The role of sea ice algae-produced carbon in Arctic and Antarctic food webs

Dependency of polar life on a threatened food source

Dissertation

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Summary

The underside of sea ice in Polar Regions represents a natural habitat for heterotrophic organisms, such as copepods and amphipods. This under-ice fauna plays a key role in transferring carbon synthesized by sea ice-associated (sympagic) microalgae into associated pelagic and benthic food webs of polar ecosystems. Animals at higher trophic levels are adapted to feed on the under-ice fauna as well as on pelagic zooplankton and nekton. Polar ecosystems thrive significantly on ice algae-produced carbon depending on different periods of the year. Thus, the under-ice fauna and the associated pelagic food web are largely affected by multi-scale climate changes accompanied by the reduction of sea ice coverage and an increasing duration of the melt season. Until now, however, the degree to which polar food webs depend on sea ice-derived carbon is unclear.

The **overall aim** of this thesis is to quantify the transfer of ice algae-produced carbon from the sea ice into the under-ice community and from there into pelagic food webs in Arctic and Antarctic ecosystems, in order to improve our understanding of the potential ecological consequences of a changing sea ice environment for marine food web dynamics. Furthermore, spatial and seasonal differences in the utilization of ice algae-produced carbon within and between both hemispheres are investigated.

The sample collection in the central Arctic Ocean was carried out during the RV '*Polarstern*' expedition ARK XXVII-3 (PS80, August-September 2012) within the Amundsen and Nansen Basins. In the Southern Ocean, samples were collected during the RV '*Polarstern*' expeditions ANT XXIX-7 (PS81, August-October 2013) in the northern Weddell Sea and ANT XXIX-9 (PS82, December 2013-March 2014) offshore from the Filchner Ice Shelf.

Trophic interactions of important representatives of Arctic and Antarctic food webs are studied using lipid fingerprinting, stable isotope analysis (SIA) of natural abundance bulk carbon and nitrogen (BSIA), and compound-specific SIA (CSIA) of fatty acids (FAs). From the distribution of algae-produced FAs in the consumers (= marker FAs), the origin of carbon produced by diatoms versus dinoflagellates in key Arctic species (**Chapter I** and **II**) and key Antarctic species (**Chapters III-VI**) is investigated. Stable isotope mixing models are used to quantify the relative contribution of bulk carbon and marker fatty acids derived from ice algae versus pelagic phytoplankton to the carbon budget of the organisms. Additionally, the stomach contents of polar cod *Boreogadus saida* (**Chapter II**) and Antarctic krill *Euphausia superba* (**Chapter IV**) are investigated to provide information on the most recent diet composition and carbon sources compared to the long-term trophic signal derived from FA proportions and stable isotope compositions.

In the Arctic food web, a high contribution of ice algal carbon with up to 90% of the carbon budget of species with a known strong sea ice association, such as the amphipods *Apherusa glacialis* and *Onisimus glacialis*, is demonstrated. The results also suggest a substantial ice algae-carbon assimilation by rather pelagic species, such as *Calanus* copepods and the pelagic amphipod *Themisto libellula* during late Arctic summer, in which sympagic carbon contributed up to 55% of the carbon budget of these species (**Chapter I**). Furthermore, a high trophic dependency of polar cod on sea ice-associated resources is shown (up to 95% ice algal carbon of body carbon), indicating their high vulnerability in regards to alterations of the sympagic food web (**Chapter II**).

Chapter III addresses differences in the utilization of ice algal carbon by different developmental stages of Antarctic krill (Furcilia larvae, juveniles, adults) during late austral winter. It is shown that young developmental stages thrive significantly on ice algae produced carbon to survive their first winter, receiving up to two thirds of their carbon uptake from ice algae. The high spatial and temporal variability in diet and carbon sources of AC0 krill (larvae, juveniles) across the sampling area in the northern Weddell Sea is discussed in **Chapter IV**. Besides young *E. superba*, the amphipod *Eusirus latircarpus* demonstrates a particularly high trophic dependency on sea ice-related primary production during late austral winter, indicating a proportional contribution of ice algal carbon of up to 67% of their energy budget. Other important energy linkers indicate a switch from a predominantly pelagic lifestyle to a strong dependency on ice algae-produced carbon as the winter season progressed (**Chapter V**). Among the other abundant euphausiids collected offshore from the Filchner-Ronne Ice Shelf, *Euphausia crystallorophias* and *Thysanoessa macrura* show that ice algal carbon can serve as important carbon source during austral summer, accounting for up to 43% of the dietary carbon in these species (**Chapter VI**).

In summary, the applied state-of-the art techniques and statistical models allow for a reliable quantification of the contribution of ice algae-produced carbon to the carbon budget of ecological key species in both Polar Regions. The results imply that functioning and carbon dynamics of food webs in both Polar Regions are likely affected by changes in sea ice coverage and thus ice algal primary production. Due to the close connectivity between the sea ice ecosystem and the pelagic system, these consequences will subsequently impact the entire polar ecosystems, their fish populations and subsequently mammal populations. Moreover, these large amounts of required carbon for the nutrition of polar food webs, currently fulfilled by ice algae, can likely not be substituted by an increased pelagic primary production.

Zusammenfassung

Die Unterseite des Meereises in den Polargebieten bietet einen natürlichen Lebensraum für heterotrophe Organismen, wie zum Beispiel für Ruderfußkrebse (Copepoda) und Flohkrebse (Amphipoda). Diese Untereisfauna spielt eine wichtige Rolle für die Weitergabe von durch Eisalgen produziertem Kohlenstoff in assoziierte pelagische und benthische Nahrungsnetze in Arktis und Antarktis. Höhere Organismen ernähren sich zum einen von diesen eis-assoziieren Organismen, aber auch von pelagischem Zooplankton und Nekton. Polare Ökosysteme können, je nach Jahreszeit, stark abhängig von dem von Eisalgen produzierten Kohlenstoff sein. Daher sind Untereis-Organismen und assoziierte pelagische Nahrungsnetze stark von klimatischen Veränderungen betroffen, die mit dem Rückgang der Meereisbedeckung und der Verlängerung der Eisschmelze einhergehen. Bis heute ist jedoch unklar, wie stark die Abhängigkeit polarer Nahrungsnetze von Eisalgenkohlenstoff ist.

Das **Ziel** dieser Arbeit ist es, zu quantifizieren, wieviel Eisalgenkohlenstoff von eis-assoziierten Organismen aufgenommen und als Nahrung an höhere Organismen in arktischen und antarktischen Nahrungsnetzen weitergeleitet wird. Dies ist wichtig, um potentielle Auswirkungen der Änderungen der Meereishabitate auf polare Ökosysteme besser abschätzen zu können. Ein weiteres Ziel ist es, regionale und saisonale Unterschiede im Transfer von Eisalgenkohlenstoff in beiden Hemispheren zu analysieren und zu vergleichen.

Die Proben für diese Arbeit wurden im zentralen Arktischen Ozean mit RV '*Polarstern*' (ARK XXVII-3, PS80) zwischen August und September 2012 im Amundsen und Nansen Becken genommen. Im Südlichen Ozean wurden Proben im nördlichen Weddellmeer zwischen August und September 2013 (ANT XXIX-7, PS81) und im südlichen Weddellmeer nahe des Filchner-Eisschelfs zwischen Dezember 2013 und März 2014 genommen (ANT XXIX-9, PS82).

Trophische Wechselwirkungen arktischer und antarktischer Schlüsselarten werden anhand der Zusammensetzung stabiler Isotope organischer Kohlenstoff- und Stickstoffkomponenten (BSIA- Bulk Stable Isotope Analysis), sowie an der Verteilung spezifischer Fettsäuren (= Markerfettsäuren), und derer isotopischer Zusammensetzung (CSIA- Compound-specific Stable Isotope Analysis) untersucht. Der Ursprung der Kohlenstoffquellen von den Algengruppen Diatomeen und Dinoflagellaten in Arktischen Organismen (**Kapitel I** und **II**) und Antarktischen Organismen (**Kapitel III-VI**) wird von der Verteilung algen-synthetisierter Fettsäuren in den Organismen abgeleitet. Basierend auf der stabilen Isotopenzusammensetzung von Algen und Organismen werden Modelle angewendet, um den prozentualen Anteil des Eisalgenkohlenstoffs im Vergleich zu pelagischem Kohlenstoff am Kohlenstoffbudget der Organismen zu bestimmen. Zusätzlich wird der Mageninhalt von Polardorsch *Boreogadus saida* (**Kapitel II**) und Antarktischem Krill *Euphausia superba* (**Kapitel IV**) untersucht, um das trophische Signal der kürzlich aufgenommenen Nahrung mit dem Signal von Fettsäuren und stabilen Isotopen zu vergleichen, das über einen längeren Zeitraum integriert wird.

Meereis-assoziierte Organismen des Arktischen Nahrungsnetzes zeigen eine starke Abhängigkeit von dem von Eisalgen produzierten Kohlenstoff. Bei den Amphipoden *Apherusa glacialis* und *Onisimus glacialis* macht Eisalgenkohlenstoff bis über 90% des Gesamtkohlenstoffbedarfs im Spätsommer aus. Weiterhin wird dargestellt, dass auch Organismen, die vorwiegend im Pelagial und in größerer Wassertiefe zu finden sind, wie Ruderfußkrebse (*Calanus* spp.) und der pelagische Amphipod *Themisto libellula*, einen Großteil ihres Kohlenstoffbedarfs (bis zu 55%) aus Eisalgen beziehen (**Kapitel I**). Ein hoher Beitrag zum Kohlenstoffbudget des Polardorsches (bis zu 95%) wird ebenfalls von Eisalgen geleistet (**Kapitel II**), was auf eine starke Anfälligkeit dieser Arten hinsichtlich klimatisch bedingter Änderungen des Meereissystems hinweist.

In **Kapitel III** werden die Unterschiede in der Aufnahme von Eisalgenkohlenstoff zwischen unterschiedlichen Entwicklungsstadien des Antarktischen Krills (Larven, Juvenile, Adulte) im Spätwinter herausgestellt. Es wird gezeigt, dass insbesondere junge Entwicklungsstadien bis zu zwei Drittel ihres Kohlenstoffbedarfs aus Eisalgen beziehen, um ihren ersten Winter zu bestehen. Die große räumliche und zeitliche Variabilität der Nahrungs- und Kohlenstoffquellenzusammensetzung larvalen und juvenilen Antarktischen Krills im nördlichen Weddellmeer ist in **Kapitel IV** diskutiert. Neben jungen Lebensstadien von *E. superba* wird die starke Abhängigkeit des Amphipods *Eusirus laticarpus* von Eisalgenkohlenstoff in **Kapitel V** erörtert, dessen Kohlenstoffbedarf bis zu 67% von Eisalgen gedeckt wird. Viele wichtige Antarktische Arten stellen ihre vorwiegend pelagische Nahrungsweise auf eisalgen-produzierten Kohlenstoff während der Winterperiode um, da organischer Kohlenstoff in der Wassersäule während des Winters stark verarmt ist (**Kapitel V**). Weiterhin wird Eisalgenkohlenstoff auch während des südlichen Sommers als wichtige Kohlenstoffquelle für die Krillarten *Euphausia crystallorophias* und *Thysanoessa macrura* von der bisher wenig untersuchten Region um das Filchner-Ronne-Eisschelf erkannt, mit Beiträgen von bis zu 43% des Energiebedarfs dieser Tiere (**Kapitel VI**).

Zusammenfassend wird dargestellt, dass die angewendeten modernen Analyseverfahren und statistischen Modelle eine zuverlässige Quantifizierung des Beitrags an Eisalgenkohlenstoff zum Kohlenstoffbedarf ökologischer Schlüsselarten in beiden Polarregionen ermöglichen. Die Ergebnisse belegen, dass die Funktionsweise und der Kohlenstofftransfer in den marinen Nahrungsnetzen der Polargebiete von den Veränderungen der Meereisbedeckung und damit der Primärproduktion durch Eisalgen sehr wahrscheinlich beeinträchtigt werden. Aufgrund der engen Verbindung zwischen Meereissystem und pelagischem Nahrungsnetz werden sich die Folgen der klimabedingten Meereisveränderung schließlich auch auf die gesamten polaren Ökosysteme, deren Fischbestände und schützenswerte Säugetiere auswirken. Des Weiteren ist es unwahrscheinlich, dass die großen Mengen an benötigtem Kohlenstoff für die Ernährung zahlreicher Schlüsselarten, die derzeit noch durch Eisalgen abgedeckt werden, durch eine verstärkte Primärproduktion im Pelagial ersetzt werden können.

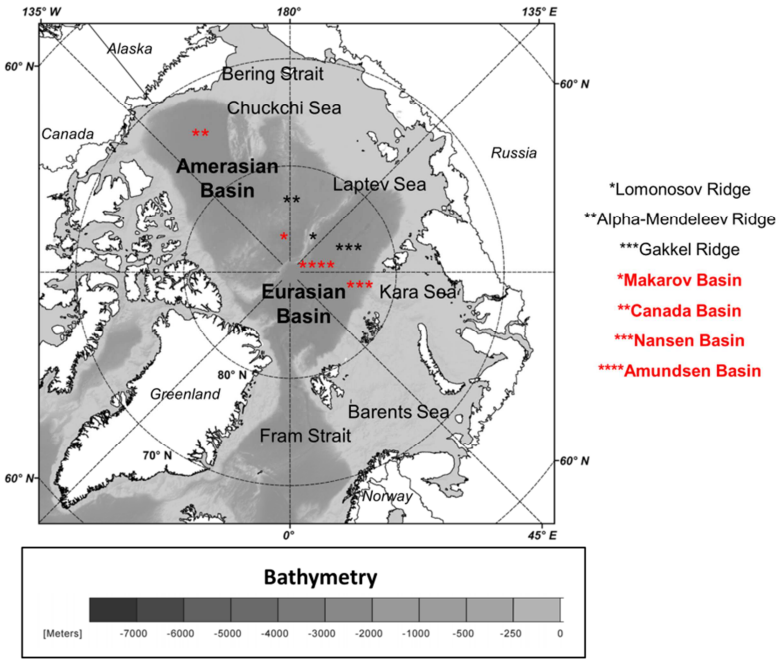
Abbreviations

AB	Amundsen Basin
BSIA	Bulk Stable Isotope Analysis
CAO	Central Arctic Ocean
Chl *a*	Chlorophyll *a*
CSIA	Compound-Specific Stable Isotope Analysis
FA	Fatty Acid
GC-c-IRMS	Gas Chromatography- combustion- Isotope Ratio Mass Spectrometry
I-POM	Ice-associated Particulate Organic Matter
NB	Nansen Basin
P-POM	Pelagic Particulate Organic Matter
SO	Southern Ocean
SUIT	Surface and Under-Ice Trawl
TL	Trophic Level

1. Introduction

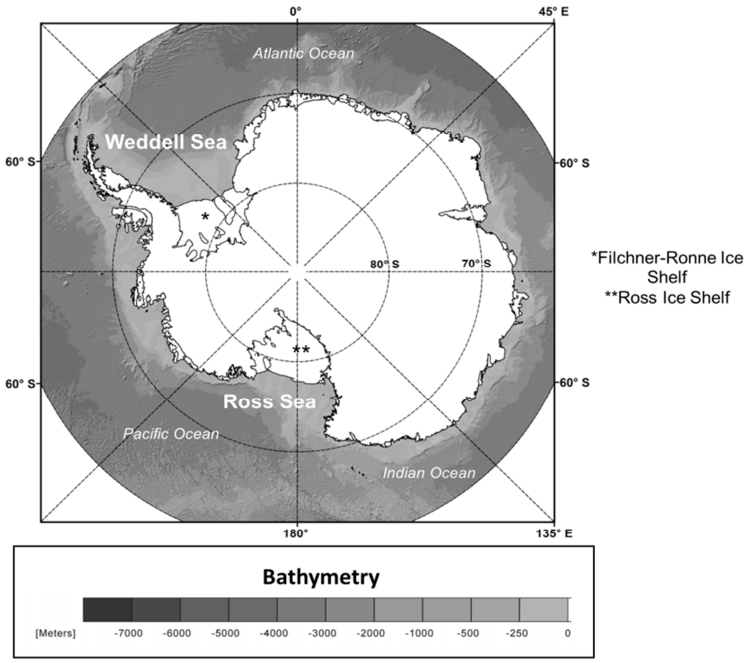
1.1 The Polar Oceans: Impact of environmental changes

In the Northern Hemisphere, north of 66°34'N, the Arctic Ocean covers an area of ~ 14 Mio. km^2 within the Arctic Circle, surrounded by the continental land masses of Europe, Asia and North America (**Figure 1**). More than half of the Arctic Ocean is occupied by shallow shelves (typically < 100 m). They play an important role in the transformation of water masses entering the global circulation, and dominate carbon fluxes and biochemical processes within the Arctic ecosystem (Aagaard et al. 1981; Stein and MacDonald 2004). Two basins, the Amerasian and the Eurasian Basin, structure the deep-sea central Arctic Ocean, divided by the Lomonosov Ridge with a sill depth of ~ 1600 m. The Amerasian Basin includes the ~ 4000 m deep Makarov Basin and the Canada Basin (~ 3800 m), separated by the Alpha-Mendeleev Ridge. The Eurasian Basin is divided by the Nansen-Gakkel Ridge into the ~ 4000 m deep Nansen Basin and the slightly deeper Amundsen Basin (~ 4500 m). The water in the Amerasian Basin originates from Pacific waters through the Bering Strait, whereas Atlantic waters enter the Eurasian Basin via the Barents Sea and Fram Strait. Unlike the surrounding shelf regions in the marginal seas, which are generally considered seasonally ice-covered waters (Polyakov et al. 2003; Shapiro et al. 2003), high-Arctic deep-sea regions north of 78°N in the Eurasian Basin, with bottom depths > 4000 m, are permanently ice-covered, with a high percentage of thick multi-year ice. Sea ice extent reaches its minimum in September (mean 5 x 10^6 km^2), and its maximum in March (mean 15 x 10^6 km^2) (Arrigo 2014).



▲***Figure 1.*** *Map of the Arctic Ocean, showing the major basins and marginal seas. Bathymetry were mapped using the IBCAO grid (Jakobsson et al. 2012).*

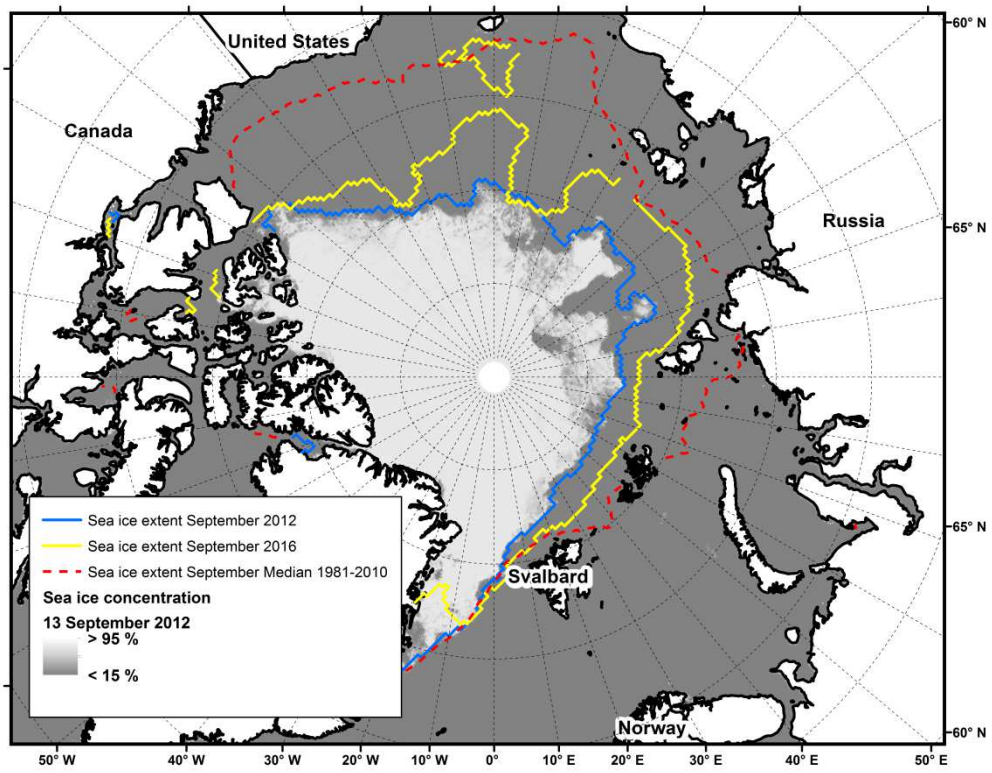
The Southern Ocean surrounds the Antarctic continent in the Southern Hemisphere, extending from the coast of Antarctica to a latitude of 60°S, comprising parts of the Atlantic, Indian and Pacific Oceans (**Figure 2**). In contrast to the Arctic, which represents a frozen ocean surrounded by continental land masses and open oceans, the frozen continent Antarctica is only surrounded by oceans. With no land barrier to the north, the average position of the Antarctic Polar Front is often used to define the northern limit of the Southern Ocean. The Antarctic marine realm is characterized by large latitudinal differences. For example, South Georgia is located at 55°S, whereas the Ross Sea extends to 75°S (Nicol et al. 2006). The Antarctic Circumpolar Current (ACC) is an important hydrographical feature in the Southern Ocean, encircling the Antarctic continent, and flowing eastwards through the Atlantic, Indian and Pacific Oceans. The ACC transports more water than any other current and is described as the most powerful current in the world (Griesel et al. 2012). Most of the sea ice around Antarctica is first-year ice (FYI), which formed during the previous fall or winter season. However, in some regions, particularly in the Weddell Sea, sea ice can be perennial, meaning it has survived at least one summer melt season. Annual fast ice in coastal regions was found to grow to a maximum thermodynamic thickness of up to 2 m (Heil et al. 1996), whereas the more dynamic pack ice rarely grows thicker than 0.3 m due to thermodynamic processes (Allison and Vvorby 1994; Jeffries et al. 1997). This is significantly thinner than Arctic FYI. Ice floes do not grow thicker due to the impact of ocean heat fluxes, wind, waves, ocean currents and tides (Worby et al. 1998). Sea ice in the Southern Hemisphere reaches a minimum of around 3 x 10^6 km^2 in February and a maximum of around 19 x 10^6 km^2 in September (Arrigo 2014). The sea ice extent minimum in the Southern Ocean is slightly lower than in the Arctic Ocean, however, the maximum is slightly larger than in the Arctic, with an area 1.5 times that of the Antarctic continent. This seasonal change from open water to sea ice cover represents one of the largest changes in physical properties on a global scale (Nicol et al. 2008).



▲***Figure 2.*** *Map of the Antarctic continent with surrounding water masses. Bathymetry were mapped using the ICCSO grid (Arndt et al. 2013).*

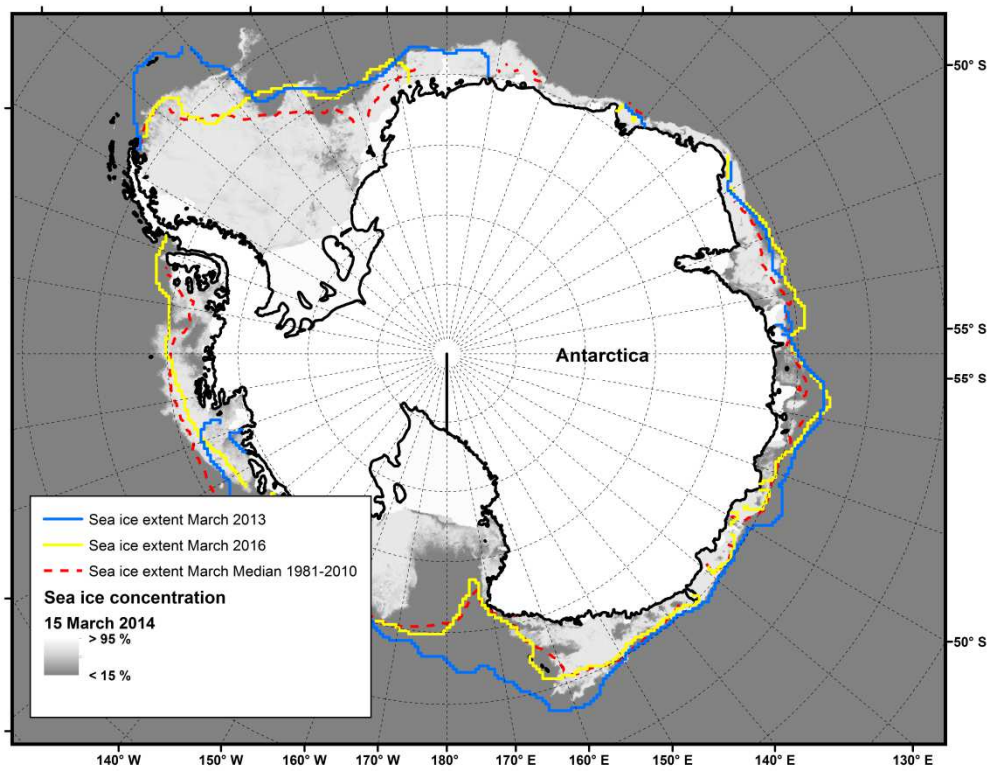
The consequences of climate change are particularly noticeable in the Polar Regions. The effect of climate change differs between the hemispheres due to considerable dissimilarities in geographical position and oceanographical structure. Numerous studies have provided evidence that the sea ice characteristics in terms of structural composition and distribution are highly sensitive to climatic conditions in both Polar Oceans (e.g. Serreze et al. 2007; Comiso et al. 2011; Renner et al. 2014). Due to increased temperatures, summer melt periods in most mid- and high-latitude regions are prolonged (Walther et al. 2002).

In the Arctic, sea ice coverage and thickness have significantly decreased in the past decades (Johannessen et al. 2004; Rigor and Wallace 2004; Comiso et al. 2008; Kwok et al. 2009; Kwok and Rothrock 2009; Markus et al. 2009; Simmonds 2015; Harada 2016), accompanied with a change of ice properties from a largely perennial ice coverage to a seasonal coverage with more open water during summer (i. e. less multi-year ice, more first-year ice) (Kwok 2007; Lindsay et al. 2009; Maslanik et al. 2011). In September 2012, the total Arctic sea ice extent, area, and thickness have had their lowest levels since satellite observations started (Comiso et al. 2008; Stroeve et al. 2008; Lindsay et al. 2009; Parkinson and Comiso 2013) (**Figure 3**). A predominantly ice-free Arctic during summer is predicted for the end of the current century (Johannessen et al. 2004).



▲***Figure 3.*** *Map of the Arctic Ocean, showing the sea ice extent during the sea ice minimum in 2012 and during the most recent summer in 2016. The comparison to the median sea ice extent (1981 to 2010) demonstrates the drastic sea ice retreat in the northern hemisphere. Sea ice concentration data were acquired from Bremen University (http://www.iup.uni-bremen.de:8084/amsr/)) (Spreen et al. 2008). Median sea ice extent data were acquired from NSIDC (Fetterer et al. 2002).*

Based on the Intergovernmental Panel on Climate Change's (IPCC) fifth assessment report, the Antarctic has responsed relatively more slowly to climate change compared to the Arctic (IPCC 2014). Thus far, global warming indicated a more localized and sometimes regionally contrasting impact regarding e.g. alterations of the sea ice cover in the Southern Ocean (Zwally et al. 2002; Massom and Stammerjohn 2010; Stammerjohn et al. 2012; IPCC 2014; Turner et al. 2014) (**Figure 4**). Overall, Antarctic sea ice extent has shown a slight increasing trend (Gagné et al. 2015; Turner et al. 2016). However, the region surrounding the Antarctic Peninsula has experienced large sea ice retreat and collapse of ice shelves (Vaughan et al. 2003; Meredith and King 2005; Paolo et al. 2015). Moreover, models predict a dramatic shrinkage of the Antarctic sea ice cover in the next century (Rind et al. 1997; Meehl et al. 2000; Liu and Curry 2010; Gutt et al. 2015).



▲***Figure 4.*** *Map of the Antarctic region, showing the sea ice extent during summer 2013 and during the most recent summer in 2016. In comparison to the Arctic, changes in sea ice extent are much less pronounced. Sources of sea ice concentration and extent as described in* ***Figure 3.***

Both Polar Regions have major influences on the global ocean and the earth's climate. Changes in polar climate regarding temperature and precipitation affect other parts of the world by e.g. increased sea levels from enhanced melting of ice sheets and glaciers, and slowing oceanic heat transport (Bintanja and Selten 2014; Slangen et al. 2014; Vihma 2014; Dutton et al. 2015; Romero and Emanuel 2017). In particular, changes in the Southern Ocean are of great significance, because many water masses are produced here and spread throughout the global ocean (Whitworth et al. 1998; Purkey and Johnson 2013; Rintoul and Naveira Garabato 2013). Changing physical parameters, including reduced ocean convection and deepwater formation are predicted to affect the thermohaline circulation and ocean ventilation, ultimately affecting ocean currents and climatic conditions in other regions of the earth (Murphy and Mitchell 1995; Budd and Wu 1998; Hirst 1999; Frankcombe et al. 2013; de Lavergne et al. 2014; Galaasen et al. 2014). Sea ice modulates the exchange of heat and mass between atmosphere and ocean, as well as the exchange of heat and moisture with the atmosphere (albedo feedback system) (Budyko 1969; Perovich et al. 2007). The shrinking cryosphere causes additional warming of the surface due to enhanced absorption of solar radiation, resulting in higher temperatures of air and ocean, which in turn, will further decrease the ice cover, particularly in the Arctic (Johannessen et al. 2004; Perovich et al. 2011; Riihelä et al. 2013; Pistone et al. 2014). In addition, thawing of permafrost is accompanied by the release of large amounts of greenhouse gases, which can further accelerate climate warming (Koven et al. 2013; Schuur et al. 2015). Changes in

landscapes due to an altered sea ice and permafrost profile will ultimately affect human communities in the Arctic and their traditional lifestyles (Durkalec et al. 2015; Pearce et al. 2015).

Environmental responses to global warming in the Polar Regions have an impact on e.g fish populations with disadvantages for local and global fisheries (Reist et al. 2006; Hollowed et al. 2013a). Rising water temperatures can trigger a poleward expansion of coldwater adapted species, causing competition of existing niches, ultimately changing prevailing community structures (Vermeij and Roopnarine 2008; Forcada and Trathan 2009; Renaud et al. 2012). As the Arctic Ocean and the Southern Ocean play a key role in global food reserve, concerns are raised about the sustainability of important coldwater fisheries resources, endangered by loss of habitat and spawning grounds (Croxall and Nicol 2004; Miller 2014; Nicol and Foster 2016). The potentially reduced role of important fisheries resources due to climatic changes in the future might affect resource management, conservation policy and traditional subsistence hunting (McBride et al. 2014). Moreover, polar organisms provide substances with nutritional value, such as Omega- fatty acids in fish and krill, with a high commercial and industrial interest and benefit for human's health (Tou et al. 2007; Nicol et al. 2012).

Another highly debated consequence of shrinking sea ice in the Arctic is the alteration of current ship transportation routes. The opening of new sea routes across the Arctic Ocean will have major trading and strategic implications for shipping, fishing and tourism. Shipping will significantly benefit from increased opportunities along high-latitude routes, for example by saving thousands of miles transisting the Northern Sea Route above Russia, enabling the reduction of time and operational costs for oil and gas industry (Xu et al. 2011). However, increased maritime traffic comes along with amplified environmental pollution for the Arctic Ocean (Ho 2010). Moreover, increased costs due to reduced transportation capabilities across frozen ground and water might be expected (Anisimov et al. 2007).

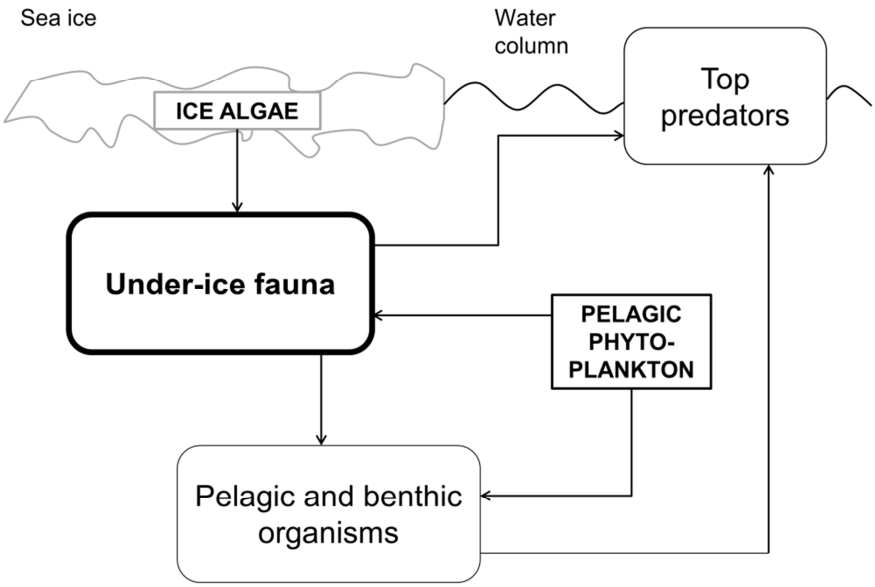
1.2 Sea ice algae-produced carbon in polar ecosystems

Pelagic and ice-associated (sympagic) microalgae constitute the basis of the marine food web, producing energy in the form of organic carbon by photosynthesis. Whereas pelagic algae exist freely moving in the water column, sea ice algae are adapted to inhabit the brine-filled interspaces in sea ice, called lacunes. Salts are rejected during freezing, and brine pockets form subsequently, enabling the formation of the unique ice-associated ecosystem (Weeks and Ackley 1986). Besides microalgae, bacteria, protists, and metazoans constitute the sea ice community (Melnikov 1997; Arrigo 2014). Ice algae are able to grow under very low light conditions (Michel et al. 1988), mostly within the bottom layer of the sea ice due to the proximity to seawater nutrients (Arrigo 2014) (**Figure 5**). The taxonomic composition of autotrophic communities in sea ice is controlled by species-specific responses to environmental conditions, including temperature, salinity, light and nutrient concentrations (Petrou and Ralph 2011). In both the Arctic and Antarctic, diatoms (Bacillariophyceae) dominate the ice-associated

microalgae communities, whereas individual sea ice communities usually consist of 30 to 70 different diatom species (Riaux-Gobin et al. 2003; Werner et al. 2007).

▲***Figure 5.*** *Layer of ice-associated microalgae on the bottom of Antarctic sea ice. Photo: Julia Ehrlich.*

Sea ice algae are an important carbon source for organisms that inhabit the sea ice itself (in-ice fauna) and for organisms dwelling at the ice-water interface, e.g. copepods, amphipods and Antarctic krill (under-ice fauna; **Figure 6**) (Aarset 1991; Siegel et al. 1992; Werner 1997; Bluhm et al. 2010; David et al. 2017). Herbivorous grazers can feed on ice algae that are released in the water column during ice melt, graze at the underside of the sea ice, e.g. found for Arctic copepods and amphipods (Sherman et al. 1988; Werner 1997), or scrape off the ice-associated material, as e.g. found for Antarctic krill (Marschall 1988). This under-ice community has a central position in the food web of polar ecosystems by transferring energy in the form of ice algae-produced carbon into the associated pelagic and benthic food webs (Laws 1985; Norkko et al. 2007; Budge et al. 2008). Animals at higher trophic levels (e.g. fishes, birds, mammals) are adapted to feed on the under-ice fauna as well as on zooplankton and nekton (Clarke et al. 2007; Harter et al. 2013; Hop and Gjøsæter 2013). The upper trophic levels thrive on carbon that was ultimately synthesized by algae and show therefore an indirect dependency on the ice algae-produced biomass. With a loss of 75-80% of the organic matter from one trophic level to another due to e.g. respiration and microbial degradation of dissolved organic matter, only a small portion of the primary produced carbon reaches the seabed, where it can be utilized by opportunistic benthic organisms (cryo-benthic coupling) (Sakshaug 2004).



▲***Figure 6.*** *Flux of ice algae-produced and pelagic produced carbon through a polar sea ice ecosystem (redrawn after Flores 2009).*

During winter, algal biomass in sea ice is usually low due to low light availability, low temperature and high salinity in the brine channels (Werner et al. 2007). In spring, increasing temperatures and light transmission, accompanied by decreasing salinity, trigger the ice algae bloom, where ice algae abundances can increase by five to seven orders of magnitude (Riaux-Gobin et al. 2003; Mundy et al. 2005). The timing of the bloom depends on the region, and thus, light availability. For example, in high-Arctic regions north of 78°N, the productive season starts in May, and thus, several weeks later than in southern Arctic regions (Leu et al. 2011). When nutrient exchange is enhanced due to larger brine volumes, sea ice blooms peak prior to ice melt, usually in late spring or early summer (Arrigo and Sullivan 1994; Garrison et al. 2005). Eventually, ice algae abundances decline when sea ice melts and nutrient limitation and grazing pressure are enhanced (Hegseth and von Quillfeldt 2002; Elliott et al. 2012). As the sea ice melt season progresses and the sea ice breaks up, a subsequent bloom of algae in the water column follows, caused by a stronger stratification of the water surface layer and increased light penetration. A secondary ice algae bloom can occur in autumn, when sea ice begins to re-form. These blooms are typically shorter and characterized by less algal biomass (Kennedy et al. 2002; Meiners et al. 2003).

The distribution of ice algal biomass is predominantly patchy (Garrison 1991; Rysgaard et al. 2001), reflecting e.g. variations in surface snow cover, which directly influences the transmission of light through the ice below (Gosselin et al. 1986; Perovich 1990). Biomass in Antarctic sea ice is generally higher compared to Arctic sea ice (Arrigo et al. 2008a; Meiners et al. 2012). The marginal ice zone (MIZ) is a region of high primary production in the Southern Ocean (Arrigo and Thomas 2004). Usually pelagic algae provide the bulk of the primary produced carbon, but in polar sea ice zones, sea ice algae can in some areas account for large parts of the primary production for long periods of

the year (Gosselin et al. 1997; Lizotte 2001; McMinn et al. 2010; Saenz and Arrigo 2014; Fernández-Méndez et al. 2015). In the Arctic, especially in spring, it was shown that sea ice algae represent an important food source for pelagic consumers during the early stages of ice melt (Michel et al. 1996; Sakshaug 2004). In the Southern Ocean, sea ice algae are assumed to represent a sufficient high-quality food source particularly during austral winter, when the pelagic primary productivity is critically low (Lizotte 2001; Arrigo and Thomas 2004; Arrigo et al. 2008a; McMinn et al. 2010).

Sea ice is a critical feature of polar ecosystems, e.g. in terms of structuring the habitat, providing food resources and shelter from predators for many organisms (Thomas and Dieckmann 2008; Gradinger et al. 2010; Arrigo 2014; David et al. 2015, 2017). Thus, alterations of sea ice properties in both Polar Regions will cause ecological responses of polar inhabitants, from individual species to community levels, such as seasonal distribution, migration patterns, reproductive success, and consequently changes in species abundances (Constable et al. 2014). For example, climate change was found to affect the reproductive grounds of krill in the Southern Ocean. Consequently, fluctuations in recruitment and populations due to reduced sea ice area of these important energy transmitters will have a cascading affect on the entire ecosystem (Walther et al. 2002; Turner et al. 2015). As a result of reduced sea ice thickness and coverage area, ice break-up and onset of the phytoplankton bloom start earlier. This has triggered an increase in overall primary production due to enhanced light availability in the water column (Arrigo and Thomas 2004; Arrigo and van Dijken 2011; Fernández-Méndez et al. 2015; Moreau et al. 2015). The response of the ice-associated primary production to changes in the sea ice environment, however, remains uncertain. For the Arctic, it has been suggested that the thinning ice cover and increased light transmittance could trigger an increase of the ice algal productivity as a result of an increased photosynthetic activity (Nicolaus et al. 2012). Other studies suggest that the declining sea ice extent will result in a drop of the ice-associated primary production (Arrigo et al. 2008b; Vancoppenolle et al. 2013), which has a direct impact on ice-associated herbivores due to reduction of their ultimate food source. For example, the dramatic decline in krill (from 38 to 75% per decade) in the south-west Atlantic was attributed to reduced abundance of ice algae (Atkinson et al. 2004). At a higher level in the food web, a likewise decrease in populations size was found for sea ice-dependent penguins, particularly Adelié and Emperor penguins (Croxall et al. 2002; Ainley et al. 2003; Jenouvrier et al. 2014). Seabirds and marine mammals with specific breeding sites associated with sea ice will be also affected by shifts in their foraging habitat and migration of their prey (Anisimov et al. 2007).

1.3 Food webs in Polar Regions

The principal structure of a marine food web represents the trophic transfer of energy through the aquatic ecosystem, combining the interactions of numerous inter-connected food chains (McCann et al. 1998). Irrespective of spatial and temporal varying trophic patterns of the highly complex food webs, they are often simplified and generalized. Here, from the pelagic/sympagic primary producers, energy is transferred as particulate

organic matter (POM) to zooplankton herbivores and thereby to higher predators, and furthermore to the microbial loop and to the benthic system directly derived from the primary producers or indirectly from zooplankton via detritus (Pomeroy 1974; Azam 1998; Clarke and Harris 2003; Clarke et al. 2007). The trophic hierarchy in the food web is reflected by a number of trophic levels, where the primary producers occupy the lowest trophic level (i.e. 1) and top predators represent the highest trophic level, integrating the number of feeding links separating a species from the primary production (Thompson et al. 2007). When organisms feed on more than one trophic level, trophic omnivory results in non-integer trophic positions (Vandermeer 2006).

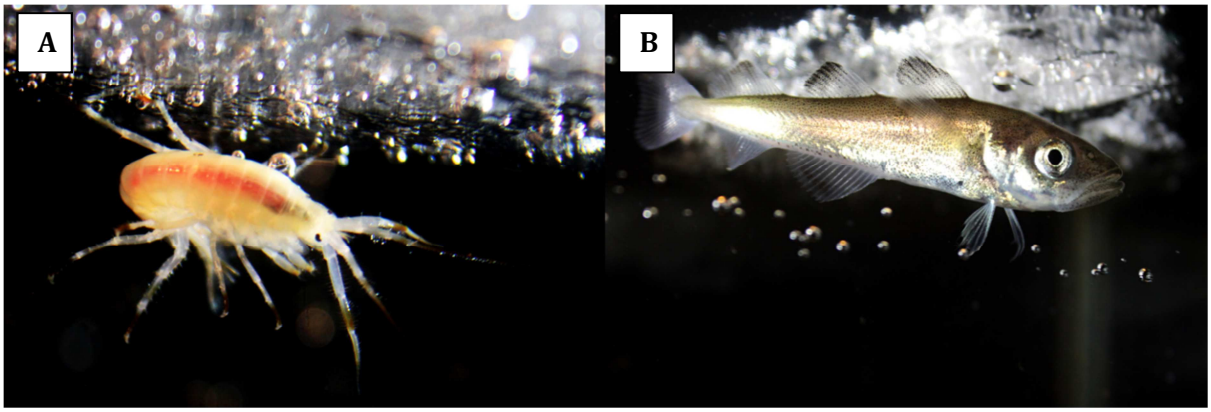
Impact of grazing, sinking fluxes, and storage of dissolved organic matter are subject to large spatio-temporal variability, influenced by multiple environmental and ecological factors, including sea ice dynamics (Frost 1991; Olli et al. 2007; Sejr et al. 2007). In previous studies, Arctic microzooplankton was estimated to consume between 20 and 100% of the entire primary production (Capriulo and Carpenter 1983; Cosper and Stepien 1984). Larger zooplankton, such as copepods and amphipods, were also found to contribute substantially to the carbon flux to higher trophic levels (Hobson et al. 2002). In the Southern Ocean, krill and salps were estimated to graze around 50% of the primary produced biomass (Pakhomov et al. 2002). However, Coyle and Cooney (1988) found that a low zooplankton population in early spring can leave a phytoplankton bloom largely ungrazed, whereas the vertical flux is reduced in autumn (Sejr et al. 2007). Furthermore, organic matter flux in bacteria can be a major pathway; it was suggested that one half of the oceanic primary production is channeled into the microbial loop, with a high variability in time and space (Azam et al. 1983; Rich et al. 1997). POM is exported towards deep waters and benthic communities (benthic-pelagic coupling) mainly by the production of fast-sinking particles, such as ungrazed algae, fecal pellets, and organic debris, the vertical migration of zooplankton, and microbial and metazoan metabolism in deep waters (Cho and Azam 1988; Longhurst et al. 1990; Piepenburg 2005; Manno et al. 2015). Moreover, carbon is transferred to the seabed in form of dissolved inorganic matter in sinking dense water, e.g. Antarctic Bottom Water and North Atlantic Deep Water. It has been estimated that up to 40% of the primary produced biomass is exported out of the mixed layer via sinking and active transport (Henson et al. 2011). When algal biomass is abundant and grazers are scarce, the vertical export of organic matter can be considerable, especially over shallow continental shelves (Lovvorn et al. 2005; Tremblay et al. 2006; McTigue and Dunton 2014). In deep-sea regions, however, food limitation for benthic organisms is increased due to the enhanced utilization by pelagic consumers (Mintenbeck et al. 2007; Smith et al. 2008). POM reaching the seafloor may be consumed upon deposition (Boetius et al. 2013), or provide long-term food sources for benthic communities (Mincks et al. 2005).

In the Arctic, zooplankton-fish connections dominate, whereas in Antarctic food webs, the interactions between zooplankton-seabird and marine mammals is more pronounced, and the connection to fish pathways is more locally restricted. Benthic-pelagic coupling is more important in Arctic food webs due to the extensive and shallow

shelf areas in the Arctic compared to the relatively deeper continental shelves in the Southern Ocean (Carmack and Wassmann 2006; Murphy et al. 2007, 2016; Smith et al. 2007; Hop and Gjøsæter 2013).

1.3.1 Arctic

Arctic food webs are typically characterized by low diversity, and biomass is often dominated by a few species due to harsh environmental conditions, causing the development of highly specialized organisms (Kosobokova and Hirche 2009; Søreide et al. 2010). Herbivorous copepods, such as *Calanus glacialis* Jaschnov (1955) and *C. hyperboreus* Krøyer (1838), dominate the zooplankton biomass in high Arctic waters, and are important algae grazers (Conover and Huntley 1991; Auel and Hagen 2002; David et al. 2015). Declining sea ice coverage could lead to alterations regarding reproduction and growth cycles of these copepods, since their life cycles are adapted to the seasonal progression of the pelagic and sympagic algae blooms (Søreide et al. 2010). A potential mismatch between the two primary production peaks of high-quality food and the reproductive cycle of key Arctic grazers may have negative consequences for the entire lipid-driven Arctic marine ecosystem. Consequently, organisms feeding on copepods directly, such as the amphipods *Gammarus wilkitzkii* Birula (1897) (**Figure 7A**) and *Themisto libellula* Lichtenstein (1822), or indirectly, such as seals and seabirds, will be affected by changes at lower trophic levels. For example, the widely distributed polar cod *Boreogadus saida* Lepechin (1774) (**Figure 7B**) were found to feed extensively on calanoid copepods, such as *C. glacialis*, and amphipods, such as *Apherusa glacialis* Hansen (1888) (Lowry and Frost 1981; Lønne and Gulliksen 1989; Scott et al. 1999; Benoit et al. 2010; Majewski et al. 2016). Both species can receive a large part of their carbon budget from sea ice algae (Søreide et al. 2006; Wang et al. 2015), transferring the sea ice-derived carbon along the marine food chain to apex predators. The energy flow from ice algae through calanoid copepods and amphipods, via polar cod to top predators, such as narwhales, belugas and seabirds (Bradstreet and Cross 1982; Welch et al. 1993), represents a strong and highly efficient pathway within the Arctic food web (Welch et al. 1992). However, the potentially high trophic dependency on ice algae as a primary carbon source reveals the weakness of this interaction in the light of ongoing changes of the sea ice environment. Declining sea ice coverage can result in lower food availability and quality for grazers (Leu et al. 2006). Reduction of spawning grounds for polar cod would additionally and ultimately affect the prosperity of end members (Moore and Huntington 2008; Li et al. 2009).



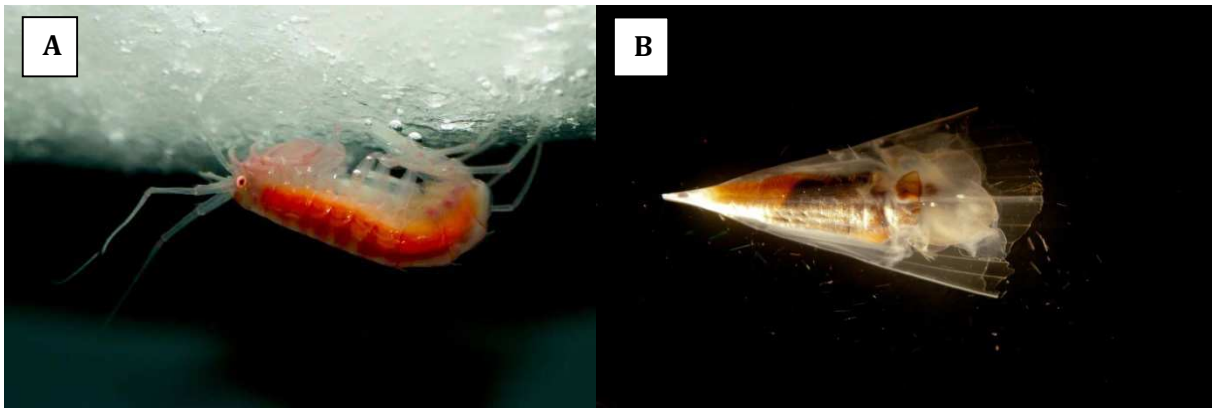
▲***Figure 7.*** *The ice-amphipod Gammarus wilkitzkii (**A**) and polar cod Boreogadus saida (**B**) as representatives of the Arctic food web. Photos: Hauke Flores.*

1.3.2 Antarctic

The Antarctic krill *Euphausia superba* Dana (1850) (**Figure 8**) is one of the most abundant metazoan species on earth in terms of numbers and biomass, and its abundance clearly dominates many Antarctic regions, constituting about 50% of the standing stock of zooplankton in the Southern Ocean (Hopkins 1985; Voronina 1998; Nicol 2006). Thus, *E. superba* constitute a major trophic link between primary production and upper trophic levels in the Antarctic. In early studies, Antarctic food chains have been simplified to algae - Antarctic krill - whales, assuming a highly efficient energy transfer due to the short trophic linkage (Murphy 1962; Hempel 1985). However, the importance of particular energy transmitters is subject to large regional variability. The Antarctic krill-based food chain is restricted spatially, and is particularly important in the seasonal ice zone (Brierley and Thomas 2002; Nicol 2006, 2008). In closer proximity to the Antarctic continent, *E. superba* are numerically replaced by another euphausiid, the ice krill *Euphausia crystallorophias* Holt & Tattersall (1906), occupying a central position in the neritic food web (Thomas and Green 1988; Schnack-Schiel and Mujica 1994). *E. superba* were frequently described as opportunistic feeders, feeding on both, ice algae and phytoplankton, and rely on ice-associated resources particularly during winter (Daly 1990; Meyer et al. 2009). Thus, changes in the sea ice environment will likely affect krill, and subsequently the functionality of this efficient food chain, with an ultimate impact on predators, such as penguins, fur seals, crabeater seals and baleen whales (Nicol et al. 2008; Trivelpiece et al. 2011).

▲***Figure 8.*** *The Antarctic krill Euphausia superba. Photo: Hauke Flores.*

Besides the young developmental stages of Antarctic krill, copepods and amphipods are important components of the under-ice fauna in the Antarctic (Marschall 1988; Aarset and Torres 1989; Garrison and Buck 1989; Flores et al. 2011, 2012a; David et al. 2017), similar to the Arctic. Moreover, the salp *Salpa thompsoni* Foxton (1961) is among the most important filter-feeding metazoans in the Southern Ocean (Huntley et al. 1989; Voronina 1998). Both, krill and salps play a major role in channeling biogenic carbon from the surface to the seabed by efficiently re-packing small particles into feces (le Fèvre et al. 1998; Perissinotto and Pakhomov 1998a; Phillips et al. 2009). Salps serve as common prey for many fish species, invertebrates and birds (Pakhomov et al. 2002). Particularly in the Antarctic, the food supply is subject to a strong seasonality. Therefore, local organisms, such as *Eusirus* spp. amphipods (**Figure 9A**) and the pteropod *Clio pyramidata* Linnaeus (1767) (**Figure 9B**), must be equipped with specialized adaption mechanisms to overcome the harsh environmental conditions, especially during winter (Hagen et al. 1993; Kattner et al. 1994).



▲***Figure 9.*** *The amphipod Eusirus sp. (**A**) and the pteropod Clio pyramidata (**B**) as representatives of the Antarctic under-ice community. Photos: Jan Andries van Franeker.*

So far, food web studies investigating the effects of climate change-induced modifications of polar ecosystems on specific organisms are rather rare. Particularly in high Arctic regions, the assessment is logistically difficult as a result of the pronounced ice cover year-round, and studies during winter are generally challenging due to environmental restrictions in both the Arctic and the Antarctic. However, alterations of the ice-associated primary production in terms of extent, timing, energy content and taxonomic composition will have dramatic consequences for the energy flux through Arctic and Antarctic ecosystems with a subsequent impact on top predator populations (e.g. van Franeker et al. 1997; Smith et al. 1999; Reid and Croxall 2001; Croxall et al. 2002; Weimerskirch et al. 2003; Wassmann et al. 2006; Clarke et al. 2007; Laidre et al. 2008; Schofield et al. 2010; Søreide et al. 2013). Thus, the quantification of the trophic dependency of polar key species on the sea ice production is crucial for the understanding of polar ecosystem dynamics and functioning, and to evaluate their future fate in the light of ongoing climate-related changes of their habitat.

1.4 Biomarker concept

In this thesis, trophic interactions were studied using lipid fingerprinting, stable isotope analysis (SIA) of natural abundance nitrogen and carbon, and compound-specific SIA of marker fatty acids (FAs). The main principle of biomarker analyses is the conservation of bioindicators, such as FAs and stable isotopes, when transferred along the marine food chain, representing the trophic 'fingerprint' of the primary producers. Tracing these biomarkers in the consumers enables the identification of certain food and carbon source preferences. The FA approach, initially demonstrated on calanoid copepods (Lee et al. 1971b), has been successfully applied over several decades in tracing or confirming predator-prey relationships in marine food webs for both marine invertebrates and fish (Fraser et al. 1989; Graeve et al. 1994b; St. John and Lund 1996; Desvilettes et al. 1997; Mohan et al. 2016b).

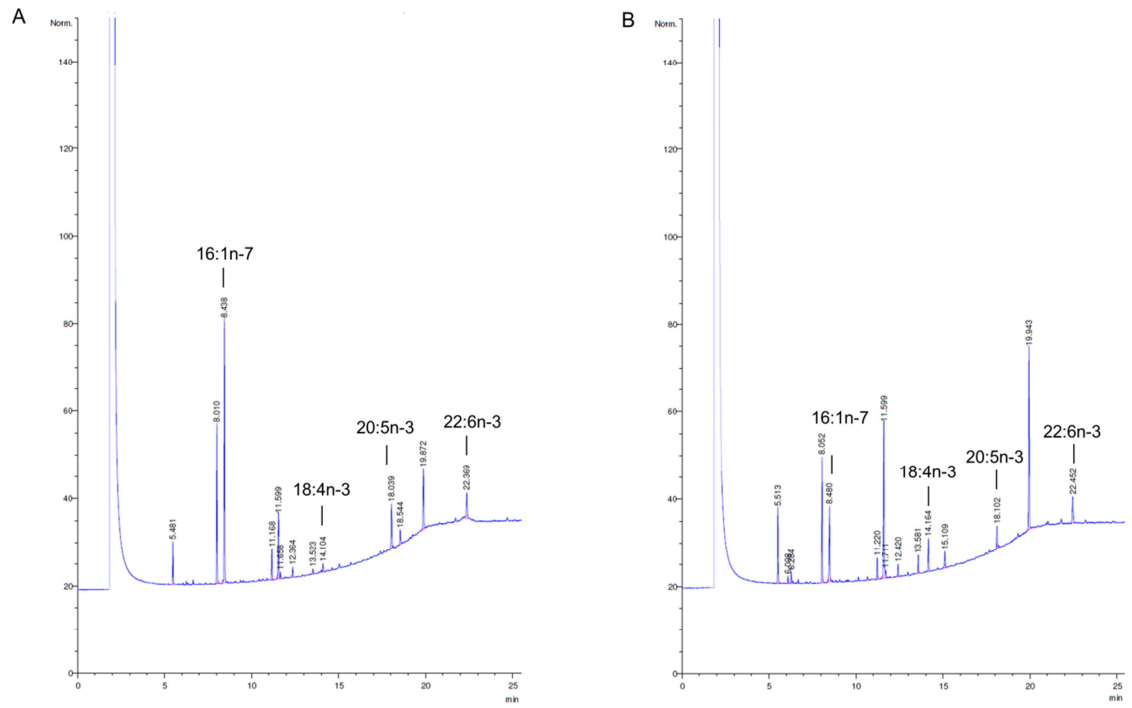
Ice algae communities are often dominated by Bacillariophyceae, simplified to diatoms (Nöthig et al. 1991; Nichols et al. 1993; Dalsgaard et al. 2003), whereas pelagic communities are often characterized by high abundances of Dinophyceae, simplified to dinoflagellates (Dalsgaard et al. 2003). The FA composition of diatoms is characterized by high abundances of C16 FAs, such as 16:1n-7 and 16:4n-1, and the polyunsaturated FA (PUFA) 20:5n-3 (Chuecas and Riley 1969; Pohl and Zurheide 1979). Dinoflagellates show high abundances of C18 FAs, especially 18:4n-3 and 18:5n-3, and the PUFA 22:6n-3 (Harrington et al. 1970; Joseph 1975). To identify the sources of energetic reserves, the proportions of diatom-derived (16:1n-7, 20:5n-3) and dinoflagellate-derived FAs (18:4n-3, 22:6n-3) in the consumers can be investigated (Viso and Marty 1993; Graeve et al. 1997; Phleger et al. 1998; Scott et al. 1999; Dalsgaard et al. 2003). To determine the degree of carnivory and identify representatives of the copepod-based food web, the proportions of long-chained FAs that originate from copepods, such as *Calanus glacialis*, *C. hyperboreus* and *C. propinquus* (20:1n-9, 22:1n-11) are analyzed (Falk-Petersen et al. 1987; Søreide et al. 2013; Virtue et al. 2016).

Tracing sea ice-derived carbon in food webs by FA analysis can be a challenge when the taxonomic composition of ice algae and phytoplankton communities are very similar, as it is often the case in Arctic and Antarctic microalgae communities. The community structure of pelagic assemblages is rather mixed, containing primarily diatoms and prymnesiophytes in addition to dinoflagellates (Bathmann et al. 1997; Gosselin et al. 1997; Arrigo et al. 1999, 2010). Stable isotope analysis can provide a valuable tool in clarifying trophic relationships when proportions of marker FAs are not sufficient to distinguish carbon pathways in consumers that are based on taxonomically diverse primary producer communities. A specific stable isotope signature reflects the diet composition of a consumer, because the contribution of carbon isotopes in the body tissue is directly related to the isotopic composition of prey items.

Photosynthesis of biomolecules in the primary producers is a mass-dependent process. The lighter ^{12}C isotope is favoured during metabolic/biochemical reactions due to a higher reactivity compared to the isotopically heavier ^{13}C. Often, the sea ice environment is depleted in dissolved carbon dioxide, because the sea ice brine channels are semi-enclosed environments, where CO_2 concentrations decrease when ice-associated primary production is high with simultaneous reduced water exchange. This consequently leads to an enrichment of the heavy carbon stable isotope ^{13}C in organic matter produced in sea ice relative to pelagic organic matter (Fry and Sherr 1984; Rau et al. 1991b; Hecky and Hesslein 1995). This isotopic difference is transferred from producer to consumer, and allows for the tracking of carbon from ice algae and pelagic algae to higher trophic levels (Hobson et al. 2002; Søreide et al. 2013; Wang et al. 2015). In the Arctic, the stable isotope approach was applied to quantify the proportion of ice algal carbon in the carbon budget of e.g. an Alaskan food web (Budge et al. 2008), and a food web in the European Arctic (Søreide et al. 2006), abundant zooplankton species in the Bering Sea (Wang et al. 2015), and polar cod in the Beaufort Sea (Graham et al. 2014).

1.5 State-of-the-Art techniques in lipid and stable isotope analyses

High Performance Liquid Chromatography (HPLC) allows identification and quantification of the lipid class composition of storage lipids and membrane lipids. Gas Chromatography (GC) or Gas Chromatography-Mass Spectrometry (GC-MS) is applied to analyze the lipid compounds after derivatization into Fatty Acid Methyl Esters (FAMEs) (**Figure 10**).



▲***Figure 10***. *GC chromatograms of Arctic ice-associated particulate organic matter (I-POM;* ***A****) and pelagic particulate organic matter (P-POM;* ***B****).*

Bulk nitrogen and carbon stable isotope ratios are determined by Isotope Ratio Mass Spectrometry (IRMS), which enables the measurement of precisely small differences in the natural abundances of isotopes such as $^{15}N/^{14}N$ and $^{13}C/^{12}C$ (BSIA- Bulk Stable Isotope Analysis) (McKinney et al. 1950; Carter and Barwick 2011; Brand and Coplen 2012).

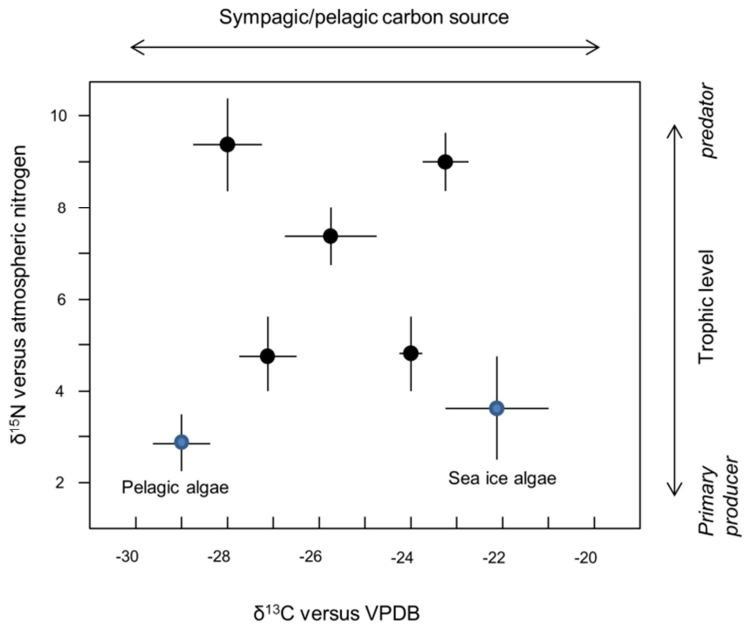
It has been common to report the isotopic results in parts per thousand (‰) in the delta (δ) notation as $\delta^{13}C$ and $\delta^{15}N$:

(1) $$ratio\ (R) = \frac{abundance\ heavy\ stable\ isotope}{abundance\ light\ stable\ isotope}$$

(2) $$\delta = \left(\frac{R_{sample}}{R_{standard}} - 1\right) * 1000$$

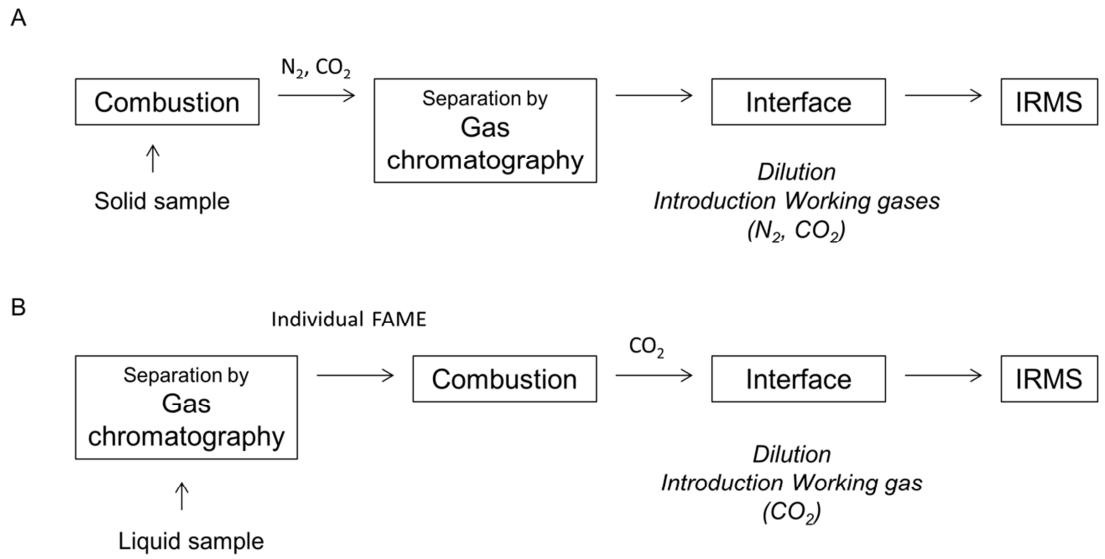
with R_{sample} representing the ratio of the sample and $R_{standard}$ representing the ratio of an international standard.

Due to the preservation of the isotopic information along the food chain, carbon stable isotope compositions $\delta^{13}C$ are used for the quantification of carbon sources in the consumers. The nitrogen isotopic composition $\delta^{15}N$ is suitable for accurately determining the trophic level of organisms. The heavy nitrogen stable isotope ^{15}N becomes enriched from one trophic level to another, reflected in increasing $^{15}N/^{14}N$ ratios relative to the baseline (Wada et al. 1987; Kaehler et al. 2000) (**Figure 11**).



▲***Figure 11.*** *Example for a polar food web based on pelagic and sympagic carbon sources. $\delta^{13}C$ mirrors the origin of the carbon, $\delta^{15}N$ displays the trophic position of the organism, represented by the black dots.*

To produce isotopic representatives of the original sample, the organic material is combusted at a high temperature (900 to 1050°C) in an oxygen atmosphere in a quartz reactor of an Elemental Analyzer (EA). The resulting N_2 and CO_2 gases are separated via an isothermal packed GC column, which enables the dual measurement of the gases. The gases are then transferred to the multicollector MS via a Conflo Interface, which ensures the appropriate dilution of the evolved gases before entering the MS (continuous flow IRMS, **Figure 12A**). Besides, pulses of Working (Reference) gases (N_2, CO_2) are introduced to facilitate raw delta value calculations (Carter and Barwick 2011). The MS is equipped with an ion source in which the entering gas molecules are ionised by collision with an electron beam (Electron Ionisation, EI). The resulting ions are focussed and accelerated through a high voltage into a magnetic field. In the case of CO_2 measurements, three ion beams for the different isotopomers $^{12}C^{16}O_2$, $^{13}C^{16}O_2$, and $^{12}C^{18}O^{16}O$ with the masses *m/z* (mass-to-charge ratio) 44, 45 and 46, respectively, are measured by Faraday cups. After signal amplification, the corresponding isotopic ratios are calculated, creating a chromatogram for ions of given *m/z*, where the peak area is proportional to the number of ions detected (Coplen et al. 1983; Meier-Augenstein 1999; Carter and Barwick 2011). The result is the isotopic abundance of the analyte gas relative to an internationally agreed zero point (primary or calibration materials), which is the Vienna Pee Dee Belemnite (VPDB) standard for the calibration of carbon measurements and atmospheric nitrogen for nitrogen measurements (Meier-Augenstein 1999; Gröning 2004; Paul et al. 2007; Carter and Barwick 2011). Quality assurance of the isotope measurements is performed by analyzing materials with defined δ values, which are calibrated versus the primary standard materials.



▲***Figure 12.*** *Simple scheme of the EA-IRMS system for the determination of bulk $\delta^{15}N$ and $\delta^{13}C$ (**A**) and the GC-c-IRMS system (**B**) for the determination of fatty acid-specific $\delta^{13}C$.*

The concept of linking GC for separating organic compounds with subsequent IRMS was evolved during the 1970s/80s (Matthew and Hayes 1978; Barrie et al. 1984). Due to the around 1990 available technique of Gas Chromatography-combustion-Isotope Ratio Mass Spectrometry (GC-c-IRMS), it is possible to analyze the stable isotope composition of single compounds (Compound-specific Stable Isotope Analysis- CSIA), such as fatty acids (Meier-Augenstein 1999, 2002; Boschker and Middelburg 2002). The compounds of interest are initially separated by GC and subsequently combusted to CO_2 (**Figure 12B**). In comparison to BSIA measurements, the isotopic information derives from individual compounds, whereas the BSIA ratios reflect complex materials, integrating widely varying structures and origins. In addition, the CSIA technique allows for considerably lower sample amounts. Due to its complexity, the analysis of samples via GC-c-IRMS is much more time consuming and technically more demanding compared to the EA-IRMS system. Both techniques have their advantages and disadvantages, and should be applied complementary to each other, where the chosen approach should match the individual scientific question.

Stable isotope mixing models (SIMMs) are frequently used as ecological tool (e.g. Lubetkin and Simenstad 2004; Inger and Bearhop 2008; Cremona et al. 2009; Graham et al. 2014; Wang et al. 2015), allowing the quantification of source contributions to a mixture, such as prey to a consumer (Phillips et al. 2005, 2014). In our study, Bayesian Stable Isotope Mixing Models, implemented in the Software packages SIAR (Stable Isotope Analysis in R) (Parnell et al. 2008, 2010) or MixSIAR (Stock and Semmens 2015), were applied to determine the relative contribution of carbon originated from ice algae versus pelagic phytoplankton to the carbon budget of Arctic and Antarctic organisms. These models allow for multiple dietary sources, from which they create potential dietary solutions as true probability solutions (posterior probability distribution). Incorporating prior information, uncertainties and fractionation factors in source

isotopic values are considered, which increases the robustness of the results from the Bayesian models compared to other modelling approaches (McCarthy 2007; Moore and Semmens 2008; Parnell et al. 2010, 2013; Gelman et al. 2014).

1.6 Objectives of this thesis

As a primary objective, this thesis aimed to quantify the extent to which ice algae-produced carbon is channeled from sea ice algae to important energy transmitters of the under-ice community, and from there into pelagic food webs in both Polar Regions (**Objective 1**). Calculating the relative contribution of sympagic versus pelagic carbon sources to the carbon budget of the investigated species ultimately allowed a comparison of the proportional flux of sea-ice derived carbon versus pelagic-derived carbon during different seasons and hemispheres. From that, we improved our understanding of the potential ecological consequences of a changing sea ice environment in the Polar Regions.

Besides the quantification of the trophic dependency of the food web on sea ice, we aimed to

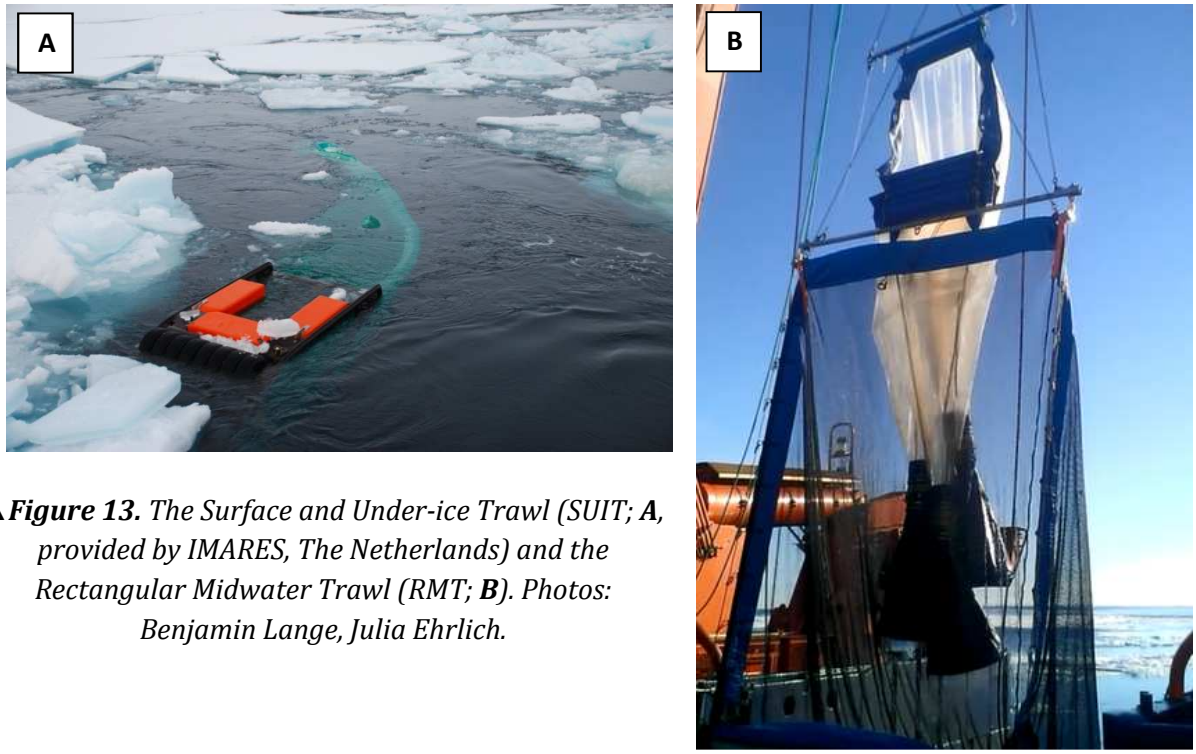
- **Objective 2**: describe trophic interactions and food web structures within Arctic (**Chapter I**) and Antarctic food webs (**Chapter V**), derived from biomarker proxies
- **Objective 3**: conduct regional comparisons of the biomarker proxies and relate the differences to environmental parameters (**Chapters I, IV, V and VI**)

The main **research questions** addressed in this thesis were:

1. Which polar organisms are most dependent on the sea ice algae biomass and are therefore most vulnerable to changes of the sea ice system?
2. Is the trophic dependency on ice algal carbon subject to seasonal and spatial variabilities? Is there a distinct difference in the overall utilization of sea ice-derived carbon between the hemispheres?
3. Which analytical/statistical approach is the most reliable for the quantification of dietary carbon in body compounds of an organism?

To accomplish the objectives and resolve the scientific questions, a comprehensive study design, combining traditional tools, i.e. stomach content analysis (e.g. Reid 1961; Hickey 1975; Matley et al. 2015) and lipid/fatty acid analysis (e.g. Gruger et al. 1964; Volkman et al. 1981; Haynes et al. 2015), with state-of-the-art techniques in the stable isotope sector was applied (e.g. Schmidt et al. 2004b; de Troch et al. 2012; Svensson et al. 2015; Taipale et al. 2015). So far, most studies tracing carbon pathways in marine ecosystems rely on either solely bulk isotopic compositions (e.g. Søreide et al. 2013; Jia et al. 2016) or, scarcer, solely compound-specific stable isotope compositions (e.g. Budge et al. 2008; Graham et al. 2014; Wang et al. 2015). In this thesis, proportional ice algal contribution estimates based on both, bulk (BSIA) and fatty acid-specific stable isotope compositions (CSIA) were provided. This enabled the comparison of the applicability and significance of both methods.

Most of the samples were collected with the SUIT (Surface and Under-Ice Trawl; van Franeker et al. 2009), which is capable of quantitatively sampling under-ice fauna (zooplankton, micronekton) in the uppermost 2 m of the water column under the sea ice, combined with simultaneous measurements of environmental parameters (e.g. sea ice thickness, water temperature and salinity) (**Figure 13A**).



▲***Figure 13.*** *The Surface and Under-ice Trawl (SUIT;* ***A****, provided by IMARES, The Netherlands) and the Rectangular Midwater Trawl (RMT;* ***B****). Photos: Benjamin Lange, Julia Ehrlich.*

Sampling was complemented by using Rectangular Midwater Trawls (RMT) for collecting comparative samples of organisms from greater depths. This pelagic trawling system enables multiple sample collection by a total of six nets with different mouth openings (1 m and 8 m) and mesh sizes for depth-stratified hauls (**Figure 13B**) (Roe and Shale 1979).

In this thesis, species that are known for their close association with sea ice, such as the Arctic ice-amphipods *Apherusa glacialis*, *Gammarus wilkitzkii* and *Eusirus holmii* and the Antarctic amphipod species *Eusirus laticarpus*, were investigated. However, 'ice-associated' does not necessarily mean that these species depend on sea ice-derived resources since preying on pelagic food sources cannot be excluded. Additionally, FA and stable isotope compositions of rather pelagic organisms, such as the Arctic amphipod *Themisto libellula* and the bipolar pteropod *Clione limacina*, were analyzed. Due to the close connectivity between sympagic and pelagic ecosystems, alterations of the sea ice system will most likely first affect ice-associated species, but will subsequently impact on the food web dynamics of the pelagic system. Therefore, it is essential to gain information not only about the directly ice-associated sympagic food web, but also about the indirectly or at a later stage affected pelagic ecosystem.

The results can be used to estimate the overall trophic flux of ice algae-produced carbon through Arctic and Antarctic ecosystems under current and future conditions. Combining knowledge on biomass and productivity of ice-associated communities in relation to environmental parameters, and the ice algal carbon flux in these communties, will allow projecting an overall ice-associated carbon flux in space and time in physical sea ice-ocean models. Ultimately, improved knowledge on the carbon flux between sea ice and the adjacent water column will enable predictions of the impact of changing sea ice habitats on food webs in polar marine ecosystems. This can help contributing to the development of sustainable approaches regarding fisheries management and ecosystem conservation.

1.7 Publication outline

This cumulative dissertation presents the research findings of my PhD project that were acquired between May 2013 and February 2017. This project was part of the Helmholtz Association Young Investigators Group *Iceflux*, under supervision of Dr. Hauke Flores. The *Iceflux* project (Ice-ecosystem carbon flux in polar oceans) aims to evaluate the contribution of ice algae-produced carbon to the food webs in both Polar Regions under consideration of changing sea ice environments.

This thesis consists of a general introduction, followed by 6 manuscripts that are either published in peer-reviewed journals or in preparation for submission (**Chapters I** to **VI**), followed by a synoptic discussion. The objectives are addressed in the chapters. The research questions are reflected in the overarching discussion.

The first two Chapters of this thesis present peer-reviewed published/accepted work, quantifying the carbon that is channeled from the Arctic sea ice to the diet of ecological key species, i.e. the Arctic under-ice fauna (**Chapter I**) and polar cod *Boreogadus saida* (**Chapter II**). The ongoing reduction of the Arctic sea ice coverage, accompanied by changes of the sea ice characteristics, make it crucial to gain information about the dependency of Arctic organisms on the sea ice algae-based primary production in order to better predict ecological consequences and trophic implications for the Arctic food web. Both datasets were conducted during RV '*Polarstern*' expedition PS80 in the central Arctic Ocean in summer 2012. In **Chapter I**, all three objectives were addressed. **Chapter II** focused on objective **1**.

In **Chapter I**, the most abundant representatives of the Arctic under-ice community, with different degree of carnivory, were submitted to fatty acid and stable isotope analysis to quantify their trophic dependency on the Arctic sea ice habitat. Results from different stable isotope approaches were compared and discussed. Furthermore, spatial variabilities in the biomarker data based on the definition of two distinct environmental regimes, the Nansen and the Amundsen Basins, were examined.

Chapter I: The importance of ice algae-produced carbon in the central Arctic Ocean ecosystem: Food web relationships revealed by lipid and stable isotope analyses.

Doreen Kohlbach, Martin Graeve, Benjamin A. Lange, Carmen David, Ilka Peeken, Hauke Flores
Field sampling for this study was performed by H. Flores, B. A. Lange, C. David and I. Peeken. Taxonomic classification was conducted by H. Flores and C. David. Laboratory analyses were accomplished by D. Kohlbach and M. Graeve. Data analyses were performed by D. Kohlbach with support from B. A. Lange and H. Flores. The manuscript was written by D. Kohlbach with contribution from all authors. This paper was published in Limnology & Oceanography (2016) 61: 2027-2044.

In **Chapter II**, a representative of the upper trophic levels, polar cod *Boreogadus saida*, was investigated in terms of its significance as ice algal carbon transmitter between zooplankton and top predators in the Arctic Ocean. The importance of ice algae-produced carbon to the carbon budget of this fish species was quantified by combining stomach content analysis with lipid and stable isotope analyses of muscle, liver and gonad tissues. As first study so far, biomarker parameters of *B. saida* caught directly from underneath the sea ice, were presented.
Chapter II: Strong linkage of polar cod (*Boreogadus saida*) to sea ice algae-produced carbon: Evidence from stomach, fatty acid and stable isotope analyses.
Doreen Kohlbach, Fokje L. Schaafsma, Martin Graeve, Benoit Lebreton, Benjamin A. Lange, Carmen David, Martina Vortkamp, Hauke Flores
Samples for this study were collected by H. Flores, C. David and B. A. Lange. Length measurements of the fish and subsampling of muscle, liver and gonad tissues were performed by H. Flores, B. A. Lange and C. David. Lipid and stable isotope laboratory analyses were accomplished by D. Kohlbach, B. Lebreton, M. Graeve and M. Vortkamp. Stomach content analyses were conducted by F. L. Schaafsma and H. Flores. Data analyses were performed by D. Kohlbach with support from B. A. Lange and H. Flores. Writing of the manuscript was realized by D. Kohlbach and F. L. Schaafsma with contribution from all authors. This paper was accepted in Progress in Oceanography (07 February 2017).

In **Chapters III** and **IV**, Antarctic krill *Euphausia superba* were investigated regarding their diet and/or carbon sources during austral winter. Due to their outstanding position in the Antarctic food web, detailed information on their dietary characteristics are crucial to estimate their fate in a changing sea ice environment. In **Chapter III,** the proportional contribution of ice algal carbon to larval, juvenile and adult krill, collected during RV '*Polarstern*' expedition PS81 in the northern Weddell Sea during winter/onset spring 2013 was quantified. **Chapter III** mainly addressed **objective 1**. In **Chapter IV**, temporal and spatial variabilities in diet and carbon sources of young Antarctic krill (AC0) from PS81 were investigated. Particularly **objective 3** was addressed in **Chapter IV**.

Chapter III focused on ontogenetic differences regarding the utilization of ice algal carbon by larval, juvenile and adult *E. superba*. This circumpolar species has a key position in linking primary production and upper trophic levels due to its enormous

abundance in the Southern Ocean. This study is the first of its kind, quantifying the assimilation of ice algae-produced carbon by *E. superba* during winter.

Chapter III: Ice algae-produced carbon ensures winter survival of young Antarctic krill *Euphausia superba*.

Doreen Kohlbach, Benjamin A. Lange, Fokje L. Schaafsma, Carmen David, Martina Vortkamp, Martin Graeve, Jan Andries van Franeker, Hauke Flores

Sample collection was carried out by C. David, F. L. Schaafsma and J. A. van Franeker. Determination of the developmental stage and length measurements were accomplished by C. David, F. L. Schaafsma and J. A. van Franeker. Laboratory analyses were performed by D. Kohlbach, M. Graeve and M. Vortkamp. Analysis of data was done by D. Kohlbach with support from B. A. Lange and H. Flores. Writing of the manuscript was realized by D. Kohlbach with contribution from all authors. This paper is in preparation for submission to Frontiers in Marine Science.

Temporal and spatial differences in diet and carbon sources of young Antarctic krill *E. superba* (larvae, juveniles) during winter in the northern Weddell Sea, based on the results from microscopic stomach analysis combined with fatty acid parameters, carbon/nitrogen compositions and bulk stable isotope compositions, were evaluated in **Chapter IV**. This study aimed to shed further light on the role of sea ice in terms of food supply for the survival of AC0 krill during their first winter.

Chapter IV: Spatio-temporal variability in the winter diet of larval and juvenile Antarctic krill (*Euphausia superba*) in ice-covered waters

Fokje L. Schaafsma, Doreen Kohlbach, Carmen David, Benjamin A. Lange, Martin Graeve, Hauke Flores, Jan Andries van Franeker

Samples were collected by F. L. Schaafsma, C. David and J. A. van Franeker. Individuals were sexed and measured by F. L. Schaafsma, C. David and J. A. van Franeker. Stomach analyses were accomplished by F. L. Schaafsma, fatty acid and stable isotope analyses were run by D. Kohlbach. C/N measurements were realized by C. David. Data was analyzed by F. L. Schaafsma and D. Kohlbach. The manuscript was written by F. Schaafsma with major contributions from D. Kohlbach. This paper is in preparation for submission to Marine Ecology Progress Series.

In **Chapters V** and **VI,** the results from the biomarker analyses of abundant Antarctic species were interpreted, in order to quantify their trophic association with the sea ice system. The determination of the sympagic dependency of Antarctic ecological key species is of high significance due to the predicted climate change-induced shrinkage of the sea ice coverage in the Southern Ocean. In **Chapter V**, representatives of the Antarctic food web in the northern Weddell Sea during austral winter 2013, collected during RV '*Polarstern*' expedition PS81, were investigated in terms of their input of sympagic produced carbon versus carbon derived from pelagic algae. **Chapter V** fulfilled **objectives 1**, **2** and **3**. In **Chapter VI**, the contribution of sympagic carbon to the carbon budget of the most abundant euphausiids collected off the Filchner Ice Shelf in austral summer 2013/14 during RV '*Polarstern*' expedition PS82 was compared, examining mainly **objectives 1 and 3**.

The utilization of ice algal carbon by the most abundant zooplankton species caught from underneath the Antarctic sea ice, to understand the role of sea ice in terms of food supply for overwintering, was investigated in **Chapter V**. Many of the investigated species are not well characterized yet in respect to their preferred carbon sources. Thus, it is of great importance to gain information on the origin of their body carbon, particularly during winter, when the water column is largely completed in nutrients and sea ice algae could present a high-quality food alternative.

Chapter V: Overwintering of Weddell Sea under-ice community strongly linked to sea ice-associated food sources.

Doreen Kohlbach, Martin Graeve, Benjamin A. Lange, Carmen David, Fokje L. Schaafsma, Jan Andries van Franeker, Martina Vortkamp, Angelika Brandt, Eva Leu, Hauke Flores

Sample collection was carried out by C. David, F. L. Schaafsma and J. A. van Franeker. Determination of the developmental stage and length measurements were accomplished by C. David, F. L. Schaafsma and J. A. van Franeker. Laboratory analyses were performed by D. Kohlbach, M. Graeve and M. Vortkamp. Analysis of data was done by D. Kohlbach with support from B. A. Lange, H. Flores, A. Brandt and E. Leu. Writing of the manuscript was realized by D. Kohlbach with contribution from all authors. This paper is in preparation for submission to Journal of Plankton Research.

In **Chapter VI**, lipid class, fatty acid and stable isotope compositions of the most abundant euphausiids collected off the Filchner Ice Shelf were analyzed and compared. The sampling region is difficult to access due to challenging sea ice conditions, even in mid-summer, which explains the very limited numbers of food web studies in this area. This study showed a comprehensive compilation of trophic interactions and carbon sources of the dominant krill species in the Southern Weddell Sea.

Chapter VI: *Euphausia superba*, *E. crystallorophias* and *Thysanoessa macrura* in the Filchner Outflow System: Variability of carbon sources during summer assessed in a lipid and stable isotope study.

Doreen Kohlbach, Martin Graeve, Benjamin A. Lange, Martina Vortkamp, Hauke Flores

Samples were collected by D. Kohlbach, B. A. Lange and M. Vortkamp. Determination of the developmental stage and length measurements were conducted by D. Kohlbach, B. A. Lange and M. Vortkamp. Laboratory analyses were performed by D. Kohlbach, M. Graeve and M. Vortkamp. Analysis of data was done by D. Kohlbach with support from B. A. Lange and H. Flores. Writing of the manuscript was realized by D. Kohlbach with contributions from all authors. This paper is in preparation for submission.

2.1 *Chapter I*

The importance of ice algae-produced carbon in the central Arctic Ocean ecosystem: Food web relationships revealed by lipid and stable isotope analyses

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Abstract

To better predict ecological consequences of changing Arctic sea ice environments, we aimed to quantify the contribution of ice algae-produced carbon (α_{Ice}) to pelagic food webs in the central Arctic Ocean. Eight abundant under-ice fauna species were submitted to fatty acid (FA) analysis, bulk stable isotope analysis (BSIA) of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopic ratios, and compound-specific stable isotope analysis (CSIA) of $\delta^{13}C$ in trophic marker FAs. A high mean contribution α_{Ice} was found in *Apherusa glacialis* and other sympagic (ice-associated) amphipods (BSIA: 87 to 91%, CSIA: 58 to 92%). The pelagic copepods *Calanus glacialis* and *C. hyperboreus*, and the pelagic amphipod *Themisto libellula* showed substantial, but varying α_{Ice} values (BSIA: 39 to 55%, CSIA: 23 to 48%). Lowest α_{Ice} mean values were found in the pteropod *Clione limacina* (BSIA: 30%, CSIA: 14 to 18%). Intra-specific differences in FA compositions related to two different environmental regimes were more pronounced in pelagic than in sympagic species. A comparison of mixing models using different isotopic approaches indicated that a model using $\delta^{13}C$ signatures from both diatom-specific and dinoflagellate-specific marker FAs provided the most conservative estimate of α_{Ice}. Our results imply that ecological key species of the central Arctic Ocean thrive significantly on carbon synthesized by ice algae. Due to the close connectivity between sea ice and the pelagic food web, changes in sea ice coverage and ice algal production will likely have important consequences for food web functioning and carbon dynamics of the pelagic system.

Introduction

Arctic sea ice coverage and thickness have significantly decreased in the past decades (Johannessen et al. 2004; Kwok et al. 2009; Maslanik et al. 2011). This has been accompanied by a dramatic loss of old, thick multi-year sea ice and a transition to a seasonal ice-dominated Arctic Ocean with more open water during summer (Kwok 2007; Lindsay et al. 2009; Maslanik et al. 2011). The loss of summer sea ice has consequences for ice algae that depend on sea ice as habitat and represent an important carbon source in high Arctic regions. Estimates of ice algal primary production range from 3 to 25% of the total primary production within Arctic marine systems (Subba Rao and Platt 1984; Legendre et al. 1992) to as high as 50 to 57% in high Arctic regions (Gosselin et al. 1997; Fernández-Méndez et al. 2015). Climate change is expected to have dramatic consequences in terms of timing, magnitude, and spatial distribution of both ice-associated and pelagic primary production, with a subsequent direct and indirect impact on higher trophic organisms such as zooplankton (Wassmann et al. 2006; Søreide et al. 2013).

The declining sea ice extent could lead to changes in the reproduction and growth cycles of some Arctic zooplankton, such as copepods, that adapt their life cycles to food availability between ice-associated and pelagic blooms (Søreide et al. 2010). Consequently, these changes at the lower trophic level may affect pelagic and benthic food webs. In order to understand how the loss of sea ice and potential changes in primary production may affect zooplankton, we need to gain insight on the importance of sea ice algae carbon to Arctic zooplankton. So far, the contribution of ice algal biomass to higher trophic levels compared to pelagic phytoplankton is scarcely investigated, particularly in the central Arctic basins. The few available studies focused on shelf-bound ecosystems (Hobson et al. 1995; Søreide et al. 2006; Budge et al. 2008).

Fatty acids (FAs) can be used as trophic markers to track predator-prey relationships within marine food webs (e.g. Falk-Petersen et al. 1998; Mayzaud et al. 2013). Certain FAs that are biosynthesized by primary producers are considered to be markers of those primary producers, and are assumed to be transferred conservatively through the marine food web (Graeve et al. 1994a; Bergé and Barnathan 2005; Budge et al. 2012). For example, Bacillariophyceae (simplified to diatoms), which often dominate algal communities in sea ice, express high amounts of the FAs 16:1n-7 and 20:5n-3, accompanied with high levels of C16 polyunsaturated FAs. Dinophyceae (simplified to dinoflagellates) are often more abundant in the water column and contain high amounts of the FA 22:6n-3 and C18 PUFAs (e.g. Dalsgaard et al. 2003). The fatty acid approach alone, however, cannot provide information on the proportional contribution of ice algae- versus pelagic phytoplankton-produced FAs, because the same FAs can originate from sea ice-diatoms or diatoms in the water column (Søreide et al. 2008). By combining FA biomarker analysis with stable isotope analysis of the bulk organic carbon content (e.g. Dehn et al. 2007; Feder et al. 2011; Weems et al. 2012) or specific compounds, such as FAs (e.g. Budge et al. 2008; Graham et al. 2014; Wang et al. 2015), it is possible to quantify the relative transfer of sea ice- and pelagic phytoplankton-derived organic matter to the consumers.

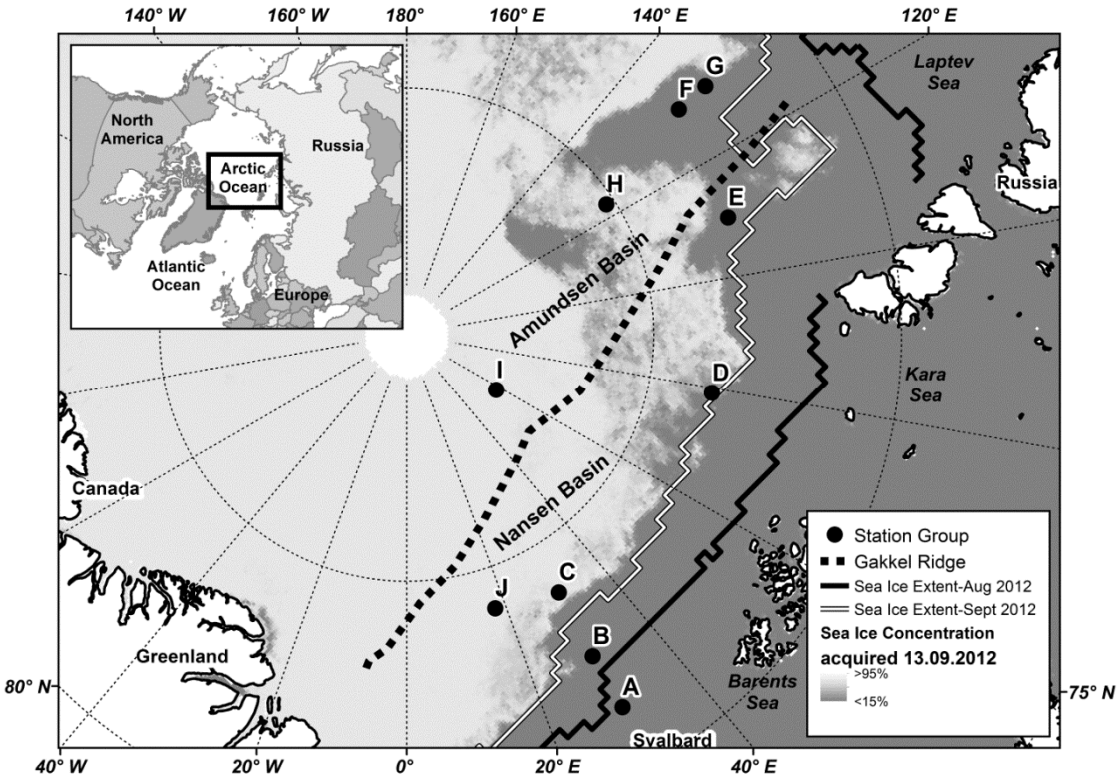
The isotopic signature of sea ice-produced carbon is assumed to be caused by a carbon-limiting environment of the sea ice system (e.g. Fry and Sherr 1984; Peterson and Fry 1987; Hecky and Hesslein 1995). The semi-closed system in sea ice results in a significantly higher ^{13}C enrichment in ice algae relative to pelagic phytoplankton. This difference in isotope values allows for the tracking of carbon from ice algae and pelagic phytoplankton to higher trophic levels (Hobson et al. 2002; Søreide et al. 2013). The quantification of ice algae-produced carbon based on bulk stable isotope parameters (BSIA), however, can be complicated by the effect of metabolic processes, e.g. isotopic routing (Gannes et al. 1997). Metabolic effects can be largely excluded when the variability of the stable isotope composition is considered only in FAs, which are not biotransformed in consumers. By using gas chromatography-combustion-isotope ratio mass spectrometry (GC-c-IRMS), it is possible to analyze the stable isotope composition of individual FAs (compound-specific stable isotope analysis- CSIA, see description of method in Meier-Augenstein 2002) with high sensitivity regarding both concentration of FAs and isotopic composition (Boschker and Middelburg 2002).

We analyzed FAs, bulk and FA-specific stable isotope compositions to describe the trophic relationships between phytoplankton, ice algae, and abundant under-ice fauna species throughout the Eurasian Basin of the Arctic Ocean during summer 2012. We also used this two-dimensional biomarker approach to estimate the relative contribution of carbon produced by sea ice algae versus pelagic phytoplankton in different macrofauna species at different levels of heterotrophy and ice association, and its sensitivity to the methodological approach chosen. According to David et al. (2015), two environmental regimes could be distinguished in our sampling area. During the sampling period, the Nansen Basin (NB) was characterized by higher salinities and nitrate concentrations compared to the Amundsen Basin (AB), among other properties. The community structure of under-ice faunal organisms was also separated according to these two environmental regimes (David et al. 2015). Besides the basin-wide perspective, we analyzed differences in the FA parameters between the two environmental regimes.

Material and Methods

Study area and sampling

The sample collection was conducted during the RV '*Polarstern*' expedition IceArc (PS80; 2 August to 7 October 2012) in the Eurasian Basin of the Arctic Ocean north of 80°N (**Figure 1, Table 1**). More detailed information on the sampling area, including ice types and properties, is given in David et al. (2015) and Fernández-Méndez et al. (2015).



▲***Figure 1.*** *Map of the sampling area during RV 'Polarstern' cruise IceArc (PS80) across the Eurasian part of the Arctic Ocean. The Gakkel Ridge geographically separates the Nansen and Amundsen Basins. Sea ice concentration for 13 September 2012 (concentration data acquired from Bremen University (http://www.iup.uni-bremen.de:8084/amsr/)) and mean sea ice extent for August and September 2012 are represented on the map (data acquired from NSIDC, Fetterer et al. 2002). Letter codes correspond to sampling locations. Station information for the individual sampling sites is given in* ***Table 1****.*

▼**Table 1.** Sample information for ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM), and under-ice fauna (UIF) collected in the Eurasian Basin of the Arctic Ocean during PS80 in 2012.

Location	Sample type	Date (m/dd/yyyy)	Station no.	Latitude (°N)	Longitude (°E)
A	P-POM	8/6/2012	209	81.296	30.103
B	UIF	8/7/2012	216	82.483	30.027
C	P-POM	8/8/2012	220	83.599	28.500
	UIF	8/9/2012	223	84.070	30.434
	I-POM	8/9/2012	224	84.051	31.112
	P-POM	8/11/2012	230	84.022	31.221
	UIF	8/11/2012	233	83.934	31.298
D	I-POM	8/14/2012	237	83.987	78.103
	P-POM	8/16/2012	244	83.551	75.583
	UIF	8/16/2012	248	83.934	75.500
	P-POM	8/18/2012	250	83.353	87.271
E	I-POM	8/20/2012	255	82.671	109.590
	UIF	8/20/2012	258	83.076	109.627
	P-POM	8/22/2012	263	83.476	110.899
F	UIF	8/25/2012	276	83.076	129.125
	I-POM	8/25/2012	277	82.883	130.130
	P-POM	8/26/2012	284	82.537	129.462
	UIF	8/26/2012	285	82.896	129.782
G	UIF	9/4/2012	321	81.717	130.033
	I-POM	9/4/2012	323	81.926	131.129
	UIF	9/5/2012	331	81.905	130.863
	UIF	9/6/2012	333	82.989	127.103
H	I-POM	9/7/2012	335	85.102	122.245
	P-POM	9/7/2012	341	85.160	123.359
	UIF	9/9/2012	345	85.254	123.842
I	I-POM	9/18/2012	349	87.934	61.217
	UIF	9/19/2012	358	87.341	59.653
	I-POM	9/22/2012	360	88.828	58.864
	UIF	9/25/2012	376	87.341	52.620
J	UIF	9/29/2012	397	84.172	17.922

Ice-associated particulate organic matter (I-POM), representative of the ice algae community, was sampled by taking ice cores at 8 sites using a 9 cm interior diameter ice corer (Kovacs Enterprises). Ice thickness of the cores varied between 0.9 and 2.0 m. Chlorophyll *a* (Chl *a*) concentrations of the entire ice cores varied between 0.4 and 6.5 mg m^{-3} (0.3 to 8 mg m^{-2}; Fernández-Méndez et al. 2015). Whole ice cores were melted in the dark at 4°C on board the ship and filtered via a vacuum pump through pre-combusted 0.7 µm GF/F filters (3.5 to 10.5 L, Whatmann, 3 h, 550 °C).

Pelagic particulate organic matter (P-POM), representative of the phytoplankton community, was collected at 8 sites by a CTD probe (Seabird SBE9+) with a carousel water sampler. Further information about the CTD probe equipment can be found in David et al. (2015). Details of the sampling procedure are accessible in Boetius et al.

(2013). The water collection was performed at the surface layer, or at the depth of the Chl *a* maximum (between 30 and 50 m). The water at the Chl *a* maximum showed Chl *a* concentrations between 0.2 and 1.2 mg m^{-3} throughout the sampling area. Depending on the P-POM biomass concentration, between 6.4 and 11.0 L of water was filtered using pre-combusted GF/F filters. All I-POM and P-POM filters were stored at -80°C until further processing.

Samples of dominant species of the under-ice community, such as copepods, ice-associated (sympagic) amphipods, pelagic amphipods, and pteropods were collected at 14 stations, with varying ice conditions, using a surface and under-ice trawl (the SUIT, van Franeker et al. 2009). Detailed information on the SUIT operation and sampling conditions during the expedition can be found in David et al. (2015).

The copepods *Calanus glacialis* and *C. hyperboreus* were sorted by developmental stages (CV and female). Due to the small organism size, *Calanus* spp. and *Apherusa glacialis* were pooled species-specifically (up to 27 individuals per sample) in order to obtain sufficient sample material for subsequent processing and analyses (**Table 2**). All samples were immediately frozen on board at -80°C in pre-combusted and pre-weighed sample vials (Wheaton, 6 h, 500°C).

▼**Table 2.** Dry weight, total lipid content (TLC) by dry weight, and fatty acid content (FAC) by dry weight of under-ice fauna species (mean ± 1 SD).

	Calanus glacialis	***Calanus hyperboreus***	***Apherusa glacialis***	***Onisimus glacialis***	***Gammarus wilkitzkii***	***Eusirus holmii***	***Themisto libellula***	***Clione limacina***
Ind./sample	15 ± 6	8 ± 5	12 ± 4	1	1	1	1	1
Dry weight/Ind. (mg)	0.6 ± 0.2	1.1 ± 0.7	4.2 ± 1.2	46.0 ± 33.4	103.2 ± 43.5	86.3 ± 21.1	64.6 ± 36.9	26.0 ± 20.6
TLC/dry weight (%)	40.5 ± 16.3	36.4 ± 15.3	42.3 ± 7.0	37.4 ± 7.9	26.5 ± 6.2	26.3 ± 9.7	35.7 ± 4.8	16.1 ± 8.7
FAC/dry weight (%)	16.9 ± 6.5	18.7 ± 9.2	29.1 ± 5.6	22.8 ± 5.6	16.1 ± 3.1	16.4 ± 6.0	24.7 ± 3.5	7.1 ± 4.0

Lipid class and fatty acid analyses

The analytical work was conducted at the Alfred Wegener Institute in Bremerhaven, Germany.
Prior to lipid extraction, all samples were freeze-dried for 24 h. Dry weights were determined gravimetrically (**Table 2**). The under-ice fauna samples were homogenized mechanically using a Potter-Elvehjem homogenizer. Total lipids were extracted using a modified procedure from Folch et al. (1957) with dichloromethane/methanol (2:1, v/v). The extracted lipids were cleaned with 0.88% potassium chloride solution. The total lipid content was determined gravimetrically (**Table 2**).
Lipid classes of the under-ice fauna species were determined directly from the lipid extracts by high performance liquid chromatography using a LaChrom Elite® chromatograph (VWR Hitachi, Germany), equipped with a monolithic silica column Chromolith® Performance-Si (VWR, Germany) and an evaporative light scattering detector Sedex 75 (Sedere, France). Further information about the chromatographic method was given by Graeve and Janssen (2009). Results of the lipid class analysis were provided as supplementary content (**Table S1**).
The extracted lipids were converted into fatty acid methyl esters (FAMEs) and free alcohols derived from wax esters by transesterification in methanol, containing 3% concentrated sulfuric acid, at 50°C for 12 h. After a subsequent hexane extraction, the FAMEs and alcohols were separated on an Agilent 6890N Network gas chromatograph (Agilent Technologies, USA) with a DB-FFAP capillary column (30 m, 0.25 mm I.D., 0.25 µm film thickness), equipped with a split injection and a flame ionization detector using a temperature program (160 to 240°C). The samples were injected at 160°C. Helium was used as a carrier gas. FAMEs were identified via standard mixtures and quantified with an internal standard (23:0) that was added prior to lipid extraction.
Fatty acids were expressed by the nomenclature A:Bn-X, where A represents the number of carbon atoms, B the amount of double bonds, and X is giving the position of the first double bond starting from the methyl end of the carbon chain. The proportions of individual FAs were expressed as mass percentage of the total FA content.

Bulk stable isotope analysis

Frozen samples were freeze-dried for 24 h, and under-ice fauna samples were mechanically homogenized prior to the BSIA. In order to get an adequate amount of sample material, individuals of *Calanus* spp. and *A. glacialis* were pooled species-specifically for each sampling site. The powdered material and filters were filled into tin capsules and analyzed with a continuous flow isotope ratio mass spectrometer Delta V Plus, interfaced with an elemental analyzer (Flash EA 2000 Series) and connected via a Conflo IV interface (Thermo Scientific Corporation, Germany).

According to the following equation, the isotopic ratios were conventionally expressed as parts per thousand (‰) in the δ notation (Coplen 2011):

(1) $\delta_x = [(R_{sample}/R_{standard}) -1] * 1000$

where x represents the heavy carbon isotope ^{13}C or the heavy nitrogen isotope ^{15}N. R_{sample} represents the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ isotope ratio relative to the corresponding standard ($R_{Standard}$). The international Vienna Pee Dee Belemnite standard was used for carbon measurements and atmospheric nitrogen for nitrogen measurements.
Since lipids have a high turnover and are depleted in ^{13}C relative to proteins and carbohydrates (Deniro and Epstein 1977), they are often removed prior to the analysis in order to reduce the variability of $\delta^{13}C$ due to seasonal fluctuations (Tamelander et al. 2006b), and to make the C:N rations more comparable among species (Søreide et al. 2006). Previous studies, however, have shown that the extraction can cause fractionations in $\delta^{15}N$ (Pinnegar and Polunin 1999; Sweeting et al. 2006). In our study, the lipids were not removed, since the removal process might create uncertain changes in the isotopic compositions, particularly in small organisms (Madurell et al. 2008; Mintenbeck et al. 2008; Kürten et al. 2012).
The calibration of the stable isotope measurements (Brand et al. 2014) was done by analyzing the secondary reference material USGS40 (certified: $\delta^{15}N$ = -4.52‰, $\delta^{13}C$ = -26.39‰, measured: $\delta^{15}N$ = -4.46‰, $\delta^{13}C$ = -26.24‰) and USGS41 (certified: $\delta^{15}N$ = 47.57‰, $\delta^{13}C$ = -37.63‰, measured: $\delta^{15}N$ = 47.12‰, $\delta^{13}C$ = -37.49‰), provided by the International Atomic Energy Agency (IAEA, Austria). The analytical errors were indicated as ± 0.2 for nitrogen and ± 0.3‰ for carbon measurements for both USGS40 and USGS41 (representing the 1 SD of 7 analyses each). For the verification of accuracy and precision, the laboratory standards Isoleucine and Acetanilide were analyzed every 5 samples, with analytical errors of ± 0.1‰ for both Isoleucine nitrogen and carbon isotope ratios, and ± 0.1 and ± 0.2‰ for Acetanilide nitrogen and carbon isotope ratios, respectively (representing the 1 SD of 7 analyses each). The samples were analyzed in duplicates, and true δ values were obtained after two-point linear normalization (Paul et al. 2007).

Compound-specific stable isotope analysis

Prior to the CSIA, FAMEs were separated from the wax ester-derived fatty alcohols in order to avoid overlapping peaks. An insufficient baseline separation between FAMEs and alcohols can potentially cause carry-over effects and, thus, potentially lead to imprecise calculations of the FAME $\delta^{13}C$ values. For this purpose, FAMEs were isolated from the fatty alcohols via column chromatography with silica gel (6%, deactivated). The FAME fraction was eluted with hexane/dichloromethane (9:1, v/v), fatty alcohols with hexane/acetone (1:1, v/v).
Carbon stable isotope ratios were determined for selected marker FAs using a Thermo GC-c-IRMS system, equipped with a Trace GC Ultra gas chromatograph, a GC Isolink and Delta V Plus isotope ratio mass spectrometer, connected via a Conflo IV interface

(Thermo Scientific Corporation, Germany). The FAMEs, dissolved in hexane, were injected in splitless mode and separated on a DB-FFAP column (60 m, 0.25 mm I.D., 0.25 µm film thickness). The $\delta^{13}C$ values of a free FA and the corresponding FAME can differ slightly due to the added methyl group during the transesterification (e.g. Budge et al. 2011; Wang et al. 2014). However, in a previous study, we did not find significant differences between the $\delta^{13}C$ values of the free FA and the FAME (e.g. 16:0 FA: -28.56 ± 0.12‰, 16:0 FAME: -28.57 ± 0.16‰; C. Albers unpubl.). Therefore, we did not correct for these potential differences.

The $\delta^{13}C$ values of the individual FAMEs were calibrated by analyzing the certified standard FAMEs 14:0 (certified: $\delta^{13}C$ = -29.98‰, measured: $\delta^{13}C$ = -29.54‰) and 18:0 (certified: $\delta^{13}C$ = -23.24‰, measured: $\delta^{13}C$ = -23.29‰), supplied by Indiana University, every 5 samples. The analytical error was ± 0.3‰ for both 14:0 and 18:0 (representing the 1 SD of 10 analyses each). Furthermore, for quality assurance and analytical precision of the determined carbon stable isotope ratios, the laboratory standard 23:0 was measured intermittently during the sample runs with an analytical error of ± 0.4% (representing the 1 SD of 10 analyses). The samples were analyzed in duplicates.

Data analysis

The species-specific FA proportions were used as an indicator of a consumer's carbon sources in the days and weeks before the sampling. Consumers at lower trophic levels, such as *Calanus* copepods, show a quick lipid turnover rate ranging between hours and days (Graeve et al. 2005).

The investigation of the FA composition variations was based on six marker FAs. The FAs 16:1n-7 and 20:5n-3 are mainly produced by diatoms and can therefore be treated as valid diatom-specific marker FAs (e.g. Graeve et al. 1997; Falk-Petersen et al. 1998; Scott et al. 1999). The FAs 18:4n-3 and 22:6n-3 are produced in high amounts by dinoflagellates and are therefore used as a dinoflagellate marker FAs (Viso and Marty 1993; Graeve et al. 1994b). Long-chained FAs 20:1 and 22:1 (all isomers) were used to indicate the presence of *Calanus* spp. within the diets of the investigated under-ice fauna species (e.g. Falk-Petersen et al. 1987; Søreide et al. 2013). A principal component analysis (PCA) was applied on the FA dataset to visualize inter-specific differences. Spatial variability in the FA patterns between the two environmental regimes characterized by David et al. (2015) were visualized with bar plots.

Similar to FAs, stable isotope compositions can provide dietary information over a longer period (Tieszen et al. 1983). Bulk $\delta^{13}C$ and FA-specific $\delta^{13}C$ values were determined to estimate the proportional contribution of ice algae-produced carbon (α_{Ice}) to the diet of the under-ice fauna species. Bayesian multi-source stable isotope mixing models (SIAR; Parnell et al. 2010) were used to determine the α_{Ice} estimates from both analyses, BSIA and CSIA. For the CSIA modeling, two different FA combinations were used: (a) 20:5n-3 and (b) 20:5n-3 + 22:6n-3, in order to account for the potentially overlapping compositions of the ice algae and phytoplankton communities. The diatom-specific FA 20:5n-3 was used in the model, because I-POM is typically dominated by diatoms (Horner 1985; Gosselin et al. 1997; Arrigo et al. 2010). However, diatoms can

also be present in P-POM (Gosselin et al. 1997; Wang et al. 2014). The dinoflagellate-specific FA 22:6n-3 was used, because the water column can contain high amounts of dinoflagellates and flagellates (Sherr et al. 1997). Besides, sea ice systems may also be dominated by flagellates, particularly during ice melt (Tamelander et al. 2009).

The models allow the incorporation of trophic enrichment factors (TEFs) to account for isotopic turnover rates in the consumers that are tissue-specific. From lower to higher trophic level, an enrichment of the heavy carbon stable isotope between 0.1 and 1‰ was often observed (DeNiro and Epstein 1978; Rau et al. 1983; Post 2002). Since the true value of the carbon TEFs in the under-ice fauna species is unknown, carbon TEFs for both BSIA and CSIA models were assumed to be zero (Budge et al. 2011; Wang et al. 2015). The models also allow the incorporation of concentration dependencies to account for different levels of the investigated marker FAs in the primary producers. The discrepancy in the proportions of 20:5n-3 between I-POM and P-POM during maximum ice in 2010 reported by Wang et al. (2015) was higher than in our dataset. However, Wang et al. (2015) did not find substantial differences between the results using models with and without concentration data. Thus, we did not incorporate concentration dependencies in our models. Due to the small sample size, the calculation of α_{Ice} was based on the mean stable isotope values, with no differentiation between the two environmental regimes, for both BSIA and CSIA data.

The ice algae-produced carbon demand of the most abundant herbivores, *C. glacialis*, *C. hyperboreus* and *A. glacialis*, was estimated by multiplying our proportional α_{Ice} derived from CSIA model b with ingestions rates (Olli et al. 2007) and observed species abundances under sea ice and in the water column (David et al. 2015; Ehrlich 2015).

All data analyses were conducted using the open-source software 'R', version 3.2.0 (R Core Team 2015). Intra-specific and inter-specific variations in fatty acid and stable isotope compositions were tested using 1-way ANOVAs followed by Tukey HSD post-hoc tests. Student´s t-tests were applied for comparisons between two groups. Prior to testing, the FA data were transformed applying an arcsine square root function following Budge et al. (2007) to improve normality. The statistical output reported in the text was summarized in **Tables 3** (ANOVAs) and **4** (t-tests).

▼**Table 3.** Statistical parameters of ANOVA tests and Tukey HSD post-hoc tests with significant results.

ANOVA					
Parameter	*n*	*F*	*df*	*p*	Tukey HSD
level FA 16:1n-7	98	28.3	7, 90	< 0.001	*A. glacialis* > all amphipod species: $p < 0.001$ *C. limacina* < all species: $p < 0.05$
level FA 22:6n-3	98	39.3	7, 90	< 0.001	*Calanus* spp. > all amphipod species: $p < 0.01$ *C. limacina* > all species (except C. *hyperboreus*): $p < 0.001$

FA: fatty acid, *n*: sample size

▼**Table 4.** Statistical parameters of Student´s t-tests with significant results.

t-test					
Parameter	*n*	*t*	*df*	*p*	
level FA 16:1n-7	19	7.1	13.6	< 0.001	I-POM > P-POM
level FA 18:4n-3	19	9.8	16.3	< 0.001	I-POM < P-POM
δ^{13}C FA 18:4n-3	12	7.3	4.7	< 0.001	I-POM > P-POM
level FA 20:5n-3	19	2.3	10.9	< 0.05	I-POM < P-POM
δ^{13}C FA 20:5n-3	13	6.4	9.9	< 0.001	I-POM > P-POM
level FA 22:6n-3	19	9.0	12.8	< 0.001	I-POM < P-POM
δ^{13}C FA 22:6n-3	11	5.9	4.4	< 0.01	I-POM > P-POM

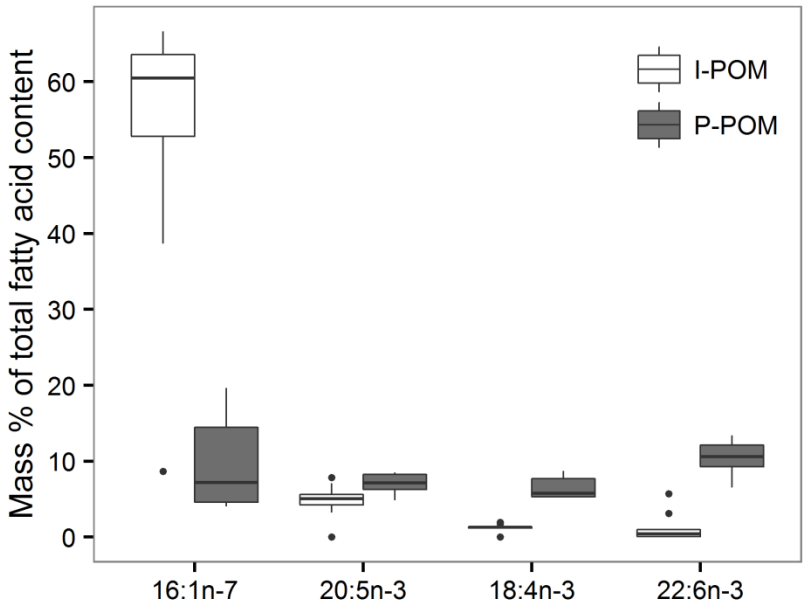
FA: fatty acid, *n*: sample size

Results

Marker fatty acid compositions

Ice-associated and pelagic particulate organic matter

The I-POM samples were dominated by the diatom-specific FA 16:1n-7, showing significantly higher levels than the P-POM samples. The proportional contributions of the second diatom-specific FA 20:5n-3 were, however, significantly lower in the I-POM samples compared to the P-POM samples. The proportions of the dinoflagellate-specific FAs 18:4n-3 and 22:6n-3 showed significantly higher values in P-POM compared to I-POM (**Figure 2**, **Tables 4** and **5**).



▲***Figure 2.*** *Relative composition of marker fatty acids (FAs) in ice-associated particulate organic matter (I-POM) and pelagic particulate organic matter (P-POM). 16:1n-7 and 20:5n-3 represent diatom marker FAs, 18:4n-3 and 22:6n-3 represent dinoflagellate marker FAs. Horizontal bars in the box plots indicate median proportional values. Upper and lower edges of the boxes represent the approximate 1st and 3rd quartiles, respectively. Vertical error bars extend to the lowest and highest data value inside a range of 1.5 times the inter-quartile range, respectively (Team 2015). Outliers are represented by the dots outside the boxes. Sample size is reported in* ***Table 5.***

Under-ice fauna species

In all species, the bulk of the determined FAs were incorporated into neutral (storage) lipids, whose proportions far exceeded the levels of polar (membrane) lipids (**Table S1**, Supplementary).

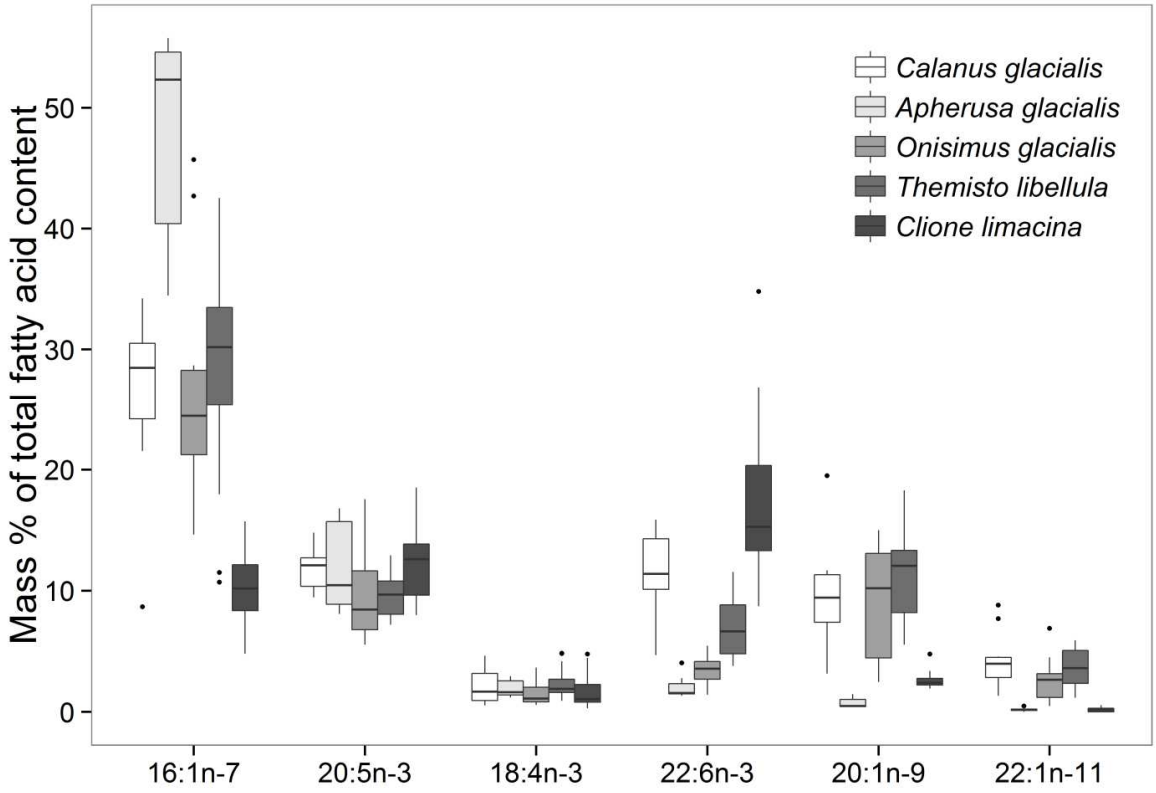
The largest variability among all species was observed in the diatom-specific FA 16:1n-7 and the dinoflagellate-specific FA 22:6n-3. The levels of the diatom-specific FA 20:5n-3 were comparable among all species, and the proportions of the dinoflagellate-specific FA 18:4n-3 were generally low in all species (**Figure 3**, **Table 5**).

▼**Table 5.** Relative composition of the most abundant fatty acids (FAs) in ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM), and under-ice fauna species (mean ± 1 SD mass % of total FA content) collected in the Nansen Basin (NB) and Amundsen Basin (AB). Not detected FAs are reported as '--'.

	I-POM	**P-POM**	***Calanus glacialis***	***Calanus hyperboreus***	***Apherusa glacialis***	***Onisimus glacialis***	***Gammarus wilkitzkii***	***Eusirus holmii***	***Themisto libellula***	***Clione limacina***
n_{NB}	1	7	3	2	4	7	5	5	2	3
n_{AB}	9	2	7	4	8	9	3	9	14	13
14:0	5.3 ± 1.5	6.0 ± 2.1	8.1 ± 1.2	4.6 ± 1.9	4.2 ± 0.4	3.4 ± 0.9	3.9 ± 0.5	3.8 ± 0.6	4.9 ± 1.3	2.6 ± 1.8
16:0	16.3 ± 4.1	20.3 ± 1.9	8.8 ± 1.5	7.3 ± 3.2	13.4 ± 0.5	11.5 ± 2.1	12.2 ± 0.8	12.7 ± 1.6	9.2 ± 1.3	12.1 ± 1.6
16:1n-7[a]	53.6 ± 17.9	9.8 ± 6.0	26.2 ± 7.3	20.3 ± 10.2	48.1 ± 8.1	27.0 ± 9.6	31.4 ± 5.6	36.4 ± 8.5	27.9 ± 8.5	10.3 ± 2.9
18:0	4.5 ± 7.5	5.3 ± 1.2	1.2 ± 0.5	1.6 ± 1.1	0.7 ± 0.2	0.5 ± 0.2	0.6 ± 0.1	0.6 ± 0.2	0.5 ± 0.1	2.8 ± 1.9
18:1n-9	7.0 ± 4.5	6.5 ± 2.5	3.6 ± 0.4	3.3 ± 0.6	7.9 ± 1.5	18.1 ± 4.4	16.1 ± 2.9	9.8 ± 1.4	8.1 ± 1.5	4.2 ± 1.3
18:1n-7	0.4 ± 0.4	1.8 ± 1.1	1.5 ± 0.4	1.8 ± 0.7	2.0 ± 0.5	3.4 ± 0.7	4.0 ± 0.5	3.0 ± 0.6	3.0 ± 0.7	4.6 ± 1.4
18:4n-3[b]	1.2 ± 0.5	6.4 ± 1.4	2.2 ± 1.6	3.0 ± 1.6	1.9 ± 0.7	1.5 ± 0.9	1.9 ± 0.5	1.5 ± 0.7	2.4 ± 1.3	1.8 ± 1.5
20:1n-9[c]	--	--	9.8 ± 4.3	8.7 ± 5.6	0.7 ± 0.4	8.9 ± 4.5	3.2 ± 2.1	4.9 ± 4.5	11.3 ± 4.1	2.7 ± 0.7
20:1n-7	--	--	0.5 ± 0.4	1.0 ± 0.9	0.5 ± 0.2	1.4 ± 0.6	0.7 ± 0.1	1.0 ± 0.5	1.5 ± 0.8	2.5 ± 0.6
20:5n-3[a]	4.8 ± 2.2	7.1 ± 1.3	11.9 ± 1.9	15.3 ± 3.7	11.7 ± 3.6	9.7 ± 3.8	12.8 ± 3.4	11.8 ± 3.3	9.7 ± 1.6	12.1 ± 2.9
22:1n-11[c]	--	--	4.3 ± 2.3	6.2 ± 4.8	0.2 ± 0.1	2.5 ± 1.6	2.1 ± 1.9	1.8 ± 1.8	3.7 ± 1.6	0.2 ± 0.2
22:6n-3[b]	1.2 ± 1.8	10.4 ± 2.1	11.4 ± 3.5	14.1 ± 7.8	2.0 ± 0.8	3.4 ± 1.3	3.3 ± 0.8	4.3 ± 1.8	7.1 ± 2.7	17.5 ± 7.0
Total	94.3	73.6	89.5	87.2	93.3	91.3	92.2	91.6	89.3	73.4

a: diatom marker FA, b: dinoflagellate marker FA, c: *Calanus* marker FA, *n*: sample size

The mean levels of 16:1n-7 in both *Calanus glacialis* and *C. hyperboreus* were lower than in all other species, except for *Clione limacina*. In contrast, their content in 20:5n-3 was high compared to the other species, with *C. hyperboreus* reaching the maximum mean value of this study. *C. glacialis* and *C. hyperboreus* contained significantly higher amounts of 22:6n-3 compared to all amphipod species (**Tables 3** and **5**). The mean level of the *Calanus*-specific FA 20:1n-9 was only higher in *Themisto libellula* relative to *Calanus* spp., and in *Onisimus glacialis* relative to *C. hyperboreus*. The second *Calanus*-specific FA 22:1n-11 was detected in generally higher amounts in both *Calanus* spp. compared to all other species. There was no significant difference found in the FA patterns between CV and female within the same *Calanus* species (t-test, $p > 0.05$).



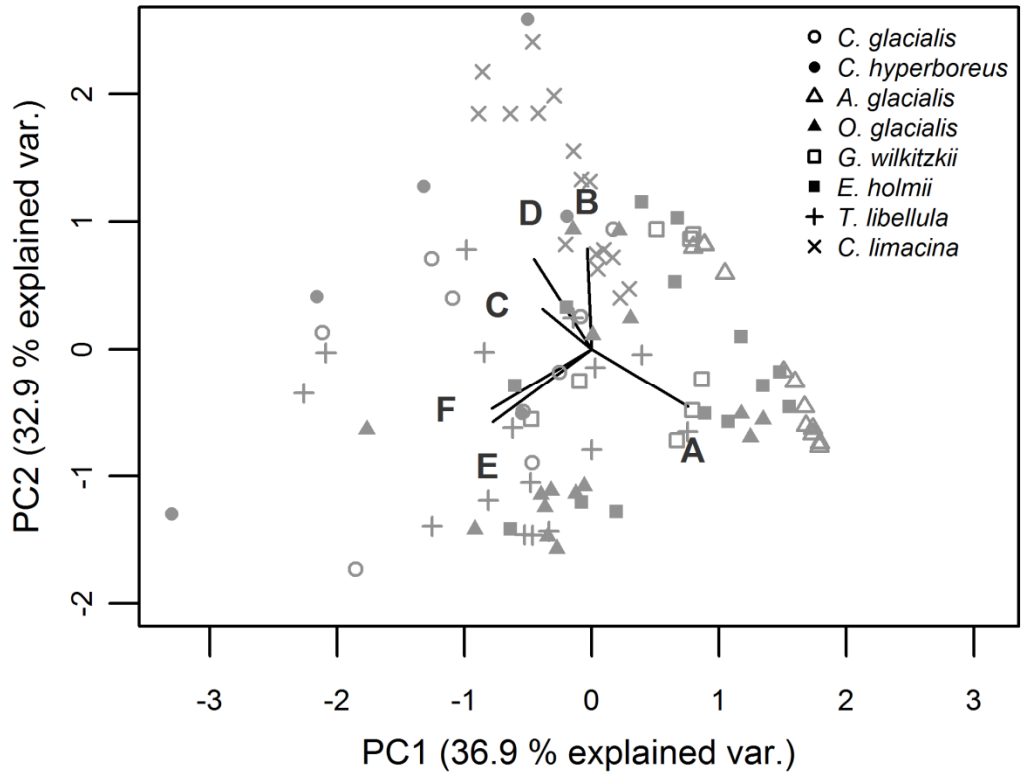
▲***Figure 3.*** *Relative composition of marker fatty acids (FAs) in selected under-ice fauna species. 16:1n-7 and 20:5n-3 represent diatom marker FAs, 18:4n-3 and 22:6n-3 represent dinoflagellate marker FAs, 20:1n-9 and 22:1n-11 represent Calanus-marker FAs. Box plot design as in* ***Figure 2****. Sample size is reported in* ***Table 5****.*

A. glacialis had a significantly higher proportion of 16:1n-7 than all other amphipod species, in addition to relatively high levels of 20:5n-3 (**Tables 3** and **5**). The levels of 20:1n-9 and 22:1n-11 were close to the detection limit in this species. *Gammarus wilkitzkii* and *Eusirus holmii* were generally similar to each other in their FA composition*. E. holmii* had the second-highest proportional content of 16:1n-7 among all amphipod species. *T. libellula* had a higher proportional content of 22:6n-3 than all other amphipods, and high levels of 20:1n-9 and 22:1n-11.

The FA 16:1n-7, which was dominant in all investigated copepods and amphipods, showed significantly lower levels in *C. limacina* compared to all other investigated

species (**Tables 3** and **5**). Conversely, the proportional contribution of 22:6n-3 was significantly higher in *C. limacina* compared to all other investigated species, except for *C. hyperboreus* (**Tables 3** and **5**). The FAs 20:1n-9 and 22:1n-11 were only found in small amounts in this species.

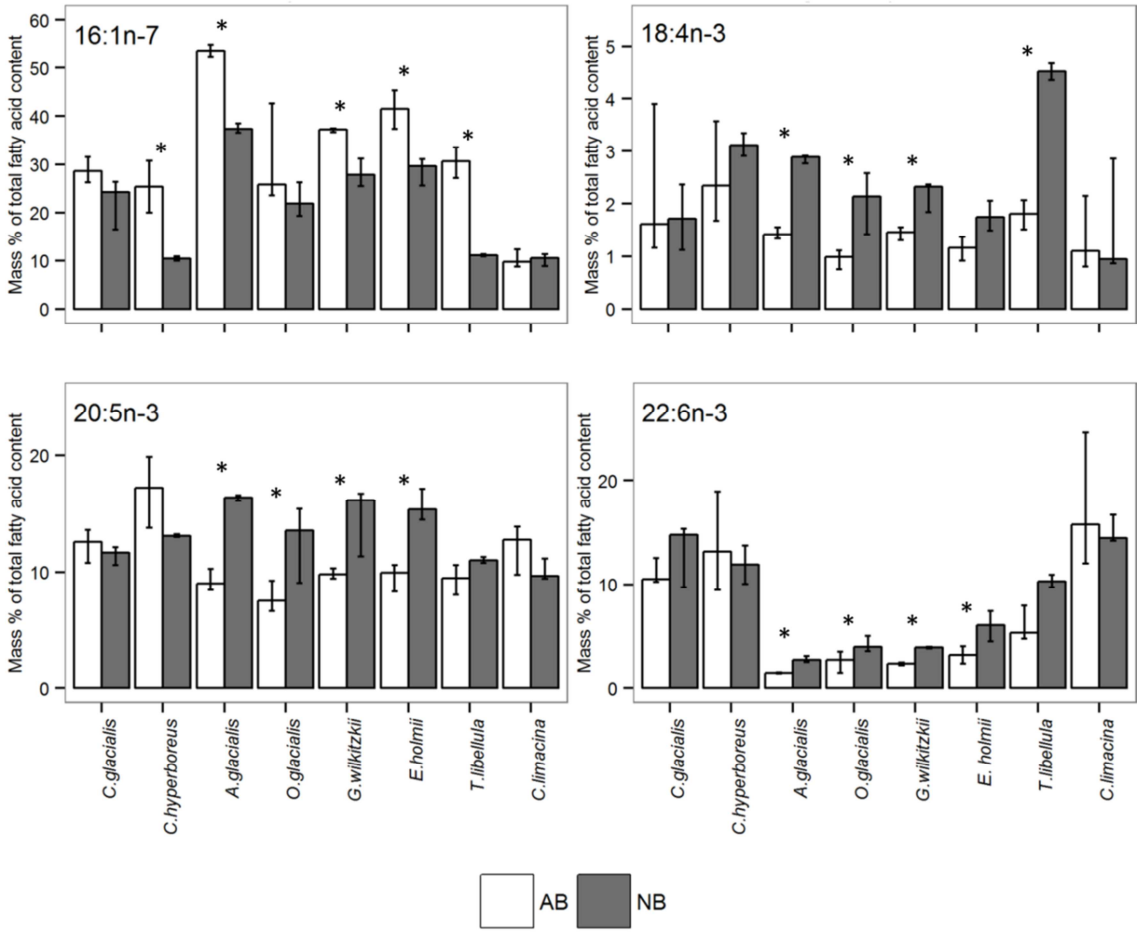
The first two principal components of the PCA explained 69.8 % of the variance in the FA data among the samples (**Figure 4**). The first axis (PCA 1) separated the sympagic amphipods with high levels of 16:1n-7 on one side from the pelagic copepods with high levels of 22:6n-3, 20:1n-9, and 22:1n-11 on the other side. The second axis (PCA 2) emphasized the difference in the marker FA proportions between the pelagic species *T. libellula* with higher levels of 16:1n-7 and both *Calanus*-marker FAs, and *C. limacina* with distinctly higher levels of 22:6n-3. In general, the FA profile of *C. limacina* was clearly isolated from all other species.



▲***Figure 4.*** *PCA biplot of marker fatty acid (FA) proportions in under-ice fauna species. Biplot arrows correspond to gradients of FAs in the PCA ordination. Diatom marker FAs: 16:1n-7 (A), 20:5n-3 (B); dinoflagellate marker FAs: 18:4n-3 (C), 22:6n-3 (D); Calanus-marker FAs: 20:1n-9 (E), 22:1n-11 (F). Sample size is reported in* ***Table 5****.*

In addition to the differences between the species, there was an intra-specific spatial variability of certain marker FA proportions observed. SUIT station 258 was located close to the Gakkel ridge, on the border between the Nansen Basin (NB) and the Amundsen Basin (AB). In general, the FA composition of individuals from station 258 demonstrated a higher similarity to the FA profiles of the same species from the AB regime. Thus, station 258 was considered as an AB regime sample for the statistical tests. In *Calanus* spp. and all five amphipod species, the proportional amount of 16:1n-7 was higher in the AB regime samples than in the NB regime samples. This pattern was

significant (t-test, $p < 0.05$) in *C. hyperboreus*, *A. glacialis, G. wilkitzkii*, *E. holmii*, and *T. libellula*, and near-significant in *O. glacialis* ($p = 0.06$). Conversely, the levels of 18:4n-3, 20:5n-3, and 22:6n-3 were significantly higher in the NB regime in *A. glacialis, O. glacialis* and *G. wilkitzkii*. In *E. holmii*, the proportions of 20:5n-3 and 22:6n-3 were significantly higher in the NB regime samples compared to the AB regime samples. In *T. libellula*, the levels of 18:4n-3, 20:1n-9 and 22:1n-11 were significantly higher in the NB regime than in the AB regime (**Figure 5**). As all but one station in the AB regime were sampled later in the season than stations in the NB regime, these patterns could reflect the seasonal progression of the system (e.g. Basedow et al. 2010). In addition, the fundamental differences in the environmental characteristics of the two regimes probably played an important role. The AB regime was characterized by lower nitrate and phosphate concentrations and lower Chl *a* concentrations in the surface layer compared to the NB regime (David et al. 2015).



▲***Figure 5.*** *Intra-specific differences in the proportions of marker fatty acids (FAs) in under-ice fauna species between Nansen Basin (NB) and Amundsen Basin (AB) regimes. Columns and error bars correspond to the median and interquartile ranges, respectively. Note: y-axes have different scales. Associated bars marked with asterisk '*' represent significant differences between the regimes (t-test, p < 0.05). Sample size is reported in* ***Table 5****.*

Bulk stable isotope compositions

Both POM types displayed the lowest δ^{15}N values between 3.5 and 6.4‰ in I-POM and between 2.1 and 5.8‰ in P-POM, representing the trophic baseline (**Table 6**). The δ^{13}C values in I-POM varied between -22.8 and -26.8‰, the P-POM δ^{13}C values varied between -25.4 and -28.7‰.

▼**Table 6.** Bulk stable nitrogen (δ^{15}N) and carbon isotope values (δ^{13}C) in ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM), and under-ice fauna species (mean ± 1 SD ‰).

	n	**δ^{15}N**	**δ^{13}C**
I-POM	6	4.8 ± 1.3	-24.9 ± 1.6
P-POM	17	4.0 ± 1.2	-27.3 ± 0.9
Calanus glacialis	4	7.5 ± 0.9	-26.8 ± 3.1
Calanus hyperboreus	4	7.8 ± 1.4	-26.6 ± 1.1
Apherusa glacialis	4	5.4 ± 0.3	-22.3 ± 1.5
Onisimus glacialis	4	7.1 ± 1.8	-22.4 ± 1.7
Gammarus wilkitzkii	4	7.1 ± 0.6	-24.4 ± 0.4
Eusirus holmii	4	10.0 ± 1.5	-23.3 ± 0.7
Themisto libellula	4	8.8 ± 1.5	-25.7 ± 1.8
Clione limacina	4	8.6 ± 0.8	-26.9 ± 0.5

n: sample size

Among the under-ice fauna species, *A. glacialis* showed the lowest δ^{15}N values between 5.0 and 5.7‰, *E. holmii* showed the highest δ^{15}N values between 8.9 and 12.2‰ (**Table 6**). The highest carbon stable isotope values were found in *A. glacialis* (-20.0 to -23.3‰). The lowest δ^{13}C values were found in *Calanus* spp., *T. libellula* and *C. limacina* (-24.1 to -31.2‰). A comparison of the bulk stable isotope ratios in POM and the under-ice fauna species between the two environmental regimes was provided in **Table S2** (Supplementary).

Compound-specific stable isotope compositions

The δ^{13}C values of 18:4n-3, 20:5n-3 and 22:6n-3 were significantly higher in the I-POM samples compared to the P-POM samples (**Tables 4** and **7**). The stable isotope values of 16:1n-7 demonstrated little variation between the two source communities.

▼**Table 7.** Carbon stable isotope values ($\delta^{13}C$) of marker fatty acids (FAs) in ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM), and under-ice fauna species (mean ± 1 SD ‰). Not detected FAs are reported as '--'.

	n	**16:1n-7**	**20:5n-3**	**18:4n-3**	**22:6n-3**
I-POM	7	-24.9 ± 4.1	-26.6 ± 2.7	-28.4 ± 3.2	-23.4 ± 3.7
P-POM	7	-26.4 ± 3.4	-35.6 ± 2.3	-39.3 ± 1.1	-35.5 ± 2.3
Calanus glacialis	10	-25.0 ± 3.8	-32.2 ± 1.7	-35.6 ± 1.8	-32.0 ± 2.1
Calanus hyperboreus	6	-27.3 ± 3.6	-32.1 ± 1.2	-36.2 ± 1.1	-33.8 ± 2.3
Apherusa glacialis	10	-24.2 ± 2.6	-26.6 ± 1.3	-29.2 ± 1.9	-28.5 ± 1.6
Onisimus glacialis	8	-22.9 ± 3.0	-28.4 ± 1.6	-32.4 ± 3.6	-30.4 ± 1.0
Gammarus wilkitzkii	4	-24.8 ± 2.1	-29.0 ± 1.0	-31.2 ± 0.9	-31.3 ± 1.5
Eusirus holmii	8	-23.4 ± 2.1	-28.9 ± 1.0	-30.1 ± 1.2	-30.4 ± 1.3
Themisto libellula	7	-23.9 ± 2.3	-31.4 ± 1.4	-35.6 ± 2.2	-33.7 ± 1.8
Clione limacina	9	-28.7 ± 1.9	-34.1 ± 1.6	--	-33.8 ± 1.1

n: sample size

There was no significant difference in the carbon stable isotope values of the individual marker FAs between the two *Calanus* species (t-test, $p > 0.05$). The mean $\delta^{13}C$ values of 18:4n-3, 20:5n-3, and 22:6n-3 were lower in both *Calanus* spp. compared to all other species, except for *T. libellula* and *C. limacina*. Among all species, *A. glacialis* displayed the highest mean $\delta^{13}C$ values of 18:4n-3, 20:5n-3 and 22:6n-3. Among the amphipods, *T. libellula* displayed the lowest mean $\delta^{13}C$ values of 18:4n-3, 20:5n-3 and 22:6n-3 (**Table 7**). A comparison of the fatty acid-specific stable isotope ratios in POM and the under-ice fauna species between the two environmental regimes was provided in **Table S3** (Supplementary).

Proportional contribution of ice algae-produced carbon

All three approaches indicated that the sympagic amphipods *A. glacialis*, *O. glacialis*, *G. wilkitzkii*, and *E. holmii* showed the highest dependency on ice algal carbon, *Calanus* spp. and *T. libellula* took an intermediate position, and *C. limacina* showed the lowest dependency (**Table 8**). The results from the SIAR models using the carbon stable isotope values of FA 20:5n-3 (model a) were similar to those from the BSIA models, and were generally higher than the α_{Ice} estimates derived from model b, which combined 20:5n-3 and 22:6n-3 (**Table 8**).

▼**Table 8.** Proportional contribution of ice algae-produced carbon (α_{Ice}) in under-ice fauna species (mean %) from SIAR mixing models based on bulk stable isotope analyses (BSIA; Table 6) and stable isotope compositions of marker fatty acids (a) 20:5n-3 and (b) 20:5n-3 + 22:6n-3 (Table 7). Ranges of α_{Ice} are shown in parentheses.

Model	BSIA	(a) 20:5n-3	(b) 20:5n-3 + 22:6n-3
Calanus glacialis	47 (10-76)	48 (20-53)	33 (26-43)
Calanus hyperboreus	39 (6-86)	40 (35-48)	25 (20-27)
Apherusa glacialis	90 (85-95)	92 (91-94)	86 (80-90)
Onisimus glacialis	87 (79-95)	77 (73-81)	61 (53-68)
Gammarus wilkitzkii	91 (88-93)	76 (63-81)	58 (48-66)
Eusirus holmii	90 (87-92)	79 (74-84)	60 (56-64)
Themisto libellula	55 (6-87)	45 (40-50)	23 (20-28)
Clione limacina	30 (16-53)	18 (13-28)	14 (10-21)

A. glacialis showed the highest α_{Ice} estimates among all species, accompanied with the lowest variation between the α_{Ice} estimates derived from the BSIA model and the two CSIA models (overall mean > 85%). Both *Calanus* spp. indicated high similarity between the estimates derived from the BSIA model and CSIA model a (BSIA: mean 43%, CSIA model a: mean 44%). Furthermore, all approaches provided similar α_{Ice} estimates for *O. glacialis*, *G. wilkitzkii*, and *E. holmii* (BSIA: mean ~ 90%, CSIA model a: mean ~ 80%, CSIA model b: mean ~ 60%). A high discrepancy between the BSIA model and CSIA model b was found in the pelagic species *T. libellula* (BSIA: mean 55%, CSIA model b: 23%) and *C. limacina* (BSIA: mean 30%, CSIA model b: mean 14%).

Ice algae-produced carbon demand

We calculated a tentative estimate of the overall demand of ice algae-produced carbon by the most abundant grazers *C. glacialis*, *C. hyperboreus* and *A. glacialis* based on the α_{Ice} values derived from CSIA model b (**Table 8**). Altogether, these species consumed between 2.9 and 8.5 mg ice algae-produced carbon m^{-2} d^{-1}. Due to its high abundance, the bulk of the ice algal carbon demand was attributed to *C. glacialis* (**Table 9**).

▼**Table 9.** Ice algae-produced carbon demand in abundant herbivores. In *Calanus* spp., only adults and CV stages were included in abundance estimates. α_{Ice} = proportional contribution of ice algae-produced carbon derived from SIAR model b (**Table 8**).

	α_{Ice}	**Ingestion rate**[1] (µg C ind.$^{-1}$ d^{-1})		**Abundance** (ind. m^{-2})		**Ice algal carbon demand** (mg C m^{-2} d^{-1})					
				Under-ice[2]	Pelagic[3]	Under-ice		Pelagic		Total	
	Mean	Min	Max	Mean	Mean	Min	Max	Min	Max	Min	Max
Calanus glacialis	0.33	6.0	18.0	6.4	1180	0.01	0.04	2.34	7.01	2.35	7.05
Calanus hyperboreus	0.25	2.8	8.4	1.0	700	0.00	0.00	0.49	1.47	0.49	1.47
Apherusa glacialis	0.86	13.0	13.0	0.6	0	0.01	0.01	0.00	0.00	0.01	0.01
Total		21.8	39.4	8.0	1880	0.02	0.05	2.83	8.48	2.85	8.53

[1]Olli et al. (2007)
[2]David et al. (2015)
[3]Ehrlich (2015)

Discussion

Variability in marker fatty acid compositions among algal communities and under-ice fauna species

In our study, the FA profiles of the I-POM samples suggested a diatom-dominated ice algal community. The small amounts of the dinoflagellate-specific FAs 18:4n-3 and 22:6n-3 in the I-POM samples indicated that a small part of the sea ice flora consisted of dinoflagellates, which was in agreement with the results of molecular analyses of the primary community structures (K. Hardge et al. subm.). Based on the marker FA proportions, the phytoplankton community consisted of a mixture of both diatoms and flagellates. The dominance of dinoflagellates in the water column and a substantially higher proportion of diatoms in the sea ice community compared to the pelagic community during our sampling were also confirmed by genome sequencing (K. Hardge et al. subm.). The lower levels of the diatom-specific FA 20:5n-3 accompanied with the distinctly higher levels of the diatom-FA 16:1n-7 in the I-POM samples compared to the P-POM samples could indicate a different diatom-community in sea ice compared to the water column. Supporting our assumption, previous studies found a dominance of pennate diatoms in sea ice versus a dominance of centric diatoms in the water column (Gosselin et al. 1997; Arrigo et al. 2010).

The FA profiles of the under-ice fauna species revealed variable associations with diatom-and dinoflagellate-related marker FAs. Although it may be possible for herbivorous invertebrates to synthesize 20:5n-3 and 22:6n-3 from 18:3n-3 (Moreno et al. 1979), FA 18:3n-3 was only found in trace amounts (< 1%) in the species from this study. This indicates that biosynthesis of 20:5n-3 and 22:6n-3 likely did not occur, and these FAs were derived through the trophic chain from algal sources.

Both *Calanus* spp. are known to be key Arctic grazers, utilizing both ice algae- and pelagic phytoplankton-derived carbon (Søreide et al. 2010; Durbin and Casas 2013). There was little difference in the FA profiles between *C. glacialis* and *C. hyperboreus*, indicating that the primary carbon sources were similar for both *Calanus* species. As frequently shown, the FA composition of Arctic *Calanus* spp. was characterized by high amounts of the diatom-specific FAs 16:1n-7 and 20:5n-3 (Graeve et al. 1994b; Wang et al. 2015). Furthermore, our results showed that both copepod species contained high amounts of the dinoflagellate-specific marker FA 22:6n-3, which together suggests sources of carbon from both diatoms and dinoflagellates.

The FA composition of the amphipod *A. glacialis* indicated a diet dominated by diatom-derived carbon, evident by high proportions of the diatom-specific FAs 16:1n-7 and 20:5n-3, accompanied by low levels of the dinoflagellate-specific FA 22:6n-3. A diatom-dominated diet is in agreement with several studies showing that *A. glacialis* primarily feeds on the under-ice flora and phytodetritus (Bradstreet and Cross 1982; Scott et al. 1999; Tamelander et al. 2006a). Together with *O. glacialis* and *G. wilkitzkii*, *A. glacialis* is known to live permanently associated with the Arctic sea ice (Poltermann 2001; Gradinger and Bluhm 2004). Thus, it is not surprising that *O. glacialis* and *G. wilkitzkii*

contained high levels of the diatom markers 16:1n-7 and 20:5n-3, with considerably lower levels of the dinoflagellate-specific FA 22:6n-3.

Calanus copepods are able to synthesize the long-chain FAs 20:1n-9 and 22:1n-11 in large amounts de novo. These FAs can also be used as trophic indicators for a copepod-related diet in higher consumers (Sargent et al. 1977; Wold et al. 2011). Accordingly, high values of the FA 20:1n-9 indicated a partly *Calanus*-based diet in the omnivorous amphipod *O. glacialis*. *G. wilkitzkii* has been reported to also feed extensively on copepods, primarily during adult stages (Scott et al. 2001). However, we found only small amounts of the *Calanus*-specific FAs 20:1n-9 and 22:1n-11 in this amphipod, indicating that *Calanus* may not have been important in their diets before the sampling.

Carnivorous amphipods, such as *E. holmii* and *T. libellula*, constitute important links between lipid-rich herbivores and top predators (Noyon et al. 2011). These two amphipod species also showed high levels of the diatom-specific FAs 16:1n-7 and 20:5n-3. In *T. libellula*, a higher proportion of the dinoflagellate-specific FA 22:6n-3 indicated a greater importance of dinoflagellate-derived carbon than in *E. holmii*. Both species, but particularly *T. libellula*, displayed elevated levels of the *Calanus*-specific marker FAs. Our findings are consistent with other feeding studies, which identified *T. libellula* as a part of the *Calanus*-based food web (Scott et al. 1999; Dalpadado et al. 2008; Kraft et al. 2013).

The carnivorous pteropod *C. limacina* is assumed to feed exclusively on *Limacina helicina* (Conover and Lalli 1974; Phleger et al. 2001). In our study, the FA composition of *C. limacina* was characterized by the lowest proportion of the diatom-specific FA 16:1n-7 and the highest proportion of the dinoflagellate-specific FA 22:6n-3, possibly reflecting a pelagic-based diet of diatoms and dinoflagellates in *L. helicina*. The pteropod *L. helicina* was first described as a pure herbivore, but more recent studies reported an omnivorous diet consisting of small copepods and juvenile *L. helicina* (Gilmer 1974; Gilmer and Harbison 1991; Falk-Petersen et al. 2001). The low levels of the *Calanus*-specific FAs found in our study in *C. limacina*, however, indicated that *Calanus* copepods were not important in the *L. helicina*-based pathway of the food web during the weeks before our sampling.

Besides the expected inter-specific variations largely confirming known feeding patterns, we also found considerable intra-specific variability in the FA profiles of the investigated under-ice fauna species. All amphipod species and *Calanus* spp. from the Amundsen Basin regime had higher proportions of the FA 16:1n-7 compared to the samples from the Nansen Basin regime. Additionally, all amphipods from the AB regime showed lower proportions of all other algal FAs than those sampled in the NB regime. The FA 16:1n-7 was largely limited to I-POM samples in our dataset. Hence, the observed variability between the two environmental regimes was probably driven by variability in ice algal communities rather than phytoplankton, assuming lipid turnover rates in these herbivores were fast compared to changes in algal composition (Graeve et al. 2005). An impact of the variability of sea ice communities on the FA composition is corroborated by pronounced differences in the community composition of protists in sea ice between the two environmental regimes (K. Hardge et al. subm.), as well as by

differing drift pathways of sea ice between the NB and the AB in 2012 (David et al. 2015).

Importance of ice algae-produced carbon to the Arctic under-ice community

In most investigated species, the α_{Ice} estimates based on BSIA were higher than those based on the single FAs. Unlike CSIA of FAs, which is limited to molecules assumed to be unchanged by metabolic processes, the interpretation of BSIA results can be more complicated. Besides the lipid components, proteins and carbohydrates are also subject to various mass-dependent metabolic processes, influencing the carbon stable isotope signal of a species. Compared to proteins and carbohydrates, lipids are more depleted in the heavy carbon stable isotope (DeNiro and Epstein 1977; Søreide et al. 2006). To correct for a potential bias in the BSIA results introduced by variability in lipid content, both *a priori* lipid removal and post-analytical corrections, e.g. with the normalization algorithm proposed by McConnaughey and McRoy (1979), have been used in previous studies. Several studies showed, however, that the extraction can cause fractionations in $\delta^{15}N$ (Pinnegar and Polunin 1999; Sweeting et al. 2006; Post et al. 2007). On the other hand, there are studies indicating that normalization models do not account for different lipid levels in different species in an appropriate way (Sweeting et al. 2006; Post et al. 2007). Therefore, we based our calculations on the non-corrected data. It remains difficult to conclude to which degree and in which species BSIA-based estimates of α_{Ice} were influenced by lipid content, taxon-specific, habitat-related, and/or trophic level-related effects on metabolically active compounds. Yet, both BSIA and CSIA-derived α_{Ice} estimates yielded a consistent hierarchical order of the investigated species, ranging from a highly sea ice algae-related trophic dependency in *A. glacialis* to a considerably lower trophic dependency on sea ice algae in *C. limacina* within the food web.

Based on the CSIA results, the isotopic values of carbon in the FAs 20:5n-3 and 22:6n-3 were used to investigate the proportional contributions of sea ice algae-produced carbon α_{Ice} versus phytoplankton-produced carbon to the body tissue of abundant under-ice fauna species. Budge et al. (2008) traced the carbon flux in an Alaskan coastal ecosystem using the stable isotope values of carbon in the FA 20:5n-3, which they assumed to represent a realistic estimate of the ice algae contribution relative to all other types of phytoplankton. Wang et al. (2015) also suggested that the use of only FA 20:5n-3 could be most accurate if diatoms dominated the POM composition. Due to the mixed taxonomic composition of the primary communities in our dataset, we additionally calculated α_{Ice} using the FA 22:6n-3 in combination with 20:5n-3 to account for the contribution of the dinoflagellate-dominated pelagic communities in our samples. To estimate the relative contribution of carbon sources to higher trophic levels, Budge et al. (2008) made several assumptions and simplifications that we also included in our study. We assumed that the major sources of FA 20:5n-3 were either ice-related diatoms or pelagic diatoms, and isotopic fractionation and routing processes were negligible. Furthermore, we assumed that our measured carbon stable isotope ratios actually reflect the ratio at the base of the food web. This means that the algae-derived lipid composition during the time of sampling was representative of the time when they were

ingested. Consumers at lower trophic levels show a quick lipid turnover rate ranging between hours and days (Graeve et al. 2005), indicating that this was indeed the case for the more herbivorous species.

The highest α_{Ice} estimates were found when only the diatom-specific FA 20:5n-3 was used (model a). The dinoflagellate-specific FA 22:6n-3 showed generally lower $\delta^{13}C$ values compared to I-POM in all under-ice fauna species. Thus, α_{Ice} estimates were considerably lower in some species when 20:5n-3 was used in combination with 22:6n-3 (model b). This indicates that the sole use of the diatom-specific FA 20:5n-3 underestimates the contribution of dinoflagellate-produced carbon when the proportion of diatoms versus dinoflagellates varies between sea ice and water column, causing a potential bias towards ice algae-produced carbon.

As expected, the sympagic amphipods showed a high trophic dependency on the ice algal production. Surprisingly, many species classified as rather pelagic also showed a considerable input of ice algae-produced carbon, further emphasizing the importance of ice algae for the entire food web. In *Calanus* spp., the estimated relative contribution of ice algae-derived carbon based on the BSIA and the CSIA profiles indicated a mix of pelagic and ice-associated carbon sources. Our results were comparable to a recent study in the Bering Sea, suggesting that the mean proportion of 20:5n-3, which originated from ice algae, was between 39 and 57% in *Calanus* spp., depending on the ice conditions (Wang et al. 2015). The reported mean α_{Ice} values for the combination of 20:5n-3 and 22:6n-3 were somewhat higher than our values, ranging between 31 and 63% (Wang et al. 2015). The ice algae-dependency of *Calanus* spp., however, seems to have a high variability, depending on region, season, and environmental properties. For example, Søreide et al. (2006) found a higher ice algae contribution for both *Calanus* copepods in autumn compared to spring, based on bulk stable isotope values.

Among the amphipods, *A. glacialis* showed the highest dependency on ice algal-produced carbon. *O. glacialis*, *G. wilkitzkii,* and *E. holmii* showed also high α_{Ice} values for both BSIA and CSIA, indicating a generally high trophic dependency on the ice algae production for all investigated sympagic amphipods, which is consistent with previous studies (Søreide et al. 2006; Tamelander et al. 2006a). In contrast, Budge et al. (2008) estimated the mean ice algae carbon contribution in *Apherusa sp.* near Barrow, Alaska, based on FA 20:5n-3, to be distinctly lower (61%) than our results. The mean proportional contributions of ice algae-produced carbon in *Onisimus sp.* and *Gammarus sp*., estimated by Budge et al. (2008), were also clearly lower than our findings (*Onisimus sp*.: 36%, *Gammarus sp*.: 46%). These differences could be explained by a combination of regional, seasonal, or inter-annual variability. In a shelf system, pelagic production may be higher due to higher nutrient and light availability, and amphipods have better access to recycled pelagic POM. In the ice-covered high Arctic deep-sea, however, ice algae represent a highly important carbon source for species, such as *A. glacialis* or *Onisimus spp*., and pelagic production is low (Fernández-Méndez 2014).

Based on FA 20:5n-3, Wang et al. (2015) reported that *T. libellula* consumed substantial amounts of ice algae-produced FAs with a proportional contribution between 47 and 63% in the Bering Sea, with variations according to ice conditions. These values

correspond well to the results of our BSIA analysis and our model a, which is based on the same FA. Our results from model b, however, indicate that the true dependency of this species on sea ice-produced carbon was probably lower when the proportional consumption of dinoflagellate-produced FAs is considered. In fact, previous studies, based on bulk stable isotope compositions, also indicate that *T. libellula* primarily depends on pelagic carbon sources (Søreide et al. 2006).

In the pteropod *C. limacina*, we found the lowest trophic dependency on ice algae-produced carbon compared to all other species, irrespective of the method and the mixing model used. A low trophic dependency (< 20%) on ice algae-produced carbon based on BSIA values was also found by e.g. Søreide et al. (2006). However, the subsequent loss of shelter from predators might be more pronounced in certain species than the dependency on sea ice in terms of food supply.

Altogether, a CSIA-based approach including the effect of multiple potential carbon producing taxa at the base of the food web (such as our model b) appears to be the most conservative approach to estimate the contribution of sea ice algae in food web studies.

We estimated the overall demand of ice algae-produced carbon by the most abundant herbivores *C. glacialis*, *C. hyperboreus* and *A. glacialis* (David et al. 2015). Due to its high abundance in the water column, the bulk of the ice algal carbon demand was attributed to *C. glacialis*. The outcome of this estimation should be considered as a minimum range, because the carbon demand of other abundant potential ice algal grazers, such as *Onisimus* spp. and *Oithona* spp., was not included in our tentative calculation (David et al. 2015). Because *C. glacialis* is known to constantly change its vertical position in the water column, it is unlikely that the estimate of α_{Ice} was biased by our sampling in the under-ice water layer. At an integrated (median) primary production rate by ice algae of about 0.7 mg C m^{-2} d^{-1} (Fernández-Méndez 2014), the minimum ice algal carbon demand of the three species in our study exceeded the ice algal primary production by a factor of 4 to 12 during the sampling period. To some extent, the apparent discrepancy between low sea ice primary production rates and high carbon demand of herbivores may reflect high ice algae production rates prior to our sampling, inferred by Boetius et al. (2013), who observed a high export of ice algae to the sea floor during August and September 2012. In the light of less than one day turnover times in herbivores (Graeve et al. 2005), however, minimum ice algal carbon demand rates ranging potentially an order of magnitude above measured in situ primary production rates of ice algae, indicating that the interaction between ice algal production and food web dynamics is far from understood. To improve the quantitative understanding of this interaction, efforts to quantify the spatio-temporal dynamics of both ice algal production and grazer populations must be considerably increased.

Conclusions

The results of this study showed an Arctic under-ice community with gradual differences in the dependency on sea ice algae-produced carbon, ranging from nearly 100% in sympagic amphipods to less than 30% in the pelagic pteropod *Clione limacina*. Particularly in ecologically important pelagic carbon transmitters, such as *Calanus* spp.

and *Themisto libellula*, the dependency on sea ice algae-produced carbon was overall significant, leading to a cumulative carbon demand that considerably exceeded sea ice algae primary production estimated in the field. With a significant dependency on sea ice algae-produced carbon in almost all investigated species, our results show that the Arctic sea ice-water interface is a functional node transmitting carbon from the sea ice into the pelagic food web. Hence, the role of zooplankton and under-ice fauna in the central Arctic Ocean may change significantly in the future, as the spatio-temporal extent of sea ice declines and its structural composition changes. Our results indicate that these changes will likely first have the most pronounced impact on sympagic amphipods, but will consequently affect food web functioning and carbon dynamics of the pelagic system.

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Supplementary

▼**Table S1.** Relative composition of most abundant lipid classes in under-ice fauna species (mean ± 1 SD mass % of total lipid content).

	Calanus glacialis	***Calanus hyperboreus***	***Apherusa glacialis***	***Onisimus glacialis***	***Gammarus wilkitzkii***	***Eusirus holmii***	***Themisto libellula***	***Clione limacina***
n	2	2	6	6	6	6	6	6
WE	72.6 ± 5.4	85.6 ± 7.5	1.5 ± 1.1	16.0 ± 11.3	4.5 ± 5.0	14.9 ± 19.9	47.4 ± 18.8	1.4 ± 0.6
TAG	1.7 ± 2.4	1.9 ± 1.9	86.4 ± 4.0	73.6 ± 11.5	80.0 ± 4.8	62.7 ± 17.5	46.1 ± 18.0	61.2 ± 29.1
PE	7.9 ± 1.8	4.3 ± 3.6	3.2 ± 1.2	2.0 ± 1.1	3.2 ± 1.2	4.9 ± 1.9	1.6 ± 0.5	8.1 ± 6.2
PC	17.1 ± 7.1	7.3 ± 5.0	6.2 ± 1.3	5.9 ± 1.6	6.5 ± 1.5	11.7 ± 8.9	4.0 ± 2.0	13.3 ± 9.3
Total	99.3	99.1	97.3	97.5	94.2	94.2	99.1	84.0
NL	75.0	88.5	90.2	91.8	89.3	81.7	94.3	72.4
PL	25.0 ± 8.8	11.5 ± 8.6	9.8 ± 2.5	8.2 ± 1.5	10.7 ± 2.9	18.3 ± 9.8	5.7 ± 1.5	27.6 ± 18.0

n: sample size, NL: neutral lipid, PC: phosphatidylcholine, PE: phosphatidylethanolamine, PL: polar lipid, TAG: triacylglycerol, WE: wax ester

▼**Table S2.** Bulk stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope values in ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM), and under-ice fauna species (mean ± 1 SD ‰). Species-specific $\delta^{15}N$ and $\delta^{13}C$ values are shown separately for Nansen (NB) and Amundsen Basin (AB) regimes.

			NB		**AB**	
	n_{NB}	n_{AB}	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$
I-POM	2	5	3.7 ± 0.3	-23.2 ± 0.6	5.3 ± 0.8	-25.7 ± 1.2
P-POM	6	11	3.3 ± 0.6	-27.2 ± 0.5	4.4 ± 1.3	-27.4 ± 1.0
Calanus glacialis	2	2	7.0 ± 1.0	-29.0 ± 3.1	8.1 ± 0.2	-24.6 ± 0.2
Calanus hyperboreus	2	2	6.8 ± 1.3	-26.8 ± 0.7	8.8 ± 0.4	-26.4 ± 1.7
Apherusa glacialis	2	2	5.4 ± 0.2	-22.1 ± 0.4	5.4 ± 0.5	-21.6 ± 2.2
Onisimus glacialis	2	2	7.6 ± 2.9	-22.9 ± 0.8	6.7 ± 0.1	-21.9 ± 1.6
Gammarus wilkitzkii	3	1	7.4 ± 0.4	-24.5 ± 0.4	6.3	-24.0
Eusirus holmii	2	2	9.1 ± 0.3	-22.7 ± 0.3	10.9 ± 1.8	-23.8 ± 0.2
Themisto libellula	1	3	7.1	-28.0	9.3 ± 1.2	-25.0 ± 1.1
Clione limacina	1	3	7.4	-26.6	8.9 ± 0.5	-26.9 ± 0.5

n: sample size

▼**Table S3.** Carbon stable isotope values ($\delta^{13}C$) of marker fatty acids (FAs) in ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM), and under-ice fauna species (mean ± 1 SD ‰). Species-specific $\delta^{13}C$ values are shown separately for Nansen (NB) and Amundsen Basin (AB) regimes. Not detected FAs are reported as '--'.

			NB	**AB**	**NB**	**AB**	**NB**	**AB**	**NB**	**AB**
	n_{NB}	n_{AB}	16:1n-7		20:5n-3		18:4n-3		22:6n-3	
I-POM	1	6	-23.3	-25.2 ± 4.4	-25.8	-26.7 ± 3.0	-26.7	-28.8 ± 3.5	-21.3	-24.1 ± 4.1
P-POM	5	2	-27.3 ± 3.7	-24.1 ± 1.2	-36.3 ± 2.3	-33.8 ± 0.7	-39.2 ± 0.7	-39.6 ± 0.6	-35.7 ± 2.7	-34.7 ± 1.2
Calanus glacialis	3	7	-29.9 ± 1.9	-22.9 ± 2.0	-32.1 ± 1.2	-31.8 ± 1.4	-35.2 ± 2.2	-35.9 ± 1.6	-31.2 ± 2.1	-32.4 ± 2.2
Calanus hyperboreus	2	4	-30.8 ± 2.4	-25.5 ± 2.7	-31.6 ± 2.0	-32.3 ± 0.9	-36.0 ± 1.2	-36.3 ± 1.2	-32.7 ± 2.0	-34.3 ± 2.5
Apherusa glacialis	3	7	-26.2 ± 2.0	-23.4 ± 2.4	-27.3 ± 0.9	-26.4 ± 1.4	-31.4 ± 1.0	-28.6 ± 1.6	-30.2 ± 1.6	-27.7 ± 1.0
Onisimus glacialis	4	4	-24.8 ± 1.3	-21.1 ± 3.1	-29.3 ± 0.7	-27.5 ± 1.8	-34.5 ± 0.4	-30.3 ± 4.7	-30.6 ± 1.2	-30.1 ± 0.7
Gammarus wilkitzkii	2	2	-26.5 ± 0.8	-23.1 ± 1.1	-29.5 ± 1.3	-28.4 ± 0.1	-31.6 ± 0.9	-30.4 ± 3.5	-30.6 ± 1.4	-32.7 ± 1.0
Eusirus holmii	2	6	-25.2 ± 0.5	-22.8 ± 2.1	-29.6 ± 1.1	-28.7 ± 1.0	-30.9 ± 0.2	-29.8 ± 1.3	-31.6 ± 0.4	-29.9 ± 1.2
Themisto libellula	1	6	-28.6	-23.2 ± 1.2	-33.4	-31.1 ± 1.2	-38.5	-35.2 ± 1.9	-33.4	-33.7 ± 2.0
Clione limacina	2	7	-29.8 ± 0.5	-28.4 ± 2.1	-33.2 ± 2.0	-34.4 ± 1.5	--	--	-33.0 ± 1.5	-34.0 ± 1.0

n: sample size

2.2 *Chapter II*

Strong linkage of polar cod (*Boreogadus saida*) to sea ice algae-produced carbon: evidence from stomach content, fatty acid and stable isotope analyses

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Abstract

The polar cod (*Boreogadus saida*) is considered an ecological key species, because it reaches high stock biomasses and constitutes an important carbon source for seabirds and marine mammals in high-Arctic ecosystems. Young polar cod (1-2 years) are often associated with the underside of sea ice. To evaluate the impact of changing Arctic sea ice habitats on polar cod, we examined the diet composition and quantified the contribution of ice algae-produced carbon (α_{Ice}) to the carbon budget of polar cod. Young polar cod were sampled in the ice-water interface layer in the central Arctic Ocean during late summer 2012. Diets and carbon sources of these fish were examined using 4 approaches: 1) stomach content analysis, 2) fatty acid (FA) analysis, 3) bulk nitrogen and carbon stable isotope analysis (BSIA) and 4) compound-specific stable isotope analysis (CSIA) of FAs. The ice-associated (sympagic) amphipod *Apherusa glacialis* dominated the stomach contents by mass, indicating a high importance of sympagic fauna in young polar cod diets. The biomass of food measured in stomachs implied constant feeding at daily rates of ~ 1.2% body mass per fish, indicating the potential for positive growth. FA profiles of polar cod indicated that diatoms were the primary carbon source, indirectly obtained via amphipods and copepods. The α_{Ice} using bulk isotope data from muscle was estimated to be > 90%. In comparison, α_{Ice} based on CSIA ranged from 34 to 65%, with the highest estimates from muscle and the lowest from liver tissue. Overall, our results indicate a strong dependency of polar cod on ice-algae produced carbon. This suggests that young polar cod may be particularly vulnerable to changes in the distribution and structure of sea ice habitats. Due to the ecological key role of polar cod, changes at the base of the sea ice-associated food web are likely to affect the higher trophic levels of high-Arctic ecosystems.

Introduction

The impact of climate change on Arctic sea ice properties, most evidently characterized by decreased sea ice coverage and thickness, has been well documented over the past decades (e.g. Johannessen et al. 1995, 2004; Rothrock et al. 1999; Kwok et al. 2009; Maslanik et al. 2011; Harada 2016). As a result, dramatic changes are expected in terms of timing, magnitude, and the spatial distribution of both ice-associated and pelagic primary production, with subsequent impacts on higher vertebrates (Wassmann et al. 2006; Søreide et al. 2013).

Polar cod, *Boreogadus saida* (Lepechin, 1774), are highly abundant in the Arctic Ocean (Falk-Petersen et al. 1986; Harter et al. 2013; Hop and Gjøsæter 2013) and play a key role in Arctic ecosystems, accounting for up to 75% of the energy transfer from the pelagic food web to endotherm predators (Bradstreet and Cross 1982; Jensen et al. 1991; Benoit et al. 2010; Rand et al. 2013). The diet of polar cod has been frequently found to be variable and associated with pelagic and benthic food webs, dominated by copepods and amphipods (Hop et al. 1997b; Christiansen et al. 2012; Renaud et al. 2012; Majewski et al. 2016; McNicholl et al. 2016). However, polar cod are assumed to rely on sea ice for foraging, spawning and shelter using cavities, gaps and rafted ice during at least a part of the larval and juvenile phase (Lønne and Gulliksen 1989; Scott et al. 1999; Gradinger and Bluhm 2004; David et al. 2016). This indicates that polar cod might show an indirect dependency on the sea ice primary production when feeding on ice-associated (sympagic) fauna (Lowry and Frost 1981; Bradstreet and Cross 1982; Budge et al. 2008).

Studies on the carbon source and diet composition of young polar cod caught directly from underneath the ice in the high Arctic are very limited (Lønne and Gulliksen 1989; Søreide et al. 2006). Moreover, the relative contribution of carbon originating from ice algae compared to pelagic phytoplankton to the carbon budget of polar cod has been scarcely quantified (Søreide et al. 2006). While the stomach content provides information on the very recent food compositions, fatty acid (FA) and stable isotope compositions give information on diet and carbon sources over a longer time span. Certain FAs are assumed to be transferred conservatively along the marine food web and are therefore called trophic markers (Graeve et al. 1994a; Falk-Petersen et al. 1998; Dalsgaard et al. 2003; Bergé and Barnathan 2005; Iverson 2009). Hence, the composition of these trophic markers in a consumer reflects the composition of FAs biosynthesized by primary producers. This qualitative investigation of predator-prey relationships based on FAs is substantially improved by its combination with stable isotope analyses of the bulk organic carbon content (BSIA- Bulk Stable Isotope Analysis) (Dehn et al. 2007; Feder et al. 2011) and/or specific FAs (CSIA- Compound-specific Stable Isotope Analysis) (Budge et al. 2008; Graham et al. 2014; Wang et al. 2015; Kohlbach et al. 2016). Algal communities differ not only in their proportions of certain FAs (Dalsgaard et al. 2003), but are also often characterized by relatively higher carbon stable isotope values (expressed as $\delta^{13}C$) in sea ice algae compared to pelagic phytoplankton (Hobson et al. 2002; Søreide et al. 2006; Budge et al. 2008). Capitalizing on this isotopic difference, the isotopic composition enables the quantification of sea ice

algae-produced carbon versus phytoplankton-produced carbon to the carbon budget of a consumer. The results of the few existing CSIA-based analyses on polar cod are controversial. A recent study based on fatty acid-specific stable isotope analyses suggested a negligible ice algal contribution (≤ 2%) to the diet of age class 0 polar cod in the ice-free Beaufort Sea at the end of summer (Graham et al. 2014). In contrast, results from an Alaskan study suggested a remarkable proportional ice algal contribution in shelf-bound adult polar cod, with values between 8 and 77%, depending on the sampling location and analytical approach taken (Budge et al. 2008). In addition, the trophic level of a consumer can be defined based on its nitrogen isotopic composition (expressed as $\delta^{15}N$) due to the stepwise enrichment in ^{15}N between each trophic level related to isotopic fractionation (Minagawa and Wada 1984; Post 2002).

Different tissue types integrate dietary information over different time spans due to varying turnover rates (Vander Zanden et al. 2015; Mohan et al. 2016a). For example, the liver is described as a metabolically active tissue, characterized by a faster turnover rate compared to the muscle tissue (Tieszen et al. 1983; Buchheister and Latour 2010). The half-life of carbon stable isotopes is only few days in liver tissue compared to multiple weeks in muscle tissue of bony fish (Suzuki et al. 2005). As a result, the combination of stomach content analysis and determination of FA and isotopic compositions on several types of tissues enables a more comprehensive investigation of the food resources used by consumers, giving information at several temporal scales and about the origin of carbon as well as ingested prey items.

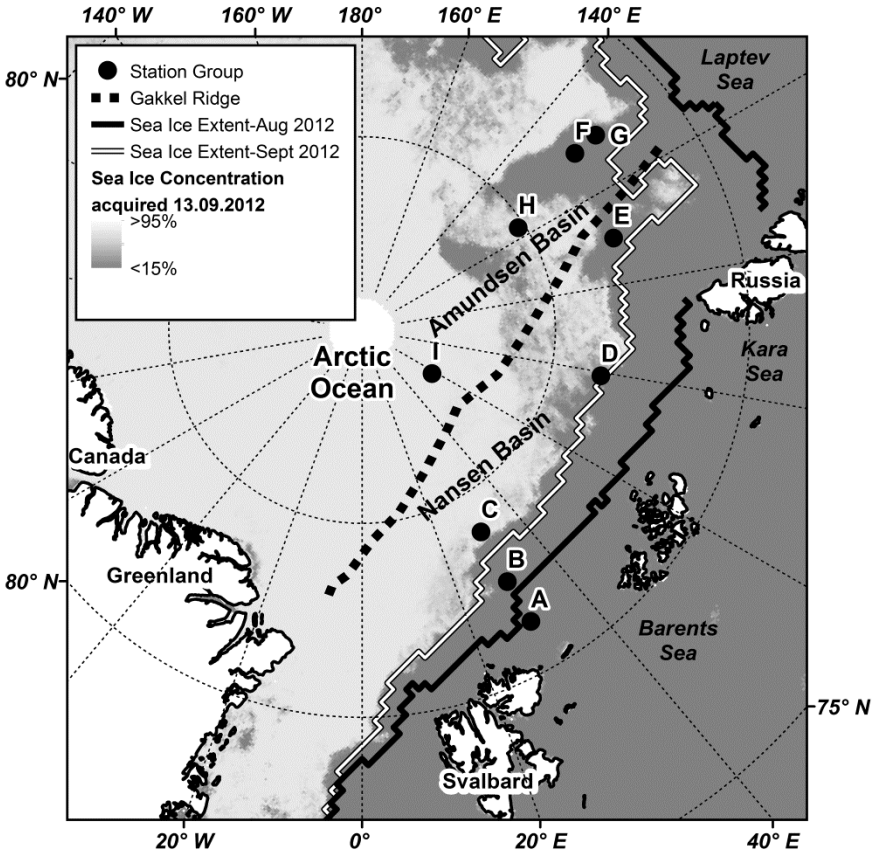
A first basin-wide survey of polar cod in the under-ice habitat indicated that the fish were widely distributed throughout the Eurasian Basin in 2012, and potentially followed the sea ice drift from the Siberian shelf across the Arctic Ocean (David et al. 2016). In the light of their good nutritional condition and potential month-long association with drifting sea ice, it was hypothesized that the Arctic under-ice habitat constitutes a favorable environment for the fish in terms of high-energetic food supply, until they reach maturity and leave the under-ice environment (David et al. 2016). We aimed to investigate this hypothesis by assessing whether the close relationship of young polar cod from the central Arctic Ocean with the sea ice is accompanied by a diet relying on food resources provided by sea ice. We combined stomach content analysis, lipid fingerprinting and the investigation of the stable isotope composition of different polar cod tissues (muscle, liver, gonads) to reveal diet composition and carbon sources of polar cod under sea ice. Furthermore, we quantified the proportional contribution of ice algae-produced carbon to the carbon budget of polar cod, based on stomach content analyses and the isotopic compositions of polar cod tissues, respectively.

Materials and Methods

Study area and sampling methods

Sample collection was conducted during the RV '*Polarstern*' expedition 'IceArc' (PS80; 2 August to 7 October 2012) in the Eurasian Basin of the Arctic Ocean (**Table 1, Figure 1**).

Detailed information on the sampling during PS80 can be found in David et al. (2016), and Kohlbach et al. (2016).



▲***Figure 1.*** *Map of the sampling area during RV 'Polarstern' cruise IceArc (PS80) across the Eurasian part of the Arctic Ocean modified after Kohlbach et al. (2016). Sea ice concentration for 13 September 2012 (concentration data acquired from Bremen University (http://www.iup.uni-bremen.de:8084/amsr/)) and mean sea ice extent for August and September 2012 are represented on the map (data acquired from NSIDC, Fetterer et al. 2002). Letter codes correspond to sampling locations. Station information for the individual sampling sites is given in* ***Table 1****.*

▼**Table 1.** Sample information for ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM), and under-ice fauna (UIF), including polar cod, collected during PS80.

Location	Sample type	Date (m/dd/2012)	Station no.	Latitude (°N)	Longitude (°E)	Water depth (m)	Sea ice coverage (%)
A	P-POM	8/6	209	81.296	30.103	710	
B	UIF	8/7	216	82.483	30.027	3610	98
C	P-POM	8/8	220	83.599	28.500	4016	
	UIF	8/9	223	84.070	30.434	4016	82
	I-POM	8/9	224	84.051	31.112	4014	
D	P-POM	8/11	230	84.022	31.221	4011	
	I-POM	8/14	237	83.987	78.103	3485	
	P-POM	8/16	244	83.551	75.583	3420	
	UIF	8/16	248	83.934	75.500	3424	56
E	P-POM	8/18	250	83.353	87.271	3508	
	I-POM	8/20	255	82.671	109.590	3569	
	UIF	8/20	258	83.076	109.627	3575	100
	P-POM	8/22	263	83.476	110.899	3606	
F	UIF	8/25	276	83.076	129.125	4188	79
	I-POM	8/25	277	82.883	130.130	4161	
	P-POM	8/26	284	82.537	129.462	4173	
	UIF	8/26	285	82.896	129.782	4174	100
G	UIF	9/4	321	81.717	130.033	4011	64
	I-POM	9/4	323	81.926	131.129	4031	
	UIF	9/5	331	81.905	130.863	4036	0
	UIF	9/6	333	82.989	127.103	4187	4
H	I-POM	9/7	335	85.102	122.245	4355	
	P-POM	9/7	341	85.160	123.359	4353	
	UIF	9/9	345	85.254	123.842	4354	62
I	I-POM	9/18	349	87.934	61.217	4380	
	UIF	9/19	358	87.341	59.653	4384	86
	I-POM	9/22	360	88.828	58.864	4374	
	UIF	9/25	376	87.341	52.620	3509	100

Ice-associated particulate organic matter (I-POM), representing the ice algae community, was sampled by taking ice cores with a 9 cm interior diameter ice corer (Kovacs Enterprises). Ice cores were melted in the dark at 4°C on board and from 0.7 to 10.5 L water were filtered using a vacuum pump through pre-combusted 0.7 μm GF/F filters (Whatmann, 3 h, 550°C). Either the whole core or the bottom part of the ice core was used. Chlorophyll *a* (Chl *a*) concentrations of the ice cores ranged from 0.4 to 6.5 mg m^{-3} (0.3 to 8 mg m^{-2}) (Fernández-Méndez et al. 2015). Pelagic particulate organic matter (P-POM), representing the phytoplankton community, was sampled using a carousel water sampler connected to a CTD probe (Seabird SBE9+). Water collection was performed at the surface layer and at the depth of the Chl *a* maximum (between 20 and 50 m). Depending on the biomass, from 2.0 to 11.0 L water were filtered using pre-

combusted GF/F filters. Chl *a* concentrations of the water column at the Chl *a* maximum ranged from 0.2 to 1.2 mg m^{-3}. All filters were stored at -80°C until further processing. Polar cod were caught with a Surface and Under-Ice Trawl (SUIT) (van Franeker et al. 2009) within the uppermost 2 m surface layer. Detailed information on the description and use of the SUIT can be found in David et al. (2015). After measurements of the total lengths (TL), and the determination of the sex, fish for the lipid and stable isotope analyses were subsampled for muscle, liver and gonad tissues. The subsamples were immediately frozen at -80°C in pre-combusted and pre-weighed sample vials (Wheaton, 6 h, 500°C). Whole fish were frozen at -20°C for stomach content analysis.

The condition index *CI* per individual fish in % was calculated as

(1) $CI = 100 * W_{ev}/WW$

where W_{ev} is the eviscerated wet weight (g) and *WW* is the wet weight (g) of the individual fish.

Stomach content analysis

Stomach content analysis was conducted at the Alfred Wegener Institute, Germany, and Wageningen Marine Research, The Netherlands. After defrosting, total and eviscerated wet weights of the fish were recorded. The stomachs extracted from the defrosted fish were either analyzed directly or preserved in a 4% hexamine-buffered formaldehyde-sea water solution until further processing. After rinsing, the stomachs were cut open and rinsed out with deionized water. The empty stomachs were weighed again. Prey items in the stomach content were identified to the lowest possible taxonomic level and counted using a Discovery V8 stereomicroscope (Zeiss, Germany). Size measurements of the prey items were done using an AxioCam HRc with AxioVision40 V 4.8.2.0 software (Zeiss, Germany). Where possible, the TLs of amphipods found in the stomachs were measured from the tip of the rostrum to the tip of the telson (mm). In addition, the urosome length was recorded in order to reconstruct the TL in broken animals, using regressions obtained from measurements on complete individuals:

Apherusa glacialis

(2) $TL = 1.5726U + 5.9316 (R^2 = 0.996)$

Themisto spp.

(3) $TL = 3.5337U + 3.9169 (R^2 = 0.906)$

where *U* is the length of the urosome (mm). For copepods, the prosome and urosome were measured when possible.

Reconstructed biomasses of the identifiable food items in the stomach were estimated by multiplying the number of individuals of a species with the mean individual dry weight (DW in mg ind^{-1}). Mean individual dry weights of amphipods were calculated using the mean length, and length-dry weight regressions of measurements performed on frozen individuals:

(4) $DW = 0.0259 * TL^{2.4503}$ $(R^2 = 0.83)$

For calculations of *Calanus* spp. total biomass, the average measured DW was used. Proportions of the different *Calanus* species in the stomach were determined according to their length frequency as found in the polar cod stomachs, and reference data for prosome lengths of *C. hyperboreus*, *C. glacialis* and *C. finmarchicus* (Madsen et al. 2001). The dry weights of harpacticoid copepods were calculated using the average lengths measured in the stomach content samples, and a length/dry weight regression from Goodman (1979). Other species mean individual dry weights were taken from Richter (1994). The DW of a decapod was estimated after Kreibich et al. (2010). Occasional finds of nauplii and of some tissues were excluded from the analyses due to their negligible numbers and low biomass.

Stomach fullness (*SF*) (Hyslop 1980) was calculated in % as

(5) $SF = 100 * W_{sc}/WW$

where W_{sc} is the stomach content weight and *WW* is the wet weight (g) of the individual fish (g).

The Index of Relative Importance (*IRI*) of the various prey species in % were calculated as

(6) $IRI = (A + B) * F$

where *A* is the relative abundance (%), *B* the biomass (%) and *F* the frequency of occurrence (%) of the prey species.

Feeding rates of polar cod were estimated with a simple exponential gastric evacuation model, using coefficients determined for polar cod at subzero temperatures by Hop and Tonn (1998). Assuming that the feeding rate equals the stomach evacuation rate, feeding rate *R* was estimated after Elliott and Persson (1978) as

(7) $R = a * e^{bT}$

where *R* is the gastric evacuation rate, *a* and *b* are absolute terms, and *T* is the temperature (°C).

Using the coefficients a = 0.018 and b = 0.14 recommended by Hop and Tonn (1998) for polar cod at subzero temperatures and a typical water temperature of -1.5°C (David et al. 2016), R = 0.0148.

The daily consumption R' in g DW ind.$^{-1}$ d^{-1} was then calculated using the equation:

(8) $$R' = 24 * \overline{W_{SC}} * R$$

where $\overline{W_{SC}}$ is the mean total stomach content dry weight (g).

The relative daily feeding rate r' in % of the mean individual dry body weight was calculated as follows:

(9) $$r' = 100 * 24 * \frac{\overline{W_{SC}}}{\overline{W_F}} * R$$

where $\overline{W_F}$ is the mean individual dry weight of the fish (g), based on an average water content of 73% (David et al. 2016).

Fatty acid analysis

Fatty acid analysis was performed on freeze-dried bulk particulate organic matter (POM), and muscle, liver, and gonad tissues of polar cod at the Alfred Wegener Institute, Germany. After homogenization, lipids were extracted using a modified procedure from Folch et al. (1957) with dichloromethane/methanol (2:1, v/v). Dry weights and total lipid content (TLC) of the different tissues were determined gravimetrically (**Table 2**).

▼**Table 2.** Lipid parameters of polar cod used in fatty acid and stable isotope analyses (mean ± 1 SD). TLC = total lipid content, FAC = fatty acid content.

Parameter	**TLC/dry weight (%)** (n = 32)	**FAC/dry weight (%)** (n = 32)
Muscle	17.1 ± 5.2	12.1 ± 5.9
Liver	78.0 ± 12.3	40.3 ± 20.1
Gonads	87.1 ± 4.9	32.5 ± 20.8

Lipid class composition of the polar cod tissues was analyzed via high-performance liquid chromatography (Graeve and Janssen 2009). The relative proportions of the most abundant lipid classes were provided as supplementary material (**Suppl. A**). The extracted lipids were converted into fatty acid methyl esters (FAMEs) and free fatty alcohols by transesterification with methanol containing 3% concentrated sulfuric acid. The fatty acid content (FAC) (**Table 2**) and the percentage of individual FAs were determined using an internal standard (23:0) added prior to lipid extraction. The individual FA data was expressed as mass percentage of the total FA content. For details on sample preparation and measurements as well as analytical equipment see Kohlbach et al. (2016).

The investigation of FA composition variations was based on the diatom-associated marker FAs 16:1n-7 and 20:5n-3 (Graeve et al. 1994b, 1997; Falk-Petersen et al. 1998; Scott et al. 1999), the dinoflagellate-associated marker FAs 18:4n-3 and 22:6n-3 (Viso and Marty 1993; Graeve et al. 1994b), and the *Calanus*-associated marker FAs 20:1n-9 and 22:1n-11 (Falk-Petersen et al. 1987).

Bulk and compound-specific stable isotope analyses

Bulk nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) stable isotope compositions (BSIA) of POM and polar cod muscle tissue were determined at the Alfred Wegener Institute, Germany. For sample preparation, measurement details and analytical equipment used for the BSIA measurements see Kohlbach et al. (2016). Lipids were not removed prior to BSIA in order to avoid inducing changes in the isotopic compositions of the fish tissue samples (Murry et al. 2006).

All isotopic compositions were expressed as parts per thousand (‰) in the δ notation as deviation from standards. Standards were the certified Vienna Pee Dee Belemnite (VPDB) and atmospheric nitrogen for measurements of $\delta^{13}C$ and $\delta^{15}N$ values, respectively.

The calibration of the isotope ratio mass spectrometer was done by measuring the secondary reference material USGS41 (certified: $\delta^{15}N$ = 47.6‰, $\delta^{13}C$ = 37.6‰, measured: $\delta^{15}N$ = 47.1‰, $\delta^{13}C$ = 35.5‰), provided by the International Atomic Energy Agency (IAEA, Vienna). The measurement errors were indicated as ± 0.2 and 0.3‰ for $\delta^{15}N$ and $\delta^{13}C$ values, respectively (represents 1 SD of 9 analyses). Furthermore, the laboratory standards isoleucine ($\delta^{15}N$ = -11.9‰, $\delta^{13}C$ = -3.1‰), peptone ($\delta^{15}N$ = 8.0‰, $\delta^{13}C$ = -15.7‰), and acetanilide ($\delta^{15}N$ = 0.8‰, $\delta^{13}C$ = -27.3‰) were analyzed every 5 samples for verification of accuracy and precision of the BSIA measurements. Measurement errors were ± 0.2 and 0.5‰ for $\delta^{15}N$ and $\delta^{13}C$ values of isoleucine (represents 1 SD of 17 analyses), ± 0.1 and 0.2‰ for peptone (represents 1 SD of 6 analyses) and ± 0.2 and 0.6‰ for acetanilide (represents 1 SD of 8 analyses), respectively.

Measurement of $\delta^{13}C$ values of extracted FAMEs from POM, muscle, liver and gonad tissues were performed at the stable isotope facility of the University of La Rochelle (LIENSs), France, using a Trace GC (Thermo Scientific, Italy), coupled with a Thermo GC Combustion III interface (Thermo Scientific, Germany) and an isotope ratio mass spectrometer (Delta V Advantage with a Conflo IV interface, Thermo Scientific, Germany). A J&W DB-23 capillary column (60 m × 0.25 mm internal diameter × 0.25 μm film) was used with helium as a carrier gas at a flow of 1 ml min^{-1} for separation of FAMEs. Samples were injected (1.5 μL) in splitless mode using a SSL injector at 240°C. Oven initial temperature was 50°C and then increased at a rate of 20°C min^{-1} until 150°C, and at a rate of 2°C min^{-1} until 240°C. The GC-c-IRMS was calibrated using a certified reference material, supplied by the Indiana University (30:0 FAME, certified: $\delta^{13}C$ = -26.3‰, measured: $\delta^{13}C$ = -26.4 ± 0.4‰). Furthermore, $\delta^{13}C$ values of the internal standard 23:0 ($\delta^{13}C$ = -30.6‰) added prior to lipid extraction was analyzed. FAME

identification was performed by comparing relative retention times of FAME samples with those of a known standard mixture (37-FAME Mix, Sigma Aldrich).

Data analysis

Correlation coefficients between abundances available prey in the water column (David et al. 2015) and number of prey found in the fish stomachs were determined by using Pearson's correlation coefficient of species abundance in the environment and in the stomachs. Association was estimated between paired samples and ranges between [-1, 1] with 0 indicating no association (**Suppl. C**). The significance of found correlations between pairs was further tested by calculating a *t*-value and corresponding *p*-value based on Pearson's product moment correlation coefficient. A full record of abundance and distribution of species living in the under-ice habitat of the Arctic Ocean during PS80 can be found in David et al. (2015). Co-occurrence of prey species in the analyzed stomachs was evaluated using a probabilistic model of species co-occurrence from Veech (2013). As this analysis is distribution-free, results can be interpreted as *p*-values (Griffith et al. 2016).

The proportional contribution of ice algae-produced carbon α_{Ice} to the diet of polar cod was estimated from the natural distribution of stable isotopes in the animal tissues (Kohlbach et al. 2016), by applying Bayesian multi-source stable isotope mixing models (SIAR, Parnell et al. 2010). These models incorporate the isotopic information of the consumers as well as the isotope values of I-POM and P-POM as representative diet sources (end member sources). SIAR models can account for trophic enrichment factors, considering tissue-specific turnover rates in the consumers (Parnell et al. 2010). For the BSIA calculations, a nitrogen trophic fractionation of 3.4‰ per trophic level (Δ_N) was assumed (Minagawa and Wada 1984). Carbon enrichment for both BSIA and CSIA calculations was assumed to be zero, because the trophic fractionation in the different fish tissues was unknown (Budge et al. 2011; Wang et al. 2015; Kohlbach et al. 2016). We took four different SIAR-based approaches to calculate α_{Ice}: 1) using the relative average biomass of the prey species in the stomachs multiplied by the percentage of ice-algae produced carbon of each prey species according to CSIA model b in Kohlbach et al. (2016); 2) using $\delta^{13}C$ of the bulk muscle tissue (BSIA); 3) using $\delta^{13}C$ values of FA 20:5n-3 (CSIA model a); and 4) using $\delta^{13}C$ values of both marker FAs 20:5n-3 and 22:6n-3 (CSIA model b). In the CSIA-based approaches, we calculated α_{Ice} separately for muscle, liver and gonad tissue.

The trophic level of polar cod was estimated as follows (Post 2002; Søreide et al. 2013):

(10) $$Trophic\ level = \lambda + (\delta^{15}N_x - [\delta^{15}N_{base1} * \alpha + \delta^{15}N_{base2} * (1 - \alpha)])/\Delta_N$$

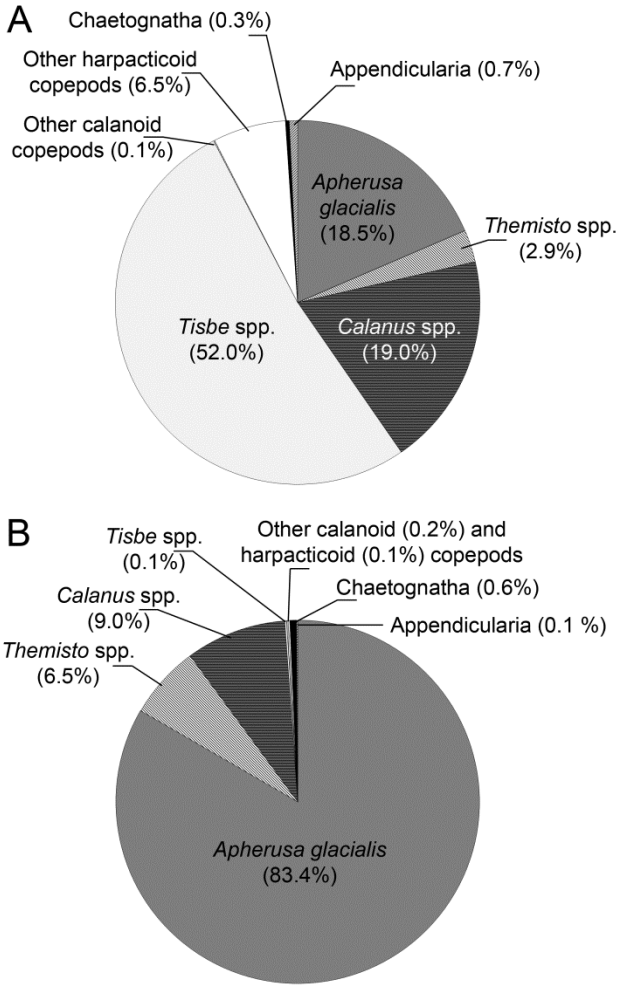
where λ represents the trophic position of the baseline (I-POM or P-POM, λ = 1). The directly measured $\delta^{15}N_x$ and $\delta^{15}N_{base}$ are the bulk nitrogen isotopic compositions of polar cod and POM, respectively. Base 1 and base 2 relate to I-POM and P-POM, respectively.

The proportion of nitrogen that derives ultimately from the baseline organism of food web 1 (= ice algae community) is represented by α.
Variations in fatty acid and stable isotope compositions between the tissue types were tested using 1-way ANOVA followed by Tukey HSD post-hoc tests. For testing between algal communities in sea ice and water column, represented by I-POM and P-POM, Student's t-tests were applied. FA data were transformed applying an arcsine square root function in order to achieve a near-normal distribution of the data. All data analyses were conducted with the program R, version 3.2.3 (R Core Team 2015).

Results

Diet composition and feeding rates

The average wet weights (3.4 ± 3.1 g), total lengths (78.4 ± 18.8 mm) and body condition indices (78.6 ± 3.6%) of the fish used for stomach content analysis (91.8% male fish) were representative of the total population sampled under sea ice in 2012 (David et al. 2016). A low percentage of empty stomachs (3.9%) with a mean stomach content wet weight of 0.1 ± 0.1 g, and a mean stomach fullness of 2.5 ± 1.7% indicated constant feeding. The stomach contents had a taxonomically diverse composition, comprising of at least 11 taxa (8 crustaceans, chaetognaths, appendicularians and 1 parasitic trematode) (**Suppl. B**). The amphipod *Apherusa glacialis* dominated in numbers and biomass in the majority of the samples (**Figure 2**). About 50% of the samples were dominated in numbers by *Tisbe* spp. In terms of biomass, however, this species contributed little to the overall diet. *A. glacialis* (62%) was the most important food item according to the index of relative importance (*IRI*). *Tisbe* spp. was the next most important food item (*IRI* 25%), despite its low total biomass (**Figure 2**). Other prey taxa found regularly in the stomachs were the amphipod *Themisto libellula,* and harpacticoid copepods other than *Tisbe* spp. The diet of fish from location D (**Table 1, Figure 1**), and one individual from location F, were dominated by large numbers of *Calanus glacialis.* The abundances of *A. glacialis* (t= 3.4, df = 7, p < 0.01), *Calanus* spp. (t= 20.7, df = 7, p < 0.001), and chaetognaths (t= 83.6, df = 7, p < 0.001) in the stomachs were each positively correlated with the abundance of these species in the under-ice surface waters (**Suppl. C**). Analysis of co-occurrence of species in the stomachs confirmed that *Tisbe* spp. co-occurred with the trematode *Hemiurus levinseni* (p = 0.02), a parasite that is hosted by calanoid copepods (Køie 2009). This parasite occurred in 14 of the 51 investigated stomachs, representing an infestation rate of 27.5%. The mean individual daily feeding rate R' was estimated at 0.01 ± 0.01 g DW ind.$^{-1}$ d^{-1}. This value corresponded to a mean relative daily feeding rate r' of 1.22 ± 1.24 % DW by body mass of the fish, based on a gastric evacuation rate R of 0.0148, an average stomach content dry weight $\overline{W_{SC}}$ of 0.03 ± 0.03 g DW and an average fish dry weight $\overline{W_F}$ of 0.88 ± 2.50 g DW.



▲***Figure 2.*** *Average stomach content of polar cod in A) relative abundance (% number ind^{-1}) and B) relative biomass (% reconstructed dry weight ind^{-1}).*

Marker fatty acid composition

Ice-associated and pelagic particulate organic matter

In the I-POM samples, the diatom-associated fatty acid 16:1n-7 was by far the most abundant marker FA, accounting on average for about 54 % of the FA composition. The second-most abundant marker FA was the diatom-associated FA 20:5n-3 (mean proportion ~ 5%). The mean contributions of the dinoflagellate-associated markers 18:4n-3 and 22:6n-3 to the FA composition were each below 2% in the I-POM samples (**Table 3**). In contrast, the P-POM samples were characterized by a more even distribution of the relative abundance of marker FAs. Here, the dinoflagellate-associated marker FA 22:6n-3 was the most abundant, with a mean relative contribution to the FA composition of about 10%. The marker FAs 18:4n-3 and 20:5n-3 showed similar mean proportions in the P-POM samples (~ 7%). These three FAs were significantly more abundant in P-POM than in I-POM samples (20:5n-3: $t = 2.3$, $df = 11$, $p < 0.05$; 18:4n-3: $t = 9.8$, $df = 16$, $p < 0.001$; 22:6n-3: $t = 9.0$, $df = 13$, $p < 0.001$). In contrast, the mean proportion of the diatom-associated marker FA 16:1n-7 in the P-POM samples (~ 10%) was significantly lower compared to the I-POM samples ($t = 7.1$, $df = 14$, $p < 0.001$).

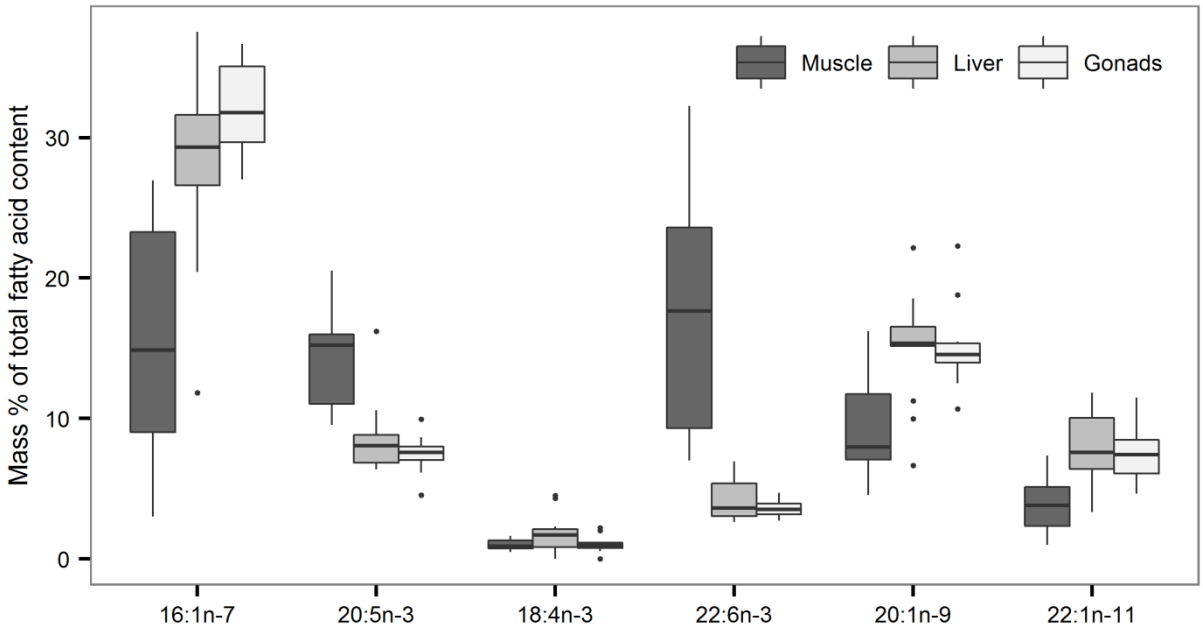
▼**Table 3.** Relative composition of most abundant fatty acids (FAs) in ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM), and the three tissue types of polar cod (mean ± 1 SD mass % of total FAs). Not detected FAs are reported as '--'. MUFA = monounsaturated FA, PUFA = polyunsaturated FA.

	I-POM ($n = 10$)	**P-POM** ($n = 9$)	**Muscle** ($n = 8$)	**Liver** ($n = 14$)	**Gonads** ($n = 10$)
14:0	5.3 ± 1.5	6.0 ± 2.1	2.9 ± 0.8	4.2 ± 0.8	4.5 ± 0.5
16:0	16.3 ± 4.1	20.3 ± 1.9	16.0 ± 2.6	10.3 ± 1.1	10.5 ± 1.0
16:1n-7	53.6 ± 17.9	9.8 ± 6.0	15.5 ± 8.7	28.4 ± 6.5	32.1 ± 3.6
18:0	4.5 ± 7.5	5.3 ± 1.2	1.6 ± 0.4	1.3 ± 0.3	1.1 ± 0.4
18:1n-9	7.0 ± 4.5	6.5 ± 2.5	6.9 ± 0.6	7.4 ± 1.0	7.1 ± 0.8
18:1n-7	0.4 ± 0.4	1.8 ± 1.1	3.4 ± 0.4	3.5 ± 0.6	3.8 ± 0.5
18:4n-3	1.2 ± 0.5	6.4 ± 1.4	1.0 ± 0.4	1.8 ± 1.3	1.1 ± 0.5
20:1n-9	--	--	9.2 ± 3.8	15.1 ± 3.8	15.2 ± 3.0
20:5n-3	4.8 ± 2.2	7.1 ± 1.3	14.4 ± 3.7	8.6 ± 2.5	7.5 ± 1.2
22:1n-11	--	--	3.9 ± 2.1	7.9 ± 2.6	7.6 ± 2.2
22:1n-9	--	--	0.6 ± 0.5	1.5 ± 0.6	1.3 ± 0.6
22:6n-3	1.2 ± 1.8	10.4 ± 2.1	17.6 ± 8.9	4.2 ± 1.5	3.5 ± 0.5
Total	94.3	73.6	93.0	94.2	95.3
MUFA	61.5 ± 13.9	21.3 ± 7.9	41.6 ± 14.4	66.0 ± 6.2	68.8 ± 3.2
PUFA	10.8 ± 3.5	46.5 ± 9.9	37.9 ± 12.5	18.3 ± 5.6	15.0 ± 2.6
∑C16/∑C18	6.8 ± 3.1	1.1 ± 0.3	2.2 ± 0.6	2.4 ± 0.7	2.9 ± 0.3
16:1n-7/16:0	3.6 ± 1.6	0.5 ± 0.3	1.0 ± 0.7	2.8 ± 0.6	3.1 ± 0.3
22:6n-3/20:5n-3	0.1 ± 0.2	1.5 ± 0.2	1.2 ± 0.4	0.5 ± 0.2	0.5 ± 0.1

Polar cod

In all three tissue types, both diatom-associated marker FAs 16:1n-7 and 20:5n-3 contributed significantly to the total fatty acid content, accounting for ~ 30% of the FA composition in muscle tissue and reaching the maximal contribution in the gonad tissue (~ 40%). The sum of the dinoflagellate-associated marker FA mean proportions of 18:4n-3 and 22:6n-3 ranged from ~ 5% in the gonad tissue to ~ 19% in the muscle tissue. The *Calanus*-associated FAs 20:1n-9 (mean ~ 9 to 15%) and 22:1n-11 (mean ~ 4 to 8%) were also abundant in all three tissues (**Table 3, Figure 3**).

Liver and gonad tissues were characterized by a significantly higher abundance of 16:1n-7 and of both *Calanus*-associated marker FAs than in the muscle tissue (16:1n-7: $F_{2, 29}$ = 15.5, Tukey HSD $p < 0.001$; 20:1n-9: $F_{2, 29}$ = 8.8, Tukey HSD $p < 0.01$; 22:1n-11: $F_{2, 29}$ = 9.5, Tukey HSD $p < 0.01$). In contrast, the polyunsaturated marker FAs 20:5n-3 and 22:6n-3 were significantly more abundant in the muscle tissue than in the other two tissues (20:5n-3: $F_{2, 29}$ = 18.1, Tukey HSD $p < 0.001$; 22:6n-3: $F_{2, 29}$ = 37.5, Tukey HSD $p < 0.001$).



▲***Figure 3.*** *Relative proportions of marker fatty acids (FAs) in muscle, liver and gonad tissue of polar cod. 16:1n-7 and 20:5n-3 represent diatom-associated FAs, 18:4n-3 and 22:6n-3 represent dinoflagellate-associated FAs, 20:1n-9 and 22:1n-11 represent Calanus-associated FAs. Horizontal bars in the box plots indicate median proportional values. Upper and lower edges of the boxes represent the approximate 1st and 3rd quartiles, respectively. Vertical error bars extend to the lowest and highest data value inside a range of 1.5 times the inter-quartile range, respectively (R Core Team 2015). Outliers are represented by the dots outside the boxes. Sample size is reported in* ***Table 3****.*

Stable isotope compositions

Ice-associated and pelagic particulate organic matter

The mean $\delta^{15}N$ values were similar in I-POM (4.8 ± 1.3‰) and P-POM (4.0 ± 1.2‰). The mean I-POM bulk $\delta^{13}C$ value (-24.9 ± 1.6‰) was considerably higher compared to P-POM (-27.3 ± 0.9‰) (**Figure 4A**). The range of mean $\delta^{13}C$ values of the four algal marker FAs was considerably larger in P-POM than in I-POM (**Table 4**). The dinoflagellate-associated marker FA 18:4n-3 had the lowest mean $\delta^{13}C$ values in both I-POM and P-POM samples of all marker FAs. The $\delta^{13}C$ values of the FAs 18:4n-3, 20:5n-3 and 22:6n-3 were significantly higher in I-POM than in P-POM (18:4n-3: $t = 7.3$, $df = 5$, $p < 0.001$; 20:5n-3: $t = 6.4$, $df = 10$, $p < 0.001$, 22:6n-3: $t = 5.9$, $df = 4$, $p < 0.01$).

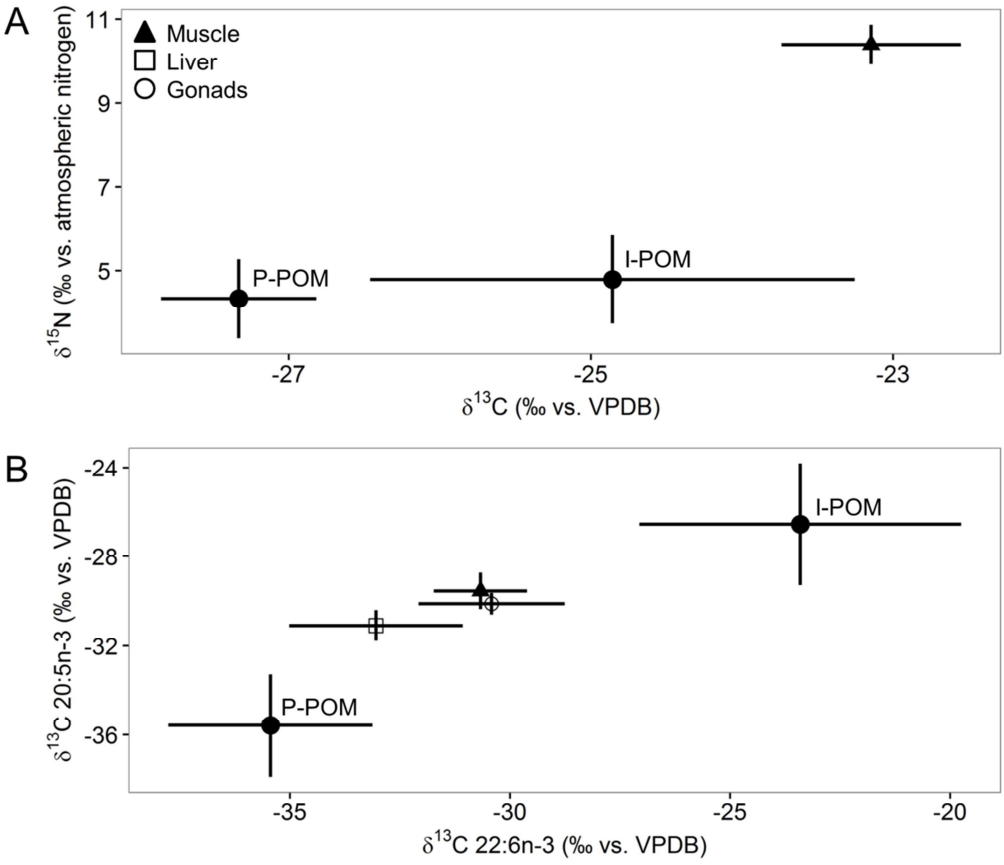
▼**Table 4.** Carbon stable isotope values ($\delta^{13}C$) of marker fatty acids in ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM), and the different body tissues of polar cod (mean ± 1 SD ‰). Not detected FAs are reported as '--'.

	I-POM ($n = 7$)	**P-POM** ($n = 7$)	**Muscle** ($n = 7$)	**Liver** ($n = 5$)	**Gonads** ($n = 5$)
16:1n-7	-24.9 ± 4.1	-26.4 ± 3.4	-23.2 ± 1.8	-25.6 ± 2.1	-24.3 ± 1.4
20:5n-3	-26.6 ± 2.7	-35.6 ± 2.3	-29.6 ± 0.8	-31.1 ± 0.7	-30.1 ± 0.5
18:4n-3	-28.4 ± 3.2	-39.3 ± 1.1	--	--	--
22:6n-3	-23.4 ± 3.7	-35.5 ± 2.3	-30.7 ± 1.1	-33.1 ± 2.0	-30.4 ± 1.7
20:1n-9	--	--	-27.1 ± 3.0	-32.8 ± 3.3	-29.5 ± 3.0
22:1n-11	--	--	-26.3 ± 1.0	-27.0 ± 0.9	-26.9 ± 0.9

Polar cod

Relative to I-POM and P-POM, the polar cod muscle tissue was enriched in ^{15}N on average by 5.6 and 6.4‰, respectively (10.4 ± 0.5‰). The trophic level of polar cod was estimated to 3.0 ± 0.2. The mean bulk $\delta^{13}C$ value of polar cod muscle (-23.2 ± 0.6‰) was higher by 1.7‰ than the mean $\delta^{13}C$ value in I-POM and by 4.1‰ compared to the P-POM samples (**Figure 4A**).

In general, the $\delta^{13}C$ values of the marker FAs were the highest in the muscle tissue and the lowest in the liver tissue (**Table 4**). The diatom-associated FA 16:1n-7 showed the highest $\delta^{13}C$ values, and the dinoflagellate-associated FA 22:6n-3 showed the lowest $\delta^{13}C$ values of all FAs in all three body tissues. Among the three tissue types, the mean $\delta^{13}C$ values of the diatom-associated marker FA 16:1n-7 showed little variation, ranging from -25.6‰ in the liver tissue to -23.2‰ in the muscle tissue. The $\delta^{13}C$ values of the diatom-associated marker FA 20:5n-3 in the muscular tissue were significantly higher relative to the liver tissue ($F_{2, 13} = 6.9$, Tukey HSD $p < 0.01$). The mean $\delta^{13}C$ values of 22:6n-3 were similar between muscle and gonads, and considerably higher compared to the liver tissue (**Table 4, Figure 4B**). Among the *Calanus*-associated marker FAs, the $\delta^{13}C$ values of 20:1n-9 were significantly higher in the muscle compared to the liver tissue ($F_{2, 13} = 4.7$, Tukey HSD $p < 0.05$), whereas the second *Calanus*-associated marker FA 22:1n-11 showed little variation between the three body tissues (-27.0 to -26.3‰).



▲*Figure 4.*

A) Bulk nitrogen ($\delta^{15}N$) and carbon stable isotope compositions ($\delta^{13}C$) in ice-associated particulate organic matter (I-POM, n = 4), pelagic particulate organic matter (P-POM, n = 17) and polar cod muscle tissue (n = 66) relative to atmospheric nitrogen and the international Vienna Pee Dee Belemnite standard (VPDB). Error bars indicate ± 1 SD.

*B) Carbon stable isotope compositions ($\delta^{13}C$) of marker fatty acids 20:5n-3 and 22:6n-3 in ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM), and the three tissue types of polar cod relative to the international Vienna Pee Dee Belemnite standard (VPDB). Plot design as in **Figure 4A**. Sample size is reported in **Table 4**.*

Proportional contribution of ice algal carbon to the diet of polar cod

Calculations of the proportional contribution of ice algae-produced carbon α_{Ice} to the diet of polar cod based on values of prey species found in the stomachs indicated that the mean contribution of ice algae to the dietary carbon uptake of fish was at least 54% (**Table 5**). This value was considerably lower than our BSIA-based estimate from the muscle tissue (95%), but in the same range as estimates based on the $\delta^{13}C$ values from the marker FAs in the different body tissues (34 to 65%). In the CSIA-based models, mean α_{Ice} was the highest in the muscle tissue (51 to 65%), and the lowest in the liver tissue (34 to 50%). The values in the gonad tissue were closer to those in the muscle tissue (50 to 59%). CSIA-based estimates from model a (20:5n-3) were higher than those from model b (20:5n-3 + 22:6n-3) in all three tissue types (**Table 5**).

▼**Table 5.** Comparison of the proportional contribution of ice algae-produced carbon α_{Ice} in the stomach content and different body tissues of polar cod (mean ± 1 SD %). Calculations of α_{Ice} in stomach contents were based on α_{Ice} of prey items estimated by Kohlbach et al. (2016). Body tissue estimates of α_{Ice} were derived from bulk stable isotope compositions (BSIA) of muscle tissue and fatty acid-specific stable isotope compositions of 20:5n-3 (model a) and 20:5n-3 + 22:6n-3 (model b) in muscle, liver and gonad tissue of polar cod.

Diet analysis	**BSIA**	**CSIA**					
Stomach	Muscle	Muscle		Liver		Gonads	
		Model a)	Model b)	Model a)	Model b)	Model a)	Model b)
54 ± 34	95 ± 5	65 ± 9	51 ± 8	50 ± 11	34 ± 11	59 ± 14	50 ± 12

Discussion

Diet composition and feeding rates

The stomach contents of polar cod caught under sea ice during PS80 were diverse in taxonomic composition, but heavily dominated by the sympagic crustaceans *Apherusa glacialis* in terms of biomass, and *Tisbe* spp. in terms of numbers. The diet of polar cod from the central Arctic under-ice habitat differed from previous diet analyses of fish collected from underneath first-year ice of the western Barents Sea in spring, which were found to be dominated by *Calanus glacialis* (Lønne and Gulliksen 1989). In the same study, fish collected from underneath multi-year ice north of Svalbard had a more diverse stomach content dominated in biomass by *Themisto libellula*, followed by *A. glacialis* (Lønne and Gulliksen 1989). The diet compositions in other studies in more open waters were dominated by *Themisto* spp. and *Calanus* spp. (Bradstreet and Cross 1982; Renaud et al. 2012; Gray et al. 2016; Majewski et al. 2016; McNicholl et al. 2016). Epi-benthic and ice-associated harpacticoid and cyclopoid copepods were found to be important in the diet of relatively small sized polar cod (56 – 159 mm) in open water during summer (Matley et al. 2013). Near the coast, polar cod have been found feeding on other benthic species (Lowry and Frost 1981; Craig et al. 1982; Gray et al. 2016). Euphausiids, gammarid amphipods and appendicularians were a major component of the diet of polar cod in the Bering and Chukchi Seas (Nakano et al. 2016). Several studies concluded that the differences in diet were most likely caused by differences in food availability (Craig et al. 1982; Lønne and Gulliksen 1989; Ajiad and Gjøsæter 1990; Gray et al. 2016; Majewski et al. 2016). This assumption is consistent with our findings, as we observed a correlation between the abundances of prey species in the upper two meters of the water column under ice (David et al. 2015) and with the stomach contents of the fish. Some studies also reported differences in diet depending on fish size, where larger fish consume larger prey or a greater variety of prey species (Bradstreet and Cross 1982; Craig et al. 1982; Ajiad and Gjøsæter 1990; Renaud et al. 2012; Matley et al. 2013; Gray et al. 2016; McNicholl et al. 2016). Renaud et al. (2012) found smaller fish (< 80 mm) feeding primarily on small copepods, whereas the diet of bigger individuals (< 135 mm) was dominated by bigger prey species, such as the pelagic amphipod *T. libellula*.

This pattern was not found in our study, probably because of the limited and small size range of our samples, or as a result of sampling from the under-ice environment, whereas the fish in the study of Renaud et al. (2012) were caught in pelagic waters of the fjords of Svalbard.

The mean relative daily feeding rate of 1.2% of the body weight determined in our study was about twice as high compared to values estimated for similar-sized polar cod in Resolute Bay (0.51% body weight d^{-1}) (Hop and Tonn 1998). It was, however, still within the range observed in fish adapted to low temperatures. For example, Flores et al. (2004) estimated a relative daily feeding rate of 1.0 to 1.5% of the body weight for the Antarctic icefish *Champsocephalus gunnari*. An experimental study showed that young polar cod (5 g WW $ind.^{-1}$) could grow at daily rations of 11 to 21 mg WW d^{-1} (*Calanus* spp.) and 25 to 44 mg WW d^{-1} (*Themisto* spp.), respectively (Hop et al. 1997a). Assuming a mean relative dry mass of 30% (*Calanus* spp.) and 20% (*Themisto* spp.) (Hop et al. 1997a) would imply that the range of daily food intake was between 4 and 9 mg DW d^{-1}. Hence, a mean daily ration of 11 mg d^{-1}, observed in our small fish (3.4 g WW $ind.^{-1}$) was well within the range allowing for positive growth. Accordingly, a mean *CI* of 78.6% and high lipid contents in liver and gonads indicated that feeding rates were sufficient to sustain a good body condition of the fish. Using our estimates of feeding rates for juvenile polar cod dwelling within the under-ice habitat in combination with the corresponding minimum mean fish abundance of 5,400 ind. km^{-2} in the research area (David et al. 2016), results in a mean minimum dry mass food demand of 81 g km^{-2} d^{-1}. According to the relative diet composition by dry mass, 55 g km^{-2} d^{-1} were attributed to *A. glacialis*, 5 g km^{-2} d^{-1} to *Themisto* spp., and 6 g km^{-2} d^{-1} to *Calanus* spp. These values were about 2 to 3 orders of magnitude below the biomass densities of these species in the under-ice habitat (H. Flores, unpubl. data). These calculations support the hypothesis that polar cod in the Eurasian Basin find sufficient food resources within the under-ice habitat, while they possibly follow the drift of sea ice across the Arctic Ocean during their first 1 to 2 years of life (David et al. 2016), even if the true polar cod abundance and food demand were underestimated due to a potentially lower catch efficiency of the SUIT (David et al. 2016).

Lipid and fatty acid profiles

The lipid content in the muscle tissue was considerably lower than in the liver, supporting the assumption that the main lipid depot in polar cod was the liver (Hop et al. 1995). The liver is the main tissue where lipogenic activity occurs, i.e. where FAs are synthesized *de novo* and FAs are modified (Henderson and Sargent 1985; Dalsgaard et al. 2003). Thus, the maintenance of the lipid levels in the liver is important for the good body condition of the organism (Hop et al. 1997a). In order to prepare for reproduction, liver lipids are transferred to the gonads (Krivobok and Tokareva 1972), which then explains the high similarity of lipid and fatty acid contents between the liver and the gonads.

We found relatively high amounts of *Calanus*-associated marker FAs in all tissues, suggesting a significant contribution of *Calanus* spp. to the diet, as reported by previous

studies (Lowry and Frost 1981; Bradstreet and Cross 1982; Falk-Petersen et al. 1987). In addition, high amounts of *Calanus*-associated FAs could also have been derived from *Calanus*-feeding amphipods, such as *T. libellula*, a locally important prey item in our study (David et al. 2015; Kohlbach et al. 2016). It has been shown that *Calanus* copepods contain high amounts of diatom-associated FAs, such as 16:1n-7 and 20:5n-3 (Kohlbach et al. 2016), which could have indirectly contributed to the signal of these markers in the polar cod tissue. High amounts of the FAs 16:1n-7 and 20:5n-3 were also found in the sympagic amphipod *A. glacialis* (Kohlbach et al. 2016), which constituted the bulk of the stomach content biomass in our study.

The biomarker ratios 16:1n-7/16:0 and ∑C16/∑C18 provide information on the relative proportions of diatoms versus flagellates in a consumer (Claustre et al. 1988/89; Viso and Marty 1993). Both biomarker ratios showed average values ≥ 1 in all three tissue types, indicating that diatoms were the most important carbon source of polar cod during our sampling period. In summary, the results from the fatty acid analysis agreed with the stomach content analysis in finding a diet predominantly consisting of copepods and amphipods, with diatoms as the primary carbon source. During our sampling period, diatoms dominated the ice algal community, whereas the phytoplankton community was dominated by dinoflagellates (Kohlbach et al. 2016; Hardge et al. 2017). Hence, a high contribution of diatoms at the base of the food web is a qualitative indication that ice algae played an important role as a carbon source for polar cod. The relative proportion of copepods versus amphipods to the carbon budget, however, cannot be quantified with FA analysis due to a lack of specific amphipod-associated marker FAs.

Polyunsaturated FAs, such as 20:5n-3 and 22:6n-3, are mainly incorporated into the cell membranes of fish to ensure their structural and functional integrity (Cowey and Sargent 1977). In contrast, 16:1n-7, 18:4n-3 and the *Calanus*-associated FAs are mainly used as storage FAs (D. Kohlbach, unpubl. data). In this study, all three tissues showed the same pattern: a higher content of storage lipids was accompanied by a higher proportional contribution of 16:1n-7, 18:4n-3 and the *Calanus*-associated markers, whereas higher contents of membrane lipids were associated with higher proportions of 20:5n-3 and 22:6n-3. Thus, a comparison of the FA profiles among the three different tissue types is difficult to accomplish due to the different levels of storage versus membrane lipids in the different tissues.

Stable isotope compositions and trophic dependency of polar cod on ice algae-produced carbon

Bulk and fatty acid-specific stable isotope compositions

The $\delta^{15}N$ values in I-POM and P-POM in our study were in the range of those $\delta^{15}N$ values measured in previous studies in the Arctic (Tamelander et al. 2006a; Søreide et al. 2013). Based on the two-source food web model described in Post (2002) and Søreide et al. (2013), polar cod occupied approximately trophic level 3, agreeing with other studies,

in which a trophic level between 3 and 4 was determined, depending on the ontogenetic stage of the fish (Hobson et al. 1995; Hobson et al. 2002; Christiansen et al. 2012).
The considerably higher $\delta^{13}C$ values in I-POM versus P-POM were consistent with the stable isotope patterns described in previous studies (Hobson et al. 1995; Søreide et al. 2006; Tamelander et al. 2006a). The isotopic difference in bulk $\delta^{13}C$ values between I-POM and P-POM in our study of 2.4‰ was considerably lower compared to measurements made around Svalbard in August where $\delta^{13}C$ values in I-POM were 7‰ higher versus P-POM (Søreide et al. 2013). A high variability of $\delta^{13}C$ values between studies was particularly evident for I-POM, possibly reflecting variations in nutrient availability and thus growth conditions, the taxonomic composition of the trophic baseline or the availability of CO_2 (Rau et al. 1992; Fry 1996; Ostrom et al. 1997). For example, the $\delta^{13}C$ values in I-POM from a food web study in the Barents Sea ranged from -21.7 to -12.6‰, and the mean of -20.3‰ was ~ 2‰ higher than the $\delta^{13}C$ values in I-POM collected farther north and within the Arctic Ocean in the following year (Tamelander et al. 2006a). This large spatial and temporal variability in I-POM $\delta^{13}C$ values highlights the importance to representatively sample potential food sources when studying trophodynamics and to be very cautious when only relying on literature values.
$\delta^{13}C$ values of FA 20:5n-3 in I-POM were ~ 9‰ higher than in P-POM, which was very similar to a previous study in Alaskan waters in August (Budge et al. 2008). In contrast, Graham et al. (2014) used a trophic baseline derived from Wang et al. (2014) where $\delta^{13}C$ values in I-POM were ~ 4‰ higher than in P-POM for both 20:5n-3 and 22:6n-3. The $\delta^{13}C$ values of 20:5n-3 in our polar cod samples were between 3 and 4.5‰ lower than in I-POM, and between 4.5 and 6‰ higher than in P-POM. The $\delta^{13}C$ values of 20:5n-3 in polar cod from the Alaskan study (Budge et al. 2008) were between 6.6 and 8.1‰ lower relative to their I-POM and between 0.5 and 2‰ higher relative to their P-POM. Juvenile polar cod caught in the Beaufort Sea during late summer (Graham et al. 2014) showed a similar depletion of ^{13}C in both 20:5n-3 and 22:6n-3 to our results, but in contrast to our study, the $\delta^{13}C$ values in both FAs were lower than their P-POM $\delta^{13}C$ values.

Proportional ice algal contribution to the carbon budget of polar cod

Three out of four approaches to estimate the proportional contribution of sea ice algae-produced carbon α_{Ice} (i.e. α_{Ice} of prey species, BSIA, and CSIA using one marker FA (model a) and CSIA using tow marker FAs (model b)) were consistent in finding that α_{Ice} accounted for more than 50% of the carbon budget of polar cod. Only estimates using the CSIA-based model b on liver tissue arrived at a relatively low value of α_{Ice} of about 34%.
The α_{Ice} estimates derived from the BSIA-based model were generally higher than the estimates based on the CSIA models and on stomach content analysis. These higher α_{Ice} values from the BSIA-based models may be related to several reasons. 1) Besides the lipid components, proteins and carbohydrates are also subject to various mass-dependent metabolic processes, which can influence the carbon isotopic composition of a species. Since lipids are more depleted in ^{13}C than other body molecules (DeNiro and

Epstein 1977; Søreide et al. 2006), they are often either removed prior to analysis or mathematical corrections are applied under consideration of the individual lipid content of a sample (e.g. McConnaughey and McRoy 1979). For both methods, advantages and disadvantages regarding applicability have been reported (Pinnegar and Polunin 1999; Sweeting et al. 2006; Post et al. 2007; Mintenbeck et al. 2008), which were discussed in Kohlbach et al. (2016). The mathematical normalization of the bulk stable isotope values (McConnaughey and McRoy 1979) led to a considerably lower α_{Ice} (~ 50%) related to its great impact on the isotopic compositions of the lipid-rich POM, and its marginal influence on the muscular polar cod compositions with its low lipid content. 2) An additional over-estimate of α_{Ice} might be caused by a trophic fractionation factor of the heavy carbon stable isotope between 0.1 and 1% per trophic level (DeNiro and Epstein 1978; Rau et al. 1983; Post 2002). The assumption of a carbon trophic fractionation factor Δ_C = 1‰ per trophic level reduced the bulk α_{Ice} estimates for polar cod considerably by ~ 20% to 74%. So far, there is no consensus whether to consider the effect of both high lipid contents and trophic enrichment factors, and we therefore did not account for these effects. The differing nature of the analytes, i.e. a mix of all biochemical body components versus individual molecules, however, may to some extent explain the consistently higher α_{Ice} values obtained with BSIA compared to the other two fatty acid-based approaches.

In contrast to BSIA, CSIA of marker FAs is limited to molecules assumed to be unchanged by metabolic processes, and is therefore independent from the chemical composition of organisms. Considering solely the diatom-associated FA 20:5n-3 (model a) resulted in higher α_{Ice} estimates compared to a combination of this FA with the dinoflagellate-associated FA 22:6n-3 (model b). Accordingly, model b represents the most conservative estimate of α_{Ice}, accounting for the contribution of both diatoms, which in our dataset dominated the sea ice algal community, and dinoflagellates, which were more important in the phytoplankton community (Kohlbach et al. 2016; Hardge et al. 2017). Assuming that both liver tissue and stomach contents are representative of more recently obtained food sources compared to the muscle tissue, however, a high consensus between stomach content-derived α_{Ice} and CSIA-based α_{Ice} from model a indicates that a potential under-estimate of α_{Ice} in model b cannot be excluded.

The liver tissue and stomach contents indicated lower α_{Ice} estimates relative to the muscle tissue. The high similarity of the α_{Ice} estimates of muscle and gonad tissues might be explained by the fact that the lipid content of the gonads originates from the liver fat, which makes the biomarker signal from the gonads older than the liver itself. In conclusion, the fish probably relied less on sea ice-derived carbon sources during the sampling period of PS80 than during the weeks before. Evidence of a massive export of ice algae shortly before PS80 sampling suggested high standing stocks of ice algae in the weeks before the sampling (Boetius et al. 2013). During our sampling, these stocks had already melted away for most of the sampling area during ice break-up, with high ice algal biomass present at only the high latitude stations with thicker sea ice (Lange et al. 2016). Therefore, the low stocks of phytoplankton in regions with low ice algal biomass became relatively more important for the food web. Ice algae, however, remained an

important carbon source for consumers of intermediate trophic levels (Kohlbach et al. 2016).

So far, studies calculating the proportional contribution of sea ice-derived carbon to the diet of polar cod are very limited. The available estimates, however, show a wide range between negligible and high importance of ice algae-produced carbon, depending on region, season, and the approach used for the calculation. The variability of α_{Ice} in polar cod could be influenced by the size composition of the fish and hence reflect ontogenetic changes in the diet (Renaud et al. 2012). Based on bulk stable isotope analyses of the muscle tissue, Christiansen et al. (2012) concluded that adult polar cod (length 141 to 185 mm), caught in fjords in NE Greenland in autumn, were highly associated with the pelagic food web. Using CSIA, Graham et al. (2014) estimated a negligible trophic dependency on ice-algae produced carbon (≤ 2%) in juvenile polar cod (length ~ 30 to 100 mm) from the Beaufort Sea in August/September. However, the specimens collected by Graham et al. (2014) were spawned in open waters and had barely started feeding yet when they were sampled, reducing the probability of ingesting ice-associated prey. Furthermore, an increased proportion of benthic prey in a shallow sea could result in a lower importance of α_{Ice}, compared to oceanic waters. Budge et al. (2008) estimated α_{Ice} ranging on average from 8 to 30% based on FA 20:5n-3, and from 65 to 77% based on FA 16:4n-1 for polar cod from coastal waters in Alaska during August, depending on the sampling site. With a similar seasonal coverage, our α_{Ice} estimates for FA 20:5n-3 were considerably higher than those reported by Budge et al. (2008), indicating that polar cod under sea ice of the central Arctic Ocean relied more on carbon produced by ice algae than in coastal areas. Assuming that the fish follow the ice drift (David et al. 2016), drifting sea ice might be an important pathway and a competitive survival trait for this species, connecting polar cod populations, endangered by climate change-related alterations of the sea ice system in high-Arctic regions.

Conclusions

This first comprehensive investigation regarding the feeding ecology of 1 to 2 year-old polar cod from the under-ice habitat of the central Arctic Ocean provides unequivocal evidence from four different approaches that polar cod associated with the under-ice habitat critically depend on carbon produced by sea ice algae during summer. By combining classical diet analysis with the analysis of stable isotopes and lipid trophic markers, the carbon flux from sea ice algae via ice-associated crustaceans to polar cod is now clearly visible. The good body condition of the fish and the viable feeding rates support the notion that the sea ice habitat can provide sufficient resources for the fish to survive drifting with sea ice across the Arctic Ocean. Understanding the sea ice – polar cod connection is important, because polar cod is a major prey of many endotherm populations around the Arctic Ocean, and a competitor to commercially exploited fishes. A strong dependency on sea ice-associated resources indicates that young polar cod from the under-ice habitat are particularly vulnerable to ramifications of the sea ice-associated food web, which are expected at the current rate of change in the distribution and structure of sea ice habitats. The ability to survive in the under-ice habitat may

constitute a unique trait of this species, enhancing genetic exchange and recruitment of populations around the Arctic Ocean. A continuing disruption of the sea ice-associated ecosystem could weaken the evolutionary advantage of this feature in terms of resilience to environmental variability and competitors.

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Supplementary

▼**Supplementary A**. Relative composition of most abundant lipid classes (mean ± 1 SD mass % of total lipids) in the three tissue types of polar cod. FFA = free fatty acid, PC = phosphatidylcholine, PE = phosphatidylethanolamine, TAG = triacylglycerol.

	Muscle (*n* = 3)	**Liver** (*n* = 3)	**Gonads** (*n* = 3)
TAG	21.7 ± 7.9	88.1 ± 4.5	85.2 ± 13.4
FFA	0.4 ± 0.7	7.1 ± 5.3	9.7 ± 13.0
PE	22.4 ± 2.6	0.6 ± 0.4	0.9 ± 0.7
PC	44.9 ± 4.6	1.5 ± 0.1	2.1 ± 0.8
Total	89.4	97.3	97.9

▼**Supplementary B.** Proportional stomach content composition by abundance, dry mass and Index of Relative Importance (*IRI*) at each station (%).

Station	216	223	248	258	276	285	321	331	345	358	376
Location	B	C	D	E	F	F	G	G	H	I	I
n	7	4	2	4	9	4	7	1	8	2	3
Relative abundance (%)											
Amphipods											
Apherusa glacialis	33.3	85.2	1.5	8.3	19.6	25.0	22.6	100.0	2.9	76.9	60.0
Themisto libellula	0	0	0	1.0	1.2	1.9	1.6	0	2.9	0	0
Themisto abyssorum	0	0	0	0	0	0	0	0	0.7	0	0
Themisto spp.	0	0	0	0	0	0	1.6	0	3.2	0	0
Unidentified amphipod	50.0	2.3	0.5	0	1.9	1.9	3.2	0	1.6	7.7	0
Copepods											
Calanus spp.	16.7	2.3	79.0	4.2	3.1	3.9	1.6	0	0.3	0	0
Euchirella spp.	0	0	0	0	0	0	0	0	0	0	10.0
Tisbe spp.	0	0	0	83.3	73.6	57.7	48.4	0	73.6	0	20.0
Harpacticoid copepod	0	1.1	0	2.1	0.6	5.8	19.4	0	13.5	0	0
Unidentified copepod	0	2.3	18.0	1.1	0.0	3.8	0.0	0	1.3	0.0	10.0
Other											
Chaetognatha	0	0	0.5	0	0	0	0	0	0	15.4	0
Appendicularia	0	6.8	0.5	0	0	0	0	0	0	0	0
Decapoda	0	0	0	0	0	0	1.6	0	0	0	0
Relative biomass (%)											
Amphipods											
Apherusa glacialis	39.2	96.5	11.8	88.0	87.4	86.9	20.1	100.0	35.3	84.7	93.2
Themisto libellula	0	0	0	5.5	2.8	3.4	0.7	0	17.9	0	0
Themisto abyssorum	0	0	0	0	0	0	0	0	4.0	0	0
Themisto spp.	0	0	0	0	0	0	0.7	0	19.9	0	0
Unidentified amphipod	58.8	2.6	3.9	0	8.2	6.7	2.9	0	19.6	8.5	0
Copepods											
Calanus spp.	2.0	0.3	67.2	4.6	1.4	1.4	0.2	0	0.4	0	0

Relative biomass (%)											
Euchirella spp.	0	0	0	0	0	0	0	0	0	0	5.2
Tisbe spp.	0	0	0	0.6	0.2	0.1	0.03	0	0.6	0	0.02
Harpacticoid copepod	0	0.01	0	0.1	0.01	0.1	0.1	0	0.7	0	0
Unidentified copepod	0	0.3	15.3	1.2	0	1.4	0	0	1.6	0	1.6
Other											
Chaetognatha	0	0	1.6	0	0	0	0	0	0	6.8	0
Appendicularia	0	0.3	0.2	0	0	0	0	0	0	0	0
Decapoda	0	0	0	0	0	0	75.3	0	0	0	0
***IRI* (%)**											
Amphipods											
Apherusa glacialis	24.2	95.5	3.5	66.2	50.9	74.7	35.0	100.0	16.5	89.4	86.7
Themisto libellula	0	0	0	1.1	0.6	0.9	0.4	0	4.5	0	0
Themisto abyssorum	0	0	0	0	0	0	0	0	0.5	0	0
Themisto spp.	0	0	0	0	0	0	0.4	0	5.0	0	0
Unidentified amphipod	72.7	1.7	1.2	0	0.8	1.4	2.0	0	2.3	4.5	0
Copepods											
Calanus spp.	3.1	0.9	77.0	3.0	0.7	0.9	0.3	0	0.1	0	0
Euchirella spp.	0	0	0	0	0	0	0	0	0	0	4.3
Tisbe spp.	0	0	0	28.9	46.9	19.3	39.7	0	64.3	0	5.7
Harpacticoid copepod	0	0.2	0	0.4	0.1	1.0	9.6	0	6.2	0	0
Unidentified copepod	0	0.5	17.6	0.4	0	1.8	0	0	0.6	0	3.3
Other											
Chaetognatha	0	0	0.5	0	0	0	0	0	0	6.1	0
Appendicularia	0	1.2	0.2	0	0	0	0	0	0	0	0
Decapoda	0	0	0	0	0	0	12.6	0	0	0	0

▼**Supplementary C.** Pearson's correlation coefficients indicating the association between paired samples found in the stomach content of polar cod (*Boreogadus saida*) and the under-ice surface water of the sampled area per station. The association ranges between [-1, 1] with 0 indicating no association.

	Stomach content					
Abundance under-ice surface	*Apherusa glacialis*	*Themisto* spp.	*Calanus glacialis*	*Tisbe* spp.	Harpacticoid copepods	Chaetognaths
Apherusa glacialis	0.793	-0.168	-0.275	-0.117	-0.149	-0.279
Themisto spp.	-0.186	0.122	-0.299	0.030	0.239	-0.296
Calanus glacialis	-0.110	-0.212	0.992	-0.259	-0.247	0.991
Tisbe spp.	0.740	0.442	-0.207	0.354	0.429	-0.207
Harpacticoid copepods	-0.039	-0.108	-0.143	0.142	-0.218	-0.145
Chaetognaths	-0.129	-0.191	0.999	-0.295	-0.223	0.999

2.3 *Chapter III*

Ice algae-produced carbon ensures winter survival of young Antarctic krill *Euphausia superba*

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Abstract

Antarctic krill *Euphausia superba* ('krill') constitute a fundamental carbon source for Antarctic seabirds and mammals, and a globally important fisheries resource. The future resilience of krill to climate change depends critically on the winter survival of young krill. To survive periods of extremely low production by pelagic algae during winter, krill are assumed to rely partly on carbon produced by ice algae. The true dependency on ice algae-produced (sympagic) carbon, however, is so far unquantified. This confounds predictions on the future resilience of krill stocks to sea ice decline. Fatty acid (FA) analysis, bulk stable isotope analysis (BSIA) and compound-specific stable isotope analysis (CSIA) of marker FAs were applied to quantify the dependency of overwintering krill in the northern Weddell Sea on ice algae-produced carbon (α_{Ice}). Our results demonstrate that the majority of the carbon uptake of overwintering young krill originates from ice algae (up to 67%), and that the dependency on ice algal carbon decreases with ontogeny (< 30% in adults). Differences between α_{Ice} estimates derived from short- versus long-term FA-specific isotopic compositions suggested that sympagic carbon gained importance as the winter progressed, and might become critical at the late winter-spring transition, before the phytoplankton bloom commences. Where the sea ice season shortens, reduced availability of ice algae might possibly not be compensated by pelagic algae during wintertime. Hence, sea ice decline could seriously endanger the winter survival of recruits, and subsequently overall biomass of krill.

Introduction

Antarctic krill *Euphausia superba* Dana (1850) (hereafter 'krill') is a highly abundant key species in the Southern Ocean ecosystem, channelling the majority of dietary carbon from marine microalgae to fishes, seabirds, and marine mammals (Hempel 1987; Ward et al. 2012). Besides their ecological importance, krill constitute an increasingly harvested fisheries resource. In the period from 2000 to 2015, the annual catch has approximately doubled, accounting for over 200,000 metric tons, which equals a total market value of 300 million US$ in 2015 (Grant et al. 2013; CCAMLR 2016). While fisheries effort increases, krill populations have suffered from sea ice decline and other climate change-related stressors (Atkinson et al. 2004; Flores et al. 2012a). In the south-west Atlantic sector of the Southern Ocean, decreasing winter sea ice extent was paralleled by a significant decline of krill abundance, indicating a pronounced dependency of krill on winter sea ice (Loeb et al. 1997; Atkinson et al. 2004, 2008; Flores et al. 2012a). Satellite observations show large regional variability with negative trends in sea ice extent (Parkinson and Cavalieri 2012) and ice season duration (Stammerjohn et al. 2012) in key areas of krill distribution (Atkinson et al. 2008). Although there remains uncertainty in sea ice extent predictions for the Southern Ocean (Turner et al. 2013), the majority of simulations indicate more widespread sea ice decline in the coming decades, particularly during winter and spring (Turner et al. 2014).

Winter survival of krill larvae is considered the most vulnerable component of their life cycle to climate change (Flores et al. 2012a). Krill spawn during austral summer, between December and March. In autumn, the larvae reach their overwintering stage, the furcilia larvae (Fraser 1937; Hempel et al. 1979). Krill larvae need to feed constantly to cover their energy demand (Quetin et al. 1994; Meyer 2012). In winter, concentrations of pelagic algae (phytoplankton) are far below critical levels to sustain their food demand (Meyer 2012). Alternatively, the productivity and/or standing stocks of 'ice algae'- microalgae living in sea ice- and other in-ice fauna are assumed to be important in the diet of krill larvae during winter (Daly 1990). Supporting this theory, primarily young developmental stages of krill were frequently found in high abundances underneath ice floes during winter (Meyer et al. 2009; Flores et al. 2012b; David et al. 2017). In addition, heterotrophic prey, e.g. copepods, can account significantly to the carbon uptake of krill larvae during winter (Meyer et al. 2009), but may in turn also depend on ice algae as a primary carbon source. Altogether, there is ample observational evidence that ice algae-produced carbon is important for the survival of krill larvae during their first winter (Daly 1990; Frazer et al. 2002; Meyer et al. 2009). In contrast, overwintering adult krill have demonstrated a combination of strategies to survive periods of starvation, e.g. by reducing metabolic rates, mobilising reserves from body tissues (Ikeda and Dixon 1982; Meyer et al. 2010), feeding on detritus (Schmidt et al. 2011) or zooplankton (Ju and Harvey 2004), or even cannibalism (Maihama and Endo 1986). Temporarily, however, adults may also rely on ice algae-produced carbon (Marschall 1988; Quetin et al. 1994).

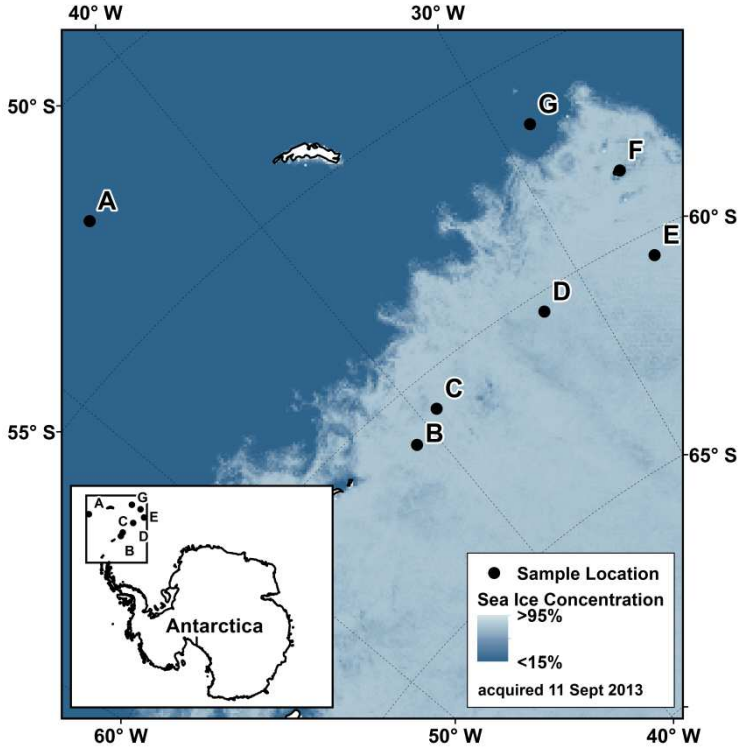
Increasing fishing effort in combination with a presumed high vulnerability of krill to climate change has raised concerns about the future sustainability of krill harvesting and its role in Antarctic ecosystems (Schiermeier 2010). In spite of extensive efforts to elucidate the winter survival of krill, the true contribution of ice algae-produced carbon to the carbon budget of overwintering krill has remained unresolved. Quantitative knowledge of the dependency of overwintering krill on ice algae-produced carbon, however, is critical for assessing the ability of krill to maintain today's population levels in regions of changing sea ice conditions. In the light of the assumed significant role of sea ice for overwintering krill, such an assessment would be crucial for future resource and conservation management.

In this study, we analysed the composition of lipid classes, fatty acids (FAs), and stable isotopes in larval, juvenile and adult krill from the northern Weddell Sea during late winter 2013. Lipid parameters provided information on energy allocation and the FA composition reflected the natural distribution of dietary FAs in krill. Certain fatty acids biosynthesised by algae are not metabolically transformed and can therefore be used as tracers of autotrophic carbon sources in food webs (Dalsgaard et al. 2003 and References therein). Some of these marker fatty acids are indicative of distinct autotrophic taxa, such as Bacillariophyceae ('diatoms'), or Dinophyceae ('dinoflagellates') (Dalsgaard et al. 2003 and references therein). In algal biomolecules, the lighter carbon stable isotope ^{12}C is more reactive during photosynthetic assimilation than the heavier ^{13}C isotope, and is therefore usually enriched. In the often carbon-limited sea ice environment, however, metabolic enrichment of ^{12}C is less pronounced (Fry and Sherr 1984; Hecky and Hesslein 1995). Hence, biomolecules synthesised by ice algae often have a higher relative content of the heavy carbon isotope ^{13}C compared to phytoplankton (Wada et al. 1987; Fischer 1991; Rau et al. 1991b). The isotopic composition of biomolecules from ice algae is transferred through the food web by organisms ingesting ice algae-produced carbon either directly or indirectly by carnivorous or detritivorous feeding. The isotopic fractionation of carbon ($\delta^{13}C$:$^{13}C/^{12}C$) has therefore been used in polar organisms to estimate their relative dependency on ice algae-produced carbon (Budge et al. 2008; Wang et al. 2015; Jia et al. 2016; Kohlbach et al. 2016). In this study, we estimated the relative dependency of krill on carbon produced by ice algae in terms of the proportional contribution of ice algae-produced carbon to the body carbon of krill (α_{Ice}), based on bulk stable isotope analysis (BSIA) and compound-specific stable isotope analysis (CSIA) of marker FAs. Quantification of the importance of ice algae-produced carbon for ecological key species is a crucial step to model the overall carbon flux in the Southern Ocean under current and future scenarios to ultimately contribute to the development of sustainable approaches in fisheries management and conservation policy.

Materials and Methods

Sample collection

Sampling was conducted during the RV '*Polarstern*' expedition PS81 (14 August-16 October 2013) in the northern Weddell Sea (**Figure 1**, **Table 1**). Detailed information on the sampling during PS81 can be found in David et al. (2017).



▲***Figure 1.*** *Map of the sampling area during 'Polarstern' expedition PS81 in the northern Weddell Sea (14 August to 16 October 2013) with sea ice concentration (Spreen et al. 2008). Sampling locations are indicated by capital letters (**Table 1**).*

▼**Table 1.** Sample information for ice algae (I), phytoplankton (P), and larval (L), juvenile (J) and adult (A) *Euphausia superba* (ES) collected during RV '*Polarstern*' expedition PS81 in the northern Weddell Sea.

Location	Station no.	Date (m/dd/yyyy)	Sample type	Latitude	Longitude
A	527-2	8/22/2013	ES (J)	-52.29	-45.07
	529-1	8/22/2013	P	-52.28	-44.25
B	549-1	8/29/2013	ES (L, J)	-61.25	-42.06
	551-1	8/31/2013	ES (A)	-61.21	-40.73
	552-1	8/31/2013	P	-61.22	-40.72
	555-1	9/1/2013	I	-61.21	-41.05
	555-24	9/4/2013	P	-60.90	-40.44
C	555-47	9/9/2013	ES (L, J)	-60.80	-39.15
D	557-2	9/10/2013	ES (L, J, A)	-59.96	-33.17
	557-3	9/11/2013	P	-59.95	-33.15
	560-2	9/11/2013	ES (L, J, A)	-60.63	-31.78
	560-3	9/12/2013	P	-60.63	-31.83
	562-5	9/12/2013	ES (L, J, A)	-60.97	-31.24
E	565-5	9/16/2013	ES (L, J)	-60.71	-27.17
	566-1	9/17/2013	I	-60.60	-27.10
	566-2	9/19/2013	ES (L)	-60.52	-26.52
	566-21	9/25/2013	ES (L)	-60.66	-26.44
	566-32	9/28/2013	P	-60.43	-25.71
	567-2	9/28/2013	ES (L)	-60.45	-25.70
F	571-1	9/30/2013	ES (L, A)	-58.43	-26.11
	577-2	10/2/2013	ES (L, J)	-58.44	-26.10
	579-2	10/2/2013	ES (J, A)	-58.46	-26.05
G	576-3	10/1/2013	P	-56.52	-28.65

The ice algae community was sampled by taking ice cores with a 9 cm interior diameter ice corer (Kovacs Enterprises). The bottom 10 cm of the ice cores were melted on board. Particulate Organic Matter (POM) from sea ice was concentrated by filtering the water from the melted ice cores via a vacuum pump through pre-combusted GF/F filters (1.0 to 1.5 L). The phytoplankton community was sampled at the chlorophyll *a* maximum depth (between 20 and 50 m) by a carousel water sampler connected to a CTD probe (Seabird SBE9+) with attached fluorometer. Depending on the biomass concentration, POM from the water column was obtained by filtering between 3 and 21 L water through pre-combusted GF/F filters. All filters were stored at -80°C until further processing.

Krill was caught in the uppermost 2 m from directly underneath the sea ice by a Surface and Under-Ice Trawl (SUIT) (van Franeker et al. 2009). A Rectangular Midwater Trawl (RMT) (Roe and Shale 1979) was used at one station (571-1). Larval krill were staged based on the number of terminal spines on the telson (Kirkwood 1982). All analysed larvae were staged as furcilia VI krill. Krill which already lost one pair of post-lateral spines from their telson (Fraser 1937), but had not yet developed external sexual characteristics, were classified as juveniles (Makorov and Denys 1981). Krill bearing

external sexual characteristics were categorized into females and males (Makorov and Denys 1981), but grouped together as 'adults' since no statistical differences in biomarker parameters were apparent. After determination of the body length and developmental stage (**Table 2**), samples were immediately frozen at -80°C in pre-combusted and pre-weighed sample vials (Wheaton, 6 h, 500°C). Analytical work took place at the Alfred Wegener Institute, Bremerhaven, Germany.

▼**Table 2.** Body length, dry mass and lipid content of krill (mean ± 1 standard deviation).

Parameter	Larvae (*n* = 14)	Juveniles (*n* = 19)	Adults (*n* = 26)
Length (mm)	11.4 ± 1.6	25.1 ± 7.8	42.7 ± 8.3
Dry mass/Individual (mg)	2.5 ± 3.1	19.0 ± 18.0	108.9 ± 81.8
Fatty acid content/Dry mass (%)	8.5 ± 10.2	5.1 ± 7.0	7.0 ± 3.5

Lipid class and fatty acid analyses

Prior to analysis, POM filters and whole krill individuals were freeze-dried for 24 h. Dry masses of krill were determined gravimetrically (**Table 2**). After homogenization, lipids were extracted with dichloromethane/methanol (2:1, v/v) (Folch et al. 1957). The lipid class composition of krill was investigated by High Performance Liquid Chromatography (HPLC) (Graeve and Janssen 2009) in order to determine ontogenetic differences in the proportions of storage and membrane lipids. Extracted lipids were converted into fatty acid methyl esters (FAME) and free fatty alcohols by transesterification with methanol, containing 3 % concentrated sulfuric acid. The proportional mass contributions of the diatom-associated marker FAs 16:1n-7 and 20:5n-3 (Graeve et al. 1994b, 1997; Falk-Petersen et al. 1998; Volkman et al. 1998; Scott et al. 1999), the dinoflagellate-associated marker FAs 18:4n-3 and 22:6n-3 (Viso and Marty 1993; Graeve et al. 1994b; Phleger et al. 1998), and the copepod-associated marker FA 20:1n-9 and 22:1n-11 (Dahl et al. 2000; Virtue et al. 2016) were analyzed via gas chromatography. The percentage of each individual fatty acid of the total fatty acid mass was determined by an internal standard (23:0) added prior to lipid extraction. The total fatty acid content was determined gravimetrically by the internal standard (**Table 2**). 16:1n-7 and 18:4n-3 are mainly incorporated in storage lipids, and 20:5n-3 and 22:6n-3 mainly serve as membrane FAs. Storage FAs are assumed to reflect the more recent carbon source composition, whereas membrane FAs are more conserved (Stübing et al. 2003). To distinguish the short- and long-term importance of diatom- versus dinoflagellate-derived carbon in the krill diet, the fatty acid ratios 16:1n-7/18:4n-3 and 20:5n-3/22:6n-3 were investigated. For details on sample preparation and measurements as well as analytical equipment see Kohlbach et al. (2016).

Bulk and compound-specific stable isotope analyses

Bulk nitrogen and carbon isotopic compositions of POM and krill were determined from freeze-dried bulk sample material (BSIA: bulk stable isotope analysis). Lipids were not removed prior to BSIA in order to avoid inducing changes in the isotopic composition of the krill samples (Mintenbeck et al. 2008). The fatty acid-specific stable isotope composition of carbon was measured in FAME derivatives of POM and krill (CSIA: compound-specific stable isotope analysis) (Kohlbach et al. 2016). Length, dry weight, lipid content and relative composition of storage and membrane lipids of krill used in BSIA and CSIA measurements were in the same range as those for lipid class and fatty acid composition (**Table 2**). All isotopic ratios were expressed in the δ notation as parts per thousand (‰) differences from the primary (calibration) standards Vienna Pee Dee Belemnite (VPDB) for carbon measurements, and atmospheric nitrogen for nitrogen measurements.

Verification of accuracy and precision of BSIA measurements was done by measuring the secondary reference material USGS41 (δ^{15}N = 47.6 ± 0.2‰, δ^{13}C = 37.6 ± 0.1‰, measured: δ^{15}N = 46.8‰, δ^{13}C = 36.8‰), provided by the International Atomic Energy Agency (IAEA, Vienna). Measurement errors were indicated as ± 0.8‰ for nitrogen and ± 0.5‰ for stable carbon measurements, respectively (representing ± 1 standard deviation of 17 analyses). Furthermore, the laboratory standards isoleucine (δ^{15}N = -11.9‰, δ^{13}C = -3.1‰) and peptone (δ^{15}N = 8.0‰, δ^{13}C = -15.7‰) were analysed every 5 samples (Sigma Aldrich). Measurement errors were ± 0.3‰ for nitrogen and ± 0.6‰ for carbon isotope ratios of isoleucine (representing ± 1 standard deviation of 16 analyses) and ± 0.3‰ for both peptone measurements (representing ± 1 standard deviation of 8 analyses). For CSIA measurements, quality assurance and analytical precision of the carbon stable isotope ratios were established by analysing the certified standard FAME 14:0 (certified: δ^{13}C = -30.0‰, measured: δ^{13}C = 29.8‰), 16:0 (certified: δ^{13}C = -30.7‰, measured: δ^{13}C = -30.2‰), and 18:0 (certified: δ^{13}C = -23.2‰, measured: δ^{13}C = -23.8‰), supplied by Indiana University, every 5 samples. Analytical error was ± 0.2‰ for 14:0 and ± 0.3‰ for both 16:0 for 18:0 (representing ± 1 standard deviation of 8 analyses). The samples were analysed in duplicates, and true δ values were obtained after two-point linear normalization (Paul et al. 2007). For details on sample preparation, measurements and analytical equipment for BSIA and CSIA see Kohlbach et al. (2016).

Quantification of ice algal carbon

We estimated the proportional contribution of sea ice algae-produced carbon α_{Ice} to the body carbon of krill from the bulk and fatty acid-specific carbon stable isotope compositions of POM from sea ice (simplified to ice algae) and the water column (simplified to phytoplankton), and krill by applying Bayesian multi-source stable isotope mixing models (MixSIAR) (Parnell et al. 2013; Stock and Semmens 2015). Trophic enrichment of ^{13}C and concentration dependencies were assumed to be zero for both BSIA and CSIA models (Budge et al. 2011; Graham et al. 2014; Wang et al. 2015). For the BSIA models, trophic enrichment of ^{15}N was assumed to be 3.4‰ per trophic level

(Minagawa and Wada 1984). For the fatty acid-specific modelling, the contribution of sea ice algae-derived carbon was calculated separately for 1) FAs associated with storage lipids (16:1n-7, 18:4n-3) and for 2) FAs associated with biomembranes (20:5n-3, 22:6n-3). Additionally, α_{Ice} was determined, weighted by the average mass proportions of storage and membrane lipids in each developmental stage, to account for differences in the contribution of the two lipid fractions to the total lipid content.

Data analysis

All performed data analyses were conducted using Software R, version 3.2.3 (R Core Team 2015). FA data were transformed applying an arcsine square root function in order to improve normality. Variations in lipid class, fatty acid and stable isotope compositions were tested using 1-way ANOVA. For testing between ice algae and phytoplankton, Student's t-tests were applied.

Results & Discussion

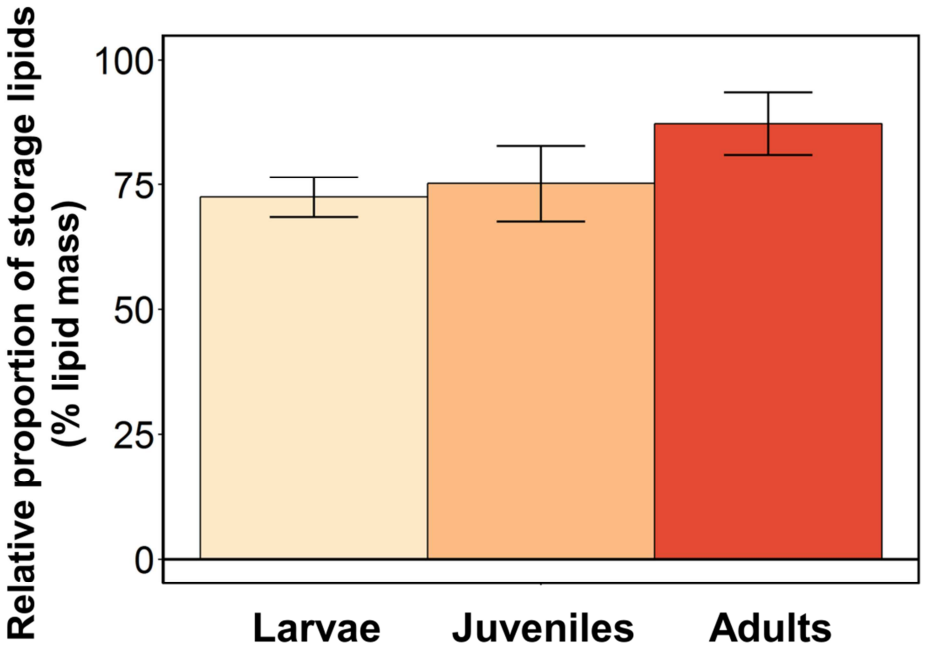
Lipid class and fatty acid compositions

Lipids provide two essential functions in living organisms: 1) they constitute structural components in membranes, and 2) they are a component for cellular energy storage (Lee et al. 2006). In most Antarctic euphausiids, energy is mainly stored in wax esters, providing long-term energy compared to triacylglycerols (TAGs), which are faster metabolized (Fricke et al. 1984; Stübing et al. 2003; Ko et al. 2015). Krill, however, mainly rely on TAGs and phosphatidylcholines (PCs) as energy stores for the survival of food-limited periods (Hagen et al. 1996). The mean proportions of PCs were very similar among the different developmental stages (41 to 42% of the total lipid content) (**Table 3**). Adult individuals, however, displayed significantly higher mean proportions of TAGs (39%) relative to larval (12%) and juvenile krill (20%). Conversely, the mean proportions of the membrane-associated phosphatidylethanolamine (PEs) were significantly lower in adult krill (10%) than in larvae (20%) and juveniles (18%). Adding TAGs, PCs and other typical storage lipids, such as sterols and free fatty acids, the lipid pool was clearly dominated by storage lipids in all three life stages. Adults, however, had a significantly higher mass proportion of storage lipids than larval and juvenile krill (ANOVA $F_{2, 20} = 4.7$, $p < 0.05$) (**Figure 2**). These ontogenetic differences in lipid class compositions were consistent with the known higher energy storage capacity of adults compared to younger stages (Meyer 2012).

▼**Table 3.** Proportions of most abundant lipid classes in krill (mean ± 1 standard deviation mass % of total lipid content).

Lipid class	**Larvae** (*n* = 7)	**Juveniles** (*n* = 9)	**Adults** (*n* = 7)	**ANOVA**		
				F	*df*	*p**
TAG	12.2 ± 10.0	20.3 ± 13.1	39.4 ± 10.8	8.1	2, 20	*
Sterols	6.4 ± 4.5	6.2 ± 2.9	2.9 ± 1.7		ns	
FFA	6.7 ± 2.0	6.1 ± 2.3	3.7 ± 1.2	4.9	2, 20	*
PE	19.8 ± 5.0	17.8 ± 6.2	9.6 ± 3.7	8.8	2, 20	*
PC	42.1 ± 7.8	42.4 ± 3.4	41.2 ± 5.0		ns	

FFA: free fatty acid, PC: phosphatidylcholine, PE: phosphatidylethanolamine, TAG: triacylglycerol
*ANOVA *p*: ns = $p > 0.05$; * $0.05 < p < 0.01$; ** $0.01 < p < 0.001$



▲***Figure 2.*** *Proportion of storage lipids in krill (mean ± 1 standard deviation %).*

In our ice algae samples, the diatom-associated marker FAs 16:1n-7 and 20:5n-3 were the most abundant marker FAs, altogether contributing over 30% to the total fatty acid mass. Conversely, the dinoflagellate-associated marker FAs 18:4n-3 and 22:6n-3 were only present in small amounts (mean < 5%), confirming the well-known dominance of diatoms in the ice algal community (Garrison and Close 1993; Lizotte 2001). In phytoplankton samples, the proportional contributions of both diatom- and dinoflagellate-associated marker FAs ranged between 5 and 10%, indicating a co-dominance of both algal taxa (Buck and Garrison 1983; Garrison et al. 1991). The pelagic algae community in the Southern Ocean often consists of a mixture of diatoms, dinoflagellates and prymnesiophytes *Phaeocystis* spp., with large variations depending on season and thus bloom situations (Burkholder and Sieburth 1961; Bathmann et al. 1997; Arrigo et al. 1999). In our study, we focused on well-known diatom- and

dinoflagellate-associated marker FAs that have been used frequently for tracking predator-prey relationships in marine food webs (Kattner et al. 1994; Hagen et al. 2001; Virtue et al. 2016).

In krill, the most abundant marker FAs were 20:5n-3 and 22:6n-3 (**Table 4**), which was in agreement with previous studies (Falk-Petersen et al. 2000; Virtue et al. 2016). Both polyunsaturated FAs were found in significantly higher concentrations in larval and juvenile krill versus adult individuals. Contrastingly, the FA profiles of adult individuals were characterized by higher amounts of 16:1n-7 compared to the younger developmental stages (**Table 4**). Hagen et al. (2001) also found higher levels of 20:5n-3 and 22:6n-3 accompanied by lower levels of 16:1n-7 in krill furcilia larvae compared to adults, suggesting that the fatty acid signatures of larvae might provide a more evident dietary input of primary synthesized FAs compared to the FA content of the adult krill.

▼**Table 4.** Proportions of marker fatty acids in krill (mean ± 1 standard deviation mass % of total fatty acid content).

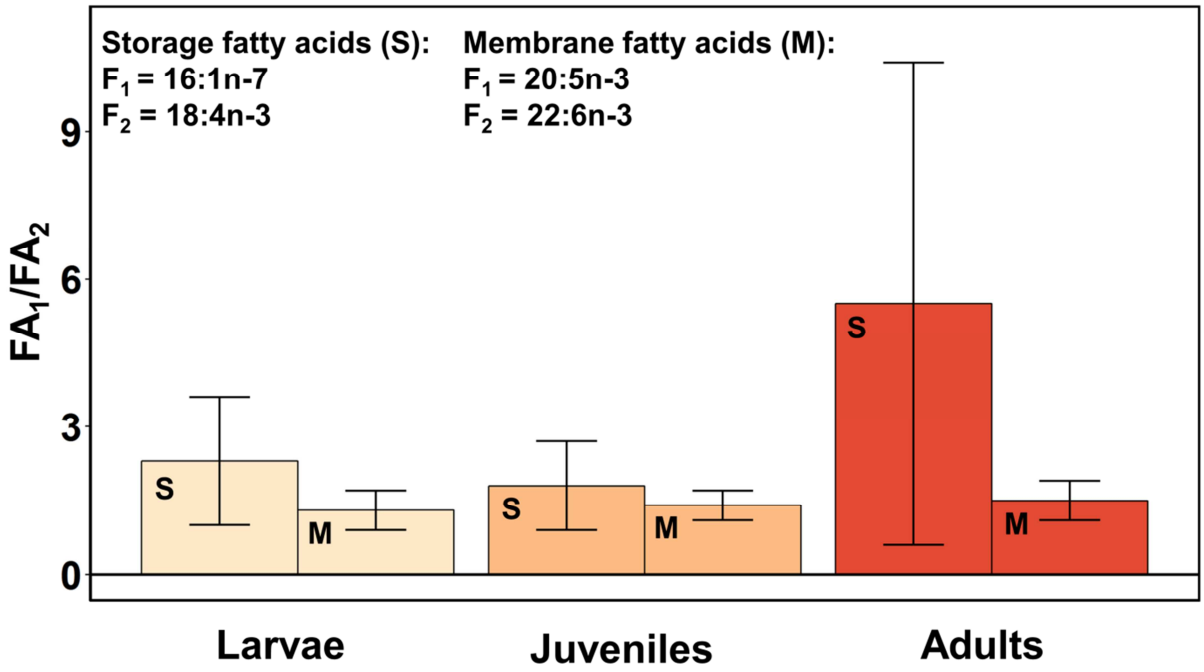
Fatty acid	**Larvae** (*n* = 14)	**Juveniles** (*n* = 19)	**Adults** (*n* = 26)	**ANOVA**		
				F	*df*	*p**
16:1n-7	4.1 ± 1.3	4.3 ± 1.2	6.7 ± 2.1	16.1	2, 56	**
18:4n-3	2.1 ± 1.3	2.7 ± 1.1	1.8 ± 0.9		ns	
20:5n-3	27.2 ± 5.3	26.1 ± 4.4	16.1 ± 2.6	49.2	2, 56	**
22:6n-3	22.2 ± 5.4	18.7 ± 4.5	11.2 ± 3.7	35.9	2, 56	**
20:1n-9	0.9 ± 0.5	0.9 ± 0.5	0.9 ± 0.4		ns	
22:1n-11	0.1 ± 0.2	0.2 ± 0.5	0.6 ± 0.3		ns	

*ANOVA *p*: ns = $p > 0.05$; * $0.05 < p < 0.01$; ** $0.01 < p < 0.001$

The diatom-associated marker FA 16:1n-7 and the dinoflagellate-associated marker FA 18:4n-3 are mainly incorporated into storage lipids, whereas the diatom-associated marker FA 20:5n-3 and the dinoflagellate-associated marker FA 22:6n-3 are predominantly incorporated in membrane lipids (Stübing et al. 2003). Hence, in this study we considered the two pairs of FAs separately in their two corresponding lipid fractions. In all three life stages and both lipid fractions of krill, the mean ratio of the diatom-associated versus dinoflagellate-associated marker FA was on average greater than 1, indicating a dominance of diatom-associated carbon sources (**Figure 3**). Furthermore, this ratio was higher in storage lipids (2.3-5.5) than in membrane lipids (1.3-1.5) in all three life stages. The two storage-associated marker FAs are metabolically more dynamic, and hence more likely to reflect dietary patterns during the sampling periods than the highly conserved membrane-associated marker FAs, which possibly still reflected in parts the trophic signal from autumn grazing (Stübing et al. 2003). This indicates that diatoms were a more important carbon source for krill during the weeks of our sampling than integrated over the months before.

Several Antarctic copepod species, including *Oithona* spp., *Metridia* spp., *Calanus propinquus* and *Calanoides acutus*, produce the long-chain FA isomers 20:1 and 22:1 *de novo* in large amounts, which can be used as carnivory marker FAs in omnivorous or carnivorous predators (Kattner et al. 1994; Cripps and Hill 1998; Ju and Harvey 2004).

The low levels of these FAs in all krill samples suggested that these copepods did not serve as major food source in the weeks before the sampling. It has to be considered, however, that the FAs 20:1n-9 and 22:1n-11 are largely egested with the krill's fecal pellets (Stübing et al. 2003, 2004). Therefore, the estimation of the absolute copepod-derived carbon uptake based on relative proportions of these FAs in the consumers can be difficult when they are metabolized quickly. Results from stomach analysis indicated that other copepod genera (*Stephos longipes*) were an important diet component at least during the hours and days of our sampling (Schaafsma et al., under review) (**Chapter IV**).



▲***Figure 3.*** *Ratios of diatom- versus dinoflagellate-associated marker fatty acids (FA) in krill (mean ± 1 standard deviation). The diatom-associated marker FA 16:1n-7 (FA_1) and the dinoflagellate-associated marker FA 18:4n-3 (FA_2) were considered storage FA (S). The diatom-associated marker FA 20:5n-3 (FA_1) and the dinoflagellate-associated marker FA 22:6n-3 (FA_2) were considered membrane FA (M).*

Quantification of carbon sources

Estimates of the proportional contribution of ice algal carbon α_{Ice} based on BSIA can be influenced by the varying metabolic fractionations of $\delta^{13}C$ in the different organic compounds, i.e. lipids, proteins and carbohydrates, of the bulk material (DeNiro and Epstein 1978; Kohlbach et al. 2016). In contrast, $\delta^{13}C$ values of trophic marker fatty acids are assumed to be unchanged by metabolic processes, and independent from the chemical composition of organisms (Kohlbach et al. 2016). CSIA allows estimating $\delta^{13}C$ in individual marker fatty acids to accurately trace and quantify sea ice-produced carbon in food webs (Wang et al. 2015; Kohlbach et al. 2016). Here, we applied for the first time both stable isotope methods to quantify the relative dependency of overwintering krill on ice algae-produced carbon.

In ice algae samples, the $\delta^{13}C$ values of the bulk algal material and the diatom-associated marker FAs (16:1n-7, 20:5n-3) were on average significantly higher by 5-6‰ compared to phytoplankton samples (**Table 5**). In the two dinoflagellate-associated marker FAs, significant differences in mean $\delta^{13}C$ values ranged between 9‰ (22:6n-3) and 14‰ (18:4n-3) (**Table 5**). Hence, in both algal communities, $\delta^{13}C$ from bulk material and marker fatty acids could be used to confidently discriminate between ice algae- and phytoplankton-associated carbon sources. The low variability of $\delta^{13}C$ values in bulk samples and fatty acids of ice algae and phytoplankton during the six-weeks sampling period of our study indicated that $\delta^{13}C$ values in krill were not significantly influenced by temporal changes in the isotopic signal of algal compounds (Graeve et al. 2005; Kohlbach et al. 2016).

▼**Table 5.** Bulk nitrogen ($\delta^{15}N$) and carbon stable isotope compositions ($\delta^{13}C$) and $\delta^{13}C$ compositions of marker fatty acids in ice algae and phytoplankton (mean ± 1 standard deviation ‰).

Stable isotope values	Ice algae	Phytoplankton	t-test *p**
BSIA			
n	15	7	
$\delta^{15}N$	4.1 ± 2.8	3.2 ± 3.0	ns
$\delta^{13}C$	-22.2 ± 4.3	-28.2 ± 0.5	**
CSIA			
n	14	6	
$\delta^{13}C$ 16:1n-7	-23.5 ± 5.8	-28.6 ± 3.0	*
$\delta^{13}C$ 18:4n-3	-31.1 ± 6.0	-44.6 ± 3.3	**
$\delta^{13}C$ 20:5n-3	-28.7 ± 3.1	-34.8 ± 2.5	**
$\delta^{13}C$ 22:6n-3	-23.5 ± 3.4	-32.7 ± 1.5	**

*t-test *p*: ns = $p > 0.05$; * $0.05 < p < 0.01$; ** $0.01 < p < 0.001$

In the krill samples, $\delta^{13}C$ values varied significantly between life stages (**Table 6**). In general, $\delta^{13}C$ values of bulk measurements and all marker fatty acids were significantly lower in adults than in younger stages (**Table 6**). BSIA-based mean proportions of ice algae-produced carbon α_{Ice} were 62% in larvae, 35% in juveniles, and 13% in adults (**Figure 4a**). This ontogenetic trend was also observed within juveniles. In BSIA measurements, krill in their first year < 25 mm had significantly higher bulk $\delta^{13}C$ values (-25.1 ± 0.7‰) than juveniles in their second year > 25 mm (-28.3 ± 1.7‰) (t-test t = 5.1, df = 8.6, $p < 0.001$). In a previous study, it has been suggested that krill transit from living in close proximity to the ice-water interface to living predominantly in the epipelagic zone when they reach a length of approximately 25 mm, which then supports the high variability in the utilization of ice algal carbon between younger juveniles < 25 mm (mean α_{Ice} = 59%) and older juveniles > 25 mm (mean α_{Ice} = 19%). In a recent study by Jia et al. (2016), bulk stable isotope data of krill collected from East Antarctica during two winter-spring transitions are compared. As found in our study, adult specimens had lower $\delta^{13}C$ values than larval and juvenile krill, suggesting that our observed ontogenetic trend of a higher utilization of ice algae carbon by younger krill is a rather common pattern in the different regions of the Southern Ocean. However, the extent of ice algal

carbon ingestion by larval krill was found to differ inter-annually, depending on sea ice properties and thus the accessibility of ice algae as a food source for krill, suggesting dietary flexibility of krill larvae during winter (Jia et al. 2016). The nitrogen stable isotope values δ^{15}N of krill (**Table 6**), which provide information on the trophic position of a consumer (Minagawa and Wada 1984), increased with ontogeny, suggesting a higher trophic level of adult versus larval and juvenile krill, which was well in agreement with previous studies (Hopkins and Torres 1989; Jia et al. 2016).

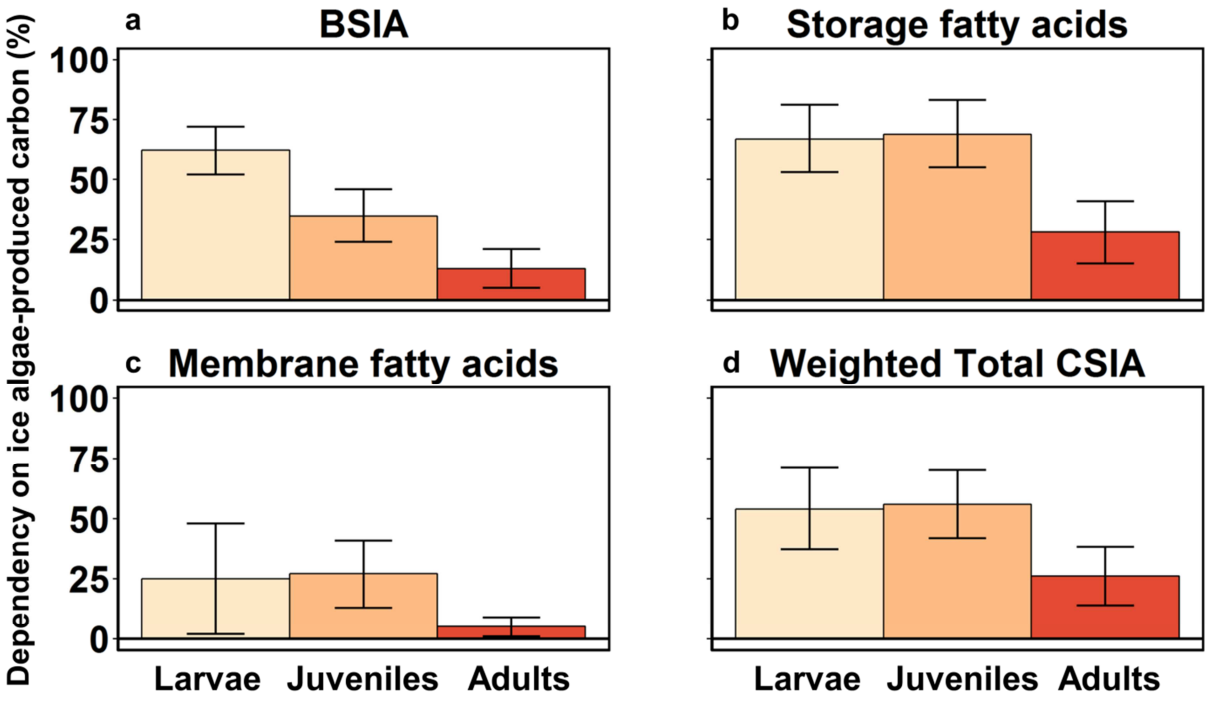
▼**Table 6.** Bulk nitrogen (δ^{15}N) and carbon stable isotope compositions (δ^{13}C) and δ^{13}C compositions of marker fatty acids in krill (mean ± 1 standard deviation ‰).

Stable isotope values	Larvae	Juveniles	Adults	ANOVA *p**
BSIA				
n	20	20	9	
δ^{15}N	3.5 ± 0.7	3.6 ± 0.6	4.4 ± 0.8	**
δ^{13}C	-24.8 ± 1.0	-26.4 ± 2.0	-28.7 ± 1.8	**
CSIA				
n	6	8	9	
δ^{13}C 16:1n-7	-30.6 ± 5.5	-32.9 ± 2.8	-38.6 ± 2.0	**
δ^{13}C 18:4n-3	-35.3 ± 2.7	-34.2 ± 1.5	-37.2 ± 0.8	*
δ^{13}C 20:5n-3	-30.9 ± 0.7	-32.0 ± 1.2	-35.9 ± 1.8	**
δ^{13}C 22:6n-3	-32.7 ± 0.9	-31.7 ± 1.5	-33.2 ± 0.8	*

*ANOVA p: ns = $p > 0.05$; * $0.05 < p < 0.01$; ** $0.01 < p < 0.001$

CSIA-based estimates of α_{Ice} were calculated separately for storage lipids and membrane lipids, integrating the trophic signal of both diatom- and dinoflagellate-associated marker fatty acids. In the CSIA-based mixing model using storage-associated FAs, mean α_{Ice} values were between 67% in larvae and 69% in juveniles, and 28% in adults (**Figure 4b**). Mean α_{Ice} values in membrane-associated FAs were considerably lower, with values between 25-27% in larvae and juveniles, and 5% in adults (**Figure 4c**). To account for the differences between storage lipids and membrane lipids in their relative contribution to lipid mass (**Figure 2**), we estimated the overall CSIA-based α_{Ice}, weighted by the proportional mass of the two lipid fractions in each life stage. As a result, the mean CSIA-based relative dependency on ice algae-produced carbon was 54% in larvae, 56% in juveniles, and 26% in adults (**Figure 4d**).

Both BSIA- and weighted CSIA-based estimates of α_{Ice} consistently showed an over 50% dependency on ice algae-produced carbon by larval krill, and a lower dependency in adults. In juveniles, differences between both approaches were likely driven by the lower δ^{13}C values of krill in their second year in the BSIA samples. CSIA-based estimates of α_{Ice} in membrane FAs probably retained in parts the trophic signal of pre-winter feeding, because these FAs are highly conserved and accumulated over long time periods (Stübing et al. 2003). Conversely, CSIA-based estimates of α_{Ice} in storage-associated FAs rather represented carbon sources during our sampling period, indicating that about two thirds of the carbon demand in larval and juvenile krill originated from ice algae in late winter. Our weighted CSIA-based estimate of α_{Ice} should therefore be considered as a conservative estimate.



▲***Figure 4.*** *Proportional contribution of ice algae-produced carbon (α_{Ice}) to the body carbon of krill (mean ± 1 standard deviation %). The BSIA-based estimates of α_{Ice} were shown in (a). The estimates in (b) and (c) were based on the stable isotope compositions of the storage fatty acids 16:1n-7 and 18:4n-3 (b), and the membrane fatty acids 20:5n-3 and 22:6n-3 (c) from CSIA measurements. The Weighted Total CSIA estimates of α_{Ice} (d) were weighted by the proportional mass of storage and membrane lipids in each life stage.*

δ^{13}C values in particulate organic matter can vary interanually, seasonally and regionally, ranging from -16 to -28‰ in ice-associated POM and from -25 to -31‰ in pelagic POM from the Weddell Sea (Rau et al. 1991b). In both algal communities, δ^{13}C from bulk material and marker fatty acids could be used to confidently discriminate between ice algae- and pelagic algae-associated carbon sources, with no overlap of the mean δ^{13}C values between sea ice –associated and pelagic algae. However, the fatty acid and stable isotope compositions varied considerably between ice algae from ice camp 1 and ice camp 2 (**Chapter V**). Such differences can occur due to variations in physical parameters, e.g. ice thickness, snow cover, and light intensity, subsequently affecting physiological processes in the ice algae. Calculating the proportional contribution of ice algal carbon for all krill samples with the ice algal isotopic signal from ice camp 1 resulted in mean α_{Ice} estimates of 69% in larvae, 72% in juveniles, and 54% in adults, based on the storage fatty acids 16:1n-7 and 18:4n-3. The potential bias introduced by calculating α_{Ice} using the ice algae δ^{13}C values from ice camp 2 for all samples, would have been larger, resulting in considerably lower estimates for all developmental stages (larvae: 54%, juveniles: 55%, adults: 44%).

Importance of ice algal carbon for overwintering

With a good agreement between both isotopic approaches, particularly in larval krill, this study demonstrates for the first time that up to two thirds of the carbon demand of

young krill during their first winter is covered from ice algae production. High abundances of young developmental stages of krill underneath ice floes suggested that feeding on sea ice biota is indeed important for their winter survival, but this behaviour may also be related to other factors, e.g. predator avoidance (Hamner et al. 1989; Meyer et al. 2009; Flores et al. 2012b; David et al. 2017). A high importance of ice algae in the diet was supported by analyses of stomach contents and fatty acid compositions, finding that diatoms were an important carbon source of young krill (Daly 1990; Schmidt et al. 2014). Stomach content and fatty acid analyses alone, however, cannot accurately discriminate between the signal of ice algae and phytoplankton, because these two communities overlap significantly in species composition (Stübing et al. 2003). Heterotrophic prey species sometimes also account for a significant part of the diet of krill (Perissinotto et al. 2000), but their link to ice algae as a carbon source is not always clear, because the trophic signal is diluted from one trophic level to another (Meyer et al. 2009; Schmidt et al. 2014). Overcoming the uncertainty of these well-established methods to reliably trace the trophic signal of ice algae, our isotopic biomarker approach provides quantitative evidence of a crucial dependency of larval krill on ice algae-produced carbon, integrated over several trophic levels.

A relatively low dependency of adult krill on ice algae-produced carbon in combination with a higher proportion of storage lipids (**Figure 2**, **Figure 4**) confirms the paradigm that adult krill survive the winter mainly by reducing metabolism and mobilising lipid reserves accumulated during summer and autumn (Meyer 2012). This assumption was supported by previous studies on the feeding behaviour of postlarval krill, reporting very low feeding rates (Morris and Priddle 1984; Quetin and Ross 1991) and no significant growth during austral winter (Kawaguchi et al. 1986; Siegel 1987). It was hypothesized that the size might be the criterion for exclusion of the larger krill to feed on sea ice algae, if they are unable to enter the narrow ice crevices (Atkinson et al. 2002). In adults and second-year juveniles, however, the signal of more recent ice algae-derived carbon uptake may have been buffered by their older and more modified lipid pool (Stübing et al. 2003). In our study, mean lipid contents in adults of 7% dry mass were at the low end of the typical range of 5-30% for winter and spring (Hagen et al. 1996; Ju and Harvey 2004), indicating that energy reserves were almost depleted. This suggests that ice algae-produced carbon could become critical for them to survive the late winter-spring period, as long as phytoplankton production remained low (Meyer 2012). Winter-feeding on sea ice biota by post-larval krill is corroborated by reported concentrations of juvenile and adult krill at the ice underside during winter and early spring (Marschall 1988; Flores et al. 2012b). Both in larvae and adults, however, our knowledge about the seasonal variability of their dependency on ice algae-produced carbon is still limited. Therefore, trans-seasonal studies on the role of ice algae in the carbon budget of krill are needed to pinpoint critical time periods for krill survival.

Krill are distributed throughout the Southern Ocean, extending over about 27 degrees of latitude, from coastal waters to deep-sea and from year-round ice-covered to virtually ice-free regions, and are adapted to survive a wide range of environmental conditions (Flores et al. 2012a). The dependency of overwintering larval and adult krill on ice

algae-produced carbon is therefore likely to vary regionally, and depend particularly on the duration of the sea ice season. A large part of the circum-Antarctic krill population (Atkinson et al. 2008) as well as major recruitment areas (Meyer 2012) and fishing grounds (Flores et al. 2012a) are found in the northern Weddell Sea. Stretching over a distance of approximately 900 km from west to east, our study area represented a major part of this key region of krill distribution and recruitment (**Figure 1**). The northern Weddell Sea has experienced a shortening of the sea ice season of about 10 days per decade between 1979 and 2006 (Flores et al. 2012a). When this trend continues, declining recruitment success, caused by reduced winter survival of larval krill, can be assumed to impact significantly on the overall krill biomass and the sustainability of the krill fishery. Besides, sea ice is also important to krill as physical shelter from predators (Hamner et al. 1989; Daly and MaCaulay 1991; Frazer et al. 2002).

In the Southern Ocean, climate change-related decline of sea ice and, consequently, ice algae production, may be balanced by an increase of overall phytoplankton productivity (Arrigo and Thomas 2004; Vancoppenolle et al. 2013). This could come at the cost of changes in phytoplankton composition towards taxa less supportive of krill, however , e.g. from diatoms to cryptophytes (Moline et al. 2004). Furthermore, as a result of a shorter sea ice season, enhanced light availability for phytoplankton growth may be counter-acted by deeper mixing due to increasing wind speeds in the future Southern Ocean (Lovenduski and Gruber 2005; Cai 2006). In the northern Weddell Sea, where this study was conducted and major krill stocks reside (Atkinson et al. 2008), chlorophyll *a* and pigment concentrations rarely exceed 0.1 mg m^{-3}, indicating near-zero phytoplankton production between April and August even in ice-free waters north of the ice edge (Comiso et al. 1993; David et al. 2017). Such low availability of phytoplankton during ice-free winters would suggest that a replenishment of up to two thirds of krill larvae's carbon demand, which is currently fulfilled by ice algae, by alternative carbon sources during winter is highly unlikely in a Southern Ocean with reduced sea ice coverage and duration. More importantly, sea ice preserves carbon in the form of ice algae and heterotrophic sea ice biota throughout the dark period, when even ice algae production is nearly zero (Arrigo and Thomas 2004). This carbon storage capacity will be reduced when delayed sea ice formation shortens the period for ice algal production before winter darkness (Arrigo and Thomas 2004). In conclusion, this study substantiates concerns with quantitative data that loss of ice algae habitat constitutes a serious threat to young overwintering krill. In regions of on-going or future sea ice decline, this could drastically affect the biomass and spatial distribution of krill populations. Due to their position as a key secondary producer in the Southern Ocean, changing krill populations could incur significant ramifications on the structure and biogeochemical cycling of Antarctic ecosystems (Schofield et al. 2010; Flores et al. 2012a).

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2.4 *Chapter IV*

Spatio-temporal variability in the winter diet of larval and juvenile Antarctic krill (*Euphausia superba*) in ice-covered waters

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Abstract

Antarctic krill *Euphausia superba* is an ecological key species in the Southern Ocean and a major fisheries resource. Due to the association of age class 0 (AC0) krill with sea ice and their need to feed during their first winter, the winter survival of AC0 krill is susceptible to changes in the sea-ice environment. However, our understanding of their overwintering diet is limited. We studied the spatio-temporal variability of AC0 krill diet during late winter using stomach content and fatty acid (FA) analysis. Stomach contents were dominated by diatoms in numbers and occasionally contained large volumes of copepods. Variability in stomach content composition was related to environmental factors including, chlorophyll *a* concentration, copepod prey abundance and sea-ice cover. In contrast, fatty acid composition was mainly related to the size composition of the krill. Seasonally changing environmental conditions were reflected in both the stomach contents and fatty acid composition of AC0 krill. Results show that overwintering AC0 krill are opportunistic feeders, with the ability to cover large parts of their carbon demand by predation. Additionally, availability of sea-ice derived food sources over a long period can significantly impact the fitness of developing AC0 krill. The spatio-temporal availability of sea-ice resources and advection pathways are, therefore, important predictors over AC0 krill over-winter survival.

Introduction

Due to the pronounced seasonality in the Polar Regions, polar species need to adapt to changes in primary production (Falk-Petersen et al. 1999; Hagen and Auel 2001). In winter, light limitation and water column mixing due to surface water cooling result in a long period of limited primary production, which can drop to nearly zero (Arrigo et al. 2008a). During the winter months, biota living in sea ice and at its underside can provide an important energy source (Eicken 1992; Quetin and Ross 2003; Flores et al. 2011, 2012b). In spring, primary production increases in the sea ice as well as in the water column. As the ice edge retreats, starting in September, a series of water column phytoplankton blooms occur (Quetin and Ross 1991; Lizotte 2001). In summer there is another peak in the water column primary production after which it starts to decrease towards winter (Quetin and Ross 1991; Lizotte 2001).

Adult Antarctic krill (*Euphausia superba*) release eggs from mid-December to April (Ross and Quetin 1986). The duration of the spawning season of krill and the number of spawning episodes that occur can be variable (Ross and Quetin 1986; Spiridonov 1995). Multiple spawning episodes increase the chance to produce larvae that reach the first feeding stage at a time when there is enough food available in the environment, since the timing and length of phytoplankton blooms are highly variable and unpredictable (Quetin and Ross 1991).

Adult *E. superba* overwinter by reducing metabolic activity in combination with opportunistic feeding and utilization of body lipids or body shrinkage (Ikeda and Dixon 1982; Meyer et al. 2010; Virtue et al. 2016). In contrast to adult krill, larvae are not able to survive long periods of starvation (Meyer et al. 2009; O'Brien et al. 2011) and the first winter is therefore considered a critical period for krill survival and recruitment (Quetin et al. 2003; Daly 2004). Krill larvae are assumed to rely on sea ice resources (Daly 1990; Meyer et al. 2002, 2012; Kohlbach et al., in preparation (**Chapter III**)), but in addition show flexible overwintering behaviour such as a delay of development, an increase of the inter-molt period, growth reduction and moderate lipid storage (Hagen et al. 2001; Daly 2004).

Krill larvae often reside directly underneath the sea ice in winter (Frazer et al. 2002; Meyer et al. 2009; Flores et al. 2012b; Schaafsma et al. 2016; David et al. 2017). Using a Surface and Under-Ice Trawl (SUIT; van Franeker et al. 2009), Schaafsma et al. (2016) conducted a large scale investigation of the krill population structure directly underneath the sea ice in the northern Weddell Sea, during the winter/early spring of 2013. The population mostly comprised larvae (furcilia) and juveniles experiencing their first winter, in the following referred to as age class 0 (AC0) krill. The AC0 krill population consisted of several cohorts, differing in size and developmental stage. The differences between these cohorts could have been caused by a dissimilar timing of spawning and/or different growth conditions due to variable environmental conditions encountered on differing advection paths (Quetin and Ross 2003; Schaafsma et al. 2016). Investigating the diet of AC0 krill can give insight in the survival through their first winter and therefore successful recruitment (Virtue et al. 2016). Due to the difficulty of sampling during winter, only a limited number of studies have been

conducted on the stomach contents of larval krill during this season (Daly 1990; Meyer et al. 2009; Schmidt et al. 2014), and food sources, and the determinants of variability in diet composition remain unclear.

The analysis of stomach content can provide essential information on the recent diet composition of a consumer. Combined with lipid and fatty acid (FA) compositions, it is possible to elucidate trophic interactions over larger temporal scales (Falk-Petersen et al. 1999; Dalsgaard et al. 2003; Kohlbach et al. 2016). Zooplankton lack the ability to biosynthesize certain FAs *de novo*. Since these specific FAs can only be produced by primary producers, they must be derived from dietary sources (Virtue et al. 2016). Such FAs are assumed to get transferred conservatively through the food web, and are therefore considered to be trophic markers (Graeve et al. 1994a; Kohlbach et al. 2016). Diatoms (Bacillariophyceae) produce high amounts of the FAs 16:1n-7 and 20:5n-3, while dinoflagellates (Dinophyceae) produce high amounts of the FAs 22:6n-3 and 18:4n-3 (Graeve et al. 1994a; Dalsgaard et al. 2003; Kohlbach et al. 2016). FAs 20:5n-3 and 22:6n-3 are mainly incorporated into polar lipids which are primarily used as structural components in membranes (Hagen et al. 2001), while 16:1n-7 and 18:4n-3 are mainly incorporated into storage lipids (Stübing et al. 2003).

Sea ice algae communities often have high proportions of diatoms compared to the underlying water column (Garrison 1991; Lizotte 2001; Søreide et al. 2010). Conversely, dinoflagellates are typically more abundant in the water column, compared to sea-ice communities (Garrison 1991; Lizotte et al. 2001; Søreide et al. 2010). The fatty acid composition of krill can therefore give some qualitative insight in the origin of dietary sources.

In this study, microscopic stomach content analysis and FA analysis were combined to gain insight into the diet and carbon sources and, subsequently, survival of *E. superba* during their first winter. The aim of this study was to evaluate temporal and spatial differences in diet of AC0 krill in late winter/onset of spring. Additional information was integrated such as the total FA content (% dry weight) and carbon/nitrogen content (C/N mass ratio), as indicators of the krill's lipid storage and body condition. Furthermore, the isotopic fractionation of carbon ($\delta^{13}C$) was investigated to confirm the source of the krill's carbon. Due to carbon limitation in the sea-ice environment, biomolecules synthesized by algae residing within the sea-ice often have a higher proportion of the heavy ^{13}C isotope over the ^{12}C isotope, compared to phytoplankton in the water column (Fry and Sherr 1984; Hecky and Hesslein 1995). The $\delta^{13}C$ values of sea ice derived carbon are therefore found to be higher compared to pelagic produced carbon (Jia et al. 2016; Kohlbach et al., in preparation (**Chapter III**)), which is transferred through the food web by direct and indirect ingestion. The isotopic composition of nitrogen ($\delta^{15}N$) was used as an indicator for trophic position (DeNiro and Epstein 1981; Minagawa and Wada 1984).

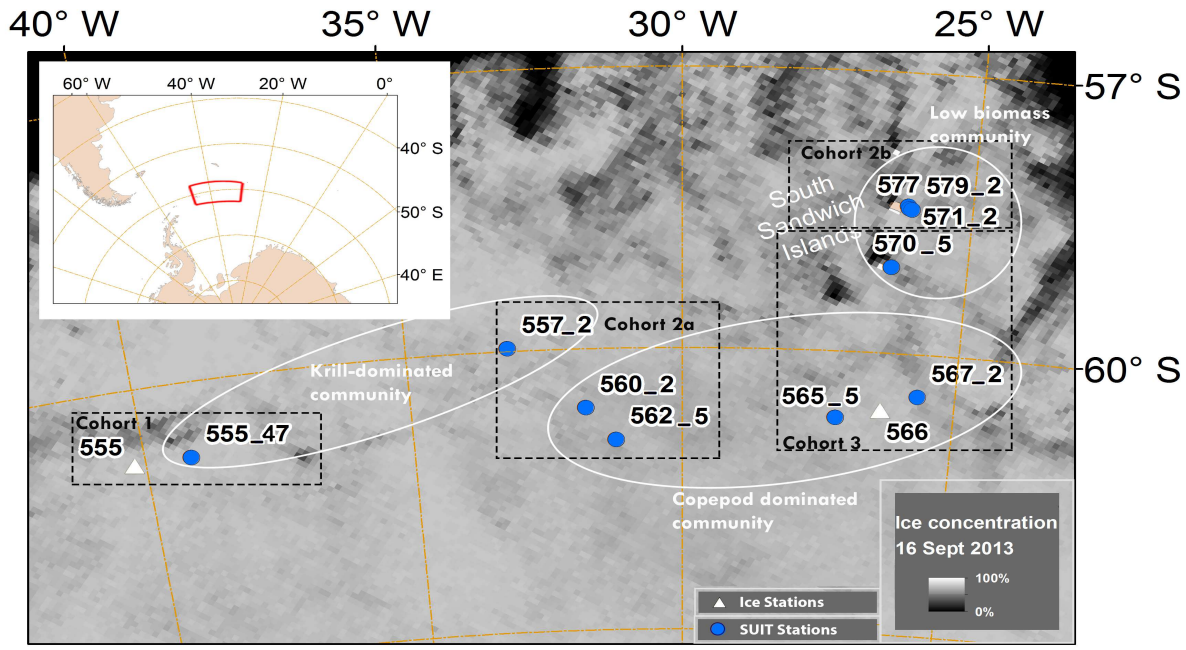
Specifically, the objectives of this study are to link the diet and FA composition to patterns in the zooplankton community as established by David et al. (2017), as a proxy for prey availability, and to investigate if the diet and FA composition follow patterns in the AC0 krill population structure. Regarding the latter objective we hypothesize that

body condition, size and development are determined by feeding history. The final objective of this study is to confirm the importance of (heterotrophic) sea ice biota in the winter diet on a relatively large spatio-temporal scale. To gain insights on the role of sea ice in the survival of AC0 krill, the effects of environmental parameters of the sea-ice habitat on stomach content and FAs were investigated.

Methods

Sampling and data collection

Sampling was performed in the northern Weddell Sea during RV Polarstern expedition PS81 (ANT-XXIX/7), between 24 August and 2 October 2013 (**Figure 1**).



▲***Figure 1.*** *Sampling locations of the SUIT, indicated with their station numbers. Sea ice concentration data were aquired on 16 September 2013. Round = SUIT hauls, triangles = stationary hauls during ice stations. Black dotted lines indicate the spatial pattern of size frequencies of age class 0 krill (Euphausia superba), as established in Schaafsma et al. (2016). Cohort numbers given to the stations with similar size frequencies of krill are indicated within the rectangle. White lines indicate the spatial pattern in the under-ice zooplankton community as established in David et al. (2017).*

The upper two meters of the water column directly underneath the sea ice was sampled using a Surface and Under Ice Trawl (SUIT, van Franeker et al. 2009). Environmental parameters, such as sea-ice concentration and thickness, and under-ice surface water temperature, salinity, and chlorophyll *a* concentration were measured during trawling using a sensor array attached in the frame of the SUIT, including an acoustic Doppler current profiler (Nortek, Aquadopp®, Norway) and a CTD probe (CTD75 M, Sea & Sun

technology, Germany) with connected altimeter (PA500/6-E, Tritech, UK). In addition, regional gridded sea ice concentrations during SUIT hauls were calculated from AMSR2 satellite data, which were acquired from the sea ice portal of the Alfred Wegener Institute (AWI, www.meereisportal.de), using the algorithm from Spreen et al. (2008). Ice floe size was estimated visually during SUIT hauls by an observer on deck. Detailed information on sampling and data collection can be found in Schaafsma et al. (2016) and David et al. (2017). Additional to trawling stations, krill were collected during sea-ice stations, by deploying the SUIT from the stationary ship in the current. *Euphausia superba* for stomach content analysis were directly preserved in a 4% hexamine-buffered formaldehyde-seawater solution. *E. superba* for C/N, fatty acid and bulk stable isotope analyses were immediately frozen at -80°C.

Stomach analysis

Prior to stomach content analysis, the preserved krill were weighed and total length (TL) was measured, to the nearest mm, from the anterior margin of the eye to the tip of the telson (Discovery method; Marr 1962). The developmental stage of furcilia larvae was determined according to Kirkwood (1982). Juveniles were distinguished from furcilia and other post-larval krill according to Fraser (1937) and Makarov & Denys (1981). A Discovery V8 stereomicroscope (Zeiss, Germany) was used for krill dissection. After removing the carapace, the stomach was taken out, transferred into a tube with 2 ml of deionized water and mixed using a vortex to break the stomachs. For each analytical sample, three stomachs abstracted from krill of comparable size were pooled together. The tube with the stomach contents was emptied into an Utermöhl sedimentation chamber, were it was left to settle for at least two hours (Schmidt et al. 2006). Identifiable prey items were counted on an Observer A1 microscope (Zeiss, Germany) at 400 x magnification in half of the counting receptacle. Rare prey items such as dinoflagellates, tintinnids, foraminiferans, radiolarians and copepod- or other zooplankton remains were enumerated in the complete receptacle at 200x magnification. Pieces of broken pennate and centric diatoms were measured in order to reconstruct the number of individual diatoms in the stomach, by dividing the average size of the complete surface area of intact diatoms with the average size of the measured pieces of that species found in the stomachs. For unidentifiable diatom pieces the average surface area of all intact diatoms was used (Garrison et al. 1987; Kang et al. 2001). The total biovolume of prey species or species group in the stomach was calculated by multiplying the number of individuals with the volume per individual from Archer et al. (1996) for dinoflagellates, Kang et al. (2001) for diatoms, Buck et al. (1992) for tintinnids and Gradinger (1999) for foraminifera. A minimum number of individual copepods per stomach was estimated on the basis of the numbers of appendages and mandibles found. The average volume of the copepods was reconstructed using the measured blade length of the mandibles found in the stomachs which were then converted into prosome length according to Karlson and Båmstedt (1994) and into body volume according to Mauchline (1998). Mandibles were not found in all stomachs containing zooplankton remains, therefore one average copepod volume was calculated

based on all mandibles found in all stomachs, which was then used for all volume calculations in all samples.

Lipid content and fatty acid analysis

The frozen individuals were freeze-dried for 24 h and the dry weights were determined gravimetrically. Lipids were extracted, with a method modified after Folch et al. (1957) using dichloromethane/methanol (2:1, v/v). The lipids were converted into fatty acid methyl esters (FAMEs) by transesterification in methanol, containing 3% sulphuric acid, at 50°C for 12 h. The FAMEs were extracted with hexane and analysed via gas chromatography. The FAMEs were identified with known standard mixtures. The total FA content and the percentage of individual FAs were quantified with an internal standard (23:0) added prior to lipid extraction. The proportions of the individual FAs were expressed as mass percentage of the total FAs. Details on the procedure and analytical equipment were reported in Kohlbach et al. (2016).

Carbon and nitrogen analysis

Krill samples for carbon and nitrogen analysis were freeze-dried for 24 h, and were mechanically homogenized prior to analyses. Up to five individuals were pooled into one sample in order to reach a minimum sample dry weight of 1 mg. Carbon and nitrogen were then analysed using a Carlo Erba CN analyser (HEKAtech GmbH, Germany).

Bulk stable isotope analysis (BSIA)

Bulk stable isotope compositions were determined with a continuous flow isotope ratio mass spectrometer Delta V Plus, interfaced with an elemental analyser (Flash EA 2000 Series) and connected via a Conflo IV Interface (Thermo Scientific Corporation, Germany). The isotopic ratios were expressed as parts per thousand (‰) in the delta notation, as deviation from the Vienna Pee Dee Belemnite standard for carbon measurements ($\delta^{13}C$), and atmospheric nitrogen for nitrogen measurements ($\delta^{15}N$). Verification of accuracy and precision of BSIA measurements was done by measuring the secondary reference material USGS41, provided by the International Atomic Energy Agency (IAEA, Vienna), which indicated errors as ± 0.8‰ for nitrogen and ± 0.5‰ for stable carbon measurements (representing ± 1 standard deviation of 17 analyses). Furthermore, the laboratory standards isoleucine and peptone were analysed every 5 samples (Sigma Aldrich), indicating errors of ± 0.3‰ for nitrogen and ± 0.6‰ for carbon isotope ratios of isoleucine (representing ± 1 standard deviation of 16 analyses) and ± 0.3‰ for both peptone measurements (representing ± 1 standard deviation of 8 analyses). For details on the verification of accuracy and precision of the BSIA measurements see Kohlbach et al. (2016).

Data analysis

The AC0 krill community was in general dominated by furcilia larvae in stage VI (FVI). The sampled population could be divided in three separate cohorts according to their

length distribution (Schaafsma et al 2016; **Table S1**, electronic supplement). The first cohort (station 555_47) was dominated by AC0 juveniles and contained a smaller proportion of FVI. The second cohort (stations 557_2 to 562_5 and 571_2 to 579_2) was dominated by FVI, with negligible amounts of other developmental stages. The third cohort was dominated by FVI, but also contained significant proportions of FV and FIV (stations 565_5 to 570_5; Fig. 1). In spite of the overlap in developmental stages between cohorts, the average length of the developmental stages differed between cohorts (Schaafsma et al. 2016; **Table S1**, electronic supplement). For example, FVI from cohort 1 and 2 were significantly larger than FVI from cohort 3 (Schaafsma et al. 2016). For this study, cohort 2 was split up into groups 2a and 2b. These krill represented AC0 krill of similar length and developmental stage, but were separated by hundreds of kilometres in space and weeks in time (**Figure 1**, **Table 1**). These four groups were used to investigate population-driven patterns in short- and long-term diet inferred from stomach contents, fatty acid composition, carbon and nitrogen content, and stable isotope composition.

▼**Table 1.** Sampling date, and parameters used for BioEnv analysis per station, including environmental parameters and abundances of dominant copepods from the ice-water interface layer.

Station nr.	Sampling date	Sea ice coverage (%)	Sea ice thickness	Sea ice roughness	Temperature (°C)	Salinity	Chl *a* (mg m^{-3})	*Calanus propinquus* (ind.m^{-3})	*Ctenocalanus* sp. (ind.m^{-3})	*Stephos longipes* (ind.m^{-3})
555_47	09-09-2013	99.5	0.475	3.734	-1.85	34.3	0.104	0.09	0.11	1.04
557_2	10-09-2013	94.0	0.700	0.833	-1.86	33.9	0.134	0.06	0.20	1.25
560_2	11-09-2013	96.0	0.525	1.030	-1.86	33.8	0.108	0.08	0.67	3.28
562_5	12-09-2013	92.5	0.525	0.969	-1.86	33.8	0.097	0.47	1.75	6.63
565_5	16-09-2013	96.5	0.525	2.297	-1.87	34.2	0.103	0.46	1.33	0.79
567_2	28-09-2013	86.5	0.675	1.148	-1.88	33.6	0.204	1.19	4.66	0.07
570_5	29-09-2013	96.0	0.425	0.853	-1.86	33.9	0.223	0.30	0.03	0.02
571_2	30-09-2013	84.0	0.225	0.829	-1.84	34.1	0.165	0.07	0.02	0.07
577_2	02-10-2013	51.5	0.475	1.207	-1.84	33.7	0.164	0.01	0.00	0.01
579_2	02-10-2013	46.0	0.575	1.504	-1.83	34.1	0.275	0.03	0.00	0.06

An analysis of the community structure of under-ice fauna in the sampling area suggested the presence of three distinctive community types, differing in the numerical and biomass composition of abundant taxa (David et al. 2017; **Figure 1**). The first community type ('krill dominated'; stations 555_47 to 557_2) was dominated by krill in terms of proportional biomass, but overall species abundances and biomasses were relatively low. The second community type ('copepod dominated'; stations 560_2 to 567_2) had high species abundances and biomasses, and was largely dominated by copepods. The third community type, comprising stations close to the sea-ice edge ('low biomass'; stations 570_5 to 579_2) was characterized by both low species abundance and low total biomass (David et al. 2017). This grouping of community types was used to investigate community-driven patterns in short- and long-term diet.

To investigate the influence of the sea-ice environment on the krill diet variability between stations, the effect of all possible combinations of measured environmental variables on the average stomach content per station was analysed using a BioEnv analysis (Clarke and Ainsworth 1993), in order to estimate the subset of environmental variables that has the highest correlation with the stomach content. The BioEnv analysis relates two distance matrices, the environmental data based on Euclidean distance and the stomach content data on Bray-Curtis dissimilarity (Clarke and Warwick 2001). Environmental variables used are listed in **Table 1**. The density of the most abundant copepod species (*Stephos longipes*, *Ctenocalanus* sp. and *Calanus propinquus*) in the under-ice surface layer were added as parameters to investigate the effect of copepods as an available food source (David et al. 2017). Stomach content, expressed as abundance as well as volume, were 4th root transformed to obtain near-normal distribution of the data assumed by the test. After data assessment using a draftsman plot, environmental data was log transformed. Only sea-ice thickness and sea-ice concentration were squared and temperature was untransformed. After data transformation, the environmental data was normalised to obtain a consistent scale by, for each parameter, subtracting the mean value and dividing by the standard deviation over all samples of that parameter. This ensures equal variances of all used parameters and therefore equal importance in the analysis (Clarke and Warwick 2001). A Mantel test was used to test the significance of the association of the environmental variables selected with BioEnv with the stomach content data using Spearman's correlation. The significance of Mantel test correlations was assessed with a bootstrapping procedure using 999 iterations.

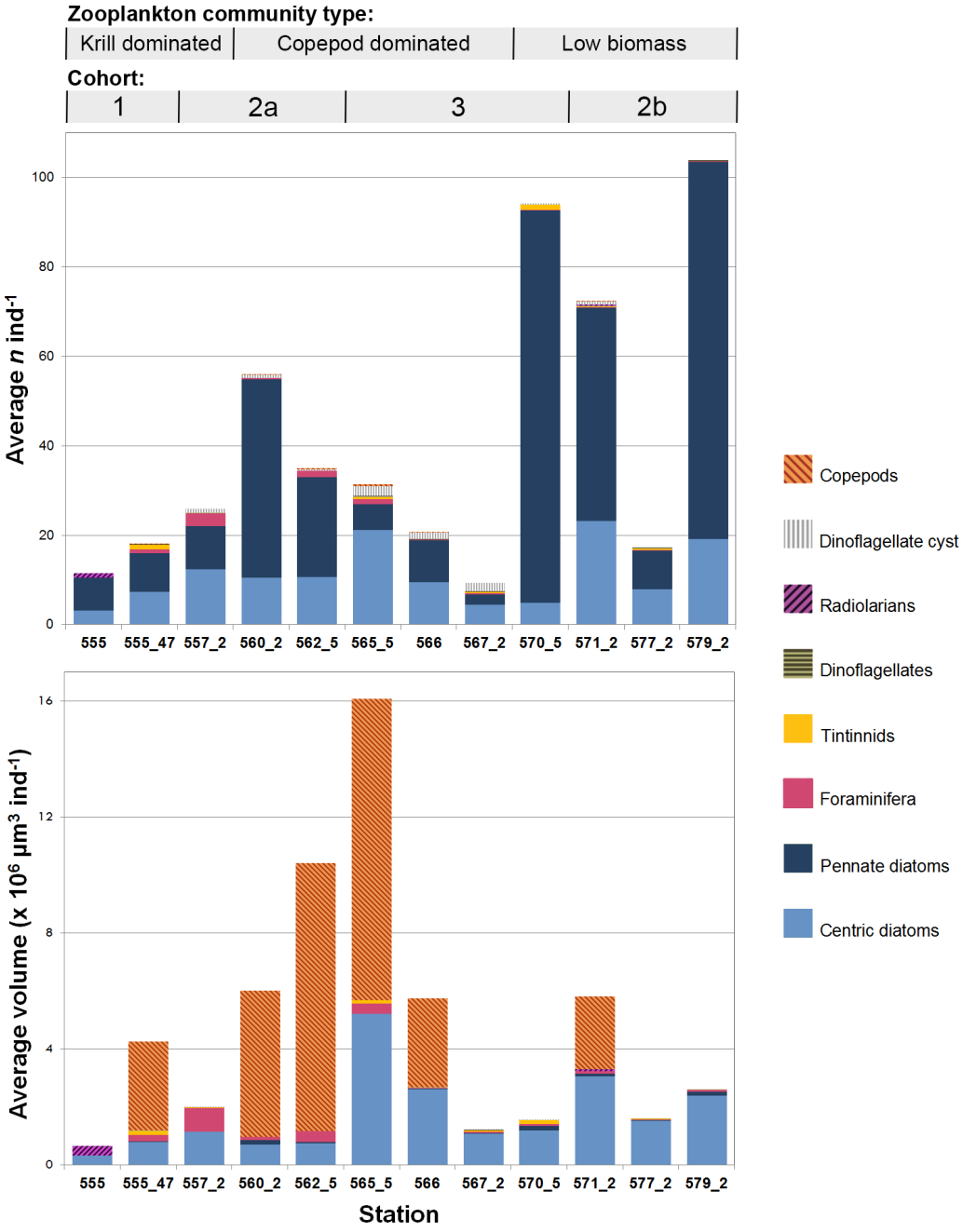
Differences between fatty acid compositions were assessed using a Principle Components Analysis (PCA), including all fatty acids that contributed more than 1% to the total amount of the krill's fatty acids. Proportions of FAs were 4th root transformed to increase importance of FAs that generally occur in low proportions (Clarke and Warwick 2001). To test whether stomach contents differed between cohort groups or community types, a multivariate generalized linear model (GLM) was used. Unlike distance-based methods, this approach does not vary in detection of between-group differences depending on variance, which increases with increasing abundance (Warton et al. 2012). Differences were assessed using 999 bootstrapping iterations.

Untransformed abundance data was used and a negative binomial distribution of data was assumed (Wang et al. 2012; Warton et al. 2012). The model assumptions of a multivariate GLM are violated when used on proportional FA data (Wang et al. 2012; Warton et al. 2012). Therefore, differences in FA composition between cohorts and community types were tested with a distance based analysis of similarities (ANOSIM), using transformed data and a Euclidean distance matrix (Clarke and Warwick 2001). Only a single AC0 krill was sampled for FA analysis from cohort 1. Therefore this cohort was excluded from all FA data analysis.
Differences in C/N ratios and bulk stable isotope compositions between cohort groups and community types were investigated using one-way ANOVA. Differences between groups were further assessed using the Tukey's HSD post hoc test. Assumptions of ANOVA were violated when assessing differences in the proportions of marker fatty acids between different groups. Therefore, a Kruskal-Wallis non-parametric test was used followed by a Dunn's test, with Bonferroni correction for multiple testing, to further investigate between group differences. All analyses were performed using R version 3.3.1, with packages vegan, ade4, ggplot2 and mvabund (R Core Team 2015). Numbers and properties of krill used for the different analyses can be found in **Tables S2** and **S3** of the electronic supplement.

Results

Stomach content analysis

Overall, the diet of AC0 krill was dominated, on average, by centric (35%) and pennate (56%) diatoms in abundance, and centric diatoms (52%) and copepods (33%) in volume (**Figure 2**). The numbers of pennate diatoms in the stomachs were considerably higher in the northernmost stations compared to all other stations (**Figure 2**, **Table 2**). Not all diatoms could be identified to species level. The pennate diatoms were dominated by species of the genus *Fragillariopsis*. Identifiable species were *Fragillariopsis curta*, *F. kerguelensis*, *F. obliquecostata* and *F. ritscheri*. Identifiable species of centric diatoms were *Actinocyclus actinochilus*, *Stellarima microtrias*, *Thalassiosira tumida*, *Thalassiosira* spp. and *Coscinodiscus* spp. *Eucampia antarctica*, *Asteromphalus* spp. and *Rizosolenia* sp. were encountered occasionally. *A. actinochilus* often represented a large part of the total reconstructed number of diatoms (over 50% in stations 555_47 – 560_2, and over 30% in stations 570_5-579_2).



▲***Figure 2.*** *Average stomach contents of age class 0 krill (Euphausia superba) per station, shown in numbers per individual krill (A) and volume of food items per individual krill (B). The bars above the graphs show how the sampled stations were grouped in under-ice surface zooplankton community type or age class 0 krill cohorts, according to David et al. (2017) and Schaafsma et al. (2016), respectively.*

Copepod appendages and mandibles that could be identified belonged to *Stephos longipes*. Copepod prosome lengths reconstructed from mandible width ranged between 0.61 and 0.85 mm. Other prey items regularly found in the stomachs were the foraminifer *Neogloboquadrina pachyderma*, the tintinnids *Laackmanniella naviculaefera*, *Cymatocylis convallaria*, *Cymatocylis vanhoeffeni* and *Codonellopsis glacialis*, and dinoflagellate cysts. Dinoflagellates were found in small numbers, some identifiable as

Protoperidinium sp. and *Dinophysis* sp. Krill setae and radiolarians were found sporadically.

There were no significant differences in stomach content between cohorts (GLM, LR = 32.83, $p > 0.05$). Differences in stomach content were found to be partially related to community types and depending on environmental factors. Using the three community types established by David et al. (2017) as station grouping factor, a significant difference was found between the stomach contents of krill from the low biomass community at the sea-ice edge and of krill from the copepod-dominated community at the centre of the sampling area (GLM, LR = 18.44, $p = 0.038$). At the centre of the sampling area copepods also dominated the stomach content of krill in terms of volume (**Figure 2**, **Table 2**).

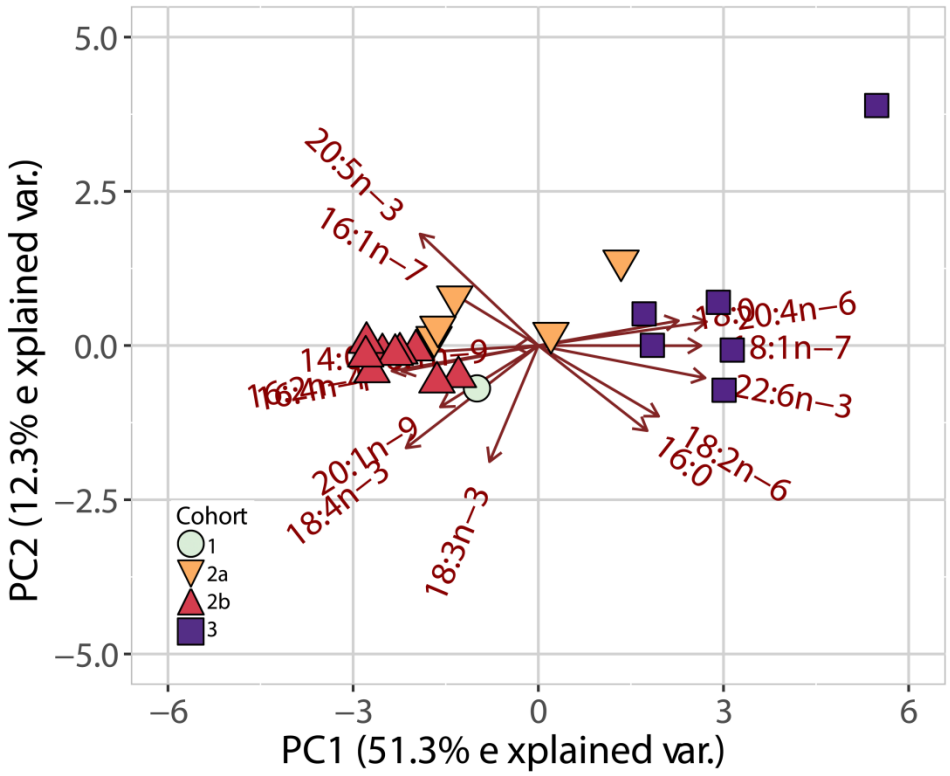
▼**Table 2.** Stomach contents of AC0 krill (*Euphausia superba*) per under-ice zooplankton community type as established in David et al. (2017). K = krill dominated community, C = copepod dominated community, L = low biomass community. *n* = number of individuals analysed, + represents a volume < 0.001 x 10^6 m^3 ind^{-1}.

Community type	**K** (*n* =19)	**C** (*n* =43)	**L** (*n* =35)
Average number (ind^{-1})			
Centric diatoms	9.45	10.97	15.02
Pennate diatoms	9.04	17.98	53.88
Foraminifera	1.74	0.58	0.2
Tintinnids	0.53	0.14	0.31
Dinoflagellates	0.16	0.12	0.2
Radiolarians	0.05	0	0.06
Dinoflagellate cysts	0.42	1.33	0.29
Unidentified round body < 20 µm	6.53	4.28	2.71
Copepods	0.05	1.05	0.34
Krill setae	1.15	0.67	1.26
Average volume (x 10^6 m^3 ind^{-1})			
Centric diatoms	2.91	3.38	4.63
Pennate diatoms	0.02	0.04	0.11
Foraminifera	0.49	0.16	0.06
Tintinnids	0.11	0.03	0
Dinoflagellates	+	+	+
Radiolarians	0.02	0	0.02
Dinoflagellate cysts	+	+	+
Unidentified round body < 20 µm	+	+	+
Copepods	1.46	5.16	0.79
Total volume (excluding krill setae)	*5.01*	*8.78*	*5.68*

BioEnv analysis showed that the numerical composition of identifiable prey items was correlated to a combination of under-ice surface chlorophyll *a* concentration, sea-ice coverage, under-ice surface salinity and the abundance of *Stephos longipes* in the ice-water interface layer (r = 0.47; Mantel test p = 0.005). Similarly, the volumetric composition of identifiable prey items in the stomach was best correlated with the under-ice surface abundance of *S. longipes* and under-ice surface chlorophyll *a* concentration (r = 0.58; Mantel test p = 0.008).

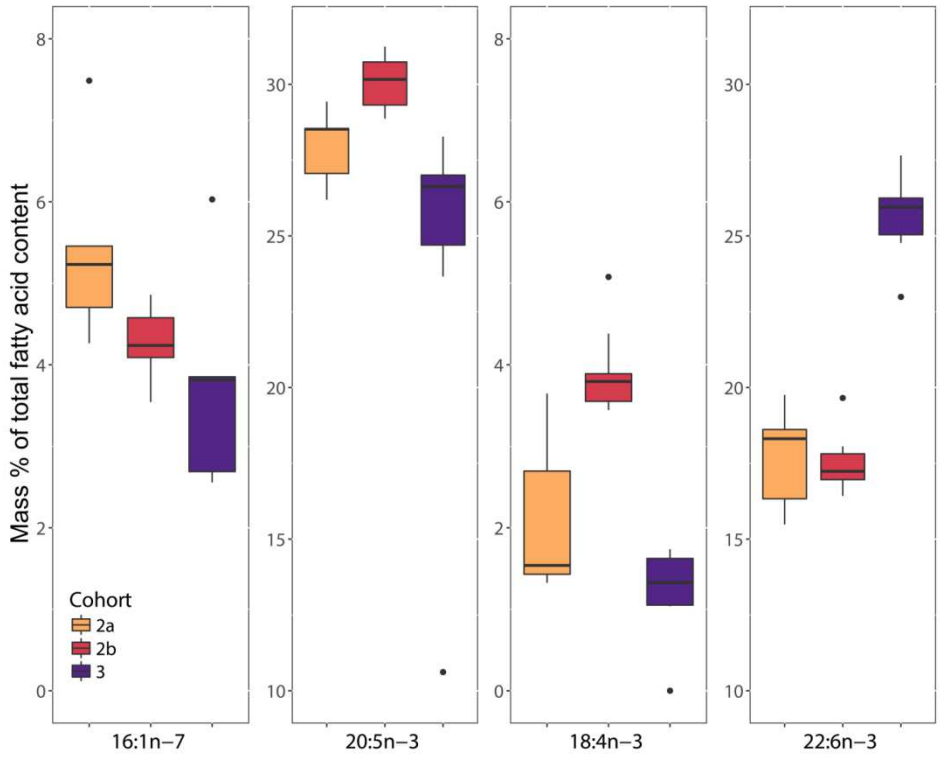
Fatty acid analysis

Using ANOSIM, a significant difference between FA profiles was found when grouped according to cohorts (R = 0.42, p = 0.001), but none when grouped according to community types. This was confirmed by the PCA analysis (**Figure 3**). The first three principal components (PCs) of the PCA analysis accounted for 74.8% of the variance between the cohorts. The first PC explained 51.3% of the variability, separating cohort 3 from the other cohorts. The FAs 14:0, 16:2n-4, 20:4n-6 and 20:5n-3 contributed most to the variability in the data. PCs 2 and 3, explaining 12.3% and 11.2% of the variability, respectively, separated cohorts 2a and 2b from each other (**Figure 3**; PC 3 not presented).



▲***Figure 3.*** *Results of a principle component analysis (PCA) using fatty acid profiles of different cohorts of age class 0 krill (Euphausia superba), showing the first and second principal components.*

Following the results of the previous analysis, four biomarker FAs were compared between cohorts (**Figure 4**). In cohort 3, the relative contribution of the diatom-associated marker FA 16:1n-7 was significantly lower compared to cohort 2a (KW, H_2 = 8.74, p = 0.01; Dunn's test, p < 0.005), and the diatom-associated biomarker FA 20:5n-3 was significantly lower compared to cohort 2b (KW, H_2 = 14.33, p < 0.0001; Dunn's test, p = 0.0003). Conversely, the dinoflagellate-associated biomarker FA 22:6n-3 was significantly higher in cohort 3 compared to the other cohorts (KW, H_2 = 28.58, p = 0.001; Dunn's test, p < 0.009). The dinoflagellate biomarker FA 18:4n-3 was significantly higher in cohort 2b compared to cohorts 2a and 3 (KW, H_2 = 13.90, p < 0.0001, Dunn's test, p < 0.02).



▲***Figure 4.*** *Proportion of biomarker fatty acids (mass % of total FA) of age class 0 krill (Euphausia superba). Cohorts are defined as in figure 1. Fatty acids 16:1n-7 and 20:5n-3 are regarded as diatoms-associated markers, 18:4n-3 and 22:6n-3 are regarded as dinoflagellate-associated markers. The horizontal black lines show the median FA proportion in a cohort. The upper and lower limits of the coloured squares indicated the 25th and 75th ‰. The upper and lower limits of the vertical line indicate the minimum and maximum FA proportion in a cohort. Black dots represent the true minimum and maximum FA proportion, but are numerically distant from the other data points and therefore considered outliers.*

Body condition

The C/N ratios of AC0 krill ranged between 3.38 and 4.10 (**Table 3**). There was a significant difference between the C/N ratio of the krill from the 'copepod dominated' community type with krill from the other community types (ANOVA, $F_{2, 24}$ = 10.81, p < 0.0001; Tukey HSD, p < 0.004). Further analysis, however, indicated that these

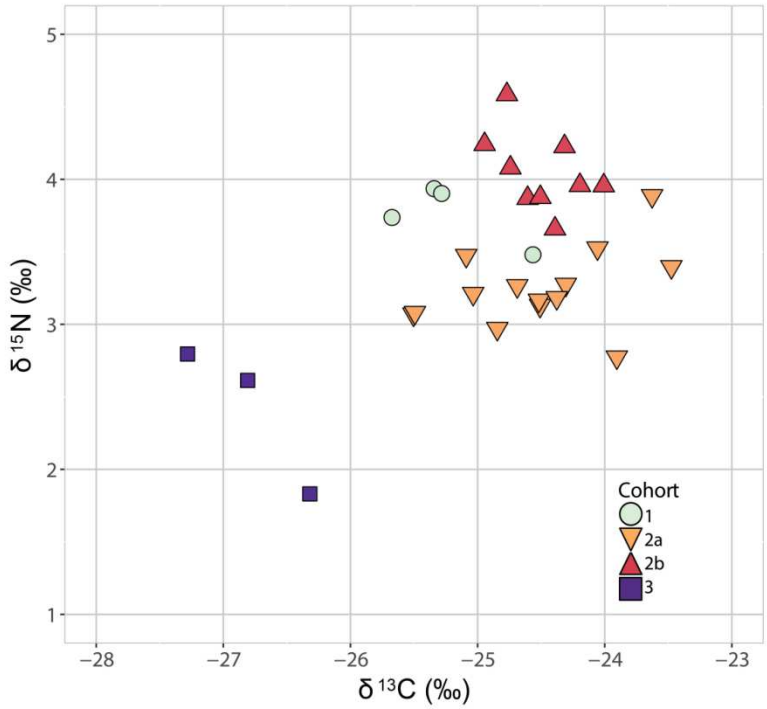
differences could be more robustly explained by differences between cohort groups. C/N ratios of AC0 krill differed significantly between all four cohort groups (ANOVA, $F_{3,23}$ = 26.6, p < 0.0001; Tukey HSD, p > 0.04), decreasing from cohort 1 to cohort 3. The individuals of cohort 2 showed a difference in C/N ratio between sampling regions, with cohort 2b being significantly higher than cohort 2a. A similar pattern was found in the total FA content of the AC0 krill (**Table 3**). There were, however, no significant differences in total FA content between cohort groups.

▼**Table 3.** Carbon content, nitrogen content, C/N ratio and total fatty acid content (standard deviation within brackets) of AC0 krill (*Euphausia superba*) per cohort.

Cohort	Carbon content (% of dry mass)	Nitrogen content (% of dry mass)	C/N ratio	Total FA content (% of dry mass)
1	40.60 (0.64)	10.12 (0.27)	4.01 (0.07)	NA
2a	39.06 (1.13)	10.59 (0.40)	3.69 (0.07)	12.48 (11.81)
2b	39.32 (1.06)	10.20 (0.21)	3.86 (0.09)	19.50 (14.55)
3	34.61 (1.00)	9.81 (0.19)	3.53 (0.10)	2.63 (2.09)

Bulk stable isotope composition

The δ^{15}N value of AC0 krill different significantly when grouped according to community types as well as cohorts. Again, further analysis indicated that the cohort grouping explained the differences more robustly. Apart from cohort 1 vs. cohort 2b, δ^{15}N values differed significantly between cohorts (**Figure 5**; ANOVA, $F_{3, 26}$ = 29.47, p = < 0.0001; Tukey HSD, p < 0.02). The average δ^{15}N value in cohort 3 (2.41) was lowest. In this cohort, δ^{15}N values did not exceed 3. The average δ^{15}N values of cohort 1 (3.72) and 2b (4.05) were somewhat higher than in cohort 2a (3.24; **Figure 5**). The δ^{13}C value of krill from cohort 3 differed significantly from all other cohorts (ANOVA, $F_{3,26}$ = 17.92, p < 0.001, Tukey HSD, p < 0.003). The δ^{13}C values of cohort 3 (average -26.8) were in general considerably lower than all values of cohort groups 1, 2a and 2b (average -25.1, -24.5, -24.5, respectively). The δ^{13}C values did not show significant differences when the krill was grouped according to community type.



▲***Figure 5.*** *Bulk stable isotope values of age class 0 krill (Euphausia superba) per cohort. Cohorts are defined as in* ***Figure 1****.*

Discussion

Stomach contents of AC0 krill in winter/early spring

The stomach contents of AC0 krill showed a variable diet in terms of taxonomic composition. Our findings were similar to those reported in winter studies conducted in the Weddell-Scotia Confluence (Daly 1990) and in the Lazarev Sea (Meyer et al. 2009). In those areas, the diet of larvae was numerically dominated by pennate diatoms, in particular *Fragillariopsis* spp., and had a heterotrophic component consisting of dinoflagellates, dinoflagellate cysts, foraminifera, tintinnids, copepod appendages and krill setae (Daly 1990; Meyer et al. 2009). Although the stomach content of AC0 krill from our study had similar autotrophic and heterotrophic proportions compared to the larvae from the Lazarev Sea, the total volume of food in the stomachs of our study was higher (Meyer et al. 2009). Aforementioned studies concluded that heterotrophic organisms are important food items for larvae and AC0 juveniles in winter. This is consistent with our findings, although the scale of our study enables us to show that the degree of utilization of this food source varies within a region and is dependent on environmental factors. The importance of heterotrophic taxa in the diet may further be under-estimated by stomach content analysis, because soft-bodied organisms such as flagellates, ciliates and turbellarians are easily digested and therefore unlikely to be found in the stomachs of the AC0 krill (Meyer et al. 2009). Studies suggest that detritus may provide an additional food source for furcilia (Daly 1990; Ju and Harvey 2004), but no further analysis was done on unidentifiable stomach items during this study. Krill

setae found in the stomachs most likely originated from moults, as no other body parts such as eye fragments were found (Meyer et al. 2009).

Many of the identified species in the krill stomachs of our study were sea-ice associated species. *Actinocyclys actinochilus* has been found in higher abundances within sea ice compared to the underlying water column (Armand et al. 2005). *Fragillariopsis* spp. such as *F. curta* and *F. cylindrus* often dominate the sea- ice algal assemblage (Nöthig et al. 1991; Garrison and Close 1993; Ugalde et al. 2016). Dinoflagellate cysts can be abundant in the sea ice and it has been proposed that sea ice is an overwintering site for resting or dormant stages (Garrison and Buck 1989). In winter/early spring, the copepod species *Stephos longipes* resides in the upper layers of the water column, but highest abundances of juvenile and adult *S. longipes* were found in the sea ice (Schnack-Schiel et al. 1995). *S. longipes* is known to migrate actively between the water column and the sea-ice habitats, and the presence of this copepod in the water column is found to be concomitant with their presence in the sea ice above (Wallis et al. 2016). The high proportional contribution of sea ice-associated species found in the stomachs of AC0 krill suggests that they were largely relying on sea ice-associated prey during winter.

Differences in stomach content could not be attributed to cohort groups and were rather related to environmental factors, such as under-ice surface chlorophyll *a* concentration and the abundance of copepods present, and to sea-ice concentration and under-ice surface water salinity. Stomach contents of AC0 krill in the central part of the study area were dominated in volume by copepods. At these stations, the highest abundance of copepods was found in the ice-water interface layer dominated by *S. longipes* and *Ctenocalanus* sp. (David et al. 2017). Furthermore, the zooplankton community in the ice-water interface was characterized by a high biomass, attributed to high numbers of amphipods, pteropods, chaetognaths and ctenophores, indicating a diverse heterotrophic food web (David et al. 2017). Exceptionally, the stomach content of AC0 krill from station 567_2 had a small total volume and no copepods were found in the krill stomachs even though they were abundant in the water column (David et al. 2017).

In the four northernmost stations, situated in relatively close proximity to the sea-ice edge, stomach contents had a low volume of copepods and a higher abundance of pennate diatoms, although these diatoms contributed little to the total volume of the stomach content. The under-ice zooplankton community structure at these stations was characterized by low abundances and biomass of zooplankton species compared to the rest of the sampling area. These stations were further characterised by higher under-ice surface chlorophyll *a* concentrations, and decreased ice floe size compared to the stations in the rest of the samling area. The last two stations also had lower sea-ice concentrations (David et al. 2017). This suggests that the sea ice had started to melt. Increased numbers of diatoms in the water column could be a result of a sea-ice edge bloom (Quetin and Ross 1991; Bianchi et al. 1992). Ackley et al. (1979) indicated that sea-ice algae and other in-ice fauna are not released into underlying water through direct melting in a single pulse, but that there is more likely a constant release occurring along the sea ice edge, where floes deteriorate through erosion by wind and waves. The increase in pennate diatoms in the stomach contents of AC0 krill is therefore likely a

result of residing closer to the sea-ice edge where the sea ice started to release its contents, and/or a phytoplankton bloom initiated. Alternatively, it is possible that sea-ice algae became more easily accessible as the sea ice began to soften and become more porous due to melt (Quetin et al. 2003).
Findings suggest that the diet of AC0 krill is a reflection of the food available and accessible in the environment. Therefore, seasonal and biogeographical patterns in food availability govern the diet of AC0 krill on the short term. Food availability, in turn, is dependent on environmental factors driven by the sea-ice, which can be the properties of the sea ice itself, but also effects caused by changes in the sea ice such as the increase in chlorophyll *a* concentration in the water column due to sea-ice melt.

Fatty acid and stable isotope composition

The FAs of all AC0 krill were dominated by 16:0, 20:5n-3 and 22:6n-3, similar to larval krill from East Antarctica (Virtue et al. 2016) and the Lazarev Sea (Hagen et al. 2001) in winter/early spring, and the western Antarctic Peninsula in winter (Ju and Harvey 2004). The polyunsaturated FAs 20:5n-3 and 22:6n-3 are mainly incorporated in phospholipids, which usually represent biomembrane components. The phospholipid phosphatidylcholine (PC), however, serves as a storage lipid for *Euphausia superba* (Hagen et al. 1996), and was the most dominant lipid class found in the AC0 krill from our study, explaining the high proportions of 20:5n-3 and 22:6n-3 (Kohlbach et al., in preparation) (**Chapter III**).
FA and lipid signatures may reflect different sources and, in omnivorous species, ingestion of both phytoplankton and zooplankton, which can complicate the interpretation of trophic relationships (Mayzaud et al. 1999; Auel et al. 2002; Dalsgaard et al. 2003). Also, the time scales for incorporation of different FAs into tissues as well as their turnover rate are often not well defined (Dalsgaard et al. 2003). Therefore, the results on the proportions of carbon, nitrogen, bulk stable isotopes and FAs of individual krill at any point in time is a reflection of integrated conditions over a period of days to months prior to collection (Daly 2004; Graeve et al. 2005; Töbe et al. 2010). Additionally, it must be considered that the relative fatty acid composition can depend on total lipid content (Stübing et al. 2003). The FA content of larvae and AC0 juveniles from our study was highly variable between individuals, which Virtue et al. (2016) previously attributed to the patchiness of the available food.
Differences in FA composition of AC0 krill were largely related to size and developmental stage reflecting the diets over a longer time span (Graeve et al. 1994a; Schmidt et al. 2006). The FA composition of furcilia has been shown to be markedly influenced by their food composition (Stübing et al. 2003). Therefore, the different fatty acid profiles as distinguished by the PCA, indicate that the dietary history of the various cohort groups was distinct.
Cohort 3 had relatively low proportions of the diatom-associated marker FAs 16:1n-7 and 20:5n-3, indicating that diatoms had a lower contribution to the diet in this cohort (Reiss et al. 2015; Virtue et al. 2016). Additionally, the krill from cohort 3 also had lower amounts of the FA 16:4n-1 which has also been found to be an important FA for diatoms

(Dalsgaard 2003). A higher contribution of dinoflagellates was confirmed by the dinoflagellate associated marker FA 22:6n-3. The FA 22:6n-3 is essential for the structure of biomembranes and is efficiently retained in body tissue (Stübing et al. 2003). The relatively high amount of FA 22:6n-3 in the krill of cohort 3 could be a result of their relative high proportion of PC compared to other cohorts (Kohlbach et al, in preparation) (**Chapter III**). However, FA 20:5n-3, which is also mainly incorporated in phospholipids, was lowest in the krill of cohort 3. Therefore, as it is known that FA 22:6n-3 accumulates when it is abundant in the diet (Schmidt et al 2006), it is an indication that AC0 krill from cohort 3 had fed more extensively on dinoflagellates in the further past compared to the other cohort groups. Conversely, the relatively low proportion of dinoflagellate-associated marker FA 18:4n-3 in cohort 3 indicates that dinoflagellates were less important in the more recent period before the sampling, because this FA metabolizes rapidly, and therefore decreases when not replaced by dietary input (Stübing et al. 2003). From fatty acids biomarkers and relatively low $\delta^{15}N$ it appears that AC0 krill from cohort 3 were feeding predominantly herbivorous in the past, and the proportion of dinoflagellates in the diet was larger compared to the other cohorts. This suggests that feeding in the further past occurred for a larger part on water column resources, based on the larger proportion of dinoflagellates often residing in the water column as opposed to the sea ice (Garrison 1991; Lizotte et al. 2001). This is supported by relatively low $\delta^{13}C$ values that also indicate less feeding on sea-ice resources and/or advection from another water mass. The relatively small size and lower C/N ratio of cohort 3, compared to the other cohort groups, strongly suggest advection through regions with poor food availability. In conclusion, it seems that cohort 3 did not encounter resource-rich sea ice during the winter months, which led to a bad condition and slow growth and/or development.

Larger juvenile krill from cohort 1 were in good condition despite low stomach content volume, indicating that rapid development to the juvenile stage may be advantageous for survival (Feinberg et al. 2006). These findings also support the idea that the ability to withstand poor food conditions increases with age (Daly 2004).

Despite their similar size and developmental stage, cohort 2b, residing close to the sea-ice edge, showed a higher proportion of dinoflagellate biomarker 18:4n-3 than cohort 2a, which could therefore reflect a regional difference in feeding conditions rather than an ontogenetic one. The relatively high proportion of this marker FA in cohort 2b suggests a relative increase in feeding on dinoflagellates at the end of the sampling season, while stomach contents suggest an increased feeding on diatoms. Although low numbers of dinoflagellates were found in the stomach of these krill, it is possible that they were feeding on athecate (naked) dinoflagellates which are easily digested. Increased feeding on athecate dinoflagellates could be a result of shifting feeding from sea-ice resources to pelagic resources at the onset of spring. The subsequent increase in feeding on diatoms, based on stomach contents analysis, could be a result of melting sea-ice, releasing its content into the water column. The average diatom biomarker FA 16:1n-7 proportion of cohort 2b, which was not higher than that of the other cohort groups, suggest that increased feeding on diatoms occurred more recent than increased

feeding on dinoflagellates. The krill from region 2b had a higher C/N ratio, suggesting that they were in better condition than the krill from cohort 2a, confirming improving conditions at the beginning of the spring bloom of ice algae and phytoplankton.

Conclusions

The diet of AC0 *Euphausia superba* shows considerable spatial and temporal variation, mirroring patterns of local food availability and environmental parameters. Heterotrophic food sources are confirmed to be important during winter, and sea-ice associated prey was important in this study. Increased feeding on autotrophic food sources occurred at the sea-ice edge during the onset of spring, and was most likely a result of increased availability of these resources, supporting the idea of opportunistic feeding. On the longer term, fatty acids and stable isotopes mirror the ontogenetic development and advection history of different cohorts rather than local food availability. Results indicate that the long-term availability of sea-ice resources during advection history has a significant influence on the fitness of AC0 krill after their first winter. Furthermore, not only extent and duration of the seasonal sea ice are important for krill recruitment (Siegel 2000; Quetin and Ross 2003; Arrigo and Thomas 2004), but also the potential of the sea-ice habitat to sustain sufficiently productive sea-ice algae communities. The biological richness of sea ice and its spatio-temporal variability as well as advection pathways of krill larvae must be represented in models predicting the over-winter survival of krill in climate change predictions and management applications.

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Supplementary

▼**Table S1**. Average length (mm) of different stages of *Euphausia superba* furcilia larvae (F) and AC0 juveniles (JUV) per station. Additionally the proportion (%) of the developmental stages in the catch per station is presented. The remainder of the proportion per station consists of sub-adult and adult krill (not shown).

	Stage							
	FIV		**FV**		**FVI**		**JUV**	
Station	mm	%	mm	%	mm	%	mm	%
555-47					13.64	24.3	16.35	75.7
557_2			11.23	0.9	12.10	68.7	16.36	29.8
560_2					11.14	88.0	17.85	8.7
562_5			8.69	3.0	10.13	88.0	18.19	2.8
565_5	5.79	19.3	6.76	38.9	8.23	41.8		
567_2	6.36	8.9	7.03	29.6	8.78	60.7	18.00	0.7
570_5	6.49	5.2	7.02	25.8	9.54	59.6	16.87	5.9
571_2	7.32	2.4	8.06	10.0	10.46	84.9	15.30	2.6
577_2					11.18	88.6	15.90	9.2
579_2	7.95	1.7	8.36	8.4	10.82	81.1	15.05	7.4

▼**Table S2**. Number of individuals (*n*), developmental stages and average length of AC0 *Euphausia superba* used for stomach analysis. FVI indicate furcilia larvae in stage six, Juv are juveniles in their first winter. The standard deviation is given within brackets.

Station	***n***	**Stages**	**Average length (mm)**	**Station**	***n***	**Stages**	**Average length (mm)**
555	1	Juv	16	566	9	FVI	8.78 (1.0)
555_47	9	FVI, Juv	14.11 (1.9)	567_2	9	FVI	9.33 (0.8)
557_2	9	FVI, Juv	15 (1.7)	570_5	6	FVI, Juv	13.5 (1.8)
560_2	11	FVI, Juv	15.62 (4.8)	571_2	11	FVI, Juv	14 (2.3)
562_5	6	FVI	11.17 (0.90)	577_2	9	FVI, Juv	13 (2.3)
565_5	8	FVI	9.71 (1.0)	579_2	9	FVI	13.08 (1.1)

▼**Table S3**. Number of individuals (*n*), developmental stage, average length and average dry weight of AC0 *Euphausia superba* used for carbon/nitrogen, fatty acid and bulk stable isotope analysis. FV and FVI indicate furcilia larvae in stage five and six, Juv are juveniles in their first winter. The standard deviation is given within brackets.

Cohort	*n*	Stages	Average length (mm)	Average DW (mg)
Carbon and nitrogen content				
1	5	FVI, Juv	17.98 (2.39)	6.74 (2.96)
2a	11	FVI	13.09 (2.56)	3.13 (1.58)
2b	7	FVI	11.36 (1.14)	1.69 (0.50)
3	4	FV, FVI	8.91 (0.30)	1.29 (1.06)
Fatty acids and total fatty acid content				
2a	5	FVI, Juv	12.37 (3.69)	2.94 (2.0)
2b	9	FVI, Juv	10.16 (3.57)	1.78 (1.8)
3	7	FV, FVI, Juv	10.35 (3.49)	1.80 (1.5)
Bulk stable istopes				
1	5	FVI, Juv	17.98 (2.4)	6.74 (3.0)
2a	14	FVI, Juv	13.09 (2.6)	3.13 (1.6)
2b	9	FVI, Juv	11.36 (1.1)	2.49 (1.6)
3	3	FVI	9.07 (0.03)	2.22 (1.1)

2.5 *Chapter V*

Overwintering of Weddell Sea under-ice community strongly linked to sea ice-associated food sources

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Abstract

Ice-associated (sympagic) microalgae are assumed to serve as high-quality food source during winter when pelagic algae biomass is critically low in the Southern Ocean. To better understand the role of sea ice and the importance of ice algae-produced carbon for the overwintering of marine organisms in the northern Weddell Sea, we investigated lipid and stable isotope parameters of abundant Antarctic under-ice species and their potential sympagic and pelagic carbon sources. Fatty acid-specific carbon stable isotope compositions were used in Bayesian stable isotope mixing models to quantify the contribution of ice algae-produced carbon (α_{Ice}) to the body carbon of the species. α_{Ice} estimates ranged from 4 to 69% with remarkable variations depending on the fatty acid used. Differences in fatty acid ratios and α_{Ice} estimates between fatty acids associated with younger versus older lipid pools suggested a switch from a negligible to a substantial dependency on sympagic food sources for many species as the winter season progressed. Winter survival by ice algae-produced carbon, however, might be endangered by climate change-related decline of sea ice and, consequently, ice algae production. Sufficient food supply by alternative carbon sources is unlikely due to the low biomass of pelagic algae during winter, impacting on species distribution patterns and ecosystem structure.

Introduction

In the Southern Ocean, ice-associated (sympagic) primary production is assumed to provide carbon to the food web when the pelagic productivity is near-zero during winter (Lizotte 2001; McMinn et al. 2010; Smith Jr. and Sakshaug 2013). Due to the high spatial and temporal variability of sea ice algal production, however, the importance of carbon synthesized by sea ice algae and transferred to the food web has been difficult to quantify (Arrigo et al. 1997). Apart from sympagic microalgae, in-ice or under-ice fauna, e.g. protozoans or small copepods, can serve as carbon sources for predatory species dwelling underneath the sea ice (Daly 1990; Schmidt et al. 2014). Particularly during winter, however, changes of sea ice extent and properties are critical for growth and production of ice-associated biota, which subsequently affects upper trophic levels (Smith et al. 1999; Clarke et al. 2007; Ducklow et al. 2007). Climate change-induced alterations of the sea ice habitat might not only have severe consequences for the sympagic ecosystem, but have potentially a strong impact on the pelagic food web as well, due to the close connectivity between sea ice and pelagic system (Flores et al. 2011; David et al. 2017). There are a few, but very abundant zooplankton species that may be important in transferring carbon from algal producers into the pelagic food web. Hence, it is critical to understand to which extent these organisms depend on sea ice algal production in order to evaluate future alterations in food web dynamics, and the subsequent effect on upper trophic levels.

As in other high latitudinal marine ecosystems, primary production in the Southern Ocean shows extreme seasonal variability, resulting in short-term food pulses. Hence, timing is a critical factor for Antarctic ecosystems. Antarctic organisms have adapted differently to prevailing environmental conditions during winter. To overcome insufficient primary production in the water column during winter, some species accumulate large lipid energy reserves in form of wax esters and/or triacylglycerols (Hagen et al. 1993; Kattner et al. 1994), such as the euphausiid *Thysanoessa macrura* (Sars, 1883) (Lee et al. 2006). Various copepod species are known to perform diapause, migrating into deeper water layers during winter (Voronina 1972), after accumulating lipids from the summer phytoplankton blooms (Lee et al. 1971a). In contrast, the copepod *Calanus propinquus* (Brady, 1883) is winter-active species (Hagen and Auel 2001), remaining in surface waters and actively feeding during winter (Marin 1988; Schnack-Schiel et al. 1991). Based on abundance data, Fisher et al. (2004) suggested a switch from pelagic to sympagic life style of e.g. the amphipod *Eusirus microps* (Walker, 1906) during winter, correlated with the availability of sea ice.

There are different types of trophic markers that can be used to identify the source of carbon biomass in grazers and predators. Certain fatty acids (FAs) are very abundant in particular algal groups, such as the FAs 16:1n-7 and 20:5n-3 for diatoms, and 18:4n-3 and 22:6n-3 for dinoflagellates (Dalsgaard et al. 2003 and references therein). Accordingly, the natural distribution of these marker FAs can be used for the differentiation between algal groups. Because these marker FAs are not subject to metabolic transformation, they can be used to trace carbon sources in the consumers. The FAs 16:1n-7 and 18:4n-3 are predominantly incorporated into storage lipids to

provide energy reserves. Conversely, the polyunsaturated FAs 20:5n-3 and 22:6n-3 are mainly incorporated into membrane lipids. Particularly 18:4n-3 was characterized as valuable short-term trophic marker fatty acid, because this FA was found to be metabolized in a short time period when not refilled by dietary sources (Stübing et al. 2003). Due to their different turnover rates, the trophic information from the storage-associated FAs is likely to reflect the recent carbon source composition more precise than the more conserved membrane-associated FAs, which, however, reflect carbon source preferences accumulated over longer time periods.

Alternatively or in addition to fatty acids, analyses of the natural abundance of nitrogen and carbon stable isotopes have frequently been used to characterize predator-prey relationships in the marine environment (e.g. Hodum and Hobson 2000; Kohlbach et al. 2016). Nitrogen stable isotope compositions (expressed in the delta notation δ^{15}N: ^{15}N/^{14}N) enable the estimation of a consumer's trophic position within the food web due to a stepwise enrichment of ^{15}N along the food chain (Wada et al. 1987; Kaehler et al. 2000). The distribution of carbon stable isotopes (δ^{13}C: ^{13}C/^{12}C) in the bulk organic content (BSIA- Bulk stable isotope analysis) or specific compounds of a sample, such as fatty acids (CSIA- Compound-specific stable isotope analysis), allows for the determination of the original carbon source in the consumer. CSIA of marker FAs represents a further development of the less specific analyses of the organic carbon compounds (Søreide et al. 2013; Ko et al. 2015), and has been applied more frequently in marine food web studies in the recent past (Budge et al. 2008; Kohlbach et al. 2016; Wang et al. 2016). The δ^{13}C composition of carbon produced by ice algae is often found to be considerably higher compared to carbon produced by pelagic phytoplankton (Fry and Sherr 1984; Hecky and Hesslein 1995). This isotopic difference is transferred conservatively from producers to consumers, and thus constitutes a valuable tool when the potential producer communities are taxonomically diverse. For example, a diatom-associated FA can either originate from sea ice diatoms or from diatoms in the water column and, thus, carbon source preferences of a given consumer are difficult to identify based on the composition of marker FAs alone (Kohlbach et al. 2016). The trophic signal from fatty acid and stable isotope compositions is integrated over days to months (Fry and Arnold 1982; Alonzo et al. 2005), and gives therefore insights into diet and carbon sources from a longer time span compared to the snapshot character of stomach content analyses.

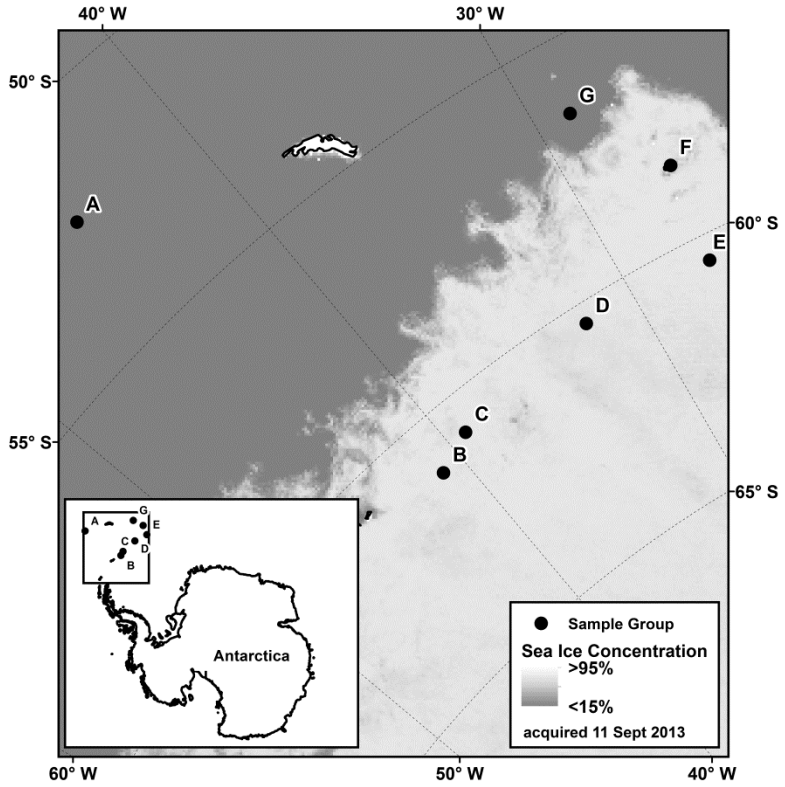
In this study, we investigated food web interactions and carbon sources of abundant under-ice fauna species during winter/onset of spring in the northern Weddell Sea based on lipid and stable isotope data. From the distribution of marker FAs in ice-associated and pelagic algae and under-ice fauna species, we traced the dietary carbon from the producers (diatoms versus dinoflagellates) to the consumers. We quantified the proportional contribution of ice algae-produced carbon α_{Ice} versus pelagic-produced carbon to the carbon budget of these ecological key species, based on fatty acid-specific stable isotope compositions. We hypothesized that ice algae-produced carbon gains importance for Antarctic organisms as winter progresses, because in late winter ice

algae might represent the only food source abundant enough to close their energy budget.

Materials and Methods

Sample collection

Sampling was conducted during RV '*Polarstern*' expedition PS81 (WISKY; 14 August to 16 October 2013) in the Weddell Sea south of 50°S (**Figure 1**). Summarized station information is given in **Table 1**. Additional information is provided in David et al. (2017) and Schaafsma et al. (2016).



▲***Figure 1.*** *Map of the sampling area during RV 'Polarstern' expedition WISKY (PS81) in the northern Weddell Sea. Letter codes correspond to grouped sampling locations. Station information for the individual sampling site is given in* ***Table 1****.*

▼**Table 1.** Station information for ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM) and under-ice fauna (UIF) collected during RV '*Polarstern*' expedition PS81.

Location	Station no.	Date (m/dd/2013)	Sample type	Latitude	Longitude
A	527-2	8/22	UIF	-52.29	-45.07
	529-1	8/22	P-POM	-52.28	-44.25
B	549-1	8/29	UIF	-61.25	-42.06
	551-1	8/31	UIF	-61.21	-40.73
	552-1	8/31	P-POM	-61.22	-40.72
	555-1	9/1	I-POM (ice camp 1)	-61.21	-41.05
	555-24	9/4	P-POM	-60.90	-40.44
C	555-47	9/9	UIF	-60.80	-39.15
D	557-2	9/10	UIF	-59.96	-33.17
	557-3	9/11	P-POM	-59.95	-33.15
	560-2	9/11	UIF	-60.63	-31.78
	560-3	9/12	P-POM	-60.63	-31.83
	562-5	9/12	UIF	-60.97	-31.24
E	565-5	9/16	UIF	-60.71	-27.17
	566-1	9/17	I-POM (ice camp 2)	-60.60	-27.10
	566-2	9/19	UIF	-60.52	-26.52
	566-21	9/25	UIF	-60.66	-26.44
	566-32	9/28	P-POM	-60.43	-25.71
	567-2	9/28	UIF	-60.45	-25.70
F	571-1	9/30	UIF	-58.43	-26.11
	577-2	10/2	UIF	-58.44	-26.10
	579-2	10/2	UIF	-58.46	-26.05
G	576-3	10/1	P-POM	-56.52	-28.65

Ice-associated particulate organic matter (I-POM) was sampled as representative of sea ice algae by taking ice cores at 2 different ice camps (**Figure 1**, **Table 1:** B, E) with a 9 cm interior diameter ice corer (Kovacs Enterprises). The bottom 10 cm of ice cores were melted on board and between 1.0 and 1.5 L water from the melted ice cores were filtered via vacuum pump through pre-combusted GF/F filters (Whatmann, 3 h, 550°C). Pelagic particulate organic matter (P-POM) was collected as representative of pelagic algae at 6 sites by a carousel water sampler on a CTD probe (Conductivity, temperature, depth: Seabird SBE9+) (**Figure 1**, **Table 1**). Depending on the biomass concentration, between 8.0 and 20.5 L water were filtered using pre-combusted GF/F filters. All POM filters were stored at -80°C.

Samples of abundant fauna from the ice-water interface layer were collected at 12 stations by a Surface and Under-Ice Trawl, (SUIT) (van Franeker et al. 2009) (**Figure 1**, **Table 1**). At station 571-1, samples were collected by a Rectangular Midwater Trawl (RMT) (Roe and Shale 1979) between 345 m and the surface (**Table 1**). There were no statistical differences in the investigated parameters between specimens caught with SUIT and specimens caught with RMT. We investigated the euphausiids *Euphausia superba* (Dana, 1850) and *Thysanoessa macrura* (Sars, 1883), the copepod species

Calanus propinquus (Brady, 1883), the amphipods *Eusirus laticarpus* (Chevreux, 1906), *Eusirus microps* (Walker, 1906) and *Cyllopus lucasii* (Bate, 1862), the gastropods *Clione limacina antarctica* (E. A. Smith, 1902), *Clio pyramidata* (Linnaeus, 1767) and *Spongiobranchea australis* (d'Orbigny, 1836), the siphonophore *Diphyes antarctica* (Moser, 1925) and the salp *Salpa thompsoni* (Foxton, 1961). *Euphausia superba* were sorted by developmental stage into larval, juvenile (first- and second-year) and adult individuals. All analyzed larvae were staged as Furcilia VI krill, based on the number of terminal spines on the telson (Kirkwood 1982). Krill which lost one pair of post-lateral spines from their telson (Fraser 1937), but with no external sexual characteristics yet, were staged as juveniles (Makorov and Denys 1981). Krill with external sexual characteristics were categorized into female and male (Makorov and Denys 1981), but grouped together as 'adults' since there were no statistical differences in biomarker parameters found. *C. propinquus* were sorted into CV and female individuals (Razouls 1994). Hereafter, the pteropod *Clione limacina antarctica* E. A. Smith (1902) was referred to as *Clione antarctica*, based on the suggestion by Gilmer and Lalli (1990) to consider the southern population as distinct species from the Arctic *Clione limacina* Phipps (1774). Length measurements were conducted on euphausiids, *C. propinquus* and *S. thompsoni* (**Suppl. A**). All zooplankton samples were immediately frozen at -80°C in pre-combusted and pre-weighted sample vials (Wheaton, 6 h, 500°C). Analytical work took place at the Alfred Wegener Institute in Bremerhaven, Germany.

Lipid class and fatty acid analyses

After freeze-drying (24 h) filters and animals, total lipids were extracted with dichloromethane/methanol (2:1, v/v) using a modified procedure from Folch et al. (1957). Dry masses were determined gravimetrically (**Suppl. A**). Lipid classes of the under-ice fauna species were determined directly from the lipid extracts via high-performance liquid chromatography. Fatty acids were determined as fatty acid methyl esters (FAMEs) via gas chromatography, after transesterification with methanol (3% sulphuric acid). Concentrations of individual fatty acids were determined with an internal standard (23:0) added prior lipid extraction. For detailed information on sample preparation and measurements as well as analytical equipment see Kohlbach et al. (2016).

The investigation of the FA compositions was based on the diatom-associated marker FAs 16:1n-7 and 20:5n-3 (e.g. Graeve et al. 1997; Falk-Petersen et al. 1998; Scott et al. 1999), the dinoflagellate-associated marker FAs 18:4n-3 and 22:6n-3 (e.g. Viso and Marty 1993; Graeve et al. 1994b), and the copepod-associated marker FAs 20:1-9 and 22:1n-11 (e.g. Falk-Petersen et al. 1987; Søreide et al. 2013). Storage FAs are assumed to reflect the more recent diet composition compared to membrane fatty acids, which are more conserved (Stübing et al. 2003). This makes it possible to integrate the dietary signal over different time scales. To distinguish the importance of diatom- versus dinoflagellate FAs in storage versus membrane lipids, the fatty acid ratios of the storage-associated FAs 16:1n-7 and 18:4n-3, and the membrane-associated FAs 20:5n-3 and 22:6n-3 was investigated. In the following, storage and membrane FAs are distinguished

into short-term (= recent) and long-term (= older) FAs, respectively. To estimate the degree of carnivory, the proportions of 18:1n-9 (Sargent and Falk-Petersen 1981; Falk-Petersen et al. 1990) and the ratio of 18:1n-7/18:1n-9, which decreases with increasing carnivory (Graeve et al. 1997; Nelson et al. 2000; Auel et al. 2002), were evaluated.

Bulk and fatty-specific stable isotope analyses

Bulk nitrogen ($\delta^{15}N$) and bulk carbon ($\delta^{13}C$) stable isotope compositions were determined from freeze-dried filters of POM and animals. For the under-ice fauna species, whole individuals were used after homogenization. From the FAME derivatives, the $\delta^{13}C$ compositions of the fatty acids 16:1n-7, 18:4n-3, 20:5n-3 and 22:6n-3 were determined. For detailed information on sample preparation and measurements as well as analytical equipment see Kohlbach et al. (2016).
All isotopic ratios were presented as parts per thousand (‰) in the delta notation ($\delta^{15}N$: $^{15}N/^{14}N$, $\delta^{13}C$: $^{13}C/^{12}C$), as deviation from atmospheric nitrogen for nitrogen measurements, and the Vienna Pee Dee Belemnite standard for carbon measurements. Verification of accuracy and precision of the BSIA measurements was done by analyzing secondary reference material USGS41 (certified: $\delta^{15}N$ = 47.6‰, $\delta^{13}C$ = 37.6‰, measured: $\delta^{15}N$ = 46.8‰, $\delta^{13}C$ = 36.8‰) provided by the International Atomic Energy Agency (IAEA, Vienna). Measurement errors were indicated as ± 0.3‰ for both stable nitrogen and stable carbon measurements. Furthermore, the laboratory standard isoleucine ($\delta^{15}N$ = -11.87‰, $\delta^{13}C$ = -3.14‰) was analyzed every 5 samples with measurement errors of ± 0.2 and 0.3‰ for stable nitrogen and carbon isotope ratios, respectively. For the CSIA measurements, quality assurance and analytical precision of the determined carbon stable isotope ratios were established by analyzing certificated standard FAME 14:0 (certified: $\delta^{13}C$ = -29.13‰, measured: $\delta^{13}C$ = -29.77‰), 16:0 (certified: $\delta^{13}C$ = -30.74‰, measured: $\delta^{13}C$ = -30.21‰) and 18:0 (certified: $\delta^{13}C$ = -23.24‰, measured: $\delta^{13}C$ = -23.78‰), supplied by Indiana University, every 5 samples. Analytical error was 0.2 ‰ for 14:0, 0.3‰ for 16:0 and 0.3‰ for 18:0 (represents 1 SD of 9 analyses each).

Data analysis

The trophic levels (TL) of the under-ice fauna species in the investigated food web were estimated from the bulk $\delta^{15}N$ and $\delta^{13}C$ compositions as follows (Two-source food web model) (Post 2002), assuming that carbon and nitrogen moved through the food web with a similar stoichiometry:

(1) $$TL = \lambda + (\delta^{15}N_x - [\delta^{15}N_{base1} * \alpha + \delta^{15}N_{base2} * (1 - \alpha)])/\Delta_N$$

where λ represents the trophic position of the baseline (I-POM or P-POM, λ= 1). The directly measured $\delta^{15}N_x$ and $\delta^{15}N_{base}$ are the bulk nitrogen isotopic compositions of the under-ice fauna species and POM, respectively. Base 1 and base 2 relate to I-POM and P-POM, respectively. Δ_N is the enrichment constant of $^{15}N/^{14}N$ (fractionation) per trophic level (assumed as Δ_N = 3.4‰) (Minagawa and Wada 1984). The proportion of nitrogen

in the investigated species that derives ultimately from the baseline organism of food web 1 (= ice algae community) is represented by α.
For the TL calculations, α was estimated as follows:

$$(2) \qquad \alpha = \frac{(\Delta_N \delta^{13}C_x - \Delta_C \delta^{15}N_x + \Delta_C \delta^{15}N_{base2} - \Delta_N \delta^{13}C_{base2})}{(\Delta_N \delta^{13}C_{base1} - \Delta_N \delta^{13}C_{base2} + \Delta_C \delta^{15}N_{base1} + \Delta_C \delta^{15}N_{base2})}$$

A trophic fractionation of carbon between 0 and 1‰ per trophic level is generally assumed (DeNiro and Epstein 1978; Rau et al. 1983), which seems to be a robust and applicable assumption when investigating a food web with multiple possible trophic pathways (Post 2002). In this study, we assumed Δ_C = 0.4‰ (Post 2002) since the true carbon enrichment factors for our investigated species were unknown. However, calculations using a varying Δ_C within the range of 0 and 1‰ resulted in negligible variations of α_{Ice} in all species (data not shown).
The $\delta^{13}C$ values of the storage-associated FA 18:4n-3 and the two membrane-associated FAs 20:5n-3 and 22:6n-3 were used to calculate the proportional contribution of ice algae-produced carbon (α_{Ice}) to the body carbon of the under-ice fauna species from Bayesian multi-source stable isotope mixing models (SIAR; Parnell et al. 2010). Due to the different isotopic turnover rates, the isotopic signal from 18:4n-3 represented the short-term trophic signal of more recent carbon sources and 20:5n-3 and 22:6n-3 represented the long-term trophic signal of older carbon sources. Trophic enrichment factors for carbon in these FAs and concentration dependencies were assumed to be zero (Budge et al. 2011; Wang et al. 2015). FA 16:1n-7 was not used for the calculations, because in all species $\delta^{13}C$ values were lower than the trophic baseline (e.g. I-POM and P-POM). We suggest that 16:1n-7 was mainly produced by sea-ice diatoms, indicated by the high $\delta^{13}C$ values in both I-POM and P-POM, and the negligible contribution of this FA to the fatty acid pool of P-POM. Thus, the 16:1n-7 signals from the P-POM samples probably stemmed from ice algae secluded into the water column, making the use of this FA for the modeling redundant. *E. superba* in their first year (larvae and juveniles) were combined as Age Class 0 (AC0) krill (Schaafsma et al. 2016) for the modeling.
To account for the spatial and temporal variability in the fatty acid and stable isotope compositions of the organisms, we grouped the samples species-specifically in four regimes (**Figure 1**, **Table 1**): a) ice-free stations (location A, abbreviated as 'ice-free') sampled at the beginning of the sampling period, b) stations in close proximity to ice camp 1 (locations B to D, abbreviated as 'ice camp 1'), c) stations in close proximity to ice camp 2 (location E, abbreviated as 'ice camp 2'), and d) northernmost stations sampled at the end of the sampling period (location F, abbreviated as 'north'). Statistical tests were only run for *E. superba*, *C. propinquus* and *E. laticarpus* due to sufficient sample size. Besides the mean α_{Ice}, we calculated α_{Ice} for each location and species using corresponding I-POM and P-POM values to account for the variability in the stable isotope data. For the individuals from location north, we used the I-POM $\delta^{13}C$ values from ice camp 2 due to the closer spatial and temporal proximity to the sampling at location north. α_{Ice} was not determined for under-ice fauna specimens from the ice-free

station (location A). Variability of biomarker parameters is discussed using the example of *E. superba*.

We calculated the number of individuals of the two most abundant species during our sampling, larval *E. superba* and *C. propinquus* (David et al. 2017) that can be sustained by available ice algae and pelagic carbon sources in the northern Weddell Sea during the winter period (122 days), based on the α_{Ice} estimates derived from the dinoflagellate-associated FA short-term 18:4n-3 and published ingestion rates (Pakhomov et al. 2004; Pakhomov and Froneman 2004). For that, typical winter bottom-ice algae biomass values (Meiners et al. 2012) and Chl *a* values from the under-ice water layer during the sampling (David et al. 2017) were converted to carbon biomass (Arrigo et al. 1998, 2010).

All data analyses were conducted using the open-source software 'R', version 3.2.3 (R Core Team 2015). In order to improve normality, the FA data were transformed following Budge et al. (2007) and applying an arcsine square root function. Pairwise testing for statistical significance between value groups was conducted with Student´s t-tests. All data were checked for normality and homogeneity by performing the Shapiro-Wilk normality test and evaluating histograms and scatter plots of the data.

Results

Lipid and fatty acid compositions

Ice-associated and particulate organic matter

In the I-POM samples, the sum of the diatom-associated marker FAs 16:1n-7 and 20:5n-3 exceeded with on average 34% considerably the sum of these marker FAs in the P-POM samples (mean ~ 12%) (**Table 2**). The contributions of both FAs 16:1n-7 and 20:5n-3 were significantly higher in the I-POM samples (mean 19% and 15%, respectively) than in the P-POM samples (mean 5% and 7%, respectively) (t-test, $p < 0.001$). In contrast, the sum of the dinoflagellate-associated marker FAs 18:4n-3 and 22:6n-3 was on average twice as high in P-POM (mean sum 12%) versus I-POM (mean sum 6%). Whereas the mean proportion of 22:6n-3 (4%) was on average twice as high than the mean proportion of 18:4n-3 in I-POM (2%), both dinoflagellate-associated FAs accounted for ~ 6% of the total FA content in P-POM (**Table 2**). The ratios of 16:1n-7/18:4n-3 (mean 10) and 20:5n-3/22:6n-3 (mean 5) suggested a dominance of diatoms versus dinoflagellates in I-POM. Mean ratios of 16:1n-7/18:4n-3 and 20:5n-3/22:6n-3 were ~ 1 in P-POM, suggesting a rather mixed taxonomic composition of diatoms and dinoflagellates in the pelagic primary producer community (**Table 2**).

▼**Table 2.** Proportions of marker fatty acids (mean ± 1 SD mass % of total fatty acids) and biomarker ratios in I-POM and P-POM (mean ± 1 SD).

Parameter	Parameter description	I-POM (n = 28)	P-POM (n = 6)
16:1n-7	Diatom-associated FA in short-term storage lipids	18.7 ± 8.7	5.1 ± 2.1
20:5n-3	Diatom-associated FA in long-term membrane lipids	15.4 ± 8.0	6.8 ± 2.9
18:4n-3	Dinoflagellate-associated FA in short-term storage lipids	2.2 ± 0.9	5.6 ± 3.4
22:6n-3	Dinoflagellate-associated FA in long-term membrane lipids	4.2 ± 1.8	6.3 ± 4.3
16:1n-7/18:4n-3	Diatom-dinoflagellate ratio in short-term storage lipids	10.1 ± 12.3	0.9 ± 0.3
20:5n-3/22:6n-3	Diatom-dinoflagellate ratio in long-term membrane lipids	4.7 ± 2.9	0.9 ± 0.1

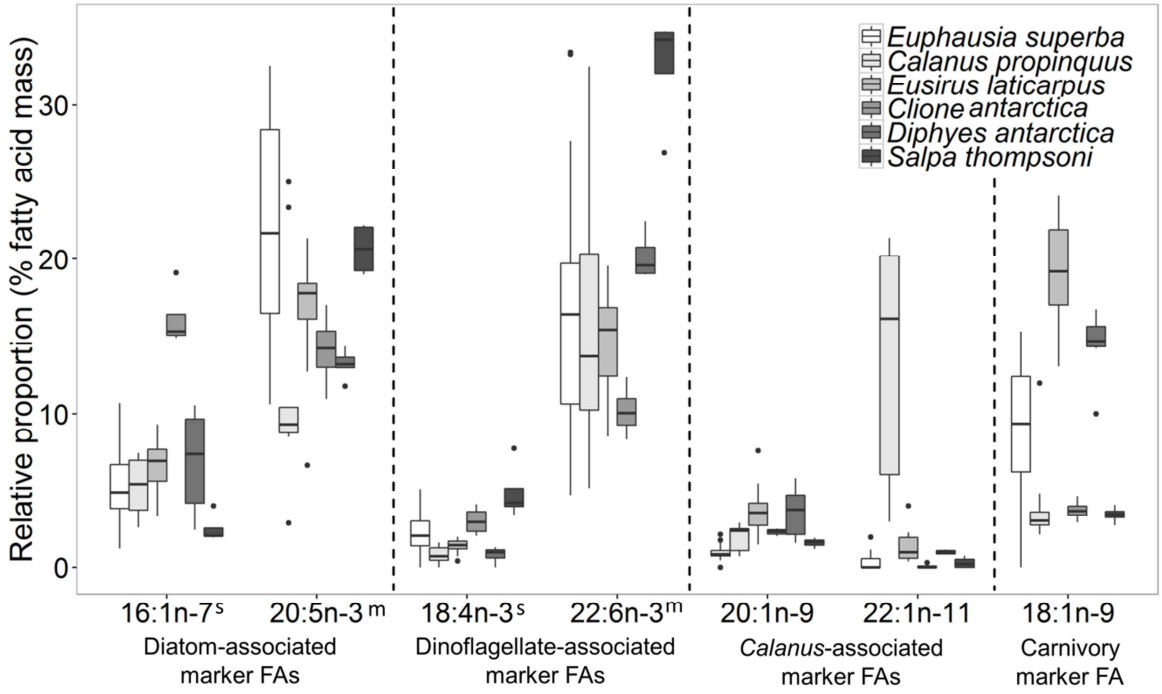
There was high variability in the FA composition between I-POM collected at ice camp 1 (n = 14) (**Figure 1**, **Table 1**: B) and I-POM from ice camp 2 (n = 14) (**Figure 1**, **Table 1**: E). I-POM from ice camp 1 revealed significantly lower proportions of 16:1n-7 (12.2 ± 5.0%) (t-test, $p < 0.001$) and 22:6n-3 (2.9 ± 1.3%) (t-test, $p < 0.001$) than I-POM from ice camp 2 (25.2 ± 6.4% and 5.5 ± 1.0%, respectively). In contrast, FA 20:5n-3 was found in significantly higher relative abundance in I-POM from ice camp 1 (19.8 ± 7.4%) versus I-POM from ice camp 2 (11.1 ± 6.2%) (t-test, $p < 0.01$). The mean proportions of 18:4n-3 were similar for both ice camps (ice camp 1: 2.1 ± 1.0%, ice camp 2: 2.3 ± 0.8%). P-POM from the ice-free station (n = 1) (**Figure 1**, **Table 1**: A) and from location north (n = 1) (**Figure 1**, **Table 1**: G) had somewhat higher proportions of 18:4n-3 (mean 9%, respectively) compared to P-POM from ice camps 1 (n = 3) and 2 (n = 1) (0 to 6%), and higher proportions of 22:6n-3 (mean 11%, respectively) compared to ice camps 1 and 2 (0 to 8%).

Under-ice fauna species

The mean proportions of the storage lipids triacylglycerols ranged from 1% in *Thysanoessa macrura* to 87% in *Clione antarctica*. In *T. macrura*, energy was mainly allocated to wax esters, accounting for ~ 37% of the lipid content. Elevated wax esters proportions were also found in the amphipods *Eusirus laticarpus* (31%) and *Eusirus microps* (13%). The mean proportions of the most abundant membrane-associated lipid class phosphatidylcholine ranged from 6 to 46%, with the lowest proportions in *C. antarctica* and the highest proportions in all euphausiids and S*alpa thompsoni* (**Suppl. B**).

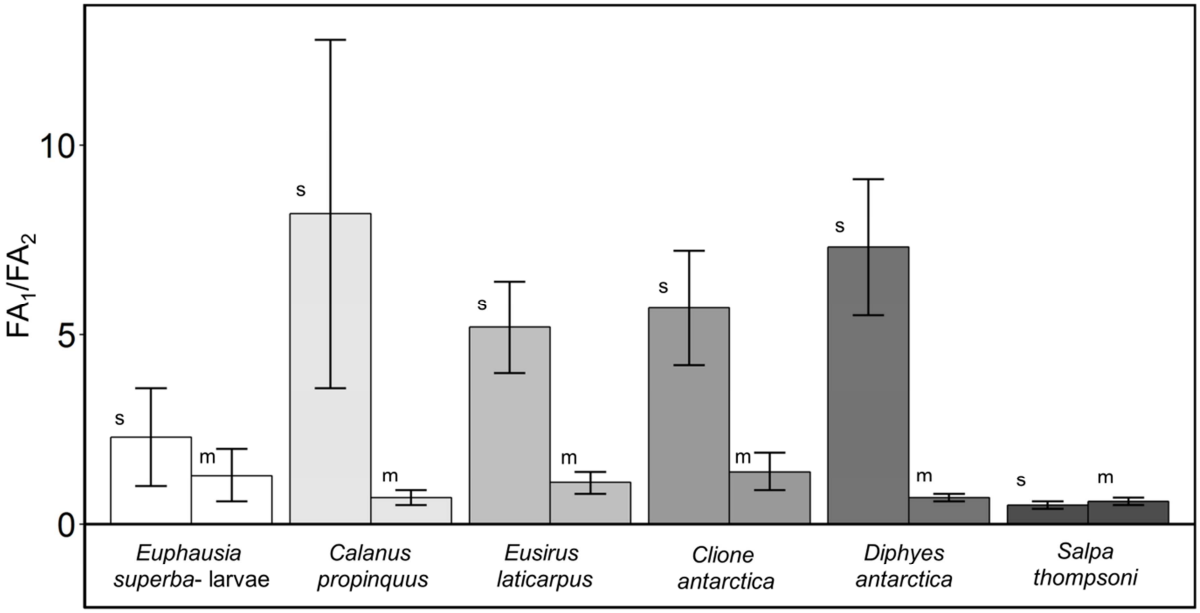
In most species, the sum of the proportions of the diatom-associated marker FAs 16:1n-7 and 20:5n-3 exceeded the sum of the proportions of the dinoflagellate-associated FAs, except for *Salpa thompsoni* (**Suppl. C**). The mean proportions of 16:1n-7 were below 10% in all species, except for *C. antarctica* (16%). In general, 20:5n-3 and the

dinoflagellate-associated FA 22:6n-3 were the most abundant marker FAs with mean contributions ranging from 12% (*C. propinquus*) to 27% (larval *E. superba*) for 20:5n-3, and 10% (*C. antarctica*) and 33% (*S. thompsoni*) for 22:6n-3, relative to the total fatty acids (**Figure 2, Suppl. C**). The relative abundance of the second dinoflagellate-associated marker FA 18:4n-3 was rather marginal in all species (mean < 5%). The marker FA profile of *C. antarctica* differed from the other species due to the highest levels of 16:1n-7 accompanied with the lowest levels of 22:6n-3. Conversely, *S. thompsoni* showed one of the lowest levels of 16:1n-7 and the highest levels of both dinoflagellate-associated marker FAs (**Figure 2**, **Suppl. C**).



▲***Figure 2.*** *Relative composition of marker fatty acids in selected under-ice fauna species (mass % of total fatty acid content). FAs 16:1n-7 and 18:4n-3 represent storage-associated short-term FAs (s), 20:5n-3 and 22:6n-3 represent membrane-associated long-term FAs (m). Horizontal bars in the box plots indicate median proportional values. Upper and lower edges of the boxes represent the approximate 1st and 3rd quartiles, respectively. Vertical error bars extend to the lowest and highest data value inside a range of 1.5 times the inter-quartile range, respectively (R Core Team 2015). Outliers are represented by the dots outside the boxes. All developmental stages of Euphausia superba were grouped. Sample size is given in* ***Suppl. C****.*

In storage-associated FAs, the ratio of 16:1n-7/18:4n-3 indicated a dominance of diatom-produced versus dinoflagellate-produced carbon in all species in recent carbon sources, except for *S. thompsoni* (**Figure 3**, **Suppl. D**). The ratio of the diatom-associated FA versus dinoflagellate-associated FA was lower in membrane-associated FAs than in storage lipids in all species, except for *S. thompsoni* (**Figure 3**). The long-term trophic ratio of 20:5n-3/22:6n-3 suggested rather mixed carbon sources for most species, with the highest impact of diatom-associated FAs in *C. pyramidata* and the highest contribution of dinoflagellate-produced carbon in *S. thompsoni* (**Figure 3**, **Suppl. D**).



▲ **Figure 3**. Ratios of diatom- versus dinoflagellate-associated marker fatty acids (FA) in krill (mean ± 1 standard deviation). The diatom-associated marker FA 16:1n-7 (FA_1) and the dinoflagellate-associated marker FA 18:4n-3 (FA_2) were considered storage FAs (s), representing the short-term trophic signal. The diatom-associated marker FA 20:5n-3 (FA_1) and the dinoflagellate-associated marker FA 22:6n-3 (FA_2) were considered membrane FAs (m), representing the long-term trophic signal. Sample size is given in **Suppl. D**.

The copepod-associated marker FAs 20:1n-9 and 22:1n-11 had generally low contributions in all species (mean < 5%), except for *C. propinquus*, which showed the highest levels of 22:1n-11 of this study (mean 13%) (**Figure 2**, **Suppl. C**). Particularly the mean proportions of the carnivory marker FA 18:1n-9 varied in a wide range between 2% (*S. australis*) and 20% (*Eusirus microps*) among the organisms. The mean ratios of 18:1n-7/18:1n-9 were < 1 for most species, except for larval *E. superba* (1.1 ± 0.2), *C. antarctica* (1.2 ± 0.1) and *S. australis* (1.9 ± 0.4). In *E. superba*, the mean ratio of 18:1n-7/18:1n-9 decreased with ontogeny (**Suppl. D**).

The proportions of 18:4n-3 were significantly higher in larvae and juvenile *E. superba* from location north compared to larvae from ice camps 1 and 2, and juveniles from ice camp 1 (**Suppl. E**). Conversely, adults from location north had significantly lower proportions of 18:4n-3 compared to adults from ice camp 1. Additionally, larvae from ice camp 2 had significantly higher proportions of 22:6n-3 compared to larvae from ice camp 1 and location north. In juveniles, the proportions of 16:1n-7 were significantly higher in specimens from ice camp 1 versus location north. Conversely, 20:5n-3 was more abundant in juveniles from location north compared to juveniles from ice camp 1.

Bulk stable isotope compositions

In I-POM, the mean $\delta^{15}N$ value was with 4.1 ± 2.8‰ somewhat higher than the mean $\delta^{15}N$ value in P-POM (3.2 ± 3.0‰). The $\delta^{13}C$ mean value in I-POM (-22.3 ± 4.3‰) was higher by ~ 6‰ compared to P-POM (-28.2 ± 0.5‰) (**Suppl. F**). I-POM from ice camp 1

(n = 7) showed somewhat higher δ^{15}N values (δ^{15}N = 5.4 ± 3.3‰) relative to I-POM from ice camp 2 (n = 7) (δ^{15}N = 2.7 ± 1.2‰). I-POM from ice camp 1 showed significantly higher δ^{13}C values (δ^{13}C = -18.9 ± 3.0‰) than I-POM from ice camp 2 (δ^{13}C = -26.0 ± 1.3‰) (t-test, $p < 0.001$).

Among the under-ice fauna species, the mean δ^{15}N values ranged from 2.5‰ (*C. propinquus* CV) to 6.9‰ (*S. australis*). In *C. propinquus*, the δ^{15}N values of CV individuals were somewhat lower than the δ^{15}N values in females. In *E. superba*, δ^{15}N values increased with ontogeny (**Table 3**). The mean bulk δ^{13}C values varied from -24.1‰ in *E. laticarpus* to -30.5‰ in *C. antarctica*. CV *C. propinquus* had slightly lower δ^{13}C values than female *C. propinquus*. The δ^{13}C values decreased with ontogeny in *E. superba* (**Table 3**).

▼**Table 3.** Bulk nitrogen (δ^{15}N) and carbon stable isotope values (δ^{13}C) in under-ice fauna species (mean ± 1 SD ‰). Based on isotopic ratios, trophic levels were calculated (mean ± 1 SD).

Species	*n*	Sex/stage	δ^{15}N	δ^{13}C	TL
Euphausia superba	20	larva	3.5 ± 0.7	-24.8 ± 1.0	0.9 ± 0.2
	20	juvenile	3.6 ± 0.6	-26.4 ± 2.0	1.0 ± 0.2
	9	adult	4.4 ± 0.8	-28.7 ± 1.8	1.4 ± 0.3
Thysanoessa macrura	2	--	5.0 ± 2.5	-29.3 ± 4.5	1.5 ± 0.8
Calanus propinquus	3	CV	2.5 ± 1.5	-29.2 ± 0.9	0.8 ± 0.1
	12	female	3.1 ± 1.6	-28.6 ± 1.5	1.0 ± 0.5
Eusirus laticarpus	8	--	6.0 ± 1.3	-24.1 ± 2.2	1.7 ± 0.5
Eusirus microps	1	--	4.4	-25.8	1.3
Cyllopus lucasii	2	--	4.5 ± 0.2	-27.7 ± 0.1	1.4 ± 0.1
Clione antarctica	5	--	4.6 ± 1.0	-30.5 ± 1.4	1.4 ± 0.3
Clio pyramidata	1	--	2.6	-26.5	0.8
Spongiobranchea australis	1	--	6.9	-29.8	2.1
Diphyes antarctica	4	--	5.2 ± 0.3	-27.6 ± 0.9	1.6 ± 0.1
Salpa thompsoni	5	--	3.5 ± 1.0	-29.7 ± 0.7	1.1 ± 0.3

Based on bulk stable isotope compositions, the highest trophic levels within the investigated food web were occupied by *S. australis* (2.1) and *E. laticarpus* (mean 1.7). The lowest TLs were determined for *C. pyramidata* (0.8) and CV *C. propinquus* (0.8). Adult *E. superba* occupied a higher TL (mean 1.4) than larval (mean 0.9) and juvenile *E. superba* (1.0) (**Table 3**).

In all three developmental stages of *E. superba,* the δ^{15}N values were the highest in individuals from location north compared to the other locations (**Suppl. G**). In larval *E. superba*, the δ^{13}C values were lower at stations located close to ice camp 2 compared to station close to ice camp 1 and location north. In general, the species-specific variability in bulk δ^{13}C values was rather low (**Suppl. G**).

Fatty acid-specific stable isotope compositions

The δ^{13}C values were significantly higher in the I-POM samples relative to the P-POM samples in all four marker FAs (t-test, $p < 0.05$) (**Suppl. F**). The mean isotopic difference between I-POM and P-POM ranged between 5‰ in 16:1n-7 and 14‰ in 18:4n-3.

Among the I-POM samples, the mean $\delta^{13}C$ values of FAs 20:5n-3 and 18:4n-3 were similar for both ice camps (20:5n-3: ice camp 1: -28.5 ± 2.4‰, ice camp 2: -28.8 ± 3.8‰, 18:4n-3: ice camp 1: -31.6 ± 5.0‰, ice camp 2: -30.7 ± 7.3‰). In contrast, the $\delta^{13}C$ values of the FAs 16:1n-7 and 22:6n-3 were significantly higher in I-POM from ice camp 2 (n = 8) (16:1n-7: -19.7 ± 4.4‰, 22:6n-3: -22.4 ± 3.7‰) compared to I-POM from ice camp 1 (n = 6) (16:1n-7: -28.6 ± 2.4‰, 22:6n-3: -25.8 ± 1.3‰) (t-test, $p < 0.05$). P-POM from location north (n = 1) had the lowest $\delta^{13}C$ values in the FAs 16:1n-7, 20:5n-3 and 22:6n-3 (16:1n-7: -31.6‰, 20:5n-3: -37.8‰, 22:6n-3: -34.7‰) compared to P-POM from the ice-free station (n = 1), ice camps 1 (n = 2) and 2 (n = 1) (16:1n-7: -24.1 to -30.2‰, 20:5n-3: -31.0 to -35.6‰, 22:6n-3: -31.2 to -32.7‰).

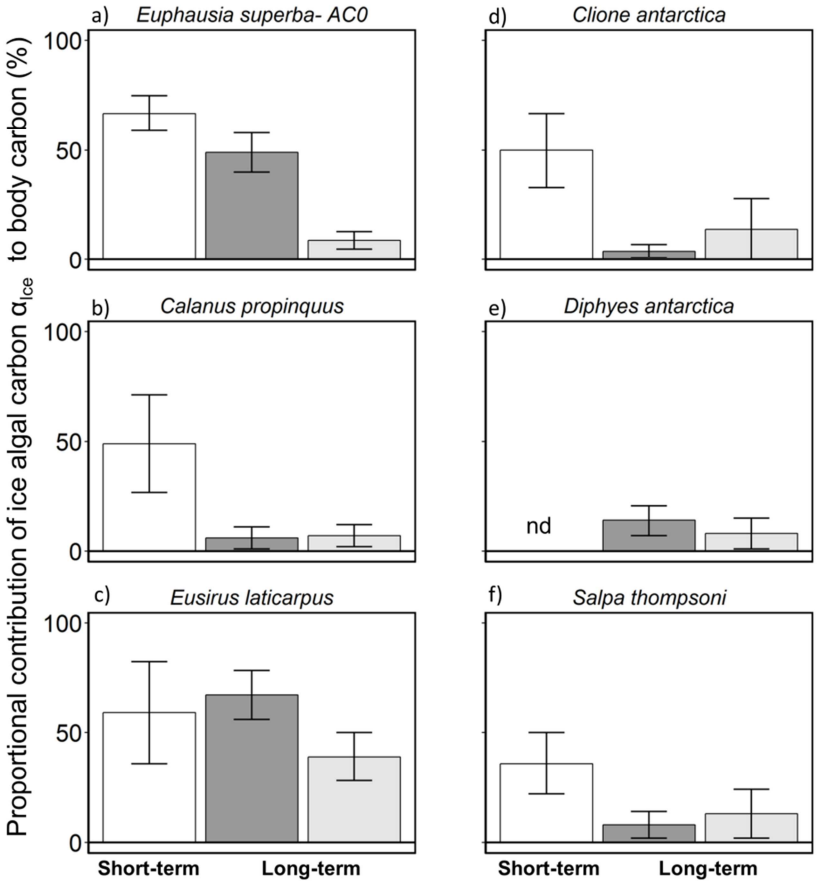
Among the under-ice fauna species, the range of $\delta^{13}C$ values was the highest in 16:1n-7 (~ 12‰) and the lowest in 22:6n-3 (~ 5‰) (**Table 4**). In most species, FA 22:6n-3 showed the highest $\delta^{13}C$ values and 18:4n-3 the lowest $\delta^{13}C$ values. In all four marker FAs, *E. laticarpus* had the highest $\delta^{13}C$ values. In general, the lowest $\delta^{13}C$ values were found in adult *E. superba*, *T. macrura* and *S. thompsoni* (**Table 4**). The variability in the fatty acid-specific $\delta^{13}C$ values between the different sampling locations was insignificant in all species (**Suppl. G**).

▼**Table 4.** Carbon stable isotope values ($\delta^{13}C$) of the storage-associated fatty acids 16:1n-7 and 18:4n-3, and the membrane-associated fatty acids 20:5n-3 and 22:6n-3 in under-ice fauna species (mean ± 1 SD ‰). Not detected FAs marked as '--'.

Species	***n***	**Sex/stage**	**16:1n-7** Diatom-associated FA in short-term storage lipids	**18:4n-3** Dinoflagellate-associated FA in short-term storage lipids	**20:5n-3** Diatom-associated FA in long-term membrane lipids	**22:6n-3** Dinoflagellate-associated FA in long-term membrane lipids
	6	larva	-30.6 ± 5.5	-35.3 ± 2.7	-30.9 ± 0.7	-32.7 ± 0.9
Euphausia superba	8	juvenile	-32.9 ± 2.8	-34.2 ± 1.5	-32.0 ± 1.2	-31.7 ± 1.5
	9	adult	-38.6 ± 2.0	-37.2 ± 0.8	-35.9 ± 1.8	-33.2 ± 0.8
Thysanoessa macrura	5	--	-41.7 ± 4.9	-37.7 ± 1.2	-35.2 ± 2.2	-33.5 ± 2.4
Calanus propinquus	7	female	-36.3 ± 2.1	-37.8 ± 1.0	-35.9 ± 0.9	-33.2 ± 1.0
Eusirus laticarpus	5	--	-29.4 ± 2.2	-34.0 ± 0.2	-30.3 ± 1.4	-29.0 ± 0.7
Eusirus microps	2	--	-34.0 ± 2.4	-35.7 ± 1.7	-34.1 ± 0.4	-31.9 ± 0.1
Cyllopus lucasii	4	--	-36.3 ± 2.5	-40.1 ± 0.2	-34.5 ± 1.1	-33.0 ± 0.7
Clione antarctica	4	--	-34.7 ± 1.3	-37.7 ± 2.4	-36.9 ± 1.0	-33.1 ± 1.2
Clio pyramidata	2	--	-38.0 ± 2.5	-37.4 ± 0.2	-34.6 ± 1.1	-31.9 ± 1.8
Spongiobranchea australis	3	--	-36.4 ± 3.9	--	-34.2 ± 1.1	-32.1 ± 0.4
Diphyes antarctica	6	--	-33.6 ± 1.2	--	-34.9 ± 0.8	-33.9 ± 0.5
Salpa thompsoni	4	--	-38.4 ± 2.0	-39.7 ± 0.6	-35.7 ± 0.9	-32.7 ± 0.7

Proportional contribution of ice algae-produced carbon

In most species, the estimates of the proportion of ice algae-produced carbon in the under-ice fauna species α_{Ice} were the lowest based on the dinoflagellate-associated long-term FA 22:6n-3 and the highest based on the dinoflagellate-associated short-term FA 18:4n-3. The estimates based on the diatom-associated long-term FA 20:5n-3 and the dinoflagellate-associated long-term FA 22:6n-3 showed a high similarity in many species, respectively. Based on the dinoflagellate-associated short-term FA 18:4n-3, the mean trophic dependency on ice algal carbon under more recent conditions varied between 36% (*S. thompsoni*) and 67% (AC0 *E. superba*). Based on the diatom-associated long-term FA 20:5n-3, mean α_{Ice} ranged from 4% (*C. antarctica*) to 67% (*E. laticarpus*) and based on the dinoflagellate-associated long-term FA 22:6n-3, mean α_{Ice} estimates were between 5% in adult *E. superba* and 39% in *E. laticarpus* (**Figure 4, Table V**). Only *E. laticarpus* suggested elevated mean α_{Ice} estimates based on all three fatty acids (39 to 67%). AC0 *E. superba* indicated a substantial proportion of ice algae carbon in their diet, based on the dinoflagellate-associated short-term FA 18:4n-3 and the diatom-associated long-term FA 20:5n-3 (mean 48 to 67%) and remarkably lower mean α_{Ice} values based on the dinoflagellate-associated long-term FA 22:6n-3 (mean 9%). Based on the diatom-associated long-term FA 20:5n-3 and the dinoflagellate-associated long-term FA 22:6n-3, *E. microps*, *C. lucasii*, *C. pyramidata* and *S. australis* displayed moderate mean α_{Ice} estimates between 13 and 30%, whereas the dinoflagellate-associated short-term FA 18:4n-3 suggested a considerably higher proportion of ice algal carbon in *E. microps*, *C. lucasii*, *C. pyramidata* (mean 42 to 55%). Distinctly lower were the mean α_{Ice} estimates for adult *E. superba*, *T. macrura, C. propinquus*, *D. antarctica and S. thompsoni* (5 to 17%) based on the diatom-associated long-term FA 20:5n-3 and the dinoflagellate-associated long-term FA 22:6n-3, whereas the dinoflagellate-associated short-term FA 18:4n-3 suggested considerably higher mean α_{Ice} values for *E. superba*, *T. macrura, C. propinquus*, *and S. thompsoni* (36 to 51%). From all three models, the lowest input of ice algal carbon was generally suggested for *S. thompsoni* (mean 8 to 36%) (**Figure 4, Table V**).



▲***Figure 4.*** *Proportional contribution of ice algae-produced carbon α_{Ice} to the carbon budget of selected under-ice fauna species (mean ± 1 SD %). Shown are ecologically important representatives of Antarctic a) euphausiids, b) copepods, c) amphipods, d) gastropods, e) siphonophores and e) salps. The calculations were based on the isotopic composition of the storage-associated fatty acid 18:4n-3, representing the short-term trophic signal and the membrane-associated fatty acids 20:5n-3 and 22:6n-3, representing the long-term trophic signal. Euphausia superba in their first year (larvae, juveniles) were grouped as AC0 krill. Sample size is given in* ***Suppl. H****. 'nd' = not determined.*

▼**Table 5.** Proportional contribution of ice algae-produced carbon to the carbon budget of under-ice fauna species (mean %). Proportions are based on short-term fatty acid (FA) 18:4n-3, representing the recent trophic signal, and the long-term FAs 20:5n-3 and 22:6n-3, representing the older trophic signal. Sample size is given in **Table 4.** Not determined: '--'.

	Proportional contribution ice algal carbon (%) to body carbon	
Species	short-term trophic signal	long-term trophic signal
Euphausia superba- AC0	67	9 to 48
Euphausia superba- adult	51	5 to 10
Thysanoessa macrura	51	12 to 17
Calanus propinquus	49	6 to 7
Eusirus laticarpus	59	39 to 67
Eusirus microps	55	21 to 30
Cyllopus lucasii	42	13 to 18
Clione antarctica	50	4 to 14
Clio pyramidata	51	16 to 23
Spongiobranchea australis	--	19 to 21
Diphyes antarctica	--	8 to 14
Salpa thompsoni	36	8 to 13

AC0 *E. superba* from stations located close to ice camp 1 indicated higher α_{Ice} values compared to individuals close to ice camp 2, based on the short-term FA 18:4n-3 (**Suppl. H**)**.** Conversely, based on long-term FA 20:5n-3, higher α_{Ice} values were determined for ACO krill at stations close to ice camp 2 versus ice camp 1 (**Suppl. H**).

Carbon demand and sustainability of abundant species

Converting typical bottom ice algal biomass values of 4.5 mg Chl *a* m^{-2} during winter (Meiners et al. 2012) to carbon biomass using typical ice algae ratios of 20-40 mg C : mg Chl *a* (Arrigo et al. 2010), results in between 90-179 mg C m^{-2} of available carbon for under ice fauna during winter. Converting pelagic biomass of 0.15 mg Chl *a* m^{-3} (David 2016), which translates into 0.3 mg Chl *a* m^{-2} related to the top 2 m of the water column, to carbon biomass with typical pelagic algae ratios of 75 mg C : mg Chl *a* (Arrigo et al. 1998), suggests 22.5 mg C m^{-2} of pelagic carbon available during winter. Using winter (defined as June to September: 122 days) metabolic energy requirements of 23 μg C $ind.^{-1}$ d^{-1} for krill larvae (Pakhomov et al. 2004) and 10 μg C $ind.^{-1}$ d^{-1} for *C. propinquus* (Pakhomov and Froneman 2004), translates to an ice algae-derived carbon demand of 1.8 mg C ind^{-1} for krill larvae and 0.6 mg C ind^{-1} for *C. propinquus*. Based on these numbers, 4-8 times more individuals of these two species can be sustained by ice algae carbon versus pelagic-produced carbon during winter (**Table 6**).

▼**Table 6.** Sustainability of the most abundant under-ice fauna species during the sampling by ice algae-produced and pelagic algae-produced carbon. α_{Ice} = proportional contribution of ice algae-produced carbon derived from SIAR model based on fatty acid 18:4n-3.

	α_{Ice} (%)	**Total winter requirement** (mg C ind^{-1})	**Ice algae-derived carbon demand during winter** (mg C ind^{-1})	**Pelagic algae-derived carbon demand during winter** (mg C ind^{-1})	**Ind. sustained by ice algae carbon** (Ind. m^{-2})	**Ind. sustained by pelagic algae** (Ind. m^{-2})
Euphausia superba (larvae)	63	2.81	1.77	1.04	**87-172**	**22**
Calanus propinquus	49	1.22	0.60	0.62	**145-289**	**36**

Discussion

Food web structure based on fatty acid and stable isotope compositions

The particularly higher proportions of the diatom-associated FA 16:1n-7 and the higher biomarker ratios 16:1n-7/18:4n-3 and 20:5n-3/22:6n-3 (Dalsgaard et al. 2003; Bergé and Barnathan 2005) in I-POM versus P-POM confirmed the dominance of diatoms over dinoflagellates in I-POM (**Table 2**), as suggested in previous studies (Garrison and Close 1993; Lizotte 2001). In the P-POM samples, the FA distribution suggested a co-dominance of diatoms and dinoflagellates (Buck and Garrison 1983; Garrison et al. 1991). The lipid class and FA profiles in our investigated under-ice fauna species largely resembled the results from previous studies on these species (**Suppl. B and C**) (Kattner et al. 1998; Falk-Petersen et al. 1999, 2000; Phleger et al. 2001; Virtue et al. 2016). The proportions of the polyunsaturated FAs 20:5n-3 and 22:6n-3 were generally high in all species, but particularly elevated in young *Euphausia superba* and *Salpa thompsoni*, which is in agreement with previous studies (Cripps et al. 1999; Falk-Petersen et al. 2000; Phleger et al. 2000; Virtue et al. 2016). The high proportions of these two long-chain FAs can be explained by the high proportions of the membrane-associated lipid classes phosphatidylcholine and phosphatidylethanolamine, in which they are predominantly incorporated in (Virtue et al. 2016), as *E. superba* and *S. thompsoni* had the highest proportions of these membrane FAs in our study (**Suppl. B**). Except for *S. thompsoni,* all investigated species suggested a high assimilation of diatom-associated carbon based on the ratio 16:1n-7/18:4n-3, which was considerably > 1 in all species (**Figure 3**, **Suppl. D**). In contrast, the carbon source composition integrated over a longer time period was apparently rather a mix of diatom- and dinoflagellate-associated origin for most species, or a dominance of dinoflagellate-produced carbon particularly in *S. thompsoni*, based on the lower ratios of 20:5n-3/22:6n-3 in the long-term lipid pool.
In all species, the proportions of the *Calanus*-associated marker FAs 20:1n-9 and 22:1n-11 were relatively low, excluding extensive feeding on *Calanus* copepods in the weeks before the sampling. The presence of these marker FAs in all species, however, indicates a certain input of primary produced carbon by feeding on *Calanus* spp. in the weeks before the sampling (**Figure 2**, **Suppl. C**). For example, other copepods than *Calanus* spp., such as *Stephos longipes*, were frequently found in the stomachs of larval and juvenile *E. superba* (Schaafsma et al., under review) (**Chapter IV**), and Ctenocalanus in adult specimens from this expedition (F. Schaafsma, pers. commun.). Besides the two *Calanus*-associated FAs, the proportions of FA 18:1n-9 and the ratio of 18:1n-7/18:1n-9 were used in previous studies to estimate the degree of carnivory of a consumer (Sargent and Falk-Petersen 1988; Falk-Petersen et al. 2000). In animals with a carnivorous diet, the ratio is assumed to be below 0.5 (Nelson et al. 2000), which was the case for all three amphipod species and *Dipyhes antarctica* (**Suppl. D**). Besides fatty acid-derived information on the lifestyle of a consumer, the nitrogen stable isotope composition $\delta^{15}N$ indicates a consumer´s trophic position and feeding behavior within the investigated food web (DeNiro and Epstein 1981; Minagawa and Wada 1984; Vander

Zanden and Rasmussen 1999), where the algal communities represent the trophic baseline. Low δ^{15}N ratios in the consumer reflect herbivorous feeding behavior, whereas predators show higher ^{15}N concentrations and thus higher δ^{15}N ratios (Owens 1987). The δ^{15}N values for I-POM and P-POM were in the range of typical ice-associated and pelagic algal communities in the Southern Ocean from previous studies (Frazer 1996; Jia et al. 2016). However, our and previous results suggested a high variability of δ^{15}N values in POM from the Southern Ocean, possibly reflecting spatial and temporal changes in concentrations and isotopic abundance of ammonium (Wada 1980; Wada et al. 1987; Rau et al. 1991b). Due to the mostly low δ^{15}N values, we concluded predominantly herbivores and omnivores in our investigated food web, supporting the composition of carnivory markers in the consumers in our study (**Table 3, Suppl. C and D**). The δ^{15}N values in *Calanus propinquus* (mean CV: 2.5‰, mean female: 3.1‰) and *Clio pyramidata* (mean 2.6‰) were lower than in both I-POM and P-POM, which might indicate a certain degree of heterotrophy in the POM samples, but also reflects the predominantly herbivorous lifestyle of these species (Hopkins and Torres 1989; Phleger et al. 2001; Hunt et al. 2008). However, both species are known to ingest heterotrophic organisms as well (Hopkins 1985; Hopkins and Torres 1989). The lower δ^{15}N values in these two species might also reflect carbon sources ingested a longer time ago or over a longer time-span, originating from a different algae regime with different isotopic signatures of the primary producers than the one found in the current sampling area. Gymnosome pteropods such as *Clione antarctica* and *Spongiobranchea australis* are considered to prey specialized on thecosomes, such as *Limacina helicina* and *C. pyramidata* (Gilmer and Lalli 1990; Hunt et al. 2008), which agrees well with the higher δ^{15}N values in *C. antarctica* and *S. australis* compared to *C. pyramidata* in our study. The amphipod *Eusirus laticarpus* and the gastropod *S. australis* pointed to rather carnivorous feeding due to the comparably higher δ^{15}N values relative to the other species (**Table 3**). The low 18:1n-7/18:1n-9 ratios in the amphipods confirmed the elevated δ^{15}N values in particularly *E. laticarpus*, but in contrast, *S. australis* showed the lowest mean 18:1n-9 levels accompanied with the highest δ^{15}N value in this study. A possible explanation for the contraindication found in *S. australis* between the two methods, could be an increase in the ratio 18:1n-7/18:1n-9 during starvation. Besides, FA 18:1n-9 can be biosynthesized in large amounts by the prymnesiophytes *Phaeocystis* spp., and might be accumulated in the consumers (Dalsgaard et al. 2003 and references therein).

Variability in fatty acid and stable isotope compositions

There was a large variability in the fatty acid and stable isotope parameters between the I-POM samples from the two ice camps. The species composition in sea ice assemblages is a product of both physical and biological processes (Lizotte 2001). For example, the process of ice formation can have an impact on the ice-associated microalgal composition. The sea ice sampled at ice camps 1 and 2 might have been formed in different areas in the Southern Ocean, consequently affecting the algal species composition within the sea ice. The physical parameters of the two ice camps did not reveal distinct differences regarding ice thickness, snow thickness and Chl *a*

concentrations both of the sea ice and in the water column at nearby SUIT stations (David et al. 2017; K. Meiners unpubl. data). However, the roughness of the ice was somewhat higher at ice camp 1 versus ice camp 2, which might have favored certain algal groups over others. Furthermore, the variability in biomarker parameters might be the result of seasonal environmental changes, as ice camp 2 was sampled approximately two weeks later than ice camp 1 (**Figure 1**, **Table 1**). The higher $\delta^{13}C$ values in ice-associated algae versus pelagic algae are a result of a CO_2 limitation in the sea ice environment versus the water column (Fry 1996). The onset of spring was apparently accompanied by enhanced ice melting, causing a decrease of ^{13}C within the sea ice due to a less restricted CO_2 environment, which might explain the lower $\delta^{13}C$ values in the I-POM samples from ice camp 2, which were located close to the ice edge, compared to ice camp 1. Due to the variability in fatty acid compositions in I-POM, also within the same ice camp, and P-POM, the observed variability in fatty acids of the under-ice fauna species between the different locations was probably driven by a spatial and temporal variability in both, ice-associated and pelagic algal communities.

The higher proportions of the dinoflagellate-associated FA 18:4n-3 in combination with a stronger dinoflagellate signal from the short-term fatty acid ratio 16:1n-7/18:4n-3 indicated a higher impact of dinoflagellate-derived carbon in the recent past in young *E. superba* located at ice-free stations and stations in close proximity to the ice edge compared to the ice-covered stations close to ice camps 1 and 2. The ingestion of secondary carbon was enhanced in *E. superba* at the northernmost stations based on higher $\delta^{15}N$ values, indicating a stronger dependence on heterotrophic food sources in regions where ice-associated microalgae might not be abundant enough or too difficult to access to meet the nutritional requirements of the animals. The high variability of fatty acid and stable isotope compositions in young krill suggest that the carbon source and diet composition of this species are highly variable and changes with changing sea ice conditions and thus food availability when the winter season progresses (Schaafsma et al., under review) (**Chapter IV**).

Contribution of ice algal carbon to the carbon budget of the under-ice fauna species

In our study, young Antarctic krill and the amphiod *Eusirus laticarpus* indicated the highest trophic dependency on ice algae-produced carbon (**Figure 4**, **Table 5**). Reports on Antarctic eusirids are rather rare and concrete numbers on the composition of their carbon sources do not exist. Before acknowledged as individual species by de Broyer and Jazdzewski (1993), *E. laticarpus* was included into the species *E. antarcticus* due to a similar morphology, and, thus, for findings on *E. laticarpus* was most likely not accounted before that time. In the recent past, the close connectivity of *E. laticarpus* with the sea ice was observed frequently. For example, Krapp et al. (2008) reported the presence of eusirid amphipods under the pack ice of the Weddell Sea and the Lazarev Sea and suggested that the underside of Antarctic pack ice might serve as a habitat for eusirids. The consistently high contribution of ice algal carbon to the body carbon of *E. laticarpus* from all three models (mean 39 to 67% of body carbon) confirmed that this species played a generally important role for the energy transfer between the sympagic

and pelagic food web, both during our sampling and also in the weeks and months before that (Flores et al. 2011).

Although dependence of young Antarctic krill *E. superba* on ice algae has been suggested by earlier authors (Daly 1990; Frazer et al. 2002; Meyer et al. 2009), our data are the first to properly quantify this. Young Antarctic krill was found to rely for about 69% on ice algae-produced carbon to survive the winter (**Figure 4, Table 5**). A lower ice dependence was observed in adult krill, but likely ice algae also become more important to them when winter progresses and their older lipid storages become depleted, which was indicated by the higher α_{Ice} values derived from 18:4n-3 (mean 51%) compared to the long-term-associated FAs 20:5n-3 and 22:6n-3 (mean 5 to 10%). We found a spatial variability in the utilization of ice algal carbon in young Antarctic krill between stations sampled earlier in the winter season close to ice camp 1 and stations sampled later in the season located farther north closer to the sea ice edge (**Suppl. H**). Accordingly, ice algae-produced carbon contributed to about 78% to the carbon budget of AC0 krill in the more southern stations, whereas the dependency on ice algal carbon was approximately 25% less in individuals sampled farther north, based on short-term FA 18:4n-3. This confirms the stronger dinoflagellate signal derived from the fatty acid compositions at stations farther north, suggesting a less sea ice-associated and more heterotrophic lifestyle of krill when other food sources than ice algal carbon become more abundant, triggered by enhanced melting and pelagic productivity at the onset of spring. Furthermore, the α_{Ice} estimates revealed that the utilization of sympagic carbon increased stronger in AC0 krill from stations in close proximity to ice camp 1 versus 1 camp 2 during the winter season, based on the α_{Ice} estimates derived from 18:4n-3 versus 20:5n-3 and 22:6n-3 (**Suppl. H**). This highlights the importance of ice algal carbon for the overwintering of young krill with great distance to open water areas and thus a strong limitation of pelagic food sources. The low spatial variability in adult krill between the different locations suggests an overwintering strategy largely independent from environmental parameters.

All other investigated species suggested a rather marginal trophic dependency on ice algae-produced carbon based on the more conserved membrane-associated fatty acids 20:5n-3 and 22:6n-3 (**Figure 4, Table 5**), likely reflecting the assimilation of predominantly pelagic food sources in autumn. However, the estimates of the proportional contribution of ice algae-produced carbon α_{Ice} in the short-term fatty acid 18:4n-3 indicated a remarkable increase in the utilization of sympagic food sources by these species as winter progressed, which was in agreement with the increased proportions of diatom-associated versus dinoflagellate-associated FAs in younger versus older lipid pool. Hence, during our sampling period, between 36 and 69% of the carbon demand of our investigated species was covered by ice algae production, indicating a surprisingly high significance of ice-associated food sources for species frequently described as predominantly relying on pelagic food sources. However, for the majority of our investigated species a certain association with sea ice at least during winter has been observed in the past. For example, the euphausiid *T. macrura* is often found at larger depths, but the occurrence of *T. macrura* underneath sea-ice of the closed pack-ice

zone in the northern Weddell Sea points to a certain association with the sympagic food web (Siegel et al. 1992; Kaufmann et al. 1995; Donnelly et al. 2006). During our study, numbers of *T. macrura* in the upper two meter of the water column under ice were low (David et al. 2017), confirming their more pelagic life style. *T. macrura* are assumed to utilize their large wax ester storage when the water column is depleted in food sources and, thus, with little urge to feed directly or indirectly via zooplankton on sea ice algae for overwintering. The surprisingly high α_{Ice} estimates based on the more recent lipid pool (mean 51%) compared to the estimates derived from the membrane-associated FAs (12 to 17%) shows that prey linked to sea ice-associated production might have an underestimated role and become important for *T. macrura* during winter, despite their presumed pelagic life style and reliance on lipid storage for winter survival.

For *C. propinquus*, it has been frequently suggested that a portion of the copepod population remains in surface waters throughout the year to feed actively under the sea ice during winter, on ice algae, detritus or metazoans associated with the sea ice (Hopkins and Torres 1989; Schnack-Schiel et al. 1991; Bathmann et al. 1993; Kattner et al. 1994). We caught *C. propinquus* from directly underneath the ice in high numbers, and our α_{Ice} estimates support the assumption that they turn to sympagic carbon sources from autumn (mean 6 to 7%, based on FAs 20:5n-3 and 22:6n-3) to winter (mean 49%, based on 18:4n-3) (**Figure 4, Table 5**).

Fisher et al. (2004) suggested a switch from a pelagic to a sympagic lifestyle in association with the availability of sea ice for the amphipod *E. microps*. In contrast, the amphipod *C. lucasii* was found in significant higher numbers in open water than under ice, based on abundance data during different seasons (Flores et al. 2011). Lancraft et al. (1991) reported generally full guts consisting of gelatinous food (siphonophores and salps) for *C. lucasii* during winter in the Weddell-Scotia Confluence, suggesting continuous feeding during winter. In contrast, Torres et al. (1994) found a significant drop in metabolism in *C. lucasii* during winter in the Scotia-Weddell Sea region and suggested starvation in the winter months for this species. The stable isotope data of *E. microps* and *C. lucasii* suggested continuous feeding and reflected that the importance of ice algal carbon increased during winter (mean 42 to 55% of body carbon), while the assimilation of ice algae-produced carbon was distinctly lower compared to *E. laticarpus* based on the older lipid pool (mean 13 to 30% of body carbon) (**Figure 4, Table 5**).

A certain association with the sympagic system was also suggested for the pteropods C. *antarctica* and *C. pyramidata* from relatively high densities under the sea ice during winter (Flores et al. 2011). C. *antarctica* is believed to prey predominantly on another thecosome pteropod, *Limacina helicina* (Conover and Lalli 1974). In the Arctic, the bipolar *L. helicina* was found to rely on the pelagic phytoplankton bloom in summer and on sea ice-derived organic matter in winter (Kobayashi 1974; Gannefors et al. 2005). Derived from that, a similar behavior might be expected in the Southern Ocean, leading consequently to an aggregation of C. *antarctica* close to the sea ice (Flores et al. 2011). Both *C. pyramidata* and the third pteropod species *S. australis* indicated a moderate assimilation of ice algal carbon based on FAs 20:5n-3 and 22:6n-3 (mean 16 to 23% of the body carbon), which was somewhat higher than in *C. antarctica* (mean 4 to 14% of

the body carbon), and increased in *C. antartica* and *C. pyramidata* as the winter period progressed based on the isotopic signal from FA 18:4n-3 to ~ 50% ice algal carbon of the body carbon (**Figure 4, Table 5**).

During winter, high quantities of food in the guts of the tunicate *S. thompsoni* were found, revealing predominantly phytoplankton, but also copepods (Lancraft et al. 1991), indicating that this species is able to continue feeding successfully even when the phytoplankton concentration is low (Hopkins 1985). Based on our calculations, the contribution of ice algal carbon to the diet of *S. thompsoni* based on the membrane fatty acids was insignificant (mean 8 to 13% of the body carbon), but increased with progressing winter season (mean 36% of body carbon) (**Figure 4, Table 5**). A significant trophic association of *D. antarctica* and ice algae, at least on long-term, could not be revealed with our data according to the low α_{Ice} values based on 20:5n-3 and 22:6n-3 (mean 8 to 14%).

In the northern Weddell Sea, the pelagic primary production during winter is very low (Comiso et al. 1993). A productivity of 1.3 mg C m^{-2} d^{-1} in the water column and 12 mg C m^{-2} d^{-1} in sea ice during late winter, as suggested by Kottmeier and Sullivan (1987), indicates that the available biomass of pelagic carbon is insufficient to satisfy the energy demands of the Antarctic food web during winter, whereas the available ice algae carbon might be sufficient to supply enough food for species that feed year-round (Lizotte 2001; McMinn et al. 2010). Our estimation of the number of individuals that can potentially be sustained by ice algae far exceeded the individuals that could be sustained by pelagic algae (**Table 6**), which highlights the importance of sympagic-derived carbon particularly during the winter season, not only for the lower trophic levels, but for the entire food web (van Franeker et al. 1997). However, the Antarctic sea ice cover is predicted to experience shrinkage by over 30% over the next 100 years in climate models due to increasing CO_2 concentrations (Rind et al. 1997; Meehl et al. 2000; Gutt et al. 2015). Accompanied with a shrinking sea ice cover, sea ice primary production is expected to drop simultaneously. Arrigo and Thomas (2004) estimated that a 50% loss in sea ice cover could result in a 86% loss in annual sea ice primary production. This loss of primary produced carbon can likely not be buffered by the expected increase in pelagic productivity (Arrigo and Thomas 2004; Vancoppenolle et al. 2013) due to the high carbon demand that pelagic algae would have to cover, when the abundances of ice algae decrease.

Conclusions

Integrated over different time scales, fatty acid and stable isotope compositions indicated that ecologically important Antarctic zooplankton temporally switched their diet from predominantly pelagic sources to a strong association with ice-associated carbon sources. The surprisingly high dependency of ecologically important pelagic carbon transmitters on ice algal carbon, such as *Euphausia superba* and *Calanus propinquus*, highlights the significant role of sea ice for the functionality and trophic dynamics of the food web in the Southern Ocean during winter, when pelagic algal biomass is critically depleted and ice algae represent an important food source meeting

the organisms' energy demands. Hence, a shrinking sea ice coverage and, thus, changing sea ice environment and ecosystem dynamics might have important consequences for the entire Antarctic food web. Minimal pelagic algal biomass during winter further enhances the threat in terms of insufficient food supply to species with the requirement to feed constantly, subsequently affecting overall species populations.

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Supplementary

▼**Supplementary A.** Length, dry mass, total lipid content (TLC) by dry mass, and fatty acid content (FAC) by dry mass in under-ice fauna species (mean ± 1 SD). Not detected: '--'.

Species	sex/stage	Ind./sample	Length (mm)	Dry mass/Ind. (mg)	FAC/dry mass (%)
Euphausia superba	larva	5 ± 3	11.4 ± 1.6	2.5 ± 3.1	8.5 ± 10.2
	juvenile	4 ± 3	25.1 ± 7.8	19.0 ± 18.0	5.1 ± 7.0
	adult	1	42.7 ± 8.3	108.9 ± 81.8	7.0 ± 3.5
Thysanoessa macrura	--	3 ± 3	47.5 ± 10.6	69.7 ± 87.5	7.0 ± 1.1
Calanus propinquus	CV	6 ± 2	4.2 ± 0.1	0.4 ± 0.1	--
	female	8.1 ± 2.4	5.4 ± 0.1	2.0 ± 1.2	5.1 ± 4.2
Eusirus laticarpus	--	4 ± 3	--	17.9 ± 15.2	5.3 ± 3.5
Eusirus microps	--	2 ± 1	--	13.5 ± 9.7	7.8 ± 5.1
Cyllopus lucasii	--	1	--	55.0 ± 13.5	5.7 ± 4.1
Clione antarctica	--	1	--	43.3 ± 21.5	7.0 ± 2.8
Clio pyramidata	--	1	--	69.5 ± 66.5	4.2 ± 4.8
Spongiobranchea australis	--	1	--	47.4 ± 30.2	7.5 ± 0.8
Diphyes antarctica	--	1	--	39.9 ± 29.2	12.7 ± 3.4
Salpa thompsoni	--	1	46.3 ± 18.6	30.2 ± 18.2	--

▼**Supplementary B.** Proportions of most abundant lipid classes (LCs) in under-ice fauna species (mean ± 1 SD mass % of total lipid content). Not detected LCs are marked as '--'. The pteropod *Clione limacina antarctica* E. A. Smith (1902) was referred to as *Clione antarctica* (Gilmer and Lalli 1990).

Species	*n*	sex/stage	TAG	WE	PE	PC
	7	larva	12.2 ± 10.0	0.1 ± 0.3	19.8 ± 5.0	42.1 ± 7.8
Euphausia superba	9	juvenile	20.3 ± 13.1	0.1 ± 0.2	17.8 ± 6.2	42.4 ± 3.4
	7	adult	39.4 ± 10.8	0.1 ± 0.1	9.6 ± 3.7	41.2 ± 5.0
Thysanoessa macrura	5	--	0.5 ± 0.5	37.1 ± 31.0	11.7 ± 12.9	41.4 ± 12.2
Calanus propinquus	9	female	58.9 ± 27.7	--	9.1 ± 6.5	14.6 ± 12.4
Eusirus laticarpus	7	--	40.8 ± 9.5	30.9 ± 18.6	4.1 ± 1.8	8.2 ± 4.3
Eusirus microps	2	--	52.4 ± 8.7	12.8 ± 16.0	5.6 ± 2.6	14.3 ± 9.2
Cyllopus lucasii	4	--	47.2 ± 27.4	3.7 ± 6.2	9.6 ± 6.9	16.5 ± 11.1
Clione antarctica	4	--	86.7 ± 1.5	0.6 ± 0.7	1.4 ± 1.0	6.2 ± 1.7
Clio pyramidata	2	--	51.5 ± 43.3	--	9.6 ± 13.5	19.4 ± 15.7
Spongiobranchea australis	3	--	53.5 ± 19.6	--	8.2 ± 3.7	23.8 ± 6.8
Diphyes antarctica	6	--	24.4 ± 15.7	4.4 ± 4.9	2.5 ± 3.8	16.0 ± 7.2
Salpa thompsoni	4	--	1.4 ± 2.7	--	3.9 ± 4.7	45.8 ± 10.5

NL: neutral lipids, PC: phosphatidylcholines, PE: phosphatidylethanolamines, TAG: triacylglycerols, WE: wax esters

▼**Supplementary C.** Proportions of marker fatty acids (FAs) under-ice fauna species (mean ± 1 SD mass % of total fatty acids). Not detected FAs are marked as '--'. The FAs 16:1n-7 and 18:4n-3 represent short-term storage FAs, the FAs 20:5n-3 and 22:6n-3 represent long-term membrane FAs.

Species	***n***	**Sex/stage**	**diatom-associated marker FA**		**dinoflagellate-associated marker FA**		***Calanus*- associated marker FA**		**Carnivory marker FA**	
			16:1n-7	20:5n-3	18:4n-3	22:6n-3	20:1n-9	22:1n-11	18:1n-9	18:1n-7
	14	larva	4.1 ± 1.3	27.2 ± 5.3	2.1 ± 1.3	22.2 ± 5.4	0.9 ± 0.5	--	6.3 ± 2.6	7.0 ± 1.2
Euphausia superba	19	juvenile	4.3 ± 1.2	26.1 ± 4.4	2.7 ± 1.1	18.7 ± 4.5	0.8 ± 0.5	0.2 ± 0.5	7.7 ± 2.4	6.4 ± 0.9
	26	adult	6.7 ± 2.1	16.1 ± 2.6	1.8 ± 0.9	11.2 ± 3.7	0.9 ± 0.4	0.6 ± 0.3	12.5 ± 1.3	7.2 ± 0.6
Thysanoessa macrura	5	--	2.3 ± 0.9	18.4 ± 5.1	0.6 ± 0.1	19.4 ± 10.1	1.6 ± 0.6	0.3 ± 0.3	10.5 ± 2.5	4.8 ± 0.5
Calanus propinquus	9	female	5.3 ± 1.8	11.9 ± 7.3	0.8 ± 0.5	16.4 ± 9.9	2.0 ± 0.9	13.3 ± 7.4	4.1 ± 3.1	1.8 ± 0.6
Eusirus laticarpus	8	--	6.5 ± 2.2	16.3 ± 4.6	1.3 ± 0.5	14.6 ± 3.7	3.8± 1.9	1.4 ± 1.2	19.3 ± 3.8	4.7 ± 1.3
Eusirus microps	2	--	7.9 ± 2.4	18.2 ± 4.2	1.1 ± 0.1	16.3 ± 2.2	2.8 ± 1.3	0.7 ± 0.4	19.5 ± 5.9	5.9 ± 0.9
Cyllopus lucasii	4	--	4.7 ± 3.8	17.3 ± 8.4	4.9 ± 5.4	21.7 ± 7.1	5.2 ± 3.6	0.8 ± 1.0	14.0 ± 12.2	4.6 ± 3.3
Clione antarctica	4	--	16.2 ± 2.0	14.1 ± 2.5	3.0 ± 1.0	10.2 ± 1.7	2.3 ± 0.2	0.1 ± 0.2	3.7 ± 0.7	4.5 ± 0.9
Clio pyramidata	2	--	4.6 ± 2.0	25.6 ± 1.9	3.6 ± 4.0	17.8 ± 3.5	1.7 ± 0.2	--	4.6 ± 4.1	2.8 ± 1.3
Spongiobranchea australis	3	--	4.7 ± 0.4	19.3 ± 3.4	0.4 ± 0.4	24.8 ± 3.3	2.7 ± 0.3	--	2.2 ± 0.3	4.2 ± 0.4
Dipyhes antarctica	6	--	6.9 ± 3.4	13.2 ± 0.9	0.8 ± 0.5	20.1 ± 1.4	3.6 ± 1.7	1.0 ± 0.1	14.4 ± 2.3	2.8 ± 0.4
Salpa thompsoni	4	--	2.5 ± 1.0	20.6 ± 1.7	4.9 ± 1.9	32.5 ± 3.8	1.6 ± 0.3	0.3 ± 0.4	3.4 ± 0.6	2.4 ± 0.5

▼**Supplementary D.** Fatty acid biomarker ratios in under-ice fauna species. The fatty acids 16:1n-7 and 20:5n-3 represent diatom-associated marker FAs, the FAs 18:4n-3 and 22:6n-3 represent dinoflagellate-associated marker FAs.

Species	***n***	**Sex/stage**	**16:1n-7/18:4n-3** Diatom-dinoflagellate ratio in short-term storage lipids	**20:5n-3/22:6n-3** Diatom-dinoflagellate ratio in long-term membrane lipids	**18:1n-7/18:1n-9** Carnivory ratio, decreasing with increasing carnivory
Euphausia superba	14	larva	2.3 ± 1.3	1.3 ± 0.7	1.1 ± 0.2
	19	juvenile	1.8 ± 0.9	1.4 ± 0.3	0.9 ± 0.3
	26	adult	5.5 ± 4.9	1.5 ± 0.4	0.6 ± 0.1
Thysanoessa macrura	5	--	4.4 ± 2.6	1.1 ± 0.3	0.5 ± 0.1
Calanus propinquus	9	female	8.2 ± 4.6	0.7 ± 0.2	0.6 ± 0.3
Eusirus laticarpus	8	--	5.2 ± 1.2	1.1 ± 0.3	0.2 ± 0.1
Eusirus microps	2	--	7.3 ± 2.4	1.1 ± 0.1	0.3 ± 0.1
Cyllopus lucasii	4	--	8.2 ± 13.4	0.8 ± 0.3	0.4 ± 0.1
Clione antarctica	4	--	5.7 ± 1.5	1.4 ± 0.5	1.2 ± 0.1
Clio pyramidata	2	--	2.6 ± 2.3	1.5 ± 0.4	0.8 ± 0.5
Spongiobranchea australis	3	--	7.0 ± 4.1	0.8 ± 0.2	1.9 ± 0.4
Diphyes antarctica	6	--	7.3 ± 1.8	0.7 ± 0.1	0.2 ± 0.1
Salpa thompsoni	4	--	0.5 ± 0.1	0.6 ± 0.1	0.7 ± 0.2

▼**Supplementary E.** Proportions of marker fatty acids (FAs) in under-ice fauna species (mean ± 1 SD mass % of total fatty acids) from the different locations. Not detected FAs are marked as '--'.

Species	Location	Fatty acid (%)			
		16:1n-7	18:4n-3	20:5n-3	22:6n-3
Euphausia superba larva	a) ice-free			--	
	b) ice camp 1 (*n* = 2)	5.5 ± 2.8	1.6 ± 0.1	28.9 ± 2.5	17.8 ± 3.2
	c) ice camp 2 (*n* = 7)	3.6 ± 1.2	1.1 ± 0.6	24.3 ± 6.2	26.8 ± 3.3
	d) north (*n* = 5)	4.2 ± 0.2	3.7 ± 0.2	30.5 ± 0.8	17.5 ± 0.4
	ANOVA *p**	--	**	--	**
Euphausia superba juvenile	a) ice-free (*n* = 1)	1.2	2.0	23.8	33.3
	b) ice camp 1 (*n* = 10)	4.9 ± 0.8	2.4 ± 1.0	24.2 ± 4.8	16.9 ± 2.3
	c) ice camp 2 (*n* = 1)	2.7	1.6	25.7	25.9
	d) north (*n* = 7)	4.1 ± 0.6	3.5 ± 1.1	29.2 ± 2.4	18.1 ± 1.8
	ANOVA *p**	*	*	*	--
Euphausia superba adult	a) ice-free			--	
	b) ice camp 1 (*n* = 16)	7.0 ± 1.9	2.2 ± 0.8	15.4 ± 2.1	10.2 ± 3.3
	c) ice camp 2			--	
	d) north (*n* = 10)	6.2 ± 2.3	1.2 ± 0.5	17.2 ± 2.9	12.9 ± 3.9
	ANOVA *p**	--	**	--	--
Thysanoessa macrura	a) ice-free (*n* = 2)	1.3 ± 0.1	0.7 ± 0.1	23.3 ± 0.8	30.5 ± 1.7
	b) ice camp 1			--	
	c) ice camp 2 (*n* = 3)	2.9 ± 0.5	0.5 ± 0.2	15.1 ± 3.3	12.0 ± 2.5
	d) north			--	
Calanus propinquus female	a) ice-free			--	
	b) ice camp 1 (*n* = 3)	6.7 ± 0.9	0.8 ± 0.3	9.2 ± 0.8	11.0 ± 2.3
	c) ice camp 2 (*n* = 4)	4.5 ± 1.9	0.3 ± 0.2	7.4 ± 4.0	13.1 ± 7.6
	d) north (*n* = 2)	3.6 ± 0.1	1.6 ± 0.1	24.2 ± 1.2	32.3 ± 0.4
	ANOVA *p**	--	*	**	**
Eusirus laticarpus	a) ice-free			--	
	b) ice camp 1 (*n* = 4)	6.0 ± 3.2	1.2 ± 0.8	13.7 ± 5.3	13.4 ± 3.8

	c) ice camp 2 (*n* = 3)	7.1 ± 0.5	1.5 ± 0.2	18.2 ± 0.8	15.6 ± 4.6
	d) north (*n* = 1)	6.4	1.4	21.4	16.4
	ANOVA *p**	--	--	--	--
Eusirus microps	a) ice-free			--	
	b) ice camp 1			--	
	c) ice camp 2 (*n* = 2)	7.9 ± 2.4	1.1 ± 0.1	18.2 ± 4.2	16.3 ± 2.2
	d) north			--	
Cyllopus lucasii	a) ice-free			--	
	b) ice camp 1 (*n* = 3)	4.4 ± 4.6	1.2 ± 1.8	15.3 ± 9.0	22.4 ± 8.6
	c) ice camp 2			--	
	d) north (*n* = 1)	5.6	11.7	23.4	19.6
Clione antarctica	a) ice-free			--	
	b) ice camp 1 (*n* = 2)	17.1 ± 2.8	3.3 ± 1.2	15.9 ± 1.6	9.0 ± 0.9
	c) ice camp 2 (*n* = 1)	14.9	3.4	13.7	10.5
	d) north (*n* = 1)	15.5	2.0	11.0	12.4
Clio pyramidata	a) ice-free			--	
	b) ice camp 1			--	
	c) ice camp 2 (*n* = 2)	4.6 ± 2.0	3.6 ± 4.0	25.6 ± 1.9	17.8 ± 3.5
	d) north			--	
Spongiobranchea australis	a) ice-free			--	
	b) ice camp 1 (*n* = 1)	5.0	--	16.5	28.3
	c) ice camp 2 (*n* = 2)	4.5 ± 0.5	0.7 ± 0.1	20.7 ± 3.5	23.0 ± 1.8
	d) north			--	
Diphyes antarctica	a) ice-free			--	
	b) ice camp 1 (*n* = 3)	9.9 ± 0.7	1.2 ± 0.1	13.3 ± 1.3	19.7 ± 1.2
	c) ice camp 2 (*n* = 2)	4.6 ± 1.2	0.4 ± 0.6	13.0 ± 0.1	21.2 ± 1.7
	d) north (*n* = 1)	2.4	0.5	13.4	19.1
Salpa thompsoni	a) ice-free			--	
	b) ice camp 1			--	
	c) ice camp 2 (*n* = 3)	2.0 ± 0.1	3.9 ± 0.5	21.1 ± 1.8	34.3 ± 0.6

d) north (n = 1)	4.0	7.7	19.3	26.9

*ANOVA p: ns = $p > 0.05$; * $0.05 < p < 0.01$; ** $0.01 < p < 0.001$

▼**Supplementary F.** Bulk nitrogen ($\delta^{15}N$) and carbon stable isotope values ($\delta^{13}C$), and fatty acid-specific $\delta^{13}C$ values in I-POM and P-POM (mean ± 1 SD ‰).

Algal community	***n***	**Bulk $\delta^{15}N$**	**Bulk $\delta^{13}C$**	***n***	**$\delta^{13}C$ 16:1n-7** Diatom-associated FA in short-term storage lipids	**$\delta^{13}C$ 18:4n-3** Dinoflagellate-associated FA in short-term storage lipids	**$\delta^{13}C$ 20:5n-3** Diatom-associated FA in long-term membrane lipids	**$\delta^{13}C$ 22:6n-3** Dinoflagellate-associated FA in long-term membrane lipids
I-POM	14	4.1 ± 2.8	-22.2 ± 4.3	14	-23.5 ± 5.8	-31.1 ± 6.0	-28.7 ± 3.1	-23.5 ± 3.4
P-POM	6	3.2 ± 3.0	-28.2 ± 0.5	7	-28.6 ± 3.0	-44.6 ± 3.3	-34.8 ± 2.5	-32.7 ± 1.5

▼**Supplementary G.** Bulk nitrogen ($\delta^{15}N$) and carbon stable isotope values ($\delta^{13}C$), and fatty acid-specific $\delta^{13}C$ values in under-ice fauna species from the different locations (mean ± 1 SD ‰). Not detected values marked as '--'.

Species	Location	Stable isotope values (‰)							
		n	bulk $\delta^{15}N$	bulk $\delta^{13}C$	*n*	$\delta^{13}C$ 16:1n-7	$\delta^{13}C$ 18:4n-3	$\delta^{13}C$ 20:5n-3	$\delta^{13}C$ 22:6n-3
Euphausia superba larva	a) ice-free	0		--	0			--	
	b) ice camp 1	9	3.4 ± 0.3	-24.4 ± 0.7	2	-33.8 ± 3.1	-31.8	-31.2 ± 0.4	-31.6 ± 0.1
	c) ice camp 2	4	2.6 ± 0.6	-26.2 ± 1.3	3	-26.8 ± 7.6	-36.7 ± 2.3	-30.8 ± 0.9	-33.3 ± 0.6
	d) north	7	4.1 ± 0.3	-24.5 ± 0.3	1	-32.1	-34.8	-30.3	-32.6
	ANOVA *p**		**	*		--	--	--	--
Euphausia superba juvenile	a) ice-free	1	2.7	-26.7	1	-36.8	-34.4	-33.5	-30.2
	b) ice camp 1	16	3.5 ± 0.6	-26.6 ± 2.2	5	-33.1 ± 2.5	-34.2 ± 1.7	-31.9 ± 1.2	-32.0 ± 1.8
	c) ice camp 2	0		--	1	-29.5	--	-32.4	-32.1
	d) north	3	4.0 ± 0.2	-25.3 ± 1.2	1	-31.9	-33.2	-30.8	-31.0
	ANOVA *p**		--	--		--	--	--	--
Euphausia superba adult	a) ice-free	0		--	0			--	
	b) ice camp 1	5	4.2 ± 1.0	-28.7 ± 0.9	6	-39.0 ± 2.2	-37.5 ± 1.0	-36.4 ± 2.0	-33.2 ± 1.0
	c) ice camp 2	0		--	0			--	
	d) north	4	4.8 ± 0.6	-28.6 ± 2.7	3	-37.9 ± 1.7	-36.7 ± 0.3	-35.0 ± 0.7	-33.2 ± 0.6
	ANOVA *p**		--	--		--	--	--	--
Thysanoessa macrura	a) ice-free	1	3.3	-26.2	2	-39.9 ± 1.9	-37.7	-32.9 ± 0.6	31.1 ± 1.3
	b) ice camp 1	0		--	0			--	
	c) ice camp 2	1	6.8	-32.5	3	-43.4 ± 7.5	--	-36.8 ± 0.8	35.1 ± 0.9
	d) north	0		--	0			--	
Calanus propinquus female	a) ice-free	0		--	0			--	
	b) ice camp 1	4	2.2 ± 1.0	-29.3 ± 0.8	3	-35.6 ± 2.3	-38.5	-35.9 ± 0.9	-33.2 ± 1.0
	c) ice camp 2	3	2.3 ± 1.7	-29.3 ± 0.4	2	-38.2 ± 2.1	--	-36.3 ± 1.0	-33.9 ± 1.4
	d) north	4	3.6 ± 0.6	-28.4 ± 1.0	2	-35.5 ± 0.3	-37.1	-36.0 ± 0.1	-34.0 ± 0.6
	ANOVA *p**		--	--		--	--	--	--
Calanus propinquus CV	a) ice-free	0		--				--	
	b) ice camp 1	1	0.8	-28.6					

	c) ice camp 2	2	3.3 ± 0.1	-29.4 ± 1.0				
	d) north	0		--				
Eusirus laticarpus	a) ice-free	0		--	0		--	
	b) ice camp 1	6	6.2 ± 1.5	-23.8 ± 2.5	5	-29.4 ± 2.2	-34.0 ± 0.2	-30.3 ± 1.4	-29.0 ± 0.7
	c) ice camp 2	0		--	0		--	
	d) north	2	5.6 ± 0.1	-25.2 ± 0.1	0		--	
	ANOVA *p**		--	--			--	
Eusirus microps	a) ice-free	0			0		--	
	b) ice camp 1	0			0		--	
	c) ice camp 2	1	4.4	-25.8	2	-34.0 ± 2.4	-35.7 ± 1.7	-34.1 ± 0.4	-31.9 ± 0.1
	d) north	0			0		--	
Cyllopus lucasii	a) ice-free	0			0		--	
	b) ice camp 1	1	4.6	-27.8	3	-35.0 ± 0.7	-39.9	-34.0 ± 0.4	-32.8 ± 0.7
	c) ice camp 2	0		--	0		--	
	d) north	1	4.3	-27.6	1	-39.9	-40.2	-36.0	-33.7
Clione antarctica	a) ice-free	0		--	0		--	
	b) ice camp 1	3	4.3 ± 1.2	-29.7 ± 1.1	2	-33.6 ± 0.4	-35.8 ± 1.7	-36.1 ± 0.7	-32.0 ± 0.2
	c) ice camp 2	2	4.9 ± 0.9	-31.7 ± 0.6	1	-36.1	-40.1	-37.8	-34.3
	d) north	0		--	1	-35.6	-38.9	-37.6	-34.0
Clio pyramidata	a) ice-free	0		--	0		--	
	b) ice camp 1	0		--	0		--	
	c) ice camp 2	1	2.6	-26.5	2	-38.0 ± 2.5	-37.4 ± 0.2	-34.6 ± 1.1	-31.9 ± 1.8
	d) north	0		--	0		--	
Spongiobranchea australis	a) ice-free	0		--	0		--	
	b) ice camp 1	0		--	1	-33.8	--	-35.2	-32.6
	c) ice camp 2	1	6.9	-29.8	2	-37.8 ± 4.5	--	-33.7 ± 0.9	-31.9 ± 0.1
	d) north	0		--	0		--	
Diphyes antarctica	a) ice-free	0		--	0		--	
	b) ice camp 1	3	5.3 ± 0.2	-27.2 ± 0.3	3	-33.4 ± 1.4	--	-34.8 ± 1.0	-33.8 ± 0.6
	c) ice camp 2	1	4.9	-28.9	2	-34.2	--	-35.4 ± 0.6	-34.2 ± 0.4

Salpa thompsoni	d) north	0	--	1	--	--	-34.4	-33.4
	a) ice-free	0	--	0		--		
	b) ice camp 1	2	2.8 ± 0.7	-29.1 ± 0.7	0		--	
	c) ice camp 2	3	4.2 ± 0.9	-30.0 ± 0.4	3	-38.1 ± 2.3	-39.5 ± 0.5	-35.4 ± 0.9	-32.3 ± 0.2
	d) north	0	--		1	-39.2	-40.4	-36.5	-33.7

*ANOVA *p*: ns = $p > 0.05$; * $0.05 < p < 0.01$; ** $0.01 < p < 0.001$

▼**Supplementary H.** Proportional contribution of ice algae-produced carbon α_{Ice} to the carbon budget of under-ice fauna species (mean %), grouped after locations close to ice camp 1 (B-D) and locations close to ice camp 2 (E-F). Proportions are based on short-term fatty acid (FA) 18:4n-3, representing the recent trophic signal, and the long-term FAs 20:5n-3 and 22:6n-3, representing the older trophic signal. Sample size is given in **Table 4.** Not determined: '--'.

	Proportional contribution ice algal carbon α_{Ice} to body carbon (%)					
	18:4n-3		20:5n-3		22:6n-3	
Species	locations B-D	locations E-F	locations B-D	locations E-F	locations B-D	locations E-F
Euphausia superba- AC0	78 ± 11	54 ± 15	43 ± 16	64 ± 13	17 ± 9	12 ± 6
Euphausia superba- adult	50 ± 13	48 ± 19	4 ± 3	6 ± 5	7 ± 4	10 ± 5
Thysanoessa macrura	--		--	7 ± 3	--	5 ± 3
Calanus propinquus- female	52 ± 22	53 ± 19	7 ± 3	17 ± 12	15 ± 12	8 ± 5
Eusirus laticarpus	61 ± 23	--	59 ± 19	--	55 ± 10	--
Eusirus microps	--	52 ± 22	--	41 ± 23	--	32 ± 22
Cyllopus lucasii	47 ± 22	37 ± 21	7 ± 5	30 ± 21	15 ± 7	16 ± 13
Clione antarctica	59 ± 22	39 ± 22	4 ± 2	5 ± 3	16 ± 13	6 ± 3
Clio pyramidata	--	47 ± 22	--	39 ± 23	--	34 ± 23
Spongiobranchea australis	--		8 ± 6	44 ± 23	15 ± 10	31 ± 22
Diphyes antarctica	--		7 ± 3	28 ± 18	9 ± 5	3 ± 2
Salpa thompsoni	--	27 ± 11	--	20 ± 13	--	14 ± 8

2.6 *Chapter VI*

Euphausia superba, *E. crystallorophias* and *Thysanoessa macrura* in the Filchner Outflow System: Variability of carbon sources during summer assessed in a lipid and stable isotope study

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Abstract

Collected off the Filchner Ice Shelf during austral summer 2013/14, the three most abundant euphausiids, *Euphausia superba*, *E. crystallorophias* and *Thysanoessa macrura*, were analyzed in regard to their lipid and stable isotope compositions. Fatty acid (FA) fingerprints of the krill species and their potential ice-associated (sympagic) and pelagic carbon sources gave insight on the relative proportions of diatom- and dinoflagellate-produced FAs. Proportions of marker FAs in all three euphausiids were similar to proportions of these FAs in pelagic algae. From the bulk nitrogen stable isotope compositions (δ^{15}N), we estimated the trophic levels (TLs), which indicated predominantly herbivorous feeding for *E. superba* (TL 1.9 ± 0.3), predominantly omnivorous feeding for *E. crystallorophias* (TL 2.7 ± 0.3) and predominantly carnivorous feeding for *T. macrura* (TL 3.5 ± 0.1). Bulk carbon stable isotope compositions (δ^{13}C) indicated a higher proportional contribution of ice algae-derived carbon α_{Ice} in *E. crystallorophias* (43 ± 6%) compared to *E. superba* (6 ± 3%) and *T. macrura* (20 ± 17%), whereas the δ^{13}C values of marker FAs suggested similar mean α_{Ice} values for *E. crystallorophias* (22 to 36%) and *T. macrura* (16 to 36%), and also the lowest mean α_{Ice} in *E. superba* (6 to 16%). In all three species, differences in dietary parameters in respect to the sampling depth were observed and were more pronounced in *E. superba* and *E. crystallorophias* than in *T. macrura*. Climate change-related changes in sea ice extent and duration might not affect *E. superba* drastically in respect of their energy supply during summer, when sufficient algal biomass in the water column is available to support their pelagic lifestyle. *E. crystallorophias* and *T. macrura*, however, potentially receive significant portions of their body carbon from ice algae, which might become difficult to buffer by pelagic food sources in a future Southern Ocean characterized by less sea ice and prolonged melt seasons.

Introduction

In the Southern Ocean, euphausiids occupy a key position regarding the assimilation of primary produced carbon, while representing a major food source for higher trophic levels, such as fish, penguins, seabirds and whales, and contribute therefore substantially to the energy turnover in Antarctic ecosystems (Nemoto and Nasu 1958; DeWitt and Hopkins 1977; Laws 1985; Pakhomov and Perissinotto 1996; Atkinson et al. 2009). Particularly *Euphausia superba* have been in the focus of numerous studies due to their high abundance in the Southern Ocean in general and their overwhelming dominance in some Antarctic regions (Hopkins 1985; Miller and Hampton 1989; Nicol 2006), resulting in a high commercial and industrial interest (Arts et al. 2001; Gigliotti et al. 2011). In coastal waters, towards the Antarctic continent, the abundance of *E. superba* decreases and the 'ice krill', *Euphausia crystallorophias*, get superior in number and importance within the neritic food web (Kühl and Schneppenheim 1986; Thomas and Green 1988; Schnack-Schiel and Mujica 1994; Falk-Petersen et al. 2000). Also highly abundant throughout the Southern Ocean with a predominantly oceanic distribution (Boysen-Ennen and Piatkowski 1988; Falk-Petersen et al. 2000), *Thysanoessa macrura* was found to sometimes even exceed *E. superba* in terms of abundance (Kittel and Stepnik 1983). *E. superba* and *E. crystallorophias* have been identified to feed predominantly as herbivores (Mauchline and Fisher 1969; Falk-Petersen et al. 2000; Schmidt et al. 2003), but omnivorous lifestyle has also been reported (Falk-Petersen et al. 1999; Perissinotto et al. 2000; Ju and Harvey 2004). In contrast, *T. macrura* is assumed to be a true omnivore with even carnivorous tendencies (Mayzaud et al. 1985; Hopkins and Torres 1989; Falk-Petersen et al. 2000).

During summer, the algal biomass in the water column is generally assumed to be sufficient to meet the requirements of the food web, and the energy transfer from phytoplankton via herbivorous zooplankton to upper trophic levels is considered the crucial step in the highly seasonal Southern Ocean (Falk-Petersen et al. 1999). On the other hand, particularly during winter, sea ice algae can serve as an alternative food source, especially in regions with a large spatial coverage of sea ice throughout the year (Ackley et al. 1979; Bartsch 1989; Meiners et al. 2012), and Antarctic food webs can significantly thrive on carbon produced by ice-associated algae (Kohlbach et al., in preparation) (**Chapter V**). Thus, climate change-related alterations of the sea ice primary production and the habitat structure may have important consequences for organisms that feed in the sea ice-water interface layer, and particularly the southeastern Weddell Sea is supposed to be extremely sensitive to climate warming (Hellmer et al. 2012).

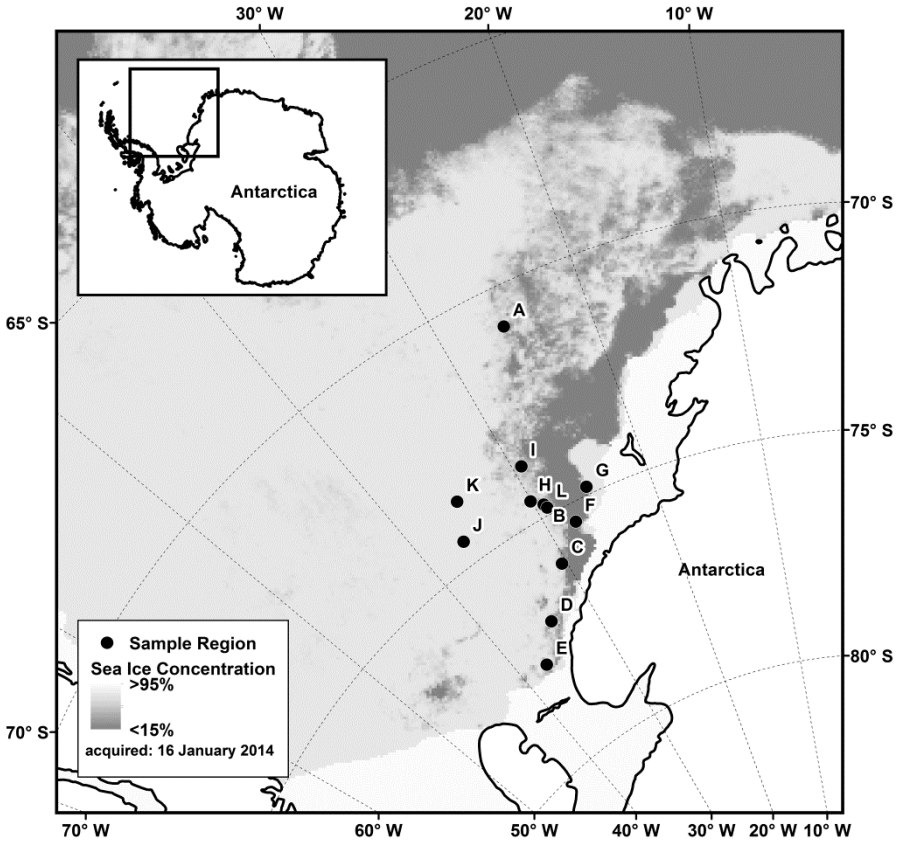
Food web studies off the Filchner-Ronne Ice shelf in the southernmost part of the Weddell Sea are generally very scarce due to its challenging sea ice conditions resulting in a difficult accessibility, even in austral summer (Kohnen 1982). The region in close proximity to the Filchner Ice Shelf has been identified as a major area for the formation of deep and bottom water in the southern Weddell Sea, where cold and fresh water from below the shelf ice interacts with warm oceanic Weddell Sea Gyre waters (Foster and Carmack 1976; Nicholls et al. 2009). As a result, our study area is considered a biological

'hotspot', causing an enhanced food availability (Knust and Schröder 2014). In the present study, samples were e.g. collected along a coastal polynya, which is generally assumed to be a site of concentrated biological activity (Arrigo and van Dijken 2003) and represents a critical habitat for a wide variety of higher trophic level organisms, which potentially prey on krill (Gill and Thiele 1997; Gilchrist and Robertson 2000).
In marine food web studies, fatty acids (FAs) and stable isotope compositions are often investigated to characterize food web relationships and to track primary produced carbon from the source to the consumers. Certain algal-produced FAs are taxon-specific and obtained solely from their diet, providing a trophic 'fingerprint', which is conserved throughout the food web (Bottino 1974; Graeve et al. 1994b; Phleger et al. 1998; Cripps et al. 1999). For example, diatoms are particularly rich in FA 16:1n-7 and polyunsaturated FA (PUFA) 20:5n-3 (Volkman et al. 1989; Nichols et al. 1993), whereas C18 FAs and 22:6n-3 are produced in high amounts by dinoflagellates (Viso and Marty 1993; Brown et al. 1997). Natural abundances of nitrogen stable isotopes ($\delta^{15}N$) enable the estimation of the trophic position, with a subsequent enrichment of the heavy nitrogen isotope ^{15}N in the consumers relative to the trophic baseline (Wada et al. 1987; Rau et al. 1991a; Schmidt et al. 2004a). Carbon stable isotope ratios ($\delta^{13}C$) might provide information on the origin of the body carbon in the consumers (Frazer 1996; Kohlbach et al. 2016). Sea ice algae often show a higher enrichment of the heavy carbon stable isotope ^{13}C resulting in higher $\delta^{13}C$ values relative to algae in the water column (Fry and Sherr 1984; Hecky and Hesslein 1995). This pattern is also transferred along the food chain, which enables the quantification of ice algae-originated carbon to the diet of the investigated organism based on the bulk organic content (BSIA- bulk stable isotope analysis) or marker FAs (CSIA- Compound-specific stable isotope analysis) (Kohlbach et al. 2016).
In this study, we investigated the carbon source composition of the three euphausiid species *E. superba*, *E. crystallorophias* and *T. macrura* during summer. For this purpose, we analyzed the lipid class, fatty acid, bulk and fatty acid-specific stable isotope compositions of juvenile and adult euphausiids and their potential carbon sources (ice-associated algae and pelagic algae). We quantified the proportional contribution of sea ice algae-produced carbon versus carbon produced by pelagic phytoplankton to the carbon budget of the euphausiids during austral summer, based on stable isotope compositions. Furthermore, we aimed to reveal if a close proximity to the surface of the sea ice was accompanied by a sea ice-associated diet of the euphausiids by sampling at different depth layers (below 200 m, 200 to surface, 50 m to surface).

Materials and Methods

Sample collection

Sampling was carried out during RV '*Polarstern*' expedition PS82 (FOS; 19 December 2013 to 5 March 2014) in the southern Weddell Sea in close proximity to the Filchner Ice Shelf south of 70°S (**Figure 1**, **Suppl. A**).



▲***Figure 1.*** *Map of the sampling area during 'Polarstern' expedition PS82 (December 2013 to 5 March 2014) off the Filchner-Ronne Ice Shelf. Letter codes correspond to sampling locations. Station information for the individual sampling site is given in* ***Suppl. A****.*

As trophic baseline for the biomarker analyses, ice-associated particulate organic matter (I-POM) was sampled by taking ice cores with a 9 cm interior diameter ice corer (Kovacs Enterprises). Bottom 10 to 40 cm of ice cores were melted and between 0.2 and 1.0 L melted water were filtered via vacuum pump through pre-combusted 0.7 µm GF/F filters in the dark at 4°C on board and (Whatmann, 3 h, 550°C). For defining the pelagic baseline, pelagic particulate organic matter (P-POM) was collected by a CTD probe (Conductivity, temperature, depth, Seabird SBE9+) with a carousel water sampler. Water collection was performed at the surface layer and at the depth of the Chlorophyll *a* maximum (between 10 and 75 m). Depending on the biomass concentration, between 3 and 11 L water were filtered using pre-combusted GF/F filters. All POM filters were stored at -80°C.

Euphausia superba, *Euphausia crystallorophias* and *Thysanoessa macrura* were collected with a Multi-Rectangular Midwater Trawl (M-RMT) (Roe and Shale 1979) at different depth layers (**Suppl. A**). Prior to determination of total length, catches were sorted species-specifically by developmental stage into juveniles and adults (CCAMLR 2011: Scheme of International Scientific Observation: Scientific Observers Manual. CCAMLR, Hobart, Australia) (**Table 1**). Samples were immediately frozen at -80°C in pre-combusted and pre-weighted sample vials (Wheaton, 6 h, 500°C). Analytical work was conducted at the Alfred Wegener Institute in Bremerhaven, Germany.

▼**Table 1.** Length and dry weights of juvenile (J) and adult (A) euphausiids (mean ± 1 SD).

	Euphausia superba	***Euphausia crystallorophias***		***Thysanoessa macrura***	
developmental stage	A	J	A	J	A
n	59	9	68	6	10
Length (mm)	40.6 ± 4.8	21.4 ± 3.0	27.2 ± 4.4	15.0 ± 1.0	16.8 ± 2.1
Dry weight/Ind. (mg)	138.2 ± 61.2	12.7 ± 8.9	46.2 ± 22.0	9.2 ± 5.0	11.6 ± 6.1

Lipid class and fatty acid analyses

Total lipids were extracted from the freeze-dried samples using a modified procedure from Folch et al. (1957) with dichloromethane/methanol (2:1, v/v). Dry weights and total lipid content were determined gravimetrically (**Table 1, Suppl. B**). Lipid class composition of the euphausiid species were determined directly from the lipid extracts via high-performance liquid chromatography (Graeve and Janssen 2009). Proportions of lipid classes were expressed as mass % of total lipid content. Fatty acids of I-POM, P-POM and euphausiid lipid extracts were converted into fatty acid methyl esters (FAMEs) by transesterification with methanol (3% sulphuric acid), and determined via gas chromatography. Fatty acid content (FAC) (**Table 2**) and individual FAs were quantified with an internal standard (23:0) added prior lipid extraction. FAs were expressed as mass % of total fatty acid content. For detailed information on sample preparation and measurements as well as analytical equipment see Kohlbach et al. (2016).

Bulk and fatty acid-specific stable isotope analyses

Bulk nitrogen ($\delta^{15}N$) and bulk carbon ($\delta^{13}C$) stable isotope compositions of I-POM, P-POM and euphausiids were determined from freeze-dried samples (BSIA). From the fatty acid extracts, $\delta^{13}C$ compositions of the diatom-associated FAs 16:1n-7 and 20:5n-3, and the dinoflagellate-associated FAs 18:4n-3 and 22:6n-3 were determined (CSIA). For detailed information on sample preparation and measurements as well as analytical equipment see Kohlbach et al. (2016).

All isotopic ratios were presented as parts per thousand (‰) in the delta notation ($\delta^{15}N$: $^{15}N/^{14}N$, $\delta^{13}C$: $^{13}C/^{12}C$), as deviation from the Vienna Pee Dee Belemnite standard for carbon measurements and atmospheric nitrogen for nitrogen measurements. Verification of accuracy and precision of the BSIA measurements was done by analyzing secondary reference material USGS41 (certified: $\delta^{15}N$ = 47.6‰, $\delta^{13}C$ = 37.6‰, measured: $\delta^{15}N$ = 46.1‰, $\delta^{13}C$ = 36.0‰) provided by the International Atomic Energy Agency (IAEA, Vienna). Measurement errors were indicated as ± 0.6‰ for stable nitrogen and ± 0.4‰ for stable carbon measurements (represents 1 SD of 12 analyses). The laboratory standard isoleucine ($\delta^{15}N$ = -11.87‰, $\delta^{13}C$ = -3.14‰) was analyzed every 5 samples with measurement errors of ± 0.4 and 0.2‰ for stable nitrogen and carbon isotope ratios, respectively (represents 1 SD of 13 analyses). For the CSIA measurements, quality assurance and analytical precision of the determined carbon

stable isotope ratios were established by analyzing the certificated standard FAMEs 14:0 (certified: $\delta^{13}C$ = -29.13‰, measured: $\delta^{13}C$ = -29.68‰), 16:0 (certified: $\delta^{13}C$ = -30.74‰, measured: $\delta^{13}C$ = -30.62‰) and 18:0 (certified: $\delta^{13}C$ = -23.24‰, measured: $\delta^{13}C$ = -24.03‰), supplied by Indiana University, every 5 samples. Analytical error was 0.3‰ for 14:0, 0.4‰ for 16:0 and 0.2‰ for 18:0 (represents 1 SD of 7 analyses each).

Data analysis

For the investigation of different lipid storage modes and the estimation of the nutritional condition of the euphausiids, the lipid content and lipid classes were determined. In order to track the trophic relationship between the primary producers and euphausiids, the proportions of marker FAs were determined, namely the diatom-associated FAs 16:1n-7 and 20:5n-3 (e.g. Graeve et al. 1997; Falk-Petersen et al. 1998; Scott et al. 1999), the dinoflagellate-associated FAs 18:4n-3 and 22:6n-3 (e.g. Viso and Marty 1993; Graeve et al. 1994b), and the *Calanus*-associated FAs 20:1-9 and 22:1n-11 (e.g. Falk-Petersen et al. 1987; Søreide et al. 2013). The biomarker ratios 16:1n-7/16:0, ∑C16/∑C18, and 22:6n-3/20:5n-3 were examined (Budge and Parrish 1998; Dalsgaard et al. 2003; Søreide et al. 2008, 2013; Wang et al. 2015) to determine the relative proportions of diatoms to flagellates in the algal assemblages and the relative proportions of diatom- versus dinoflagellate-produced FAs in the euphausiids (Claustre et al. 1988/89; Viso and Marty 1993). To estimate the degree of carnivory, the levels of the FA 18:1n-9 (Sargent and Falk-Petersen 1981; Falk-Petersen et al. 1990) and the ratios of 18:1n-7/18:1n-9 (Graeve et al. 1997; Auel et al. 2002) were determined.
The trophic levels (TL) of the euphausiids were estimated from the bulk $\delta^{15}N$ and $\delta^{13}C$ compositions as follows (Two-source food web model) (Post 2002), assuming that carbon and nitrogen moved through the food web with a similar stoichiometry:

$$(1) \qquad TL = \lambda + (\delta^{15}N_x - [\delta^{15}N_{base1} * \alpha + \delta^{15}N_{base2} * (1 - \alpha)])/\Delta_N$$

where λ represents the trophic position of the baseline (I-POM or P-POM, λ = 1). $\delta^{15}N_x$ and $\delta^{15}N_{base}$ represent the bulk nitrogen isotopic compositions of the euphausiids and the primary producers, respectively. Base 1 and base 2 relate to I-POM and P-POM, respectively. Δ_N is the trophic enrichment of $^{15}N/^{14}N$ per TL and was assumed with 3.4‰ (Minagawa and Wada 1984). α represents the proportion of nitrogen in the investigated species that derives ultimately from the sea ice algae.
For the TL calculations, α was estimated as follows:

$$(2) \qquad \alpha = \frac{(\Delta_N\delta^{13}C_x - \Delta_C\delta^{15}N_x + \Delta_C\delta^{15}N_{base2} - \Delta_N\delta^{13}C_{base2})}{(\Delta_N\delta^{13}C_{base1} - \Delta_N\delta^{13}C_{base2} + \Delta_C\delta^{15}N_{base1} + \Delta_C\delta^{15}N_{base2})}$$

The trophic enrichment of carbon (Δ_C) is generally assumed between 0 and 1‰ per TL (Deniro and Epstein 1978; Rau et al. 1983). In this study, we assumed Δ_C = 0.4‰ (Post 2002) since the true carbon enrichment factors for our investigated species were

unknown. However, calculations using a Δ_C within the range of 0 and 1‰ resulted in negligible variations of α (data not shown).

Based on Bayesian multi-source stable isotope mixing models (SIAR; Parnell et al. 2010), the proportional contribution of ice algae-produced carbon α_{Ice} to the diet of the euphausiids was determined from the bulk and fatty acid-specific stable isotope values. Trophic enrichment factors for carbon and concentration dependencies were assumed to be zero (Budge et al. 2008, 2011; Wang et al. 2015). For the CSIA calculations, the $\delta^{13}C$ values of the diatom-associated FAs 16:1n-7 and 20:5n-3 and the dinoflagellate-specific FAs 18:4n-3 and 22:6n-3 were separately used in the models. To asses differences in storage-associated and membrane-associated lipid pools (Stübing et al. 2003), representing younger and older lipid pool, respectively, we furthermore combined the isotopic information of the storage-associated FAs 16:1n-7 and 18:4n-3 and the membrane-associated FAs 20:5n-3 and 22:6n-3 in the modeling (Kohlbach et al., in preparation) (**Chapter III**).

Besides inter-specific differences, we assessed differences in the species-specific fatty acid and stable isotope compositions of the euphausiids with regard to the sampling depth. We grouped the samples as following: 1) individuals caught between 50 m and the surface, 2) individuals caught between 200 m the surface and 3) individuals caught below 200 m.

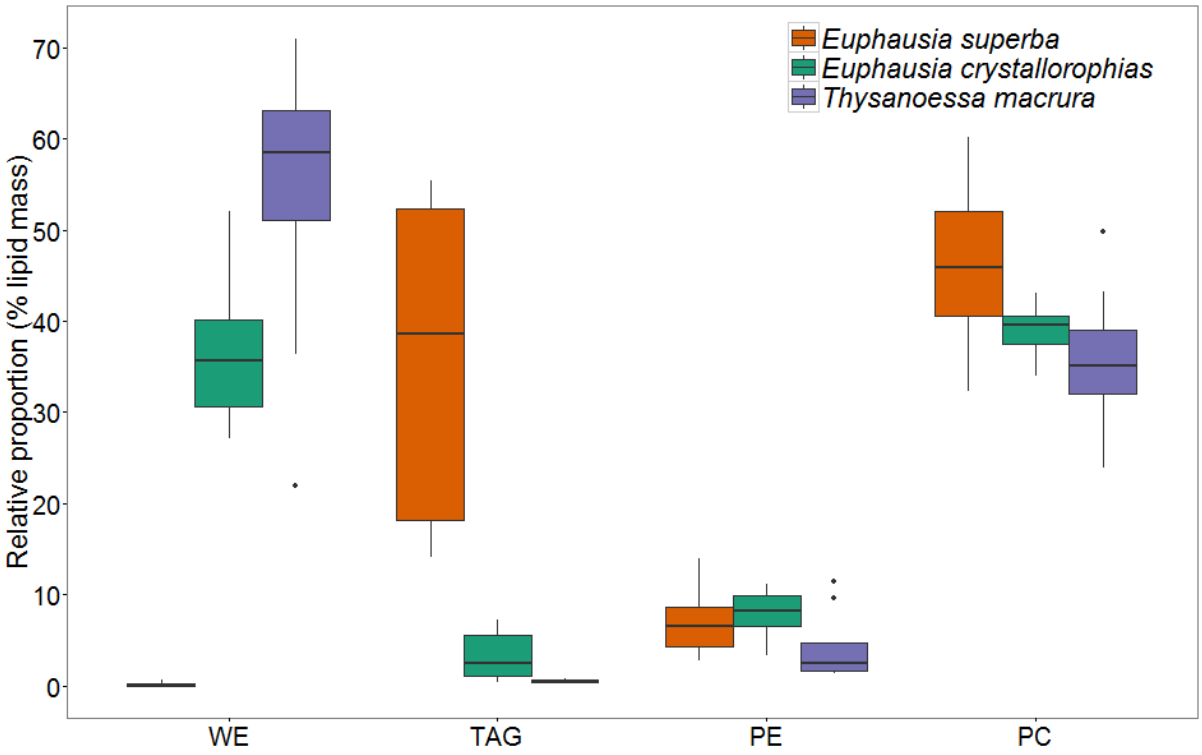
All data analyses were conducted using the open-source software 'R', version 3.0.1 (R Core Team 2015). Testing for statistical significance of the results was conducted with 1-way ANOVAs followed by Tukey HSD post-hoc tests as well as Student´s t-tests. All data were checked for normality and homogeneity by performing the Shapiro-Wilk normality test and evaluating histograms and scatter plots of the data. In order to improve normality, the FA data were transformed following Budge et al. (2007) and applying an arcsine square root function.

Results

Lipid class compositions

Thysanoessa macrura had a significantly lower total lipid content related to the dry weight than *Euphausia superba* and *Euphausia crystallorophias* (ANOVA, $p < 0.001$) (**Suppl. B**). The mean proportions of storage versus membrane lipids were each about 50% in *E. superba*, *E. crystallorophias* and adult *T. macrura* (**Suppl. B**). Only in juvenile *T. macrura*, the proportions of the storage lipids (mean 65%) took a larger part than the membrane lipids. Triacylglycerols (TAGs) dominated the neutral lipid pool in *E. superba* (mean 36%) and were, in contrast, found in only low amounts in juveniles and adults of *E. crystallorophias* (mean < 4%) and *T. macrura* (mean < 1%) (**Figure 2**, **Suppl. B**). Wax esters (WE) were determined in high proportions in *E. crystallorophias* (mean 34 to 45%) and showed the highest proportions in *T. macrura* (mean 51 to 64%), and were somewhat higher in juveniles compared to adults of both species, respectively. Among the membrane lipids, phosphatidylcholines (PCs) and phosphatidylethanolamines (PEs) were the most abundant lipid classes in all samples (**Figure 2**, **Suppl. B**). The highest

concentrations of PCs were found in *E. superba* and the highest proportions of PEs were detected in *E. crystallorophias* versus the other two species, respectively.



▲**Figure 2.** *Relative composition of lipid classes (LCs) in Euphausia superba, Euphausia crystallorophias and Thysanoessa macrura. Horizontal bars in the box plots indicate median proportional values. Upper and the lower edges of the boxes represent the approximate 1st and 3rd quartiles, respectively. Vertical error bars extend to the lowest and highest data value inside a range of 1.5 times the inter-quartile range, respectively (R Core Team 2015). Outliers are represented by the dots outside the boxes. Sample size was reported in* ***Suppl. B****. WE: wax esters, TAG: triacylglycerols, PE: phosphatidylethanolamines, PC: phosphatidylcholines.*

Marker fatty acid compositions

Ice-associated and pelagic particulate organic matter

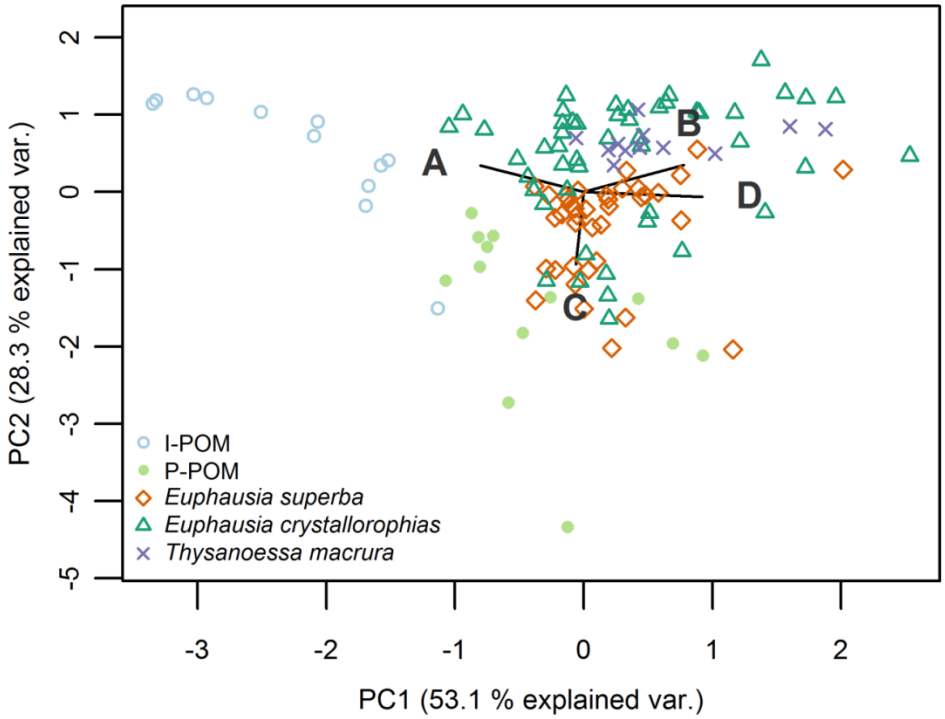
The FA composition of I-POM was clearly dominated by the diatom-associated FA 16:1n-7, whereas the proportions of the four algal marker FAs were more evenly distributed in the P-POM samples (**Table 2**). In the I-POM samples, 16:1n-7 took up 40% of the total FA content, whereas this FA was found in significantly lower concentrations in P-POM (mean 10%) compared to I-POM (t-test, $p < 0.001$). The proportions of the second diatom-associated FA 20:5n-3 showed similar levels in I-POM (10%) and P-POM (12%). The FA composition of P-POM was characterized by more than twice as high proportions of the dinoflagellate-associated FA 18:4n-3 (mean 7%) compared to I-POM (t-test, $p < 0.001$). The biomarker ratios of 16:1n-7/16:0, ∑C16/∑C18 and 22:6n-3/20:5n-3 indicated considerably higher proportions of diatom-associated FAs versus dinoflagellate-associated FAs in the I-POM samples and a higher proportion of dinoflagellate-associated FAs in the P-POM samples (**Table 2**).

▼**Table 2.** Proportions of marker fatty acids (FAs) in ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM) and juvenile (J) and adult (A) euphausiids (mean ± 1 SD mass % of total FA content). Fatty acid content (FAC) is expressed in relation to dry weights. Not detected FAs are marked as '--'.

	I-POM	**P-POM**	***Euphausia superba***	***Euphausia crystallorophias***		***Thysanoessa macrura***	
developmental stage	--	--	A	J	A	J	A
n	12	13	37	7	42	5	8
16:1n-7	42.7 ± 16.3	9.5 ± 5.2	10.2 ± 3.2	7.0 ± 4.4	11.1 ± 6.3	7.5 ± 3.2	4.3 ± 3.3
18:1n-9	7.5 ± 10.3	5.7 ± 2.6	10.8 ± 2.0	24.6 ± 9.0	26.2 ± 8.7	10.6 ± 2.3	13.4 ± 0.7
18:1n-7	0.5 ± 1.5	1.5 ± 1.5	7.2 ± 0.9	10.5 ± 2.0	11.3 ± 2.4	4.0 ± 0.6	4.0 ± 0.8
18:4n-3	2.6 ± 1.5	6.6 ± 3.2	4.1 ± 1.5	3.3 ± 2.1	1.6 ± 1.6	0.7 ± 0.5	0.7 ± 0.3
20:5n-3	9.8 ± 5.0	12.4 ± 3.4	15.8 ± 3.7	17.7 ± 3.2	17.7 ± 4.3	16.5 ± 1.6	17.1 ± 3.4
22:6n-3	1.0 ± 1.9	8.3 ± 4.2	10.4 ± 2.8	13.1 ± 7.2	10.1 ± 4.3	10.8 ± 1.2	13.3 ± 3.9
20:1n-9	--	--	1.2 ± 0.5	0.9 ± 0.3	0.8 ± 0.6	0.5 ± 0.3	0.7 ± 0.2
22:1n-11	--	--	0.4 ± 0.2	--	0.2 ± 0.4	--	0.1 ± 0.1
FAC/dry weight	--	--	8.8 ± 3.2	13.4 ± 5.7	14.9 ± 6.4	23.3 ± 3.9	22.5 ± 8.9
16:1n-7/16:0	2.0 ± 0.6	0.6 ± 0.3	0.5 ± 0.2	0.5 ± 0.3	0.9 ± 0.5	0.4 ± 0.2	0.2 ± 0.2
∑C16/∑C18	7.3 ± 5.0	0.8 ± 0.4	1.2 ± 0.2	0.6 ± 0.2	0.6 ± 0.3	1.7 ± 0.4	1.2 ± 0.2
22:6n-3/20:5n-3	0.2 ± 0.5	0.7 ± 0.3	0.6 ± 0.1	0.8 ± 0.3	0.6 ± 0.2	0.7 ± 0.1	0.8 ± 0.1

Euphausiids

The proportions of the total fatty acid content relative to the dry weight were significantly higher in *T. macrura* versus *E. superba* and *E. crystallorophias*, and also higher in *E. crystallorophias* compared to *E. superba* (ANOVA, $p < 0.001$) (**Table 2**). In general, the four algal FAs were evenly distributed in the euphausiids (**Table 2**). The concentrations of the diatom-associated FAs 16:1n-7 and 20:5n-3 (mean 21 to 29%) were approximately twice as high as the concentrations of the dinoflagellate-associated FAs 18:4n-3 and 22:6n-3 in all three species (mean 12 to 16%). The greatest difference between the species was found in the proportions of the diatom-associated FA 16:1n-7, which ranged from 4% in adult *T. macrura* to 10% in *E. superba* and 11% in adult *E. crystallorophias* (ANOVA, $p < 0.05$). The proportions of the dinoflagellate-associated FA 18:4n-3 were significantly higher in *E. superba* (mean 4%) versus *T. macrura* (mean 0.7%) (ANOVA, $p < 0.001$). Furthermore, the proportions of 18:4n-3 were significantly higher in juvenile *E. crystallorophias* than in adult *E. crystallorophias* (t-test, $p < 0.05$). In contrast, the abundances of the PUFAs 20:5n-3 and FAs 22:6n-3 ranged in a narrow interval from 16 to 18% and from 10 to 13% in all species, respectively. The proportions of the *Calanus*-associated marker FAs 20:1n-9 and 22:1n-11 were generally low in all euphausiid species. Yet, their levels were significantly higher in *E. superba* relative to the other two species (ANOVA, $p < 0.001$). The ratio of $\sum$C16/$\sum$C18 revealed a higher abundance of C18 fatty acids in *E. crystallorophias* versus *E. superba* and *T. macrura*, whereas the other biomarker ratios did not reveal much variability between the species (**Table 2**). The PCA of the distribution of the marker FAs in POM and the euphausiids explained 81.4% of the variance in the dataset, and revealed a clear distinction of the FA proportions between the primary communities (e.g. I-POM and P-POM) and the three euphausiid species (**Figure 3**). The first axis represented the remarkably higher proportions of 16:1n-7 in I-POM compared to P-POM and the euphausiids on one side, and the higher levels of 20:5n-3 and 22:6n-3 in the euphausiids versus I-POM on the other side. In general, a higher similarity in the marker FA proportions to the FA proportions in P-POM was indicated for all three krill species. The second axis highlighted the great similarity in the FA proportions between *E. crystallorophias* and *T. macrura*, and the difference to *E. superba* that was mainly driven by the higher proportions of 18:4n-3.



▲**Figure 3.** *PCA biplot of marker fatty acid (FA) proportions in ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM) and the euphausiids. Biplot arrows correspond to gradients of FAs in the PCA ordination. Diatom-associated marker FAs: 16:1n-7 (A), 20:5n-3 (B); dinoflagellate-associated marker FAs: 18:4n-3 (C), 22:6n-3 (D). Sample size is reported in* ***Table 2****.*

E. superba and *E. crystallorophias* caught between 50 m and the surface had significantly higher proportions of the diatom-associated FA 16:1n-7 than individuals caught between 200 m and the surface as well as below 200 m (ANOVA, $p < 0.01$) (**Suppl. C and D,** respectively). The proportions of the diatom-associated FA 16:1n-7 were significantly higher in *T. macrura* sampled between 50 m and the surface relative to individuals caught between 200 m and the surface (ANOVA, $p < 0.05$) (**Suppl. E**). Furthermore, the proportions of the second diatom-associated FA 20:5n-3 were significantly higher in *E. superba* collected between 50 and 0 m and also in individuals collected between 200 m and the surface compared to *E. superba* caught below 200 m (ANOVA, $p < 0.01$). In contrast, the proportions of the dinoflagellate-associated FA 22:6n-3 were significantly higher in *E. superba* and *E. crystallorophias* collected between 200 and 0 m than in individuals collected between 50 m and the surface (ANOVA, $p < 0.01$) (**Suppl. C and D,** respectively). The levels of dinoflagellate-associated FA 22:6n-3 were somewhat higher in *T. macrura* caught between 200 and 0 m compared to the other two depth layers (**Suppl. E**).

Bulk and fatty acid-specific stable isotope compositions

Ice-associated and pelagic particulate organic matter

The bulk $\delta^{15}N$, bulk $\delta^{13}C$ values and the $\delta^{13}C$ values in all four marker fatty acids were significantly higher in I-POM versus P-POM (**Table 3**).

▼**Table 3.** Bulk nitrogen ($\delta^{15}N$) and carbon stable isotope values ($\delta^{13}C$), and $\delta^{13}C$ in the diatom-associated marker fatty acids 16:1n-7 and 20:5n-3, and the dinoflagellate-associated marker fatty acids 18:4n-3 and 22:6n-3 in ice-associated particulate organic matter (I-POM) and pelagic particulate organic matter (P-POM) (mean ± 1 SD ‰).

Stable isotope values	I-POM	P-POM	t-test p*
n	6	21	
bulk $\delta^{15}N$	3.7 ± 4.3	0.6 ± 1.3	*
bulk $\delta^{13}C$	-8.9 ± 5.3	-29.3 ± 2.3	**
n	7	7	
$\delta^{13}C$ 16:1n-7	-10.2 ± 6.1	-38.7 ± 3.3	**
$\delta^{13}C$ 18:4n-3	-16.9 ± 6.2	-42.8 ± 1.9	**
$\delta^{13}C$ 20:5n-3	-16.4 ± 5.2	-38.2 ± 3.2	**
$\delta^{13}C$ 22:6n-3	-19.6 ± 4.2	-35.3 ± 1.9	**

*t-test *p*: ns = $p > 0.05$; * $0.05 < p < 0.01$; ** $0.01 < p < 0.001$

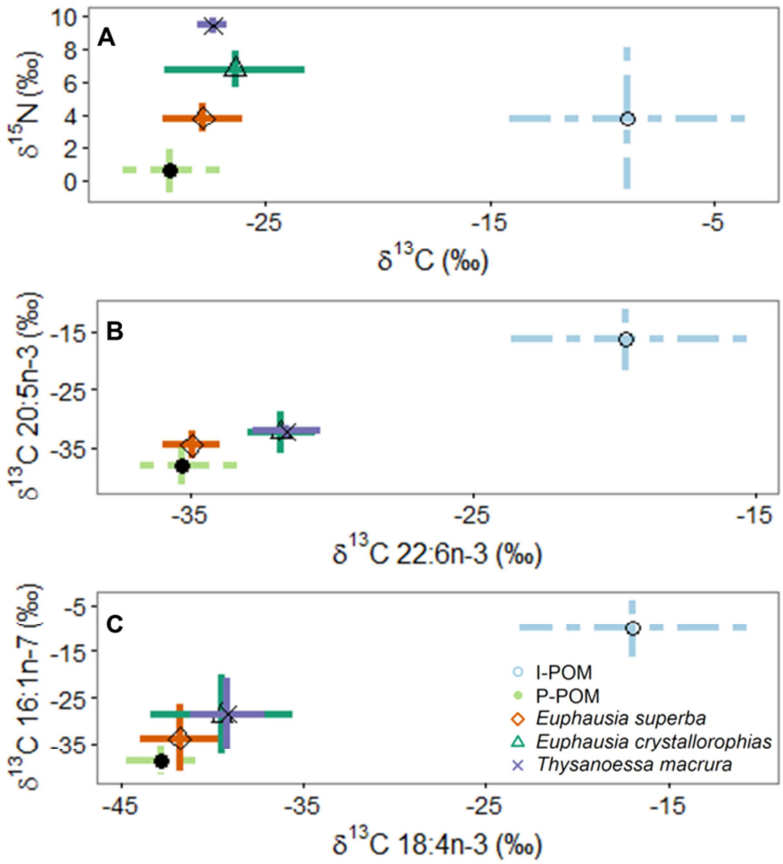
Euphausiids

The bulk $\delta^{15}N$ values in *T. macrura* were significantly higher compared to *E. superba* and *E. crystallorophias* (ANOVA, $p < 0.001$) (**Table 4**). Furthermore, the $\delta^{15}N$ values in *E. crystallorophias* were significantly higher than in *E. superba* (ANOVA, $p < 0.001$). The bulk $\delta^{13}C$ values in *E. crystallorophias* were somewhat higher compared to *E. superba* and *T. macrura*, but did not show significant differences between the species (**Table 4**).

▼**Table 4.** Trophic indicators for estimation of degree of carnivory based on fatty acid ratio 18:1n-7/18:1n-9 and trophic levels (TLs) of euphausiids based on bulk stable isotope compositions.

	Euphausia superba	***Euphausia crystallorophias***		***Thysanoessa macrura***	
developmental stage	A	J	A	J	A
18:1n-7/18:1n-9	0.7 ± 0.1	0.5 ± 0.1	0.5 ± 0.2	0.4 ± 0.1	0.3 ± 0.1
bulk $\delta^{15}N$	3.8 ± 0.9	5.8 ± 0.5	6.8 ± 1.1	9.2	9.5 ± 0.7
bulk $\delta^{13}C$	-27.9 ± 1.7	-26.0 ± 3.7	-26.4 ± 3.1	-27.6	-27.2 ± 0.9
TL	1.9 ± 0.3	2.4 ± 0.1	2.7 ± 0.3	3.5	3.5 ± 0.2

The $\delta^{13}C$ values of 20:5n-3 in *E. crystallorophias* (-32.4 ± 3.6‰) and *T. macrura* (-32.3 ± 1.0‰) were somewhat higher compared to *E. superba* (-34.6 ± 2.4‰), but with no statistical differences. A larger discrepancy was found for the $\delta^{13}C$ ratios of 22:6n-3, which were significantly higher in *E. crystallorophias* (-31.8 ± 1.2 ‰) and *T. macrura* (-31.6 ± 1.2‰) relative to *E. superba* (-35.0 ± 1.0‰) (ANOVA, $p < 0.001$). The FAs 16:1n-7 and 18:4n-3 showed also a high similarity between *E. crystallorophias* (-28.8 ± 8.6‰ and -39.4 ± 3.9‰) and *T. macrura* (-28.7 ± 7.6‰ and -39.1 ± 2.0‰). Both FAs were somewhat higher in both species compared to *E. superba* (-33.8 ± 7.3‰ and -41.8 ± 2.1‰) (**Figure 4**).



▲**Figure 4.** *A) Bulk stable nitrogen ($\delta^{15}N$) and carbon isotope ratios ($\delta^{13}C$) in ice-associated particulate organic matter, pelagic particulate organic matter and the euphausiids relative to atmospheric nitrogen and Vienna Pee Dee Belemnite (VPDB) standard, respectively. Error bars correspond to ± standard deviation. Sample size for euphausiids is reported in* ***Table 5****.*
B) Carbon stable isotope ratios ($\delta^{13}C$) of the membrane-associated marker fatty acids 20:5n-3 and 22:6n-3 in I-POM, P-POM and the euphausiids relative to VPDB. Error bars correspond to ± standard deviation. Sample size for E. superba is reported in ***Table 5****.*
C) Carbon stable isotope ratios ($\delta^{13}C$) of the storage-associated marker fatty acids 20:5n-3 and 22:6n-3 in I-POM, P-POM and the euphausiids relative to VPDB. Error bars correspond to ± standard deviation. Sample size for E. superba is reported in ***Table 5****.*

In *E. superba*, the $\delta^{13}C$ values of 16:1n-7 and 22:6n-3 were significantly higher in individuals caught between 50 and 0 m compared to krill caught between 200 m and the surface (ANOVA, $p < 0.05$). Additionally, the bulk $\delta^{13}C$ values in *E. superba* sampled between 50 m and the surface and between 200 m and the surface were somewhat higher in comparison to *E. superba* sampled below 200 m. (**Suppl. C**). In *E. crystallorophias* caught between 50 m and the surface, bulk $\delta^{13}C$ values were significantly higher than individuals collected between 200 m and the surface and below 200 m (ANOVA, $p < 0.01$) (**Suppl. D**). In *T. macrura*, the $\delta^{13}C$ values of 16:1n-7 were somewhat higher in individuals caught between 50 and 0 m compared to specimens caught between 200 m and the surface (**Suppl. E**).

Trophic positions

Based on the bulk stable isotope compositions, *T. macrura* occupied the highest TL (3.4 to 3.6), *E. crystallorophias* took an intermediate position (2.0 to 3.2) and *E. superba* showed the lowest TL estimation among the euphausiids (1.4 to 2.9) (**Table 4**). The TL estimate for juvenile *E. crystallorophias* was somewhat lower compared to adult *E. crystallorophias*, whereas *T. macrura* did not reveal differences between the developmental stages. Based on the ratio of 18:1n-7/18:1n-9, the degree of carnivory was significantly higher in *T. macrura* due to higher proportions of 18:1n-9 versus 18:1n-7 than in both *E. superba* and *E. crystallorophias*, and also higher in *E. crystallorophias* versus *E. superba* (ANOVA, $p < 0.05$). The levels of FA 18:1n-9 were significantly higher in adult *T. macrura* compared to juvenile *T. macrura* (t-test, $p < 0.01$) (**Table 2**), which resulted in a lower 18:1n-7/18:1n-9 ratio (**Table 4**), indicating a somewhat higher degree of carnivory in adults versus juveniles.

Contribution of ice algae-produced carbon to the diet of the euphausiids

All seven stable isotope approaches consistently suggested a low proportional ice algal contribution to the carbon budget of *E. superba*, ranging from 5 to 18% (**Table 5**). The bulk $\delta^{13}C$ values indicated a substantial contribution of ice algae carbon to the diet of *E. crystallorophias* (mean 43%), which was approximately twice as high as in *T. macrura* based on the bulk parameters (mean 20%). All CSIA models suggested a very similar range of α_{Ice} estimates for *E. crystallorophias* and *T. macrura* (mean 16 to 36%) (**Table 5**). In all three species, the highest α_{Ice} estimates derived from FA 16:1n-7. The α_{Ice} estimates derived from the model combining the storage-associated FAs 16:1n-7 and 18:4n-3 were in the same range as the estimates deriving from the membrane-associated FA 20:5n-3 and 22:6n-3 in each species, respectively.

▼**Table 5.** Proportional contribution of ice algae-produced carbon α_{Ice} to the diet of juvenile (J) and adult (A) euphausiids (mean ± 1 SD %), based on bulk and fatty acid-specific stable isotope values.

α_{Ice}	*Euphausia superba*	*Euphausia crystallorophias*	*Thysanoessa macrura*
n	23	28	3
bulk	6 ± 3	43 ± 6	20 ± 17
n	14	7	10
16:1n-7	18 ± 7	36 ± 14	36 ± 10
18:4n-3	6 ± 3	23 ± 17	16 ± 7
16:1n-7 + 18:4n-3	6 ± 2	25 ± 15	17 ± 6
20:5n-3	16 ± 6	27 ± 8	27 ± 4
22:6n-3	5 ± 2	22 ± 5	23 ± 4
20:5n-3 + 22:6n-3	8 ± 6	24 ± 4	25 ± 3

Discussion

Lipid and fatty acid compositions

Particulate organic matter

Diatoms are generally the most abundant inhabitants of sea ice in Polar Regions (Bartsch 1989; Garrison and Buck 1989; Garrison 1991). The phytoplankton community in the Southern Ocean can regionally and seasonally be dominated by diatoms, but flagellates and *Phaeocystis spp.* assemblages can also occur as major components (Burkholder and Sieburth 1961; Arrigo et al. 1999). In the present study, the dominance of diatom algae in the I-POM samples was indicated by the considerably higher proportions of the diatom-associated FA 16:1n-7 and the high ratios of 16:1n-7/16:0 and ∑C16/∑C18 relative to P-POM (Nichols et al. 1986; Bergé and Barnathan 2005). In contrast, the dominance of dinoflagellates in the pelagic algae community was suggested by the significantly higher levels of the dinoflagellate-associated marker FAs 18:4n-3 and 22:6n-3 and the higher ratio of 22:6n-3/20:5n-3 (Harrington et al. 1970; Graeve 1993; Viso and Marty 1993) in comparison to the I-POM samples. The high proportions of the diatom-associated FA 20:5n-3 in both I-POM and P-POM were pointing to a mixed community structure in the pelagic assemblages. The relative range of the marker FA proportions was rather large for both I-POM and P-POM, suggesting a high variability in the taxonomic composition of the primary communities throughout the sampling area.

Euphausiids

The lipid levels in *Thysanoessa macrura* (30 to 35%) were higher compared to *Euphausia crystallorophias* (23%) and *Euphausia superba* (21%), which was also found in other studies and were generally in the same range as previously reported values (Hagen 1988; Hagen and Kattner 1998; Kattner and Hagen 1998; Falk-Petersen et al. 1999). However, the total lipid levels in our adult *E. crystallorophias* rather correlated with levels found in this species in late winter/early spring (21%) reported by Falk-Petersen et al. (2000) and were considerably lower than in adult individuals from summer with on average 35% per dry weight (Falk-Petersen et al. 1999, 2000). This might be the result of environmental differences, because the Filchner region is even in midsummer mostly ice-covered, whereas the individuals referred to in Falk-Petersen et al. (2000) were caught in the more northern Weddell Sea (Kattner and Hagen 1998), an area with comparably more and larger open water areas during summer. The reproduction period of *E. superba* ranges from November to April (Quetin et al. 1994). In contrast, in *E. crystallorophias*, spawning takes place between November and December and thus before the onset of the phytoplankton bloom (Harrington and Thomas 1987). *T. macrura* spawns between September and November (Nordhausen 1994), which indicates the independency of this euphausiid from the phytoplankton bloom for providing external energy. According to the different spawning cycles, the higher lipid levels in *T. macrura* and *E. crystallorophias* compared to *E. superba* could be explained by the replenishment of energy reserves after the spawning, whereas the reproduction of *E.*

superba was still ongoing during the sampling period (January/February). However, considering the polar lipid phosphatidylcholine as storage depot besides WEs and TAGs, as suggested by Hagen et al. (1996) and Mayzaud (1997) for high-latitude euphausiids, all three species indicated large energy reserves (> 80% of total lipid content). Wax esters provide a long-term energy depot since they are incorporated and utilized at a slower rate than triacylgylcerols (Benson et al. 1972; Lee et al. 2006). In *E. superba*, only traces of WEs were found, whereas TAGs dominated the storage lipid fraction, supporting the findings of previous studies (Clarke 1984; Falk-Petersen et al. 2000; Hagen et al. 2001). The principal lipid composition of *E. crystallorophias* and *T. macrura* was found to be very similar, with WEs as main lipid depot (Bottino 1975; Hagen and Kattner 1998).

The distribution of the marker FAs in all three euphausiids was consistent with previous studies (Bottino 1974; Kattner and Hagen 1998; Yang et al. 2016). The moderate levels of the diatom-associated FA 16:1n-7 accompanied with high proportions of the second diatom-associated FA 20:5n-3, but also high concentrations of the dinoflagellate-associated FA 22:6n-3 in all three species, however, did not allow for a distinct differentiation on the preferred carbon source. The ratio of 16:1n-7/16:0 indicated a dominance of dinoflagellate-produced carbon in all three euphausiids, particularly in *T. macrura*. The ratio of ∑C16/∑C18, however, indicated a higher impact of diatom-produced carbon in *E. superba* and particularly juvenile *T. macrura*. Based on the ratio of 22:6n-3/20:5n-3, diatom-produced carbon dominated in all three species. All biomarker ratios in all three species showed similar values to our P-POM samples, suggesting that the origin of carbon was mixed as the taxonomic composition of particularly the algal community in the water column.

Trophic positions

We investigated three different fatty acid- and stable isotope-derived indicators of the euphausiids' trophic position and the degree of carnivory. 1) High concentrations of phytoplankton-derived FA 18:1n-7 can indicate a primarily herbivorous diet of a consumer, whereas high levels of 18:1n-9 might reflect the degree of animal dietary input (Falk-Petersen et al. 2000; Broglio et al. 2003). The ratio of 18:1n-7/18:1n-9 was the highest in *E. superba* (mean 0.7) and the lowest in *T. macrura* (mean 0.3 to 0.4). *E. crystallorophias* was characterized by significantly higher levels of 18:1n-9, but also high concentrations of 18:1n-7 compared to the other two euphausiids, which was also found by Yang et al. (2016). However, the particularly in *E. superba* and *E. crystallorophias* from the literature varying proportions of carnivory marker 18:1n-9 might indicate the more opportunistic feeding behavior of both species. 2) High concentrations of the *Calanus*-associated marker FAs 20:1n-9 and 22:1n-11, which are biosynthesized by calanoid copepods (Ackman et al. 1970; Ratnayake and Ackman 1979), can give further evidence on the degree of carnivory (Kattner and Hagen 1995). In previous studies, all three species have been identified to feed on copepods occasionally (Atkinson and Snyder 1997; Cripps et al. 1999; Perissinotto et al. 2000; Ju and Harvey 2004). However, the low levels of the *Calanus*-associated markers in all three krill species lead to the

conclusion that calanoid copepods, such as *Calanoides acutus* and *Calanus propinquus*, were not important food items in the weeks before the sampling. 3) δ^{15}N values give information on the trophic position, showing an subsequent enrichment of the heavy nitrogen isotope ^{15}N in the consumers relative to the trophic baseline as carnivory increases (Wada et al. 1987; Rau et al. 1991a; Schmidt et al. 2004a). The δ^{15}N values suggested the highest degree of carnivory for *T. macrura,* occupying the highest trophic level (mean 3.5), and the lowest animal ingestion by *E. superba* (mean TL 1.9). The algal concentrations in the water column and/or sea ice were apparently high enough in the weeks prior sampling to support the predominantly herbivorous lifestyle of *E. superba* (Marr 1962; Clarke 1980), with no need to switch to omnivorous feeding. The considerably lower trophic level estimation for *E. crystallorophias* (mean 2.4 to 2.7) compared to *T. macrura* and yet considerably higher TL estimation compared to *E. superba* indicated a predominantly omnivorous diet for this species, which is consistent with previous findings (Falk-Petersen et al. 1999). In early studies, *T. macrura* was found to tend towards carnivorous feeding during late summer and early autumn (Hopkins 1985; Hopkins and Torres 1989). *T. macrura* in our study apparently fed strictly on animals, reflected by the lipid parameters and elevated nitrogen stable isotope values (Rau et al. 1991a), indicating a higher degree of carnivory than suggested by previous studies (Falk-Petersen et al. 1999).

Stable isotope compositions

During austral summer, pelagic POM in the Southern Ocean is characteristically depleted in ^{13}C, and thus, isotopically lighter than ice-associated POM (Rau et al. 1982; Wada et al. 1987; Fischer 1991; Fontugne et al. 1991). This was also the case for the bulk and fatty acid-specific δ^{13}C values in our study, allowing for the quantification of the relative importance of ice-associated food sources in the diet of the euphausiids. To date, fatty acid-specific stable isotope compositions are not available for none of the three euphausiid species from the Filchner region. However, bulk stable isotope compositions are published from several regions of the Southern Ocean, particularly for *E. superba*. For example, by Wada et al. (1987) reported δ^{13}C values for adult *E. superba*, collected in austral summer in the Australian sector of the Southern Ocean between ~ 900 m depth and the surface, was with -29.3‰ somewhat lower than our values (mean -27.9‰). In contrast, the δ^{13}C values in *E. superba* collected in Prydz Bay were with -25.0 ± 0.3‰ slightly higher than in our study (Hodum and Hobson 2000). The δ^{13}C values in *E. superba* collected from the Weddell Sea in March ranged between ~ -25 and -32‰ (Rau et al. 1991a), suggesting a high taxon-specific variability of the stable isotope composition, probably reflecting the spatial and temporal variability in the taxonomic structure of the primary producers. Stable isotope studies on the other two euphausiids are much scarcer. The δ^{13}C values in *E. crystallorophias* collected in Prydz Bay (Hodum and Hobson 2000) were with on average -25.3‰ marginally higher than our values (mean -26.0 to -26.4‰). The δ^{13}C values in juvenile *E. crystallorophias* collected in summer from East Antarctica reported by Giraldo et al. (2011) were also somewhat higher than in our study (-24.4 ± 0‰). *T. macrura* showed bulk δ^{13}C values of ~ -28.5‰

in a previous study (Rau et al. 1991a), which was similar to our results (mean -27.2 to -27.6‰). The bulk $\delta^{13}C$ values in *T. macrura* collected from the northern Weddell Sea during winter (Kohlbach et al., in preparation) (**Chapter V**) were considerably lower (mean -29.2‰) compared to the specimens in this study (mean -27.2‰). This might be explained by the particularly differing stable isotope compositions in the ice-associated algal assemblages between both studies. The bulk $\delta^{13}C$ values in the I-POM samples from the winter study were significantly lower (mean -23.5‰) than in the I-POM samples from this study (mean -8.9‰), which was also the case for all four marker fatty acids. This indicates a different taxonomic composition of primary producers in sea ice between the two seasons and regions, consequently affecting the stable isotope compositions of the consumers. In contrast, the bulk $\delta^{13}C$ values and $\delta^{13}C$ values of the FAs 18:4n-3, 20:5n-3 and 22:6n-3 in P-POM between the two studies were similar, suggesting less spatial and seasonal variability within the pelagic algal community compared to the sea ice community. Only the $\delta^{13}C$ values of FA 16:1n-7 were significantly higher in individuals caught close to the surface compared to individuals caught at greater depths in all three euphausiids. This highlights the importance of this FA for the differentiation between sympagic and pelagic produced carbon, as I-POM and P-POM also showed the largest difference in their $\delta^{13}C$ values among the marker FAs. Consequently, a distinct determination of the carbon source origin, i.e. sympagic versus pelagic diatoms, in the consumers is possible.

Drivers of variability in fatty acid and stable isotope compositions

The western part of the study area was characterized by low Chl *a* concentrations in the water column (Knust and Schröder 2014), indicating a low pelagic algae biomass. This supports well our findings of the highest concentrations of the diatom-associated FA 16:1n-7 and the highest $\delta^{13}C$ values, accompanied by the lowest proportions of the dinoflagellate-associated markers in *E. superba* and *E. crystallorophias* from the westernmost stations (region J), indicating an elevated input of ice algal carbon in this region. In contrast, the highest Chl *a* concentrations were found off the eastern Weddell Sea shelf (Knust and Schröder 2014), where the proportions of 16:1n-7 were generally low and the proportions of the dinoflagellate-associated FA 22:6n-3 were high in both krill species (region G). This might indicate the opportunistic feeding style of *E. superba* and *E. crystallorophias*, able to utilize carbon originating from different microalgae taxa and adapting to the availability of pelagic or sympagic carbon sources.

I-POM samples from the eastern shelf-station 146 (**Figure 1**: region G) showed considerably lower proportions of 16:1n-7 (mean 13.0%) compared to all other stations (mean 39.5 to 60.4%), accompanied by the highest proportions of the dinoflagellate-associated FA 22:6n-3 (mean 4.3%), which was below 1% in the other regions. Furthermore, particularly the bulk $\delta^{13}C$ values were lower at this station (mean -17.9‰) compared to the other stations (mean -3.7 to -10.8‰), indicating an elevated concentration of pelagic algae in the sea ice in this area, which can regionally occur (Garrison and Buck 1989). P-POM from this region (St. 140) was also considerably different to all other stations, characterized by lower proportions of 16:1n-7 (mean

1.7%) versus the other regions (mean 4.8 to 17.7%), and high proportions of the dinoflagellate-associated marker FA 18:4n-3 (mean 14.0%) versus the other regions (mean 3.8 to 9.0%). Dieckmann et al. (1991), Garrison (1991) and Ackley and Sullivan (1994) suggested that the composition of sea ice communities are shaped by physically distinct sea ice environments and could reflect the ability to adapt to different physicochemical and biological features among the ice habitats. For example, Dieckmann et al. (1991) indicated that e.g. nutrient limitation, particularly of silicate, can limit the growth of diatoms in sea ice, which consequently leads to different algal assemblages with a dominance of autotrophic flagellates. Furthermore, gradients in light, temperature and salinity can affect the vertical heterogeneity in ice floes (Garrison 1991). Also phytoplankton assemblages in the Southern Ocean can be extremely diverse regarding both taxonomy and size (Smith Jr. and Sakshaug 2013), which accordingly might influence their biomarker characteristics, such as isotopic signature (Montoya 1990; Rau et al. 1990). Furthermore, Rau et al. (1989) suggested that high concentrations of CO_2 (aq) could possibly mask the depletion of ^{13}C in P-POM. Due to the geographically varying physical characteristics and environmental conditions in our sampling area, the formation of different primary assemblages is the natural result. Overall, the variability in the biomarker parameters was more pronounced in the sea ice-associated primary community, suggesting that environmental parameters and seasonal progression might have had a larger impact on the sea ice-associated algal community.

Besides geographically-related differences, the biomarker parameters might have been influenced by the regionally varying bathymetric conditions. Whereas nitrate, silicate and phosphate concentrations did not show significant differences between the station groups (K. Ksionszek unpubl.), the water depths varied strongly within the sampling areas. For example, deep sea-station 3 (**Figure 1**: region A) showed the lowest concentrations of the diatom-associated marker 16:1n-7 with the highest concentrations of both membrane-associated FAs 20:5n-3 and 22:6n-3 in *E. superba* and *T. macrura*. Furthermore, species-specific differences in the FA patterns might partly be explained by the seasonal progression of the system. *E. crystallorophias* collected in the same area within a span of ~ 5 weeks (**Figure 1**: regions B and L) showed a stronger dinoflagellate-related signal earlier in the season. However, the bulk $\delta^{13}C$ values were much lower beginning-mid February (mean -28.7‰) than beginning of January (mean -24.9‰), possibly indicating a change in taxonomic composition of the carbon sources introduced by changing environmental parameters depending on the month and, thus, bloom situations (Garrison 1991; Bathmann et al. 1997; Arrigo et al. 1999). Additionally, the degree of carnivory was higher in January versus February, suggesting a somewhat higher input of secondary carbon earlier in the season.

Contribution of ice algae-produced carbon to the carbon budget of the euphausiids

All stable isotope mixing models agreed in finding that the utilization of ice algal carbon by *E. superba* in the weeks before the sampling was rather marginal (5 to 18%). However, in Kohlbach et al. (in preparation) (**Chapter III**), we demonstrated that sea ice

algae contributed significantly to the diet of particularly young developmental stages of *E. superba* during winter in the northern Weddell Sea (up to 67% of the carbon budget). In contrast, Schmidt et al. (2003) assumed a predominantly pelagic feeding pattern of larval *E. superba* rather than feeding within the sea ice in autumn in the Lazarev Sea, based on bulk isotopic compositions, leading to the assumption of seasonally changing feeding histories for this species. Indeed, many Antarctic species, including adult *E. superba* and *T. macrura*, were found to switch their diet and thus their carbon supply from predominantly pelagic resources to sympagic food sources as the winter season progressed (Kohlbach et al., in preparation) (**Chapter V**). This was indicated by higher α_{Ice} estimates derived from the storage lipid pool, which reflects the more recent carbon composition from the sampling period compared to the more conserved membrane lipids, likely representing trophic signals partly from the weeks and months before the sampling (Stübing et al. 2003). However, in this study, there was no difference found between the younger and older lipid pool, suggesting that the carbon source preferences of the euphausiids were not subject to large changes over several weeks.

The bulk $\delta^{13}C$ values suggested a significant utilization of sympagic carbon by *E. crystallorophias* (mean 43%), and a considerably lower importance of the ice algae-produced carbon in *T. macrura* (mean 20%). The fatty acid-specific $\delta^{13}C$ values indicated generally lower α_{Ice} estimates for *E. crystallorophias* (mean 22 to 36%) compared to the BSIA results, which was in the same range as for *T. macrura* (25 to 27%). In Kohlbach et al. (2016), we suggested that the most reliable α_{Ice} estimates might derive from both FAs, 20:5n-3 and 22:6n-3, when a mixed taxonomic composition of the primary communities is expected. BSIA results, in contrast, might be influenced by metabolic processes, especially at higher trophic levels (Gannes et al. 1997). The FA patterns of *E. crystallorophias* and *T. macrura* were rather similar, which then supports their similar α_{Ice} estimates from the CSIA models. In a zooplankton study in the ice-covered Weddell Sea during summer, *E. crystallorophias* were found closely associated with the pack ice near the continent (Boysen-Ennen et al. 1991). Furthermore, Falk-Petersen et al. (1999) collected *E. crystallorophias* during summer in the Lazarev Sea over the shelf directly linked with ice floes and suggested that this species is well adapted to utilize both carbon from the pelagic bloom and ice-associated carbon. Due to their primarily occurrence in high-Antarctic regions, *E. crystallorophias* have to overcome the most extreme environmental conditions of all euphausiids (Kattner and Hagen 1998), and might therefore be the most likely candidate with the need to equip with a high degree of adaptability regarding alterations and fluctuations of their food sources.

The distribution of the marker FAs and the $\delta^{13}C$ values suggested a higher proportion of ice algae-derived carbon versus phytoplankton-derived carbon in individuals caught in close proximity to the surface compared to individuals sampled at greater depths, particularly pronounced in the carbon composition of *E. superba* and *E. crystallorophias*. Lascara et al. (1999) found that in summer, only 25% of the *E. superba* biomass was positioned deeper than 50 m, based on the results of multiple cruises west of the Antarctic Peninsula. Krill change their vertical position constantly (Kalinowski 1978; Godlewska and Klusek 1987; Taki et al. 2005), for example to find shelter from

predators at greater depths (Ritz 1994). However, our biomarker parameters indicated that the krill caught close to the surface also fed at the surface, and therefore indicated a higher trophic dependency on sea ice algae than individuals located at greater depths.
All three species have been documented in association with the sea ice in the past, to a greater or lesser extent, and seasonally also actively feeding on sea ice biota, but are also known to thrive significantly on phytoplankton blooms (Falk-Petersen et al. 2000). According to Hellmer et al. (2012), the area around the Filchner Trough is extremely sensitive to the climate warming-related changes, subsequently resulting in an increased import of warm water masses into the deep southern ice-shelf cavity, and the resulting higher temperatures might cause increased melting at deep ice-shelf bases, such as the Filchner-Ronne Ice Shelf (Rignot and Jacobs 2002; Pritchard et al. 2012). Our dietary estimates provide a valuable insight into the feeding history of abundant euphausiid species, which are often overshadowed by the more frequently investigated *E. superba*. The results from this study suggest that ice algae might serve as important dietary alternative to pelagic algae particularly for *E. crystallorophias*. The lack of stable isotope data for *E. crystallorophias* and *T. macrura*, however, emphasizes the need for further investigations of the feeding characteristics of the Southern Oceans' ecological key species to gain more information on their fate in respect to proceeding changes of Antarctic ice-associated ecosystems.

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Supplementary

▼**Supplementary A.** Station information for ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM), *Euphausia superba* (ES), *Euphausia crystallorophias* (EC) and *Thysanoessa macrura* (TM) collected during PS82 in the Filchner outflow system. Region letters correspond to station grouping presented in **Figure 1**.

Region	Date (m/dd/yyyy)	Sample type	Station no.	Depth at station (m)	Sampling depth (m)	Latitude	Longitude
A	1/2/2014	ES, EC, TC	3	3154-3203	200-0	-70.87	-25.77
B	1/3/2014	P-POM	4	424	30	-74.68	-29.75
	1/3/2014	EC	7	398-423	250-160, 100-0	-74.73	-29.80
	1/4/2014	P-POM	14	500	20	-74.83	-28.21
C	1/5/2015	P-POM	22	406	20	-76.18	-30.00
	1/5/2014	I-POM	26	473	--	-76.05	-31.01
	1/6/2014	P-POM	31	685	10	-75.94	-31.66
	1/6/2014	I-POM	36	462	--	-75.92	-30.75
	1/7/2014	P-POM	38	462	40	-76.08	-30.45
	1/7/2014	ES, EC	42	445-469	200-0	-76.07	-30.27
	1/8/2014	EC	51	255-376	200-0	-76.32	-28.97
D	1/9/2014	P-POM	55	373	25	-76.99	-33.51
	1/10/2014	P-POM	61	1133	31	-77.10	-36.40
	1/10/2014	ES, EC	65	1100-1126	200-0	-77.10	-36.43
	1/11/2014	P-POM	70	491	20	-77.01	-34.05
	1/11/2014	TC	76	765-825	700-500	-76.99	-34.56
	1/12/2014	P-POM	80	377	15	-77.06	-33.61
	1/13/2014	ES, EC	83	419-457	350-200, 50-0	-77.03	-33.68
	1/13/2014	I-POM	h02	--	--	-77.16	-34.53
	1/14/2014	P-POM	87	273	14	-76.97	-32.94
	1/14/2014	EC	90	336-380	100-50, 50-0	-76.93	-32.73
E	1/15/2014	P-POM	93	399	12	-77.64	-35.17
	1/15/2014	EC, TC	100	583-588	200-50	-77.69	-35.87
	1/16/2014	P-POM	104	1194	15	-77.92	-37.99

	1/16/2014	EC, TC	107	1192-1216	700-500, 500-200	-77.92	-38.00
	1/17/2014	TC	117	1022-1065	500-200	-77.60	-38.90
F	1/19/2014	P-POM	121	288	35	-75.50	-27.45
	1/19/2014	EC	124	279-288	250-200, 200-100	-75.50	-27.45
	1/20/2014	ES, EC	133	358-366	200-50	-75.33	-27.62
	1/20/2014	EC	135	365-370	200-0	-75.32	-27.64
G	1/21/2014	P-POM	140	520	10	-74.83	-25.83
	1/21/2014	I-POM	146	702	--	-74.83	-25.12
	1/21/2014	ES, EC	147	655-694	600-0	-74.82	-25.22
H	1/22/2014	ES, EC	155	1538-1814	200-0	-74.57	-28.30
I	1/23/2014	P-POM	156	3250	20	-73.47	-29.68
	1/23/2014	P-POM	160	2285	20	-74.07	-28.95
H	1/25/2014	P-POM	173	529	20	-74.50	-30.99
	1/25/2014	ES, EC	177	516-533	200-50, 50-0	-74.55	-30.95
J	1/27/2014	P-POM	197	400	30	-74.67	-36.50
	1/27/2014	ES	199	422-425	50-0	-74.60	-36.36
	1/28/2014	P-POM	207	1719	50	-74.27	-35.55
K	1/29/2014	I-POM	214	2287	--	-73.89	-35.45
	1/30/2014	P-POM	219	3109	35	-73.50	-34.61
	1/30/2014	P-POM	222	2846	35	-73.64	-35.14
J	1/31/2014	ES, EC	227	624-859	50-0	-74.32	-37.67
	1/31/2014	P-POM	228	554	25	-74.33	-37.79
	2/1/2014	ES, EC, TC	234	636-891	500-200, 50-0	-74.28	-37.86
	2/2/2014	P-POM	240	440	20	-74.67	-39.03
	2/3/2014	EC, TC	247	395-424	50-0	-74.55	-37.76
	2/3/2014	EC, TC	250	380-383	50-0	-74.52	-37.49
	2/3/2014	P-POM	252	388	25	-74.49	-37.53
	2/4/2014	P-POM	258	592	20	-74.51	-35.57
	2/4/2014	I-POM	259	623	--	-74.51	-35.65
	2/5/2014	I-POM	265	654	--	-74.41	-33.41
	2/6/2014	P-POM	271	756	50	-74.49	-33.14

L	2/9/2014	P-POM	302	425	37	-75.09	-28.75
	2/9/2014	EC	304	416-437	350-200	-75.09	-28.76
	2/10/2014	ES, EC, TC	317	805-868	500-200, 200-50, 50-0	-74.65	-28.84
	2/10/2014	P-POM	318	424	40	-74.72	-29.36
	2/11/2014	EC	322	429-435	50-0	-74.66	-29.92

▼**Supplementary B.** Proportions of most abundant lipid classes and total of storage lipids (SL) in in juvenile (J) and adult (A) in euphausiids (mean ± 1 SD mass % of total lipid content).

	Euphausia superba	***Euphausia crystallorophias***		***Thysanoessa macrura***	
developmental stage	A	J	A	J	A
n	9	2	6	2	6
WE	0.2 ± 0.2	44.5 ± 10.8	33.9 ± 5.8	63.7 ± 6.7	50.8 ± 18.1
TAG	35.7 ± 17.8	1.5 ± 0.9	3.9 ± 2.9	0.7 ± 0.1	0.5 ± 0.2
PE	6.8 ± 3.3	7.6 ± 5.1	7.9 ± 2.6	1.9 ± 0.5	5.0 ± 4.4
PC	46.4 ± 8.6	41.2 ± 2.8	38.2 ± 2.7	30.7 ± 6.1	37.3 ± 8.8
SL	45.1 ± 11.1	48.8 ± 8.1	44.8 ± 5.3	65.5 ± 5.9	53.9 ± 15.9
TLC/dry weight (%)	21.2 ± 7.0	23.1 ± 11.7	22.9 ± 9.6	30.0 ± 9.3	35.4 ± 11.3

TAG: triacylglycerol, PC: phosphatidylcholine, PE: phosphatidylethanolamine, WE: wax ester

▼**Supplementary C**. Fatty acid and stable isotope parameters in *Euphausia superba* collected at different depth layers.

		%								‰			
depth	*n*	16:1n-7	20:5n-3	18:4n-3	22:6n-3	*n*	bulk δ^{15}N	bulk δ^{13}C	*n*	δ^{13}C 16:1n-7	δ^{13}C 18:4n-3	δ^{13}C 20:5n-3	δ^{13}C 22:6n-3
50-0	19	12.2 ± 3.1	16.4 ± 1.4	3.8 ± 0.7	9.1 ± 1.2	13	3.7 ± 0.5	-27.6 ± 1.8	7	-28.6 ± 6.9	-40.6 ± 2.2	-33.7 ± 2.9	-34.3 ± 1.0
200-0	13	8.2 ± 1.8	17.7 ± 2.9	4.7 ± 2.6	12.4 ± 3.6	7	4.2 ± 1.4	-27.8 ± 1.4	5	-39.5 ± 1.8	-42.9 ± 1.3	-36.1 ± 1.1	-35.8 ± 0.7
< 200	6	8.5 ± 0.8	13.0 ± 2.2	4.5 ± 1.1	9.8 ± 1.1	2	3.2 ± 0.3	-29.9 ± 0.1	2	-38.1 ± 2.5	-43.2 ± 0.8	-34.1 ± 1.0	-35.1 ± 0.4

▼**Supplementary D.** Fatty acid and stable isotope parameters in *Euphausia crystallorophias* collected at different depth layers. Not detected parameters are marked as '--'.

	%								‰			
depth	*n*	16:1n-7	20:5n-3	18:4n-3	22:6n-3	*n*	bulk δ^{15}N	bulk δ^{13}C	*n*	δ^{13}C 16:1n-7	δ^{13}C 18:4n-3	δ^{13}C 20:5n-3	δ^{13}C 22:6n-3
50-0	10	16.5 ± 6.1	16.9 ± 3.3	1.5 ± 0.6	6.3 ± 1.6	4	6.0 ± 0.8	-21.9 ± 2.0	2	-26.8 ± 15.8	--	-34.0 ± 2.8	-31.1 ± 1.1
200-0	25	9.7 ± 5.6	17.8 ± 4.2	1.8 ± 1.7	11.5 ± 4.3	18	7.0 ± 1.0	-26.8 ± 2.7	5	-29.6 ± 6.7	-39.4 ± 3.9	-31.7± 1.8	-32.1 ± 1.3
< 200	14	7.8 ± 4.7	18.0 ± 4.7	2.3 ± 2.4	10.8 ± 3.7	6	6.4 ± 1.1	-28.0 ± 2.4	--	--	--	--	--

▼**Supplementary E.** Fatty acid and stable isotope parameters in *Thysanoessa macrura* collected at different depth layers. Not detected parameters are marked as '--'.

	%								‰			
depth	*n*	16:1n-7	20:5n-3	18:4n-3	22:6n-3	*n*	bulk δ^{15}N	bulk δ^{13}C	*n*	δ^{13}C 16:1n-7	δ^{13}C 18:4n-3	δ^{13}C 20:5n-3	δ^{13}C 22:6n-3
50-0	2	10.0 ± 4.0	17.6 ± 0.9	0.5 ± 0.7	11.4 ± 1.9	--	--	--	2	-21.5 ± 5.4	-37.1	-32.7 ± 0.7	-31.5 ± 1.5
200-0	2	2.3 ± 1.0	18.9 ± 4.6	0.6 ± 0.2	16.4 ± 5.2	1	9.6 ± 0.5	-27.1 ± 0.7	2	-34.1 ± 4.1	-40.5 ± 1.8	-32.4 ± 1.4	-31.7 ± 1.0
< 200	9	5.3 ± 3.0	16.3 ± 2.6	0.8 ± 0.3	11.6 ± 2.8	2	9.0	-27.8	6	-29.2 ± 7.9	-38.8 ± 2.5	-32.1 ± 1.2	-31.6 ± 1.4

3. Discussion

3.1 Quantifying dietary contributions of ice algal produced carbon: Methodological aspects

To study trophic relationships and the interaction between primary producers and consumers, various approaches have been used. Besides the isotopic composition of bulk organic content (BSIA- Bulk stable isotope analysis) (e.g. Hobson et al. 2002; Søreide et al. 2006; Jia et al. 2016), individual biomolecules, such as fatty acids, can be studied in order to estimate the importance of a given carbon source (e.g. sympagic, pelagic, terrestrial) within an ecosystem (CSIA- Compound-specific stable isotope analysis) (Budge et al. 2008; Wang et al. 2015; Mohan et al. 2016b). Whereas the BSIA approach tends to overestimate the importance of sympagic carbon in a consumer (see 3.1.2, **Chapters I** and **II**), it remains difficult to decide, which marker fatty acid (FA) most accurately represents the contribution of carbon sources in the consumers.
Most commonly used is the stable isotope composition of the diatom-associated FA 20:5n-3 (**Chapters I-III**, **V** and **VI**). The application of this FA is suggested, because 20:5n-3 is one of the most abundant FAs in marine species. 20:5n-3 is produced by both sympagic and pelagic diatoms. Thus, high proportions of 20:5n-3 in a consumer from an environment with high abundances of pelagic diatoms make it impossible to distinguish the carbon source preferences of this organism. The single use of 20:5n-3 might not represent a marine ecosystem well, which is characterized by high numbers of dinoflagellates in the water column, as discussed in **Chapter I**. Thus, adding the isotopic information of a dinoflagellate-associated FA to the calculations might be a reasonable modification to avoid the introduction of a bias from excluding an important carbon source, which was also considered in food web studies by e.g. Graham et al. (2014) and Wang et al. (2015). Without exception, the estimates of the contribution of ice-algae carbon were higher derived from the model using only 20:5n-3 in all species investigated in the studies of this thesis compared to the estimates from the model incorporating the isotopic signals from both 20:5n-3 and 22:6n-3. In contrast, the estimates from both models for zooplankton from the Bering Sea were more similar to each other or even higher when using the combination of 20:5n-3 and 22:6n-3 instead of only 20:5n-3 (Wang et al. 2015). This emphasizes the need to assess, which approach is the most dependable. The applicability of the different approaches differs from study to study, with a strong dependency on the composition of the primary communities and environmental conditions.

Budge et al. (2008) used the diatom-associated FA 16:4n-1, in addition to 20:5n-3, to quantify the carbon sources in an Alaskan shelf food web. The species analyzed in the present study, however, revealed generally lower proportions of this FA. Hence, the determination of the stable isotope composition would have been accompanied by a tendency for higher error-proneness when analyzing molecules quantitatively close to the detection limit of the measuring system. The derived $\delta^{13}C$ values would not

have been reliable and would most likely have led to false or inaccurate estimates of the proportional contribution of a carbon source.

A more comprehensive approach was applied in **Chapters III**, **V** and **VI**, where the trophic signal derived from 'short-term' and 'long-term' fatty acids was distinguished. Storage fatty acids are assumed to experience a faster turnover rate than membrane fatty acids that are conserved in cell membranes over a longer period (Stübing et al. 2003). Differentiating the isotopic pattern between storage ('more recent') and membrane fatty acids ('less recent') revealed a remarkable increase in the utilization of ice algal carbon from pre-winter to winter in Antarctic under-ice fauna species. In contrast, Arctic under-ice organisms did not indicate time-dependent variabilities in the dependency on ice algae-produced carbon, which emphasized the value of this approach when investigating seasonal patterns in dietary compositions.

Besides the application of Bayesian stable isotope mixing models (Parnell et al. 2013), which were used to estimate the relative contribution of ice algal carbon in this study, more simple model structures can be applied, such as proposed by Budge et al. (2008). In this two-end member mixing model, only one FA is considered at a time. Applying this model to the Arctic food web dataset, resulted in similar estimates to the estimates from the Bayesian mixing models derived from the δ^{13}C compositions of FA 20:5n-3. In contrast to the estimates from the Software R -based modeling with SIAR (Parnell et al. 2008) or MixSIAR (Stock and Semmens 2015), the results can, however, suggest a carbon proportion considerably below 0% or higher than 100%, when the δ^{13}C values of the consumers are either lower or higher than both baseline communities (ice algae and pelagic algae).

Besides the stable isotope signal from a fatty acid, the isotopic compositions of fatty alcohols, which serve as long-term lipid reserves incorporated in wax esters, can potentially provide useful information on the origin of carbon sources in wax-ester containing consumers. Wax esters typically do not occur in algae, but the wax ester alcohols in herbivorous zooplankton are either biosynthesized *de novo*, by utilizing algal proteins and carbohydrates, or are produced by modification of algal fatty acids (Lee et al. 2006). The δ^{13}C compositions of the fatty alcohol 16:1n-7 in the wax-ester containing species *Calanus* spp., *E. holmii* and *T. libellula* from the CAO were similar to the δ^{13}C values of the fatty acid 16:1n-7, demonstrating the lowest values in *C. hyperboreus* and the highest values in *E. holmii* (**Table 1**). This FA is produced by algae, and thus, the information on the origin of the carbon is likely transferred along the marine food chain and is incorporated in the alcohol that is produced from FA 16:1n-7. *Calanus* copepods accumulate large amounts of the long-chain FAs and fatty alcohols 20:1n-9 and 22:1n-11 (Sargent and Falk-Petersen 1988). The δ^{13}C values of 20:1n-9 and 22:1n-11 were higher in the fatty alcohols compared to the FAs in all species. The long chain FAs are usually not primary produced and therefore copepods need to build them from scratch, which might be one explanation for the differing stable isotope compositions between fatty alcohol and fatty acid. To my knowledge, δ^{13}C values of wax ester alcohols have not been used so far for tracking trophic pathways in marine studies or quantifying carbon

sources in consumers. These biomolecules might be valuable trophic markers in this context, and the applicability of fatty alcohols as carbon source proxies should be in the focus of future stable isotope-based food web studies.

▼**Table 1.** Comparison of carbon stable isotope compositions $\delta^{13}C$ of corresponding fatty acids and fatty alcohols in wax ester-containing species.

Species	**FATTY ACID $\delta^{13}C$**			**FATTY ALCOHOL $\delta^{13}C$**		
	16:1n-7	20:1n-9	22:1n-11	16:1n-7	20:1n-9	22:1n-11
Calanus glacialis	-25.0 ± 3.8	-31.5 ± 1.9	-27.4 ± 1.7	-24.7 ± 4.1	-28.3 ± 1.5	-26.4 ± 1.4
Calanus hyperboreus	-27.3 ± 3.6	-30.0 ± 1.9	-27.5 ± 1.4	-27.2 ± 4.2	-28.8 ± 1.3	-27.1 ± 1.5
Eusirus holmii	-23.4 ± 2.1	-28.6 ± 0.7	-26.3 ± 1.1	-21.3	-27.4	-25.2
Themisto libellula	-23.9 ± 2.3	-29.0 ± 0.5	-27.6 ± 0.9	-23.8 ± 2.5	-28.0 ± 0.7	-26.1 ± 0.6

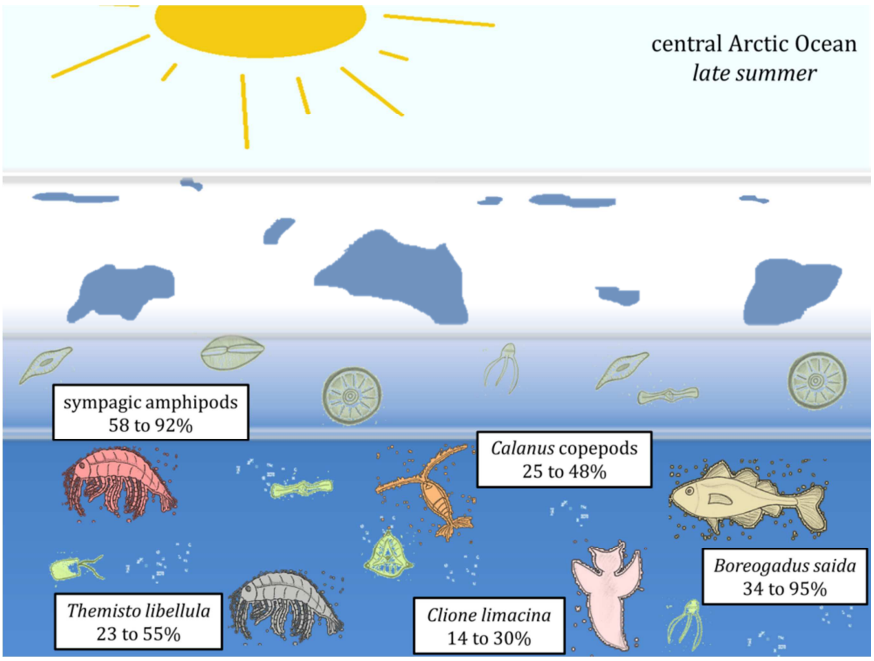
$\delta^{13}C$ values that do not allow for a distinct differentiation between ice algae and phytoplankton due to overlapping $\delta^{13}C$ values make the determination of the quantitative importance of ice algal carbon to the food web impossible or with large uncertainties. Søreide et al. (2006) showed that ice-associated particulate organic matter (I-POM) can occasionally be dominated by pelagic algae such as *Fragilariopsis oceanica* (in spring) or *Chaetoceros spp.* (in autumn; facultative I-POM), resulting in $\delta^{13}C$ highly depleted in ^{13}C, similar to pelagic particulate organic matter (P-POM). Thus, the distinct discrepancy of $\delta^{13}C$ values between ice-associated algae and pelagic algae does not always occur (Fry and Wainright 1991; Lovvorn et al. 2005; Kohlbach et al. unpubl.). Brown and Belt (2012) highlighted another possible limitation when using the stable isotope approach for determining carbon source preferences. They pointed out that the isotopic data do not sufficiently differentiate between carbon derived from bacterial, meiofaunal or sea ice algae production. A relatively novel approach, promising a precise alternative to trace ice algae-derived carbon in Arctic food webs is the use of the sea ice diatom biomarker IP_{25}. This highly branched isoprenoid alkene is assumed to be biosynthesized selectively by certain Arctic sea ice diatoms, particularly during the spring bloom (Belt et al. 2007; Brown et al. 2011, 2016). Other HBIs (highly branched isoprenoids) are produced by Antarctic marine diatoms, and were e.g. used for the estimation of the contribution of sea ice-derived organic matter to the diet of Antarctic fishes (Goutte et al. 2014b) and Antarctic seabirds and seals (Goutte et al. 2014a). In future studies, reliable data on the degree of sea ice algae-based feeding of marine organisms could be gained by combining the evaluation of this sea ice marker with the established analyses of FA proportions and stable isotope compositions of marker FAs.

3.2 Importance of ice algae-produced carbon to the Arctic food web

Sea ice can be very productive and seasonally host large assemblages of diatoms and other algal groups (Mock and Gradinger 1999; Boetius et al. 2013). The sea ice algae bloom occurs in spring, depending on the region with later blooms in higher latitude regions, and provides a high-quality food source prior to the phytoplankton bloom. Subsequently, the timing of the phytoplankton bloom is determined by the timing of the sea ice melt. The estimation of the contribution of the ice-associated primary production to the net primary production in the Arctic has a large range (3 to 57%) (Subba Rao and Platt 1984; Gosselin et al. 1997; Fernández-Méndez et al. 2015). Consequently, further research in specific regions of the Arctic Ocean is required, in order to improve our understanding of the trophic interactions between ice-associated (sympagic) and pelagic ecosystems in the Arctic Ocean.

A great number of herbivorous fauna is specialized to graze on ice-associated organic matter and transfer the ice algae-produced carbon into pelagic and benthic Arctic food webs (Michel et al. 1996; Werner 1997; Falk-Petersen et al. 2008; Campbell et al. 2016). However, Arctic sea ice coverage and thickness have significantly decreased in the past decades (Johannessen et al. 2004; Comiso et al. 2008; Kwok and Rothrock 2009; Maslanik et al. 2011; Harada 2016), accompanied by a decline in ice-associated primary production. So far, little is known about the contribution of ice algal biomass to lower

consumers and higher trophic levels compared to pelagic phytoplankton on multiple spatial and temporal scales (Hobson et al. 1995; Søreide et al. 2006; Budge et al. 2008). This study provided a unique dataset on the proportional contribution of ice algal carbon to the most important grazers in the central Arctic Ocean (CAO) as well as pelagic zooplankton (**Chapter I**), and a representative of the upper trophic levels, polar cod (**Chapter II**). The results demonstrated a generally high trophic dependency of numerous important carbon transmitters on the sea ice production in the CAO during late summer (**Figure 1**). In the sympagic amphipods *Apherusa glacialis*, *Onisimus glacialis*, *Gammarus wilkitzkii* and *Eusirus holmii*, ice algal carbon contributed up to 92% to their carbon budget. Moreover, the predominantly pelagic amphipod *Themisto libellula* and the *Calanus* copepods *Calanus glacialis* and *C. hyperboreus* acquired ice algae-produced carbon to a large extent. Only the pteropod *Clione limacina* received the majority of their dietary carbon from pelagic resources. Polar cod *Boreogadus saida* showed a high variability of the carbon source estimates based on the different model approaches, but the results suggested a generally high importance of sympagic carbon to their diet (**Figure 1**).



▲**Figure 1.** *Proportional contribution of ice algae-produced carbon to the carbon budget of under-ice fauna species in the central Arctic Ocean during late summer (PS80). Estimates are derived from* ***Chapters I*** *and* ***II****, based on the bulk organic content and the fatty acids 20:5n-3 and 22:6n-3.*

3.2.1 Foundation of every food web study: the trophic baseline

The taxonomic composition of pelagic algal communities (represented by P-POM) and ice-associated primary producer communities (represented by I-POM) varies through time and space. Thus, the fatty acid and isotopic compositions of the trophic baseline (i.e. I-POM and P-POM) in this study (**Chapters I** and **II**) can only be understood as a 'late summer signal', representing the sampling region in the CAO. For both I-POM and

P-POM, the proportions of marker FAs and the bulk and fatty acid-specific stable isotope compositions had a large variability across the sampling area, demonstrating substantial differences between the algal assemblages from the Nansen Basin (NB) and the Amundsen Basin (AB) (**Chapter I**: **Figure 1**).

Due to increased seasonal light availability for ice-associated POM compared to algae in the water column (Gradinger et al. 2009), and a limitation of CO_2 in the semi-closed system of the sea ice environment compared to the water column, the $\delta^{13}C$ values are often elevated in ice algae in comparison to pelagic phytoplankton (Fry and Sherr 1984). However, the ice algae and pelagic algae communities can also temporally and spatially differ in their taxonomic compositions, and the CO_2 concentration is subject to variations, which ultimately affects the isotopic signal of the sympagic primary producers.

The $\delta^{13}C$ compositions of primary producer communities showed also a large variation within and between other studies in the Arctic. Søreide et al. (2008) reported differences in the bulk $\delta^{13}C$ values due to different taxonomic compositions of the primary producers and also between different sampling seasons accompanied with different bloom situations in high-Arctic Svalbard. For example, algae sampled in May showed a higher enrichment of ^{13}C in both I-POM (mean -18.2‰) and P-POM (mean -23.5‰) compared to I-POM (-24.6‰) and P-POM (mean -26.3‰) collected during August (Søreide et al. 2008). In comparison, I-POM from the northern Fram Strait, collected in May/June, revealed considerably lower bulk $\delta^{13}C$ values (mean -28.0‰) compared to the findings from Søreide et al. (2008), which were even lower than the P-POM $\delta^{13}C$ values from this study (mean -25.9‰) (Kohlbach et al. unpubl.). Wang et al. (2014) determined fatty acid-specific $\delta^{13}C$ values in I-POM and P-POM during maximum ice extent in March, melting during May and June, and ice-free conditions between June and July in the Bering Sea. They found a discrepancy of approx. 3.5‰ in the $\delta^{13}C$ values of FA 20:5n-3 between I-POM sampled during maximum ice (mean -26.5‰) and I-POM sampled during ice melt (~ -22.5‰). The I-POM $\delta^{13}C$ values of 22:6n-3 were also lower during maximum ice content (~ -23.8‰) versus melting conditions (~ 21‰). In contrast, the $\delta^{13}C$ values in P-POM revealed a lower variability between the different ice situations (20:5n-3: ~ -29 to -30‰, 22:6n-3: ~ -26 to -27.5‰) (Wang et al. 2014).

These results imply that the seasonal, temporal and spatial variability of the baseline isotopic signals, representing bloom progression and environmental properties, is a big constraint when quantifying the importance of given carbon sources to consumers from the isotopic compositions of I-POM and P-POM (Tamelander et al. 2009). Thus, most reliable carbon source estimates can only derive from a food web system where carbon sources and consumers were sampled in the same region during the same period of the year.

3.2.2 Consumption of ice algal carbon: Do season and region matter?

The primary production in the CAO is generally assumed to be low as a result of the sea ice coverage during most periods of the year (Gosselin et al. 1997). Therefore, it seems natural that many organisms have adapted to the strongly limited food availability in the water column, particularly during Polar Night, by utilizing sea ice algae-produced carbon. Lower temperatures during winter result in a thicker ice pack and larger sea ice extent. Therefore, it could be speculated that the trophic dependency on the sea ice production is generally higher during winter due to the lack of food alternatives and might be highest during spring when the ice algae blooms starts. So far, our food web study is the only in the CAO, and provides the only information on the assimilation of ice algal carbon during late summer. Thus, investigating food web interactions during spring and winter in the CAO are the crucial step to reveal seasonal variability present in the utilization of ice algae-produced carbon.

The higher contribution of ice algal carbon to the carbon budget of many zooplanktonic species during spring compared to summer revealed by Søreide et al. (2013) supports the hypothesis of the highest utilization of sympagic carbon when the ice is thicker and the availability of pelagic algae is more restricted (**Table 2**). However, the results from Wang et al. (2015) do not indicate clear differences in the utilization of ice algal carbon by *Calanus* spp. and *T. libellula* during different seasons in the Bering Sea. This might reflect regional and thus environmental differences as well as the availability of nutrients and light between the region around Svalbard, the Bering Sea and the CAO, influencing growth and availability of sympagic and pelagic carbon sources during different periods of the year. The ice algae growth in the CAO is characterized by a different seasonal progression compared to regions with seasonal ice cover. The sea ice algae bloom in the CAO occurs approximately 2 months after the ice-associated bloom in lower latitude Arctic regions such as the Bering Sea and Svalbard (Leu et al. 2015). The melting rate in coastal and near-shelf regions is a lot faster and terminates the bloom earlier than in CAO regions. Consequently, biomass in the sea ice can be high in the central Arctic even during late summer (Gosselin et al. 1997; Melnikov et al. 2002; Lange 2016). The sampling for this study was conducted during a post-bloom situation, which was indicated by a high export of sea ice algae to the sea floor before the sampling period (Boetius et al. 2013). During PS80, all but one station was ice-covered (satellite observations indicated ice coverage between 46 and 100%). In contrast, the sample collection during summer in the Bering Sea took place under ice-free conditions (Wang et al. 2015), and mostly ice-free conditions during summer around Svalbard (Søreide et al. 2013).

Differences between the results from the different datasets might partly be explained by differences in the methodologies applied. The estimates presented in Søreide et al. (2013) derive from the bulk organic content, whereas the calculations in Wang et al. (2015) were based on fatty acid-specific stable isotope compositions. In this Arctic study (**Chapter I**), the difference between BSIA and CSIA estimates (model b: 20:5n-3 + 22:6n-3) ranged from 4% in *A. glacialis* to 33% in *G. wilkitzkii*, which indicates that the

potential uncertainties can vary by an order of magnitude. Furthermore, it has to be considered that the range presented in Budge et al. (2008) is based on the FAs 16:4n-1 and 20:5n-3, whereas in Wang et al. (2015) the $\delta^{13}C$ values of different combinations of the FAs 16:1n-7, 20:5n-3 and 22:6n-3 were investigated. This emphasizes how many factors can influence the result from a carbon source mixing model, and that the interpretation needs to be done very carefully, considering individual parameters of the given study design.

▼**Table 2**. Regional and seasonal variability in the ice algae contribution to the carbon budget of important Arctic carbon transmitters.

Species	Region	Season	mean % Ice algae contribution	Parameter	Reference
Calanus glacialis	Svalbard	spring summer	40-60 0-20	bulk $\delta^{13}C$	Søreide et al. (2013)
	CAO	summer	47 33-48	bulk $\delta^{13}C$ FA $\delta^{13}C$	this study
Calanus hyperboreus	Svalbard	spring summer	20-50 0-40	bulk $\delta^{13}C$	Søreide et al. (2013)
	CAO	summer	39 25-40	bulk $\delta^{13}C$ FA $\delta^{13}C$	this study
Calanus spp.	Bering Sea	winter spring summer	30-63 27-63 31-54	FA $\delta^{13}C$	Wang et al. (2015)
Apherusa glacialis	Svalbard	spring summer	40-60 20	bulk $\delta^{13}C$	Søreide et al. (2013)
	CAO	summer	90 86-92	bulk $\delta^{13}C$ FA $\delta^{13}C$	this study
Apherusa spp.	Alaska	summer	61-72	FA $\delta^{13}C$	Budge et al. (2008)
Onisimus glacialis	Svalbard	summer	30	bulk $\delta^{13}C$	Søreide et al. (2013)
	CAO	summer	87 61-77	bulk $\delta^{13}C$ FA $\delta^{13}C$	this study
Onisimus spp.	Alaska	summer	36-80	FA $\delta^{13}C$	Budge et al. (2008)
Gammarus wilkitzkii	Svalbard	summer	10-40	bulk $\delta^{13}C$	Søreide et al. (2013)
	CAO	summer	91 58-76	bulk $\delta^{13}C$ FA $\delta^{13}C$	this study
Gammarus spp.	Alaska	summer	46-79	FA $\delta^{13}C$	Budge et al. (2008)
Themisto libellula	Svalbard	summer	0	bulk $\delta^{13}C$	Søreide et al. (2013)
	Bering Sea	winter spring summer	47-51 36-55 38-72	FA $\delta^{13}C$	Wang et al. (2015)
	CAO	summer	55 23-45	bulk $\delta^{13}C$ FA $\delta^{13}C$	this study

Species	Region	Season	mean % Ice algae contribution	Parameter	Reference
Clione limacina	Svalbard	summer	0	bulk $\delta^{13}C$	Søreide et al. (2013)
	CAO	summer	30 14-18	bulk $\delta^{13}C$ FA $\delta^{13}C$	this study

In most investigated under-ice fauna species, the $\delta^{15}N$ values were higher in the Amundsen Basin (AB) regime than in the Nansen Basin (NB) regime (**Chapter I**). Conversely, the $\delta^{13}C$ values followed this pattern in many under-ice fauna species, particularly in *Calanus* spp. and *Themisto libellula*. These three species also had the highest variability in the ice algal-produced carbon contribution between the two environmental regimes. For example, the bulk stable isotope composition and the $\delta^{13}C$ values of FA 20:5n-3 indicated a considerably higher contribution of ice algal carbon to *C. glacialis* from the AB regime (BSIA: mean 63%, CSIA 20:5n-3: mean 33%) compared to individuals from the Nansen Basin (BSIA: mean 39%, CSIA 20:5n-3: 20%). An even higher discrepancy in the utilization of ice algal carbon was found in *T. libellula*, indicating that on average 79% of their ingested carbon was originated from sea ice algae in the AB regime versus 27% in the NB regime, based on BSIA measurements, and 49% versus 21% based on the $\delta^{13}C$ values of 20:5n-3. In the sympagic amphipods *A. glacialis*, *O. glacialis, G. wilkitzkii*, and *E. holmii*, differences between the two environmental regimes were not clearly evident, because the variability of $\delta^{13}C$ values was generally low in these species due to their consistently high trophic dependency on ice algae. Altogether, these results imply that the food web in the AB regime was both more heterotrophic and more sea ice-dependent than in the NB regime. This confirms results from David et al. (2015) who suggested a higher heterotrophy in the AB regime than in the NB regime based on the variability in species abundances. Furthermore, there were fundamental differences regarding the environmental characteristics and the physical and chemical properties of the water column between the two regions. All but one station in the AB regime was sampled later in the season, and showed lower nitrate, phosphate and Chlorophyll *a* (Chl *a*) concentrations in the surface layer than the stations in the NB regime. These factors probably limited the availability of algal food in the water column, and enforced the orientation of pelagic consumers towards more heterotrophic and more ice-associated carbon sources. Due to enhanced melting and ice break-up at the stations in the AB, the availability of food sources associated with sea ice other than algae, such as in-ice meiofauna, further supports the more heterotrophic character of the ecosystem in the AB regime (David 2016).

Dividing the PS80 stations in stations with low distance to the ice edge (< 50 km) and stations with high distance to the ice edge (> 100 km), revealed a large difference in the contribution of ice algal carbon to the diet of particularly *C. glacialis*. At stations close to the ice edge, ice algal-produced carbon was estimated to contribute to on average 27% to the carbon budget of this species, whereas ~ 44% of the carbon at stations far away from the ice edge originated from sympagic food sources. A similar result, albeit with a lower difference, was found for *T. libellula*, which also demonstrated a higher trophic dependency on ice algal carbon for individuals sampled far from the ice edge (mean 50%) versus individuals collected close to the ice edge (mean 38%).

The SUIT stations 358 and 376 during PS80 (**Chapter I**: **Figure 1**, **Table 1**) represented high-latitude stations, which were characterized by a larger ice thickness compared to the other stations (Lange 2016). The high-latitude ice stations 349 and 360 were multi-

year ice stations, station 335 was characterized by a mixture of multi-year ice and first-year ice, whereas all other stations were covered by first-year ice. Fernández-Méndez et al. (2015) estimated the sympagic primary production (PP) with up to 60% of the total PP at stations in close proximity to the north pole during this cruise. Based on the findings of high productivity and high Chl *a* concentrations in sea ice at high-latitude stations in previous studies (Gosselin et al. 1997; Melnikov 1997), Lange (2016) suggested that this high sympagic biomass and productivity might be a common characteristic for sea ice at high latitudes in late summer. Due to lower solar radiation, thicker sea ice and lower atmospheric temperatures at high latitudes, the sea ice experiences lower melt rates during Polar Day, which results in higher biomass standing stocks of sea ice algae in regions > 85°N compared to lower latitude regions (Lange 2016). Conversely, due to the dense sea ice cover, pelagic algae have little chance to receive efficient sunlight for intense growing periods. These factors led to the assumption that ice algal carbon was of higher importance as a food source for more opportunistic feeders, such as *Calanus* copepods, at these high-latitude stations compared to stations with more open water during the sampling period, and thus, a higher availability of pelagic algae. Indeed, calculating the proportional contribution of ice algal carbon with high-latitude station-specific δ^{13}C values of I-POM, indicated a considerably higher dependency on sympagic carbon versus pelagic carbon by *C. glacialis* at station 376 of ~ 63% compared to stations located in the NB with ~ 35% ice-associated carbon in their energy budget, based on the δ^{13}C values of FA 20:5n-3.

Our results highlight a large variability regarding the importance of ice algal carbon for the food web throughout the central Arctic Ocean. Regions at lower latitudes are characterized by a longer ice-free period, which allows for a longer and likely more intense phytoplankton bloom after the sea ice recedes. In comparison, in high-Arctic regions, which are even in summertime mostly ice-covered, and assumed that the productivity by ice algae is proportional to the sea ice coverage, ice algae carbon might be the only available carbon source for most periods of the year, explaining the considerably higher proportions of ice algal carbon to the carbon budget of the under-ice fauna species from the CAO. Based on these results, it can be argued that the trophic dependency of Arctic organisms in oceanic deep-sea regions on ice algae is much greater than previously thought. Therefore, it is of crucial importance to characterize and quantify the overarching interactions between important carbon transmitters in order to accurately assess the ecological implications of a changing Arctic sea ice environment on large temporal and spatial scales.

3.2.3 How big is the impact of the changing sea ice environment on top predators?

Studies quantifying the trophic dependency on ice algal carbon by organisms from upper trophic levels (TLs), such as fishes, seals or whales, are even more scarce than for lower TLs. For one, sampling in the Arctic Ocean is logistically difficult due to the heavy ice conditions during long periods of the year, particularly in high-Arctic regions. Moreover, higher organisms are not as abundant, and thus, not as easily collected as zooplankton,

and the sampling is accompanied by strict regulations regarding the acquisition of sample material.

Another complication when investigating trophodynamics of higher predators is the evaluation of the results. Higher organisms do not receive carbon directly from the primary producers, but by often various preys from multiple TLs, and show therefore a 'diluted' biomarker signal. For example, the $\delta^{13}C$ composition of a predator is influenced by metabolic processes of the organic compounds, such as elongation and desaturation of FAs (Monson and Hayes 1982), which are assumed to result in a enrichment of ^{13}C and thus increasing $\delta^{13}C$ values with increasing TL. Unfortunately, the species-specific degree to which the carbon stable isotope signal is altered from prey to predator, is still unknown, but is assumed to be as high as 1‰ per TL (DeNiro and Epstein 1978; Rau et al. 1983). This uncertainty potentially leads to an overestimation of the ice algae dependency of an organism, when the trophic enrichment is not considered (see **Chapter II**). However, it is assumed that these metabolic processes in marine vertebrates regarding specific marker FAs, such as 20:5n-3 and 22:6n-3, are rather negligible (Tocher 2003). Nevertheless, when investigating the bulk organic content of organisms, besides fatty acids, proteins and carbohydrates are subject to metabolic alterations. Measurements of bulk stable isotope compositions are therefore more likely to produce results with a bias toward a higher contribution of sympagic carbon. In comparison to organisms from lower TLs, which show a lipid turnover rate of hours to days (Graeve et al. 2005), the lipid turnover of e.g. fish was found to be ~ 3 weeks (Kirsch et al. 1998), and can accordingly be expected to be longer in top predators, such as seals and whales. That means that the trophic signal of top predators does not reflect the current composition of carbon sources, but the ingested carbon sources integrated over several weeks. Accordingly, the most representative results in food web studies with higher organisms are received when potential carbon sources are sampled a certain time in advance, to accurately reflect the dietary signal of the available carbon sources for the consumers.

In **Chapter II**, essential and new insights on the composition of carbon sources of an important predator and energy link in the central Arctic Ocean were provided. It was demonstrated that polar cod *Boreogadus saida* caught from underneath the sea ice in the CAO during late summer acquired substantial amounts of ice-associated carbon (**Figure 1**), apparently by feeding on ice-associated copepods and amphipods. A high spatial variability and dependency on environmental properties for this species can be derived from the highly differing results conducted by Budge et al. (2008) and Graham et al. (2014). Whereas the individuals from the Beaufort Sea received their dietary carbon almost exclusively from pelagic resources, a large proportion of ice algal carbon with up to 77% was ingested by polar cod off the coast of Barrow, Alaska (**Table 3**). Different seal species from the Bering Sea indicated a general high trophic dependency on ice algae-derived carbon during different seasons (Wang et al. 2016), whereas the seals caught in Alaskan waters during summer had a rather mixed carbon source

composition, receiving carbon from both sympagic and pelagic sources (Budge et al. 2008) (**Table 3**).

▼**Table 3**. Regional and seasonal variability in the ice algae contribution to the carbon budget of higher trophic levels and top predators.

Species	Region	Season	mean % ice algae contribution	Parameter	Reference
Polar cod	Alaska	summer	8-77	FA $\delta^{13}C$	Budge et al. (2008)
	Beaufort Sea	summer	1-2	FA $\delta^{13}C$	Graham et al. (2014)
	CAO	summer	95 34-65	bulk $\delta^{13}C$ FA $\delta^{13}C$	this study
Bearded seals	Alaska	summer	0-57	FA $\delta^{13}C$	Budge et al. (2008)
	Bering Sea	spring-summer	61-80	FA $\delta^{13}C$	Wang et al. (2016)
Ringed seals	Alaska	summer	7-62	FA $\delta^{13}C$	Budge et al. (2008)
	Bering Sea	fall-winter spring-summer	24-42 21-60	FA $\delta^{13}C$	Wang et al. (2016)
Spotted seals	Bering Sea	fall-winter	51-62	FA $\delta^{13}C$	Wang et al. (2016)
Bowhead whales	Alaska	spring/fall	0-44	FA $\delta^{13}C$	Budge et al. (2008)

These studies give clear evidence that top predators can thrive significantly on ice algae-produced carbon across the Arctic Ocean during different periods of the year. Changes within the ice-associated communities regarding e.g. their composition or energy content will likely affect the energy flux through the ecosystem with inevitable consequences for end members. For example, in recent studies, the great sensitivity of Arctic marine mammals regarding the climate change-related alteration of their habitat, such as ice-associated seals, polar bears and narwhales has been demonstrated (Tynan and DeMaster 1997; Ainley et al. 2003; Derocher et al. 2004; Laidre and Heide-Jørgensen 2005; Laidre et al. 2008; Hamilton et al. 2016; Huntington et al. 2016). The alterations of the sea ice system might result in a permanent habitat change or even habitat loss for many organisms along the marine food chain, which is particularly severe when a species is highly specialized in terms of diet composition and seasonal environmental parameters (Laidre et al. 2008).

Habitat changes within the Arctic ecosystem might trigger alterations of e.g. seasonal distributions, the nutritional condition and reproduction ability, which will ultimately affect the population structure and size of the species (Tynan and DeMaster 1997; Stempniewicz et al. 2016; Wauchope et al. 2016). These changes are likely to affect polar cod populations, which constitute an important prey for Arctic marine mammals and may diminish the food resource for seals, whales and consequently polar bears (Nahrgang et al. 2014). In contrast, it has been argued that an earlier ice break-up and more open-water areas, particularly in shelf areas during Polar Night, due to the increasing temperatures, might have a positive effect on survival of young polar cod and could thus result in an increasing polar cod population (Bouchard and Fortier 2008, 2011), which is also a likely scenario for their competitors. A potentially reduced role of polar cod in the future can likely be buffered by invasive species, such as Atlantic cod *Gadus morhua*, which have already expanded into the Barents Sea and the deep-sea regions of the Arctic Ocean (Hollowed and Sundby 2014; Kjesbu et al. 2014; Kunz et al. 2016). However, the potential competition with invading species for space might force local species to migrate into habitats with less favorable conditions in terms of food quality and supply and spawning conditions, ultimately affecting the population density negatively (Clark et al. 2003; Brander 2007; Renaud et al. 2012). Growth and reproductive processes of fishes are critically depending on the environmental temperature, and only occur within a species-specific temperature range. Hence, the conquest of new habitat for invasive species can only be successful when these species are able to adapt to new environmental conditions, including harsh conditions and food limitation during Polar Night (Hollowed et al. 2013b; Berge et al. 2015; Stige et al. 2015).

The diet of polar bears consists mainly of ringed seals and, to a lower extent with a higher geographical variability, bearded seals (Lønø 1970; Stirling and Øritsland 1995; Derocher et al. 2002; Thiemann et al. 2008). Based on results from Wang et al. (2016), ringed seals receive up to 60% of their energy from ice-associated carbon sources during the spring-summer transition in the Bering Sea. Assuming that the polar bear diet in this region consists to ~ 60% of ringed seals by number, as reported by Derocher et

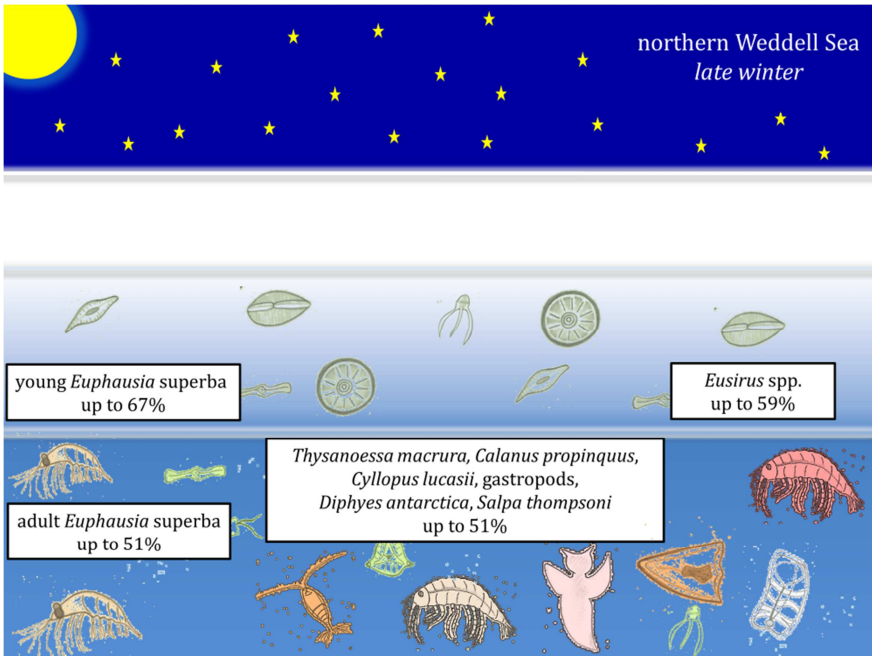
al. (2002) for polar bears in likewise shelf-bound regions close to Svalbard, the proportional contribution of ice algal carbon to the carbon budget could be as high as 36%. However, under the current climatic trends, polar bears will have less opportunity to hunt seals during spring to accumulate their annual fat reserves. Derived from that it was assumed that polar bears will react to climate change by adapting to predominantly terrestrial food sources, and thus shifting to a more opportunistic feeding behavior (Derocher et al. 2013; Gormezano and Rockwell 2013; Rode et al. 2015). However, a recent study gives evidence that the increased nest predation of land-based bird eggs might be insufficient to maintain polar bears, resulting in continued decline of their body condition in ice-free periods (Dey et al. 2016). Overall, numerous studies suggest a dramatic decrease in polar bear numbers due to continuing sea ice loss (e.g. Obbard et al. 2016; Regehr et al. 2016).

3.3 Importance of ice algae-produced carbon to the Antarctic food web

In the Southern Ocean (SO), Antarctic krill *Euphausia superba* and copepods dominate the zooplanktonic communities, and play a similar role as an energy linkage to amphipods in Arctic food webs (Hernández-León et al. 2000; Li et al. 2001; Pakhomov and Froneman 2004; Tanimura et al. 2008; Ducklow et al. 2012). Environmental changes and modifications of the primary producer communities, however, are predicted to have a negative effect on the highly specialized krill grazing (McClatchie and Boyd 1983; Moline et al. 2004). For example, in the region of the western Antarctic Peninsula, sea ice retreated significantly (Meredith and King 2005; Paolo et al. 2015) and the net primary production declined during the past three decades due to climate change, which was accompanied by a change in the taxonomic composition of pelagic primary assemblages (Moline et al. 2004; Montes-Hugo et al. 2009; Mendes et al. 2013). As a result of changing environments, krill numbers have shown a decreasing trend between 38 and 75% per decade (Atkinson et al. 2004). In contrast, salps, which can be highly abundant throughout the SO, might actually profit from the ecosystem changes (Perissinotto and Pakhomov 1998b; Pakhomov et al. 2002; Loeb and Santora 2012). They are believed to possibly replace krill in number and significance since they have a less sea ice-related lifestyle and are more likely to succeed in a warmer habitat with a lower sea ice coverage (Smith et al. 1999; Smetacek and Nicol 2005; Ducklow et al. 2007; Murphy et al. 2007; Montes-Hugo et al. 2009). Salps are mostly restricted to warmer water masses (Siegel et al. 1992; Park and Wormuth 1993), and are therefore often geographically excluded from *E. superba* (Hosie 1994; Pakhomov et al. 1994), but the higher seawater temperatures might push salps to high-latitude Antarctic regions, which would have important consequences for the regional food web and the carbon flux within (Perissinotto and Pakhomov 1998a, 1998b; Henschke et al. 2016). Unlike krill, salps are not considered being a major link to higher trophic levels. Thus, an increasing salp abundance paralleled by decreasing krill abundance might reduce food availability for fish and higher predators (Steinberg et al. 2012; McBride et al. 2014). Moreover, krill distribution patterns are changing, in relation to changing chlorophyll concentrations and sea ice extent (Murphy et al. 2007; Montes-Hugo et al. 2009). A southward shift of

krill would consequently lead to decreased abundances of krill-dependent predators, with a possible shift from a krill to a more copepod-dominated ecosystem (Murphy et al. 2007; Hill et al. 2012). The results presented in this thesis might give this assumption of a threatened krill additional support by demonstrating that young *E. superba* fed substantially on ice-associated resources to survive winter (**Figure 2**, **Chapters III** and **V**), whereas the salp *Salpa thompsoni* indicated the lowest dependency on sea ice algae carbon in the Weddell Sea food web. However, an increase in the dependency on ice algae-produced carbon was found for this species as the winter season progressed (**Chapter V: Figure 3**).

Only the amphipod *Eusirus laticarpus* demonstrated a substantial acquisition of ice algal carbon during the sampling period in late winter as well as in the weeks before that (**Figure 2**, **Chapter V: Figure 3**). This suggests that many Antarctic species adapted to the high food limitation in the Southern Ocean by e.g. relying on lipid reserves, which they backfill with phytoplankton bloom-carbon, or overcome by starvation. However, all investigated under-ice fauna species were able to switch their predominantly pelagic lifestyle in the pre-winter period to rely considerably on sympagic carbon, when the water column is still depleted in food sources during late winter. Most of the species did not gain much attention in previous studies, so that even basic trophic information are scarce. Hence, this study with particular on the quantification of their carbon sources fills a large knowledge gap regarding the lifestyle and feeding behavior of Antarctic zooplankton species during winter (**Chapters III-V**) and summer (**Chapter VI**), as the number of studies on carbon source preferences of these species is much more limited than in the Arctic food web (Jia et al. 2016).



▲**Figure 2.** *Proportional contribution of ice algae-produced carbon to the carbon budget under-ice fauna species in the northern Weddell Sea during winter (PS81). Estimates are derived from* ***Chapter V****, based on the short-term fatty acid 18:4n-3.*

3.3.1 Exceptional role in the Antarctic food web: Antarctic krill Euphausia superba

Antarctic krill *Euphausia superba* is regionally a keystone species in the food web of the SO (Hopkins 1985; Miller and Hampton 1989; Krafft et al. 2015; Ratnarajah et al. 2016). Thus, this species deserves more attention, particularly considering that the scientific views on their fate in the course of climate change are rather diverse and speculative (Nicol 2006; Hill et al. 2013).

The results from this study suggested that the degree of utilization of ice algae-produced carbon by *E. superba* in the SO is a result of multiple ontogenetic and environmental factors. Relatively low, yet variable trophic dependency on ice algal carbon was found for adult krill in the beginning of winter (**Chapters III** and **V**) in the Weddell Sea and during summer in the Filchner area (**Chapter VI**), possibly reflecting the availability of certain food sources and variability of environmental conditions during different seasons and in different regions. During winter, the importance of the sea ice algae primary production decreased with ontogeny, and indicated a strongly ice algae-based diet for larvae (**Chapter III**), supporting previous studies (Meyer et al. 2002, 2009, 2012; Jia et al. 2016). In contrast to adult krill, which showed a surprisingly flexible feeding behavior (Perissinotto et al. 2000; Schmidt et al. 2006), young developmental stages are more sensitive to the availability of food. The dependency of larvae on sea ice algae as a food source is particularly critical when the sea ice environment and parameters change, since the availability of sympagic food sources is a function of timing and extent of the sea ice (Quetin et al. 2007). The life cycle of krill is strongly linked to environmental parameters, including sea ice duration and characteristics. Thus, the distribution of krill and consequently of the krill-based food web depends on the winter extent of sea ice due to the tight connection between sea ice and krill's reproductive success, survival and recruitment (Nicol 2006; Wiedenmann et al. 2009; Reiss et al. 2015; Kawaguchi 2016). The high trophic dependency on ice algae for overwintering by larval and juvenile krill in combination with their limited physiological flexibility in terms of utilizing different food sources, overwintering strategies and restriction to surface waters compared to adults (Quetin et al. 2003; Arndt and Swadling 2006; Clarke and Tyler 2008; Flores et al. 2012a), leave young Antarctic krill highly vulnerable in the light of ongoing sea ice decline, with consequences for survival and thus population size. Besides alterations of the sea ice system, the rising temperatures of the ocean can function as a stressor, because krill is adapted to low and stable temperatures of its natural environment (Whitehouse et al. 2008; Flores et al. 2012a). The majority of the krill population is located in the south-western region of the Atlantic Sector (Atkinson et al. 2008), where climate change has shown a particularly large impact regarding temperature rise and increasing ocean acidification (Meredith and King 2005; Kawaguchi et al. 2013). In contrast, longer open water seasons might support adult krill stocks due to the prolonged availability of pelagic algae and/or prey (reviewed by Flores et al. 2012a).

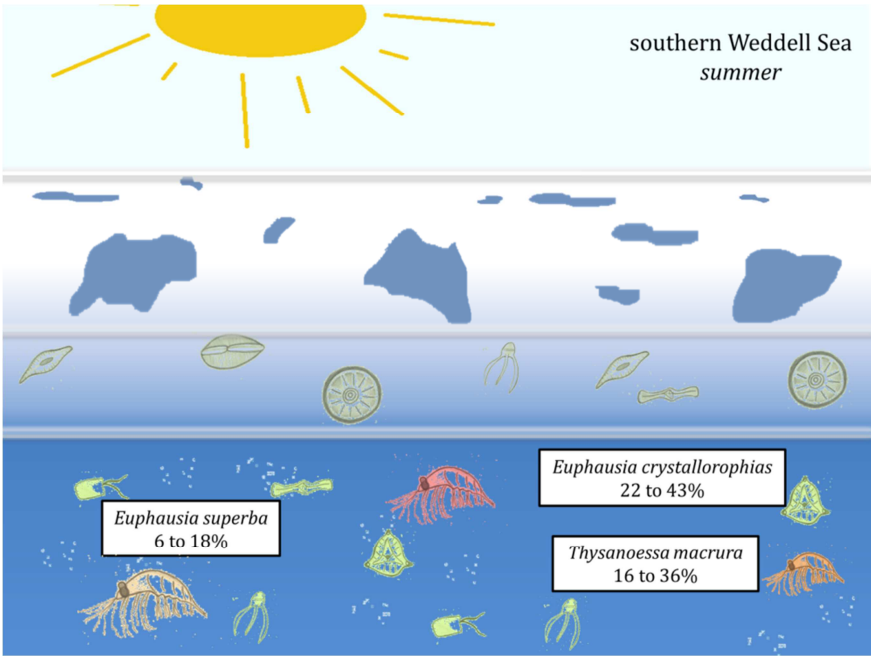
Despite the extensive research over the past century on *E. superba*, it is still unclear how and if this species will be capable to adapt to changing environmental parameters in the

SO. A reduction of the krill population during the past decades has already been detected since the 1970s (Loeb et al. 1997; Atkinson et al. 2004), and also in numbers of krill-dependent predators (Reid and Croxall 2001; Forcada et al. 2005; Trivelpiece et al. 2011; Seyboth et al. 2016). Kawaguchi et al. (2013) suggested that continued ocean acidification might cause the collapse of the krill population by 2300. However, the long-term reduction of the overall krill abundance is still under debate (Nicol and Brierley 2010; Atkinson et al. 2012; Steinberg et al. 2015). In contrast, others assume that krill might be equipped with a high potential of resilience and adaption on a molecular basis to withstand future changes of their habitat (reviewed by Flores et al. 2012a). Melbourne-Thomas et al. (2016) suggested that sea ice decline might not affect krill populations negatively due to a larger area of potential larvae habitat under warm conditions. These ambiguous results highlight the importance of combined and further analyses of the effects of sea ice alterations, ocean properties, food availability and krill distribution to confidently predict the fate of Antarctic krill in a changing Southern Ocean (Constable et al. 2014).

3.3.2 The unattended krill: Euphausia crystallorophias and Thysanoessa macrura

The colloquial expression 'ice krill' used for *Euphausia crystallorophias* implies a certain association of this krill species with sea ice. For one, this species is particularly found in shelf regions close to the Antarctic continent, which are characterized by heavy ice conditions almost year-round. But do they also feed on 'ice'? Up to date, nearly nothing is known about the trophic relationship between ice algae and the two 'outsider' euphausiid species *Euphausia crystallorophias* and *Thysanoessa macrura*. In comparison to the research on *E. superba*, krill food web studies addressing the euphausiid species *E. crystallorophias* and *T. macrura* are much more sparse, likely explainable by their considerably lower abundance in many Antarctic regions, even though they can contribute significantly to the overall biomass in the SO (McLeod et al. 2010). In shelf ecosystems, *E. crystallorophias* substitute the position of *E. superba* in respect of structuring the food web (Sala et al. 2002; Smith et al. 2007), and its trophic importance is fundamental to the continental plateau zone, constituting an important link between primary production and coastal top predators (Pakhomov and Perissinotto 1996).

Thus far, *E. crystallorphias* were regurlarly described as major phytoplankton grazer (Pakhomov and Perissinotto 1997), with a grazing impact accounting generally for < 4%, increasing up to 90% of total primary production (Pakhomov and Perissinotto 1996). This study indicated that the trophic dependency on ice algae-produced carbon of these species might be remarkable (**Chapter VI**). *E. crystallorophias*, sampled off the Filchner Ice Shelf, had an ice algal carbon contribution of up to more than 40% of their dietary carbon during summer (**Figure 3, Chapter VI**), suggesting that the term 'ice krill' is not a coincidence. Both *E. crystallorophias* and *T. macrura* demonstrated a higher dependency on ice algal carbon compared to *E. superba* in our study, indicating that these species require more attention in order to gain a better understanding of their future response to the warming seas in their habitat.



▲***Figure 3.*** *Proportional contribution of ice algae-produced carbon to the carbon budget of three krill species from the southernmost region of the Weddell Sea during summer (PS82). Estimates are derived from* ***Chapter VI****, based on the bulk organic content and the fatty acids 16:1n-7, 18:4n-3, 20:5n-3 and 22:6n-3.*

The geographic separation between coastal *E. crystallorophias* and deep-sea pelagic *E. superba* was related to abiotic factors of their particular habitat, as *E. crystallorophias* are adapted to low temperatures and the presence of sea ice, which would make this species particularly vulnerable to the warming in the Southern Ocean, ultimately affecting their abundances in the future (Lee et al. 2013; Cascella et al. 2015; Steinberg et al. 2015). The distribution of *E. crystallorophias* was found to be correlated in time and space with sea ice retreat. Thus, a change in distribution patterns would be expected as sea ice systems change (Ducklow et al. 2007; Ross et al. 2008). One predicted consequence of the climate warming is the poleward relocation of certain species, which has already been demonstrated for e.g. copepods, to ensure their comfortable temperature (Beaugrand et al. 2009; Mackey et al. 2012), and was also determined for *E. superba* (Ross et al. 2014). In the case of *E. superba*, the southward migration could result in an enhanced competition with *E. crystallorophias*, which naturally inhabit the southernmost regions of the SO (Flores et al. 2012a). The poleward shift of *E. superba* habitat may result in a decreasing overall production and abundances in a reduced area closer to the Antarctic continent (McBride et al. 2014).

In previous studies, there was no long-term trend in *T. macrura* abundances found (Ross et al. 2008). In contrast to *E. superba*, which is predicted to be affected negatively by climate change, increased growth rates of *T. macrura* might occur in regions with warming trends, such as the Antarctic Peninsula (Driscoll et al. 2015). Steinberg et al. (2015) reported a significant increase in *T. macrura* abundances over a time series from 1993 to 2013 in the northern region off the Western Antarctic Peninsula, explained by increasing primary production. Increased *T. macrura* biomass could potentially buffer

some of the *E. superba* loss, but with unknown impacts on their predators due to energetic differences between the two euphausiids (Richerson 2015). The omnivorous/carnivorous feeding strategy during summer off the Filcher-Ronne-Ice-Shelf (**Chapter VI**) suggests that the high adaption to utilize multiple food sources is favorable in a changing environment. However, the increased dependency on sea ice-derived food sources at the end of winter (**Chapter V**) suggested that changes of the sea ice system will consequently affect this euphausiid species, at least when food in the water column is strongly limited in the dark season.

3.4 Impact of ice algae as food source: Comparison between the hemispheres

Whereas the Arctic expedition PS80 took place during late summer, the sampling during PS81 in the SO was conducted during winter, which makes the comparison of the two datasets slightly more complicated. However, both sampling areas were largely covered with sea ice in the beginning of the expeditions, followed by the break up and melting of the ice by the end of the sampling period (David et al. 2015, 2016, 2017). The zooplanktonic under-ice community in the CAO consisted of more ice-associated species than during PS81 in the SO, where pelagic species dominated. In both hemispheres, copepods were most abundant, followed by amphipods in the Arctic and euphausiids (mainly *Euphausia superba*) in the Antarctic (David 2016).

Based on the proportion of ice algae-derived carbon as a food source and thus carbon source preferences, we categorized the investigated organisms into predominantly sympagic, sympagic/pelagic, and predominantly pelagic species (**Table 4**). This classification was based on fatty acid 18:4n-3, which is assumed to represent the recent lipid pool and thus the isotopic signal during the sampling period, and the more conserved fatty acids 20:5n-3 and 22:6n-3, which are accumulated over a longer period and thus represent an older trophic signal than the storage FA 18:4n-3 (**Chapter III**). The Arctic dataset was characterized by a balanced composition of sympagic and pelagic species, which did not show a high variability of the ice algal signal between younger and older lipid pools. In contrast, the Antarctic dataset was clearly dominated by organisms characterized by predominantly pelagic feeding behavior, based on the conserved fatty acids, possibly representing the isotopic signal from before the sampling period, which can thus be considered as pre-winter signal (‘autumn signal’). The more recent trophic signal (‘winter signal’), however, suggested a dietary switch as the winter season progressed to a higher dependency on ice algal carbon by all species, resulting in the classification as sympagic/pelagic species (**Table 4**).

▼**Table 4.** Summary of the proportional contribution of ice algal carbon to key organisms from the central Arctic Ocean (PS80) and the Southern Ocean (PS81). Mean contribution values (± 1 SD) are based on stable isotope compositions of fatty acids (FA) 18:4n-3, 20:5n-3 and 22:6n-3. For the Antarctic species, the isotopic composition of 20:5n-3 and 22:6n-3 was assumed to reflect the 'Autumn trophic signal', and 18:4n-3 was assumed to reflect the 'Winter trophic signal'.

ARCTIC			**ANTARCTIC**			
Lifestyle	**Species**	**% Ice algae contribution *-Summer signal-***	**Species**	**% Ice algae contribution *-Autumn signal-***	**Species**	**% Ice algae contribution *-Winter signal-***
sympagic	*Apherusa glacialis* *Onisimus glacialis* *Gammarus wilkitzkii* *Eusirus homii*	66 ± 18	--	--	--	--
sympagic/ pelagic	*Calanus glacialis* *Calanus hyperboreus* *Themisto libellula*	33 ± 11	*Euphausia superba*- larvae *Euphausia superba*- juveniles *Eusirus laticarpus* *Eusirus microps*	37 ± 22	all species	52 ± 9
pelagic	*Clione limacina*	17 ± 1	*Euphausia superba*- adults *Thysanoessa macrura* *Calanus propinquus* *Cyllopus lucasii* *Clione antarctica* *Clio pyramidata* *Spongiobranchea australis* *Diphyes antarctica* *Salpa thompsoni*	13 ± 6	--	--

Considering our investigated species as significant and abundant representatives of their respective sympagic and pelagic habitats, it can be derived that the under-ice community received half of their dietary carbon from ice-associated food sources during late summer in the CAO. Approximately the same proportional amount of ice algal carbon was ingested by Antarctic under-ice fauna species during winter in the northern Weddell Sea. In contrast, the Antarctic food web was approximately two times less dependent on sea ice algae as a carbon source before winter started, suggested by the long-term trophic signal. In the Antarctic, none of the species could be identified as predominantly sympagic feeders; the highest proportion of ice algal carbon was ingested by young *E. superba* and *Eusirus laticarpus*, where ice algae carbon contributed up to 67% of their energy budget. However, the fundamental differences of the environmental structures between the sampling areas and periods, such as sea ice coverage, ice thickness, snow coverage, and food availability (David 2016) have to be considered for the comparison of their degree of sea ice association.

In the CAO, the copepods *Calanus glacialis* and *Calanus hyperboreus* were the most abundant species in the first 2 m of the water column. *Apherusa glacialis* was the dominant amphipod species (David et al. 2015). Based on their individual daily ingestion rates, abundances under the ice during the sampling, and the contribution of ice algae-produced carbon to their energy budget based on fatty acid 18:4n-3, the ice algal carbon demand of these three grazers was estimated to be up to 0.22 mg C m^{-2} d^{-1} during the sampling period (**Table 5**). The ice algal primary production during PS80 ranged from 0.1 to 13 mg C m^{-2} d^{-1} (Fernández-Méndez et al. 2015). Based on that, the ice algal carbon demand of these grazers potentially exceeded the ice algae production in some regions throughout the sampling area. This mismatch between production and demand, however, might have been expected, because the primary production was shutting down at the end of the sampling period.

In the northern Weddell Sea, krill accounted for 60% of the mean biomass over all stations, dominated by larval and juvenile *E. superba*. The second-most abundant species was the copepod *Calanus propinquus* (David et al. 2017). Based on their abundances beneath the sea ice and their ingestion rates, their ice algal carbon demand was estimated with up to 0.07 mg C m^{-2} d^{-1} (**Table 5**). In spring, primary production rates in sea ice in the Southern Ocean can be as high as 1250 mg C m^{-2} d^{-1}, as found in platelet ice in McMurdo Sound (Grossi et al. 1987; Arrigo et al. 1995). However, in autumn the primary production in sea ice from the Weddell sea was estimated between 0.02 and 0.25 mg C m^{-2} d^{-1} (Mock 2002). This suggests an overall high seasonal and spatial variability in sea ice productivity, and possibly high variability regarding the supply of sufficient carbon to support the food web. Due to lacking information on the primary productivity by ice algae during the sampling period in the Weddell Sea, the sustainability of the under-ice community by the ice algae production is unknown. All of these Arctic and Antarctic key species, except for *A. glacialis*, were found in considerably higher abundances in the water column than directly underneath the sea ice (Ehrlich 2015; David 2016), leading to a higher overall ice algal carbon demand.

▼**Table 5.** Ice algal carbon demand in the most abundant under-ice fauna species during late summer in the central Arctic Ocean and during late winter in the Weddell Sea, based on individual ingestion rates, abundances under the ice, and the proportional contribution of ice algae-produced carbon to their body carbon (based on FA 18:4n-3) during the sampling periods.

	ARCTIC			**ANTARCTIC**	
	Calanus glacialis	*Calanus hyperboreus*	*Apherusa glacialis*	*Euphausia superba*- AC0	*Calanus propinquus*
Ingestion rate (µg C Ind. d^{-1})	6-18[a]	3-8[a]	13[a]	23[b]	10[c]
Under-ice abundance (Ind. m^{-2})	0.04-30.5[d]	0-4.9[d]	0.003-2.2[d]	0.01-3.6[e]	0.02-2.4[e]
Ice algae contribution (%)	34	28	82	69	49
Ice algal carbon demand (µg C m^{-2} d^{-1})	0.08-186.7	0-11.5	0.03-23.5	0.16-57.3	0.98-11.7
	0.1-221.7 µg C m^{-2} d^{-1} ice algal carbon demand during summer			**1.1-69.0 µg C m^{-2} d^{-1}** ice algal carbon demand during winter	

[a]Olli et al. 2007
[b]Pakhomov et al. 2004
[c]Pakhomov and Fronemann 2004
[d]David et al. 2015
[e]David et al. 2017

Copepods and other small zooplankton are important indicators of the impact of climate change on an ecosystem, because their populations are strongly linked to environmental conditions. Due to the high biomass contributions of, in particular, copepods and Antarctic krill to the Arctic and Antarctic under-ice community, these species will likely have a large impact on future ecosystem functioning of their respective ecosystems. In the Arctic, there is already ample evidence indicating the effects of climate change on copepods will subsequently impact commercially important predatory species (Beaugrand et al. 2002; Chiba et al. 2006; Hunt et al. 2011). A similar scenario is predicted for copepods in the Southern Ocean (Mackas and Beaugrand 2010; Constable et al. 2014).

The lipid-based energy flux from Arctic copepods to predatory species enables the maintenance of large stocks of fish and mammals in the Arctic Ocean, and is therefore of great importance for Arctic ecosystem functioning (Scott et al. 2002; Falk-Petersen et al. 2004). Copepods are known to thrive significantly on ice algal and phytoplankton spring blooms (Tremblay et al. 2006; Forest et al. 2011; Durbin and Casas 2013). The seasonal timing of the blooms is critical for successful reproduction, growth and survival of copepod offspring, ultimately fueling the Arctic food web (Gosselin et al. 1997; Darnis et al. 2012; Post et al. 2013). Sea ice thinning accompanied by an increased melt season, and an earlier onset of the phytoplankton bloom leads to a disruption of the seasonality of the two blooms, and consequently creates a mismatch in the reproductive cycle of copepods, reducing the ecological success of this species (Søreide et al. 2010; Leu et al. 2011), with consequences for the dependent food web (Moody et al. 2012; Ji et al. 2013). Studies predict shortening of the diapause in copepods, accompanied by higher metabolic rates and reduced body size and lipid storage, as well implications for their egg production and indirect impacts via changes in ice cover, salinity and food availability (Jung-Madsen et al. 2013; Mayor et al. 2015; Wilson et al. 2016). The diapause of copepods is of great importance for the global biogeochemical cycling, because the accumulation of lipids at the ocean surface and subsequent respiration of them transports large amounts of carbon into the deep ocean (Jónasdóttir et al. 2015; Baumgartner and Tarrant 2017). The distribution pattern of *C. glacialis* was determined to change with a poleward shift into the Arctic deep-sea basins (Slagstad et al. 2011). Due to the heavier ice conditions in high-Arctic regions, and their proven ability to feed on sea ice algae, ice algae-produced carbon might become even more important for this species in the future, possibly sustained by high ice algal standing stocks in high-Arctic regions (Lange 2016). However, the thinner ice cover allows for increased solar irradiance, which might in turn reduce the food quality of ice algae (Leu et al. 2010).

Sea ice is used as a habitat, provides protection from predators and offers attractive feeding grounds (Meyer et al. 2009; Flores et al. 2012a). Clearly visible is the effect of climate change on reproductive grounds of Antarctic krill, and thus, their recruitment success due to the sea ice decline, particularly near the Antarctic Peninsula (Flores et al. 2012a). Krill density in summer has been found to be positively correlated with sea ice edge extent in the preceding winter (Atkinson et al. 2004). For the end of the 21st

century, models predict that winter sea ice extent will reduce by 30-35% around the edges of the marginal sea ice along the eastern Weddell Sea toward King Haakon VII Sea, accompanied by a decrease in seasonal duration of sea ice by up to 40 days (Piñones and Fedorov 2016). Furthermore, an overall decline of 51% in the area of krill spawning habitat is projected, considering decreased sea ice coverage and Chl *a* availability, particularly affecting the northern Weddell Sea and the eastern Ross Sea. However, assuming a 25% increase in Chl *a* suggests a general improvement of krill's habitat by 43%, mostly in regions that support krill's growth at present (Piñones and Fedorov 2016). Krill have a longer life cycle (up to 7 years) than copepods (several months to 2 years) and are thus affected on a wider temporal and spatial scale (Siegel and Loeb 1995; Smetacek and Nicol 2005). Habitat and food source loss due to sea ice decline have been often predicted to result in dramatic krill population decline, when winter survival cannot be assured. During late summer and fall, food availability in the Southern Ocean allows for sufficient feeding and accumulation of lipid reserves. However, sea ice biota becomes more important for krill during winter (**Chapter III**). This period is especially critical for young developmental stages as they need to feed constantly to grow successfully into juveniles the following spring (Meyer 2012).

In the Arctic, rising temperatures and reduced sea ice cover have resulted in an increase in total primary productivity, which was quantified by a 20% increase of net primary production by phytoplankton between 1998 and 2009, and also the increased probability of phytoplankton blooms beneath snow-covered sea ice due to a thinner and more dynamic ice pack (Arrigo and van Dijken 2011, 2015; Assmy et al. 2017). Enhanced primary production due to climatic changes was also described for the Southern Ocean (Boyd et al. 2015; Moreau et al. 2015). This can potentially lead to a higher secondary production, depending on the organism's ability to adapt to the changing climatic conditions. Unlike highly ice algal-dependent species, such as *A. glacialis*, organisms predominantly feeding on phytoplankton will probably be favored by higher water column productivity, ultimately defining winners and loosers of climate change in both Polar Oceans (Somero 2010; LaRue et al. 2013). However, during winter, extreme algal biomass limitation in the water column in combination with a decreased ice-associated primary productivity due to sea ice loss will become critical regarding the sustainability of winter-active species in both Polar Oceans.

Both polar ecosystems demonstrated a strong linkage to ice-associated primary production, in the Arctic during late summer and in the Antarctic during winter. The impact on the overall carbon flux through the food web will be dependent on species-specific responses in individual physiology, seasonal timing, population structure and geographical distribution, and their subsequent consequences for higher trophic levels, biodiversity and ecosystem services (Walther et al. 2002). Particularly for the Southern Ocean, environmental responses to climatic changes are often ambigious and regionally constrasting, which complicates predictions on ecological responses of individual species and ultimately the entire ecosystem.

4. Conclusion and Outlook

Climate change affects the entire planet on physical, ecological, social and economical levels, and the Polar Oceans are among the fastest-changing environments on earth. In the Polar Regions, changes of the sea ice system, such as the decline of sea ice thickness and coverage are particularly pronounced in the Arctic, and more locally restricted in the Southern Ocean. In both Polar Regions, environmental alterations will affect the energy flow from lower to higher trophic levels, and ultimately humans that depend on these ecosystems. Thus, knowledge on the role of sea ice and the implications of its changes for ecosystem dynamics and functioning is crucial as climate change is expected to accelerate in the future.

This study provides insights into the transfer of ice algae-produced carbon from the sea ice into the associated sympagic and pelagic under-ice communties in Arctic and Antarctic food webs. The results imply that food webs in the Arctic Ocean and in the Southern Ocean thrive significantly on carbon produced by sea ice-associated microalgae, and bring thus quantitative evidence on the vulnerability of Arctic and Antarctic ecosystems to alterations of the sea ice properties. A future diminished role of the ice-associated primary production, and thus, an expected mismatch between the carbon demand of ice-associated organisms and the primary production will ultimately affect population structure of key energy transmitters with negative consequences up to the highest trophic levels in both Polar Oceans. To assess overarching shifts in trophic interactions and ecological implications, however, the little information from the few studies so far on the trophodynamics of end members in polar food webs must clearly be increased.

In the future, we have to improve our understanding of the vulnerability and resilience of polar ecosystems regarding climate change-induced environmental alterations and resulting ecological responses both on species and population level, in shelf-bound and deep-sea Polar Regions, during different seasons and bloom situations. Such knowledge is crucial for the determination of changes regarding biodiversity, population structures and ecosystem functioning, consequently affecting management of commercially important fisheries resources, and conservation policy. Assessments of food web dynamics are essential for the parameterization and validation of statistical models and/or pan-Arctic/pan-Antarctic ecosystem models, which are able to simulate future scenarios in Arctic and Antarctic ecosystems. Based on the contribution of ice algal carbon as food source in marine systems, the carbon flux through the entire ecosystem can be characterized under present conditions and future changes.

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The 'original' German/Dutch Iceflux team in June 2013:
Top from the left: Benjamin Lange, Doreen Kohlbach, Fokje Schaafsma, Carmen David, Michiel van Dorssen, Martina Vortkamp, Hauke Flores
Bottom from the left: André Meijboom, Jan Andries van Franeker

Statutory Declaration

(According to § 7 (4) doctoral degree regulations of the MIN Faculty)

Eidesstaatliche Erklärung

(Gem. § 7 (4)- PromO)

I herby declare, on oath, that I have written the present dissertation by my own and have not used other than the acknowledged resources and aids.

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg,
Hamburg, den

Signature
Unterschrift

<u>Paper 1</u>: The importance of ice algae-produced carbon in the central Arctic Ocean ecosystem: Food web relationships revealed by lipid and stable isotope analyses

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This paper was published in Limnology & Oceanography.

Samples were collected by H. Flores, B. A. Lange, C. David and I. Peeken. The study was designed by **D. Kohlbach** and H. Flores. All laboratory analyses were conducted by **D. Kohlbach**, with the help of M. Graeve. **D. Kohlbach** evaluated the results with the help of B. A. Lange and Hauke Flores. **D. Kohlbach** accomplished the data analyses with support of B. A. Lange. **D. Kohlbach** wrote the first version of the manuscript. All authors contributed to the final manuscript.

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<u>Paper 2</u>: Strong linkage of polar cod *(Boreogadus saida)* to sea ice-algae-produced carbon: Evidence from stomach, fatty acid and stable isotope analyses

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<u>Paper 3</u>: Ice algae-produced carbon ensures winter survival of young Antarctic krill *Euphausia superba*

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<u>Paper 4</u>: Spatio-temporal variability in the winter diet of larval and juvenile Antarctic krill *(Euphausia superba)* in ice-covered waters

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<u>Paper 5</u>: Overwintering of Weddell Sea under-ice community strongly linked to sea ice-associated food sources

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<u>Paper 6</u>: *Euphausia superba*, *E. crystallorophias* and *Thysanoessa macrura* in the Filchner Outflow System: Variability of carbon sources during summer assessed in a lipid and stable isotope study

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Samples were collected by **D. Kohlbach**, B. A. Lange and M. Vortkamp. The study was designed by **D. Kohlbach** and H. Flores. Laboratory analyses were conducted by **D. Kohlbach** with the help of M. Graeve and M. Vortkamp. **D. Kohlbach** evaluated the results and accomplished the data analyses with the help of B. A. Lange and H. Flores. **D. Kohlbach** wrote the first version of the manuscript.

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