the 'whos, hows, and whys' of the high 1193 Arctic ecosystem: 1194 The largest number of samples to assess biodiversity ever collected at such a high spatiotemporal resolution in the central Arctic Ocean will allow for a 1195 comprehensive ecosystem description from viruses to fish and squid for all 1196 1197 seasons along the drift. 1198 • Unprecedentedly high winter standing stocks and activity levels of organisms 1199 in the largely unstudied high Arctic polar night were observed. • The biological property measurements in a diverse range of seasonally-1200 1201 occurring habitats were conducted, including in-depth characterizations of 1202 biological hotspots (e.g., pressure ridges, meltwater layers). 1203 Rate measurements for key biological processes (e.g., primary and bacterial • production, zooplankton grazing and respiration rates) throughout all seasons 1204 1205 provide a crucial foundation for the parameterization of biogeochemical 1206 models over complete annual cycles. 1207 • The largest sequencing effort for polar ecosystems will provide a benchmark 1208 for biodiversity change (Mock et al., 2022). 1209 Cross-cutting analysis have revealed that Central Arctic biological processes 1210 can affect the atmospheric composition during the melt season (Yue et al., 1211 2023) and have the potential to impact cloud processes (Creamean et al., 1212 2022). 1213 MOSAiC ECO supported a large and diverse suite of projects covering either • 1214 a particular season or environment, or a full year, which will enable us to 1215 obtain a wealth of knowledge on specific aspects of species biology and 1216 ecology, and a better understanding of seasonal changes in these aspects. 1217 1218 The co-located, in-depth characterization of environmental conditions driven by the 1219 interdisciplinary character of MOSAiC allows to link biological observations to abiotic 1220 driving factors (e.g., for fast transition periods that are hard to predict in terms of 1221 timing), and in turn to determine when biological interactions are likely the main 1222 driving force of ecosystem dynamics (Behrenfeld, 2010). As one example, nutrients, 1223 representing one major controlling factor of Arctic productivity (Randelhoff et al., 1224 2020; Tremblay et al., 2015), indicate strong spatial differences across water masses 1225 along the drift (Schulz et al., 2023b) that dominate variability due to potential signals 1226 of seasonal uptake and limitation dynamics. The presence of surface ocean nitrate 1227 concentrations around 2 µM at the end of summer and into fall at >84 °N warrant 1228 close inspection concerning the dynamics supplying nutrients to the sunlit layers, 1229 potentially indicating iron limitation of primary production in Nansen Basin 1230 (Rijkenberg et al., 2018). This could lead to a paradigm shift in our understanding of 1231 Arctic primary production (Ardyna and Arrigo, 2020; Tremblay et al., 2015; 1232 Wassmann and Reigstad, 2011). The large imprint that water masses had on 1233 important environmental drivers such as nutrient concentrations illustrate that many 1234 statements about the Arctic cannot be generalized but need to be region-specific.

1235 The interdisciplinary approach of MOSAiC will also allow us to better 1236 parameterize and map cross-disciplinary linkages that may not be obvious a-priori. 1237 For example, sea ice algae might change the energy absorption of ice and ocean 1238 (Manizza et al., 2013), thereby affecting Arctic heat budgets along the atmosphere-1239 ice-ocean continuum (Shupe et al., 2022). New tools such as hyperspectral imagers 1240 deployed on remotely operated vehicles (see case study 1) may enable 1241 comprehensive mapping of ice algae potentially facilitating improved guantitative 1242 evaluation of biological effects on ice transmission and heat budgets.

Comprehensive studies of a number of periodically-occurring habitats found 1243 1244 them to be biological hotspots, including meltwater-influenced systems and pressure 1245 ridges. Unique habitat-specific processes may provide major additions to fluxes of 1246 energy and matter; thus, their quantification is needed for a complete view on high 1247 Arctic biogeochemistry and ecology. Our data will allow us to evaluate the relative 1248 role of these short-lived hotspot habitats compared to the perennial habitats, such as 1249 level sea ice. Several of these habitats develop during the summer season (e.g., 1250 melt ponds, meltwater layers, unconsolidated water-filled voids in pressure ridges), 1251 but later in the year may have residual structuring of habitats, which affect 1252 organismal life strategies during different periods of the annual cycle. While these features primarily form during the summertime, their altered states can persist into 1253 1254 later seasons and even the following year. For example, remnants or "fingerprints" of 1255 these hotspots may be identifiable, such as refrozen melt ponds or refrozen 1256 (consolidated) voids in ridges, and characterized during the winter season as 1257 overwintering habitats for a range of Arctic organisms.

1258

1259 4.2. Challenges and Lessons Learned

1260 MOSAiC observations and samples were conducted year-round, often in challenging 1261 conditions. This required frequently adapting standard ship and on-ice operations 1262 and team operations as well as adjusting the science objectives. Given the major 1263 focus of MOSAiC on interactions between atmosphere, sea ice, and ocean, we 1264 intentionally limited our work program to focus on the ecological and biogeochemical 1265 components that are relevant for the sea ice and upper ocean, excluding the deepest 1266 water layers and the benthos. Additionally, in an effort to focus on measurements that would elucidate biological feedbacks in the Arctic climate system, we did not 1267 1268 include observations of megafauna, such as sea birds and mammals, although they 1269 provide important ecosystem services and are highly impacted by climate change 1270 (Hamilton et al., 2022).

1271 Some unique challenges we addressed in the preparation phase were related 1272 to potential impacts of the anticipated long-term drift on the scientific data collection. 1273 Key adaptations were made in conjunction with other science teams and the ship's 1274 crew (see section 2.4 for details). Additionally, during the preparation phase, we took 1275 steps to train and prepare field personnel to execute a variety of tasks and protocols 1276 encompassing a broader range of activities than they would have been responsible 1277 for within an expedition of narrower scope than MOSAiC. Building competencies and 1278 redundancies in the skill sets of field personnel was important to realizing the diverse 1279 work program. However, it was not always possible, and in some instances gaps in 1280 our time-series measurements exist because it was not feasible for the field team to 1281 accomplish all the tasks (see Section 3.4). Additional modifications were necessary onboard based on expected irregular disturbances (e.g., storms, ice break-up) as 1282 1283 well as unexpected events (e.g., the COVID-19 outbreak). In the future, improved 1284 prioritization of sample collections, development of more semi-automated sampling 1285 and processing devices, and increased training on unfamiliar data logging routines 1286 will strengthen execution of complex work programs. Our experience with MOSAiC 1287 ECO work will also provide us with the opportunity to better determine which suites 1288 of properties are most needed for addressing future questions and objectives related 1289 to high Arctic ecosystem changes.

1290 Our data analyses will need to disentangle temporal versus spatial aspects to 1291 observed changes in biological properties and ecological processes over the course 1292 of the drift. This can be nicely illustrated by the development of nitrate concentrations 1293 over the course of the expedition (Figure 9E). Even though nitrate is considered one 1294 of the two major limiting factors for Arctic primary production (Tremblay et al., 2015), 1295 its concentrations increased over the main microalgal growing season, i.e., from 1296 March to July. While this seems counterintuitive at first, it can be explained by the 1297 drift of the ice floe into areas with increasingly larger influence by nitrate-rich Atlantic 1298 water masses (Rabe et al., 2022; Schulz et al., 2023b). Such water mass effects 1299 also influence other measured parameters such as DOM characteristics (Gonçalves-1300 Araujo et al., 2016, Kong et al., under review), and potentially the presence or 1301 absence of certain organismal groups and species (Kaiser et al., 2022). Also, the 1302 faster-than-expected drift speed of the main MOSAiC floe resulted in earlier arrival 1303 into Atlantic inflow-influenced waters and proximity to the ice edge, resulting in 1304 significant deformation and instability of the first Central Observatory. Therefore, 1305 after the logistical departure in May 2020, the ice camp had to be relocated to a 1306 different part of the original ice floe and a second Central Observatory was 1307 established. While these aspects are part of the nature of a drift campaign, their influence on how one can interpret our observations is central to our understanding 1308 1309 of ecosystem processes during the MOSAiC field year.

1310

1311 4.3. Ecosystem research in the context of Arctic System Science

1312 MOSAiC was designed to improve our understanding of the governing principles of 1313 the Arctic climate system and thus can be used in an earth system science 1314 approach. This is particularly urgent as the Arctic is warming four times faster than 1315 the global average (Rantanen et al., 2022). Developing baseline knowledge on the 'who', 'how', and 'why' of the high Arctic was the foundational principle of the 1316 1317 ecosystem science program, and the data already demonstrate multiple connections 1318 within the ecosystem compartments and to the whole Arctic system including the 1319 presence of INPs of marine biological origin (Creamean et al., 2022). The Arctic 1320 Ocean can be both a source and sink for greenhouse gases, like CO₂ and methane. 1321 Annual cycles of fluxes of such substances are currently being investigated in 1322 relation to bacterial biodiversity, algal activity, and respiration. For instance, it is

1323 expected that a combination of the broad scope of information from several MOSAiC 1324 science teams will help resolve the "ocean methane paradox" explaining periodically 1325 enhanced CH₄ concentrations in ocean surface waters (Rees et al., 2022). Great 1326 uncertainty exists regarding the future role of the Arctic Ocean as a source or sink for 1327 CO₂, where melting of sea ice combined with increased productivity could regionally 1328 lead to an intensified sink (Rees et al., 2022), while other Arctic areas might 1329 experience a reduction of carbon fixation and export due to increased sea ice meltinduced stratification (von Appen et al., 2021). Other processes which can potentially 1330 lead to CO₂ outgassing by the Arctic Ocean include decreased solubility driven by 1331 1332 warmer temperatures, equilibration with the atmosphere (Cai et al., 2010; Else et al., 1333 2013), or wind-driven mixing of surface waters with more carbon-rich subsurface 1334 layers (Lannuzel et al., 2020). MOSAiC ECO data will fill important regional and pan-1335 Arctic knowledge gaps in our understanding and may help to determine those 1336 mechanisms that will drive the effects of climate change on the Arctic carbon cycle. 1337 A set of different ecosystem and fully coupled Arctic Ocean models will be 1338 essential tools for integrating information across the ecosystem and the entire Arctic 1339 system using MOSAiC data, targeting not only specific questions like carbon cycling 1340 in the Arctic or production of climate relevant greenhouse gases, but also 1341 transferring these process-focused knowledge gains into products to understand 1342 climate change on larger regional and temporal scales. The unprecedented increase 1343 in knowledge on biodiversity and gene expressions in relation to environmental 1344 variables (Mock et al., 2022) will allow for the application of models to elucidate 1345 metabolic and energetic fluxes within the Arctic microbial consortia (Succurro and 1346 Ebenhöh, 2018). This combined application of different model types (e.g. see will be 1347 an important tool to differentiate the intertwined role of spatial and temporal

1348 variability in MOSAiC data sets.

1349

1350 **5. OUTLOOK**

The knowledge created by the ecological research during MOSAiC will provide a
lasting legacy for future studies focusing on the Arctic System. For the first time,
biodiversity and ecosystem functioning were studied on multiple trophic levels over a
full seasonal cycle using traditional and novel approaches.

The legacy of MOSAiC goes beyond publications, developing novel sampling 1355 1356 approaches and the openly accessible data archives. Indeed, the open and growing 1357 network of researchers across many nations and disciplines can be expected to 1358 have a lasting effect on Arctic marine research, particularly considering the high 1359 number of early career scientists that are already involved. New spin-off projects initiated through MOSAiC include projects on microbial processing and 1360 1361 biogeochemical modeling, remote sensing of under-ice blooms, sea ice-ecosystem 1362 modeling, and a yearround ecosystem study in an Arctic fjord. The gained 1363 knowledge will help to evaluate the importance of the Arctic for climate regulation. 1364 Although incomplete, several publications have demonstrated the broad range of 1365 currently known ecosystem services provided by the Arctic marine system to 1366 humans including regulation of greenhouse gases and biodiversity (Malinauskaite et 1367 al., 2019). MOSAiC-based knowledge will also support political decision-making 1368 processes through, e.g., Arctic Council initiatives on the management of Arctic 1369 marine ecosystems (e.g. PAME). Although MOSAiC ECO covers a very broad range of ecological topics and will fill many knowledge gaps, many research questions 1370 1371 remain unanswered or are now newly defined. The free, findable, accessible, 1372 interoperable, and reusable MOSAiC data will be a major milestone of success, 1373 providing together with the gained knowledge, the backbone for interdisciplinary 1374 marine Arctic research for decades to come.

1375 The broad range of realized measurements and samples from MOSAiC ECO 1376 will make it possible to move from the observed answers of the 'who' and 'how' to developing process-based mechanistic understanding of the 'why', also by means of 1377 1378 modeling approaches (see below). Mechanistic understanding in turn will allow 1379 moving beyond the specific locations and conditions during our observational period. 1380 The observation of high levels of biomass presence and organismal activity during 1381 the months-long cold and dark polar night, for example, provides the foundations for 1382 new investigations regarding overwintering mechanisms, strategies, and 1383 physiological adaptations. The combination of rate measurements, observations on 1384 different life stages, physiological and food web experimental work, as well as 1385 information originating from metagenomics and metatranscriptomics will allow an 1386 improved understanding the current overwintering mechanisms. Also, it will provide 1387 improve scenarios regarding the potential impacts of a future warmer Arctic with a reduced and changed ice cover, for example on effects on winter survival, annual 1388 1389 productivity, and biogeochemical cycles. Here, synergies between the ECO team 1390 and the BGC science with its focus on trace and greenhouse gases as well as 1391 cycling of sulfur, nitrogen and carbon will be essential. Entrainment of the detected 1392 processes and rates into ecosystem and biogeochemical models will also greatly 1393 improve the validity of such future scenario estimations. While a one-year field-1394 period cannot observe climate change trends directly, MOSAiC science is a step-1395 change in Arctic ecosystem understanding that will provide a baseline upon which future changes can be identified, while also providing the potential for improved 1396 1397 projections of future changes based on the advanced process-based interdisciplinary 1398 understanding.

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- 1400

1401 Data accessibility statement

- Drift track data for each MOSAiC leg is available via Pangaea (Haas, 2020; Kanzow,2020; Rex, 2021a, 2021b, 2020).
- 1404 Combined surface ocean temperature and salinity from different sensors as
- described in (Schulz et al., 2023b) is available via the Arctic Data Center (Schulz et al., 2023a),
- 1407 Air temperatures at 2 m over the MOSAiC floe are available at the Arctic Data Center1408 (Cox, 2023).
- 1409 Incoming PAR data was derived from radiation station measurements published at
- 1410 PANGAEA (Nicolaus et al., 2023b, 2023a, 2022a).
- 1411 Data publication of nutrient data is under way. Data is available upon request from
- 1412 Sinhué Torres-Valdes (sinhue.torres-valdes@awi.de). Other metadata shown is
- 1413 either available in the supplementary information or will be published together with
- 1414 the data once quality controlled, and are available from the authors upon request.
- 1415

1416 Author contributions

- 1417 Developed the concept and design: AAF and RRG with input from co-authors
- 1418 Conducted the field sampling: AAF, CJMH, CJA, YB, JPB, JB, DB, RGC, GC, EJC,
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Tables

Table 1. MOSAiC ecosystem core measurements. Catalog of biological and

2148 biogeochemical properties and processes measured during the MOSAiC expedition.

2149 Additional geochemical properties (i.e. gases) were measured by the MOSAiC

Biogeochemistry Team. Details can be found in the supplementary Table S2.

	Sampled	
ECO variable	environments	Method
Nutrients (nitrate+nitrite, ammonium,		
phosphate, silicic acid, dissolved organic	Water column, ice,	Colourimetric continuous
nitrogen, dissolved organic phosphorus)	special habitats	flow; AA3 (SEAL)
Dissolved oxygen (DO)	water column	Winkler titration
Carbonate chemistry: total alkalinity (TA)	water column, special	
and dissolved inorganic carbon DIC)	habitats	VINDTA
Carbonate chemistry: TA, DIC	ice, special habitats	Coulometry/ VINDTA
		TOC-VCPN, high
Dissolved organic carbon (DOC) and	water column, ice,	temperature catalytic
nitrogen (DON), concentrations	special habitats	combustion
Dissolved organic matter characterization	water column, special	Ultrahigh resolution mass
and chemometrics	habitats	spectrometry
	water column, ice,	
Particulate organic carbon and nitrogen	special habitats,	%C, %N, δ ¹³ C, δ ¹⁵ N; EA-
(POC and PON); stable isotopic	short- and longterm	IRMS (Flash 2000-Delta
composition and concentrations	sediment traps	V Plus, Thermo Scientific)
	water column, ice,	
	special habitats,	
	short- and longterm	
POC and PON, concentrations	sediment traps	Euro EA 3000, HEKAtech
		Photometrically after
Biogenic silica (bSi)	water column, ice,	NaOH digestion
Oceanic particle size spectra and		Optical - Underwater
distributions	Water column	Vision Profiler (UVP)
	water column, ice,	Fluorometric analyses of
Chlorophyll a (Chl-a)	special habitats	extractd samples
	water column, ice,	High Performance Liquid
Pigment biomarkers	special habitats	Chromatography (HPLC)
		Attune NxT
		(ThermoFisher) and Facs
Enumeration and diversity of prokaryotes,	water column, ice,	Calibur (Becton Dickson)
eukaryotic microbes and viruses	special habitats	flow cytometers (FCM)
	water column, ice,	
	special habitats,	
Diversity and abundance of protists	sediment traps	Inverse light microscopy
	water column, ice,	
Diversity of prokaryotes and eukaryotic	special habitats,	16S/18S rRNA amplicon
microbes	underway	sequencing (Illumina)

	water column, ice,	Illi una lus a
Metagenomes	special nabitats	Illumina
	water column, ice,	
Metatranscriptomes	special habitats	Illumina
	water column, ice,	
	special habitats,	
Primary productivity (NPP)	underway	¹⁴ C-based incubations
Net community production (NCP)	surface water	MIMS O ₂ /Ar
	water column, ice,	
	special habitats,	
Bacterial productivity (BP)	underway	3H-leucine incubations
		FRRF; FastOcean with
	water column, special	FastAct /Fastact2
PSII fluorescence-based photophysiology	habitats	(Chelsea Tech)
Mesozooplankton: abundance/distribution	water column	Microscopy, Zooscan
Small mesozooplanton:		
abundance/distribution	water column	Microscopy, Zooscan
Macrozooplankton:		
abundance/distribution	water column	Microscopy, Zooscan
Macrozooplankton: biomarkers	water column	diverse
Macrozooplankton: carbon & nitrogen	water column	Elemental analyser
Surface mesozooplankton: biomarkers	water column	diverse
Surface mesozooplankton: carbon &		
nitrogen	water column	Elemental analyser
Surface mesozooplankton: individual		
respiration	water column	optodes
Deep mesozooplankton: biomarkers	water column	diverse
Deep mesozooplankton: carbon &		
nitrogen	water column	Elemental analyser
Deep mesozooplankton: individual		
respiration	water column	optodes
Mesozooplankton: high vertical		
resolution distribution	water column	Microscopy, Zooscan
Under-ice fauna: abundance/distribution	ice	Microscopy
Grazing rates (microzooplankton &		
copepods)	water column	experiments
Egg production (copepods)	water column	experiments
Gut contents & DNA (fish, copepods,		
amphipods)	water column	Microscopy, scales, DNA
Energy content macrofauna	water column	oxygen calorimeter

- 2153 Figures
- 2154





Figure 1. MOSAiC expedition track. Passive periods of drift are shown in solidcolored lines, with each color-coded line delineating one of the MOSAiC legs. Dates are periods of each leg and dates shown in parentheses identify passive drift periods per leg. Dotted lines depict transit tracks of the ship initially and for repositioning after legs 3 and 4. The solid grey line approximates the location of the Gakkel Ridge between the Amundsen and Nansen Basins. The approximate sea ice edge at the

- annual maximum (Mar 5, 2020) and minimum (Sept 15, 2020) is also shown.
- 2163 Modified after (Shupe et al., 2020).
- 2164



2166 Figure 2. Ecosystem compartments and processes of the Central Arctic.

- 2167 Illustrated are the primary components and processes investigated by the ECO team
- 2168 during the MOSAiC (Multidisciplinary drifting Observatory for the Study of Arctic
- 2169 Climate) expedition.
- 2170



Figure 3. Main sampling locations and measurement sites of the first MOSAiCCentral Observatory

2174 in April 2020. Map background shows the airborne laser scanner (ALS) image from 2175 April 23, 2020 with grey areas indicating no data. White, brighter areas depict sea ice 2176 of greater elevation (i.e. ridge sails). Some site locations were approximate due to active ice dynamics. Sites labeled "old" were previously active sampling locations, 2177 2178 but were no longer accessible and maintained after the winter. The primary water column sampling locations during October 2019 and May 2020 were conducted at 2179 2180 RV Polarstern (black) and Ocean City (yellow square). Common ice coring sites are 2181 shown in purple and approximately 1 km from RV Polarstern. The map had been 2182 simplified to show main sampling and measurement positions for the ecosystem work program. Additional MOSAiC measurement sites from teams ATMO, ICE, and 2183 2184 OCEAN can be viewed in the respective MOSAiC Overviews by Nicolaus et al. (2022b), Rabe et al. (2022) and Shupe et al. (2022). 2185 2186



2188 Figure 4. Main sampling locations and measurement sites of the second

2189 **MOSAiC Central Observatory during summer 2020.** Primary water column

sampling was from RV *Polarstern* (light blue, lower righthand side). Ocean City did
 not have a CTD-rosette system. FYI coring site was an original portion of the FYI site

- 2192 established in Oct 2019. SYI coring site adjacent to FYI shown here was a reserve
- 2193 SYI site identified earlier, but was not actively sampled. Original SYI coring site is not
- 2194 depicted in this map as that part of the ice floe detached from the main floe. SYI
- coring in June and July 2020 occurred near Alli's ridge. ECO Lodge was established
- beyond the perimeter of the logistics area. The map had been simplified to show
- 2197 main sampling and measurement positions for the ecosystem work program.
- 2198 Additional MOSAiC measurement sites from teams ATMO, ICE, and OCEAN can be
- viewed in the respective MOSAiC Overviews by Nicolaus et al. (2022b), Rabe et al.
- 2200 (2022) and Shupe et al. (2022).
- 2201



2203 Figure 5. Main sampling locations and measurement sites of the third MOSAiC 2204 **Central Observatory during late summer 2020.** The background of the map is an aerial photo of the ice floe (photo credit S. Graupner). Primary water column 2205 2206 sampling was from RV Polarstern (light blue, lower righthand side). Ocean City did 2207 not have a CTD-rosette system. Ice cores (not new ice formations) in August and 2208 September 2020 were sampled from a single site (yellow area). New ice formation 2209 and waters from the upper ocean (1-2m) were sampled at RS, OC, ROV, and Luna leads. ECO Lodge (red square) was established adjacent to Ocean City lead, 2210 2211 approximately 300 m from the ship. The map had been simplified to show main 2212 sampling and measurement positions for the ecosystem work program. Additional 2213 MOSAiC measurement sites from teams ATMO, ICE, and OCEAN can be viewed in 2214 the respective MOSAiC Overviews by Nicolaus et al. (2022b), Rabe et al. (2022) and 2215 Shupe et al. (2022).



Figure 6. Ecosystem observations and measurements during the field phase of MOSAiC. Each row shows the dates of a sampling event for a specific type of gear (e.g. Polarstern-CTD) or sampling activity (e.g. FYI coring). Solid lines indicate instrumentation deployed through the ice for a continuous period. A number of parameters are collected from an individual sampling event, such as deployment of the Polarstern-CTD rosette system. Alternating white and grey horizontal bars at the bottom of the chart indicate the MOSAiC leg. Colored horizontal bars indicate from

the Polarstern-CTD rosette system. Alternating white and grey horizontal bars at the
bottom of the chart indicate the MOSAiC leg. Colored horizontal bars indicate from
which Central Observatory (CO) samples were collected. Dashed red line boxes
identify the periods when RV Polarstern was transiting to/from an ice floe. LOKI =
Light-frame On-sight Key species Investigation system (zooplankton camera
system). ROV nets = Plankton nets towed by a Remotely Operated Vehicle. LISST =
Laser In-Situ Scattering and Transmissometer (particle counter). FYI = First Year

- 2229 Ice. SYI = Second Year Ice.
- 2230



2231 2232 Figure 7. Distribution of CTD-rosette-based water column samples for nutrients, Chl-a, and total DNA in depth and time. Discrete samples (while 2233 2234 circles) for the upper 400 m (A, C, and E) and for full depth (0-4000 m; B, D, and F) 2235 are overlain on temperature contours with isotherms shown by thin, solid lines. 2236 Temperature data shown here are from temperature sensors mounted to the CTD-2237 rosette system. During mid-March to May 2020, the Polarstern-CTD was not 2238 operational due to the closure of the ice hole alongside the ship; water column 2239 sampling was limited to the upper 1000 m using the OC-CTD-rosette system. A) Nutrient samples collected in the upper 400 m; B) Nutrient samples collected over 2240 2241 the full water column depth; C) Chl-a samples collected in the upper 400 m; D) Chl-a 2242 samples collected over the full water column depth; E) Total DNA samples collected

in the upper 400 m; F) Total DNA samples collected over the full water column

2244 depth.

2245



2246

Figure 8. Ecological sea ice core pooling and processing. Full length cores were sectioned in the field and placed in prelabeled melt bags. Filtered seawater (FSW) was added onboard to each melt bag, and after complete melt, pooled sample were parsed for different properties. When possible, 2 ECO pools were generated. Properties collected from each pool are shown, see Table 1 for abbreviation explanations. Additional samples were collected from SALO18 and DIC/TA cores as well as additional bottom sections.



2255

Figure 9. Environmental conditions over the annual cycle. A) latitude (°N), B) air 2256 and C) surface ocean temperature (blue) and salinity (grey) at 10 ± 3 m depth, D) 2257 incoming PAR (photosynthetically active radiation, 400-700 nm, measured as photon 2258 flux density), and E) surface ocean nutrients (nitrate+nitrite, silicic acid, and 2259 2260 phosphate) from the upper 30 m water depths. Grey shaded areas indicate transit 2261 periods. Here, latitude and nutrients are from the location of RV Polarstern, while 2262 PAR, water temperature, and surface air temperature are representative of CO 2263 conditions.





Figure 10. Dominant pelagic (water column) and sympagic (ice-associated)

2266 **protists during the MOSAiC cruise.** A) dinoflagellate belonging to

2267 Gymnodiniaceae, B) unidentified flagellate, C) *Pseudo-nitzschia* sp. and D) *Melosira*

arctica from water column samples; E) and F) unidentified flagellates, G) Nitzschia

2269 *frigida* and H) *Navicula* sp. from bottom sea ice samples.



2270

Figure 11. Zooplankton and fish species caught during the MOSAiC cruise. A) 2271 2272 Apherusa glacialis, B) Themisto libellula, C) Eukrohnia hamata, D) Aglantha digitale, E) Botrynema ellinorae, F) Calanus hyperboreus, G) Microcalanus sp., H) Oithona 2273 2274 similis, I) Metridia longa, J) Paraliparis bathybius, K) from top to bottom: Haddock 2275 (Melanogrammus aeglefinus), 2 x Atlantic cod (Gadus morhua), Beaked redfish 2276 (Sebastes mentella), Haddock (Melanogrammus aeglefinus); L) Boreogadus saida. The specimens A - I were obtained with the LOKI (Lightframe on-sight key species 2277 2278 investigation), further sampling methods were J) zooplankton ring net, K) longlines, 2279 and L) ROVnet camera.



2280 2281 Figure 12. Sediment trap material from winter vs summer. Overview images of

sediment trap material from A) January 14, and B) July 21, 2020. 2282



Figure 13. A variety of different seawater and sea ice habitats sampled over the

2285 drift year. A) Frost flowers developing on a refrozen lead on March 11, 2020; B) Sampling an open lead on 22, 2020; C) New ice formation on a lead located near 2286 ECO Lodge 2 on September 07, 2020; D) Sampling new ice and direct under-ice 2287 waters from a lead located near ECO Lodge 2 on September 12, 2020; E) 2288 2289 Underwater photos of ice blocks within an open lead from July 01, 2020 and F) from 2290 the same location on 29, 2020, showing the development of thin, stratified fresh and brackish layers within leads. G) Jaridge Observatory from the surface with piled up 2291 2292 ice blocks on June 26, 2020; H) Underwater photo of ice blocks in Jaridge 2293 Observatory with strands of Melosira; I) Refrozen surface of a melt pond showing 2294 large aggregate material through the ice surface from Aug 21, 2020; and J) Melt 2295 pond sampling from August 31, 2020.



- 2296
- 2297 Figure 14. Components of the multidisciplinary ridge sampling strategy during
- 2298 **MOSAIC**. Schematic representation of the sampling strategy of sea ice ridges
- 2299 developed by the HAVOC project-, including autonomous systems (e.g. thermistor
- strings), coring and drilling, sampling of ice and void water in the ridge keel, as well
- as ROV- and sediment trap-based measurements, with the former including
- 2302 zooplankton net tows and various sensor-based measurements (including
- 2303 hyperspectral imager mapping of the ice underside, see Figure 16).



2304

Figure 15. The Jaridge ridge sampling areas during summer 2020. A) Shows an aerial image of the study area with ponded level ice and the Jaridge ridge sampling

2307 site. Shading in B) indicates ice draft from the ROV multibeam sonar with keel

2308 depths of the pressure ridge exceeding 7 m, and red stars indicate locations of

2309 deployed sediment traps, and the blue star the location of underwater hyperspectral

imager (UHI) data collection shown in Figure 16.



Figure 16. Determination of ice algal habitable space in pressure ridges and

2313 level sea ice using underwater hyperspectral image (UHI) information. A) An

example of composite RGB (red, green, and blue) image of one area along the ridge

flank transect (blue star in Figure 15b) compared to model results to estimate B)

relative algal quantity estimated via the Relative ice algal Biomass Index (RBI), and

C) inhabited area based on support vector machine (SVM) machine learning

2318 approaches of sea ice using the signature of the spectral light transmitted through

- the ridge (Lange et al., submitted).
- 2320



2323 Figure 17. Transformations of energy, carbon and nitrogen by

2324 mesozooplankton in the upper water column and near the sea ice-ocean

2325 **boundary.** Arrows indicate transformation rates and component linkages that were

2326 quantified; red arrows show incorporation of carbon/nitrogen while blue arrows show

2327 export of carbon/nitrogen from the organisms. Characteristics of each ecosystem

2328 component that were measured indicated inside boxes.
- 2329 Supplementary Information
- 2330

Supplementary information

Table S1. Project-specific contributions to the ECO work program. Information
 on Project Title, PI, involved institutions, funding agencies, and science foci.

Table S2. List of ECO sampling events based on rosette casts and optical

particle profiling. Event Operation IDs, date and time, location and bottom depth for
 PS-CTD rosette, OC-CTD rosette and LISST casts as well as UVP profiles.

Table S3. Overview on sample processing and applied methods. Detailed
overview of sampled parameters, applied methods, responsible PIs, coverage, and
estimated number of samples. The table represents an extended version of Table 1
from the main document.

2342

2337

Table S4. Overview of quantitively analyzed zooplankton sampling events and
collected samples. Samples were collected via LOKI (up to 20 frames sec-1), UVP,
multinet (MN), ring nets (RN), Nansen net (NCN) and a net mounted on an ROV
(ROVN), from Nov. 2019 to Oct. 2020. For each month, the number of samples is
given; depth strata MN: 2000-1000-500-200-50-0 m; depth strata NCN: 1000-200 m
& 200 - 0 m.

2349

Table S5. List of ECO sampling events for zooplankton and fish sampling.

Event Operation IDs, date and time, location (of *RV Polarstern*), and bottom depth

- 2352 for all zooplankton and fish sampling events for multinets (NM), Light-frame On-sight
- 2353 Key species Investigation system (LOKI), Ring nets, Nansen Nets, long lines,
- remotely operated vehicle nets (BEAST), finish rods and Gill nets.
- 2355

Table S6. List of ECO sampling events for first and second year ice. Event
 Operation IDs, date and time, location and bottom depth for all common time-series

- 2358 ice coring activities at the first and second year ice (FYI and SYI) coring sites.
- 2359
- Table S7. List of ECO sampling events for event driven sampling and intense
- 2361 observation periods (IOPs). Event Operation IDs, date and time, location and
- bottom depth for event-driven sampling of direct under ice water, leads, melt ponds,
- new ice formation as well as high frequency IOP sampling.