Life in the polar oceans: the role of sea ice in the biology and ecology of marine species

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CONTENTS

CHAPTER 1

General introduction

This thesis is about the polar oceans and their seasonal sea-ice cover which support rich foodwebs. Human-induced stressors like fisheries and climate change may directly affect the functioning of these foodwebs. Under such conditions the management and conservation of the marine living resources in these areas require optimal understanding of ecosystem functioning. This thesis contributes to this demand by providing dedicated studies of the environmental conditions and associated life forms directly under the sea ice.

SEA ICE

The presence of sea ice provides a unique feature of the polar oceans (Ackley & Sullivan 1994). The annual cycles of freezing and melting occurring in the Arctic and Southern Oceans cause tremendous changes in sea-ice cover during the year, resulting in large-scale cycles that are of great influence on many processes in these oceans (Dieckmann & Hellmer 2003; Massom & Stammerjohn 2010). In the Arctic Ocean the sea-ice cover is at its maximum extent at approximately 15.5 x 10^6 km^2 in March and at its minimum at approximately 7.5 x 10^6 km^2 in September. In the Southern Ocean the seasonal pattern is reversed, with a maxiumum sea-ice cover of 19 x 10^6 km^2 in September and a minimum in February, covering approximately 3.8 x 10^6 km^2 (Fig. 1.1; Comiso 2003). The minimum sea-ice cover is reached a month earlier than the maximum in the Arctic, due to accelerated warming as a result of relatively warm water surrounding the Southern Ocean (Comiso 2003). This is already one example of differences between the Arctic and Antarctic sea ice caused by the Arctic Ocean being surrounded by land while the Southern Ocean surrounds the Antarctic continent. There are several oceanic fronts surrounding Antarctica providing an oceanographic northern boundary to the Southern Ocean (Orsi et al. 1995).

Although from a distance the ice-covered oceans may seem like a uniform landscape, the many processes that are present make it a highly dynamic system and an ever changing physical feature of the polar oceans (Ackley & Sullivan 1994; Massom & Stammerjohn 2010). On a large scale, as well as a micro scale, sea ice has different structures and properties, which are mostly determined by environmental

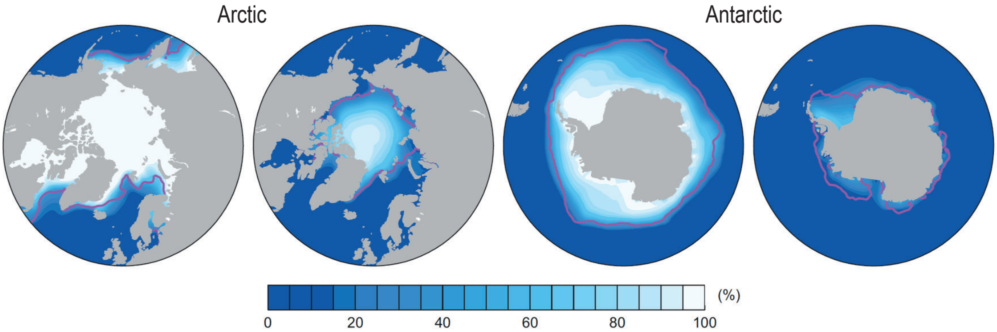


Figure 1.1: Maps showing the average sea-ice concentration (1986-2005) of the polar regions in September and February. The pink line marks the observed average concentration limit of 15% (from Collins et al. 2013, with data from Comiso & Nishio 2008).

conditions during sea-ice formation (Weeks & Ackley 1982; Massom & Stammerjohn 2010). A distinction is made between pack ice, drifting on the ocean, and (land-) fast ice, which is attached to either the coast, ocean bottom or to grounded ice bergs. Sea ice can, furthermore, be perennial or seasonal. Perennial sea ice does not completely melt away for one or multiple summer seasons (ice which is then referred to a second-year ice and multi-year ice or MYI, respectively), while seasonal sea ice does (newly formed summer ice is also known as first-year ice or FYI). The period in which a certain part of the ocean is covered with sea ice can vary, depending on e.g. latitude, and therefore, it should be taken into account that the timing of seasonal changes in sea-ice cover is regionally variable (Horner et al. 1992).

Sea ice starts to form in autumn when air temperature and irradiance are decreasing (Constable et al. 2014). Small ice crystals, also known as frazil ice, can form at the surface or float up towards the surface when formed in deeper water layers (Horner et al. 1992). In the Antarctic, ocean swells penetrate from higher latitudes which, in combination with high wind speeds, causes newly formed frazil ice to agglomerate into pancake ice that eventually grows into larger ice floes (Fig. 1.2). This results in ice dominated by a granular structure (Weeks & Ackley 1982; Horner et al. 1992; Ackley & Sullivan 1994; Eicken 2003). As surrounding land masses dampen sea water conditions, newly formed sea-ice in the Arctic is mainly composed of ice crystals forming a thin, continuous sheet of ice also known as nilas. When this ice grows further it will form ice that mainly has a columnar texture, which forms when larger elongated ice crystals freeze together, and which is also known as congelation ice (Eicken 2003).

Snow cover can affect the growth of sea ice and is higher in the Antarctic than in the Arctic. Due to the insulating properties of snow and its higher reflective power (or albedo) compared to ice, increasing snow cover usually results in a reduction in ice growth and, therefore, in thinner ice (Eicken 2003; Haas 2003). However, high snow cover can push the sea-ice surface below the sea water, causing its surface to be flooded, shifting the growth place from the bottom of the sea ice to the surface of the sea ice or the bottom of the snow pack (Eicken 2003). Surface flooding hardly ever occurs in the Arctic (Eicken 2003). When the ice melts, it either melts from the bottom or at the surface, the latter generating melt ponds on top of the sea ice (Eicken 2003). Melting at the surface is currently the dominant process in the Arctic (Fig. 1.2), while melting from the bottom or margins dominantly occurs in the Antarctic (Eicken 2003). One factor influencing this process in the Arctic is fresh water inflow mainly from the Siberian continent. This cold water forms a stable layer obstructing heat coming from the warmer Atlantic inflow water underneath (Haas 2003).

Sea ice is reshaped continuously due to influences of internal stressors, wind, ocean currents and the passage of storms (Massom & Stammerjohn 2010). This results in the formation of assemblages of ice floes of different sizes, ice types and ages, variation in snow cover thickness, and the formation of cracks, leads and polynyas with open water (Haas 2003; Massom & Stammerjohn 2010). Furthermore, the existing ice can thicken due to over-rafting and the formation of pressure ridges. This is a result of ice floes being pushed together when the direction and speed of the drift of the sea ice changes under the influence of wind and currents (Haas 2003; Massom & Stammerjohn 2010). Due to its confinement by land, the sea ice in the

Arctic Ocean is usually more deformed and more pressure ridges are present (Haas 2003). Therefore, the sea ice covering the Arctic Ocean is often older and thicker than that of the Southern Ocean. In the Southern Ocean the ice drifts away from the continent to open sea and thus to relatively warmer waters (Haas 2003).

The annual growth and melt of sea ice is the most prominent physical process in the polar oceans which has a major impact on marine life (Brierley & Thomas 2002). It changes light availability and temperature regionally and locally, variables which are already extreme at high latitudes (Swadling et al. 1997). However, life in the polar oceans has adapted to live in this harsh environment and utilize the sea ice that forms a particular habitat in these oceans. Sea ice provides a substrate for life but can also form a barrier, restraining access to the ocean water. The bottom of the food chain in oceans is formed by algae, the primary producers. Large scale cycles of sea-ice formation and melt influence the availability of light and nutrients for primary production in the water column, but also within the sea ice, that hosts a community of sea-ice algae and other in-ice fauna (Constable et al. 2014). To distinguish algae growing within the sea ice from algae living in the water column, they are usually referred to as ice algae and phytoplankton, respectively. The sea ice, furthermore, has other functions for higher trophic levels regarding basic animal needs such as reproduction and shelter for predation. Due to the harsh environment and primary production cycles, higher trophic levels also show large adaptations to seasonal and regional changes in food availability.

Figure 1.2: Pancake ice drifting on the Southern Ocean (left), and a melt pond on the surface of Arctic sea ice (right).

PRIMARY PRODUCTION

When sea-ice forms, most of the salt is concentrated in liquid inclusions in the solid ice, which is referred to as brine (Eicken 1992; Eicken 2003). A fraction of this brine is retained within the pores of the sea ice, steadily increasing the salinity therein. The majority of the brine is, however, expelled from the ice over time (Eicken 1992; Eicken 2003). Therefore, with time, the brine within the ice is replaced by less saline sea water or brine from lower ice layers by processes such as gravity drainage (Eicken 2003). The ejected, cold brine is denser than the underlying water, causing it to sink and resulting in a deepening of the mixed layer (Eicken 1992). Therefore, freezing and melting processes influence the fresh water budget, the distribution of salt and, consequently, the mixed layer depth (MLD) of the oceanic water through, amongst other things, brine expulsion during sea-ice formation and fresh water pulses from melting sea ice (Legendre et al. 1992; Massom & Stammerjohn 2010; Comiso 2003; Constable et al. 2014). Changes in MLD have a marked influence on the primary production in the water column (Constable et al. 2014).

The microbial community, including algae, bacteria and protozoans, that is still substantial in the surface water, are incorporated within the sea ice as it forms, as they are being scavenged from the water column by new-formed ice crystals rising to the surface or enclosed within the forming ice (Weeks & Ackley 1982; Ackley & Sullivan 1994; Lizotte 2003; Arrigo & Thomas 2004). In the early stage of ice formation, the in-ice community is likely similar to that of the underlying water column during formation (Gradinger & Ikävalko 1998; Arrigo & Thomas 2004). However, as the sea ice ages, the in-ice population and its dominant species shift (Arrigo & Thomas 2004). For example, the number of larger centric diatoms are often replaced by smaller pennate diatoms over time, and bacterial diversity tends to decrease (Arrigo & Thomas 2004). In-ice communities are subjected to extreme fluctuations in salinity to which they must adapt (Arrigo & Thomas 1994), because the brine within the sea ice changes in salinity over time (Eicken 2003). In addition, there are also extreme fluctuations in temperature, light, nutrient and chemical (for instance oxygen) concentrations. Therefore, in-ice assemblages are restructured depending on species specific temperature and salinity tolerances and the ability to acclimatize physiologically to changing environmental conditions (Lizotte 2003).

Apart from a microbial community, the sea-ice can also be inhabited or colonized by highly specialized small animals such as turbellarians, nematodes, rotifers and copepods (Schnack-Schiel et al. 1998; Schnack-Shiel 2003). Sea ice can differ in its ecological role in the life-cycle of these species, partly attributed to the sea ice being FYI or MYI (Schnack-Schiel 2003). Rotifers are only recorded in the Arctic sea-ice, while copepods and nematodes dominate the metazoan community in the Antarctic (Gradinger 1999; Swadling et al. 1997; Schnack-Schiel et al. 1998; Schnack-Schiel 2003). The distribution of metazoans within the sea ice has been found to depend on the size and spatial arrangements of brine channels and pores (Cross 1982; Krembs et al. 2001; Schnack-Schiel 2003). The biomass and species richness of all life within the sea ice is generally highly variable over both small and large scales, and shows a high degree of patchiness (Garrison 1991; Swadling et al. 1997; Gradinger 1999).

As the mixed layer deepens due to brine expulsion, nutrients might be brought to the surface, but phytoplankton is also being mixed away from the surface where light availability is highest. This deepening, therefore, often results in a reduction of primary production in the water column (Eicken 1992; Constable et al. 2014). Consequently water column primary production is generally very low during winter, and algae residing in the sea-ice may be the only, albeit highly concentrated, source of primary production during this season (Arrigo & Thomas 2004). The platform provided by sea ice enables algae and other organisms to remain in the surface where light is still available (Arrigo & Thomas 2004).

Sea-ice melt, initiated in late spring/summer, once more results in marked changes in both sea ice and water column primary production. Sea-ice algae and other in-ice fauna are released into the water column together with nutrients and other particulates (Leventer 2003; Boetius et al. 2013). The melt water, furthermore, forms a relatively stable layer on top of the denser sea water due to its low salinity. Together with an increase in light availability, due to both the time of year and the reduced inhibition by sea-ice, this often results in the initiation of phytoplankton blooms (El-Sayed 1971; Bianchi et al. 1992; Legendre et al. 1992). In the Southern Ocean, spring phytoplankton blooms start to occur in October and from then move poleward in the wake of the melting sea-ice edge (Brierley & Thomas 2002). The area in which the sea ice is melting, called the marginal ice zone (MIZ), is regarded as a highly productive zone (Legendre et al 1992; Leventer 2003). Phytoplankton blooms in the Southern Ocean also occur in other areas such as shallow waters, onsets ranging from October to January, showing high variability between regions and years (Thomalla et al. 2011; Llort et al. 2015). In the Arctic, spring blooms also occur when sea ice melts but phytoplankton blooms have been seen underneath the summer Arctic sea ice as well (Horvat et al. 2017). Even without blooms, particles or detritus, and organisms that are released from the sea ice can be important for pelagic grazers, and the link between the surface waters and the deep ocean (Bradstreet & Cross 1982; Leventer 2013). Sinking ice algae have, for example, been found to be an important food source for benthic organisms (Boetius et al. 2013).

HIGHER TROPHIC LEVELS

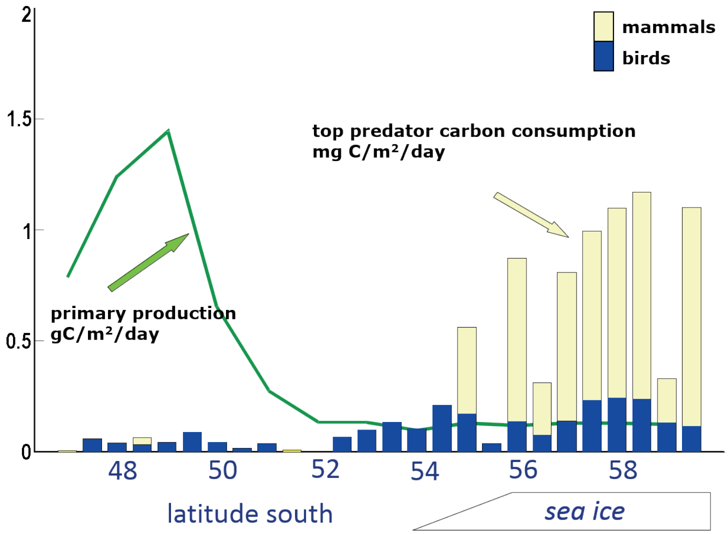
The polar regions are home to unique fauna, evolutionary adapted to life at low temperatures and/or the (seasonal) presence of sea ice. The ones regarded as most charismatic by most people, and which are also the best visible, are the top predators. Top predators living in the polar oceans include seals, whales and flying birds, and, furthermore, penguins in the Southern Ocean and polar bears (*Ursus maritimus*) in the Arctic Ocean (Ainley et al. 2003a; Kovacs et al. 2011). Many species reside in the Arctic and Southern Oceans seasonally and exploit the open water, moving along with the retreating sea ice. An example are several tubenosed bird species found in the open water area of the Antarctic, and sometimes, but not always, concentrated along the sea-ice edge (Van Franeker et al. 1992). Other species have specific adaptations to be able to reside in the pack- or fast-ice year-round. The sea ice is used as a platform for reproduction by many seals and the emperor penguin. Species that reproduce in the pack ice time this in such way that their young become independent in late summer/early autumn, when food availability is highest (Finley et al. 1983; Ainley et al. 2003a). Mammals and birds also use the sea ice as a platform for resting and moulting (Ainley et al. 2003a; Kooyman et al. 2004). Top predator species residing in ice-covered regions have specific adaptations to deal with the sea ice blocking the water from the air that they need to breathe (Finley et al. 1983; Ainley et al. 2003a). Adélie and emperor penguins can hold their breath much longer than penguins residing in open water areas, enabling them to cover large distances underneath ice floes (Watanuki et al. 1997; Ponganis et al. 2000; Ainley et al. 2003a). Sea-ice obligate whale species often lack a dorsal fin which enables them to break through thin ice with their back, such as the bowhead whale and beluga, or use their pointy rostrum, such as the minke whale (Moore et al. 2000; Ainley et al. 2003a). In thicker ice, they are, however, dependent on polynyas and leads (Stirling 1980; Ainley et al. 2003a). Polynyas appear due to ice being blown offshore by winds, or can occur offshore under the influence of bathymetry, for example, due to shelf topography or warmer sub-surface water currents rising over ridges (Stirling 1980; Brierley & Thomas 2002). These areas are relatively predictable and persistent, remaining open throughout the winter or open at same time each year (Stirling 1980; Ainley et al. 2003a). Leads and polynyas are additionally important because they offer feeding opportunities for birds and mammals (Brierley & Thomas 2002). Many sea-ice obligate species have a preference for a specific type of ice that they are able to exploit best (Ainley et al. 2003a; Kooyman et al. 2004).

The presence of top predators provides evidence that sea-ice has an important function in food provisioning (Van Franeker et al. 1997). Highest densities of Antarctic top predators were found associated with sea ice (as opposed to open water), in ice-covered areas where phytoplankton measurements suggested low primary production in the water column (Fig. 1.3; Van Franeker et al. 1992; Van Franeker et al. 1997). This indicated that, despite low phytoplankton concentrations, the sea-ice habitat provides sufficient food for top predators to be able to e.g. survive and reproduce, and, furthermore, that large populations of krill and other zooplankton prefer to summer in the sea-ice covered waters. Bird, seal and whale densities along edge and further in pack ice did not indicate a specific more favourable feeding condition in the MIZ (Van Franeker et al. 1992). The top predators of the Southern and Arctic Oceans are known to feed mainly on crustacea, fish and cephalopods. Zooplankton and nekton distribution and abundance have been found to be structured by the sea ice and its dynamics of growth and decay, in addition to fronts, currents and bathymetry (Swadling et al. 2010). Therefore, the sea-ice habitat greatly influences the quantity and quality of food available for top predators, inspiring research on the role and importance of sea ice in the life cycle of marine animals living in the (seasonally) ice-covered oceans.

LIFE UNDERNEATH THE ICE: ZOOPLANKTON AND NEKTON

Investigations of zooplankton and nekton within the sea-ice environment have provided evidence that life cycles and seasonal use of the sea-ice habitat are in multiple ways adapted to the fluctuation in food availability related to the seasonally changing environment. Similar to top predators, zooplankton and nekton species living in the polar oceans time life cycle events with peaks in production. For instance, species use elevated ice-algae or phytoplankton availability, resulting from blooms, to gain energy for reproduction. Species time spawning events to ensure that their offspring can make optimal use of the phytoplankton blooms and the adults can use elevated production to fatten up for winter (Søreide et al. 2010). Organisms are attracted to the surface water to feed on algae, protists and bacteria covering the

Figure 1.3: Rates of primary production (green line) and top predator consumption expressed in carbon consumption (columns) in the Weddell Sea in the summer of 1988/1989. The latitudes that were covered with sea ice are presented on the x-axis (From Van Franeker et al. 1997).



bottom of the sea ice or material that is released from it (Arrigo & Thomas 2004). In addition, many species use the topographical features of the sea ice as a hiding place for predators which, besides the top predators, can include fish, squid, and ctenophores (Pakhomov et al. 1996; Nesis et al. 1998; Gradinger & Bluhm 2004).

Invertebrates showing an association with sea ice are mainly crustacea (copepods, amphipods and euphausiids), but e.g. ctenophores, polychaetes and larval forms of several organisms can also be found (Gulliksen & Lønne 1991; Flores et al. 2011). There are many organisms that occur in high abundances and are suggested to play a pivotal role in the polar ecosystems. However, Antarctic krill (*Euphausia superba*) and polar cod (*Boreogadus saida*) are considered to be key species in the Southern and Arctic Oceans, respectively, due to their high abundances, widespread distribution and role in carbon transfer between the sea-ice habitat and top predators. Antarctic krill is the largest species of the euphausiids occurring in the Southern Ocean. There are, in addition, a wide range of organisms feeding on the different life stages of Antarctic krill (Hamner et al. 1989; Ainley et al. 1991; Reid et al. 1996; Scolardi et al. 2006). Polar cod is a major food source for many bird and seal species in the Arctic (Welch et al. 1992). As consumers of ice-associated copepods and amphipods, they are responsible for the majority of the energy transfer between the sea-ice habitat, other fish, and top predators (Bradstreet & Cross 1982; Lønne & Gulliksen 1989; Welch et al. 1992). Both Antarctic krill and polar cod thus have a major impact on lower and higher trophic levels (Benoit et al. 2010; Flores et al. 2012b).

Zooplankton and nekton abundance and distribution have been found to differ between different depth layers, indicating that some species are utilizing the sea-ice habitat directly, and are thus ice-associated either year-round or during parts of the year. However, other species that are perhaps not directly related to sea ice can benefit from zooplankton concentrating in the surface as a food source, which is reflected in both diel and/or seasonal vertical migration patterns. Diel vertical migration (DVM) is suspected to occur due to a trade-off between food availability, energy budget and predation risk (Youngbluth 1975; Quetin et al.

1996; Flores et al. 2014). For example, adult Antarctic krill have been found to dwell in the surface to feed at night and in deeper layers to avoid predation during the day (Zhou & Dorland 2004; Siegel 2005; Flores et al. 2012a). Reversed DVM patterns have been found, for instance at South Georgia, likely to avoid being preyed upon by fish as opposed to top predators (Kalinowski & Witek 1985 in Godlewska 1996). Fish species usually regarded as mesopelagic or bathypelagic, e.g. *Electrona antarctica, Gymnoscopelus braueri, Bathylagus antarcticus* and *Notolepis coatsi*, have been found to migrate to the surface at night particularly during winter (Kaufmann et al. 1995; Hunt et al. 2011), attracted towards the surface to forage (Ainley et al. 1991).

A seasonal change in depth distribution can be a result of overwintering strategy. For instance, to cope with food scarcity many species overwinter in deeper waters where they reduce their metabolism and/or rely on reserves (Hagen 1999). Copepod species such as *Calanus hyperboreus* and *C. glacialis* in the Arctic (Conover & Siferd 1993 and references therein) and *Calanoides acutus* in the Antarctic (Conover & Huntley 1993), overwinter at depth in diapause, a period in which growth and development is suspended. Other animals, for example carnivorous chaetognaths, are able to feed on their prey year-round, but can show seasonal vertical migration as they follow the migration patterns of their food (Torres et al. 1994). Apart from the general vertical distribution change between seasons, the amplitude and rhythm of DVM can show variation between seasons and even regions (Atkinson et al. 1996; Taki et al. 2005; Berge et al. 2009). This was also found during the Arctic winter, where some species continued DVM even during the polar night (Berge et al. 2009). Depth distribution can likewise vary within species between different developmental stages (Hagen 1999), probably because younger individuals have different food requirements and predators than the older individuals (Siegel 2005). Furthermore, the seasonal presence or absence of sea ice can change the vertical and horizontal distribution within species. For example, crustacea, such as amphipods and ostracods, were found spending the entire day at depth in open water, but were found to occupy surface layers when residing underneath the ice during the same season (Ainley et al. 1986). There are also species that have a preference for dwelling in either open or ice-covered waters.

STUDYING THE ICE-COVERED ENVIRONMENT

Despite past research efforts, the question of how the presence or absence of seasonal pack ice influences the community structure and, species' horizontal and vertical distribution remains. Due to the inaccessibility of the under-ice surface, zooplankton and nekton populations that concentrate in its proximity are hard to quantify (Gulliksen & Lønne 1989; Van Franeker et al. 1992). When using conventional sampling gear, abundance estimates are often integrated over a large depth range and the sea-ice habitat is disturbed by ice breaking ships while sampling (Brierley et al. 2002). Additionally, many trawls cannot be used in ice-covered regions and other methods such as baited traps do not give information on habitat selection (Gradinger & Bluhm 2004). The community at the under-ice surface has been studied using SCUBA, remotely operated vehicles (ROV), and pumps through core holes or acoustic techniques. However, the horizontal range of these observations is very limited (Brierley & Thomas 2002). Furthermore, information on the means of utilization of sea-ice by different marine organisms, species interactions and trophic pathways remain incomplete (Kędra et al. 2015). Consequently, the understanding of sea-ice ecology has been hampered by the difficulty to collect sufficient samples to identify large-scale spatial trends (Brierley & Thomas 2002).

To overcome this limitation a Surface and Under Ice Trawl (SUIT) was developed, enabling the exploration of the upper 2 meter underneath the sea ice (Van Franeker et al. 2009), which will further be referred to as the under-ice surface layer or the ice-water interface layer (Fig. 1.4). Investigations using SUIT have given insight in the differences in zooplankton distribution and community structure between open and ice-covered waters. Additionally, the large difference with other depth layers showed that the ice-water interface is an important layer that deserves to be considered separately when studying the marine community in polar oceans. Studies using SUIT in the Antarctic demonstrated that the surface zooplankton community assemblage responded to the presence of sea ice in all seasons sampled, which included summer, autumn and winter (Flores et al. 2011). Furthermore, evidence suggests that the ice-water interface can provide an important temporary habitat for a variety of species (Flores et al. 2011). Antarctic krill was found in the under-ice surface water year-round, and not only in the MIZ but also deep into the pack ice (Flores et al. 2012a). Comparing different depth layers in open as well as ice covered waters, the Antarctic krill were found to concentrate in the under-ice surface during summer. During autumn adults were most abundant in open water and more dispersed over a wider depth range compared to the surface layer underneath young ice. Larvae were, however, most abundant underneath the sea ice during this season. A smaller krill species, *Thysanoessa macrura*, was more abundant in deeper water compared to the surface layer, and no difference in distribution was found between open water and ice-covered water (Flores et al. 2012a).

Investigations have shown that animals do not only respond to sea-ice cover but also changes in thickness distribution (Flores et al. 2012b). Other studies also found a preference of certain ice-associated species with a certain ice type (Hop et al. 2000). For example, the population structure and abundance of the Arctic amphipod *Gammarus wilkitzkii* has been found to differ with differing ice conditions (Beuchel & Lønne 2002). Antarctic krill abundance was also found to be linked to the under-ice topography (Brierley et al. 2002).

Knowledge required to describe and understand zooplankton and nekton distribution, and the degree of association with the sea ice is very limited, particularly because there are seasonal, regional and annual differences (Welch et al 1992; Wallis et al 2016). Year-round sampling is often limited though necessary to fully understand the implication of seasonal changes in sea-ice for life cycle strategies (Bathmann et al 1993; Schnack-Schiel 2003). In order to gain insights in the ecological adaption to the sea-ice habitat, a better understanding of population structure in under-ice habitat is desirable (Welch et al. 1992; Beuchel & Lønne 2002). Generally, studies on a larger horizontal scale are lacking but would help identifying the occurrence and preference of ice-associated species in sea ice with certain properties. Despite recent advances (Kohlbach et al. 2016; 2017; 2018), the importance of the quality and quantity of in-ice assemblages as a carbon source for under-ice fauna is currently poorly understood (Søreide et al. 2010). Together with increased knowledge on the ecological niche of ice-associated species and trophic relationships between species, such information would help to predict the effect of large scale changes in sea-ice extent and thickness (Welch et al 1992; Gradinger & Bluhm 2004), which are expected consequences of ongoing climate change. Furthermore, such information is necessary to aid management directed to improve the sustainability of current and future fisheries.

Figure 1.4: The Surface and Under Ice Trawl deployed in the water and ready to sample (left), and hauled out of the water by the A-frame of RV Polarstern (right).

SEA ICE AND CLIMATE CHANGE

The climate has been changing, under human influence, causing a warming of the atmosphere and oceans (Stocker et al. 2013). The increase in the global temperature has already had a marked imact on the Arctic Ocean. Despite the total sea-ice cover fluctuating annually, the sea-ice cover and extent show an overall decline since 1978, and an even more rapid decline has been found since 1996 (Bjørgo et al. 1997; Cavalieri et al. 1997; Parkinson et al. 1999; Comiso et al 2012). Trends in sea ice from 1979/1980 to 2010/2011 showed significant changes, indicating both a later advance and an earlier retreat (Stammerjohn et al. 2012). The largest changes were observed in the eastern Siberian/Chukchi/western Beaufort region and the Kara/Barents sea region (Stammerjohn et al. 2012). In addition to observed changes in cover and extent, the Arctic sea ice has been thinning. The proportion of FYI, as opposed to MYI, has increased from 38% in the spring of the mid-1980s to 55% in 2007, and even 72% in 2008 (Stroeve et al. 2012). The year 2010 showed a record low of sea ice older than 5 years (Comiso et al. 2012; Stroeve et al. 2012). Thinning of the sea ice favours an even stronger areal retreat during summer (Haas et al. 2008). Other consequences of thinning ice could be that it becomes more saline, less deformed and more fragile (Nicolaus et al. 2012). Additional expected consequences are changes in the timing of phytoplankton blooms, a longer period of increased light availability and changes in MLD (Venergas & Drinkwater 2001; Meredith & King 2005; Ardyna et al 2014). An increased number and longer presence of dark open water areas and melt ponds on the sea-ice surface will decrease the surface albedo resulting in an increase in the absorption of solar radiation, as opposed to reflection, which accelerates warming (Stoeve et al. 2012). Therefore, a continuing increase in energy absorption by the ocean and light transmission into the ocean are expected, resulting in a further increase in sea-ice retreat and more input of solar heat in the ocean's surface water (Nicolaus et al. 2012). This could also lead to a change in the dominant sea-ice melt area, at the bottom of the sea ice instead of the top (Hardge et al. 2017). Global warming and the resulting changes in sea-ice properties has consequences for marine life. For example, northward shift in the distribution of usually more temperate species has already been found in the Arctic region as a consequence of warming ocean waters. Under the influence of Atlantic inflow water, several species of cephalopods have been found to have expanded their northward distribution and certain species have spread into the Barents Sea (Golikov et al. 2013). Similar trends have been found for fish species such as Atlantic cod (*Gadus morhua*) and capelin (*Mallotus vilosus*; Orlova et al. 2009; Hop & Gjøsæter 2013).

In the Antarctic, environmental change has been less obvious and causes of it are uncertain (Turner et al. 2009a; Stocker et al. 2013). The scientific understanding of the small observed increase in sea-ice extent is low due to uncertainties in the estimated natural variability in the region (Stocker et al. 2013). Based on modelling exercises, the total length of the sea-ice season has been slightly increasing or decreasing depending on the model used, but an increase in overall Antarctic sea-ice extent since 1979 is suggested to be likely (Stocker et al. 2013). However, regional trends in sea-ice extent have been observed and showed an increase in some areas, while it decreased in others (Fig. 1.5; Cavalieri et al. 1997). In the Western Antarctic Peninsula region, the sea-ice extent has been declining strongly between 1979 and 2008, while it has been somewhat increasing in the Ross Sea (Turner et al. 2009b). Furthermore, the Antarctic Peninsula/Bellinghausen Sea region showed a later sea-ice advance and earlier sea-ice retreat, whereas the western Ross Sea region showed the opposite, thus an earlier sea-ice advance and later retreat (Stammerjohn et al. 2012). The Western Antarctic Peninsula has also been the region of the Southern Ocean where the greatest increase in air temperature has been recorded (King 1994). Although long-term trends in sea-ice thickness are not available for the Southern Ocean (Bracegirdle et al. 2008), reconstructions suggest that between 80 to 140°E, the thickness has been declining during the second half of the 20th century (Turner et al. 2009a). In addition, a loss of mass of the Antarctic ice sheet (the vast mass of glacial ice that covers the Antarctic continent and surrounding seas), has been observed over the last two decades (Stocker et al. 2013). As in the Arctic region, changes in extent and/or thickness of the sea ice will have consequences for the ecosystem functioning.

FISHERIES

In addition to warming of the oceans, polar regions are rich in valuable marine resources and therefore subject to commercial fisheries. Species currently harvested in the Southern Ocean include Antarctic krill, Patagonian toothfish (*Dissostichus eleginoides*), Antarctic toothfish (*Dissostichus mawsoni)* and on a smaller scale mackerel icefish (*Chamsocephalus gunnari*). Krill have been commercially harvested since the 1970s.

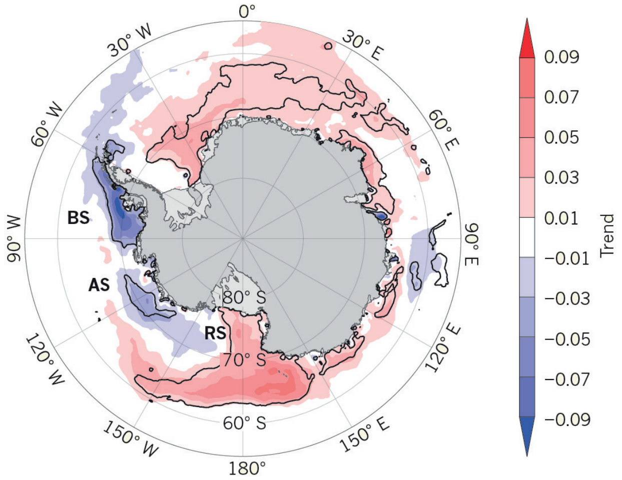


Figure 1.5: The change in fractional ice coverage per decade calculated over the period 1979-2012. Bold lines indicate a change that is statistically different ($p < 0.05$). (From King 2014, with data from the National Snow and Ice Data Center, Boulder, USA).

Currently, most krill fishing occurs in the Atlantic sector of the Southern Ocean, around South Georgia, the South Orkney Islands and the Antarctic Peninsula. Fisheries in the Southern Ocean are regulated by the Commission on the Conservation of Antarctic Marine Living Resources (CCAMLR 2017), which is part of the Antarctic Treaty system. The intention of CCAMLR is to conserve living resources and prevent overexploitation, in other words, using an ecosystem and precautionary approach for harvesting resources. Most of the krill catch is used for domestic animal and aquaculture feed, but its use as a food supplement for its omega-3 fatty acids is growing. Additionally, krill are used for sport fishing bait, for human consumption, for pharmaceuticals, or as a source of chitin and its derivative chitasan, which both have a wide variety of uses (Nicol et al. 2000a; Nicol 2018). Ongoing research is necessary to continue the assessment of krill distribution and stock size, and the relationship between marine resources, fisheries, top predators and sea ice, to evaluate the potential cumulative effects resulting from a changing climate (CCAMLR 2017).

Fishing in the Arctic occurs in permanently or seasonally ice-free waters (AMSA 2009). Fishing is performed on e.g. capelin, herring (*Clupea* spp.), Atlantic cod, saithe (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*), pollack (*Pollachius pollachius*), Arctic haddock (*Melanogrammus aeglefinus*), blue whiting (*Micromesistius poutassou*), Greenland halibut (*Reinhardtius hippoglossoides*), Pacific salmon (*Oncorhynchus* spp.), shrimp and snow crab (*Chionoecetes opilio*; Lindholt 2006). Polar cod, mainly utilized for fish meal and oil, has been intensively fished by the former USSR, Norway, Denmark and Germany in the past, but is currently only exploited in a minor way (FAO 2018). The reduction and thinning of the Arctic sea ice has had implications, such as longer seasons of navigation and new access to regions that previously were difficult to reach (AMSA 2009). Currently, fisheries mostly take place in the parts of the Arctic Ocean comprising the Exclusive Economic Zones (EEZ) of Canada, Denmark (Greenland), Norway, Russia and the USA. Knowledge on the Arctic ecosystem is necessary to protect natural resources in the international waters of the central Arctic Ocean, or high Arctic, when it becomes increasingly accessible for commercial fisheries and when currently intensively harvested sub-Arctic fish stocks expand northward. In 2017, the EU and nine major fishery nations agreed to not fish the high seas of the central Arctic Ocean commercially, but focus on first understanding the marine ecology and fish stock dynamics, and on developing a management plan (Hoag 2017).

THESIS OUTLINE

The aim of this thesis is to acquire knowledge on the association of key species with the sea-ice habitat by looking at several aspects of their life cycle and biology. Furthermore, the aim is to increase knowledge on the functioning of polar food webs. The final objective is to estimate the level at which polar ecosystems and their key inhabitants are affected by changing sea-ice habitats by investigating the distribution, population structure, diet and energy density of trophic key species in the under-ice habitat. Specific goals are to:

- Assess the abundance and distribution of trophic key species in the under-ice habitat;
- Estimate the importance of sea ice-derived carbon sources (ice algae, sea-ice microfauna) for trophic key species.
- Increase knowledge on the functioning of polar food webs.

Although Antarctic krill (*Euphausia superba*, hereafter krill) has been studied extensively, many questions remain unanswered. This is in part caused by their large flexibility in behaviour resulting in annual, regional and seasonal differences, which also varies with ontogeny (Atkinson et al. 2008; Flores et al. 2012b). Particular knowledge gaps addressed in this thesis are regarding larval and juvenile krill during winter time, when young Antarctic krill are known to reside in the under-ice surface layer. As they hatch in the preceding summer, larval and juvenile krill have to deal with the harsh conditions of their first winter, which is regarded a critical period for krill survival. The role of sea ice herein is expected to be significant, but particularly large scale observations are scarce. Especially for sustainable fisheries management it is important to ensure that new recruits survive to reproductive age, hence the need to gain insight into the critical winter period. Therefore, it was investigated how young, age class 0 Antarctic krill use the sea ice during winter. This was done, firstly, by looking at their population dynamics and composition in the ice-water interface and comparing that to deeper water layers (**Chapter 2**). Secondly, the diet, and the contribution of sea-ice associated food sources of young krill was studied. By looking at a large population and its structure as investigated in **Chapter 2**, it was possible to draw conclusions on drivers of spatial variability in the diet (**Chapter 3**). By using different methods to examine the diet, temporal variability and effects on body condition could be studied.

Although krill is a key species, it is not the only species in the diet of top predators. The top predator's diet depends on season and region, and variability can have an effect on e.g. the growth of offspring. Furthermore, diel and seasonal shifts in vertical distribution alter the availability of prey for top predators between seasons and/or different times of day (Ainley et al. 1991). To make a good estimate of the value of a species as a food source as well as for making energy flux and food web models, a good estimate of the energetic value of different prey species is necessary. Therefore, the energetic density of a variety of zooplankton and nekton species caught in the Southern Ocean was measured. Measurements were compared with values from literature, resulting in a review summarizing what is currently known about the energetic value of species, and the source and degree of variation of energetic values between and within species (**Chapter 4**). Furthermore, the review gives a good overview of available data enabling the identification of knowledge gaps.

In the Arctic, young, one- or two-year-old, polar cod have been found to dwell in the under-ice surface layer. Although this was known, David et al. (2016) conducted the first large scale investigation of the abundance and distribution of polar cod in the ice-water interface layer using SUIT. The study resulted in the hypotheses that young polar cod use the sea ice as a transport mechanism and suggested that the fish found in the central Arctic Ocean originated from spawning grounds in the shelf regions of the Kara and Laptev Seas. In order to investigate the importance of sea ice as a food source for polar cod, a diet study, using a similar multiple method approach as to Antarctic krill, was conducted (**Chapter 5**). Stomach content analysis gave insights in the species composition of the diet, while fatty acid and stable isotope analyses revealed the proportional contribution of ice-algal produced carbon in different tissues of the fish.

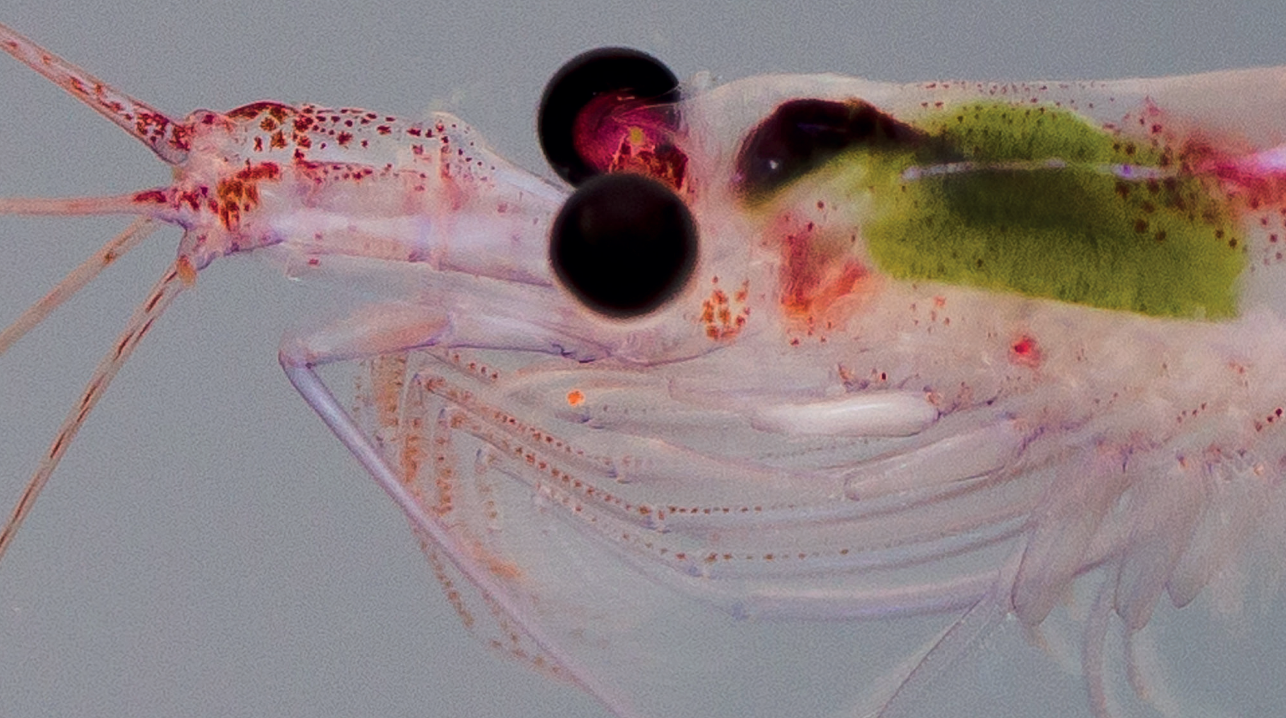
Apart from polar cod, amphipods constitute a major part of the zooplankton community associated with the sea-ice food web. The amphipod *Apherusa glacialis* is a highly abundant, ice-obligate species and an important link in between sea-ice and the pelagic food webs. Studies have shown that it feeds on sea-ice resources at least during summer. But how the sea-ice structures the *A. glacialis* population and consequently how this changes with a changing sea-ice habitat is largely unknown. Small scale studies, often performed by SCUBA diving, yield variable results. The relationship of this amphipod with general properties of the Arctic environment would be helpful to gain insight in preferred habitats and large-scale consequences of a reduction in sea ice. Therefore, the effect of sea ice and other environmental parameters on the abundance and distribution of this species has been examined. The results of a research expedition conducted north of Svalbard were compared with results from a another research expedition (David et al. 2015), which was conducted in the Eurasian basin of the Arctic Ocean (**Chapter 6**).

In the final chapter (**Chapter 7**) the findings of this thesis are discussed. The order of the chapters is based on geography for clarity, starting with the Southern Ocean chapters followed by Arctic Ocean chapters. The general discussion will, however, be structured per topic based on the above mentioned aims. Recommendations for further research are given.

CHAPTER 2

Size and stage composition of age class 0 Antarctic krill (*Euphausia superba*) in the ice-water interface layer during winter/early spring

Fokje L. Schaafsma, Carmen David, Evgeny A. Pakhomov, Brian P.V. Hunt, Benjamin A. Lange, Hauke Flores, Jan Andries van Franeker



ABSTRACT

The condition and survival of Antarctic krill (*Euphausia superba*) strongly depends on sea ice conditions during winter. How krill utilize sea ice depends on several factors such as region and developmental stage. A comprehensive understanding of sea ice habitat use by krill, however, remains largely unknown. The aim of this study was to improve the understanding of the krill's interaction with the sea-ice habitat during winter/early spring by conducting large-scale sampling of the ice–water interface (0–2 m) and comparing the size and developmental stage composition of krill with the pelagic population (0–500 m). Results show that the population in the northern Weddell Sea consisted mainly of krill that were <1 year old (age class 0; AC0), and that it was comprised of multiple cohorts. Size per developmental stage differed spatially, indicating that the krill likely were advected from various origins. The size distribution of krill differed between the two depth strata sampled. Larval stages with a relatively small size (mean 7–8 mm) dominated the upper two metre layer of the water column, while larger larvae and AC0 juveniles (mean 14–15 mm) were proportionally more abundant in the 0- to 500-m stratum. Our results show that, as krill mature, their vertical distribution and utilization of the sea ice appear to change gradually. This could be the result of changes in physiology and/or behaviour, as, e.g., the krill's energy demand and swimming capacity increase with size and age. The degree of sea ice association will have an effect on large-scale spatial distribution patterns of AC0 krill and on predictions of the consequences of sea ice decline on their survival over winter.

INTRODUCTION

During winter, a large part of Antarctic krill's (*Euphausia superba*) habitat is ice-covered (Meyer et al. 2002a). At the onset of freeze-up and ice formation, in autumn, substantial pico-microplankton populations remain in the surface water and are incorporated into the newly formed ice (Eicken 1992; Arrigo & Thomas 2004). Deep vertical mixing and low light intensity suppress water column phytoplankton production during the winter months, during which the biota growing in and on the underside of the sea ice represent an important energy resource for krill larvae and adults (Eicken 1992; Quetin & Ross 2003; Flores et al. 2012a). Unlike adults, larval krill cannot employ survival strategies such as utilizing storage lipids or reducing metabolism or protein catabolism when starving. Therefore, sea-ice resources are considered critical for the winter survival of larval and juvenile krill (Daly 1990; Meyer et al. 2002b; Meyer 2012). This dependency can also explain the positive correlation between sea-ice extent and population size (Atkinson et al. 2004). The dependency of larval krill on sea ice makes krill an important link between the ice and other environments by feeding on ice organisms, by excreting faeces to the water column and benthos, and by serving as an important food source to predators (Eicken 1992; Van Franeker et al. 1997; Flores et al. 2012a).

Despite the recognized role of sea ice in krill's life cycle, information on how krill utilize and interact with the sea ice–ocean environment remains limited. There is evidence that the interaction of krill with sea ice varies with sea-ice properties (Murphy et al. 2004), season, region, and developmental stage of the krill (Quetin et al. 1994; Murphy et al. 2004; Flores et al. 2012a). These factors could have an effect on the distribution of *E. superba* (Nicol 2006). Observed distribution patterns of different krill size classes may be attributed to advection from different krill stock sources (Siegel 2012), differences in physiology, e.g. swimming ability and/or transport mechanisms due to different environmental conditions. This will be influenced by the timing of krill spawning. A combination of behavioural and physical factors can cause spatial aggregation of krill of a certain size range or maturity (Kils 1979; Quetin & Ross 1984; Daly & Macaulay 1991), resulting in schools or swarms with similarly sized individuals (Watkins 2000; Kawaguchi et al. 2010).

The onset of krill spawning is influenced by winter sea-ice extent and the duration of the sea-ice cover (Pakhomov 2000; Siegel 2000). The duration of the spawning season and the number of spawning episodes that occur within one season can be variable (Ross & Quetin 1986; Spiridonov 1995). In general *E. superba* releases eggs from mid-December to April (Ross & Quetin 1986), with the highest intensity in late December and January (Pakhomov 1995; Spiridonov 1995). The larvae have a complex developmental process going through several stages, namely nauplius I–II, metanauplius, calyptopis I–III and furcilia I–VI (Fraser 1936; Bargmann 1945; Marr 1962; Jia et al. 2014).

Late-stage furcilia (III–VI) have been reported during the onset of winter within the marginal ice zone of the Scotia and Weddell seas. Here, furcilia VI were not commonly found before August, effectively about 150–180 days after the spawning (Daly 1990; Siegel 2000). Nevertheless, in the Bransfield Strait furcilia VI larvae have been found as early as the beginning of winter, and are numerous by spring (Ross & Quetin 1986). During their first winter/early spring furcilia generally develop into juveniles (age class 0) at a length of approximately 15 mm (Siegel 1987). The krill remain in the juvenile stage in their second year (age class 1). At the end of their second year the juveniles become sub-adults, and from the third year onwards, all krill are mature adults (Siegel 1987). Post-larval krill can have a great overlap in size. Juveniles can grow up to 36 mm (Siegel 1987), while females can become mature from 33 mm onwards (Siegel 2012).

Knowledge on the abundance and distribution of different age classes of krill, as well as the interaction of krill with sea ice, is crucial for better predictions of krill recruitment and understanding krill population structure and krill dispersal, particularly in the face of potential sea-ice reductions due to climate change (Brierley et al. 2002; Daly 2004; Ross et al. 2004; Sologub & Remelso 2011; Flores et al. 2012b). Pelagic trawls generally undersample the top 1–10 m of the water column, and hydro-acoustic technology is also lacking the ability to explore the upper metres of the water column (Pakhomov 2000; Brierley et al. 2002; Flores et al. 2012a). Therefore, earlier length– frequency analyses of krill, which can be important to find connections between sub-populations, have probably underestimated late larval and early juvenile krill due to a general undersampling of the surface layer and, in particular, the sea-ice underside (Melnikov & Spiridonov 1996,; Frazer et al. 2002; Atkinson et al. 2008; 2012; Kawaguchi et al. 2010). To overcome this limitation a Surface and Under Ice Trawl (SUIT) was used in this study, enabling large-scale sampling of the upper two metres of the water column under the sea ice (Van Franeker et al. 2009; Flores et al. 2012a; 2014).

The macrozooplankton/micronekton community residing within the under-ice surface layer has previously been shown to differ from the epipelagic layer in terms of species composition, community structure and species density (Flores et al. 2012a; 2014). In this study, krill assemblages were investigated from different depth strata of the northern Weddell Sea during austral winter/early spring. Specifically, we aimed to characterize the population structure of krill at the sea-ice interface in terms of length and developmental stage composition and examine habitat partitioning of different krill life stages between the sea-ice interface and the water column. Using a comparative approach, we aim to improve our understanding of the relative importance of the sea ice–ocean interface in the life cycle of krill.

METHODS

SAMPLE AND ENVIRONMENTAL DATA COLLECTION

Sampling was performed in the northern Weddell Sea during research cruise PS81 (ANTXXIX/7) on board RV Polarstern, between 24 August and 2 October 2013 (Fig. 2.1a). The upper two metres of the water column directly under the sea ice were sampled using a Surface and Under Ice Trawl (SUIT; Van Franeker et al. 2009). The trawl has a steel frame with a 2 x 2m net opening, with a 7-mm half-mesh commercial shrimp net over 1.5 m width, and a 0.3-mm mesh plankton net over 0.5 m width. Floats attached to the top of the frame keep the net at the surface or directly under the ice. The SUIT shears out to the side of the ship, sampling away from the ship's wake and under relatively undisturbed sea ice (Van Franeker et al. 2009; Suppl. mat. in Flores et al. 2012a).

The SUIT frame is equipped with a sensor array containing an acoustic Doppler current profiler (ADCP, Nortek Aquadopp, Norway), which measures the velocity and probe (CTD75 M, Sea & Sun Technology, Germany) with built-in fluorometer (Cyclops, Turner Designs, USA), which measures water temperature, salinity and water column chlorophyll *a* concentration. Data gaps in the CTD measurements caused by low battery voltage were filled using complementary datasets from the shipboard sensors (temperature, salinity and chlorophyll *a* at stations 557_2, 560_2 and at station 562_5 only for chlorophyll *a*), using correction factors determined by linear regression. Connected to the CTD probe was an altimeter (PA500/6-E, Tritech, UK) which measured the distance between the net and the sea-ice underside, and it was used to calculate ice thickness. Gaps in the data were filled by constructing a linear model between the CTD ice thickness and ADCP depth in order to derive ice thickness from ADCP depth alone. The set of values for sea-ice thickness along a sampling profile was used to calculate a sea-ice roughness coefficient. A detailed description of the acquisition and calculation of environmental parameters can be found in David et al. (2015). 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). The measured and calculated environmental parameters are shown in Table S2.1 in Supplement 2A.

In total 11 under-ice SUIT stations were completed, four during the day and seven at night. Net tows were conducted at a speed of 1.8–3 km. The volume of water filtered was estimated for each haul by multiplying the mean current velocity with the trawl duration and the opening area, and it ranged between 558.10 and 3177.83 m^3 for the plankton net. Further details of sampling are given in Supplement 2A (Table S2.1).

The 0- to 500-m stratum was sampled in ice-covered waters with double oblique hauls using a rectangular midwater trawl (RMT). The trawl consisted of an RMT-1 with a 0.33-mm mesh mounted above an RMT-8 with a mesh size of 4.5 mm at the opening and 0.85 mm at the cod end. The net openings were 1 and 8 $m^{2,}$ respectively. A flowmeter (Hydro Bios, Kiel) was mounted in the mouth of the RMT-8 to measure the water volume filtered. Net tows were conducted at a speed of 2–2.5 km. Nine hauls were completed in ice-covered areas, six during the night, two during the day and one during twilight. The volume of water filtered by the RMT-1 ranged between 1055 and 4280 m^3. Further details of sampling are given in Supplement 2A (Table S2.2).

Samples for krill length–frequency analysis from both nets were preserved in a 4 % hexamine-buffered formaldehyde–sea water solution. Krill from all samples were counted, and total length was measured, to the nearest mm, from the anterior margin of the eye to the tip of the telson (Discovery method; Marr 1962).

Larvae were staged based on the number of terminal spines on the telson according to Kirkwood (1982). Krill that have lost one pair of post-lateral spines from their telson (Fraser 1936), but do not show sexual characteristics yet (Makarov & Denys 1981) are defined as juveniles. The sexual maturity of postlarval individuals was further staged according to Makarov & Denys (1981).

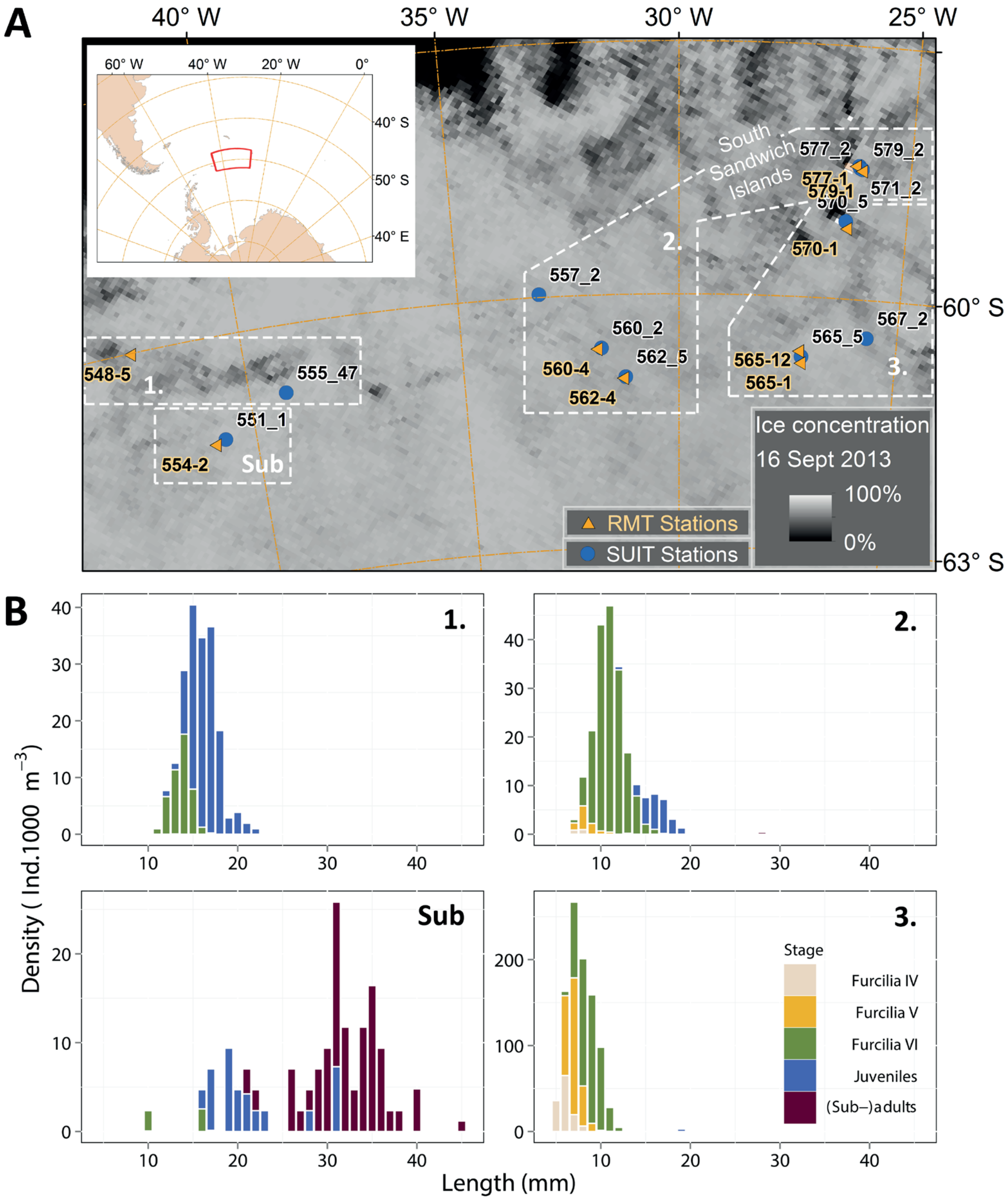


Figure 2.1: Spatial pattern in *Euphausia superba* size frequencies. A) SUIT and RMT sampling locations, indicated with their station numbers, with ice concentration on 16 September 2013. Dashed rectangles show the spatial size distribution of the krill. ‘Sub’ represents the station dominated by sub-adult krill, 1 to 3 are the stations dominated by AC0 krill, grouped in stations with similar krill size distributions according to the cluster analysis. B) length frequency distributions of krill as in mapped clusters.

Because the SUIT's shrimp net and the RMT-8 undersample small krill (<20 mm; Siegel 1986, Flores et al. 2012a) and the catch of larger krill was low throughout the sampling area, only data from the SUIT's plankton and the RMT-1 nets were used for further analyses. As a result, abundances of larger krill ([20 mm) were likely underestimated (Siegel 1986), and this study focuses on larval and juvenile krill that are born in the preceding summer, and which are further referred to as age class 0 (AC0) krill. For comparison between stations and nets, areal and volumetric densities were calculated (ind. m^{-2} and ind. m^{-3}, respectively).

STATISTICAL ANALYSIS

Cluster analysis was performed to analyse similarity of length class frequencies between stations, using Euclidean distance. In order to compare length distributions regardless of varying krill abundances at each station, numbers were standardized to percentages. Stations were grouped using the average linkage method, which was found to work well with suspected unequal cluster sizes and small sample sizes (Ferreira & Hitchcock 2009; Saraçli et al. 2013).

Differences in mean length within stages and between clusters were investigated using one-way ANOVA. Between-group differences were assessed with the Tukey HSD post hoc test. Differences in total abundance per sampling depth were investigated using the nonparametric Wilcoxon rank-sum test due to unequal variances. Differences in size distribution between depth layers were investigated using the Kolmogorov–Smirnov test.

A mixture distribution was fitted to the total catch per size class in ind.1000 m^{-3}, using the maximum likelihood fitting programme CMIX (De la Mare 1994). This model assumes that the sampled population is a mixture of cohorts or age classes and that each group can be described by a parametric distribution. The model provides relative abundance estimates for each cohort (Shelton et al. 2013). The best fitting model was further evaluated using a Chisquare goodness-of-fit test. All analyses were performed using R statistical software, version 3.0.3 (R Core Team 2014). The CMIX R package was downloaded from the Australian Antarctic Division website (http://www.antarctica.gov.au/science/southern-oceanecosystems-environmental-change-and-conservation/southern-ocean-fisheries/fish-and-fisheries/conservation-andmanagement/cmix).

RESULTS

ENVIRONMENTAL CONDITIONS

At the western side of the sampling area, the sea ice extended to ~59°S in August and increased to ~58°S from mid-September onward. At the eastern side, the sea-ice extent increased to ~56°S in September. Under-ice water properties, measured with the SUIT sensor array, showed low variability throughout the sampling area. Surface temperatures and salinities were on average -1.84 ± 0.012°C and 34.14 ± 0.11, respectively. Chlorophyll *a* concentrations of the subsurface waters ranged from 0.097 to

0.134 mg m^{-3} during August/early-September and showed somewhat higher values ranging from 0.164 to 0.275 mg m^{-3} during late-September/beginning of October. Sea-ice concentrations, in the sampling area, were in general between 86 and 100%, except at the end of September/beginning of October, when four stations (570–579) where sampled north of 60°S. At these stations, sea-ice coverage decreased to about 50%. Although the size of the ice floes decreased, sea-ice thickness was still within the range (0.30–0.70 m) of the preceding stations, with one exception (station 571_2, 0.23 m). The sea-ice roughness coefficient ranged from 0.8 to 3.7, with the highest values at stations 555_47 and 565_5. Snow cover was present at all stations ranging from 0.05 to 0.6 m. Further details of sea-ice parameters and snow cover are given in Supplement 2A (Table S2.1).

STAGE COMPOSITION AND LENGTH-FREQUENCY DISTRIBUTION OF KRILL IN THE UNDER-ICE SURFACE LAYER

At most stations sampled with the SUIT, furcilia VI was the dominant stage. Furcilia V and juveniles also had relatively high proportional abundances. Low proportional abundances were recorded for furcilia IV, sub-adult and adult stages. Figure 2.2 shows the total length and stage composition of krill larvae in the 0- to 2-m depth layer. Sub-adults and adults were only caught in the under-ice surface layer at night, which is consistent with the findings in a previous winter study in the Lazarev Sea (Flores et al. 2012a). Station 551_1 was the only station where mostly sub-adults were caught. The other stations consisted of predominantly AC0 krill. Cluster analysis revealed that these AC0-dominated stations can be divided into three geographically distinct groups, which differed in krill size and developmental stage composition (Figs. 2.1a; 2.3). The first cluster consisted of station 555_47, which was dominated by juveniles with a mean length of 15.69 mm (Figs. 2.1b; 2.3). The second cluster consisted of stations dominated by furcilia VI (Figs. 2.1b; 2.3). Small numbers of juveniles, and occasionally sub-adults, adults and furcilia V were also present

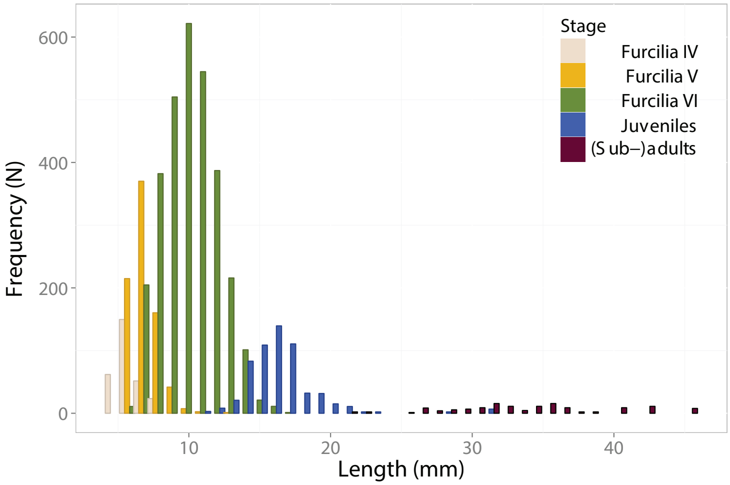


Figure 2.2: Length frequency distribution of *Euphausia superba* per developmental stage in number caught (N) in the upper two meters of the water column under ice (all SUIT stations combined).

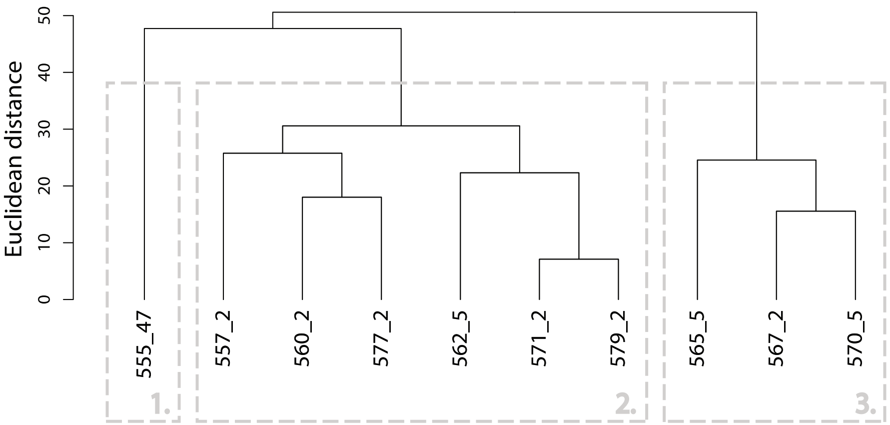


Figure 2.3: Dendrogram of the cluster analysis comparing the similarity of the length distribution of AC0 *Euphausia superba* in the upper two meters of the water column under ice. The left cluster consists of a station dominated by juveniles, the middle cluster consists of stations dominated by furcilia VI and the right cluster consists of stations with furcilia IV, V and VI.

in the second cluster stations. The mean length of the krill in this cluster was 11.85 mm. The third cluster was dominated by furcilia V and VI with a mean length of 7.92 mm and had a relatively large proportion of furcilia IV (Figs. 2.1b; 2.3). Although there was an overlap in developmental stages among clusters, the average length per developmental stage differed spatially (Fig. 2.4). The average size of furcilia V and VI was significantly different between each cluster (ANOVA $F = 505.9$, $p < 0.001$; Tukey HSD, $p < 0.001$). Furcilia V were significantly larger in Cluster 2 than in Cluster 3, and absent from Cluster 1. Furcilia VI were significantly larger in Cluster 1 than in Cluster 2 and 3, and smallest in Cluster 3 (Fig. 2.4). For juveniles, the average size in station 551_1 was significantly larger than all other stations (ANOVA $F = 57.11$, $p < 0.001$; Tukey's HSD, $p < 0.02$).

COMPARISON OF THE UNDER-ICE SURFACE TO THE 0-500M STRATUM

Krill volumetric density (ind. m^{-3}) was significantly higher in the 0- to 2-m under-ice surface layer than in the 0- to 500-m stratum (Wilcoxon, $U = 97$, $p < 0.001$; Fig. 2.5a), while areal density (ind. m^{-2}) was significantly higher in the 0- to 500-m stratum than in the under-ice layer (Wilcoxon, $U = 18$, $p = 0.016$; Fig. 2.5b). Average abundance estimates from the SUIT catches ranged from 0.09 to 3.60 individuals m^{-2} and in the RMT catches from 0 to 46.03 individuals m^{-2}. A summary of both depth layers and average length per station is given in Supplement 2A (Tables S2.3 & S2.4). The length–frequency distribution of the part of the population sampled in the 0- to 500-m stratum differed significantly from the distribution in the upper 2 m under the ice (KS test, $D_{47} = 0.47$, $p < 0.001$). The proportion of small furcilia (<10 mm) in the 0- to 500-m stratum was lower compared to the under-ice layer, while the opposite pattern was observed for larger krill (15–20 mm, Fig. 2.6).

Densities at night did not statistically differ from densities during the day (Wilcoxon, 0–2 m: $U = 10$, $p =$

1; 0–500 m: $U = 3$, $p = 0.4$; Fig S2.1, Supplement 2B). The total size distribution in the 0- to 2-m depth layer of age class 0 (AC0) krill at night was not significantly different from the distribution at day (KS test, $D_{20} = 0.25$, $p = 0.56$). Although statistically there was also no difference in the day and night size distribution in the 0- to 500-m depth layer (KS test, $D_{20} = 0.35$, $p = 0.17$), AC0 krill <8 mm and >15 mm were not found in this depth stratum during the day but only at night (Fg. S2.2, Supplement 2B).

The cohort mean lengths as determined by the mixture distribution analyses were similar for both SUIT and RMT samples (Fig. 2.7). The mixture distribution analysis derived from CMIX (De la Mare 1994) showed that the best fit of expected densities vs. observed densities was obtained with four components (0–2 m: $Chi^2 = 0.997$, 0–500 m: $Chi^2 = 0.999$; Fig. 2.7). One component represented subadults and adults, which were 1+ years old. The other components were krill larvae and juveniles that were in their first year, indicating that they represented three separate cohorts. Comparing the cohort mean sizes as determined from the mixture distribution analysis with the clusters using measured krill body length, indicated that there was one cohort (mean length 0–2 m: 7.27 mm, 0–500 m: 7.06 mm) that corresponds with the third cluster containing furcilia IV, V and small furcilia VI. One cohort (mean length 0–2 m: 9.90 mm, 0–500 m: 10.90 mm) corresponds with the second cluster of mainly furcilia VI. The last cohort (mean length 0–2 m: 14.42 mm, 0–500 m: 15.42 mm) corresponds with the first cluster that contains furcilia VI and AC0 juveniles.

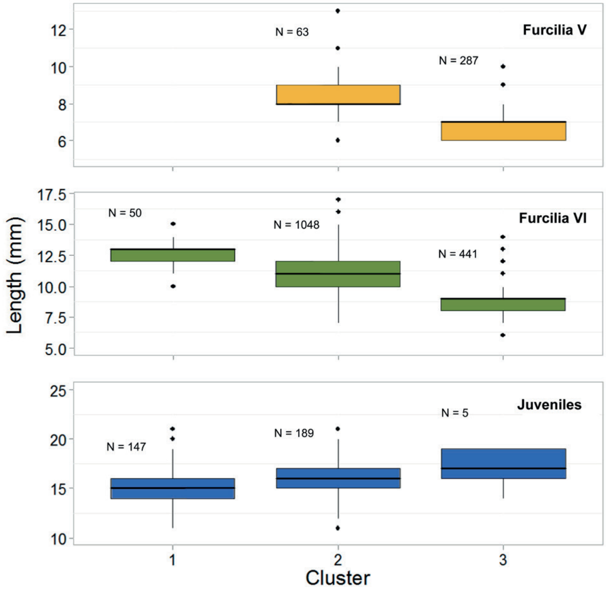


Figure 2.4: Size characteristics of the three most abundant stages of *Euphausia superba* (furcilia V, VI and juveniles) per cluster in the SUIT catches. Clusters are defined as in Figures 2.1a and 2.3. The horizontal black lines show the median length in a cluster. The upper and lower limits of the coloured squares indicated the 25th and 75th percentile. The upper and lower limits of the vertical line indicate the minimum and maximum length of that stage in a cluster. Black dots represent the true minimum and maximum lengths, but are numerically distant from the other data points and therefore considered outliers. N represents the number of individuals.

DISCUSSION

KRILL POPULATION STRUCTURE

Primarily AC0 krill were found in both the under-ice surface (0–2 m) and the 0- to 500-m strata of the

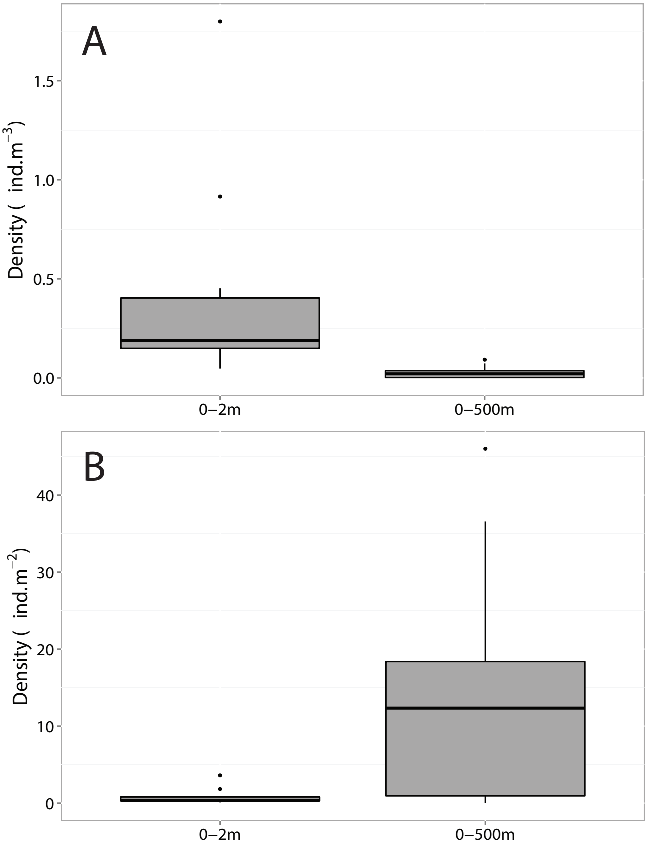


Figure 2.5: Comparison of the volumetric density in ind. m^{-3} (A) and areal density in ind.m^{-2} (B) of *Euphausia superba* in the surface layer (0-2 m) and the 0-500 m layer under ice. The horizontal black lines show the median density in a depth stratum. The upper and lower limits of the grey squares indicated the 25th and 75th percentile, thus 50% of all stations have densities between these limits. The upper and lower limits of the vertical line indicate the minimum and maximum density of the stations in a depth stratum. Black dots represent the true minimum and maximum densities, but are numerically distant from the other data points and therefore considered outliers.

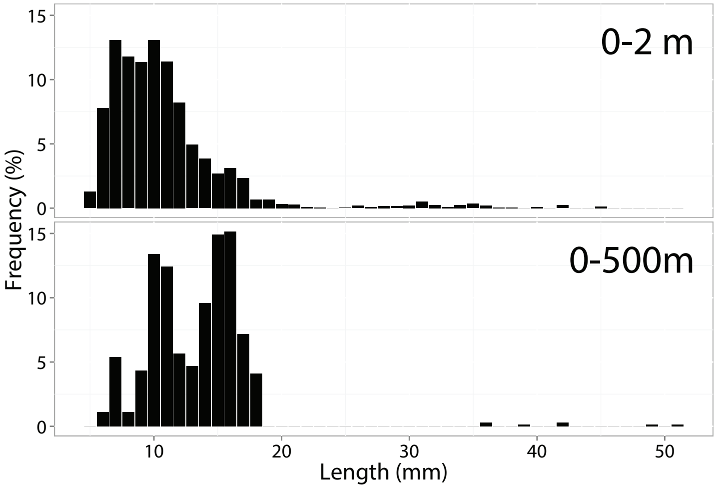


Figure 2.6: Relative distribution of length classes of *Euphausia superba* within the under-ice surface (0-2 m) and the water column under ice (0-500 m).

northern Weddell Sea during winter/early spring. The comparison of krill abundances should be considered with caution because the effect of, e.g., towing speed, sea-ice conditions or other factors on the catch efficiency of both nets is not precisely known (Flores et al. 2012a; 2014). Hunt et al. (2014) showed that, at least in the eastern part of the sampling area, AC0 krill were migrating from the ice–water interface down to <20 m at night. Therefore, it should be kept in mind that the AC0 krill found in the 0- to 500-m stratum are most likely still caught in the upper part of the water column (Hunt et al. 2014). Additionally, there is probably a degree in overlap of krill found in both depth layers due to diel vertical migration. It should also be kept in mind that the RMT samples in the wake of the ship and therefore in disturbed sea-ice conditions. Earlier comparisons of SUIT and RMT data also indicated that the RMT does not sample the ice–water interface well (Flores et al. 2011; 2012a; 2014). Abundances calculated from the SUIT catch are probably underestimations due to the low efficiency of the SUIT to sample krill from sea-ice crevices and over-rafted ice floes, where larval krill have been found to reside (Frazer et al. 2002; Meyer et al. 2009; Flores et al. 2012b). Although krill abundances at stations where the sea ice was relatively rough were not lower than in other stations, the abundance estimates in 0- to 2-m depth stratum presented in this study should be regarded as a minimum estimates.

In the upper 0–2 m furcilia VI were most abundant, while in the 0- to 500-m stratum juveniles dominated. Previous studies, conducted in the Scotia/Weddell Sea and western Antarctic Peninsula (WAP) during late winter/early spring, also found furcilia VI as the dominant stage in the under-ice surface, which was sampled using 1 m^2 Ring and Reeve nets and/or divers (Daly 1990; Quetin et al. 2003; Ross et al. 2004). The majority of furcilia VI from our study were similar in size or even larger than those found in other winter studies, and in some instances, our furcilia VI were comparable to studies done in autumn (Daly 2004; Ross et al. 2004 and references therein).

Juveniles in the present study had a size distribution comparable to juveniles sampled from the WAP during January 2002 (Siegel et al. 2003) and were larger than juveniles found in the Scotia/Weddell Sea during winter (Daly 2004), but also than juveniles found in ice–water interface in the western Weddell sea in March/April (Melkinov & Spiridonov 1996). In the latter study, furcilia VI were also abundant, however, in contrast to the juveniles, on average larger than the individuals found in our study (Melkinov & Spiridonov 1996). The larger size range of the furcilia VI and AC0 juveniles of our study compared to the smaller size range reported by Melkinov & Spiridonov (1996) could possibly be explained by the former belonging to different cohorts, while the latter potentially belongs to the same or less cohorts.

Remarkably, our results show that size per developmental stage differed between stations. Furcilia IV, V and VI caught at stations 565_5, 567_2 and 570_5 were small compared to late-stage furcilia caught in other winter studies. Quetin et al. (2003) found that larval krill collected during September of two different years had the same developmental stage despite showing clear differences in total length. They also documented that larvae collected from underneath the ice in July were significantly larger than those collected from open water, although their developmental stages were the same. This suggested

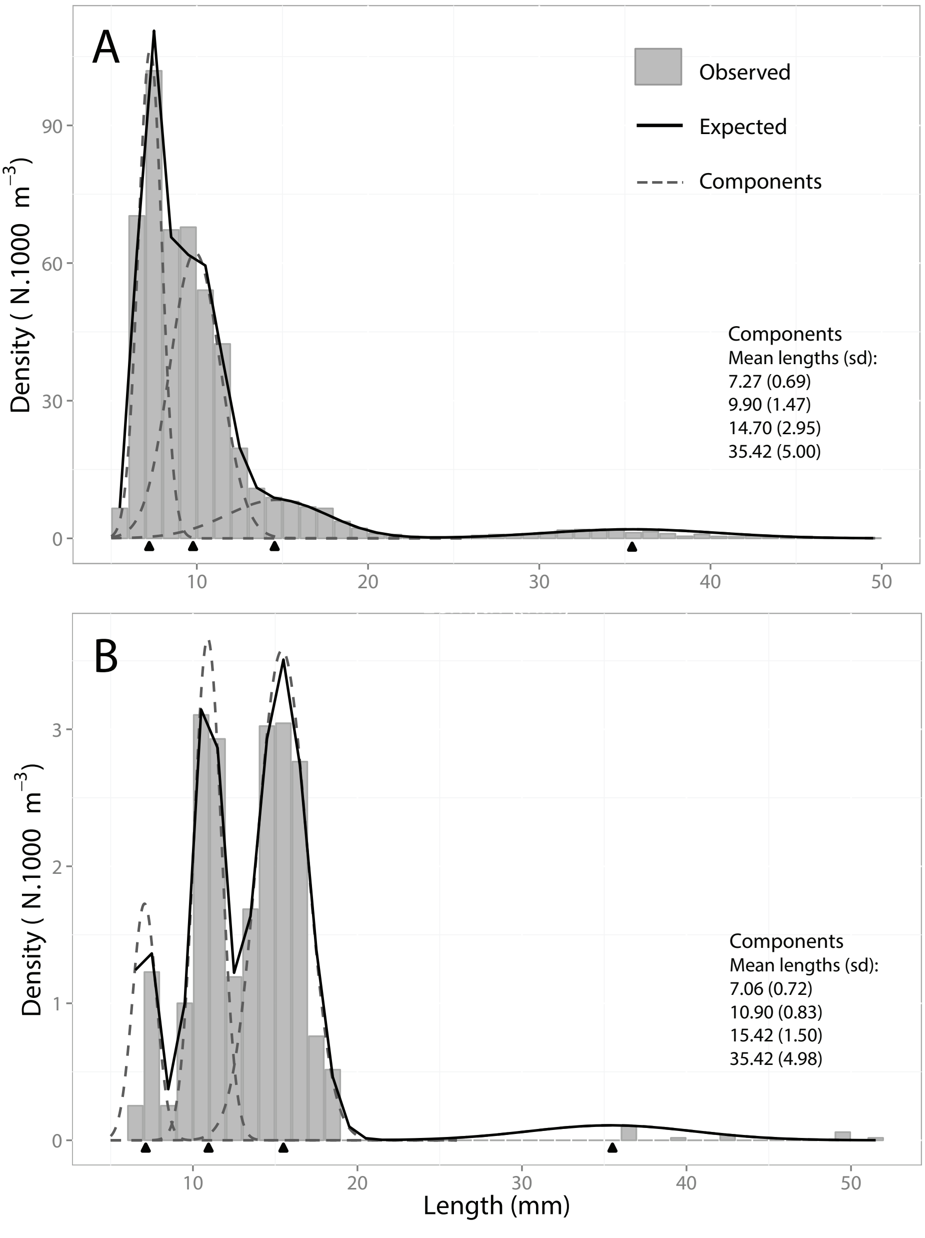


Figure 2.7: Size frequency distribution of *Euphausia superba* from different depth layers analysed using CMIX. Grey bars show the observed distribution, the black line shows the expected distribution (total) which can be subdivided into four components or age groups (dark grey dashed lines). Mean krill lengths and standard deviation (in parentheses) of all components are shown within the figure. A) 0-2 m layer (Chi^2=0.997). B) 0-500 m layer (Chi^2=0.999).

that developmental progression may be temporally less variable than the growth rate (Quetin et al. 2003; Pakhomov et al. 2004). Differences in developmental stages and sizes within developmental stages could be explained by dissimilar timing of spawning or different growth conditions of the larval krill caused by variable encountered environmental conditions (Quetin & Ross, 2003). Both could be a result of either multiple spawning episodes arising from a prolonged reproductive season, and therefore multiple cohorts originating from the same population, or the influx of larval krill from different locations (Quetin & Ross 2003). This would also explain the various cohorts we found within the AC0 krill population as established by the mixture distribution and cluster analyses.

The appearance of multiple developmental stages within the clusters indicated that there were at least three cohorts, though it is possible that these cohorts comprised multiple age groups that merged during an earlier stage. Growth experiments have demonstrated that AC0 krill show little or no growth in winter and that inter-moult periods can increase from 19 days in autumn to 40 days in winter, although the latter depends on the feeding conditions (Quetin et al. 2003; Daly 2004). This indicates that length per developmental stage in winter could potentially be more influenced by conditions that allow larvae to achieve a greater length and weight prior to overwintering (Quetin et al. 2003). Therefore, the observed variability of size within larval stages may possibly be a result of differences in environmental conditions experienced by larvae, such as different feeding conditions or unequal growth periods, before the onset of winter.

DRIVERS OF LARVAL DISTRIBUTION

Both the timing of reproduction and the geographic origin of the AC0 krill population influence their transport and therefore their distribution pattern. The large-scale distribution of furcilia has often been assumed to be affected primarily by sea surface circulation (Daly 1990; Pakhomov 2000). However, as young krill are known to reside at the ice–water interface, within crevices and unconsolidated ridges along the under-ice surface or between over-rafted ice floes, the transport and distribution of krill could also be influenced by ice drift (Daly 1990; Thorpe et al. 2007; Meyer et al. 2009). Sea ice moves differently than the underlying water mass, due to the combined influence of wind, ocean currents and mechanical stress (Thorpe et al. 2007). In addition, the ocean surface temperature and salinity gradients are modified by the ice such that the surface currents are very different to those expected when sea ice is not present (Murphy et al. 2004). If larval transport is affected by a combination of surface currents and sea-ice drift, then larval transport processes are even more complex than previously assumed, since they depend on sea-ice extent, and the locations of boundaries and fronts (Fach et al. 2002).

Particle-tracking models using ocean circulation and sea-ice drift patterns (Murphy et al. 2004; Thorpe et al. 2007) suggest that larvae are possibly carried into the northern Weddell Sea area with north-easterly currents from major spawning grounds in the Scotia Sea, north and west of the Antarctic Peninsula, or from the central or south-eastern Weddell Sea, adjacent to the Lazarev Sea (Daly 1990; Melkinov & Spiridonov 1996). Reproduction in the Scotia Sea and the Antarctic Peninsula area typically starts earlier than in the south-eastern Weddell and Lazarev Seas (Spridonov 1995). It is thus a possibility that the larger and older krill from cluster 1 could have originated from the Scotia Sea or the tip of the Antarctic Peninsula, advected by the eastward-flowing current of the northern Weddell Gyre. The smaller and younger krill from cluster 3 may be a result of spawning in the central Weddell Sea. This depends, however, strongly on environmental conditions (Murphy et al. 2004). If the krill larvae remain in the upper layers of the water column, the ocean circulation and ice drift models suggest that larvae originating from the Scotia Sea would potentially move northward. However, in some years it was found that the krill from this flow would be transported back around the South Sandwich Islands into the Weddell Sea (Murphy et al. 2004).

The general pattern of sea-ice drift in the northern Weddell Sea would indicate that krill associated with the sea ice would have come from farther south within the Weddell Sea (Murphy et al. 2004; Schwegmann et al. 2011). The reproductive season in the Weddell and Lazarev Seas is typically short due to sea-ice conditions. The northward extension of sea ice in the Weddell Sea during January 2013, however, was unusually high and sea-ice melt was slow (Vizcarra 2013). This could have caused a spatially less synchronized maturation rate of the krill and thus a higher variation in timing of krill mating, likely leading to an increase in the number of spawning episodes (Spiridonov 1995). It is therefore also a possibility that all the AC0 krill found in our study have originated from within the Weddell Sea and that the different cohorts are a result of a long reproductive season with multiple spawning episodes. More research on the larval origin in the northern Weddell Sea is required.

COMPARISON OF DIFFERENT DEPTH LAYERS

Our results show that the size composition of AC0 krill in in the upper two meters underneath the sea ice was different from the rest of the water column (0–500 m). Although absolute size ranges were similar in both depth layers, the size and stage structure of krill sampled from deeper waters was skewed more towards juvenile krill, while krill sampled from the ice–water interface layer were skewed more towards furcila IV, V and small furcilia VI. A similar pattern was observed west of the Antarctic Peninsula by Frazer et al. (2002), who observed a higher proportion of AC0 juveniles in the 0- to 300-m depth range compared to larval/juvenile krill collected by divers within the under-ice surface layer during late winter.

Differences in sea-ice association, overwintering strategies, and/or vertical migration between larval krill and adult krill have been previously noted (Nast 1979; Daly & Macauley 1991; Quetin et al. 1994; Meyer et al. 2002a; 2010; Flores et al. 2012a). Most studies, however, only compared larvae or juveniles with post-larval krill or adults, or made no distinction between furcilia stages, AC0 juveniles and/or AC1 juveniles. Based on length–frequency distributions, Daly & Macaulay (1991) suggested that *E. superba* in the marginal ice zone make a transition from living in close proximity of the ice–water interface to the epipelagic zone when they reach ~25 mm in length. However, no late-stage furcilia were caught in their study, and hence, no comparison could be made between late-stage furcilia and

AC0 juveniles (Daly & Macaulay 1991). It is therefore possible that this transition already starts earlier.

Results of our study suggest that while first-year juveniles may still inhabit the ice–water interface, they already are in the process of transiting to deeper layers or/and increasing the amplitude of their vertical migration. The large proportion of small furcilia in the 0- to 2-m depth layer was found at both day and night in similar abundances. Regarding the 0- to 500-m stratum, we note from the outset that there were only 2 daytime RMT tows. Differences in size structure between day and night, and between nets, were therefore in all likelihood influenced by differences in horizontal distribution and the small sample size. Keeping this caveat in mind, it is apparent that the ≤ 8-mm-size class was completely absent from the day time RMT tows, when the SUIT demonstrated that this population sector was abundant at the sea-ice surface (Supplement 2B, Fig. S2.2). The appearance of the relatively small proportion of ≤ 8 mm krill and of >15 mm krill in the 0–500 m at night agrees well with the SUIT data (and multi-net data from Hunt et al. 2014) which demonstrated a downward nighttime migration of at least a portion of the AC0 krill population into the water column below the sea ice, where they would be caught by the RMT.

Frazer et al. (2002) proposed that behavioural or physiological differences associated with developmental stages may be responsible for the different larval and juvenile proportions observed in the different depth layers. It has been suggested that the downward movement of euphausiids results from passive sinking and that this behaviour is used to save energy (Rudjakov 1970; Youngbluth 1975). Krill is a relatively heavy species that uses a considerable amount of its energy to maintain at a constant depth. It is also documented that krill density and sinking speed increases with size (Kils 1982). As a consequence their energy expenditure to remain at a fixed depth increases exponentially with body weight. Additionally, the ability of larvae to withstand poor food conditions increases with age (Daly 2004) suggesting that krill, as it matures, would benefit from saving energy by sinking during a passive stage, instead of maintaining its position near the under-ice surface. This would also provide growing krill with access to a larger foraging field which is beneficial in the highly patchy environment.

The vertical distribution of krill appears to be a constant trade-off between food availability, energy budget and predation risk (Youngbluth 1975; Quetin et al. 1996; Watkins 2000; Ross et al. 2014). Sub-adult and adult krill show variation in vertical migration behaviour and depth of occurrence, depending on region and season (Mauchline & Fisher 1969; Marr 1962; Pakhomov 1995; Watkins 2000; Flores et al. 2012a; Siegel 2005). In a multi-seasonal study from the Lazarev Sea comparing the surface layer with deeper depth strata, the post-larval *E. superba* distribution patterns are variable and different from that of AC0 krill (Flores et al. 2014). The trade-off of AC1 juveniles and (sub-) adults is likely different from that of larvae and AC0 juveniles due to, e.g., different (vertebrate) predators and/or food requirement (Quetin et al. 1996; Siegel 2005; Flores et al. 2012a).

CONCLUSIONS

The Antarctic krill population sampled in the northern Weddell Sea during winter/early spring consisted mainly of late-stage furcilia and AC0 juveniles belonging to multiple cohorts. The different cohorts may reflect the influx of krill sub-populations from several regions or of a prolonged reproductive season resulting in multiple spawning episodes within a region, with variation in the growth of individuals due to environmental variability. In a variable environment, an increase in the number of spawning episodes in a single season would theoretically increase reproductive success (Ross & Quetin 2000). Our findings suggest that the northern Weddell Sea could possibly be an area where sub-populations with different temporal or spatial origin converge. To more accurately understand these processes, investigating the ice–water interface on a larger scale is necessary.

This study provides evidence for variations in the vertical distribution and sea-ice association between different developmental stages of AC0 krill during winter. The fact that such differences can already be seen within the first year of *E. superba*'s life suggests that this transition is gradual. This change is likely a result of physiological and behavioural development and ecophysiological trade-offs, causing larger individuals to gradually disperse into deeper layers, under the conditions prevailing during the present study. The preference for different habitats by krill at different developmental stages likely plays an important role in the large-scale spatial distribution of krill, as transport processes between water column and ice vary (Thorpe et al. 2007). The association of younger krill with sea ice also indicates that the effect of sea-ice decline on the survival of AC0 krill over winter may vary between krill with different sizes or developmental stages. Differences found in surface waters and deeper layers suggest that, by sampling predominantly deeper layers with conventional pelagic nets, the composition, distribution and abundance of krill populations may not be adequately represented.

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SUPPLEMENT 2A: Additional information on SUIT and RMT sampling and the Antarctic krill (*Euphausia superba*) length distribution in both nets.

Table S2.1: SUIT sampling scheme (0-2 m depth) and environmental conditions during sampling.

Station	Date	Time (UTC)	Latitude South	Longitude West	Trawled distance (m)	Ice cover-age (%)	Snow thickness (m)	Ice thick-ness (m)	Ice rough-ness
551_1	31-08-2013	00:50	61.2258	40.7325	834.15	87.5	0.2 - 0.5	0.300	NA
555_47	09-09-2013	13:52	60.8036	39.1553	1760.86	99.5	0.2 - 0.5	0.475	3.734
557_2	10-09-2013	23:16	59.9706	33.1667	1428.52	94.0	0.075	0.700	0.833
560_2	11-09-2013	21:51	60.6306	31.7897	1289.63	96.0	0.1	0.525	1.030
562_5	12-09-2013	20:46	60.9775	31.2433	945.84	92.5	0.25	0.525	0.969
565_5	16-09-2013	16:53	60.7111	27.1769	928.29	96.5	0.25	0.525	2.297
567_2	28-09-2013	23:11	60.4542	25.7028	558.10	86.5	0.6	0.675	1.148
570_5	29-09-2013	22:19	59.0036	26.0419	1524.35	96.0	0.15	0.425	0.853
571_2	30-09-2013	09:50	58.4225	26.1219	1987.17	84.0	0.05	0.225	0.829
577_2	02-10-2013	12:12	58.4464	26.1031	3177.83	51.5	0.2 - 0.5	0.475	1.207
579_2	02-10-2013	23:36	58.4600	26.0556	2730.73	46.0	NA	0.575	1.504

Table S2.2: RMT sampling scheme.

Station	Date	Time (UTC)	Latitude South	Longitude West	Sampling depth (m)
548_5	29-08-2013	00:35	60.0000	42.4358	500
554_2	01-09-2013	02:29	61.2531	40.9217	500
560_4	12-09-2013	03:16	60.6219	31.8347	500
562_4	12-09-2013	19:17	60.9736	31.2389	200
565_1	16-09-2013	09:38	60.7667	27.1392	500
565_12	17-09-2013	05:32	60.6258	27.1842	500
570_1	29-09-2013	18:36	59.1486	26.2658	600
577_1	02-10-2013	11:21	58.4006	26.1442	500
579_1	02-10-2013	21:44	58.4567	26.0053	600

Table S2.3: Comparison of *Euphausia superba* size and distribution in the 0-2 m surface layer and the 0-500 m layer in ice covered waters.

	0-2 m (SUIT)	0-500 m (RMT)
N	4789	724
Average length (mm) (± sd)	11.06 (5.11)	13.28 (4.23)
Geometric mean length (mm)	10.28	12.74
Modal length (mm)	10	16
Average (N.m^{-2})	0.79	13.87
Geometric mean (N.m^{-2})	0.63	6.18
Average (N.m^{-3})	0.39	0.027
Geometric mean (N.m^{-3})	0.35	0.027

Table S2.4: Comparison of *Euphausia superba* catch and average size per station in the 0-2 m surface layer and the 0-500 m layer in ice covered waters. Positioning of stations on the same row indicate a comparable geographic location.

0-2 m (SUIT)				0-500 m (RMT)			
Station	N	N.m^{-2}	Average length (mm)	Station	N	N.m^{-2}	Average length (mm)
				548_5	394	46.03	15.23
551_1	141	0.34	30.05	554_2	2	0.95	42.5
555_47	333	0.38	15.69				
557_2	643	0.90	13.46				
560_2	142	0.22	12.25	560_4	47	17.84	10.89
562_5	185	0.39	11.34	562_4	0	0	-
565_5	850	1.83	7.19	565_1	2	0.58	11.0
				565_12	73	18.39	7.77
567_2	1004	3.60	8.12				
570_5	227	0.30	10.06	570_1	9	0.92	16.22
571_2	705	0.71	10.30				
577_2	150	0.09	11.57	577_1	124	36.58	11.39
579_2	409	0.30	11.17	579_1	73	9.87	12.0

SUPPLEMENT 2B: Differences between day and night size frequency and abundance of Antarctic krill (*Euphausia superba*) in the 0-2 m and 0-500 m depth layers.

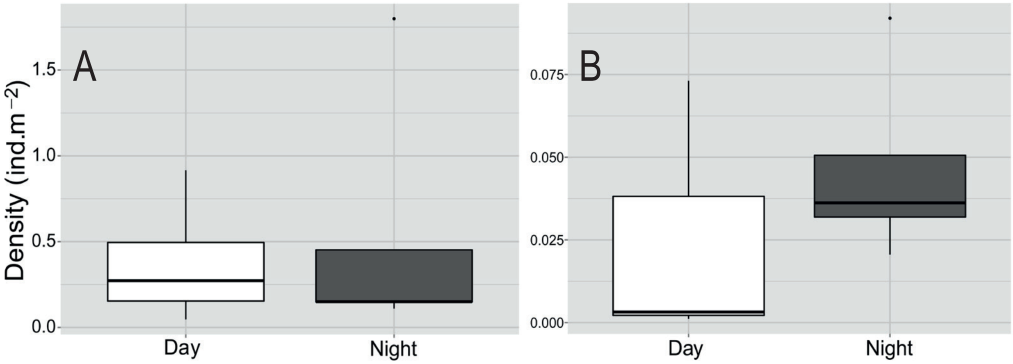

Figure S2.1: Abundances of age class 0 Antarctic krill (*Euphausia superba*) caught during the day (white) and during the night (dark grey) in the 0-2 m (A) and the 0-500 m (B) depth layers. Number of stations (N) are given in parentheses. The horizontal black lines show the median abundance in the stations. The upper and lower limits of the coloured squares indicated the 25th and 75th percentile. The upper and lower limits of the vertical line indicate the minimum and maximum density. Black dots represent the true minimum and maximum densities, but are numerically distant from the other data points and therefore considered outliers.

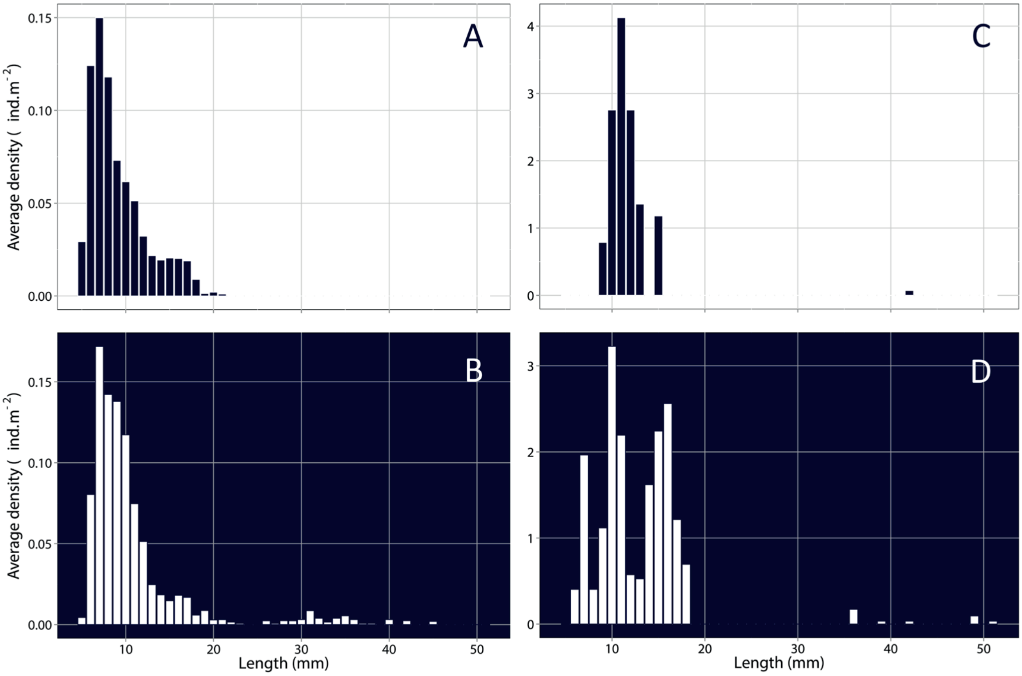

Figure S2.2: Size distribution of Antarctic krill (*Euphausia superba*) caught during the day (white background) and during the night (dark blue background) in the 0-2 m (A & B) and the 0-500 m (C & D) depth layers.

CHAPTER 3

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. The winter survival of age class 0 (AC0) krill is susceptible to changes in the sea-ice environment due to their association with sea ice and their need to feed during their first winter. However, our understanding of their overwintering diet and it's variability is limited. We studied the spatio-temporal variability of the diet in four cohorts of AC0 krill in the Northern Weddell Sea during late winter 2013 using stomach contents, fatty acid (FA) and bulk stable isotope analysis (BSIA). Stomach contents were dominated by diatoms in numbers and occasionally contained large volumes of copepods. Many of the prey species found in the stomachs were sea ice-associated. Our results show that the diet of overwintering AC0 krill varies significantly in space and time. Variability in stomach content composition was related to environmental factors, including chlorophyll *a* concentration, copepod abundance and sea-ice cover. In contrast, FA composition mainly varied between cohorts indicating variation in the long-term diet. The condition of the AC0 krill was reflected in FA and BSIA analysis, suggesting that the availability of sea-ice derived food sources over a long period may impact the condition of developing AC0 krill significantly. The spatio-temporal availability of sea-ice resources is a potentially important factor for AC0 krill winter survival.

INTRODUCTION

Due to the pronounced seasonality in the Polar regions, polar species need to adapt to drastic changes in primary production (Falk-Petersen et al. 1999; Hagen & Auel 2001). In the Southern Ocean, light limitation and water column mixing due to surface water cooling result in a long period of near-zero primary production during wintertime (Arrigo et al. 2008). During the winter months, biota living in sea ice and at its underside can provide an important energy source (Eicken 1992; Quetin & Ross 2003; Flores et al. 2011; 2012a). 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 & Ross 1991; Lizotte 2001). In late summer there is another peak in the water column primary production after which it starts to decrease towards winter (Quetin & Ross 1991; Lizotte 2001).

Adult Antarctic krill (*Euphausia superba*) release eggs from mid-December to April (Ross & Quetin 1986). The duration of the spawning season of krill and the number of spawning episodes that occur can be variable (Ross & 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 & Ross 1991).

Adult *E. superba* overwinter by reducing metabolic activity in combination with opportunistic feeding and utilization of body lipids or body shrinkage (Ikeda & 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; Flores et al. 2012b). Krill larvae are assumed to rely on sea-ice resources (Daly 1990; Meyer et al. 2002a; Meyer 2012), but in addition show flexible overwintering behaviour such as a delay of development, an increase of the inter-moult period, growth reduction and moderate lipid storage (Daly 2004; Hagen et al. 2001).

Krill larvae often reside directly underneath the sea ice in winter (Chapter 2; Frazer et al. 2002; Meyer et al. 2009; Flores et al. 2012a; David et al. 2017). Using a Surface and Under-Ice Trawl (SUIT; van Franeker et al. 2009), a large-scale investigation of the krill population structure directly underneath the sea ice in the northern Weddell Sea during winter/early spring of 2013 was conducted (Fig. 3.1; Chapter 2). The population mostly comprised larvae (furcilia) and juveniles experiencing their first winter, subsequently referred to as age-class 0 (AC0) krill. The AC0 krill population consisted of several spatially separated cohorts, differing in size and developmental stage composition. 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 (Chapter 2; Quetin & Ross 2003; Schwegmann 2012). Furthermore, the metazoan community structure in the ice-water interface layer in the northern Weddell Sea showed a distinct spatial structure, consisting of three distinct community types which could be attributed to spatially and seasonally varying environmental conditions (David et al. 2017). These observations indicated that the environmental regime in the northern Weddell Sea was influenced by various interacting drivers, such as ocean currents, phytoplankton and ice algae concentrations and sea-ice drift, creating a heterogeneous pattern of food availability and food composition for overwintering krill. This is important, because growth and development of overwintering larval krill are strongly influenced by food supply and food type (Daly 1990; Ross et al. 1988; Ross & Quetin 1989).

Investigating the diet of AC0 krill can give insight in the survival through their first winter (Virtue et al. 2016). Due to the difficulty of sampling during winter, only a limited number of studies describe the stomach contents of larval krill during this season (Daly 1990; Ju & Harvey 2004; Meyer et al. 2009; O'Brien et al. 2011). Due to the small spatial coverage of these studies, determinants and variability of diet composition remain unclear. The analysis of stomach contents 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. Hence, these essential FAs produced by primary producers are not metabolically modified and can be used as trophic markers to trace back dietary carbon sources (Lee et al. 1971; Graeve et al. 1994a; Virtue 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 18:4n-3 and 22:6n-3 (Graeve et al. 1994a; Dalsgaard et al. 2003 and references therein). Sea-ice algae communities often contain high proportions of diatoms compared to the underlying water column (Garrison 1991; Lizotte et al. 2001). Conversely, dinoflagellates are typically more abundant in the water column, compared to sea-ice communities (Garrison 1991; Lizotte et al. 2001). The fatty acid composition of krill can therefore give some qualitative insight in the origin of carbon in dietary sources.

The aim of this study was to evaluate temporal and spatial differences in diet of AC0 krill in late winter/early spring. Microscopic stomach content analysis and FA analysis were combined to gain insight into the diet and carbon sources of *E. superba* during their first winter. Additional information was integrated such as carbon/nitrogen content (C/N mass ratio), as indicators of the krill's lipid storage and body condition. Furthermore, the isotopic fractionation of carbon ($\delta^{13}C$:$^{13}C/^{12}C$) was measured to assess the potential contribution of ice algae-derived carbon to the diet of overwintering krill. This is possible, because the $\delta^{13}C$ values of sea-ice derived carbon are often higher compared to pelagic produced carbon (Fry & Sherr 1984; Hecky & Hesslein 1995; Jia et al. 2016; Kohlbach et al. 2016). The isotopic composition of nitrogen ($\delta^{15}N$: $^{15}N/^{14}N$) was used as an indicator of trophic position (DeNiro & Epstein 1981; Minagawa & Wada 1984).

We used this comprehensive methodical approach for a detailed analysis of the spatial variability of the trophic ecology of overwintering krill across a geographically large research area in the northern Weddell Sea, aiming to:

(1) assess the importance of sea ice-associated carbon sources in the diet of overwintering krill;

(2) investigate the association of the diet composition with spatio-temporal patterns in the environmental properties of the research area;

(3) analyse correlations between the size and stage composition of different krill cohorts and recent and long-term dietary sources.

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 (Fig. 3.1). The upper two meters of the water column directly underneath the sea ice was sampled using a Surface and Under-Ice Trawl. 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, and varied between 10m and <1km diameter. Detailed information on sampling and data collection can be found in David et al. (2015) and Chapter 2. 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 (1936) 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 stomach wall. For each analytical sample, up to three stomachs abstracted from krill of comparable size were pooled together. The tube with the stomach contents was emptied into an Utermöhl sedimentation chamber, where 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

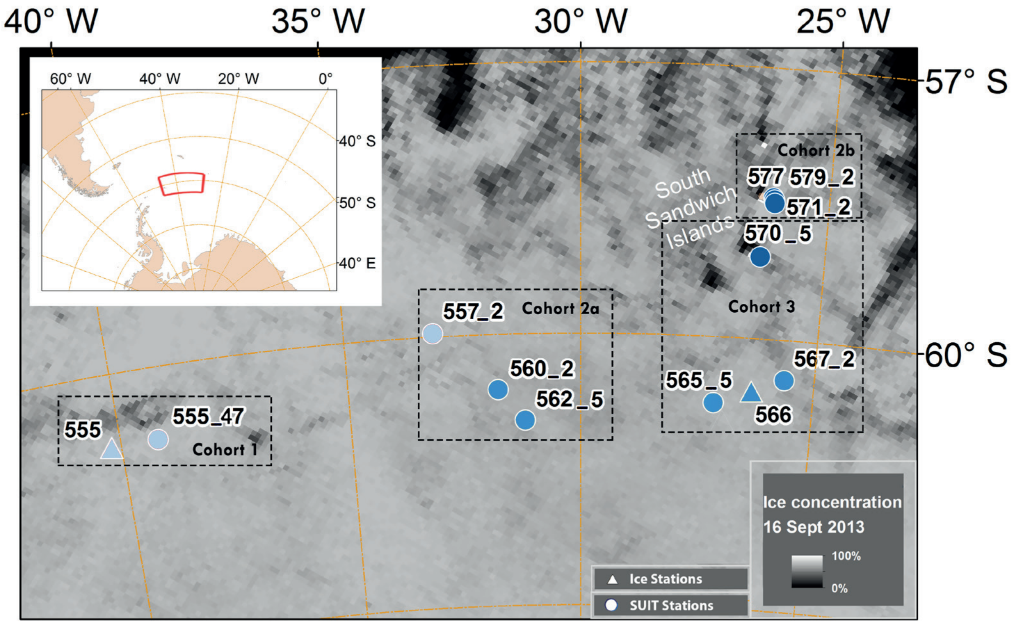

Figure 3.1: Sampling locations of the SUIT, indicated with their station numbers. Sea-ice concentration data were aquired on 16 September 2013. Round = SUIT hauls, triangles = stationary hauls during ice stations. Black dotted lines indicate the spatial pattern of cohorts of age class 0 krill (*Euphausia superba*), as established in Chapter 2. Cohort numbers are indicated within their respective rectangle. Stations are collored according to the spatial pattern in the under-ice zooplankton community as established by David et al. (2017). Light blue = "krill-dominated" community, blue = "copepod-dominated" community, dark blue = "low biomass" community.

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. When copepod remains were found in a sample, the number of copepods was estimated to be one, unless there was evidence that the remains originated from more than one individual, e.g. more than one urosome or genital segment. To estimate total biovolume of copepods in krill stomachs, the number of individuals was multiplied with a volume of 13.4 x 10^6 µm^3 per individual, based on the prosome length from stomach content analysis in Meyer et al. (2009) which was converted into volume according to Mauchline (1998).

FATTY ACID ANALYSIS

Up to ten individuals were pooled into one sample in order to obtain a sufficient sample material for subsequent analyses. The frozen samples 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)

Up to ten individual krill were pooled into one sample in order to obtain sufficient sample material for analyses. Bulk stable isotope (BSI) 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). Samples of particulate organic matter (POM) from surface water and sea-ice were collected to provide a baseline for BSIA. Measurements confirmed that the $\delta^{13}C$ values were significantly higher in sea-ice derived carbon compared to carbon derived from the water column (t-test, $t_{10.9} = 5.2$, $p < 0.01$; Kohlbach et al, 2017). There also was no overlap between the $\delta^{13}C$ values of sea-ice POM and water column phytoplankton POM, confirming that these can be recognized as distinct carbon sources (Kohlbach et al. 2017).

Table 3.1: Sampling dates and parameters used for BioEnv analysis per station, including environmental parameters and abundances of dominant copepods from the ice-water interface layer (0-2 m).

Station	Sampling date (dd-mm-yy)	Sea-ice coverage (%)	Sea-ice thickness (m)	Sea-ice rough-ness	Temper-ature (°C)	Salin-ity	Chl a (mg m-3)	*Calanus propin-quus* (ind.m^{-3})	*Cteno-calanus* 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

DATA ANALYSIS

The AC0 krill population 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 (Chapter 2; Table S3.1, Supplement 3). 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. 3.1). In spite of the overlap in developmental stages between cohorts, the average length of the developmental stages differed between cohorts. For example, FVI from cohort 1 and 2 were significantly larger than FVI from cohort 3 (Chapter 2). Average lengths and proportions of developmental stages per cohort can be found in Chapter 2 and Table S3.1 of the supplement. 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 (Fig. 3.1, Table 3.1). 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 contents, and bulk stable isotope composition.

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; Fig. 3.1). The first community type ('krill dominated'; stations 555_47 to 557_2) was dominated by krill in terms of proportional biomass (> 65%), 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 (> 72 % in terms of abundance). 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-associated patterns in short- and long-term diet.

To investigate the relationship between the sea-ice environment and 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 & Ainsworth 1993), which evaluates the subset of environmental variables that has the highest correlation with the stomach contents. The BioEnv analysis relates two distance matrices, the environmental data based on Euclidean distance and the stomach content data on Bray-Curtis dissimilarity (Clarke & Warwick 2001). Environmental variables used are listed in Table 3.1. 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 contents, expressed as abundance as well as volume, were 4th root transformed to increase importance of food items that generally occur in low abundances (Clarke & Warwick 2001). After data assessment using a draftsman plot, sea-ice thickness and sea-ice concentration were square-transformed, and all other environmental data except temperature were log-transformed. After data transformation, the environmental data were 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 & 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.

To test whether numerical stomach content composition differed between cohort groups or under-ice 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 abundances (Warton et al. 2012). Differences were assessed using 999 bootstrapping iterations. Untransformed abundance data were used, and a negative binomial distribution of data was assumed (Wang et al. 2012; Warton et al. 2012). Assumptions were checked by plotting the residuals versus the fits (Wang et al. 2012).

The variability in fatty acid compositions was 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 & Warwick 2001). Only a single AC0 krill was sampled for FA analysis from cohort 1. Therefore this cohort is shown in the PCA analysis results but was further excluded from all FA data analyses. Differences in FA composition between cohorts and community types were tested with a distance-based Analysis of Similarity (ANOSIM), using 4th root-transformed data and a Euclidean distance matrix

(Clarke & Warwick 2001).

Differences in individual marker FAs, C/N ratios and BSI compositions between cohort groups and community types were investigated using one-way ANOVA, followed by a non-parametric Tukey's HSD post hoc test. Statistical significance was set at $\alpha = 0.05$. All analyses were performed using R version 3.3.1, with packages vegan, ade4, ggplot2 and mvabund (R Core Team 2015). Details on the properties of krill used for the different analyses can be found in Tables S3.2 and S3.3 of Supplement 3.

RESULTS

STOMACH CONTENT ANALYSIS

The diet of AC0 krill was dominated, on average, by centric (35%) and pennate (56%) diatoms in abundance, and centric diatoms (58%) and copepods (26%) in estimated volume (Fig. 3.2). Not all species could be identified to species level. The relative abundance of pennate diatoms in the stomachs was considerably higher in the northernmost stations compared to all other stations (Fig. 3.2; Table 3.2). The pennate diatoms were dominated by species of the genus *Fragilariopsis*. Identifiable species were *Fragilariopsis 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 *Rhizosolenia* sp. were encountered occasionally. *Actinocyclus actinochilus* often represented a large part of the total reconstructed number of centric diatoms (over 50% in stations 555_47 - 560_2, and over 30 % in stations 570_5 - 579_2).

The only copepod appendages that could be identified belonged to *Stephos longipes*. Other prey items regularly found in the stomachs were the foraminifer *Neogloboquadrina pachyderma*, the tintinnids *Laackmanniella naviculaefera, Cymatocylis convallaria, Cymatocylis vanhoeffeni* and *Codonellopsis glacials*, and dinoflagellate cysts. Dinoflagellates were found in small numbers, some identifiable as *Protoperidinium* spp. and *Dinophysis* spp. Krill setae and radiolarians were found sporadically.

There were no significant differences in stomach contents between cohorts (GLM, LR = 32.83, $p > 0.05$). Differences in stomach contents were found to be partially related to under-ice community types and depending on environmental factor levels. 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 northern sea-ice edge versus krill from the copepod-dominated community in 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 contents of krill in terms of volume (Fig. 3.2; Table 3.2).

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

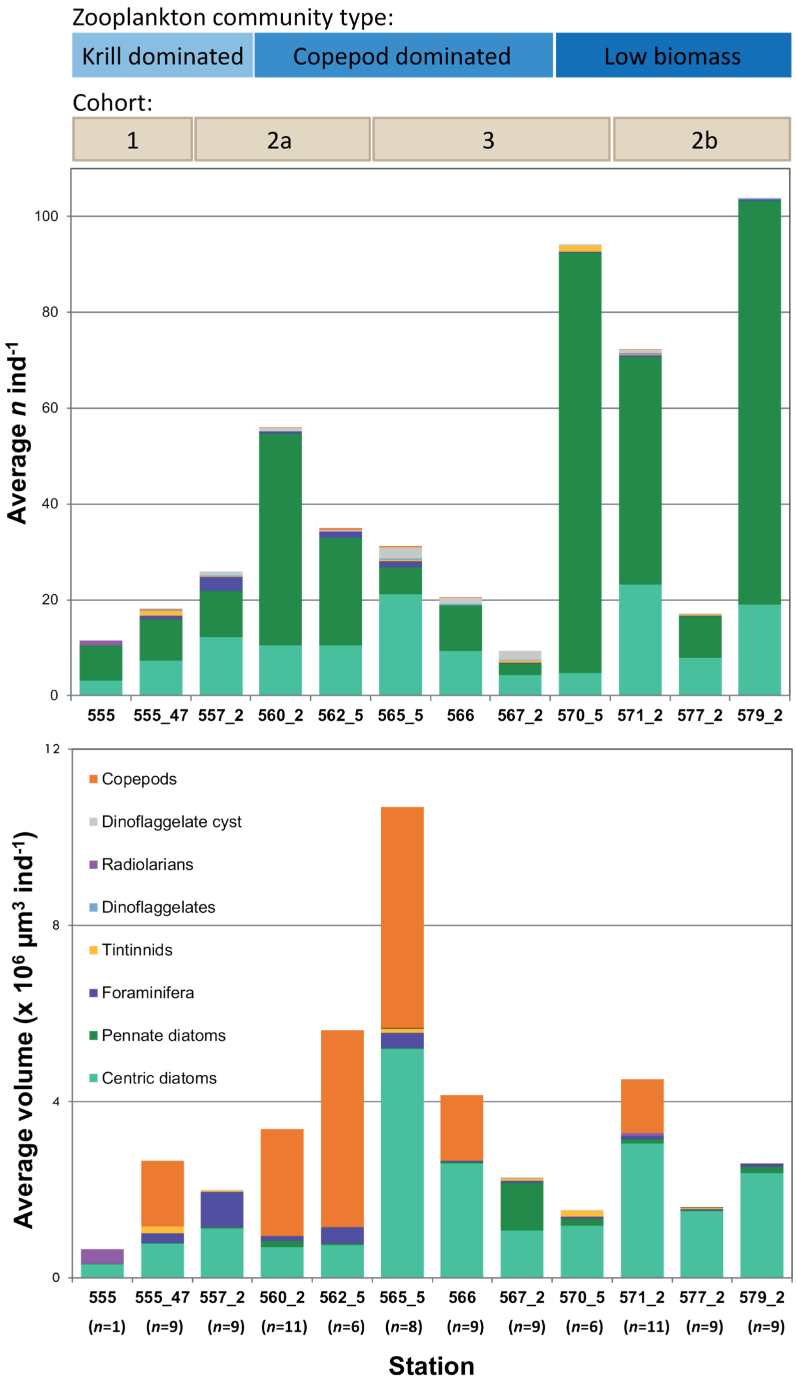

Figure 3.2: Average stomach contents of age class 0 krill (*Euphausia superba*) per station, shown in numbers per individual krill (A) and estimated volume of food items per individual krill (B). The bars above the graphs show how the sampled stations were grouped in under-ice surface zooplankton community type or age class 0 krill cohorts, according to David et al. (2017) and Chapter 2, respectively. *n* represents the number of individuals analysed.

the under-ice surface abundance of *S. longipes* and under-ice surface chlorophyll *a* concentration ($r = 0.58$; Mantel test $p = 0.006$).

FATTY ACID ANALYSIS

Using ANOSIM, a significant difference between FA profiles was found when the AC0 krill were grouped according to cohorts ($R = 0.42$, $p = 0.001$), but none when they were grouped according to community types. This was confirmed by the PCA analysis (Fig. 3.3). The first three principal components (PC) 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, 16:4n-1, 20:4n-6, 20:5n-3 and 18:1n-7 contributed most to the variability in the data. The FA composition per cohort is given in table S3.4 (Supplement 3).

Following the results of the previous analysis, four biomarker FAs were compared between cohorts (Fig.

Table 3.2: Average stomach content composition of AC0 krill (*Euphausia superba*) per under-ice zooplankton community type as established by David et al. (2017). K = krill dominated community, C = copepod dominated community, L = low biomass community. *n* = number of individuals analysed, + represents a volume < 0.01 x 10^6 µm^3 ind^{-1}.

Community type	K (*n*=19)	C (*n*=43)	L (n=35)	Total (*n*=97)
Average number (ind^{-1})				
Centric diatoms	9.45	10.97	15.02	12.14
Pennate diatoms	9.04	17.98	53.88	29.18
Foraminifera	1.74	0.58	0.2	0.67
Tintinnids	0.53	0.14	0.31	0.28
Dinoflagellates	0.16	0.12	0.2	0.15
Radiolarians	0.05	0	0.06	0.03
Dinoflagellate cysts	0.42	1.33	0.29	0.77
Unidentified round body < 20 µm	6.53	4.28	2.71	4.15
Copepods	0.05	1.05	0.34	0.6
Krill setae	1.15	0.67	1.26	0.98
Average volume (x 10^6 µm^3 ind^{-1})				
Centric diatoms	2.91	3.38	4.63	3.74
Pennate diatoms	0.02	0.04	0.11	0.06
Foraminifera	0.49	0.16	0.06	0.19
Tintinnids	0.11	0.03	0	0.06
Dinoflagellates	+	+	+	+
Radiolarians	0.02	0	0.02	0.01
Dinoflagellate cysts	+	+	+	+
Unidentified round body < 20 µm	+	+	+	+
Copepods	0.71	2.49	0.38	1.38
Total volume (excluding krill setae)	5.01	8.78	5.68	6.92

3.4). In cohort 3, the relative contribution of the diatom-associated marker FA 16:1n-7 was significantly lower compared to cohort group 2a (ANOVA, $F_{2, 18} = 5.18$, $p = 0.02$; Tukey's HSD, $p = 0.01$), and the diatom-associated marker FA 20:5n-3 was significantly lower compared to cohort group 2b (ANOVA, $F_{2, 18} = 5.19$, $p = 0.02$; Tukey's HSD, $p = 0.01$). Conversely, the dinoflagellate-associated marker FA 22:6n-3 was significantly higher in cohort 3 compared to the other cohorts (ANOVA, $F_{2, 18} = 41.57$, $p < 0.0001$, Tukey's HSD, $p < 0.0001$). The dinoflagellate-associated marker FA 18:4n-3 was significantly higher in cohort group 2b compared to cohorts 2a and 3 (ANOVA $F_{2, 18} = 32.28$, $p < 0.0001$, Tukey's HSD, $p < 0.0001$).

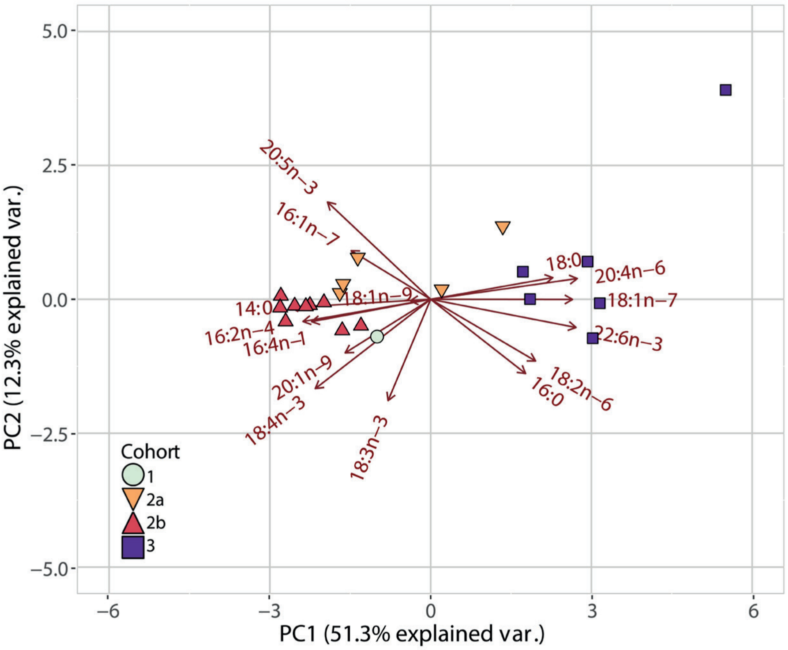

Figure 3.3: Results of a principle component analysis (PCA) using fatty acid profiles of different cohorts of age class 0 krill (*Euphausia superba*), showing the first and second principal components. Every point represents a replicate sample.

BODY CONDITION

The C/N ratios of AC0 krill ranged between 3.38 and 4.10 (Table 3.3). There was a significant difference between the C/N ratio of the krill from the 'copepod dominated' community type versus krill from the other community types (ANOVA, $F_{2, 24} = 10.81$, $p < 0.0001$; Tukey HSD, $p < 0.004$). However, testing for differences between cohort groups within community types indicated that these differences could be 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 group 1 to cohort group 3. The C/N ratio of cohort group 2b was significantly higher than that of cohort group 2a (Tukey HSD, $p = 0.005$). A similar pattern was found in the total FA content of the AC0 krill (Table 3.3). There were, however, no significant differences in total FA content between cohort groups.

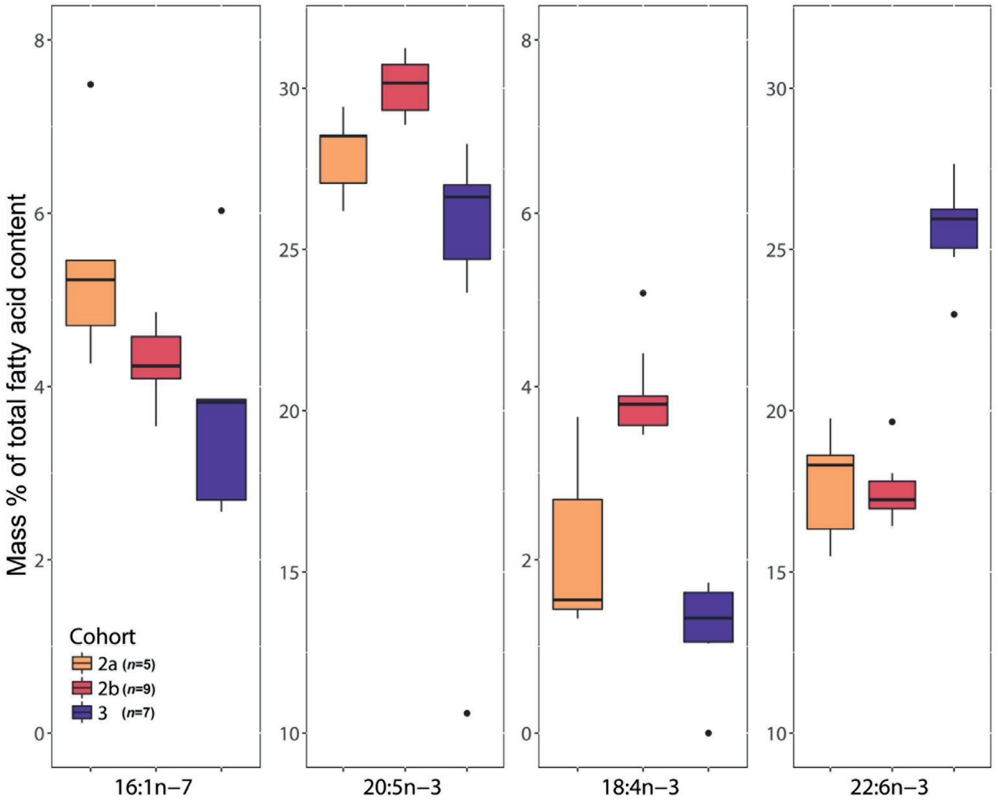

Figure 3.4: Proportion of biomarker fatty acids (mass % of total FA) of age class 0 krill (*Euphausia superba*). Cohorts are defined as in Figure 3.1. Fatty acids 16:1n-7 and 20:5n-3 are regarded as diatoms-associated markers, 18:4n-3 and 22:6n-3 are regarded as dinoflagellate-associated markers. The 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 percentile. The upper and lower limits of the vertical line indicate the minimum and maximum FA porportions in a cohort excluding the outliers (represented by dots), which are numbers that are 1.5 times less or greater than the lower or upper percentiles respectively.

BULK STABLE ISOTOPE COMPOSITION

The δ^{15}N value of AC0 krill differed significantly between both community types and cohorts (ANOVA, $F_{2,27} = 16.86$, $p < 0.001$ and $F_{3,26} = 29.47$, $p < 0.001$, resp.). 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 cohort groups (Fig. 3.5; 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 significantly higher than in cohort 2a (3.24‰; Fig. 3.5; Tukey HSD, $p < 0.02$). The δ^{13}C values of cohort 3 (average -26.8‰) were significantly lower than all values of cohort groups 1, 2a and 2b (average -25.1‰, -24.5‰, -24.5‰, respectively; ANOVA, $F_{3,26} = 17.92$, $p < 0.001$, Tukey HSD, $p < 0.003$). The δ^{13}C values did not show significant differences when the krill were grouped according to community type.

Table 3.3: Average 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)

DISCUSSION

STOMACH CONTENTS AND FATTY ACIDS OF AC0 KRILL IN WINTER/EARLY SPRING

The stomach contents of AC0 krill showed a variable diet in terms of taxonomic composition. In general, the diet of larvae were numerically dominated by diatoms, in particular the pennate species *Fragilariopsis* spp., and had a heterotrophic component consisting of foraminifera, tintinnids, dinoflagellates, dinoflagellate cysts, and copepod appendages. This is consistent with findings of winter studies conducted in the Weddell-Scotia Confluence (Daly 1990) and in the Lazarev Sea (Meyer et al. 2009; Schmidt et al. 2014), although the scale of our study enables us to show that the degree of utilization of these food sources vary within a region and correlates with environmental factors.

The importance of heterotrophic taxa in the diet may be under-estimated by stomach content analysis,

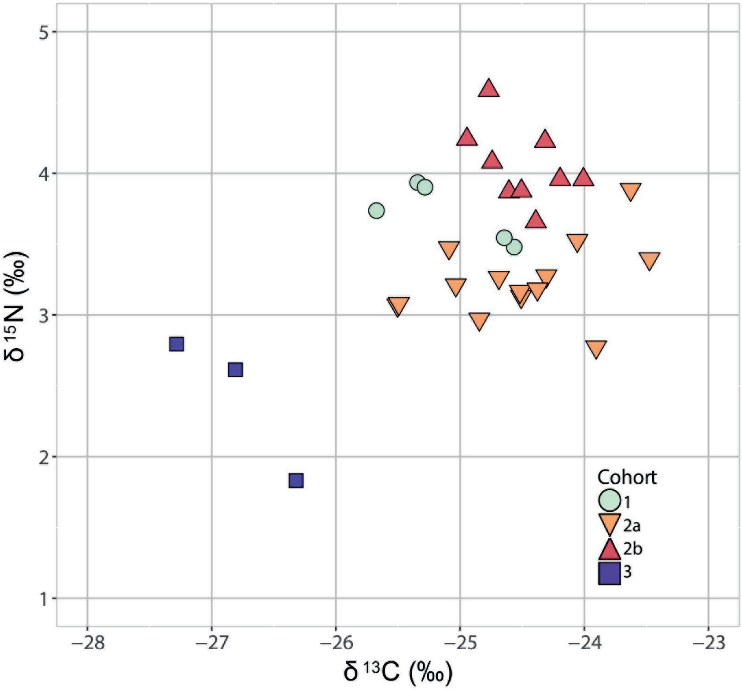

Figure 3.5: Bulk stable isotope values of age class 0 krill (*Euphausia superba*) per cohort. Cohorts are defined as in Figure 3.1. Every point represents a replicate sample.

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 & Harvey 2004), but no further analysis was done on unidentifiable stomach items during this study. The lack of copepod mandibles in the AC0 krill stomachs could be an indication that the copepod appendages found originated from moults The reconstructed volume of the copepods in the stomachs could therefore represent an over-estimate, although feeding on copepods during winter is common (Meyer et al. 2009; Többe et al. 2010). Moults were, furthermore, sparse in the SUIT samples compared to live copepods (David et al. 2017), indicating a low encounter probability in the under-ice layer. This is probably due the fact that moults tend to sink quickly and therefore only stay in the under-ice habitat for a very short time (Frangoulis et al. 2005).

In general, 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 (O'Brien et al 2011, Virtue et al. 2016) and the Lazarev Sea (Hagen et al. 2001) in winter/early spring, and the western Antarctic Peninsula in winter (Ju & Harvey 2004). FAs are typically components of different classes of lipids. The marker FAs 20:5n-3 and 22:6n-3 are mainly incorporated into phospholipids (Hagen et al. 2001). The phospholipid phosphatidylcholine (PC) was the most dominant lipid class found in the AC0 krill from our study (Kohlbach et al. 2017), explaining the high proportions of these FAs. While phospholipids usually represent biomembrane components, PC also serves as a storage lipid for *Euphausia superba* (Hagen et al. 1996). The marker FAs 16:1n-7 and 18:4n-3 are mainly incorporated into other storage lipids (Stübing et al. 2003).

SEA-ICE ASSOCIATION OF PREY

Many of the identified species in the krill stomachs of our study were sea-ice associated species. *Actinocyclus actinochilus* has been found in higher abundances within sea ice compared to the underlying water column (Armand et al. 2005). *Fragilariopsis* spp. such as *F. curta* and *F. cylindrus* often dominate the sea-ice algal assemblage (Nöthig et al. 1991; Garrison & 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 & Buck 1989). The copepod *Stephos 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). Abundances of juvenile and adult *S. longipes* were highest in the sea ice during winter/early spring (Schnack-Schiel et al. 1995; Mauchline 1998).

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. This was confirmed by the δ^{13}C values, which suggested that the AC0 krill had continuous access to sea-ice associated food sources (Kohlbach et al. 2017).

RELATIONSHIP BETWEEN DIET AND ENVIRONMENT

The stomach contents, reflecting the recent diet, were related to environmental factors, such as under-ice surface chlorophyll *a* concentration and the abundance of copepods present, sea-ice concentration, and under-ice surface water salinity. The results on the proportions of carbon, nitrogen, BSI 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). FA and BSI thus reflect the diet over a longer term which explains why their variability could not be attributed to environmental factors measured during sampling.

Stomach contents of AC0 krill in the central part of the study area contained considerable volumes of copepods. At these stations, the highest abundances of copepods were found in the ice-water interface layer, dominated by *S. longipes* and *Ctenocalanus* spp. (David et al. 2017). The central part of the study area was further characterized by a high biomass zooplankton community in the ice-water interface, consisting 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, despite their abundance in the water column (David et al. 2017). This could be due the extreme dominance of *Ctenocalanus* spp. at this station (Table 3.1), which are not a food source of larval krill (Töbe et al. 2010).

The under-ice zooplankton community structure at the four northernmost stations was characterised by low abundances and biomass of species compared to the rest of the sampling area (David et al. 2017). These stations were further characterised by relatively higher under-ice surface chlorophyll *a* concentrations and limited ice floe size (David et al. 2017). This suggests that the sea ice had started to melt. 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 (Ackley et al. 1979), and/or a phytoplankton bloom started (Quetin & Ross 1991; Bianchi et al. 1992). 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).

Our 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 other effects, such as the increase in chlorophyll *a* concentration in the water column due to sea-ice melt.

RELATIONSHIP BETWEEN DIET AND SIZE/DEVELOPMENTAL STAGE

The FA composition of furcilia has been shown to be markedly influenced by their food composition (Stübing et al. 2003). FA and lipid signatures may reflect different food 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). It must be considered that the relative fatty acid composition can depend on total lipid content (Stübing et al. 2003). The total 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. Nevertheless, the AC0 krill in this study showed distinct FA profiles, BSI values and C/N ratios, indicating that the dietary history of the various cohort groups was different and are related to differences in size and development. The lack of relationship between stomach contents and cohort groups suggests that there was no size restriction in the utilization of various prey.

The time scales for incorporation of carbon, nitrogen and of different FAs into tissues as well as their turnover rates are often not well defined (Dalsgaard et al. 2003). However, for e.g. FAs it is assumed that FAs incorporated in storage lipids reflect a more recent carbon source compositions compared to FAs incorporated in membrane components such as phospholipids (Stübing et al. 2003). Therefore, the differences found between cohort groups during this study using a variety of analyses, suggest that the availability and/or utilization of food sources changed over time.

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 groups 2a and 2b showed some differences in several analyses. This suggests that they encountered distinct environmental conditions during advection from their spawning area or areas (Chapter 2). The krill from cohort group 2b had a higher C/N ratio than the krill from cohort group 2a, suggesting that they were in better condition, likely due to ice edge feeding, as would be expected at the beginning of a spring bloom of ice algae and phytoplankton.

The relatively high proportion of the dinoflagellate-associated marker FA 18:4n-3 in cohort 2b suggests a relative increase in feeding on dinoflagellates at the end of the sampling season. A similar enhanced feeding on dinoflagellates during the winter/spring transition was also found in East Antarctica, based on FA analysis (Virtue et al 2016). While the aforementioned study suggests that diatoms were not a major food source during this time of year (Virtue et al. 2016), our cohort 2b had a relatively high proportion of the diatom-associated marker FA 16:1n-7 and on average the highest number of diatoms in their stomachs. The proportion of FA 16:1n-7 was also similar to that of AC0 krill from cohort 2a, caught earlier in the season. Possible explanations for contradictions between FA and stomach content analyses of cohort 2b are increased feeding on athecate (naked), easily digested dinoflagellates, and/or that the increased feeding on diatoms had occurred only recently.

Cohort 3 had relatively low proportions of the diatom-associated marker FAs 16:1n-7 and 20:5n-3, indicating that diatoms had a consistently lower contribution to the diet of this cohort compared to the other cohorts (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).

The relatively low proportion of the dinoflagellate-associated marker FA 18:4n-3 in cohort 3 either indicates that dinoflagellates were less important in the more recent period before the sampling, or that the krill from cohort 3 have recently been starving. This FA metabolizes rapidly, and is found to decrease when not replaced by new dietary input (Stübing et al. 2003). The relatively high amount of the dinoflagellate-associated marker FA 22:6n-3 in the krill of cohort 3 could be a result of their relative high proportion of the phospholipid PC compared to other cohorts (Kohlbach et al. 2017). However, FA 20:5n-3, also usually incorporated in PC, was lowest in the krill of cohort 3, strongly indicating that AC0 krill from cohort 3 had fed more extensively on dinoflagellates in the more distant past compared to the other cohort groups. 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 suggests that feeding in the more distant past occurred to a larger extent on pelagic resources, which are scarce during winter. The relatively low $\delta^{15}N$ value suggests that AC0 krill from cohort 3 were feeding predominantly herbivorous in the past, while the other cohorts were feeding more omnivorously. This was based on the mostly low $\delta^{15}N$ values in sea-ice and pelagic POM (Kohlbach et al. under review). Results show that compensating a lack of sea-ice resources with heterotrophic pelagic food sources, as seemed to be the case during one year in East Antarctica (Jia et al. 2016), is not a general pattern in the Southern Ocean during winter. The combined results, including the relatively small size and lower C/N ratio of cohort 3, strongly suggest advection through regions with poor food availability, probably related to regional properties of the sea-ice habitat as supported by different $\delta^{13}C$ values.

CONCLUSION

During winter in the northern Weddell Sea, sea-ice associated prey were crucially important in the diet of AC0 *Euphausia superba*. Data mirrored patterns of local food availability, influenced by the sea-ice environment. Differences in size and development of AC0 krill are a result of differences in the earlier food availability.

This study shows that there is considerable temporal and spatial variation in the diet of AC0 krill within a season, and adds insight on how this can relate to the environment and the condition of the krill. Dietary differences found between groups in variable physiological states indicate that the long-term availability of sea-ice resources during advection over winter could have a significant influence on the condition of AC0 krill. The potential of the sea-ice habitat to sustain sufficiently productive sea-ice algae communities may, be an important factor for AC0 krill to survive their first winter. Further investigation of the relationship between diet, environmental factors and food availability can improve our understanding of AC0 krill over-wintering. A better understanding of within-season and annual variations will help to predict the consequences of environmental change.

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SUPPLEMENT 3: Additional information on the sampled population of AC0 Antarctic krill (*Euphausia superba)*, the krill used for various analyses and the fatty acid composition.

Table S3.1: Average length (mm) of different stages of *Euphausia superba* furcilia larvae (F) and age class 0 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 S3.2: Number of individuals (n), developmental stages and average length of AC0 *Euphausia superba* used for stomach content 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 S3.3: Number of measured replicates (n), total number of individuals used, developmental stages, 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 deviations of length and dry weight are given within brackets.

Cohort	n	Total number of individuals	Stages	Average length (mm)	Average DW (mg)
Carbon and nitrogen content					
1	5	5	FVI, Juv	17.98 (2.39)	6.74 (2.96)
2a	11	26	FVI	13.09 (2.56)	3.13 (1.58)
2b	7	20	FVI	11.36 (1.14)	1.69 (0.50)
3	4	16	FV, FVI	8.91 (0.30)	1.29 (1.06)
Fatty acids and total fatty acid content					
2a	5	31	FVI, Juv	12.37 (3.69)	2.94 (2.0)
2b	9	75	FVI, Juv	10.16 (3.57)	1.78 (1.8)
3	7	50	FV, FVI, Juv	10.35 (3.49)	1.80 (1.5)
Bulk stable isotopes					
1	5	5	FVI, Juv	17.98 (2.4)	6.74 (3.0)
2a	14	51	FVI, Juv	13.09 (2.6)	3.13 (1.6)
2b	9	36	FVI, Juv	11.36 (1.1)	2.49 (1.6)
3	3	17	FVI	9.07 (0.03)	2.22 (1.1)

Table S3.4: Average fatty acid composition of age class 0 *Euphausia superba* per cohort, expressed as average % of total fatty acids. The standard deviation is given in brackets. n represents the number of replicates measured.

Fatty acid	**Cohort** 1 (n = 1)	2a (n = 5)	2b (n = 9)	3 (n = 7)
14:0	5.86	4.38 (1.0)	5.08 (0.3)	2.13 (0.2)
i-15:0	0	0	0	0
a-15:0	0	0.04 (0.1)	0	0
15:0	0	0.11 (0.1)	0.06 (0.1)	0
16:0	19.16	17.21 (0.5)	16.54 (0.4)	17.84 (1.9)
16:1(n-7)	6.31	5.43 (1.1)	4.28 (0.4)	3.64 (1.1)
16:1(n-5)	0	0.08 (0.1)	0.17 (0.3)	0.06 (0.1)
16:2(n-4)	2.82	1.71 (1.1)	1.42 (0.4)	0.19 (0.3)
16:3(n-4)	0	0.16 (0.2)	0.29 (0.6)	0
16:4(n-1)	0.80	0.97 (0.6)	1.61 (0.6)	0.13 (0.3)
18:0	1.4	1.08 (0.1)	1.08 (0.3)	1.81 (0.5)
18:1(n-9)	8.42	6.46 (1.5)	5.83 (0.7)	6.78 (3.4)
18:1(n-7)	6.44	7.00 (0.6)	5.64 (0.1)	7.86 (0.8)
18:1(n-5)	0	0.06 (0.1)	0.02 (0.1)	1.17 (2.7)
18:2(n-6)	2.30	2.25 (0.1)	2.10 (0.2)	2.50 (0.4)
18:3(n-6)	0	0.166 (0.2)	0.35 (0.2)	0
18:3(n-3)	0.82	0.39 (0.3)	0.93 (0.1)	0.71 (0.3)
18:4(n-3)	2.10	2.13 (0.9)	3.91 (0.5)	1.20 (0.6)
20:0	0	0	0	0
20:1(n-9)	0.60	1.06 (0.2)	1.23 (0.5)	0.61 (0.4)
20:1(n-7)	0	0.10 (0.1)	0	0
20:2(n-6)	0	0.10 (0.1)	0.04 (0.1)	0
20:3(n-6)	0	0.10 (0.1)	0	0
20:4(n-6)	1.02	1.31 (0.3)	0.80 (0.0)	2.09 (0.2)
20:3(n-3)	0	0.06 (0.1)	0.07 (0.2)	0
20:4(n-3)	0	0.38 (0.3)	0.53 (0.2)	0.16 (0.3)
20:5(n-3)	24.90	27.95 (1.2)	30.02 (0.8)	24.13 (5.7)
22:1(n-11)	0	0.63 (0.7)	0.03 (0.1)	0.05 (0.1)
22:1(n-9)	0	0.38 (0.6)	0.03 (0.1)	0
22:5(n-3)	0	0.60 (0.5)	0.44 (0.2)	0.22 (0.3)
22:6(n-3)	17.04	17.70 (1.6)	17.49 (0.9)	26.72 (3.0)
24:1(n-9)	0	0	0	0

CHAPTER 4

Review: the energetic value of zooplankton and nekton species of the Southern Ocean

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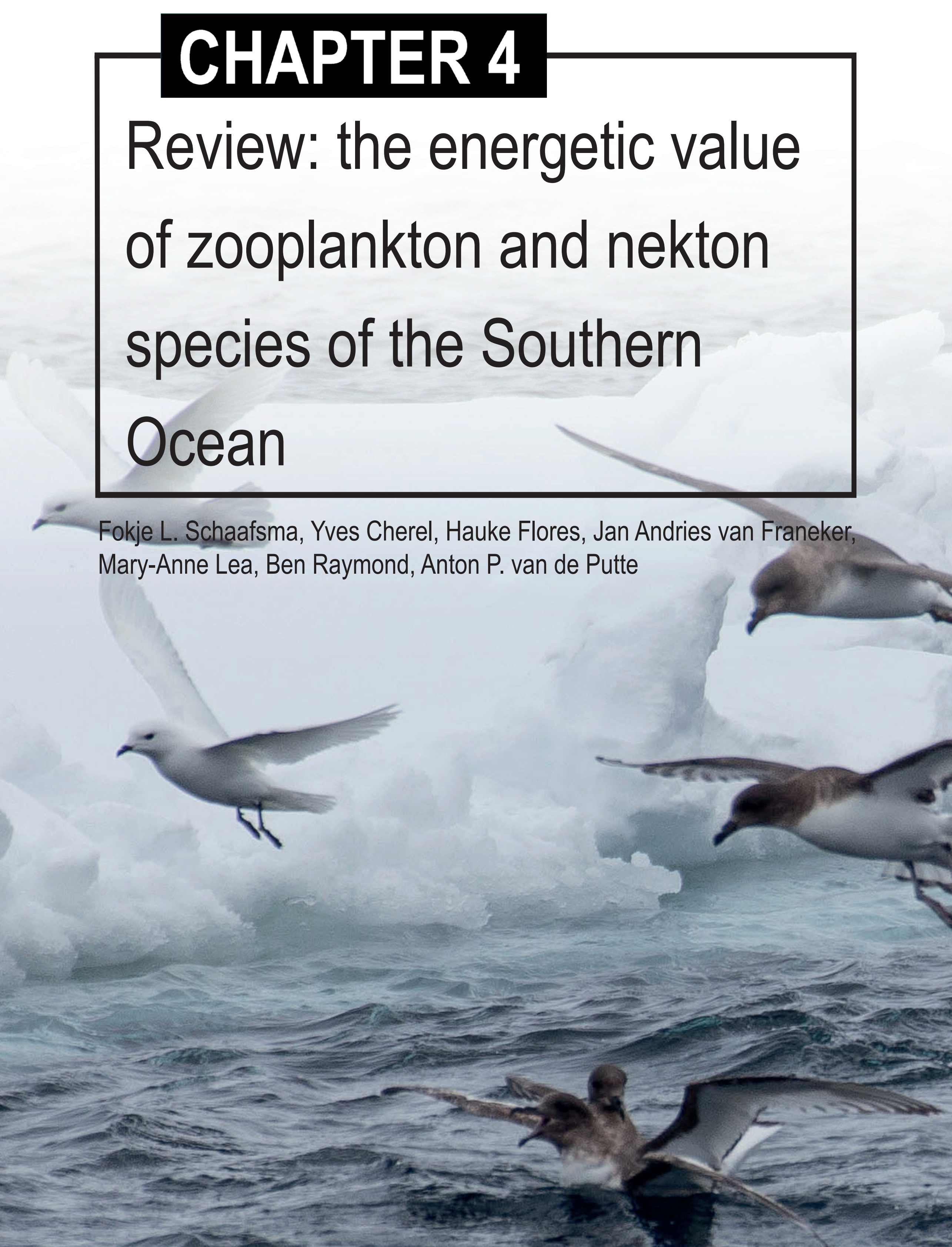

ABSTRACT

Understanding the energy flux through food webs is important for estimating the capacity of marine ecosystems to support stocks of living resources. The energy density of species involved in trophic energy transfer has been measured in a large number of small studies, scattered over a 40 year publication record. Here, we reviewed energy density records of Southern Ocean zooplankton, nekton and several benthic taxa, including previously unpublished data. Comparing measured taxa, energy densities were highest in myctophid fishes (ranging from 17.1 to 39.3 kJ g^{-1} DW), intermediate in crustaceans (7.1 to 25.3 kJ g^{-1} DW), squid (16.2 to 24.0 kJ g^{-1} DW) and other fish families (14.8 to 29.9 kJ g^{-1} DW), and lowest in jelly fish (10.8 to 18.0 kJ g^{-1} DW) , polychaetes (9.2 to 14.2 kJ g^{-1} DW) and chaetognaths (5.0 to 11.7 kJ g^{-1} DW). Data reveals differences in energy density within and between species related to size, age and other life cycle parameters. Important taxa in Antarctic food webs, such as copepods, squid and small euphausiids, remain under-sampled. The variability in energy density of *Electrona antarctica* was likely regional rather than seasonal, although for many species with limited data it remains difficult to disentangle regional and seasonal variability. Models are provided to estimate energy density more quickly using a species' physical parameters. It will become increasingly important to close knowledge gaps in order to improve the ability of bioenergetic and food-web models to predict changes in the capacity of Antarctic ecosystems to support marine life.

INTRODUCTION

The Southern Ocean is home to some of the largest populations of top predator species worldwide such as penguins, flying birds, seals and whales. It comprises the sub-Antarctic and Antarctic regions and is here defined as the water masses south of the Subtropical Front (STF), which separates the surface waters of the Southern Ocean from the warmer and more saline surface waters of subtropical circulations (Orsi et al. 1995; Belkin & Gordon 1996). In order to predict consequences of challenges to top predators, such as from climate change and increased fisheries, and to develop adequate conservation measures, a quantitative understanding of the energy flux in the ecosystem is important. The energy content of species is a key factor in models of energy flux in food webs and in the studies of trophic relationships between species (Van de Putte et al. 2006).

The life cycle and physiology of a species can strongly influence its energetic value. Organisms often have seasonal cycles in lipid content and consequently energy density (Hislop et al. 1991; Tierney et al. 2002). This is generally associated with the annual reproductive and feeding cycles (Hislop et al. 1991). Many species, for instance, acquire energy for reproduction and therefore have a high energy value just before spawning, and a lower one afterwards (Norrbin & Båmstedt 1984; Van de Putte et al. 2006; Fenaughty et al. 2008). Particularly in crustaceans, energy densities can vary between sexes (Färber-Lorda et al. 2009a). Lipid storage is used as buoyancy control in many marine animals, causing differences in energy content between animals with a different vertical distribution (Lawrence 1976). Furthermore, lipid content changes with size and age, greatly influencing energy content (Tierney et al. 2002; Färber-Lorda et al. 2009a; Färber-Lorda & Mayzaud 2010). Energy allocation for different purposes, such as growth or reproduction, most likely occur simultaneously, but one purpose may dominate over others depending on locality and season (Båmstedt 1986).

Within a single species, the energetic value can vary between region or seasons, due to differences in the type or amount of food (Williams and Robins 1979; Tierney et al. 2002; Van de Putte et al. 2006). Temperature and changes in food can, furthermore, influence the energy storage function of prey species (Ruck et al. 2014). Specifically at higher latitudes, the Southern Ocean experiences strong seasonality, with drastic changes in light availability between seasons and massive changes in sea-ice cover in many parts. In winter, the phytoplankton growth in the water column of both ice-covered and open water is greatly reduced (Arrigo et al. 1998; 2008). In ice-covered waters, algae and other fauna within and at the underside of the sea ice may provide the only source of primary production (Chapter 3; Eicken 1992; Quetin & Ross 2003; Arrigo et al. 2008; Flores et al. 2011; 2012a; Meiners et al. 2012). A patchy and seasonally changing food distribution can cause frequent periods of starvation. Therefore, organisms living in harsher environment tend to have higher energy content, as they have adapted to the lower degree of predictability of food availability, and energy content and lipid stores of organisms tend to increase towards higher latitudes (Norrbin & Båmstedt 1984; Falk-Petersen et al. 2000).

The winter food scarcity has resulted in different overwintering strategies used by zooplankton and nekton living in the Southern Ocean such as relying on lipids reserves, reducing metabolic activity, dormancy, feeding on sea-ice resources, opportunistic feeding, combustion of tissue, or a combination of these (Chapter 3; Torres et al. 1994; Schnack-Schiel et al. 1998; Meyer et al. 2009; Kohlbach et al. 2017). Species need to make optimal use of periods of high production, for instance to "fatten up" for winter and/or to gain enough energy for reproduction. Timing of reproduction can be important to ensure winter survival of young stages. Many species, therefore, have a specific strategy to make optimal use of spring phytoplankton blooms, which in ice covered waters is initiated by sea ice melt, or the peak summer phytoplankton production during their life cycle (Quetin & Ross 1991; Lizotte 2001).

The overwintering strategy utilized by zooplankton and nekton influences its seasonal physiology and consequently, energetic density. Species relying on reserves in winter often have a low energetic value by the end of this season (Torres et al. 1994). Organisms that have accumulated lipids for a time of low phytoplankton availability have a relatively high lipid content and high energetic values. Therefore, higher energetic values are often found in herbivores in certain seasons (Donnelly et al. 1994). Species can also have a 'business as usual' overwintering strategy, encompassing opportunistic feeding combined with some combustion of tissue (Torres et al. 1994). This strategy is, for instance, adopted by deeper living zooplanktivorous species which do not necessarily experience a food decline during the winter months, as they have access to e.g. calanoid copepods that sink out of the euphotic zone to overwinter in diapause (Bathmann et al 1993; Torres et al. 1994; Kruse et al. 2010). Many larger crustaceans adopt a mixed strategy comprising a combination of opportunistic feeding, combustion of body mass, a lowered metabolic rate and, occasionally, negative growth (Ikeda & Dixon 1982; Quetin & Ross 1991; Torres et al. 1994). In general, the food supply is more variable for pelagic species as opposed to benthic species, as seasonal changes are less pronounced in deeper waters. Pelagic species often have a higher and more variable energy density compared to benthic species. This is attributed to the generally more variable food supply for pelagic species as opposed to benthic species, as seasonal changes are less pronounced in deeper waters (Norrbin & Båmstedt 1984).

Predation, seasonality, and subsequent life cycle strategy, has influenced the behaviour and distribution of zooplankton and nekton species. This has consequences for the availability of zooplankton and nekton as a food source for predators, for example, prey species have different depth distribution between seasons (Ainley et al. 1991; Ainley et al. 2006; Greely et al. 1999; Flores et al. 2014), prey species shift their horizontal distribution depending on growth and retreat of sea ice (Van Franeker 1992; Van Franeker et al. 1997; Flores et al. 2011) or schooling behaviour of prey species changes with food availability, seasons and/or regions which can change the catchability of this prey species for predators (Hamner et al 1989; Kawaguchi et al 2010). Therefore, the quality (in terms of energetic value) of available prey may change between seasons, possibly influencing the physiology, distribution and behaviour of predators (Ainley et al. 2015).

Information on the energetic value of prey can be used to predict the behaviour and population dynamics of predators, and to gain insight into key trophic interactions between species (Trathan et al. 2007). It is furthermore important for the calculation of the energy flux through trophic levels of marine ecosystems (Goldsworthy et al. 2001; Lea et al. 2002), the investigation of the importance of a particular prey species in the diet of a predator (Cherel & Ridoux 1992; Lea et al. 2002) and for the use in bioenergetics models (e.g. Hartman and Brandt 1995). The aim of this review is to summarize the knowledge on the energy density of zooplankton and nekton species of the Southern Ocean, for the potential utilization in trophodynamic studies and bioenergetic models. Although the focus is on zooplankton and nekton, benthic species are included. Previously unpublished data are also included in this study.

METHODS

SOUTHERN OCEAN ENVIRONMENTAL FRAMEWORK

South of the STF, the Southern Ocean comprises different water masses and zones with distinct characteristics, separated from each other by several fronts and currents, and is thus not ecologically uniform (Pakhomov & McQuaid 1996; Belkin 2007). Large regions such as the continental shelf and slopes, sub-Antarctic and Antarctic Island groups, features of different fronts, the deep ocean, banks and basins and large gyre systems can be separated having distinct environmental features (Grant et al. 2006). The dominating current of the Southern Ocean is the Antarctic Circumpolar Current (ACC), driven by westerly winds (Orsi et al. 1995; Belkin 2007). The surface water of the ACC has a northern boundary at the Sub-Antarctic Front (SAF). Within the ACC, the Antarctic Polar Front (APF) marks the boundary between warmer sub-Antarctic water and cold Antarctic surface water. The surface waters of the ACC do not show a clear boundary to the south, its properties being rather uniform from the APF to the continental margins. However, in the underlying circumpolar deep water a Southern Boundary (SB) of the ACC occurs (Orsi et al. 1995), which has been found to also influence the physical features of the overlying water (Nicol et al. 2000b; Dinniman et al. 2011). The Weddell and Scotia Seas also have different characteristics and they are separated by the Weddell-Scotia confluence separating the ACC from the Weddell gyre (Orsi et al. 1995; Belkin 2007). Although, the ACC consisting of aforementioned fronts is the classical view based on studies mainly conducted in the Drake Passage, the frontal structure can be more complex in different areas. More details on this can be found in Sokolov & Rintoul (2009). Along the margins of the continent there is a westward current, the Antarctic Slope Current. The waters of the continental shelf and the oceanic waters are separated by the Antarctic Slope Front (Jacobs et al. 1991), which in areas where the continental shelf is narrow coincides with the slope current (Heywood et al. 1998). In between the major currents there are various eddies, the largest being the Weddell Gyre and the Ross Gyre (Riffenburgh 2007). Temperature and salinity gradients often coincide with the shelf breaks leading to a separation between coastal and oceanic areas (Ainley & Jacobs 1981; Van de Putte 2008). Broadly, the oceanic area south of the APF can be separated in (from north to south) a permanent open ocean zone, a seasonal ice zone (SIZ) and a coastal and continental shelf zone, which are regarded as different sub-systems with specific mechanisms controlling nutrient and phytoplankton dynamics (Tréguer & Jacques 1992). More information in biogeographic regions can be found in De Broyer & Koubbi (2014).

MEASURING ENERGY DENSITY

Bomb calorimetry

Bomb calorimetry is the most direct method to analyse the energy content of a species. A bomb calorimeter establishes the energy density (the amount of energy per unit mass) of a plant or animal tissue sample by measuring the heat released when that sample is completely oxidized. The sample is placed in a combustion chamber filled with oxygen, which is surrounded by water. After ignition, the temperature rise in the surrounding water is measured and converted to calorific density. If a sample causes 1000 g of water to rise with 1°C, the calorific content of the sample is 1 kilocalories (kcal; Shul'man 1974; Robbins 1983). The calorific density (cal g^{-1} weight) will then depend on the weight of the sample. To determine the whole-body energy density of an animal using bomb-calorimetry, the animal is dried and homogenized. After ignition in the bomb calorimeter, the calorific density of the tissue per gram dry weight (DW) is obtained, DW representing the weight of the organic and inorganic contents of the body without any water. Following the Système international d'unités (SI), energetic densities are expressed in Joule (J) or Kilojoules (kJ). One kilocalorie equals 4.184 kilojoules.

Depending on the intended use of the data, the energy density can be expressed in several ways. Expression in kJ g^{-1} wet weight (WW) can be useful in studies of trophic relationships and predator distribution/abundance, for instance to translate energetic requirements into food requirements (in number of individuals or kg) and is thus relevant for ecological considerations (Båmstedt 1986; Van Franeker 1992; Flores et al. 2008). However, the wet weight energy content of an individual is strongly related to its water content, the determination of which is a potential source of error. Samples are often weighed after being stored frozen and freezing samples causes dehydration. Calculating the 'wet' energetic value can therefore be skewed, as a lower water content will result in a higher wet weight energetic value (Hislop et al. 1991). Using fixation solutions also often results in loss of water or lipids and can therefore bias the relationship between WW, DW, chemical composition and energy content (Lamprecht 1999). Therefore, expression of energy density in kJ g^{-1} DW can be a better tool for comparison of the energy density within and between species.
As DW includes inorganic material, expression of the energetic density in kJ g^{-1} ash free dry weight (AFDW), representing the mass of only the organic part of the body or tissue, can in some cases be a more suited unit of measurement, for instance for growth and translocation studies (Lamprecht, 1999). For energy comparison between tissues it is also more useful to use AFDW, because different tissues often have different ash contents (Lamprecht, 1999). Although literature sources suggest that ash content can be determined by using the residue in the calorimeter cup after combustion (Lamprecht 1999), the more accurate determination is to make an independent estimate of the ash content of an organism (Paine 1971; Craig et al. 1978; Cherel & Ridoux 1992).

Measurements of organisms with a high ash content can yield unrealistic energetic values. Ash consisting of high proportions of $CaCO_3$ or other decomposable salts, can cause endothermic reactions when subjected to the high temperatures present in the bomb calorimeter, leading to a loss of heat within the calorimeter and consequently an underestimation of the energy density (Paine 1964; Paine 1971). This error increases with increasing ash content (Paine, 1971). Therefore, caution should be taken with ash contents higher than 25% (Paine 1971). Determination of the proportion of ash can also lead to errors due to the decomposition of salts (Paine 1971)

Measurements of energetic values lower than 17 kJ g^{-1} AFDW (the energetic density of carbohydrates) should be considered with caution, as they may be due to a wrong determination of ash content or to contributions of inorganic reactions during burning (Lamprecht 1999). Even though substances with lower calorific values exist, such as pyruvic acid and glycine etc., it is unlikely that these substances substantially lower the energetic values of an individual organism (Paine 1971).

A bomb calorimeter typically oxidizes nitrogen to a greater degree than most aquatic organisms (except microorganisms), giving a higher estimate of energy than is actually available to a consumer. To account for this extra energy a nitrogen correction can be used (Kersting 1972; Salonen et al. 1976). However, for such a correction it is necessary to know the amount of nitrogen in the sample, and correction can possibly vary depending on the organism (Kersting 1972). The energy density values obtained by bomb calorimetry are usually not corrected for nitrogen and may thus be slightly overestimated.

Bomb calorimetry measures the energy content of an organism as a whole. Part of this energy can, however, not be used by the consumer because food is often not completely digested or metabolized. Incomplete catabolism of protein leaves compounds (ammonium, urea, uric acid, creatinine) that are lost in urine (Brody 1945; FAO 2003). The digestibility of chitin, the main component of the exoskeleton of crustacea, can differ between species (Danulat 1987; Jackson et al. 1992), and carbohydrates can have indigestible parts often referred to as dietary fibre (FAO, 2003). The energy density determined using bomb calorimetry is thus the gross energy of an organism. This, in contrast to e.g. metabolizable energy or digestible energy, represents the total amount of energy that is potentially available (Brody 1945; Brett & Groves 1979; FAO 2003). For detailed studies that, for instance, require knowledge on digestible energy, correction factors and recommendations can be found in Brody (1945) and the FAO (2003). Although analysing fresh tissue is best when using bomb calorimetry, freezing is regarded as the most suitable preservation method for samples, as chemical preservation methods (e.g. ethanol or formaldehyde) significantly affect the results (Giguère et al. 1989; Benedicto-Cecilio & Morimoto 2002; Hondolero et al. 2012)

Proximate composition

Apart from ash and water fractions, organisms have an organic fraction that can be regarded as being composed of lipids, proteins and carbohydrates. By analysing the relative proportion of these components in the body of an organism, the energetic value can be reconstructed using energetic conversion factors

(Paine 1971).

The energy content of the different fractions can show slight variations due to differences in molecular structure (Båmstedt 1986), but conversion factors commonly used are 23.64 kJ g^{-1} AFDW (5.65 kcal g^{-1}) for proteins and 16.97 kJ g^{-1} AFDW (4.1 kcal g^{-1}) for carbohydrates (Brett & Groves 1979). For lipids, an energy content of 39.54 kJ g^{-1} AFDW (9.45 kcal g^{-1}) has often been used (Paine 1971 and references therein; Brett and Groves 1979). These values represent gross energy content of the compounds (Brody 1945; Bret & Groves 1979), which, similar to bomb calorimetry, does not take into account potential differences in digestibility between animals and substrates, and lost protein compounds (Brody 1945; FAO 2003). A factor of 36.40 kJ g^{-1} AFDW (8.7 kcal g^{-1}) is suggested to be more appropriate for lipids, because lipid content in the body may be overestimated due to impurities in the lipid extract (Craig 1977; Craig et al. 1978). This may, however, vary between methods used (FAO, 2003). As the energy density of lipids is almost twice as high as that of protein, higher lipid contents often result in a higher energetic value (Anthony et al. 2000). Therefore, differences in the lipid content of organisms can often predict differences in energy density. There are exceptions to this rule, however, as the energy density can also change significantly due to changes in, e.g., water or protein content, particularly during growth (Shul'man 1974; Donnelly et al. 1994). In addition, changes in protein content cause greater changes in an organisms weight compared to lipids (Shul'man 1974).

As carbohydrates usually contribute very little to the total dry body composition, this constituent is sometimes not considered in proximate analysis (Craig et al. 1978). The protein content of a body is sometimes estimated by measuring the total nitrogen content of a sample and then multiplying this with a factor 6.25, which is known as the Kjeldahl method (Craig et al. 1978). The protein content estimated using this method is often referred to as crude protein. For the energetic contribution of chitin to the total energy density the same conversion factor as for carbohydrate is usually used (Clarke 1980; Donnelly et al. 1994). Such factors cannot always accurately represent the potentially large variability of energy content of proximate compounds. Therefore, estimating the energetic content by means of proximate compositions is potentially subject to more error than bomb calorimetry (Henken et al 1986; Kamler 1992; Hartman & Brandt 1995; Higgs et al 1995).

Several studies found a good agreement between energy densities estimated using proximate composition and measured with bomb calorimetry (Paine 1971; Vollenweider et al. 2011). Other studies, however, found significant discrepancies between energy densities established using both proximate composition and bomb calorimetry (Craig et al 1978; Henken et al 1986; Kamler 1992). Energetic densities based on proximate composition were on average 4.4% higher than values obtained with bomb calorimetry in Craig et al. (1978), while they were on average 3-4% lower in Henken et al. (1986). The conversion factors do not take into account potential differences in heat of combustion of protein, depending on their amino acid composition, or the contribution of dietary fibre to carbohydrates, which has a lower energetic density (FAO 2003). Furthermore, methods used for measuring the relative contribution of different proximate compounds, as well as calculation of the energetic value, often differ between studies (Henken et al. 1986). Therefore, bomb calorimetry is considered the preferable method for energy density estimation (Henken et al. 1986; Kamler 1992; Hartman & Brandt 1995; Higgs et al. 1995). An advantage of proximate composition measurements is that changes in energy density can be related to changes in particular components that can give additional information on, e.g., ecological strategies, feeding activity, trophodynamics and reproductive status (Lawrence & Guille 1982; McClintock & Pearse 1987; Donnelly et al. 1994). A clear recommendation on the preservation of samples for proximate composition analysis was not found, but samples are usually processed directly or stored frozen.

Water content, carbon content and energy density

A relationship between energy density and water content is often found, showing an increase in water content with decreasing energy content (on a WW basis) and vice versa (Båmstedt 1981; Torres et al. 1994; Hartman & Brandt 1995). This can be attributed to water and lipids or protein replacing each other, depending on age, season and reproductive state (Torres et al. 1994; Hartman & Brandt, 1995; Lea et al. 2002; Tierney et al. 2002; Van de Putte et al. 2006). For example the water content increases when lipids (or protein) are combusted (Torres et al. 1994). The relationship between water, lipid and protein content in fish changes with age because younger individuals would use the protein to build up the body, but when growth ceases and protein metabolism stabilizes, the fish switch to the accumulation of fat (Shul'man 1974). Protein growth occurs in adult fishes in the form of gonad development (Shul'man 1974). Protein and lipid accumulation can however also depend on availability and composition of food. For example, in two species of anchovy with similar energy densities, one species had less available food, was larger at same age and contained more protein and less fat, while the other species had more food available, was fatter but also smaller and contained less protein (Shul'man 1974). The water content/energy density (WW) relationship is also common in crustaceans (Torres et al. 1994). Exceptions are found, however, in for instance decapod, amphipod and krill species, where water and lipids do not replace each other but increase or decrease simultaneously, or where changes in one of the fractions do not lead to changes in the other (Torres et al. 1994).

Relationships have also been found between total carbon content and energy density. Platt & Irwin (1973), Salonen et al. (1976), Finlay & Uhlig (1981), Gnaiger & Bitterlich (1984) and Normant et al. (2002) show regressions to calculate energy density. Different studies show relationships using different parameters and variable methods to establish both carbon content and energy density, making it hard to compare them. Measurements were done on phytoplankton (Platt & Irwin 1973), protozoa (Salonen et al 1976; Finlay & Uhlig 1981) and crabs (Normant et al. 2002). Platt & Irwin (1973) make a regression calculating calories mg^{-1} DW using the total % carbon, while Salonen et al. (1976) calculate kJ g^{-1} AFDW using the total % carbon, the former having a negative intercept, while the latter has a positive one. The relationship found by Normant et al.(2002), between kJ g^{-1} DW and % carbon, also has a negative intercept, and a relatively low R^2 (0.61), suggesting that a relatively low proportion of the variability was explained by the regression. Finlay & Uhlig (1981) calculate energy density in terms of kJ g^{-1} DW based om mg C mg^{-1} DW. Färber-Lorda et al. (2009a) shows a regression between carbon and energy in krill, with values based on mg ind^{-1} and J ind^{-1}. In addition to regressions, factors to convert carbon to energy density were suggested. Salonen et al. (1976) suggested a conversion factor of 45.7 kJ (AFDW) g^{-1} organic carbon, while Finlay & Uhlig suggested 46 kJ g^{-1} organic carbon. A conversion factor of 50.2 kJ g^{-1} C was suggested based on measurements on the amphipod *Themisto compressa*, caught in the North Atlantic (Williams & Robbins 1979). Due to differences in regression slopes and intercepts, measured species or species groups, and differences in units used, it remains unclear if the conversion factors and regressions can be used in a general context. It is also likely that season, region, organism, size and age will affect the carbon – energy density relationship, and these influences need to be assessed. Therefore, carbon content was not used in this review to estimate the energy density of species.

DATA AND STATISTICS

In this review, we aimed to express all energy density values in kJ g^{-1} DW for species comparison and in kJ g^{-1} WW for use in ecological studies. When possible, the energy density values obtained from literature were recalculated to kJ g^{-1} DW and/or kJ g^{-1} WW, by using given energy densities, species weights or water contents reported in the references concerned. Energy density values, determined by proximate composition, were calculated by the original authors using a factor of 36.40 kJ g^{-1} AFDW for the conversion of the lipid fraction unless stated otherwise. Protein values represent actual measurements derived from true protein content analysis. When crude protein measurements were used in the original paper this is specified. We also calculated energy densities from references reporting only proximate composition values (usually given in %WW), using the above mentioned conversion factors. When the carbohydrate fraction was not given in the source, we assumed it to be the remainder of 100% minus the other fractions (water content, lipids, carbohydrate, protein, ash and, where relevant, chitin). The lengths of fish reported in this review are given in standard length (SL), measured from the most forward part of the head to the end of the vertebrae. Some lengths are given in total length (TL), which is measured from the most forward part of the head to the end of the caudal fin.

Previously unpublished data obtained during two expeditions have been included in this review. Individual zooplankton and nekton species were collected on board the RV Polarstern in the Weddell Sea (PS81: August-October 2013) and in the Lazarev Sea (PS89: December/January 2014/2015), using Rectangular Midwater Trawls (RMT) and Surface and Under-Ice Trawls (SUIT). Details on sampling procedures, research area and environmental conditions for PS81 and PS89 can be found in Chapter 2 and Flores et al. (2015) respectively. After collection, zooplankton and nekton species were frozen at -20°C. Before the analysis of energetic value, samples were defrosted, blotted dry, and length and WW were measured. Then samples were freeze-dried until complete desiccation and re-weighted to determine DW and water content. After homogenization, a subsample of approximately 0.5 g was used for calorimetry. If necessary, individuals were pooled in order to obtain a sufficient amount of material to enable energy density measurements. The energy density (in kJ g^{-1} DW) of samples was determined with an isoperibol bomb calorimeter (IKA C2000 basic), calibrated with benzoic acid. Benzoic acid (29.62 kJ g^{-1} DW) was added to samples that were too small to obtain a minimum sample weight of 0.5 g. Some jelly fish body parts did not combust in the bomb calorimeter, most likely due to high ash contents (> 75 %DW). These tissues were then measured again using a sample consisting of half tissue, half benzoic acid. The AFDW of the jelly fish was obtained by drying a homogenized sample to constant mass at 60°C, followed by 6 hrs incineration at 500°C.

In datasets with a sufficient sample size, energy densities were compared using two-way ANOVA followed by a non-parametric Tukey's HSD post hoc test. Linear relationships between DW and energy content were established using ln-transformed data (Van de Putte et al. 2006). Linear relationships between water content and wet weight energy density were also investigated. Slopes and intercept of regression models were compared using ANCOVA (Hartman & Brandt 1995). All analyses were performed with R version 3.3.1 (R Core Team 2015). Seasons listed within the tables are defined as stated by the authors, or as summer for December to January, autumn for March to May, winter for June to August and spring for September to November. It should be kept in mind that environmental conditions may vary within a month depending on region. All data used in this review, including the previously unpublished data, are available as part of the SCAR Southern Ocean Diet and Energetics Database, which is a compilation of diet and energetics data from Southern Ocean studies. More information on use and contributing can be found at https://www.scar.org/data-products/southern-ocean-diet-energetics/.

ENERGY DENSITY OF ZOOPLANKTON AND NEKTON SPECIES

GENERAL OVERVIEW

Energetic densities of zooplankton and nekton species from sub-Antarctic and Antarctic waters collected and found in the literature included crustaceans, such as copepods, euphausiids, amphipods, mysids and decapods, fish, squid, and gelatinous species. The numbers of records varied greatly between groups and species. Some species have been given more attention than others which is often related to their abundance, importance in the diet of top predators, commercial interest and catchability. Fig. 4.1 shows an overview of all reported dry weight energy densities per species group and the locations at which recorded animals were sampled.

The majority of measurements of energy content in Antarctic crustaceans were conducted on euphausiids. The most comprehensive studies of energy density of crustaceans other than euphausiids were conducted by Donnelly et al. (1994) and Torres et al. (1994), using proximate composition. These studies provide, to our knowledge, almost the only records of energy densities of copepod, amphipod, decapod,

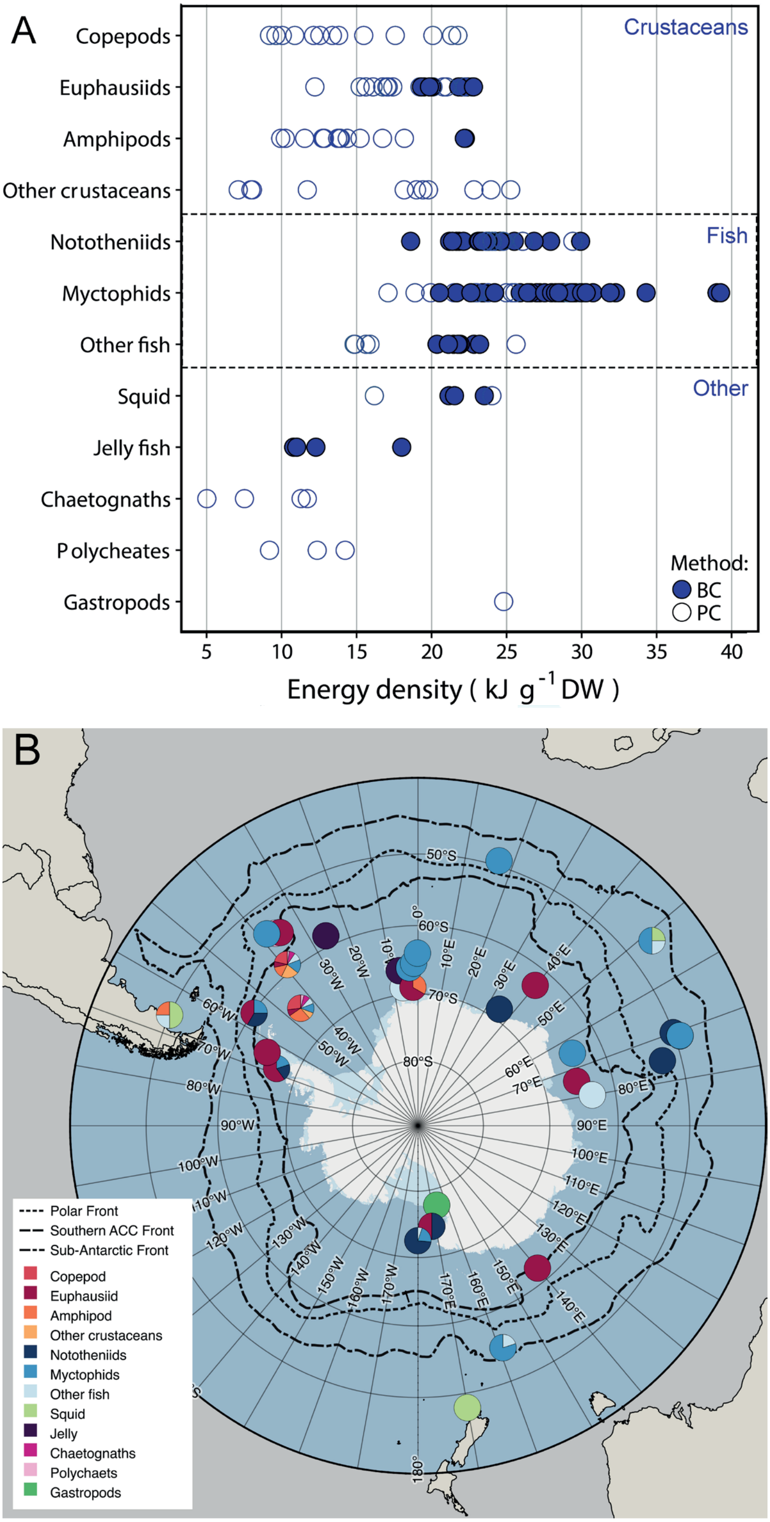

Figure 4.1: A) Overview of energy density records per species group. One point represents an average energetic value per species and per record. A distinction is made between measurements done using bomb calorimetry (BC) and proximate composition (PC). Note that one literature source can contain multiple energy density records, for instance of different species or developmental stages, and that, therefore, one point does not represent one literature source. B) Overview map of energy density records, including several fronts. One point on the map represents one source. Therefore, a single point can include multiple measurements on a single species or measurements of multiple species from a single group. Approximate locations were derived from the source material. The map was made using Quantarctica from the Norwegian Polar Institute (Matsouka et al. 2018). Mean front positions were taken from Sokolov and Rintoul (2009). Previously unpublished data is included.

mysid and ostracod species, which were caught in autumn and winter in the northwestern Weddell Sea and the southern Scotia Sea respectively. Donnelly et al. (1994) noted that their estimates of energy density are in general relatively low due to the incomplete recovery of organic material during analysis. Copepods showed a wide range of dry weight energy density values including very low values. Other low values were in general found for amphipods and ostracods. Amphipods have the highest skeletal ash, suggesting a more robust exoskeleton compared to copepods, euphausiids, decapods and mysids (Percy & Fife 1981; Torres et al. 1994). This can result in a lower dry-weight energy density because smaller proportion of the DW encompasses organic material. Amphipods furthermore have the highest chitin content (Donnelly et al. 1994; Torres et al.1994). However, two measurements on amphipods using bomb calorimetry yielded an energy density similar to the other crustaceans. It is unclear if this was is an artefact of the different methods used, as all other energy densities were estimated using proximate composition, or due to a different life cycle and/or distribution of the species. Ostracods had a low lipid content and slightly higher ash content compared to other crustaceans except amphipods (Donnelly et al. 1994).

In terms of energetic measurements, fish are the most studied organisms in the Southern Ocean. The main focus lies on nototheniid, myctophid and bathylagid species. The lipid content of myctophids is in general high, while nototheniids are more variable in composition, which shows a difference between the two families that is possibly related to habitat use (Lenky et al. 2012). This is reflected in their dry-weight energy density, which was generally high for myctophids, while for nototheniids it ranged from values similar to crustaceans to values similar to myctophid fish. Dry-weight energetic densities of fish from other families, including *Bathylagus antarcticus* and *Notolepis coatsi*, were also comparable to those of crustaceans or the lower end of the range of nototheniids (Fig. 4.1). A similar range was found for squid.

Dry weight energy densities of other groups showed relatively low values with the exception of a gastropod species, *Clione limacina antarctica* (Bryan et al. 1995). Measuring the energy content of gelatinous species is difficult due to their low proportion of organic material (high ash content), and high water content. A large part of the inorganic ash can be attributed to salt, a result from the large volume of sea water constituting the bulk of the organism's tissue (Percy & Fife 1981; Norrbin & Båmstedt 1984). In jellyfish is thought that residual water remains, even after drying to constant mass. This residual water is estimated to be 11.7% DW (Larson 1986; Doyle et al. 2007). For these reasons bomb calorific measurements and proximate composition estimates of gelatinous species should be considered with caution (Doyle et al. 2007). The high ash content can furthermore explain the low dry weight energy density values of gelatinous species such as jelly fish, salps and siphonophores.

CRUSTACEANS

Copepods

Copepods are the numerically dominant zooplankton group and often also dominate in biomass (Foxton 1956; Schnack-Schiel et al. 2001; Atkinson et al. 2012; David et al. 2017). Therefore, they are an important part of the diet of many zooplankton, fish and some top predator species (Laws 1977; Gon & Heemstra 1990; Hubold & Ekau 1990; Bocher et al. 2002; Van Franeker et al. 2002). Many species found in the Antarctic and sub-Antarctic regions have a wide distribution and are found north of the STF, sometimes even as far north as the Arctic Ocean (Kouwenberg et al. 2014). Of the total 388 species that have been reported to occur in the Southern Ocean, 53 are endemic south of the APF (Kouwenberg et al. 2014) and often rare. Many copepods can also be found residing within the sea-ice (Schnack-Schiel et al. 2001; Arndt & Swadling 2006).

The energy densities of copepods estimated in Donnelly et al. (1994) ranged between 9.0 and 21.8 kJ g^{-1} DW. Highest energy densities were from *Paraeuchaeta antarctica* (21.8 kJ g^{-1} DW), *Calanus propinquus* (21.3 kJ g^{-1} DW) and *Calanoides acutus* (17.6 kJ g^{-1} DW) which were all caught in autumn. All three species have a wide distribution and occur from south of the STF to the Antarctic continent (Kouwenberg et al. 2014). The other species analysed in Donnelly et al. (1994) showed energy densities below 13.8 kJ g^{-1} DW. An overview of recorded copepod average energy density measurements including, where possible, values expressed in kJ g^{-1} WW can be found in Table 4.1.

Some observations on energy content of copepods by Donnelly et al. (1994) can be explained by their life cycle, overwintering strategy and/or food. Species such as *C. acutus* and *C. propinquus* are mainly herbivorous and have high lipid levels (Donnelly et al. 1994), resulting in a relatively high energy density. More omnivorous species, such as *Euchirella rostromagna* and *Gaetanus tenuispinus*, or carnivorous species, such as *Heterorhabdus* spp., have lower lipid levels (Donnelly et al. 1994). There are, however, exceptions to this pattern: the carnivorous *Paraeuchaeta antarctica* was found to have a high lipid content and the herbivorous *Rhincalanus gigas* a relatively moderate lipid content, the latter attributed to their more flexible two-year life cycle including a delayed reproduction (Donnelly et al. 1994). *Heterorhabdus austrinus* continues to feed during winter which is reflected in higher protein content and lower lipid content compared to its congener *H. farrani*, which does not feed during winter. Their estimated energy content was however similar (12.13 kJ g^{-1} DW; Donnelly et al. 1994).

All species that were analysed in two seasons showed a similar or lower energy density in winter compared to autumn, except for *Rhincalanus gigas*. *Calanoides acutus* overwinters at depth in diapause and did not show a difference in proximate composition between seasons which could be attributed to its reduced metabolic rates (Donnelly et al. 1994). This could also be the case for *R. gigas*, although this species has also been found to feed and reproduce during winter (Atkinson 1998). *Calanus propinquus,* overwintering using a combination of continuous feeding, reduction in body integrity and combustion of energy reserves, shows an increase in water levels, and a decrease in chitin content and lipid levels from autumn to winter (Donnelly et al. 1994). As *C. propinquus* relies on energy reserves, their energy content can be expected to show large variations between seasons. Changes from autumn to winter were observed in the composition of *Paraeuchaeta antarctica* which was suggested to be a consequence of reproductive demand. Their energy content was, however, similar in both seasons (Donnelly et al. 1994). Studies on the lipids of copepods indicated that seasonal as well as regional variability of lipid content can be found within species, due to differences in food availability, type of food and overwintering strategy (Hagen et al. 1993; Donnelly et al. 1994).

Euphausiids

Euphausiids are a major component of Southern Ocean ecosystems. The three most studied species of Euphausiacea are *Euphausia superba, Thysanoessa macrura* and *Euphausia crystallorophias*. *Euphausia superba* has a circumpolar distribution, from south of the polar front to the continental shelf, with a majority of the total stock found in the regions of the Antarctic Peninsula and the Scotia Arc (Atkinson et al. 2008;

Table 4.1: Overview of the average energy density of copepod species from Donnelly et al. (1994). All values were estimated using proximate composition (PC). *n* represents the number of samples measured. Where this expresses samples of pooled individuals, this is indicated with (p). The standard deviation is given where available (±).

SEASON	LOCATION	*n*	MEAN WW (g)	WATER CONTENT (%)	ENERGY DENSITY		METHOD	SOURCE
					kJ g^{-1} WW	kJ g^{-1} DW		
Calanoides acutus								
Autumn	Weddell sea	2 (p)	0.20	86.0	2.51	17.57	PC	Donnelly et al. 1994*
Winter	Scotia sea	2 (p)	0.78	84.2 ± 0.1	2.51	15.48	PC	Donnelly et al. 1994
Calanus propinquus								
Autumn	Weddell sea	2 (p)	0.19	74.0	5.44	21.34	PC	Donnelly et al. 1994
Winter	Scotia sea	2 (p)	0.49	84.6 ± 0.5	2.09	13.39	PC	Donnelly et al. 1994
Euaugaptilis laticeps								
Autumn	Weddell sea	1 (p)	0.04	83.7	1.67	10.04	PC	Donnelly et al. 1994
Paraeuchaeta antarctica								
Autumn	Weddell sea	1 (p)	0.22	79.3	4.60	21.76	PC	Donnelly et al. 1994
Winter	Scotia sea	2 (p)	0.33	84.2 ± 1.8	3.35	20.08	PC	Donnelly et al. 1994
Euchirella rostromagna								
Winter	Scotia sea	1 (p)	0.15	84.5	1.26	9.20	PC	Donnelly et al. 1994
Gaetanus tenuispinus								
Autumn	Weddell sea	1 (p)	0.25	85.0	1.67	12.13	PC	Donnelly et al. 1994
Winter	Scotia Sea	3 (p)	0.19	82.6 ± 0.9	2.09	12.13	PC	Donnelly et al. 1994
Heterorhabdus austrinus								
Winter	Scotia Sea	1 (p)	0.22	88.7	1.26	12.13	PC	Donnelly et al. 1994
Heterorhabdus farrani								
Winter	Scotia Sea	1 (p)	0.17	89.5	1.26	12.13	PC	Donnelly et al. 1994
Metridia gerlachei								
Autumn	Weddell sea	1 (p)	0.78	90.4	1.26	10.88	PC	Donnelly et al. 1994
Winter	Scotia sea	1 (p)	0.46	91.0	0.84	9.62	PC	Donnelly et al. 1994
Rhincalanus gigas								
Autumn	Weddell sea	1 (p)				12.55	PC	Donnelly et al. 1994
Winter	Scotia sea	4 (p)	0.82	91.0 ± 0.3	1.26	13.81	PC	Donnelly et al. 1994

* A factor of 4.19 was used to convert calories to joules

Pakhomov et al. 2000; Flores et al. 2012a). *Thysanoessa macrura* has a similar distribution but can also be found north of the SAF (Pakhomov et al. 2000; Atkinson et al. 2012; Flores et al. 2012a; Cuzin-Roudy et al. 2014). The distribution and density of *E. superba* has been related to sea ice, although this association differs between seasons, while the smaller *T. macrura* can be found in ice-covered waters but is less ice-associated and often occupies a deeper stratum (Nordhausen 1994; Flores et al. 2012a; Haraldsen & Siegel 2014). *Euphausia crystallorophias* is neritic and found close to the Antarctic continent (Nordhausen 1994; Pakhomov & Perissinotto 1996), where they reside in ice-covered waters year round. For all krill species, larvae, juveniles and adult have different physiological, metabolic and functional adaptions and can therefore have different habitat requirements (Cuzin-Roudy et al. 2014). The largest species, *E. superba*, is the most heavily studied due to its high total biomass, its importance in the diet of many top predators and because it is a target species of a growing fishery (Atkinson et al. 2012).

The lowest average energetic density for *E. superba* was 15.2 kJ g^{-1} DW for adults during autumn, estimated using proximate composition (Torres et al. 1994). The highest density found in the literature is 22.7 kJ g^{-1} DW of gravid females at South Georgia during summer (Clarke 1980), although another source reports a somewhat lower energetic density for gravid females (20.1 kJ g^{-1} DW) found at Elephant Island (Ishii et al. 2007). Both aforementioned energy densities were estimated using proximate composition, but differences in methodological details used could have resulted in different values. Ishii et al. (2007), for instance, did not take the chitin fraction into account and details on the methods used for different components are undescribed. For the energy densities of *T. macrura, E. crystallorophias* and *Euphausia frigida*, estimates using bomb calorimetry, proximate composition and calculations using published equations (Färber-Lorda 1986; Torres et al. 1994, Ainley et al. 2003b, Ruck et al. 2014), suggest that the energy density of these krill species are similar to that of *E. superba*. Bomb calorific measurements on adult and juvenile *T. macrura* from the southern Indian Ocean showed that individuals at one station (6.12 and 5.35 kJ g^{-1} WW, respectively) had higher WW energy density values than individuals from another station (5.52 and 4.76 kJ g^{-1} WW, respectively; Färber-Lorda 1986). A measurement of the mesopelagic, circumpolarly distributed *Euphausia triacantha* (Piatkowski 1985; Atkinson et al. 2012) showed that this species had a relative low energy density compared to the other euphausiid species from the same study (Torres et al. 1994). An overview of recorded euphausiid average energy density measurements including, where possible, values expressed in kJ g^{-1} WW can be found in Table 4.2.

The energy density of *E. superba* varies between regions, seasons, sexes and states of sexual maturity. Mature females have a high energy density and lose up to 55-58% of their lipids when spawning, resulting in a lower energetic value (Clarke 1980; Färber-Lorda et al. 2009b). *Euphausia superba* spawns from December to April with a peak in January (Ross & Quetin 1986; Pakhomov 1995; Spiridonov 1995). During summer the energetic density of males is relatively low compared to juveniles and females (Clarke 1980; Färber-Lorda et al. 2009a). Studies suggest that this is due to differences in lipid accumulation, which was found to be low in males and at a maximum in maturing females, although a lot of variance was found (Pond et al. 1995;

Mayzaud et al. 1998; Färber-Lorda et al. 2009a; Ruck et al. 2014). Lower lipid content in males is assumed to be a result of a higher investment of energy in growth in order to increase reproductive success (Ruck et al. 2014). Virtue et al. (1996) suggested that low accumulation of lipids in male krill is a result of a higher sexual activity. Multiple linear regressions between dry weight, carbon content, and lipid content versus energy content of *E. superba*, reported as values individual^{-1}, can be found in Färber-Lorda et al. (2009a).

Table 4.2: Overview of the average energy density of several euphausiid species ±, were available, the standard error (SE) or standard deviation (SD) as given in the original source. Methods (MTD) used for energy density estimates are bomb calorimetry (BC), micro-bomb calorimetry (MBC), proximate composition (PC) or are calculated using published equations from Färber-Lorda et al. (2009a; Calc). Energy densities given in italics represent values that were converted using information from the given sources. *n* represents the number of samples measured. Where this expresses samples of pooled individuals, this is indicated with (p). SIO = Southern Indian Ocean.

SEASON	LOCATION	*n*	STAGE	WATER CONT. (%)	ENERGY DENSITY kJ g^{-1} WW	ENERGY DENSITY kJ g^{-1} DW	MTD	SOURCE
Euphausia superba								
Summer	South Georgia	5-20	Female (gravid)	*76.0*	5.45^{1,2}	*22.66*	PC	Clarke 1980
	Elephant Is.	4	Female (gravid)	*75.9* ± 0.4 SE	4.80^{1,3} ± 0.05 SE	*20.08*	PC	Ishii et al. 2007
	SIO	7	Female (spent)		4.88 ± 0.78*		BC	Färber-Lorda et al. 2009a
	Lazarev Sea	3 (p)	Female	73.8 ± 1.9 SD	5.54 ± 0.73 SD	22.27 ± 0.72 SD	BC	This study (PS89)
	SIO	15	Female		6.31 ± 0.88*		BC	Färber-Lorda et al. 2009a
	WAP	(p)	Female			22.00 ± 0.3 SE	BC	Ruck et al. 2014
	Elephant Is.	2	Female	*77.7* ± 1.3 SE	4.16^{1,3} ± 0.33 SE	*17.41*	PC	Ishii et al. 2007
	South Georgia	5-20	Male	80.05	3.83^{1,2}	*19.22*	PC	Clarke 1980
	SIO	10	Male		4.76 ± 0.96*		BC	Färber-Lorda et al. 2009a
	WAP	(p)	Male			19.50 ± 0.5 SE	BC	Ruck et al. 2014
	Elephant Is.	4	Male	*78.9* ± 0.5 SE	3.73^{1,3} ± 0.12 SE	*15.61*	PC	Ishii et al. 2007
	Elephant Is.	2	Male (sub-ad.)	*77.9* ± 0.3 SE	4.09^{1}, 3 ± 0.03 SE	*17.11*	PC	Ishii et al. 2007
	Lazarev Sea	2 (p)	Juvenile	75.1 ± 3.5 SD	5.63 ± 1.19 SD	22.38 ± 0.44 SD	BC	This study (PS89)
	SIO	10	Juvenile		5.59 ± 0.76*		BC	Färber-Lorda et al. 2009a
	WAP	(p)	Juvenile			20.80 ± 1.7 SE	Calc	Ruck et al. 2014
	Elephant Is.	1	Juvenile	78.30	4.0^{1,3}	*16.74*	PC	Ishii et al. 2007
	WAP	9		77.0 ± 2.7 SD	*5.01*	21.8 ± 0.7 SD	BC	Nagy and Obst 1992
				75.7	4.86	*20.0*	PC	Yanagimoto et al. 19795
	East Antarctica	1			4.47		BC	Tamura and Konishi 2009
Autumn	NA			*75*	5.31	*22.22*	PC	Márquez et al. 19785
	Weddell Sea	23	Adult	73.3 ± 3.4 SD	4.07^{6}	*15.24*	PC	Torres et al. 1994
	NA			*76.5*	*4.71*	20.0	BC	Jackson 1986
Winter	Scotia Sea	32	Adult	77.3 ± 3.4 SD	3.80^{6}	*16.75*	PC	Torres et al. 1994
Thysanoessa macrura								
Summer	WAP	(p)				28.5 ± 2.8 SE	Calc	Ruck et al. 2014
	SIO	1 (p)	Adult		5.52		MBC	Färber-Lorda 1986
	SIO	1 (p)	Adult		6.12		MBC	Färber-Lorda 1986
	SIO	1 (p)	Juvenile		4.76		MBC	Färber-Lorda 1986

Table 4.2 continued.

SEASON	LOCATION	*n*	STAGE	WATER CONT. (%)	ENERGY DENSITY kJ g^{-1} WW	kJ g^{-1} DW	MTD	SOURCE
	SIO	1 (p)	Juvenile		5.35		MBC	Färber-Lorda 1986
	SIO			*74.2*	*5.42*	*21.00*	PC	Färber-Lorda et al. 2009b
Autumn	Weddell Sea	1 (p)		70.4	5.04[6]	*17.02*	PC	Torres et al. 1994
Winter	Scotia Sea	6 (p)		76.9 ± 1.2 SD	3.72[6]	*16.10*	PC	Torres et al. 1994
Euphausia crystallorophias								
Summer	Ross Sea	4 (?)	Adult			*19.33*	BC	Ainley et al. 2003b
	WAP	(p)				21.8 ± 0.8 SE	Calc	Ruck et al 2014
Autumn				80.6	3.85	*19.85*	BC	Green and Gales 1990
				71.7	6.45[4]	*22.79*	BC	Green and Gales 1990
Euphausia triacantha								
Winter	Scotia Sea	9 (p)		76.1 ± 3.6 SD	2.92[6]	*12.22*	PC	Torres et al. 1994
Euphausia frigida								
Summer	SIO	1 (p)			4.62		MBC	Färber-Lorda 1986

[1] Energy density calculated with an energetic value of 39.54 kJ g^{-1} AFDW (9.45 kcal g^{-1}) for lipids
[2] A factor of 4.1864 was used to convert calories to joules
[3] Energy density calculated excluding chitin
[4] Sample taken from bird stomach contents, in which the energetic value is potentially overestimated due to water removal in stomach.
[5] from Barrera-Oro 2002
[6] A factor of 4.19 was used to convert calories to joules

Similar differences in lipid content between males and females were found for *T. macrura* (Färber-Lorda & Mayzaud 2010). The lipid content of *E. superba* and *T. macrura* showed a high local variability in several studies (Pond et al. 1995; Hagen et al. 1996; Mayzaud et al. 1998; Färber-Lorda et al. 2009a; Färber-Lorda & Mayzaud 2010; Ruck et al. 2014; Kohlbach et al. 2017). In *E. superba* lipid, but also protein content, was found to be highly variable within a single population during several seasons, and the variety within a season can be greater than between seasons (Torres et al. 1994; Mayzaud et al. 1998; Ruck et al. 2014). This intra-seasonal variation can be attributed to a patchy and/or regionally variable distribution of available food (Chapter 3; Mayzaud et al. 1998; Ruck et al. 2014; Virtue et al. 2016)

As the spawning seasons of *T. macrura* and *E. crystallorophias* are somewhat earlier in the year compared to *E. superba*, differences in timing of the peak energetic value can be expected between species. The spawning season for *T. macrura* ranges from June to January with a peak from September to November (Haraldsson and Siegel 2014), while *E. crystallorophias* spawn in November/December (Pakhomov & Perissinotto 1996; Falk-Petersen et al. 2000). Both species use energy reserves accumulated in summer and autumn to overwinter and reproduce, which ensures that their larvae can feed on the spring phytoplankton blooms (Falk-Petersen et al. 2000; Vallet et al. 2011). *Euphausia superba* needs the spring and summer phytoplankton blooms for sexual maturations, mating and egg development (Cuzin-Roudy et al. 1999). Due to the lack of data, however, these differences in life cycles do not become clear in a seasonal variability of their energetic density. Regarding lipid contents, *E. crystrallorophias* showed steady decrease of lipid content over winter and the following spawning period in spring. Lipid content increased again in late spring/

summer which was found to coincide with elevated chlorophyll *a* content in the water column (Clarke 1984). Larger sized individuals of *E. triacantha* showed a higher lipid level and a lower water content than smaller sized individuals. Seasonal changes in composition suggests that this species combusts tissue during winter (Torres et al. 1994).

Amphipods

The 820 amphipod species recorded in the Southern Ocean occupy a very wide variety of ecological niches and have a large range of feeding strategies (Dauby et al. 2001; De Broyer et al. 2001; Dauby et al. 2003; Zeidler & De Broyer 2014). The amphipods can be divided in gammarid and hyperiid amphipods. The gammarid amphipods are mainly benthic with few pelagic species. Some gammarids, such as species from the genus *Eusirus*, have been found closely related to the sea-ice underside (Flores et al. 2011; David et al 2017). The hyperiid amphipods are mainly pelagic and have been found to be important prey species for top predators such as several bird species (Ridoux 1994; Bocher et al. 2001). The swarming *Themisto gaudichaudii* occurs in high abundances in the sub-Antarctic and Antarctic regions (Kane 1966).

The energy density of several amphipod species from the Weddell and Scotia Seas was estimated using proximate composition by Torres et al. (1994). The lowest value of 9.9 kJ g^{-1} DW, was from the gammarid amphipod *Parandania boecki* collected in winter (Table 4.3). This species also had the highest water content and is the deepest living. It has furthermore been found to have low lipid levels and to be feeding on coelenterates (Reinhardt & Van Vleet 1986). The highest energetic density of 18.2 kJ g^{-1} DW, was from the hyperiid amphipod *Cyllopus lucasii* collected in autumn (Torres et al. 1994). The relatively high energy density expressed in kJ g^{-1} WW is a result of the water content of 68.7% (of WW), which is relatively low compared to that of other amphipods or euphausiids.

Both *C. lucasii* and *Primno macropa* showed a significant decline in energy density in winter compared to autumn (Torres et al. 1994). This could be a result of reproductive activity, but considering what is known about the timing of reproduction, most likely a result of lipid combustion. This was supported by an increase in water content with decreasing lipid content. *Cyllopus lucasii* furthermore showed significant variability in lipid content between regions (Torres et al. 1994). *Themisto gaudichaudii* had a very low energy density of 12.7 kJ g^{-1} DW, during wintertime. It was suggested to be a result of reproductive activity, as their reproduction peak is in spring. Mayzaud and Boutoute (2015) found that *T. gaudichaudii* (females), which continues to feed carnivorously over winter, had a relatively stable lipid content year-round. A bomb calorimetry measurement of *T. gaudichaudi* yielded an average energy density of 22.1 kJ g^{-1} DW (Ciancio et al. 2007). Torres et al. (1994) suggested a mixed overwintering strategy for all examined hyperiid amphipods. The gammarid amphipods examined in Torres et al. (1994) are all deeper living species and a business-as-usual overwintering strategy was suggested.

An energy density of 22.3 kJ g^{-1} DW was found for the gammarid *Eusirus microps* during summer in the Lazarev Sea (PS89). *Eusirus microps* has been found in the surface of both open and ice-covered waters

Table 4.3: Overview of the average energy density of amphipod species. Values were estimated using proximate composition (PC) and one using bomb calorimetry (BC). Energetic values in italics represent values that were converted using information from the given source. *n* represents the number of samples measured. Where this expresses samples of pooled individuals, this is indicated with (p). The standard deviation is given where available (±).

SEASON	LOCATION	*n*	MEAN WW	WATER	ENERGY DENSITY		METHOD	SOURCE
			(g)	CONT. (%)	kJ g^{-1} WW	kJ g^{-1} DW		
Cyphocaris faueri **(gammarid)**								
Autumn	Weddell sea	6	22.0	76.4 ± 5.8	2.42	*10.25*	PC	Torres et al. 1994*
Cyphocaris richardi **(gammarid)**								
Autumn	Weddell sea	5	28.8	74.7 ± 2.5	2.92	*11.54*	PC	Torres et al. 1994
Winter	Scotia sea	5	22.6	74.8 ± 2.6	3.84	*15.24*	PC	Torres et al. 1994
Parandania boecki **(gammarid)**								
Winter	Scotia sea	2 (p)	18.5	83.7 ± 2.3	1.62	*9.94*	PC	Torres et al. 1994
Eusirus microps **(gammarid)**								
Summer	Lazarev sea	1 (p)	44.1 ± 1.7	80.7 ± 4.4	4.51	*22.25*	BC	This study (PS89)
Cyllopus lucasii **(hyperiid)**								
Autumn	Weddell sea	12	19.8	68.7 ± 4.2	5.69	*18.18*	PC	Torres et al. 1994
Winter	Scotia sea	8	21.3	77.6 ± 2.1	2.87	*12.81*	PC	Torres et al. 1994
Hyperia macrocephala **(hyperiid)**								
Autumn	Weddell sea	1	30.0	72.8	3.77	*13.86*	PC	Torres et al. 1994
Hyperiella antarctica **(hyperiid)**								
Autumn	Weddell sea	1 (p)	9.6	86.7	1.71	*12.86*	PC	Torres et al. 1994
Primno macropa **(hyperiid)**								
Autumn	Weddell sea	2 (p)	14.3	70.6 ± 1.7	4.92	*16.73*	PC	Torres et al. 1994
Winter	Scotia Sea	2 (p)	14.7	76.5 ± 0.2	3.23	*13.74*	PC	Torres et al. 1994
Themisto gaudichaudii **(hyperiid)**								
Winter	Scotia Sea	2 (p)	17.0	77.4 ± 0.5	2.88	*12.74*	PC	Torres et al. 1994
	Patagonia	3 (p)	3-12	86.0	3.11	*22.19*	BC	Ciancio et al. 2007
Vibilia stebbingi **(hyperiid)**								
Autumn	Weddell sea	1 (p)	11.5	71.4	4.11	*14.37*	PC	Torres et al. 1994
Winter	Scotia sea	3 (p)	10.5	72.5 ± 5.2	3.83	*13.93*	PC	Torres et al. 1994

* A factor of 4.19 was used to convert calories to joules

during summer (Flores et al. 2011) and winter (Flores et al. 2011; David et al. 2017). All energy density values of amphipods are listed in Table 4.3.

Other crustacea

Energy density values of crustaceans of the orders Decapoda, Mysida and the class Ostracoda were also found in Donnelly et al. (1994) and Torres et al. (1994). Their energy densities, estimated using proximate composition, ranged from 19.0 to 25.3 kJ g^{-1} DW, 18.2 to 24.0 kJ g^{-1} DW, and 7.1 to 11.7 kJ g^{-1} DW, respectively. The decapod *Pasiphaea scotiae* had a higher energy density in autumn compared to winter, while the opposite was found for the decapod *Petalidium foliacium*. The species from Torres et al. (1994) are all deeper living animals, although ostracods have also been found in the under-ice surface (David et al. 2017). Recorded energy density measurements including, where possible, values expressed in kJ g^{-1} WW are listed in Table 4.4.

FISHES

In general, there is a strong distinction between coastal and oceanic fish assemblages (Hubold 1991; Kock 1992). The families Myctophidae, Bathylagidae, Gonostomatidae and Paralepidae dominate the fish community of the Southern Ocean's oceanic waters (Kock 1992; Flores et al. 2008; Duhamel et al. 2014). The oceanic myctophids, or lanternfishes, dominate the meso- and bathypelagic zones in term of species richness, abundance and biomass (references in Duhamel et al 2014). The cold waters of the Antarctic continental shelf and slope are dominated by the Nototheniidae (Eastman & Eakin 2000; Van de Putte 2008), which

Table 4.4: Overview of the average energy density of other crustacean species. All values were estimated using proximate composition (PC). Energetic values in italics represent values that were converted using information from the given sources. The mean size of the decapods and mysids represents the carapace length, for ostracods it represents the sphere diameter. *n* represents the number of samples measured. Where this expresses samples of pooled individuals, this is indicated with (p). The standard deviation is given where available (±).

SEASON	LOCATION	*n*	MEAN WW (g)	WATER CONT. (%)	ENERGY DENSITY kJ g^{-1} WW	kJ g^{-1} DW	METHOD	SOURCE
***Pasiphaea scotiae* (decapod)**								
Autumn	Weddell sea	6	21.7	63.2 ± 2.7	8.40	*22.82*	PC	Torres et al. 1994*
Winter	Scotia sea	8	21.3	63.3 ± 2.1	6.97	*19.00*	PC	Torres et al. 1994
***Petalidium foliacium* (decapod)**								
Autumn	Weddell sea	1	17.0	71.8	5.58	*19.77*	PC	Torres et al. 1994
Winter	Scotia sea	3	13.3	67.4 ± 3.3	8.24	*25.27*	PC	Torres et al. 1994
***Boreomysis rostrata* (mysid)**								
Winter	Scotia sea	2	10.0	75.8 ± 0.9	4.40	*18.17*	PC	Torres et al. 1994
***Eucopia australis* (mysid)**								
Winter	Scotia sea	2	13.0	77.8 ± 1.8	5.32	*23.96*	PC	Torres et al. 1994
***Gnathophausia gigas* (mysid)**								
Winter	Scotia sea	4	16.8	69.4 ± 4.4	5.95	*19.43*	PC	Torres et al. 1994
***Conchoecia antipoda* (ostracod)**								
Winter	Scotia Sea	1 (p)		87.8	1.67	11.72	PC	Donnelly et al. 1994*
***Conchoecia belgicae* (ostracod)**								
Winter	Scotia Sea	1 (p)		85.9	1.26	7.95	PC	Donnelly et al. 1994
***Conchoecia hettacra* (ostracod)**								
Winter	Scotia Sea	1 (p)		84.1	1.26	7.11	PC	Donnelly et al. 1994
***Gigantocypros mulleri* (ostracod)**								
Winter	Scotia sea	4	16.3	91.3 ± 0.4	0.70	8.06	PC	Torres et al. 1994

* A factor of 4.19 was used to convert calories to joules

are mainly benthic or bentho-pelagic (La Mesa et al. 2004). Other families significantly contributing to the Southern Ocean fish fauna are the Liparidae, Zoarcidae and Macrouridae (Duhamel et al. 2014). The neritic species composition differs between the continental areas, SIZ and around the (sub-)Antarctic islands (Kock 1992). In some species, the larval stages have a different (vertical) distribution pattern than adult individuals of the same species (e.g. Hubold 1990).

The availability of previously unpublished data and data of individual fish kindly provided by colleague researchers, allows for a more detailed description and analysis of the energetic density of the nototheniid *Pleuragramma antarctica*, the myctophids *Electrona antarctica, Gymnoscopelus braueri* and the bathylagiid *Bathylagus antarcticus.*

Pleuragramma antarctica

The notothenoid *Pleuragramma antarctica* is the most abundant pelagic fish in the high-Antarctic coastal regions, with an extended range to the South Shetland and South Orkney Islands (Eastman & Hubold 1999; La Mesa et al. 2004; Donnelly & Torres 2008; Van de Putte 2008). It is an important prey species for many fish species and (Eastman 1985) and top predators, including flying birds (Van Franeker et al. 2001), seals (Southwell et al. 2012 and references therein) and penguins (Ainley et al. 1998; Cherel & Kooyman 1998),

Reported and measured average energy density values of *Pleuragramma antarctica* ranged from 21.7 to 27.9 kJ g^{-1} DW (both summer Ross Sea). In East Antarctica, the energy density increased with age, from 21.8 kJ g^{-1} DW to 25.5 kJ g^{-1} DW in small (52-95 mm) and large, adult (> 105 mm) individuals, respectively (Van de Putte et al. 2010). The water content showed an opposite trend and was higher in the younger group (87.9%) compared to the older one (70.2%; Van de Putte et al. 2010). The energy density of juvenile fish showed a lot of variation, possibly attributed to variability in foraging success (Van de Putte et al. 2010). Therefore, despite differences between size classes, there was no (linear) relationship between size and energy density within the small group. An overview of recorded average energy density measurements of *Pleuragramma antarctica* including, where possible, values expressed in kJ g^{-1} WW can be found in Table 4.5.

The relatively low energy density of young *Pleuragramma antarctica* could possibly be due to their small size. The energy density of adult *Pleuragramma antarctica* is closer to that of the myctophid fishes, and evidence suggest that the energy density of adults would be even higher in fully grown individuals (Van de Putte et al. 2010). This suggestion is supported by a relatively high energetic density of larger fish from the Ross Sea (Lenky et al. 2012). This increased energy density could be a result of increased lipid content, which increases with age and size. This increase is suggested to be needed for buoyancy, in order to compensate for increasing weight, rather than an energy storage, as it is assumed that sufficient copepod and euphausiid prey are available for *Pleuragramma antarctica* year round, and because large lipid stores were still found in this fish after winter (Gon & Heemstra 1990; Friedrich & Hagen 1994; Hubold & Hagen 1997). However, there is also evidence that *Pleuragramma antarctica* is cannibalistic from a study conducted in late spring (Eastman 1985). The difference in energy density between juvenile and adult fish can also be

Table 4.5: Average energy densities of *Pleuragramma antarctica*, measured using bomb calorimetry (BC). Numbers in italics represent values that were converted using information from the given sources. Sizes are in standard length. *n* represents the number of samples measured. Where this expresses samples of pooled individuals, this is indicated with (p). Where available, the standard error or standard deviation as given in the original source is added (±).

SEASON	LOCATION	*n*	MEAN SIZE (mm)	MEAN WW (g)	MEAN DW (g)	WATER CONTENT (%)	ENERGY DENSITY kJ g^{-1} WW	ENERGY DENSITY kJ g^{-1} DW	MTD	SOURCE
Summer	Ross Sea	(p)	134[1] ± 21 SE	23.7 ± 15.2 SE	*4.2*	82.1	5	*27.93*	BC	Lenky et al. 2012
	Ross Sea		70-120					*21.76*	BC	Ainley et al. 2003
	WAP		89.9 ± 4.3 SE					24.6 ± 0.4 SE	BC	Ruck et al. 2014
Autumn	East Antarctica	14	52-95	1.6 ± 0.6 SD	0.2 ± 0.1 SD	87.9 ± 1.1 SD	2.64 ± 0.25 SD	21.83 ± 0.44 SD	BC	Van de Putte et al. 2010
	East Antarctica	2	>105	6.1 ± 0.1 SD	1.8 ± 0.04 SD	70.2 ± 2.8 SD	7.59 ± 0.65 SD	25.52 ± 1.18 SD	BC	Van de Putte et al. 2010

[1] measured in total length (TL)

explained by the higher investment in protein growth rather that lipid accumulation, which is a common phenomenon in fish (Shul'man 1974). No data on energy density are available for the spawning season, presumably occurring in winter and spring, with a possible extended season into December in the Ross Sea (Vacchi et al. 2004).

Other Nototheniidae

High energy densities of 29.9 and 29.4 kJ g^{-1} DW were reported for *Dissostichus mawsoni* (Antarctic toothfish) and *Dissostichus eleginoides* (Patagonian toothfish), respectively (Durand & Nicolle 1980; Lenky et al. 2012). *Dissostichus mawsoni* occurs mainly in high Antarctic waters. *Dissostichus eleginoides* is more distributed in the northern parts of the Southern Ocean, particularly around the sub-Antarctic islands, and around the southern tip of South America (Duhamel et al. 2014). A significant proportion of the diets of *Dissostichus* spp. consists of other fish (Kock 1992). *Dissostichus* spp. are of great commercial interest and are harvested using longlines. All notothenioids lack a swim bladder. Most species are heavier than sea water but still relatively light in weight compared to other teleosts (Eastman & DeVries 1982). Together with *Pleuragramma antarctica* and likely *Aethotaxis mitopteryx*, *D. mawsoni* accumulates lipids to achieve neutral buoyancy (Eastman & DeVries 1982; Kock 1992; Lenky et al. 2012). Juvenile *D. mawsoni* gradually become more buoyant with increasing size until they reach neutral buoyancy with adulthood at an approximate length of 81 cm SL (Near et al. 2003).

The energy density of other nototheniid species found in the literature ranged from 18.6 kJ g^{-1} DW for *Trematomus scotti* to 26.8 kJ g^{-1} DW for *Trematomus lepidorhinus* (proximate composition, Lenky et al. 2012), both caught in the Ross sea during summer. Of the species listed in Lenky et al. (2012), *Lepidonotothen squamifrons, Trematomus bernacchii, Trematomus hansoni, Trematomus pennelli* and *T. scotti* are benthic species (Eastman & DeVries 1982; Lenky et al. 2012). Therefore, they are suggested to have less lipids and a higher proportion of ash (Hagen et al. 2000; Lenky et al. 2012). Furthermore *Trematomus* spp., *Notothenia coriiceps* and *Gobionotothen gibberifrons* mainly feed on benthic organisms which can have a relatively low- energetic value such as polychaetes, molluscs and amphipods (Kock 1992; Lenky et al. 2012). *Trematomus lepidorhinus* feeds away from the bottom and possibly has more fat to increase buoyancy, explaining its higher energetic density (Lenky et al. 2012), although *L. squamifrons* has also been suggested to feed on both benthic and pelagic organisms (Kock 1992). Similar to *Pleuragramma antarctica*, the lipid content of *T. lepidorhinus* is known to increase with increasing size and weight (Friedrich & Hagen 1994).

Champsocephalus gunnari and *Chaenocephalus aceratus* have a northerly distribution usually occurring close to the APF, while the distribution of *Channichthys* spp. is limited to the Kerguelen Plateau (Duhamel et al. 2014). These species have similar energetic densities while they utilize different food sources (Kock 1992). An overview of recorded average energy density measurements of nototheniid fish species including, where possible, values expressed in kJ g^{-1} WW can be found in Table 4.6. Due to recent changes in the classification, former separate families are now included in the family Nototheniidae and the new proposed sub-families of the fish are given in brackets in the table (Duhamel et al. 2014). The energy densities of gonad, liver and muscle tissue of several nototheniid fish were measured separately using bomb calorimetry by Vanella et al. (2005). In most investigated species, the AFDW energy densities were highest in the liver (Vanella et al. 2005).

Table 4.6: Overview of the average energy density of several nototheniid species. Sub-families are given in brackets. Energy densities were measured using bomb calorimetry (BC) and proximate composition (PC). Energy densities in italics represent values that were converted using information from the given sources. *n* represents the number of samples measured. Where this expresses samples of pooled individuals, this is indicated with (p). The standard error (SE) or standard deviation (SD) as given in the original source are added where available (±). The mean size is given in standard length (SL) unless otherwise indicated.

SEASON	LOCATION	*n*	MEAN WW	WATER	ENERGY DENSITY		METHOD	SOURCE
			(g)	CONT. (%)	kJ g^{-1} WW	kJ g^{-1} DW		
Champsocephalus gunnari **(Channichthyinae)**								
Autumn	Kerguelen Is.	3	311.7 ± 16.1 SD	76.7 ± 2.0 SD	5.4 ± 0.3 SD	23.2 ± 0.6 SD	BC	Lea et al. 2002
	Scotia Sea	3	437[1] ± 15 SD	81.0 ± 0.4 SE	*4.65*	*24.74*	PC[2,3]	Oehlenschläger 1991
Spring	Kerguelen Is.			80.1	*4.74*	23.84	PC[3]	Durand and Nicolle 1980
Chaenocephalus aceratus **(Channichthyinae)**								
Autumn	Scotia sea	10	497[1] ± 34 SD	81.2 ± 0.8 SE	*4.56*	*24.24*	PC[2,3]	Oehlenschläger 1991
Channichthys rhinoceratus **(Channichthyinae)**								
Spring	Kerguelen Is.			82.8	*3.97*	23.09	PC[3]	Durand and Nicolle 1980
Dissostichus mawsoni **(Dissostichinae)**								
Spring	McMurdo	1		68.6	9.40	*29.94*	BC	Lenky et al. 2012
Dissostichus eleginoides **(Dissostichinae)**								
Spring	Kerguelen Is.			69.4	*9.00*	*29.42*	PC[3]	Durand and Nicolle 1980

Table 4.6 continued

SEASON	LOCATION	*n*	MEAN WW	WATER	ENERGY DENSITY		METHOD	SOURCE
			(g)	CONT. (%)	kJ g^{-1} WW	kJ g^{-1} DW		
Pagothenia borchgrevinki **(Trematominae)**								
Spring	McMurdo 2006	1 (p)	182^1 ± 3 SE	77.2	5.6	24.56	BC	Lenky et al. 2012
	McMurdo 2006	4	205^1 ± 26 SE	77.6 ± 3.1 SE	5.3 ± 1.3 SE	23.66	BC	Lenky et al. 2012
	McMurdo 2007	4	235^1 ± 27 SE	76.0 ± 2.5 SE	5.7 ± 1.1 SE	23.75	BC	Lenky et al. 2012
Trematomus bernacchii **(Trematominae)**								
Spring	McMurdo 2006	(p)	146^1 ± 18 SE	78.3	4.7	21.66	BC	Lenky et al. 2012
	McMurdo 2007	(p)	164^1 ± 25 SE	77.4	5.0	22.12	BC	Lenky et al. 2012
	McMurdo 2007	4	189^1 ± 22 SE	76.2 ± 3.0 SE	5.5 ± 1.3 SE	23.11	BC	Lenky et al. 2012
Trematomus hansoni **(Trematominae)**								
Spring	McMurdo Sound	7	211^1 ± 262 SE	76.7 ± 2.0 SE	5.4 ± 0.9 SE	23.18	BC	Lenky et al. 2012
Trematomus pennellii (Trematominae)								
Spring	McMurdo Sound	1 (p)	141^1 ± 16 SE	78.3	4.6	21.20	BC	Lenky et al. 2012
Trematomus eulepidotus **(Trematominae)**								
Summer	Ross Sea	(p)	196^1 ± 31 SE	75.6	5.7	23.36	BC	Lenky et al. 2012
Trematomus lepidorhinus **(Trematominae)**								
Summer	Ross Sea	(p)	274^1 ± 56 SE	71.3	7.7	26.83	BC	Lenky et al. 2012
Trematomus scotti **(Trematominae)**								
Summer	Ross Sea	(p)	129^1 ± 7 SE	78.5	4.0	18.60	BC	Lenky et al. 2012
Lepidonotothen squamifrons **(Trematominae)**								
Summer	Ross Sea	(p)	224^1 ± 317 SE	81.3	4.00	21.39	BC	Lenky et al. 2012
Spring	Kerguelen Is.			79.8	4.78	23.67	PC^3	Durand and Nicolle 1980
					5.00			Goldsworthy et al. 2001
Notothenia rossi **(Nototheniinae)**								
Spring	Kerguelen Is.			76.7	6.07	26.07	PC^3	Durand and Nicolle 1980
Notothenia neglecta **(Nototheniinae)**								
Autumn	Scotia sea	3	317^1 ± 51 SD	78.4 ± 1.0 SE	5.35	24.77	$PC^{2,3}$	Oehlenschläger 1991
Gobionotothen gibberifrons **(Gobinototheninae)**								
Autumn	Scotia sea	13	377^1 ± 17 SD	79.8 ± 0.4 SE	4.85	24.05	$PC^{2,3}$	Oehlenschläger 1991

[1] measured in total length (TL)
[2] crude protein measurement used
[3] carbohydrates not measured.

Electrona antarctica

Electrona antarctica is a circumpolar, widely distributed mesopelagic species found at and south of the APF (Duhamel et al. 2014). It has been found to be an important prey species for flying birds in the Weddell and Scotia Seas (Ainley et al. 1991). Records of the average energy density of *E. antarctica* showed a range between 18.9 kJ g^{-1} DW, for fish from the Scotia Sea during spring (proximate composition, Donnelly et al. 1990), and 34.3 kJ g^{-1} DW, for fish from the Kerguelen plateau during winter (bomb calorimetry, Lea et al. 2002). The lower range of values found in the literature were usually estimates made using proximate composition. Average recorded energy density measurements of *E. antarctica* including, where possible, values expressed in kJ g^{-1} WW are listed in Table 4.7.

The energy content of *E. antarctica* generally increased with increasing size (Donnelly et al. 1990; Van de Putte et al. 2006; Van de Putte et al. 2010). Van de Putte et al. (2006) showed that the energy density of *E. antarctica* strongly increased with size in age class 0, and slows down from the second year onward while the variation increases. This trend is confirmed in fish from East Antarctica and the Lazarev Sea in several seasons (Fig. 4.2a). This size-energy density relationship suggests that the small fish invest more of their energy in growth compared to the older individuals, probably due to the need to grow quickly in order to avoid predation (Van de Putte et al. 2006).

Donnelly et al. (1990) found an increase in lipid and energy content from spring to autumn, and from autumn to winter (Table 4.7), and suggested that this might be due to the accumulation of reserves for winter and early spring. In contrast, however, the data from the Lazarev Sea suggest highest energy densities in summer, decreasing towards autumn and winter. In general, energy density of *E. antarctica* was higher in the Lazarev Sea compared to East Antarctica and Macquarie Island (Fig. 4.2a). Available measurements of individual fish, depicted in Fig. 4.2, allowed for a statistical comparison. The energy density of fish from the Lazarev Sea in summer was significantly higher than all other data (ANOVA $F_{24, 254} = 36.8$, $p < 0.001$; Tukey's HSD, $p < 0.0001$), while the energy density of fish caught in East Antarctica in autumn was significantly lower than all other locations (Tukey's HSD, $p < 0.03$). Based on current available science, *E. antarctica* is assumed to spawn year-round with a peak in late summer/early autumn, or late spring/summer (Donnelly et al. 1990). In contrast, Gon & Heemstra (1990) suggested a peak spawning season in autumn/winter. However, the energetic content of maturing gonads does not appear to contribute significantly to the total energy content of the fish (Donnelly et al. 1990). Therefore, the main driver for differences in energy density is probably food composition, which differs for *E. antarctica* depending on area and season (Flores et al. 2008). The relationship between DW (in %WW) and wet weight energy density was similar in fish from all seasons and regions (ANCOVA, $p > 0.05$; Fig. 4.2b).

Gymnoscopelus braueri

Gymnoscopelus braueri is also a circumpolar, widely distributed species found between de SAF and the SACCF (Duhamel et al. 2014). Recorded average energy densities of *G. braueri* ranged from 19.9 kJ g^{-1} DW in fish from the Scotia Sea during spring (proximate composition, Donnely et al. 1990) to 39.0 kJ g^{-1} DW in fish from the vicinity of Macquarie Island during summer (bomb calorimetry, Tierney et al. 2002). An overview of recorded average energy density measurements of *G. braueri* including, where possible, values expressed in kJ g^{-1} WW can be found in Table 4.8.

Tierney et al. (2002) found a strong difference in calorific value between size classes in summer. Fish <40 mm had a significantly higher dry weight energy density compared to larger individuals, which is in contrast to *E. antarctica*. Interestingly, the small fish also had a significantly higher water content (Tierney

Table 4.7: Overview of the average energy densities of *Electrona antarctica*. In the 'method' column the method used for energetic value determination is indicated, where BC is bomb calorimetry and PC is proximate composition. Numbers in italics represent values that were converted using the energetic values, wet weights, dry weights and water contents from the given sources. *n* represents the number of samples measured. Where this expresses samples of pooled individuals, this is indicated with (p). The standard error (SE) or standard deviation (SD) where available. The mean size is given in standard length (SL) unless otherwise indicated.

SEASON	LOCATION	*n*	MEAN SIZE (mm)	MEAN WW (g)	MEAN DW (g)	WATER CONTENT (%)	ENERGY DENSITY kJ g^{-1} WW	ENERGY DENSITY kJ g^{-1} DW	MTD	SOURCE
Summer	Macquarie	20	50.4 ± 13.1 SD	1.9 ± 1.5 SD	0.6 ± 0.5 SD	69.9 ± 4.3 SD	9.04 ± 1.889 SD	30.76 ± 8.30 SD	BC	Tierney et al. 2002
	Lazarev Sea	31	49.1 ± 16.8 SD^1	1.4 ± 1.4 SD	0.5 ± 0.5 SD	73.3 ± 7.2 SD	9.94 ± 1.11 SD	32.26 ± 1.15 SD	BC	This study (PS89)
	WAP		76.5 ± 3.8 SE					31.9 ± 0.29 SE	BC	Ruck et al. 2014
	Elephant Island	3				71.7 ± 0.6 SE	8.55 ± 0.19 SE^2	*30.21*	PC	Ishii et al. 2007
Autumn	East antarctica	22	57.4 ± 21.2 SD	2.6 ± 2.5 SD	0.7 ± 0.8 SD	73.7 ± 4.0 SD	7.26 ± 1.68 SD	27.21 ± 2.76 SD	BC	Van de Putte et al. 2010
	Lazarev Sea	113	47.6 ± 15.9 SD	1.8 ± 1.8 SD	0.6 ± 0.6 SD	68.4 ± 4.1 SD	9.35 ± 1.58 SD	29.4 ± 1.80 SD	BC	Van de Putte et al. 2006
	Weddell Sea	27	61.9	3.9	*1.2*	68.7 ± 3.4 SD	6.73	*21.5*	PC	Donnelly et al. 1990*
						68.2	9.11	*28.65*	BC	Green and Gales 1990
Winter	Lazarev Sea	74	52.6 ± 19.5 SD	2.4 ± 3.5 SD	0.8 ± 1.2 SD	71.3 ± 4.2 SD	8.35 ± 1.82 SD	28.77 ± 2.67 SD	BC	Van de Putte 2008
	Kerguelen	5	64.5 ± 8.6 SD	3.2 ± 1.8 SD	*1.3*	60.8 ± 8.8 SD	13.3 ± 2.6 SD	34.3 ± 3.8 SD	BC	Lea et al. 2002
	Scotia Sea	35	68.3	5.6	*1.7*	69.6 ± 3.7 SD	*7.71*	*25.36*	PC	Donnelly et al. 1990
Spring	Ross Sea	(p)	81^1 ± 10 SE	*7.4 ± 2.5 SE*	*2.3*	69.6	9.0	*29.61*	BC	Lenky et al. 2012
	Scotia Sea	16	66.1	3.8	*1.2*	69 ± 3.7 SE	5.86	*18.9*	PC	Donnelly et al. 1990

Table 4.8: As table 7 but for *Gymnoscopelus braueri*

SEASON	LOCATION	*n*	MEAN SIZE (mm)	MEAN WW (g)	MEAN DW (g)	WATER CONTENT (%)	ENERGY DENSITY kJ g^{-1} WW	ENERGY DENSITY kJ g^{-1} DW	MTD	SOURCE
Summer	South Georgia	3				66.1 ± 1.5 SE	9.06	*29.85*	PC	Clarke & Prince 1980
	Macquarie	18	78.2 ± 35.3 SD	5.3 ± 5.7 SD	1.94 ± 2.2 SD	69.4 ± 8.4 SD	10.91 ± 1.51 SD	39.03 ± 14.33 SD	BC	Tierney et al. 2002
Autumn	Weddell Sea	3	101.3	8.74	*2.9*	66.6 ± 2.2 SD	7.94	*23.77*	PC	Donnelly et al. 1990*
	Lazarev Sea	20	87.3 ± 18.1 SD	6.3 ± 5.3 SD	1.9 ± 1.7 SD	69.5 ± 4.0 SD	8.86 ± 1.42 SD	29.37 ± 1.51 SD	BC	Van de Putte et al. 2006
Winter	Scotia Sea	23	81.2	5.83	*1.9*	67.2 ± 2.3 SE	7.52	*22.93*	PC	Donnelly et al. 1990
	Lazarev Sea	3 (p)	49.7 ± 9.0 SD1	0.7 ± 0.5 SD	0.3 ± 0.2 SD	62.1 ± 2.0 SD	10.68 ± 0.24	29.17 ± 1.31 SD	BC	This study (PS81)
Spring	Ross Sea	(p)	101^1 ± 7 SE	9 ± 1.9 SE	*2.8*	68.5	9.3	*29.52*	BC	Lenky et al. 2012
	Scotia Sea	3	110.3	9.2	*3.3*	64.2 ± 2.5 SD	7.14	*19.94*	PC	Donnelly et al. 1990

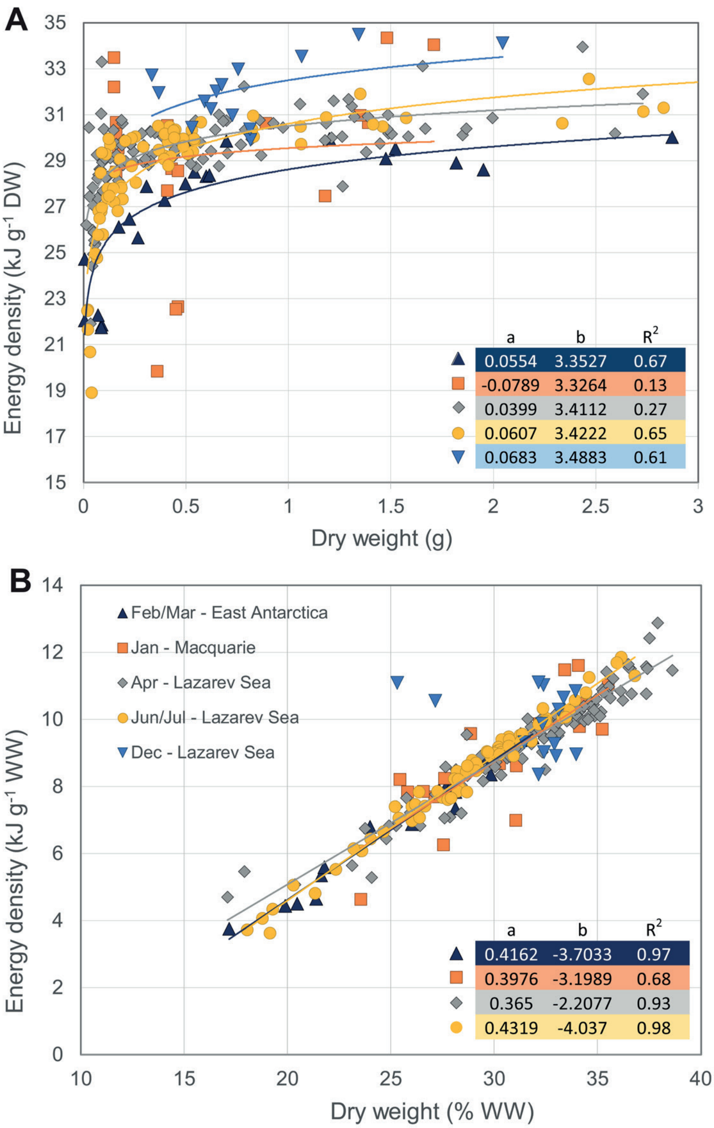

Figure 4.2: *Electrona antarctica*; A) the relationship between DW and energy density g^{-1} DW including the parameters for the linear regression of ln(y) = a + b ln(x), and the corresponding power function $y = x^b e^a$ and, B) the relationship between percentage dry weight (DW) and energy density g^{-1} wet weight (WW) including regression parameters of the linear regression lines y = ax + b. Regression parameters are depicted in the figures. Data were obtained from Tierney et al. 2002 (Macquarie Island), Van de Putte et al. 2010 (East Antarctica, February-March), Van de Putte et al. 2006 (Lazarev Sea, April), Van de Putte 2008 (Lazarev Sea, June/July) or collected during PS89 (Lazarev Sea, December). All measurements were done using bomb calorimetry. The legend, depicted in B, indicates month and location of data collection. No regression was fitted for the December-Lazarev Sea data in B, due to two individuals that had divergent dry weights.

et al. 2002). This pattern was, however, not confirmed by data from the Lazarev Sea in autumn where the dry weight energy density did not differ in different sized fish (Van de Putte et al. 2006). Within the size classes found in Tierney et al. (2002) there was no (linear) relationship between size and dry weight energy density (Fig. 4.3a). The data from Macquarie Island (Tierney et al. 2002) and the Lazarev Sea (Van de Putte et al. 2006 and PS81) allowed for statistical comparison, which showed that the energy density of *G. braueri* >40 mm did not vary significantly between seasons and regions, even in the relatively small fish from winter (ANOVA, $F_{3,35} = 0.288$, $p = 0.83$).

In fish > 40 mm, the relationship between water content and wet weight energy density of *G. braueri* from the Lazerev Sea in April and the Macquarie region in January show similar slopes (Fig. 4.3b) suggesting that there is no evidence that tissues replacing the body water are markedly different between seasons and/or regions (ANCOVA, $p > 0.05$). As the small fish from the Macquarie region have a relatively high energy density, the intercept of this regression is significantly higher compared to regressions of the other data (ANCOVA, $p < 0.05$).

Other myctophids

The average energy density of other myctophid species reported in the literature range from 17.1 kJ g^{-1} DW

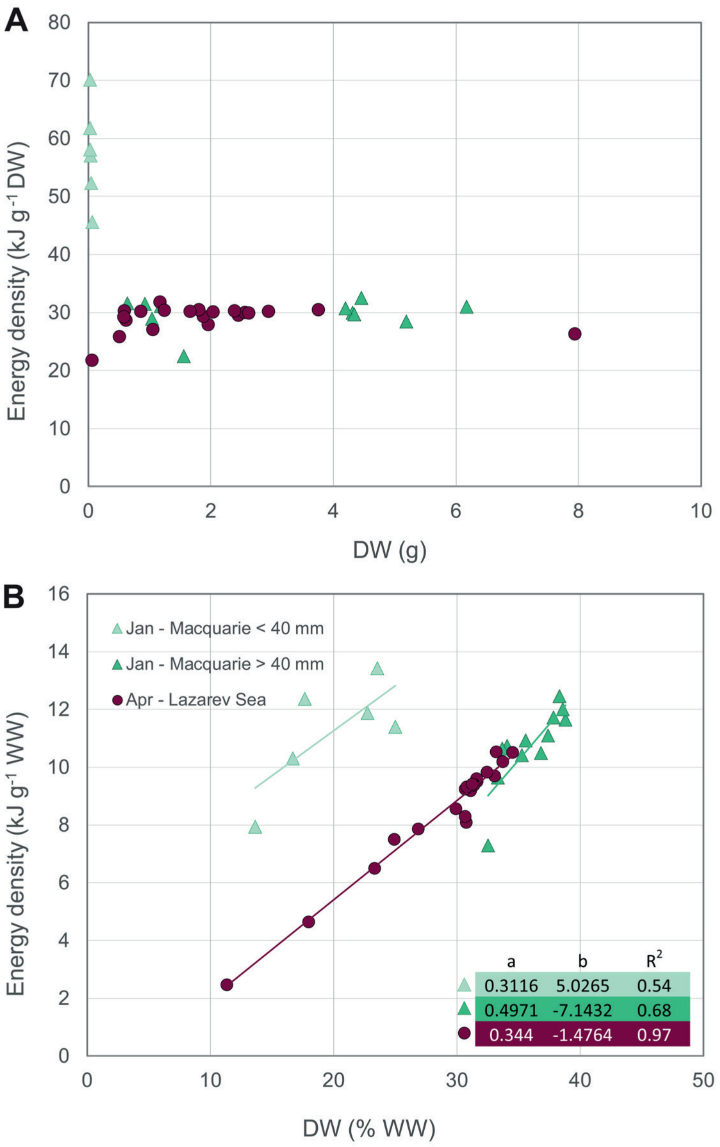

Figure 4.3: *Gymnoscopelus braueri;* A) the relationship between DW and energy density g^{-1} DW and, B) the relationship between percentage dry weight (DW) and energy density g^{-1} wet weight (WW) including parameters of the linear regression lines y = ax + b. Regression parameters are depicted in the figure. Data were obtained from Tierney et al. 2002 (Macquarie Island, January) and Van de Putte et al. 2006 (Lazarev Sea, April). Due to significant differences in energetic density, data from Tierney et al. (2002) were separated in individuals <40 mm and >40 mm. All measurements were done using bomb calorimetry. Legend indicates month and location of data collection.

of *Protomyctophum tenisoni* and *Protomyctophum bolini* caught in the Scotia Sea during winter (proximate composition, Donnelly et al. 1990) to 39.3 kJ g^{-1} DW of *Protomyctophum andriashevi* caught in the vicinity of Macquarie Island during summer (bomb calorimetry, Tierney et al. 2002). Similiar to *G. braueri*, Tierney et al. (2002) found several, but not all, other myctophid species in which small individuals (<40 mm SL, approximately) had a significantly higher dry weight energy density such as *Gymnoscopelus fraseri, P. andriashevi, P. bolini* and *Lampanyctus archirus*. In contrast to the other species, the water content of *G. fraseri* and *P. andriashevi* did not differ significantly between size classes (Tierney et al. 2002). An overview of recorded average energy density measurements of myctophid fish species including, where possible, values expressed in kJ g^{-1} WW are listed in Table 4.9.

Of the species listed, *P. tenisoni, Electrona carlsbergi, G. fraseri* and *Gymnoscopelus piabilis* occur mainly in the sub-Antarctic zone, while the other species occur south of the PF or have a more wide distribution. *Protomyctophum tenisoni, E. carlsbergi, Gymnoscopelus ophistopterus* and *Gymnoscopelus microlampas* have relatively low energy densities considering what can be assumed for lipid rich myctophid species. Lea et al. (2002) found that *P. tenisoni* had a relatively low lipid content compared to other investigated myctophid fishes. *Electrona carlbergi* was however lipid-rich in this study (Lea et al. 2002).

Bathylagus antarcticus

Of the two main species of Bathylagidae (*Bathylagus tenuis* and *Bathylagus antarcticus*) found in the meso- and bathypelagic zones of the Southern Ocean, *B. antarcticus* has the more southern distribution (Duhamel et al. 2014). Recorded average energy densities of *B. antarcticus* ranged from 14.8 kJ g^{-1} DW, estimated in fish from the winter Scotia sea using proximate composition (Donnelly et al. 1990), to 22.8 kJ g^{-1} DW measured in fish from the spring Ross Sea using bomb calorimetry (Lenky et al. 2012). Average recorded energy density measurements of *B. antarcticus* including, where possible, values expressed in kJ g^{-1} WW are listed in Table 4.10.

The dry weight energy density of *B. antarcticus* caught in the Lazarev Sea in April (Van de Putte et al. 2006) did not differ significantly from fish caught in the vicinity of Macquarie Island in January (Tierney et al. 2002), even though the latter fish were larger (Fig. 4.4a). In both seasons/regions, the energy density did not change with changing sizes. Water content of *B. antarcticus* was significantly higher in April than it was in January, resulting in a lower wet weight energy density in the Lazarev Sea in April compared to the Macquarie region in January. The relationship between wet weight energy density and proportional dry weight found by Van de Putte et al. (2006) suggested that water is replaced with low energy tissue. This relationship is, however, different in the fish from Tierney et al. (2002), where energy density is relatively low compared to other fish species from the same study, but the wet weight energy density increases relatively fast with decreasing water content (Fig. 4.4b).

Table 4.9: Overview of the average energy density of several myctophid species. Energy density measurement were done using bomb calorimetry (BC) and proximate composition (PC). Energy densities in italics represent values that were converted using information from the given sources. *n* represents the number of samples measured. Where this expresses samples of pooled individuals, this is indicated with (p). The standard error (SE) or standard deviation (SD) are given where available. The mean size is given in standard length (SL) unless otherwise indicated.

SEASON	LOCATION	*n*	MEAN WW (g)	WATER CONT. (%)	ENERGY DENSITY kJ g^{-1} WW	ENERGY DENSITY kJ g^{-1} DW	MTD	SOURCE
Gymnoscopelus ophistopterus								
Autumn	Weddell Sea	6	108.8	80.1 ± 3.3 SD	4.58	*23.02*	PC	Donnelly et al. 1990*
Gymnoscopelus fraseri								
Summer	Macquarie Is.	18 (p)	35-78	73.1 ± 4.0 SD	*7.89*	29.32 ± 8.62 SD	BC	Tierney et al. 2002
Winter	Kerguelen	5	66.2 ± 7.1 SD	62.6 ± 10.1 SD	10.2 ± 3.5 SD	27.0 ± 2.9 SD	BC	Lea et al. 2002
Gymnoscopelus piabilis								
Winter	Kerguelen Is.	5	187.6 ± 32.0 SD	68.5 ± 3.0 SD	9.5 ± 1.7 SD	30.0 ± 30.0 SD	BC	Lea et al. 2002
Gymnoscopelus nicholsi								
Summer	Elephant Is.	3		76.7 ± 0.7 SE	5.82 ± 0.2 SE1	*24.98*	PC	Ishii et al. 2007
Autumn				67	8.43	*25.55*	PC	VNIRO, 2000
				66.4	9.58	*28.51*	BC	Green & Gales 1990
Winter	Kerguelen Is.	1	128	66.8	9.80	28.00	BC	Lea et al. 2002
	Scotia Sea	1	148	59.6	11.75	*29.08*	PC	Donnelly et al. 1990
Spring	Ross Sea	(p)	149^2 ± 7 SE	64.9	10.3	*29.34*	BC	Lenky et al. 2012
Gymnoscopelus microlampas								
Summer	Macquarie Is.	6 (p)	84-122	74.7 ± 1.3 SD	*5.72*	22.62 ± 1.14 SD	BC	Tierney et al. 2002
Electrona subaspera								
Summer	Macquarie Is.	6 (p)	10-117	72.1 ± 1.7 SD	*7.41*	26.56 ± 1.15 SD	BC	Tierney et al. 2002
Winter	Kerguelen Is.	3	92.7 ± 7.5 SD	72.3 ± 1.6 SD	7.4 ± 1.0 SD	26.6 ± 2.1 SD	BC	Lea et al. 2002
Electrona carlsbergi								
Summer	South Georgia	3		71.2 ± 0.3 SE	6.57	*22.84*	PC	Clarke & Prince 1980
				72.7	*5.87*	*21.50*	PC	VNIRO, 2000
	Possession Is.	3	78.8 ± 4.6 SD	70.2 ± 0.4 SD	7.0 ± 0.2 SD^3	23.5 ± 0.4 SD^3	BC	Cherel & Ridoux 1992
	Elephant Is.	3		73.8 ± 0.7 SE	6.92 ± 0.1 SE	*26.41*	PC	Ishii et al. 2007
	Macquarie Is.	6 (p)	*26-97*	*76.7 ± 5.2 SD*	*5.05*	21.67 ± 3.2 SD	BC	Tierney et al. 2002
Winter	Kerguelen Is.	6	84.7 ± 3.6 SD	67.0 ± 3.2 SD	8.6 ± 1.2 SD	25.9 ± 3.2 SD	BC	Lea et al. 2002
Spring	Ross Sea	(p)	72 ± 6 SE^2	73.9	6.1	*23.37*	BC	Lenky et al. 2012
Krefftichthys anderssoni								
Summer	Possession Is.	2	47.7 ± 9.2 SD	69.3 ± 1.4 SD	8.1 ± 0.3 SD^3	26.4 ± 0.1 SD^3	BC	Cherel & Ridoux 1992
	Macquarie Is.	18 (p)	40-69	69.8 ± 1.9 SD	*8.32*	27.54 ± 2.8 SD	BC	Tierney et al. 2002
Autumn				66.6	10.12	30.30	BC	Green & Gales 1990
Protomyctophum tenisoni								
Summer	Macquarie Is.	6 (p)	43-51	73.2 ± 1.1 SD	*5.50*	20.53 ± 0.65 SD	BC	Tierney et al. 2002
Winter	Kerguelen Is.	1	45	74.6	6.1	24.2	BC	Lea et al. 2002
	Scotia Sea	3	*47*	72.2 ± 0.6 SD	*4.75*	*17.09*	PC	Donnelly et al. 1990

Table 4.9 continued.

SEASON	LOCATION	*n*	MEAN WW (g)	WATER CONT. (%)	ENERGY DENSITY kJ g^{-1} WW	kJ g^{-1} DW	MTD	SOURCE
Protomyctophum andriashevi								
Summer	Macquarie Is.	12 (p)	23-51	*75.7 ± 5.3 SD*	*9.54*	39.26 ± 21.48 SD	BC	Tierney et al. 2002
Protomyctophum bolini								
Summer	Macquarie Is.	18 (p)	29-61	*73.5 ± 3.9 SD*	*7.42*	28.0 ± 10.61 SD	BC	Tierney et al. 2002
Winter	Scotia Sea	6	48.3	74.6 ± 1.4 SD	4.34	*17.09*	PC	Donnelly et al. 1990
Protomyctophum parallelum								
Summer	Macquarie Is.	6 (p)	20-48	*70.9 ± 3.6 SD*	*8.23*	28.27 ± 12.28 SD	BC	Tierney et al. 2002
Lampanyctus archirus								
Summer	Macquarie Is.	18 (p)	35-147	*78.5 ± 3.4 SD*	*6.12*	28.47 ± 14.43 SD	BC	Tierney et al. 2002

1 a lipid factor of 39.6 kJ g^{-1} used for energy density estimation
2 measured in total length (TL)
3 Sample taken from bird stomach contents, in which the energetic value is potentially overestimated due to water removal in stomach
* A factor of 4.19 was used to convert calories to joules

Other fishes

An overview of recorded average energy density measurements of five fish species other than the ones listed above including, where possible, values expressed in kJ g^{-1} WW can be found in Table 4.11. The families to which the species belong are given in the table. Among these fishes, *Paradiplospinus gracilis* had the highest mean energy density of 25.6 kJ g^{-1} DW. The lowest values were found in *Notolepis coatsi* from autumn and winter in the Weddell-Scotia Seas sector (14.9 and 15.6 kJ g^{-1} DW, respectively). Both measurements were done using proximate composition. Ciancio et al. (2007) list another 9 species of which the distribution in the Southern Ocean is limited to the Patagonian shelf. Their energy density (measured using bomb calorimetry) ranged from 16.2 kJ g^{-1} DW for *Genypterus blacodes* (Ophidiidae) to 26.2 kJ g^{-1} DW for *Eleginops maclovinus* (Eleginopidae; Ciancio et al. 2007).

OTHER SPECIES

Squid

Squid are often a part of, or even dominate in some seasons, the diet of many top predators (Klages 1989; Ainley et al. 1991; Cherel et al. 1996; Kirkman et al. 2000; Van Franeker et al. 2001). Therefore, an indication of their energy density is highly relevant in trophic and ecosystem studies. Although measurements of squid are limited, reported values suggest that the energy density of squid increases with increasing latitudes (from the tropics to Southern Ocean), and that the energy density of squid in the Southern Ocean is comparable with that of nototheniid fish. Squid are difficult to catch with scientific sampling gear (Rodhouse et al. 2014), explaining the limited amount of measurements on this group (Table 4.12). Therefore, we have included some energetic density measurements from regions other than the Southern Ocean in this section for comparison.

Croxall & Prince (1982) provide an overview of energy densities of cephalopods from different locations.

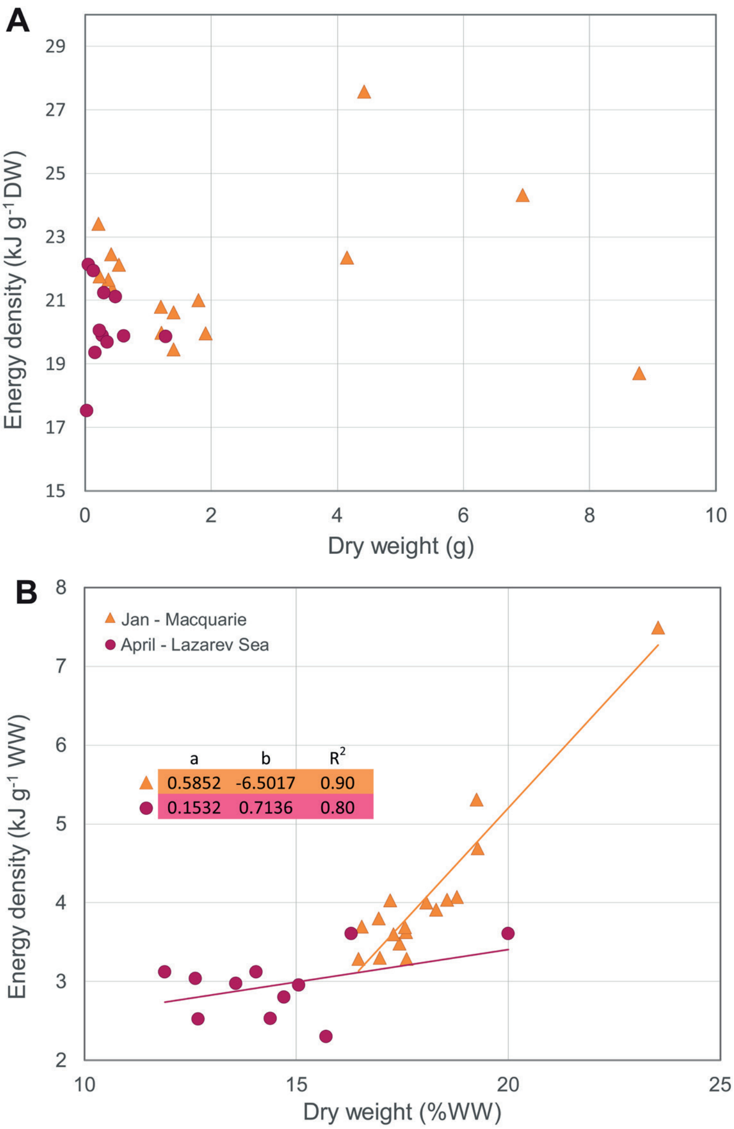

Figure 4.4: *Bathylagus antarcticus*; A) the relationship between DW and dry weight energy density and, B) the relationship between percentage dry weight (DW) and energy density g^{-1} wet weight (WW) including parameters of the linear regression lines y = ax + b. Regression parameters are depicted in the figure. Data were obtained from Tierney et al. 2002 (Macquarie Island, January) and Van de Putte et al. 2006 (Lazarev Sea, April). All measurements were done using bomb calorimetry. Legend indicates month and location of data collection.

The reported values ranged from 14.9 to 19.9 kJ g^{-1} DW. The cephalopods listed in Croxall & Prince (1982), belong to the families Loliginidae, Octopodidae, Ommastrephidae, Onychoteuthidae and Sepiidae. Of the reported species only the squid *Doryteuthis gahi* occurs south of the STF, over the Patagonian shelf in the sub-Antarctic region (Rodhouse et al. 2014). It had an energy density of 16.2 kJ g^{-1} DW (Ferreyra in Pandit and Magar, 1972). Ciancio et al. (2007) reported an energy density of 21.2 kJ g^{-1} DW for *D. gahi*. They, furthermore, reported the energy density of *Illex argentinus*, also caught over the Patagonian shelf (Table 4.12; Ciancio et al. 2007)

Moroteuthis ingens is a very abundant species in the Southern Ocean. The mantle and tentacles of *M. ingens*,

Table 4.10: Overview of the average energetic densities of *Bathylagus antarcticus*. Energy density measurements were done using bomb calorimetry (BC) and proximate composition (PC). Energetic values in italics represent values that were converted using information from the given sources. *n* represents the number of samples measured. Where this expresses samples of pooled individuals, this is indicated with (p). The standard error (SE) or standard deviation (SD) as given in the original source are added where available. The mean size is given in standard length (SL) unless otherwise indicated.

SEASON	LOCATION	*n*	MEAN SIZE (mm)	MEAN WW (g)	MEAN DW (g)	WATER CONTENT (%)	ENERGY DENSITY kJ g^{-1} WW	ENERGY DENSITY kJ g^{-1} DW	MTD	SOURCE
Summer	Macquarie Is.	18	116.8 ± 35.4 SD	14.2 ± 14.2 SD	2.70 ± 2.8 SD	81.7 ± 1.9 SD	3.93 ± 1.17 SD	21.43 ± 4.88 SD	BC	Tierney et al. 2002
Autumn	Lazarev Sea	7	77.6 ± 23.4 SD	3.1 ± 3.6 SD	0.40 ± 0.4	85.6 ± 2.5 SD	2.92 ± 0.42SD	20.36 ± 1.32 SD	BC	Van de Putte et al. 2006
	Weddell Sea	32	77.2	3.8	*0.5*	85.9 ± 2.0 SD	2.24	*15.89*	PC	Donnelly et al. 1990*
Winter	Scotia Sea	16	90	7.8	*0.9*	88.4 ± 1.4 SD	1.72	*14.83*	PC	Donnelly et al. 1990
Spring	Ross Sea	(p)	151[1] ± 20 SE	38.6 ± 18.2 SE	*4.9*	87.3	*2.9*	22.83	BC	Lenky et al. 2012
	Scotia Sea	8	99.4	5.8	*0.9*	85.1 ± 2.1 SD	2.22	*14.89*	PC	Donnelly et al. 1990

[1] measured in total length (TL)

* A factor of 4.19 was used to convert calories to joules

collected from the stomach contents of king penguins at Possession Island in summer, had an energy density of 23.5 kJ g^{-1} DW, measured using bomb calorimetry (Cherel & Ridoux 1992). Proximate composition values of *M. ingens* caught near New Zealand (Vlieg 1984), result in an estimated energy density of 24.0 kJ g^{-1} DW. The mantle, fins and tentacles of *M. ingens*, had a similar energy density of approximately 23 kJ g^{-1} DW. The energy density of the inner organs was higher (25.7 kJ g^{-1} DW), which is probably caused by ingested food residing in the stomach (Vlieg 1984) or lipids stored in the digestive gland (Phillips et al. 2001).

Two species of squid that are not known to reside in sub-Antarctic or Antarctic waters (Rodhouse et al. 2014), but which have been found in the stomachs of penguin species, had energy densities of 24.7 kJ g^{-1} DW (*Sepiotheuthis australis*) and 23.4 kJ g^{-1} DW (*Nototodarus gouldi*; Green & Gales 1990). Clarke et al. (1985) measured the energy density of several species of squid caught in the North-East Atlantic Ocean. The energy value ranged from 17.5 kJ g^{-1} DW (1.8 kJ g^{-1} WW; *Mastigoteuthis* sp.) to 21.5 kJ g^{-1} DW (2.7 kJ g^{-1} WW; *Histioteuthis* sp.). The energy value per gram WW was highly variable due to different types of buoyancy regulation used by different squid species, resulting in large differences in water content between species. This did however not result in large differences in the energy density per gram DW, the range of which was limited (Clarke et al. 1985).

Gelatinous zooplankton

A large biomass component of marine ecosystems is formed by gelatinous zooplankton (McInnes et al. 2017). The gelatinous zooplankton include for instance Ctenophora, or comb jellies, and Cnidaria, including Scyphozoa and Hydrozoa. The latter class contains

Table 4.11: Overview of the average energy density of several fish species. Families are given in brackets. Energy density measurements were done using bomb calorimetry (BC) and proximate composition (PC). Energy densities in italics represent values that were converted using information from the given sources. *n* represents the number of samples measured. Where this expresses samples of pooled individuals, this is indicated with (p). The standard deviation (SD) is given where available. The mean size is given in standard length (SL).

SEASON	LOCATION	*n*	MEAN WW (g)	WATER CONT. (%)	ENERGY DENSITY		MTD	SOURCE
					kJ g^{-1} WW	kJ g^{-1} DW		
***Notolepis coatsi* (Paralepididae)**								
Autumn	Weddell Sea	5	62.4	82.2 ± 2.7	2.65	*14.89*	PC	Donnelly et al. 1990*
Winter	Scotia Sea	5	63.4	79.4 ± 3.4	3.22	*15.63*	PC	Donnelly et al. 1990
Summer	East Antarctica	3	168 ± 52.2	79.8 ± 1.3	4.42 ± 0.33	21.90 ± 0.73	BC	Van de Putte et al. 2010
***Paradiplospinus gracilis* (Gempylidae)**								
Summer	Possesion Is.	1	168.7	78.9	4.6[1]	21.8[1]	BC	Cherel & Ridoux 1992
Winter	Scotia Sea	2	325.5	69.1 ± 2.4	7.92	*25.63*	PC	Donnelly et al. 1990
***Antimora rostrata* (Moridae)**								
Summer	Macquarie	2 (p)	227 – 225	80.1 ± 1.0	*4.33*	*21.75* ± 2.28	BC	Tierney et al. 2002
***Stomias gracilis* (Stomiidae)**								
Summer	Macquarie	18(p)	130 – 278	77.8 ± 3.1	*5.15*	23.20 ± 2.99	BC	Tierney et al. 2002
***Micromesistius australis* (Gadidae)**								
	Patagonia	3	140-150	78.5	4.54	*21.12*	BC	Ciancio et al. 2007

[1]Sample taken from bird stomach contents, in which the energetic value is potentially overestimated due to water removal in stomach

* A factor of 4.19 was used to convert calories to joules

Table 4.12: Overview of the average energy density of Southern Ocean squid species. In the method (MTD) column the method used for energetic value determination is indicated, where BC is bomb calorimetry and PC is proximate composition. Energetic values in italics represent values that were converted using the energetic values, wet weights and dry weights from the given source. *n* represents the number of samples measured.

SEASON	LOCATION	*n*	MEAN WW (g)	WATER CONT. (%)	ENERGY DENSITY		MTD	SOURCE
					kJ g^{-1} WW	kJ g^{-1} DW		
Doryteuthis gahi								
				80.9	3.09[1]	*16.18*	PC	Pandit and Magar 1972
	Patagonia	8	60-90	76.6	4.95	*21.16*	BC	Ciancio et al. 2007
Moroteuthis ingens								
Summer	Possession Is.	1		76.0	5.6[2]	23.51[2]	BC	Cherel and Ridoux 1992
	New Zealand	6	356	80.3	*4.73*[3]	*24.02*[3]	PC	Vlieg 1984
Illex argentinus								
	Patagonia	4	210-415	76.7	5.01	*21.52*	BC	Ciancio et al. 2007

[1] Based on measurements of water content, lipids (x 39.7 kJ g^{-1}) and crude protein

[2] Mantle and tentacles

[3] Based on crude protein

the order Siphonophora from which species such as *Diphyes antarctica* can dominate the epipelagic layer particularly during autumn and winter (Flores et al. 2014). Gelatinous species have often been viewed as an unimportant prey item for many organisms, due to both their low energetic value and the difficulty in detecting gelatinous prey with conventional diet assessments methods (e.g. stomach content analysis, leading to potential underestimation of their prevalence as a prey item; McInnes et al. 2017). However, they have been found to be more than an incidental part of the diet of many larger animals (Fig. 4.5), including albatrosses and Adélie penguins in the Southern Ocean (Jarman et al. 2013; Thiebot et al. 2016; McInnes et al. 2017; Thiebot et al. 2017;). Although secondary ingestion cannot be excluded when using DNA analysis, results suggest that they are common prey item (Jarman et al. 2013; McInnes et al. 2017). Video observations captured Adélie penguins feeding on jellyfish, even when other prey were available (Thiebot et al. 2016; Thiebot et al. 2017). Certain jellyfish species are regularly invested with parasitic amphipods, and although there was no evidence that the penguins were targeting these, they may prove to be a profitable addition (Thiebot et al. 2016).

Two species of Scyphozoa were measured from both the winter Weddell Sea (PS81) and the summer Lazarev Sea (PS89) using bomb calorimetry (Table 4.13). The energetic density of *Periphylla periphylla* was on average 20.4 kJ g^{-1} DW during winter. Samples consisted of one small individual (93.5 g WW) and several larger individuals, with a WW ranging from 470 to 499 g. The average winter energy density of *P. periphylla* was higher compared to 10.8 kJ g^{-1} DW during summer. The latter measurements were however performed on small individuals with an average WW of 7.0 g. This suggests that season has an influence on the energy density of *P. periphylla,* although there could also be an influence of size. No difference was found in the energy density of *Atolla* spp. between seasons. The average energy density of *Atolla* spp. was 11.0 kJ g^{-1} DW during winter and 12.3 kJ g^{-1} DW during summer. The water content of the scyphozoa caught during both winter and summer were similar and usually in between 90 and 95% WW. It should be kept in mind that these individuals were weighed after having been frozen. Due to the potential error in that measurement, energy densities are not given in kJ g^{-1} WW. High ash contents may have resulted in an underestimation of the dry weight energy densities of these Scyphozoa.

Observations showed that Adélie penguins often attacked the gonads and/or oral arms of jelly fish specifically, and that there was a relationship between the penguin attacks and the visible presence of gonads (Thiebot et al. 2016). Gonads from *P. periphylla* caught in the summer Lazarev Sea showed a higher energetic density than other body parts (Table 4.14). Doyle et al. (2007) and Milisenda et al. (2014) also found that gonads had a higher energy content than oral arm or bell tissue, with the exception of one species in which the oral arms yielded a similar energy density as the gonads (Doyle et al. 2007). The energy densities of the bell and collar tissue of *P. periphylla* were very low and likely unrealistic (Table 4.14; Doyle et al. 2007). These tissues also had very high ash contents (Table 4.14), although ash content was high in general when compared to other animals.

A measurement using bomb calorimetry on a sample of pooled anterior nectophores of the siphonophore

Figure 4.5: Antarctic Petrels (*Thalassoica antarctica*) feeding on gelatinous species in the Lazarev Sea during summer.

Diphyes antarctica from winter Weddell Sea (PS81) resulted in an energy density of 12.0 kJ g^{-1} DW (4.0 kJ g^{-1} WW). The ash content of *D. antarctica* has been reported to be close to 60% (Donnelly et al. 1994).

Proximate compositions of ctenophore and cnidarian species were measured by Clarke et al. (1992) and Donnelly et al. (1994), which included the species *Beroe* spp. (Clarke et al. 1992), *Pleurobrachia* sp. (Clarke et al. 1992), *Calycopsis borchgrevinki* (Clarke et al. 1992; Donnelly et al. 1994), *Botrynema brucei* (Clarke et al. 1992), *Diphyes antarctica* (Clarke et al. 1992; Donnelly et al. 1994), *P. periphylla* (Donnelly et al. 1994) and *Atolla wyvillei* (Clarke et al. 1992; Donnelly et al. 1994). The water content of all species was > 95% WW, while the ash content ranged between 50 and 73% DW (Clarke et al. 1992; Donnelly et al. 1994). Apart from residual water, there is evidence that suggests that gelatinous species also contain a proportion of amino-carbohydrate which is missed by conventional assay techniques. Furthermore, a proportion of the protein potentially consists of glycoproteins that can be missed or underestimated depending on the technique used (Clarke et al. 1992). This could explain why energy density calculated using proximate composition is far lower than the energy density of carbohydrates, and is an unreliable method for estimating energy density of gelatinous species (Clarke et al. 1992; Donnelly et al. 1994).

Pelagic tunicates, or salps, that occur in the Southern Ocean are widely distributed and can form an important part of the total metazoan biomass, particularly in relatively warm water masses (Pakhomov 2004; Pakhomov et al. 2011). The proximate composition of the pelagic tunicates *Salpa fusiformis, Salpa* *thomsoni* and *Ihlea racovitzai* were measured by Clarke et al. (1992), Donnelly et al. (1994), Dubischar et al. (2006) and Dubischar et al. (2012). Despite similar complications as for other gelatinous zooplankton, some of the sources report an energy density estimate. Dubischar et al. (2012) estimated the WW energy density of *S. thompsoni* and *I. racovitza*i to be 0.2 and 0.4 kJ g^{-1} (using the conversion factors 4.1 kcal g^{-1} for protein and 9.3 kcal g^{-1} for lipids), which would correspond to 3.1 kJ g^{-1} DW and 6.7 kJ g^{-1} DW, respectively. They did find that the energy density of *I. racovitzai* was approximately twice as high than that of *S. thompsoni*, mainly due to differences in the amount of protein. The amount of protein found by Donnelly et al. (1994) was a lot lower. The proximate composition did not markedly differ between seasons in both studies, suggesting that lipids are not accumulated (Donnelly et al. 1994; Dubischar et al. 2012). Clarke et al. (1992) calculated an energy density of 4.58 kJ g^{-1} DW for *S. fusiformis*. When comparing solitary forms with aggregate forms of *S. thompsoni* measured from the Bellinghausen Sea in autumn, the amount of protein and lipids were higher in the former, which would result in a higher energy density for the solitaries when converted (5.3 kJ g^{-1} DW as opposed to 3.2 kJ g^{-1} DW; Dubischar et al. 2006). The reported energy densities for salps are also lower than that of carbohydrates (Clarke et al. 1992). Questions still remain regarding the digestibility of salps. It is suggested that they can be digested entirely but also only partly due to the cellulose-like tunicin present in the tunica (Dubishar et al. 2012 and references therein). Gili et al. (2006) proposed that the salps' stomach

Table 4.13: Average energy density of scyphozoans ± standard deviation. *n* represents the number of samples measured.

SEASON	LOCATION	*n*	MEAN DW (mg)	WATER CONTENT (%)	ENERGY DENSITY kJ g^{-1} DW	METHOD	SOURCE
Periphylla periphylla							
Winter	Weddell Sea	8	22.0 ± 9.1	93.6 ± 1.7	20.43 ± 1.13	BC	This study (PS81)
Summer	Lazarev sea	9	0.8 ± 0.9	89.0 ± 6.1	10.85 ± 2.57	BC	This study (PS89)
***Atolla* sp.**							
Winter	Weddell Sea	5	1.6 ± 0.7	93.0 ± 2.7	11.16 ± 3.79	BC	This study (PS81)
Summer	Lazarev sea	16	1.0 ± 0.3	93.2 ± 1.6	12.29 ± 1.41	BC	This study (PS89)

Table 4.14: The energy density ± standard deviation of different body parts from the scyphozoan *Periphylla periphylla*, caught in the summer Lazarev Sea. Measurements were done using bomb calorimetry. Replicate measurements were performed on the body parts of a single individual.

	MEAN WW (g)	MEAN DW (g)	WATER CONTENT (%)	ASH CONTENT (% DW)	ENERGY DENSITY	
					kJ g^{-1} DW	kJ g^{-1} AFDW
Intestine	385.27	18.31	95.25	66.27 ± 0.39	6.73 ± 0.27	19.96
Gonads	113.12	7.66	93.23	41.57 ± 2.52	13.28 ± 0.12	22.73
Bell	94.46	3.66	96.12	74.90 ± 0.93	1.15 ± 0.28	4.59
Tentacles	123.02	5.61	95.44	55.89 ± 4.47	8.06 ± 2.32	18.27
Collar	259.09			75.30 ± 0.51	1.47 ± 0.33	5.97

may be the main source of energy when preyed upon.

Chaetognaths, polychaetes and gastropods

Other pelagic zooplankton species for which reported energy densities were found, included cheatognaths, polychaetes and a gastropod (Table 4.15). Chaetognaths, such as *Eukrohnia hamata, Sagitta gazellae* and *Sagitta marri*, can form a major part of the mesopelagic zooplankton community and are important carnivorous predators (Pakhomov et al. 1999; Flores et al. 2014). These three species are the most abundant in the epipelagic and have a wide, circumpolar distribution (David 1958). Their distribution in the water column has been found to follow increased abundances of their prey, larval krill and copepods (David et al. 2017).

Estimated energy density using proximate composition are available for the three species of chaetognaths and two species of polychaetes in Donnelly et al. (1994). The dry weight energy density of chaetognaths ranged between 5.0 kJ g^{-1} DW of *S. gazellae* caught in autumn and 11.7 kJ g^{-1} DW of *E. hamata* caught during winter. The energy densities of *E. hamata* and *S. gazellae* were higher in winter than in autumn. Seasonal changes in energy content are suggested to be a result of trophodynamics (Donnelly et al. 1994).

Table 4.15: Average energy density of chaetognath, polychaete and a gastropod species. Energy densities in italics represent values that were converted using information from the given sources. *n* represents the number of samples measured. Where this expresses samples of pooled individuals, this is indicated with (p). Standard deviation is given were available. All measurements were done using proximate composition (PC).

SEASON	LOCATION	*n*	MEAN WW	WATER	ENERGY DENSITY		MTD	SOURCE
			(mg)	CONT. (%)	kJ g^{-1} WW	kJ g^{-1} DW		
Eukrohnia hamata								
Autumn	Weddell Sea	1 (p)	0.456	95.0	0.42	7.53	PC	Donnelly et al. 1994*
Winter	Scotia Sea	1 (p)	2.00	91.8	0.84	11.72	PC	Donnelly et al. 1994
Sagitta gazellae								
Autumn	Weddell Sea	1 (p)	4.36	95.1	0.42	5.02	PC	Donnelly et al. 1994
Winter	Scotia Sea	3 (p)	1.36	93.5 ± 1.1	0.42	7.53	PC	Donnelly et al. 1994
Sagitta marri								
Winter	Scotia Sea	1 (p)	0.67	90.8	1.26	11.30	PC	Donnelly et al. 1994
Vanadis antarctica								
Autumn	Weddell Sea	1	1.09	86.3	2.09	14.23	PC	Donnelly et al. 1994
Tomopteris carpenteri								
Winter	Scotia Sea	1 (p)	0.76	87.7	1.26	9.20	PC	Donnelly et al. 1994
Summer	South Georgia	5		84.5	*1.92*	12.37[1]	PC	Clarke et al. 1992
Clione limacina antarctica								
Spring	McMurdo Sound	4 (p)				*24.81*[2]	PC	Bryan et al. 1995

[1] calculated using the values 39.5 kJ g^{-1} for lipids and 23.9 kJ g^{-1} for protein

[2] calculated using 39.5 kJ g^{-1} for lipids

* A factor of 4.19 was used to convert calories to joules

Sagitta marri had a winter energy density of 11.3 kJ g^{-1} DW. All chaetognath species had high water and ash contents.

The polychaetes *Vanadis antarctica* and *Tomopteris carpenteri* are both oceanic species that can be found in the entire water column (Boysen-Ennen & Piatkowski 1988; Fernández-Álamo & Thuesen 1999). They had estimated energy densities of 14.2 kJ g^{-1} DW during autumn and 9.2 kJ g^{-1} DW during winter respectively (Donnelly et al. 1994). The energy density of *T. carpenteri* was also estimated from individuals caught near South Georgia. The reported value of 12.4 kJ g^{-1} DW was calculated using the values 39.5 kJ g^{-1} for lipids and 23.9 kJ g^{-1} for protein (Clarke et al. 1992).

A proximate composition estimate of the pelagic gastropod *Clione limacina antarctica* from the McMurdo Sound yielded an energy density of 24.8 kJ g^{-1} DW (Bryan et al. 1995). This gastropod can be very abundant in certain seasons or areas, and contains defensive chemicals to defend itself against predation (Bryan et al. 1995). An overview of the energy densities of the abovementioned species can be found in Table 4.15.

Benthic invertebrate species

McClintock et al. (1987; 1989; 2004; 2006) reported energy densities of benthic echinoderms, sponges and a tunicate. All estimates of the energy density of these species were done using proximate composition. The sea stars *Granaster nutrix* and *Neosmilaster georgianus* were investigated in McClintock et al. (2006). Measurements were done on the pyloric caeca and body wall separately which yielded 24.8 and 8.5 kJ g^{-1} DW for *G. nutrix*, and 26.5 and 14.1 kJ g^{-1} DW for *N. georgianus,* respectively. The energy densities of the body walls of 13 echinoderm species from McMurdo Sound ranged from 10.5 (*Odontaster meridionalis*) to 18.2 (*Porania antarctica*) kJ g^{-1} DW (McClintock 1989). The proximate composition of different body parts of the aforementioned study can be found in McClintock & Pearse (1987). The energy densities of 17 species of benthic sponges from McMurdo Sound ranged from 5.1 kJ g^{-1} DW (*Sphaerotylus antarcticus*) to 17.4 kJ g^{-1} DW (*Dendrilla membranosa*; McClintock 1987). The energy density of the benthic tunicate *Distaplia cylindrica* was estimated at 14.7 kJ g^{-1} DW (McClintock et al. 2004). This benthic tunicate had a lower water content and higher protein content compared to the pelagic tunicates (Donnelly et al. 1994; McClintock et al. 2004; Dubischar et al. 2012).

An energy density of 21.8 kJ g^{-1} DW was estimated using proximate composition for the nemertean *Parborlasia corrugatus*, collected in the McMurdo Sound during spring (Heine et al. 1991). Three bivalve species from the Patagonian shelf, *Aulacomya atra, Perumytilus purpuratus* and *Mytilus edulis*, yielded energy densities of 19.2, 20.0 and 17.9 kJ g^{-1} DW, respectively. Animals were measured without shells using bomb calorimetry (Ciancio et al. 2007).

DISCUSSION

DATA GAPS

There is a focus on certain species, but the Southern Ocean is composed of different biogeographical regions that can have a distinct biodiversity and community structure, and specific key species. For instance, for euphausiids many studies focus on *Euphausia superba* but other species can be of high importance in certain areas. In the continental shelf region, *Euphausia crystallorophias* is an important food source, for instance for Adélie penguins in the Ross Sea and at Adélie Land (Ainley et al 1998; Cherel 2008), and for minke and blue whales (Laws 1977; Ishii et al. 1998). The euphausiid *Euphausia vallentini* can be a major food source for many sea birds in particular biogeographic regions, for instance at Heard Island and the Crozet Islands (Ridoux 1994; Deagle et al. 2007). Several amphipod species are found in the diet of many bird species (Hindell 1989; Ridoux 1994; Van Franeker et al. 2001), although their contribution to the diet varies significantly between regions. The hyperiid amphipod *Themisto gaudichaudii*, for example, has a wide distribution and is found in variable amounts in the diet of many species, but seems to be an important prey item in the region of the Kerguelen Islands particularly (Bocher et al. 2001). Similarly, the copepod *Paraeuchaeta antarctica* has been found to be abundant in the diet of bird species in the Kerguelen region (Bocher et al. 2002).

A better seasonal or regional coverage of the energy density of species is desirable as it can give insight into a species life cycle and behaviour, because several top predator species show a change in diet between seasons (Ridoux 1994). For example, the fish feeding Cape petrel switches to a squid dominated diet in the Weddell/Scotia Sea in autumn (Ainley et al. 1991), while the Arctic tern (*Sterna paradisaea*) feeds mainly on *Electrona antarctica* in spring, but on Antarctic krill in autumn (Ainley et al. 1991). Adélie penguins in the Ross Sea, feeding mainly on krill at the start of the season, increased their proportion of fish in the diet together with their foraging trip duration. This is likely a result of a change in food availability due to increased predation pressure by the penguins themselves (Ainley et al. 2015).

There are many species groups that are overlooked as they are not known to be an important part of the diet of top predators, but which can reach high numbers and biomasses in certain habitats or seasons and are therefore important parts of the Southern Ocean food web. These include previously mentioned groups such as salps (Pakhomov et al. 2002), chaetognaths, siphonophores, ctenophores, gastropods (Hunt et al. 2008; Flores et al. 2011; 2014), other small krill species such as *Euphausia frigida*, but also benthic species such as bivalves and limpets (Favero et al. 1997; Ainley et al. 2003b). Furthermore, a better coverage of the energy density of Southern Ocean species can help to predict what happens if prey distribution changes. For example, research has shown that areas dominated by Antarctic krill may be replaced with a dominance of salps due to warming waters (Pakhomov et al. 2002; Atkinson et al. 2004; Ross et al. 2014), which may have significant food web implications. An effect of food availability on annual fledging mass of Macaroni penguin chicks was shown at Bird Island, South Georgia (Waluda et al. 2012). The fledging mass of penguin chicks could be related to the energy density of the prey in combination with prey size and mobility, and was highest in years where *E. superba* dominated the diet, and lowest when there were large proportions of fish and other crustaceans, such as *T. gaudichaudii* and *E. frigida* (Waluda et al. 2012). In contrast, male Adélie penguin chicks had a higher proportion of fish in the diet and were growing faster than female chicks, which ate higher proportions of krill (Jennings et al. 2016). Model simulations also suggested that penguin chicks that supplemented their diet with fish (*Pleuragramma antarctica*), instead of feeding solely on Antarctic krill, would be heavier and more likely to recruit (Chapman et al. 2011). The quantity of milk fat of fur seals (*Arctocephalus gazella*) at Kerguelen was found to be influenced by the proportion of myctophids in the diet (Lea et al. 2006).

The energy density of a prey species might change as consequence of warming temperatures. Oxygen consumption and metabolic rate have been found to increase with increasing temperature across species (Brockington & Clarke 2001). This could not only lead to smaller sized individuals (Atkinson 1994; Daufresne et al. 2009; Baudron et al. 2014), but also to changes in community structure due to a need for increased consumption leading to, for example, changes in predator-prey interactions or intraspecific competition (Bruno et al. 2015). The reduction in body size with increasing temperature has been found for many myctophid fish species, which could potentially lead to these fish shifting to a different size of prey or becoming a less valuable food source for predators (Saunders & Tarling 2018). In addition, the energy allocation (for instance, towards growth or build-up of reserves) has been found to change under different temperature conditions in a study on zoarcid fish species (Brodte et al. 2006).

Although for all types of studies using a species specific energy density value it would be preferable to use an estimate that is specific for e.g. region, season and body size, a generalized estimate of the energy density of a species could be useful in cases where this is not available. For many species, however, only a single record of their energy density exists. Many records also often consist of one individual or a single pooled sample. Therefore, more measurements are necessary to validate and generalize energy densities of species, and sources of variation within species. For *E. antarctica* there are relatively many individual records (284), which yield a mean energy density of 30.26 kJ g^{-1} DW and 8.94 kJ g^{-1} WW. Results have shown, however, that sources of variation include size and region. Another way to estimate a mean value could be by using a median value of all recorded mean energy densities, which would result in median values of 29.61 kJ g^{-1} DW and 9.08 kJ g^{-1} WW for *E. antarctica* and 21.9 kJ g^{-1} DW and 5.01 kJ g^{-1} WW for *E. superba*. For the latter species it is, however, clear that the energy densities differ between sexes and developmental stages, while regional differences are uncertain. For aforementioned estimates only bomb calorimeter measurements were used.

Measuring energy density using bomb calorimetry and proximate composition are time consuming. Therefore increased information on relationships between energy density and other, more easy to measure, parameters could be helpful. These may include insights in the effect of size/age/maturity on energy density within species and variation between seasons and regions. Also, relationships between water content or proportion of body carbon and energy density, including more information on differences and similarities between, for example, species, families and classes, would be useful to evaluate the accuracy of values used. In addition, it would increase the precision of studies and models based on energy density, when using values that take interspecific variation into account. Currently, regressions are generally limited to certain fish species and on an individual basis for Antarctic krill (Färber-Lorda et al. 2009a). In order to obtain such correlations, measurements on individuals are most useful. A standard bomb calorimeter needs, however, quite a large dry weight sample and thus for measuring small animals it is necessary to have access to a micro-bomb calorimeter.

SIZE/AGE - ENERGY DENSITY RELATIONSHIPS

Relationships between size and dry weight energy density are found for fish but differ between species. A positive relationship between size and dry weight energy density was found for the myctophids *Gymnoscopelus piabilis, Electrona carlsbergi* (Lea et al. 2002) and *E. antarctica*. For other fish species such as *Bathylagus antarticus* (Tierney et al. 2002; Van de Putte et al. 2006), *Pleuragramma antarctica* (Van de Putte et al. 2010) and other fish from the study of Lea et al. (2002), no relationship was found, and fish had the same dry weight energy density regardless of size. In addition, Tierney et al. (2002) found negative relationships between size and dry weight energy density. Most relationships are, however, not linear but show differences between size classes. Therefore, as recommended by Van de Putte et al. (2006), it is useful to separate energy densities in age or size classes, using distinct energy densities for each age group. In particular in trophodynamic studies and research on prey utilization of species, as predators are known to often feed on a particular prey size (Van Franeker et al. 2001). However, again more data is needed to see if size/energy density relationships show a general trend rather than an incidental occurrence, and, if differences are found, to be able to characterize the size classes between which differences occur. The available data on *Gymnoscopelus braueri* show an example where there is a (negative) relationship in one dataset but none in the other (Tierney et al. 2002; Van de Putte et al. 2006). Furthermore, it is currently unclear how energy density in young fish is allocated because not all small specimens show increased energy density with decreasing water content, as would be expected (Tierney et al. 2002).

In krill, and most likely other crustaceans, there are marked differences in energy density between developmental stages. Predators have been found to have a higher proportion of female krill in their diet, probably also due to their larger size (Reid et al. 1996). It would be useful to gain information on the energy densities of krill based on size, as predators also prey upon particular sizes, and sizes of different developmental stages usually overlap. For instance, fulmarine petrels consume krill of approximately 35 mm (Van Franeker et al. 2001), which is a size including both juvenile and sub-adult krill (Siegel 1987; Siegel 2012). For species other than *E. superba* and fish, size or developmental stage specific data is lacking completely, although data suggest that there may be differences in energy density between size classes, for example in the jelly fish *Periphylla periphylla*.

WATER CONTENT - ENEGRY DENSITY RELATIONSHIPS

The relationship between water content and energy content (in kJ g^{-1} WW) can help estimating the energy density based on water content (usually expressed in DW as a percentage of WW), in which case only the determination of wet weight and dry weight or water content is needed (Hartman and Brandt 1995). The relationship between water content and energy density (WW) of *E. antarctica* was similar between seasons and regions, and thus a single regression model, using all available individual measurements, should give good, generally useful parameters for the estimation of energy density on a WW basis given the water content:

$$ED_{WW} = 0.393 * P_{DW} - 2.977 \quad (R^2 = 0.93, n = 252)$$

Where ED_{WW} represents the energy density in kJ g^{-1} WW and P_{DW} the dry weight as a percentage of WW.

Using the available individual data of *G. braueri* a generalized regression model would yield similar parameters:

$$ED_{WW} = 0.344 * P_{DW} - 1.539 \quad (R^2 = 092, n = 33)$$

This model does however exclude the smaller fish (<40 mm) from Tierney et al. (2002) which had a significantly higher energy density than the larger fish, for which the cause remains unclear. The slopes of the models for *E. antarctica* and *G. braueri* differed significantly from each other (ANCOVA, $p = 0.006$).

Differences in regression slopes between fish species (Van de Putte et al. 2006; Van de Putte et al. 2010) reveals that the relationship between water content and energy density (WW) differ between families at least. Hartman and Brandt (1995) suggested that similar models can be used for fish within the same order or family, but recommended using species-specific models when available, especially in species which show marked seasonal changes in energy density. In this review, individual data on *Bathylagus antarcticus* showed that the relationship can also differ between seasons and/or regions. Furthermore, the different feeding habitats and wide range of energy densities of nototheniid fishes suggest that there might be large differences in water content/energy density relationships between species of the same family. Similar modelling was done by Ciancio et al. (2007), including crustaceans, fish and cephalopods. They also found that same genus models would produce similar results as species-specific models, although this was not the case for some groups which were less well represented by aggregated models and for which species-specific models were recommended. Therefore, more individual data is needed to establish regression models for different species, compare the relationship between water content and energy density within families and evaluate if the established regression models can be used in a general manner, also for taxa other than fish.

CONCLUSION

A large amount of data is available on the energy density of potential prey species in the Southern Ocean. The available data are, however, strongly skewed towards a few large, abundant and relatively easily accessible taxa. Furthermore, information on the seasonal and regional variability of energy densities is still limited in most species. This information, however, would be key to the improvement of bio-energetic models and food web models. Bomb calorimetry is hitherto regarded as the most accurate method for energy density measurements. However, proximate composition analysis at various levels can provide a range of additional parameters often used in ecological studies. Important taxa for the energy flux of Antarctic food webs remain under-sampled. In a changing Southern Ocean, smaller zooplankton and gelatinous species may become more abundant. Such a shift would likely change food web energetics significantly at various levels, affecting the carrying capacity of the ecosystem for top predators and harvesting of living resources. It will therefore become increasingly important to include small and gelatinous zooplankton in energy flux models and ecosystem studies, warranting the need for more energetic measurements of these organisms.

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CHAPTER 5

Strong linkage of polar cod (*Boreogadus saida*) to sea ice-algae procuced 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 icewater 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 & 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 & 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 & Gulliksen 1989; Scott et al. 1999; Gradinger & 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 & Frost 1981; Bradstreet & 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 & 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 & 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 & 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. 2016). 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 & 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 5.1, Fig. 5.1). Detailed information on the sampling during PS80 can be found in David et al. (2015; 2016), and Kohlbach et al. (2016).

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 precombusted 0.7 mm 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} (0.3–8 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 chlorophyll *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

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

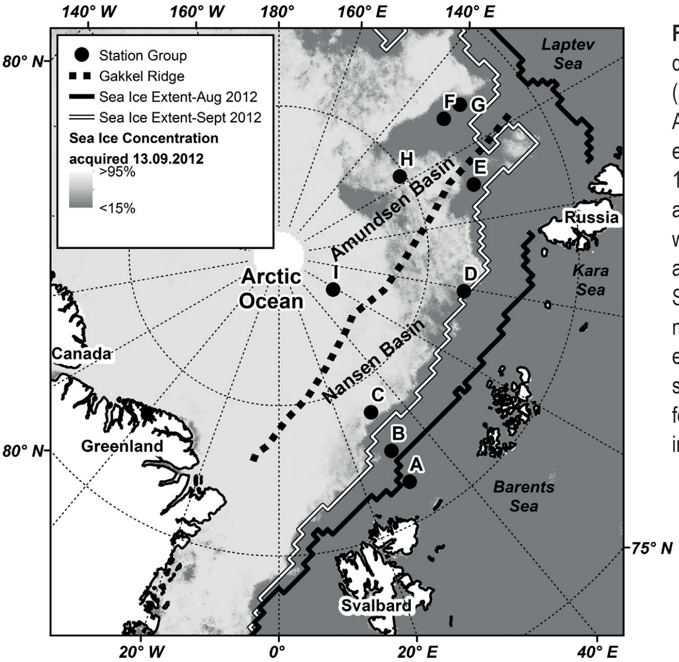

Figure 5.1: Map of the sampling area during RV 'Polarstern' cruise IceArc (PS80) across the Eurasian part of the Arctic Ocean modified after Kohlbach et al. (2016). Sea-ice concentration for 13 September 2012 (concentration data acquired from Bremen University (http://www.iup.uni-bremen.de:8084/amsr/)) 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 5.1.

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% hexaminebuffered 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

Table 5.1: 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	
	P-POM	8/11	230	84.022	31.221	4011	
D	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
	P-POM	8/18	250	83.353	87.271	3508	
E	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	110.889	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	82.926	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	89
	i_POM	9/22	360	88.828	58.864	4374	
	UIF	9/25	376	87.341	52.620	3509	100

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 AxioVision 40 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

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

Themisto spp.

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

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:

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

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

$$SF = 100 * W_{SC}/WW \quad (5)$$

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

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

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

$$R = a * e^{bT} \tag{7}$$

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 & 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:

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

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:

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

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 5.2). Lipid class composition of the polar cod tissues was analyzed via high-performance liquid chromatography (Graeve & Janssen 2009). The relative proportions of the most abundant lipid classes were provided in the supplementary material (Table S5.1). 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 5.2) 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

Table 5.2: Lipid parameters of polar cod used for 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

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 & 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 ANALYSIS

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 x 0.25 mm internal diameter x 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: $\delta^{13}C = -26.4 \pm 0.4‰$). 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. The significance of found correlations between pairs was further tested by calculating a t-value and corresponding pvalue 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 & 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):

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

where λ represents the trophic position of the baseline (I-POM or P-POM, $\lambda = 1$). 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%)

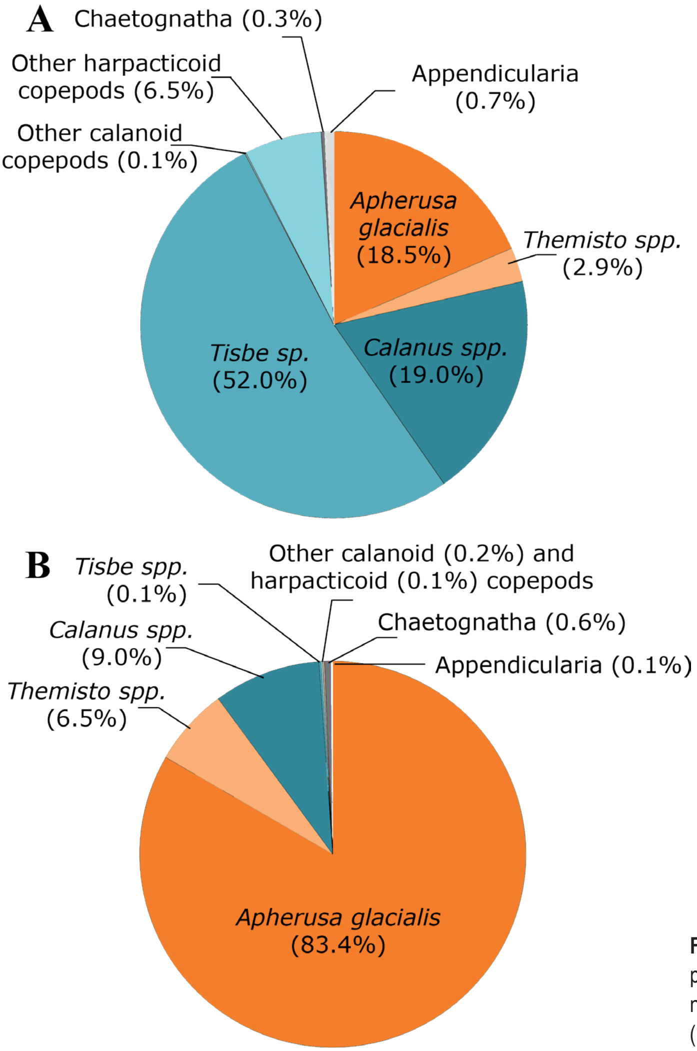

Figure 5.2: Average stomach content of polar cod in (A) relative abundance (% number ind.$^{-1}$) and (B) relative biomass (% reconstructed dry weight ind.$^{-1}$).

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; Supplement 5, Table S5.2). The amphipod *Apherusa glacialis* dominated in numbers and biomass in the majority of the samples (Fig. 5.2). 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 (Fig. 5.2). 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 5.1, Fig. 5.1), and one individual from location F, were dominated by large numbers of *Calanus glacialis*. The abundances of *A. glacialis* (t_7= 3.4, $p < 0.01$), *Calanus* spp. ($t_7 = 20.7$, $p < 0.001$), and chaetognaths ($t_7 = 83.6$, $p < 0.001$) in the stomachs were each positively correlated with the abundance of these species in the under-ice surface waters (Suppl. 5, Table S5.3). 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.

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 <2% in the I-POM samples (Table 5.3). 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: $t_{11} = 2.3$, $p < 0.05$; 18:4n-3: $t_{16} = 9.8$, $p < 0.001$; 22:6n-3: $t_{13} = 9.0$, $p < 0.001$). 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 ($t_{14} = 7.1$, $p < 0.001$).

Polar cod

In all three tissue types, both diatom-associated marker FAs 16:1n-7 and 20:5n-3 contributed significantly

Table 5.3: Relative composition of the 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.

Fatty acids	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

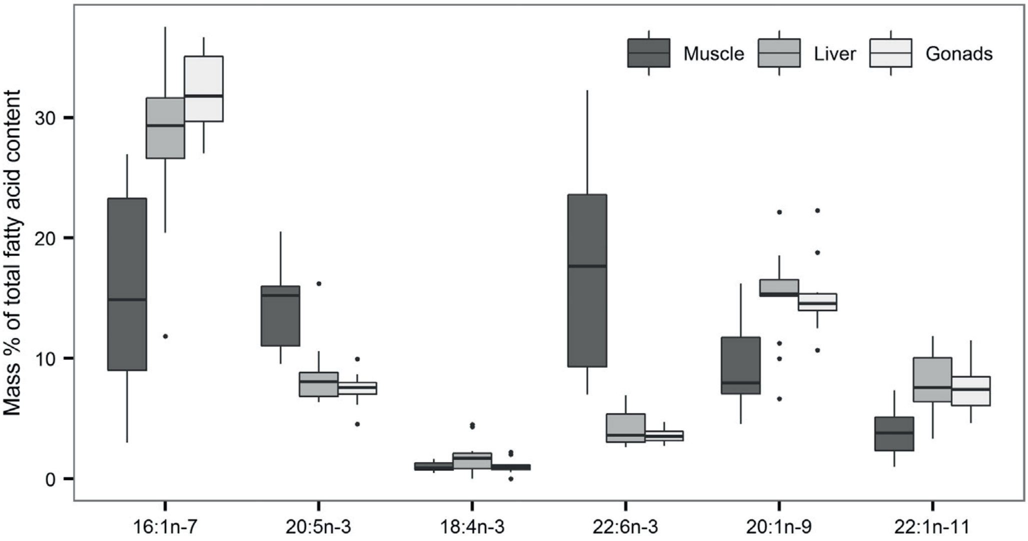

Figure 5.3: Relative proportions of marker fatty acids (FAs) in muscle, liver and gonad tissue of polar cod. 16:1n-7 and 20:5n-3 represent diatom-associated FAs, 18:4n-3 and 22:6n-3 represent dinoflagellate-associated FAs, 20:1n-9 and 22:1n-11 represent *Calanus*-associated FAs. Horizontal bars in the 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 5.3.

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 9–15%) and 22:1n-11 (mean 4–8%) were also abundant in all three tissues (Table 5.3, Fig. 5.3). 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 $p < 0.001$).

STABLE ISOTOPE COMPOSITION

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‰; Fig. 5.4A). 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 5.4). 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: $t_5 = 7.3$, $p < 0.001$; 20:5n-3: $t_{10} = 6.4$, $p < 0.001$; 22:6n-3: $t_4 = 5.9$, $p < 0.01$).

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 (Fig. 5.4A).

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 5.4). 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 5.4, Fig. 5.4B). 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‰).

PROPORTIONAL CONTRIBUTION OF ICE ALGAL CARBON TO POLAR COD DIET

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 5.5). 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 (34–65%). In the CSIA-based models, mean α_{Ice} was the highest in the muscle tissue (51–65%), and the lowest in the liver tissue (34–50%). The values in the gonad

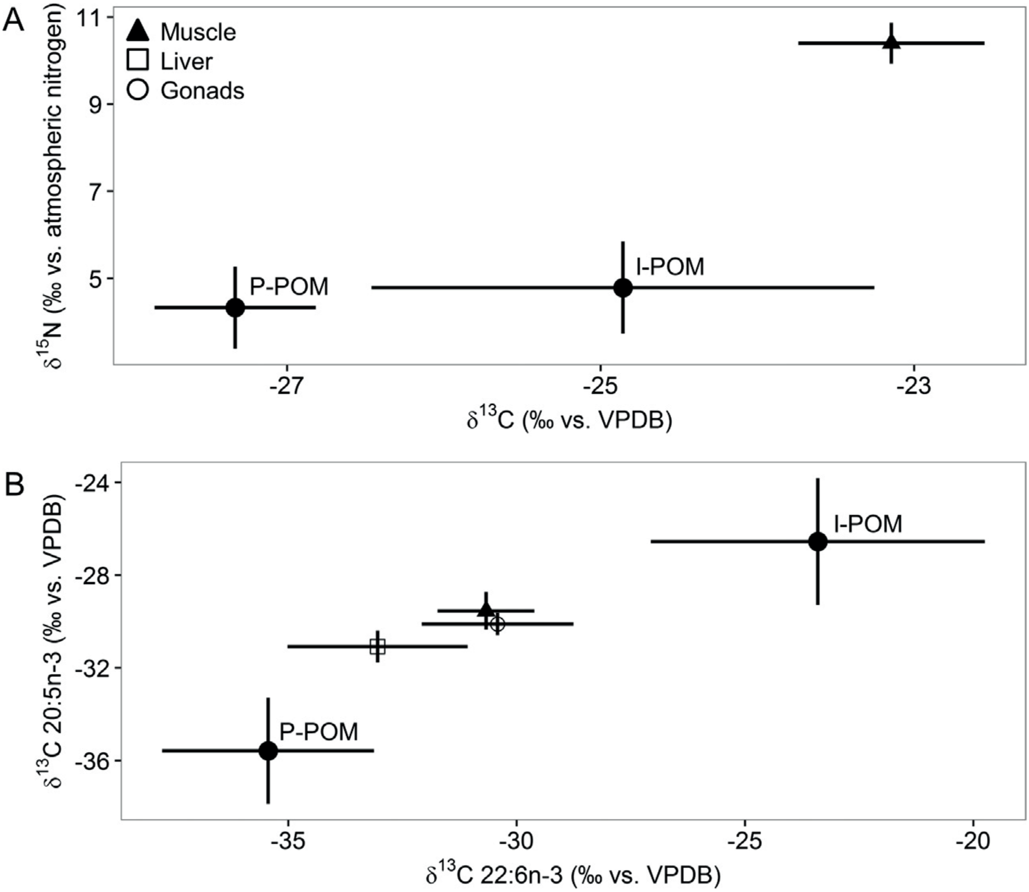

Figure 5.4: (A) Bulk nitrogen ($\delta^{15}N$) and carbon stable isotope compositions ($\delta^{13}C$) in ice-associated particulate organic matter (I-POM, n = 6), pelagic particulate organic matter (P-POM, n = 17) and polar cod muscle tissue (n = 66) relative to atmospheric nitrogen and the international 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 Fig. 5.4A. Sample size is reported in Table 5.4.

Table 5.4: 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 '–'.

Stable isotopes	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

Table 5.5: 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

tissue were closer to those in the muscle tissue (50–59%). 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 5.5).

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 & 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 & Gulliksen 1989). The diet compositions in other studies in more open waters were dominated by *Themisto* spp. and *Calanus* spp. (Bradstreet & 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 & 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 studiesconcluded that the difference in diet were most likely caused by differences in food availability (Craig et al. 1982; Lønne & Gulliksen 1989; Ajiad & 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 & Cross, 1982; Craig et al. 1982; Ajiad & 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 & 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 1.0–1.5% 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– 21 mg WW d^{-1} (*Calanus* spp.) and 25–44 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 5400 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 2–3 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 1–2 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 & 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 & 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 & Frost 1981; Bradstreet & 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 ΣC16/ΣC18 provide information on the relative proportions of diatoms versus flagellates in a consumer (Claustre et al. 1988/89; Viso & 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 & 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 COMPOSITION AND TROPHIC DEPENDENCY OF POLAR COD ON ICE

ALGAL-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. 2006; 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, 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. 2006). 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. 2006). 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 two 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 & 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 & McRoy 1979). For both methods, advantages and disadvantages regarding applicability have been reported (Pinnegar & 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 & 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 & Epstein 1978; Rau et al. 1983; Post 2002). The assumption of a carbon trophic fractionation factor $\Delta_C = 1‰$ 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 during our sampling. 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 141–185 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 30–100 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 1–2 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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SUPPLEMENT 5: Additional information lipid classes and stomach contents of polar cod (*Boreogadus saida*), including the correlation with the under-ice zooplankton community.

Table S5.1: 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	0.34 ± 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

Table S5.2: Proportional stomach content composition by abundance, dry mass and Index of Relative Importance (IRI) at each station (%).

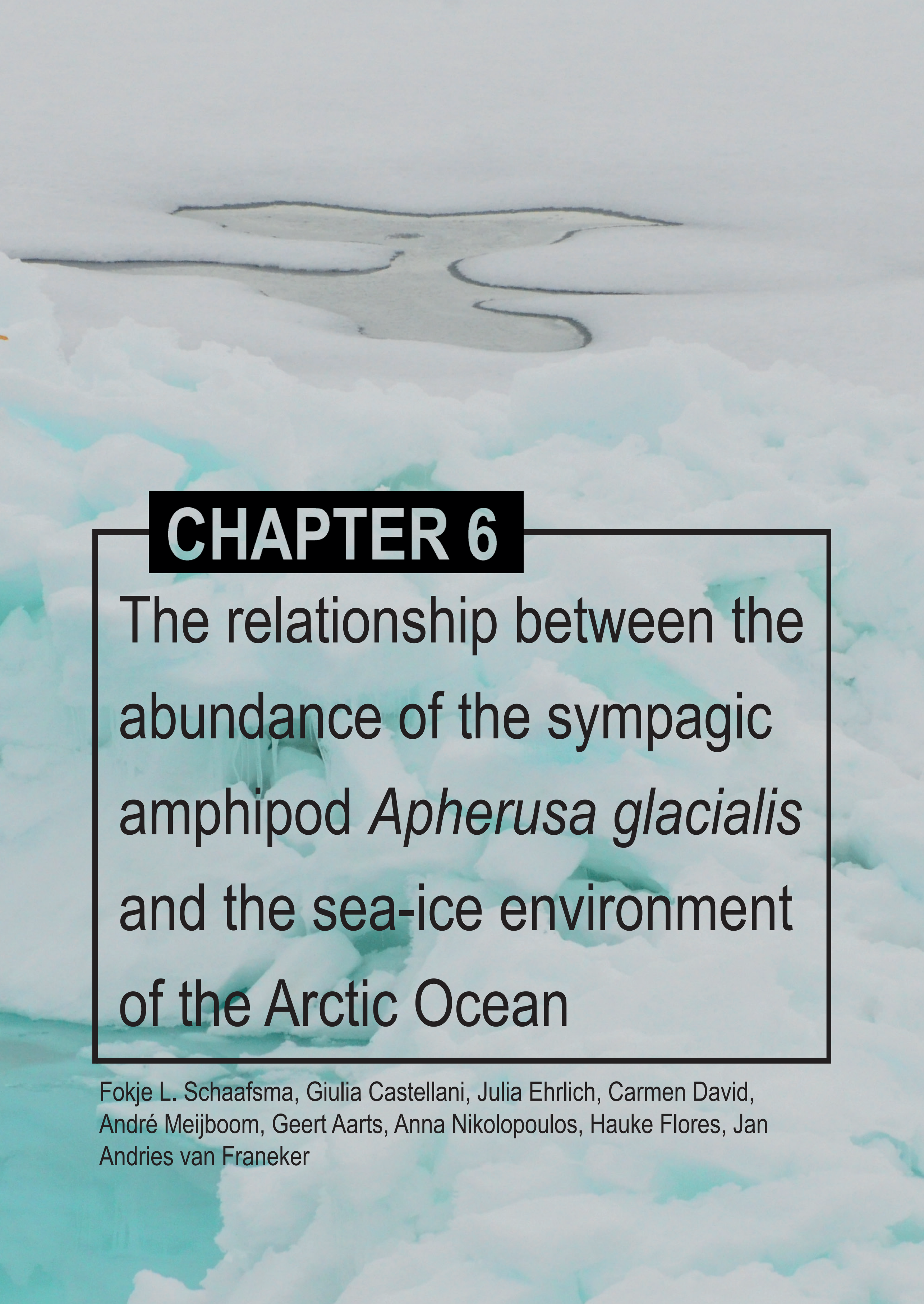
Station	216	223	248	258	276	285	321	331	345	358	376
Location	B	C	D	E	F	F	G	G	H	I	I
n	7	4	2	4	9	4	7	1	8	2	3
	Relative abundance (%)										
Amphipods											
Apherusa glacialis	33.3	85.2	1.5	8.3	19.6	25.0	22.6	100.0	2.9	76.9	60.0
Themisto libellula	0	0	0	1.0	1.2	1.9	1.6	0	2.9	0	0
Themisto abyssorum	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	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	0	1.1	0	2.1	0.6	5.8	19.4	0	13.5	0	0
Unidentified	0	2.3	18.0	1.1	0.0	3.8	0	0	1.3	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

Table S5.2 continued.

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 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	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
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	0	0.01	0	0.1	0.01	0.1	0.1	0	0.7	0	0
Unidentified	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	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	0	0.2	0	0.4	0.1	1.0	9.6	0	6.2	0	0
Unidentified	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

Table S5.3: 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



CHAPTER 6

The relationship between the abundance of the sympagic amphipod *Apherusa glacialis* and the sea-ice environment of the Arctic Ocean

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ABSTRACT

Amphipods are an important part of the Arctic marine community and recognized as a central species in the sea-ice ecosystem. The amphipod *Apherusa glacialis* is often abundant in the ice-water interface layer. Earlier studies showed that structures of sea-ice, such as floe size and presence of ridges, are important determinants for distribution patterns of this species. The aim of this study is to investigate large-scale relationships between the abundance and distribution of *Apherusa glacialis* and several biological and environmental variables during spring, using data obtained simultaneously over a scale of kilometres with a Surface and Under Ice Trawl (SUIT). The best single explanatory variable influencing the abundance of *A. glacialis* was chlorophyll *a*, suggesting that food availability was an important factor driving the amphipods distribution during spring. Data from a summer study in the high Arctic were added to investigate seasonal variation. These results indicated that temperature and salinity, with significant effects of sea ice structures, were important for explaining the amphipod's abundance and distribution. Despite a relatively small dataset, findings suggest that factors driving the the abundance and distribution of *A. glacialis* differs between seasons, likely due to a shift in the trade-off between food availability and predation.

INTRODUCTION

Amphipods are an important part of the Arctic marine community and recognized as a central group in the sea-ice ecosystem (Berge et al. 2012). They are particularly important at the underside of Arctic sea ice which forms a distinct habitat with specific environmental conditions (Werner & Gradinger 2002; David et al 2015). Arctic amphipods have been found to be an important link between sea-ice algae and intermediary as well as higher trophic level consumers, including fish, sea birds and marine mammals (Brown et al 2017; Kohlbach et al 2017). With the receding sea ice, there is a growing need to understand the impact of potential changes in sea-ice conditions on these sympagic grazers.

Apherusa glacialis is often the most abundant amphipod in the ice-water interface (Cross 1982; Gulliksen 1984; Lønne & Gulliksen 1991a; Gradinger et al 2010; David et al. 2015; Brown et al 2017). This herbivorous/ detrivorous (Poltermann 2001) amphipod reproduces in winter (Berge et al. 2012). The release of juveniles from the brood pouch occurs mostly in March (Poltermann et al. 2000). However, juveniles are released from brood pouches in subsequent batches over time, ensuring that at least part of the young amphipods are exposed to favourable environmental conditions (Poltermann et al. 2000). *Apherusa glacialis* has a short life-span, matures relatively early and produces a high number of eggs (Poltermann et al. 2000). Although *A. glacialis* has been found to in deeper strata during winter (Berge et al. 2012), they have mostly been found closely related to sea ice year round (Werner & Auel 2005).

Different studies, mainly conducted in spring and summer, have investigated the influence of sea-ice properties on the distribution of *A. glacialis* and yielded a variety of results. Ice-floe size and structure of the lower ice surface have been suggested to influence the population structure of the amphipod (Beuchel & Lønne 2002). Results from the study of Gradinger et al (2010) suggested that *A. glacialis* show increased abundances at pressure ridges, particularly at ridges between 3 and 6m depth. Abundances on ridges were also more variable than under flat ice (Gradinger et al 2010). Several studies report high abundances or a concentration of *A. glacialis* at ice-floe edges (Cross 1982; Gulliksen 1984; Lønne & Gulliksen 1991a; 1991b; Poltermann 1998; Hop et al. 2000). Abundances at floe edges seem to depend on floe size and sea-ice concentration (Hop et al. 2000). In contrast, Werner & Gradinger (2002) did not find a clear distributional differences in relation to distance from floe edgeindependent of season. In addition to elevated abundance at floe edges, Poltermann (1998) found high numbers of *A. glacialis* at thin, translucent floes with flat and smooth under-ice surfaces, which is not only in contradiction with the results of Gradinger et al. (2010), but also with those of Cross (1982) who found higher abundances underneath rough ice compared to flat ice. Other studies agreed with the results of Poltermann (1998), showing that *A. glacialis* (adults and juveniles) abundances were higher under flat or dome-shaped sea-ice than under ridges (Lønne & Gulliksen 1991b; Hop et al. 2000). Low abundances of *A. glacialis* have been associated with low temperature, high salinity and high algal biomass within ice (Werner & Gradinger 2002). Therefore, abundance is suggested to be positively related to thinner ice or melting conditions due to the availability of algae in soft, porous ice

(Werner & Gradinger 2002). In addition, a patchy distribution of *A. glacialis* has been observed, including juveniles clinging to clumps and strands of ice algae (Cross 1982).

Different findings also occur with respect to sea-ice microstructures. *Apherusa glacialis* were observed in small pockets and burrows in the ice (Gulliksen 1984) and some were found associated with brine channels (Cross 1982). In other studies, however, there was no association with cracks or brine channels (Lønne & Gulliksen 1991a) and the amphipods were not observed within the ice (Poltermann 1998).

The relationship of *A. glacialis* with the properties of sea-ice seems to differ between regions. However, the majority of the studies on abundance and distribution of *A. glacialis* were conducted in the Barents Sea (Gulliksen 1984; Gulliksen & Lønne 1989; Lønne & Gulliksen 1991a; 1991b) and the Fram Strait/Greenland Sea (Werner 1997a; Werner & Gradinger 2002; Beuchel 2000; Werner & Auel 2005), and many areas in the Arctic Ocean still lack coverage. Furthermore, annual (Lønne & Gulliksen 1991b) and seasonal variation in both abundance and distribution has been found (Werner & Gradinger 2002; Werner & Auel 2005). Additionally, most studies have been conducted by divers using handheld nets or pumps to sample sympagic fauna, allowing for investigations only at a relatively small spatial scale.

Summarizing, earlier studies showed that mesoscale, but also small and microscale, structures of sea-ice are important for distribution patterns of *A. glacialis* (Hop et al. 2000). However, this species is widely distributed and variation in structuring factors have been found between studies. More information on the abundance and distribution of *A. glacialis*, factors affecting variations in its abundance and a better temporal and spatial coverage is important to estimate its total production, role in carbon transfer and role in the food web (Dalpadado et al. 2001). In addition, the relationship between abundance and distribution with sea-ice properties on a larger scale would be useful to predict consequences of changes in the sea-ice habitat on a pan-Arctic scale. Therefore, the aim of this study is to investigate springtime relationships between the abundance and distribution of *A. glacialis* and several environmental characteristics on a large scale, by using biological and environmental data obtained simultaneously over a scale of kilometres with a Surface and Under Ice Trawl (SUIT). Furthermore, oceanographic parameters, such as mixed layer depth, were added, resulting in a high resolution environmental data set. Results are compared with a summer study in the high Arctic (David et al. 2015), to investigate if relationships will differ as the season progresses, as suggested by findings from aforementioned previous studies.

MATERIALS AND METHODS

DATA COLLECTION

Sampling was performed during Polarstern expedition "TRANSSIZ" (PS92) in 2015. The expedition was conducted north of Svalbard between 19 May and 28 June 2015. The area included the Svalbard shelf and slope, the Sophia basin and the Yermak plateau (Fig. 6.1). In total 15 under-ice sampling stations were completed during PS92. The environmental variables of PS92 per station can be found in Table 6.1.

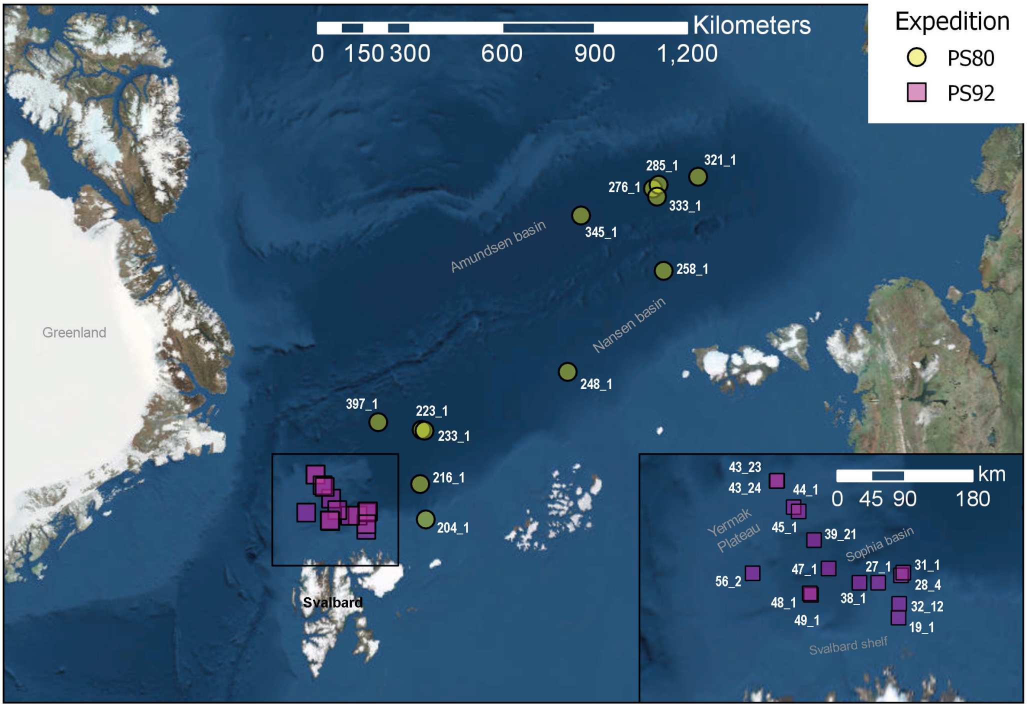

Figure 6.1: Map of SUIT (Surface and Under Ice Trawl) stations conducted during Polarstern expeditions “IceARC” (PS80) in 2012 and “TRANSSIZ” (PS92) in 2015. Numbers next to the sampling locations represents station numbers.

The upper two meters of the water column directly underneath the sea ice were sampled using a SUIT (Van Franeker et al. 2009). The SUIT has a steel frame with a 2x2 net opening and floats attached to the top to keep the net at the surface or directly under the ice. The SUIT shears out to the side of the ship, sampling away from the ship’s wake and under relatively undisturbed sea ice (Van Franeker et al. 2009). The frame contains a 7-mm half-mesh commercial shrimp net over 1.5 m width, and a 0.3-mm mesh plankton net over 0.5 m width. Due to the size of *Apherusa glacialis*, only the individuals caught in the plankton net were used for quantitative analysis.

Animals were preserved in a 4% hexamine buffered formaldehyde-sea water solution. Amphipods from all samples were counted and the total length (TL) was measured from the tip of the rostrum to the tip of the telson using a stereomicroscope (Zeiss, Discovery V8, Germany) with a digital camera and coupled image analysis software. For comparison between stations, areal densities (ind. m^{-2}) were calculated using trawled distances obtained from sensor measurements. During the expedition, deeper strata were sampled using a Rectangular Midwater Trawl (RMT). No *A. glacialis* were caught with the RMT except for a few individuals caught in the 0-50m depth layer and one individual in the 50-200m depth layer at station 43_23.

The SUIT frame is equipped with a sensor array containing an Acoustic Doppler Current Profiler (ADCP, Nortek Aquadopp®, Norway), which measures the velocity and direction of water passing through the net, and a CTD probe (CTD75 M, Sea & Sun Technology, Germany) with built-in fluorometer (Cyclops, Turner Designs, USA), which measures water temperature, salinity and surface water chlorophyll *a* concentration. Chlorophyll *a* concentration is used as a proxy for algal biomass in the under-ice surface water. Connected to the CTD probe was an altimeter (PA500/6-E, Tritech, UK) which measured the distance between the net and the sea ice underside, and which was used to obtain ice thickness profiles over the entire haul. Under-ice light levels were measured using two RAMSES spectral radiometers (Trios GmbH, Germany). The sensor measurements were used to calculate sea-ice properties per station as described below. Due to failure of the CTD, environmental data were incomplete at stations 31_1 and 32_12.

The mixed layer depth (MLD) was estimated from hydrographic data as the maximum depth at which the potential density is within 0.1 kg m^{-3} of the surface value (Peralta-Ferriz 2015), here taken as the density

STN	Date	LAT	LON	COV	DFT	RDP	RID
19_1	27-05-2015	81.0194	19.8700	24.9	0.96	2.38	1.39
27_1	31-05-2015	81.3764	17.7575	90.8	0.98	3.31	6.27
28_4	02-06-2015	81.5194	19.4258	97.1	1.17	2.33	4.37
31_1	03-06-2015	81.5572	19.5669	NA	NA	NA	NA
32_12	07-06-2015	81.1822	19.7164	NA	NA	NA	NA
38_1	09-06-2015	81.3233	16.3183	94.9	1.11	3.38	4.83
39_21	12-06-2015	81.6558	11.8269	70.2	1.46	2.88	11.40
43_23	16-06-2015	82.1586	7.0925	32.9	1.62	4.23	1.56
43_24	16-06-2015	82.1525	7.0503	63.8	1.09	2.18	6.94
44_1	17-06-2015	81.9419	9.2719	71.7	3.52	5.90	2.58
45_1	17-06-2015	81.9156	9.8058	82.1	1.68	4.20	3.41
47_1	19-06-2015	81.3881	13.6531	89.3	1.43	3.10	5.20
48_1	21-06-2015	81.025	12.9578	69.2	1.58	2.94	5.77
49_1	21-06-2015	81.0378	12.8364	94.7	1.70	4.60	4.87

STN	RD3	CHL	TMP	SAL	BTM	IIC	MLD	PSW	APH
19_1	0.35	3.52	-1.26	33.89	188.5	0.46	36.6	15.8	1.39
27_1	2.61	4.61	-1.44	33.45	827.9	0.46	26.7	52.4	0.63
28_4	0.87	2.30	-1.42	34.08	928.2	0.55	18.8	28.7	0.17
31_1	NA	NA	NA	NA	1050.5	0.97	28.7	42.5	2.00
32_12	NA	NA	NA	NA	335.6	2.25	28.7	31.7	3.54
38_1	2.76	8.78	-1.66	33.72	2249.1	1.88	29.7	60.3	0.60
39_21	2.85	0.45	-1.83	33.85	1971.8	0.22	78.1	98.9	0.09
43_23	0.78	0.27	-1.80	34.05	791.3	0.37	36.6	105.8	0.03
43_24	0.00	0.25	-1.80	34.24	794.3	0.25	59	62	0.04
44_1	1.55	0.39	-1.77	34.16	808.4	0.18	59	62	0.02
45_1	2.04	0.52	-1.74	34.32	913.6	0.25	53.4	63.3	0.02
47_1	2.08	10.58	-1.68	33.38	2139.1	0.70	23.7	71.2	2.15
48_1	1.77	2.83	-1.48	33.51	2047.7	0.31	8.9	67.3	0.63
49_1	3.25	5.58	-1.61	33.43	2080.2	0.59	27.7	60.3	0.68
56_2	5.87	1.97	-1.72	33.96	848.8	0.42	25.7	85.1	0.41

Table 6.1: The environmental properties and abundance of *Apherusa glacialis* per station from PS92. LAT = latitude, LON = longitude, COV = sea ice cover during trawling (%), DFT = sea-ice draft (m), RDP = average ridge depth (m), RID = number of ridges km^{-1}, RD3 = number of ridges over 3 m deep km^{-1}, CHL = surface water chlorophyll *a* concentration (mg m^{-3}), TMP = surface water temperature (°C), SAL = surface water salinity, BTM = bottom depth (m), IIC = in-ice chlorophyll *a* concentration (mg m^{-2}), MLD = mixed layer depth (m), PSW = polar surface water layer (m) and APH = *A. glacialis* (n m^{-2}).

at 3 m depth (3 dbar). As an alternative, MLD was also estimated according to Shaw et al. (2009), as the maximum depth where the potential density is within 20% of the density difference between the surface (3 m depth) and 100 m depth. The value used was the one that fitted the particular station best based on density profiles. The hydrographic data (vertical profiles of temperature and salinity) were provided from the on-board standard SBE911+ CTD/rosette water sampler system or, in some cases when such profiles were lacking, from Jamstec eXpendable CTDs (XCTD; Nikolopoulos et al. 2016; Peeken et al. 2016). In addition to MLD the actual depth of the Polar Surface Water layer (PSW; Rudels et al. 2000) was used as a variable. The MLD and PSW don't necessarily coincide (Table 6.1). In the current analyses the measurements obtained from CTD stations closest to the SUIT stations, in space and time, were used.

SEA-ICE PROPERTIES

The combination of measurements collected with the SUIT's CTD and ADCP allow the calculation of sea-ice draft. The draft is the sea-ice thickness below the water line. The procedure is explained in detail in Castellani et al. (in preparation) and Lange (2017) and only a summary is provided here. Sea-ice draft is the depth of the SUIT, minus the distance between the SUIT and the bottom of the ice. These pieces of information are combined and corrected for the movement of the SUIT, i.e. pitch and roll, The distance trawled is retrieved by GPS information. The identification of ridges along the SUIT profile follows Castellani et al. (2014; 2015) and Rabenstein et al. (2010). Ice draft local minima deeper than a threshold value of 1.5 m (Castellani et al. 2015) along the SUIT profile are identified as potential ridges. In order to be recognized as two separated topographic elements, adjacent minima need to be separated by a draft point shallower than half the depth of the first minima. The number of ridges identified is used to calculate the ridge density per profile (n km^{-1}). The depth of identified ridges along a SUIT profile is used to calculate the average ridge depth per station. Moreover, ridges deeper than 3m are selected as a separate variable, since *A. glacialis* were found having elevated abundances at 3-6m deep ridges in the study of Gradinger et al. (2010)

Retrieval of in-ice chlorophyll *a* is based on the under-ice hyperspectral measurements taken with the RAMSES sensors mounted on the SUIT frame. The correlation between spectral shape of under-ice light measurements and chlorophyll *a* has been already used by several studies in the Arctic (Mundy et al. 2007; Lange et al. 2016; Lange et al. 2017) and in the Antarctic (Melbourne-Thomas et al. 2015) to infer chlorophyll *a* content without the disruption of the sea-ice. Among several methods existing (see Lange et al. 2016 for a review), the most widely used is the normalized differences indices (NDI). As in Castellani et al. (in preparation), the use of NDI method is justified for the present data set because it minimizes the variability introduced by latitudinal differences and the differences in sea-ice properties that can affect light transmission. Two different algorithms for PS80 and for PS92 were used because the two expeditions have been carried out in different seasons: PS80 covers summer conditions, i.e. a melting stage, absence of snow on sea ice and presence of melt ponds; PS92 covers spring conditions, i.e. with relatively thick snow cover at each sampling station. For PS80 the algorithm from Lange et al. (2016) developed for this data set was used (see their Table 3). The NDI algorithm for PS92 was developed by merging this data set with data collected in the same season and in the same location two years later (expedition PS106 in 2017 on board of the RV Polarstern) as described in Castellani et al. (in preparation).

DATA ANALYSIS

A principal component analysis (PCA) was performed to assess similarity in environmental variables between PS92 stations using mixed layer depth (MLD), depth of polar surface water (PSW), surface water salinity (SAL), surface water temperature (TMP), water column chlorophyll *a* concentration (CHL), in-ice chlorophyll *a* concentration (IIC), sea ice cover (COV), sea ice draft (DFT), average number of ridges km^{-2} (RID) and average number of ridges >3m thick km^{-2} (RD3). For the PCA analysis, the environmental data were normalized to obtain a consistent scale and equal variances (Clarke & Warwick 2001). Differences in amphipod abundance or environmental variables between regions and expeditions were tested using a non-parametric Wilcoxon Rank Sum test. Statistical significance was set at $\alpha = 0.05$.

The variability in *A. glacialis* abundance as a function of each individual environmental variable was studied by modelling these as smooth function using generalized additive models (Wood 2006; IJsseldijk et al. 2015). Data exploration was carried out prior to analyses. The presence of outliers was investigated using Cleveland dotplots, collinearity was assessed using scatterplots and Pearson correlation coefficients (Ieno & Zuur 2015). From PS92, the stations 31_1 and 32_12 were removed from the analysis due to missing environmental data. The response variable was the number of *A. glacialis* caught at a certain station with the logarithm of the trawled distance as offset to take into account the differences in sampled distance. The response variable was assumed to follow a negative binomial distribution with log link. Since the number of sampling stations was relatively low, the degrees of freedom for each smooth (k) were set at a maximum of 4 to avoid over-complicated models. A leave-one-out likelihood based cross validation was used to select the best model. The corrected Akaike's Information Criterion (AICc), suitable for small sample sizes, was also used to compare the models (Sugiura 1978). A likelihood ratio test based on Chi-square statistics was used to assess if a particular environmental variable explained the variation in amphipod abundance significantly. Statistical significance was set to $\alpha = 0.05$. The significance and explanatory power were investigated for each environmental variable separately.

To investigate the consistency of results over multiple seasons and investigate if drivers of *A. glacialis* abundance remain the same over time, the analysis was repeated with the addition of data from the "IceARC" (PS80) expedition conducted in 2012 (Fig. 6.1). During Polarstern expedition PS80 (2 August – 29 September 2012), samples and environmental data were obtained from the Eurasian part of the Arctic Ocean deep-sea basin in a similar manner as during PS92. Details on the environmental conditions at sampled stations are listed in Table S6.1 of Supplement 6A and David et al. (2015). Due to the small sample size, the data of PS80 was added to the dataset of PS92, instead of analysed seperately, to increase model performance. One station (station 204_1, PS80) was conducted in open water. This single station showed marked differences in environmental properties resulting in outliers (David et al. 2015). Because the aim of this study was to investigate the influence of sea-ice properties on amphipod abundance, it was excluded from the analysis. The *A. glacialis* abundance at this station was the lowest recorded value from both expeditions (0.01 ind. m^{-1}). In-ice chlorophyll *a* was not used in this analysis due to incomplete data.

In addition to modelling the *A. glacialis* abundance as a function each individual environmental variable, a forward selection procedure was used to investigate the effect of additional variables on the models. This was not possible when using only the PS92 data because the number of stations was too low. Auto-correlation plots were used to assess independence of sampling stations, quantile-quantile plots to verify normality and the residuals versus the fitted values were plotted to assess the homogeneity of variance (Zuur et al. 2012). All analyses were performed using R version 3.4.4 (R Core Team, 2018) with packages 'mgcv', 'stat', 'ggbiplot' and 'sme'.

RESULTS

APHERUSA GLACIALIS IN THE REGION NORTH OF SVALBARD DURING SPRING

All SUIT stations conducted during PS92 were in ice-covered waters. Station bottom depth at the Svalbard shelf and slope ranged between 189 and 1051 m, in the Sophia basin between 1972 and 2249 m. At the Yermak Plateau the station bottom depth ranged from 791 m to 914 m. In the under-ice surface layer, chlorophyll *a* concentrations ranged from 0.25 – 10.58 mg m^{-3}, in-ice chlorophyll *a* concentration from 0.18 and 2.25 mg m^{-3}, temperature from -1.83 to -1.26°C and salinity from 33.38 to 34.32. The sea-ice draft was on average 1.57 ± 0.68 m (standard deviation), with an average ridge depth of 3.49 ±1.05 m. During SUIT hauls, 5.06 ± 2.67 ridges km^{-1} were encountered on average, of which 2.06 ± 1.52 reached deeper than 3 meters.

The PCA analysis, with the first principal component explaining 36.8% of the variance, separates the Yermak plateau stations from the Svalbard shelf/slope and Sophia basin stations (Fig. 6.2a). The separation seems to be mainly driven by mixed layer depth, chlorophyll *a*, temperature and salinity, and less by sea-ice parameters such as ice cover and ridge densities. The abundance of *A. glacialis* was significantly different between the Yermak Plateau stations with the Svalbard shelf/slope (Wilcoxon Rank Sum, $U = 17$, $p < 0.05$) and Sophia basin stations (Wilcoxon Rank Sum, $U = 24$, $p < 0.01$). The abundances at the latter two regions did not differ from each other (Wilcoxon Rank Sum , $U = 8$, $p = 0.6$). The average *A. glacialis* abundance was 0.04 ± 0.03 ind. m^{-2} at the Yermak Plateau, 1.02 ± 0.76 ind. m^{-2} at the Sophia deep and 0.73 ± 0.61 ind. m^{-2} at the Svalbard shelf/slope (Fig. 6.2b). Overall, the abundance of *A. glacialis* ranged from 0.02 to 3.5 ind. m^{-2}, with an average of 0.83 ind. m^{-2} (Table 6.1).

The length-frequency of *A. glacialis* showed a bimodal distribution in all stations. The first peak occurred at approximately 2.5 mm, slightly increasing towards 3.5 mm over time within PS92. The second mode was found at approximately 8 mm, which also seemed to be slightly increasing with time. The larger individuals

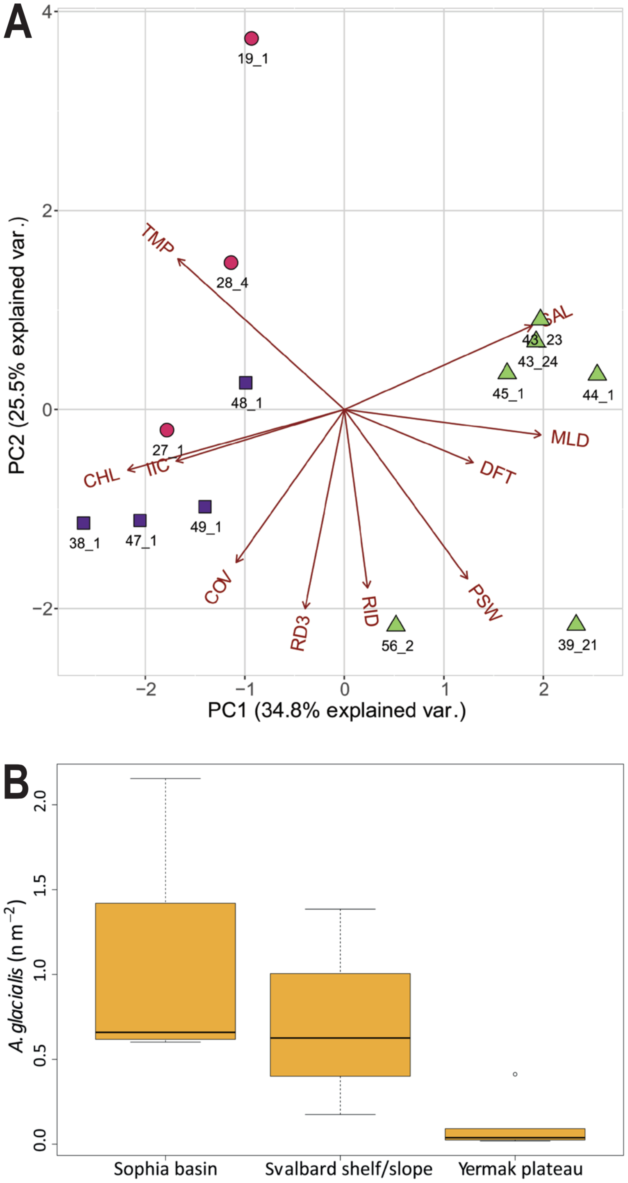

Figure 6.2: Results of a principal component analysis (PCA) using environmental variables (A), showing the first and second principal component. Each point represents a PS92 station. Station locations are indicated with a triangle for Yermak Plateau stations, a round for Svalbard slope stations and squares for Sophia Basin stations. COV = sea ice cover during trawling (%), DFT = sea-ice draft (m), RDP = average ridge depth (m), RID = number of ridges km^{-1}, RD3 = number of ridges over 3 m deep km^{-1}, CHL = surface water chlorophyll *a* concentration (mg m^{-3}), TMP = surface water temperature (°C), SAL = surface water salinity, IIC = in-ice chlorophyll *a* concentration (mg m^{-2}), MLD = mixed layer depth (m) and PSW = polar surface water layer (m). The abundance of *Apherusa glacialis* in the different regions is shown in (B). The horizontal black lines show the median density in a depth stratum. The upper and lower limits of the yellow squares indicate the 25th and 75th percentile, thus 50% of the stations have abundances between these limits. The upper and lower limits of the vertical line indicate the minimum and maximum density of the stations in a depth stratum. Black dots represent the true minimum and maximum densities, but are numerically distant from the other data points and therefore considered outliers.

dominated the samples in the first four stations of the expedition (19_1 to 31_1), with the proportion of smaller individuals ranging from 5.9 to 44.1%. The proportion of smaller individuals increased to 61 and 65% at stations 32_12 and 38_1, respectively, and increased even further to > 84.5% at the last four stations. Unfortunately, the number of amphipods found at the Yermak Plateau stations was too small to obtain a reliable length-frequency distribution. As an exception, at station 56_2, considered a Yermak Plateau station but taken late in the cruise, the proportion of small individuals was 93.6%.

RELATIONSHIP WITH ENVIRONMENTAL VARIABLES

Water column chlorophyll *a* was correlated with in-ice chlorophyll *a* (Pearson correlation = 0.7), and inversely correlated with salinity (Pearson correlation = -0.7). Sea-ice draft was highly correlated with average ridge depth (Pearson correlation = 0.8), and temperature was correlated with the depth of polar surface water (Pearson correlation = 0.8; Fig. 6.3).

The best single explanatory variable influencing the abundance of *A. glacialis* was surface water chlorophyll *a* (CHL), with abundances increasing with increasing values (Table 6.2). Other variables that significantly influenced *A. glacialis* abundance were salinity (SAL), sea-ice draft (DFT), in-ice chlorophyll *a* (IIC), mixed layer depth (MLD) and temperature (TMP). The *A. glacialis* abundance as a function of the aforementioned significant continuous covariates is shown in Fig. 6.4. An overview of all covariates can be found in Fig. S6.1 of Supplement 6B, which also includes model diagnostics.

COMPARISON WITH THE EURASIAN BASIN DURING SUMMER

In order to provide a general overview of similarities and differences between expeditions PS80 (summer) and PS92 (spring), boxplots of environmental properties and amphipod abundances are provided (Fig. 6.5). Some properties were not significantly different between expeditions, but showed a marked difference in variability, such as temperature and ridge density. This could reflect the extreme values at the Yermak Plateau in PS92 or the large spatial sampling scale during PS80 (David et al. 2015; Fig. 6.1). The abundance

Table 6.2: The explanatory power of environmental parameters on *Apherusa glacialis* abundance during spring (PS92). Models with the highest cross-validation log-likelihood (CVlik) and corrected Akaike's Information Criterion (AICc) are highlighted in bold. S(X) represents the smooth function of the covariate X, edf is effective degrees of freedom. The significance of the smooth function is represented as the adjusted R^2, the Chi^2 value and the *p*-value. CHL = surface water chlorophyll *a* concentration (mg m^{-3}), SAL = surface water salinity, DFT = sea-ice draft (m), RDP = average ridge depth (m), PSW = polar surface water layer (m), RD3 = number of ridges over 3 m deep km^{-1}, IIC = in-ice chlorophyll *a* concentration (mg m^{-2}), MLD = mixed layer depth (m), TMP = surface water temperature (°C), COV = sea ice cover during trawling (%) and RID = number of ridges km^{-1}.

covariate	CVlik	AICc	edf	Explained deviance	R^2	Chi^2 value	*p* value
s(CHL)	**-87.5**	**169**	2.82	88.63	0.824	93.48	**<0.001**
s(SAL)	-91.4	179.7	1.96	66.11	0.31	32.24	**<0.001**
s(DFT)	-91.6	186.5	1	16.97	0.406	5.51	**0.019**
s(RDP)	-94.8	188.9	1.23	13.58	0.412	4	0.11
s(PSW)	-95.7	188.2	1	7.61	0.388	1.55	0.213
s(RD3)	-96.7	189.4	1	0.09	0.185	0.01	0.903
s(IIC)	-96.9	185.1	2.13	51.67	0.567	15.68	**0.001**
s(MLD)	-116.5	187.3	2.37	51.23	0.214	16.56	**0.001**
s(TMP)	-117.3	187.9	2.35	48.58	0.443	13.54	**0.008**
s(COV)	-146.4	191.6	1.86	18.03	0.277	2.1	0.327
s(RID)	-147.2	189.1	1	2.26	0.255	0.58	0.445

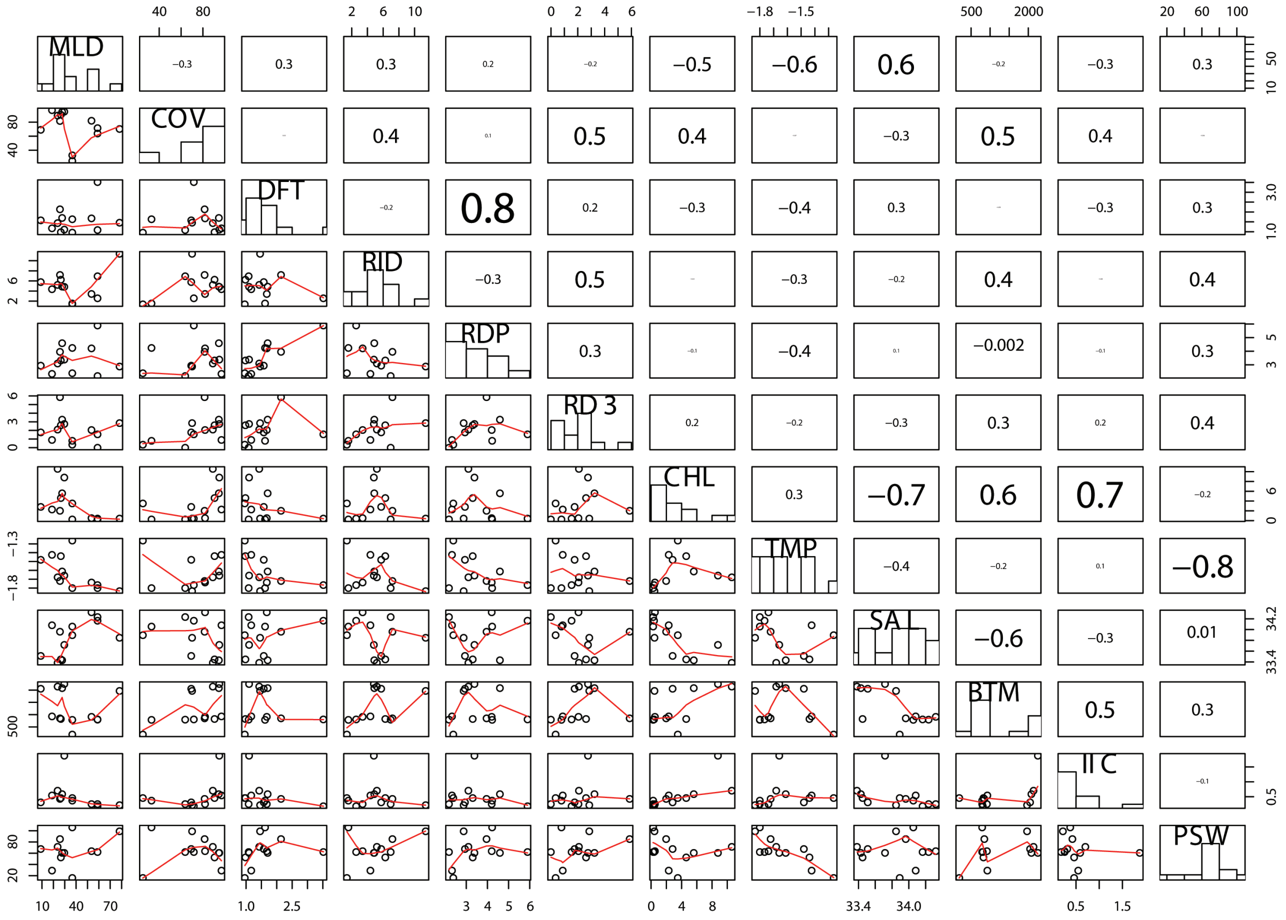

Figure 6.3: Pairwise corraltion plot of environmental variables in spring (PS92). The values in the upper level plots are Pearson correlation coefficients (Zuur et al. 2009). MLD = mixed layer depth (m), COV = sea ice cover during trawling (%), DFT = sea-ice draft (m), RID = number of ridges km^{-1}, RDP = average ridge depth (m), RD3 = number of ridges over 3 m deep km^{-1}, CHL = surface water chlorophyll *a* concentration (mg m^{-3}), TMP = surface water temperature (°C), SAL = surface water salinity, BTM = bottom depth, IIC = in-ice chlorophyll *a* concentration (mg m^{-2}) and PSW = polar surface water layer (m).

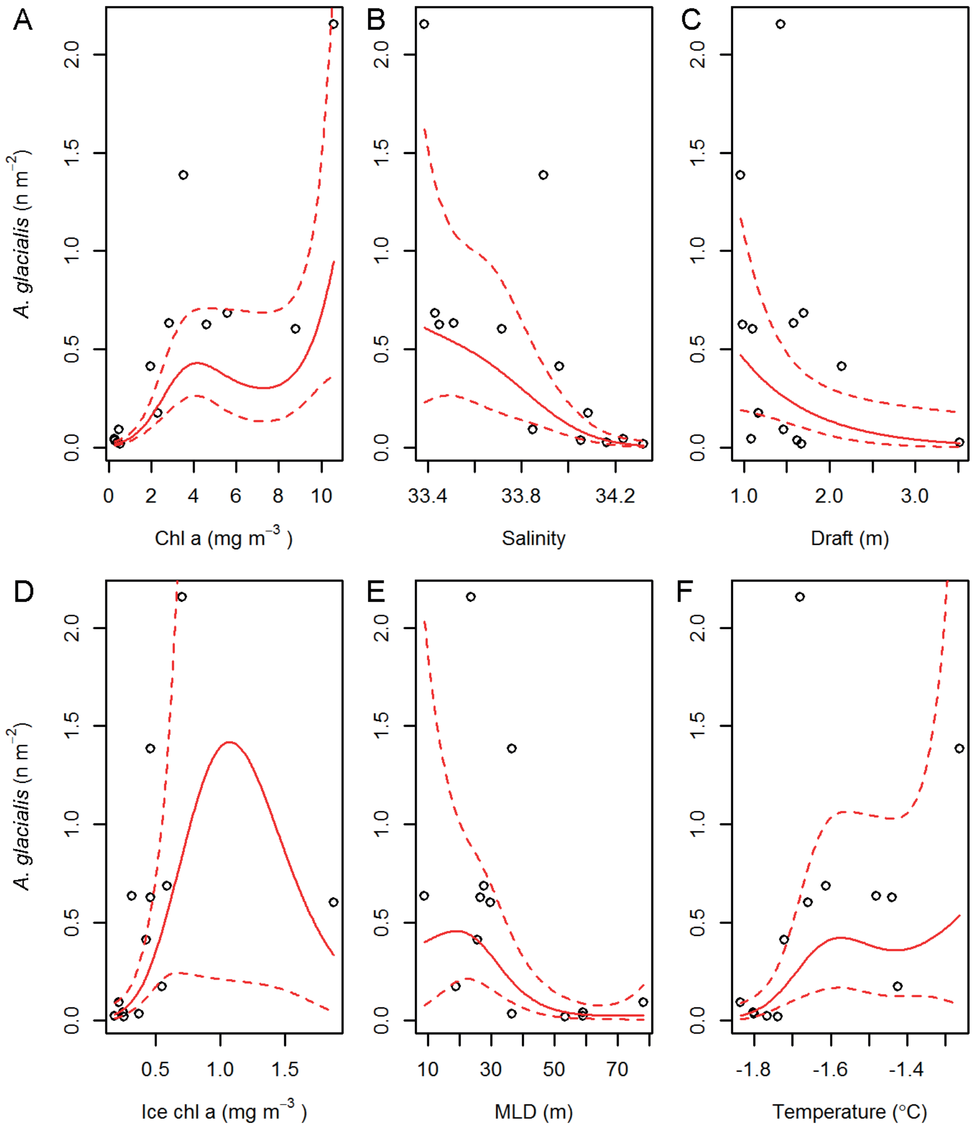

Figure 6.4: The abundance of *Apherusa glacialis* (n m^{-2}) in spring (PS92) as a function of environmental variables that showed a significant effect: water column chlorophyll *a* (A), salinity (B), sea-ice draft (C), in-ice chlorophyll *a* (D), mixed layer depth (E) and temperature (F) The estimated abundance based on the fitted GAM is shown as a red line. The 95% confidence interval is indicated by dotted lines.

of *A. glacialis* was lower during PS92 compared to PS80 (Wilcoxon Rank Sum, $U = 110$, $p = 0.03$). The environmental variables that were significantly different between expeditions were mixed layer depth (Wilcoxon Rank Sum, $U = 18$, $p < 0.01$), depth of polar surface water (Wilcoxon Rank Sum, $U = 131$, $p < 0.001$), sea-ice draft (Wilcoxon Rank Sum, $U = 20$, $p < 0.01$), average ridge depth (Wilcoxon Rank Sum, $U = 20$, $p < 0.01$), number of ridge deeper than 3m (Wilcoxon rank sum, U = 30, p = 0.02), salinity (Wilcoxon

Rank Sum, $U = 0$, $p < 0.001$), surface water chlorophyll *a* concentration (Wilcoxon Rank Sum, $U = 13$, $p < 0.001$). The concentration of in-ice chlorophyll *a* did not significantly differ between expeditions (Wilcoxon Rank Sum, $U = 13$, $p = 0.06$), but only few measurement were available for PS80 ($n = 5$) which thus may offer an incomplete view of the entire sampling area.

Salinity was inversely correlated with polar surface water depth (Pearson correlation = -0.7), and water column chlorophyll *a* was correlated with in-ice chlorophyll *a* (Pearson correlation = 0.7). Average ridge depth was highly correlated with sea-ice draft (Pearson correlation = 0.8) and the number over ridges over 3 m thick km^{-1} (Pearson correlation = 0.6; Fig. 6.6).

The best single explanatory variables influencing the abundance of *A. glacialis* were temperature (TMP)

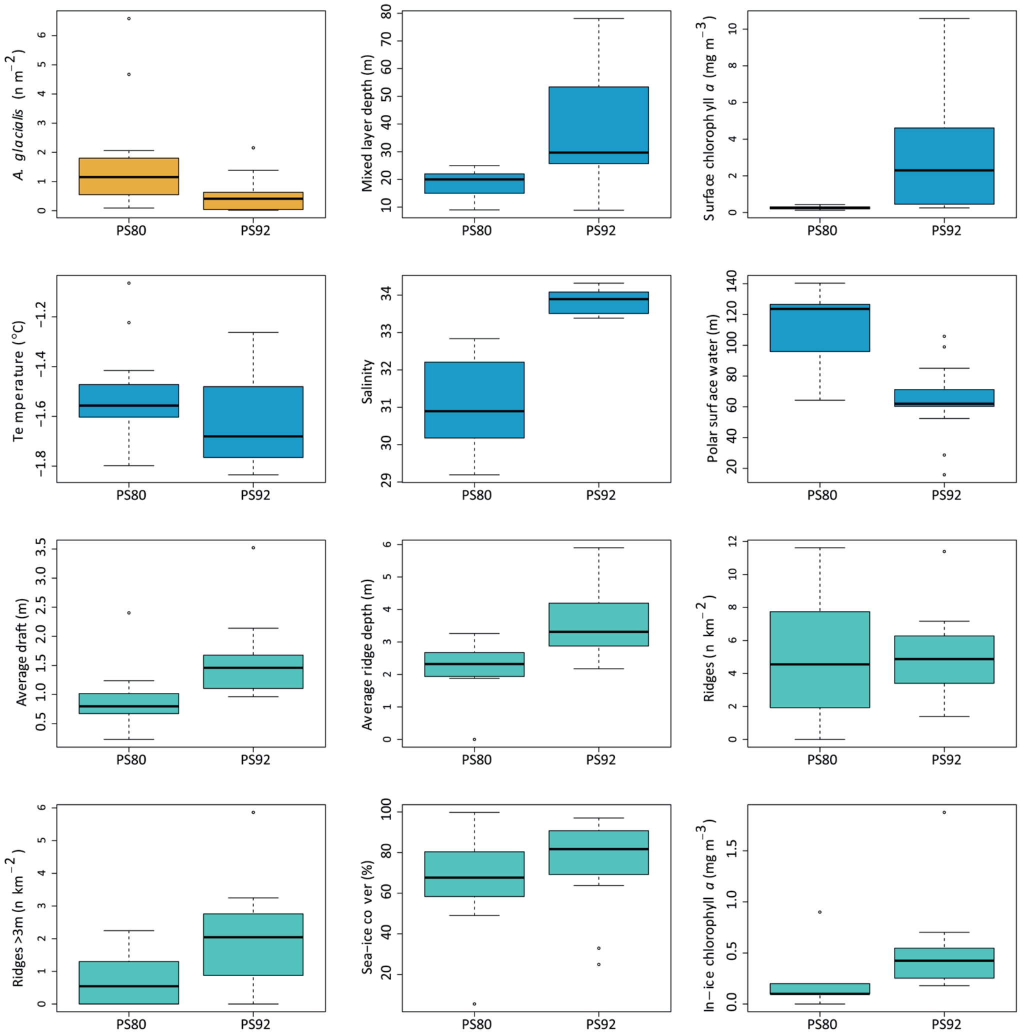

Figure 6.5: Comparison of expeditions PS80 and PS92 including *Apherusa glacialis* abundance (yellow), several surface water properties (blue) and several sea-ice properties (blue-green).

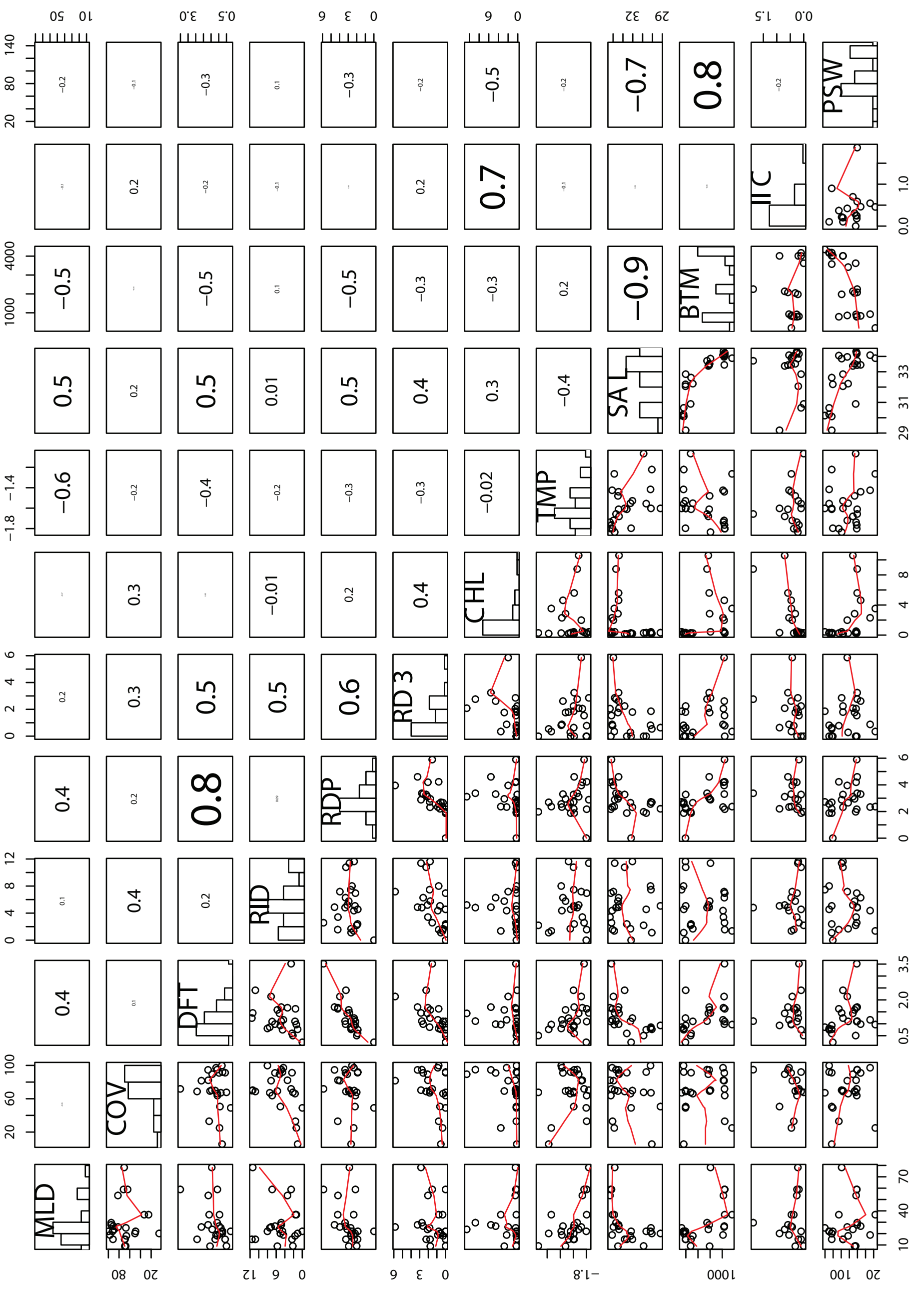

Figure 6.6: Pairwise corraltion plot of environmental variables in spring and summer (PS92 and PS80). The values in the upper level plots are Pearson correlation coefficients (Zuur et al. 2009). MLD = mixed layer depth (m), COV = sea ice cover during trawling (%), DFT = sea-ice draft (m), RID = number of ridges km^{-1}, RDP = average ridge depth (m), RD3 = number of ridges over 3 m deep km^{-1}, CHL = surface water chlorophyll a concentration (mg m^{-3}), TMP = surface water temperature (°C), SAL = surface water salinity, BTM = bottom depth, IIC = in-ice chlorophyll *a* concentration (mg m^{-2}) and PSW = polar surface water layer (m).

and salinity (SAL; Table 6.3). Highest abundances seemed to occur at intermediate values of both variables. Other variables that significantly influenced *A. glacialis* abundance were the number of ridges km^{-1} (RID), sea-ice draft (RDP), mixed layer depth (MLD) and the factor 'Expedition'. The *A. glacialis* abundance as a function of the aforementioned significant continuous covariates is shown in Fig. 6.7. An overview of all covariates can be found in Supplement 6C. The forward selection procedure, using the single best variable temperature (TMP) as a starting point, showed that the model improved when the average ridge depth (RDP) was added, resulting in a CV log-likelihood of 174.72 (Table 6.4). Adding more variables did not improve the model. There was minimal auto-correlation between stations. Model diagnostics can be found in Supplement 6C.

Table 6.3: The explanatory power of environmental parameters on *Apherusa glacialis* abundance using spring and summer data (PS80 and PS92). Models with the highest cross-validation log-likelihood (CVlik) and corrected Akaike's Information Criterion (AICc) are highlighted in bold. s(X) represents the smooth function of the covariate X, edf is effective degrees of freedom. The significance of the smooth function is represented as the adjusted R^2, the Chi^2 value and the *p*-value. Abbreviations of the environmental variables as in Table 6.1.

covariate	CVlik	AICc	edf	Explained deviance	R^2	Chi^2 value	*p* value
s(TMP)	**-180.9**	363	2.54	41.77	0.004	23.63	**<0.001**
s(SAL)	-181	362.4	2.42	42.44	-0.222	24.41	**<0.001**
EXP	-182.7	366	1	20.17	-0.023	-2.63	**0.009**
s(RID)	-183.8	368	1	14.62	0.024	4.21	**0.04**
s(RDP)	-184.3	368.8	1.82	22.69	0.087	11.78	**0.004**
s(COV)	-186.1	371	1	5.06	-0.025	1.88	0.17
s(RD3)	-186.2	372.2	1	1.12	0.019	0.43	0.51
S(PSW)	-186.6	370.3	1	7.38	0.059	1.98	0.16
s(CHL)	-187.2	373.3	1.3	2.36	-0.012	0.15	0.806
s(DFT)	-187.3	371.6	1.17	6.21	0.043	3.29	0.127
s(MLD)	-202.2	**360.9**	1	33.63	-0.53	21.73	**<0.001**

DISCUSSION

APHERUSA GLACIALIS IN THE AREA NORTH OF SVALBARD DURING SPRING

The PS92 *Apherusa glacialis* abundances, ranging from 0.02 to 3.5 ind. m^{-2}, could be considered as relatively low compared to other studies, although most of these studies show a very high variation. For example, Gulliksen (1984) showed abundances ranging from 1 to 118 ind. m^{-2} under the multi-year pack ice of Franz Josef Land, while numbers between 0 and 2488 ind. m^{-2} under were found in the multi-year pack ice of the Barents Sea (Gulliksen & Lønne 1989) and the abundance under the multi-year ice of the Svalbard/Fram strait region varied between 8 and 2196 ind. m^{-2} (Lønne & Gulliksen 1991a). Studies reporting abundance estimates within a similar range as our study are, for example, Werner & Gradinger (2002) with 1.9 ind.

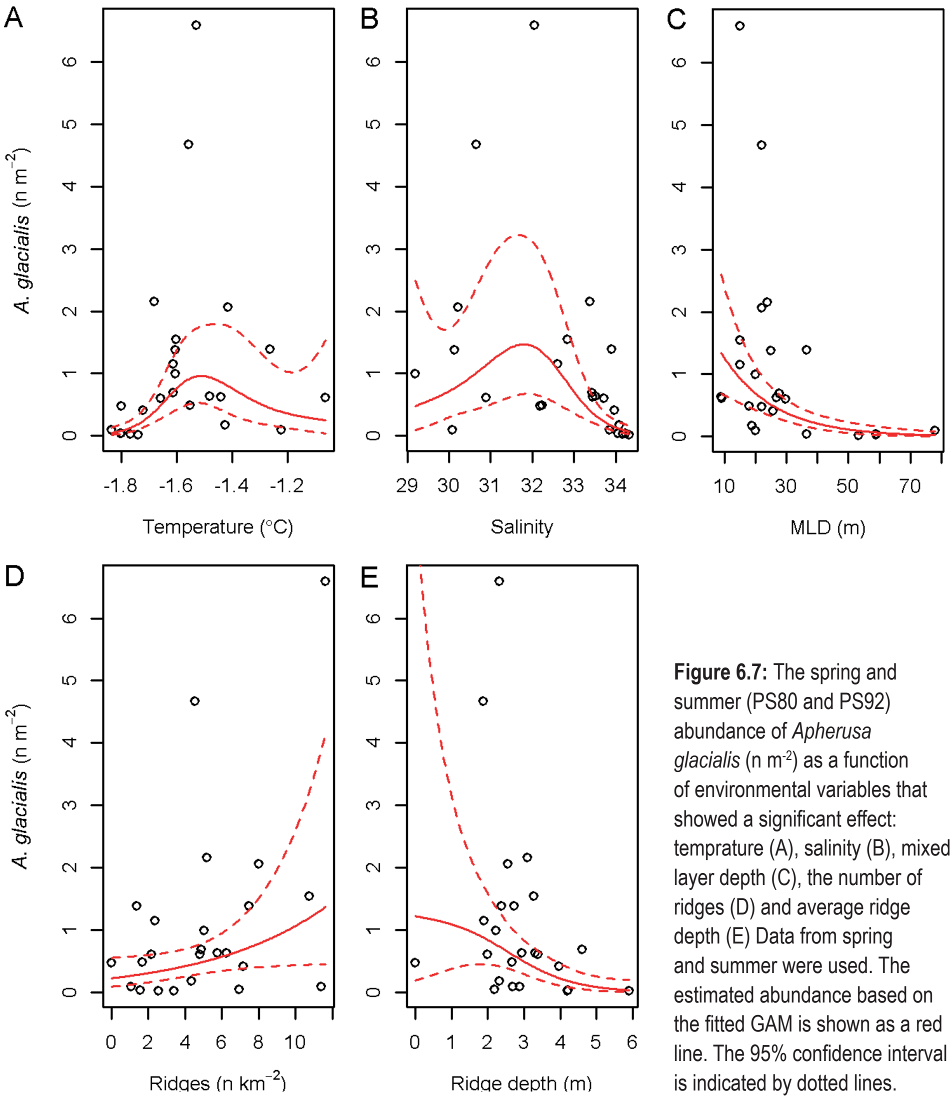

Figure 6.7: The spring and summer (PS80 and PS92) abundance of *Apherusa glacialis* (n m^{-2}) as a function of environmental variables that showed a significant effect: temprature (A), salinity (B), mixed layer depth (C), the number of ridges (D) and average ridge depth (E) Data from spring and summer were used. The estimated abundance based on the fitted GAM is shown as a red line. The 95% confidence interval is indicated by dotted lines.

m^{-2} in the Fram Strait/Greenland Sea during spring (May/June) and Werner & Auel (2005) with 2.1 ind m^{-2} in the same area during winter. An average *A. glacialis* abundance of 7.7 ind m^{-2} was reported by Brown et al. (2017) for the area north of Svalbard and the Nansen basin in July. An overview of literature reporting amphipod abundances can be found in Hop et al. (2000).

The reported large variability of under-ice abundances may reflect differences in the spatial scale of sampling. Numbers estimated using pumps or frames sample small areas and are likely to be highly variable, as they cannot account for mesoscale variability of abundance around the sampling spot. In addition, methods using scuba maybe biased towards sampling in places with high abundances (Cross 1982; Lønne &

Table 6.4: Results of the forward selection procedure using leave-one-out likelihood cross-validation. s(x) represents a smooth function of the covariate x. A model was considered improved when the addition of a covariate increased its likelihood with at least 2 (indicated in bold). Abbreviations of the environmental variables as in Table 6.1.

	Step 0	Step1	Step2	Step3	Step4
Intercept	-184.92	-	-	-	-
s(TMP)	-	**-180.94**	-	-	-
s(SAL)	-	-180.97	-187.83	-186.13	-193.61
EXP	-	-182.71	-183.02	-177.97	-180.52
s(RID)	-	-183.8	-195.17	-179.5	-178.49
s(RDP)	-	-184.31	**-174.72**	-	-
s(COV)	-	-186.14	-183.91	-178.24	-177.23
s(RD3)	-	-186.24	-182.04	-174	-
S(PSW)	-	-186.59	-192.39	-207.07	-195.21
s(CHL)	-	-187.25	-185.21	-176.9	-181.95
s(DFT)	-	-187.29	-178.56	-175.24	-174.01
s(MLD)	-	-202.19	-203.25	-186.75	-177.35

Gulliksen 1991b; Hop et al 2000), in which case reported numbers might represent the abundances found at a patch. In contrast, the SUIT samples over several kilometres, giving a more robust average estimate over a larger area due to the averaging of local aggregations and stretches of low abundances. However, the SUIT does not quantitatively sample topographical features providing protection from the trawl, such as ridges, over-rafted floes and crevices. This could lead to an underestimation of abundance when the amphipods accumulate close to these structures.

Near Franz Josef land and the northern Barents Sea in summer, Polterman et al. (2000) found a length distribution of *A. glacialis* similar to our study, with juveniles ranging from 4-6 mm and adults ranging from 8–13 mm. The cohorts were slightly larger than the individuals from our study which could be explained by the sampling being performed later in time (July/August). They suggest that the adults are approximately 1.5 years old, based on mating taking place during winter (Melnikov 1997). Another similar length distribution was found by Cross (1982) in an Canadian inlet. During May, two cohorts were found with average sizes of 3.3 and 8.9 mm. Somewhat larger cohorts were found in July with average sizes of 5.7 and 11.4 mm. A two cohort population structure was also found north of Svalbard during September although the sizes of the respective cohorts were closer together than found in our and other studies (Beuchel & Lønne 2002), which could suggest earlier reproduction or higher growth rates of the amphipods during their first year. Assuming that each mode in the size distribution represents one year class, the finding of two cohorts corresponds with general assumption that *A. glacialis* has one reproduction cycle per year and a maximum age of two years (Cross 1982; Poltermann 1998; Beuchel & Lønne 2002).

RELATIONSHIP WITH ENVIRONMENTAL VARIABLES DURING SPRING

The single best explanatory variable influencing the *A. glacialis* abundance during PS92 was surface water chlorophyll *a* concentration, indicating that food is the main driver of the amphipod's distribution during spring. Surface water chlorophyll *a* concentration was correlated to in-ice chlorophyll *a* concentration, which had a lower albeit significant influence on the *A. glacialis* abundance. *Apherusa glacialis* mainly grazes on the sea-ice underside and has been found to feed on strands of algae attached to the sea ice (Bradstreet & Cross 1982; Werner 1997b; Scott et al. 1999; Poltermann 2001). In addition, their diet has been found to be dominated by detritus, consisting of plant material, animal remains (including former sea-ice algae and in-ice fauna), bacteria and fungi (Scott et al. 1999; Poltermann 2001). Fatty acid and stable isotope analyses suggested that of 85% of the carbon in the tissue of *A. glacialis* is derived from sea-ice algae (Kohlbach et al. 2016).

An increase in *A. glacialis* abundance was related to lower mixed layer depth, higher temperature, lower salinity, thinner sea ice and higher chlorophyll *a* concentration. These are all factors indicating an onset of sea-ice melt which has likely increased both chlorophyll *a* concentration and the accessibility of in-ice algae (or its detritus) as a food source (Bradstreet & Cross 1982; Werner 1997b). The increased surface water chlorophyll *a* concentration could be a result of a phytoplankton bloom. Observations made by divers showed, however, that increase surface water chlorophyll *a* could also be a result of small strands of microalgae that were likely sloughed off the sea ice (Cross 1982).

Abundances were lowest at the Yermak plateau stations, at which the water column properties showed no indication of sea-ice melt and, likely as a result, a low chlorophyll *a* concentrations. In addition to the water column properties themselves, there are other processes in this area that could influence zooplankton abundance. Amphipods could be detached from the sea ice due to increased swell (Hop et al. 2000), because the Yermak plateau is subject to enhanced tidal variability with strong tidal currents over its slopes, leading to increased internal wave activity and enhanced mixing of water masses (Padman & Dillon 1991; Fer et al. 2015).

RELATIONSHIP WITH ENVIRONMENTAL VARIABLES USING DATA FROM TWO SEASONS

Temperature, and in somewhat lesser extend salinity, were the best single explanatory variables, explaining the overall variation in *A. glacialis* abundance when combining the results of the spring and summer expeditions, with highest densities found at intermediate values. In addition, there was an influence of the average ridge depth, with highest numbers found underneath sea ice with ridges of intermediate size, while decreasing with increasing ridge depth. Ridge depth was highly correlated to sea-ice draft and enhanced the model when added as a variable to the temperature smoother. Furthermore, an increase in the number of sea-ice ridges had a positive effect on the number of amphipods.

In most biological systems, there are several environmental processes taking place, and the variables describing these processes (e.g. temperature, salinity, sea-ice conditions) are often highly correlated (Burnham & Anderson 2002). The effects of sea ice on physical, oceanographic and biological features can be very complex and variable (Castellani et al. 2017). Consequently, pin-pointing which variable is most influential on the distribution of a species is extremely challenging (Braunisch et al. 2013). With small sample sizes, such as in our study, it can be difficult to unravel these effects, particularly when there is large variability in environmental characteristics due to a large spatial sampling scale and seasonal changes. By combining the data from both seasons, the sample size is increased, but a variation in the deteminants of amphipod abundance between seasons may become less clear. However, despite the small sample size, this study shows some evidence for environmental drivers of the large-scale abundance of *A. glacialis.*

Results suggest that there is variability in the relationship between *A. glacialis* and environmental parameters between seasons. Findings indicate that under-ice topography and oceanographic features have an increased influence on *A. glacialis* abundance when summer data is added, as opposed to food concentration during spring. Although inter-annual differences cannot be excluded, seasonal variability in factors influencing *A. glacialis* abundance can be a result of a changing trade-off between food availability and predation pressure. The need for food may be higher in spring due to the necessity to replenish lipid reserves (Bradstreet & Cross 1982). Predation has been suggested to increase when the season progresses (Hop et al. 2000). *Apherusa glacialis* is an important prey species of polar cod (*Boreogadus saida*) in the Central Arctic Ocean (Chapter 5). During PS80, the stomach contents of the polar cod were dominated by *A. glacialis* in terms of biomass (Chapter 5). Although birds were observed feeding on polar cod during PS92, indicating its presence, only a small number of fish were caught in the under-ice surface layer (unpublished data). Despite a potentially low catch efficiency by the SUIT, this is an indication that the polar cod abundance was a lot lower in the area during PS92 than during PS80. In addition, a preliminary investigation of the stomach contents of the polar cod caught during PS92 showed that the fish were mainly feeding on *Calanus* spp. and the contribution of *A. glacialis* to the diet was negligible. The abundance of *Calanus* spp. in the under-ice surface layer was approximately six-fold higher during PS92 compared to PS80, except for at the Yermak Plateau stations (unpublished data; David et al. 2015). The difference in the abundance of *Calanus* spp. between seasons could be a result of the copepod's seasonal change in vertical distribution, leaving the surface waters and moving to deeper layers, which occurs from August onwards (Conover 1988; Kosobokova 1999; Daase et al. 2008). This indicates that the predation pressure on *A. glacialis* was perhaps not only low during PS92 due to the smaller number of fish, but also due to the larger presence of another species serving as a food source. It also shows that the need for sea-ice structures to avoid predators could be higher during summer compared to spring. In future studies it would be interesting to investigate if the relationship with environmental characteristics is different for juvenile and adult *A. glacialis*, because the food availability/predation trade-off likely differs in with size (Quetin et al. 1996).

In conclusion, warming temperatures and loss of sea ice due to climate change may have different impacts on the *A. glacialis* distribution. Increased light availability may enhance primary production within sea ice, and possibly also in the water column (Tedesco et al. 2012; Fernández-Méndez et al. 2015). It could also change the timing of peak primary production and affect the distribution of species differently causing a shift in community structure, the consequences of which are currently unclear. The development of sea-ice algal assemblages within or under ice as well as detritus production may be hampered by a later sea-ice formation and earlier sea-ice melt (Melnikov et al. 2001; Lavoie et al. 2005). Loss of sea-ice structures and increasing temperature may negatively influence *A. glacialis* abundance due to increased predation. Further research is, however, needed to fully understand the impact of a changing environment. Although there was no evidence of *A. glacialis* occupying deeper water layers in the ice-covered oceanic waters, the abundance and vertical distribution of *A. glacialis* in open waters should be investigated. Nevertheless, this study provides the first insight in large-scale relationships between environmental parameters and *A. glacialis* abundance, including physical and oceanographic characteristics of both water column and sea ice.

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SUPPLEMENT 6A: Additional information on samples station and environmental variables during PS80.

Table S6.1: The environmental properties and abundance of *Apherusa glacialis* per station from PS80. LAT = latitude, LON = longitude, COV = sea ice cover during trawling (%), DFT = sea-ice draft (m), RDP = average ridge depth (m), RID = number of ridges km^{-1}, RD3 = number of ridges over 3 m deep km^{-1}, CHL = surface water chlorophyll *a* concentration (mg m^{-3}), TMP = surface water temperature (°C), SAL = surface water salinity, BTM = bottom depth (m), IIC = in-ice chlorophyll *a* concentration (mg m^{-2}), MLD = mixed layer depth (m), PSW = polar surface water layer (m) and APH = *A. glacialis* (n m^{-2}).

STN	Date	LAT	LON	COV	DFT	RDP	RID
204_1	05-08-2012	81.4545	31.0793	31.10	0.06	0.00	0.00
216_1	07-08-2012	82.4863	30.0068	67.70	0.51	1.99	2.18
223_1	09-0-2012	84.0685	30.4708	69.62	1.24	2.32	11.62
233_1	11-08-2012	84.0420	31.2758	68.91	2.40	3.26	10.78
248_1	16-08-2012	83.9338	75.5073	66.27	1.10	2.67	1.67
258_1	20-08-2012	82.7407	109.6442	91.22	0.59	1.89	2.38
276_1	25-08-2012	83.0730	129.1293	99.82	0.80	2.55	8.02
285_1	26-08-2012	82.8942	129.8230	91.94	0.75	1.88	4.55
321_1	04-09-2012	81.7197	130.0348	50.47	0.93	2.22	5.04
333_1	06-09-2012	82.9910	127.0912	5.43	0.77	2.68	1.09
345_1	09-09-2012	85.2542	123.8868	67.23	0.86	2.73	7.47
397_1	29-09-2012	84.1675	17.9292	49.07	0.23	0.00	0.00

STN	RD3	CHL	TMP	SAL	BTM	IIC	MLD	PSW	APH
204_1	0.00	0.28	0.87	31.81	464	-	9		0.01
216_1	0.00	0.30	-1.06	30.89	3616.8	0	9	64.3	0.61
223_1	1.79	0.20	-1.53	32.05	4018.9	0.2	15	95.9	6.59
233_1	2.25	0.13	-1.60	32.83	4011.2	0.1	15	95.9	1.54
248_1	0.28	0.28	-1.55	32.23	3423.1	-	18	83.1	0.49
258_1	0.00	0.15	-1.61	32.61	3574	-	15	123.6	1.15
276_1	0.81	0.25	-1.42	30.21	4188.5	-	22	129.6	2.06
285_1	0.00	0.33	-1.56	30.65	4170	0.1	22	129.6	4.67
321_1	0.63	0.33	-1.60	29.19	4011.9	0.9	20	123.6	0.99
333_1	0.55	0.19	-1.22	30.08	4186.7	-	20	123.6	0.09
345_1	1.87	0.44	-1.60	30.14	4353.8	-	25	140.4	1.38
397_1	0.00	0.27	-1.80	32.18	4025.7	-	22	120.7	0.47

SUPPLEMENT 6B: Model results using spring data (PS92)

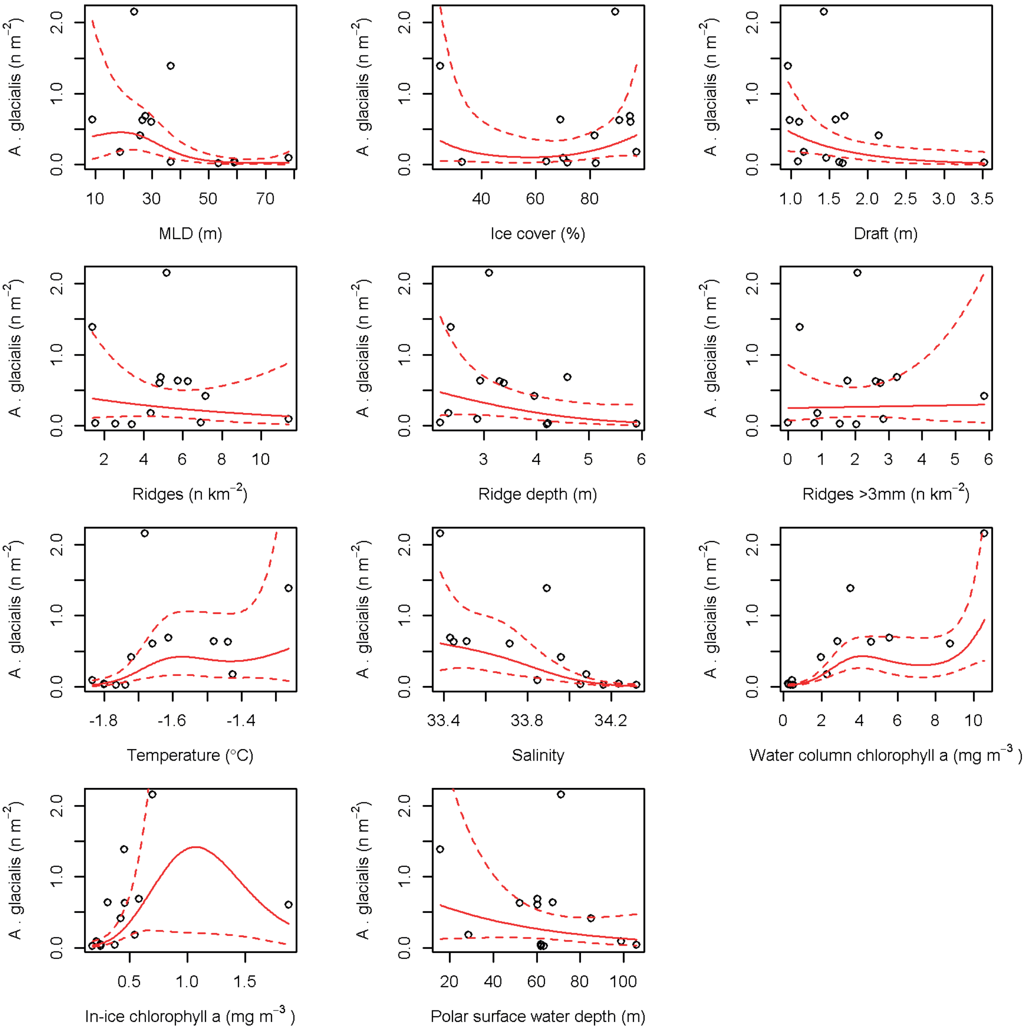
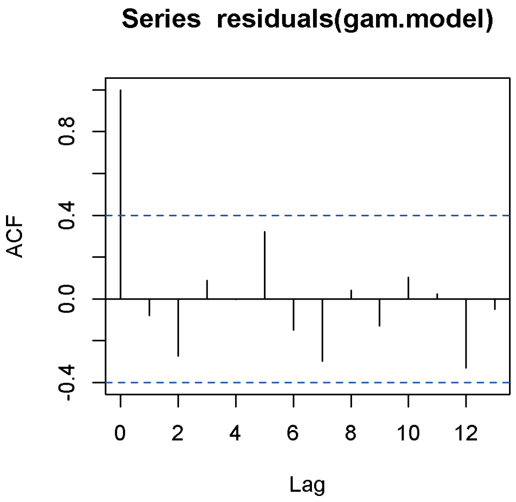


Figure S6.1: The abundance of *Apherusa glacialis* (n m^{-2}) as a function of spring environmental variables. The estimated abundance based on the fitted GAM is shown as a red line. The 95% confidence interval is indicated by dotted lines.

Figure S6.2: Plot of autocorrelation in model residuals using water column chlorophyll *a* as variable, which had the best explanatory power for explaning variation in *Apherusa glacialis* abundance during spring.



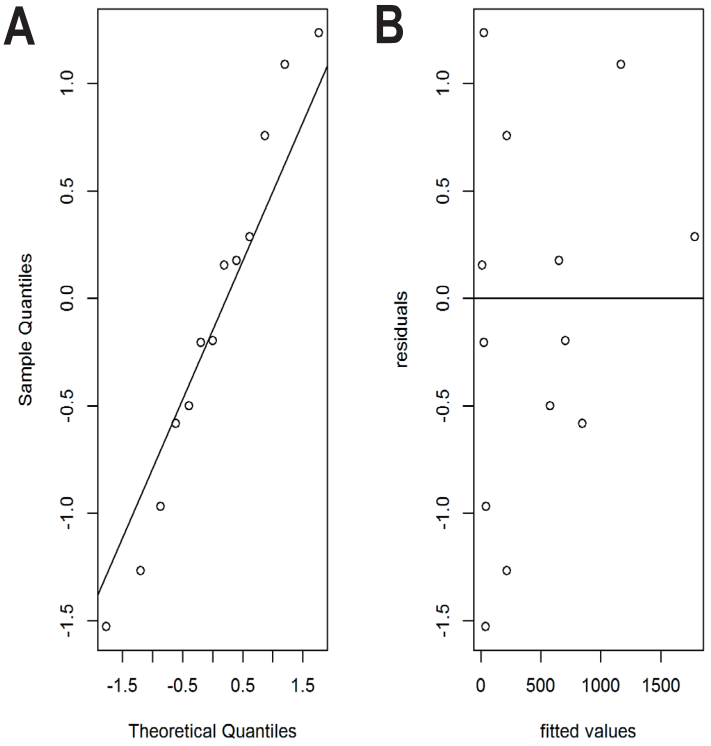


Figure S6.3: Model diagnostics for a GAM using water column chlorophyll *a* as variable: quantile-quantile (q-q) plot (A) and the fitted values vs. the residuals (B).

SUPPLEMENT 6C: Model results using spring and summer data (PS92 & PS80)

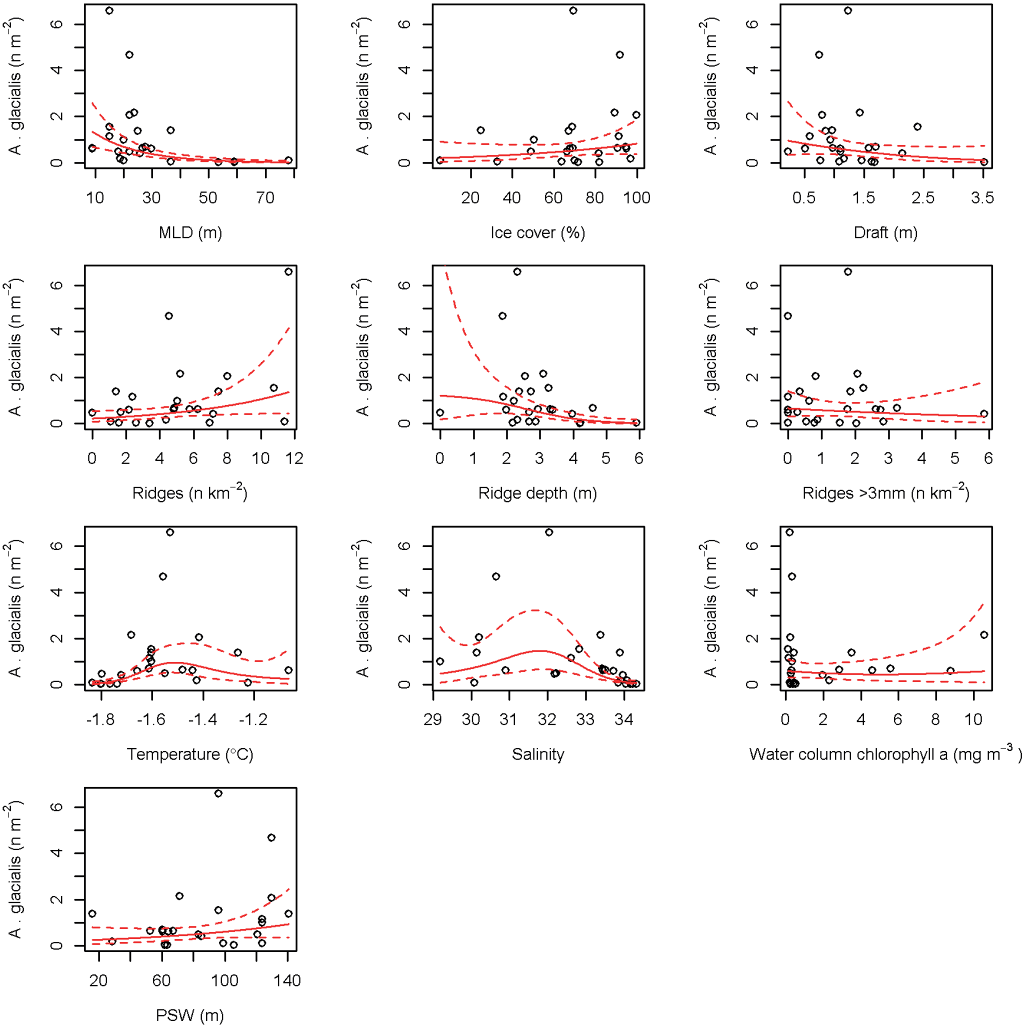
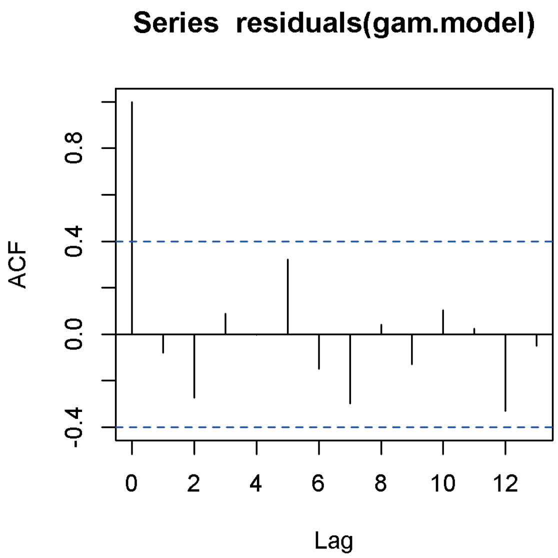


Figure 6.4: The abundance of *Apherusa glacialis* (n m^{-2}) as a function of environmental variables using spring and summer data. The estimated abundance based on the fitted GAM is shown as a red line. The 95% confidence interval is indicated by dotted lines.

Figure S6.5: Plot of autocorrelation in model residuals using temperature and average ridge depth as variables, which together had the best explanatory power for explaning variation in *Apherusa glacialis* abundance when data of both spring and summer were included.



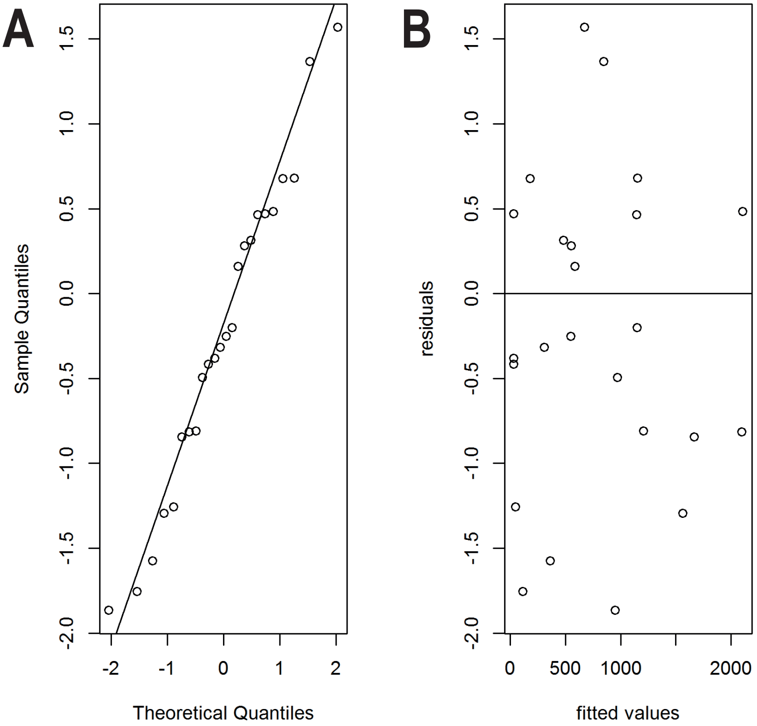
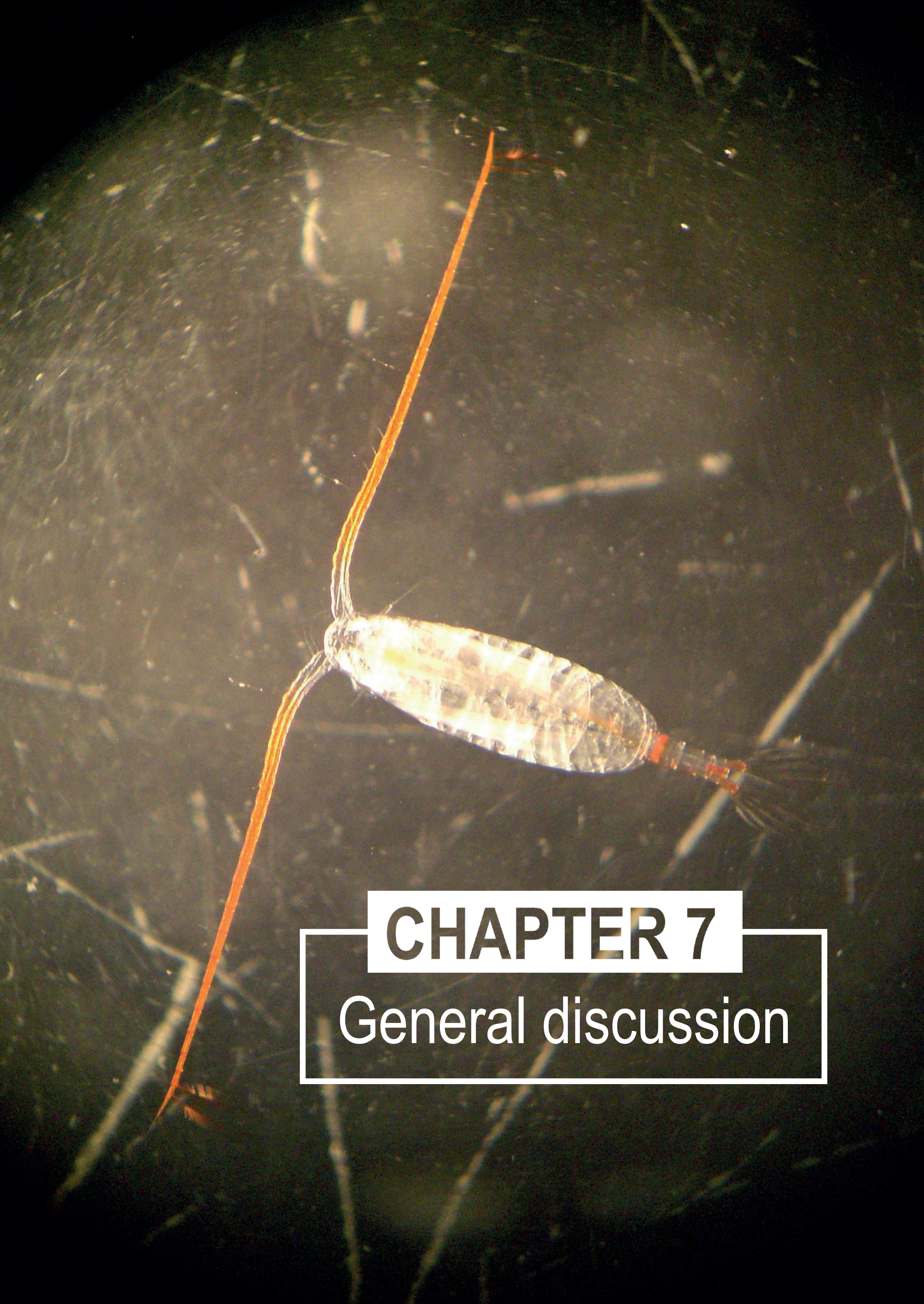


Figure S6.6: Model diagnostics for a GAM using temperature and average ridge depth as variables: quantile-quantile (q-q) plot (A) and the fitted values vs. the residuals (B).

The amphipod *Apherusa glacialis*.



CHAPTER 7

General discussion

The aim of this thesis was to gain insight in the role of sea ice in supporting life in the polar oceans. The polar oceans do not consist of one single ecosystem but can be regarded as multiple ecosystems in which sea ice is an important habitat. Furthermore, these ecosystems are subject to strong seasonal effects, resulting in a variety of life cycle strategies of polar organisms, in which the role of sea ice can change throughout a year. Despite a tremendous increase in the understanding of polar marine life during recent decades, many knowledge gaps still exist, which can be mainly attributed to sampling difficulties and logistical constraints. In this thesis, several knowledge gaps were addressed, which include large spatial scale studies on the biology and ecology of key species such as larval and juvenile krill (*Euphausia superba*) in the under-sampled winter season of the Southern Ocean, and the ice-associated amphipod *Apherusa glacialis* and one-and two-year-old polar cod (*Boreogadus saida*) in the under-sampled central Arctic Ocean. In addition, regional, inter-specific and intra-specific variability in the energetic value of Southern Ocean marine prey species were investigated to aid the understanding of consequences of changes in prey species distribution for predators. These studies on the distribution, diet and energy density of species contribute to the understanding of underlying ecological processes in the sea-ice food web and life in seasonally ice-covered waters (Flores et al. 2011).

In this final chapter, the main results and conclusions of the thesis are discussed, including the role of sea ice in structuring populations of ice-associated species and its importance as a food source. The effects of sea-ice on both the horizontal and vertical distribution of key species and the seasonal variability in sea-ice utilization by species are considered. The investigated regions mainly consist of oceanic areas covered with pack-ice and the results of the work presented will, therefore, be discussed in this context. However, the shelf and slope areas of the polar regions may show a markedly different species assemblages, differences in species behaviour and environmental differences due to, for example, the presence of land-fast ice as opposed to free-drifting oceanic pack ice. These differences between oceanic and coastal waters will not be discussed in detail here. It should be kept in mind, however, that there is a shallow, broad continental shelf covering >50% of the Arctic Ocean. A somewhat deeper shelf, which can be very wide in certain areas, covers approximately 13.4% of the Southern Ocean south of 60°S (Harris et al. 2014). Continental shelf and slope areas can play a role in the life cycle of species such as, for example, polar cod, of which older individuals are demersal along the Arctic shelf regions (Gulliksen & Lønne 1989).

Where the chapters in this thesis were introduced in the sense of the two polar regions, this synthesis tries to discuss the ecosystem implications of climate change in a coherent context. This is a challenging exercise as information on drivers of species distributions, means of sea-ice utilization and potential flexibility for dealing with a changing environment is still largely missing. Nevertheless, the findings of this thesis provide information necessary for assessing consequences of climate change for both polar ecosystems and food webs.

ABUNDANCE, DISTRIBUTION AND POPULATION STRUCTURE OF KEY SPECIES IN THE UNDER-ICE HABITAT

To date, there is little information available on large-scale distribution patterns and populations structures of organisms in seasonally ice-covered waters. Chapter 2 contributes to this knowledge gap, by a study on the age class 0 (AC0) Antarctic krill population, providing important insights in their distribution in the ice-water interface of the northern Weddell Sea during winter/early spring.

AC0 larval (furcilia) and juvenile krill were found in the proximity of the sea-ice habitat in the northern Weddell Sea during winter/early spring. They performed diel vertical migrations (DVM) moving downwards during the night. Variability in vertical distribution was found to be related to developmental stage. Adult and sub-adult *E. superba* were found in low abundances in the under-ice surface layer only at night. Highest abundances of AC0 krill in the ice-water interface layer were found in the pack-ice were the larvae were youngest and smallest. The total abundances of AC0 krill in deeper water layers varied greatly over the entire sampled region. The sampled population could be divided into several cohorts which likely originated either from different regions or from different spawning batches (Chapter 2). Differences in the sizes of both furcilia and AC0 juveniles collected in other studies suggested that the spawning season of Antarctic krill can be quite long, but also that there are potential regional and annual differences in the timing and duration of spawning (Spiridonov 1995). Differences in the timing and duration of reproduction was shown to be a consequence of the timing of elevated primary productivity, for example due to latitude, with lower latitudes having an earlier onset of spring (Spiridonov 1995). Adult krill use spring and summer phytoplankton blooms for gonad maturation and egg development. The number of spawning episodes and length of the spawning season have also been found to depend on food availability (Ross & Quetin 1986; Quetin et al. 1994).

Ice-algal and phytoplankton blooms usually show a patchy distribution. Consequently, a heterogenous larval krill population can be a result of variation in adult krill maturation due to differences in food encountered (Spiridonov 1995). Adequate food availability is extremely important during this period, as maturing is an energetically demanding process, which is supported by the difference in energy density between gravid and spent female krill, with the latter being relatively energy depleted (Chapter 4 and references therein). Furthermore, the timing and duration of reproduction has been related to the timing of sea-ice retreat in the Western Antarctic Peninsula (WAP) region, with earlier spawning in years when sea ice retreated relatively late (Quetin et al. 1994; Spiridonov 1995). Earlier spawning has been suggested to result in higher recruitment, as a consequence of a longer development time before the onset of winter, and the increased potential for multiple spawning episodes (Quetin & Ross 1991; Kawaguchi & Satake 1994; Siegel & Loeb 1995). Apart from variation found in the developmental stages between cohorts, large differences were found in size per developmental stage, indicating that the growth rates of cohorts had been unequal.

While Antarctic krill is an important species in the Antarctic, the amphipod *A. glacialis* is an important part of under-ice mesozooplankton community of the Arctic Ocean. In Chapter 6, the distribution of the *A.*

glacialis was investigated. The encountered *A. glacialis* in the sampling area north of Svalbard during spring, showed two size/age classes indicating a two-year life span, corresponding with findings of other studies (Cross 1982; Poltermann 1998; Beuchel & Lønne 2002). A prominent low amphipod abundance was found underneath the sea-ice covering the Yermak Plateau. The average abundances of *A. glacialis* were lower in spring compared to summer in the Eurasian part of the central Arctic Ocean deep sea basins (Chapter 6). Large region-based spatial patterns could not be detected in the summer data, which was in contrast to distributional patterns shown for other species in that study, such as the pelagic amphipod *Themisto libellula* and the copepod *Calanus hyperboreus* which could be related to large-scale basin-specific environmental parameters such as water column chlorophyll *a* concentration, sea-ice cover and salinity (David et al. 2015). One- and two-year old polar cod abundance was positively correlated with the *A. glacialis* abundance (David et al. 2016). One could conclude that polar cod follow their prey (Chapter 5), although the positive correlation of polar cod and *A. glacialis* could also be a result of a preference for similar environmental characteristics.

Due to the smaller difference in ice cover between seasons in the Arctic Ocean (larger proportional area of multi-year ice) compared to the Southern Ocean, Arctic ice-associated species such as sympagic amphipods have been suggested to be stronger adapted to life in the sea-ice habitat than species in the Antarctic, such as Antarctic krill (Schnack-Schiel 2003). Amphipods are motile species with appendages that are well suitable for clinging on a substrate (Gulliksen & Lønne 1989). *Apherusa glacialis* has also been reported at the sea-ice underside during winter (Werner & Auel 2005), while larval and juvenile Antarctic krill have been found to reside in the under-ice surface during autumn and summer (Flores et al 2012a), suggesting that both species are likely able to utilized the sea-ice habitat year-round. In contrast to *A. glacialis*, the young krill usually show diel vertical migration, the amplitude of which depends on season (Chapters 2 & 6; Quetin & Ross 1991; Flores et al. 2012a). The studies demonstrate the importance of sampling the under-ice surface waters in order to get an adequate view of the abundance, distribution and population dynamics of ice-associated species such as AC0 Antarctic krill in the Southern Ocean and *A. glacialis* in the Arctic Ocean.

RELATIONSHIP WITH SEA-ICE AND ENVIROMENTAL CHARACTERISTICS

How the abundance and size/age structure of AC0 Antarctic krill relates to particular sea-ice properties remains uncertain, as the sea ice in the sampled region was too heterogenous and the sample size too small to uncover patterns (Chapter 2). The oceanographic properties of the underlying water column were quite homogenous apart from small differences in the last stations of our sampling area that showed evidence of sea-ice melt (David et al. 2017). Other studies, conducted by divers, suggested that AC0 krill had a preference for highly deformed, over-rafted and thicker ice, where they can hide between ledges which shelter them from currents and predation (Frazer et al. 2002; Meyer et al. 2017). Predators of larval Antarctic krill include ctenophores and amphipods (Hamner et al. 1989). Despite difficulties in explaining the observed variability in AC0 krill distribution patterns, the general low abundances of other zooplankton, particularly copepods, in the under-ice surface layer at the stations in the northernmost part of the sampling area, could be a response to a reduction of sea-ice coverage, resulting in an increased water column productivity (David et al. 2017). These northwestern stations were also situated in shallower waters. This could be evidence of a restructuring of the zooplankton community with species moving to different depth layers or species adapting their vertical migration patterns, as has been found for copepods in the shallow waters around South Georgia (Atkinson et al. 1996). However, no obvious differences in the abundance and distribution were seen for AC0 krill in this area (Chapter 2), indicating that their vertical distribution is mainly driven by developmental stage rather than other factors.

The abundance and distribution of *A. glacialis* was related to sea-ice and oceanographic properties in the Arctic Ocean (Chapter 6). During spring, the water column chlorophyll *a* concentration, which was correlated with in-ice chlorophyll *a* concentrations, had the highest explanatory power for explaining the variation in *A. glacialis* abundance. When combining data from both spring and summer, temperature and salinity had the highest explanatory power, with highest densities occurring at intermediate values of both environmental properties. Indices of sea-ice structures, such as average ridge depth and the number of ridges at a station were also of influence. Although interacting effects cannot be revealed due to the small sample size, the results of this study suggest that relationships between *A. glacialis* abundance and environmental properties differs between seasons, which could be a result of a changing energy gain/predator avoidance trade-off.

The spring relationship between *A. glacialis* abundance and food availability could be a result of the amphipods's need to replenish lipid reserves after the winter months. Despite observations of the amphipods in the under-ice surface, Berge et al. (2012) found that *A. glacialis* moves to deeper water layers of the central Arctic Ocean during winter, and hypothesized that this is to avoid being exported out of the Arctic Ocean. The deep water currents go against the direction of the sea-ice drift and will transport the amphipod back to areas with extensive sea-ice cover (Berge et al. 2012). In addition, *A. glacialis* was found carrying eggs, suggesting that part of its energy reserves will be necessary for reproduction during the winter months (Poltermann et al. 2000; Berge et al. 2012).

A lower predation pressure during spring could explain why food availability would be the main driver of *A. glacialis* abundance. Plenty of shelter is still being provided by the sea ice and its structures, Additionally, a reduced predation pressure on *A. glacialis* can be a result of a high concentration of other prey species such as *Calanus* spp., which are still residing in the surface layers during this season (Conover 1988; Lønne & Gabrielsen 1992; Daase et al. 2008). Thus, a changing zooplankton community structure and melting of the sea ice during summer likely changes the energy gain/predator avoidance trade-off, leading to the distribution becoming more determined by thicker sea-ice and the presence of structures, such as sea-ice ridges, as opposed to food quantity (Chapter 6). Apart from at the Yermak Plateau, chlorophyll *a* concentrations were generally higher during spring compared to summer. Nevertheless, the amphipods found in summer were mainly feeding on sea-ice resources and their lipid contents were high, indicating that they were in good condition and that there was sufficient food to be found in the sea-ice habitat during this season (Kohlbach et al. 2016). Sea-ice food sources are better accessible during summer due to the melting of sea ice (Werner & Gradinger 2002).

Apart from using ocean currents as a transport mechanism to return or remain in ice-covered areas, the different direction of sea-ice drift and underlying water masses has been proposed to be of influence on transport processes of several species. Sea-ice is proposed to be used as a transport mechanism by young polar cod to move out of their nursery grounds, which allows them to avoid competition with earlier hatchers that are bigger and have moved to deeper water layers (David et al. 2016; Geoffroy et al. 2016). DVM has been proposed as a means of transport for larval Antarctic krill (Meyer et al. 2017). Moving to deeper water layers during the night, the larvae are transported to another location by currents before they ascent back to the sea-ice underside during the day, which is hypothesized to enhance foraging success in a patchy food environment (Meyer et al. 2017).

The relationship between sea-ice characteristics and species abundances is very complex. Results show that the nature of this relationship may change with season, region and developmental stage and is influenced by factors such as community structure, food availability and behavioural interactions, for example due to a need to move to a differnt location.

IMPORTANCE OF SEA-ICE DERIVED CARBON SOURCES

The observed size difference within developmental stages suggests that the growth rate varied between AC0 Antarctic krill cohorts. The study of larval and juvenile krill indicated that sea-ice derived carbon sources are very important for krill populations residing in ice-covered waters during winter (Chapter 3). Not only consisted most of the krill stomach contents of food items closely associated with sea ice, stable isotopes and fatty acids confirmed that sea-ice associated carbon sources are an important food source over a larger temporal scale (Chapter 3). Although exact turnover times of fatty acids are largely unknown, the proportion of sea-ice algae-derived carbon was approximately 2/3 in storage fatty acids, which have a shorter turnover time, while it was lower in the membrane fatty acids, which have a longer turn over time (Kohlbach et al. 2017), suggesting that the utilization of sea-ice derived food sources increased with seasonal progression. In addition, the AC0 krill showed low lipid levels suggesting that their reserves were low, also indicating that sea-ice derived food sources may not support high growth rates during wintertime, but are potentially critical for their survival in the under-ice habitat (Chapter 3). Variation in the stomach contents of AC0 krill in the northern Weddell Sea mirrored variation found in the zooplankton community structure (David et al. 2017), suggesting that feeding occurred opportunistically.

In a study from the same expedition, AC0 krill caught below the ice-water interface (~11m depth) showed increased feeding on zooplankton and detritus during the night (Halbach 2015), providing further evidence for opportunistic feeding behaviour. Although the AC0 krill from our study were caught at different times of day, no differences in the average diet composition were found between day and night (unpublished data), confirming that variation was a result of differences in food availability rather than sampling time (Chapters 2 & 3). In addition, Halbach (2015) found that, in the pack-ice region, increased feeding activity was related to increased food availability in the sea ice. It is clear that food items released or associated with sea ice provide the main food source in ice-covered waters during winter (Chapter 3; Halbach 2015; Kolhbach et al. 2017; Meyer et al 2017). AC0 *E. superba* caught with a Rectangular Midwater Trawl (RMT) in the South Georgia region during mid-winter, had full stomachs which was related to high phytoplankton biomass in this region (Meyer et al. 2017). This indicated that the young krill residing in open water were able to find ample food (Halbach 2015). Daly (2004) found lower krill abundances in the open waters of this area compared to ice-covered waters and, furthermore, found that young krill continued feeding at the under-ice surface even when phytoplankton concentration increased with the melting sea ice. This suggest that AC0 krill prefer to reside underneath the ice for more reasons than solely food abundance (Marshall 1988; Meyer et al. 2009). This is supported by the high recruitment of Antarctic krill found after years with a high sea-ice extent (Kawaguchi & Satake 1994; Siegel & Loeb 1995). Lower energy expenditure due to protection from currents has been proposed to be an advantage of residing between sea-ice structures (Meyer et al. 2017), although passive sinking, resulting in DVM, has also been suggested to be energy saving behaviour (Youngbluth 1975). The multiple advantages of sea ice for young Antarctic krill raises the question on the suitability of open water as a habitat during winter.

Further support for the importance of sea-ice resources arises from differences found in fatty acids and

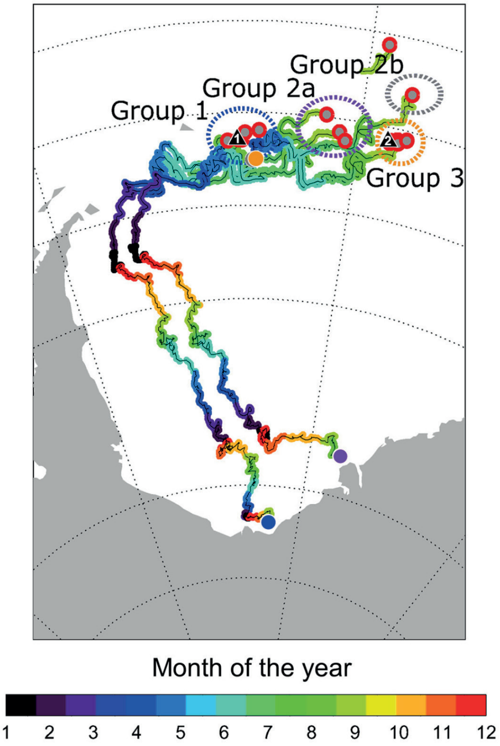


Figure 7.1: Backward-projected drift trajectories of sea-ice areas from Chapters 2 & 3. The specific ice area is tracked backwards until the ice reaches a position next to a coastline, or the ice concentration at a specific location reaches a threshold value of <40% when ice parcels are considered lost (Krumpen et al. 2016). Stations with a distance <60 km to each other were represented as one dot. Triangular symbols mark the approximate position of the two ice camps discussed in Chapter 3. Dashed circles, grouping stations by krill cohort, are distinguished by different colours. Dots in corresponding colours mark the back-tracked origin of sea-ice drift trajectories from these station groups. Colour code of drift trajectories represent the monthly sea-ice position (from Kohlbach et al. 2017).

stable isotopes between cohorts. Findings indicated that a lower availability of sea-ice resources over a larger time-scale can negatively impact the condition of krill larvae residing in ice-covered waters (Chapter 3). The results suggest that spawning time and location have a marked influence on the development of larval krill during advection due to the encountered food availability, which thus likely impacts their survival rate. This emphasizes the importance of multiple spawning batches in a reproductive season. The impact of potential environmental changes on food availability and quality is variable between regions and should be evaluated at the spawning areas and the subsequent nursery and feeding grounds at a population level. Modelling the advection pathway of AC0 krill from the winter Weddell Sea indicated that they originated from the north-western Weddell Sea, from April onwards (Meyer et al. 2017). The sea-ice found at the different sampling locations of the cohorts showed different sea-ice drift histories, parts of which originated near the coast in the southern part of the Weddell Sea (Fig. 7.1; Kohlbach et al. 2017). Together with differences in the isotopic signatures of the ice-algae from different ice floes sampled during the study (Kohlbach et al. 2017), this suggests that there is indeed a variation in sea-ice algae and other in-ice fauna assemblages found in different ice floes depending on timing and origin of sea-ice formation.

The high ingestion of pennate diatoms by AC0 Antarctic krill and the slightly higher surface water chlorophyll *a* at the northernmost stations was likely a result of the ice starting to melt. However, due to the low abundance of zooplankton grazers at these stations, reduced competition could also be a factor. The reduced competition could again be a result of a shift in vertical distribution of e.g. copepods, due to changes in depth allocation of resources and/or ocean floor depth (David et al 2017). In contrast, Meyer et al. (2017) did not find an increase in diatoms in the stomach contents of krill from the north-east area, which could be a result from the krill being caught at deeper water layers as they were sampled with RMT and Bongo nets that do not sample the surface very well and require open water to be handled in. Results indicate that a combination of studies on different spatial scales can be beneficial to obtain a complete view of a species biology and ecology, as studies on a small scale can obtain a biased picture due to the sampling of particular features and a lack of coverage of certain habitat types, while studies on a larger scale may obtain a more general picture, but can overlook certain particular important features of a habitat due to a lack of detail. In addition, it again marks the importance of sampling the ice-water interface layer, as certain analyses on krill from other sampling sites can yield different results.

In the Arctic, the one- and two-year old polar cod were also found feeding on species that were closely associated with sea ice such as *A. glacialis* and the copepod *Tisbe* spp. in summer (Chapter 5). This importance of sea-ice associated food sources was again supported by fatty acid and stable isotope analyses. The fish were, furthermore, in good condition as suggested by the high total lipid content of the liver (Chapter 5) and high energy density (David et al. 2016). Compared to Southern Ocean species, the energy density of the polar cod (David et al. 2016) was similar to that of myctophid fish, or the highest values found in notothenoid fish, which represented the highest energy densities of all taxa investigated (Chapter 4). This indicates that polar cod provide a high quality food source for top predators residing in the ice-covered region.

The differences in the estimated proportion of ice-algal produced carbon between tissues suggests that the polar cod had been feeding more on ice-associated food sources before the time of sampling than during sampling, although exact turnover of carbon rates are also unknown (Chapter 5). Other studies estimating the proportion of ice-algal produced carbon in the tissue of polar cod show ranges between negligible and high importance (Budge et al. 2008; Christiansen et al. 2012; Graham et al. 2014). This could be influenced by the fish's food, the size of which tends to increase with increasing fish size (Renaud et al. 2012) or which can have a different composition when the fish reside in open water and/or shelf regions (Graham et al. 2014; Budge et al. 2008).

Other species that are regarded as less ice-associated, such as *Calanus* spp. and *Themisto libellula*, were found to be part of the diet of polar cod (Chapter 5). Whereas the input of ice-algal produced carbon in these less ice-associated species is still considerable (Kohlbach et al. 2016), this could potentially lower the sea-ice algal isotopic signal of the fish. However, *Calanus* spp and *T. libellula* have a wide depth distribution and are regularly found in the ice-water interface (David et al. 2015). As young polar cod are not known to occupy deeper water layers in the oceanic part of the central Arctic Ocean, the ice-water interface can be regarded as the sole feeding ground of young polar cod in this region during the summer season. Estimates of daily consumption compared to food availability have indicated that sufficient food is available in the under-ice surface to support polar cod growth (Chapter 5). Future investigations on the diet of polar cod and the abundance and distribution of its prey can give further insight in feeding behaviour, and potential seasonal and regional variation. The use of a combination of methods that all deliver specific information has already been suggested to be an effective way of studying a species feeding habits (Schmidt et al. 2006).

Studying the energy density and proximate composition of species does not give direct information on the diet, but can help to gain information on feeding activity, trophodynamics and life cycle strategy (Chapter 4). For example, decreasing lipid reserves, and concomitant energy density, during winter can be found in species that rely on energy reserves during this season (Chapter 4 and references therein). Seasonal and regional differences between a size/weight/energy density relationship within species gives information on variability in the availability and quality of food for these species. In addition, the relationship between size and energy density gives information on energy allocation in individuals of varying age or developmental stage (Chapter 4 and references therein). For many species in the Southern Ocean, sufficient seasonal and regional coverage for assessing such life cycle strategies and relationships is currently lacking (Chapter 4).

Findings show that, for species inhabiting the ice-water interface layer, sea ice can provide an important direct or indirect food source. The presence of this food source, and the consequences it has on the distribution of species, has major implications for the structure of polar food webs.

POTENTIAL IMPACTS OF CLIMATE CHANGE

A changing climate, and subsequent changing environment, might initiate a mismatch between timing of spawning or maturation and the peak in food availability. Although species are able to adapt to gradual changes, the question is if climate change does not accelerate too fast for species to cope with. The concept that the survival of early stages of marine animals, which are usually regarded as the most vulnerable, depends on a match or mismatch with timing of peak (primary) productivity is quite old (Cushing 1969; Durant et al. 2007 and reference therein). Many studies on the phenology of a wide variety of organisms observed an advanced timing of reproduction resulting from a warming climate, or reported a mismatch between the two events (e.g. Visser et al. 1998; Parmesan & Yohe 2003; Philippart et al. 2003; McKinnon et al. 2012). This raises the question whether marine organisms can sufficiently adapt to environmental changes to retain the synchronized timing between food demand and availability, the latter including accessibility as well as quality, particularly in the polar regions where the productive season is short. For example, the timing of reproduction and development of the Arctic copepod *Calanus glacialis* and its offspring are synchronized with distinct ice-algal and phytoplankton blooms. Here, a potential mismatch may occur due to an expected shortening of the time between these blooms (Hirche & Kobosokova 2007; Søreide et al. 2010). The demand for energetic resources during egg maturation as well as for larvae to develop might present a similar problem for *E. superba* as for *C. glacialis* (Siegel & Loeb 1995; Ross & Quetin 2000). However, certain species or developmental stages of species may be more flexible than others. Adult krill, for example, show a wide range of behaviour regarding feeding, schooling/aggregating, vertical distribution and DVM, suggesting that they are quite resilient to environmental change (Flores et al. 2012b).

The timing of sea-ice formation and the associated growth of ice-algal and in-ice fauna may significantly affect its assemblage. This may have an influence on both the food quality and quantity (Quetin et al. 2007), potentially important for the survival of zooplankton such as AC0 krill (Chapter 3). The positive relationship between winter sea-ice extent, early spawning and high recruitment found in earlier studies could be a result of a good match between food availability/quality and the timing of reproduction. A study conducted in the coastal region of the WAP showed that phytoplankton biomass and species composition were related to winter sea-ice cover and summer stratification strength (Rozema et al. 2017). Increased winter sea-ice cover led to a stronger stratification in summer, supporting high phytoplankton biomass dominated by diatoms (Montes-Hugo et al. 2008; Saba et al. 2014; Rozema et al. 2017). In years with less winter sea ice, the summer mixed layer depth remained deeper and less stable, resulting in lower biomass with larger fractions of smaller sized phytoplankton such as haptophytes (Rozema et al. 2017). This shows that environmental changes may alter the microbial composition in a way that it becomes an unsuitable food source for Antarctic krill and maybe other species (Rozema et al. 2017). Especially in the WAP region this might have a substantial impact on the food web, where the greatest increase in air temperature has been observed (King 1994) and where the majority of the krill fishery is currently situated (CCAMLR 2017). A similar increase in small picophytoplankton, such as the pan-Arctic species *Micromonas*, as opposed to larger phytoplankton, is expected in a warming, less ice-covered Arctic ocean (Li et al. 2009). However, the increase of small phytoplankton might also be a result of higher stratification (Li et al. 2009), indicating a difference in response to environmental changes between both polar regions likely due to the geographical distinction and the difference in fresh water inflow from the continent. Changes in the size distribution of the phytoplankton community may have significant consequences for the food web (Sommer et al. 2007; Li et al. 2009). In addition, a shift to smaller zooplankton under warming conditions is expected (Richardson 2008). The size of an organism can have a marked influence on its energy density (Chapter 4), potentially altering its quality as a food source (Saunders & Tarling 2018). Furthermore, the energy density of a species may be markedly influenced by its diet, as shown for *Electrona antarctica* (Chapter 4) and polar cod (Hop et al. 1997a).

Changes in sea-ice concentration or properties, warming ocean water and perhaps subsequent changing circulation patterns, may also result in a redistribution (both horizontally and vertically) of zooplankton and nekton species which can alter the type of food available for top predators. Less cold-adapted species, such as fish in the northern hemisphere and salps in the southern hemisphere, have already been observed to migrate to higher latitudes (Atkinson et al. 2004; Wassmann et al. 2011; Mackey et al. 2012). Apart from changes in environmental conditions such as increasing temperature, this could also be a result of a shift in the available food spectrum, as, for example, salps feed better on smaller phytoplankton than krill (Schofield et al. 2010). Furthermore, ice-obligated species such as *A. glacialis*, may retreat with the sea-ice in the Arctic Ocean (David et al. 2015). The severity of these impacts may differ regionally. For example, in the Arctic Ocean, the diet of Brünnich's guillemots (*Uria lomvia*) and black legged kittiwakes (*Rissa tridactyla*) has shifted from polar cod dominated to capelin dominated. As these fish species have a similar size and energy density, the impact of such a shift is likely limited (Hop & Gjosæter 2013), although effects of this change in diet was suggested to have a negative effect on the growth rate of guillemot chicks (Gaston et al. 2005). For other top predators, the effects may be more severe. In the Antarctic, krill and salps are an example of species replacing each other that are significantly different in size, energy density, behaviour and vertical distribution (Chapter 4; Atkinson et al. 2004). Consequences can be especially large for central-place foragers such as breeding sea birds and seals (Weimerskirch & Cherel 1998; Durant et al. 2007). However, it is also possible that predator and prey follow the same environmental variables, not leading to a mismatch.

The thinning or loss of sea ice due to global warming also means a decrease of available substrate as a (foraging) habitat. The advantage of being able to utilize the sea-ice as a resource that, for instance, polar cod has over sub-Arctic and more temperate species maybe lost when sea ice retreats. Sea ice as a substrate has additional benefits such as the above mentioned decrease in energy expenditure, protection against predation and niche differentiation (Kils 1982; Marshall 1988; Atkinson et al. 2008; Berge et al. 2012), which will disappear with the thinning or retreat of sea ice. In addition, an association with sea ice has an influence on the advection of species. Without the sea ice young polar cod, for example, may lose the ability to move from their nursery ground into the central Arctic ocean (David et al. 2016).

FUTURE RESEARCH AND CONCLUDING REMARKS

The magnitude and variability of sea-ice primary production in the polar oceans remains unclear. Modelling studies showed that primary production in the Arctic may increase within the sea ice and decrease in the water column as a result of a decreasing sea-ice extent and a thinning of the ice (Tedesco et al. 2012). Other studies expect that phytoplankton production increases for the same reasons: due to enhancement of available light in the water column (Fernández-Méndez et al. 2015). In the Southern Ocean, a southward shift of winter sea ice is expected to reduce ice-algal productivity due to lower light availability at higher latitudes (Flores et al. 2012b). The development of ice-algal and in-ice fauna assemblages over time, and the relationships with abiotic factors are currently very poorly understood because it is difficult to study (Garrison & Buck 1991; Bluhm et al. 2018). This knowledge is important to assess the suitability of ice-algal and phytoplankton assemblages as a food source for ice-associated species, and to predict the potential consequences of change. Other potential components of the sea-ice food web such as bacteria and other in-ice fauna, detritus and large sub-ice algal aggregations are often not taken into account in food web studies and their role should thus be further investigated (Nöthig & Gowing 1991; Tedesco et al. 2012; Fernández-Méndez et al. 2015).

For both fisheries management and conservation it is important to increase the knowledge on the earlier life stages of marine polar species. Information on spawning and nursery grounds, advection and other environmental factors, necessary for successful recruitment, should be investigated. Sufficient recruitment is important to ensure that the part of the stock that is harvested or preyed upon is replaced. More knowledge on the availability and differences in energetic quality of prey species for top predators is useful to conduct ecosystem-based studies. Hereby it is not only meaningful to study the harvested species but also other species, in order to assess their quality as a potential food source as the distribution and thus availability/catchability of prey species might change.

Many studies stress the need for an increase in temporal and spatial coverage to investigate the importance of sea ice for life in the polar oceans (e.g. Dieckmann & Hellmer 2003; Smetacek & Nicol 2005), and to further help to apprehend the role of sea ice in species' life cycles. In particular, the relationships of animals with sea ice in the seasons other than summer are largely unknown. Overwintering strategies are key in the life cycles of polar species (Bathmann et al. 1993) and more information of this under-sampled season is necessary to fully understand the impact of environmental changes. However, it is also of paramount importance to repeat studies and surveys in regions and seasons that have already been covered, not only to be able to monitor change, but also to be able to disentangle regional variation from annual variation. More studies are needed to specifically capture polar habitat dynamics at a large scale, comparing areas with open water, smooth ice, melting (or forming) sea-ice and shallow waters. Such knowledge can help to evaluate the flexibility of particularly ice-obligate and young individuals. To understand the effect of the presence of sea-ice on the community structure, distribution and behaviour of under-ice fauna, more comparisons between open water and sea-ice covered water within a region and seasons should be performed. This can aid in predicting the potential consequences of sea-ice change or loss. In addition, studies of the surface layer of open water maybe also be important, as demonstrated by the diel vertical migration that species are performing here (Flores et al. 2011).

The research described in this thesis provides insights in the roles of sea ice in the life cycle of polar species by investigating the under-ice surface on a large spatial scale, including population structures and distribution patterns (Chapters 2 & 6). In summary, the food directly and indirectly provided by sea ice, in the form of ice-algae and in-ice fauna at the under-ice surface, attached algal strands, released material and the accumulation of ice-associated species, can provide an ecological niche for species able to utilize this food source. Hereby, potential inter- and intra-specific competition, such as suggested for polar cod, can be avoided (Chapter 5). Sea-ice may provide an opportunity for species to take advantage of the many other benefits provided by sea-ice without being deprived of food, and vice versa. Findings suggest that the trade-off between food availability, energy expenditure and predation pressure is an continuous determinant of how the sea-ice habitat is used by ice-associated species, and that factors influencing this trade-off include ontogeny, life cycle events and the presence or absence of other species in the under-ice surface layer (Chapters 2, 3, 4 & 6). The different roles that sea ice can have, e.g. food provisioning, transport and shelter against predation or currents, occur simultaneously, although one role can be more dominant, depending on season (Chapters 2, 5 & 6).

The availability of a concentrated food source on this two-dimensional platform is of significant importance to the food webs in the polar oceans (Bradstreet & Cross 1982). The availability of a substrate affects the species assemblage, diet and the vertical distribution of non-substrate bound species (Kaartvedt 1996; Flores et al. 2012a; Gray et al. 2016). In the polar oceans, the sea-ice provides an additional substrate to the ocean floor. In addition, sea ice can form a predictable source of food, including material sinking from it (Michel et al. 2002). The influence sea ice has on the abundance and vertical distribution of species, or developmental stages within species, affects the availability and quality of food for (top) predators (Chapters 2 & 4), further stressing the large effect sea ice has on polar food webs.

Despite differences in seasonal sea-ice coverage between the Arctic and Antarctic, there is a lot of evidence that species in both oceans have adapted to utilize the sea ice as a platform providing many cumulative benefits. Although this thesis does not cover all the aspects of the life histories of key species, nor offers a complete view of the sea-ice food web, findings indeed show that sea ice has many important functions for marine life, and that it is pivotal in the functioning of polar ecosystems. The knowledge necessary for predicting consequences of environmental change is still far from complete and no direct management solutions can be provided. However, the results suggest that even species that seem to be able to occupy other niches or utilize other food sources than the one provided by sea ice, do not only benefit from the sea-ice habitat, but can also be negatively affected by a loss of sea ice or its structures. Sea ice provides a unique habitat with unique species, and deserves protection and a careful management, especially before new or increased efforts of harvesting marine living resources are made.

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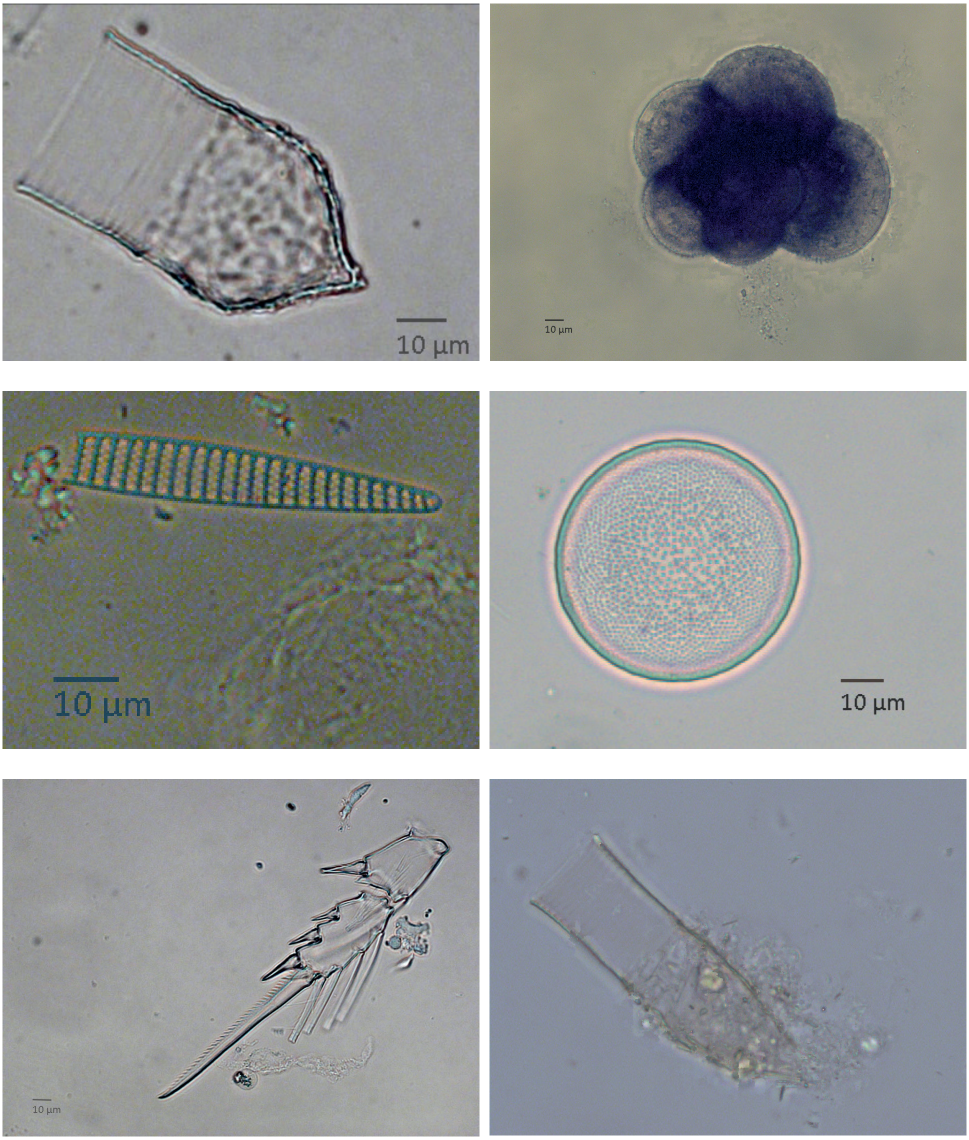

Pictures of items found in the stomachs of larval and juvenile Antarctic krill (*Euphausia superba*), taken using a microscope. Top: a shell of the tintinnid *Codonellopsis glacialis* (left) and the foraminifer *Neogloboquadrina pachyderma* (right). Middle: the pennate diatom *Fragilariopsis kerguelensis* (left) and a centric diatom (right). Bottom: a zooplankton appendage (left) and a shell of the tintinnid *Laackmanniela naviculaefera*.

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de Rutte



Neumayer-Station
AWI
HELMHOLTZ
GEMEINSCHAFT

ADDENDA

SUMMARY

A unique feature of the polar oceans is formed by sea ice. The annual cycle of freezing and melting causes tremendous seasonal variation in ice-cover. Other factors, such as wind and ocean currents, cause a continuous reshaping of the sea ice resulting in assemblages of ice of different sizes and structures. This highly dynamic feature forms a habitat for life in the polar ocean. Sea ice and its seasonal changes influence the physical features of the environment, such as light availability and water column properties, resulting in fluctuating rates of primary production both within the sea ice and in the water column. This has a large impact on the food availability for higher trophic levels, which also use the sea ice for e.g. reproduction and as a shelter for predation. Zooplankton and nekton species living underneath the sea-ice of the polar oceans have in different ways adapted to the fluctuation in food availability and their seasonally changing habitat. Life cycle events, such as reproduction, are often timed to coincide with peaks in primary production. Furthermore, several species developed different overwintering strategies to cope with the food scarcity during this season, such as relying on reserves, lowering metabolism or shifting diet. Antarctic krill (*Euphausia superba*) and polar cod (*Boreogadus saida*) are considered to be key species of the under-ice surface water in the Southern and Arctic Oceans, respectively.

Information on how organisms utilize the sea-ice habitat remains incomplete. The understanding of sea-ice ecology has been hampered by the difficulty to collect sufficient samples that allow the identification of large-scale spatial trends. The Surface and Under Ice Trawl (SUIT) was developed to overcome this limitation and has already been used to gain insight in the differences in zooplankton distribution and community structure between open and ice-covered waters in the Southern Ocean. Further knowledge on how polar species utilize the sea ice and how the sea ice affects their distribution is necessary to predict the consequences of ongoing climate change. Particularly in the Arctic a marked decrease in sea-ice cover and thickness has been recorded over the last decades. But also in the Antarctic regional changes in air temperature and sea-ice extent have been observed. Knowledge on the sea-ice associated food web is, furthermore, important for aiding management directed to improve sustainability of ongoing and future fisheries. Antarctic krill and several fish species are harvested in the Southern Ocean, and a northward expansion of commercially harvested fish stock from the sub-Arctic region has been observed.

The aims of this thesis were to gain knowledge on the association of marine species with the sea-ice habitat and the functioning of polar marine food webs by assessing the abundance and distribution of species in ice-covered oceans, the important of sea-ice derived carbon sources, and the variability in energy density of marine species.

In the Southern Ocean, the winter season has been regarded as a critical period for larval and juvenile Antarctic krill that hatched in the previous summer (age class 0 or AC0 krill). In Chapter 2, the population structure of AC0 Antarctic krill was studied to investigate their population structure at the ice-water inter-

face layer and look at habitat partitioning of different developmental stages between different depth layers. The SUIT was used to sample the upper two meters of the water column underneath sea ice and a Rectangular Midwater Trawl (RMT) was used to sample deeper water layers. Results showed that the population of AC0 krill in the ice-water interface could be divided in geographically distinct cohorts based on size and developmental stage composition and that the size of the same developmental stages differed between regions. The differences between cohorts could be a result of a different time of spawning and/or different growth rates caused by variability in environmental conditions encountered during advection. The behaviour and physiological differences associated with developmental stages likely cause a change in distribution in the water column. In general, the volumetric density of the AC0 krill was significantly higher in the under-ice surface layer compared to the 0-500m depth stratum, indicating that the composition, abundance and distribution may not be represented well if only conventional pelagic sampling gear is used.

To further look at the utilization of the sea-ice habitat, the diet of the AC0 krill during winter was investigated (Chapter 3). Multiple methods were used to study spatial and temporal variability in the diet. Stomach content gives information on the most recent feeding of a consumer, while both fatty acid and stable isotope analyses provide information on trophic interaction over a larger temporal scale. The stomach contents of AC0 krill contained mainly centric and pennate diatoms in terms of abundance, and centric diatoms and copepods in terms of biomass. Identifiable food items mainly consisted of species that are known to reside within or close to the sea-ice. Variation in the stomach content of AC0 krill between stations was mirrored in variation in the zooplankton community assemblage, which was investigated in an earlier study. Differences in fatty acids profiles and stable isotope values were found between cohorts. The fatty acids profile of the cohort with the smallest krill showed the largest difference with the other cohorts. In addition, this cohort had the lowest $\delta^{15}N$ and $\delta^{13}C$ values which are used as proxies for heterotrophy and the contribution of sea-ice algal produced carbon to the diet, respectively. This cohort also had the lowest C/N ratio, which is used an indicator for lipid storage and body condition. Results suggest that sea-ice resources are the main food source for AC0 krill residing in ice-covered waters during late winter. A lack over sea-ice resources over a longer period may negatively affect the AC0 krill's condition in ice-covered waters.

Another method for studying trophic interactions is studying the energy density of species, which can be used in food web models and for understanding the energy flux in an ecosystem. Prey quality can influence the distribution, behaviour and physiology of predators. The energetic density of a species can be influenced by their diet, physiology and by life cycle events. To investigate the variability in energy density between zooplankton and nekton species and causes of variability within species, the current knowledge on energy density of Southern Ocean species was reviewed (Chapter 4). Previously unpublished data was included. Fish were the most studied organisms regarding energy density measurements. For crustacean species, most measurements were conducted on Antarctic krill, which showed varying energy densities between sexes and developmental stages. For the myctophid fish *Electrona antarctica* a relationship between size and energy density was found. In addition, relationships between water content and energy density

were shown for *Electrona antarctica, Gymnoscopelus braueri* and *Bathylagus antarcticus*, the latter showing seasonal variation. For most Southern Ocean marine species, little data was available and a proper regional and seasonal coverage was lacking. Several methods used to measure the energy density of marine species are described and discussed.

In the Arctic Ocean, one- and two-year old polar cod are known to reside in the under-ice surface waters. The diet of polar cod was investigated to assess if the fish relies on food provided by sea ice in this habitat (Chapter 5). Similar to Chapter 2, multiple methods are used to study diet composition and carbon sources, including stomach content, fatty acid and stable isotope analyses. In addition, the proportional contribution of ice algal-produced carbon was quantified. Different polar cod tissues were investigated. Stomach contents consisted mainly of the copepods *Tisbe* spp. and *Calanus* spp., and the amphipod *Apherusa glacialis* in terms of numbers, and of *A. glacialis* in terms of biomass. Feeding rates were sufficient to sustain a good body condition. The lipid content was highest in the liver, suggesting that this is the main lipid depot of polar cod. Ice algal-produced carbon contributed over 50% to the carbon in the tissues of the fish. Results indicate that the sea ice provides sufficient resources for polar cod in the central Arctic Ocean. A loss of sea ice, resulting from climate change, can weaken the advantage of being able to exploit the sea-ice habitat that polar cod has over potential competitors.

Amphipods are an important part of the Arctic marine community, with *A. glacialis* often being the most abundant in the ice-water interface. The influence of sea-ice properties on the distribution of *A. glacialis* has previously been investigated on a small-sale in research mainly conducted by divers. Different studies report a variety of results, including high numbers of the amphipod found underneath both highly-structured and smooth ice. In Chapter 6, the spring relationship between *A. glacialis* abundance and distribution, and environmental properties was investigated on a large scale, using data on sea-ice topography, water column properties and oceanographic features. Although, the sample size was too small to unravel likely interacting effects that explain the overall variation, some evidence for environmental drivers of the large-scale abundance of *A. glacialis* were found. The variable that best explained the abundance of the amphipod during spring was chlorophyll *a* concentration. When data collected during a summer expedition was added, the variables explaining the abundance best were temperature, salinity and sea-ice structures. This indicated that the trade-off between food availability and predation pressure, and therefore the main driver of *A. glacialis* distribution, changes between seasons.

The findings of this thesis contribute to the understanding of the biology and ecology of key species in the sea-ice food web and life in ice-covered waters. The sea ice habitat provides many functions for organisms in the polar oceans. The dominant role of sea ice for a certain species can shift with, for example, season or age. Regardless of food provisioning being the main reason for species to make use of this substrate or not, species residing underneath it largely feed of sea-ice associated food sources. The unique habitat that sea ice provides deserves careful management.

SAMENVATTING

Een uniek kenmerk van de poolzeeën is de aanwezigheid zee-ijs. De jaarlijks terugkerende cyclus van bevriezen en smelten zorgt voor een enorme variatie in zee-ijs bedekking tussen seizoenen. Andere factoren, zoals wind en zeestroming, zorgen voor een onafgebroken vervorming van het zee-ijs wat resulteert in een verzameling van ijs van verschillende leeftijden en structuren. Dit dynamische zee-ijs vormt een habitat voor leven in de poolzeeën. De kenmerken van het zee-ijs en de veranderingen hierin tussen seizoenen hebben een grote invloed op de fysieke kenmerken van het gehele milieu, zoals beschikbaarheid van licht en eigenschappen van de waterkolom, met als gevolg fluctuerende hoeveelheden primaire productie in zowel het zee-ijs als de waterkolom. Dit heeft een grote invloed op de voedselbeschikbaarheid voor hogere trofische niveaus, die het zee-ijs bijvoorbeeld ook voor voortplanting of als schuilplaats gebruiken. Soorten zoöplankton en nekton die in de poolgebieden onder het zee-ijs leven hebben zich op verschillende manieren aangepast aan de variatie in beschikbaar voedsel en hun tussen seizoenen veranderende habitat. Gebeurtenissen in de levenscyclus, zoals voortplanting, zijn qua timing vaak aangepast om samen te vallen met pieken in primaire productie. Daarnaast hebben ettelijke soorten verschillende strategieën ontwikkeld voor het omgaan met voedselschaarste in de wintermaanden, zoals het gebruiken van reserves, verlaging van het metabolisme of het veranderen van dieet. Antarctische krill (*Euphausia superba*) en Arctische kabeljauw (*Boreogadus saida*) worden gezien als sleutelsoorten in, respectievelijk, de Zuidelijke en de Arctische Oceanen.

Kennis over hoe organismen het zee-ijs als habitat gebruiken is nog steeds incompleet. Het begrip van zee-ijs ecologie wordt gehinderd door logistieke beperkingen in het verzamelen van voldoende monsters die nodig zijn om grootschalige ruimtelijke trends te ontdekken. De 'Surface and Under Ice Trawl' (SUIT) werd ontwikkeld om deze beperking te overwinnen en werd gebruikt om inzicht te krijgen in de verschillen in de verspreiding van zoöplankton tussen open water en met zee-ijs bedekt water in de Zuidelijke Oceaan. Meer kennis over het gebruik van zee-ijs door verschillende soorten en het effect van zee-ijs op hun verspreiding is nodig om consequenties van de huidige klimaatverandering te kunnen voorspellen. Een afname in zee-ijs bedekking en de dikte van zee-ijs is vooral in de Arctische Oceaan in de laatste decennia waargenomen. Maar ook in het Antarctische gebied zijn er veranderingen in temperatuur en zee-ijs bedekking geconstateerd. Informatie over de voedselketen die geassocieerd is met zee-ijs kan daarnaast belangrijk zijn voor het maken van duurzaam visserijbeleid. In de Zuidelijk Oceaan worden Antarctische krill en verscheidene vissoorten commercieel bevist. Daarnaast is een noordwaartse verspreiding van commercieel beviste soorten in het subarctische gebied waargenomen.

Het doel van dit proefschrift is om kennis te vergaren over associatie van mariene soorten met het zee-ijs habitat en het functioneren van mariene voedselketens door de hoeveelheid en verspreiding van soorten in de met zee-ijs bedekte oceanen te bestuderen. Daarnaast werd het belang van koolstofbronnen uit zee-ijs en de variatie in de energie-inhoud van mariene soorten bekeken.

In de Zuidelijke Oceaan wordt de winter gezien als een periode die kritiek is voor larvale en juveniele Antarctische krill geboren in de zomer ervoor (leeftijdsklasse 0). In Hoofdstuk 2 is de populatie structuur van krill in leeftijdsklasse 0 bestudeerd om meer te weten te komen over deze structuur in het oppervlakte water onder ijs. Daarnaast is gekeken naar de verspreiding van ontwikkelingsstadia in verschillende diepte lagen. De SUIT werd gebruikt om de bovenste 2 meter van de waterkolom onder ijs te bemonsteren, terwijl een 'Rectangluar Midwater Trawl' (RMT) werd gebruikt voor de bemonstering van diepere waterlagen. De resultaten lieten zien dat de leeftijdsklasse 0 populatie in geografisch verdeelde cohorten kon worden verdeeld, gebaseerd op lengte en ontwikkelingsstadium. De lengte van dezelfde ontwikkelingsstadia verschilde tussen deze cohorten. Deze verschillen tussen cohorten kunnen een gevolg zijn van variatie in paaitijd of variatie in groei door verschillen in voedselvoorziening gedurende de ontwikkeling. Het gedrag en de fysieke verschillen behorende bij een ontwikkelingsstadium zorgen waarschijnlijk voor een verandering in de verspreiding in de waterkolom. Over het algemeen was de krill dichtheid per volume hoger in de oppervlakte laag onder ijs dan in de bovenste 500 meter van de waterkolom, wat laat zien dat de samenstelling, hoeveelheid en verspreiding van jonge krill niet goed wordt weergegeven wanneer alleen standaard vistuig zoals de RMT wordt gebruikt.

Het dieet van Antarctische krill in leeftijdscategorie 0 werd onderzocht om verder inzicht te krijgen in hoe het zee-ijs als habitat wordt gebruikt (Hoofdstuk 3). Verschillende methoden werden gebruikt om de ruimtelijke en tijdelijke variatie in het dieet te bestuderen. De maaginhoud geeft informatie over de meest recente voeding van een consument, terwijl zowel vetzuur als stabiele isotopen analyse informatie geeft over trofische interacties over een langere tijd. De maaginhoud van Antarctische krill in leeftijdsklasse 0 bevatte qua aantallen vooral centrische en pennate diatomeeën en qua biomassa vooral centrische diatomeeën en roeipootkreeftjes. Items in het dieet die geïdentificeerd konden worden lieten zien dat het dieet vooral bestond uit soorten die geassocieerd zijn met zee-ijs. Variatie in de maaginhoud van de jonge krill tussen regio's was kwam overeen met variatie in de structuur van de zoöplanktongemeenschap in het oppervlakte water onder ijs. Vetzuren en stabiele isotopen verschilden tussen cohorten, met name van het cohort met de kleinste krill larven in vergelijking met de andere cohorten. Dit eerstgenoemde cohort had daarnaast ook de laagste δ^{15}N en δ^{13}C waarden, die, respectievelijk, gebruikt worden als maat voor heterotrofie en de mate van bijdrage van koolstofbronnen uit zee-ijs aan het dieet. Ten slotte had dit cohort de laagste koolstof/stikstof ratio, wat gebruikt word als een maat voor vetopslag en algemene conditie. De resultaten suggereren dat organismen in, of geassocieerd met, zee-ijs de belangrijkste voedselbron vormen voor krill van leeftijdsklasse 0 die aan het eind van de winter onder het zee-ijs leven. Een gebrek aan deze voedselbron kan negatieve gevolgen hebben voor de jonge krill in het zee-ijs habitat.

Een andere manier om trofische interacties te bestuderen is door het kijken naar de energie-inhoud van soorten, wat gebruikt kan worden in modellen van de voedselketen en het begrijpen van de energieflux in een ecosysteem. De kwaliteit van een prooi kan de verspreiding, het gedrag en de fysiologie van een predator beïnvloeden. De energie-inhoud van een soort kan worden beïnvloed door hun dieet, fysiologie en gebeurtenissen in de levenscyclus. Om de variatie in energie-inhoud tussen verschillende soorten zoöplankton en nekton te bestuderen is een review gemaakt van de huidige kennis op dit gebied (Hoofdstuk 4) inclusief tot dusver ongepubliceerde data. De meeste energie-inhoud metingen waren gedaan op vissoorten. Binnen de kreeftachtigen was Antarctische krill de meest bestudeerde soort, waarbij verschillen in energie-inhoud werden gevonden tussen seksen en ontwikkelingsstadia. Een relatie tussen lengte en energie-inhoud werd gevonden voor de vis *Electrona antarctica*. Daarnaast werden relaties gevonden tussen het percentage water in het lichaam en energie-inhoud voor de vissen *Electrona antarctica, Gymnoscopelus braueri* en *Bathylagus antarctica*, met seizoens variatie in de laatstgenoemde. Voor de meeste mariene soorten in de Zuidelijke Oceaan waren weinig gegevens beschikbaar, waardoor de mate van variatie tussen regio's en seizoenen onduidelijk blijft. Verschillende methoden die gebruikt worden om energie-inhoud te meten worden besproken en bediscussieerd.

In de Arctische Oceaan is bekend dat één en twee jaar oude Arctische kabeljauw dicht onder het zee-ijs leven. Het dieet van Arctische kabeljauw werd bekeken om te beoordelen of de vis in dit habitat afhankelijk is van voedsel geleverd door zee-ijs (Hoofdstuk 5). Net als in Hoofdstuk 2 worden er meerdere methoden gebruikt om dieet samenstelling en koolstofbronnen te onderzoeken, zoals maaginhoud, vetzuur en stabiele isotopen analyses. Daarnaast werd de percentuele bijdrage van door ijsalgen geproduceerd koolstof aan de weefsels van de vis gekwantificeerd. Onderzoek werd gedaan aan verschillen weefsels van Arctische kabeljauw. De maaginhoud bestond qua aantallen vooral uit de roeipootkreeftjes *Tisbe* spp. en *Calanus* spp., en de vlokreeft *Apherusa glacialis*. Qua biomassa bestond de maaginhoud vooral uit *A. glacialis*. Er was voldoende voedsel beschikbaar om een goede lichamelijke conditie in stand te houden. De hoeveelheid lipiden was het hoogste in de lever, wat suggereert dat dit de voornaamste opslagplaats voor lipiden is in Arctische kabeljauw. Koolstof, geproduceerd door ijs-algen, droeg meer dan 50% bij aan de totale hoeveelheid koolstof in de weefsels van de vis. De resultaten geven aan dat het zee-ijs voldoende rijkdommen bevat om Arctische kabeljauw in de centrale Arctische Oceaan van voedsel te voorzien. Arctische kabeljauw heeft een voordeel ten opzichte van mogelijke concurrenten doordat deze vis de rijkdommen van het zee-ijs kan benutten. Wanneer het zee-ijs verdwijnt, als een gevolg van klimaatverandering, kan dit voordeel verdwijnen.

Vlokreeften vormen een belangrijk onderdeel van de Arctische mariene gemeenschap. *Apherusa glacialis* is een soort die vaak hoge aantallen voorkomt in het oppervlakte water onder ijs. Het effect van eigenschappen van zee-ijs op de verspreiding van *A. glacialis* is eerder op kleine schaal onderzocht, vaak met behulp van duikers. Verschillende voorgaande studies hebben verschillende resultaten gevonden, waarbij bijvoorbeeld grote hoeveelheden vlokreeften zijn gevonden onder zowel ijs met veel structuur als onder ijs met een heel glad oppervlak. In Hoofdstuk 6 werd de relatie tussen de verspreiding van *A. glacialis* en de eigenschappen van zee-ijs over een grote schaal onderzocht in de lente, waarbij gegevens over zee-ijs topografie, eigenschappen van de onderliggende waterkolom en oceanografische kenmerken werden gebruikt. Ondanks dat het aantal bemonsteringsplekken te klein was om op elkaar inwerkende effecten die de variatie in aantallen verklaren te ontrafelen, werd er bewijs gevonden voor invloeden van omgevingsfactoren op de verspreiding van *A. glacialis* op grote schaal. Van de gebruikte variabelen verklaarde de concentratie chlorofyl *a* de hoeveelheid vlokreeften het beste. Wanneer gegevens verzameld in de zomer werden toegevoegd aan de analyse, verklaarden temperatuur, zoutgehalte en structuren in het zee-ijs de hoeveelheid amphipoden het beste. Dit suggereert dat de trade-off tussen voedselbeschikbaarheid en predatiedruk, en dus de sturende factor voor *A. glacialis* verspreiding, veranderd met de seizoenen.

De bevindingen van dit proefschrift dragen bij aan het begrijpen van de biologie en ecologie van sleutelsoorten in de zee-ijs gerelateerde voedselketen en van het leven in de met ijs bedekte oceanen. Het zee-ijs habitat vervult veel functies in het leven van organismen in de poolzeeën. De belangrijkste rol die zee-ijs heeft in het leven van een bepaalde soort kan veranderen met bijvoorbeeld de seizoenen of met leeftijd. Ongeacht of voedselvoorziening de belangrijkste reden voor het gebruik van zee-ijs door organismen is of niet, eten soorten die direct onder het zee-ijs leven vaak van zee-ijs geassocieerde voedselbronnen. Het unieke habitat dat zee-ijs vormt verdient behoedzaam management.

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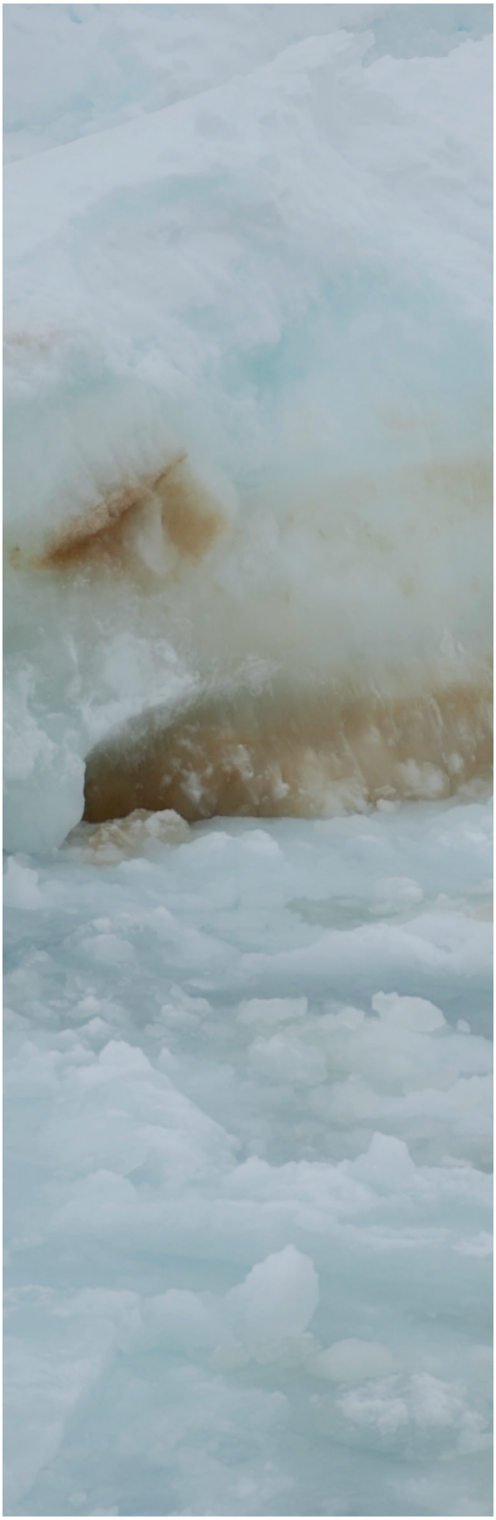

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