

**Life before the seafloor: Assessing community structure and distribution of larval benthic
invertebrates in the Western Canadian Arctic.**

By

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Thesis Abstract

The Arctic contains diverse assemblages of benthic invertebrates integral to ecosystem processes such as carbon cycling. Many benthic invertebrates have pelagic larval stages (meroplankton) that are sensitive to environmental conditions such as temperature; thus, understanding environmental influences on long-term changes in benthic invertebrate communities requires monitoring meroplankton. However, in the Western Canadian Arctic (WCA), meroplankton remain understudied due to microscopic sizes, limited resemblance to adult stages, and morphological similarity among taxa. This thesis uses multiple monitoring methods to examine meroplankton community structure during August in the WCA relative to oceanographic conditions and adult populations. A 10-year taxonomic dataset (2012–2024) revealed strong interannual variability in meroplankton abundance (11–324 ind. m⁻³), suggesting that yearly differences in oceanographic conditions influence larval populations. Although, spatial distribution was patchy, larval abundance was consistently highest at the surface (0–50 m), particularly in shallow waters (≤ 100 m) on the Mackenzie Shelf and within embayments. Environmental modelling indicated that higher meroplankton abundance was associated with warmer surface waters (0–50 m), suggesting elevated temperatures may benefit larval development and growth. To improve species-level detection, community DNA (net DNA; plankton nets) and environmental DNA (eDNA; water samples) were analyzed at 10 stations in 2024. Metabarcoding detected a greater number of meroplankton (112 taxa) relative to morphology-based taxonomy (6 taxa). At the surface (0–50 m), net DNA detected higher richness than eDNA (55 and 36 taxa, respectively), and each method characterized distinct communities. Despite these differences, meroplankton sampling approaches showed limited spatial overlap to adult communities, reinforcing the spatial decoupling of pelagic larvae from

local adult populations. Meroplankton richness at the surface increased with earlier ice break-up, suggesting that longer periods of primary productivity may support extended larval production. Furthermore, richness at the surface was best explained by high chlorophyll fluorescence and salinity, highlighting the combined influence of phytoplankton biomass and stratification on larvae. Together, these findings identify environmental variables influencing meroplankton communities in the WCA and demonstrate that incorporating metabarcoding greatly improves detection of larvae and characterization of phenological patterns. Extending metabarcoding across multiple-years and seasons will further improve understanding of inter-annual and seasonal variability in meroplankton community composition in the changing Arctic.

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I would like to extend my gratitude to the members of my MSc committee, Dr. Margaret Docker and Dr. John O'Brien for their helpful suggestions and comments. Thank you to the Inuvialuit Game Council for all of their guidance and input on sampling within their traditional waters. Thank you to the dedicated team apart of the Fisheries and Oceans Canada (DFO) Canadian Beaufort Sea Marine Ecosystem Assessment for field sample collection (Andy, Jane, Chloe, Judy, Krystal, Caity, Annlise, and Michelle) as well as Captain Dan Mose and the crew navigating the F/V Frosti. Thank you to Dr. V. Roy (DFO Quebec) for analyzing benthic invertebrate samples, Dr. K. Westfall for analyzing eDNA samples and guiding me through bioinformatics, and the DFO freshwater institute genetics team (Denise, Rob, and Erin) for their guidance on DNA extractions and PCR. Lastly, thank-you to the DFO Marine Conservation Targets (MCT) for providing funding for this project.

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Field sampling for this project was done within the marine waters of the Inuvialuit Settlement Region, while data analysis and writing was completed on the territory of the Anishinaabeg, Inninewak, Anishinewak, Dakota Oyate, Denesuline, and the Homeland of the Red River Métis. As a settler, my presence on these lands is shaped by colonialism. I am committed to conducting research in ways that respect Indigenous sovereignty, uphold community priorities, and contribute to the self determined futures of the Nations whose lands and waters supported this work.

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Contribution of Authors

Chapter 1

Mia-May Grabovac led the data analysis and writing of the manuscript. Methodology and collection of meroplankton was conducted as part of the Beaufort Regional Ecosystem Assessment (BREA; 2012–2014) and the Canadian Beaufort Sea Marine Ecosystem Assessment (CBS-MEA; 2017–2024) collected by Dr. Alexis Burt and Mia-May Grabovac (2023–2024). Morphological taxonomic assignments were done by Cyril Aubry at Université Laval, the taxonomy team at Biologica in Victoria, B.C., and confirmed by Moira Galbraith at the Institute of Ocean Sciences (Sidney, B.C). Environmental data was collected by Jane Eert and processed by Dr. William Williams, Ryan Galley, and Dr. Lauren Dares. Dr. Andrea Niemi, Dr. Patricia Ramey-Balci, Dr. Margaret Docker, and Dr. John O’Brien provided guidance and revisions.

Chapter 2

Collection of meroplankton for morphological analysis, DNA, and environmental DNA (eDNA) were done by Mia-May Grabovac and Krystal Woodard as part of CBS-MEA. Environmental data was collected by Jane Eert and Chloe Immonen, and processed by Dr. William Williams, Ryan Galley, and Dr. Lauren Dares. Collection of adult benthic invertebrates was done by Caitlin Allison, Michelle Kamula, and Annlise Guillemard. Confirmation of benthic individuals was completed by the benthic ecology team at the Maurice Lamontagne Institute, DFO Quebec, Mont-Joli, Canada and the Université Laval. Morphological analysis of meroplankton were done by Cyril Aubry at Université Laval, the taxonomy team at Biologica in Victoria, B.C., and confirmed by Moira Galbraith at the Institute of Ocean Sciences (Sidney, B.C). Dr. Kristen Westfall developed the methodology for eDNA and bulk DNA extractions, while also aiding in

data analysis (bioinformatics). Mia-May Grabovac, Denise Tenkula, Rob Bajno, and Erin Spice ran bulk DNA extractions and library preparation. Mia-May Grabovac led the data analysis and writing of the manuscript, with Dr. Andrea Niemi, Dr. Patricia Ramey-Balci, Dr. Kristen Westfall, Dr. Margaret Docker, and Dr. John O'Brien providing revisions.

Thesis Format

This thesis is formatted as a grouped manuscript composed of two independent chapters containing their own introduction, methods, results, discussion, and conclusion. A general introduction and conclusion are included.

Thesis Introduction

The Arctic makes up approximately 70% of Canada's coastline (Niemi et al. 2024) and supports some of the highest invertebrate diversity living in and on the seafloor of Canadian waters (Wei et al. 2020). Benthic invertebrates play a critical role in maintaining the integrity and stability of Arctic ecosystems (Chen, 2021; Descôteaux et al., 2021), serving important functions such as nutrient cycling, food for higher trophic-level predators, habitats for other organisms, and include commercially important species (Comeau et al., 1998; Alvsvåg et al., 2009; Chen, 2021). Benthic invertebrate communities serve as a link between the benthic and pelagic ecosystems (Ershova et al., 2019; Descôteaux et al., 2021; Niemi et al., 2024). For example, benthic invertebrates redistribute resources including organic matter between the benthic and pelagic environments by consuming sinking sea ice algae and phytoplankton, zooplankton fecal pellets, and sinking carcasses of fish and marine mammals (Ershova et al. 2019; Niemi et al. 2024).

The distribution, diversity, and abundance of seafloor invertebrates is impacted by environmental drivers such as food supply, depth, temperature, and salinity (Gimenez, 2004; Roy et al., 2014, 2015; Grebmeier et al., 2018; Niemi et al., 2020). Food supply in the form of sinking particulate organic matter (POM) (i.e., phytoplankton, ice algae, dead organic matter) has been shown to support diverse and abundant benthic invertebrate populations (Darnis et al. 2012), particularly evident in shallow areas with high POM flux, resulting in strong benthic-pelagic coupling (Stasko et al. 2018). These benthic 'hotspots' (Wei et al. 2020) provide important feeding areas in the Arctic for higher trophic level predators such as Pacific walrus (*Odobenus rosmarus divergens*), gray whales (*Eschrichtius robustus*), bearded seals (*Erignathus barbatus*), diving birds, and fish (Logerwell et al., 2011; Ershova et al., 2019; Descôteaux et al., 2021; Niemi et al., 2024). However, increases in depth influence food supply to benthic communities,

as POM flux takes longer to sink to the seafloor and is thus more likely to be consumed by pelagic grazers and microbial communities (Steinberg et al., 2008; Roy et al., 2015a). Thus, diversity and abundance of benthic invertebrates can decrease or show a hump-shaped relationship with depth depending on conditions of overlying waters (Levin et al. 2001; Stasko et al. 2018; Wei et al. 2020; Ehrman et al. 2022).

In addition to food supply, inter-annual variability in temperature and salinity can influence the behaviour and physiological responses of benthic invertebrates such as the timing of reproduction or release of eggs/larvae (Morgan, 1995; Darnis et al., 2012; Roy et al., 2014). At larger scales (100s of km), increasing air temperature can influence the timing of sea-ice breakup, which controls the timing of phytoplankton blooms and consequently the period of greatest POC flux to the seafloor (Roy et al., 2014; Roy et al., 2015b; Michelsen et al., 2017). A delay in POC flux to the seafloor may alter the timing of reproduction in benthic invertebrates, which can impact population abundance measured the following season. Given the rapid environmental change occurring in the Arctic (Rantanen et al. 2022), gaining a more comprehensive understanding of benthic invertebrates and their life history strategies has become increasingly important (Bilous et al. 2022; Deb and Bailey 2023; Niemi et al. 2024). Furthermore, the consequences of climate change will not just impact benthic adult stages but will influence larval benthic invertebrates (meroplankton) residing in the water column, far above the seafloor. Thus, inclusion of meroplankton in benthic invertebrate monitoring programs is essential for a more holistic understanding of changes to the ecosystem (Ehrman et al. 2022).

Most benthic invertebrates have a bi- or multi-phasic life cycle containing a less motile or sessile (i.e., sedentary) adult stage residing in or on the seafloor, and a free-floating, microscopic larval stage located in the water column (Levin & Bridges, 1995; Calado & Leal,

2015; Silberberger et al., 2016; McBride et al., 2024). Meroplankton rely on external energy sources such as phytoplankton (i.e., planktotrophic) or internal yolk reserves (i.e., lecithotrophic) (Mileikovsky 1971; Pechenik 1999). However, feeding strategies, behaviour, and development of meroplankton vary widely among benthic invertebrate species (Thorson 1950; Mileikovsky 1971; Pechenik 1999) depending on environmental and geographical variables (Levin & Bridges, 1995; Eckman, 1996; Stanwell-Smith et al., 1999).

While feeding and developing in the plankton, ocean currents disperse meroplankton to local or regional habitats beyond spawning areas (Silberberger et al. 2016). Dispersal and survival of meroplankton, along with post-settlement life stages (e.g., juveniles) support the long-term persistence of benthic invertebrate communities (Cowen & Sponaugle, 2009; Short et al., 2013; Silberberger et al., 2016; Ronowicz et al., 2024) by contributing to the distribution and regulation of adult population dynamics (Cowen & Sponaugle, 2009; Short et al., 2013; McBride et al., 2024). As meroplankton grow and develop in the water column, they are subjected to different environmental variables than adult or juvenile life stages such as sea surface temperature and ice-mediated ecosystem phenology (Ehrman et al., 2022). It is essential to understand how meroplankton are impacted by conditions within their habitat, as seasonal or inter-annual environmental variability within the water column can influence meroplankton growth and survival to the next life stage, impacting future benthic invertebrate populations (Thorson, 1950; Bendtsen & Hansen, 2013).

Study Region: The Western Canadian Arctic

The Western Canadian Arctic (WCA) (approx. 68°N, -114°W) contains the marine waters of the Inuvialuit Settlement Region (ISR) which includes the Tarrum Niruyutait and Anguniaqvia niqiqyuam Marine Protected Areas (TNMPA and ANMPA, respectively) (Figure 1). Habitats

within the WCA are diverse and characterized by seasonal and inter-annual variability in physical, chemical, and biological conditions (Carmack and Macdonald 2002), which influence and support unique assemblages of mammals (Walkusz et al., 2012; Chambault et al., 2018; Mayette et al., 2023), fish (Walkusz et al., 2011; Majewski et al., 2017; Bilous & Dunmall, 2020), and benthic invertebrates (Darnis et al. 2012; Roy et al. 2015; Stasko et al. 2018). Environmental heterogeneity in the WCA is caused by variability in ocean circulation, surface layer temperature, salinity-driven stratification, sea ice, and primary production phenology (Niemi et al. 2020; Wassmann et al. 2021; Bilous et al. 2022). Meroplankton can adapt to habitat variability unless the environmental factors exceed average tolerance ranges thereby impacting survival (Thorson, 1950; Mileikovsky, 1971; Clough et al., 1997; Allen, 2008; Short et al., 2013; Schroeder et al., 2023). Thus, a comprehensive knowledge regarding the responses of meroplankton to environmental factors within their habitats is critical in understanding how meroplankton community structure may react, persist, and influence adult populations under environmental variability (Eckman, 1996; Gimenez, 2004; Chen, 2021).

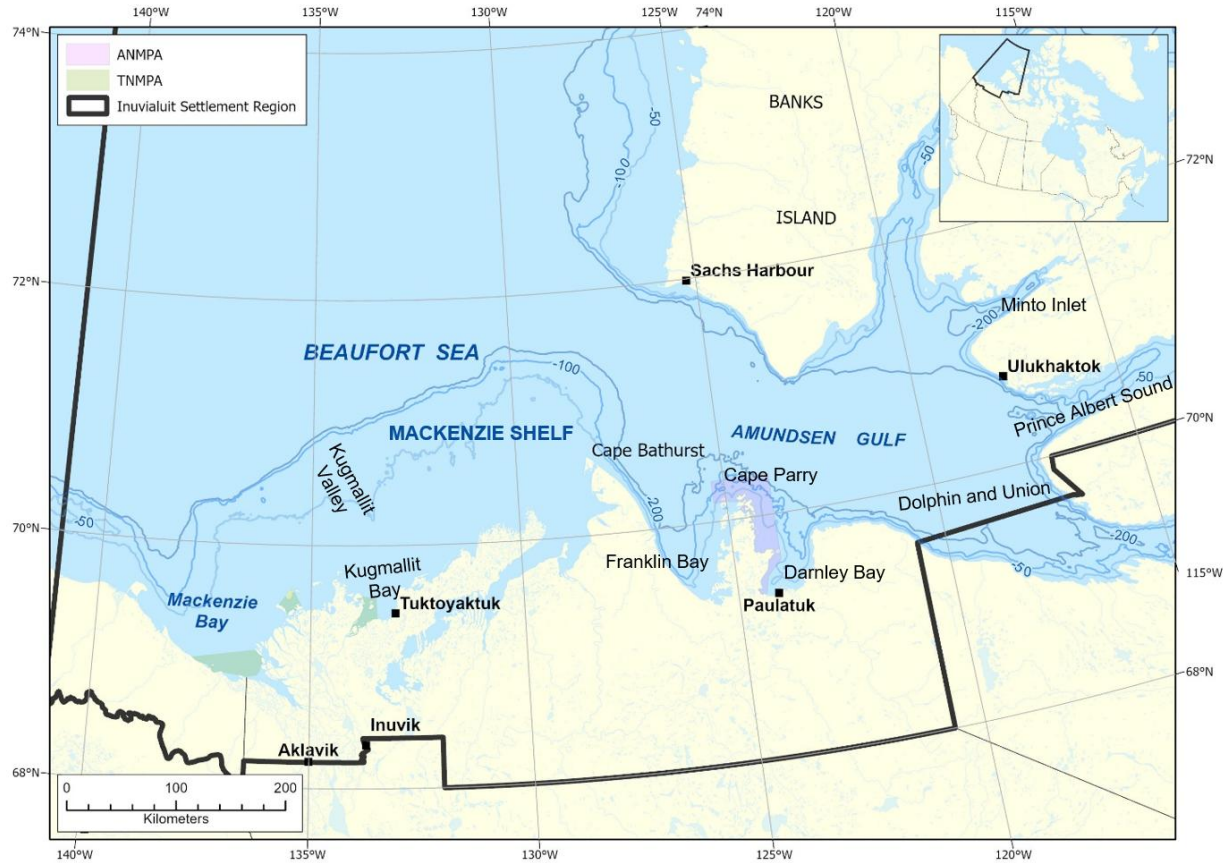


Figure 1. Location of the Western Canadian Arctic. Includes an outline of the Inuvialuit Settlement Region (ISR) in black, the communities of the ISR, and both Tarnum Nirvutait (green) and Anguniaqvia niqiqyuam (purple) Marine Protected Areas.

Circulation Patterns

The passive drifting of meroplankton in the water column subject them to the influence of natural large and small-scale currents which determine dispersal location (Clough et al. 1997; Bendtsen & Hansen, 2013). Surface circulation (i.e., upper 50 m of ocean water) in the study area is influenced by the anticyclonic Beaufort Gyre centered offshore in the Canada Basin (Carmack & Macdonald, 2002; Barber et al., 2010; Forest et al., 2011). The Gyre causes surface waters to flow onto the Mackenzie Shelf and into the Amundsen Gulf near Banks Island, which then exit Amundsen Gulf near Cape Bathurst (Figure 1.2) (Barber et al. 2010). Subsurface currents of Pacific and Atlantic water origins (i.e., the Beaufort Undercurrent) flowing along the

Mackenzie Shelf also enter Amundsen Gulf near Banks Island (Figure 2), carrying offshore nutrients to the shelf and gulf (Aagaard 1984; Carmack & Macdonald, 2002). Thus, meroplankton located in surface and subsurface currents within the Amundsen Gulf are generally transported in the same direction (Barber et al. 2010). Additionally, storms and smaller-scale circulation such as eddies (Porter et al., 2020 Descôteaux et al., 2021; Kubryakov et al., 2021) would influence the dispersion of meroplankton in the Amundsen Gulf (Clough et al., 1997; Schlüter & Rachor, 2001; Largier, 2003; Cowen & Sponaugle, 2009).

In the WCA, there is high variability in wind-driven surface currents that occur over short time scales (Ehrman et al., 2022), which could transport meroplankton located near the surface (i.e., upper meters of the ocean) across the Amundsen Gulf or between the Mackenzie Shelf and gulf (Descôteaux et al. 2021). For example, surface drifters have been observed to travel from one end of the WCA to the other in a matter of weeks in response to prevalent winds (Niemi et al. 2020). Alterations in meroplankton distribution pathways can be positive, if carried to new, favourable habitats allowing the expansion of local communities (Clough et al. 1997). Repetitive strong wind events give benthic invertebrates located in coastal areas potential to expand their populations into offshore or open water (Eckman, 1996). Changes in dispersal may also negatively impact meroplankton community structure by increasing mortality risk if meroplankton get carried to unfavourable areas containing high predator abundances, low food availability, or unfavourable temperatures for development (Bendtsen and Hansen 2013; Silberberger et al. 2016).

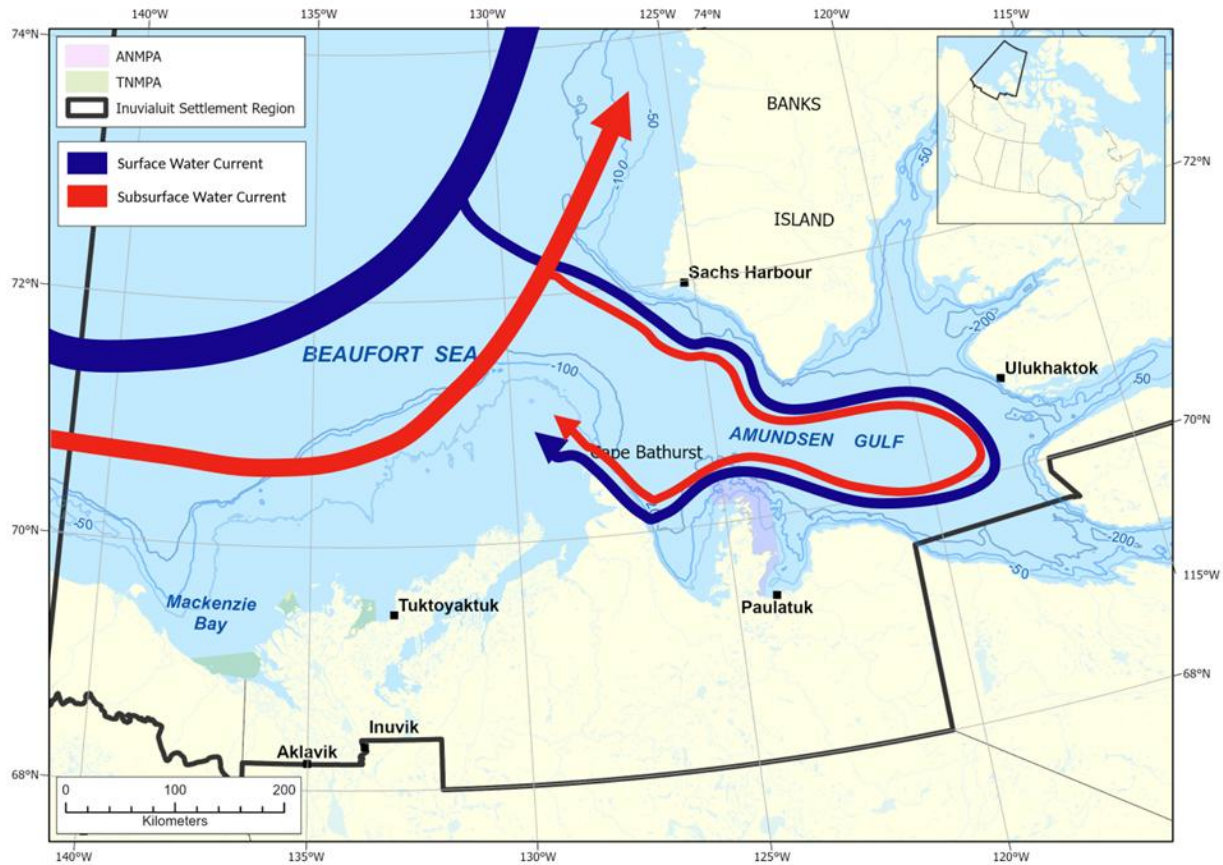


Figure 2. Large-scale circulation patterns within the study region. Shows the movements of surface (blue) and subsurface (red) currents of the Beaufort Sea and Amundsen Gulf.

Temperature

Water temperature can influence metabolism and growth rates of meroplankton by having an inverse relationship with planktonic larval duration (PLD) and directly influencing survival which impacts community structure (O'Connor et al., 2007; Cobb et al., 2008, Deb & Bailey, 2023). Temperature tolerance is species-specific (Cobb et al., 2008; Schlüter & Rachor, 2001), with many meroplankton adapting to a range of temperatures within their habitat. Generally, meroplankton adapted to colder climates have a longer PLD in the range of weeks to months due to slower growth rates and metabolism (Cowen & Sponaugle, 2009; O'Connor et al., 2007). In the Barents Sea region, the cold surface temperatures, where meroplankton are most abundant,

have been hypothesized to decrease the metabolic rate of meroplankton such that they require less food, but a longer development time (Descôteaux et al., 2021). The PLD of meroplankton taxa in the WCA is unknown, but cold surface temperatures similar to the Barents Sea may indicate adaptation for slower growth rates increasing PLD and time in the pelagic habitat.

Spatiotemporal variability in sea surface temperature (SST) in the WCA can alter the growth rates and metabolism of meroplankton which impact their PLD in the pelagic habitat (Cowen and Sponaugle 2009). Extreme temperature fluxes (e.g., heat waves) have been known to impact abundances of benthic invertebrate communities at all life stages (Atkinson 1994; Ershova et al. 2019), but warming SST can have varying degrees of impact on populations at a regional level (Wassmann et al. 2021). A marine heatwave in the Eastern Bering Sea (EBS) from 2018–2019 increased metabolic demand of larval and juvenile snow crabs (*Chionoecetes opilio*), leading to high mortality and population decline (Szuwalski et al. 2023). Such extreme temperature anomalies have not yet been observed in the WCA; thus, it is important to assess temperature variation within and between specific regions to better comprehend the impacts of temperature on meroplankton communities.

Food Availability

Although reproduction in benthic invertebrates varies among species and locations, studies have suggested that many taxa time release of meroplankton to maximize food availability for larval growth and development (Fernandes et al. 2012; Fachon et al. 2025). This suggests phytoplankton primary productivity as a key driver of the spatial and temporal release of meroplankton into the water column (Kuklinski et al. 2013; Descôteaux et al. 2021). In turn, meroplankton production may be indirectly affected by inorganic nutrients and light availability through their control on phytoplankton dynamics (Ardyna et al., 2011; Ehrman et al., 2022; Frey

et al., 2022; Deb & Bailey, 2023). In Arctic systems, nutrients and light availability in the water column is controlled by physical processes such as stratification and sea ice dynamics (Ardyna et al. 2014). Variability in the strength of stratification and timing of ice break-up can alter primary production and affect associated ecosystem interactions such as benthic-pelagic coupling (Sallon et al., 2011; Ehrman et al., 2022) and distribution of organisms such as meroplankton in the water column (Cobb et al., 2008; Ardyna et al., 2011).

Stratification can limit nutrient availability to the euphotic zone, which directly influences the abundance and vertical distribution of phytoplankton and indirectly impacts the vertical position and composition of meroplankton in the water column (Mundy et al., 2009; Ardyna et al., 2014; Scheifele et al., 2021; Ehrman et al., 2022; Frey et al., 2022). In the WCA, stratification and structure of the water column are driven by salinity. The surface mixed layer (0–50 m) overlies a layer of Pacific-origin water (50–200 m), and the deeper layer of Atlantic water origin (>200 m) (Carmack and Macdonald 2002; Niemi et al. 2024). The surface layer is relatively low in salinity and nutrient concentrations and is influenced by river discharge in nearshore and Mackenzie Shelf areas (Carmack and Macdonald 2002; Stasko et al. 2018; Solomon et al. 2021) as well as seasonal ice melt (Wassmann et al. 2021; Niemi et al. 2024). The Pacific layer is characterized by moderate salinity (31–33) and temperatures (-1.5–3°C) that shift seasonally and contain high concentrations of dissolved nutrients (Niemi et al. 2020). The Atlantic water mass (>200 m) has high salinity (34) and year-round temperatures of 0–3°C (Niemi et al. 2020).

Phytoplankton production in the WCA is limited to the surface mixed layer, due to periodic replenishment of nutrients coinciding with optimal light conditions (Niemi et al. 2024). The main source of nutrients to the surface layer is in the lower Pacific layer, and areas of upwelling that

promote mixing of nutrients from deeper waters to the surface have greater primary productivity than nutrient poor (i.e., oligotrophic) areas (Mundy et al., 2009; Ardyna et al., 2011). The WCA has strong upwelling events near Cape Bathurst and around the ANMPA (Figure 1) that promote nutrient replenishment in the surface layer and enhance primary productivity for grazers like zooplankton (Williams & Carmack, 2008; Roy et al., 2015; Niemi et al., 2020; Ehrman et al., 2022).

The relationship between meroplankton distribution and areas of relatively high primary production remains unclear (Metaxas 2001), but, like many zooplankton species (Folt & Burns, 1999; Darnis & Fortier, 2014), meroplankton may be inclined to congregate in areas of increased phytoplankton (i.e., food availability) such as the surface mixed layer (Metaxas 2001; Michelsen et al. 2017). Additionally, areas of increased primary productivity or where stratification is weaker due to vertical mixing may be essential locations for meroplankton growth and development, and important in the maintenance of future benthic invertebrate communities. Considering the effects of stratification on primary production, meroplankton community structure could be influenced indirectly by the strength of stratification across the WCA. Thus, understanding the significance of stratification on meroplankton across the WCA is important to consider, as stronger stratification is expected in the WCA by the end of the century (Ehrman et al. 2022) due to seasonal ice melt occurring more rapidly and earlier each season (Ardyna and Arrigo 2020).

Sea ice modulates the delivery of light and heat to the water column, directly influencing the timing and magnitude of primary production and indirectly impacting release of larval benthic invertebrates into the water column (Drobot 2003; Gully et al. 2022). Phytoplankton are controlled seasonally, with changes in composition and abundance occurring in spring when the

ice melts, and again in summer and fall when nutrients are depleted and ice forms (Darnis and Fortier 2014; Hoover et al. 2021). Sea ice in the WCA forms in early to mid-October and fully covers surface waters by November (Carmack and Macdonald 2002). Spring is when ice begins to melt and increased nutrient and light concentrations promote growth of larger phytoplankton such as diatoms (Cobb et al., 2008; Ardyna et al., 2011; Darnis & Fortier, 2014). Once nutrients are depleted in summer and fall, smaller phytoplankton taxa like flagellates become dominant (Ardyna et al. 2011).

The spring phytoplankton bloom in the WCA is essential for many zooplankton species that utilize the bloom for development (Folt & Burns, 1999; Darnis & Fortier, 2014; Smoot & Hopcroft, 2017). Meroplankton may also be released around the phytoplankton blooms to maximize food intake for growth which occurs in coastal high Arctic fjords (Michelsen et al. 2017). However, many meroplankton (e.g., lecithotrophic species) do not need to rely on the spring blooms or can utilize lower quality food (Descôteaux et al. 2021). Thus, seasonal shifts in phytoplankton may be more important for adult benthic communities, as many may use sinking POM from phytoplankton blooms to fuel reproduction, thereby releasing larvae when phytoplankton are less abundant under post-bloom conditions (Thorson, 1950; Descôteaux et al., 2021). Understanding the dynamics between sea ice duration and meroplankton abundance over time and space may provide insights as to the possible linkage between variability in sea ice relative to inter-annual variability of meroplankton communities in the WCA.

Research Relevance

Environmental variability across the WCA will continue to influence meroplankton communities both directly and indirectly (Pechenik, 1999; Cowen & Sponaugle, 2009; Silberberger et al., 2016). Meroplankton are known to be adaptable to natural changes in their habitats (Thorson, 1950; Clough et al., 1997; Chen, 2021), but under projected Arctic climate

change scenarios, failure to adapt and the risk of population decline is of increasing concern (Monteiro et al. 2023). Environmental shifts affecting circulation patterns (Cowen & Sponaugle, 2009; Silberberger et al., 2016; Niemi et al., 2024), increased SST (O'Connor et al., 2007; Ershova et al., 2019), water column stratification (Smoot and Hopcroft 2017), declining sea ice (Nichols et al., 2004; Sallon et al., 2011; Gully et al., 2022), and associated alterations to primary production (Carmack & Macdonald, 2002; Rey et al., 2022; Bravo et al., 2024; Niemi et al., 2024) are occurring and expected to continue; influencing population dynamics of larval benthic invertebrate communities (Atkinson, 1994; Cowen & Sponaugle, 2009; McBride et al., 2024; Ronowicz et al., 2024). Additionally, changes to the environment may impact the life stages of organisms at varying degrees of intensity such that adult benthic invertebrates may have less intense responses to environmental variability at the surface than pelagic larval stages (Ehrman et al. 2022). Thus, monitoring the response of benthic invertebrates under projected environmental change at all life stages is essential for understanding current and future population dynamics.

Efforts to monitor seafloor invertebrates have been implemented throughout the WCA (Nichols et al., 2004; Cobb et al., 2008; Logerwell et al., 2011; Renaud et al., 2015; Niemi et al., 2020; Bilous et al., 2022, 2024), but monitoring programs have not considered how meroplankton communities are changing and the subsequent implications on the distribution and abundance of adult benthic invertebrates. Meroplankton remain understudied in the WCA because of their microscopic sizes, patchy distributions (Bowden et al. 2009; Ershova et al. 2019), and being unrecognizable from their adult stages (Bowden et al. 2009) which makes them difficult to identify. Furthermore, many species of meroplankton are morphologically similar to one another (Ershova et al., 2019; Descôteaux et al., 2021), which creates challenges in using

morphological taxonomy to monitor communities. Morphological taxonomy is used in the WCA for monitoring zooplankton communities but often leave meroplankton only identified to broad taxonomic categories (e.g., phylum or order). Thus, alternative sampling approaches such as DNA metabarcoding, which involves the detection of multiple taxa from one mixed sample, have been recommended to help obtain more detailed knowledge of meroplankton community composition (Ruppert et al. 2019; Spear et al. 2021).

Application of metabarcoding in marine environments have substantially increased in studies looking at distribution, density, population dynamics, and taxonomic composition of fish (Oka et al. 2021; Larson et al. 2022), zooplankton (Djurhuus et al. 2018; Ershova et al. 2021), and meroplankton (Ershova et al., 2019 Descôteaux et al., 2021). For meroplankton, bulk organismal (known here as net DNA) samples have been collected using conventional surveying methods (i.e., zooplankton nets) and genetic material extracted using previously established techniques (Lindeque et al. 2013; Berry et al. 2023), which has increased detection of species substantially. In a study done using metabarcoding to look at zooplankton communities in the northern Barents Sea by Ershova et al. (2019), they found detected species richness three to four times higher in net DNA extraction relative to morphological taxonomy. Alternatively, environmental DNA (eDNA) has provided similar benefits but is a less invasive method using shed genetic material (e.g., feces, skin, or hair) or small organisms (e.g., zooplankton) collected from environmental samples such as water, air, or sediments (Muha et al. 2017; Chen 2021). Leduc et al. (2019) found that out of 202 invertebrate genera found across three locations in the Canadian Arctic using eDNA, only 9–15% were also identified through species collection.

Incorporation of metabarcoding has helped to improve knowledge on ecological communities relative to taxonomy (Baker et al. 2016); however, there are limitations in using

this method in lieu of taxonomy that should be taken into consideration. Often, false detection occurs from prolonged eDNA persistence in the water (Collins et al. 2018), or from contamination of DNA samples during collection or extraction (Ershova et al. 2019; Berry et al. 2023). Persistence of eDNA in the water is impacted by abiotic factors such as temperature and biotic factors such as microbial communities, which can preserve eDNA in nature from weeks to years (Thomsen and Willerslev 2015; Collins et al. 2018). Biases in Polymerase Chain Reaction (PCR) can also result in misrepresentation of community composition due to better amplification of DNA in some organisms relative to others (Ershova et al. 2021). Lastly, reference databases lacking genetic information of benthic invertebrates and challenges in finding universal primer sets to bind to all taxa can result in underrepresentation of species within communities (Chen 2021). To properly identify an organism using metabarcoding, reference sequences need to be present in databases such as GenBank (Rodríguez-Ezpeleta et al. 2021). However, in understudied areas such as coastal Arctic regions, only 50% of known invertebrates may be present in databases, which limits identifying individuals to lower taxonomic levels (Lacoursière-Roussel et al. 2018). In Arctic regions such as the WCA, metabarcoding has yet to be incorporated but could complement morphological taxonomy to help provide a more complete understanding of community composition, distribution of individuals within ecosystems, and relationships to the environment (Deiner et al. 2017; Ruppert et al. 2019).

Thesis Objectives

The overarching aim of my thesis research was to use an integrated monitoring approach to provide a comprehensive assessment of meroplankton community structure in the Western Canadian Arctic relative to oceanographic conditions and their adult life stages. The first chapter analyzed a long-term taxonomic and environmental dataset (2012–2024) to assess spatiotemporal

variability in meroplankton abundance in relation to environmental variables (i.e., ice break up, temperature, salinity, fluorescence, depth) and water column structure. It was hypothesized that meroplankton abundance will show no increasing or decreasing temporal trend. It was predicted that meroplankton abundance will vary between years but be the highest and most consistently observed in the surface mixed layer (0–50 m) where food (i.e., phytoplankton) is most abundant. It was hypothesized that variability in meroplankton abundance would be the result of year-specific oceanographic conditions. It was predicted that years with higher meroplankton abundance would be most influenced by ice break-up such that these years with a shorter open water period (i.e., ice break-up closer to August) would have delayed phytoplankton blooms and release of meroplankton by benthic invertebrates. Furthermore, it was expected that years with lower meroplankton abundance in August would be influenced by higher temperatures in the surface mixed layer due to increased temperatures accelerating meroplankton growth and development causing larvae to settle to the seafloor quicker.

The objective of my second chapter was to incorporate metabarcoding sampling approaches (net DNA, eDNA) in 2024 to analyze meroplankton community composition and richness relative to local adult communities and environmental variables in the WCA. It was hypothesized that meroplankton community structure will differ depending on the sampling approach used such that net DNA and eDNA would identify meroplankton to lower-level taxa (i.e., to species-level) than morphological taxonomy. It was expected that meroplankton would show a decoupling and spatial mismatch in community composition between benthic invertebrate early and adult life stages, as colder water temperatures resulting in longer larval development times likely dispersed meroplankton far from spawning adult populations prior to sampling. Lastly, it was hypothesized that food availability, a determinant in timing and location

of meroplankton in the water column, would be the most important environmental variable determining spatial distribution of meroplankton communities. It was predicted that stations with higher chlorophyll fluorescence (an indicator of phytoplankton biomass) would have higher meroplankton richness, as increased phytoplankton would provide meroplankton with abundant food for growth and development.

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Chapter 1. Environmental influence on spatiotemporal variability of larval benthic invertebrates in the Western Canadian Arctic

Abstract

Benthic invertebrate populations, integral to Arctic ecosystem processes, are influenced by environmental variability, requiring monitoring programs to understand responses to ongoing climate change. Traditional monitoring overlooks environmentally sensitive pelagic larval stages (meroplankton), despite their importance in shaping distribution and composition of adult seafloor invertebrates. Using morphological analysis, this study used a 10-year meroplankton dataset (2012–2024) to evaluate environmental variables influencing spatiotemporal patterns in meroplankton community structure during August in the Western Canadian Arctic (WCA). Mean meroplankton abundance varied substantially among years (11–324 ind. m⁻³), suggesting that meroplankton communities are influenced by inter-annual changes in oceanographic conditions. Polychaetes (85–2143 ind. m⁻³) and bivalves (37–5852 ind. m⁻³) dominated numerically, with shifts in their relative contributions driving inter-annual variability in meroplankton abundance. Echinoids, gastropods, and cirripeds were consistently present but less dominant relative to bivalves and polychaetes, while groups such as Brachyura and Bryozoa were rare or absent, likely reflecting seasonal phenology or sampling limitations. High abundances were consistently observed on the Mackenzie Shelf at depths ≤ 100 m, within embayments (Franklin and Darnley Bays), and at stations around the Anguniaqvia niqiqyuam Marine Protected Area (ANMPA). Furthermore, meroplankton were significantly more abundant in the surface layer (0–50 m) relative to the Pacific (50–200 m) or Atlantic (> 200 m) layers. Environmental modelling revealed higher meroplankton abundance in the surface layer significantly correlated to warmer surface waters, suggesting that moderate warming enhances larval growth for taxa with small,

low-metabolic larvae such as bivalves and polychaetes. This study identified meroplankton dynamics under environmental variability in the Western Canadian Arctic, providing implications for benthic population connectivity and recruitment. Future work incorporating molecular methods (e.g., metabarcoding) will be essential for resolving species-specific dynamics, improving understanding of meroplankton phenology, and predicting how benthic communities may respond to continued environmental change.

Introduction

Environmental variability across the Arctic Ocean creates heterogeneous habitats that contribute to unique and diverse assemblages of benthic invertebrates (Bluhm et al. 2011; Michel et al. 2012; Roy et al. 2015). Benthic invertebrates play a critical role in maintaining the integrity and stability of Arctic ecosystems (Descôteaux et al., 2021; Chen, 2021), serving important functions such as nutrient cycling, food for upper trophic-level predators, habitats for other organisms, and include commercially important species (Comeau et al., 1998; Alvsvåg et al., 2009; Chen, 2021). Many benthic invertebrates are low in mobility or sessile, and thus rely on a free-living, pelagic larval stage (i.e., meroplankton) to aid in distribution (Levin & Bridges, 1995; Calado & Leal, 2015; Silberberger et al., 2016; McBride et al., 2024). Dispersive meroplanktonic life stages are beneficial for the long-term persistence of benthic invertebrate communities (Cowen & Sponaugle, 2009; Short et al., 2013; Silberberger et al., 2016; Ronowicz et al., 2024), but can also negatively influence adult population dynamics depending on survival under different pelagic conditions (Cowen & Sponaugle, 2009; Short et al., 2013; McBride et al., 2024).

Meroplankton community structure is influenced by seasonal and inter-annual changes in environmental conditions. (Bendtsen & Hansen, 2013; Pandori & Sorte, 2019; Bashevkin et al., 2020; Chen, 2021). For example, ocean currents disperse meroplankton away from adult spawning areas, which can then establish adult populations up to hundreds of kilometers away depending on pelagic larval duration (Roughgarden et al., 1988). However, changes to natural distribution pathways from winds or storms may also disperse larvae to undesirable habitats impacting settling individuals (Bhaud, 2000; Holmes et al., 2004). Additionally, sea surface temperature (SST) can influence larval duration in the water column (O'Connor et al., 2007;

Cobb et al., 2008), which alters timing of metamorphosis to sedentary life stages (Cowen & Sponaugle, 2009). The distribution and persistence of meroplankton in the water column is also related to the availability and quantity of food, specifically phytoplankton, that is influenced by salinity-driven stratification and sea ice dynamics (Highfield et al., 2010; Ardyna et al., 2011; Frey et al., 2022; Ronowicz et al., 2024).

In an Arctic context, meroplankton are sensitive to environmental shifts affecting circulation patterns (Cowen & Sponaugle, 2009; Silberberger et al., 2016; Niemi et al., 2024), increased water temperature (O'Connor et al., 2007; Ershova et al., 2019), strengthened water column stratification (Smoot & Hopcroft, 2017), declining sea ice (Nichols et al., 2004; Sallon et al., 2011; Gully et al., 2022), and associated alterations to primary production (Carmack & Macdonald, 2002; Rey et al., 2022; Bravo et al., 2024; Niemi et al., 2024). Meroplankton are adaptable to natural environmental variability within the pelagic habitat (Thorson, 1950; Clough et al., 1997; Chen, 2021), but under projected Arctic climate change scenarios, conditions beyond their adaptability threshold and the risk of population decline is of increasing concern (Atkinson, 1994; Cowen & Sponaugle, 2009; Monteiro et al., 2023; McBride et al., 2024; Ronowicz et al., 2024).

Given ongoing environmental change occurring across the Arctic (Rantanen et al., 2022), a more comprehensive knowledge of Arctic meroplankton communities is needed to better understand benthic invertebrate life history strategies in the face of climate change (Bilous et al., 2022; Deb & Bailey, 2023; Niemi et al., 2024). Meroplankton have been examined in Arctic regions such as the Barents Sea (Kuklinski et al., 2013; Descôteaux et al., 2021), Chukchi Sea (Ershova et al. 2019), and around Svalbard and Norway (Silberberger et al., 2016; Michelsen et al., 2017), but remain understudied in areas such as the Western Canadian Arctic (WCA). The

WCA (68°N, -114°W) is characterized by seasonal and inter-annual variability in physical, chemical, and biological conditions (Carmack & Macdonald, 2002). Due to projected environmental change, efforts to monitor ecologically and culturally important seafloor invertebrates within this region have been well implemented (Nichols et al., 2004; Cobb et al., 2008; Logerwell et al., 2011; Renaud et al., 2015; Niemi et al., 2020; Bilous et al., 2022, 2024). However, monitoring programs have not considered if meroplankton communities are changing and the subsequent implications on the distribution and abundance of adult benthic invertebrates.

Using a long-term (2012–2024) dataset, the aim of the present study was to provide a spatiotemporal analysis of meroplankton abundance across the WCA and address relationships to water column structure and environmental variables. It was hypothesized that meroplankton abundance would show no significant spatiotemporal trend across the WCA. It was predicted that meroplankton abundance would vary between years, but highest abundances would be within the surface mixed layer (0–50 m) where phytoplankton is most abundant. It was also hypothesized that meroplankton would be influenced by year-specific oceanographic conditions. It was expected that years with higher meroplankton abundance in August would be linked to later ice break-up resulting in a delayed phytoplankton bloom and subsequent triggered release of meroplankton by benthic invertebrates. Furthermore, it was expected that years with lower meroplankton abundance would be influenced by higher temperatures at the surface (0–50 m) that accelerate meroplankton development and settlement to the seafloor.

Methods

Sample Collection

Multi-year sampling (2012–2014, 2017–2019, 2021–2024) was conducted in the WCA (Figure 1.1) from a stern trawler (F/V Frosti) at depths ranging from 20 to 1250 m. Due to a larger coverage of stations and to keep season consistent for temporal analyses, only stations sampled within the month of August were included in the study. Out of all stations within the study period, four had no meroplankton identified within taxonomic samples, and two had missing abundance data and thus were omitted from further analyses. Over the 10-year study period, 245 samples were collected at 125 stations from August 2nd to 31st. A complete summary of sampling stations used within the study is provided in Appendix 1.1.

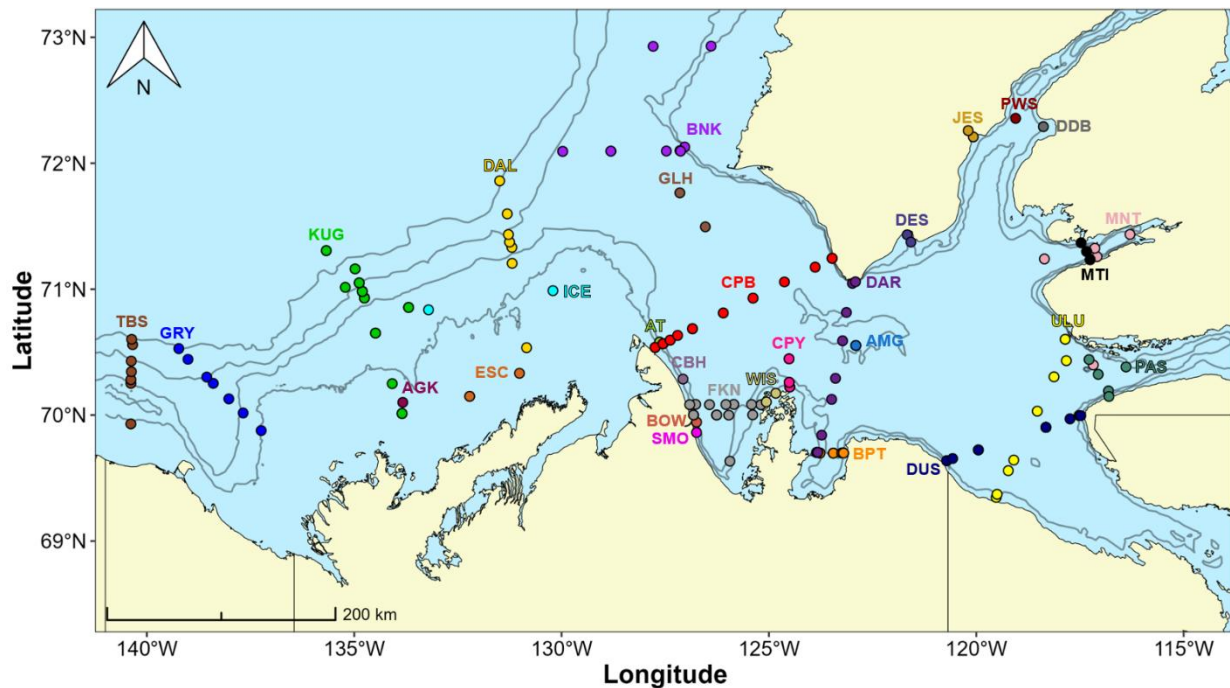


Figure 1.1. Meroplankton sampling stations in the Western Canadian Arctic from 2012–2014, 2017–2019, and 2021–2024. Sampling was done as part of the Fisheries and Oceans Canada Beaufort Regional Ecosystem Assessment (BREA) (2012–2014) and the Canadian Beaufort Sea Marine Ecosystem Assessment (CBS-MEA) (2017–2019; 2021–2024) programs. Stations are identified by transect name.

Meroplankton

Collection of meroplankton was conducted by a vertical net tow at each station starting 5 m off the bottom to the surface using either a Hydrobios Midi Multinet (MPS) (net opening 0.25 m²; 150 µm mesh screen) or a Ring net (RNG) (net opening 0.5 m; 150 µm mesh screen) when stations were ≤ 20 m. A flow meter was attached to each net to determine the volume of water filtered (m³). The MPS contained five nets that opened independently to sample pre-determined depth strata within the water column. Meroplankton were collected in the surface mixed layer (SML), defined as the waters between 0–50 m based on known ocean structure in the region (Carmack and Macdonald, 2002). Additionally, meroplankton samples were collected for the Pacific water mass (50–200 m), and Atlantic water mass (> 200 m) (Figure 1.2), depending on the depth of the station. The RNG net collected a single depth-integrated sample at the shallow stations. Samples from each net was sieved over a 145 µm mesh screen and fixed in a borax-buffered seawater solution with a final concentration of 4% formaldehyde (gram:gram).

Meroplankton were counted within a sub-sample taken with a Henson-Stempel pipette. A minimum of 300 individuals were counted which included both holo- and meroplankton and identified to the lowest possible taxonomic level using morphological analysis. Species/taxon abundance (ind. m⁻³) in each net sample were determined by multiplying the raw counts by the sub-sample fraction and then dividing by the volume of water (m³) that passed through the zooplankton net. Meroplankton were defined as spending a portion of their life cycle in the pelagic environment before settlement to a benthic stage (Clough et al. 1997). Accordingly, holoplanktonic taxa (e.g., copepods, chaetognaths) and species defined as hyper-benthic by Arctic Traits Database (e.g., amphipods, shrimp) were excluded from the meroplankton dataset. The cnidarian genus *Obelia* was retained because its life cycle includes a medusa stage that

produces pelagic larvae (Boero et al. 2007). When needed, rare taxa identified to a genus or species level at less than 10 samples over the 10-year study period were grouped to a higher taxonomic level where the majority of individuals had been identified. For example, the species *Chionocetes opilio* observed in one sample and was grouped into the infraorder Brachyura.

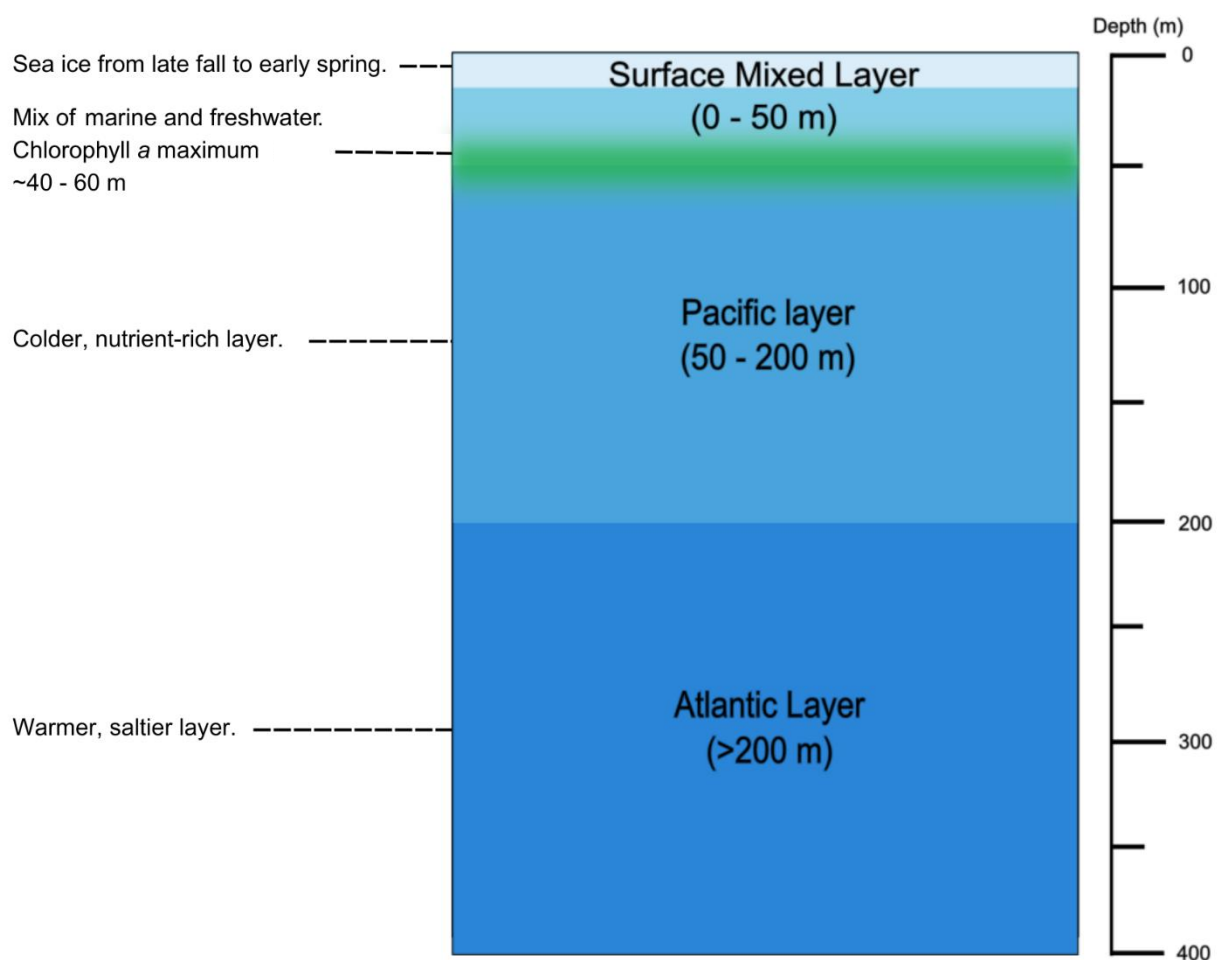


Figure 1.2. The three water masses of the Western Canadian Arctic. Adapted from Stasko et al. (2018).

Environmental Variables

At all stations, temperature ($^{\circ}\text{C}$), salinity, and chlorophyll fluorescence (mg m^{-3} , used as a proxy for phytoplankton biomass) were measured using a rosette mounted Seabird SBE9+ CTD, except for 2012 and 2013 when a SBE25 was used (Eert et al. 2015). All data was collected from

the downcast. To examine environmental relationships with meroplankton in the SML, temperature, salinity, and fluorescence were calculated by averaging CTD values over 0–50 m. To examine environmental relationships with meroplankton over the water column, temperature, salinity, and fluorescence were calculated by averaging CTD values from the bottom to surface at each station. Ice break-up dates were obtained from multi-satellite sensor data (AVHRR+VIIRS; <https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html>) at 0.25° resolution and processed at the Freshwater Institute, DFO, Winnipeg, MB. Following Walsh et al. (2022), break-up date was defined as the last day for which ice concentration over the preceding two weeks exceeded a threshold calculated as the maximum winter mean minus two standard deviations or when ice remained below 15% concentration. Ice break-up dates were then used to determine the number of ice-free days, defined as the number of days between the station sampling date and break-up date at each station. Out of 245 samples, 20 with incomplete environmental data (i.e., one or more variables missing) were removed from environmental datasets to prevent complications in analysis and avoid reducing the validity of the statistical test (Kang 2013).

Statistical Analyses

Meroplankton Spatiotemporal Analyses

To examine spatiotemporal variability in meroplankton abundance within the WCA, abundances at each station and year were plotted together using a bubble map. To determine if there were temporal changes in the taxonomic composition and abundance of meroplankton groups, relative abundance (%) for each taxon were calculated as the taxon abundance divided by total meroplankton abundance multiplied by 100. Taxa with the highest relative abundance

across multiple sampling years were then plotted separately on bubble maps for visualizing taxon-specific spatiotemporal changes. Lastly, to determine how often taxonomic groups were present within the 10-year study period, Frequency of occurrence (%) was calculated by dividing number of samples where taxa were observed divided by total number of samples ($n = 245$) and multiplied by 100.

Meroplankton abundance within each water mass were pooled across all years and log-scaled box plots were used to show the mean abundance of meroplankton within each water mass (i.e., SML 0–50 m, Pacific 50–200 m, Atlantic >200 m). The data was log transformed to reduce skewness and improve visualization of changes in meroplankton abundance over the water column. Significant differences in meroplankton abundance among water masses was determined using a non-parametric Kruskal-Wallis test. When the overall result was significant, post-hoc pairwise comparisons (i.e., Dunn’s test) were conducted to identify which water masses differed from each other. Prior to analysis, data was examined for normality using the Shapiro-Wilk test and for homogeneity of variance using Levene’s test. Neither raw or transformed data (i.e., log and square root) met assumptions of normality and/or equal variance across water masses. Stacked bar plots were used to visualize inter-annual variability in % relative abundance of meroplankton by station and water mass. All graphs for univariate analyses were generated using the package *ggplot2* (Wickham, 2016) and statistics done using *rstatix* (Kassambara, 2025). in R (Version 4.5.2; R Core Team, 2025) and RStudio (Version 2026.01.1+403; Posit Team, 2025)

Environmental Analyses

The relationship between meroplankton abundance and environmental variables temperature, salinity, fluorescence, number of ice-free days, and station depth and year ($n = 10$)

as a random effect was modelled using a generalized linear mixed-effects model (GLMM) with a log-link function. Meroplankton abundance fit a Gamma distribution. Prior to model selection, environmental variables were examined for interrelationships and skewness using a matrix of pairwise scatterplots (i.e., Draftsman plots) in Jamovi v2.17. Variables were examined for co-linearity and none showed high correlation to each other (Pearson co-efficient ≥ 0.95). Thus, all environmental variables were retained for further analyses. To weigh environmental data equally, all fixed effects were standardized using Z-scores. The data was assessed in R and RStudio using packages *mgcv* (Wood 2017), *fitdistrplus* (Delignette-Muller and Dutang, 2015), and *corrplot* (Wei & Simko, 2024).

Separate GLMMs were fitted for meroplankton abundance in the SML (SML model) and for abundance over the full water column (average model). Predictors in the final models followed a backwards selection process based on the lowest Akaike Information Criterion (AIC) value. Model adequacy was evaluated which included assessing residual structure (i.e., heteroscedasticity, nonlinearity, mean-variance mismatch), global model fit (uniformity of simulated residuals), overdispersion, zero-inflation, multicollinearity using variance inflation factors (VIFs), and residual spatial autocorrelation (Moran's I). Models were assessed using the packages *performance* (Lüdtke et al. 2021) and *DHARMa* (Hartig 2024) in RStudio.

Meroplankton abundance was also modelled for each year separately using generalized linear models (GLMs) with a log-link function. Similar to the SML and average models, GLMs included meroplankton abundance (response), and temperature, salinity, fluorescence, number of ice-free days, and depth (predictors). Separate models were assessed for the SML and full water column for each year. Final model selection was based on the lowest AIC value. To evaluate performance and reliability for each year-specific GLM, diagnostic checks were completed for

dispersion, multicollinearity on models with two or more variables, and residual structure (heteroscedasticity, nonlinearity, mean-variance mismatch, Cook's distance).

Results

Spatiotemporal Trends in Abundance

Within the 10-year study period, mean meroplankton abundance varied by an order of magnitude among years with no distinct trend (Table 1.1). Mean meroplankton abundance ranged from 11 ± 3 ind. m^{-3} in 2017 ($n = 17$) to 324 ± 98 ind. m^{-3} in 2024 ($n = 28$). Meroplankton abundance was highest in 2012, 2019, and 2024 with peaks in abundance found at stations DAL_01 (2313 ind. m^{-3} ; Mackenzie Shelf), BPT_05 (805 ind. m^{-3} ; Darnley Bay), and CPY_02 (2395 ind. m^{-3} ; Cape Parry) respectively (See Figure 1.1 and Thesis Introduction Figure 1). On the Mackenzie Shelf (approx. 142°W – 130°W ; Figure 1.1), higher abundances were observed at stations with depths of ≤ 100 m (Figure 1.3). Within the Amundsen Gulf (approx. 130°W – 115°W ; Figure 1.1), meroplankton abundance was highest at stations closer to shore and within embayments including Franklin Bay (FKN stations), Darnley Bay (BPT stations), and Minto Inlet (MTI and MNT stations) (Figure 1.1). Additionally, meroplankton were occasionally abundant at stations near the ANMPA (CPY stations; Figure 1.1), especially in 2024.

Table 1.1. Yearly mean ($\pm$ standard error) meroplankton abundance (ind. m^{-3}) and number of stations sampled per year in the Western Canadian Arctic.

Year	Mean abundance	Standard error	# of stations
2012	127	82	28
2013	19	8	26
2014	79	16	39
2017	11	3	17
2018	97	52	12
2019	166	44	25

2021	82	22	23
2022	78	29	24
2023	26	9	23
2024	324	98	28

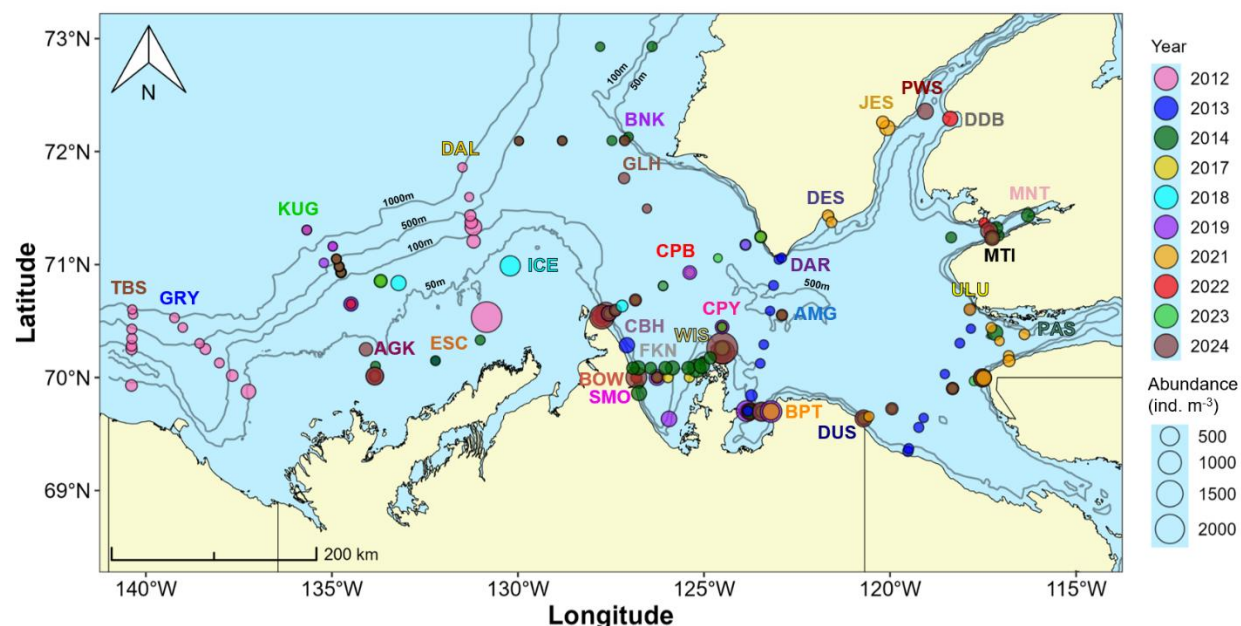


Figure 1.3. Meroplankton abundance between 2012 and 2024 in the Western Canadian Arctic. Year is represented by colour and abundance by circle size. Stations may overlap and are identified by transect name.

A total of 10 meroplankton taxa were identified over the 10-year study period (Figure 1.4). The taxa are primarily identified at the class level. Taxa with the highest frequency of occurrence were Polychaeta, Bivalvia, and Echinoidea, while the taxa with the lowest occurrence were Asteroidea, Bryozoa, Brachyura, and Decapoda (Table 1.2). Polychaete abundances ranged from 85 to 2143 ind. m⁻³ and were most abundant in 5 of the 10 years, with the highest relative abundance in 2018 (83.3%) (Figure 1.4). Bivalve abundance ranged from 37 to 5852 ind. m⁻³ and were most abundant in 2023 (44.2%) and 2024 (64.4%) (Figure 1.4). In 2014, 2019, and 2021, more than one taxon dominated meroplankton abundance. Polychaetes and bivalves were most

abundant in 2014 (33.5% and 34.1% respectively) and 2019 (40.8% and 45.1% respectively), whereas polychaetes (30.8%) and echinoids (31.8%) were most abundant in 2021.

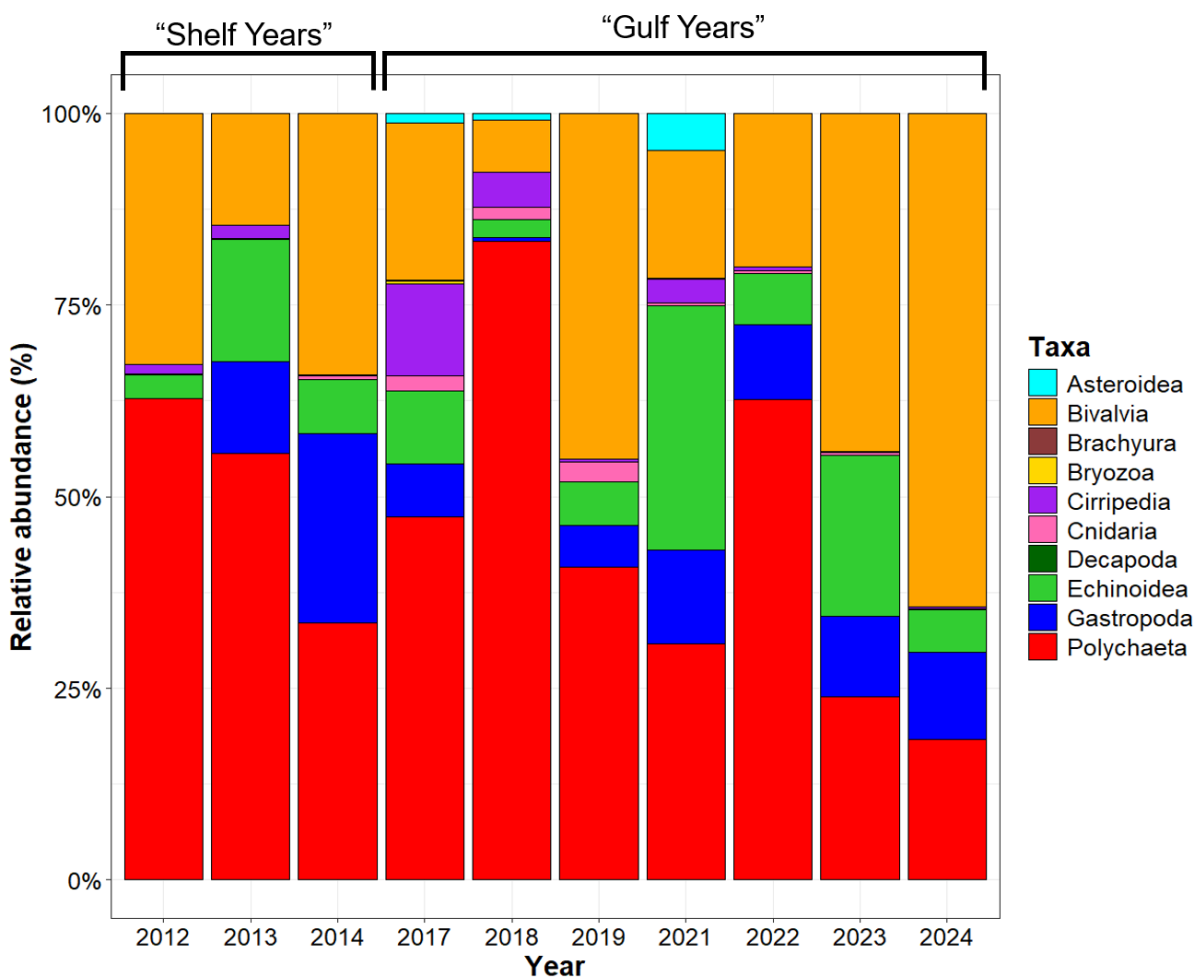


Figure 1.4. Relative abundance (% of total meroplankton) of taxa for each year within the study period. “Shelf Years” include years where the majority of sampling took place on the Mackenzie Shelf. “Gulf Years” include years where sampling primarily occurred in the Amundsen Gulf (Figure 1.1).

The distribution of polychaetes and bivalves followed similar patterns to total meroplankton abundance (Figure 1.3). Polychaete abundance was higher on the Mackenzie Shelf, at stations ≤ 100 m, with highest abundance at a 75 m station (DAL_01, 1270 ind. m^{-3}) in 2012 (Figure 1.5 A). Within the Amundsen Gulf, polychaetes were abundant at stations in-shore and within embayment’s including Franklin Bay, Darnley Bay, Minto Inlet, and around the

ANMPA. Polychaete abundance was highest at a 20 m station nearest Cape Bathurst (CPB_01, 588 ind. m⁻³) in 2022. Bivalve abundance on the Mackenzie Shelf was lower relative to polychaetes (Figure 1.5 B) but had the highest abundance at the shallowest DAL station in 2012 (1001 ind. m⁻³). Within the Amundsen Gulf bivalves were abundant at stations ≤ 100 m especially within Franklin and Darnley bays and around the ANMPA. Bivalve abundance in Amundsen Gulf was highest in 2024 at a 75 m station (CPY_02, 1720 ind. m⁻³), located within the ANMPA.

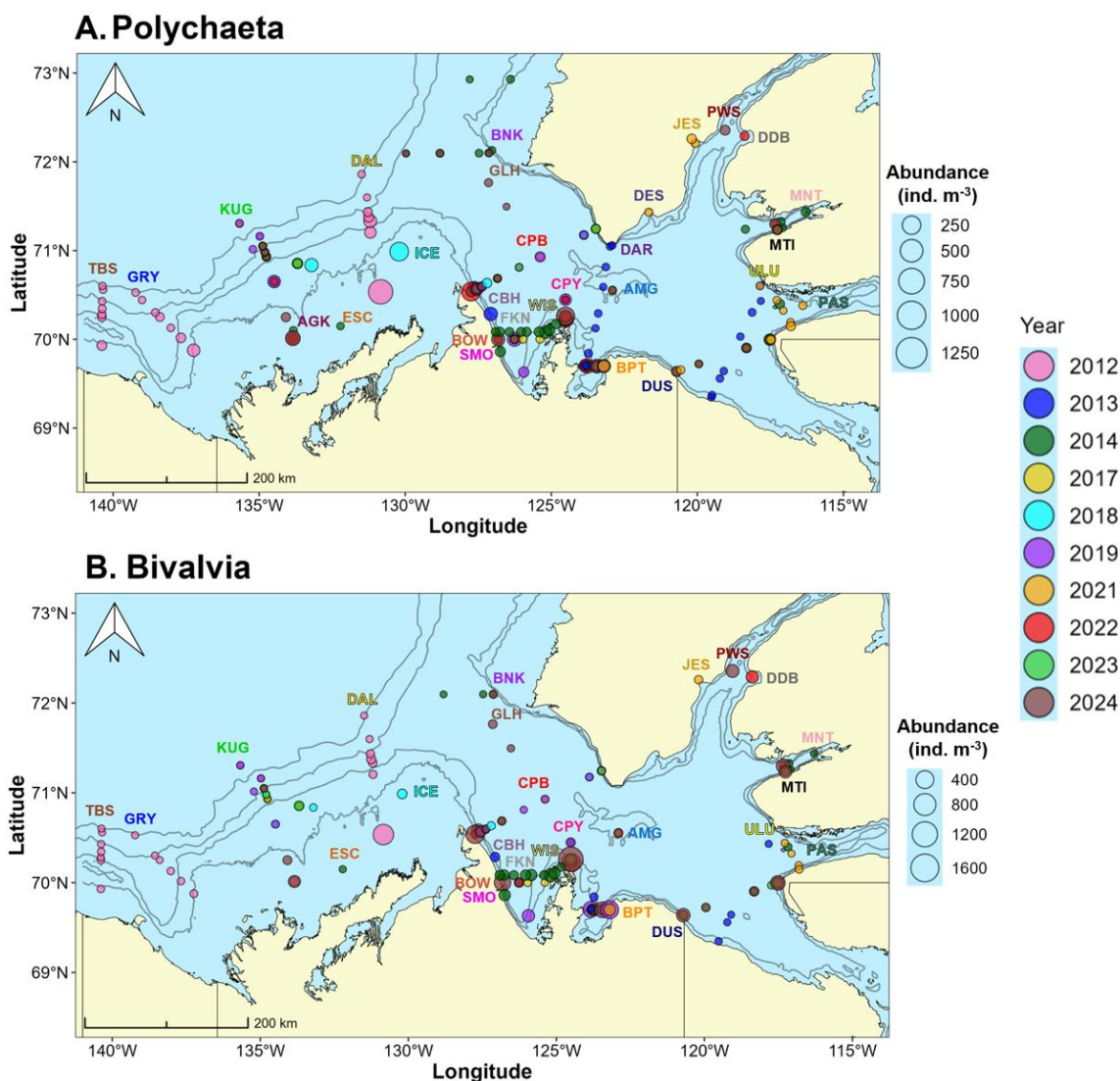


Figure 1.5. Abundance of A) Polychaeta and B) Bivalvia at each sampling station within the 10-year study period. Abundance is represented by circle size on the maps, while colour represents year. Stations may overlap and are identified by transect name.

Out of the 10 meroplankton taxa, Polychaeta, Bivalvia, Cnidaria, Echinoidea, and Cirripedia occurred within all years of the study period, but polychaetes had the highest frequency of occurrence (92.7%) followed by bivalves (71%) and echinoids (69.8%) (Table 1.2). Polychaetes, bivalves, and echinoids had the highest frequency of occurrence in 2012 at 100%, 96%, and 89% of stations, respectively. Polychaete occurrence was lowest in 2023 (74% of stations), while bivalves were lowest in 2013 (38% of stations) and echinoids in 2022 (33% of

stations). Taxa with the lowest average frequency of occurrence included Brachyura (4.8%), Decapoda (1.6%), and Bryozoa (< 1%).

Table 1.2. Average frequency of occurrence (%) of meroplankton taxa identified from 245 samples between 2012 and 2024 ($n = 10$) in the Western Canadian Arctic.

Taxon	Occurrence by year	Frequency of occurrence (%)
Asteroidea	4/10	6.5
Bivalvia	10/10	71
Brachyura	6/10	4.8
Bryozoa	2/10	< 1
Cirripedia	10/10	36.3
Cnidaria	10/10	19.6
Decapoda	2/10	1.6
Echinoidea	10/10	69.8
Gastropoda	9/10	52.2
Polychaeta	10/10	92.7

Meroplankton abundance differed significantly among water masses (Kruskal-Wallis $H_2 = 156.02$, $P < 0.0001$; Figure 1.6) and was consistently lowest in the Atlantic layer (mean of 3 ± 0.44 ind. m^{-3} , $n = 72$) contributing < 6% to total meroplankton over the years (Figure 1.7).

Abundance in the Atlantic water mass differed significantly from the Pacific water mass ($Z = 4.45$, $P < 0.0001$), which had a mean abundance of 5 ± 3 ind. m^{-3} ($n = 146$) and contributed 1% (2022) to 22% (2017) of total meroplankton abundance. Abundance was consistently highest in the surface mixed layer (SML), contributing between 72% (2017) to 98% (2022) of total meroplankton abundance within the water column. Mean abundance of the SML, 46 ± 18 ind. m^{-3} ($n = 206$), was significantly higher than meroplankton mean abundance in the Atlantic ($Z = 11.42$, $P < 0.0001$) and Pacific ($Z = 8.53$, $P < 0.0001$) water masses (Figure 1.6). The relative abundance of meroplankton within water masses also differed among years (Figure 1.8).

Meroplankton in the Atlantic water mass was dominated by polychaetes (> 60%) in all 10 years. In the Pacific water mass, the relative abundance of meroplankton taxa varied among years, with a greater number of taxa present relative to the Atlantic water mass (Figure 1.8). In contrast, the SML had fewer taxa present, but the dominant taxa showed greater inter-annual variability than the dominant taxa of the Pacific layer (Figure 1.8).

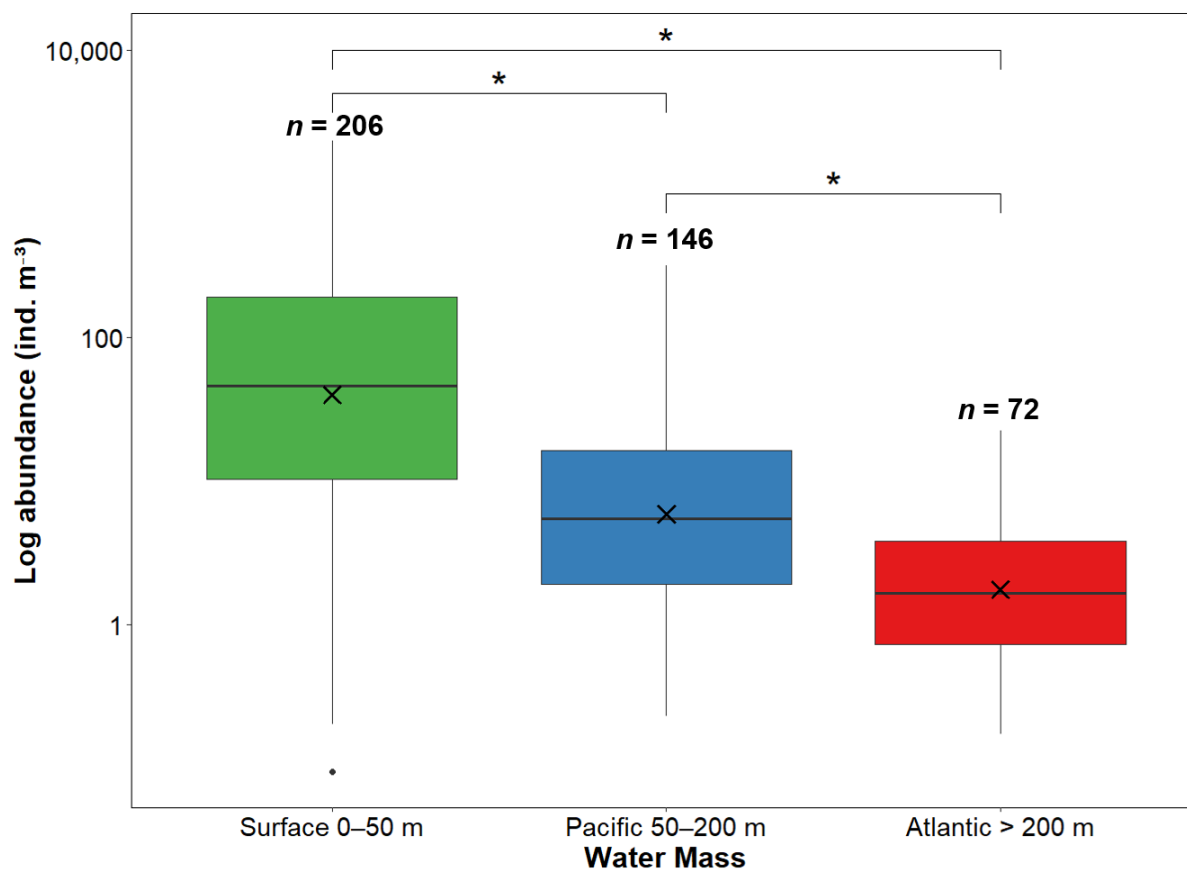


Figure 1.6. Meroplankton abundance in the surface (0–50 m), Pacific (50–200 m), and Atlantic (> 200 m), water masses in the Western Canadian Arctic. Number of samples per water mass are indicated on the plot. Bold horizontal line within each box represents the median, the x indicates the mean, and box spans the interquartile range, encompassing the middle 50% of data. Whiskers extend to the range of the data. Asterisks indicate significant pairwise differences among methods ($\alpha = 0.05$; associated statistics in the text).

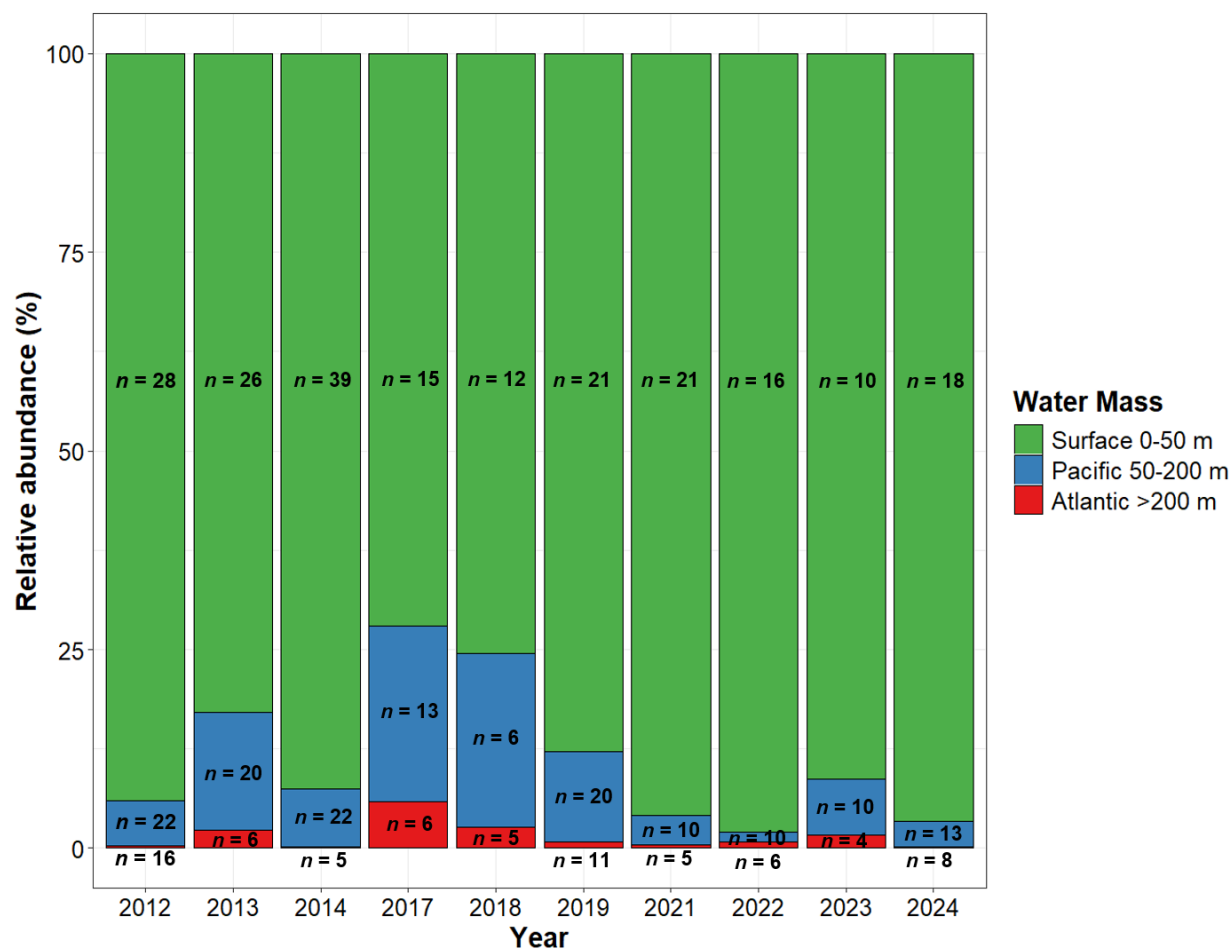


Figure 1.7. Relative abundance of meroplankton (% of total) in the surface (0–50 m), Pacific (50–200 m), and Atlantic (> 200 m) water masses of the Western Canadian Arctic between 2012 and 2024. n = number of samples per water mass.

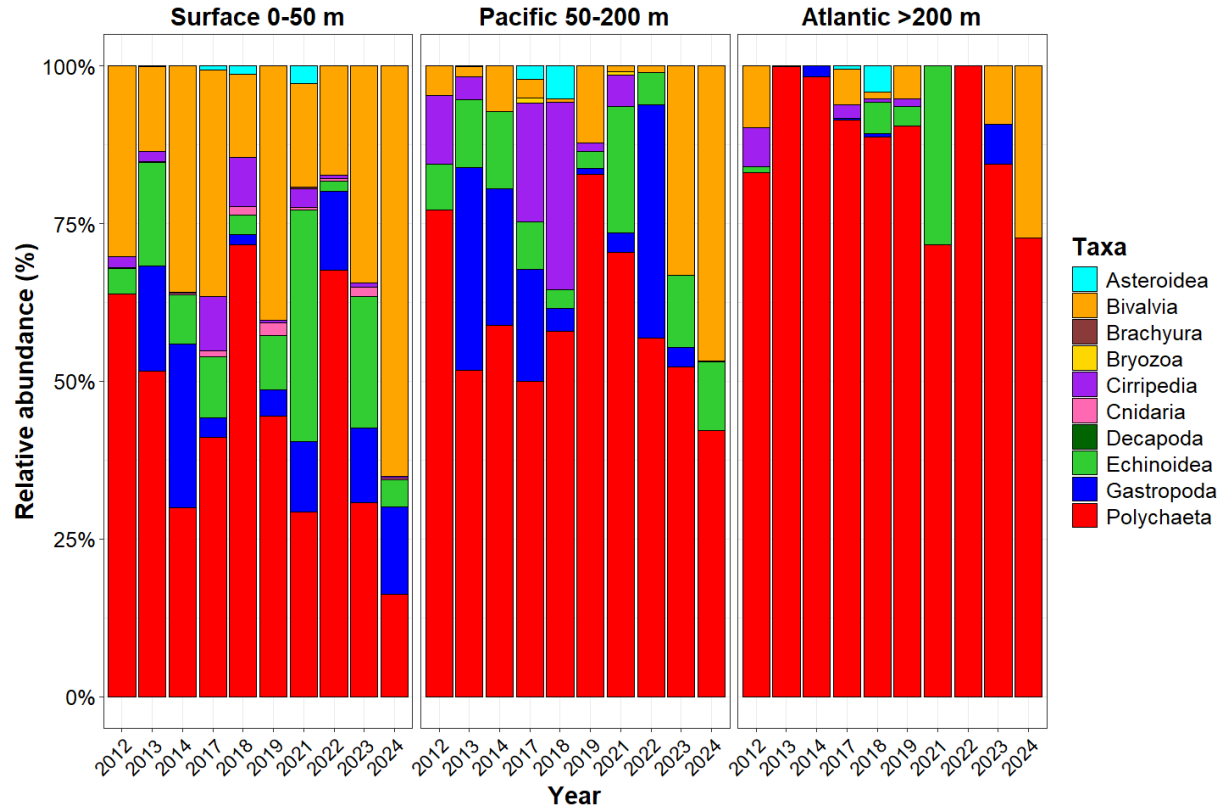


Figure 1.8. Relative abundance (% of total meroplankton) of taxa in the surface (0–50 m), Pacific (50–200 m), and Atlantic (> 200 m) water masses of the Western Canadian Arctic between 2012 and 2024.

Meroplankton Abundance and Environmental Variables

Within the WCA, inter-annual variability was observed among all measured environmental variables (Figure 1.9 A–D). Mean temperature within the SML ranged between 0.9°C in 2013 and 3.2°C 2024 with notable peaks in 2017, 2019, and 2021 and decreases in 2018, 2022, and 2023 (Figure 1.9 A). Surface water freshening was evident in 2013 and 2022 indicated by salinities of < 29 (Figure 1.9 B). Additionally, upwelling of Pacific waters in 2014 and 2023 were evident by surface waters > 30. Fluorescence ranged from 0.313 mg m⁻³ to 0.688 mg m⁻³ with maximum values in 2024. The number of Ice-free days prior to sampling showed high interannual variability (Figure 1.9 D), ranging from 21 (2013) to 68 days (2019).

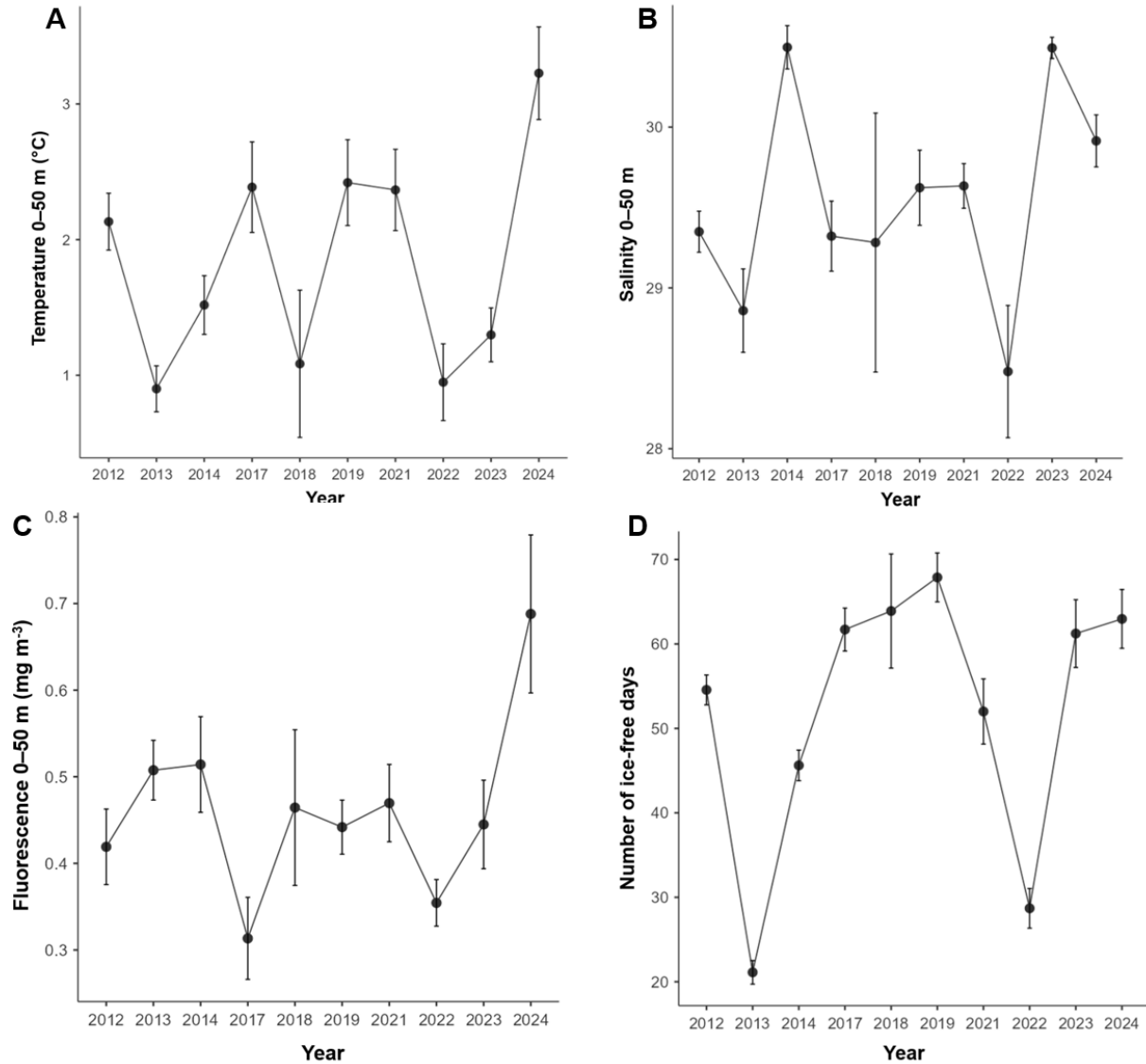


Figure 1.9. Mean surface mixed layer temperature (A), salinity (B), and chlorophyll fluorescence (C) in the Western Canadian Arctic study area and the number of ice-free days (D) prior to sampling between 2012 and 2024. Error bars represent the standard error.

Mixed effects modelling revealed that year explained 19.8% of the variation within meroplankton abundance in the SML (intercept = 0.35, SD = 0.59). Temperature had the largest effect on meroplankton abundance in the SML (estimate = 0.60, $t_{181} = 4.59$, $P < 0.0001$) followed by station depth (estimate = -0.57, $t_{181} = -5.73$, $P < 0.0001$). Salinity in the SML (estimate = 0.43, $t_{181} = 3.26$, $P = 0.0011$), and number of ice-free days (estimate = 0.39, $t_{181} = 3.01$, $P = 0.0026$)

also significantly influenced meroplankton abundance. For the average model, final predictors included temperature, number of ice-free days, and station depth as fixed effects, and year as a random effect. The random effect year accounted for 11.7% of the variation in meroplankton abundance over the water column (intercept = 0.19, SD = 0.44). Station depth had the most significant effect on meroplankton abundance over the water column (estimate = -0.94, $t_{220} = -11.88$, $P < 0.0001$) followed by temperature (estimate = 0.65, $t_{220} = 5.94$, $P < 0.0001$) and number of ice-free days (estimate = 0.35, $t_{220} = 2.90$, $P = 0.0037$).

Generalized linear models revealed year-specific environmental influence not identified by the SML and average models (Table 1.3). Relative to other environmental variables, temperature in the SML had the most significant effect on meroplankton abundance in 2012, 2019, and 2024. Salinity in the SML had the most significant effect on meroplankton abundance in 2013, 2014, and 2017, while fluorescence in the SML influenced meroplankton abundance the most in 2018 and 2023. Number of ice-free days had significant influence on meroplankton abundance only in 2014. No measured environmental variables influenced meroplankton abundance in 2021. Year-specific GLMs for average environmental variables showed slightly different results than the GLMs for the SML (Table 1.4). Temperature was most influential in 2017, whereas salinity has the most significant effect in 2014, 2019, and 2023. In 2018 and 2022 meroplankton abundance was most affected by fluorescence whereas station depth was the only significant factor in 2013.

Table 1.3. Best fit environmental predictors of meroplankton abundance in the surface mixed layer (0–50 m) for each year.

Year	Driver	Estimate	t-statistic	Res.df	P-value	Number of stations
2012	SML temperature	1.24	3.31	21	0.0034	25
	SML salinity	1.20	2.24		0.036	

	Station depth	-0.39	-2.35		0.029	
2013	SML temperature	1.43	1.96		0.0063	
	SML salinity	1.75	2.24	22	0.0009	26
	Station depth	-1.37	-3.25		0.0037	
2014	SML temperature	0.82	2.21		0.003	
	SML salinity	1.95	5.84	32	< 0.0001	36
	Ice free days	0.80	2.51		0.017	
2017	SML salinity	2.14	5.62		0.0002	
	SML fluorescence	1.56	3.19	10	0.0097	14
	Station depth	1.16	2.75		0.021	
2018	SML fluorescence	0.84	2.81	8	0.023	10
2019	SML temperature	0.95	4.01		0.0011	
	SML salinity	0.63	2.54	15	0.019	20
	Ice free days	0.43	1.70		0.11	
	Station depth	-0.36	-1.71		0.11	
2021	None	-	-	-	-	17
2022	SML temperature	1.24	3.48		0.0059	
	SML fluorescence	1.43	2.29	10	0.045	14
	Station depth	-0.99	-4.01		0.0025	
2023	SML fluorescence	-0.98	-3.32	7	0.013	9
2024	SML temperature	0.67	2.34		0.0071	
	SML salinity	0.95	2.66	12	0.021	17
	SML fluorescence	0.22	2.17		0.051	
	Station depth	-0.38	-1.82		0.091	

Table 1.4. Best fit environmental predictors of meroplankton abundance over the water column for each year.

Year	Driver	Estimate	t-statistic	Res.df	P-value	Number of stations
2012	Temperature	0.74	3.74	21	0.0012	25

	Ice free days	-1.30	-3.23		0.004	
	Station depth	-0.79	-5.49		< 0.0001	
2013	Station Depth	-1.56	-2.99	24	0.0063	26
	Salinity	2.51	5.42		< 0.0001	
2014	Ice free days	0.67	1.98	33	0.056	37
	Station depth	-3.67	-6.77		< 0.0001	
	Temperature	-0.66	-3.03		0.0091	
2017	Station depth	-0.45	-2.03	14	0.062	17
2018	Fluorescence	0.98	3.29	8	0.011	10
	Salinity	-0.84	-3.23		0.0041	
2019	Station depth	-0.59	-3.20	21	0.0043	24
	Temperature	0.68	2.93		0.0099	
2021	Station depth	-1.24	-3.52	16	0.0029	19
	Fluorescence	2.97	4.14		0.0007	
2022	Station depth	-0.85	-1.87	17	0.079	20
2023	Salinity	-2.26	-4.84	20	< 0.0001	22
	Temperature	0.52	2.53		0.019	
2024	Ice free days	0.64	2.47	22	0.022	26
	Station depth	-1.30	-3.59		0.0017	

Discussion

Meroplankton Spatiotemporal Variability

Meroplankton in the Western Canadian Arctic showed no increasing or decreasing trend in abundance over the 10-year study period. Variability in abundance indicates a patchy distribution likely influenced by local hydrodynamic processes. For example, the Mackenzie

River plume can act as a physical barrier to offshore larval transportation (Ayata et al. 2011), explaining higher meroplankton abundance at inner and middle shelf stations (≤ 100 m) relative to stations at the outer shelf and slope. The extent of the Mackenzie River plume is altered seasonally and annually due to variation in winds and extent of open water (Carmack and Macdonald 2002). Winds from the east can influence upwelling, potentially retaining meroplankton in the plume which spreads further offshore. Conversely, periods with absent or strong winds from the west can carry the plume and associated meroplankton towards the Amundsen Gulf (Carmack and Macdonald 2002). However, for meroplankton distribution to be influenced by the Mackenzie River plume, meroplankton would have to be within the upper 5–10 m of the water column. Thus, for meroplankton located outside of the influence of the plume, other mesoscale (tens to 100s of km) oceanic processes such as eddies could affect distribution. Eddies cause localized recirculation of water outside the flow of major currents, resulting in the retention of small, passively moving organisms such as meroplankton (Largier, 2003; O'Connor et al., 2007; Cowen & Sponaugle, 2009; Barber et al., 2010; Kubryakov et al., 2021). Eddies and adjacent winds could explain high meroplankton abundance observed at stations along coasts, including the ANMPA area, and in embayments (i.e., Franklin Bay and Darnley Bay). Additionally, the semi-enclosed nature of the bays and slower flow of nearshore waters may further increase retention of meroplankton at these locations (Metaxas, 2001; Largier, 2003).

Drivers of Interannual Variability in Meroplankton

While processes such as currents influenced inter-annual meroplankton distribution, variability in abundance among years was primarily driven by temperature in the SML (0–50 m) followed by biological processes associated with longer open-water periods. Temperature in the SML has higher variability than the lower Pacific or Atlantic water layers due to dynamic sea ice

and surface mixing processes that influence the heat content (Cobb et al. 2008; Wassmann and Reigstad 2011; Darnis and Fortier 2014; Ardyna and Arrigo 2020; Niemi et al. 2024). Increased meroplankton abundance, especially in 2012, 2019, and 2024, associated with higher water temperature suggests thermal conditions enhanced growth and development (Pappalardo et al. 2025). Larval survival likely increased with warmer waters in the SML by reducing time meroplankton spend in the pelagic habitat, decreasing risk in mortality through predation, missing seasonal declines in phytoplankton for planktotrophic individuals, and overdispersion to unfavourable habitats (Kirby et al. 2008).

Timing of ice break-up had a weaker effect on meroplankton abundance than temperature in the SML, and little to no influence in years with high abundance such as 2012 and 2024. Initially, it was expected that higher meroplankton abundance would be linked to later ice break-up, due to a delayed phytoplankton bloom and subsequent meroplankton production. However, high meroplankton abundance was associated with longer open water periods, indicating that early triggering of meroplankton release in response to the phytoplankton bloom that immediately follows ice breakup may benefit the detection of meroplankton in the SML during August. Small meroplankton only a few micrometers in size (e.g. bivalves, polychaetes, echinoids) were detected in the SML frequently and could benefit from a longer open water period due to their low metabolic demand allowing them to consume smaller phytoplankton (e.g., dinoflagellates and ciliates) following the spring phytoplankton bloom (Lindeque et al., 2013; Descôteaux et al., 2022). However, the consumption of the phytoplankton by the smaller-sized meroplankton did not drive a significant correlation between chlorophyll fluorescence and meroplankton abundance.

Meroplankton Community Composition and Abundance within the WCA

Inter-annual variability in meroplankton community structure within the WCA reflected changes primarily in two dominant groups, bivalves and polychaetes. Bivalve larvae occurred frequently in 2012 (96% of stations), 2019 (92% of stations), and 2024 (86% of stations) when mean SML temperatures were high. In this study, stations with the highest recorded surface temperatures also had some of the highest bivalve abundances such as a 40 m station in Cape Parry (CPY_01) in 2024 (8.3°C) with 687 ind. m⁻³, a 20 m station in Cape Bathurst (CPB_01) in 2024 (6.4°C) with 707 ind. m⁻³, and a 20 m station (DAL_01) on the Mackenzie Shelf in 2012 (5.2°C) with 1001 ind. m⁻³. These high abundances agree with studies from Arctic and boreal regions, where larval bivalve veligers also peaked in abundance with high water temperature (Kirby et al., 2008; Fachon et al., 2025; Schrage et al., 2026).

Bivalves and polychaetes are known to dominate late summer meroplankton communities, as observed in the nearby Beaufort Sea (Smoot and Hopcroft 2017) and within other Arctic regions (Fetzer & Arntz, 2008; Kuklinski et al., 2013; Descôteaux et al., 2021; Schrage et al., 2026). However, in some Arctic areas, dominant meroplankton taxa differ seasonally, with groups such as cirripeds (barnacles) driving abundances around the time of the phytoplankton bloom (Highfield et al. 2010). Earlier reproductive periods could explain why cirripeds, though frequently observed, were in low relative abundances during the study period. Differences in meroplankton phenology could also explain rare occurrence of taxa such as Bryozoa, which mostly spawn either in time with the spring phytoplankton bloom or in late autumn/early winter if larvae have internal nutrition reserves (i.e., lecithotrophic) (Silberberger et al., 2016; Descôteaux et al., 2021; Weydmann-Zwolicka et al., 2021; Pappalardo et al., 2025). Furthermore, bryozoan species that do spawn in late summer often have short larval stages that remain close to the seafloor (Kuklinski et al. 2013; Silberberger et al. 2016). This corresponds to

bryozoan larvae observed during the study period, which were reported at three stations (FKN_04 in 2017; PAS_01 and PAS_10 in 2021) in the bottom water mass. Other notably rare taxa for this study area included brachyuran crabs, which were found mainly in Cape Bathurst (CPB), and the east side of the study area (MTI, DUS, PAS, and ULU). To fulfill high metabolic demand, early larval stages of brachyuran crabs such as *Chionoecetes opilio* spawn with the phytoplankton bloom, usually having later stage zoea or megalopa larvae during late summer (Comeau et al. 1998; Jadamec et al. 1999; Orensanz et al. 2004). Additionally, these crab larvae are often larger in size and actively swim within the water column, which can contribute to their low abundance as they may evade vertically towed plankton nets (Questel et al. 2013; Ershova et al. 2019).

Meroplankton Distribution in the Water Column

Spatial and inter-annual variability in abundance have been reported for mero- and holoplankton communities in the study area, the nearby Beaufort Sea (Smoot and Hopcroft 2016; Niemi et al. 2020), and across Arctic regions (Auel and Hagen 2002; Ershova et al. 2019; Schrage et al. 2026). Yet, meroplankton abundance showed a consistent decline from the surface to deeper water masses, similar to holoplanktonic communities. Declining meroplankton abundance with depth is likely linked to optimal conditions for primary productivity in the SML (Darnis and Fortier 2014; Ardyna and Arrigo 2020). It would be advantageous for greater meroplankton abundance at the surface where currents and winds are more dynamic for dispersal relative to slower and more stable subsurface currents in Pacific and Atlantic water masses (Carmack and Macdonald 2002; Byers and Pringle 2006; Ehrman et al. 2022). It is also common for holo- and meroplankton distribution over the water column to be organized by developmental stage, as seen for species such as *Calanus hyperboreus* (Falk-Petersen et al. 2009; Darnis and

Fortier 2014). Earlier and smaller meroplankton developmental stages may be more buoyant and float closer to the surface (Ayata et al. 2011; Meyer-Kaiser et al. 2022; Fachon et al. 2025). Mortality also increases with larval development, with as little as 1% of spawning individuals settling onto the seafloor (Mileikovsky 1971). This could explain lower abundances of meroplankton in deeper water masses, reflecting larvae closer to settling into juvenile or adult stages. However, organization of developmental stages in the water column can be species specific (Ayata et al. 2011; Meyer-Kaiser et al. 2022; Fachon et al. 2025) and would need to be verified through identification of species and their larval developmental stages (e.g., size estimates) within each water mass.

It is important to note that while higher abundance of larvae in the SML coincided with a greater number of meroplankton groups, it is not necessarily a reflection of greater richness. For example, Smoot and Hopcroft (2017) found that even though zooplankton abundance was higher above 50 m, richness increased with depth. Meroplankton richness can not be directly assessed in this study as species-level identification is required. However, identification of meroplankton to lower taxonomic levels is challenging with morphological analysis and requires expertise to properly identify species (Bowden et al. 2009; Ershova et al. 2019; Ruppert et al. 2019; Descôteaux et al. 2021). To mitigate these challenges, metabarcoding approaches could be applied to plankton tows or environmental (e.g., water) samples (Ershova et al. 2019). Incorporating metabarcoding methods could also help to understand within-group interannual trends in community structure and responses to environmental variables that is difficult to assess using taxonomy.

Conclusion

The present study provided the first in-depth assessment into spatiotemporal trends and environmental influence on meroplankton abundance within the Western Canadian Arctic. Consistent with the initial hypotheses, meroplankton abundance showed no temporal trend over the 10-year period and was highest within the surface mixed layer. Highest abundance was consistently observed at stations ≤ 100 m deep on the Mackenzie shelf, around the ANMPA, and within Amundsen Gulf embayments. Contrary to what was expected, temperature rather than number of ice-free days had the strongest influence on meroplankton abundance in the SML, suggesting that direct physiological effects are likely more important than bottom-up food web effects. Release of meroplankton in the WCA may be closely tied to changes in temperature, with warmer temperatures more optimal for growth and development. Though this study provides further understanding of meroplankton abundance and distribution within the WCA, it is not without limitations. For example, without seasonal information, it is not known how meroplankton composition may have varied earlier in the open water period relative to August or during the phytoplankton bloom relative to the post-bloom conditions of the WCA. Examining seasonal variation could highlight peaks in abundance for specific meroplankton groups, providing further insights into why taxa such as Bryozoa are low in abundance during August. High-level taxonomic identification is another limitation, with broad meroplankton taxa underestimating potential spatiotemporal variability in meroplankton richness and within-group community composition. It is recommended to incorporate species-level identification of meroplankton using molecular approaches such as metabarcoding. Information from metabarcoding can offer insight into environmental drivers impacting meroplankton richness and

provide information on life-history strategies for ecologically important species within the Western Canadian Arctic.

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Appendix I

Table A 1.1. August sampling stations in the Western Canadian Arctic including coordinates (DD, decimal degrees), water depth (m), year station was sampled and samples collected during that year (*T* = taxonomic samples, *S* = stratified sampling, and *E* = environmental variables [temperature, salinity, fluorescence, number of ice-free days]).

Station ID	Latitude (DD)	Longitude (DD)	Depth (m)	2012	2013	2014	2017	2018	2019	2021	2022	2023	2024
AGK_01	70.101	-133.829	32			T/S/E							
AMG_03	70.5530	-122.9050	640						T/S/E	T/S/E	T/S/E	T/S/E	T/S/E
AT_01	70.5796	-127.6371	60								T/S/E	T/S/E	T/S/E
BNK_01	72.129	-127.031	50			T/S/E							
BNK_02	72.097	-127.473	350			T/S/E							
BNK_03	72.0932	-129.9720	367			T/S/E							T/S/E
BNK_04	72.0950	-128.8070	382			T/S/E							T/E
BNK_05	72.928	-127.792	251			T/S/E							
BNK_06	72.93	-126.395	58			T/S/E							
BNK_07	72.0982	-127.1410	209			T/S/E							T/S/E
BPT_01	69.7037	-123.8200	41		T/S/E	T/S/E			T/S/E				
BPT_01b	69.6983	-123.7692	75							T/S/E	T/S/E		
BPT_02	69.6997	-123.7870	67		T/S/E	T/S/E							
BPT_03	69.6984	-123.4388	125		T/S/E	T/S/E			T/S/E	T/S/E		T/S/E	T/S/E
BPT_04	69.6982	-123.2420	72		T/S/E	T/S/E							
BPT_05	69.7009	-123.1945	40		T/S/E	T/S/E			T/S/E	T/S/E			

DAR_01	69.704	-123.822	44		T/S/E								
DAR_02	69.841	-123.728	65		T/S/E								
DAR_03	70.125	-123.488	209		T/S/E								
DAR_04	70.292	-123.395	359		T/S/E								
DAR_05	70.59	-123.224	510		T/S/E								
DAR_06	70.815	-123.132	350		T/S/E								
DAR_07	71.046	-122.987	209		T/S/E								
DAR_08	71.059	-122.913	80		T/S/E								
DDB_01	72.2906	-118.3821	46								T/S		
DES_01	71.432	-121.665	24							T/S/E			
DES_02	71.374	-121.576	55							T/S/E			
DUS_02	69.6379	-120.7034	100							T/E	T/E	T/E	T/S/E
DUS_03	69.6537	-120.5722	220							T/E			
DUS_04	69.7235	-119.9500	350								T/S/E	T/E	T/E
DUS_07	69.9032	-118.3335	500				T/S/E	T/S/E	T/S/E	T/S/E	T/S/E	T/S/E	T/S/E
DUS_09	69.9708	-117.7325	200									T/E	
DUS_10	69.9950	-117.5180	100				T/S/E	T/S/E	T/S/E	T/S/E	T/E	T/E	T/E
DUS_11	69.996	-117.481	43							T/S/E			
ESC_03	70.332	-131.015	18			T/S/E							
ESC_04	70.086	-132.144	20		T/S/E	T/S/E							
FKN_01	70.0015	-126.8185	50				T/S/E				T/S/E		T/S/E
FKN_03	70.0015	-126.2507	200				T/S/E		T/S/E		T/S/E	T/S/E	T/S/E

FKN_04	70.0015	-125.9660	150				T/S/E						
FKN_06	70.0015	-125.4060	50				T/S/E						
FKN_07	69.6321	-125.9431	82						T/S/E				
FRK_01	70.0823	-125.1980	36			T/S/E							
FRK_02	70.0823	-125.4200	79			T/S/E							
FRK_03	70.0847	-125.8550	126			T/S/E							
FRK_04	70.0867	-126.0420	202			T/S/E							
FRK_05	70.0838	-126.4300	228			T/S/E							
FRK_06	70.0872	-127.7300	125			T/S/E							
FRK_07	70.0897	-126.9190	39			T/S/E							
GLH_01	71.7633	-127.1387	430										T/S/E
GLH_02	71.4947	-126.5278	450										T/E
GRY_01	69.877	-137.243	46	T/S/E									
GRY_02	70.017	-137.678	76	T/S/E									
GRY_03	70.129	-138.023	199	T/S/E									
GRY_04	70.252	-138.399	346	T/S/E									
GRY_05	70.302	-138.556	502	T/S/E									
GRY_06	70.443	-139.008	760	T/S/E									
GRY_07	70.528	-139.23	1041	T/S									
ICE_01	70.836	-133.208	66					T/S/E					
ICE_03	70.988	-130.208	43					T/S/E					
JES_01	72.209	-120.072	32							T/S			

JES_01.1	72.259	-120.195	40							T/S			
KUG_01	70.0115	-133.8437	20	T/S		T/S/E	T/S/E	T/S/E			T/S/E		T/S/E
KUG_01b	70.2498	-134.0834	40										T/S/E
KUG_01c	70.6487	-134.4753	60					T/S/E	T/S/E		T/S/E		
KUG_02	70.8497	-134.6758	75	T/S/E		T/S/E	T/S/E					T/E	
KUG_03	70.9300	-134.7543	200	T/S/E		T/S/E	T/S/E				T/S/E	T/E	T/E
KUG_04	70.9812	-134.8050	350	T/S/E		T/S/E	T/S/E	T/S/E	T/S/E		T/S/E	T/S/E	T/S/E
KUG_05	71.0487	-134.8720	500	T/S/E		T/S/E	T/S/E		T/S/E		T/S/E	T/E	T/S/E
KUG_06	71.1573	-134.9798	750	T/S/E					T/S/E				
KUG_07	71.2852	-135.1045	1000	T/S/E			T/S/E		T/S/E				
KUG_08	71.015	-135.216	1250						T/S/E				
MNT_01	71.2316	-118.3690	215			T/S/E							
MNT_02	71.2594	-117.0840	281			T/S/E							
MNT_03	71.3253	-117.1500	155			T/S/E							
MNT_04	71.3944	-117.1960	80			T/S/E							
MNT_05	71.4347	-116.3010	154			T/S							
MTI_03	71.3682	-117.4730	150								T		
MTI_04	71.2988	-117.3387	175								T		T
MTI_05	71.2345	-117.2690	280					T/S		T/S	T/S	T/S	T/S
PAS_01	70.441	-117.2808	300							T/S/E			
PAS_02	70.3236	-117.0598	280							T/S/E			
PAS_03	70.3823	-116.3892	190							T/S			

PAS_05	70.1921	-116.8125	182							T/S/E			
PAS_05B	70.148	-116.8015	50							T/S/E			
PWS_05	72.3566	-119.0509	78										T/S/E
SMO_01	69.862	-126.745	40			T/S/E							
TBS_01	69.93	-140.386	50	T/S/E									
TBS_02	70.252	-140.385	77	T/S/E									
TBS_03	70.281	-140.385	203	T/S/E									
TBS_04	70.345	-140.373	350	T/S/E									
TBS_05	70.429	-140.376	501	T/S/E									
TBS_06	70.559	-140.343	774	T/S/E									
TBS_07	70.602	-140.366	1040	T/S/E									
ULU_01	69.347	-119.52	41		T/S/E								
ULU_02	69.371	-119.498	77		T/S/E								
ULU_03	69.559	-119.228	197		T/S/E								
ULU_04	69.643	-119.096	348		T/S/E								
ULU_05	70.031	-118.529	451		T/S/E								
ULU_06	70.304	-118.126	351		T/S/E								
ULU_07	70.432	-117.828	92		T/S/E								
ULU_08	70.6016	-117.8550	210		T/S/E					T/S/E			
WIS_01	70.1046	-125.0620	55			T/S/E							
WIS_02	70.1735	-124.8345	44			T/S/E							

Chapter 2. Metabarcoding reveals patterns in richness and distribution of larval benthic invertebrates in the Western Canadian Arctic

Abstract

Pelagic larval stages (meroplankton) play a key role in determining the distribution and composition of benthic invertebrates on the Arctic seafloor. Information on how environmental variables influence meroplankton richness and distribution is critical, as meroplankton survival is highly sensitive to oceanographic change which influences development to juvenile or adult life stages. However, knowledge of meroplankton community structure remains limited in areas such as the Western Canadian Arctic (WCA) due to challenges with identifications to lower taxonomic levels using morphological taxonomy. This study applied metabarcoding sampling approaches to increase understanding of meroplankton community structure in relation to local adult benthic invertebrate communities and environmental conditions. Community (net) DNA ($n = 10$ plankton nets) and environmental DNA (eDNA; $n = 10$ water samples) methods detected substantially higher richness (112 taxa) than morphological taxonomy (6 taxa), while also detecting taxa not previously recorded in the region. At the surface (0–50 m), higher meroplankton richness was detected in net DNA (55) compared to eDNA (36), reflecting known differences in DNA origin, persistence, and transport. Meroplankton communities at the surface (net DNA, surface eDNA) and 5–10 m off the seafloor (bottom eDNA, $n = 10$) revealed differing patterns in richness and distribution likely from bottom communities reflecting a mixture of larval and adult DNA. Meroplankton composition at the surface showed limited spatial overlap with adult benthic invertebrates observed in ($n = 8$ box cores) and on ($n = 9$ trawls) sediments, supporting the hypothesis that long-distance dispersal decouples larval stages from adult spawning populations. Patterns of surface meroplankton richness showed a positive correlation

with number of ice-free days, suggesting earlier ice break-up extends primary productivity and prolongs larval production. Though driven by ice-mediated ecosystem phenology, environmental analyses indicated that meroplankton community composition at the surface was best explained by increased fluorescence and salinity, reflecting combined influence of food availability and stratification-driven habitat conditions. These findings highlight the importance of integrating molecular tools for a comprehensive understanding of seafloor invertebrate communities in the WCA. It is recommended for future work to expand on reference databases for Arctic marine invertebrates and look at seasonal variability in shaping meroplankton community structure.

Introduction

Many benthic invertebrates have a bi- or multi-phase life cycle containing a low motile or sessile (i.e., sedentary) adult stage residing in or on the seafloor, and a free-floating, pelagic larval stage referred to here as meroplankton. (Levin & Bridges, 1995; Calado & Leal, 2015; Silberberger et al., 2016; McBride et al., 2024). Through ocean currents, meroplanktonic life stages aid in the dispersal and maintenance of benthic invertebrate populations (Cowen & Sponaugle, 2009; Short et al., 2013; Silberberger et al., 2016; Ronowicz et al., 2024). However, meroplankton have also been recognized as limiting factors in the long-term preservation of benthic invertebrate community structure within ecosystems due to sensitivity to changes in water temperature, salinity, primary productivity, and sea ice dynamics (Thorson 1950; Thorson 1966; Cowen and Sponaugle 2009; Shanks 2009; Pandori and Sorte 2019; Ronowicz et al. 2024). Within the upper water column (i.e., 0–50 m) meroplankton are subjected to different environmental conditions than juvenile or adult benthic life stages and may respond to environmental variables differently (Ehrman et al., 2022). In addition, meroplankton behaviour and development are different than benthic life stages and largely variable across benthic invertebrate species (Thorson 1950; Mileikovsky 1971; Pechenik 1999). Thus, to gain a more holistic understanding of benthic invertebrate population dynamics, establishing a region-specific knowledge of meroplankton community composition, distribution, and relationships to environmental variables is critical (Calado & Leal, 2015; Fuchs et al., 2020; Trembl et al., 2015).

Despite the importance of meroplankton in benthic invertebrate life cycles, they are often overlooked in benthic and zooplankton studies due to their microscopic sizes, being unrecognizable from adult stages, and looking morphologically similar to one another (Bowden et al. 2009; Ershova et al. 2019; Descôteaux et al. 2021). This becomes challenging in

constructing lower-level taxonomic identifications (e.g., to genus or species) of individuals using morphological taxonomy (Gluchowska et al. 2016). Thus, metabarcoding sampling approaches using bulk organismal (hereafter referred to as net DNA) or environmental DNA (eDNA) have been recommended to obtain more detailed information of meroplankton community structure (Ruppert et al. 2019; Spear et al. 2021).

Use of molecular approaches to detect of many organisms within a single sample (i.e., metabarcoding) in marine environments have substantially increased in studies examining community structure of fish (Oka et al. 2021; Larson et al. 2022), zooplankton (Djurhuus et al. 2018; Ershova et al. 2021), and meroplankton (Ershova et al. 2019; Descôteaux et al. 2021). For meroplankton, bulk samples have been collected using conventional surveying methods (i.e., zooplankton nets) and genetic material extracted using previously established techniques (Lindeque et al. 2013; Berry et al. 2023), which has significantly increased detection of species. A study from the northern Barents Sea by Ershova et al. (2021) found zooplankton richness to be three to four times higher in net DNA samples compared to morphological taxonomy. Environmental DNA has provided similar benefits but is a less invasive method using shed genetic material from an organism (i.e., feces, skin, or hair) collected from environmental samples such as water or sediments (Muha et al. 2017; Chen 2021). Leduc et al. 2019 found that out of 202 invertebrate genera identified across three locations in the Canadian Arctic using eDNA, only 9–15% were also identified morphologically.

Incorporation of metabarcoding has helped to improve knowledge on ecological communities relative to morphological taxonomy (Baker et al. 2016); however, there are limitations in using this method in lieu of morphological taxonomy that should be taken into consideration. Often, false detection of species occurs from prolonged eDNA persistence in the

water that degrades quality (Collins et al. 2018) or from contamination of DNA samples during collection or extraction (Ershova et al. 2019; Berry et al. 2023). The persistence of eDNA in the water is controlled by abiotic factors such as temperature and biotic factors such as microbial communities, such that eDNA may remain detectable within the water column from weeks to years depending on conditions (Thomsen and Willerslev 2015; Collins et al. 2018). Additionally, reference databases lacking genetic information of benthic invertebrates can result in underrepresentation of species within communities (Chen 2021). To detect an organism using metabarcoding, reference sequences need to be present in databases such as GenBank (Rodríguez-Ezpeleta et al. 2021). However, in understudied areas such as coastal Arctic regions, only half of known benthic invertebrates are present in databases, which limits identifying individuals to lower taxonomic levels (Lacoursière-Roussel et al. 2018). In Arctic regions such as the Western Canadian Arctic (WCA), morphological taxonomy used to monitor meroplankton have only provided higher-level taxonomic identifications (e.g., class or family), which can result in broad assumptions on meroplankton community dynamics, but fails to understand species-level composition and distribution within the environment. Thus, incorporation of metabarcoding would complement morphological taxonomy to help provide a more complete understanding of community composition, distribution of individuals within ecosystems, and relationships to environmental conditions (Deiner et al. 2017; Ruppert et al. 2019).

Using meroplankton data collected from 10 sites within the WCA during an offshore survey conducted in August 2024, the main objectives of this study were to use metabarcoding sampling approaches (net DNA, eDNA) to examine meroplankton distribution, composition, and richness relative to local adult communities and environmental variables. It was hypothesized that meroplankton community structure would differ depending on the sampling approach used

such that net DNA and eDNA would detect more taxa at lower levels (i.e., species or genus) than morphological taxonomy. It was expected that meroplankton would show a decoupling and spatial mismatch in community composition compared to adult life stages, as colder water temperatures resulting in longer larval development times likely dispersed meroplankton far from spawning adult populations prior to sampling. Lastly, it was hypothesized that food availability, important for growth and development, would be the most important environmental variable influencing distribution of meroplankton communities such that stations with higher fluorescence would have higher meroplankton richness.

Methods

Sample Collection

Samples were collected in the Western Canadian Arctic (including the Mackenzie Shelf and Amundsen Gulf) (see Thesis Introduction Figure 1) in 2024 from a stern trawler (F/V Frosti). Sampling was conducted between the 9th and 24th of August at ten stations (Figure 2.1) representing a wide range of depths and oceanographic conditions within the WCA (Table 2.1).

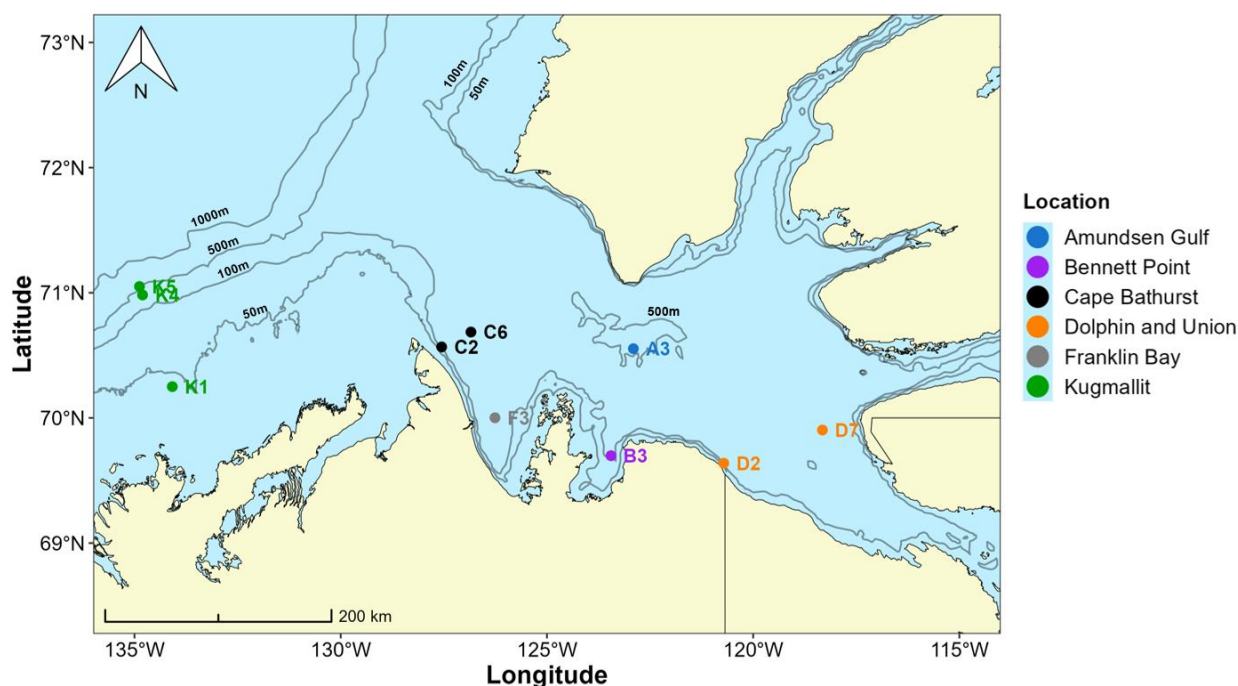


Figure 2.1. Station locations in the Western Canadian Arctic where meroplankton and adult benthic invertebrate samples were collected in August 2024. Station locations colour coded by region. Further station details in Table 2.1.

Table 2.1. Sampling location/stations in the Western Canadian Arctic including station code, coordinates (DD, decimal degrees), sampling date (day/month/year) water depth (m), and type of samples collected (*E* = *eDNA*, *N* = *net DNA*, *X* = *meroplankton for morphological taxonomy*, *B* = *adults collected using box cores*, and *T* = *adults collected using trawls*).

Location/Station	Station code	Latitude (DD)	Longitude (DD)	Date	Depth (m)	Sample type
Amundsen Gulf/AMG_03	A3	70.5533	-122.9171	24.08.2024	640	E/N/X/B/T
Bennett Point/BPT_03	B3	69.6975	-123.4342	21.08.2024	125	E/N/X/T
Cape Bathurst/CPB_02	C2	70.5650	-127.5534	13.08.2024	128	E/N/X/B/T
Cape Bathurst/CPB_06	C6	70.6877	-126.8341	14.08.2024	300	E/N/X/B/T
Dolphin and Union/DUS_02	D2	69.6397	-120.7017	29.08.2024	100	E/N/X/B/T
Dolphin and Union/DUS_07	D7	69.8968	-118.325	28.08.2024	500	E/N/X/B/T

Franklin Bay/FKN_03	F3	69.9985	-126.2518	22.08.2024	215	E/N/X/B/T
Kugmallit/KUG_01B	K1	70.2498	-134.0834	07.08.2024	40	E/N/X
Kugmallit/KUG_04	K4	70.9835	-134.7965	08.08.2024	350	E/N/X/B/T
Kugmallit/KUG_05	K5	71.0521	-134.8617	09.08.2024	500	E/N/X/B/T

Taxonomy sample collection and processing

Meroplankton

Meroplankton samples for morphological analysis were collected by conducting a vertical tow from 50 m to the surface with a Hydrobios Midi Multinet (MPS) (0.5 m², 150 µm mesh screen). This surface layer generally has the highest zooplankton abundance and concentration of chlorophyll *a* of the water column (Darnis et al., 2014). A flow meter attached to the net was used to determine the volume of water filtered (m³). Each sample was concentrated on a 145 µm mesh screen, transferred to a Nalgene sample bottle, and then fixed in a borax-buffered seawater solution with a final concentration of 4% formaldehyde (gram:gram). Meroplankton were counted within a sub-sample taken with a Henson-Stempel pipette. A minimum of 300 individuals were counted which included both holo- and meroplankton and identified to the lowest possible taxonomic level. Meroplankton samples were sent and analyzed using the same morphological keys for zooplankton to the Université Laval, Quebec City, Canada and Biologica Environmental Sciences (for stations B3 and F3), Victoria, Canada.

Adult Benthic Invertebrates

Adult benthic invertebrates were sampled with different methods to encompass both epifaunal and infaunal communities (living on and in seafloor substrates respectively) (see Table 3.1). Epifauna were collected at nine stations using a Benthic Beam Trawl (BBT; High-Life 3 m

trawl) with a 0.63 cm square mesh cod-end and towed for ten minutes. The net depth was recorded using a Marport sensor, and trawl speed was measured three times during each deployment using the ship's Global Positioning System (GPS). Following protocols from Niemi et al. (2020), epifaunal invertebrates were separated from non-target specimens (e.g., fish) immediately on deck and brought to the ship's laboratory for further processing. Specimens were then sorted and identified to the lowest possible taxonomic level, usually species, weighed, and enumerated. Individuals for which identification was uncertain were photographed and frozen at -50°C for subsequent identification at the Maurice Lamontagne Institute, DFO Quebec, Mont-Joli, Canada. Infauna were collected at eight stations (Table 3.1) using a 0.5 m² box corer (Precision Enterprises, Dartmouth, NS). Following Niemi et al. (2020), infauna samples were taken above the clay layer, which occurred at depths ranging from 7 to 25 cm among stations. After residual water was drained from the core's surface, sediment from approximately half of each core (~0.25 m²) was gently sieved over a 0.5 mm stainless steel mesh using seawater, to remove all sediments. All infauna on the sieve was then transferred to benthic jars and preserved with 4% borax-buffered formaldehyde. Infauna were later sorted from the sediment using a stereomicroscope, identified, and enumerated at the benthic ecological laboratory, Université Laval, Quebec, Canada.

Metabarcoding: Sample Collection and Extraction

Net DNA

Samples for net DNA were collected using the same MPS system as for the morpho-taxonomic samples. A single net sampled the surface layer of the water column (0–50 m depth) which was sieved over a 145 µm mesh screen and fixed in 95% ethanol. To minimize

contamination between samples, all equipment (i.e., gloves, forceps, sieve) and work surfaces were cleaned with ELIMINase (Deacon Labs Inc.) between samples and stations.

For laboratory processing, lab surfaces and equipment were cleaned using a 15% bleach solution (left for 10 min), followed by ElimINASE. For each station, the bulk zooplankton samples were inverted ~30 times and subsampled into six 50 mL falcon tubes. Samples were then centrifuged for 10–15 min at 5000 rpm, and the majority of the ethanol supernatant was removed. The remaining pellet and residual liquid from the six tubes were pooled, inverted 30 times, and redistributed into two 50 mL falcon tubes. Material from one falcon tube was homogenized for 30 s using a PowerGen 1000 S1 homogenizer (Fisher Scientific; New Hampshire, United States). Following homogenization, 5 mL of the sample was aliquoted into five 2 mL safe-lock tubes (1 mL per tube). To minimize cross contamination when homogenizing, the blade on the homogenizer was soaked in a 25% bleach solution for 10 min and rinsed three times with deionized (DI) water. One extraction blank (1 mL of 99% ethanol) was included per station. All aliquots and blanks were placed with caps removed in a Vacufuge (Eppendorf; Hamburg, Germany) for approximately 3 h until all excess ethanol was evaporated.

Extraction of DNA was performed in a clean laboratory following protocols from the DNeasy Blood and Tissue Kit (QIAGEN; Hilden, Germany) with the following modifications: 1) 900 μ L of ATL buffer added to each aliquot; 2) bead homogenization of aliquots (5 mm stainless steel beads) using a Tissue Lyser II (QIAGEN, Hilden, Germany) at 30 hertz for 10 s; 3) 100 μ L of proteinase-K added and aliquots incubated for 2 h at 56 °C; 4) 20 μ L RNaseA added to lysate and incubated at room temperature for 10 min; 5) lysates transferred to 15 mL falcon tubes, mixed with 2 mL of AL buffer and ethanol, and loaded onto spin columns for multiple rounds; 6) spin columns washed with 500 μ L AW1 and AW2 and incubated at room temperature for 2 min

before centrifuging; 7) an additional dry spin after adding AW2 at 13,200 rpm for 3 min to ensure the membrane was dry; and 8) DNA eluted in 300 μ L of AE buffer. Quantity and quality of DNA were assessed using a Qubit fluorometer (Fisher Scientific), Nanodrop 2000 (Fisher Scientific), and 2% pre-cast agarose e-gels (Invitrogen; California, USA). The three aliquots with the highest DNA concentration (i.e., highest Qubit reads and strongest e-gel bands) and best quality DNA (i.e., best 260/280 and 260/230 reads on the nanodrop) were selected and pooled to form a single station level subsample for further analyses.

Environmental DNA (eDNA)

Environmental DNA (eDNA) samples were collected at surface and bottom depths using 8 L Niskin bottles mounted on a 16-bottle rosette water sampler equipped with a Seabird SBE9+ (CTD) and a handheld Smith-Root sampler with self-preserving filters (Thomas et al. 2019). A 0.22 μ m pore size filter was used for meroplankton, consistent with previous Arctic marine studies (e.g., Ershova et al., 2021; Galaska et al., 2023; Kawakami et al., 2023). Surface eDNA (0–50 m) consisted of integrated water collected from four depths (i.e., 5 m, 10 m, 20 m, chlorophyll (chl) *a* maximum). The chl *a* maximum was identified from peak fluorescence measured by the CTD, usually occurring between 40 and 50 m. This sampling design was used to help ensure comparability with net DNA and taxonomic samples collected over the same depth range (0–50 m). Bottom eDNA was collected from 5–10 m above the seafloor depending on weather conditions during sampling. Environmental DNA was collected at the bottom of the water column as sampling followed the spring phytoplankton bloom, when meroplankton may reside closer to the bottom in preparation for settlement to the seafloor (Highfield et al. 2010; Descôteaux et al. 2021).

A total of 4 L of water was filtered for the surface (1 L of water from each of the four surface depths) and bottom samples. Filters were stored at -80°C in sterile packaging provided by Smith-Root until extraction. Sampling for eDNA at associated depths was done in triplicate to account for variability in DNA recovery. Between samples and stations, all equipment and working surfaces were cleaned with ELIMINase. Additionally, to monitor potential contamination during sample collection, 1 L of MilliQ water was filtered as a field control sample at each station. MilliQ water was used instead of the ship's reverse osmosis (RO) water to reduce the risk of contamination, however due to logistical constraints in shipping MilliQ water to the research vessel, controls were limited to one litre per station.

Samples and blanks were processed at the Environmental Genomics Laboratory (Fisheries and Oceans Canada Pacific Biological Station, Nanaimo, BC) for extraction, PCR and library preparation, and bioinformatics. Environmental DNA was extracted using a DNeasy Blood and Tissue Kit following the manufacturer's protocols with the following modifications: 1) filters incubated in 720 µL ATL buffer; 2) 80 µL of proteinase-K added and samples incubated for 2 h at 56 °C; 3) 4 µL of RNase A (100 mg/mL) added to lysate; and 4) 200 µL of the AL buffer and ethanol added to lysate prior to spin column purification with repeated rounds of adding lysate to the spin column. An extraction blank was completed for each batch of extractions (23 samples plus one blank) as part of the negative control system.

PCR and Library Preparation

A ~313 base pair (bp) fragment from the 5' region of the COI gene (Leray et al. 2013) was used and included the forward primer mlCOIintF 5'-GGWACWGGWTGAACWGTWTAYCCYCC-3' and reverse primer jgHCO2198 5'-TAIACYTCIGGRTGICCRAARAAYCA-3'. This primer set was validated and proved efficient

across phyla such as Arthropoda, Mollusca, Cnidaria, Annelida, Chordata, Echinodermata, and Bryozoa (Leray et al. 2013). To reduce tag jumping in eDNA amplicon pools, mirrored septamer tags were attached to the 5' end of each forward and reverse primer (Carøe & Bohmann, 2020). To increase positional diversity for net DNA subsamples and eDNA samples, 0–4 additional nucleotides with a minimum of three mismatches between them were added. Triplicate Polymerase Chain Reactions (PCR) were performed at a final volume of 25 μ L with the following reagents at final concentration for net DNA: 1x buffer; 0.2 mg/mL bovine serum albumin (BSA); 2.5 mM $MgCl_2$; 0.2 mM dNTPs; 0.2 μ M each of forward and reverse primers; and 1 U of Taq. Reagents for eDNA at final concentration were as follows: 1x HotStarTaq MasterMix; 0.2 mg/mL BSA; and 0.3 mM of forward and reverse primers. Cycling conditions for PCR consisted of a denaturing step of 5 min for net DNA and 15 min for eDNA at 95°C followed by 35 cycles of denaturation at 95°C for 30 s; annealing at 54°C for 90 s; extension at 72°C for 60 s; and a final extension at 72°C for 10 min. To monitor for reagent contamination, a no template control (NTC) was added during PCR and downstream library preparation.

Library preparation for net DNA, eDNA, blanks, and NTCs was completed following the PCR-free Tagsteady protocol (Carøe and Bohmann 2020). Triplicate PCRs were pooled at a final volume of 75 μ L. To normalize the amount of amplified DNA from each eDNA sample and marker, relative strength of PCR products was assessed on pre-cast 3% agarose gels (BioRad). Products were scored by eye based on strength of the band, and a sample volume between 5 μ L (strongest band) and 50 μ L (no visible band) was added to one of 41 twin-tagged pooled libraries. Due to lower number of subsamples for net DNA ($n = 21$), the normalization step into library pools was omitted and each subsample treated as its own library (21 libraries total).

Libraries were purified with SPRI beads at 1.8x for net DNA and 1.5x for eDNA to remove extra primers, enzymes, and unused dNTPs.

Libraries were quantified on a Qubit prior to adaptor ligation (1:10,000 dilution). Briefly, 2 pmol of each library was adjusted to 30 μ L for end repair using EBT buffer (10 mM Tris-HCl, 0.05% Tween-20, 4.945 mL molecular grade water). End repair for each library included the following reagents at final concentration: 0.1875 U/ μ L Klenow fragment, 0.5 U/ μ L T4 PNK, 0.125 mM dATP, 1x T4 DNA ligase buffer, and reaction booster (1.25% PEG, 20mM NaCl, 0.1 mg/mL BSA). Plates were incubated at 37°C for 30 min followed by 65°C for 30 min. Full-length Y-adapters with 3' dT overhangs (xGen™ UDI-UMI Adapters from IDT) with the Illumina TruSeq backbone were added to each amplicon library. The Y-shaped adapters were ligated to each other by the manufacturer and consist of 3' dT overhangs containing dual matching indices for identifying tag-jumping on the flow cell. Adapters (3 μ L) were ligated to amplicon libraries with the following reagents at final concentration: 1x T4 DNA ligase buffer, 6.25% PEG, 8 U/ μ L T4 DNA ligase. Plates were incubated at 20°C for 30 min then 65°C for 10 min.

Each library was purified using 2x volume and 1.5x volume SPRI beads for net DNA and eDNA, respectively and quantified using the NEBNext™ Library Quant Kit for Illumina following manufacturer protocols. Equimolar amounts of each library were pooled into a final sequencing library with a final molarity of 12 nM in 250 μ L volume for net DNA and 6.7 nM in 175 μ L volume for eDNA. A final size selection step using 1.7x SPRI beads was conducted to remove residual fragments less than 100 base pairs (bp) and checked using 1% pre-cast agarose gels. The final net DNA library was sequenced on one lane of an Illumina NovaSeqX instrument using a 300 cycle (PE2x150bp) kit. For eDNA, the final library was sequenced on one lane of an

Illumina NextSeq instrument using a 300 cycle (PE2x150 bp) kit. Both net DNA and eDNA sequencing was completed at GenomeQuebec, Montréal, QC.

Bioinformatics

Illumina TruSeq adapters from forward and reverse sequences and terminal end bases (i.e., ambiguous nucleotides) were removed until all sequences indicated high quality read scores (Phred score > 33). Sequences shorter than 100 bp after trimming were discarded to maintain meaningful sequence lengths for downstream bioinformatics. For pooled eDNA libraries, inline barcodes were demultiplexed to identify sequences belonging to each station. An initial demultiplexing step sorted sequences based on a strict match (up to one bp mismatch) followed by a second demultiplexing using a relaxed sequence matching step (up to three bp mismatches). Primers were trimmed from forward and reverse sequences with degenerate bp included for broad taxonomic coverage. Sequence pairs where both forward and reverse primers were not found were discarded to ensure only amplicon-targeted sequences were kept for downstream analyses. A maximum of two bp mismatches were allowed in primer recognition. All adapter and primer trimming and demultiplexing was done using Cutadapt v5.1 (Martin, 2011).

To avoid truncated or poor-quality consensus sequences (Callahan et al. 2016), only forward sequences were used for downstream analyses as they are more reliable for clustering and taxonomic assignments (Antich et al. 2021). Forward sequences containing ambiguous nucleotides or those outside of the expected amplicon range for COI (i.e., < 100 bp, > 400 bp) were discarded using Vsearch v2.30.4 (Rognes et al., 2016). Within and across samples, sequences amplified during PCR were dereplicated and collapsed into one representative sequence using Vsearch. Dereplicated sequences were then clustered into metagenomic operational taxonomic units (OTUs) based on a clustering distance threshold of one nucleotide

using SWARM v2.0 (Mahé et al., 2015). Compared to previous clustering methods, SWARM clustering is highly reliable as it removes centroid selection and reduces likelihood of arbitrary or inaccurate OTUs (Mahé et al., 2014).

Following clustering, a chimera check, defined as two replicated sequences of differing species combining during PCR (Edgar et al. 2011), was done using Vsearch. Chimeras can result in false detections of species and were thus removed to avoid inflation of richness (Edgar et al. 2011; Callahan et al. 2016). An OTU table was created prior to taxonomic assignment in eDNAFlow v1.0 (Mousavi-Derazmahalleh et al., 2021). All OTUs were BLASTed against the MIDORI2 unique COI database (GB255) using BLAST+ (Camacho et al., 2008). Taxonomic assignment used the eDNAFlow lowest common ancestor algorithm with default parameters of 97% sequence similarity and 100% sequence length. If an OTU shared > 97% similarity to two or more taxa, they were assigned to the next taxonomic level up. Additionally, if matches to reference sequences were less than 100%, sequences remained unassigned. A final taxon table was generated in R v4.5.2 (R Core Team, 2024) by collapsing all OTUs with identical taxonomic assignment and summing reads across replicates within each sample.

Data Processing

For eDNA, associated depths (surface and bottom) were analyzed separately as there was high likelihood of capturing two different communities (e.g., early versus late meroplankton stages). Triplicate eDNA samples at each station were combined for the datasets. To remove any possible sources of contamination, sequences of taxa found in station or extraction blanks were subtracted from sequences of taxa found in the subsequent station sample as they were processed simultaneously. Furthermore, sequences found in the NTCs were subtracted from taxa sequences at all stations as they were processed concurrently during library preparation. Following the

removal of blanks, any taxa with ≤ 5 sequences at a station were considered ‘undetected’ and removed from the dataset.

Environmental Sampling

At all stations, temperature ($^{\circ}\text{C}$), salinity, and chlorophyll fluorescence (mg m^{-3} , used as a proxy for phytoplankton biomass) were measured using a rosette mounted Seabird SBE9+ CTD. All data was collected from the downcast. To examine environmental relationships with meroplankton at the surface, temperature, salinity, and fluorescence within the surface mixed layer (SML) at each station were calculated by averaging CTD values over 0–50 m. To examine environmental relationships with meroplankton at the bottom, temperature and salinity were calculated by averaging three CTD measurements 5–10 m above the sea floor. As expected, fluorescence levels were negligible in bottom waters below the photic zone and were thus excluded from subsequent analyses.

Ice break-up dates were obtained from multi-satellite sensor data (AVHRR+VIIRS; <https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html>) at 0.25° resolution and processed at the Freshwater Institute, Fisheries and Oceans, Canada. Following Walsh et al. (2022), break-up date was defined as either the last day for which ice concentration over the preceding two weeks exceeded a threshold calculated as the maximum winter mean minus two standard deviations or remained below 15% concentration within the grid. Ice break-up dates were then used to determine the number of ice-free days, defined as the number of days between the sampling date and break-up date at each station.

Statistical Analysis

Within the meroplankton datasets (i.e., surface eDNA, bottom eDNA, net DNA, and taxonomy), only meroplankton were retained for analyses in the present study. Accordingly, holoplanktonic taxa (e.g., copepods, chaetognaths) were excluded from the datasets. The cnidarian genus *Obelia* was retained because its life cycle includes a medusa stage that produces pelagic larvae (Boero et al. 2007). Hyper-benthic taxa (e.g., shrimp, amphipods) were also excluded in the meroplankton and epifaunal datasets as they live at the sediment water interface and their potential for vertical migration make them difficult to classify as strictly benthic. Additionally, parts of specimens, unidentifiable juvenile individuals, and any infaunal or epifaunal taxa that did not have a meroplanktonic stage in their life cycle, based on literature from the Arctic Traits Database were removed. Three polychaete worms in the infaunal dataset (*Glyphanostomum pallescens*, *Paradiopatra quadricuspis*, and *Praxillura longissima*) lacked life history information on the presence of a meroplanktonic stage, however pelagic larval development was reported in the Arctic Traits Database for a majority of other taxa in the family or genus. Thus, these three polychaetes were retained in the infaunal dataset. To avoid over-estimating richness, higher level taxa (e.g., genus or family) were retained in meroplankton and adult (i.e., epi- and infaunal datasets) only when no corresponding lower-level identifications were present in the dataset. For example, the taxa Ampharetidae spp. was excluded from the infaunal data when a species level assignment of *Amphicteis gunneri* was already identified. Final meroplankton and adult richness was defined as number of species and taxa including genus or family.

For each sampling approach and associated depth (i.e., net DNA [0–50 m], surface eDNA [0–50 m], and bottom eDNA [5–10 m off seafloor]), species accumulation curves were generated to determine whether sampling effort for metabarcoding approaches was adequate to characterize

regional taxon richness. Sequencing-depth rarefaction curves were generated for each sampling approach and depth to evaluate whether sequencing effort (number of reads) was sufficient to characterize meroplankton OTU richness. Pie charts showed the contribution of each phylum to total taxon richness for each method and sampling depth, expressed as the percentage of taxa belonging to that phylum relative to the total richness (i.e., number of taxa within each phylum divided by total richness x 100). Venn diagrams were also used to visualize shared taxa among sampling approaches and associated depths. Differences among sampling approaches and associated depths were assessed using non-parametric Kruskal-Wallis tests for total meroplankton richness and richness for the three phyla with the highest % contribution to total richness. When the overall test was significant, post-hoc test pairwise comparisons (i.e., Dunn's test) were conducted to identify differences among sampling approaches and depths. Results were visualized using boxplots. Prior to this analysis, data were examined for normality using the Shapiro-Wilk test and for homogeneity of variance using Levene's test. Neither raw or transformed data (i.e., log and square root) met assumptions of normality and/or equal variance across sampling approaches or depths. Plots were generated using R (Version 4.5.2; R Core Team, 2025) and RStudio (Version 2026.01.1+403; Posit Team, 2025) with the packages *vegan* (species accumulation and rarefaction curves; Oksanen et al. 2025), *ggplot2* (pie charts and box plots; Wickham et al. 2019), and *VennDiagram* (Chen, 2022). Statistics were done in R and RStudio using the package *rstatix* (Kassambara, 2025).

Multivariate analyses were used to examine meroplankton community composition among metabarcoding sampling approaches and associated depths, and between meroplankton and adult benthic invertebrate communities. Prior to analysis, two datasets were created by combining data from metabarcoding sampling approaches and associated depths (i.e., the

meroplankton dataset) and metabarcoding sampling approaches, associated depths, and adult sampling approaches (i.e., the adult/meroplankton dataset). When combining the meroplankton and adult/meroplankton datasets, taxon/species identifications were grouped to a common higher-level classification when the level of taxonomic identification varied among sampling approaches. For example, bottom eDNA detected two species in the family Maldanidae (*Rhodine gracilior* and *Maldane sarsi*), whereas net DNA only identified to family, then the species in the meroplankton dataset these were lumped as Maldanidae spp. Meroplankton and adult/meroplankton presence-absence data were converted to resemblance matrices using the Sørensen-Dice index, which quantifies the proportion of shared taxa between samples, ranging from “0” (no shared taxa) to “1” (identical composition) (Clarke and Gorley 2015). Principal Coordinate Ordination (PCO) plots were then generated separately for the two datasets (PRIMER v7 + PERMANOVA). Taxa with a Pearson correlation coefficient of ≥ 0.65 with the ordination axes were overlaid as vectors on the PCO plots, where the arrows point in the direction of maximal variation in community composition, and their length reflects the strength of the relationship (Ramette 2007).

Permutation Multivariate Analysis of Variance (PERMANOVA; 9999 permutations) was used to test the null hypothesis that community composition does not differ between sampling approaches and associated depths nor between meroplankton and adult benthic communities. When significant effects were detected, pair-wise comparisons were used to determine which groups differed. Since PERMANOVA is sensitive to within group variability (dispersion), homogeneity of multivariate dispersion was assessed prior to analyses using PERMDISP. A Principal Coordinates Ordination plot was also generated for the environmental data (i.e., temperature, salinity, fluorescence, number of ice-free days, station depth). Prior to analysis,

environmental variables were examined for interrelationships and skewness using pairwise scatter plots (i.e., Draftsman plots) in PRIMER. Variables showing strong skewness (i.e., surface temperature) were log-transformed. Variables were examined for co-linearity and none showed high correlation to each other (Pearson co-efficient ≥ 0.95). Thus, all environmental variables were kept for further analyses. Environmental variables were standardized using Z-scores, and a resemblance matrix was generated using Euclidean Distance.

To examine relationships among patterns in meroplankton, benthic adult communities, and environmental variables, the “Relate” function (PRIMER v7 + PERMANOVA) was used to test the congruence between resemblance matrices using Spearman rank correlations. The null hypothesis was that there is no relationship between the compared matrices, with Spearman rank correlation coefficients (ρ or ρ_{ho}) approaching “1” indicating strong similarity in spatial patterns (9999 permutations). To examine the extent to which environmental variables explained variation in the meroplankton community composition, a distance-based linear model (DistLM) was performed using environmental variables as predictors and a resemblance matrix of meroplankton presence/absence data as the response. A stepwise selection procedure based on Akaike Information selection Criterion corrected for small sample size (AICc) was used to identify the best fit model. Results were visualized using distance-based redundancy analysis (dbRDA; Legendre & Anderson, 1999) which illustrated relationships between meroplankton community structure and the environmental variables most strongly associated with observed variation.

Results

Meroplankton Community Structure

A total of 112 taxa were detected using the combined metabarcoding sampling approaches (net DNA [0–50 m], surface eDNA [0–50 m], bottom eDNA [5–10 m off the seafloor]), with substantial overlap between taxa (Figure 2.2). Metabarcoding detected more species/taxa than morphological taxonomic analysis, which identified six meroplankton taxa with no species-level identifications (i.e., four to class-level, one to subclass, one to genus). Net DNA detected 55 meroplankton taxa including 45 species, eight genus, and two family-level identifications. Surface eDNA detected 36 taxa, of which 28 were to species and eight to genus. Lastly, bottom eDNA detected 84 taxa including 64 to species, 16 to genus, and four to family. None of the species accumulation curves for the sampling approaches and associated depths reached an asymptote (Figure 2.3). However, sequencing-depth rarefaction curves levelled off at approximately 55, 30, and 80 OTUs for net DNA, surface eDNA, and bottom eDNA, respectively (Figure 2.4).

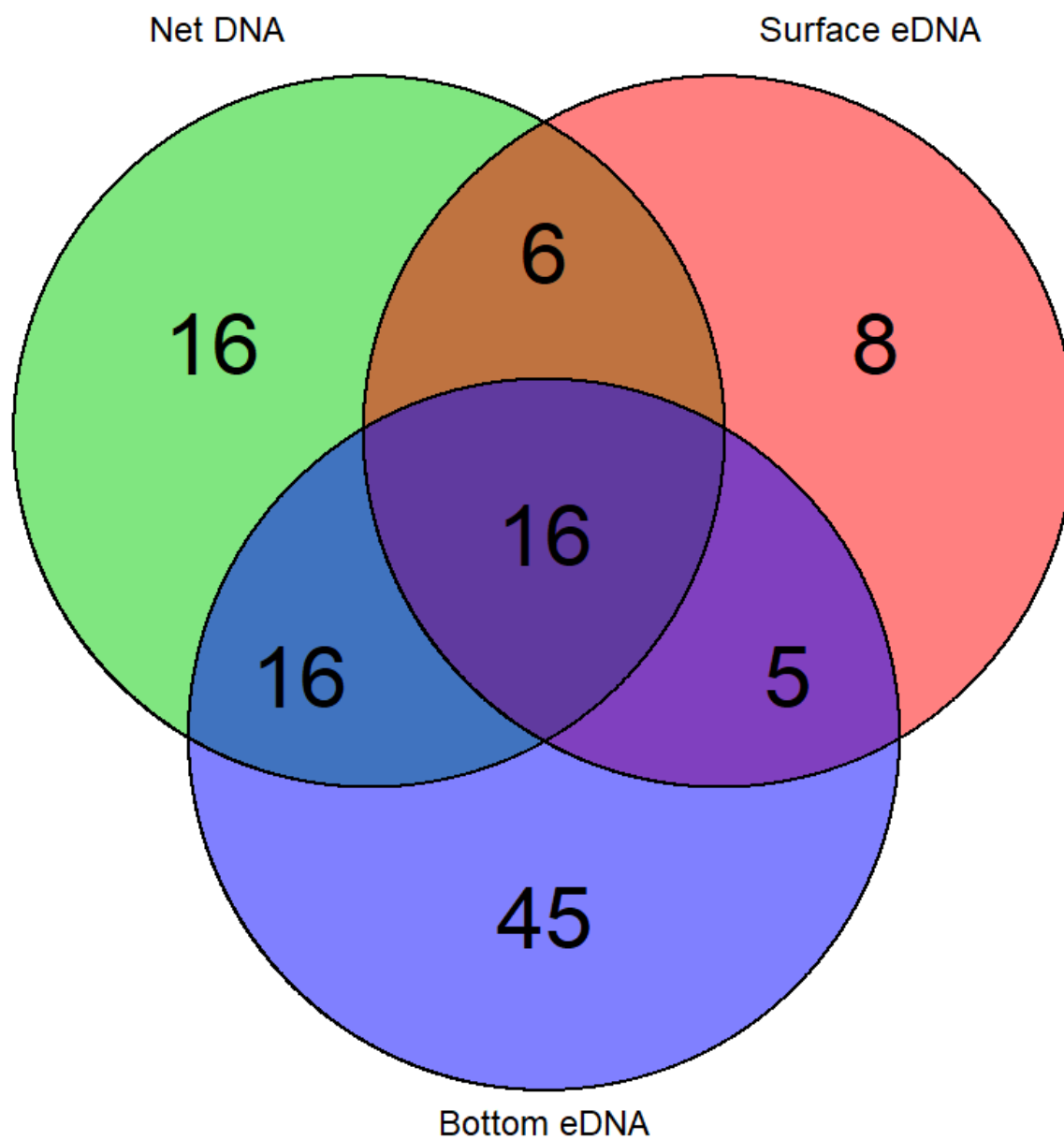


Figure 2.2. Venn diagram showing the number of species/taxa shared among and unique to net DNA (0–50 m), surface eDNA (0–50 m), and bottom eDNA (5–10 m off the seafloor) samples.

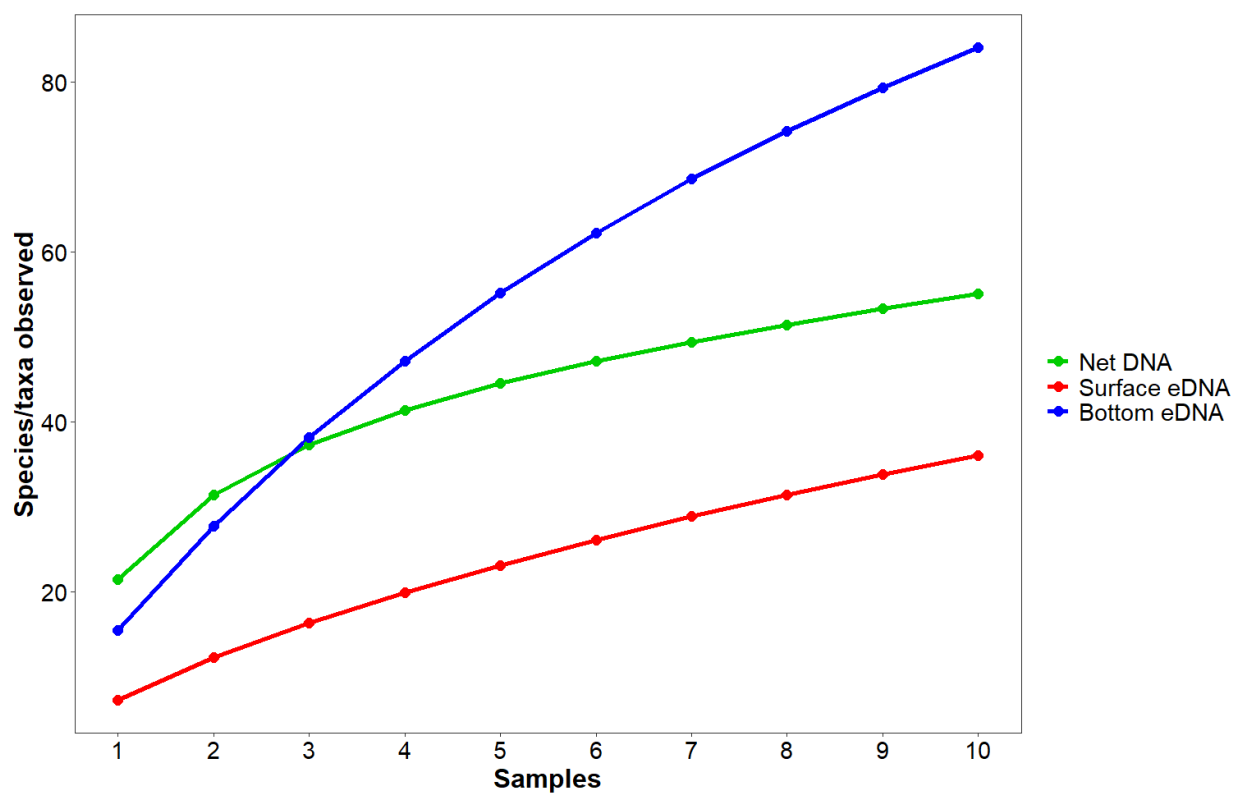


Figure 2.3. Meroplankton species accumulation curves identified by metabarcoding of A) net DNA (0–50 m), B) surface eDNA (0–50 m), and C) bottom eDNA (5–10 m off the seafloor) taken in the Western Canadian Arctic.

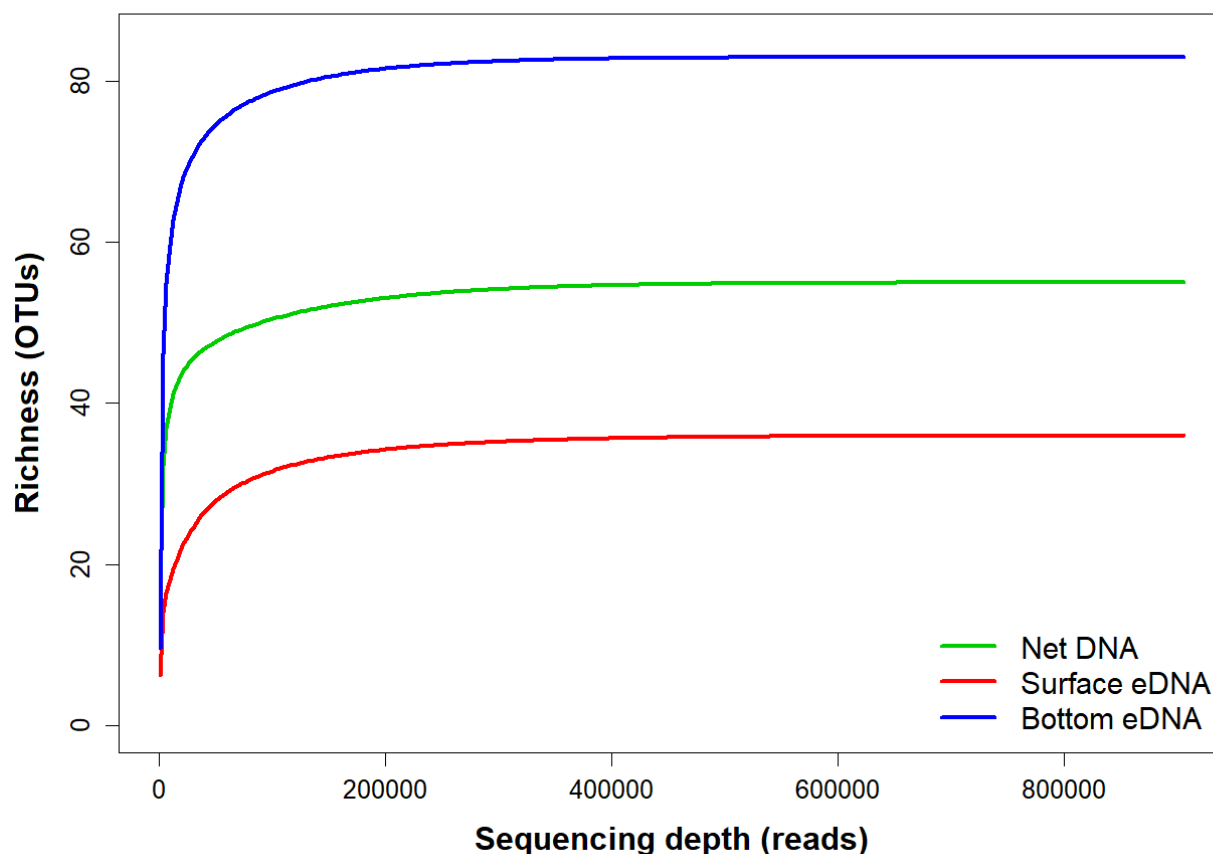


Figure 2.4. Rarefaction curves showing the observed species richness (operational taxonomic units; OTUs at 97% similarity) as a function of sequencing depth (number of reads) for net DNA (0–50 m), surface eDNA (0–50 m), and bottom eDNA (5–10 m off the seafloor).

The number of phyla detected was highest in bottom eDNA ($n = 10$), followed by net DNA ($n = 7$) and surface eDNA ($n = 4$) (Figure 2.5). Annelida, Mollusca, and Echinodermata consistently accounted for the largest proportion of taxon richness across all methods and sampling depths, with Annelida contributing 45.8–55.6%, Mollusca 16.9–25.0%, and Echinodermata 13.9–19.3% (Fig. 2.5 A–C). Surface and bottom eDNA both most frequently detected the bivalve *Kurtiella* sp. (90% of stations), whereas net DNA most frequently detected the bivalve *Macoma balthica* (100% of stations).

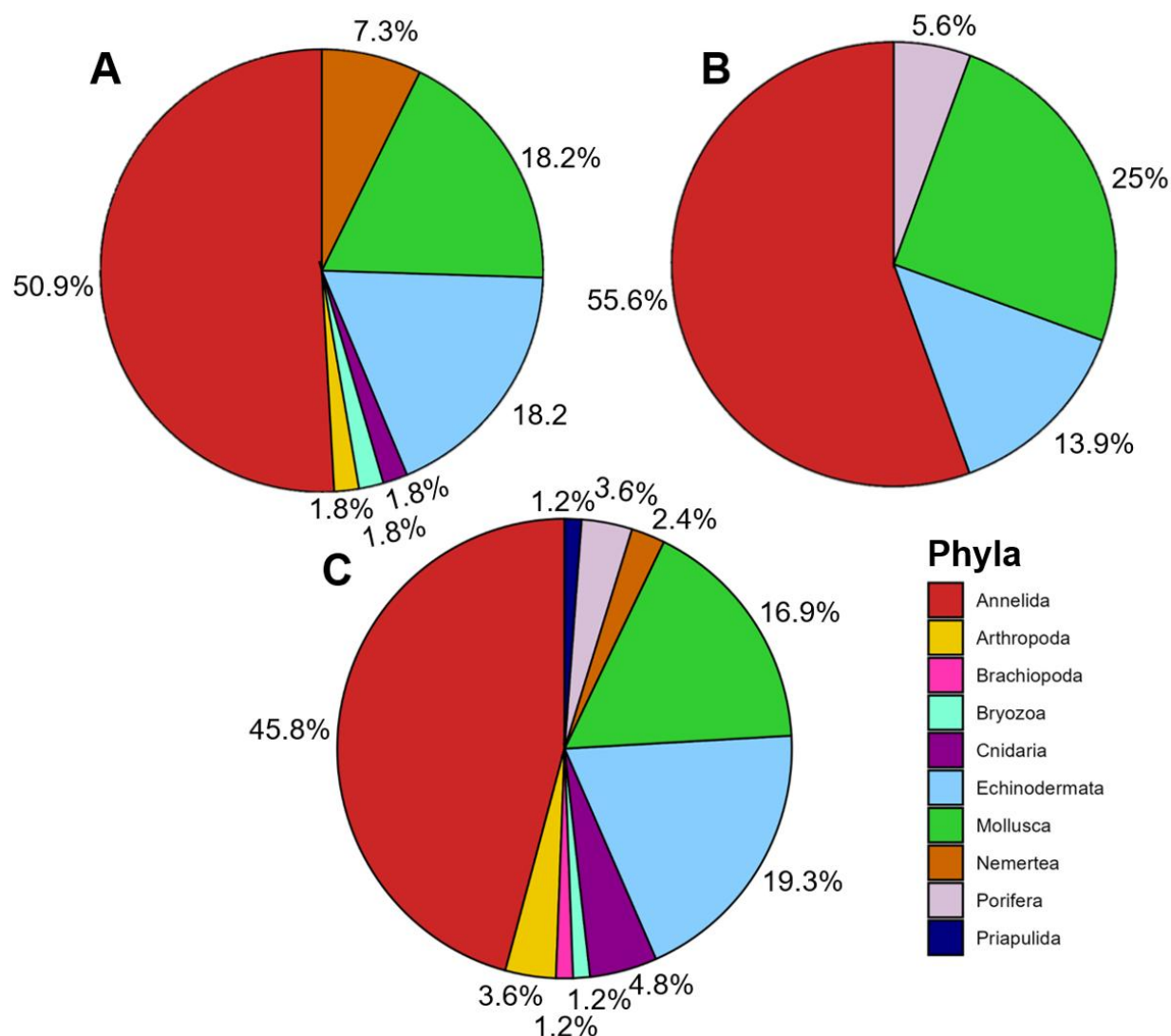


Figure 2.5. Percent contribution of each Phylum to total richness in A) net DNA (0–50 m), B) surface eDNA (0–50 m), and C) bottom eDNA (5–10 m off the seafloor).

Meroplankton richness was highest for surface meroplankton (net DNA and surface eDNA) at station D2 in Dolphin and Union Strait, while station C2 in Cape Bathurst showed the highest richness for bottom eDNA (Figure 2.6). The Kugmallit stations on the Mackenzie Shelf (Figure 2.1) had the lowest overall richness, with station K5 showing the lowest richness for net DNA and bottom eDNA and K4 as the lowest for surface eDNA. Meroplankton richness significantly varied between sampling approaches and depths ($H_2 = 12.72$, $p = 0.0017$). Richness

in surface eDNA samples (Figure 2.7), was significantly lower than both net DNA ($Z = 3.47$, $P < 0.001$) and bottom eDNA ($Z = -2.44$, $P = 0.015$). Within the three most frequently occurring taxa (Echinodermata, Mollusca, Polychaeta), richness also differed significantly among sampling approaches and depths (Table 2.2). At the surface, net DNA detected significantly higher meroplankton richness for all three phyla compared to eDNA (Table 2.2). However, both methods detected similar group richness across regions, with consistently high richness at Dolphin and Union, Amundsen Gulf, and Bennett Point, and low richness at Kugmallit (Figure 2.8). Richness patterns across depths also differed depending on the sampling approach (Table 2.2). For molluscs, bottom eDNA richness was significantly lower than net DNA, but did not differ from surface eDNA (Table 2.2). In contrast, polychaete and echinoderm richness in bottom eDNA was similar to net DNA, but significantly higher than surface eDNA. Spatially, bottom eDNA differed compared to net DNA and surface eDNA (Figure 2.8). In particular, Kugmallit stations showed variable richness among taxonomic groups in bottom eDNA, whereas Cape Bathurst stations showed consistently high richness.

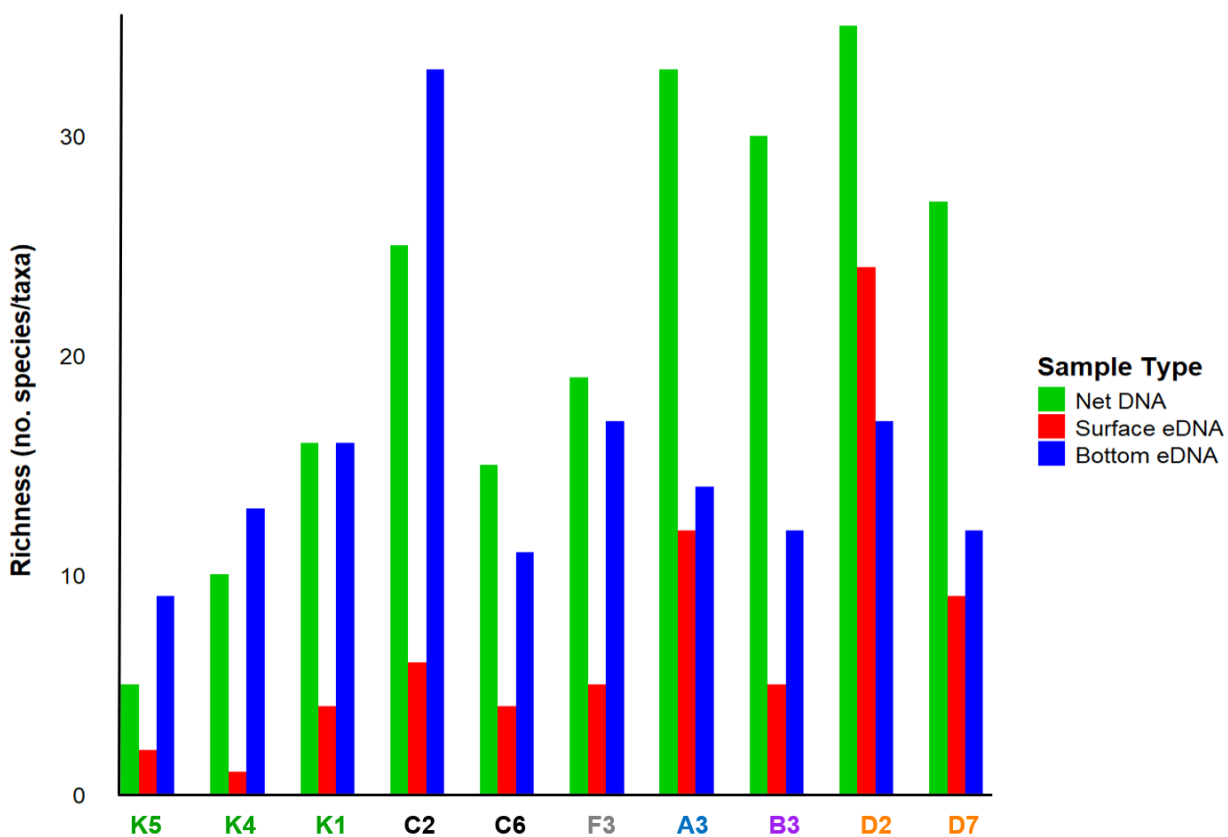


Figure 2.6. Meroplankton species/taxon richness at each station for net DNA (0–50 m), surface eDNA (0–50 m), and bottom eDNA (5–10 m off the seafloor). Stations are ordered along the x-axis by longitude (west to east) across the study area (Figure 2.1).

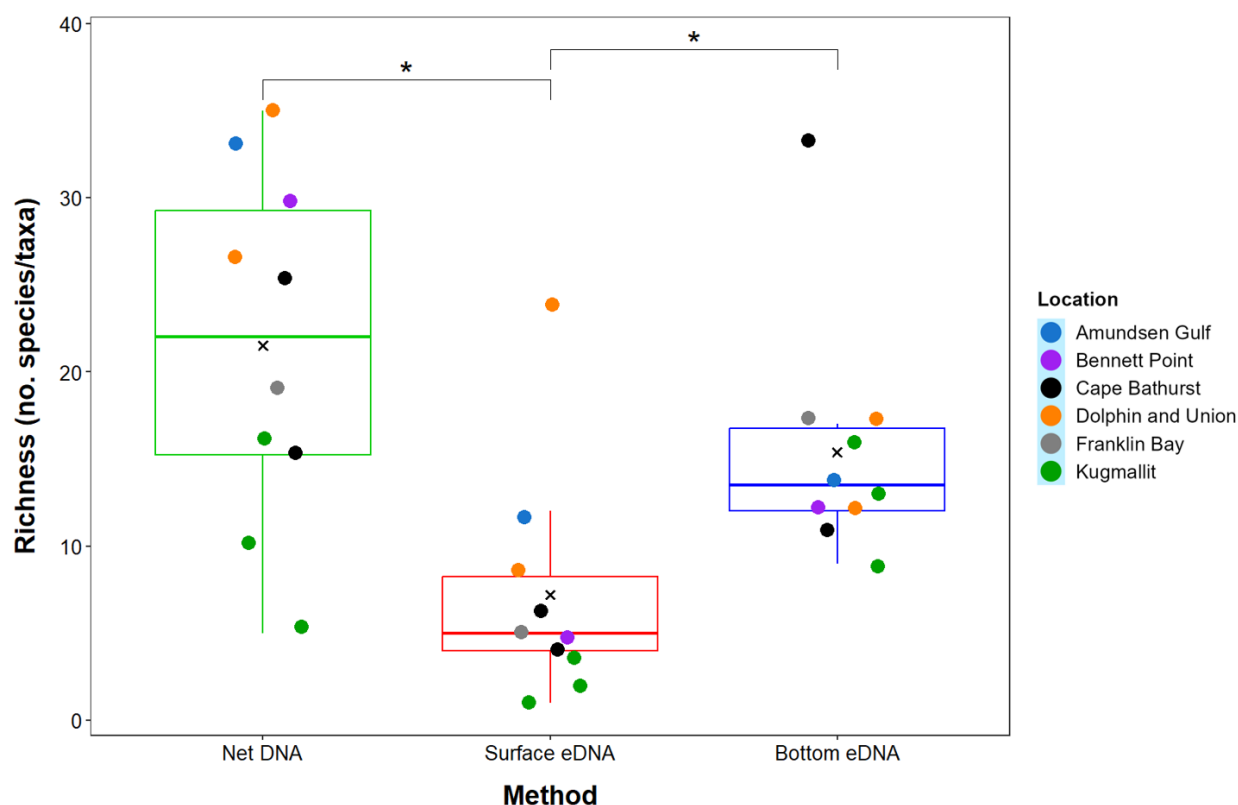


Figure 2.7. Meroplankton richness detected in net DNA (0–50 m), surface eDNA (0–50 m), and bottom eDNA (5–10 m off the seafloor). Bold horizontal line within each box represents the median, the x indicates the mean, and box spans the interquartile range, encompassing the middle 50% of data. Whiskers extend to the range of the data, and jittered points represent sampling station, colour coded by locations within the Western Canadian Arctic. Asterisks indicate significant pairwise differences among methods ($\alpha = 0.05$; associated statistics in the text).

Table 2.2. Pairwise differences in polychaete, echinoderm, and mollusc species/taxon richness among sampling approaches and associated depths (based on Dunn’s post-hoc test).

Major taxa group	Method 1	Method 2	Z-stat	P-value
Echinodermata	Bottom eDNA	Surface eDNA	-2.59	0.01
Echinodermata	Bottom eDNA	Net DNA	-0.34	0.74
Echinodermata	Surface eDNA	Net DNA	2.25	0.025
Mollusca	Bottom eDNA	Surface eDNA	-0.34	0.74
Mollusca	Bottom eDNA	Net DNA	2.21	0.027
Mollusca	eDNA top	Net DNA	2.54	0.011

Polychaeta	Bottom eDNA	Surface eDNA	-2.34	0.019
Polychaeta	Bottom eDNA	Net DNA	0.97	0.33
Polychaeta	Surface eDNA	Net DNA	3.31	< 0.001

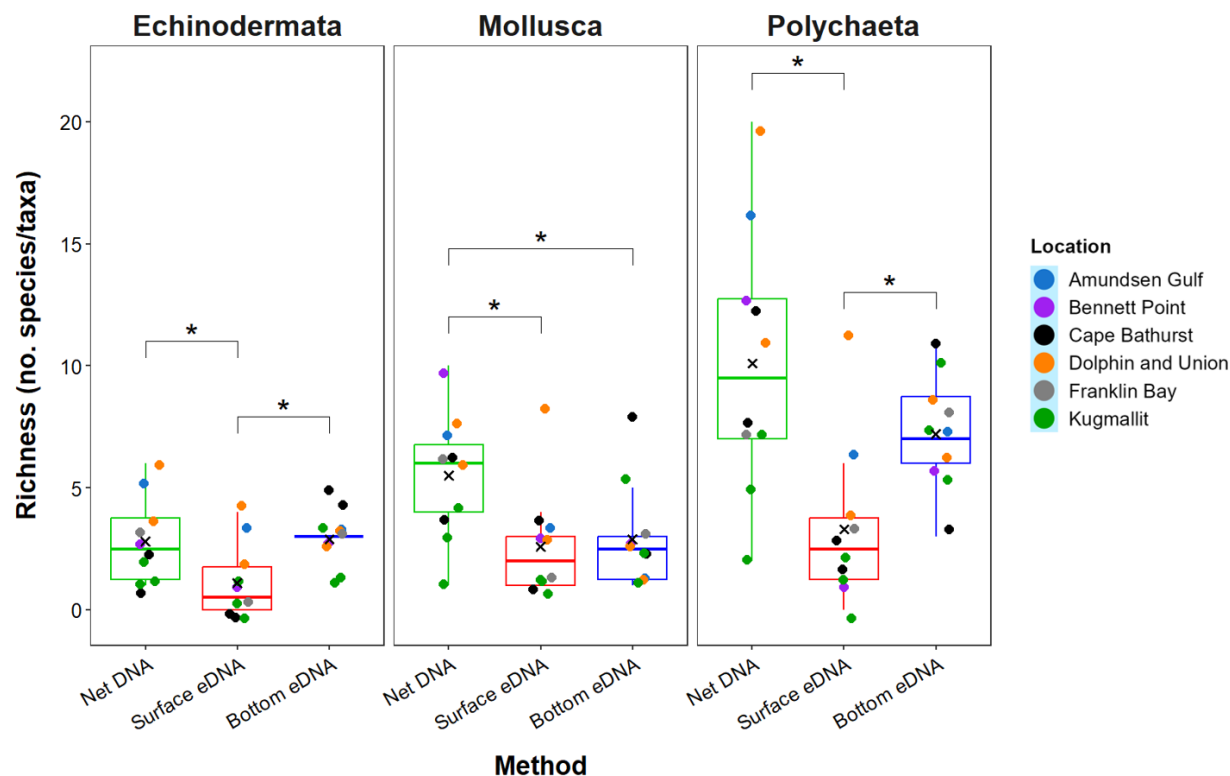


Figure 2.8. Echinoderm, mollusc, and polychaete, species/taxon richness in net DNA (0–50 m), surface eDNA (0–50 m), and bottom eDNA (5–10 m off the seafloor). Bold horizontal line within each box represents the median, the x indicates the mean, and box spans the interquartile range, encompassing the middle 50% of data. Whiskers extend to the range of the data, and jittered points represent sampling station, colour coded by locations within the Western Canadian Arctic. Asterisks indicate significant pairwise differences among methods ($\alpha = 0.05$; associated statistics in Table 2.2).

Principle Coordinate Ordination analysis of meroplankton community composition (presence/absence) based on net DNA, surface eDNA, and bottom eDNA samples explained 42.1% of the total variation in the data. Samples clustered based on metabarcoding sampling approaches and sampling depth, with net DNA, surface eDNA, and bottom eDNA samples forming three significantly distinct groups in ordination space (Figure 2.9; PERMANOVA, $P =$

0.0001, pseudo- $F_{2, 27} = 5.97$). Post hoc pairwise PERMANOVA tests indicated that surface meroplankton communities in net DNA and eDNA samples differed significantly ($t = 2.88$, $P = 0.0001$). Communities in bottom eDNA samples also differed significantly from surface meroplankton communities detected in net DNA ($t = 2.61$, $P = 0.0001$) and surface eDNA ($t = 1.87$, $P = 0.0001$). Additionally, PERMDISP analysis showed a significant difference in dispersion between bottom eDNA and net DNA ($t = 3.16$, $P(\text{perm}) = 0.013$), with net DNA showing lower dispersion (i.e., more tightly clustered) and less variability among samples. Meroplankton distribution patterns at the surface were significantly correlated between eDNA and net DNA samples (Figure A2.1 and A2.2; RELATE analysis: $\rho = 0.502$, $P = 0.0013$), whereas bottom eDNA samples (Appendix II Figure A2.3) were not significantly correlated with either surface eDNA or net DNA (RELATE analysis: $\rho = 0.135$, $P = 0.196$; $\rho = -0.172$, $P = 0.807$ respectively).

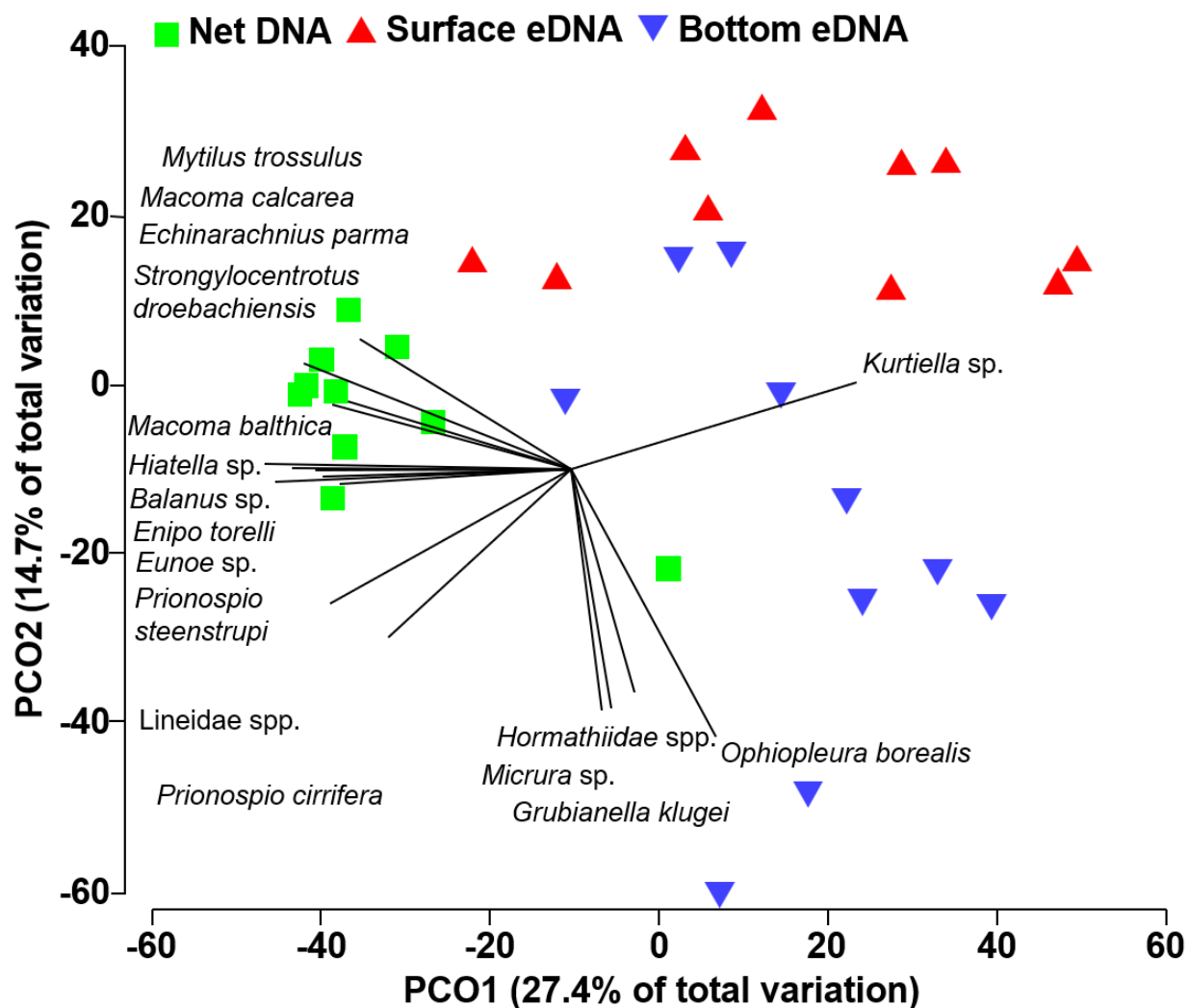


Figure 2.9. Principal Coordinates Ordination of meroplankton presence/absence based on Sørensen similarity net DNA (0–50 m), surface eDNA (0–50 m), and bottom eDNA (5–10 m off the seafloor) samples. Differences in meroplankton community composition among sampling methods and associated depths were statistically significant ($P = 0.0001$, pseudo- $F_{2, 27} = 5.97$). Species vectors shown for Pearson correlation of ≥ 0.65 .

Meroplankton and adult community structure

Principle Coordinate Ordination analysis including meroplankton (net DNA, surface eDNA, bottom eDNA) and adult benthic invertebrates (box core and trawl) based on presence/absence data explained 35.2% of total variation in the data and separated samples into five distinct groups in ordination space (Figure 2.10; PERMANOVA, $P = 0.0001$, pseudo- $F_{4,35} =$

7.36). Post hoc pairwise PERMANOVA tests showed that benthic adult communities in box cores differed significantly from meroplankton communities for each sampling approach and depth (net DNA, $t = 3.06$, $P = 0.0003$; surface eDNA, $t = 2.90$, $P = 0.0003$; bottom eDNA, $t = 2.29$, $P = 0.0002$). Adult communities in trawl samples also differed significantly from meroplankton communities for each sampling approach and depth (net DNA, $t = 3.34$, $P = 0.0003$; surface eDNA, $t = 3.18$, $P = 0.0004$; bottom eDNA, $t_1 = 2.44$, $P = 0.0003$). Spearman rank correlations, indicated that adult community distribution patterns from the box core (Appendix II Figure A2.4) were not significantly correlated with surface meroplankton distributions (net DNA RELATE analysis: $\rho = -0.368$, $P = 0.915$; surface eDNA RELATE analysis: $\rho = -0.165$, $P = 0.767$), and were weakly correlated with meroplankton in bottom samples (bottom eDNA bottom RELATE analysis: $\rho = 0.378$, $P = 0.05$). Adult spatial patterns based on trawl samples (Appendix II Figure A2.5) were significantly correlated with bottom meroplankton distribution (bottom eDNA RELATE analysis: $\rho = 0.604$, $P = 0.0008$), but not with observed patterns at the surface (surface eDNA RELATE analysis: $\rho = 0.092$, $P = 0.319$; net DNA RELATE analysis: $\rho = -0.066$, $P = 0.615$).

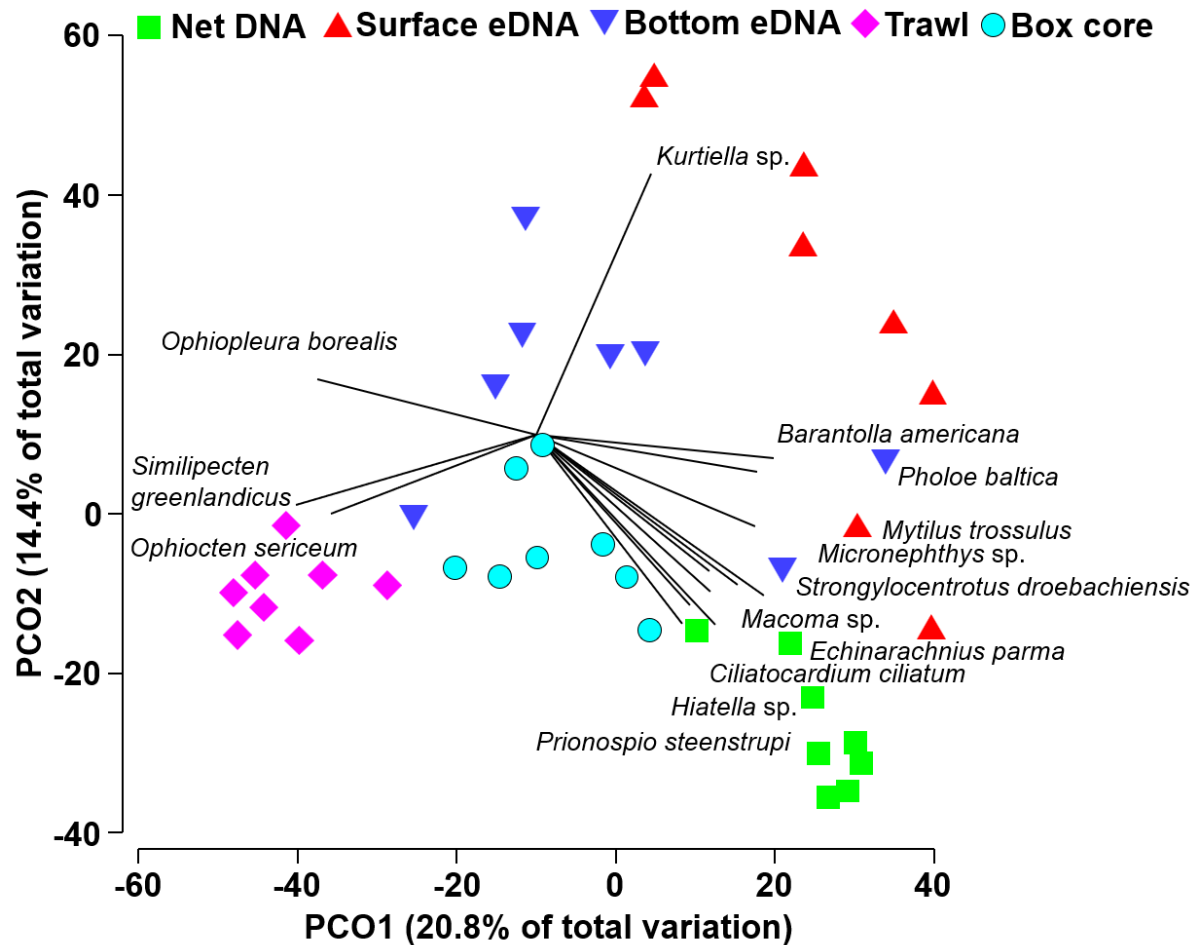


Figure 2.10. Principal Coordinates Ordination of meroplankton and adult presence/absence data based on Sørensen similarity for meroplankton samples in net DNA (0–50 m), surface eDNA (0–50 m), and bottom eDNA (5–10 m off the seafloor), and adult samples in trawl and box core samples. Differences in meroplankton community composition among sampling methods and associated depths were statistically significant ($P = 0.0001$, pseudo- $F_{4,35} = 7.36$). Species vectors based on Pearson correlation of ≥ 0.65 .

Principal Coordinate Ordination analysis of environmental variables from samples in the upper 0–50 m of the water column and 5–10 m off the sea floor explained 82.8% and 95.5% of the total variation in the data respectively (Appendix II Figure A2.6 -A2.7). Spatial patterns in the upper 0–50 m of the water column (Appendix II Figure A2.6) were significantly correlated with surface meroplankton community patterns detected using eDNA (RELATE analysis: $\rho = 0.45$, $P = 0.0064$) but not with those using net DNA (RELATE analysis: $\rho = 0.25$, $P = 0.13$).

Spatial patterns based on environmental variables 5–10 m above the seafloor (Appendix II Figure A2.7) were also correlated with bottom meroplankton community spatial patterns based on eDNA (RELATE analysis: $\rho = 0.61$, $P = 0.0003$). The DistLM analysis identified environmental predictors of meroplankton community composition. For surface communities based on eDNA, fluorescence in the upper 0–50 m of the water column was the most significant environmental predictor (Table 2.3). The first two dbRDA axes explained 100% of fitted variation and 37.13% of total variation in the surface eDNA resemblance matrix. For surface communities detected by net DNA, salinity in the upper 0–50 m of the water column was the most significant predictor, explaining 100% of fitted variation and 27.5% of total variation in the dbRDA. Station depth (m) was the most significant predictor of bottom meroplankton community composition in eDNA samples (Table 2.3; DistLM), explaining 100% and 29.69% of the fitted and total variation of the dbRDA, respectively. Linear regression analyses (Figure 2.11) showed significant relationships between surface (eDNA and net DNA) meroplankton richness and environmental variables. Fluorescence (0–50 m) was significantly related to richness in both surface eDNA ($R^2 = 0.55$, $F_{1,8} = 9.74$, $P = 0.014$) and net DNA ($R^2 = 0.72$, $F_{1,8} = 20.1$, $P = 0.002$). Similar patterns were observed for salinity (0–50 m) (surface eDNA: $R^2 = 0.53$, $F_{1,8} = 9.14$, $P = 0.016$; net DNA: $R^2 = 0.70$, $F_{1,8} = 18.7$, $P = 0.003$), and the number of ice-free days (eDNA: $R^2 = 0.75$, $F_{1,8} = 24.4$, $P = 0.001$; net DNA: $R^2 = 0.67$, $F_{1,8} = 16.2$, $P = 0.004$).

Table 2.3. Best fit environmental predictors of meroplankton community composition for surface (eDNA, net DNA) and bottom (eDNA) of the water column.

Method	Variable	SS (trace)	AICc	R ²	Res.DF	Psuedo-F	P-value
Surface eDNA	Fluorescence 0–50 m	8087.9	77.94	0.37	8	4.73	0.0011
Net DNA	Salinity 0–50 m	3680.6	74.62	0.27	8	3.0	0.0078

Bottom	Station depth	8403.9	81.61	0.30	8	3.40	0.0002
eDNA							

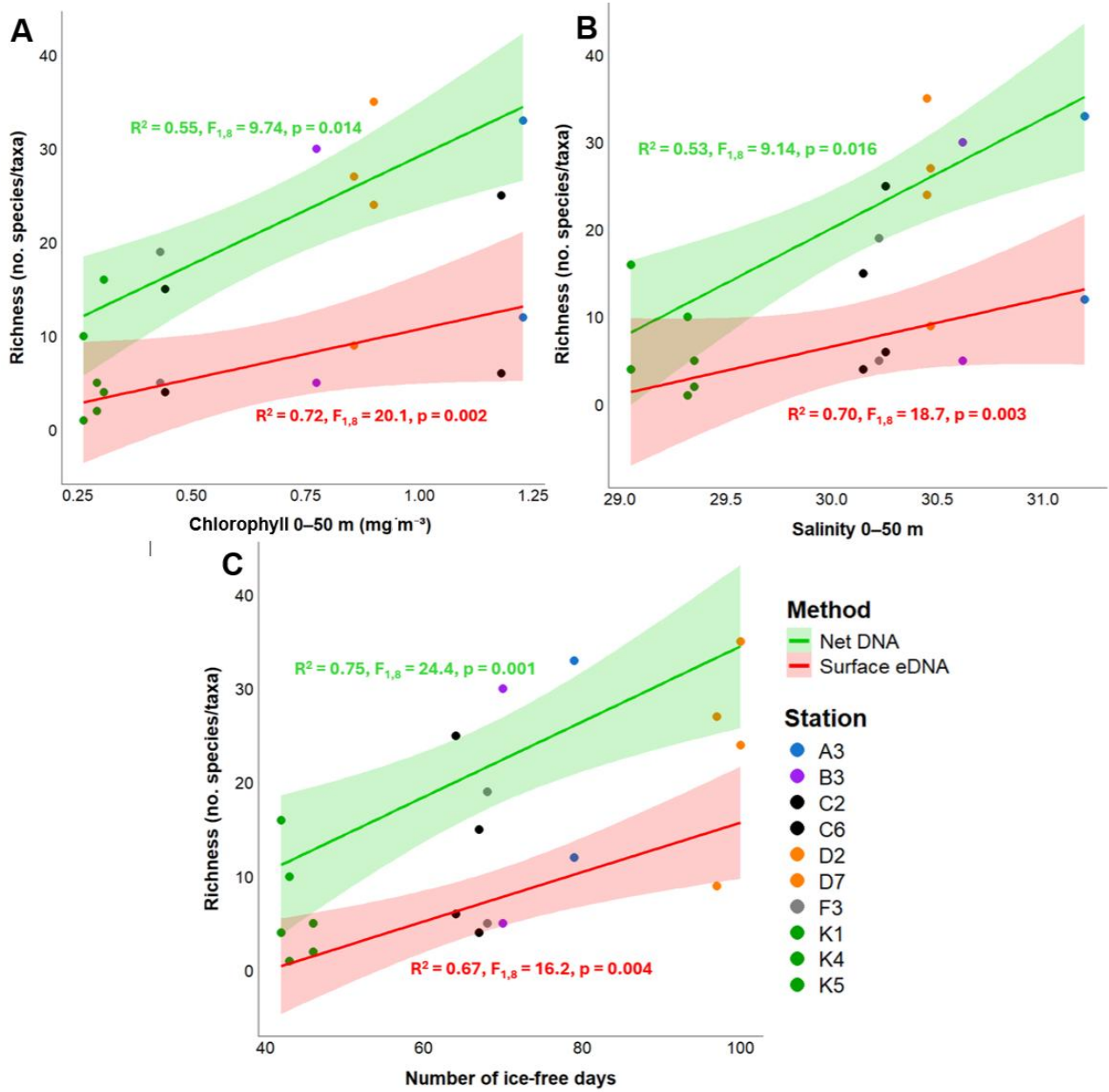


Figure 2.11. Relationship between meroplankton richness at the surface (eDNA top [red]; net DNA [green]) and A) salinity (0–50 m), B) fluorescence (0–50 m), and C) number of ice-free days.

Discussion

Incorporation of net DNA and eDNA sampling substantially improved characterization of meroplankton communities across the Western Canadian Arctic compared with morphological taxonomy alone. Most importantly, metabarcoding resolved taxonomic identification to the genus and species level and detected phyla not previously reported in meroplankton surveys, including Nemertea and Porifera. In addition, metabarcoding enabled tentative species level identification for taxa that have previously been identified only at higher taxonomic levels in benthic surveys. For example, meroplankton of the sea urchins *Strongylocentrotus droebachiensis* and *Strongylocentrotus pallidus* were commonly detected in surface waters indicating that *Strongylocentrotus* sp. reported from benthic surveys (Roy et al. 2015; Niemi et al. 2020) likely represents two species. Sequencing of adults of both *Strongylocentrotus* species from the WCA will be needed to confirm their presence in benthic communities. However, even with the higher number of taxa detected by metabarcoding, species accumulation curves indicated that neither barcoding sampling approach fully sampled the meroplankton richness, likely because of the small sample size for each method ($n = 10$). This suggests that additional sampling would likely reveal a greater number of benthic invertebrate taxa in the region. Nonetheless, incorporation of metabarcoding, to our knowledge, provided the most comprehensive assessment of meroplankton species richness in the WCA to date.

More generally, both metabarcoding sampling approaches consistently detected the same dominant phyla including Annelida, Echinodermata, and Mollusca, which is also consistent with previous observations of community composition from other meroplankton surveys conducted in the Arctic during the summer (e.g., Descôteaux et al., 2021; Ershova et al., 2019; Michelsen et al., 2017; Schrage et al., 2026). These dominant phyla are also consistent with the composition of

adult benthic invertebrate communities reported across the WCA in box core and trawl surveys (Cusson et al. 2007; Roy et al. 2015; Niemi et al. 2020) indicating that metabarcoding was able to sample the major taxonomic groups contributing to regional benthic diversity while improving taxonomic identification of their meroplankton stages.

Metabarcoding methods also detected taxa in the meroplankton that, to our knowledge, had not been previously reported from adult populations within the study area. The Nemertean genus *Cephalothrix* was detected in surface waters at six out of ten sampling stations, in the WCA. However, Nemertea are commonly observed in the WCA benthic infaunal communities, and other *Cephalothrix* species including *C. linearis* and *C. spiralis* have been reported from the Eastern Canadian Arctic and Hudson's Bay (Fisheries and Oceans Canada, 2026). More recently, *Cephalothrix iwatai*, previously reported only throughout the coast of Japan, was detected by metabarcoding in the northern Barents Sea and Fram Strait (Ershova et al. 2019; Schrage et al. 2026). Together these observations suggest that *Cephalothrix* may be more widely distributed in the Arctic including the WCA but may have remained undocumented possibly due to limitations in species-level identification. Alternatively, the detection could reflect a false positive metabarcoding assignment resulting from incomplete reference databases.

Despite the improved taxonomic identification provided by metabarcoding, some taxa could still only be identified to the class or family level, highlighting the limited representation of Arctic invertebrates in current DNA databases such as GenBank and Barcode of Life Data System (BOLD) (also see Ershova et al., 2019). In the WCA, of the 436 epi- and infaunal species with a potential meroplanktonic life stage, only 48% currently have COI reference sequences available in these databases. Expanding barcode libraries by sequencing adult benthic invertebrates would further improve species level identifications, support community

assessments, and benefit future monitoring efforts of early life stages in the WCA and across Arctic in general.

Although net DNA and eDNA detected many of the same meroplankton taxa, including benthic invertebrates commonly found in the WCA such as the polychaete *Barantolla americana* and the echinoderm *Gorgonocephalus arcticus* (Niemi et al. 2020; Roy and Niemi 2025), important differences in meroplankton richness and community composition were also observed. Surface water eDNA consistently detected lower meroplankton richness than net DNA, likely reflecting lower concentrations of meroplankton DNA in water samples that can reduce detection of species (Doloiras-Laraño et al. 2023). Additionally, eDNA is susceptible to biases affecting taxonomic detection including false positive detections, DNA fragmentation, and degradation (Barnes and Turner 2016; Múrria et al. 2024).

In Arctic environments, cold water temperatures may slow DNA degradation, prolonging the persistence and transport of DNA fragments in surface waters, increasing the potential detection of meroplankton taxa not locally present at the time of sampling (Barnes and Turner 2016; Leduc et al. 2019). On the other hand, increased microbial activity in surface waters may accelerate DNA degradation and further reduce eDNA detection of meroplankton (Barnes and Turner 2016; Collins et al. 2018; Leduc et al. 2019). Thus, net DNA metabarcoding likely provides a closer representation of the local meroplankton community composition and richness at the surface due to physical collection of organisms rather than extracellular DNA (Deiner et al. 2017; Doloiras-Laraño et al. 2023; Múrria et al. 2024). Nonetheless, eDNA complemented net sampling by detecting smaller ($< 150 \mu\text{m}$) and rare species that can pass through plankton nets (e.g., $150 \mu\text{m}$ mesh), (Djurhuus et al. 2018; Descôteaux et al. 2021) such as sponge (Porifera) larvae of *Halichondria panicea* and *Polymastia* sp. (ranging from $2\text{--}4 \mu\text{m}$ in size). In addition,

the net sampling may have missed detecting species that may avoid nets such as the crab *Hyas coarctatus* (Porter et al. 2008; Djurhuus et al. 2018; Choi et al. 2024), which are taxa of importance to local communities. However, sole detection of *H. coarctatus* in bottom meroplankton communities could indicate a reproductive and spawning event may have occurred earlier in the summer.

Meroplankton community richness was higher 5–10 m above the seafloor relative to the surface layer (0–50 m), and contained numerous taxa not found at the surface. However, interpretation of eDNA from bottom waters is complicated due to DNA from adult benthic organisms likely present in the water above the seafloor resulting from sediment resuspension or movement of mobile epifauna (Múrria et al. 2024). This is supported by the relatively high similarity in spatial patterns between bottom eDNA and infaunal (37.8% similarity) and epifaunal (60.4% similarity) communities, as well as the detection of benthic invertebrate taxa that lack a pelagic larval life stage such as the snail *Buccinum* sp., sea star *Hymenaster pellucidus*, and the isopod *Munnopsis typica* (Martel et al. 1986; Levin and Bridges 1995; McEdward and Miner 2001). Alternatively, differences in community composition between eDNA bottom and adult samples may truly represent settling meroplankton or demersal taxa. For example, *Hemithiris psittacea*, a small bivalve with a cephalula larva that remains near the seafloor (Kuzmina 2021), was detected exclusively in bottom eDNA samples potentially reflecting a pre-settlement demersal stage. However, this species occurred only at one station (C2), limiting broader interpretation. Thus, it remains challenging to distinguish whether taxa detected in bottom eDNA represent meroplanktonic or adult life stages.

At the genus and species levels, meroplankton composition in surface waters differed substantially from the composition of adult benthic invertebrate communities. This decoupling

likely reflects a combination of reproductive timing and oceanographic transport. Meroplankton detected in surface waters may represent taxa spawning in late summer (near or during August) as well as those that spawned earlier in the season and whose larvae may have been subsequently carried across the WCA by surface currents. Thus, larval distribution does not necessarily correspond to local distributions of adult populations.

The frequent detection of the bivalve *Kurtiella* sp. in surface waters illustrates this pattern. This genus was commonly detected in meroplankton communities using eDNA, yet adult records from the WCA outside of this study are limited. For example, *Kurtiella tumida* has been previously reported from the Mackenzie Shelf in 1974 (Cusson 2018), and occurred at low abundance ($< 1 \text{ ind. m}^{-2}$) within the Kugmallit region in 2018. Although *K. tumida* typically occur in intertidal to shallow subtidal environments, it has also been recorded at depths up to 1000 m (Ockelmann and Muus 1978; Li et al. 2012). It may be that adult *Kurtiella* sp. primarily occur outside of sampling stations, particularly in intertidal habitats, while their pelagic larvae are transported offshore by surface currents without successfully settling due to unfavourable environmental conditions. Alternatively, adults may occur within the sampling region but remain underrepresented in benthic surveys because of their size (1.2–6 mm) and associations with burrowing invertebrates, making them difficult to collect using box cores (Scott 1987).

In contrast, surface meroplankton communities at the surface did not include larvae from several common epifaunal species within the WCA such as the brittle star *Ophiosten sericeum* and bivalve *Similipecten greenlandicus*. Although, little is known about the reproductive timing of these species, their absence from surface samples collected in early August may indicate that spawning occurred earlier in the season, likely coinciding with the spring phytoplankton bloom

when food availability is expected to be high for larval growth and development. (Highfield et al. 2010; Kuklinski et al. 2013; Basch and Pearse 2022).

At the regional scale, meroplankton richness within surface waters increased longitudinally from west (Kugmallit) to east (Dolphin and Union Strait), a pattern likely tied to ice-mediated ecosystem phenology. In 2024, locations within Dolphin and Union Strait (D2 and D7) experienced approximately 50–55 more ice-free days prior to sampling than Kugmallit stations (i.e., K1, K4, and K5). A longer open water period increases light availability thereby extending the phytoplankton growing season (Ardyna et al. 2014). Stations with longer open-water periods also have increased wind and surface currents, bringing in more meroplankton taxa from other locations (Carmack and Macdonald 2002; Descôteaux et al. 2021). Furthermore, the longer open water season captured during the study likely caught more of the reproductive season of benthic invertebrates, thereby increasing richness and abundance and detections of meroplankton from local benthic invertebrate communities within the SML (Frey et al. 2022). As such, the lower meroplankton richness observed at Kugmallit may reflect later seasonal development rather than inherently lower richness. If sampled later in the season, after a longer ice-free period, Kugmallit surface waters may have had similar meroplankton richness as observed in Dolphin and Union Strait during the study.

Beyond these regional differences, local environmental conditions also influenced meroplankton distribution in the surface mixed layer. Meroplankton richness detected from eDNA was positively correlated with chlorophyll as measured by fluorescence, a proxy for phytoplankton biomass. This relationship is consistent with the predominance of planktotrophic taxa, which comprised 58.2% and 52.8% of meroplankton detected by net DNA and eDNA, respectively. Consequently, the growth and development of a majority of meroplankton benefit

from increased phytoplankton biomass and may actively position themselves in areas where food is most abundant, especially within oligotrophic areas (Folt and Burns 1999; Metaxas 2001; Patuła et al. 2026). In the WCA this corresponds to the subsurface chlorophyll *a* (chl *a*) maximum. In the study period the sub surface chl *a* maximum ranged between 3.8 and 68 m. Within Kugmallit and Franklin Bay, the chl *a* maximum occurred below 50 m such that the eDNA sampling and surface net tows did not capture meroplankton associated with the layer of maximum phytoplankton biomass.

Salinity was strongly correlated with the number of meroplankton taxa detected by net DNA. Correlation with salinity could represent influences of stratification on phytoplankton biomass which indirectly affects meroplankton (Ardyna et al. 2011, 2014; Frey et al. 2022). Strong stratification in the water column can reduce meroplankton richness by restricting vertical mixing of nutrients to the surface mixed layer, essential for phytoplankton growth (Metaxas 2001; Patuła et al. 2026). Alternatively, salinity could directly affect water mass structure which influences meroplankton distribution. Lower salinity at the surface impacts small taxa such as bivalve veligers which may have limited ability to move between or tolerate strong changes in density between the Pacific derived and surface water masses (Metaxas 2001).

Although chl *a* fluorescence, salinity, and stratification were associated with meroplankton richness and composition in this study, results should be interpreted with caution since sampling occurred at a single time point. These environmental conditions are highly dynamic and vary seasonally and interannually (Highfield et al. 2010; Kuklinski et al. 2013; Questel et al. 2013; Brandner et al. 2017; Descôteaux et al. 2021). For example, in high Arctic Fjords Michelsen et al. (2017) found meroplankton composition and abundance differed between winter, early summer, and late summer, with different environmental variables significantly

influencing composition based on the time of year. Seasonal changes in community composition have also been determined as a main driver of meroplankton communities in other Arctic (Kuklinski et al. 2013; Questel et al. 2013; Descôteaux et al. 2021) and Antarctic (Stanwell-Smith et al. 1999; Bowden et al. 2009) regions.

Conclusion

Metabarcoding revealed a rich meroplankton community in surface waters within the Western Canadian Arctic. Net DNA detected greater richness of meroplankton in surface waters relative to eDNA but underrepresented smaller or less common taxa such as Porifera. Meroplankton at the surface also differed from bottom communities, likely indicating a mixture of meroplankton and adult DNA when sampling 5–10 m off the seafloor. Method and depth-based differences in community structure from the present study can help inform monitoring protocols for meroplankton communities within the WCA. Higher meroplankton richness across the WCA was correlated with longer open water periods, indicating a strong relationship between meroplankton spawning and ice-associated phenology. Meroplankton community structure at the surface was further linked to water column structure and food availability, as locations with increased vertical mixing and thus fluorescence supported higher meroplankton richness. However, meroplankton in the WCA are also shaped by seasonal oceanographic conditions (Kuklinski et al. 2013; Descôteaux et al. 2021). Thus, lack of seasonal data should be considered when making inferences for environmental variables influencing meroplankton community structure. As originally hypothesized, meroplankton at the surface showed spatial mismatch and decoupling from local adult seafloor invertebrate communities. These findings suggest that life stages of seafloor invertebrates within the WCA are influenced by different oceanographic conditions, with meroplankton richness and distribution influenced by surface-layer processes

such as surface phytoplankton abundance and currents. Decoupling of community composition between life stages gives valuable insight into benthic invertebrate life history strategies and highlights potential new species present within the WCA. Continued sampling and sequencing of adult benthic invertebrates will be essential for confirming these species and improving reference databases for remote Arctic regions.

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Appendix II

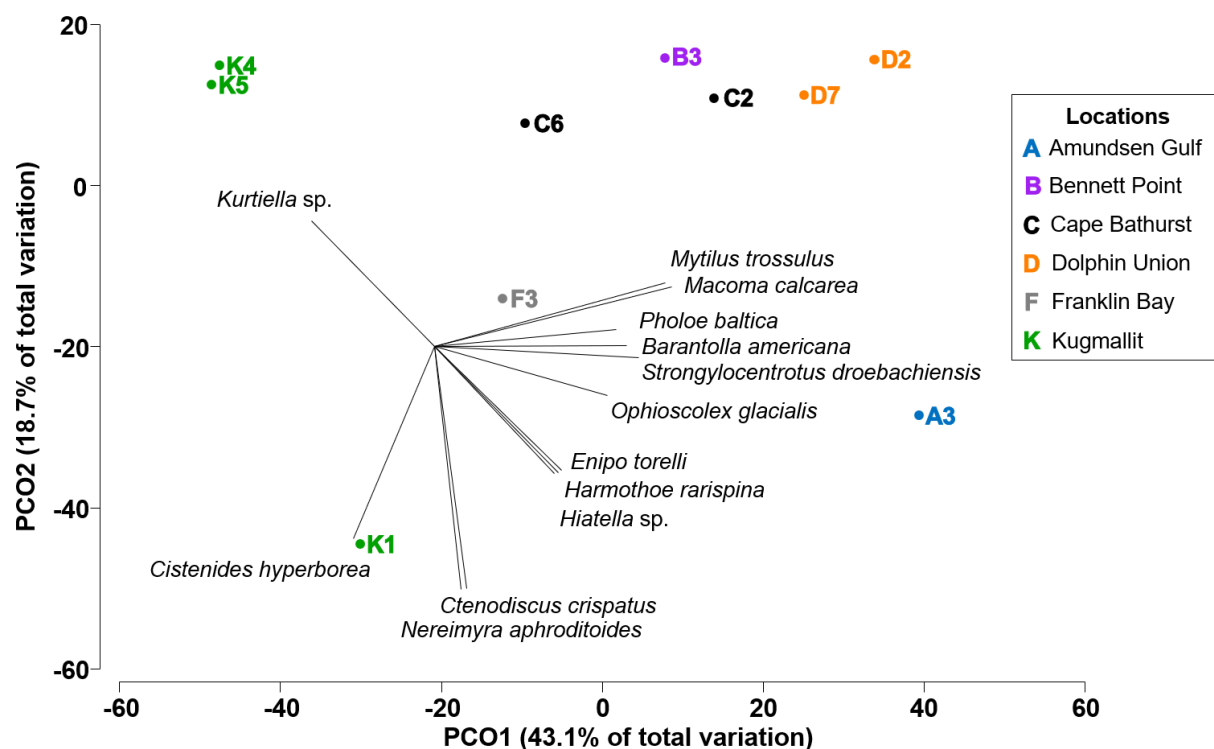


Figure A2.1. Principal Coordinates Ordination of meroplankton presence/absence data based on Sørensen similarity for surface eDNA samples ($n = 10$). Samples are labelled with station code names and colour coded based on location within the Western Canadian Arctic. Species vectors based on Pearson correlation of ≥ 0.65 .

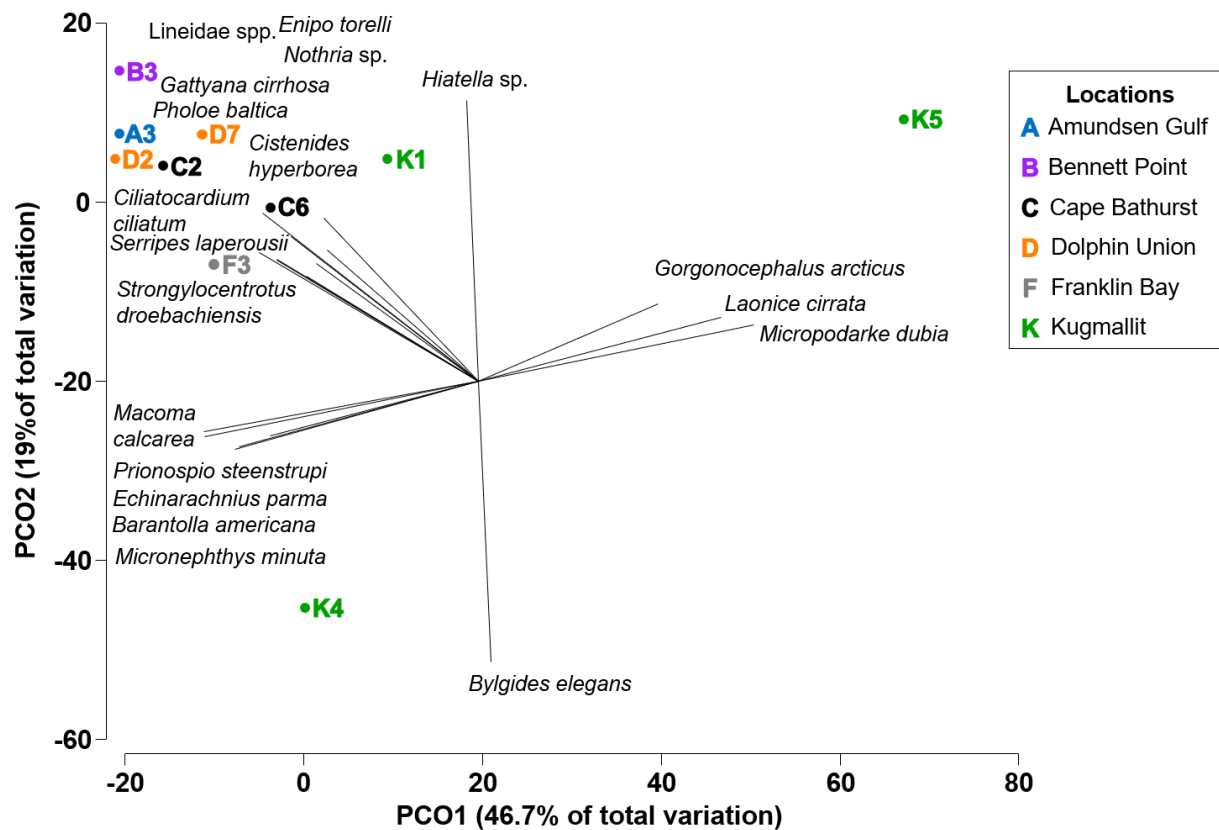


Figure A2.2. Principal Coordinates Ordination of meroplankton presence/absence data based on Sørensen similarity for net DNA samples ($n = 10$). Samples are labelled with station code names and colour coded based on location within the Western Canadian Arctic. Species vectors based on Pearson correlation of ≥ 0.65 .

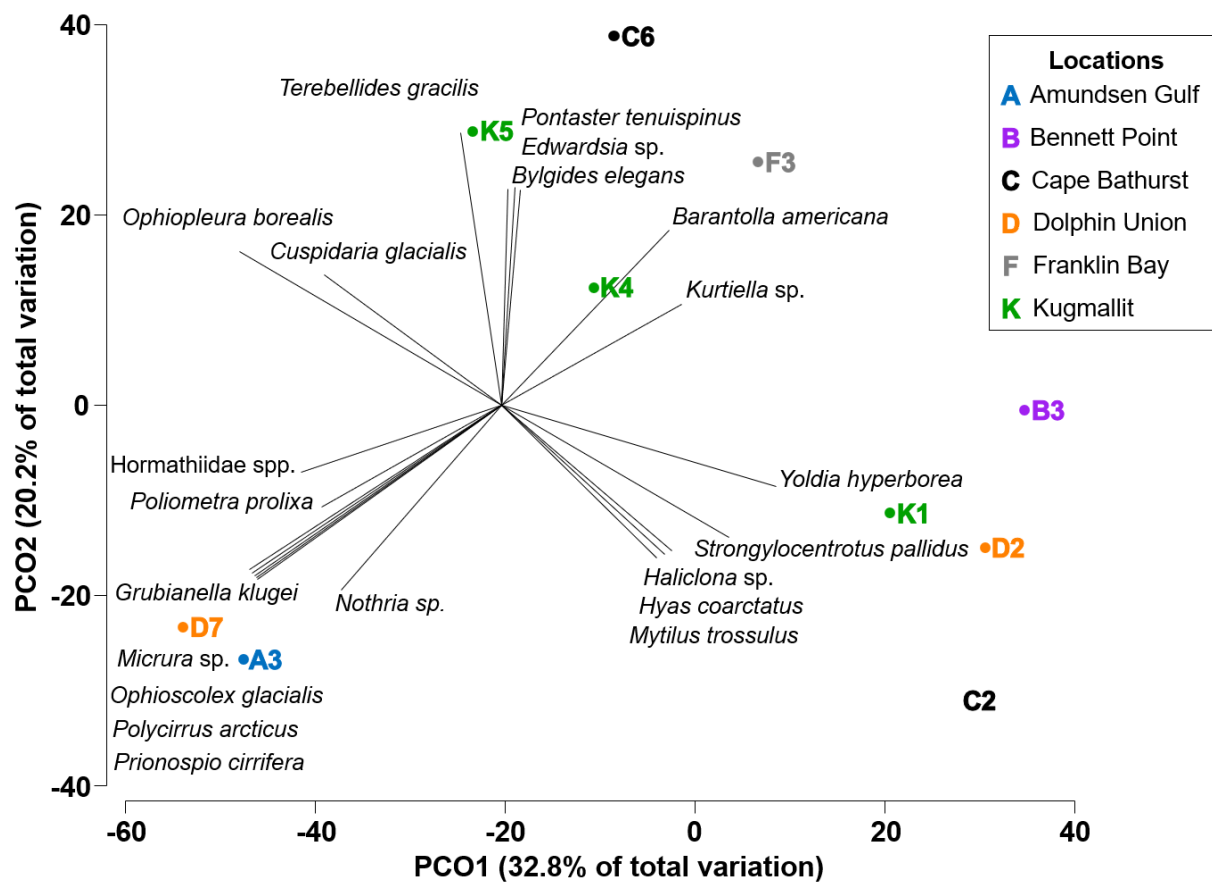


Figure A2.3. Principal Coordinates Ordination of meroplankton presence/absence data based on Sørensen similarity for bottom eDNA samples ($n = 10$). Samples are labelled with station code names and colour coded based on location within the Western Canadian Arctic. Species vectors based on Pearson correlation of ≥ 0.65 .

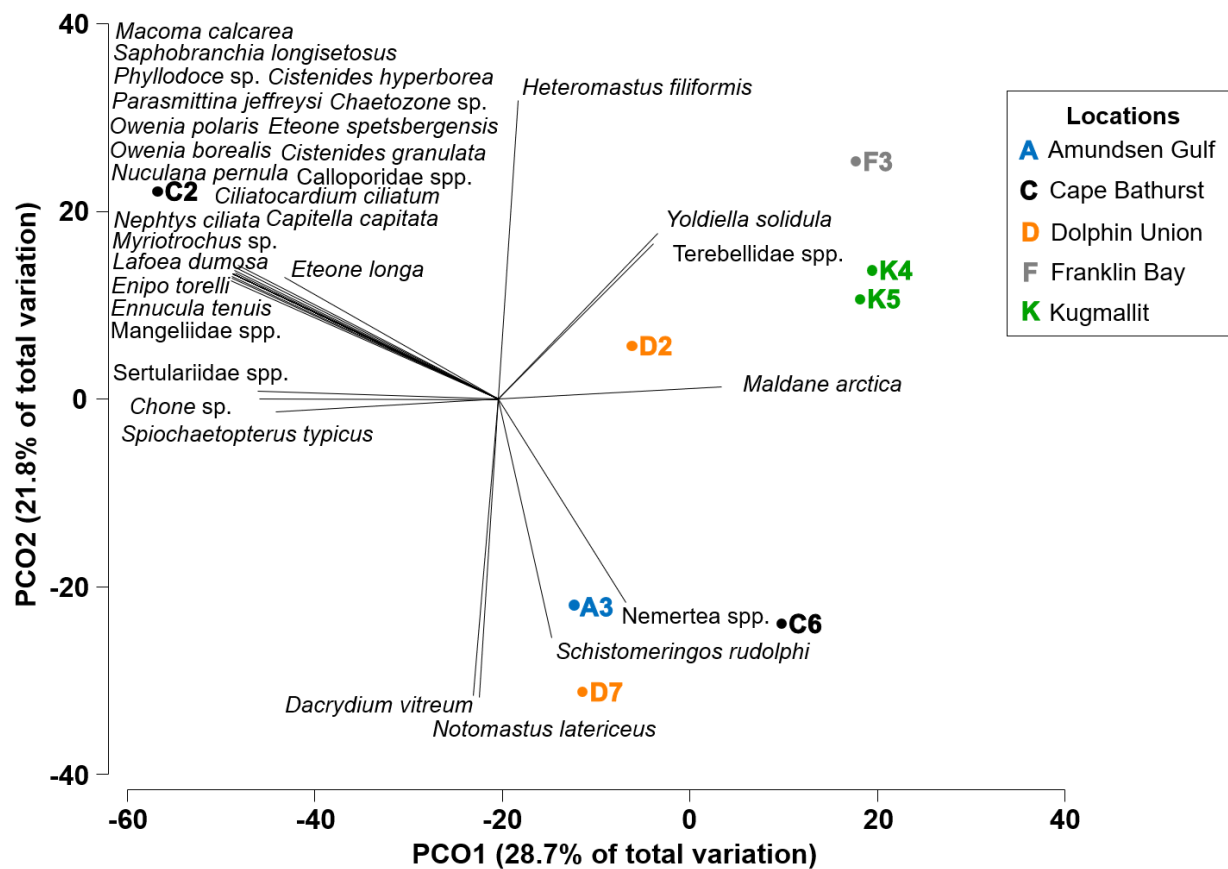


Figure A2.4. Principal Coordinates Ordination of adult benthic invertebrate presence/absence data based on Sørensen similarity for box core samples ($n = 8$). Samples are labelled with station code names and colour coded based on location within the Western Canadian Arctic. Species vectors based on Pearson correlation of ≥ 0.65 .

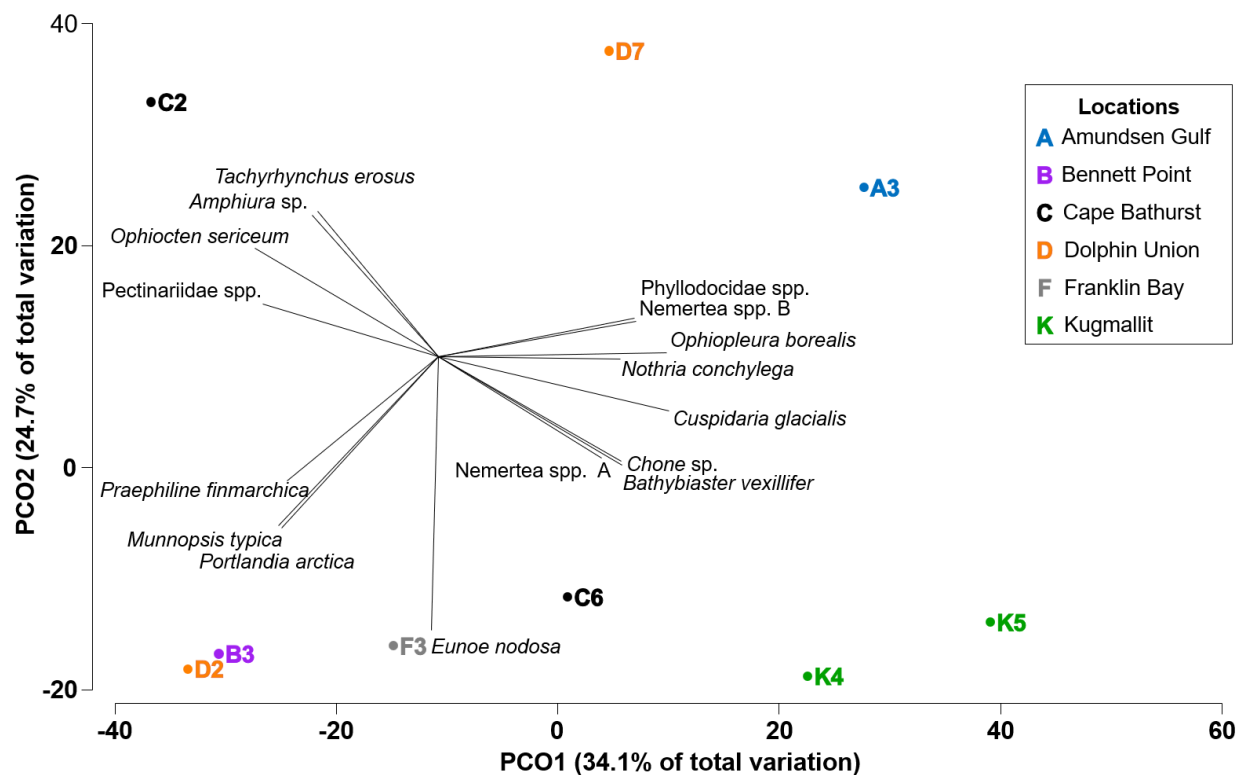


Figure A2.5. Principal Coordinates Ordination of adult benthic invertebrate presence/absence data based on Sørensen similarity for benthic beam trawl samples ($n = 9$). Samples are labelled with station code names and colour coded based on location within the Western Canadian Arctic. Species vectors based on Pearson correlation of ≥ 0.65 .

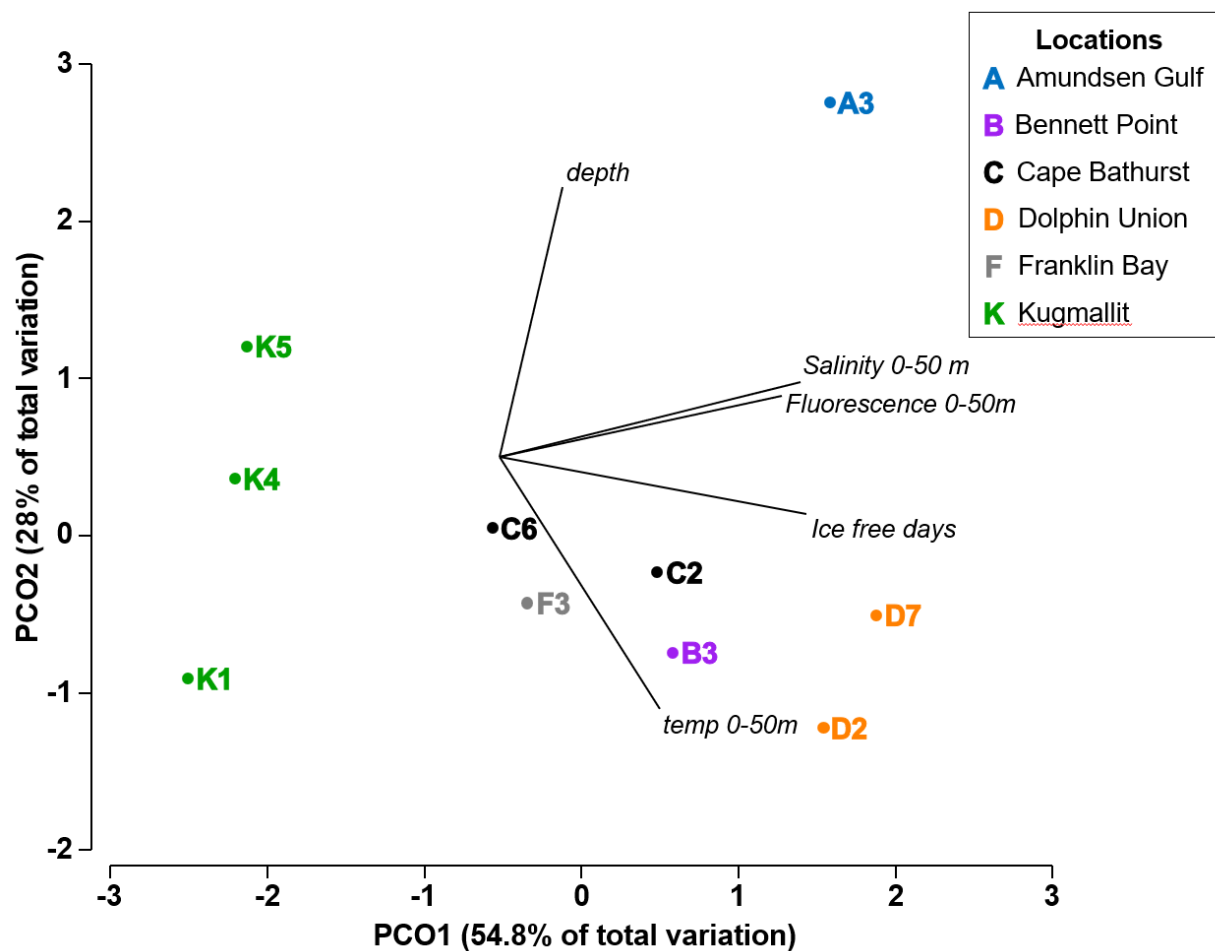


Figure A2.6. Principal Coordinates Ordination of environmental variables based on Euclidean distance for surface (0–50 m) samples ($n = 10$). Samples are labelled with station code names and colour coded based on location within the Western Canadian Arctic. Environmental vectors based on Pearson correlation of ≥ 0.65 .

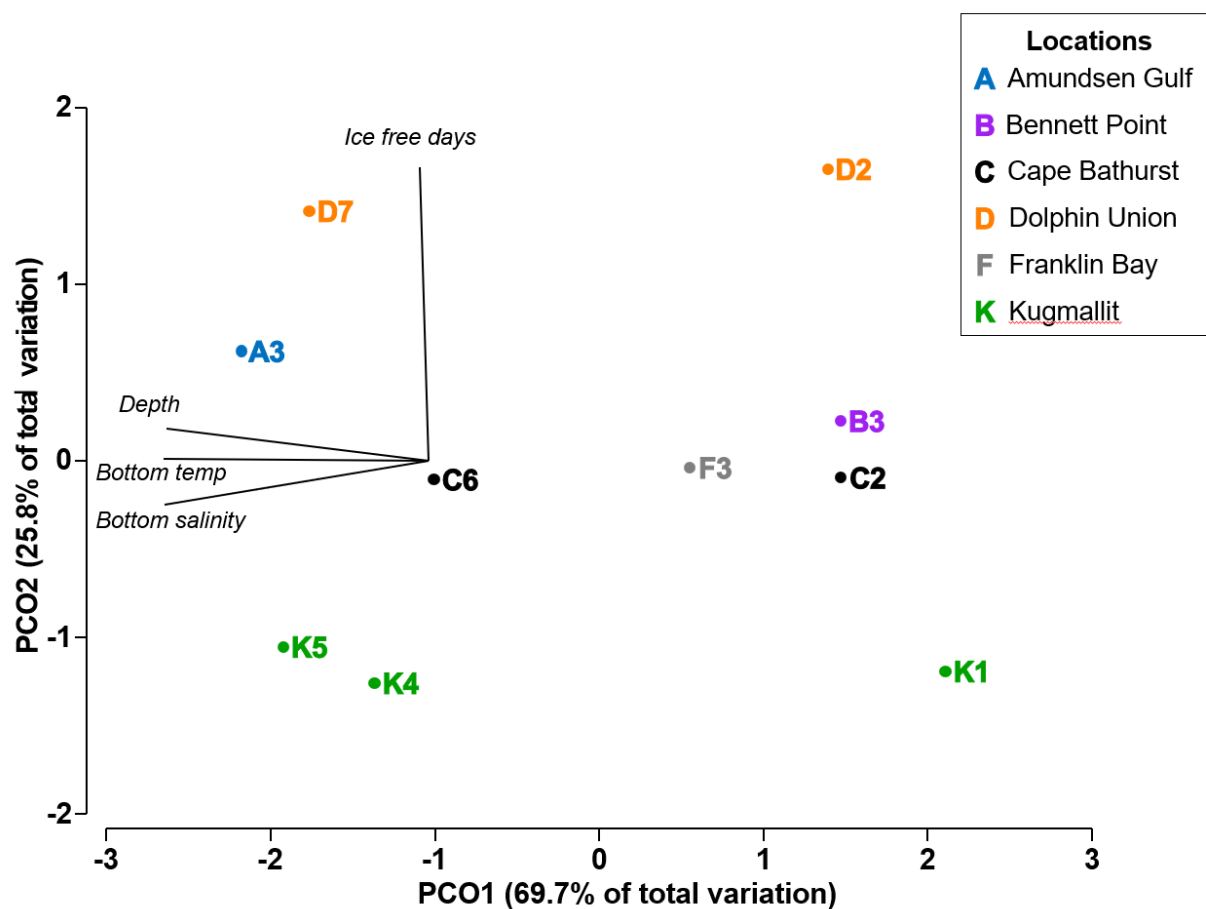


Figure A2.7. Principal Coordinates Ordination of environmental data based on Euclidean distance for bottom (5–10 m off the seafloor) samples ($n = 10$). Samples are labelled with station code names and colour coded based on location within the Western Canadian Arctic. Environmental vectors based on Pearson correlation of ≥ 0.65 .

General Conclusions

My thesis provided the first assessment of meroplankton community structure within the Western Canadian Arctic, integrating taxonomic and metabarcoding methods to better understand how larval benthic invertebrates respond to their environment. My thesis showed evidence of meroplankton utilizing surface waters (0–50 m) through detecting high meroplankton abundance and richness within the surface mixed layer. Furthermore, my thesis demonstrated pronounced interannual variability in meroplankton abundance, and how environmental conditions at the surface such as temperature and ice-mediated ecosystem phenology influence community structure. These results highlight the susceptibility meroplankton survival to surface conditions, and therefore the vulnerability of meroplankton populations to future environmental changes affecting the SML such as increased water column stratification (Smoot and Hopcroft 2017; Ardyna and Arrigo 2020; Ehrman et al. 2022; Niemi et al. 2024).

Contrary to the initial hypothesis, increased meroplankton abundance at the surface (0–50 m), was closely associated with higher temperature, especially in high abundance years such as 2012, 2019, and 2024. These years showed increased composition of taxa such as Bivalves, which are often associated with higher temperatures to accelerate growth and increase survival to juvenile life stages (Atkinson, 1984; O'Connor et al., 2007; Descôteaux et al., 2021). Additionally, meroplankton community structure was linked to longer open-water periods, with meroplankton richness showing an increase from east to west of the WCA. This association is likely tied to ice-mediated ecosystem phenology, as primary productivity at the surface is closely linked to sea ice dynamics, with an earlier break-up providing an extended phytoplankton growth period, distribution area for meroplankton, and reproductive season for benthic invertebrates

(Frey et al. 2022). Thus, increased number of meroplankton taxa observed at Dolphin and Union Strait in 2024 were likely associated to an earlier start to the phytoplankton growing season.

A limitation of the present study is the influence of environmental variables on meroplankton was analyzed on a regional scale, which restricts understanding of how meroplankton variability occurs in the presence of local oceanographic processes such as upwelling events. This could be addressed by analyzing specific environmental processes not typically modelled on a regional scale, such as upwelling events around the ANMPA. Furthermore, lack of seasonal sampling limits understanding of the progression of meroplankton release/presence from ice covered to ice-free conditions. Under-ice or ice-edge eDNA sampling through water collection could be implemented, as evident in studies detecting fish and benthic invertebrates (Lacoursière-Roussel et al., 2018; Nomura et al., 2022; Kawakami et al., 2025). However, logistical gaps such as ice thickness, use of automated eDNA samplers in extreme cold (i.e., winter) conditions, and accessibility of ice-edge sampling during spring melt or fall freeze-up would need to be taken into consideration. Nevertheless, seasonal data could help identify periods of peak abundance for specific meroplankton groups and clarify why certain taxa, such as Bryozoa, are low in abundance during August (Highfield et al. 2010; Kuklinski et al. 2013; Questel et al. 2013; Brandner et al. 2017; Descôteaux et al. 2021).

The application of metabarcoding sampling approaches (net DNA and eDNA) in my thesis expanded understanding of meroplankton community composition at a scale not possible through morphological taxonomy alone. Metabarcoding detected 112 benthic taxa with meroplankton life stages within the WCA, expanding the six taxa identified at the class level using taxonomy. Metabarcoding sampling approaches also identified taxa not previously observed in epi- and infaunal records such as the nemertean genus *Cephalothrix* and sea urchins *Strongylocentrotus*

droebachiensis and *Strongylocentrotus pallidus*, providing a new resource to better understand adult taxonomy. These findings show how metabarcoding complements morphological taxonomy by providing further understanding into richness, composition, and environmental variables influencing these components. In addition to taxonomy in monitoring meroplankton abundance, it is recommended to continue incorporation of metabarcoding for monitoring meroplankton long-term to address potential changes in meroplankton richness or community composition within the Western Canadian Arctic.

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