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Sea ice dependence in Arctic marine organisms: life cycles, resource use, and trophic linkages

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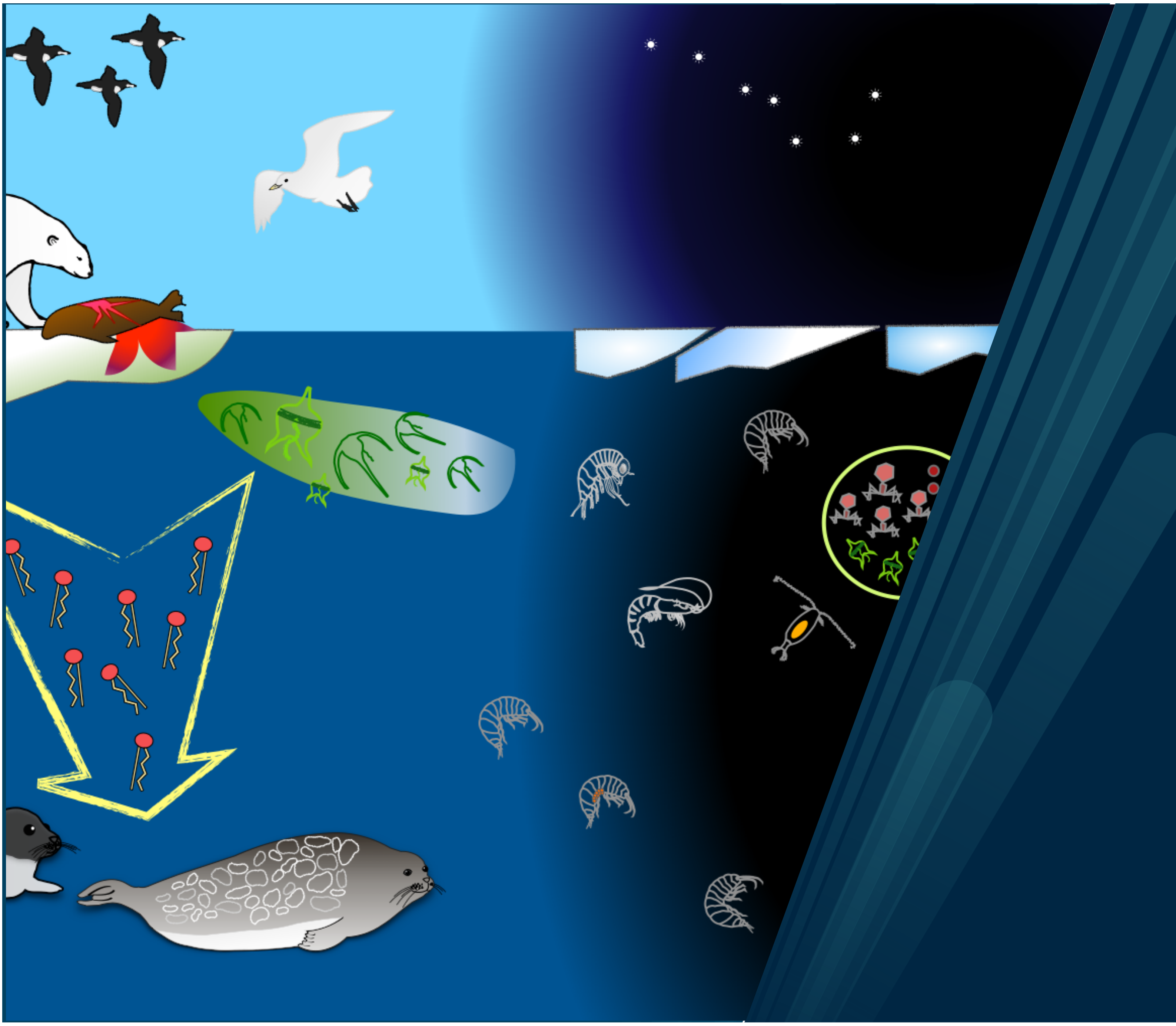

To Know the Dark

To go in the dark with a light is to know the light.
To know the dark, go dark. Go without sight,
and find that the dark, too, blooms and sings,
and is traveled by dark feet and dark wings.
Wendell Berry, 1970

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Summary

Climate warming in the Arctic has resulted in widespread changes in the physical oceanographic characteristics of the Arctic Ocean. One particularly visible change is the loss of sea ice both basin-wide and in the surrounding shelf seas. Arctic sea ice loss is occurring at such a rapid rate that future summers are predicted to become mostly ice-free. Compared to other Arctic shelf seas, the Barents Sea has experienced the largest declines in sea ice extent, with much of this loss occurring during winter. The Barents Sea also serves as a transitional space between the Atlantic and Arctic Oceans, where water masses from both oceans meet. The marginal ice zone, defined as the outer rim of Arctic sea ice extent, has experienced a continual northward retreat out of the Barents Sea. The unique physical oceanographic characteristics of the Barents Sea, namely the presence of Atlantic water and sea ice cover, further drive the biological productivity found within this area.

In response to the changes in the physical drivers within this ecosystem, a range of species-, community-, and population-level biological responses have already begun. Marine mammals have experienced population declines, benthic communities have undergone rapid restructuring of community composition, and many sub-Arctic boreal fishes have moved northward following their thermal tolerances. Sea ice itself is a unique habitat for a wide range of species assemblages, and the biological consequences of a seasonally available habitat are currently unknown. This thesis is an observational body of work that explored sea ice dependencies of various Arctic marine organisms.

Paper I explored if a pelagic phase could be part of the life cycle of a so-far presumed fully sea-ice associated amphipod, *Apherusa glacialis*, and indeed found that *A. glacialis* was also regularly found in the pelagic realm on a pan-Arctic scale. In an aggregated data set covering over 70 years, several dozen studies, and many depth-stratified tows, *A. glacialis* was found in different depths and water masses, albeit with no seasonal patterns to its pelagic occurrences. Analysis of size distributions found the majority of recently hatched juveniles of *A. glacialis* associated with the sea ice habitat during spring, supporting previous findings. The findings in

this paper imply a more complex life history in terms of habitat use than previously assumed and provide evidence that *A. glacialis* should be regarded rather as a cryopelagic species.

Paper II investigated differences in resource use for three abundant zooplankton (*Calanus glacialis, Thysanoessa inermis,* and *Themisto libellula*) and two sea-ice associated amphipod (*A. glacialis* and *Gammarus wilkitzkii*) species in the European Arctic. These five species differ both in their dietary preferences (herbivorous, omnivorous, carnivorous) and in how they have adapted to the Arctic seasonal cycle (overwintering in diapause–a state of arrested development, business-as-usual–unaffected by seasonality, or flexibility–a mix of using stored energy reserves and feeding). Considering these various categories, this research explored seasonal (rarely studied polar night versus commonly studied polar day) diet changes within these species using a comprehensive combination of lipid storage patterns, fatty acid composition, and compound-specific stable isotope values of individual trophic biomarker fatty acids. The findings in this paper provide evidence of polar night feeding in all five species, regardless of dietary preferences or overwintering strategies. Additionally, herbivorous species shifted their nutrition from primary producers to other food sources. The overwintering strategy of flexibility could potentially be more wide-spread than previously described for zooplankton and sea-ice amphipod species.

Exploring trophic links further, Paper III quantified contributions of ice-associated and pelagic carbon sources to diets of two different Arctic seal species, harp (*Pagophilus groenlandicus*) and ringed (*Pusa hispida*) seals. These are two seal species whose dependence on the sea ice habitat differs where ringed seals are considered more ice dependent. Carbon end-member support to seal diet (via blubber analysis) was quantified using compound-specific stable isotope ratios of fatty acids in specific primary producer (phytoplankton and ice algae) tropic biomarkers. Fatty acid patterns indicated dietary niche separation between harp and ringed seals. However, the seasonal sea ice-associated carbon pathway contributed equally and substantially to both harp and ringed seal diet. These findings indicate that although harp and ringed seals consume different prey items, their prey items are supported by sea ice carbon in similar ways.

The main findings of this thesis demonstrate that in this time of transition–where sea ice is still present but receding–Arctic marine organisms exhibit a wide range of sea ice dependence. While harp and ringed seals displayed strong seasonal associations to the sea ice habitat (in terms of energetic sources), zooplankton and sea ice amphipod species had varying degrees of trophic plasticity (documented here as, for example, polar night feeding activity and being supported by pelagic carbon). The present study increases the knowledge of potential biological responses to the current state of the Arctic.

List of papers

I. Kunisch EH, Bluhm BA, Daase M, Gradinger R, Hop H, Melnikov I, Varpe Ø, Berge J (2020) Pelagic occurrences of the ice amphipod *Apherusa glacialis* throughout the Arctic. Journal of Plankton Research 42:73-86. https://doi.org/10.1093/plankt/fbz072

II. Kunisch EH, Graeve M, Flores H, Gradinger R, Varpe Ø, Bluhm BA. Do Arctic zooplankton feed during polar night? Insights into trophic transfer as revealed by lipids, fatty acids, and compound-specific stable isotopes. Advanced manuscript.

III. Kunisch EH, Graeve M, Gradinger R, Haug T, Kovacs KM, Lydersen C, Varpe Ø, Bluhm BA (2021) Ice-algal carbon supports harp and ringed seal diets in the European Arctic: evidence from fatty acid and stable isotope markers. Marine Ecology Progress Series 675:181-197. https://doi.org/10.3354/meps13834

Data repositories

Paper I: https://doi.org/10.21334/npolar.2020.9167dae8
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Publications not related to doctoral thesis, but published during thesis work

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

Drivdal M, **Kunisch EH**, Bluhm BA, Gradinger R, Falk-Petersen S, Berge J (2021) Connections to the deep: deep vertical migrations, an important part of the life cycle of *Apherusa glacialis*, an Arctic ice-associated amphipod. Frontiers in Marine Science 8:772766. https://doi.org/10.3389/fmars.2021.772766

Kuehne LM, Rolls RJ, Brandis KJ, Chen K, Fraley KM, Frost LK, Ho SS, **Kunisch EH**, Langhans SD, LeRoy CJ, McDonald G (2022) Benefits of permanent adoption of virtual conferences for conservation ecology and ecologists. Conservation biology: the journal of the Society for Conservation Biology e13884. https://doi.org/10.1111/cobi.13884

Conceptual figures

Conceptual species illustrations and figures in this thesis were made by the author (E. Kunisch). I modified various figures from other papers, where the authors are credited. Figures made by others are credited.

Co-author contributions

	Paper I	Paper II	Paper III
Concept and idea	BB, ØV, JB	EK, BB	EK
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Abbreviations

$\delta^{13}C$ – Carbon isotope value

$\delta^{13}C_{FA}$ – Compound specific stable isotope values of fatty acids

CSIA – Compound specific stable isotope analysis

DHA – Docosahexaenoic acid, 22:6(n-3)

DIC – Dissolved inorganic carbon

EPA – Eicosapentaenoic acid, 20:5(n-3)

GC – Gas chromatography

HPLC – High performance liquid chromatography

IRMS – Isotope ratio mass spectrometry

MUFA – Monounsaturated fatty acids

PE – Phosphatidylethanolamine

PI – Phosphatidylcholine

POM – Particulate organic matter

iPOM – sea ice-derived particulate organic matter

pPOM – pelagic particulate organic matter

PUFA – Polyunsaturated fatty acids

SFA – Saturated fatty acids

TAG – Triacylglycerols

WE – Wax esters

1. Introduction

Ecosystems are shaped by the continual and complex interactions between abiotic and biotic factors. Ecological studies explore how these factors influence one another, and how they contribute to ecosystem functioning (Margalef 1963). Ecosystem states are the attributes of an ecosystem at a particular time (Suding & Hobbs 2009). For example, if an aquatic ecosystem is defined by the amounts of aquatic plants, amphipods, and fish, then a state space is defined as, "the three-dimensional space of all possible combinations of the amounts of these variables" with ecosystem dynamics defined as a movement through this space (Suding & Hobbs 2009). Because species, both in their abundance and diversity, play essential roles within ecosystems (McCann 2000), it has been of long interest how communities transition from one stable state to another in a fixed environment (Lewontin 1969, Holling 1973).

Alternative stable states in ecology are defined in two different ways. The first definition is from the variable point of view. Variables are from a community perspective, such as community composition or population density (Beisner et al. 2003). As defined by Suding & Hobbs (2009), there are multiple alternative basins of attraction within a system, with the ability to support different communities (ball-in-cup diagram, Fig. 1A). Within a basin (or state) there is some degree of resiliency, or the amount of change variables can undergo but remain within the same state (Suding & Hobbs 2009). Large perturbations, such as changes in community composition, can push variables out of one basin into another. This movement is commonly known as a tipping point/regime shift. Once in a new basin, variables persist unless subjected to another large perturbation (Beisner et al. 2003). In the marine ecosystem, one example of alternative stable states is the presence/absence of a keystone species (a particular species that helps to hold a system together) (Paine 1966, Simenstad et al. 1978). Variable shifts are assumed to occur within a constant environment (Beisner et al. 2003). The second definition focuses on how the environment affects ecosystems (May 1977). Instead of a shift in variables, a shift in the environment (parameter) is rather causing a state change (examples listed in Fig. 1B). Variables are then corresponding to the environmental change, and the relevant dynamics within the new environment is different (Beisner et al. 2003).

While it is argued that multiple stable states are often too subtle to detect (Knowlton 2004), ecosystems can undergo abrupt regime shifts from one state to another (Scheffer et al. 2001). In the marine environment, regime shifts can also occur as a result of human stressors, such as resource overexploitation and the impacts of coastal development (Mora et al. 2011, Ling et al. 2015). Large-scale oceanic climatic-shifts can also trigger regime shifts (Hare & Mantua 2000), resulting in complex biological feedbacks (Scheffer et al. 2001, Vollset et al. 2022). Tipping points can also serve as points of no return, not allowing for variables or parameters (Fig. 1) to return back to their original state (Duarte et al. 2012).

Polar marine ecosystems are characterized by sea ice presence and low temperatures that further influence biological processes. In these systems, the most prominent environmental driver is the seasonality of the solar cycle. Sea ice naturally expands and contracts relative to the annual cycle of sunlight, expanding when the sun is absent (winter) and contracting when the sun is present (summer). Focusing on the Arctic, the Arctic Ocean and its surrounding shelf seas are in a state of flux (Duarte et al. 2012). Arctic sea ice loss is occurring at a rapid rate, exceeding modelled projections (Jeffries et al. 2013). From 2002 to the present day, extremes in September sea ice minima have become the norm rather than anomalies (Serreze 2003, Stroeve et al. 2008, 2012). The Arctic sea ice pack is becoming both younger and thinner (Maslanik et al. 2011, Renner et al. 2014). Less sea ice cover increases ocean surface warming, creating positive feedback loops in sea ice decline (Steele et al. 2008, Stroeve et al. 2012). Arctic sea ice decline is further intensified by the incoming flow of Atlantic Water (Lind et al. 2018, Wang et al. 2020). Atlantic Water, responsible for the major heat input into the Arctic Ocean, has increased in temperature and salinity (Beszczynska-Moeller et al. 2012), thus contributing to Arctic “Atlantification.” Future summers in the Arctic Ocean are forecasted to transition to mostly ice-free (Overland & Wang 2013). The concept of ecosystem resilience, hence, poses interesting questions during a seemingly rapid reorganization of the Arctic marine ecosystem (Holling 1973, Elmqvist et al. 2003).

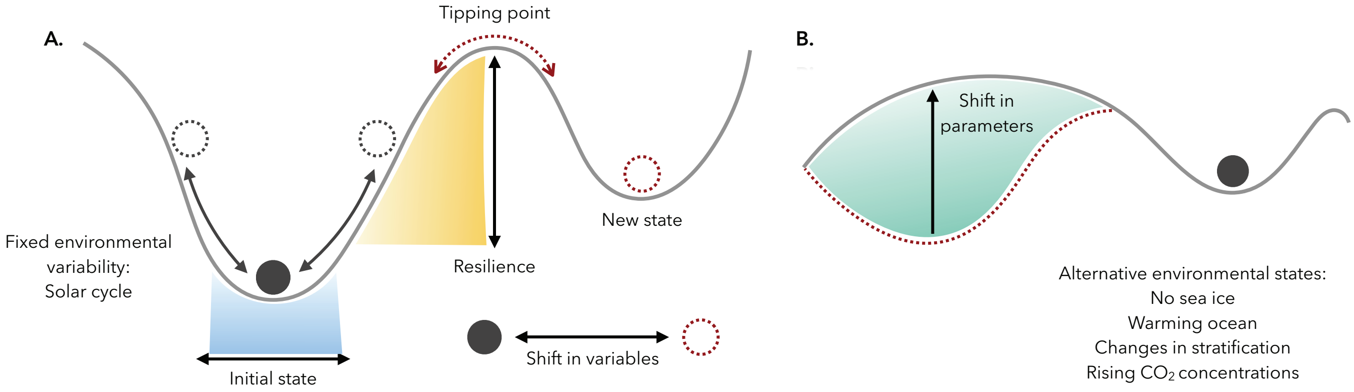


Figure 1. Two-dimensional ball-in-basin theoretical models displaying A) a shift in variables causing the ball to move from one basin to another (labelled as states). And B) environmental changes on the community or ecosystem level. As defined in Beisner et al. (2003), "a shift in parameters causes the landscape itself to change, resulting in movement of the ball." In the bottom left of figure A, fixed Arctic variability is listed and in bottom right of the figure B, alternative environmental (parameter) Arctic shifts are listed. (Figures adapted from Beisner et al. (2003) and Fiorentino & Montana-Hoyos (2014)).

Sea ice itself is a unique habitat for a wide range of species assemblages, including representatives of nearly all size classes: from Archaea and meiofauna living within brine channels (Deming & Collins 2017, Bluhm et al. 2018) to marine mammals who use sea ice as a platform to breed, hunt, or travel (Kovacs et al. 2011). A range of biological responses across trophic levels to environmental changes (a parameter shift, Fig. 1B) in the Arctic has already begun (Post et al. 2013). Sea ice loss has resulted in short-term behavioral responses in Arctic marine mammals, such as the Pacific walrus (*Odobenus rosmarus divergens*) transitioning from sea ice to coastal haul-outs (Jay et al. 2012). Sea ice-associated amphipods are commonly found at the ice-water interface and are strongly linked to Arctic sea ice habitat (both as a substrate and as a source of food resources). How these amphipods overwinter and survive periods of low food resources is less clear (Arndt & Swadling 2006). In Arctic fjords, increases in sea surface temperatures and the expansion of ice-free periods triggered a regime shift, which resulted in a rapid restructuring of benthic community composition (Kortsch et al. 2012). Furthermore, warming of the sub-Arctic seas has resulted in the poleward expansions of marine species following their thermal tolerances (Hastings et al. 2020) resulting in the borealization of Arctic shelf communities (Polyakov et al. 2020). How sea ice-associated organisms will respond to a seasonally absent habitat, and with potential future competition from boreal species, is relatively unknown.

For example, if the more Arctic *Calanus glacialis* is outcompeted by the borealization of its southerly congener, *Calanus finmarchicus*, what would be the consequences? Results from a trait-based (as opposed to species-based) model suggests zooplankton resiliency in the face of Arctic ecosystem change (Renaud et al. 2018). At the base of many Arctic food webs, *Calanus* spp. copepods serve as important links between primary producers and the higher levels of marine food webs. *Calanus* spp. copepods dominate in mesozooplankton biomass and convert much of their plankton-based diet into large stores of lipids (Conover & Huntley 1991, Falk-Petersen et al. 2009). Using *Calanus* spp. body size as a trait (with lipid content as a function of body size), modelled results suggest energy transfer in marine food webs would be equally efficient with smaller sized individuals due to faster population turnover rates (Renaud et al. 2018). In this scenario, *C. glacialis* would adopt a more boreal lifestyle, co-existing with *C. finmarchicus*, resulting in an alternative stable state.

Because of the rate of environmental changes occurring within the Arctic Ocean, marine primary production dynamics in Arctic food webs are of particular concern. Primary producers are critical in the transformation of atmospheric CO_2 into organic carbon. This energy is transferred to heterotrophs, establishing the trophic baseline in many marine food webs. In the Arctic marine realm, primary production has an early peak in sea ice-associated (sympagic) algae production, followed by a secondary peak in phytoplankton production in the water column (Leu et al. 2011, Ji et al. 2013). The phenology of sympagic production is related to sunlight and latitudinal gradients (Leu et al. 2015). Sea ice algal blooms are also affected by seasonal ice melt and the amount of snow cover, further regulating the amount of light available for autotrophic algal growth. Several environmental factors operate synergistically (*i.e.*, nutrient availability, temperature, availability of inorganic carbon, etc.) during sea ice algal bloom succession (Reitan et al. 1994, Leu et al. 2020). As sea ice becomes thinner and covers less area with climate warming, this has resulted in both under-ice and autumn phytoplankton blooms (Ardyna et al. 2014, 2020, Assmy et al. 2017). Indeed, phytoplankton production over the Arctic Ocean has increased by 30% since the late 1990s (Arrigo & van Dijken 2015). In comparison to phytoplankton production, sympagic production is generally lower, with a shorter and regionally variable season in ice-covered regions. Sympagic production, however, is important for first-order consumers that time their life-history strategies in order to feed on this early food source (Conover & Huntley 1991, Søreide et al. 2010, Varpe 2012). Collectively these primary consumers play a critical role in energy transfer to higher trophic-level species in Arctic marine ecosystems.

The overall goal of my thesis research was to better understand the role sea ice plays for Arctic marine fauna. I first assessed the habitat use of a common sympagic amphipod to determine whether it was only associated with the sea ice habitat as previously assumed. Second, I investigated both trophic structure and carbon sources in Arctic marine food webs. I did this by exploring seasonal differences in zooplankton and sympagic amphipod diets using molecular (fatty acids and lipids) approaches; and quantified the contribution of sympagic and pelagic carbon to marine mammal diets with elemental (carbon isotopes of fatty acids) approaches.

2. Background

The three papers included in my thesis are observational bodies of work from the organismal point of view (section 2.1). Paper I challenged me to think about how a sympagic amphipod could persist in the absence of its primary sea ice habitat. From this work, I began thinking about the Arctic in a fundamentally different way. To put it simply, I asked, how does sea ice biologically matter? Papers II and III delve into this question from a food web perspective, therefore a background on my approaches (sections 2.2 – 2.4) is given.

2.1 An overview of the studied species

In Paper I, I investigated a possible pelagic life cycle of a common and endemic Arctic amphipod, *Apherusa glacialis*. *A. glacialis* is ubiquitous and distributed on a pan-Arctic scale within the sea ice habitat (CAFF 2017, Hop et al. 2021). Typically, *A. glacialis* is found under sea ice at the ice-water interface with smaller individuals found within brine channels. *A. glacialis* has typically been thought of as autochthonous (or permanent resident) of the sea ice habitat because of where it was most often found. *A. glacialis* has a life span of approximately two years (Beuchel & Lønne 2002), suggesting that this amphipod overwinters at least once during its lifetime (Poltermann et al. 2000). It was previously assumed that as sea ice melted or was exported out of the Arctic Ocean, *A. glacialis* was lost to the water column and died (Arndt & Pavlova 2005, Hop & Pavlova 2008). During polar night, however, Berge et al. (2012) found *A. glacialis* in deep, northward-moving Atlantic Water (between 200 and 2000 m) in good condition. Berge et al. (2012) suggested an adaptive-advection model where *A. glacialis* could increase its survival by overwintering in the Atlantic Water inflow. Assuming *A. glacialis* employed an overwintering vertical migration strategy (similar to *Calanus* spp.), *A. glacialis* would return to ice-covered areas in the northward flowing Atlantic Water at depth. These findings led to the exploration of how often *A. glacialis* was found away from its presumed sea ice habitat.

Recent research has found higher than expected biological activity during polar night in many Arctic invertebrate and vertebrate species, contradicting long-assumed paradigms (Berge et al. 2015b a, 2020). If organisms are more active during polar night than previously assumed, are they surviving off accumulated lipids, continually feeding, or is it a combination of both? Arctic zooplankton and sympagic amphipods have evolved different types of overwintering strategies to cope with seasonally less-productive time periods and are adapted to the Arctic seasonal cycle. Strategies range from diapause (a period of arrested development, surviving off stored energy pools) to business-as-usual (continued feeding year-round, with no reduction in metabolism) (Hagen 1999). In the middle of these opposing strategies is flexibility, defined as using a mix of energy stores and opportunistic feeding (Hagen 1999).

For me, the motivation for Paper II was a natural extension of Paper I. Therefore, in Paper II, I focused on two sympagic amphipods and three pelagic zooplankton species (Fig. 2) whose diets and overwintering strategies differ. Sympagic amphipods, when found within the sea ice habitat, have overlapping dietary preferences. *A. glacialis*, classified as herbivorous–detritivorous (Werner 1997, Poltermann 2000), has a flexible overwintering strategy in the sea ice habitat (Werner & Auel 2005). *Gammarus wilkitzkii* has an opportunistic feeding strategy (herbivorous, carnivorous, detritivorous) (Poltermann 2001). While an overwintering strategy for *G. wilkitzkii* has not been determined, I categorized it having a business-as-usual strategy based on previous in-ice research findings (Poltermann 2001). The overwintering feeding strategies of sympagic amphipods away from sea ice are unknown. Additionally, I included three zooplankton species: *Calanus glacialis, Thysanoessa inermis,* and *Themisto libellula. C. glacialis* is a primarily herbivorous copepod that vertically migrates to depth in autumn and overwinters in a dormant state of diapause (Ackman 1989, Falk-Petersen et al. 2009). The euphausiid *T. inermis* is considered herbivorous–omnivorous (dependent on the time of year) and has a flexible overwintering strategy (Sargent & Falk-Petersen 1981, Hagen 1999, Dalpadado et al. 2008). *T. libellula*, a carnivorous amphipod, is less affected by seasonality in regards to its diet, and has a business-as-usual overwintering strategy (Hagen 1999, Kraft et al. 2013).

In Paper III, I again chose organisms whose dependence on the sea ice habitat differs. I investigated potential niche differences (explored by dietary differences and carbon sourcing) between two ice-associated seal species (Fig. 2). Harp seals (*Pagophilus groenlandicus*) are a North Atlantic species that annually migrates northward into their Arctic feeding areas (Stenson et al. 2020). As harp seals move from their southerly drift-ice breeding areas to their northerly feeding areas, they are likely to encounter a variety of prey items in both sympagic and pelagic habitats. Their diets are indeed variable by both season and region (Nilssen et al. 1995a b, Lawson & Hobson 2000). Ringed seals (*Pusa hispida*) are an Arctic circumpolar species. Because of their wide pan-Arctic range, their diet is also known to vary (Holst et al. 2001, Thiemann et al. 2007). However, ringed seals in the Svalbard region are tightly coupled both to tidewater glacier fronts and the retreating sea-ice edge (Hamilton et al. 2015, 2019).

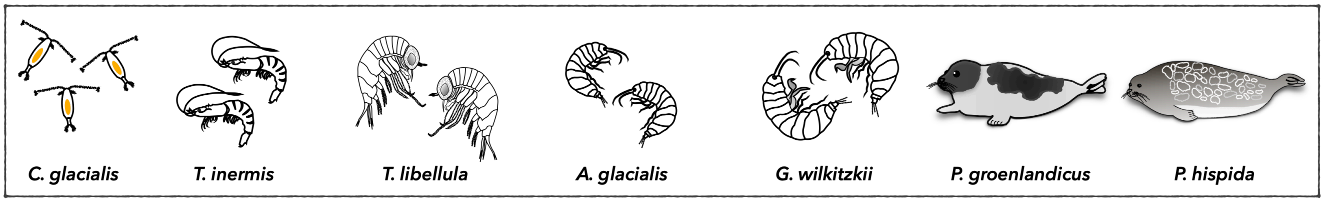


Figure 2. The species studied in this thesis.

In my papers, I explored the possibility of phenotypic plasticity in the studied species as it relates to the trajectory of Arctic ecosystem states. Phenotypic plasticity is defined as the capacity of a single genotype to exhibit variable phenotypes (Whitman & Agrawal 2009), and influences how organisms respond to different environments (DeWitt & Scheiner 2004). As my thesis deals with dietary differences (in seals) and whole-body biochemical compositions (in zooplankton and sympagic amphipods), I investigated differences in trophic plasticity of these species during different seasons. Plasticity can play an important role in organismal adaptations as it can be favored over a fixed response when predictable environmental changes occur. Organismal adaptations occur on the morphological, behavioral, and/or physiological levels (West-Eberhard 1989, Whitman & Agrawal 2009). For example, reproductive plasticity is found in the Arctic *C. glacialis*, as it ranges from using stored energy to being reliant on food resources for reproduction (Varpe et al. 2009, Daase et al. 2013).

2.2 Fatty acids

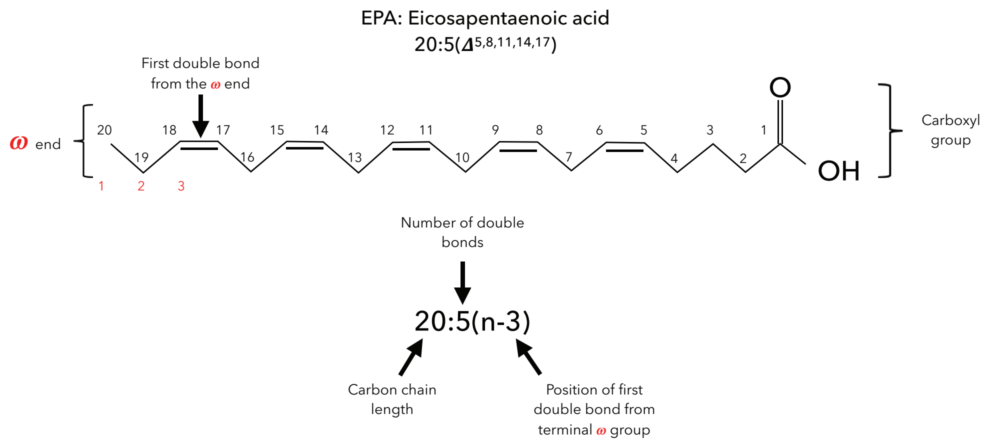
Fatty acids (Box 1) are among the most important molecules in aquatic food webs. These compounds are important structural components in cell membranes and necessary for somatic growth and are also integral components of fats that provide long-term energy storage. Marine environments are important pools for the essential n-3 and n-6 long-chain polyunsaturated fatty acids (PUFA) (Budge et al. 2014). For many species, these fatty acids must be acquired through diet. Therefore, fatty acids are commonly studied to determine consumer diets within marine food webs (Lee et al. 1971, Falk-Petersen et al. 1990, Graeve et al. 2005, Søreide et al. 2013). Unlike direct diet studies that use stomach content analysis, fatty acid analysis can provide a more qualitative overview of energy assimilated on a longer time scale.

Many marine primary producers have unique fatty acid profiles, allowing for the determination of different sources of primary producers to zooplankton consumers, thereby serving as trophic biomarkers within food web studies (Dalsgaard et al. 2003). Diatoms (Class Bacillariophyceae) and dinoflagellates (Infraphylum Dinoflagellata) are two main phytoplankton groups in the world's ocean. Diatoms are abundant at high latitudes where they are often the main primary producers and exporters of organic carbon (Malviya et al. 2016). Focusing on the sea ice habitat, the microalgal community found within polar sea ice is often dominated by diatoms, including first-year sea ice (Fahl & Kattner 1993, Leu et al. 2006, Fernández-Méndez et al. 2018, Hop et al. 2020). Diatoms also contribute the most to the particulate organic matter of sea ice (Van Leeuwe et al. 2018). Although dinoflagellates occur in sea ice, they are often more abundant in pelagic phytoplankton communities (Okolodkov & Dodge 1996). In younger sea ice habitats, dinoflagellates can be outcompeted by diatoms (Kauko et al. 2018).

Box 1. Fatty acid nomenclature

Fatty acids are carboxylic acids (containing a terminal carboxyl group, (C(=O)OH)) with hydrocarbon chains. While the carboxylic acids can range from 4 to 36 carbon atoms in length, the most commonly occurring fatty acids have even numbers of carbon atoms in chains of 12 to 24 in length. Fatty acids range from having unbranched chains that are fully saturated (having no double bonds) to having one or more double bonds.

Fatty acids are commonly presented as their trivial name (e.g., EPA, or Eicosapentaenoic acid) or in shorthand notation. Shorthand notation specifies chain length, the number of double bonds, and the position of the first double bond from the terminal methyl (ω) group (denoted by the red numbers below). Systematic nomenclature indicates the location of double bonds from the carboxyl group (also referred to as the front end), designated by the delta (Δ). To illustrate the fatty acid structure, each line segment shown in the zigzag structure below represents a single bond between adjacent carbon atoms (denoted by the black numbers).



Saturated fatty acids (SFA): fatty acids that do not have double bonds between carbon atoms (*i.e.,* 14:0, 16:0, 18:0)
Monounsaturated fatty acids (MUFA): fatty acids with one double bond between carbon atoms (*i.e.,* 16:1(n-7), 18:1(n-9))
Polyunsaturated fatty acids (PUFA): fatty acids with two or more double bonds between carbon atoms, usually refers to those that have one CH_2 between the double bonds (*i.e.*, 16:4(n-1),18:4(n-3), 22:6(n-3))
Omega-3 (n-3) fatty acids: fatty acids with the first double bond on the third carbon atom from the methyl terminus of the carbon chain
Omega-6 (n-6) fatty acids: fatty acids with the first double bond on the sixth carbon atom from the methyl terminus of the carbon chain

Modified from Twining et al. 2016

Diatoms and dinoflagellates have distinct fatty acid chemical compositions, which can be used to distinguish them from other microalgal groups and from each other. Diatoms are characterized by 14:0, 16:0, 16:1(n7), other C16 polyunsaturated fatty acids (PUFA) such as 16:4(n-1), as well as 20:5(n-3) (Viso & Marty 1993, Dunstan et al. 1994, Jónasdóttir 2019). Through a series of catalytic reactions, biosynthesis of fatty acids results in the generation of 16:0 in diatoms (Zulu et al. 2018). Through desaturation and elongation, 16:0 can be further converted into other fatty acids (see Box 2, Fig. 3). While diatoms contain other fatty acids such as 18:4(n-3) and 22:6(n-3), they are generally not considered robust diatom fatty acid biomarkers (Fahl & Kattner 1993). In comparison, dinoflagellates have higher amounts of the fatty acids18:4(n-3) and 22:6(n-3) (Viso & Marty 1993, Mansour et al. 1999), and these fatty acids often used as trophic biomarkers for dinoflagellates. Dedicated research in this field has identified many other fatty acids that are also used as trophic biomarkers (Kelly & Scheibling 2012, Parrish 2013). Thus, the differences in fatty acid compositions of diatoms and dinoflagellates (among other microalgae) promote their utilization as trophic biomarkers in diet studies using fatty acid analysis. The specific biomarkers used in Papers II and III are denoted in Table 1.

While both diatoms and dinoflagellates have unique fatty acid signatures (Mansour et al. 1999, Parrish 2013), they occur in both sea ice and the water column. Thus, the quantification of fatty acids cannot explicitly differentiate between sympagic and pelagic algae (Søreide et al. 2008). Fatty acids can be present in relatively minor proportions, or fatty acid contributions can overlap (Falk-Petersen et al. 1998), confounding results. Because of these reasons, I included stable isotope analysis as an additional method to separate carbon sources to answer my research questions (detailed in section 2.3).

Herbivorous calanoid copepods, especially those species found in polar regions, capitalize on plankton blooms in order to survive periods of low food supply. *Calanu*s spp. can de novo synthesize a primarily plankton-based diet into long-chain monounsaturated fatty acids (MUFA), and the 20:1 and 22:1 MUFA are typically characteristic for these species (Fig. 4). Therefore, 20:1(n-9) and 22:1(n-11) are generally regarded as *Calanus* spp. trophic biomarker fatty acids. The biosynthetic pathway (see Box 2) to produce 20:1(n-9) and 22:1(n-11) is from the elongation of 18:0 and 20:0 (Kattner & Hagen 1995).

Box 2. Biosynthetic pathways of fatty acids

Fatty acids can undergo both desaturation–the introduction of additional double bonds, or elongation–an enzymatic reaction that extends the carbon chain. Both desaturation and elongation can occur either on the methyl or front-end. *β*-oxidation is a process where fatty acids are broken down to produce energy.

16:1(n-7) is formed by a Δ9 desaturation of 16:0, a common biosynthetic pathway of diatoms. This pathway extends further, forming other C16 PUFA. 18:1(n-9) is the precursor to all n3 and n6 PUFA. 18:2(n-6) and 18:3(n-3) are two types of essential fatty acids. Essential fatty acids in vertebrate species (including humans) are so named because they are needed for optimal function and survival but cannot be de novo synthesized (*i.e.*, they must be acquired via diet). However, vertebrates possess the metabolic pathways necessary to further desaturate and elongate the n-3 PUFA to form other highly unsaturated fatty acids (Rosenthal 1987, Bell & Tocher 2009, Castro et al. 2016). Photosynthetic marine organisms (the primary producers) have long been considered the major source of the n-3 and n-6 PUFA. However, many heterotrophic protists and invertebrates can also produce long-chain PUFA de novo (Kabeya et al. 2018, Monroig & Kabeya 2018).

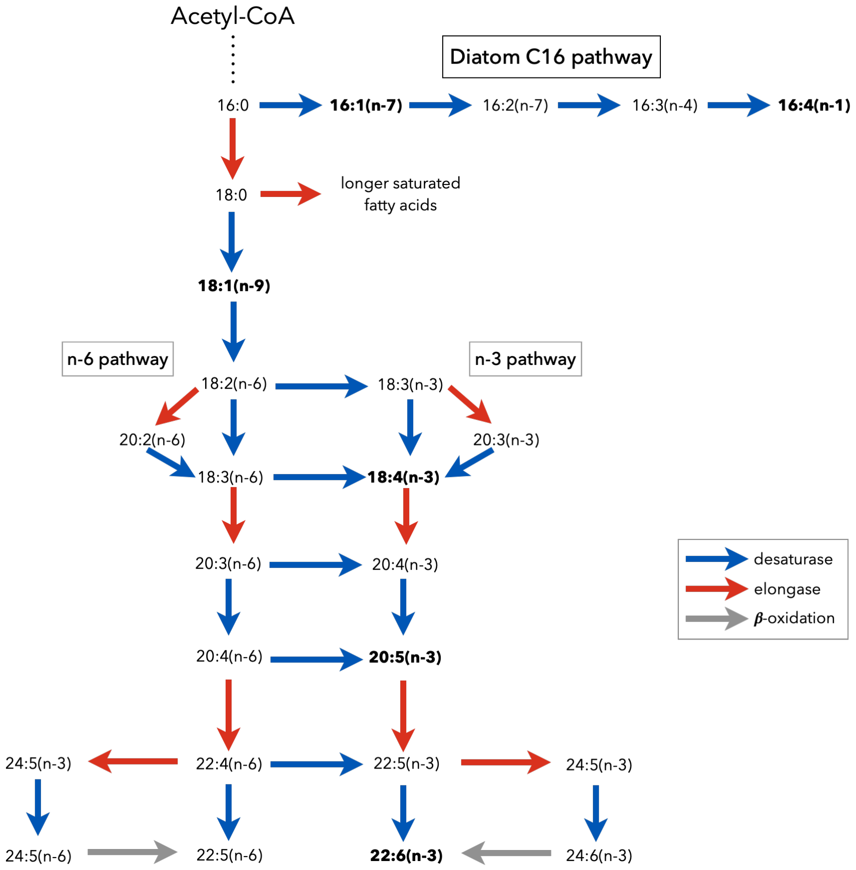


Figure 3. Fatty acid biosynthesis, modified from Monroig & Kabeya (2018). Fatty acids commonly used as trophic biomarkers are denoted in bold (and in Table 1). Blue arrows represent desaturase, red arrows represent elongase, and grey arrows represent *β*-oxidation.

Box 2 (continued).

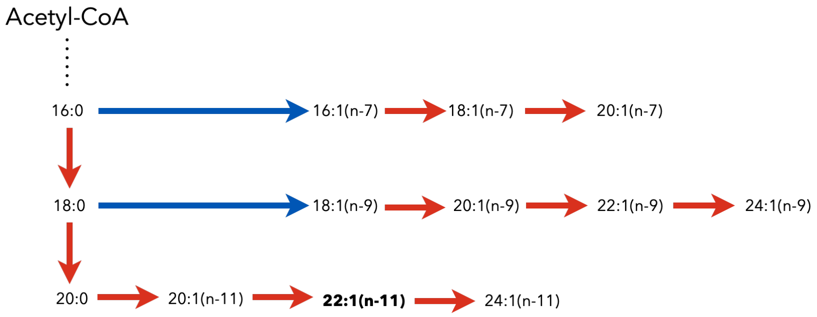


Figure 4. Fatty acid biosynthesis in herbivorous calanoid copepods, modified from Dalsgaard et al. (2003). Blue arrows represent desaturase and red arrows represent elongase. 22:1(n-11), commonly used as a trophic biomarker, is denoted in bold.

Table 1. Trophic marker fatty acids and what they indicate in pelagic and sympagic food sources. Falk-Petersen et al. 1987, 1999 [a], Graeve et al. 1994 a b, 1997 [b], Scott et al. 2002 [c], Auel et al. 2002 [d], Dalsgaard et al. 2003 [e].

Fatty Acid	Trophic Biomarker
16:1(n-7)	Diatoms at spring bloom stage (a, b)
20:5(n-3)	Diatoms (a, b)
18:4(n-3)	Dinoflagellates (a, e)
22:6(n-3)	Flagellates (a, b, d)
18:1(n-9)	Carnivory (a, b)
22:1(n-11)	*Calanus* spp. (a, b)
∑15:0, ai15:0, i15:0, 17:0	Bacteria (e)

2.3 Stable isotopes

Stable isotopes (Box 3) function like enhanced fingerprints from Earth. They can be tracers of element origin, integrating ecological processes both in space and time. Isotopes have broad applications, from paleontology (Casey & Post 2011) to planetary science (Anbar 2004). The analysis of stable isotopes for the lightest elements (Hydrogen, Carbon, Nitrogen, Oxygen, and Sulfur) that contribute to the cycling of organic matter are widely used in ecological studies (Fry 2006). During photosynthesis, carbon fixation of CO_2 occurs in photoautotrophs, resulting in the isotopic fractionation of carbon isotopes (Fry 1996). Many photosynthetic primary producers set the isotopic baseline. Carbon isotope values have been widely used to infer primary producer sources (carbon end members) to consumers within a food web, given that the carbon isotope values of various primary producers differ.

Organic carbon in sea ice-covered pelagic ecosystems originates primarily from ice algae and phytoplankton. Ice algae and phytoplankton often have distinct carbon isotope signatures (δ^{13}C). Sea ice algae compete for light and space in a closed, carbon-limiting system that has limited exchange with the underlying water column (Horner & Schrader 1982, Fry & Sherr 1984). Subsequently, bulk δ^{13}C values of ice algae are often higher when compared to phytoplankton values (Gradinger 2009, de la Vega et al. 2019). Limitations in bulk stable isotope analysis occur when carbon isotope values of primary producers overlap, preventing accurate source discrimination. In the Arctic, bulk carbon values of ice algae and phytoplankton can overlap depending on ice algal biomass and when sampling takes place (Søreide et al. 2006, Tremblay et al. 2006). Because of these limitations, the field of stable isotope ecology has extended increasingly towards compound-specific stable isotope analysis (CSIA, Box 4).

Contrary to bulk isotope analysis–yielding a single ratio encompassing a mixture of all organic compounds in a given sample (Fig. 5)–CSIA operates on a molecular level, determining isotope values of individual organic compounds (see Box 4). The incorporation of CSIA into ecological studies can thus provide more detail into the pathways and fate of organic compounds. Thus, the incorporation of CSIA in diet studies of Arctic taxa provides further differentiation between carbon sources, improving the resolution of these carbon pathways throughout food webs (Budge et al. 2008).

Box 3. Stable isotopes: notations and definitions

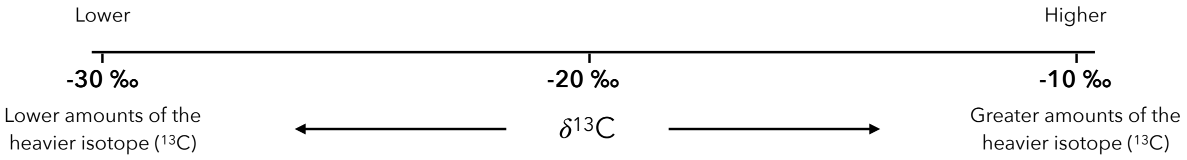
Isotopes are atoms of the same element that have different numbers of neutrons (but the same numbers of protons and electrons). This means that isotopes of the same element have similar charges but different masses. For example, carbon occurs naturally in three isotopes: carbon 12 (6 neutrons), carbon 13 (7 neutrons), and carbon 14 (8 neutrons). Said a different way, isotopes of carbon have six protons and electrons, but a carbon atom with a mass of 13 (written as ^{13}C) has one more neutron than carbon 12 (^{12}C).

Isotope values have a specific δ notation, which is a measurement of difference. δ values are "% indicators" of the heavier isotope because of the linear relationship between the δ values and isotope content (Fry 2006). The δ is expressed in ‰ (permil) units and is quantified as a deviation from a known, international reference standard in parts per thousand:

$$\delta X\ (‰) = [(R_{sample} / R_{standard}) - 1] \times 1000$$

Where X is an isotope (e.g.,^{13}C) and R is the corresponding ratio of isotopes (e.g., $^{13}C/^{12}C$)

This means the higher the δ value, the greater amounts of the heavier isotope, and the lower the δ value, the lower amounts of the heavier isotope.



Useful definitions (as defined in Kendall & Caldwell 1998):
Isotopic fractionation–preferential accumulation of one isotope relative to another (usually by chemical/physical processes). Results in a change in the relative proportions of isotopes due to equilibrium or kinetic processes.

Equilibrium fractionations–redistribution of isotopes of an element among various species/compounds. In these reactions, the heavier isotope preferentially accumulates in the species/compound with higher energy.

Kinetic fractionations–occurring outside of isotopic equilibriums where forward and backward reactions rates are different. These are common in biological processes. For example, organisms preferentially use the lighter isotope because it is energetically less costly. This results in isotope values becoming higher from source to consumer. For example, both metabolism and isotopic turnover can cause isotopic fractionations (reviewed in Twining et al. 2020).

Isotopic turnover-the time it takes for stable isotopes in tissues to be replaced by the stable isotopes in the diet. Turnover times vary dependent on species and animal tissues (Fry & Arnold 1982, Tieszen et al. 1983).

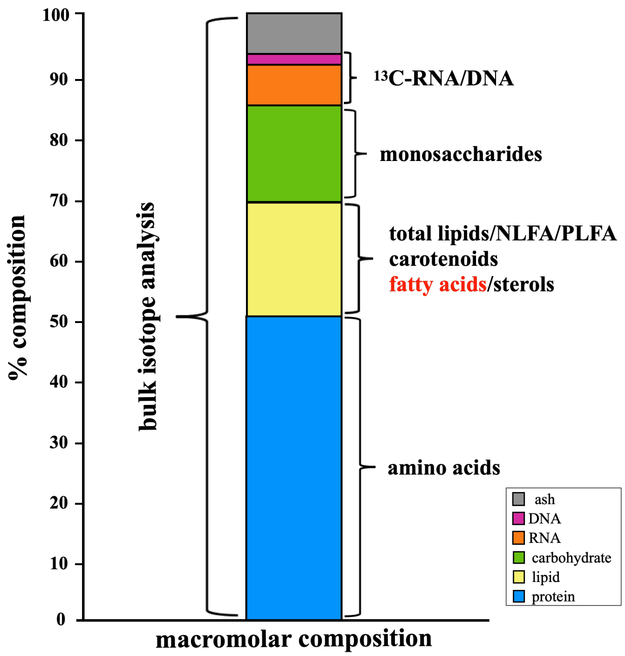


Figure 5. Organic compounds in bulk versus compound specific stable isotope analysis (modified from Twining et al. (2020)). NLFA-neutral lipid fatty acids; PLFA-phospholipid fatty acids. Fatty acids (used for Papers II and III in this thesis) depicted in red.

2.4 Lipid classes

In Paper II, I included major lipid classes, along with fatty acid analysis, to investigate the overwintering strategies of zooplankton and sympagic amphipods. Lipids (Box 5) serve as energy reserves for zooplankton (Hagen & Auel 2001) and aid in buoyancy control because of their low density compared to saltwater. Herbivorous marine zooplankton consume comparatively lipid-poor phytoplankton, converting this dietary energy into lipid-rich storage (Kattner & Hagen 1995). This strategy enables zooplankton to capitalize on relatively short pulses of primary productivity. It has resulted in unique life-history traits of marine zooplankton, particularly how they store excess energy for periods of little to no productivity. Common lipids are storage (*i.e.*, neutral) lipids which include triacylglycerols (TAG), wax esters (WE), and polar (*i.e.*, membrane) lipids, such as the phospholipids (Ventura 2006). TAG are considered pools of short-term energy reserves and WE long-term storage deposits (Lee et al. 1971). For example, in *Calanus* spp., assimilated dietary fatty acids (Box 2) are further esterified with de novo synthesized fatty alcohols, stored as WE in their oil sacs (Sargent & Henderson 1986).

Box 4. Applications of stable isotopes in ecology

Bulk isotope analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) is widely used in marine food webs because these isotopes function in predictable ways between prey and consumer tissues (Michener & Schell 1994). In ecology, bulk stable isotopes of carbon and nitrogen provide information on carbon sources, trophic position and movement, and niche space within food webs (DeNiro & Epstein 1978, Fry & Sherr 1984, Hobson 1999).

At the bulk carbon level, the difference between trophic levels is often small (0 – 1 ‰) thus often neglected when it comes to diet inferences (DeNiro & Epstein 1978). Because of the small difference between trophic levels, carbon is widely used to infer primary producer support (carbon end members) to consumers within a food web. Limitations to bulk carbon analysis arise when carbon values of primary producers overlap, presenting source discrimination. Bulk nitrogen enrichment is larger, varying between 2 – 4 ‰ in consumers relative to their diet (Minagawa & Wada 1984). A mean value of $\delta^{15}N$ equaling 3.4 ‰ has been suggested between trophic levels (Post 2002), which results in sufficient resolution to use $\delta^{15}N$ to establish the trophic position of organisms within a food web. Variation in trophic baselines ($\delta^{13}C$ and $\delta^{15}N$) can exceed the trophic discrimination between animal and diet, confounding trophic position interpretations.

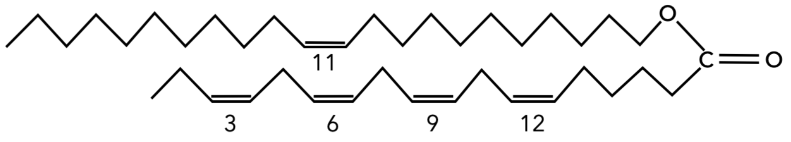
Ecological dietary tracing has expanded into applying compound-specific stable isotope analysis (CSIA, Nielsen et al. 2018). Here I highlight carbon isotope values of fatty acids (CSIA-FA, $\delta^{13}C_{FA}$). Incorporating CSIA-FA into ecological studies can better differentiate between carbon sources and their assimilation pathways throughout food webs (Budge et al. 2008). Although CSIA-FA can be a powerful tool to better understand broad patterns, it is arguably more challenging to interpret because less is known on the isotopic fractionation of individual fatty acids for many organisms.

Box 5. Lipid classes

Lipids are a large class of biomolecules. Lipids are further defined by their broad range of chemical structures, functions, and specific polarity. In general, lipids are more hydrophobic than amino acids and carbohydrates. Fatty acids provide the structural function to many lipids and are essentially the building blocks within cell membranes (De Carvalho & Caramujo 2018).

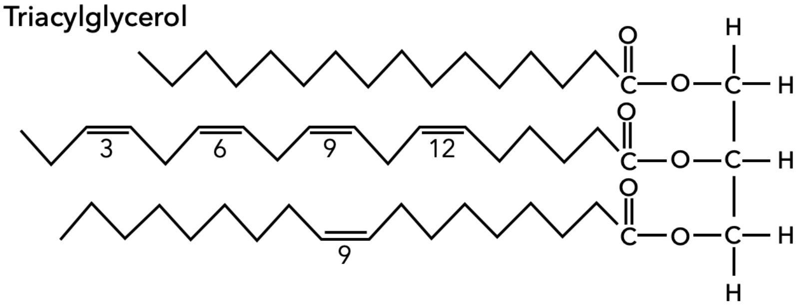
Wax esters (WE) are the main storage lipid in deep, vertical migrating zooplankton, such as *Calanus* spp. (Lee et al. 2006). They consist of long chain monounsaturated fatty acids (MUFA) and fatty alcohols, mainly from the 20:1 and 22:1 isomers (Graeve et al. 1994b). They contain one fatty acid with an ester bond to a long-chain fatty alcohol.

Wax Ester



Triacylglycerols (TAG) have a glycerol molecule, which is an alcohol with three carbon and five hydrogen atoms and three hydroxyl (OH) groups. Fatty acids are attached to the three carbons of this glycerol molecule (via an ester bond). TAG are so named because they consist of three fatty acids and a glycerol.

Triacylglycerol



Phospholipids are a class of polar lipids (chemical structure not shown) found in euphausiids and other marine zooplankton. They are important components of cell membranes. The tails of phospholipids are usually comprised of fatty acids, namely 16:0, 20:5(n-3), and 22:6(n-3) (Lee et al. 2006).

3. Thesis aims and objectives

In this thesis, I investigated the biological responses of Arctic marine organisms to their sea ice habitat during a period of sea ice decline. As illustrated in Figure 6, I explored the potential of organisms once thought of as exclusively sympagic to not only have a more comprehensive habitat range but behavioral plasticity (as indicated by the dotted arrow, Paper I). Using trophic biomarkers and lipid classes, I investigated the seasonal and spatial variability of resource use within an Arctic food web (Paper II). Paper III explores the overall fate of sympagic and pelagic carbon sources (as indicated by the fatty acid molecules within the arrow) to upper trophic predators within one season.

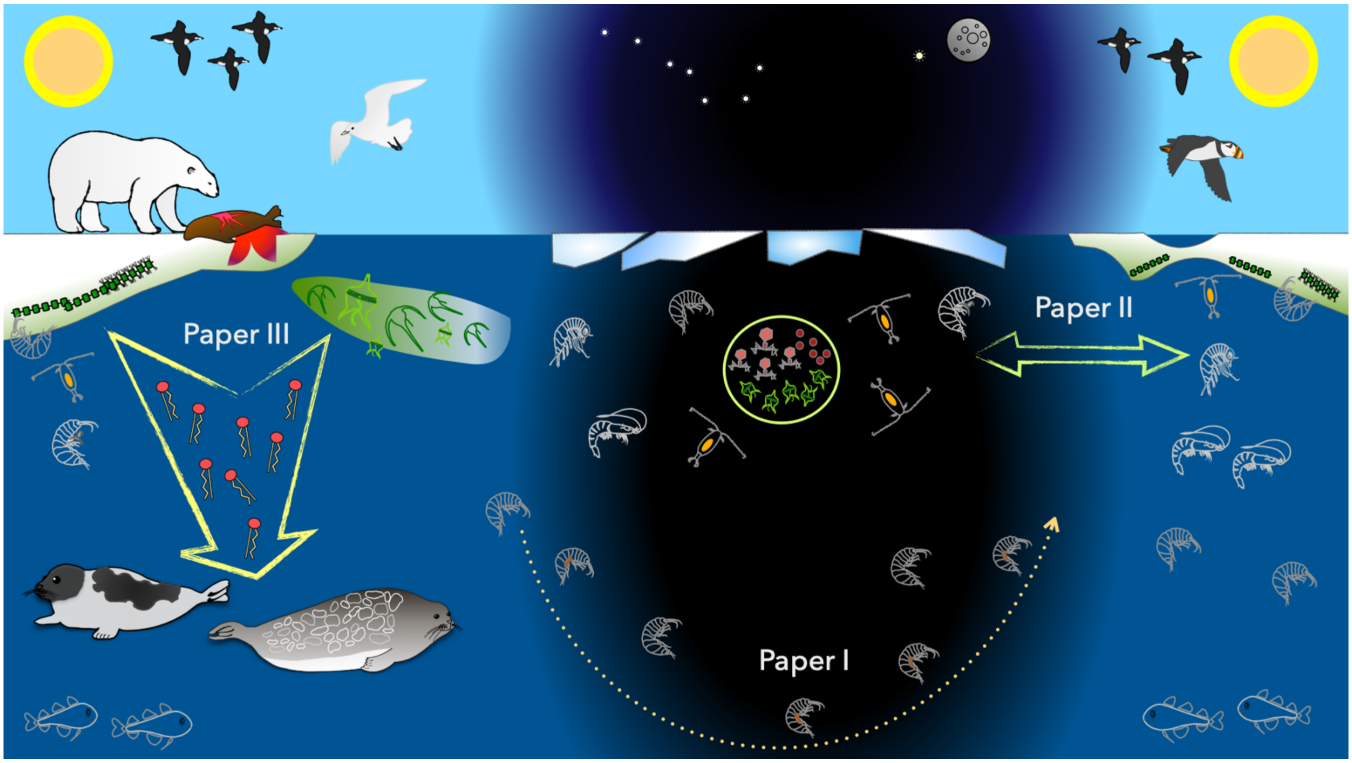


Figure 6. Conceptual presentation of the topics covered in my thesis. For organism symbols of study species, see Figure 2.

3.1 Main questions asked in the three papers

The following research questions and hypothesis were addressed in this thesis:

Paper I
When in the annual cycle is *Apherusa glacialis* found in the water column?

Are there any seasonal patterns of *A. glacialis* at depth, further explaining *A. glacialis* life history strategies?

> Hypothesis I: *A. glacialis* is only found in the pelagic realm during polar night, similar to previous findings.

Paper II
How do Arctic zooplankton and sympagic amphipods sustain polar night activity in relation to the more productive polar day?

> Hypothesis I: If changes in lipid classes and fatty acids occurred during the polar night, these would differ by overwintering strategies (diapause, flexibility, and business-as-usual).
>
> Hypothesis II: Zooplankton has low seasonal variability in the $\delta^{13}C_{FA}$ values of trophic biomarker fatty acids because of no expected switch from ice-algal carbon during the polar day to pelagic carbon sources during the polar night.
>
> Hypothesis III: Sympagic amphipods have high seasonal variability in the $\delta^{13}C_{FA}$ values of trophic biomarker fatty acids because of an expected switch from ice-algal carbon sources during the polar day to pelagic carbon sources during the polar night.

Paper III
How do sympagic and pelagic production support Arctic seal diets?

> Hypothesis I: Even if fatty acid compositions of the two primary production sources were similar, sympagic algae would have $\delta^{13}C_{FA}$ values higher than pelagic algae values.
>
> Hypothesis II: Fatty acid profiles would be similar between harp and ringed seals, given their dietary overlap.
>
> Hypothesis III: Sympagic carbon is more likely to contribute to the diet of ringed seals because of their stronger association with sea ice.

4. Methods

4.1 Study Region

The work in this thesis has both a pan-Arctic area of study (Paper I) with a particular focus on the northern Barents Sea and the region north of Svalbard (Papers I, II and, III). In the focused study region for Papers I – III, biological productivity is strongly tied to physical oceanographic characteristics, namely the presence of Atlantic water and seasonal sea ice cover (Wassmann et al. 2020).

The Barents Sea, a large inflow shelf sea, is a transitional space consisting of southerly Atlantic water mixing with colder Arctic water masses in the north (Fig. 7). The Fram Strait, a deep passageway located west of the Svalbard archipelago, further defines the study area. Situated between Greenland and Svalbard, the Fram Strait is a large two-way conduit connecting the North Atlantic and Arctic Oceans. Within the western side of the Fram Strait, sea ice and Arctic water masses flow southward (reviewed in Bluhm et al. (2015)). On the eastern side, the Fram Strait brings large volumes of warm and saline Atlantic water into the Arctic Ocean (Hop et al. 2006). The core of Atlantic water as it flows past northwest Svalbard is located at depth, between 75 and 500 m (Beszczynska-Möller et al. 2011). Atlantic water in the Barents Sea Branch is further modified as it travels northward, mixing with polar and coastal waters (Slagstad & McClimans 2005). Furthermore, Atlantic water in the northern Barents Sea can also be found near or at the surface (Rudels et al. 2013). Another characteristic of the Barents Sea is the presence of the marginal ice zone. This zone–defined as the outer rim of the seasonal ice zone domain–is a transitional zone between open water and dense, drifting sea ice. This zone is considered ecologically important because of its seasonal pulse of relatively intense productivity (Wassmann et al. 2006) that supports marine food webs, including higher trophic levels (Falk-Petersen et al. 1998).

Arctic sea ice minima (measured when sea ice extent is at its lowest, usually in September) and maximums (measured when sea ice extent is at its largest, often in March) have experienced drastic declines (Fig. 7). Compared to the other seasonally ice-covered Arctic shelf seas, the Barents Sea has experienced the largest declines in sea ice extent, with the majority of this loss occurring in winter (Onarheim & Årthun 2017, Onarheim et al. 2018). The future northern Barents Sea is forecasted to become more Atlantic-like, warmer and less-stratified (Lind et al. 2018). During June and July 2017 (data collection for Papers II and III), all sea ice encountered was first-year ice. The in-ice chlorophyll *a* concentrations in June and July 2017 ranged from 0.11 to 0.39 mg m^{-2} (Castellani et al. 2020). No sea ice was encountered during sampling in January 2017; sampling occurred within smaller sea ice fragments within the marginal ice zone during January 2018.

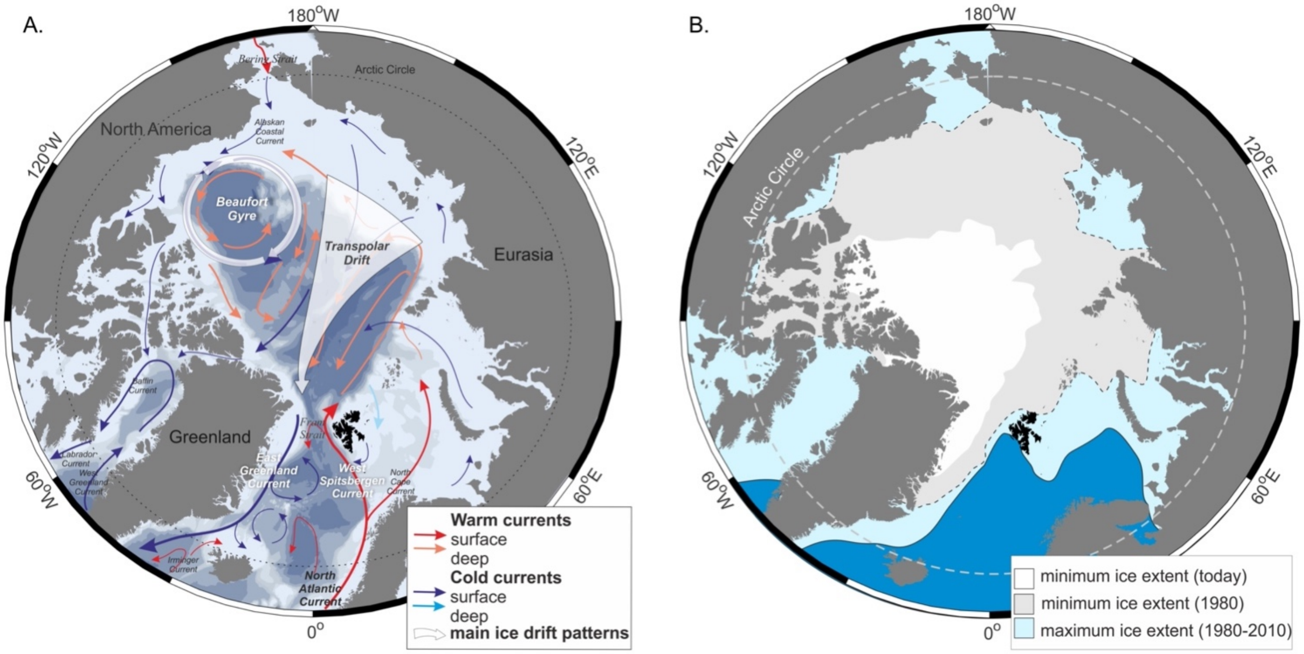


Figure 7. Pan-Arctic map (A) with advective currents displayed (modified from Hunt et al. 2016), and (B) Pan-Arctic sea ice extent. Svalbard (in both A and B) is denoted in black (Figure 7 credit: M. Daase).

4.2 Paper I: Pan-Arctic sympagic amphipod database

To test my main hypothesis, the spatial and temporal distribution of *A. glacialis* was explored in three ways. First, a previously constructed database compiled by the Norwegian Polar Institute for the Circumpolar Biodiversity Monitoring Program was used. This database also included amphipod data from the Arctic Ocean Diversity Census of Marine Life project. Second, additional pelagic records for this database were sought out by contacting many (30+) Arctic marine zooplankton ecologists inquiring if *A. glacialis* was ever found in their pelagic net samples (complete list in Paper I). Finally, targeted net sampling was conducted during a 2017 field collection during the polar night. Compiling records across 71 years meant a diversely collected dataset, further described in Paper I. Additionally, hydrographic data (temperature and salinity) were included on a subset of *A. glacialis* pelagic presences near Svalbard, to investigate the relationship of their presence in specific water masses. Atlantic Water was defined as salinity > 34.92 and temperature > 2 °C (Beszczynska-Moeller et al. 2012, Walczowski 2013, Menze et al. 2019). To further explore the life cycle strategies of *A. glacialis*, both published and unpublished records of body size and sex ratio throughout the year from a 30-year period were included in Paper I.

4.3 Sample collection for Papers II and III

For Paper II, zooplankton and sympagic amphipods were collected during three expeditions in 2017 and 2018 in the Barents Sea and Arctic Ocean (Paper II, Fig. 1). Two expeditions occurred during the polar night (January 2017 and 2018) and one during the polar day (between 3 June and 14 July 2017). Organisms were collected using a variety of pelagic and under-ice nets (described in detail in Papers I and II). Adult or pre-adult stages were collected for each species.

For Paper III, sea-ice algae and phytoplankton were collected throughout the study area (Paper III, Fig. 1). Particulate organic matter within sea ice (iPOM) was mainly collected by taking ice cores. The bottom 5 cm of each ice core was cut off and melted onboard the ship in a 4 °C dark room. Ice-algae aggregates floating in auger holes were collected by hand and placed into 50 ml Falcon tubes (Fisher Scientific). Particulate organic matter from the phytoplankton community (pPOM) was collected mainly using a CTD rosette water sampler (Seabird SBE9+) at the chlorophyll maximum layer (between 6 and 40 m). iPOM and pPOM were filtered onto 0.7 µm pre-combusted GF/F filters (Whatman, Merck) for laboratory analysis. Seal blubber was collected from harp and ringed seals on 11 September 2016 and between 26 June and 21 September 2017, respectively. I analyzed full-depth (from skin to muscle) blubber samples.

4.4 Papers II and III: Biochemical methods and laboratory analysis

Laboratory analysis is explained in brief. For full details, please refer to Papers II and III.

Before lipid extraction, samples were freeze-dried for 24 h (Rudy et al. 2016). Animal samples were mechanically homogenized, and POM filters were placed in an ultrasonic bath. Lipids were then extracted using dichloromethane/methanol 2:1 v/v (Folch et al. 1957). Next, lipids were converted to fatty acid methyl esters (Kattner & Fricke 1986), and their compositions were analyzed using a gas chromatograph (GC-6890N, Agilent Technologies). Compound specific stable isotope analyses of fatty acid methyl esters (from animal and POM samples, Box 4) were determined using gas chromatography combustion isotope ratio mass spectrometry (GC-c-IRMS, Thermo Scientific). Lipid class composition analysis was done using high-performance liquid chromatography (HPLC, VWR Hitachi) on extracted lipids from zooplankton (Graeve & Janssen 2009). Fatty acids are presented in shorthand notation, A:B(n-x), further described in Box 1. Fatty acid data are expressed as a percentage of each fatty acid relative to the sum of all fatty acids identified. All reported $\delta^{13}C_{FA}$ values are relative to the Vienna Pee Dee Belemnite (VPDB) reference standard.

4.5 Statistical methods

I applied a variety of data analytical approaches in this thesis. The datasets in Paper I represent a pan-Arctic synthesis of disparately collected pelagic records of *A. glacialis*, therefore staying at a descriptive level. I applied univariate statistics for all three papers. For Papers II and III, I also applied multivariate statistical analysis, multivariate models, and Bayesian models. Correspondence analysis was used to visualize fatty acid compositional data (Papers II and III) and lipid class data (Paper II). In Papers II and III, I used a canonical correspondence analysis to determine if certain environmental variables influenced fatty acid composition within species and if station location influenced POM differences, respectively. Nonmetric multidimensional scaling was also applied in Paper III. In Paper III, I chose a Bayesian stable isotope mixing model (Parnell et al. 2013, Stock et al. 2018, van de Schoot et al. 2021) to estimate the proportional contributions of sympagic and pelagic carbon to Arctic seal diets. For those estimates I used the $\delta^{13}C_{FA}$ values of two diatom-associated fatty acids and two dinoflagellate-associated fatty acids (Table 1). I used R to construct figures and for analytical workflow (version 4.0.3, R Core Team 2020). Specific R packages are denoted within Papers I – III.

5. Key findings

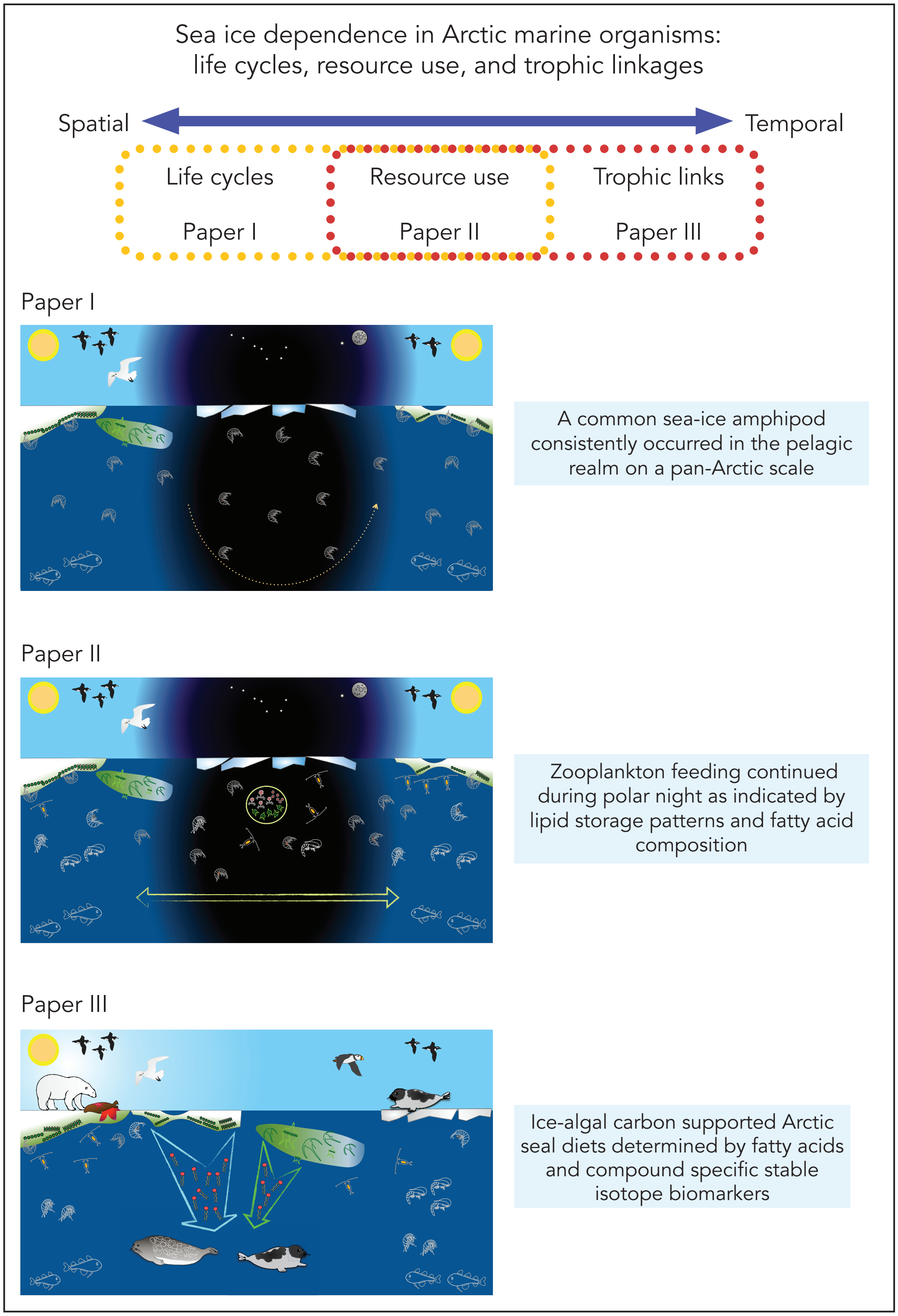


Figure 8. Conceptual presentation of the main findings for the papers included in my thesis.

5.1 Paper I – Pelagic occurrences of the ice amphipod *Apherusa glacialis* throughout the Arctic

Over 71 years, the sympagic amphipod *A. glacialis* was also consistently found in the pelagic environment. *A. glacialis* abundances in pelagic net hauls were generally low, apart from some tows to the surface that reported counts in the 1000s per tow. We found pelagic occurrences in both Pacific and Atlantic sectors of the Arctic Ocean, on the shelves, and in the deep basins (Paper I, Fig. 1). Pelagic occurrences of *A. glacialis* were reported in 506 tows to the surface and in 121 depth-stratified layers (defined here as depth-stratified tows that did not terminate at the ocean surface). Pelagic records surrounding the Svalbard archipelago showed that *A. glacialis* could be found in both Atlantic and Arctic water masses at any time of the year (Paper I, Fig. 5). Our findings contrasted the original hypothesis, that *A. glacialis* would only occur in the pelagic realm during polar night. We found no seasonal differences in pelagic occurrences both in the regional focus and in the overall pan-Arctic perspective. Our pan-Arctic synthesis of *A. glacialis* body sizes and sex ratios supported previous findings that juvenile offspring are likely released in late winter/early spring and are found under the ice. We also found a much higher proportion of females than males in the under-ice habitat, suggesting that adult males comprise approximately 25% of the sex ratio, or perhaps are shorter-lived than females. This study demonstrated that *A. glacialis* can no longer be regarded solely as an autochthonous sympagic species. However, sea ice is still part of its life-history strategy, evidenced by the younger *A. glacialis* found in the under-ice habitat. From these findings, we suggested an updated model on *A. glacialis* life history (illustrated in Paper I, Fig. 7) with three possible scenarios. First, both sexes employ a seasonal vertical migration; second, only female *A. glacialis* undergo a seasonal vertical migration from sea ice; or third, *A. glacialis* instead has a high degree of plasticity and inhabits both the sympagic and pelagic habitats at any given time.

5.2 Paper II – Do Arctic zooplankton feed during polar night? Insights into trophic transfer as revealed by lipids, fatty acids, and compound-specific stable isotopes

We found evidence of polar night feeding in all study species regardless of overwintering strategies. This finding is contrary to the first hypothesis, but in the sense that overwintering strategies have perhaps not been correctly understood. Two primarily herbivorous species (*A. glacialis* and *C. glacialis*) showed evidence of continuous feeding activity throughout the year–

switching to an omnivorous strategy in the polar night–evidenced by their fatty acid compositions (Paper II, Fig. 3). Habitat and season were influential factors in the fatty acid composition for *A. glacialis*, *C. glacialis*, and *T. libellula*, further suggesting that dietary fatty acids reflect the variability of primary producer communities in different habitats.

Accumulated lipid composition differed between species (Paper II, Fig. S2), consistent with previous research (reviewed in Paper II). *T. inermis* had relatively higher concentrations of membrane phospholipids, than the 'classic' storage lipids, setting this species apart in terms of lipid storage. The sympagic amphipods (*A. glacialis* and *G. wilkitzkii*) had similarly high investments in TAG. Furthermore, the lipid classes in *G. wilkitzkii* and *T. libellula* overlapped, supporting the trophodynamic similarities between these species (Auel & Werner 2003). *C. glacialis* invested mainly in wax esters. This lipid class was also found in *T. libellula*, which consume *Calanus* spp. (Kraft et al. 2015).

For the zooplankton, most δ13CFA values of the trophic biomarker fatty acids did not differ between polar day and night. This partially supports our second hypothesis, in that we expected low seasonal variability in the δ13CFA values in zooplankton because of no expected switch from ice-algal to pelagic carbon between seasons. Sympagic amphipods had significantly higher $\delta^{13}C_{FA}$ values for the diatom- [16:1(n-7), 20:5(n-3)] and dinoflagellate-associated [22:6(n-3)] fatty acids during the polar day when compared to polar night (Paper II, Fig. 5). This finding lends partial support to the third hypothesis, that sympagic amphipods would have high seasonal variability in $\delta^{13}C_{FA}$ values. Sympagic amphipods have strong seasonal affinities to the sea ice habitat, and the higher $\delta^{13}C_{FA}$ values are most likely a reflection of iPOM being seasonally more variable than pPOM (Paper III).

5.3 Paper III – Ice-algal carbon supports harp and ringed seal diets in the European Arctic: evidence from fatty acid and stable isotope markers

As hypothesized, we found differences in both fatty acid composition and the $\delta^{13}C_{FA}$ values of specific trophic biomarkers in sea ice algae and phytoplankton. The application of compound specific stable isotope analysis resulted in clear separations between sea ice algae and phytoplankton $\delta^{13}C_{FA}$ values (Paper III, Fig. 3). Specifically, the $\delta^{13}C_{FA}$ values of the four fatty acids [16:1(n-7), 20:5(n-3), 18:4(n-3), 22:6(n-3)] differed significantly ($p \leq 0.001$) between iPOM and pPOM, enabling their use for the mixing model estimations of carbon sourcing.

Contrary to our expectations, harp and ringed seals were strongly separated in their fatty acid compositional patterns, indicating a significant degree of trophic niche separation between species (Paper III, Fig. 4B). *Calanus* spp. trophic biomarkers were present in harp seal blubber, indicating they were feeding on a *Calanus* spp.–derived food chain. Based on the methods applied in this study, both harp and ringed seals had substantial contributions (≥ 69%) of sea-ice-derived carbon in their diets (reflected in their blubber, Fig. 9). Contrary to the third hypothesis, that sympagic carbon would be more likely to contribute to the diet of ringed seals because of their stronger association with sea ice, we instead found that sympagic carbon supported both harp and ringed seals similarly over the summer and into autumn.

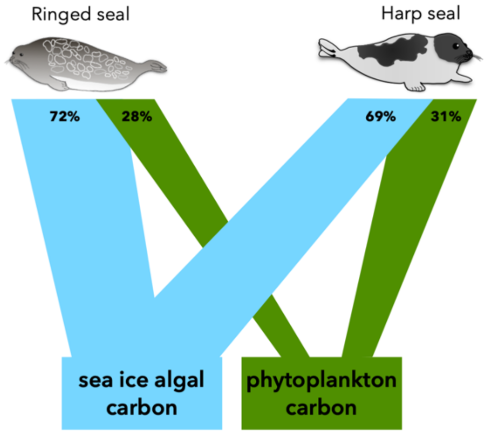


Figure 9. Conceptual figure of mixing model results. Thickness of lines represent the relative contributions of carbon sources (% denoted within lines).

6. Discussion

I return to the posed overarching thesis question; how does sea ice biologically matter? In Paper I, our findings demonstrated that *A. glacialis* does not exclusively use the sea ice habitat. However, early life stages and females seasonally found within the sea ice habitat indicate that *A. glacialis* will capitalize on this habitat when it is available. Indeed, in Paper II, we find that *A. glacialis* diet is seasonally provided by the sympagic habitat, further supporting the conclusions made in Paper I. In Paper II, we found evidence of polar night feeding in all the studied species, including nutritional shifts from primary producers to other food sources. Finally in Paper III, we find that sympagic carbon contributed substantially to the diets of both harp and ringed seals. Based on these conclusions, I think the answer to my overarching thesis question is that the biological importance of sea ice most likely lies on a gradient. While some species seem to be strongly supported by the sea ice habitat during certain times of the year, other species seem to be biologically active no matter if the sea ice habitat is present or not. However, can polar night activity persist without the seasonal input of what the sea ice habitat provides, in terms of shelter and food? It is then important to note the limited scale (both spatial and temporal) of the studies included in this thesis. Ecological systems have variable ranges of spatial, temporal, and organizational scales (Levin 1992). Environmental observations are limited in these ranges, resulting in perceptions that are "a low-dimensional slice through a high-dimensional cake" (Levin 1992). The discussion of plasticity in Arctic organisms, hence, should acknowledge the problem of ecosystem scales.

6.1 Behavioral and trophic plasticity in Arctic marine species

The designation of *A. glacialis* as an autochthonous resident of the sea ice habitat is the result of it being named as such. In early Arctic expeditions, *A. glacialis* was in fact classified as a pelagic species (Barnard 1959). As *A. glacialis* was later found in rather large numbers at the sea ice-water interface on a pan-Arctic scale, it became designated by where it was predominantly located (Melnikov 1997, Poltermann et al. 2000, Beuchel & Lønne 2002). At the same time, *A. glacialis* was described as cryopelagic with individuals being found in deep water (as reviewed in Melnikov (1997)). But is there a greater biological implication to these scientific designations?

In light of Arctic sea ice loss, the idea of *A. glacialis* employing a seasonal vertical migration then becomes a compelling alternative to a fully-sympagic *A. glacialis* life history strategy (Berge et al. 2012). Furthermore, if *A. glacialis* was so tightly coupled (*i.e.*, a permanent resident) to an ephemeral sea ice habitat (Arndt & Pavlova 2005), how would it able to maintain its population abundance on a pan-Arctic scale? The findings in Paper I provide some support to the conceptual adaptive-advection model (Berge et al. 2012). The overall patterns we found in Paper I, however, proved to be inconclusive on whether *A. glacialis* conducted a vertical overwintering migration within its life cycle. Yet continuing this story further, our results from a particle-tracking model demonstrate that a seasonal vertical migration strategy increases distribution and abundance of *A. glacialis* on a pan-Arctic scale (Drivdal et al. 2021).

Greater plasticity in life history traits than previously assumed have also been documented in other sympagic amphipods species. In Svalbard fjords, *G. wilkitzkii* has been found alive at the sea floor (Arndt et al. 2005). Two other common sympagic amphipod species, *Onisimus glacialis* and *O. nanseni*, have also been described as only temporary occupants of the sea ice habitat (Melnikov & Kulikov 1980). *O. glacialis* has also been found in deep water (Melnikov 1997) with females often absent from sea ice, suggestive of a pelagic reproductive strategy (Arndt & Beuchel 2006). Plasticity of habitat use by sea ice amphipods may then be an adaptive trait allowing for population maintenance in an often-ephemeral sea ice habitat. In the pelagic realm, recent studies on *Calanus* spp. in the same study area found these species to be distributed throughout the water column during polar night (Daase et al. 2014, 2018, Basedow et al. 2018, Daase & Søreide 2021). For *C. finmarchicus*, a sub-Arctic/boreal copepod, one hypothesis put forth by Espinasse et al. (2022) suggests that surface copepods could be using polar surface waters to be transported southward back into Atlantic Water, thus ensuring return to favorable breeding areas. Contrary to the paradigm that entire populations of these copepods overwinter at depth, these findings rather suggest some degree of individual plasticity where some individuals are in diapause while others are more active within the water column.

The findings in Paper II suggest continued polar night feeding in all studied species. This work further supports the idea that polar night is not a dormant phase for all Arctic taxa and challenges the paradigm of whole population-level behaviors. Long-standing empirical and theoretical bodies of work demonstrate that as food becomes limiting, diet diversity increases in consumers (Schoener 1971, Roughgarden 1972, Krebs et al. 1977). These studies operate under the assumption that individuals within populations behave in similar ways. However, there is a growing body of evidence that diet specialization often occurs at the individual level (Tinker et al. 2008, Woo et al. 2008, Matich et al. 2011). While dietary specialization is harder to discern for individual marine invertebrates than for marine vertebrates, there are examples of diet diversity. *C. glacialis* transitions to omnivory–carnivory outside of the spring bloom (Cleary et al. 2017) and Arctic hyperiid pelagic amphipods consume a wide range of available food sources (Legeżyńska et al. 2012). Therefore, we suggest that the overwintering strategy of flexibility could potentially be more wide-spread than previously described (Hagen 1999), depicted in Figure 10.

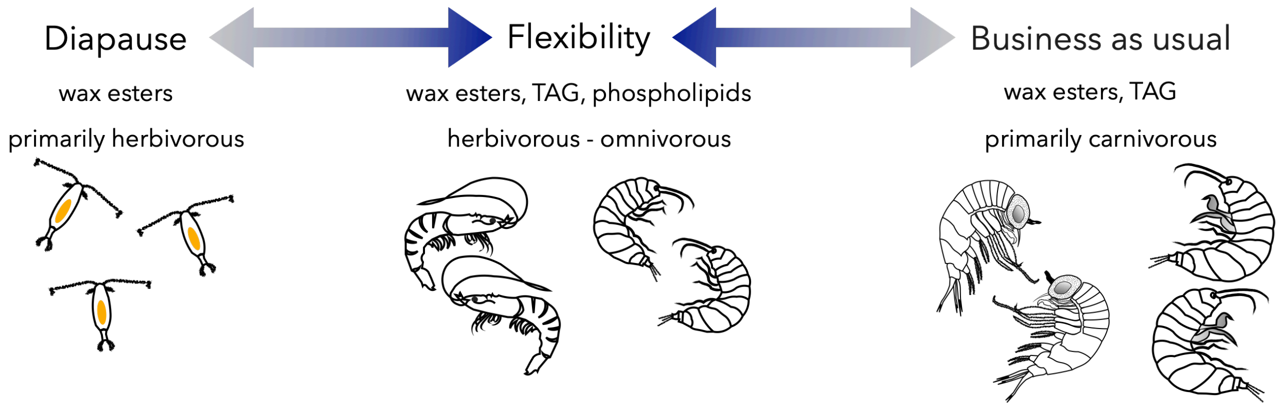


Figure 10. Studied species from Paper II with their overwintering strategies, based on how they store lipids and their dietary preferences. Arrows indicate that flexibility is larger than previously assumed.

Returning to the issue of ecosystem scale, the advective nature of the study area could influence the polar night feeding activity observed in the studied species. The Atlantic Water inflow is a large source of nutrients and zooplankton biomass to the Arctic Ocean throughout the year (Codispoti et al. 2013, Basedow et al. 2018). This suggests that food is readily available throughout the year for all the species studied, compared to other Arctic areas, although questions remain on the quality of food for herbivorous species. For these, along with a more omnivorous lifestyle, another option would be to consume degraded sea ice algae. Degraded sea ice algae and their resting spores can persist within sea ice over winter (Olsen et al. 2017). As the thinner and weaker ice present in today's Arctic (Zhang et al. 2012, Kwok et al. 2013) is exposed to more wave action, this could result in the increased flushing of the particulate organic matter of sea ice (iPOM) into the surrounding water column. Regardless, overwintering survival for the primarily herbivorous species (Fig. 10) depends on the ability to build up adequate energy stores during the more productive parts of the year. It remains to be seen if polar night feeding activity rather reflects the failure to acquire enough energy stores earlier in the year, or how particular resource allocation decisions affect overall life history strategies (Stearns 1992).

Moving up the food web, in Paper III I found dietary fatty acid composition separation between harp and ringed seals–two near-apex predators in the study system. Previous research has demonstrated some degree of niche separation between these species via foraging behavior differences and stomach content analysis, yet with some degree of overlap (Wathne et al. 2000, Ogloff et al. 2019). Our findings in Paper III further support dietary niche separation between harp and ringed seals, and modelled results indicated strong sympagic sources of carbon to both harp and ringed seal diets. Our findings suggest that while harp and ringed seal diets are different, seal prey rely on sympagic and pelagic endmember production in similar ways.

The temporal and spatial resolutions (differences in scale) differed in Papers II and III. In Paper II, we investigated seasonal differences–resulting in more varied observations–and found that Arctic invertebrates exhibited some degree of dietary plasticity. Paper III, in contrast, drew conclusions from a shorter timeframe, late summer/early autumn. Paper III is also limited in the temporal resolution of our applied methods, as seal blubber turnover of assimilated dietary fatty acids reflect a time period of weeks to several months (Tollit et al. 2010). Additionally, the lack of investigation in the spatial variability between food webs in our study area likely plays a role in our findings. In other marine ecosystems, overlapping but discrete food webs support higher trophic level dietary generalists (Montevecchi et al. 2009), for which Matich et al. (2011) argue that individual predators likely "exploit resources from different food webs without significant movement between resource patches." Within our study area, the marine ecosystem has various energy pathways (Pedersen 2022). We focused on two pathways, the sympagic and pelagic, and generally assumed somewhat localized primary production. The sympagic and pelagic food webs in our system overlap during certain times of the year. The majority of sea ice-algal bloom biomass is funneled into pelagic (and benthic) food webs (Michel et al. 1996, Søreide et al. 2013). Additionally, sympagic amphipods also consume phytoplankton (Paper II, Søreide et al. 2013) and *Calanus* spp. target both sympagic and pelagic blooms (Søreide et al. 2010), demonstrating species overlap in food webs. Hence even as seals prey upon more pelagic invertebrates and/or fish species, these prey items can still carry a sympagic signal based on the seasonal overlap of the two habitats.

6.2 Carbon isotopes in marine food web studies

As sea ice extent shrinks within the Arctic Ocean, this will ultimately affect the amount of sympagic production available within Arctic marine food webs. Paper III contributes to the current understanding of how sympagic production supports higher trophic level taxa within Arctic marine food webs. However, the incorporation of compound-specific stable isotope values of individual fatty acids in food web studies can be challenging to interpret (Box 4). While the caveats associated with this approach are discussed in Paper III, I highlight two here in particular.

Stable isotopes of POM are useful in determining the trophic baseline for food web studies, and to highlight the seasonal support the sympagic and pelagic habitats provide in polar ecosystems (St John Glew et al. 2021). There are many synergistic, temporal processes at play when characterizing POM. In both the sea ice and pelagic habitats, primary producer community composition, the availability of dissolved inorganic carbon (DIC), the isotopic fractionation that occurs during photosynthesis, and nutrient availability all affect the δ^{13}C values of POM (Goericke & Fry 1994, Laws et al. 1997, Popp et al. 1999, Gradinger 2009, Van Leeuwe et al. 2018). Similar effects apply when assessing the $\delta^{13}C_{FA}$ values of individual fatty acids. Results from a repeated sampling study in landfast ice showed that the $\delta^{13}C_{FA}$ values of trophic biomarker fatty acids and δ^{13}C values of bulk particulate organic carbon (POC) occasionally overlapped between sympagic and pelagic habitats (Leu et al. 2020). In this study, higher $\delta^{13}C_{FA}$ values from sea ice occurred during nitrate-limiting conditions and when DIC concentrations were indicative of bloom development (Leu et al. 2020). Was enough of this seasonal variation in POM captured to make subsequent ecological interpretations in Paper III? For highly mobile near-apex predators, I argue that enough spatial resolution was covered for seals that are known to travel throughout the Barents Sea and Arctic Ocean on foraging trips.

The premise of using $\delta^{13}C_{FA}$ values of trophic biomarker fatty acids in a food web context is that carbon source endmembers, here sympagic algae and phytoplankton, have different values. The application of $\delta^{13}C_{FA}$ values of specific trophic biomarkers found in sea ice algae and phytoplankton in food web studies have been measured in few studies, yet almost all sectors of the Arctic. When viewed together (Fig. 11), there is indeed consistent separation between iPOM and pPOM which validates this approach on a study-by-study basis. There is also large spatiotemporal variability in these values, again demonstrating that sampling time and which fatty acids are chosen certainly affects the subsequent interpretations in food web studies.

Further discussed in Papers II and III, the utilization of δ^{13}C values of biomarker fatty acids is also likely influenced by still largely undetermined isotopic fractionation as fatty acids move through the food web. My mixing model analysis is anchored in the finding that isotopic fractionation was negligible for the 20:5(n-3) and 22:6(n-3) fatty acids within specific tissues of three vertebrate species (Arctic eider ducks (*Polysticta stelleri* and *Somateria fischeri*) and Atlantic pollock (*Pollachius virens*)) (Budge et al. 2011, 2016). By and large, however, isotopic fractionation remains unknown for fatty acids and their enzymatic pathways (see Boxes 3 and 4), and fatty acid modifications via bioconversions (Box 2). It is also important to acknowledge that $\delta^{13}C_{FA}$ values are also affected by the metabolic processes and lipid dynamics within organisms (Chamberlain et al. 2004, Gladyshev et al. 2016, Taipale et al. 2021). My studies (Papers II and III) occur at a time when kinetic fractionation remains largely unknown.

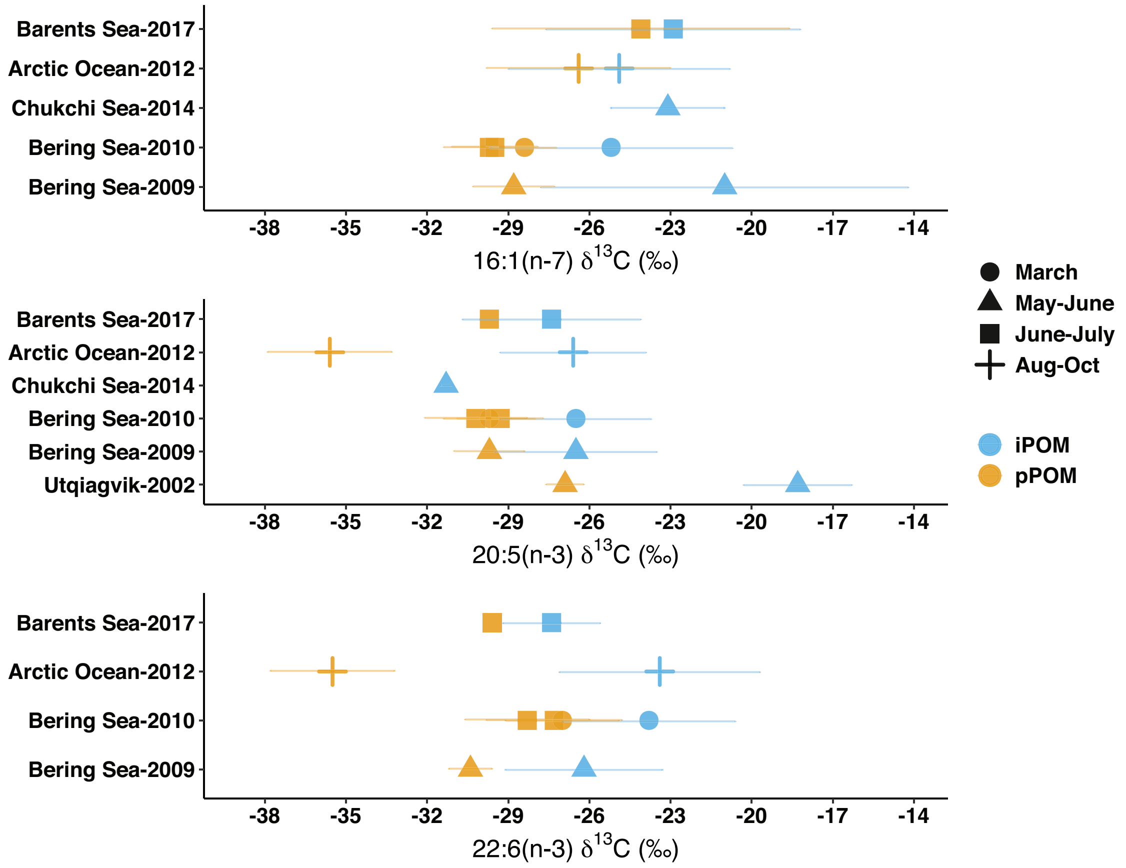


Figure 11. A synthesis of $\delta^{13}C_{FA}$ values of three trophic biomarker fatty acids commonly used in Arctic food web studies. Studies are organized by region on the y-axis, shapes indicate the time of year when sampling occurred, and color indicates iPOM or pPOM. Data points and horizontal lines are published means and standard deviations, respectively. Data sources: Barents Sea (Paper III), central Arctic Ocean (Kohlbach et al. 2016), Chukchi Sea (Schollmeier et al. 2017), Bering Sea (Wang et al. 2014), Utqiagvik (formerly Barrow)/coastal Alaska (Budge et al. 2008). Gaps in region or POM indicate that these data were not available. [Note: In Paper III, the published pPOM values included pPOM values from the Arctic Ocean 2012 study (further discussed in Paper III). For Barents Sea 2017 in this figure, the pPOM values from the sampled year are instead shown.]

7. Considerations for future studies

As the Arctic Ocean transitions from mostly ice-covered to mostly ice-free, many questions remain on the biological responses of Arctic marine organisms. A widely agreed upon standardized sampling protocol for those who study iPOM in Arctic marine food webs would be hugely beneficial. This protocol could include collecting enough samples for both bulk and compound-specific stable isotope analysis from a given location and time point. Even though compound-specific stable isotope analysis is both costly and labor-intensive, having sampled POM filters on reserve would still be useful for future analysis. A common sampling template of a suite of isotopes (δ^{13}C, δ^{15}N, δ^{18}O, δ^{34}S, δ^{2}H) could be used in assessing the trophic baseline for future studies. Including multiple isotopes (instead of two) can potentially be more robust in determining the flow of organic matter (Peterson et al. 1985). For example, the inclusion of δ^{18}O in studying a not so sympagic, blue Arctic Ocean may prove to be beneficial, given that δ^{18}O is considered a robust tracer of ocean salinity (Bigg & Rohling 2000), and can be used in the exploration of how freshwater runoff (from Arctic rivers) influences the marine environment (Cooper et al. 2005). Tracking animal movement and seasonal migration patterns could be accomplished via the analysis of δ^{2}H, on both the bulk and compound-specific levels, as δ^{2}H values have been shown to be robust tracers in tracking animal movement and migration patterns in that regard (Hobson 1999, Fogel et al. 2016).

Shifts in the isotopic baseline can be challenging to overcome, and further complicates comparisons to past studies (Casey & Post 2011). However, always sampling the primary producers for their inclusion in all food web studies is a good first step. On a bulk isotope level, the inclusion of first-order consumers, such as filter-feeding herbivorous copepods and mussels have been used as proxies of the trophic baseline in pelagic food webs (Kling et al. 1992, Post 2002). Currently, I would not recommend substituting a first-order consumer for trophic baseline studies on a compound-specific stable isotope level because of the unknowns surrounding kinetic isotopic fractionations. However, future studies of POM that include the compound-specific stable isotope analysis of fatty acids should allow for the inclusion of the taxonomic composition of POM, as it will help in deciphering biochemical patterns (Leu et al. 2020).

Future food web studies should account for humans and their overwhelming influence on ecosystems (Strong & Frank 2010, Worm & Paine 2016). For example, a less-quantified factor in the variation of $\delta^{13}C_{FA}$ values in POM can be attributed to the overall decline in $\delta^{13}C$ values in DIC within the Arctic. de la Vega et al. (2019) calculated a -0.011 ‰ decline in $\delta^{13}C$ DIC values over a 30-year period, which was attributed to the increase of anthropogenic carbon dioxide (CO_2) in the Arctic Ocean. Better known as the Suess effect, the increase in CO_2 emissions causes declines in baseline $\delta^{13}C$ values in the global ocean (Keeling 1979). While correction factors are not yet available on a compound-specific stable isotope level, future food web studies should include correction factors for this effect on a bulk $\delta^{13}C$ level (available as a package in R, Clark et al. 2021). The inclusion of a DIC correction factor will prove informative, as the latest CO_2 reading (as of this writing) was 417.88 parts per million (ppm, keelingcurve.ucsd.edu).

Isotopic data, especially in the Arctic, are now widespread. These data are found in a plethora of studies spanning from the Arctic deep sea up to the Arctic atmosphere (Morin et al. 2013, Melaniuk et al. 2022). A recent call to action by Pauli et al. (2017) argued for a world-wide collection of publicly available isotope data, similar to sequence data in GenBank (https://www.ncbi.nlm.nih.gov/genbank/). Recently, IsoBank–a centralized repository for isotopic data–was created (https://isobank.tacc.utexas.edu/). Given the importance of using isotopes in Arctic isotopic baseline studies and food web research, future studies should consider contributing to this repository as it will benefit the entire scientific community.

Exploring dietary resources in organisms that are not found within their presumed sea ice habitat will help us better understand a future blue Arctic Ocean. In Paper I, my co-authors and I make the argument that when *A. glacialis* is present at the ice, it is also likely present in the water column. Future sea ice studies on sympagic amphipods (or other fauna) could conduct a few pelagic tows to first establish if any sympagic amphipods are at the same time in the pelagic realm. Second, biochemical compositions on any amphipods that are caught at depth (along with POM!) could help us understand the potential use of secondary pelagic habitats and dietary resources for sympagic amphipods. A similar approach could be conducted for *Calanus* spp., that seem to be active within the water column during polar night while some individuals also overwinter at depth. Bioenergetics of the studied Arctic invertebrates are complex as these organisms are seemingly resilient in their physiological adaptations to little/no food (see Hirche 1989). Experimental work exploring how biogeochemical and physiological processes affect both fatty acids and isotopic values will be informative for the current methods used in field studies. I also suggest that future field studies should allow for the simultaneous inclusion of experimental work.

Future studies that capture more of the seasonal and regional variations in POM will provide a better and perhaps much needed understanding of how the isotopic values in primary producers change as the sea ice habitat recedes. This will result in a more comprehensive understanding of changes in the trophic baseline. Similar to POM, exploring time periods outside 'normal' summer/autumn sampling periods might provide certain insights into yet-undetermined differences in food resources and habitat use. For example, exploring time periods outside of late summer/autumn could provide key information about the impacts of seasonality on diets (e.g., how much do harp seals feed on non-Arctic species during their annual migration).

8. Conclusions

With widespread sea ice loss in the Arctic marine environment, future tipping points in this ecosystem are likely intertwined, possibly resulting in cascading interactions (e.g., less sea ice increases ocean surface warming thereby changing ocean stratification) (Duarte et al. 2012). Others have argued a tipping point was already passed in 2006, when sea ice extent dramatically receded in the study region, affecting individual ringed seal foraging behavior as seals travelled even further northward to the sea ice edge (Hamilton et al. 2015). Furthermore, the Svalbard ringed seal population, of which I have sampled from, has markedly declined since the 2006 decline in sea ice extent (AMAP 2017) and is currently listed as vulnerable (artsdatabanken.no). This suggests that short-term individual responses could result in negative long-term consequences on a population level.

Behavioral and trophic plasticity, occurring on the individual level, is generally assumed to be a short-term, low-cost response to environmental change. Theoretically, plasticity can be a favored trait when *predictable* environmental changes occur (Chevin et al. 2013). In highly stochastic, unpredictable environments, modelled results indicate plasticity could result in a mismatch with a corresponding phenotype (Ashander et al. 2016). This means an organism adapted to one environment experiences a reduction in fitness when in an alternative environment (DeWitt & Yoshimura 1998). If 2006 was indeed a tipping point, this theory could partially explain ringed seal population decline. Phenotypic-environmental mismatch could also imply changes in the competitive advantage of some species over others. As environmental tipping points in the Arctic marine ecosystem are likely intertwined, I hence argue that as this system transitions to alternative states, unpredictable and stochastic biological responses could also occur.

The main findings of my thesis show that in this time of transition–where sea ice is still present but receding–the biological responses of organisms are varied. It seems that as some species display strong associations to the sea ice habitat (in terms of energetic sources), others display varying degrees of trophic plasticity (polar night feeding activity). However, sea ice is more than a sympagic food source–it serves as a habitat for a myriad of different taxa. While we find year-round pelagic occurrences of *A. glacialis*, it is challenging to predict if the pelagic realm could then serve as a suitable alternative habitat throughout its life-span. Hop et al. (2021) found a pan-Arctic decline of *G. wilkitzkii*, coinciding with the decline of older, multi-year sea ice. This finding demonstrates that yet-undetermined consequences are on the horizon, as the sea ice habitat changes and shrinks in extent.

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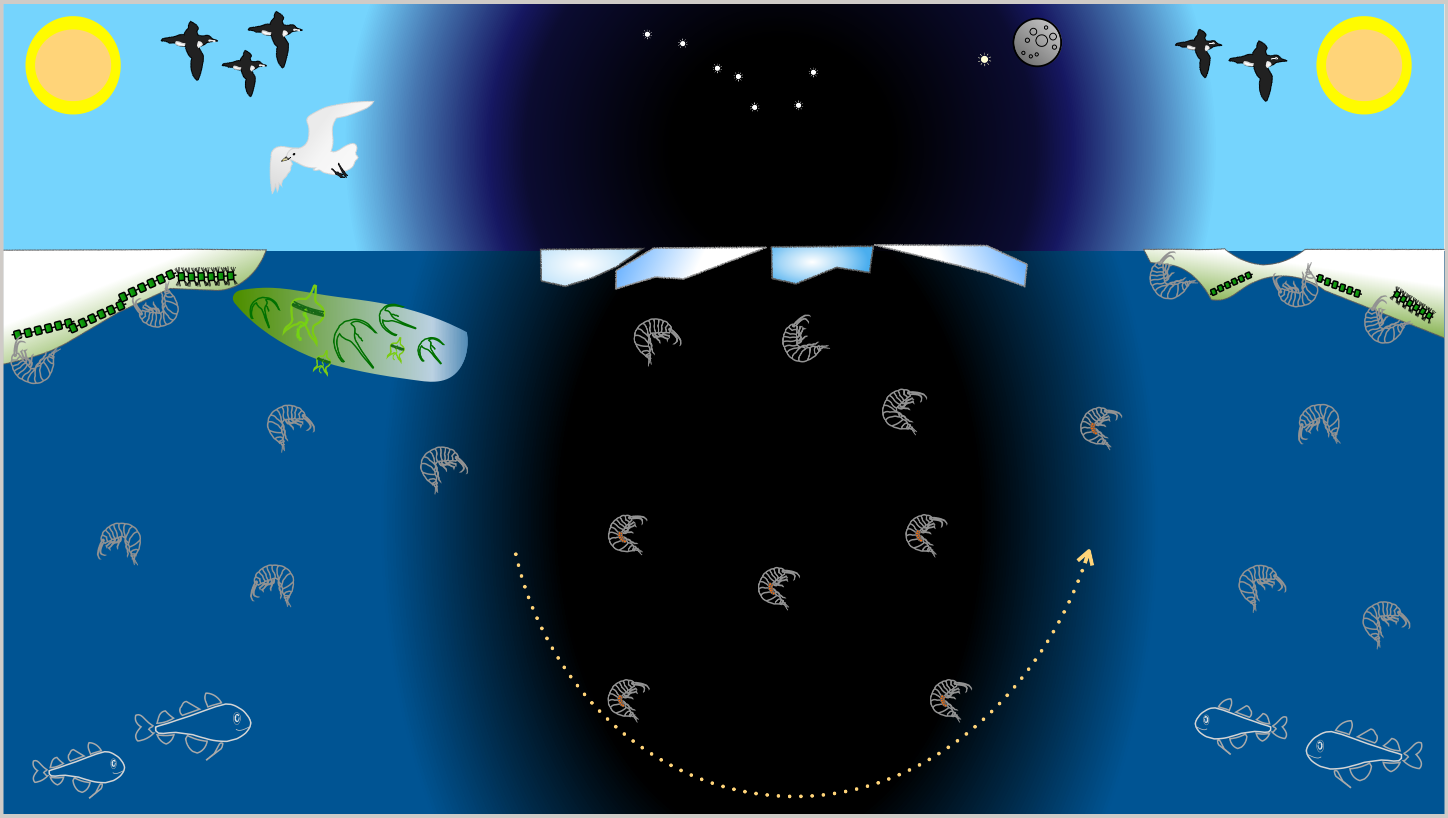
Paper I



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ORIGINAL ARTICLE

Pelagic occurrences of the ice amphipod *Apherusa glacialis* throughout the Arctic

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Apherusa glacialis is a common, sea ice-associated amphipod found throughout the Arctic Ocean and has long been considered permanently associated with the sea ice habitat. However, pelagic occurrences of *A. glacialis* have also been reported. It was recently suggested that *A. glacialis* overwinters at depth within the Atlantic-water inflow near Svalbard, to avoid being exported out of the Arctic Ocean through the Fram Strait. This study collated pelagic occurrence records over a 71-year period and found that *A. glacialis* was consistently found away from its presumed sea ice habitat on a pan-Arctic scale, in different depths and water masses. In the Svalbard region, *A. glacialis* was found in Atlantic Water both in winter and summer. Additionally, we analyzed *A. glacialis* size distributions throughout the year, collected mostly from sea ice, in order to elucidate potential life cycle strategies. The majority of young-of-the-year *A. glacialis* was found in the sea ice habitat during spring, supporting previous findings. Data on size distributions and sex ratios suggest a semelparous lifestyle. A synchronous seasonal vertical migration was not evident, but our data imply a more complex life history than previously assumed. We provide evidence that *A. glacialis* can no longer be regarded as an autochthonous sympagic species.

KEYWORDS: Arctic; sea ice fauna; life history; pelagic; spatial and temporal scales; *Apherusa glacialis*

INTRODUCTION

Polar marine ecosystems are characterized by low water temperatures and sea ice presence, which further influence biological processes. Additionally, extreme seasonality (Leu *et al.*, 2015) and the unique species association with sea ice have led to distinct life history adaptations within a seasonally disparate environment. For example, Arctic copepods, such as *Calanus glacialis*, are able to time offspring release and also mature in the photic zone when food resources are optimal and subsequently overwinter at depth in diapause (Søreide *et al.*, 2010; Varpe, 2012). Sea ice itself is a unique habitat for a wide range of species assemblages that live within brine channels and at the ice–water interface (Bluhm *et al.*, 2010, 2018). Ice-associated (sympagic) amphipods are strongly linked to Arctic sea ice habitat, though how they overwinter and survive periods of low food resources is currently unknown (Arndt and Swadling, 2006).

Apherusa glacialis is one of the 5 common, endemic Arctic amphipods (along with *Gammarus wilkitzkii*, *Eusirus holmii*, *Onisimus nanseni* and *O. glacialis*) found underneath sea ice with small individuals and juveniles also occurring within brine channels. With the exception of *E. holmii*, these amphipods have typically been considered permanent residents (autochthonous) of sea ice, with their entire life cycle to occur within the sea ice habitat (Gulliksen and Lønne, 1991; Lønne and Gulliksen, 1991b; Macnaughton *et al.*, 2007). *A. glacialis* is considered semelparous (Poltermann, 2000; Beuchel and Lønne, 2002), likely reaching sexual maturity at 1 year. It is assumed that *A. glacialis* mate at the onset of polar night (Melnikov, 1997) and incubates its eggs over the winter, similar to other Arctic amphipods (Węsławski and Legeżyńska, 2002). Developing juveniles are released from the female marsupial pouch the following year (late winter/early spring), when sea ice algal food conditions are optimal (Melnikov, 1997). *A. glacialis* has a short life span of approximately 2 years (Beuchel and Lønne, 2002) and is numerically the most abundant when compared to the other aforementioned ice-associated Arctic amphipods (Bradstreet and Cross, 1982; Hop *et al.*, 2000; Gradinger *et al.*, 2010). This 2-year life span suggests that *A. glacialis* overwinters once in its lifetime (Poltermann, 2000). However, *A. glacialis* colonizes young, first-year ice sooner than other ice amphipods (Gulliksen and Lønne, 1989), and higher abundances of *A. glacialis* in first-year ice (Bradstreet and Cross, 1982; Arndt and Lønne, 2002) implies that a horizontal movement to colonize new ice habitats.

When drifting sea ice habitat melts or is exported out of the Arctic Ocean, it is assumed that *A. glacialis* is lost to the water column, with little to no chance of survival, especially when sea ice is exported out of the Arctic Basin (Arndt and Pavlova, 2005; Hop and Pavlova, 2008). This led to the question, how are they able to maintain a viable population within this drifting and often ephemeral habitat? In early scientific reports, *A. glacialis* was in fact classified as a strictly pelagic amphipod species in the central Arctic Basin even when sea ice was present (Barnard, 1959). Several publications recorded *A. glacialis* and also *G. wilkitzkii* in open water in the Canadian Basin (Harding, 1966), Arctic Ocean (Melnikov, 1997, 1989), Greenland Sea (Werner *et al.*, 1999) and Fram Strait and Svalbard area (Arndt and Pavlova, 2005). It has earlier been suggested that *A. glacialis* employs a vertical migration strategy (Melnikov, 1989) and that *G. wilkitzkii* is able to overwinter in shallow benthic habitats (Poltermann, 1998; Arndt *et al.*, 2005).

In January 2012 near the Svalbard Archipelago, *A. glacialis* was found in all net tows ($n = 4$) in deep water between 200 and 2000 m (Berge *et al.*, 2012), which resulted in the introduction of a conceptual model that *A. glacialis* could potentially occupy habitats other than sea ice. *A. glacialis* was found in warmer subsurface water originating from the Atlantic Ocean (Berge *et al.*, 2012). Northward flowing Atlantic Water near Svalbard contributes to basin-wide advection processes of surface and deep water within the Arctic Ocean and further influences the movement of Arctic zooplankton and sea ice biota (Bluhm *et al.*, 2015; Wassmann *et al.*, 2015; Hop *et al.*, 2019). Therefore, the Berge *et al.* (2012) model suggests that a primary effect of being at depth in the Atlantic inflow area is that *A. glacialis* avoids being exported out of the Arctic Ocean, though some population loss still occurs via sea ice export through Fram Strait (Hop and Pavlova, 2008). If *A. glacialis* employed a vertical migration strategy, it would be able to re-colonize the sea ice habitat the following spring. Detaching from the sea ice habitat prior to or during the polar night could be a favorable life history strategy because food sources are scarce and predation rates would be lower at depth. Migration in the Arctic—a common phenomenon found in other Arctic zooplankton (Daase *et al.*, 2013)—is from cold surface waters to warmer water at depth. Female *A. glacialis* found at depth were gravid (Berge *et al.*, 2012), and warmer waters do support faster rates of egg development and maturation in mesozooplankton (McLaren, 1963). Furthermore, the sufficient lipid stores found in the deep-water *A. glacialis* (Berge *et al.*, 2012) suggest an adequate energy supply for overwintering.

Here we address the open questions regarding the vertical distribution and life cycle of *A. glacialis* by using the most complete available data set of its occurrence in the water column on a pan-Arctic scale. The main question of our study was rather simple, yet fundamental for our general understanding of the life history of *A. glacialis*:

how often is *A. glacialis* found in the water column? Our secondary objective was to determine if there were any seasonal patterns of *A. glacialis* at depth, further informing on their life cycle strategies.

METHOD

Pelagic occurrences of *A. glacialis*

Pan-Arctic historical data of A. glacialis

The spatial and temporal distribution of *A. glacialis* was investigated using data sets spanning the entire Arctic Ocean over a 71-year period, through accessing databases and individual records. *A. glacialis* data were extracted from existing pelagic zooplankton records compiled by the Arctic Ocean Diversity Census of Marine Life project, stored within the Ocean Biogeographic Information System (www.obis.org). We additionally compiled data from published and unpublished pelagic records of *A. glacialis* within the Arctic through literature searches and directly from individual researchers (see Acknowledgments). In total, we compiled $n = 715$ confirmed the presence of pelagic records (Supplementary Table S1). 'Records' refer to the following 3 distinct types of data: a net haul where (i) *A. glacialis* was found in the water column, but no associated depth stratum was reported, (ii) *A. glacialis* was found within a plankton tow to the surface, or (iii) *A. glacialis* was found within a depth-stratified plankton tow. In the third case, depth-stratified data were treated as individual records (*i.e.* if 1 depth-stratified tow found *A. glacialis* at 4 discrete depths, these were treated as 4 individual records). A record may contain one or more individuals. Of these 715 records, 627 had corresponding vertical tow information. While some records contained both presence and absence, this was not indicative of all records. Because of the gaps in confirmed absence data, we included presence-only records in order to investigate if *A. glacialis* is wholly dependent on the sea ice habitat within its life. The records spanned all months of the year from 1947 through 2018, though after 5 records reported in 1947, there was a 19-year gap until 1967 and a 14-year gap from 1988 to 2001. Likely, these gaps do not represent true absences of the species in planktonic environments but rather less research efforts. Within the tow records, 15 different net types with corresponding vertical tow information were used (Supplementary Table S1). Nets differed in mesh sizes and diameter openings, and presumably in towing speeds throughout the water column, adding an unquantifiable degree of bias. Data from more common sea ice sampling using e.g. suction pumps while scuba diving (Lønne, 1988) were not included due to the pelagic focus of this study.

New original data from the Svalbard region

A new field sampling campaign targeted the Svalbard region close to the Berge *et al.* (2012) study. In January 2017, there was a focused effort to search for deep water *A. glacialis* onboard the R/V *Helmer Hanssen* between 80°N–82°N and 12°E–22°E. At 5 stations, a depth stratifying Multinet was deployed in the deep Arctic basin down to 1800 m. Other nets ($n = 80$) deployed for different research objectives, including Multinets deployed in shallower layers (deepest depths ranged from 600 to 145 m) were also checked for the presence of *A. glacialis*. In summary, the following nets were used: a depth-stratified zooplankton Multinet sampler (Hydro-Bios, Kiel, Germany) equipped with 5 nets of 0.25 m^2 aperture with mesh size of 180 or 64 μm, a WP2 (Hydro-Bios, Kiel, Germany) with 90 μm mesh, an MIK net (Method Isaac Kidd-a large ring net with 3.14 m^2 opening and 1.5 mm mesh, transitioning to a 500 μm mesh for the bottom 1.5 m) and a Harstad pelagic trawl with an 8 mm mesh. Sea ice was not encountered during the expedition.

Data integration and analysis

Different studies provided estimates of *A. glacialis* occurrences as individuals m^{-3}, individuals m^{-2}, number of individuals found, or presence only. Additionally, in some datasets, *A. glacialis* was originally calculated as abundances per 100 m^{-3}, and these abundances were recalculated to abundances m^{-3} to compare with other datasets. We divided the pelagic presence records of *A. glacialis* into 3 groups. The first group consisted of $n = 88$ records with geographic position (latitude and longitude) and calendar date only. These records were included in the spatial mapping of the pelagic occurrence of *A. glacialis* on a pan-Arctic scale but were not included in additional analysis because of the lack of corresponding depth information. The second group ($n = 506$) contained geographic position, calendar date, and *A. glacialis* quantified from tows to the surface. In the literature, amphipods found within sea ice are commonly reported as individuals m^{-2} (Horner *et al.*, 1992; Arndt and Swadling, 2006). In order to compare abundance estimates from pelagic tows to the surface to those quantified within sea ice, we recalculated abundance of individuals m^{-3} by depth of the entire sampled water column and report these as individuals m^{-2}. The third group ($n = 121$) additionally reported *A. glacialis* from depth-stratified tows. The uppermost Multinet sections (*i.e.* the ones that terminated at the surface) were not included in the third group but instead included within the second group (tows to the surface). *A. glacialis* found in depth-stratified tows were only reported in the depth strata they were present, and not in the depth strata they were absent. This implies that we do not have all the information on the entire tow (or where the tow began), only sections of a depth-stratified tow where depth-specific distribution for *A. glacialis* was reported. Therefore, we can only report these data as abundance m^{-3}. Given that the data were not normally distributed, a Kruskal–Wallis test was used to test for differences in *A. glacialis* abundances. Data analysis was conducted using R (version 3.6), and maps were created with the PlotSvalbard package (version 0.8.5; Vihtakari, 2019).

Hydrographic information for Atlantic Water in the Svalbard region

Recent hydrographic information (water temperature and salinity) were used to investigate the relationship between *A. glacialis* occurrences within specific water masses near Svalbard. For a subset of recent cruises in the Atlantic inflow gateway to the Arctic, hydrographic data were available from conductivity-temperature-depth (CTD) profiles (Supplementary Table S2). Data were used from January (11 casts from years 2012, 2014, 2015, 2016, 2017), May (6 casts from 2003, 2005, 2014), July (14 casts from 2004, 2011, 2013) and August (9 casts from 2010, 2014, 2016 and 2018). We used the CTD cast geographically closest to the location of a given depth-stratified zooplankton tow. Profiles of potential temperature (T) and salinity (S) were binned every meter. Based on these binned values, T-S plots were made to identify characteristic water masses in which *A. glacialis* had been found. Atlantic Water is defined as $S > 34.92$ and $T > 2°C$ (Beszczynska-Möller *et al.*, 2012; Walczowski, 2013; Menze *et al.*, 2019).

A. glacialis body sizes and sex ratios

We approached the potential life cycle strategies of *A. glacialis* by presenting a pan-Arctic synthesis of *A. glacialis* body sizes and information on when young-of-the-year was present. Previously published and unpublished body length data along with information on life stage and sex were collected from a 30-year period (1979 through 2017) and from all months of the year (Supplementary Table S3). Body size was determined as the length (mm) from the distal end of rostrum to the base of the telson. The majority of the size data (70%) were provided pre-sorted into 3 size classes (Melnikov, 1997; Poltermann *et al.*, 2000; I. A. Melnikov, unpublished results; M. Poltermann, unpublished results): 1–2 mm (newly hatched), 3–6 mm (juveniles), and 7–16 mm (adults). Twelve percent of the tows to the surface were reported as 'juveniles' and 'adults' (Hopky *et al.*, 1994a, b), and we assigned 'juveniles' to the 3–6 mm size class and 'adults' to the 7–16-mm size class. For the majority of measured individuals, sex ratio was also reported, while for a subset of the data, only sex ratio and not size was reported. Polar night months (November through February) were pooled because of otherwise low sample sizes. Remaining months are presented individually.

RESULTS

Pelagic occurrences of *A. glacialis*

A total of 715 *A. glacialis* presence records occurred on a pan-Arctic scale between 58.7°N and 88.5°N latitude (Fig. 1A). The majority of all records (89%) were from the summer months (July, August and September, Fig. 1B), both for tows to the surface and depth-stratified tows (Fig. 1C), reflecting the generally higher research effort during the short Arctic summers. The remaining 11% of pelagic presence records were distributed over the rest of the calendar year. Some records reported counts in net hauls ranging from 1 to 1890 individuals; since most of these records also contained abundances reported per m^{-2} or m^{-3}, we report them as such in order to compare with other records.

Tows to 0 m that contained A. glacialis

Out of 506 tows to the surface, including Multinets that terminated at the surface, 85% (430 records) were located on the Canadian Beaufort Sea shelf and slope (Fig. 1A and C). Tows started at varying depths (deepest depth ranged from 2350—2 m). When reported, total abundances of *A. glacialis* ranged from 0.023 to 143 animals m^{-2} (mean 10.2, median 2.8) Surprisingly, *A. glacialis* was consistently found within pelagic tows during the entire year (Fig. 2) but with no difference in abundance between months (Kruskal–Wallis test, $P = 0.7$). There were tows ($n = 19$) where abundance was not calculated, but the number of *A. glacialis* was reported: 1–30 individuals (mean 4.1, median 2.0). These tows were taken during January, June, July, and August.

Depth-stratified tows that contained A. glacialis

A. glacialis was found in a total of $n = 121$ depth-stratified layers [*i.e.* tows that did not terminate at the surface (0 m)]. Similar to the tows to the surface, *A. glacialis* was found on a pan-Arctic scale, but in water layers mostly shallower than 1000 m (Fig. 3A). *A. glacialis* was observed in almost all months of the year, with the majority of records from January, July, August and September (Fig. 3B). Out of the 121 tows, 36% ($n = 44$) occurred within the photic

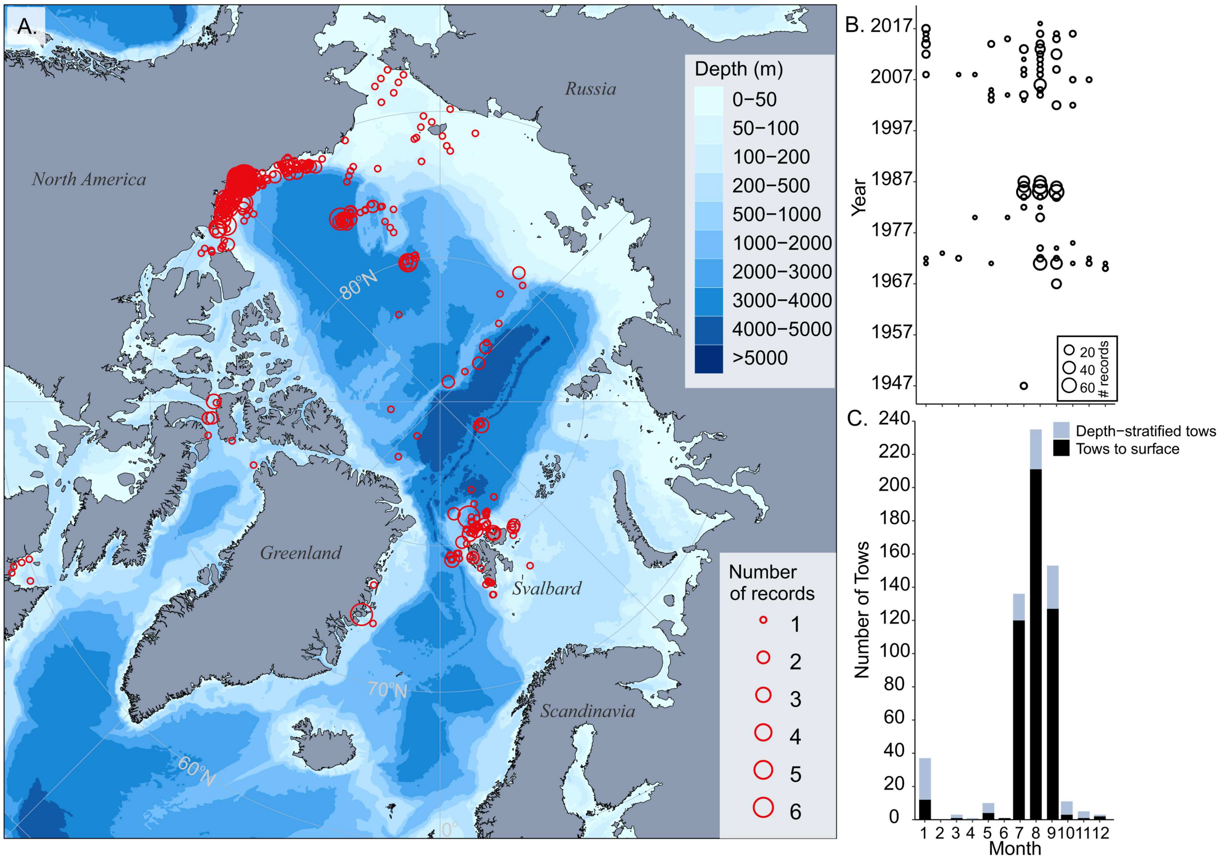

Fig. 1. **A–C**. **A.** Spatial distribution of all pelagic records of *A. glacialis*, including records with no corresponding tow information. Circle size represents number of records within a reported geographic position. **B.** Circle size represents the same records shown in **A** but organized by month and year. **C.** All tow records (tows to the surface and depth-stratified tows) that contained the presence of *A. glacialis* within different months.

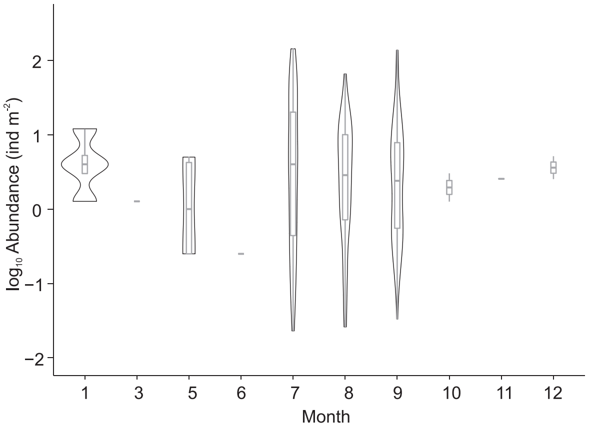

Fig. 2. Log10 of *A. glacialis* abundance (individuals m^{-2}) found in all tows to the surface. Violin plot (box shows median and interquartile range, whiskers show 95% confidence interval) within density of data (shape width depicts frequencies of values). Months 1 and 5 have only 1 whisker, due to the small ranges of *A. glacialis* abundances.

zone (0—200 m) or crossed into the photic zone from a deeper depth. Abundances of *A. glacialis* in these layers (deepest depth range 382—41 m, shallowest depth range 160—13 m) were reported as: 0.004–1 m^{-3} and 1 to 3 individuals. One tow in the near surface layers quantified *A. glacialis* as 0.02 m^{-2}. Seventy-five depth-stratified tows (62%) occurred within or crossed into the 200—1000 m depth layer, with abundances of 0.0004–1 m^{-3} and 1–6 individuals, respectively. *A. glacialis* occurred in 2 depth-stratified tows deeper than 1000 m with reported abundances of 0.002 m^{-3} and 2 individuals.

A. glacialis in the Svalbard region

During the 2017 *Polar Night* cruise, *A. glacialis* was present in 7 out of 20 tows to the surface between 80°N and 82°N. Tows to the surface started from 400 to 100 m, and within these 7 tows, we collected a total of 54 individuals. Within 2 Multinet layers (800—400 m), we found 2 *A. glacialis*. All animals found were alive, including 8 gravid females and 1 female with an empty brood pouch. Regarding pelagic occurrences coupled with hydrographic information around the Svalbard region, *A. glacialis* was found on the shelf, inside the Arctic Rijpfjorden, as well as off-shelf both west and north of the Svalbard Archipelago (Fig. 4). *A. glacialis* was found in Atlantic Water (> 2°C)

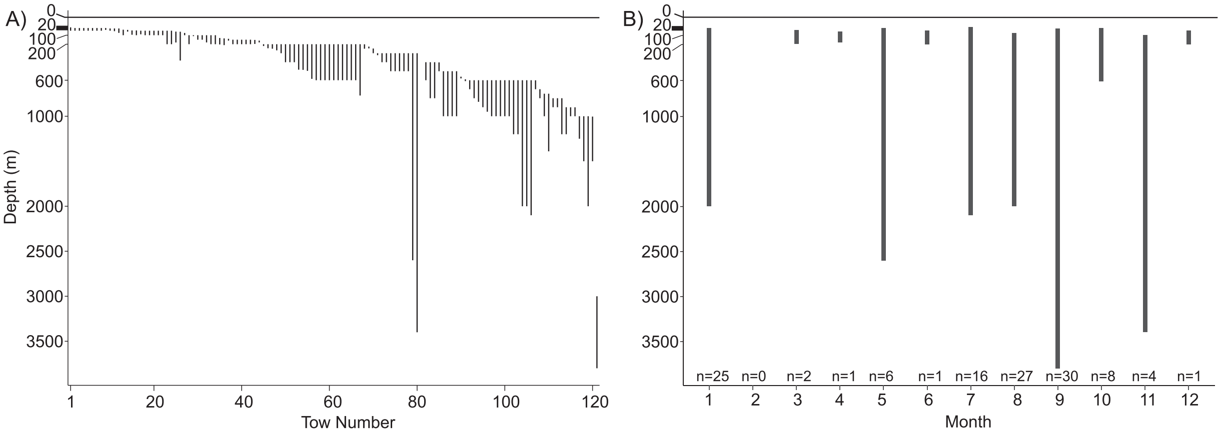

Fig. 3. A. Vertical distribution of depth-stratified tows. Depth-stratified tows are individually plotted and organized by increasing shallowest depth. **B**. Minimum and maximum of depth-stratified tows, organized by month and depth (m). Total number of depth-stratified tows per month are shown.

during all months of the year, regardless of location, but was also found in other water masses (Fig. 5). There was no obvious pattern of overwintering at depth in Atlantic Water.

A. glacialis body sizes and sex ratios

We collected a total of 15 056 body size measurements, mostly from the sea ice habitat. Most researchers sampled ice-associated *A. glacialis* (88%, $n = 13\ 261$ individuals) directly under sea ice using scuba equipment with a plankton hand net or electric suction sampler. The remaining individuals (12%, $n = 1\ 795$ individuals) were collected in depth-stratified tows and tows to the surface. The smaller juvenile size class (1–2 mm) was found between November and June and was the dominating size class during the months of March through May (Fig. 6A). During the summer months in the sea ice habitat (June–September), *A. glacialis* was represented mostly by the older juvenile and adult size classes. Adults were absent in March and close to absent in April in the size data set (Fig. 6A). While there was some overlap of the measurement and sex ratio datasets, a subset of data contained only sex ratios (and no body size measurements). Compared to males, there was a much higher proportion of females found in sea ice throughout the sampled months (Kruskal–Wallis test, $P = 0.02$). Females dominated the sex ratio at all times of the year (Fig. 6B), contributing 70% during summer (July and August) and winter (December and January) and over 90% in late winter/early spring (February through April). All adults found in January [from Berge *et al*. (2012) and the 2017 *Polar Night* cruise] were females. Interestingly, we found 1 juvenile at depth during the 2017 *Polar Night* cruise, similar to the 2012 study (Berge *et al*., 2012).

DISCUSSION

Pelagic occurrences of *A. glacialis*

Our results demonstrate that *A. glacialis* is consistently found in the pelagic environment on a pan-Arctic scale in areas similar to the sympagic distribution of *A. glacialis* (CAFF, 2017). We recorded pelagic occurrences both on the shelves and in the basin in both the Pacific and Atlantic sectors of the Arctic Ocean. There are noticeable gaps of pelagic occurrences within the Russian shelf seas although *A. glacialis* has been found there within the sea ice habitat (CAFF, 2017). We believe that these gaps are due to the lack of sampling or lack of reporting in the available literature and do not represent a true biological pattern. It seems likely that when there is sympagic presence of *A. glacialis*, there are also pelagic occurrences, based on the similarities of our results to known sympagic distributions (CAFF, 2017).

Our vertically integrated pelagic abundances of *A. glacialis* are on a similar order of magnitude compared to the reported ranges of abundances of *A. glacialis* in Arctic sea ice (Hop *et al*., 2000). A more detailed comparison of absolute abundances between and within habitats is not possible because of the various sampling methods applied. Different plankton nets and mesh sizes used in different habitats and habitat dimensions most likely affect both the catchability of *A. glacialis* and subsequent abundance estimates of pelagic records. Despite the gear bias, however, it is apparent that distribution is patchy in both habitats, the water column and the sea ice. The distribution of sympagic amphipods is horizontally patchy (Lønne and Gulliksen, 1991a,b; Swadling *et al*., 1997), and they are often unevenly distributed among different ice features such as ridges and level ice (Arndt and Pavlova, 2005; Gradinger *et al*., 2010). In the water

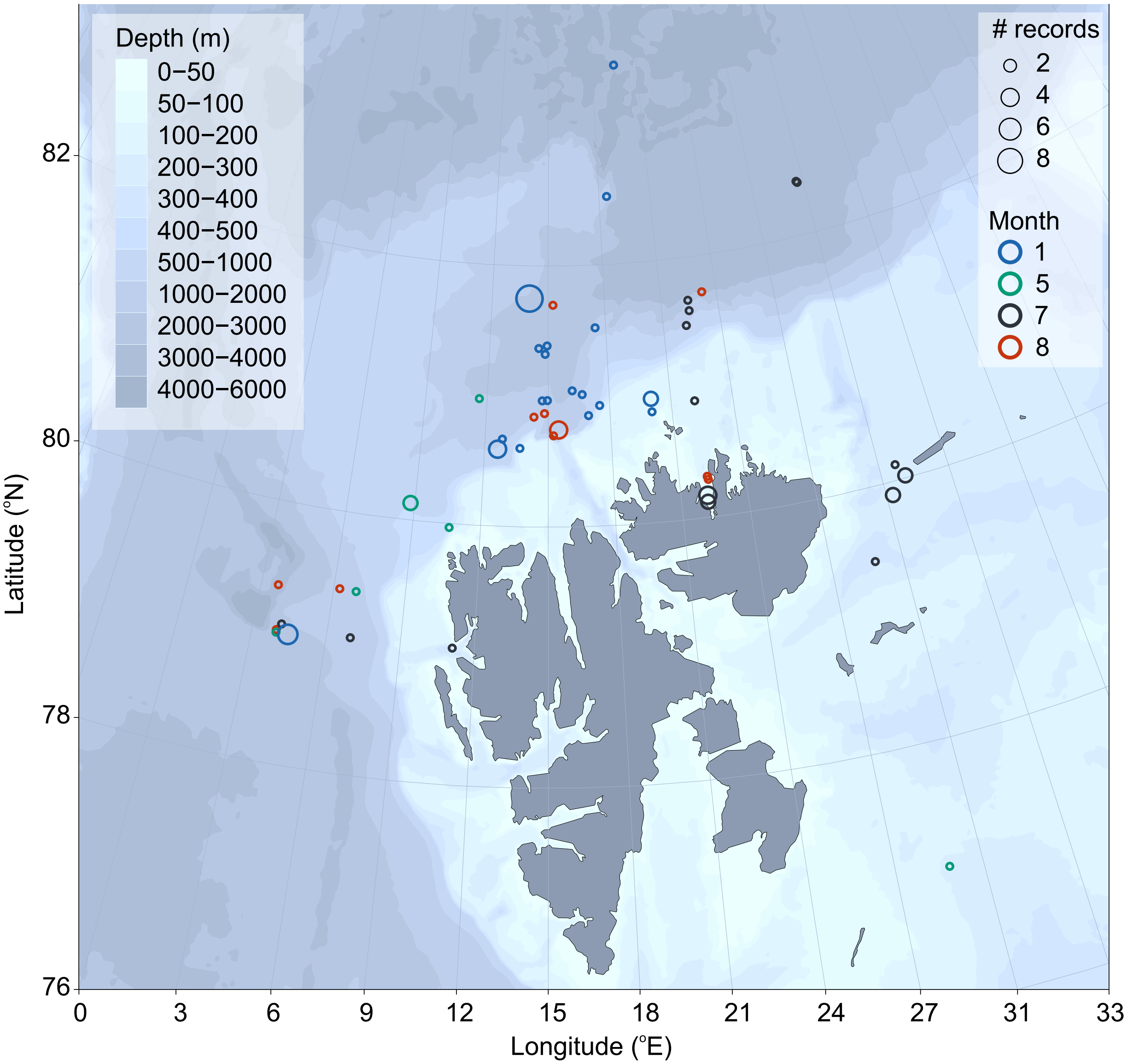

Fig. 4. Occurrence of *Apherusa glacialis* in tows to surface and depth-stratified tows in the Svalbard region. Circle size represents the number of tows of *A. glacialis* within a reported geographic position, color represents month. Tows within this region include January (2012, 2014–2017), May (2003, 2005, 2014), July (2004, 2011, 2013) and August (2010, 2014, 2016, 2018). Bathymetry is derived from IBCAO v3.0 500-m RR grid.

column, abundances were generally low, although in some tows to the surface up to hundreds of individuals were reported. Although we cannot entirely rule out that the pelagic occurrences of *A. glacialis* are due to them being lost from the sea ice habitat and that they are sinking to the sea floor, pelagic individuals occurred in areas covered by sea ice outside the melt season. Overall, our findings suggest that *A. glacialis* is not a true autochthonous species, but rather one that integrates a pelagic-sympagic coupling within its life.

We conclude that *A. glacialis* is capable of inhabiting the water column at any time of the year, even when sea ice is present. This species is rather mobile and moves between ice floes and can therefore colonize first-year ice (Lønne and Gulliksen, 1991a). No clear seasonal pattern in their pelagic occurrence was observed, although there were relatively few occurrences from the polar night compared to Arctic summer. This is in part due to the general undersampling of the polar night. Furthermore, finding *A. glacialis* both in shallower depths and in deep water during the polar night supports recent findings that many pelagic organisms maintain activity during the winter (Berge *et al.*, 2015). Even though *A. glacialis* was found in deep water during periods of assumed low

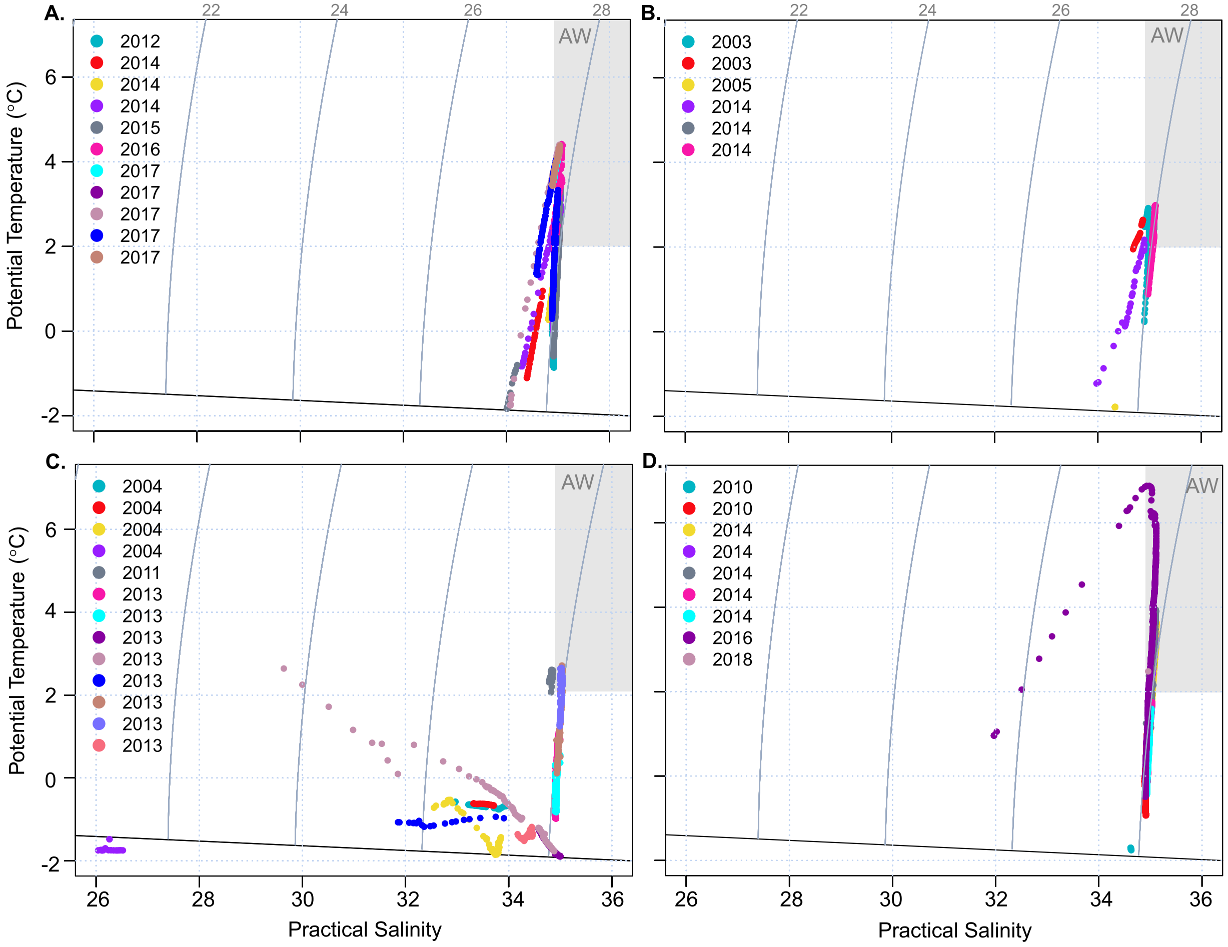

Fig. 5. A–D: Occurrence of *A. glacialis* in all tows in the Svalbard region related to available CTD salinity and temperature profiles. Boxes indicate approximate position of Atlantic water. TS-diagrams of water depths where *A. glacialis* were found in **A.** January, **B.** May, **C.** July and **D.** August. For information on the full-depth profiles (*i.e.* the depths where *A. glacialis* was not found, please see Supplementary Fig. 1).

surface water food availability (*i.e.* polar night), they were also found in deep water during months when sympagic food sources were presumably available. For example, *A. glacialis* was found under ice and considered highly reliant on the surrounding sympagic food sources (Kohlbach *et al.*, 2016) during the same summer months we find conspecifics in deep water. The overall seasonal patterns of *A. glacialis* in deep water do not follow patterns of *Calanus hyperboreus* that employs a deep overwintering migration strategy and a synchronous ascent to the surface after winter (Hirche, 1997). Our depth-stratified records with no clear seasonal pattern of *A. glacialis* occurrences suggest some plasticity in their life history strategy.

Greater plasticity in life history traits than previously assumed has also recently been documented in abundant Arctic pelagic species. Specifically regarding the paradigm that entire populations overwinter at depth, it has been found that *Calanus finmarchicus* and *C. glacialis* are also distributed throughout the water column during the polar night (Daase *et al.*, 2014, 2018; Basedow *et al.*, 2018). Regarding ice amphipod species, pelagic occurrences of *G. wilkitzkii, Onisimus glacialis* and *O. nanseni* in the Fram Strait at different seasons (Werner, 2006) have so far been interpreted as a potential dead end of their life cycles (Werner *et al.*, 1999). However, *G. wilkitzkii* has been found alive at the sea floor in both Svalbard fjords (Arndt *et al.*, 2005) and in NE Greenland (R. Fredriksen and B.A. Bluhm, pers. comm.) where ice exits the Arctic during late summer. Furthermore, *O. glacialis* females are often absent from sea ice, suggesting reproduction elsewhere (Arndt and Beuchel, 2006), and this species has been found in vertical plankton tows in deep water (Melnikov, 1997). Both *O. glacialis* and *O. nanseni* have in fact been previously described as temporary occupants of sea ice (Melnikov and Kulikov, 1980). Because *A. glacialis* is found

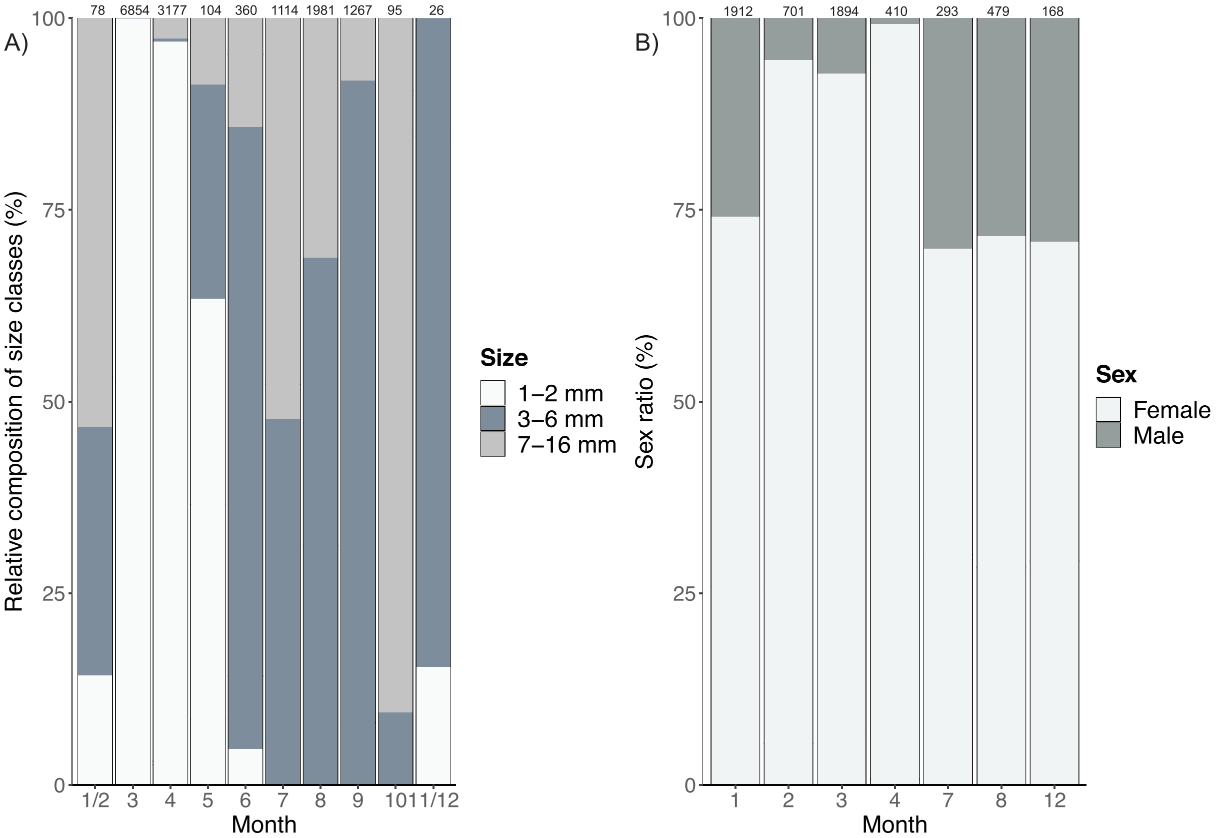

Fig. 6. Relative contribution of (**A**) size classes and (**B**) sex ratios of *A. glacialis* across seasons, pooled across years. Size classes represent freshly hatched (1–2 mm), later juvenile (3–6 mm) and adult stages (> 7 mm). Records are mostly from sea ice-associated sampling. Sample numbers for each month(s) provided above bars.

both under sea ice and in deep water, it is possible that there could be cryptic genetic variation within discrete populations, although there is no current evidence to support this. Incorporating molecular analysis into future population studies would provide insight into this question. Regardless, it is clear that higher degrees of plasticity exist than what has been previously assumed in various Arctic crustaceans.

An added benefit of *A. glacialis* vertically migrating within the Atlantic Water inflow is that individuals would be transported back into the Arctic Ocean leading to reduced advective losses at the population scale (Berge *et al.*, 2012). Surface and deep-water currents carry large volumes of warm and saline Atlantic Water into the Arctic Ocean via the Fram Strait and West Spitsbergen Current, with small amounts of Atlantic Water returning southward via bifurcation and eddy recirculation (Hattermann *et al.*, 2016). The core of Atlantic Water around the northwest Svalbard archipelago is found between 75 and 500 m in epipelagic and mesopelagic water depths, thereby isolated from sea ice and the colder and fresher surface water layer (Aagaard *et al.*, 1981; Beszczynska-Möller *et al.*, 2011; Pérez-Hernández *et al.*, 2017). Atlantic Water is also found close to or at the sea surface north of the Barents Sea (Rudels *et al.*, 2013; Lind *et al.*, 2018). Furthermore, the speed of Atlantic Water inflow can vary both within and between seasons, which can affect the overall distribution of planktonic organisms (Hop *et al.*, 2019). Berge *et al.* (2012) estimated return speeds at 2–3 months if *A. glacialis* was within the core of Atlantic water.

Within our dataset, *A. glacialis* was consistently present in both Arctic and Atlantic Waters, although there was no seasonality of where they were found when. This finding does not wholly support the hypothesis put forth by Berge *et al.* (2012), but we cannot entirely refute it either. There seems to be no overall synchronous movement within the population, though the *A. glacialis* individuals found within the Atlantic Water would have the added benefit of being transported back into the Arctic Ocean. While it is uncertain how far *A. glacialis* could be transported back into the central Arctic Ocean within their life cycle, this open question could be resolved within a particle tracking model (Döös *et al.*, 2017), releasing particles at specific depths within the Arctic Ocean in scenarios with and without sea ice.

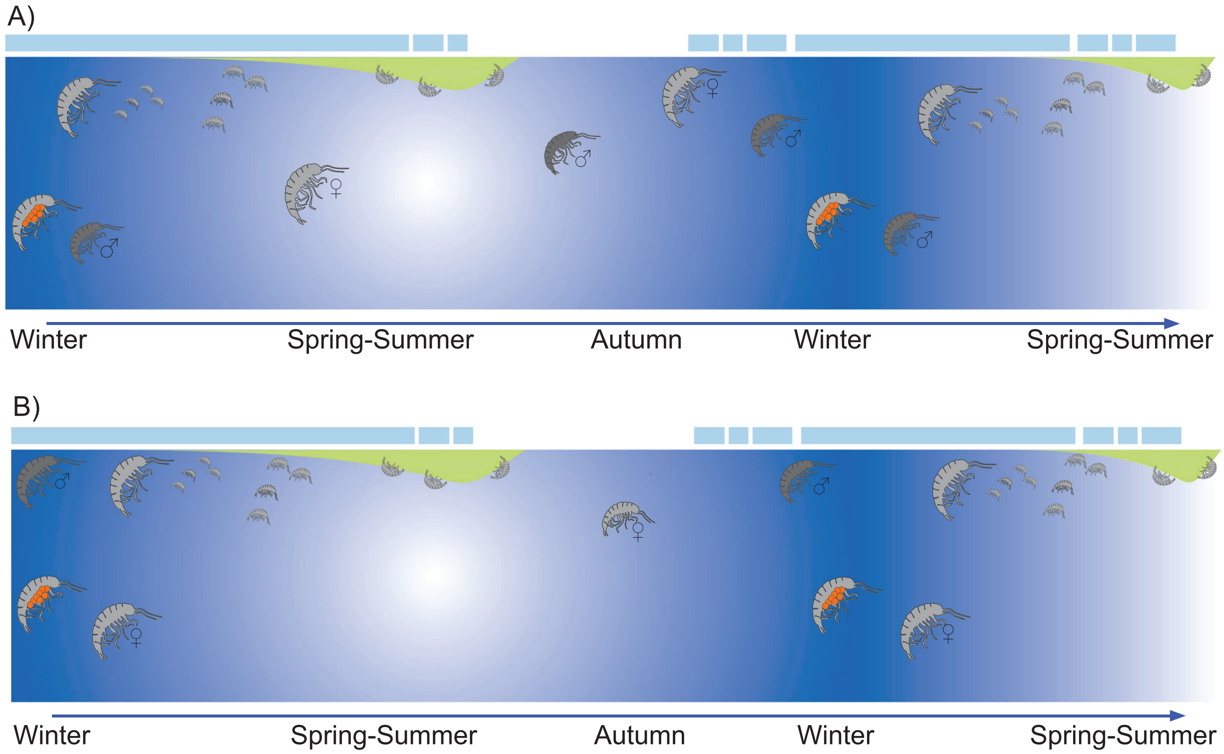

Fig. 7. Conceptual illustrations of proposed life history strategies of *A. glacialis*, for one calendar year. Light blue indicates ice cover, green indicates ice algal bloom and blue shading indicates seasonality. **A**. A scenario where adults of *A. glacialis* are distributed both under ice and in the water column year-round, and females (both gravid and those not carrying eggs) employ vertical movement. **B**. A scenario where only *A. glacialis* females (both gravid and those that are not carrying eggs) undergo a vertical migration away from sea ice during polar night.

A. glacialis life history, revisited

Within our pelagic dataset, we cannot conclude whether all *A. glacialis* found at depth were in good body condition or 'dead sinkers'. However, the few records when body condition was reported (Berge *et al.*, 2012), or observed by the authors, demonstrate that all *A. glacialis* found (regardless of depth or season) were in good body condition and that some were gravid females. An intriguing result is that when we searched for *A. glacialis* in deep water during the polar night in 2017, we again found gravid females similar to the previous findings (Berge *et al.*, 2012).

Information on body size and sex ratios throughout the year can provide insights into life history strategies (Varpe and Ejsmond, 2018). Melnikov (1997, 1989) concluded that reproduction of *A. glacialis* occurs during polar night, although it is unknown at what depths mating occurs. The present study supports the previous findings that juvenile offspring are likely released in late winter/early spring, evidenced by a strong increase in the number of the smallest size class found under sea ice at this time (Melnikov, 1989; Poltermann *et al.*, 2000). As the summer progresses, we document a development into the next size class with the largest proportion of adults occurring during autumn. The apparent low proportion of adults found under sea ice during the winter/early spring also supports earlier findings (Werner and Auel, 2005) and coincides with adult occurrences in the water column during these same months in the present study. While it has been suggested that *A. glacialis* breeds only once during its lifetime (Melnikov and Kulikov, 1980; Poltermann *et al.*, 2000), juveniles are released in successive batches through time based on our dataset and previous studies (Poltermann *et al.*, 2000; Beuchel and Lønne, 2002). Thus, our findings further support that *A. glacialis* is semelparous (Varpe and Esjmond, 2018).

In all months sampled, there was a much higher proportion of females than males in the under ice habitat, although relative adult percentages were low in the spring months. Our data suggest that adult males comprise 25% of the sex ratio consistently throughout all the months but February to April, similar to previous studies of *A. glacialis* (Melnikov and Kulikov, 1980; Poltermann *et al.*, 2000). One reason for this could be that amphipod males are generally underestimated because it is much more difficult to positively identify male sex organs (minute genital papillae) compared to female oostegites (Chapman, 2007). This same bias, however, would apply to other sympagic amphipods, but the *A. glacialis* sex ratio is in stark contrast to the other ice amphipods. *G. wilkitzkii* has a 1:1 sex ratio (Poltermann *et al*., 2000), while *O. nanseni* and *O. glacialis* fluctuated between 1:1 and a dominance of either males or females depending on time of year (Arndt and Beuchel, 2006). Higher male amphipod mortality (Thurston, 1972; Powell and Moore, 2007) or males having a smaller seasonal presence (for example, males having a large role during mating, but few roles outside of mating) could be the cause of skewed sex ratios observed. For *A. glacialis*, it could be that males die soon after breeding, resulting in their particular scarcity during February to April.

Linking the data on body sizes, sex ratios and pelagic occurrences, we suggest an updated conceptual model of *A. glacialis* life history (Fig. 7). We envision possibly 3 different scenarios. Based on the findings that there can be *A. glacialis* individuals anywhere at any time, it could be that adult females and males are distributed both under ice and in the water column year-round (Fig. 7A). The second scenario suggests that only females undergo a vertical migration away from sea ice, supported by our findings of gravid females in deep water during the polar night (Fig. 7B). The third scenario (not pictured) is that this species has developed a high degree of plasticity to inhabit both the sea ice and water column, though how it will adapt to ice-free summers is unknown.

CONCLUSION

We found clear evidence that *A. glacialis* regularly occurs within the pelagic realm, during all seasons. The scant records on body condition suggest that *A. glacialis* can successfully inhabit pelagic habitats. The data provide some support to the conceptual adaptive-advection model suggested by Berge *et al*. (2012), though our data are inconclusive on whether *A. glacialis* conducts a vertical overwintering migration and if ice drift versus water current speed makes return possible within their short life cycle. Given that *A. glacialis* is relatively mobile, can successfully inhabit different under ice structures and is found in the pelagic environment on a pan-Arctic scale, we suggest that *A. glacialis* does move in and out of the sea ice habitat and can no longer be regarded solely as an autochthonous sympagic species.

While we have demonstrated that *A. glacialis* is not as dependent on sea ice as previously assumed, sea ice habitat is still a critical part of their life history strategy, evidenced by the hatching and maturation of young *A. glacialis* in the under ice habitat. Due to climate change, the decline of Arctic sea ice extent basin-wide (Stroeve and Notz, 2018) with concomitant loss of multiyear sea ice (Kwok and Rothrock, 2009; Maslanik *et al*., 2011) has the potential to trigger ecosystem-level perturbations and affects species that inhabit sea ice, including *A. glacialis*. Both multiyear sea ice and pressure ridges provide a longer lasting habitat for ice-associated organisms (Gradinger *et al*., 2010) than thinner and smoother first-year ice. As thinner and weaker ice drifts and melts faster (Zhang *et al*., 2012; Kwok *et al*., 2013) and is exposed to more wave action, this could result in the flushing of species more easily into the surrounding water. Additionally, these changes in Arctic sea ice will result in a different under ice light environment, potentially resulting in higher predation rates from visual predators (Varpe *et al*., 2015). A complete pelagic lifestyle may be more energetically demanding (Seibel and Drazen, 2007). Increases in locomotion in order to search for food, mates and avoid predators can possibly affect metabolic rates and overall fitness of *A. glacialis*.

In conclusion, the combination of the occurrence of early life stages and females within the sea ice habitat, along with ice-algal food sources making up large proportions of adult diet, suggests that *A. glacialis* will capitalize on this habitat when available. This study gives evidence, however, that *A. glacialis* does not exclusively use the sea ice habitat, allowing them to potentially adapt to future ice-free scenarios. Therefore, a more comprehensive understanding is needed of its life history and how presence away from sea ice contributes to their overall strategy. Plasticity among organisms inhabiting under ice habitat may be an adaptive trait allowing populations to sustain themselves in an ephemeral sea ice habitat. Knowing that other Arctic ice amphipods can also occur away from sea ice, future research could investigate this phenomenon in more regional or seasonal detail, especially in areas with pronounced sea ice loss.

SUPPLEMENTARY DATA

Supplementary data is available at *Journal of Plankton Research* online.

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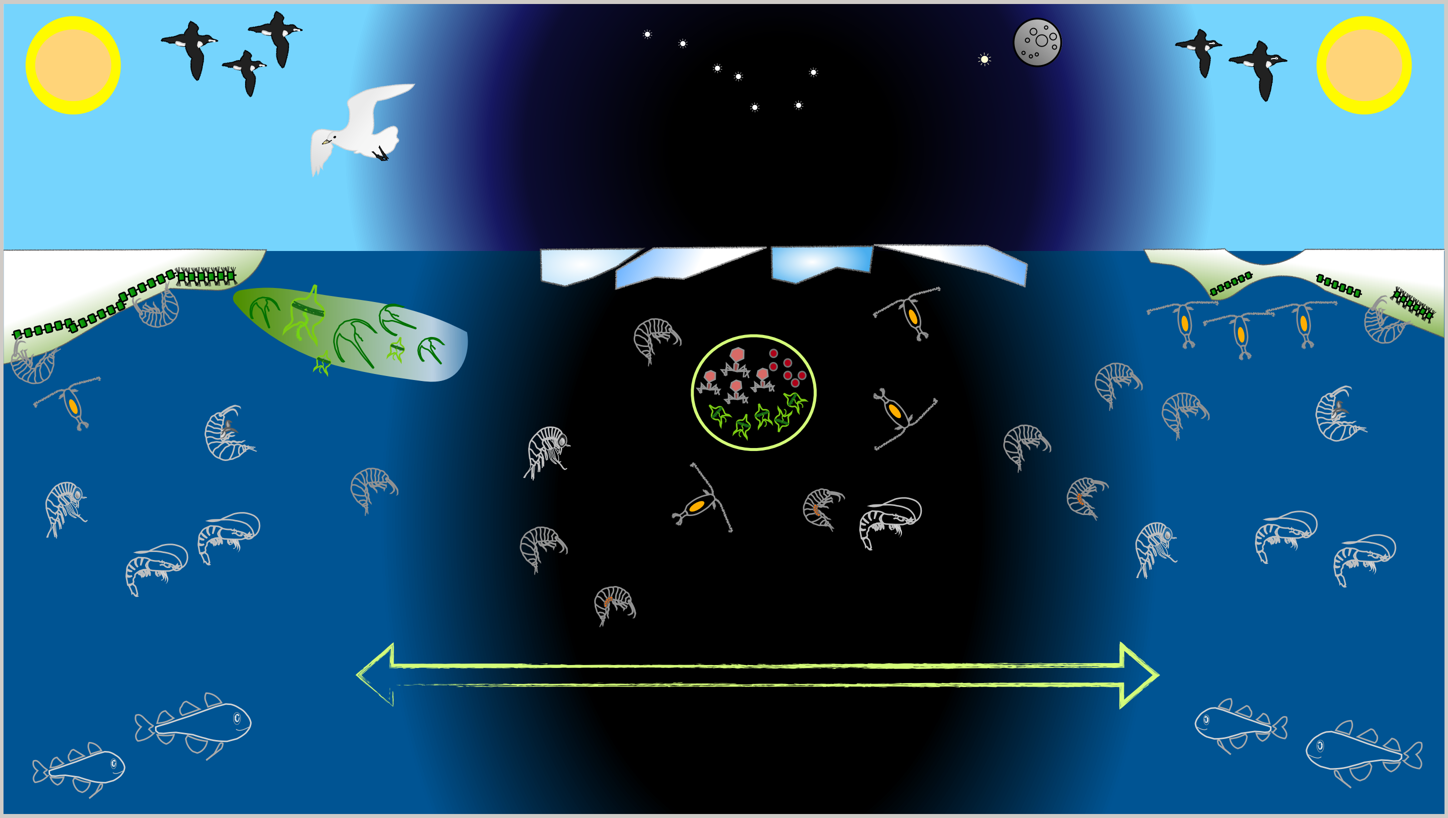
Paper II



Title: Do Arctic zooplankton feed during polar night? Insights into trophic transfer as revealed by lipids, fatty acids, and compound-specific stable isotopes

Running page head:

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Abstract:

During the productive polar day, zooplankton and sea-ice amphipods are known to have a critical role in energy transfer from primary producers to higher trophic-level species in Arctic marine ecosystems. Recent polar night studies on zooplankton and sea-ice amphipods suggest higher levels of biological activity than previously assumed. However, it is unknown if these invertebrates maintain polar night activity on stored lipids, opportunistic feeding, or a combination of both. To assess how zooplankton and sea-ice amphipods support themselves on seasonally varying resources, we studied their lipid classes, fatty acid compositions, and compound-specific stable isotopes of trophic biomarker fatty acids during polar day (June/July) and polar night (January). Lipid storage and fatty acid results confirm previously described polar day dietary sources in all species. However, we found evidence of polar night feeding activity in all species, including shifts in nutrition from primary producers to other food sources. Sympagic-, pelagic-, and *Calanus* spp.-derived carbon sources supported zooplankton and sea-ice amphipods in both seasons. We provide the first evidence on polar night feeding of sea-ice amphipods in the pelagic realm.

Keywords: Arctic Ocean, zooplankton, polar night, lipids, fatty acids, compound-specific stable isotopes, sea ice, sea-ice amphipods

INTRODUCTION

Seasonality is a periodic and predictable feature in almost all ecosystems, resulting in temporally distinct abiotic and biotic events (Lieth 1974). High latitude environments have short productive seasons and many organisms therefore have limited time windows for growth, reproduction, and energy storage. In polar marine environments, the extremes of seasonal light availability result in highly pulsed primary production events (Clarke 1988, Ji et al. 2013, Leu et al. 2015), leading to many life hitory adaptations in Arctic organisms (McNamara & Houston 2008, Varpe 2017).

For Arctic marine zooplankton, these adaptations to reduced food availability during winter include reduced feeding rates, shifts in dietary items, and/or overwintering in various states of arrested development. Additionally, many herbivorous zooplankton species accumulate large amounts of lipid reserves during the biologically productive season (Hagen & Auel 2001, Lee et al. 2006). The reproductive strategies of herbivorous zooplankton are well-adapted to the Arctic seasonal cycle, ranging from using stored energy for reproduction to being reliant on food resources in order to produce offspring (Varpe et al. 2009, Daase et al. 2013). In contrast, omnivorous and carnivorous zooplankton consume food and reproduce year-round, seemingly less affected by seasonality (Sargent & Falk-Petersen 1981, Kraft et al. 2012, Legeżyńska et al. 2012). Overwintering strategies proposed for polar zooplankton range from diapause (a period of arrested development, surviving off stored energy pools) to business-as-usual (continued feeding year-round, with no reduction in metabolism) (Hagen 1999). In the middle of these opposing strategies is flexibility, defined as using a mix of energy stores and opportunistic feeding (Hagen 1999). In most studies, overwintering strategies are explained from the perspective of biologically productive periods, and overall activity of the zooplankton community is considered to be low during the polar night. Recent research has found higher than expected biological activity during polar night, contradicting long-assumed paradigms (Berge et al. 2015b, Berge et al. 2020).

These studies show that biological activity can remain high for many organisms in the absence of light and photosynthetic production (Berge et al. 2015a). During polar night, Arctic marine zooplankton take cues from moonlight and weak twilight in order to vertically migrate (Last et al. 2016, Cohen et al. 2021). Diapausing species like *Calanus* spp. have been found to ascend from overwintering depths to surface waters as early as January (Błachowiak-Samołyk et al. 2015, Daase et al. 2018), where alternative prey availability sustains polar night activity (Hobbs et al. 2020). While overwintering strategies are less clear for ice-associated (sympagic) Arctic amphipods, recent studies suggest that the pelagic realm may serve as suitable habitat during polar night (Berge et al. 2012, Kunisch et al. 2020). As these findings demonstrate higher levels of activity than previously assumed, it remains to be seen if zooplankton and sympagic amphipods are maintaining activity on stored lipids alone, opportunistically feeding, or a combination of both. The flexibility overwintering strategy could then be perhaps used more often by more species than previously described (Hagen 1999), particularly for primarily herbivorous species.

This study explored potential seasonal diet changes for Arctic zooplankton and sympagic amphipods. We focused on five species, whose diet and overwintering strategies differ. *Calanus glacialis*, a primarily herbivorous copepod, converts much of its plankton-based diet acquired from surface layers during seasonal phytoplankton blooms into large stores of wax ester lipids

(Sargent et al. 1981, Scott et al. 2002). *C. glacialis* can also be omnivorous at all stages of their development (Campbell et al. 2009). In our study area, *C. glacialis* is found to transition to omnivory during periods of low algal biomass (Søreide et al. 2008). In autumn, *C. glacialis* vertically migrates to depth and overwinters in a dormant state of diapause, surviving on wax ester stores and reduced metabolism (Ackman 1989, Falk-Petersen et al. 2009). Life history strategies of the euphausiid *Thysanoessa inermis* are somewhat comparable to *Calanus* spp., as *T. inermis* consumes phytoplankton when available (Sargent & Falk-Petersen 1981). However, *T. inermis* overwinters in an active state, and is thus considered herbivorous–omnivorous dependent on the time of year (Sargent & Falk-Petersen 1981, Dalpadado et al. 2008). Lipid storage in euphausiids is connected to life stage and reproductive effort and varies from a mix of wax esters and triacyclglycerols (TAG), to a dominance in phospholipids (Falk-Petersen et al. 2000). Therefore, *T. inermis* has been classified as having a flexible overwintering strategy (Hagen 1999). *Themisto libellula*, a pelagic hyperiid amphipod, is a visual and opportunistic predator with a preferred diet of *Calanus* spp. copepods (Scott et al. 1999, Dalpadado et al. 2008), even during polar night (Kraft et al. 2013). Although wax esters are the preferred storage lipid for herbivorous zooplankton, *T. libellula* also has high amounts of this lipid due to their consumption of *Calanus* spp., along with producing TAG (Kraft et al. 2015). *T. libellula* is considered to have a 'business-as-usual' overwintering strategy (Hagen 1999).

Sympagic amphipods, when found within the sea ice habitat, have overlapping dietary preferences. *Apherusa glacialis* feeds mostly on sea-ice algae, but also on phytodetritus, and is classified as herbivorous–detritivorous (Werner 1997, Poltermann 2001). Compared to other sympagic amphipods, *A. glacialis* is considered lipid-rich, storing their lipids as TAG (Scott et al. 1999, Kohlbach et al. 2016). *A. glacialis* has a flexible overwintering strategy when found in the sea ice habitat (Werner & Auel 2005). *Gammarus wilkitzkii* is mostly carnivorous, with the ability to prey on *A. glacialis* as well as pelagic copepods (Werner et al. 2002). However, *G. wilkitzkii* has also been classified as detritivorous, necrophagous, and herbivorous, indicating an opportunistic feeding strategy (Poltermann 2001, Werner & Auel 2005). Compared to *A. glacialis*, *G. wilkitzkii* has lower relative amounts of TAG (Scott et al. 1999). Accumulation of wax esters in *G. wilkitzkii* has been attributed to their consumption of calanoid copepods (Werner & Auel 2005). Based on these findings, we categorized *G. wilkitzkii* to have a business-as-usual overwintering strategy.

We first studied the overwintering strategies of these five species in terms of their lipid storage patterns. Energy accumulations into lipids such as wax esters, TAG, and phospholipids are used as energy stores for zooplankton and sympagic amphipods living in food-limited extremes, as hypothesized by Hagen & Auel (2001). In our study, high investments in wax esters are interpreted as an overwintering strategy at rest (*i.e.,* diapause); or, to a lesser extent, consumption of organisms with high amounts of wax esters. Lipid accumulation via TAG can reflect opportunistic and year-round feeding behavior (Hagen & Auel 2001 and references therein), thus a more business-as-usual strategy. Flexible strategies represent a mix of these two storage lipid classes, along with potential investments into membrane phospholipids.

Second, we investigated the fatty acid composition of the studied species using a trophic biomarker approach as fatty acids provide specific information on diet sources (Sargent & Whittle 1981; Graeve et al. 1994b). Two main sources of primary productivity in Arctic pelagic marine systems are sea-ice algae (often dominated by diatoms (Bacillariophyceae), Leu et al. 2006, Søreide et al. 2006) and phytoplankton (with dinoflagellates (Dinoflagellata), diatoms, and others as main contributors, Booth & Horner 1997, Sherr et al. 2003). Abundant fatty acids in diatoms are 16:1(n-7) and 20:5(n-3) (Viso & Marty 1993, Reitan et al. 1994, Jónasdóttir 2019). Dinoflagellates have higher amounts of the 18:4(n-3) and 22:6(n-3) fatty acids (Viso & Marty 1993, Graeve et al. 1994b). During polar night, both diatoms and dinoflagellates can be found within the water column (Błachowiak-Samołyk et al. 2015, Vader et al. 2015), though with lower fatty acid contributions to particulate organic matter when compared to polar day (Marmillot et al. 2020, Kohlbach et al. 2021). While 16:1(n-7) is the precursor of 18:1(n-7) through chain elongation (Sargent & Henderson 1986), 18:1(n-9) can be produced by consumers (Graeve et al. 1994a) and can serve as a biomarker for carnivory. Other trophic biomarkers, such as 22:1(n-11), are also used as an indication of carnivory on *Calanus* spp. in higher trophic level consumers (Graeve et al. 1994b). Bacterial production in the Arctic Ocean can, at times, be as high as primary production (Wheeler et al. 1996), and is also available in the water column throughout the polar night (Iversen & Seuthe 2011). Thus, we included bacterial biomarkers which are represented by the odd-chained, branched fatty acids (15:0 and 17:0) (Dalsgaard et al. 2003, Parrish 2013).

Third, we investigated the seasonal patterns of the trophic biomarker fatty acids within each species. This was done by combining trophic biomarker fatty acid proportions with their individual carbon isotope values, or $\delta^{13}C_{FA}$. Most organic carbon in Arctic pelagic ecosystems originates from sea ice algae and phytoplankton. In particular, diatom- and dinoflagellate-associated fatty acids [16:1(n-7), 20:5(n-3), 18:4(n-3), and 22:6(n-3)] can have higher $^{13}C_{FA}$

values in ice algae when compared to phytoplankton due to carbon limitation in the sea-ice habitat (Horner & Schrader 1982, Fry & Sherr 1984). These carbon sources are then channeled through zooplankton and sympagic amphipods (Wang et al. 2015, Kohlbach et al. 2016, Ehrlich et al. 2021). When consumers catabolize isotopic compounds, it often results in a shift from lower to higher δ^{13}C values (^{13}C/^{12}C ratio) because of the preferential uptake of ^{12}C in enzymatic reactions (DeNiro & Epstein 1978). We expected similar trends using $\delta^{13}C_{FA}$ values and expected those consumers feeding on sea-ice algae would have relatively higher $\delta^{13}C_{FA}$ values than those feeding on phytoplankton.

We hypothesized that if changes in lipid classes and/or fatty acids occurred in the study species during polar night, these would differ by overwintering strategies: diapause, flexibility, and business-as-usual. Following this, we investigated if fatty acid composition differed by season and habitat. We further hypothesized that zooplankton (*C. glacialis*, *T. inermis*, *T. libellula*) would have low seasonal variability in the $\delta^{13}C_{FA}$ values of trophic biomarker fatty acids. We hypothesized high seasonal variability in the $\delta^{13}C_{FA}$ values of trophic biomarker fatty acids in the sympagic amphipods *A. glacialis and G. wilkitzkii*, because of an expected switch from ice-algae based carbon sources during the polar day to pelagic carbon sources during the polar night.

METHODS

Study area and zooplankton sampling

Sampling was conducted during three expeditions in 2017 and 2018 in the Barents Sea and the Nansen Basin (Fig. 1). Two expeditions occurred in January 2017 and 2018 (polar night conditions) on the R/V Helmer Hanssen; the third expedition on the R/V Polarstern (PS106) occurred between 3 June and 14 July 2017 (polar day conditions).

During the January expeditions, zooplankton and sympagic amphipods were collected from various depths using a depth-stratified zooplankton Multinet sampler (Hydro-Bios, Kiel, Germany) equipped with five nets of 0.25 m^2 aperture with a mesh size of 180 µm. Organisms were collected from 800 – 400 m and 400 – 100 m (January 2017), and 200 – 100 m (January 2018). Organisms were also sampled using pelagic nets towed to the surface (Table 1 and Kunisch et al. 2020). No sea ice was encountered in January 2017; sampling occurred in-between smaller sea ice fragments in the marginal ice zone in 2018.

In June–July 2017, sampling occurred in predominantly pre-bloom situations within first-year sea ice areas. Four different types of nets were used to sample both pelagic and sympagic organisms. A zooplankton net (mounted to a remotely operated underwater vehicle, ROVnet) consisted of a polycarbonate frame (40 x 60 cm) and 500 µm mesh size (Macke & Flores 2018, Wollenburg et al. 2020). This net was operated at three specific depths under the ice: directly under-ice, 5 and 10 m water depth. A Surface and Under-Ice Trawl (SUIT) (0.15 mm mesh size) was also used directly under-ice (Van Franeker et al. 2009). To sample the pelagic community, a rectangular midwater trawl (RMT, 5.5 mm and 330 µm mesh sizes) and a bongo net (180 µm mesh size) targeted the upper 100-300 m of the water column.

As soon as organisms (Table 2) were collected, they were sorted by species and placed into pre-combusted and pre-weighed 8 mL borosilicate vials or wrapped in aluminum foil (not pre-combusted) and placed into air-tight bags. Samples were frozen at -80 °C until analysis. Our interest was in the seasonal differences within species, and not among life stage within species. Hence, we attempted to collect adult life stages for each species. For *C. glacialis* we collected overwintering copepodite stages CV and adult females (AF) in January 2017 and CIV in January 2018. Upon arrival to the laboratory, samples were stored in -80 °C until laboratory analysis.

Table 2. Overview of the species included in the study. Zooplankton overwintering strategies are listed (Hagen 1999 [a]). For the sympagic amphipods, we report what is known from polar day while found in association with sea ice (Poltermann 2001 [b], Werner & Auel 2005 [c]). Based on these findings, we suggest the following overwintering strategies (flexible and business-as - usual). Total sample sizes (N = number of individuals) for fatty acid and $\delta^{13}C_{FA}$ (together denoted as FA, because these data are from the same individuals) and total sample sizes for lipid class determination (LC) are shown.

Species	Taxon	Overwintering strategy	Polar day diet	FA N Polar day	LC N Polar day	FA N Polar night	LC N Polar night
C. glacialis	Calanoid copepod	Diapause	Primarily herbivorous (a)	187	127	70	70
T. inermis	Euphausiid	Flexible	Omnivorous (a)	62	62	11	11
T. libellula	Hyperiid amphipod	Business-as-usual	Primarily carnivorous (a)	31	26	10	10
A. glacialis	Calliopiid amphipod	Flexible	Primarily herbivorous (c)	170	150	13	11
G. wilkitzkii	Gammarid amphipod	Business-as-usual	Primarily carnivorous (b)	14	14	8	8

Fatty acid and lipid class analysis

All laboratory analyses were conducted at the Alfred Wegener Institute in Bremerhaven, Germany. Prior to lipid extraction, organisms were removed from -80 °C freezers and freeze-dried for 24 h (Rudy et al. 2016). Samples were mechanically homogenized, and lipids were extracted using dichloromethane/methanol 2:1 v/v (Folch et al. 1957). Total lipid mass of each sample was determined gravimetrically. Lipid class analysis was conducted using High

Performance Liquid Chromatography on aliquots of the extracted lipids (Graeve & Janssen 2009). Extracted lipids were converted into fatty acid methyl esters by transesterification using methanol with a 3% solution of concentrated sulfuric acid. Fatty acid methyl esters were quantified with an internal standard, tricosanoic acid methyl ester (23:0) (Supelco, Germany), that was added prior to lipid extraction. Detailed information on analytical measurements and equipment is further described in Kunisch et al. (2021). Detection limits were based on a certified reference material (Supelco 37 Component fatty acid methyl ester mix), which was 10 – 20 ng per component. Fatty acids are presented in shorthand notation, *i.e.*, A:B(n-x), where: A indicates the number of carbon atoms in the straight fatty acid chain, B represents the number of double bonds present, n represents the position of the terminal methyl group and x denotes the position of the first double bond from the terminal end. Proportions of individual fatty acids are expressed as mass percentages of total fatty acid content. While all fatty acids were examined for analysis, we also highlighted known trophic biomarker fatty acids (Table 3).

Table 3. Trophic markers identified in fatty acid contributions of pelagic and sympagic food sources. TAG: triacyclglycerols. [(Falk-Petersen et al. (1987, 1999, 2000) (a), Graeve et al. (1994b a, 1997) (b), Auel et al. (2002) (c), Scott et al. (1999, 2002) (d), Kattner & Hagen (1995) (e), Dalsgaard et al. (2003) (f), (Lee et al. 2006) (g)]

Fatty Acid	Trophic Biomarker	Lipid class, function
16:1(n-7)	Diatoms at spring bloom stage (a, b)	TAG (d), Storage (d)
20:5(n-3)	Diatoms (a, b)	Phospholipids (a), Biomembranes (d), TAG (d)
18:1(n-9)	Carnivory (a, b)	TAG (g)
18:4(n-3)	Dinoflagellates (a, f)	Storage (e)
22:6(n-3)	Flagellates (a, b, c)	Phospholipids (a), Biomembranes (d)
22:1(n-11)	*Calanus* spp. (a, b)	Storage (a)
∑15:0, *ai*15:0, *i*15:0, 17:0	Bacteria (f)	

Compound-specific stable isotope analysis

Carbon stable isotope ratios of fatty acid methyl esters ($\delta^{13}C_{FA}$) of tissue samples were analyzed using a Trace Ultra gas chromatograph (GC), a GC Isolink system and Delta V Plus isotope ratio mass spectrometer (IRMS), connected via a Conflo IV interface (Thermo Scientific Corporation, Germany). Samples were injected in splitless mode and separated on a DB-FFAP column (60 m, 0.25 mm I.D., 0.25 µm film thickness) using temperature programming. The limit of detection was comparable to the methods described above. The $\delta^{13}C_{FA}$ values were calibrated using certified, referenced standards of 14:0 [$\delta^{13}C$: -29.98‰], 16:0 [$\delta^{13}C$: -30.74‰], 18:0 [$\delta^{13}C$: -23.24‰], and 20:0 [$\delta^{13}C$: -30.68‰] (supplied by Indiana University, USA). To ensure accuracy and precision (± 0.8‰ for GC-IRMS), certified standards were analyzed before and after sample runs in the GC-IRMS. All reported $\delta^{13}C_{FA}$ values are relative to Vienna Pee Dee Belemnite (VPDB) using the standard notation $\delta^{13}C_{FA}$ (‰) = $[(R_{sample} / R_{standard}) - 1] \times 1000$, where R is the corresponding ratio of $^{13}C/^{12}C$.

Multi- and univariate statistical analysis of fatty acid and lipid class data

Data analysis was conducted in R version 4.0.3 (R Core Team, 2020). We used both the tidyverse (Wickham et al. 2019) and vegan (Oksanen et al. 2020) packages for figures (unless otherwise noted) and analytical workflow. For lipid class analysis, a correspondence analysis (CA) on the relative proportions (mass % of sum) was conducted to determine how various lipid classes contributed to dissimilarity among species. We focused on two neutral lipids, wax esters, and TAG, and two polar phospholipids (phosphatidylethanolamine (PE) and phosphatidylcholine (PC)). To test for seasonal differences between lipid class proportions within species, we used the Kruskal-Wallis rank sum tests followed by Dunn's test for pairwise comparisons. This non-parametric approach was chosen because of unequal sample sizes.

Fatty acid datasets for each species were first visualized using a CA. Because fatty acid null values have biological meaning, these values were retained within the dataset. Canonical correspondence analysis (CCA) was then conducted on the significant fatty acids ($\alpha = 0.05$, determined via the *envfit* function) to examine which environmental variables might influence fatty acid composition. Separate CCA models were run for each species.

The following environmental variable groups were included in the CCA models within species: water mass, season (polar day/night), and location. For water mass, temperature (T) and salinity (S) data were derived from conductivity-temperature-depth (CTD) profiles from PS106 (Heuzé et al. 2018, Nikolopoulos et al. 2018) and the polar night expeditions. We included CTD data from the location nearest to the sampled zooplankton, often from the same station. Mean profiles of T and S were averaged over the sampled net depth (*i.e.*, if a zooplankton tow was 100 – 0 m). These values were then made categorical and binned into four distinct water masses: Polar surface water, modified Atlantic water, Atlantic water, and Arctic intermediate water (following the definition by Priou et al., 2021 for this region). For species sampled under ice via the ROVnet, we used under-ice T-S values from the same stations and depths, reported in Wollenburg et al. (2020). There were some stations where zooplankton and sympagic amphipods were collected with the ROVnet and did not have corresponding T-S values. We binned these in a separate category, under-ice. Sampled months (January, June, July) were binned into two different seasons: polar night (January) and polar day (June and July). Location (shelf, shelf break, basin) was defined by bottom depth. We designated shelf for any station that was sampled at < 400 m, shelf break stations with bottom depths between 401 – 2500 m, and basin stations with bottom depths > 2500 m (Bluhm et al. 2020).

In some cases, we found high levels of covariation between the location and water mass variables within species (e.g., if all species were found in the same water mass within a particular location, Fig. S1). For example, *T. inermis* was only found Atlantic Water in our study, where it normally resides (Dalpadado & Skjoldal 1996). Therefore *T. inermis* fatty acids could only be tested on the influence of location and season. Given that the location and water mass variables were at times linked to one another, we then chose one variable (location or water mass) that explained more of the variation in the model. These variables were then tested with season to see if they influenced fatty acid profiles within each species. Environmental variable significance was tested using a permutation test with 999 permutations. Additionally, seasonal differences on trophic biomarker fatty acids and their carbon isotope values were univariately tested using Kruskal-Wallis rank sum tests followed by a Dunn's test for pairwise comparisons.

RESULTS

Zooplankton

We found no differences between *C. glacialis* stages; hence findings were pooled within the species group. *C. glacialis* stored lipids primarily as wax esters in both seasons (Fig. 2, Table S1) and had higher relative amounts of wax esters in January compared to June/July (KW-Dunn $p = 0.03$). The trophic biomarkers 16:1(n-7), 20:5(n-3), and 22:1(n-11) contributed the most to *C. glacialis*, regardless of season (Fig. 3, Table S2). The contribution of the carnivory biomarker

18:1(n-9) in *C. glacialis* was significantly higher in January when compared to June/July (p = 0.03). Fatty acids acquired from *de novo* biosynthesis [22:1(n-11), 22:1(n-9), and 20:1(n-11)] (Graeve et al. 1994b) and two diatom-associated fatty acids [16:4(n-1) and 20:5(n-3)] significantly contributed to the CA patterns (Fig. 4). While visually the CA lacked a clear seasonality pattern, permutational test results from the CCA determined that water mass (p = 0.03) and season (p = 0.005) significantly explained the fatty acid patterns of *C. glacialis* (Table S2). $\delta^{13}C_{FA}$ values ranged from -32‰ to -30.1‰ for diatom-associated fatty acids [16:1(n-7), 20:5(n-3)] and -32.4‰ to -29.2‰ for dinoflagellate-associated fatty acids [18:4(n-3), 22:6(n-3)] (Fig. 5). In comparison, the *Calanus* spp. trophic biomarker 22:1(n-11) $\delta^{13}C_{FA}$ values ranged from -27.4‰ to -26.9‰ (Table S4). The $\delta^{13}C_{FA}$ values of the trophic biomarker fatty acids did not differ seasonally (Fig. 5).

T. inermis accumulated similar proportions of wax esters, TAG, and phospholipids in January compared to June/July with highest investments into wax esters and PC (Fig. 2, Table S1). The diatom marker 20:5(n-3) and carnivory biomarkers 16:0 and 18:1(n-9) contributed most to the body biochemical composition of *T. inermis*, in both seasons (Fig. 3, Table S2). *T. inermis* also accumulated similar amounts of the diatom-associated 20:5(n-3) in both seasons. Fatty acids significantly contributing to the CA patterns in *T. inermis* were diatom- and dinoflagellate-associated, namely 16:1(n-7), 16:4(n-1), 20:5(n-3), 18:4(n-3), and 22:6(n-3) (Fig. 4). Permutational test results from the CCA determined that neither location nor season significantly explained differences in seasonal fatty acid patterns (Table S3). $\delta^{13}C_{FA}$ values ranged from 32.5‰ to -30‰ for the diatom-associated fatty acids, similar to *C. glacialis* (Fig. 5, Table S4).

The $\delta^{13}C_{FA}$ value of 18:4(n-3) was lower in *T. inermis* compared to *C. glacialis* (January: 34.2‰, June/July: -37‰).

T. libellula amassed mostly neutral lipids in both seasons. Wax esters were significantly more abundant in June/July when compared to January (p = 0.02). As these are relative contributions, the opposite was true for TAG, which were significantly more abundant during January opposed to June/July (p = 0.02). *T. libellula* also accumulated phospholipids (PE and PC), yet in comparatively smaller proportions and without seasonal differences (Table S1). *T. libellula* accumulated significantly higher amounts of the carnivory biomarker 18:1(n-9) (p = 0.001) in January when compared to June/July (Fig. 3). The opposite was true for the *Calanus* spp. trophic biomarker [22:1(n-11)] of which *T. libellula* had significantly higher amounts in June/July when compared to January (p = 0.005, Fig. 3). This trend was evident in all *Calanus* spp. fatty acids combined (Σ 20:1, 22:1, p = 0.005, Table S2). The 20:1 and 22:1 fatty acids also contributed to the overall patterns and a clear seasonal separation in the *T. libellula* CA (Fig. 4). Permutational test results from the CCA indicated that only season significantly explained (p = 0.01) these patterns (Table S3). The mean $\delta^{13}C_{FA}$ values of the carnivory marker 18:1(n-9) ranged from -31.6‰ to -30.6‰ between June/July and January with no significant seasonal differences (Fig. 5). The dinoflagellate-associated 18:4(n-3) had significantly higher $\delta^{13}C_{FA}$ values in January compared to June/July (p = 0.04).

Sympagic amphipods

A. glacialis had significantly higher proportions of TAG in January when compared to June/July (p = 0.02). TAG was the dominant lipid regardless of season with relatively less storage investments in phospholipids (PC) and wax esters (Fig. 2). The diatom-associated 16:1(n-7) was particularly abundant in *A. glacialis* in both seasons (Fig. 3); yet January *A. glacialis* had significantly higher contributions of 16:1(n-7) compared to June/July (p = 0.003). In June/July, *A. glacialis* had significantly higher contributions of the diatom-associated 20:5(n-3) and dinoflagellate-associated 18:4(n-3) compared to January (p = 0.002 for both fatty acids). Only one June/July sample had the *Calanus* spp. biomarker 22:1(n-11), while all January *A. glacialis* samples had accumulated this fatty acid biomarker (Table S2). *A. glacialis* also had significantly higher proportions of the carnivory biomarker 18:1(n-9) in January (p = 0.04), though proportions were overall low in both seasons. Reflecting the above patterns, the *A. glacialis* CA resulted in clear separation by season along axis 1 (Fig. 4). January *A. glacialis* fatty acid patterns were driven by the contribution of 22:1(n-11). Permutational test results from the CCA indicated that season (p = 0.001) and location (p = 0.03) significantly explained *A. glacialis* fatty acid patterns (Table S2). There were significantly higher $\delta^{13}C_{FA}$ values of the two diatom-associated fatty acids and one dinoflagellate-associated fatty acid in June/July when compared to January (16:1(n-7) p = 0.04, 20:5(n-3) p = 0.002, 22:6(n-3) p = 0.04, Fig. 5). *A. glacialis* had higher $\delta^{13}C_{FA}$ values of the bacteria biomarker 15:0 in June/July (-22.7‰) compared to January (-34‰), though this finding was not significant (Fig. S3, Table S4).

G. wilkitzkii overall had somewhat similar patterns compared to *A. glacialis*, storing lipids mostly as TAG during both seasons but also – in low proportions – as wax esters and phospholipids (Fig. 2, Fig. S2). We found no significant differences in lipid class composition between January and June/July. Relative contributions of seasonal fatty acids were highest for 16:1(n-7) and 18:1(n-9) (Fig. 3, Table S2). January *G. wilkitzkii* accumulated significantly higher proportions of the dinoflagellate-associated 18:4(n-3) compared to June/July ($p = 0.003$, Fig. 3), which also contributed to its seasonal separation in fatty acids (Fig. 4). June/July *G. wilkitzkii* accumulated significantly higher amounts of the carnivory biomarker 18:1(n-9) ($p = 0.02$), and was further characterized by zooplankton feeding, indicated by the contributions of the 20:1 and 22:1 monounsaturated fatty acids (MUFA) along with the other carnivory biomarker 16:0 (Figs. 3 and 4). While a seasonal separation along axis 2 in the *G. wilkitzkii* CA was evident, permutational test results from the CCA indicated that neither season nor location were significant (Table S2). *G. wilkitzkii* had significantly higher $\delta^{13}C_{FA}$ values of the dinoflagellate-associated 22:6(n-3) in June/July (-30.4‰) when compared to January (-34.2‰, $p = 0.02$). Diatom marker $\delta^{13}C_{FA}$ values were also higher in June/July yet that difference was not statistically significant (Fig. 5).

DISCUSSION

C. glacialis – diapause, but also flexible

We found that the neutral lipid storage patterns in *C. glacialis* followed previously reported seasonal trends, in that *C. glacialis* accumulated high amounts of wax esters in order to survive food-limited periods (Sargent & Falk-Petersen 1988, Ackman 1989). In January *C. glacialis*, total lipids per dry mass was low for both sampled years (12% and 33%), compared to high summer values in other studies (≥ 56%, Scott et al. 2000). Thus January *C. glacialis* would be categorized as lipid-poor (Hirche & Kattner 1993). Low lipid levels in winter *Calanus* spp. are not unusual as a large wax ester pool might instead be allocated for gonad development and/or egg production (Conover 1967, Graeve et al. 2020). However, these low lipid levels were also comparable to surface-dwelling, non-diapausing *Calanus* spp. (Kattner & Krause 1989), suggesting that individuals lacking adequate lipid stores to overwinter would then remain active near the surface (Hobbs et al. 2020).

The saturated fatty acids are the main dietary precursors of the *de novo* synthesized 20:1 and 22:1 fatty acids and alcohols (Kattner & Hagen 1995), which provide high amounts of energy within *Calanus* spp. wax esters (Scott et al. 2002). January *C. glacialis* had significantly higher contributions of the dietary precursors 16:0 and 18:0 (Table S2), suggesting that this lipid synthesis pathway was most likely active during polar night. Fatty acid assimilation in *Calanus* spp. ranges between days to weeks (Graeve et al. 2005). Thus, we suggest that January *C. glacialis* was omnivorous, based on the significantly higher proportions of the carnivory biomarker 18:1(n-9) and saturated fatty acids during polar night. As previously mentioned with lipid storage patterns, reproductive investments also influence fatty acid composition of overwintering *C. glacialis* (Hirche & Kattner 1993). We acknowledge that at a population level, *C. glacialis* overwinters and survives on stored lipids alone (Hirche 1989). However, *Calanus* spp. in our study area are often distributed throughout the water column during polar night (Daase et al. 2014, 2018, Daase & Søreide 2021). These findings suggest some degree of individual plasticity, where some individuals are in diapause while others are more active in the water column. In fact, *C. glacialis* in this area has been shown to rather carnivorous outside the spring bloom, feeding on metazoan prey (Cleary et al. 2017). Our fatty acid and lipid findings lend support to a more flexible overwintering lifestyle (consistent also with Berge et al. 2020).

Diatom- and dinoflagellate-associated fatty acids are incorporated almost unchanged into wax esters of *Calanus* spp. (Lee 1975, Graeve et al. 1994b). Both in our study area and in other parts of the Arctic, the $\delta^{13}C_{FA}$ values of marker fatty acids are higher in sea ice algae when compared to phytoplankton (Wang et al. 2014, Kohlbach et al. 2016, Kunisch et al. 2021). For example, the $\delta\ ^{13}C_{FA}$ value of 20:5(n-3) in iPOM was -27.4‰, and -37.6‰ in pPOM (Kunisch et al. 2021), and -31.9‰ in *C. glacialis,* suggesting a diet consisting of both pelagic and sympagic carbon sources (Kohlbach et al. 2016). In other trophic biomarkers however (16:1(n-7) and 22:6(n-3)), our $\delta\ ^{13}C_{FA}$ values measured in *C. glacialis* was lower than those of pPOM (Kunisch et al. 2021), suggesting that these $\delta\ ^{13}C_{FA}$ values either reflected rather phytoplankton-dominated carbon sources. There was an insignificant but general trend that the $\delta^{13}C_{FA}$ values of the diatom- and dinoflagellate-associated fatty acids were all higher (by approximately 1‰) in January *C. glacialis* when compared to June/July. Calanoid copepods apparently lack the enzymes needed to bioconvert 18:3(n-3) into polyunsaturated fatty acids (Bell & Tocher 2009), thus we can assume here that the diatom- and dinoflagellate-associated fatty acids (minus 16:1(n-7)) and their carbon content all derive from dietary sources. However, the lack of polar night $\delta^{13}C_{FA}$ values of iPOM and pPOM, and knowing that the $\delta^{13}C_{FA}$ values of fatty acids are modified by metabolic rates and life stages (Graeve et al. 2005, 2020, De Troch et al. 2012), it is challenging to seasonally compare the $\delta^{13}C_{FA}$ values in *C. glacialis*.

T. inermis – flexible

T. inermis has a life span of three to four years (Dalpadado & Skjoldal 1996), having developed unique overwintering strategies in order to survive periodic seasons of lower food availability. Throughout the productive season, *T. inermis* converts large portions of consumed diet into storage lipids, mainly wax esters and TAG (Falk-Petersen et al. 2000). We instead found that *T. inermis* had higher concentrations of phosphatidylcholine (membrane phospholipid) in both seasons (≥ 33%) compared to the other species in our study (< 10%). This higher investment into membrane lipids set *T. inermis* apart from the other studied species in terms of lipid storage (Fig. S2). Phospholipids are not typically used for energy reserves in many pelagic species (Lee et al. 2006). However, phosphatidylcholine is used as an energy reserve for Antarctic euphausiids (Saether et al. 1985, Stübing et al. 2004), resulting in distinct lipid storage patterns in euphausiids when compared to other zooplankton. During autumn, *T. inermis* accumulate large lipid stores (55% of dry mass), though these stores are reduced to around 10% in winter (Falk-Petersen 1981, Falk-Petersen et al. 1982, 2000). We found similar levels in January *T. inermis* (7%). Euphausiids have the capacity to cyclically shrink their bodies and sexually regress due to food limitations or as an overwintering survival mechanism (Ikeda & Dixon 1982, Kawaguchi et al. 2007, Huenerlage et al. 2016), possibly confounding the interpretation of our lipid findings.

June/July *T. inermis* fatty acid composition indicated a diet supported by both diatom- and dinoflagellate-associated fatty acids, including other C16 polyunsaturated fatty acids (PUFA). While this supports previous findings from the Barents Sea (Dalpadado et al. 2008), *T. inermis* are also opportunistic foragers, acting as omnivores–carnivores, depending on season and body size (Falk-Petersen et al. 2000, Søreide et al. 2006, Huenerlage et al. 2015). We found support in opportunistic omnivory, indicated by the presence of the *Calanus* spp. fatty acids and the carnivory biomarker 18:1(n-9) in *T. inermis*. We conclude that *T. inermis* successfully overwinters on a combination of stored lipids and alternative food sources, similar to previous findings (Huenerlage et al. 2015).

Compared to the $\delta^{13}C_{FA}$ values of the diatom- and dinoflagellate-associated fatty acids in iPOM and pPOM from June/July, *T. inermis* had either lower values than both iPOM and pPOM [16:1(n-7), 18:4(n-3)], equivalent to pPOM [22:6(n-3)], or in between iPOM and pPOM [20:5(n-3)] (Kunisch et al. 2021). If we assume negligible effects of isotopic fractionation (Budge et al. 2008) the *T. inermis* values suggest this species is supported by both sympagic and pelagic carbon, similar to earlier studies using bulk $\delta^{13}C$ (Søreide et al. 2006, 2013). Based on the seasonal presence of the 22:1(n-11) fatty acid in *T. inermis*, we also suggest that carbon derived from the *Calanus* spp. food web supports *T. inermis* year-round.

T. libellula – business-as-usual

January *T. libellula* accumulated an average of 25% total lipids/dry mass, though the range of total lipids was wide between samples (5% – 66%, Table S1). The disparity in total lipids could perhaps be attributed to the fact that *T. libellula* is an opportunistic carnivore that demonstrates some degree of dietary plasticity at the individual level. Wax esters are a major lipid class of *T. libellula* during winter, comprising ≥ 77% of body mass (Kraft et al. 2015, Kohlbach et al. 2021). It has been suggested that high amounts of wax esters are rather indicative of *T. libellula* prey, the wax ester-dominant *Calanus* spp. (Noyon et al. 2011, Kraft et al. 2015). Interestingly, January *T. libellula* in our study had considerably less wax esters (31%) and a high proportion of TAG (51%). Because TAG indicates year-round feeding activity (Lee et al. 2006), we suggest that January *T. libellula* was foraging on other types of prey in addition to *Calanus* spp.

We found *T. libellula* fatty acid composition was influenced by season, similar to previous findings (Mayzaud & Boutoute 2015). The diatom-associated 16:1(n-7) contributed to June/July diet, likely due to the consumption of herbivorous grazers and the seasonal availability of algal food sources. Although *T. libellula* is mostly carnivorous, diatoms and dinoflagellates have been found in their stomach contents throughout the year (Dalpadado et al. 2008, Kraft et al. 2013). It is unknown if the presence of this alga in their stomachs is a result of direct ingestion or digested with the copepod prey. In January, diatom- and dinoflagellate-associated fatty acids were also present in *T. libellula* – along with lower amounts of 22:1(n-11), the *Calanus* spp. biomarker, and higher amounts of 18:1(n-9), the carnivory biomarker. Collectively, these findings could be suggestive of alternative, herbivorous prey available in our study area. The Atlantic Water inflow transports large amounts of other zooplankton prey through our study area throughout the year (Hop et al. 2006, Basedow et al. 2018). At the same time, *Calanus* spp. fatty acids were also present in *T. libellula*, demonstrating the importance of *Calanus* copepods as an important food source throughout the year (Dalpadado et al. 2008, Kraft et al. 2013).

For a year-round active predator such as *T. libellula*, January $\delta^{13}C_{FA}$ values of POM-derived fatty acids were variable. While the origin of the $\delta^{13}C_{FA}$ values in POM remain unclear, we can say that the carbon pathway from diatoms and dinoflagellates supports *T. libellula* throughout the year based on the continual presence of these biomarkers in January and June/July.

A. glacialis – flexible in the absence of sea ice

A. glacialis accumulate up to 50% total lipids/dry mass during the productive polar day (Scott et al. 1999, Werner & Auel 2005, Kohlbach et al. 2016). These energy stores are likely catabolized during the food-limited polar night, since the lipid content has been reported to decline to ~20% total lipids towards the end of winter (March/April, Werner & Auel 2005). The January *A.*

glacialis from the pelagic realm in our study had a mean of 48% of total lipids/dry mass, similar to previously sampled January *A. glacialis* at depth (Berge et al. 2012). Our January *A. glacialis* not only had lipid levels comparable to its summer conspecifics (Scott et al. 1999), but also had levels comparable to overwintering *Calanus* spp. (Falk-Petersen et al. 2009). These comparable lipid levels would also aid *A. glacialis* in neutral buoyancy at depth, similar to *Calanus* spp. (Campbell & Dower 2003). Based on these comparisons, *A. glacialis* has adequate lipid stores to perform seasonal vertical migrations (Berge et al. 2012, Drivdal et al. 2021). Regardless of the differences in total lipids, January TAG deposits were significantly higher than June/July, suggestive of continued feeding activity.

In the winter sea ice habitat, diatom-associated 16:1(n-7) contributed 3% – 37% of *A. glacialis* diet (Werner & Auel 2005). Given that *A. glacialis* can have a more pelagic lifestyle than previously assumed (Berge et al. 2012, Kunisch et al. 2020), it is possible that the higher contributions of 16:1(n-7) were from pelagic diatoms. Fatty acid turnover for *A. glacialis* is unknown, but in a benthic freshwater gammarid amphipod, *Pallaseopsis quadrispinosa*, turnover for 16:1(n-7) was higher than for other fatty acids, suggesting a rapid assimilation of this fatty acid from a diatom-fed diet (Taipale et al. 2021). During November/December in the northern Barents Sea, 16:1(n-7) proportion was low (mean, 7%) in both iPOM and pPOM (Kohlbach et al. 2021). However, 16:0 in iPOM and pPOM had similar mean amounts in November/December (24% – 26%) when compared to June/July iPOM (34%) and pPOM (26%) (Kohlbach et al. 2021, Kunisch et al. 2021). 16:0 – a fatty acid precursor in the diatom C16 pathway – from algal diet can be biosynthesized into 16:1(n-7) in herbivorous *Calanus* copepods (Dalsgaard et al. 2003). Thus, we cannot rule out that this pathway exists for other herbivorous species, and that *A.*

glacialis fed on pelagic diatoms during the polar night, though the overall abundance of pelagic diatoms is low at that time. *A. glacialis* found in sea ice are also classified as detrivorous, ingesting crustacean remains (Poltermann 2001). We found comparably small, seasonal contributions of the *Calanus* spp. biomarkers [20:1 and 22:1 MUFA] in *A. glacialis* diet. In our study area, there were high amounts of dead copepods in the water column in January (Daase & Søreide 2021), as was also observed in other years (Daase et al. 2014). If *A. glacialis* was to encounter dead copepods, copepod carcasses could serve as a source of lipid-rich food (Bickel & Tang 2010) during polar night.

Even though June/July *A. glacialis* was sampled from sea ice, the $\delta^{13}C_{FA}$ values of the diatom-associated fatty acids in *A. glacialis* were similar to pPOM [16:1(n-7)], or in between iPOM and pPOM values [20:5(n-3)] (Kunisch et al. 2021). *A. glacialis* $\delta^{13}C_{FA}$ values were even lower than both iPOM and pPOM in both dinoflagellate-associated fatty acids [18:4(n-3), 22:6(n-3)] (Kunisch et al. 2021). These results suggest a low contribution of ice-algal carbon supporting *A. glacialis*. This could be because we sampled early in pre-bloom situations, when compared to higher contributions of ice-algal carbon support for *A. glacialis* later in the season (August/September, Kohlbach et al. 2016). However, the $\delta^{13}C_{FA}$ values of both diatom-associated fatty acids, along with 22:6(n-3), were all significantly higher in June/July in *A. glacialis* when compared to January, demonstrating seasonal support of diatom and dinoflagellate produced carbon. We cannot discount the fact that the variation in $\delta^{13}C_{FA}$ values of *A. glacialis* are a result of metabolism and/or isotopic turnover rather than of recent dietary inputs.

***G. wilkitzkii* – business-as-usual**

In the sea ice habitat, *G. wilkitzkii* accumulates comparatively lower amounts of total lipids than *A. glacialis* with levels remaining steady during the productive season (mean 20% of dry mass) and dropping to 10% by the end of winter (March/April, Werner & Auel 2005). Interestingly, our findings were opposite in that *G. wilkitzkii* collected from ice in June/July had slightly lower total lipid values (10%) than the pelagic *G. wilkitzkii* sampled in January (20%). The range of total lipids/dry mass in January are suggestive of continuous feeding activity in at least some *G. wilkitzkii*. Furthermore, there was evidence of some overlap of lipid class composition between *G. wilkitzkii* and *T. libellula* (Fig. S2), further supporting the previously stated trophodynamic similarities between these species (Auel & Werner 2003). *G. wilkitzkii* had similar proportions of wax esters throughout the year, which is attributed to the consumption of *Calanus* copepods rather than lipid storage (Scott et al. 2001). With relatively high investments into TAG during both sampling periods, we suggest year-round feeding activity for *G. wilkitzkii*.

The patterns of *G. wilkitzkii* fatty acid composition between seasons supports our lipid class findings. Towards the end of winter (March/April) the decrease in total lipids was associated with decreases in the diatom-associated fatty acids, and an increase in the carnivory marker 18:1(n-9) (Werner & Auel 2005). However, our January *G. wilkitzkii* had similar amounts of diatom-associated fatty acids when compared to June/July, with a decrease in 18:1(n-9). The differences in these findings could be attributed to sampling times, as we sampled *G. wilkitzkii* much earlier in the winter when compared to Werner & Auel (2005). Our June/July fatty acid composition findings are comparative to previous in-ice studies, in that *G. wilkitzkii* assimilated diatom-associated fatty acids along with high contributions of 18:1(n-9) (Scott et al. 1999). In the sea ice habitat, *G. wilkitzkii* has a broad feeding strategy (Poltermann 2001). Thus, it is assumed that the presence of diatom- and dinoflagellate-associated fatty acids in *G. wilkitzkii* diet is at least in part because of direct ingestion of microalgae (Scott et al. 2001, Werner & Auel 2005). The presence of *Calanus* spp. biomarkers in *G. wilkitzkii* in our study, however, also indicated copepod consumption throughout the year.

June/July *G. wilkitzkii* had significantly higher $\delta^{13}C_{FA}$ values in 22:6(n-3) than in January. In comparison, the $\delta^{13}C_{FA}$ value in 22:6(n-3) in *G. wilkitzkii* (-30.4 ‰) was lower than the corresponding $\delta^{13}C_{FA}$ values in iPOM and pPOM (Kunisch et al. 2021). Without knowing how or if these $\delta^{13}C_{FA}$ values might vary between the direct intake of microalgae versus ingesting herbivorous prey, it is difficult to determine herbivory from $\delta^{13}C_{FA}$ values in *G. wilkitzkii*.

Limitations and knowledge gaps of trophic marker approaches

Although we have used fatty acid biomarkers to interpret dietary carbon sources in zooplankton and sympagic amphipods, caution should be exercised for comparisons between species. *Calanus* spp. are unique in that they can elongate saturated fatty acids into MUFA (e.g., 14:0 to 20:1), as well as elongate 16:1(n-7) into 22:1 (Sargent & Henderson 1986, Dalsgaard et al. 2003). Diatom- and dinoflagellate-associated fatty acids in *T. libellula* diet are assumed to be routed through prey, while *G. wilkitzkii* are thought to directly ingest microalgae (Poltermann 2001). We therefore attempted to limit our comparisons to within species. Recent genetic work has found that many marine invertebrates have the ability to *de novo* synthesize *n*-3 PUFA (omega-3 fatty acids), challenging the trophic marker concept (Kabeya et al. 2018). In our study, *n*-3 PUFA [18:4(n-3), 20:5(n-3), 22:6(n-3)] were assumed to originate from primary producers.

As we neither yet know how these genes for PUFA synthesis are expressed nor if they are present in our study species, it remains unknown how much *n*-3 PUFA could be biosynthesized as opposed to assimilated. Future fatty acid studies incorporating molecular analysis, in addition to tracer-based experiments, could provide insight into the dietary-driven strategies of many zooplankton species found in seasonally disparate environments.

Spatial variability in the $\delta^{13}C_{FA}$ values of iPOM and pPOM in June/July 2017 (Kunisch et al. 2021) likely affect our comparisons of these values as carbon baselines to zooplankton and sympagic amphipods. Because we sampled in pre-bloom situations in June/July, it is possible that the $\delta^{13}C_{FA}$ values in zooplankton and sympagic amphipods still reflected a late-winter signal. However, carbon turnover rates remain unknown in many species, especially during less-productive periods. Isotopic turnover (the time it takes for stable isotopes in tissues to be replaced by stable isotopes from diet) in bulk $\delta^{13}C$ can be up to 77 days for coastal Arctic amphipods during winter (Kaufman et al. 2008). If slow turnover such as 77 days had occurred in our studied species, it is possible that our January $\delta^{13}C_{FA}$ values are rather representative of a late autumn phytoplankton bloom. If both situations were to be the case, we argue that our seasonal comparisons are still valid since we essentially are comparing feeding activities between productive and less productive periods. It is important to acknowledge that $\delta^{13}C_{FA}$ values are affected by metabolic processes, lipid dynamics, and – largely unquantified – isotopic fractionation (Chamberlain et al. 2004, Bec et al. 2011, Gladyshev et al. 2016, Carter et al. 2019). Comparing consumer $\delta^{13}C_{FA}$ values to baseline POM sources means that we have assumed isotopic equilibriums within species and between seasons. However, the overall influences of these processes in our study species are unknown. We recognize that many processes likely affect the $\delta^{13}C_{FA}$ values, as zooplankton and sympagic amphipods all possess unique traits (such as partially surviving off stored energy pools) in order to survive periods of low food availability.

Seasonal food web drivers – considerations and recommendations

The key to making polar night feeding possible for zooplankton and sympagic amphipods may lie in the advective nature in our study area. The Atlantic Water inflow is a large source of nutrients and zooplankton biomass throughout the year (Codispoti et al. 2013, Basedow et al. 2018). This suggests relatively higher quantities of food for all the species in our study than elsewhere in the Arctic, though questions remain on the quality of food for herbivorous species. Higher quality foods generally enhance individual fitness (Stephens & Krebs 1986). Furthermore, food quality can change $\delta^{13}C_{FA}$ values, linked to the isotopic turnover of lipids (Chamberlain et al. 2006). While our findings suggest overwintering on a combination of both stored energy reserves and food intake in our study species, we did not determine the effects of food quality. Open questions on polar night feeding activities could be explored with a fitness optimization model, put forth by Burian et al. (2020), especially for scenarios with and without the seasonal input of sympagic algae.

Besides advective inputs, the microbial loop has the potential to sustain polar food webs during winter (Azam et al. 1991, Manganelli et al. 2009), as it plays a fundamental role in the reworking of dissolved organic carbon (Calleja et al. 2013). While bacterial inputs to zooplankton and sympagic amphipods were not explicitly resolved in our study, there was evidence of bacterial fatty acids in all our studied species (Fig. S3). Contributions of these biomarkers were low (≤

3%), but we found that the compound specific stable isotope approach revealed seasonal fluctuations in $\delta^{13}C_{FA}$ values. Seasonal fluctuations suggest differential sources, unknown metabolic effects within species, or both. Despite the low abundance of bacterial markers, we were able to determine corresponding $\delta^{13}C_{FA}$ values demonstrating the utility of combining these approaches to track bacterial inputs to the food web that normally have relatively low contributions.

CONCLUSIONS

We found evidence of polar night feeding activity in all species, regardless of dietary differences of overwintering strategies. This finding is contrary to our first hypothesis, but in the sense that overwintering strategies have perhaps not been correctly understood. What we found was that trophic plasticity may occur on an individual level within zooplankton and sympagic amphipod populations, regardless of season. Furthermore, a possibly broader definition (or gradient) of a flexible overwintering strategy – regardless of dietary preferences – should be recognized. Based on our findings, we suggest a more flexible overwintering strategy for the primarily herbivorous *C. glacialis* and *A. glacialis* than previously assumed, and that *G. wilkitzkii* has a business-as-usual strategy during polar night. We confirm that habitat and season were influential factors in the fatty acid composition for *C. glacialis*, *T. libellula*, and *A. glacialis*. These findings suggest that dietary fatty acids reflect the variability of primary producer communities in different habitats. We found little seasonal variation in the trophic biomarker $\delta^{13}C_{FA}$ values in zooplankton (hypothesis two). Confirming our third hypothesis, we found that $\delta^{13}C_{FA}$ values in sympagic amphipods did vary by season, especially for *A. glacialis*. Sympagic amphipods have strong seasonal affinities to sea ice habitat, and the higher $\delta^{13}C_{FA}$ values are most likely a reflection of iPOM being seasonally more variable than pPOM (Kunisch et al. 2021). However, we cannot discount the fact that other endogenous factors are also driving changes in the $\delta^{13}C_{FA}$ values in both zooplankton and sympagic amphipods.

Our study provides clear evidence for polar night feeding for all taxa involved, including shifts in nutrition from primary producers to other food sources. We suggest that *Calanus* spp. also functions as a carbon source (via the presence of *Calanus* spp. trophic biomarkers) supporting all other species in our study, regardless of habitat. We provide further evidence that the notion of polar night as a dormant phase should be phased out. However, overwintering survival for many zooplankton and sympagic amphipods depends on the ability to build up adequate energy stores during parts of the year, and the persistence of sufficient resources in both pelagic and sympagic habitats in the changing Arctic ecosystem.

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FIGURES

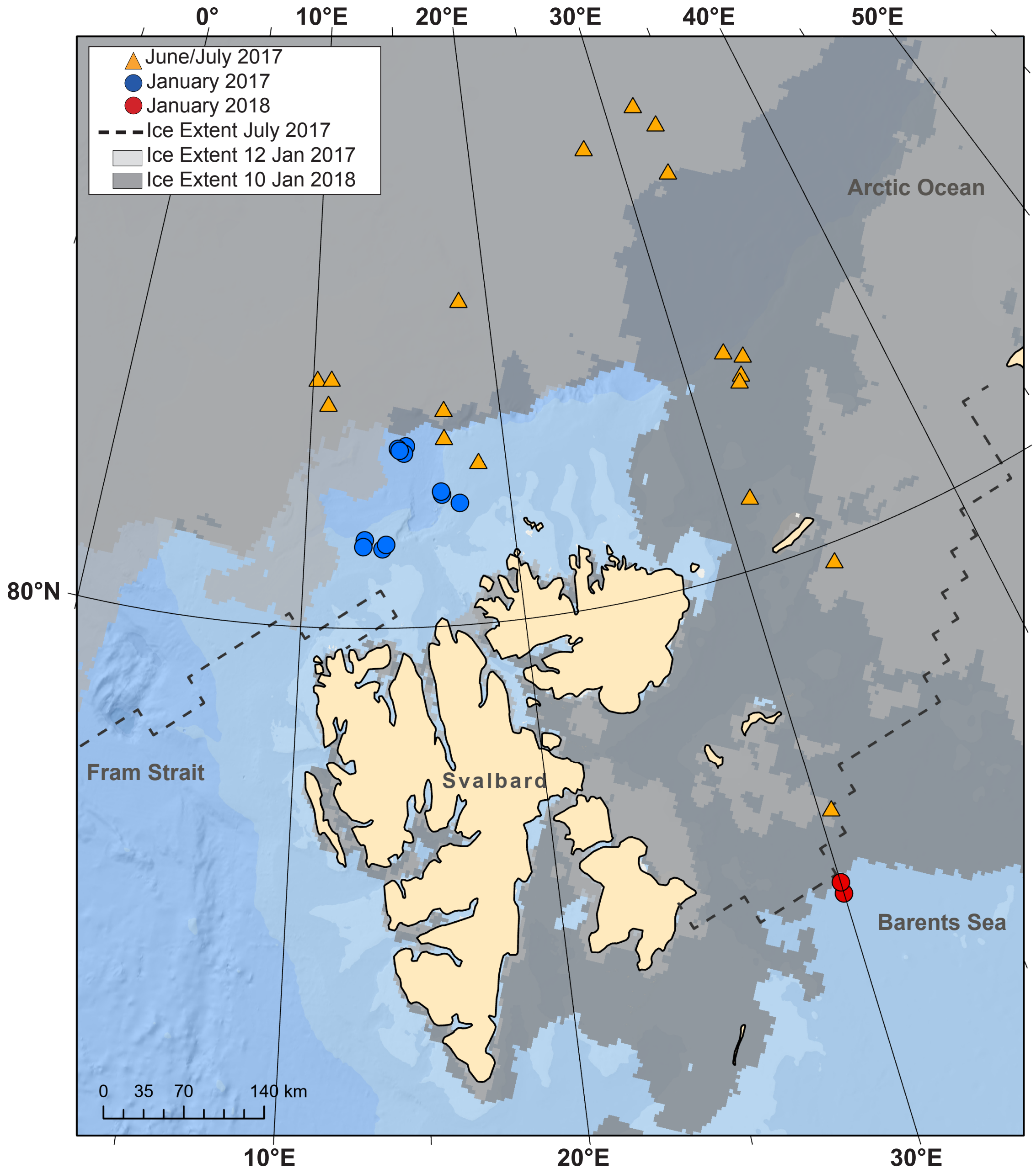


Figure 1. Station locations (triangles-June/July, circles-January) denote zooplankton collection sites. Sea ice extent data for 12 January 2017 and 10 January 2018 acquired from the University of Bremen (Spreen et al. 2008). Sea ice extent for the month of July 2017 denoted by the black dashed line (data from the National Snow and Ice Data Center, Fetterer et al. 2017). Map created with ArcGIS Pro 2.8.2.

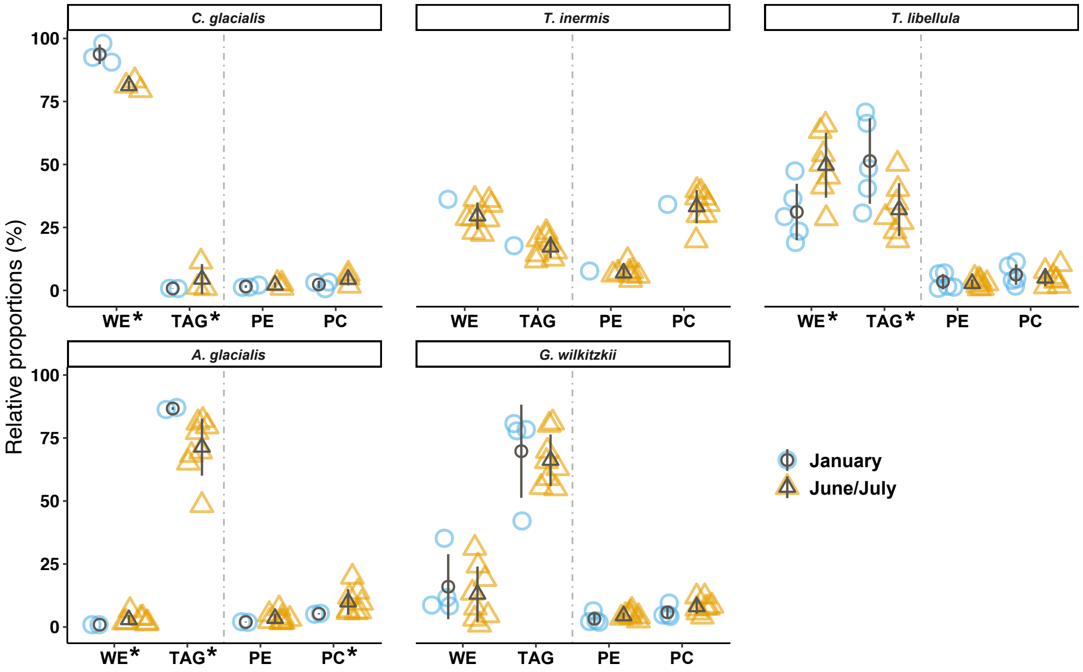


Figure 2. Seasonal lipid class differences organized by species. Displayed are wax esters (WE), triacyclglycerols (TAG), Phosphatidylethanolamine (PE), and Phosphatidylcholine (PC). Lipid class data are presented as relative proportions (mass %) of total lipids. Shapes and colors represent samples (note many individuals/sample, see Table 2): circles represent January and triangles, June/July. Note: all lipid classes in Janaury *T. inermis* lack corresponding means and standard deviations (grey shapes/lines) because there was only one sample (of many pooled individuals, Table 2).

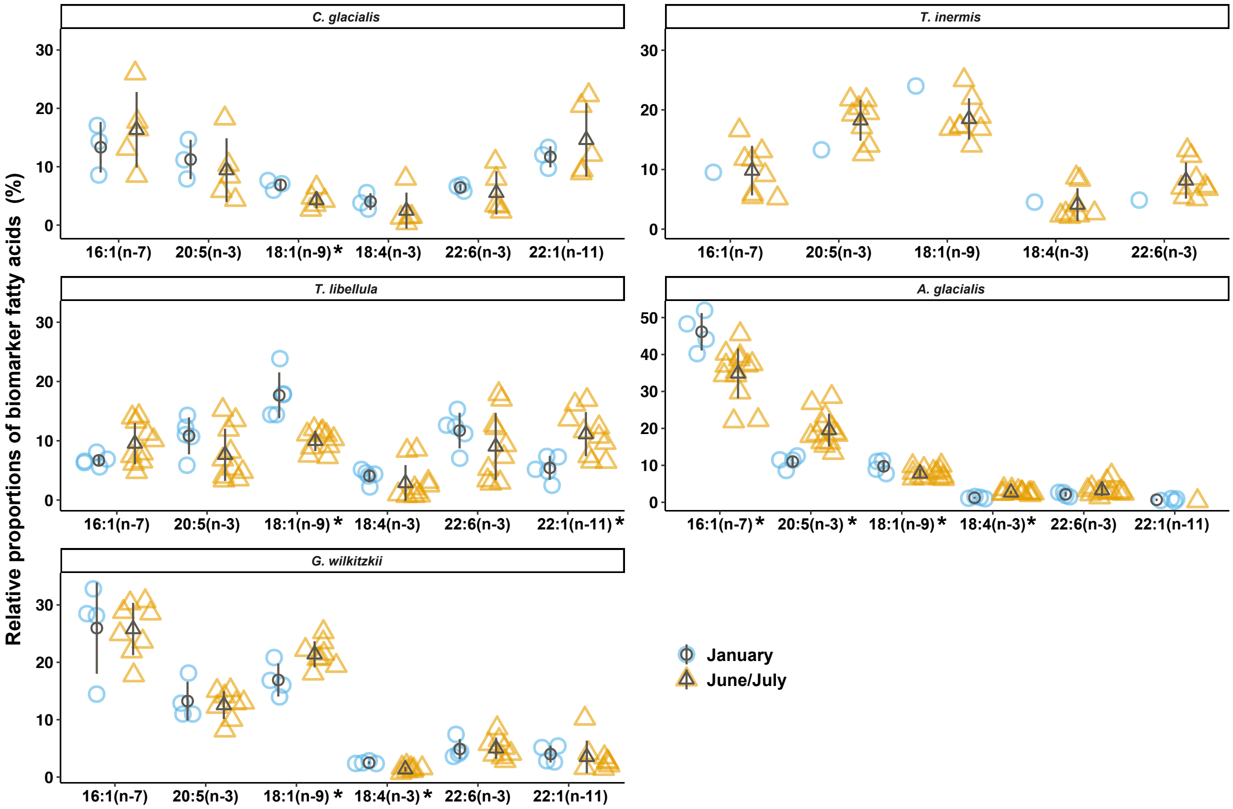


Figure 3. Relative composition of biomarker fatty acids (mass % of total fatty acids), organized by species. Shapes and colors represent samples (note many individuals pooled/sample, see Table 2): open blue circles, January and open orange triangles, June/July. Grey shapes represent means, vertical grey lines represent corresponding standard deviations of the mean. Note: all fatty acids in January *T. inermis* and 22:1(n-11) in June/July *A. glacialis* lack corresponding means and stadard deviations (grey shapes/lines) because there was only one sample (of many pooled individuals, Table 2).

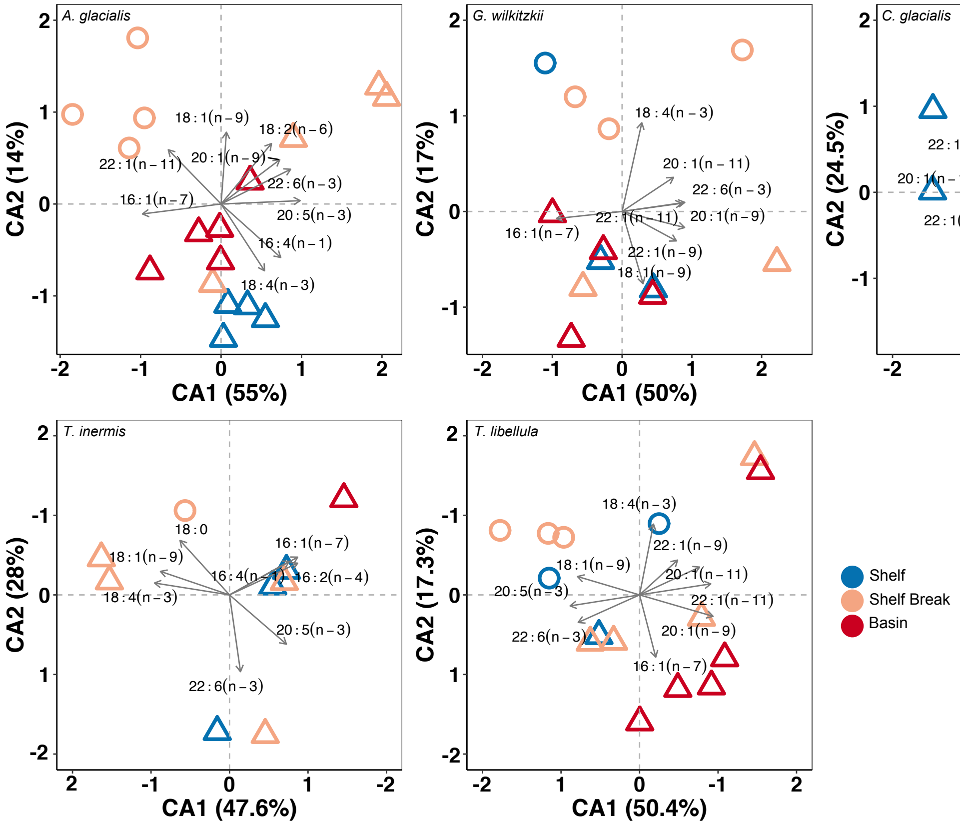


Figure 4. Correspondence analysis (CA) biplots on all fatty acids, displayed for each species, from all stations. Arrows depict directionality of significant and trophic biomarker fatty acids (see Table 2 for descriptions) in the ordination plane. Shapes indicate time of year: circles-January, open triangles-June/July, colors indicate location.

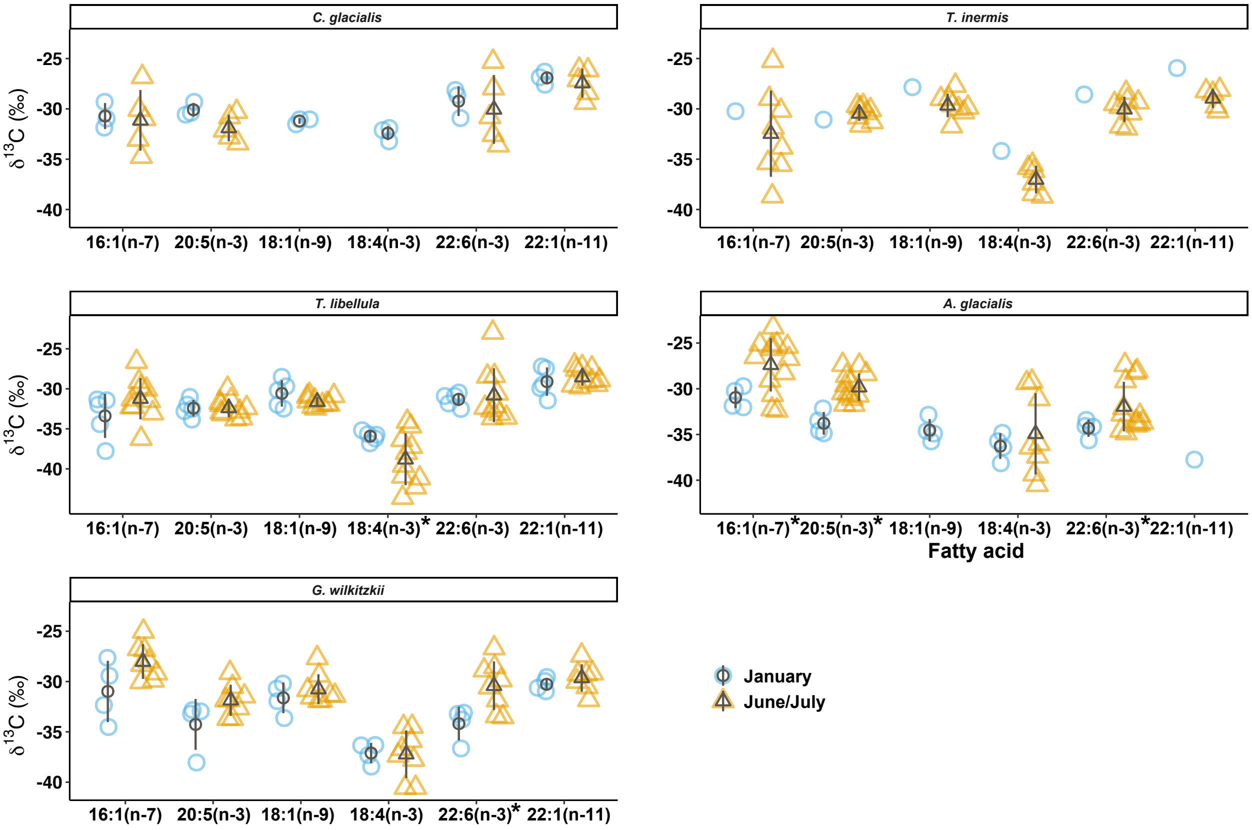


Figure 5. $\delta^{13}C_{FA}$ values of biomarker fatty acids, organized by species. Shapes and colors represent samples (note many individuals pooled/sample, see Table 2): open blue circles, January and open orange triangles, June/July. Grey shapes represent means, vertical grey lines represent corresponding standard deviations of the mean. Note: all fatty acids in January *T. inermis* and 22:1(n-11) in January *A. glacialis* lack corresponding means and stadard deviations (grey shapes/lines) because there was only one sample (of many pooled individuals, Table 2).

SUPPLEMENTARY FIGURES

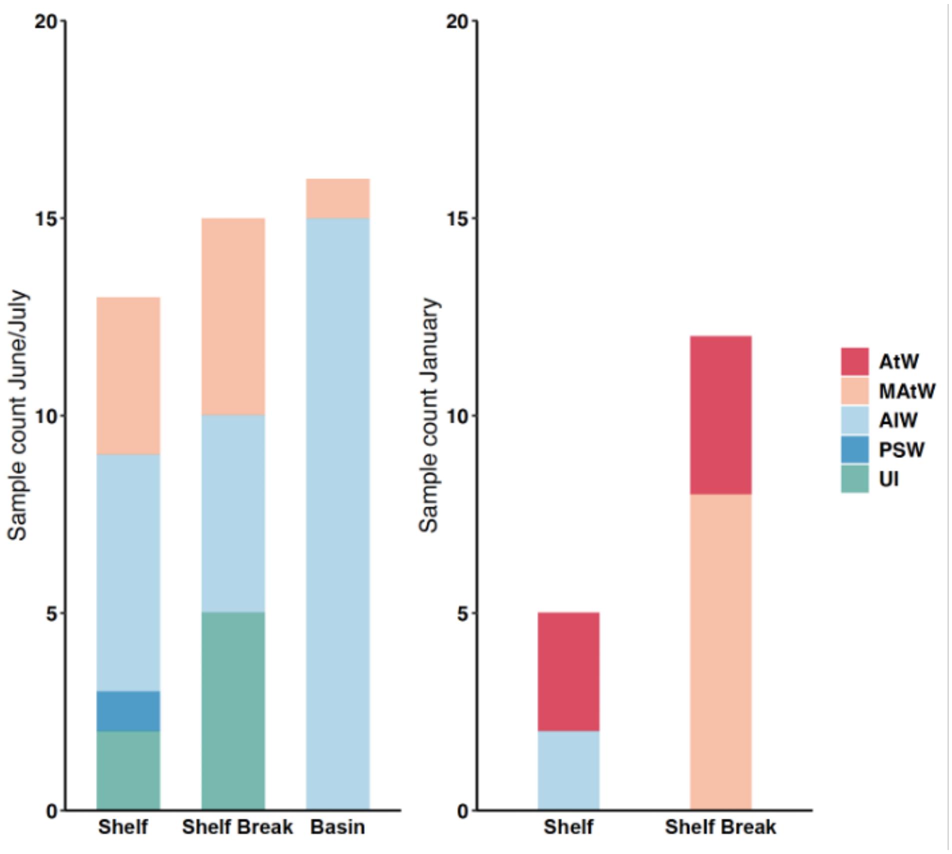


Figure S1. Water mass at locations of sampled zooplankton and sympagic (sea ice-associated) amphipods in June/July and January. AtW: Atlantic Water, MAtW: Modified Atlantic Water, AIW: Arctic Intermediate Water, PSW: Polar Surface Water, UI: Under Ice.

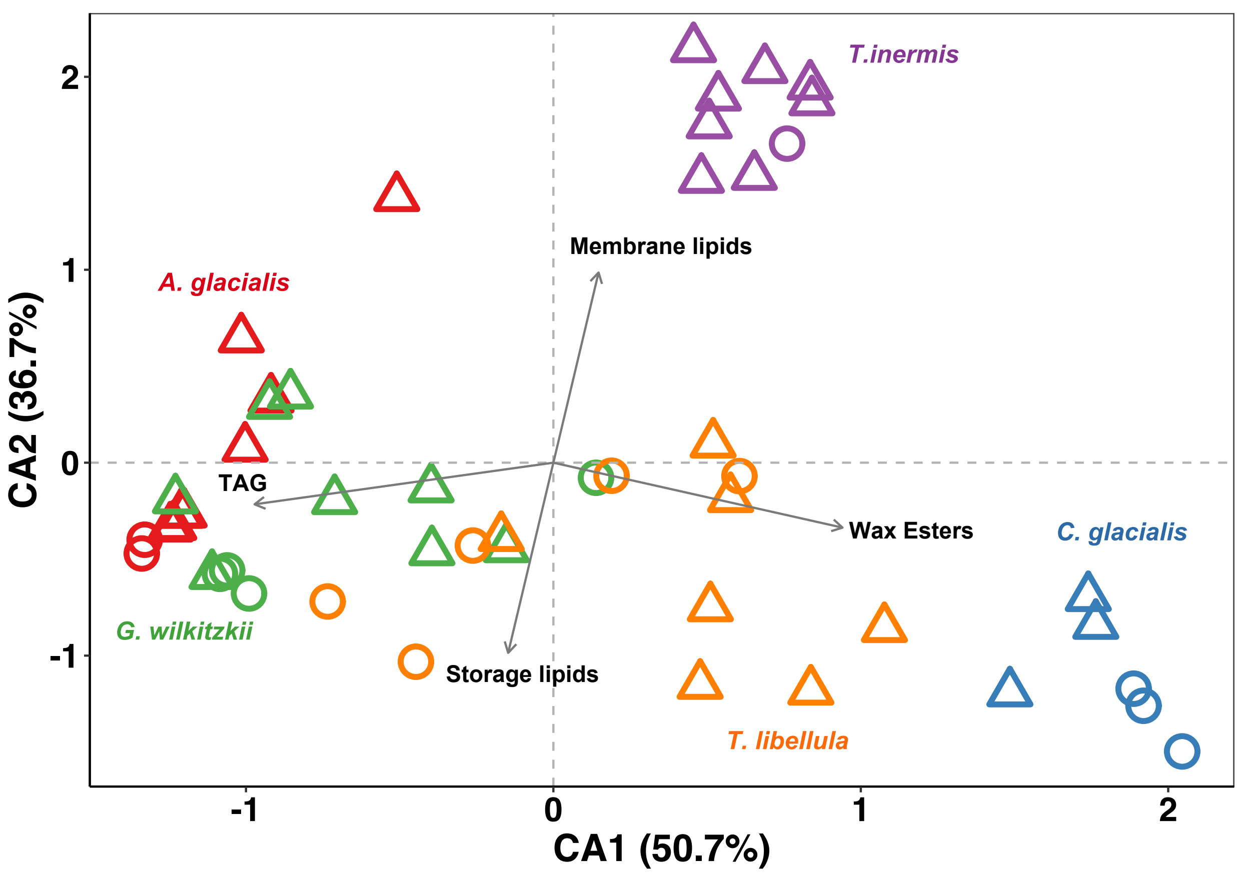


Figure S2. Correspondence analysis on lipid class proportions (%) between species. Biplot arrows depict directionality of significant lipid classes, TAG (triacyclglycerols), membrane (polar) lipids, and storage (neutral) lipids, and wax esters. Shapes indicate time of year: circles- January, triangles-June/July. Colors indicate species.

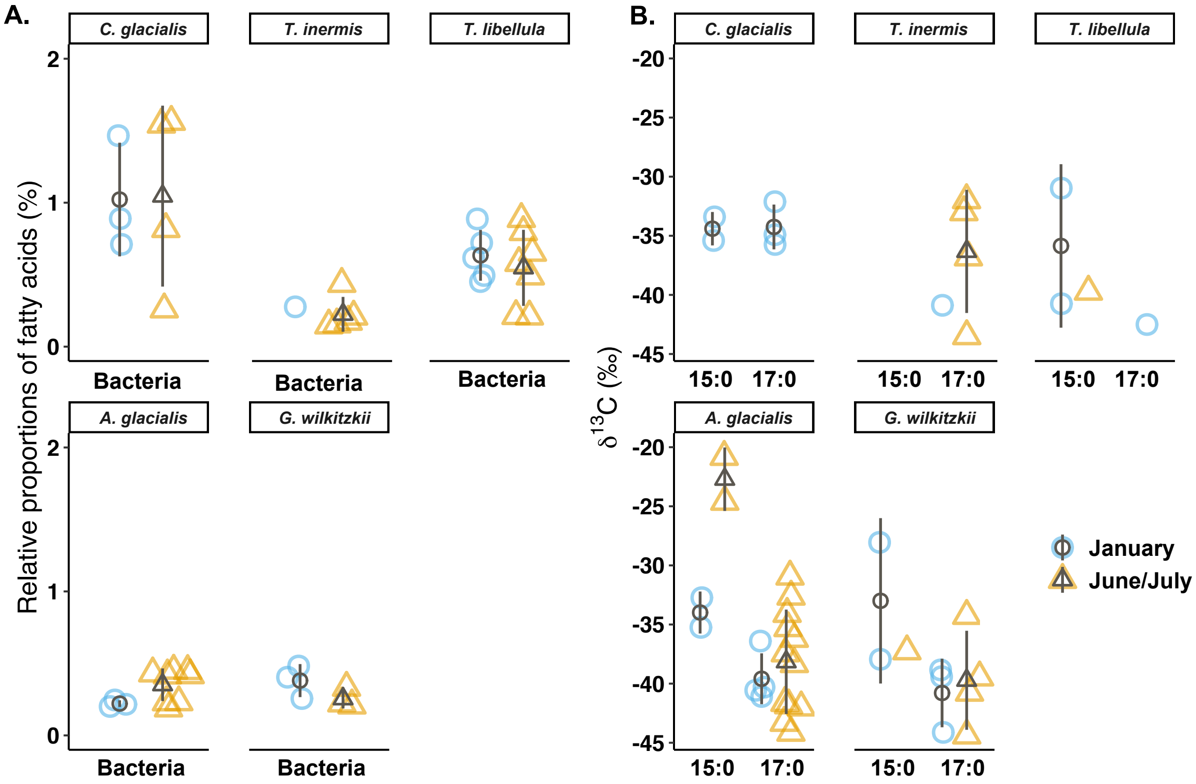


Figure S3. Fatty acid proportions for A) bacterial fatty acids [sum of odd chained, branched fatty acids] and B) $\delta^{13}C_{FA}$ values of 15:0 and 17:0 [bacterial biomarker fatty acids], organized by species. Shapes and colors represent samples (note many individuals pooled/sample, see Table 2): circles, January and triangles, June/July. Grey shapes represent means, vertical grey lines represent corresponding standard deviations of the mean. Note: January fatty acids in *T. inermis* and $\delta^{13}C_{FA}$ 17:0 in *T. inermis* and *T. libellula* lack corresponidng means and standard deviations (grey shapes/lines) because there was only sample (of many pooled individuals, Table 2).

TABLES

Table 1. Sample information for species sampled during January 2017, June/July 2017, and January 2018. Samples were analyzed for lipids, fatty acids, and carbon isotope values of fatty acids (see Table 2 for sample sums).

Date	Station	Latitude (°N)	Longitude (°E)	NET	Sampled depth (m)	Species	N
11 January 2017	NS1	80.60	13.68	WP2	100-0	*C. glacialis*	35
		80.64	13.85	Pelagic Trawl	155-0	*T. libellula*	1
	NS4	80.67	12.84	MIK	317-0	*A. glacialis*	1
		80.62	12.77	Pelagic Trawl	245-0	*T. libellula*	1
12 January 2017	NS6	81.38	14.95	Multi Net	800- 400	*A. glacialis*	1
13 January 2017		81.35	14.67	Pelagic Trawl	199-0	*G. wilkitzkii*	2
						T. inermis	11
						T. libellula	4
		81.33	14.84	MIK	160-0	*A. glacialis*	6
						G. wilkitzkii	1
						T. libellula	2
		81.37	14.53	WP2	100-0	*C. glacialis*	25
	NS9	81.00	16.65	MIK	400-0	*A. glacialis*	5
		81.03	16.62	Multi Net	400-0	*G. wilkitzkii*	1
14 January 2017	NS10	80.93	17.50	MIK	250-0	*G. wilkitzkii*	4
10 June 2017	27	81.91	10.22	ROV	under ice	*A. glacialis*	30
						C. glacialis	37
11 June 2017	28	81.91	10.99	ROV	under ice	*A. glacialis*	20
15 June 2017	32	81.72	10.86	ROV	under ice	*A. glacialis*	3
					5	*T. libellula*	1
25 June 2017	45	78.11	30.48	ROV	under ice	*A. glacialis*	15
					10	*C. glacialis*	60
				by hand	surface	*A. glacialis*	1
27 June 2017	49	79.88	33.89	BONGO	238-0	*C. glacialis*	30
						G. wilkitzkii	1
						T. inermis	12
						T. libellula	13
29 June 2017	50	80.55	31.24	SUIT	under ice	*A. glacialis*	6
						G. wilkitzkii	1
						T. inermis	2
1 July 2017	63	81.46	32.81	SUIT	under ice	*A. glacialis*	20
	64	81.41	32.62	RMT	100-0	*C. glacialis*	30
						T. inermis	3
2 July 2017	65	81.59	33.24	SUIT	under ice	*T. inermis*	3
	66	81.66	32.32	SUIT	under ice	*A. glacialis*	5
						G. wilkitzkii	1
						T. inermis	21
						T. libellula	2
5 July 2017	70	83.11	32.80	SUIT	under ice	*G. wilkitzkii*	1
						T. libellula	2
6 July 2017	72	83.49	33.12	SUIT	under ice	*A. glacialis*	11
						G. wilkitzkii	2
7 July 2017	73	83.68	32.05	SUIT	under ice	*A. glacialis*	19
						T. libellula	5
8 July 2017	74	83.48	27.91	SUIT	under ice	*A. glacialis*	15
						C. glacialis	30
						G. wilkitzkii	4
		83.46	28.12	RMT	100-0	*T. libellula*	4
10 July 2017	76	82.49	18.36	SUIT	under ice	*A. glacialis*	20
						G. wilkitzkii	2
						T. libellula	1
		82.49	18.27	RMT	100-0	*T. libellula*	1
11 July 2017	79	81.66	17.03	SUIT	under ice	*A. glacialis*	5
						T. inermis	11
						T. libellula	1
12 July 2017	80	81.45	16.95	SUIT	under ice	*G. wilkitzkii*	2
						T. inermis	4
13 July 2017	83	81.25	18.61	RMT	100-0	*T. inermis*	6
						T. libellula	1
9 January 2018	B34	77.55	30.01	Pelagic Trawl	108-0	*T. libellula*	5
10 January 2018	B34	77.47	29.99	Multinet	200-100	*C. glacialis*	10

SUPPLEMENTARY TABLES

Table S1. Lipid class composition (% total lipids) of the studied species (± standard deviation). nd = not determined, N = sample size. Displayed are wax esters (WE), triacyclglycerols (TAG), Phosphatidylethanolamine (PE), Phosphatidylcholine (PC). Lipid class data are presented as relative proportions (mass %) of total lipids. For January *C. glacialis* total lipids/dry mass (%), sample size (n = 60), indicated by **.

Species	N	Season	Dry Mass (mg)	Lipid Mass (mg)	Total Lipid (mg ind.-1)	Total lipids/dry mass (%)	WE (%)	TAGs (%)	PE (%)	PC (%)	Neutral lipid (%)	Polar lipid (%)
C. glacialis	127	June/July	nd	nd	0.2 ± 0.03	nd	81.3 ± 1.9	4.5 ± 6	2.1 ± 1.1	4.5 ± 2.4	92.4 ± 3.7	7.6 ± 3.7
	70	January	54.6 ± 82.3	5.3 ± 3	0.3 ± 0.4	22.7 ± 14.7 **	93.7 ± 3.9	0.8 ± 0.1	1.6 ± 0.5	2.4 ± 1.5	95.7 ± 2.1	4.3 ± 2.1
T. inermis	62	June/July	nd	nd	3.7 ± 2.8	nd	29.6 ± 5.3	17.2 ± 4.3	7 ± 2.3	33.2 ± 7	57.6 ± 4	42.4 ± 4
	11	January	481.20	339.2	3.2	7.3	36.2	17.8	7.7	34.2	57.9	42.1
T. libellula	26	June/July	nd	nd	12.5 ± 15.6	nd	49.7 ± 12.9	32.1 ± 11	2.7 ± 1.6	4.9 ± 3.2	90.6 ± 6	9.5 ± 6
	10	January	97.3 ± 52.4	43.7 ± 27.1	23.3 ± 26.8	25.4 ± 25.1	31.14 ± 11.2	51.4 ± 17	3.5 ± 3.1	6.3 ± 4.1	89.6 ± 7.2	10.4 ± 7.2
A. glacialis	150	June/July	nd	nd	0.9 ± 0.6	nd	2.9 ± 1.9	71.4 ± 11.3	3.4 ± 1.9	9.9 ± 5.1	82.5 ± 9.8	17.5 ± 9.8
	11	January	7.9 ± 0.7	3.8 ± 1	0.76 ± 0.7	48.1 ± 36	0.9 ± 0.007	86.7 ± 0.6	2 ± 0.2	5.2 ± 0.3	91.4 ± 1	8.6 ± 1
G. wilkitzkii	14	June/July	47.6 ± 36.2	25.7 ± 39.7	4.2 ± 6.3	10.4 ± 4.6	13 ± 11	66.2 ± 10.2	4.5 ± 1.3	8.1 ± 2.8	86.7 ± 4.4	13.3 ± 4.2
	8	January	114.4 ± 107.5	22.7 ± 19.4	7.6 ± 5.5	20 ± 14.8	16 ± 13	69.8 ± 18.5	3.2 ± 2.1	5.8 ± 2.5	90.3 ± 5.3	9.7 ± 5.3

Table S2. Fatty acid composition of study species, displayed by month sampled (June/July, January). nd = not determined, SFA = saturated fatty acids, MUFA = monounsaturated fatty acids, PUFA = polyunsaturated fatty acids, sd = standard deviation. Sample sizes listed in Table 2.

	C. glacialis		*T. inermis*		*T. libellula*		*A. glacialis*		*G. wilkitzkii*	
	June/July	January	June/July	January	June/July	January	June/July	January	June/July	January
Fatty Acid	MEAN ± SD		MEAN ± SD		MEAN ± SD		MEAN ± SD		MEAN ± SD	
14:0	3.8 ± 1.9	4.7 ± 1.7	2 + 0.5	2.4	3.4 ± 1.7	2.3 ± 0.6	3.8 ± 0.8	3.9 ± 0.2	2.4 ± 1	3 ± 1.9
phytol	0.3 ± 0.1	0.3 ± 0.1	nd	nd	0.2 ± 0.003	0.2	nd	nd	nd	nd
ai-15:0	nd	0.4 ± 0.1	0.2	nd	0.2	0.3 ± 0.1	nd	nd	0.1	0.1
i-15:0	0.6 ± 0.4	0.2 ± 0.1	0.2	0.3	0.3 ± 0.1	0.4 ± 0.1	nd	nd	nd	0.1 ± 0.01
15:0	0.4 ± 0.1	0.5 ± 0.2	0.2 + 0.03	nd	0.3 ± 0.1	0.3 ± 0.1	0.2 ± 0.02	0.2 ± 0.02	0.2 ± 0.01	0.3 ± 0.1
16:0	6.8 ± 1.2	8.5 ± 0.8	19.7 + 1.2	20.4	9.7 ± 3.9	12.1 ± 2.4	14.3 ± 1.6	14.4 ± 1.1	11.3 ± 0.9	11.7 ± 2.1
16:1(n-7)	16.3 ± 6.5	13.3 ± 4.3	9.8 + 4.2	9.5	9.3 ± 3.4	6.7 ± 0.9	34.9 ± 6.8	46.2 ± 5.1	25.8 ± 4.6	26 ± 8
16:1(n-5)	0.5 ± 0.3	0.8 ± 0.3	0.2 + 0.1		0.3 ± 0.1	0.3 ± 0.1	0.2 + 0.02	0.4 ± 0.2	0.2 ± 0.01	0.2 ± 0.03
16:2(n-4)	0.7 ± 0.1	0.7 ± 0.1	0.7 + 0.2	0.6	0.3 + 0.1	0.3 ± 0.1	1.2 ± 0.3	0.8 ± 0.2	0.6 ± 0.1	0.5 ± 0.1
16:3(n-4)	0.9 ± 0.6	0.7 ± 0.6	0.4 + 0.1	0.2	0.4 ± 0.02	0.3 ± 0.1	0.8 ± 0.2	0.5 ± 0.1	0.4 ± 0.1	0.4 ± 0.2
16:4(n-1)	1.2 ± 1.5	0.6 ± 0.3	0.5 + 0.2	0.3	0.7 ± 0.6	0.3 ± 0.1	2.7 ± 0.7	0.8 ± 0.2	0.8 ± 0.3	0.5 ± 0.2
17:0	0.9 ± 0.5	nd	nd	nd	nd	nd	0.2 ± 0.02	nd	nd	nd
17:1(n-8)	0.5 ± 0.1	nd	nd	nd	nd	nd	nd	nd	nd	nd
18:0	0.5 ± 0.1	0.9 ± 0.3	1.5 + 0.3	1.7	0.7 ± 0.5	1.2 ± 0.4	0.9 ± 0.2	1.4 ± 0.7	0.8 ± 0.1	0.8 ± 0.2
18:1(n-9)	4.3 ± 1.4	6.9 ± 0.9	18.5 + 3.5	24.0	10.1 ± 1.6	17.7 ± 3.9	7.8 ± 1.3	9.8 ± 1.7	21.4 ± 2.3	16.9 ± 2.9
18:1(n-7)	1.5 ± 0.2	1.1 ± 0.2	9.2 + 0.5	9.2	2.5 ± 0.9	4.5 ± 1	2.5 ± 0.3	2.2 + 0.4	4.8 + 0.4	4.9 ± 0.5
18:1(n-5)	1.1 ± 0.4	0.8 ± 0.04	0.2 + 0.04	nd	1.1 ± 0.2	0.9 ± 0.3	nd	nd	0.7 ± 0.1	0.6 ± 0.2
18:2(n-6)	1.9 ± 1.2	2.1 ± 0.7	1.6 + 0.3	2.0	1.7 ± 0.4	2.4 ± 0.5	1.2 ± 0.3	1.1 ± 0.1	1.5 ± 0.2	1.7 ± 0.4
18:3(n-3)	0.5 ± 0.1	1.1 ± 0.5	1.1 + 0.4	0.8	0.8 ± 0.3	1 ± 0.3	0.6 ± 0.2	0.5 ± 0.1	0.5 ± 0.1	0.8 ± 0.3
18:3(n-6)	nd	0.4 ± 0.3	0.3 + 0.2	nd	nd	0.3 ± 0.1	0.7 ± 0.3	0.7 ± 0.1	nd	0.5 ± 0.1
18:4(n-3)	2.5 ± 3.1	4 ± 1.4	4.1 + 2.8	4.5	2.7 ± 2.9	4.1 ± 1.1	2.6 ± 0.5	1.2 ± 0.3	1.3 ± 0.4	2.5 ± 0.2
20:0	0.3 ± 0.01	nd	nd	nd	nd	nd	nd	nd	nd	nd
20:1(n-11)	0.9n ± 0.6	0.8 ± 0.1	0.3 + 0.1	nd	4.4 ± 2.3	3.4 ± 1.9	nd	nd	0.5 ± 0.3	0.7 ± 0.2
20:1(n-9)	21.6 ± 3.7	18.3 ± 5.2	1.6 + 0.4	2.8	19.8 ± 6.7	10 ± 6.5	0.9 ± 0.3	0.8 ± 0.2	4.2 ± 1.7	3.8 ± 1.3
20:1(n-7)	1 ± 0.4	0.3 ± 0.1	0.3 + 0.03	0.4	1 ± 0.2	0.8 ± 0.4	0.7 ± 0.2	0.6 ± 0.2	0.7 ± 0.2	0.5 ± 0.1
20:2(n-9)	0.8	nd	nd	nd	nd	nd	nd	nd	nd	nd
20:3(n-3)	nd	nd	nd	nd	nd	nd	0.7	nd	nd	nd
20:4(n-3)	0.7 ± 0.2	1 ± 0.2	0.5 + 0.1	0.4	0.5 ± 0.2	0.7 ± 0.2	0.7 ± 0.2	0.4 ± 0.1	0.4 ± 0.1	0.7 ± 0.3
20:4(n-6)	nd	0.4 ± 0.2	0.5 + 0.1	0.4	0.4 ± 0.1	0.7 ± 0.4	0.5 ± 0.2	0.4 ± 0.1	0.6 ± 0.2	0.5 ± 0.1
20:5(n-3)	9.4 ± 5.5	11.2 ± 3.4	18.3 + 3.4	13.3	9.1 ± 6.5	10.8 ± 3.1	19.5 ± 4.4	11 ± 1.7	12.5 ± 2.4	13.2 ± 3.4
22:1(n-11)	14.6 ± 6.3	11.7 ± 1.8	nd	nd	10.3 ± 4.4	5.4 ± 2	0.2	0.7 ± 0.3	3.5 ± 2.8	4 ± 1.5
22:1(n-9)	3.6 ± 1.4	1.7 ± 0.2	1.3 + 0.3	1.8	2.4 ± 0.9	1.3 ± 0.1	0.5 ± 0.1	nd	1 ± 0.3	0.8 ± 0.3
22:1(n-7)	0.5 ± 0.1	0.3 ± 0.1	nd	nd	0.6 ± 0.3	0.3 ± 0.1	nd	nd	nd	nd
22:5(n-3)	0.7	0.4 ± 0.05	0.8 + 0.3	nd	0.6 ± 0.2	0.5 ± 0.01	0.5 ± 0.2	nd	nd	0.4 ± 0.2
22:6(n-3)	5.5 ± 3.7	6.4 ± 0.6	8.2 + 3	4.9	9.6 ± 5.7	11.7 ± 3	3.3 ± 1.6	2.2 ± 0.6	5 ± 1.9	4.9 ± 1.7
∑ SFA	12.1 ± 3	15.1 ± 2.5	23.3 + 1.8	24.9	14.1 ± 3.9	16.3 ± 2.6	19.2 ± 1.6	19.9 ± 1.6	14.5 ± 1.6	15.8 ± 4.1
∑ MUFA	64.8 ± 6.5	56 ± 3.4	41 + 3.2	47.7	60.6 ± 12.2	50.9 ± 6.4	47 ± 5.5	60.6 ± 2.6	62.6 ± 4.1	58.1 ± 2.2
∑ PUFA	22.9 ± 6.7	28.5 ± 5	35.7 + 4.5	27.5	25.3 ± 10.6	32.7 ± 4.7	33.8 ± 6.7	19.6 ± 2.7	23.3 ± 3.8	26.2 ± 5.9
∑15:0,17:0, ai-15	1 ± 0.4	1 ± 0.4	0.2 + 0.1	0.3	0.3 ± 0.3	0.6 ± 0.2	0.4 ± 0.1	0.2 ± .02	0.3 ± 0.1	0.4 ± 0.1

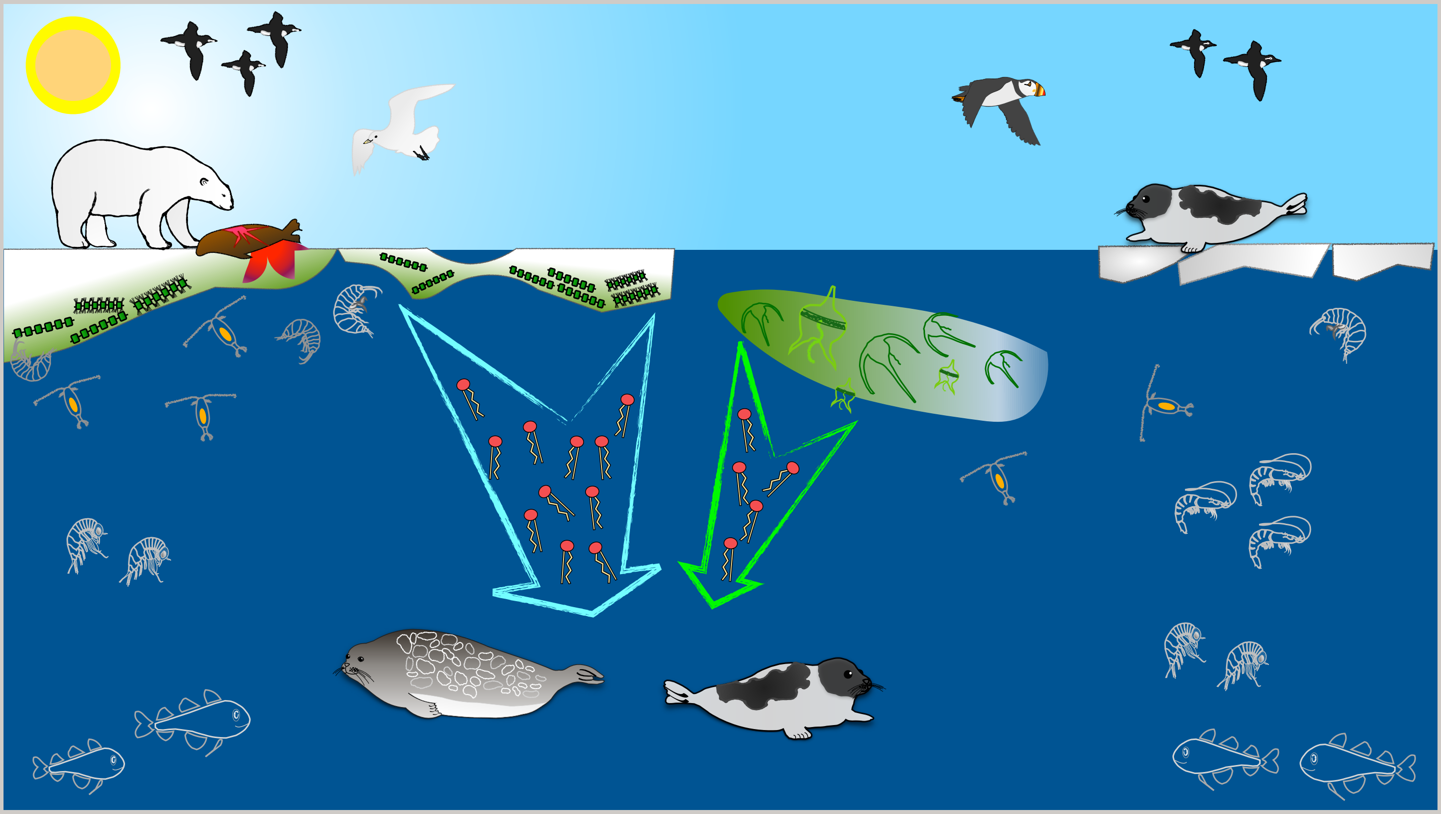
Table S3. Constrained correspondence analysis (CCA) statistical results for studied species.

Species	Variable	df	Chi-square	F	Pr(>F)	significance
A. glacialis	season	1	0.04	17.95	0.001	***
	location	2	0.01	2.88	0.034	*
	Residual	13	0.03			
G. wilkitzkii	season	1	0.01	2.11	0.11	
	location	2	0.02	1.27	0.27	
	Residual	8	0.05			
C. glacialis	season	1	0.05	8.53	0.005	**
	water mass	4	0.14	5.34	0.034	*
	Residual	2	0.01			
T. inermis	season	1	0.00	0.51	0.71	
	location	2	0.03	1.55	0.20	
	Residual	5	0.05			
T. libellula	season	1	0.04	4.45	0.012	*
	water mass	3	0.05	1.90	0.09	.
	location	2	0.04	2.23	0.07	.
	Residual	8	0.07			

Table S3. $\delta^{13}C_{FA}$ values of fatty acids in study species, displayed by month sampled (June/July, January). nd = not determined, sd = standard deviation. Sample sizes listed in Table 2.

	C. glacialis		*T. inermis*		*T. libellula*		*A. glacialis*		*G. wilkitzkii*	
$\delta^{13}C_{FA}$ values (‰)	June/July	January	June/July	January	June/July	January	June/July	January	June/July	January
Fatty Acid	MEAN ± SD		MEAN ± SD		MEAN ± SD		MEAN ± SD		MEAN ± SD	
14:0	-23.4 ± 1.7	-26.4 ± 1.2	-22.7 ± 1.4	-25.4	-25 ± 0.8	-25 ± 1.2	-23.5 ±1.8	-25.9 ± 1	-25.3 ± 0.9	-24.8 ± 2.2
15:0	nd	-34.4 ± 1.4	nd	nd	-39.7	-35.9 ± 7	-22.7 ± 2.7	-34 ± 1.8	-37.3	-33 ± 7
16:0	-32.3 ± 1.8	-30.7 ± 0.7	-29.9 ± 1.2	-28.7	-32.3 ± 1.1	-31.3 ± 1.4	-26.9 ± 2.7	-30.2 ± 1.1	-29.3 ± 1.9	-30.9 ± 1.5
16:1(n-7)	-31.1 ± 3	-30.7 ± 1.3	-32.5 ± 4.3	-30.2	-31.2 ± 2.6	-33.4 ± 2.8	-27.4 ± 2.9	-31 ± 1.2	-28 ± 1.7	-31 ± 3.1
16:1(n-5)	-31	nd	nd	nd	nd	nd	nd	nd	nd	nd
16:2(n-4)	-37	-31.2 ± 3.2	-30.5 ± 1.5	-29.5	nd	-31.9 ± 3.1	-37.9 ± 3.9	-38 ± 0.6	nd	-31 ± 16.7
16:3(n-4)	-34.9 ± 5	-35.7 ± 3.4	-29.5 ± 1.6	-30.4	-37.5	nd	-35.5 ± 2.6	-37.8 ± 2.7	-36.6 ± 0.3	-38 ± 6.4
17:0	nd	-34.3 ± 1.9	-36.3 ± 5.2	-40.9	nd	-42.5	-38.2 ± 4.4	-39.6 ± 2.2	-39.7 ± 4.2	-40.8 ± 2.9
18:0	nd	-34.3 ± 1.8	-30 ± 2.2	-30	-35.6 ± 3.4	-34.8 ± 3.8	-34.7 ± 2.9	-31.8 ± 0.9	-34.3 ± 2.4	-36.4 ± 3.3
18:1(n-9)	nd	-31.2 ± 0.3	-29.7 ± 1.2	-27.9	-31.6 ± 0.6	-30.6 ± 1.7	nd	-34.5 ± 1.2	-30.8 ± 1.5	-31.6 ± 1.5
18:1(n-7)	-35.9 ± 2	-27.1 ± 2.1	-28.9 ± 1.2	-27.3	-29.7 ± 2.2	-29.8 ± 1.3	-32.9 ± 2.4	-31.2 ± 1	-26.2 ± 1.4	-29.1 ± 2.3
18:1(n-5)	nd	nd	nd	nd	-39.8	nd	nd	nd	nd	nd
18:2(n-6)	-40.2 ± 0.2	-33.8 ± 0.7	-39.9 ± 2.2	-37.5	-39.2 ± 2.3	-38.9 ± 2.3	-39.1 ± 2.7	-39.6 ± 2.2	-40.1 ± 2.6	-39.3 ± 2.4
18:3(n-3)	nd	-34.6 ± 0.2	nd	-38.6	-35.5	-37.7 ± 2	nd	-36.2 ± 2.3	nd	-38.5 ± 3
18:3(n-6)	nd	nd	nd	nd	nd	nd	-33.2 ± 2.8	-37.9 ± 0.4	nd	-36.4 ± 8.2
18:4(n-3)		-32.4 ± 0.7	-37 ± 1.4	-34.2	-38.8 ± 3.2	-35.9 ± 0.6	-34.9 ± 4.5	-36.3 ± 1.4	-37.2 ± 2.4	-37.1 ± 1
20:0	-37.3 ± 0.01	nd	-37.3 ± 1.3	nd	nd	nd	-37.2 ± 2.3	nd	nd	nd
20:1(n-11)	nd	nd	nd	nd	-27.2 ± 0.6	-30.1 ± 2.1	nd	nd	nd	nd
20:1(n-9)	nd	nd	nd	nd	-28.5 ± 0.3	-29.8 ± 1.3	nd	nd	-31.9	nd
20:1(n-7)	-30.5 ± 2.2	-28.7 ± 1.1	-31.9 ± 2.7	-28.6	-28.3 ± 2.3	-28 ± 2.9	-31.9 ± 1.9	-37.3 ± 0.2	-33.2 ± 4.3	-30.6 ± 0.3
20:2(n-6)	nd	nd	nd	nd	-34.2 ± 2.1	-36.2 ± 1.4	nd	nd	nd	nd
20:3(n-3)	nd	-27.7	nd	nd	nd	-32.9 ± 1	nd	-33.9 ± 2.1	nd	nd
20:4(n-3)	nd	-31.3 ± 0.9	-36	nd	-31.7	-34 ± 0.5	-33 ± 3.5	-33.9 ± 0.8	-34	-34.7 ± 0.8
20:4(n-6)	nd	nd	-36.4	nd	nd	-36.6	-34 ± 1.7	nd	-33.4 ± 1.4	-34.3
20:5(n-3)	-31.9 ± 1.3	-30.1 ± 0.7	-30.5 ± 0.7	-31.1	-32.4 ± 1.2	-32.4 ± 1	-29.8 ± 1.5	-33.8 ± 1.2	-31.9 ± 1.6	-34.3 ± 2.5
21:0	-35.3 ± 3	nd	-39.6	nd	nd	nd	nd	nd	nd	nd
22:0	-29.5	-27.3 ± 1.3	nd	nd	nd	-34.4	nd	nd	nd	nd
22:1(n-11)	-27.4 ± 1.4	-26.9 ± 0.7	-29 ± 1	-26	-28.5 ± 1.1	-29.1 ± 1.8	nd	-37.8	-29.7 ± 1.4	-30.3 ± 0.6
22:1(n-9)	-24.2 ± 4	-26.2 ± 1.5	nd	nd	-28.3 ± 1.4	-30.7 ± 4.7	nd	nd	nd	nd
22:1(n-7)	nd	-27.9 ± 6.7	nd	nd	nd	nd	nd	nd	nd	nd
22:2(n-6)	-27.6 ± 1.7	nd	nd	nd	-30.1 ± 0.9	nd	nd	nd	nd	nd
22:6(n-3)	-30.1 ± 3.4	-29.2 ± 1.5	-30 ± 1.3	-28.6	-30.8 ± 3.4	-31.3 ± 0.8	-32 ± 2.7	-34.3 ± 0.9	-30.4 ± 2.4	-34.2 ± 1.7

Paper III



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Ice-algal carbon supports harp and ringed seal diets in the European Arctic: evidence from fatty acid and stable isotope markers

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ABSTRACT: Sea-ice declines in the European Arctic have led to substantial changes in marine food webs. To better understand the biological implications of these changes, we quantified the contributions of ice-associated and pelagic carbon sources to the diets of Arctic harp and ringed seals using compound-specific stable isotope ratios of fatty acids in specific primary producer biomarkers derived from sea-ice algae and phytoplankton. Comparison of fatty acid patterns between these 2 seal species indicated clear dietary separation, while the compound-specific stable isotope ratios of the same fatty acids showed partial overlap. These findings suggest that harp and ringed seals target different prey sources, yet their prey rely on ice and pelagic primary production in similar ways. From Bayesian stable isotope mixing models, we estimated that relative contributions of sympagic and pelagic carbon in seal blubber was an average of 69% and 31% for harp seals, and 72% and 28% for ringed seals, respectively. The similarity in the Bayesian estimations also indicates overlapping carbon sourcing by these 2 species. Our findings demonstrate that the seasonal ice-associated carbon pathway contributes substantially to the diets of both harp and ringed seals.

KEY WORDS: Carbon source · Climate change · Food webs · Compound-specific stable isotopes · Foraging · Pinnipeds · Sea-ice algae · Phytoplankton

1. INTRODUCTION

Niche partitioning theory states that species coexisting in the same foraging space are expected to have different diets or resource use, effectively limiting competition (MacArthur 1958). In the European Arctic, harp (*Pagophilus groenlandicus*) and ringed (*Pusa hispida*) seals are found in similar habitats for at least part of the year, along the sea-ice edge and in coastal Svalbard waters during spring and summer (Hamilton et al. 2021). They often target similar ice-associated prey (Nilssen et al. 1995b, Labansen et al. 2007, Lindstrøm et al. 2013), but exhibit some niche separation via differences in foraging behavior (dive depth, size of prey selected; Wathne et al. 2000). Trophic niche partitioning can be characterized by dietary composition but also by which carbon end members (i.e. autotrophic primary producers) support their prey sources, and both aspects are studied here. In the Arctic specifically, some of the organic carbon of their prey can be traced back to sea-ice primary production (Kohlbach et al. 2017), an early-

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season energy source that fuels food webs within the Arctic (Ji et al. 2013). Arctic sea-ice declines have already resulted in breeding and foraging habitat reductions for harp and ringed seals (Hamilton et al. 2017, 2019, Stenson et al. 2020). These pinnipeds will likely encounter increased competition in the remaining sea-ice areas from boreal species shifting northward (Kovacs et al. 2011, Øigård et al. 2013) and from each other, given that they are increasingly overlapping in some areas of their Barents Sea distributions (Bengtsson et al. 2020). The overall reduction or loss of sea-ice primary production and its cumulative effects on food webs are currently unknown, though harp seals are showing declining body condition that is thought to be due to competition with other predators, including the large standing stock of Atlantic cod *Gadus morhua*, which has shifted northward in the Barents Sea region (Stenson et al. 2020).

Harp and ringed seals are 2 ice-associated seals, but the nature of their dependence on sea ice differs. Both species are monitored in the study region and are harvested for subsistence (harp seals, Greenland) or commercially (ringed seals, Svalbard). Harp seals are a North Atlantic drift-ice breeding species that migrates into the High Arctic for summer feeding (Stenson et al. 2020). They associate with sea ice most of the year but can spend time in open-water areas outside the moulting and breeding seasons; therefore, their diets are particularly variable by season and region (e.g. Nilssen et al. 1995a,b, Lawson & Hobson 2000, Stenson et al. 2020). Harp seals from the Greenland and White Seas perform seasonal migrations from southerly breeding areas, where they use drift or land-fast ice, northward to the sea-ice edge north of Svalbard for summer and autumn foraging (Haug et al. 1994, Folkow et al. 2004). These foraging migrations are important for regaining energy stores used during the breeding and moulting seasons in the spring (Nilssen et al. 1997).

Ringed seals are a circumpolar Arctic species that is highly reliant on sea ice throughout the year (Laidre et al. 2008). Their diet is also known to vary regionally and seasonally (Holst et al. 2001, Thiemann et al. 2007, Bengtsson et al. 2020). In Svalbard, ringed seal movement and diving patterns suggest that adult animals forage primarily at tidewater glacier fronts (Hamilton et al. 2016, 2019) and trends in the recent decade show that they are retracting into these Arctic refugial areas as sea-ice declines continue (Hamilton et al. 2019). Young ringed seals do not stay coastal in summer; they migrate north to the sea-ice edge to forage (Freitas et al. 2008, Hamilton et al. 2015). Despite having to travel longer to reach the sea ice in recent years, they are still undertaking these foraging migrations (Hamilton et al. 2015).

For many Arctic organisms, sympagic (ice-associated) primary production is an essential early-season energy source (McMahon et al. 2006, Søreide et al. 2010, Ji et al. 2013). This production supports prey of higher trophic levels such as seabirds and walrus *Odobenus rosmarus rosmarus* (Cusset et al. 2019, Yurkowski et al. 2020). In the Eurasian Basin, which is partially covered by sea ice year-round, sympagic carbon contributed as much as 92% to the diets of various under-ice and pelagic zooplankton and between 34 and 65% for various tissues of polar cod *Boreogadus saida* (Kohlbach et al. 2016, 2017). In the seasonally ice-covered Bering Sea, sympagic primary production has also been shown to make high contributions to the diets of ice-associated seals, with estimates ranging from 62 to 80% for bearded seals *Erignathus barbatus*, 21 to 60% for ringed seals, and 51 to 62% for spotted seals *Phoca largha* (Wang et al. 2016). It is unknown whether Arctic seal diets in the European Arctic also have similarly high contributions of sea-ice algal-sourced carbon, as pelagic primary production would be expected to be more important in the seasonal ice-covered zones.

Organic carbon in sea-ice-covered ecosystems originates primarily from ice algae and phytoplankton. These primary producers often have distinct carbon isotope signatures ($\delta^{13}C$), largely due to the fact that sea-ice algae compete for light and space in a closed carbon-limiting system that has minimal exchange with the underlying water column (Horner & Schrader 1982, Fry & Sherr 1984, Kennedy et al. 2002). As a result, bulk $\delta^{13}C$ values of ice algae are often higher when compared to phytoplankton values (Gradinger 2009, de la Vega et al. 2019), though these values can overlap with one another depending on ice algal biomass and the time of year when sampling takes place (Søreide et al. 2006, Tremblay et al. 2006, Gradinger 2009). Bulk stable isotope analysis of carbon is most widely used (de la Vega et al. 2019), but delivers a single value encompassing a mixture of all organic compounds. In contrast, compound-specific stable isotope analysis provides more detailed information on the sources of individual compounds, such as fatty acids, which in themselves can be used as tracers in food web studies (Middelburg 2014, Burian et al. 2020).

Complementary to isotopic research, the trophic biomarker approach is a selective process involving certain marker fatty acids that can be used to determine consumer diets and energy flow within food webs (Lee et al. 1971, Sargent & Whittle 1981, Falk-

Petersen et al. 1990). Two of the most abundant fatty acids in Bacillariophyceae, or diatoms, are 16:1(n-7) and 20:5(n-3) (Viso & Marty 1993, Reitan et al. 1994, Jónasdóttir 2019). Sea ice in general and specifically first-year sea-ice algal communities are often dominated by diatoms (Leu et al. 2006, Søreide et al. 2006, Fernández-Méndez et al. 2018), which contribute the highest algal fraction to sea-ice particulate organic matter (Van Leeuwe et al. 2018). Dinoflagellates (Dinophyceae) also have characteristic marker fatty acids, namely, higher amounts of 18:4(n-3) and 22:6(n-3) (Viso & Marty 1993, Graeve et al. 1994). These fatty acids are characteristic for diatoms or dinoflagellates occurring in sea ice and/or water (Søreide et al. 2008), but again these specific fatty acids in particulate organic matter inside sea ice can have higher $\delta^{13}C$ values (Wang et al. 2014). Thus, combining marker fatty acids with their individual stable isotope values, or $\delta^{13}C_{FA}$, may provide further differentiation between carbon sources and their assimilation pathways throughout food webs (Budge et al. 2008).

The overarching objective in this study was to identify potential trophic niche differences between harp and ringed seals from 2 angles: firstly, by identifying potential differences in dietary items (fatty acid analysis), and secondly, by identifying potential differences in carbon sourcing from phytoplankton and ice algae (isotopic ratio analysis). To address these 2 aspects, we used fatty acids and $\delta^{13}C_{FA}$ to (1) determine any differences in sea-ice algae and phytoplankton values, (2) evaluate potential dietary fatty acid compositional differences between harp and ringed seals, and (3) estimate the relative contribution of sympagic and pelagic primary production to harp and ringed seal diets using the $\delta^{13}C_{FA}$ values of 4 trophic biomarker fatty acids. Based on previous studies documenting differences in $\delta^{13}C_{FA}$ values in ice algae and phytoplankton (Budge et al. 2008, Wang et al. 2014), we first predicted that even if the fatty acid compositions of the 2 primary production sources were similar, sympagic algae would have $\delta^{13}C_{FA}$ values higher than pelagic values. Second, we hypothesized that fatty acid profiles would be similar between the 2 seal species given their dietary overlap. Third, we hypothesized that sympagic carbon is more likely to contribute to the diet of ringed seals because of their stronger association with sea ice.

2. MATERIALS AND METHODS

To address our first hypothesis, we examined the fatty acid compositions and specific $\delta^{13}C_{FA}$ values of sea-ice algae and phytoplankton in summer and determined if there were differences between the 2 sources of primary production. To address hypothesis 2, we tested if harp and ringed seals differed in their blubber fatty acid compositions and the $\delta^{13}C_{FA}$ values of the trophic biomarker fatty acids. Finally, to address hypothesis 3, differences in the $\delta^{13}C_{FA}$ values between sympagic and pelagic sources were used to quantify the contribution of these different carbon sources to the harp and ringed seal diets.

2.1. Study area and sample collection

Sea-ice algae and phytoplankton were collected north of Svalbard, over the Yermak Plateau, in the northern Barents Sea and in the Nansen Basin (Fig. 1). Sample collection of particulate organic matter from sea-ice algae and phytoplankton occurred during 2 consecutive cruises onboard the RV 'Polarstern' (Fig. 1). From 3 to 15 June 2017, the RV 'Polarstern' was anchored to an ice floe north of Svalbard. During this time, the ice floe drifted approximately 100 km, circling above the Yermak Plateau (Fig. 1). From 25 June to 14 July, the RV 'Polarstern' traveled north through the Barents Sea and into the deep Nansen Basin. Sample collection occurred at various stations throughout this area (Table 1). In-ice chlorophyll *a* ranged from 0.11 to 0.39 mg m^{-2} (Castellani et al. 2020), and all sea ice encountered during both cruises was first-year ice.

Particulate organic matter within sea ice (iPOM) was collected by taking ice cores with a 9 cm inner diameter ice corer (Kovacs Enterprises). The bottom 5 cm of each ice core was cut off and melted onboard the ship in a 4°C dark room. To obtain more material, ice-algae aggregates floating in auger holes were opportunistically collected by hand and placed into 50 ml Falcon tubes (Fisher Scientific). During 3–15 June, iPOM was collected from 7 ice cores and 4 floating ice-algae aggregates. During 25 June–14 July, iPOM was collected from 17 ice cores taken at 5 ice stations and 6 hand-collected ice-algae aggregates were collected at 3 ice stations. Particulate organic matter from the phytoplankton community (pPOM) was also collected during both cruises. During 3–15 June, only one pPOM water sample (at 30 m) ended up being usable and was taken by hand through a hole in the sea ice using a Kemmerer water sampler (Eijkelkamp). During 25 June–14 July, pPOM was collected at 12 different stations using a CTD rosette water sampler (Seabird SBE9+) at the chlorophyll maximum layer (between 6 and 40 m). All samples

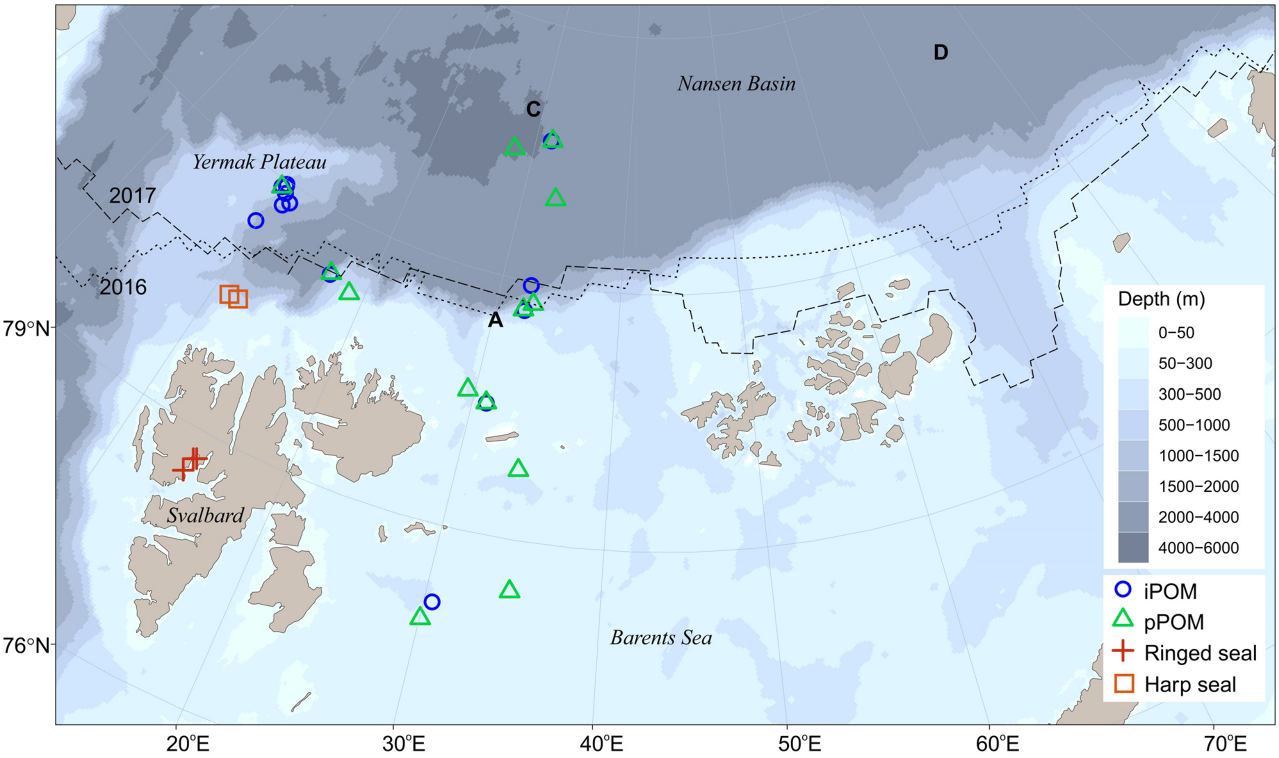

Fig. 1. Map of the study area. Black lines show minimum September sea-ice extent in 2016 (dotted line) and 2017 (dashed line; data: National Snow and Ice Data Center, Fetterer et al. [2017]). A, C, and D refer to pPOM stations included from Kohlbach et al. (2017). The study area map was generated with the ggOceanMaps package (Vihtakari 2020)

were filtered onto 0.7 µm pre-combusted GF/F filters (Whatman, Merck). Filtered samples were subsequently wrapped in aluminum foil and stored in a −80°C freezer until analysis.

Harp seals (n = 25) were shot for scientific purposes on ice floes north of Svalbard (80.52°–80.55° N, 11.4°–11.8° E), and samples were collected on 11 September 2016 (Fig. 1). Ringed seals were shot (n = 20) during an annual sport hunt that occurs in Svalbard each summer and autumn. Ringed seal samples were collected in Eckmanfjorden (78.49–78.66° N, 14.40–14.58° E), Svalbard, between 26 June and 21 September 2017 (Fig. 1). Seal age was determined by counting cementum layers of sectioned teeth (mostly canines) (Scheffer 1950). For both species, ages <1 yr were considered young of the year, ages 1–5 yr as juveniles, and seals ≥6 yr as adults (Lydersen & Gjertz 1987). Full-depth (from skin to muscle) blubber samples were taken from the trunk of the seal bodies immediately after collection, wrapped in aluminum foil and frozen at −20°C until arrival at the laboratory, where they were subsequently stored at −80°C until analysis. Blubber tissue fatty acids reflect signatures of acquired prey items consumed over time periods from weeks to months in seals (Nordstrom et al. 2008, Tollit et al. 2010). While different sections of blubber can reflect different time periods of when prey was acquired (Strandberg et al. 2008), we were interested in the cumulative incorporation of diet and carbon sources, and hence homogenized the whole blubber column.

2.2. Fatty acid analysis

All laboratory analyses were conducted at the Alfred Wegener Institute in Bremerhaven, Germany. Prior to lipid extraction, POM samples were removed from −80°C freezers and freeze-dried for 24 h. Seal blubber was first thawed in a refrigerator, and a longitudinal slice (from skin to muscle) was cut using a clean scalpel on a glass plate. The skin and any attached muscle tissue were cut away, and one blubber sample was analyzed per individual. Blubber samples were placed on individual pieces of aluminum foil and freeze-dried for 24 h (Rudy et al. 2016) leaving 2–9 g (dry mass) of blubber per individual.

Samples were mechanically homogenized, and lipids were extracted using dichloromethane/methanol 2:1 v/v (Folch et al. 1957). Total lipid mass of each sample was determined gravimetrically. Lipids were

Table 1. Sample information for particulate organic matter from sea ice (iPOM) and phytoplankton (pPOM) collected from the Yermak Plateau (PS106.1), Barents Sea (PS106.2), and Nansen Basin (PS106.2), and for harp and ringed seals. Samples were analyzed for fatty acids (FA) and carbon isotope values of fatty acids ($\delta^{13}C_{FA}$). Sea-ice coverage was acquired from the Copernicus Marine Service (https://marine.copernicus.eu/), which provides daily ice cover by 10 km^2 for pack ice (POM and harp seal locations) and 1 km^2 for land-fast ice (ringed seal locations)

Group	Sample type	Data	N	Date	Latitude (°N)	Longitude (°E)	Station	Sea-ice coverage (%)
POM, PS106.1	iPOM	$\delta^{13}C_{FA}$, FA	1	2 June 2017	81.411	9.786	19	91
	iPOM	$\delta^{13}C_{FA}$, FA	1	4 June 2017	81.964	10.243	21	96
	iPOM	$\delta^{13}C_{FA}$, FA	2	7 June 2017	81.942	10.308	24	95
	iPOM	$\delta^{13}C_{FA}$, FA	2	9 June 2017	81.909	10.006	26	93
	pPOM	FA only	1	9 June 2017	81.909	10.006		93
	iPOM	FA only	2	11 June 2017	81.867	10.557	28	99
	iPOM	$\delta^{13}C_{FA}$, FA	2	14 June 2017	81.798	11.285	31	100
	iPOM	$\delta^{13}C_{FA}$, FA	1	15 June 2017	81.731	10.858	32	100
POM, PS106.2	pPOM	$\delta^{13}C_{FA}$, FA	1	25 June 2017	77.894	30.045	44	61
	iPOM	$\delta^{13}C_{FA}$, FA	7	25 June 2017	78.111	30.479	45	63
	pPOM	$\delta^{13}C_{FA}$, FA	1	26 June 2017	78.405	34.703	47	28
	pPOM	$\delta^{13}C_{FA}$, FA	1	27 June 2017	79.815	34.018	48	70
	pPOM	$\delta^{13}C_{FA}$, FA	1	28 June 2017	80.515	30.972	50	94
	iPOM	FA only	2	29 June 2017	80.508	30.984		86
	pPOM	FA only	1	30 June 2017	81.750	32.938	57	95
	iPOM	$\delta^{13}C_{FA}$, FA	7	2 July 2017	81.655	32.342	66	98
	pPOM	FA only	1	2 July 2017	81.664	32.237		98
	iPOM	$\delta^{13}C_{FA}$, FA	2	3 July 2017	81.958	32.482	67	95
	pPOM	FA only	1	5 July 2017	83.000	33.162	69	90
	iPOM	$\delta^{13}C_{FA}$, FA	3	6 July 2017	83.661	31.581	73	91
	pPOM	$\delta^{13}C_{FA}$, FA	1	7 July 2017	83.664	31.721		92
	pPOM	FA only	1	8 July 2017	83.473	28.055	74	83
	iPOM	$\delta^{13}C_{FA}$, FA	2	12 July 2017	81.308	16.886	80	78
	pPOM	$\delta^{13}C_{FA}$, FA	1	12 July 2017	81.326	16.928		78
	pPOM	$\delta^{13}C_{FA}$, FA	1	13 July 2017	81.205	18.835	83	89
	pPOM	FA only	1	14 July 2017	80.611	29.489	85	73
Harp		$\delta^{13}C_{FA}$, FA	25	11 Sep 2016	80.517	11.400		4
Ringed		$\delta^{13}C_{FA}$, FA	3	26 June 2017	78.491	14.400		20
		$\delta^{13}C_{FA}$, FA	6	29 Aug 2017	78.491	14.400		20
		$\delta^{13}C_{FA}$, FA	2	9 Sep 2017	78.491	14.400		50
		$\delta^{13}C_{FA}$, FA	3	17 Sep 2017	78.664	14.582		5
		$\delta^{13}C_{FA}$, FA	6	21 Sep 2017	78.684	14.754		0

then converted into fatty acid methyl esters by using a solution of 3% concentrated sulfuric acid in methanol and heating for 4 h at 80°C (Kattner & Fricke 1986). Subsequently, fatty acid methyl esters were quantified using an Agilent 6890N gas chromatograph (Agilent Technologies) with a DB-FFAP capillary column (60 m, 0.25 mm i.d., 0.25 µm film thickness) supplied with a splitless injector and a flame ionization detector using temperature programming. Helium was used as the carrier gas. Fatty acid methyl esters were quantified with an internal standard, tricosanoic acid methyl ester (23:0) (Supelco), that was added prior to lipid extraction. The detection limit based on the certified reference material (Supelco 37 Component fatty acid methyl ester mix) was 10–20 ng per component. Clarity chromatography software system (version 8.2.0, DataApex) was used for chromatogram data evaluation. Fatty acids are presented in shorthand notation, i.e. A:B(n-x), where A indicates the number of carbon atoms in the straight fatty acid chain, B represents the number of double bonds present, n represents the terminal methyl group and x denotes the position of the first double bond from the terminal end. Proportions of fatty acids are expressed as mass percentages of total fatty acid content.

2.3. Compound-specific stable isotope analysis

Carbon stable isotope ratios of fatty acid methyl esters ($\delta^{13}C_{FA}$) of both POM and seal samples were analyzed using a Trace Ultra gas chromatograph (GC), a

GC Isolink system, and a Delta V Plus isotope ratio mass spectrometer (IRMS), connected to a Conflo IV interface (Thermo Scientific Corporation). Samples were injected in splitless mode and separated on a DB-FFAP column (60 m, 0.25 mm i.d., 0.25 µm film thickness) using temperature programming (Kohlbach et al. 2016). The limit of detection was comparable to the methods described above. The $\delta^{13}C_{FA}$ values were calibrated using certified standards of 14:0 ($\delta^{13}C$: −29.98‰), 16:0 ($\delta^{13}C$: −30.74‰), 18:0 ($\delta^{13}C$: −23.24‰), and 20:0 ($\delta^{13}C$: −30.68‰) (supplied by Indiana University, USA). To ensure accuracy and precision (±0.8‰ for GC-IRMS), certified standards were analyzed before and after sample runs in the GC-IRMS. All reported $\delta^{13}C_{FA}$ values are relative to Vienna Pee Dee Belemnite (VPDB) using the standard notation $\delta^{13}C_{FA}$ (‰) = $[(R_{sample} / R_{standard}) - 1] \times 1000$, where R is the corresponding ratio of $^{13}C/^{12}C$.

2.4. Data analysis

All data analyses were conducted in R version 4.0.2 (R Core Team 2020). The fatty acid data sets from POM and seals were visualized using correspondence analysis (CA) on non-standardized multivariate data using the vegan package (Oksanen et al. 2020). This analysis, with its inherent chi-square distance measure, was selected because of its ability to handle data zeros and compositional data (Greenacre 2011). As these characteristics are inherent in fatty acid data sets, the CA was deemed the most appropriate. Because POM was collected over a broad spatial area, the variance due to station location was removed using a canonical CA (Palmer 1993). Differences between iPOM and pPOM were then tested using a permutation test on the constrained correspondence analysis. A permutational ANOVA between harp and ringed seal fatty acid compositional data was conducted to determine if seal species differed by fatty acid composition. Tests were based on 999 free permutations to test the significance of location and species on the fatty acid profiles of POM and seal groups, respectively.

The 4 specific trophic biomarker fatty acids [16:1(n-7), 20:5(n-3), 18:4(n-3), and 22:6(n-3)] were examined in greater detail, as they were the basis of our trophic biomarker modeling approach. To increase replication and better capture variability in the $\delta^{13}C_{FA}$ values from pelagic POM, we included additional data originating from the same region north of Svalbard and the Nansen Basin from a study conducted in 2012 (Kohlbach et al. 2017). A Mann-Whitney *U*-test for differences between sample years (2012 and 2017) in the biomarker fatty acid $\delta^{13}C_{FA}$ values found no statistical difference (significance was set at $\alpha = 0.05$). We then tested for differences among (1) the mass percentages of the trophic biomarker fatty acids between POM groups and (2) their $\delta^{13}C_{FA}$ values between POM groups using the non-parametric Mann-Whitney *U*-test that is robust for small data sets.

To better visualize differences in all $\delta^{13}C_{FA}$ values between harp and ringed seals, we chose a non-metric multidimensional scaling (NMDS) ordination because $\delta^{13}C_{FA}$ values are negative. Out of the 34 fatty acids present in seal blubber, 20 common fatty acids that had corresponding $\delta^{13}C_{FA}$ values were selected for both seal species. To determine if harp and ringed seals differed by the $\delta^{13}C_{FA}$ values, we conducted a permutational ANOVA between groups, based on Euclidean distance (Anderson 2017). Similar to the POM data set, we also investigated the 4 trophic biomarkers in greater detail. We used a Mann-Whitney *U*-test to test for the differences in their $\delta^{13}C_{FA}$ values between harp and ringed seals.

Differences between age classes in both bulk isotopes and fatty acids have been previously reported for harp and ringed seals (Lawson & Hobson 2000, Young et al. 2010). We explored whether this difference was reflected in the $\delta^{13}C_{FA}$ values of the trophic biomarkers, in order to determine if age-specific modeling should be conducted. Differences between age classes (young of the year, juveniles, adults) was tested using Kruskal-Wallis rank sum tests as they are appropriate for uneven sample sizes. We found no significant difference between age classes within species groups and therefore pooled all age classes within species.

The proportional contributions of sympagic and pelagic carbon in seal blubber were estimated using the available $\delta^{13}C_{FA}$ values of the 4 trophic biomarker fatty acids (mean and standard deviation) of iPOM and pPOM in a Bayesian stable isotope mixing model with the MixSIAR package (Stock & Semmens 2016a, Stock et al. 2018). Because we used the $\delta^{13}C_{FA}$ values of 4 biomarker fatty acids, and our question focuses on carbon sourcing to blubber, isotopic fractionation was assumed to be zero following similar studies (Budge et al. 2008, Wang et al. 2016). Mixing models were run with 50 000 iterations (where the first 25 000 iterations were discarded). Since the objective of this modeling approach was focused on carbon sourcing, we included a residual error term as recommended by Stock & Semmens (2016b). Modeled estimates of proportional contributions of iPOM and pPOM in seal blubber sum to 1 (100 %). This means that seals with minimal sympagic input would have an estimated iPOM contribution near zero. Modeled outputs are reported as the mean contribution of iPOM and pPOM contributions to seal blubber, along with their standard deviation and 95 % credibility intervals, i.e. Bayesian confidence intervals.

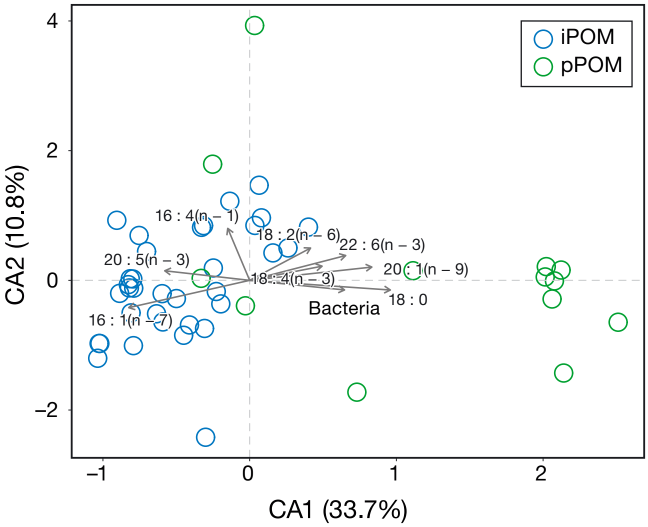

Fig. 2. Correspondence analysis (CA) biplot of 33 compositional fatty acids in particulate organic matter from sea ice (iPOM) and phytoplankton (pPOM). Biplot arrows correspond to significant contribution of fatty acids in the CA ordination. Axis labels indicate percent variance explained for each axis

3. RESULTS

3.1. Particulate organic matter fatty acids and biomarker $\delta^{13}C_{FA}$ values

Fatty acid composition between iPOM and pPOM was significantly different ($p = 0.001$) when accounting for the variation due to station locations. The CA axes accounted for 41 % of the variability on the fatty acid composition pattern, most likely due to spatial and temporal variability (Fig. 2). Diatom marker fatty acids [16:1(n-7), 20:5(n-3), and 16:4(n-1)] contributed significantly ($p = 0.001$) to the separation of iPOM from pPOM. The dinoflagellate marker fatty acids [18:4(n-3) and 22:6(n-3)] contributed significantly ($p = 0.001$) to pPOM separation, along with 18:0 and bacterial fatty acids (sum of the odd-chain saturated and branched fatty acids across stations) (Fig. 2). Of the 33 fatty acids found in all iPOM samples across stations, 3 dominated in mass contribution: 16:0 (mean 20.9 ± 4.5 %), 16:1(n-7) (mean 34.2 ± 11.1 %) and 20:5(n-3) (mean 11.0 ± 5.3 %) (Fig. 3A, Table S1 in the Supplement at www.int-res.com/articles/suppl/m675p181_supp.pdf). Of the 24 fatty acids found in all pPOM samples across stations, there were again 3 that dominated: 16:0 (mean 25.5 ± 3.3 %), 16:1(n-7) (mean 16.5 ± 12.0 %), and 18:0 (mean 25.2 ± 11.0 %) (Fig. 3A, Table S1).

The mass percentages of the diatom biomarker fatty acids 16:1(n-7) and 20:5(n-3) were significantly different between POM groups ($p \leq 0.0001$, Mann-

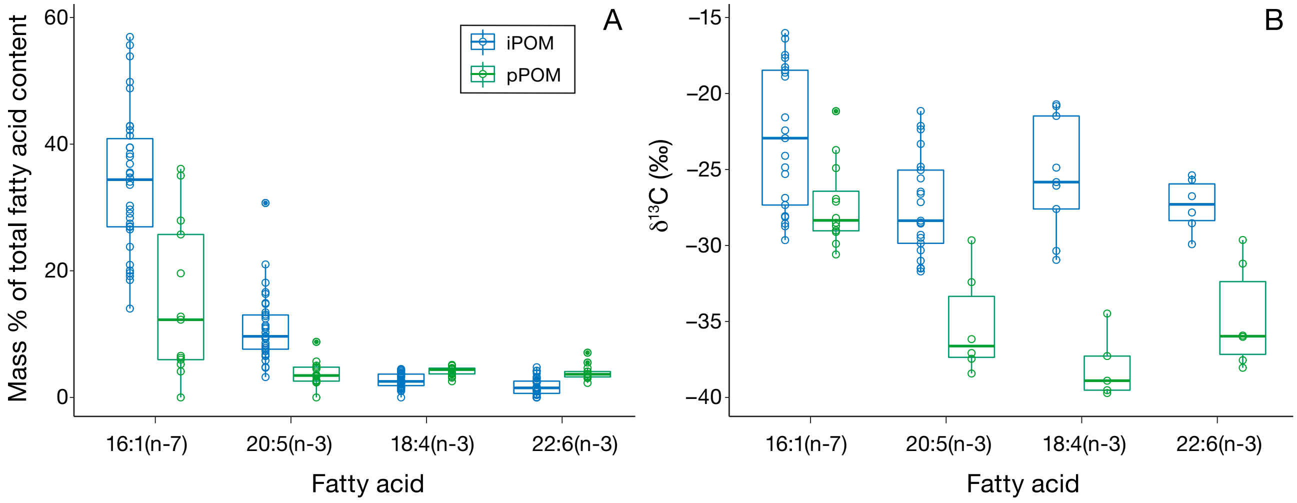

Fig. 3. Relative composition of (A) marker fatty acids and (B) their $\delta^{13}C_{FA}$ values compared between POM groups (iPOM: particulate organic matter from sea ice; pPOM: particulate organic matter from phytoplankton). 16:1(n-7) and 20:5(n-3) represent diatom fatty acids; 18:4(n-3) and 22:6(n-3) represent dinoflagellate fatty acids. Horizontal bars within box plots indicate median proportional values; upper and lower portions of the boxes are the approximate 1st and 3rd quartiles. Vertical error bars extend towards the lowest and highest data within a range of 1.5 times the inter-quartile range. Open and closed circles represent data points (closed circles are outliers)

Table 2. Carbon stable isotope means of available $\delta^{13}C_{FA}$ values for the 4 biomarker fatty acids included in this study. Mean (±1 SD) ‰ values of iPOM in 2017 and 2012, pPOM in 2017 and 2012, and of harp seal blubbers sampled in 2016 and ringed seal blubbers sampled in 2017

Fatty acid	iPOM 2017 n = 11 stations	pPOM (2017 & 2012) n = 12 stations	Harp seals 2016 n = 25	Ringed seals 2017 n = 20
16:1(n-7)	−22.87 ± 4.67	−27.32 ± 2.77	−28.26 ± 0.40	−27.11 ± 1.15
20:5(n-3)	−27.37 ± 3.26	−35.20 ± 3.42	−29.55 ± 0.51	−28.54 ± 0.57
18:4(n-3)	−25.41 ± 3.86	−38.45 ± 2.24	−32.99 ± 0.51	−32.62 ± 1.14
22:6(n-3)	−27.35 ± 1.75	−34.73 ± 3.48	−27.93 ± 0.56	−28.16 ± 0.58

Whitney *U*-test). In comparison, the dinoflagellate biomarker fatty acids were found in relatively smaller amounts in both iPOM [18:4(n-3) mean: 2.8 ± 1%; 22:6(n-3) mean: 2.0 ± 1.2%] and pPOM [18:4(n-3) mean: 4.1 ± 0.8%; 22:6(n-3) mean: 4.0 ± 0.5%]. Regardless of their relative contributions to POM, they were also found to be significantly different ($p < 0.0001$, Mann-Whitney *U*-test) between POM groups (Fig. 3A).

The $\delta^{13}C_{FA}$ values of the 4 marker fatty acids differed significantly ($p \leq 0.005$, Mann-Whitney *U*-test) between iPOM and pPOM samples, with higher $\delta^{13}C$ values for iPOM (range: −27.35 to −22.87‰) than pPOM (range: −38.45 to −27.32‰) for each of the 4 fatty acids (Fig. 3B), enabling their use for the mixing model estimations of carbon sourcing (Table 2).

3.2. Harp and ringed seal fatty acids and $\delta^{13}C_{FA}$ values

Based on the relative abundance of all fatty acids found in seal blubber (Table S1), there was significant ($p = 0.001$) group separation between species. The CA axes accounted for 70% of the variability in the fatty acid composition pattern (Fig. 4A). Within the first ordination axis of all fatty acids, the diatom biomarkers 16:1(n-7) and 20:5(n-3), and the dinoflagellate marker 18:4(n-3), were more prevalent in the harp seal samples, while the dinoflagellate biomarker 22:6(n-3) was more prevalent in the ringed seal samples (Fig. 4A). The separation of seal blubber composition along the first axis was primarily driven by the monounsaturated fatty acids (MUFAs) with 16, 18, and 20 carbon atoms. Both seal species had assimilated 20:1 and 22:1 MUFAs, including their specific isomers, with slightly higher levels in ringed seals. The *Calanus* spp. biomarker fatty acids [sum of 20:1(n-9) and 22:1(n-11)] contributed more to the ringed seals than to the harp seals. Despite group separation, the same fatty acids contributed the high-

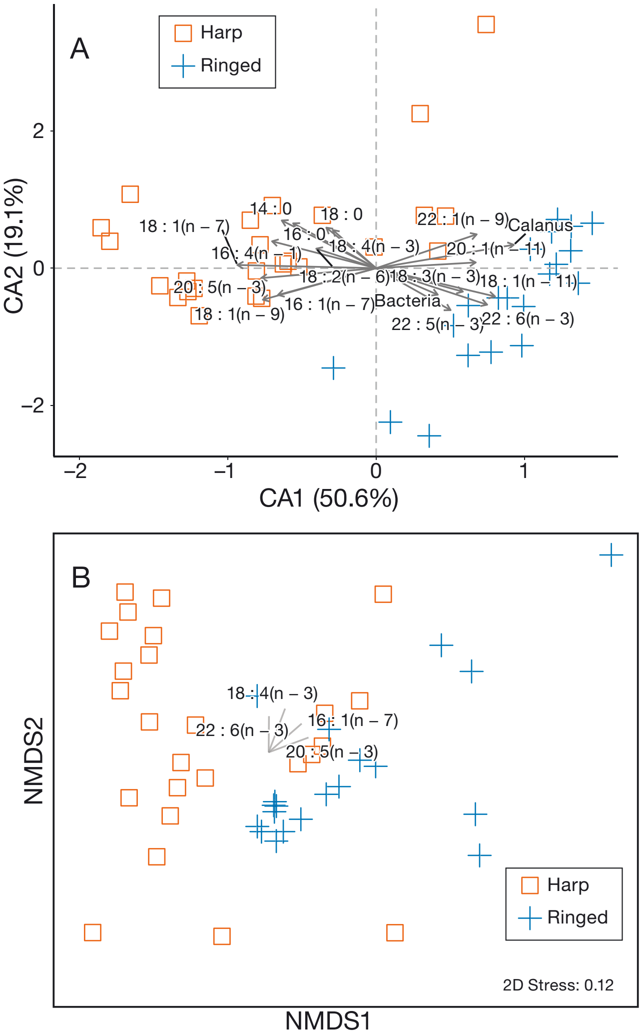

Fig. 4. Harp and ringed seal patterns of fatty acids and their carbon isotope values. (A) Correspondence analysis (CA) biplot of 34 compositional fatty acids in harp and ringed seals. Biplot arrows correspond to significant contributions from fatty acids in the CA ordination. Axis labels indicate percent variance explained for each axis. (B) Nonmetric multidimensional scaling of the $\delta^{13}C_{FA}$ values for 20 fatty acids in the blubber of harp and ringed seals. Biplot lines depict directions of marker fatty acids

est mean (±SD) mass percentages for both seal species: 14:0 (5.2 ± 0.5% in harp seals, 3.3 ± 0.3% in ringed seals), 16:0 (9.3 ± 1.4% in harp, 7.0 ± 1.4% in ringed), the 18:1 MUFA family (26.8 ± 1.2% in harp, 24.9 ± 1.2% in ringed), and 20:1(n-9) (7.7 ± 2.3% in harp, 12.3 ± 2% in ringed) (Table S1).

The NMDS ordination for $\delta^{13}C_{FA}$ values in harp and ringed seal blubber showed significant separation between the 2 seal species ($p = 0.001$), though with more overlap than the fatty acid data (Fig. 4B). The separation was prominent along NMDS axis 1 and associated with 20:5n-3 and 16:1n-7, with no separation along NMDS axis 2. The $\delta^{13}C_{FA}$ values of many fatty acids fell in a similar range for both harp and ringed seals (Fig. S1 in the Supplement). For the 4 biomarker fatty acids, ringed seals had significantly higher $\delta^{13}C_{FA}$ values for 16:1(n-7) and 20:5(n-3) than harp seals, while there were no significant differences between the $\delta^{13}C_{FA}$ values for 18:4(n-3) and 22:6(n-3) between the seal species (Table 2, Fig. 5).

3.3. iPOM and pPOM contributions to seal blubber — from mixing models

Mixing models using the 4 trophic biomarker fatty acids estimated the proportional contribution (1 = 100%) of iPOM and pPOM $\delta^{13}C_{FA}$ in seal blubber. Mixing models including both seal species estimated the group mean iPOM contributions to harp seals to be 0.69 ± 0.08 and pPOM to be 0.31 ± 0.08. For ringed seals, mean iPOM contributions were 0.72 ± 0.07 and pPOM contributions were 0.28 ± 0.07 (Table 3).

Table 3. Estimates of iPOM and pPOM contributions (mean ± 1 SD with 95% Bayesian credible intervals) to harp (2016) and ringed (2017) seals from stable isotope mixing models using the 4 marker fatty acids (shown in Table 2)

	N	Mean ± SD	Lower 95% credible interval	Higher 95% credible interval
Harp seal				
iPOM	25	0.69 ± 0.08	0.54	0.85
pPOM		0.31 ± 0.08	0.15	0.46
Ringed seal				
iPOM	20	0.72 ± 0.07	0.59	0.86
pPOM		0.28 ± 0.07	0.14	0.41

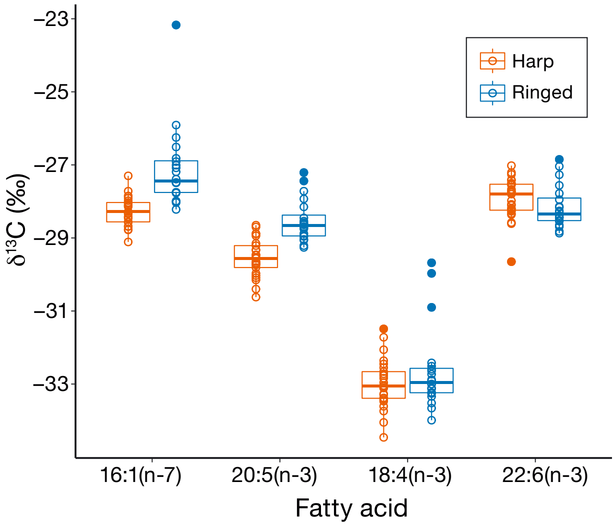

Fig. 5. Trophic biomarker $\delta^{13}C_{FA}$ values compared between seal species. Horizontal bars within box plots indicate median proportional values; upper and lower portions of the boxes are the approximate 1st and 3rd quartiles. Vertical error bars extend towards the lowest and highest data within a range of 1.5 times the inter-quartile range. Open and closed circles represent data points (closed circles are outliers)

4. DISCUSSION

4.1. Fatty acids in iPOM and pPOM

The overall fatty acid composition in our iPOM samples was similar to that in other Arctic studies (Falk-Petersen et al. 1998, Budge et al. 2008, Kohlbach et al. 2016). The diatom marker 16:1(n-7) contributed the highest mass percentage in our iPOM samples, and the ratio of 16:1(n-7)/16:0 was >1 in our iPOM samples also suggesting a dominance of diatoms (Graeve et al. 1994). The second diatom marker 20:5(n-3) also had considerably higher proportions in iPOM compared to pPOM (Leu et al. 2006). Interestingly, in the Bering Sea, Wang et al. (2014) found that 20:5(n-3) contributed more than 16:1(n-7), the opposite of our findings, which could be related to differing diatom community composition or differing bloom growth conditions and phenology. Budge et al. (2008) suggested that the combination of high contributions of 16:1(n-7) and low levels of polyunsaturated fatty acids (PUFAs) (in their case, 18.5%) might be an indication of rapid algal growth conditions. The average contribution of 16:1(n-7) in the present study was 34%, with moderate levels of total PUFAs (22.8%), which is not clearly indicative of rapid growth conditions. Based on metabarcoding from the sea-ice cores sampled at our ice stations in 2017, dinoflagellates were present (B. Hassett pers. comm.). This is consistent with earlier findings (Booth & Horner 1997) and supported by the presence of 18:4(n-3) and 22:6(n-3) in our iPOM samples. Dinoflagellates and the haptophyte *Phaeocystis pouchetti* can be common in several Arctic ice habitats, including the snow–ice interface of first-year ice, in refrozen leads, and in melting ice (Tamelander et al. 2009, Assmy et al. 2017, Fernández-Méndez et al. 2018), and our late ice stations occurred during advanced stages of melt.

The major contributing fatty acids found in our pPOM samples were also similar to data from other Arctic food web studies (Falk-Petersen et al. 1998, Wang et al. 2014, Kohlbach et al. 2016). During a seasonal study in a High Arctic fjord (Kongsfjorden, Svalbard) near our study area, the flagellate markers 18:4(n-3) and 22:6(n-3) had even higher contributions in pPOM when compared to our values (Mayzaud et al. 2013). These findings suggest differences in nutrient availability or species composition between these areas. In addition to the protist taxa discussed, the occurrence of bacteria (the odd-chain saturated and branched fatty acids) in both iPOM and pPOM demonstrates that POM constitutes a complex mix of microbial species (Kirst & Wiencke 1995) with strong potential for seasonal and regional changes driven by bloom phenology.

4.2. δ^{13}C differences in biomarker fatty acids between habitats

The differences we found in the $\delta^{13}C_{FA}$ marker values between iPOM and pPOM is the key prerequisite to using these trophic markers in the subsequent mixing models. This finding is in agreement with an earlier study from the Nansen Basin when both first-year and multi-year ice were studied (Kohlbach et al. 2016: $\delta^{13}C_{FA}$ iPOM: −28.4 to −23.4‰; $\delta^{13}C_{FA}$ pPOM: −39.3 to −26.4‰) and with a study of seasonal first-year ice in the Bering Sea (Wang et al. 2014: $\delta^{13}C_{FA}$ iPOM: −26.5 to −21.0‰; $\delta^{13}C_{FA}$ pPOM: −30.4 to −27.0‰). Leu et al. (2020) found an increasing trend in $\delta^{13}C_{FA}$ values in a seasonally sea-ice-covered fjord in Svalbard throughout spring (April–May), suggesting that bloom succession and an increase in under-ice light play a role in these values, similar to seasonal changes determined by bulk δ^{13}C values. To date, studies investigating $\delta^{13}C_{FA}$ values of individual fatty acids in POM throughout the Arctic are not as ubiquitous compared to studies of bulk δ^{13}C POM. Isotopic enrichment in bulk δ^{13}C values in iPOM over pPOM is seasonally and regionally variable, depending on environmental and physiological factors in addition to taxonomic community composition and biomass, which can be minimal or absent at times (de la Vega et al. 2019, Leu et al. 2020).

4.3. Fatty acid composition of harp and ringed seals

Although we cannot determine exactly where the harp seals from this study were foraging, it is likely they were following the sea-ice-edge in the weeks or months before collection (Stenson et al. 2020). The presence of the *Calanus* spp. trophic biomarkers in their blubber suggest that they were feeding on a *Calanus* spp.-derived food chain (Sargent & Falk-Petersen 1988). This food chain supports a variety of their major prey items. During late summer and early autumn in the northern Barents Sea, harp seals feed on pelagic crustaceans such as krill (*Thysanoessa* spp.), hyperiid amphipods *Themisto libellula*, and polar cod (Lydersen et al. 1991, Nilssen et al. 1995b, Falk-Petersen et al. 2004). These species, also supported by the *Calanus* spp. food chain, can have high levels of 16:1(n-7) and 20:5(n-3) (Auel et al. 2002, Falk-Petersen et al. 2000, Kohlbach et al. 2017).

The diet of ringed seals is often dominated by polar cod (e.g. Labansen et al. 2007), but they also consume a mix of other fishes and crustaceans (Gjertz & Lydersen 1986, Weslawski et al. 1994). Along the west coast of Svalbard, ringed seal diet (determined from the same fjord as the animals in the present study) has recently been shown to be dominated by polar cod (Bengtsson et al. 2020). 16:1(n-7) and 20:5(n-3), while slightly lower in ringed seals than in harp seals, were still major contributing fatty acids, similar to that found in previous studies (Thiemann et al. 2007, Cooper et al. 2009). Regardless of season, ringed seals from the Bering and Chukchi Seas (Wang et al. 2016) had higher contributions of 16:1(n-7), 20:5(n-3), and 22:6(n-3), and lower contributions of 18:4(n-3) than the ringed seals from this study, potentially resulting from differences in the biomarker-producing algal communities as indicated in the observed differences in the iPOM and pPOM fatty acids (Wang et al. 2014).

4.4. Carbon sourcing to seal diets

Based on the 4 specific trophic biomarkers, we found that part of the species separation is due to significantly higher $\delta^{13}C_{FA}$ values of 16:1(n-7) and 20:5(n-3) in ringed seals compared to harp seals. This finding indicates that ringed seals assimilated more sympagic fatty acids compared to harp seals. Our ringed seals had similar $\delta^{13}C_{FA}$ values of the diatom marker 20:5(n-3) (−28.5‰) to Bering Sea ringed seals (−29.2‰; Wang et al. 2016), yet were more negative when compared to ringed seals from land-fast ice in

Utqiaġvik, Alaska (−26.4‰) (Budge et al. 2008). For the $\delta^{13}C_{FA}$ values for 18:4(n-3) and 22:6(n-3), the ringed seals in this study had higher values compared to the ringed seals in the Bering Sea (Wang et al. 2016). No comparable values are currently available for harp seals.

Our modeling results showed that both harp and ringed seal diets are strongly supported by sea-ice-derived carbon sources. It should be noted that in addition to different carbon sources, other factors might be contributing to these differences (see section 4.5). Regardless of year or region, earlier studies also found that harp seal diet is supported by sea-ice production and a diatom-based food web (Falk-Petersen et al. 2004, 2009). In late summer and early autumn, harp seals maintain strong affinities to the marginal ice zone (Folkow et al. 2004, Nordøy et al. 2008), due to the seasonally strong pulses of marine productivity in this area (Falk-Petersen et al. 1990, Wassmann et al. 2020). Modeled results of sea-ice-derived carbon contributions to various harp seal prey items found that iPOM contributed up to 55% in the amphipod *T. libellula* (Kohlbach et al. 2016), and up to 65% in polar cod (Kohlbach et al. 2017). If we follow the sea-ice carbon pathway from the prey of the seals, it is plausible that at the time of the year the harp seals in this study were collected (before their long southward migration), sympagic carbon sources contributed more to their diet than pelagic carbon.

For ringed seals, the maximum value estimates of sea-ice-derived carbon contributions were similarly high when compared to other modeled values. In the Pacific Arctic, sea-ice-derived carbon in ringed seal blubber ranged from 24 to 60% in the Bering Sea, depending on time of year (Wang et al. 2016), and up to 62% in land-fast ice off the coast of Utqiaġvik, Alaska (Budge et al. 2008). Despite minor methodological differences between the studies, there is strong overall agreement on the high contributions of ice-derived carbon to ringed seal diets. Land-fast ice is seasonally present where the ringed seals from this study were captured (Nilsen et al. 2008), which could have potentially supported the high sympagic contributions found in their blubber. In turn, land-fast ice can contain substantial amounts of ice algae that become available for the marine food web (Thyrring et al. 2017). Similar to harp seals, ringed seals replenish energy stores that were used during the spring (Ryg et al. 1990, Young & Ferguson 2013). An alternative to land-fast ice-derived carbon sources, late summer/early autumn foraging trips to the ice edge (Freitas et al. 2008, Lone et al. 2019) could also explain the high iPOM contributions in their blubber. Based on the methods applied in our study, we conclude that both species of ice seals had substantial contributions of sea-ice-derived organic carbon in their diets (which were reflected in their blubber). These data are consistent with observations from other Arctic areas for both ice seals and their prey.

4.5. Model sensitivity and caveats

Modeling carbon contributions from sea ice and phytoplankton to blubber in near-apex predators warrants a discussion of both model sensitivities and caveats.

4.5.1. Issue 1

The fatty acid biomarkers used for this study were selected because they remain unmodified as they move through the marine food web (Dalsgaard et al. 2003). Almost all PUFAs originate from primary producers but can undergo trophic modifications as they pass upwards in a food chain (Bell & Tocher 2009). Vertebrates are unable to synthesize PUFAs de novo, and these essential fatty acids must be acquired through their diet (Tinoco 1982). However, vertebrates possess metabolic pathways to further desaturate and elongate the n-3 PUFAs (Rosenthal 1987) to form other highly unsaturated fatty acids (Bell & Tocher 2009). It has been shown that some pinniped species can modify various dietary fatty acids differently while consuming the same prey type, demonstrating the variability of assimilation within consumers (Rosen & Tollit 2012). Therefore, we combined fatty acids with their $\delta^{13}C_{FA}$ values in our study, in order to provide a finer resolution of the trophic biomarkers of interest.

4.5.2. Issue 2

It is well known that Bayesian model results can be skewed when not accounting for trophic fractionation (i.e. the amount of variation in the $\delta^{13}C$ and $\delta^{15}N$ values between prey and predators) in bulk carbon and nitrogen isotopes in diet reconstruction studies (Bond & Diamond 2011). Our study avoided this potential pitfall because we worked with compound-specific stable isotope values of carbon of individual trophic marker fatty acids. However, we assume here that fatty acids are integrated into seal blubber with little to no modification of their carbon chain, thus displaying unchanged $\delta^{13}C_{FA}$ values (Issue 1). Isotopic fractionation, particularly for 2 of the primary producer fatty acids used in this study, was found to be negligible for Arctic eider ducks (*Polysticta stelleri* and *Somateria fischeri*) and Atlantic pollock *Pollachius virens* (Budge et al. 2011, 2016). Experimental work on these vertebrate species found no trophic discrimination of the 20:5(n-3) and 22:6(n-3) $\delta^{13}C_{FA}$ values in either adipose tissue or serum, suggesting unmodified uptake of these fatty acids (Budge et al. 2011, 2016). These findings would then justify subsequent studies using no fractionation factor when quantifying carbon contributions to diet using trophic marker fatty acids (Kohlbach et al. 2016, 2017, Wang et al. 2016). The modeled results of sea-ice carbon to seal prey in this region (see section 4.4) would hence further support the relatively high contributions we found in the modeled results for seals. Using the $\delta^{13}C_{FA}$ values of only 20:5(n-3) and 22:6(n-3) in our mixing model (rather than all four), for comparability with Wang et al. (2016), the estimated contributions of sympagic carbon in seal blubber were even higher for both species in the present study (≥79%). These differences show that the mixing model approach is also sensitive to which fatty acids are chosen as biomarkers for diatoms and dinoflagellates.

Including isotopic fractionation terms into the model would certainly be more accurate, but to our knowledge only few data are available for higher marine organisms (see above). Furthermore, experimental work has shown that $\delta^{13}C_{FA}$ values of PUFAs can also be modified via fractionation when being incorporated into lipids in various tissues (Gladyshev et al. 2016), or by metabolic processes (Chiapella et al. 2021). Although it is difficult to map the individual steps of isotopic fractionation into total metabolism, we recognize a need for increased attention towards the kinetics of metabolic processes. This will better our understanding of the processes that cause fractionation, resulting in better application of $\delta^{13}C_{FA}$ values in quantitative models. Nonetheless, our results can be over- or under-estimations due to shifting trophic baselines in aquatic ecosystems (de la Vega et al. 2019, Casey & Post 2011) and the complexities of isotopic discrimination in marine mammals (Newsome et al. 2010).

4.5.3. Issue 3

We found high contributions of iPOM in the seals' diets. This result is, at first sight, surprising given that the contribution of sea-ice production is generally lower than pelagic primary production and the productive season in ice is short and regionally variable in seasonal ice-covered regions. Sympagic production in the Barents Sea along the spring ice edge ranges between 4.9 and 55 mg (0.0049–0.055 g) C m^{-2} d^{-1} (McMinn & Hegseth 2007), which is at least one order of magnitude below pelagic gross primary production in this region, which is estimated at 0.19 to 0.85 g C m^{-2} d^{-1} (Svensen et al. 2019). Ice algal production in the Northern Barents Sea is estimated to be approximately 5.3 g C m^{-2} yr^{-1} (Hegseth 1998), while the deep Arctic basins can have daily rates as high as 0.013 to 0.069 g C m^{-2} d^{-1} (Gosselin et al. 1997, Fernández-Méndez et al. 2015). Again, this annual estimate is well below the phytoplankton production on the nutrient-rich inflow shelves such as the Barents Sea (over 70 g C m^{-2} yr^{-1}) but in the same range as phytoplankton production in the central Arctic Ocean (Wiedmann et al. 2020). It should be noted that the highest phytoplankton production contributions occur in ice-free areas and, as such, might not be an important carbon source for the ice-based seals. Consequently, if seal foraging occurred over large parts off the shelves in deep ice-covered Arctic waters or if they spent a considerable amount of time close to sea ice, relatively high contributions of ice algal carbon could be expected.

4.5.4. Issue 4

Assumptions were made with spatial and temporal variability of POM, and sampling did not always occur within optimal time frames. We sampled POM from a large geographic area, in order to capture more of the variation of the $\delta^{13}C_{FA}$ values. We believe this was an appropriate approach, given that these seals are highly mobile predators within the European Arctic.

Pelagic $\delta^{13}C_{FA}$ values were included from a different year, which is suboptimal because sea-ice- and pelagic-derived carbon sources likely vary in their contribution to consumers temporally (as well as spatially). While the temporal mismatch between sampling of carbon end members and seal sampling is not ideal, we argue that the variation in pPOM carbon isotope values has been shown to be rather minor between years and seasons in the study area region (Søreide et al. 2006: bulk $\delta^{13}C$: −24.6 to −21‰; Tamelander et al. 2006: bulk $\delta^{13}C$: −26.5 to −23.0‰). When comparing $\delta^{13}C_{FA}$ values, our pPOM values are similar to published results from the Nansen Basin (see section 4.2). iPOM values, however, are both regionally and seasonally variable in this and other study areas, but interannual variation is not higher than seasonal and regional variation of iPOM (Søreide et al. 2006, Tamelander et al. 2006).

We did not always sample seal tissues in the optimal time frame relative to source turnover. The slight off-set of end-member sampling and seal sampling is preferred because of the turnover time needed to assimilate dietary fatty acids in seal blubber (Tollit et al. 2010). Fatty acids found in blubber reflect a time period of weeks to several months for seals (Nordstrom et al. 2008, Tollit et al. 2010). We hence evaluate the mismatch of end-member sampling and seal sampling as comparatively minor for pPOM, though iPOM estimates could be more heavily affected. Given that our estimates of iPOM contributions are very high, even a somewhat lower estimate would not change the conclusion substantially, since estimates of 40–60% iPOM contribution would still be considered high and confirm the conclusion of a strong and rather similar ice association for both species. Seasonal or monthly variation in the contribution of iPOM can be expected (Wang et al. 2016) but was not resolved in our study.

5. CONCLUSIONS

In summary, we found differences in both fatty acids and the $\delta^{13}C_{FA}$ values of specific trophic biomarkers in sympagic algae and phytoplankton as hypothesized. In contrast to our expectations, the 2 seal species were strongly separated in all fatty acid patterns, indicating a significant degree of dietary niche separation. Even though we found no differences in age classes for the 4 trophic biomarkers, our sample sizes were relatively small and disproportionate within age classes; hence, we recommend a complementary study where age-class differences could be more thoroughly explored. Finally, we hypothesized that sympagic carbon would be more likely to contribute to the diet of ringed seals because of their stronger association with sea ice. Instead, we found that sympagic carbon supported both harp and ringed seals similarly over the summer and into autumn (June, August, and September).

Since 2011, the Eurasian Basin has been almost ice free at the end of summer, with <10% sea-ice coverage remaining, and this area has experienced a continual northward retreat of sea-ice extent (Polyakov et al. 2017). Concomitantly, occurrences of new Atlantic fish species have been found in ringed seal diet (Bengtsson et al. 2020), as these boreal species expand into the Arctic (Renaud et al. 2012). Regardless of these changes, sea ice is still seasonally present within the European Arctic, and both harp and ringed seals continue to associate with this habitat. Their continued association with sea ice is reflected in their foraging behavior (Hamilton et al. 2016, 2021) and migratory patterns (Stenson et al. 2020), and is still apparent in the carbon sourcing to their diet (the present study). Given the current state of sea-ice loss in the Northern Barents Sea (Perovich et al. 2020), it remains to be seen if these seals will transition to a more open-water dominated lifestyle and diet, opt for potentially longer migration routes to the ice edge, or experience population size declines.

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