

**Feeding activity of larval and juvenile Antarctic krill  
*Euphausia superba* in open water, the marginal ice  
zone and pack ice region in late winter in the Scotia  
Sea and the northern Weddell Sea**

**Bachelorarbeit**

im Studiengang Bachelor of Science Biologie an der  
Philipps-Universität Marburg,  
in Zusammenarbeit mit dem Alfred-Wegener-Institut in Bremerhaven

vorgelegt von

**Laura Halbach**

(laurahalbach@web.de)

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1. Gutachterin, extern: Prof. Dr. Bettina Meyer (Universität Oldenburg)
2. Gutachter, intern: Prof. Dr. Lothar Beck (Universität Marburg)
3. Gutachter, intern: Dr. Barbara Kostron (Universität Marburg)

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## Vorwort

Die vorliegende Bachelorarbeit wurde im Rahmen des Bachelor Studiengangs Biologie an der Philipps-Universität-Marburg in Kooperation mit dem Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar-und Meeresforschung (AWI) in Bremerhaven durchgeführt.

Die Probennahme, sowie weitere Datenerhebungen erfolgten auf der Expedition ANT-XXIX/7 an Bord des Forschungsschiffes „Polarstern“ unter Leitung von Prof. Dr. Bettina Meyer im Sommer 2013 (s. Expeditionsbericht Meyer and Auerswald 2014). Die Probenanalyse wurde von Februar bis April 2014 am AWI in Bremerhaven durchgeführt.

Nach Zustimmung beider Betreuer, Prof. Dr. Bettina Meyer, sowie Prof. Dr. Lothar Beck wurde die Arbeit in Form eines wissenschaftlichen Papers in englischer Sprache verfasst.

## Danksagung

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## Zusammenfassung

Eine erfolgreiche larvale Überwinterung von Antarktischem Krill, *Euphausia superba*, (Krill) beeinflusst maßgeblich dessen Populationsgröße. Das Ausmaß der winterlichen Meereisbedeckung wurde hierbei als Faktor diskutiert, der eine erfolgreiche larvale Entwicklung begünstigt. Der genaue Vorteil der winterlichen Meereisbedeckung für die larvale Entwicklung bleibt jedoch weitestgehend unklar.

Das Ziel dieser Studie war es, die Hypothese zu testen, dass Krilllarven in den Packeis Regionen in besserer Kondition sind (bezüglich der Körperlänge, Trockengewicht, Fressaktivität und des Mageninhalts) als im offenen Wasser. Dafür wurde die Kondition der Krill Larven (Furcilia (F) III-IV und juvenile) im offenen Wasser (OW), der Marginalen Eis Zone (MIZ1+2) und in der Packeis Region (Ice Camp1+2) im Vergleich zu Konzentrationen von Chlorophyll *a* (Chl *a*) und partikulärem organischen Kohlenstoff (POC) in der Wassersäule und im Eis, untersucht. Zusätzlich wurden Unterschiede in der Nahrungsaufnahme von Krilllarven während des Tages und während der Nacht geprüft.

Es zeigte sich, dass sich die Krilllarven aus den Packeis Regionen insgesamt nicht in besserer Kondition als die Larven aus dem OW befanden. Obwohl die Larven von Ice Camp1 die größte Körperlänge (Mittelwert (MW) 15.69 mm) und das größte Trockengewicht (MW 4.59 mg) besaßen, wurden signifikante Unterschiede mit Krill aus dem OW nur in der Körperlänge gefunden. Die Stadiumszusammensetzung der Larven war außerdem sehr ähnlich in OW und Ice Camp1 (einige F6er und überwiegend Juvenile). Krilllarven von Ice Camp2 hatten die kleinsten Körperlängen (MW 7.96 mm) und das geringste Trockengewicht (MW 0.50 mg), die Stadiumszusammensetzung reichte von F3-F6. Die große Biomasse in dem Meereis der Packeis Regionen (Ice Camp1: 21.78  $\mu\text{g L}^{-1}$  Chl *a* und 400.55  $\mu\text{g L}^{-1}$  POC; Ice Camp2: 12.68  $\mu\text{g L}^{-1}$  Chl *a* und 330.2  $\mu\text{g L}^{-1}$  POC) konnte nur zu einem geringen Teil von den Krilllarven genutzt werden. Dies konnte anhand ihrer geringen Fressaktivität und dem geringen Mageninhalt festgestellt werden. In Ice Camp2 konnte eine tägliche vertikale Migration (DVM) der Krilllarven beobachtet werden. Tagsüber hielten sich die Larven in direkter Nähe zum Meereis auf und nachts in den oberen 20 m der Wassersäule. Ergebnisse der Mageninhaltsanalysen zeigten, dass Krill tagsüber vorwiegend Diatomeen und Dinoflagellaten gefressen hat, während Zoopankton

und Detritus überwiegend in der Nacht als Nahrung diente. Die beobachtete DVM könnte als Strategie dienen, neue Gebiete im Eis zu erreichen, die neue potentielle Nahrungsangebote für Krill bereitstellen. Denn die untersuchten Konzentrationen von Chl  $a$  und POC in Eiskernen zeigten, dass die Nahrung in den Packeis Regionen sehr heterogen verteilt ist.

Im Gegensatz zu den Packeis Regionen konnte das große Nahrungsangebot im OW und im Wasser von MIZ1 (MIZ1:  $0.73 \mu\text{g L}^{-1}$  Chl  $a$  und  $39.06 \mu\text{g L}^{-1}$  POC; OW:  $0.52 \mu\text{g L}^{-1}$  Chl  $a$  und  $38.3 \mu\text{g L}^{-1}$  POC) auch von Krill genutzt werden. Dies wurde anhand ihrer hohen Fressaktivität und einem größeren Mageninhalt aufgezeigt. Die MIZ scheint das Gebiet zu sein, das für das Wachstum und das Überleben der Krilllarven am förderlichsten ist. Zum einen haben sie dort genügend Nahrung und zum anderen bietet das MIZ durch die Eisbedeckung den Larven Schutz vor Predatoren. Ergebnisse der Mageninhaltsuntersuchungen zeigten, dass Detritus eine wichtige Nahrungsquelle in der MIZ sein kann.

## Abstract

A successful larval overwintering is a major factor determining population sizes of Antarctic krill, *Euphausia superba* (hereafter krill). A high population recruitment success of krill was linked to years with more extensive sea ice in the previous winter. However, the benefit of the winter sea ice cover for a successful larval development during winter remains unclear.

The aim of the present study was to test the hypothesis that larval krill in pack ice regions are in better condition in terms of food supply and feeding activity than larvae from OW regions. Therefore, the condition of larval krill (furcilia (F) III–VI as well as juveniles) was investigated in open water (OW), the marginal ice zone (MIZ1+2) and the pack ice region (Ice Camp1+2) during late winter, in relation to Chlorophyll *a* (Chl *a*) and particulate organic carbon (POC) concentrations in the water column and in the sea ice. In addition, differences in the dietary intake of larval krill during the day and night were examined.

Overall, krill larvae from pack ice regions were not in better condition than in OW. Although, krill larvae caught at Ice Camp1 had the largest body lengths (mean 15.69 mm) and highest dry weights (mean 4.59 mg), only the body lengths showed significant differences with larval krill from OW and stage composition was similar (few F6 and mostly juveniles). Larval krill of Ice Camp2 had the smallest body lengths (mean 7.96 mm) and dry weights (mean 0.50 mg) while stage composition ranged from F3-F6. The high amount of available food sources within the sea ice (Ice Camp1: 21.78  $\mu\text{g L}^{-1}$  Chl *a* and 400.55  $\mu\text{g L}^{-1}$  POC; Ice Camp2: 12.68  $\mu\text{g L}^{-1}$  Chl *a* and 330.2  $\mu\text{g L}^{-1}$  POC) was used only to a small extent by krill larvae, which is reflected by their lowest feeding activities and relatively empty stomachs. At Ice Camp2, larval krill was observed performing diel vertical migration (DVM). During the day larval krill was closely associated with the sea ice, whereas during the night they descended into the upper 20 m of the water column. Stomach content analyses showed that larval krill consumed diatoms and dinoflagellate primary during the day, while zooplankton and detritus predominated in the diet during the night. In pack ice regions where food abundance in the sea ice is patchy, the DVM could serve as a strategy to exploit potentially new feeding grounds.

In contrast to the pack ice regions, the food availability for larval krill was high at OW and MIZ1, reflected by higher feeding activities and higher stomach contents of larval krill, together with high Chl *a* and POC concentrations in the water (MIZ1: 0.73  $\mu\text{g L}^{-1}$  Chl *a* and 39.06  $\mu\text{g L}^{-1}$  POC; OW: 0.52  $\mu\text{g L}^{-1}$  Chl *a* and 38.3  $\mu\text{g L}^{-1}$  POC). The MIZ may represent a beneficial nursery area for larval krill. On the one hand, they have a sufficient amount of food to grow and on the other hand the MIZ provides sheltered areas as protection from predators and currents. The high amount and largest diameter of detritus pieces in larval stomachs found at MIZ2 suggest detritus is an important food source in this area.

# 1 Introduction

Antarctic krill, *Euphausia superba*, (hereafter krill) is a central component of the Southern Ocean ecosystem. Krill serves as a link between primary and secondary producers and higher-level predators from fish and birds to seals, penguins and whales (Meyer et al. 2009). This key position in the Antarctic food web implies top-down and bottom-up regulation control through grazing and predation cascades (Atkinson et al. 2008). The total biomass of krill is estimated to be approximately 170 million tons (Siegel 2005) with large impact on biogeochemical cycles (von Bodungen et al. 1986; Le Fèvre et al. 1998; Tovar-Sanchez et al. 2007). The krill fishery, still expanding, is the largest in the Southern Ocean (Siegel 2005; Croxall and Nicol 2004).

Although, krill is claimed to be one of the best-studied pelagic animals, there are still uncertainties about crucial parts of its ecology (Nicol et al. 2003). The larval phase of its life cycle in association with the winter sea ice cover or its migration behaviour, remain poorly understood (Nicol 2006; Meyer et al. 2009).

Larval stages are known to be the most vulnerable phases in the lifecycle of various marine invertebrates and their development success influence population size (Töbe et al. 2009). Spawning of krill takes place during austral summer. Young larvae develop through a series of stages during summer and winter to post-larval juveniles in the following spring (Meyer et al. 2009). Therefore, recruitment success of krill depends on larval survival during winter when food in the water column is limited (Quetin and Ross 1991; Siegel 2005; Quetin et al. 2007) and large parts of the Southern Ocean are covered with sea ice (Nicol 2006). Thus, krill overwintering can be seen as a critical phase in the lifecycle. In this context, several studies have shown a close correlation between the winter sea ice extent and the recruitment success of krill (Kawaguchi and Satake 1994; Siegel and Loeb 1995; Atkinson 2004). High krill densities in summer were linked to years with extensive sea ice the previous winter (Kawaguchi and Satake 1994; Siegel and Loeb 1995). Hence, the winter sea ice extent plays a key role in larval krill overwintering population success. In addition, several studies showed that larvae associated with sea ice

are in better condition than larvae from open water (OW) regions (Quetin and Ross 1991; Daly 2004; Meyer et al. 2009).

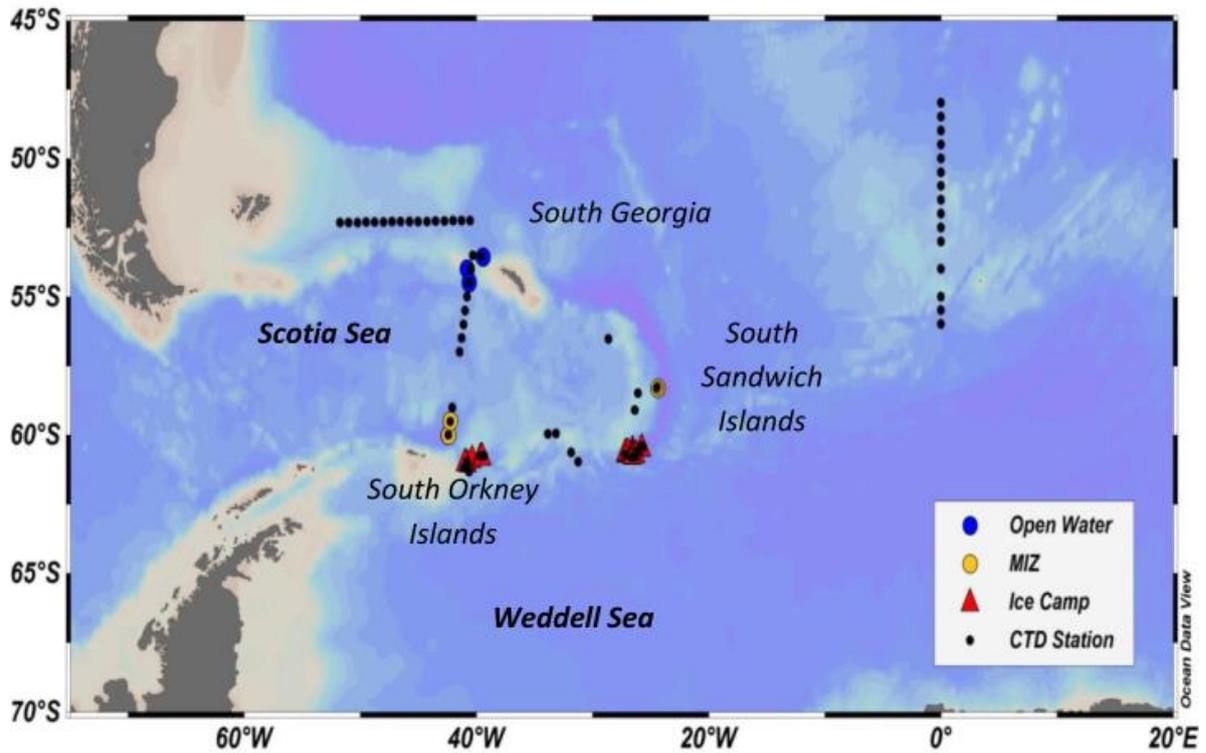
However, the benefits of winter sea ice for successful larval development and the feeding behaviour of krill larvae in sea ice habitats remain unclear. Due to the difficulties of working in the winter sea ice zone, data covering the condition of larval krill and their habitat are scarce for the austral winter (Atkinson et al. 2002; Frazer et al. 2002). Despite various uncertainties about krill's overwintering, different studies demonstrated that krill uses different strategies and physiological adaptations to survive the winter when food availability is low. Adult krill display a flexible behaviour to cope with the severe winter condition of low food supply by using its lipid reserves and reducing its metabolic rates (Meyer et al. 2009). With this strategy they are able to survive for longer than 200 d without food (Kawaguchi et al. 1986; Quetin and Ross 1991) and even body shrinkage was observed after long periods of starvation (Quetin and Ross 1991). Unlike adults, krill larvae have low lipid reserves (Hagen et al. 2001) and cannot sustain longer periods of starvation (Meyer and Oettl 2005). It is assumed that the larvae cannot cover their metabolic demands due to the low phytoplankton concentrations in the water column during winter, so they utilise other food sources in addition (Quetin et al. 2003). Observations of larval krill grazing on the underside of ice floes suggest sea ice algae as an alternative food source for krill larvae during the winter (Daly 1990; Quetin and Ross 1991; Meyer et al. 2002). Sea ice can contain Chlorophyll *a* concentrations 10-100 times higher than in the water column below (Garrison et al. 1986; Garrison and Buck 1991) and ice algae can be released into the water by brine channels in sea ice, movements of ice floes and melting processes (Meyer et al. 2009). In addition, heterotrophic organisms (e.g. dinoflagellates, tintinnids, copepods) as well as detritus might be an additive food source for larval krill during winter (Kawaguchi et al. 1986; Huntley et al. 1994; Schmidt et al. 2006). High abundances of larval krill were also recorded in specific over-rafted ice regions, suggesting that the sea ice serves also as protection for predators and shelter from currents (Frazer et al. 2002; Meyer et al. 2009). Several studies (Everson 2000; Zhou and Dorland 2004) have shown that the vertical migration behaviour performed by adult krill is not strongly linked to the winter sea ice cover. Unfortunately larval krill migration patterns and behavioural strategies are very poorly understood (Everson 2000).

Knowledge about the migration behaviour of larval krill could be of great importance to understand the interaction of larval krill with sea ice as a whole.

The aim of the present study was to test the hypothesis that larval krill from the pack ice regions are in better conditions than larvae from OW regions in terms of body length, dry weight, feeding activity and stomach content. Furthermore, we investigated the feeding behaviour of larvae over 24 h cycles in relation to their daily vertical movement behaviour. For implementing these goals we sampled larval krill in OW regions without winter sea ice coverage, in the marginal ice zone (MIZ1 and 2) and in pack ice regions (Ice Camp1 and 2). The study was part of the expedition ANT XXIX/VII, from the 14<sup>th</sup> of August to the 16<sup>th</sup> of October 2013, and of the project PACES II (Polar regions and Coast in a changing Earth System).

## 2 Materials and Methods

### 2.1 Sampling area



**Fig. 1** Cruise track with CTD (Conductivity Temperature Depth) and larval krill sampling stations (highlighted in colour) in open water (OW), the marginal ice zone (MIZ) and in the pack ice at two ice camps, where krill was caught and used for further analyses. (Cantzler et al. 2014)

Sampling took place in the Scotia Sea and northern Weddell Sea during late austral winter from 14<sup>th</sup> August to 16<sup>th</sup> October 2013. On the expedition three transects were performed (Fig. 1). The first transect was completed off the continental coast of Patagonia with a west-east direction towards South Georgia along 52 °S from 51 °W to 40 °W. The second transect followed with a north-south direction from 53 °S to 61 °S and from 40 °W to 42 °W towards the South Orkneys Islands. The last transect was performed from 55 °S to 48 °S on the Greenwich Meridian at 0 °W. After the second transect two Ice Camps were established, the first at 61 °S 41° W south-east of the islands, from 1<sup>st</sup> until 10<sup>th</sup> September (hereafter named as “Ice Camp1”), the second ice camp at 60 °S 27 °W south of the South Sandwich Islands from 17<sup>th</sup> until 28<sup>th</sup> of September (hereafter named as “Ice Camp2”). Larvae were caught in the pack ice zone (at Ice Camp1 and 2), in the OW from 53°S 39°W to 54°S 40°W and in the MIZ from 59 °S 42 °W to 60 °S 42 °W.

## 2.2 Sea ice conditions

When the ice zone was reached, daily ice observations (Ice coverage in % and ice thickness) were performed by several scientists observing from the bridge of the ship.

## 2.3 Analyses of Chlorophyll *a* and particulate organic carbon

### *In the water column*

Water samples from 0 to 200 m depth were taken with a rosette water sampler fitted with 24 Niskin bottles (12 L each) of a SBE 911 conductivity temperature depth (CTD) system (Sea Bird Electronics Inc., USA). For Chlorophyll *a* (Chl *a*) measurements one litre water samples from defined depths were filtered on glass microfiber filters ( $\varnothing$  25 mm) (GF/F Whatman International Ltd., England) with a pressure of 200 mbar. Filters were transferred in centrifuge tubes filled with 6 ml 90 % acetone as well as 1 cm<sup>3</sup> of glass beads and stored for at least 30 min and up to 24 hrs in the dark. For Chl *a* extraction the tubes were placed in a grinder for 25 sec, followed by a centrifugation at -10 °C for 5 minutes at 4,000 rpm. Then, fluorescence was measured with a Turner 7000D fluorimeter (Turner designs, USA).

Water samples (0.5 to 1 L volume) for particulate organic carbon (POC) analyses were filtered onto 25 mm diameter pre-combusted glass microfiber filters (GF/F Whatman International Ltd., England). Filters were dried over night at 50 °C and stored at -20 ° for later analyses at the Alfred-Wegener-Institute (AWI). Back at the AWI, filters were thawed, moistened with 0.88 % KCl, to remove inorganic carbon and dried for at least 12 hrs at 60 °C. Thereafter, filters were pressed to pellets and measured in a Carlo Erba CN analyser (HEKAtech GmbH, Germany). Acetanilide was used as a standard.

### *In ice cores*

At both ice stations, ice cores were taken using a Kovacs Mark II ice corer (0.09 m internal diameter), powered with an electric drill. Sea ice thickness, snow coverage and sea ice temperature were noted. At camp1 ice cores were sampled at five sampling sites located around the diving hole. At each site three 1m<sup>2</sup> areas were cleared of snow cover and

three ice cores were taken from each square, respectively. During camp2, sampling was performed on three transects ('ROV', 'POL', 'EB'). On each transect, three ice cores were taken every second meter. Ice cores were sealed in plastic tubes and stored immediately in a freezer room (-24 °C), where they were sectioned into 10 to 20 cm slices. The sea ice slices were melted in the dark at -4 °C in sealed plastic containers with added filtered sea water to avoid osmotic stress (200 ml per cm ice core length) (Meiners et al. 2011). After 24 to 36 hours when the sea ice was melted, subsamples were taken (0.5-1 L) for Chl *a* and POC measurements as outlined above.

## 2.4 Krill sampling

In OW larval krill was collected using Rectangular Midwater Trawls-8 and 1 (RMT 8 and 1) for depths to 100 m equipped with 850 µm and 350 µm cod end meshes, respectively. In addition, larval krill was sampled with a Bongo net (200 µm mesh and a 5 L closed cod end), which was towed vertically from 200 m to the surface at 1 m s<sup>-1</sup> (range: 0.7 – 1 m sec<sup>-1</sup>). Also, the ship's well shaft was used to catch krill by pumping water through the well shaft from under the ship in 11 m water depth into a flow through container with a 200 µm mesh.

During ice camp work, larvae were sampled at the diving hole with the use of hand nets and by scientific divers using the plankton pump system MASMA (MAnguera SubMArina). The MASMA, consisting of a motor-driven centrifugal pump, filtered seawater through a zooplankton net with 200 µm mesh size and a 2 L cod end, which was located inside an airtight container. Water masses were transported through a tube with 5 cm internal diameter and a maximum length of 50 m towards the container (0.1 m<sup>3</sup> min<sup>-1</sup>), where larvae were collected. At Ice Camp2 krill was also caught over 24 hrs during ten consecutive days with a fishpump by Aqualife Products (BP40). This pump was subsequently installed on board ship and seawater was pumped continuously (900 m<sup>3</sup> per hour) through the well shaft onto a sieve, where the larvae could be collected and frozen in a -80 °C freezer.

## 2.5 Morphometrics of freshly caught krill

At each station freshly caught krill larvae and juveniles were identified to stage according to Fraser (1936). Larvae were defined in the present study until the juvenile stage. Under a stereomicroscope, body length was measured from the anterior tip of the rostrum to the end of the telson, while carapace length was measured from the anterior tip of the rostrum to the posterior notch of the carapace (Meyer et al. 2010). The size of the DG was measured along its longest horizontal axis (Nicol et al. 2004) and its relative length in relation to the carapace length was calculated (Equ. 1), as it provides information about the recent feeding activity of larvae (Shin 2000; Nicol et al. 2004; O'Brien et al. 2010). Larval krill at MIZ2 could not be analysed for their feeding activity. In addition, the coloration of the DG of each animal was determined in order to indicate feeding preferences on different food sources (Kawaguchi et al. 1986, 1999; Nicol et al. 2004). After processing, larvae were immediately frozen in liquid nitrogen and stored at -80 °C for later analysis of dry weight, stomach content etc. at the AWI.

$$\text{Relative DG length} = \frac{\text{DG length [mm]}}{\text{carapace length [mm]}} \cdot 100 \quad (1)$$

## 2.6 Dry weight analysis

Larval krill were thawed, rinsed briefly with de-ionised water and then blotted dry on absorbent paper. Krill were weighted before and after lyophilisation on a Mettler UM3 microbalance (Mettler-Toledo AG, Switzerland).

## 2.7 Stomach content analysis

### 2.7.1 Stomach preparation

Stomachs of krill larvae were dissected on ice from freshly caught krill on board Polarstern and afterwards frozen at -80 °C as well as from frozen animals back at the AWI. Each larva was placed on ice and the carapace exoskeleton was opened with help of a scalpel, so that the stomach could be taken out. Stomachs of several individuals were pooled and put together in an Eppendorf vial with Milli-Q water. Stomachs were emptied by gentle agitation of the vial on a vortex mixer for a few seconds until all stomachs were

opened. The sample was transferred into an Utermöhl chamber and allowed to settle for at least 2 hours. No preservative was added and each sample was analysed on the same day. No stomachs could be analysed from larval krill at MIZ1.

### 2.7.2 Microscopic analysis of stomach content

Using an inverse Zeiss IM microscope, rare items such as large zooplankton pieces, large diatoms or tintinnids were counted first by scanning the complete chamber at x250 magnification. Small and common items such as small diatoms or detritus were counted along two transects, vertically and horizontally across the whole diameter of the chamber at x250 magnification. Counted numbers were extrapolated for the whole chamber. Identifications were based on (Scott and Marchant 2005). Pictures of unidentifiable items were taken with an attached camera to make later comparisons and identification possible. In addition, the total stomach fullness of each sample of the fishpump time series was estimated (modified after Gradinger and Bluhm (2010)). Ten randomly chosen fields of view were semi-quantitatively estimated for the total content of each selected field e.g. 25 % of the field of view is covered by food items, and the number of identifiable items (as a % of the total visible items).

All further used values are averaged per individual for one chamber.

### 2.7.3 Scanning electron microscopy analyses

Scanning electron microscopy (SEM) was used to gain closer insight into the stomach content and digestion processes. One sample from Ice Camp2 was transferred on a filter and dried over night at 60 °C. Afterwards, the filter was attached on an aluminium SEM stub and coated with a thin layer of gold/palladium in an ion coater.

## 2.8 Statistical analyses

Statistical analyses were carried out using R 3.1.2 (R Core Team 2014). The significance level for all tests was set as  $p < 0.05$ .

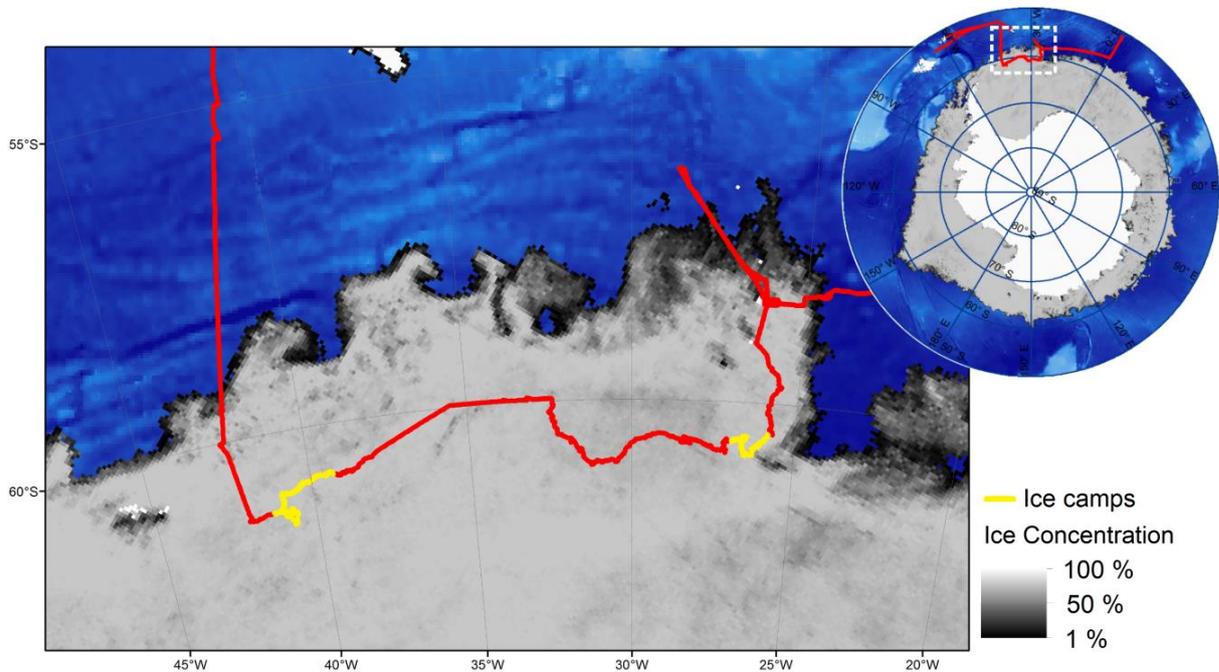
*Feeding activity:* For testing differences between regions a nested linear mixed-effects model was calculated using the lme4 package (Bates et al. 2014). For the Satterthwaite

Approximation the lmerTest was used (Kuznetsova et al. 2014). With this model a post-hoc test “Tukey-test” (Hothorn et al. 2008) was performed.

*Body length+dry weight:* For testing differences between regions a Welch-ANOVA was employed. For multiple comparisons a Games-Howell post hoc test was applied.

## 3 Results

### 3.1 Sea ice coverage



**Fig. 2** Expansion and concentration of sea ice in late austral winter on the 2th of September 2013. The rectangle indicates the area where krill larvae were caught. The map is based on satellite images of AMSR2 by the University of Bremen.

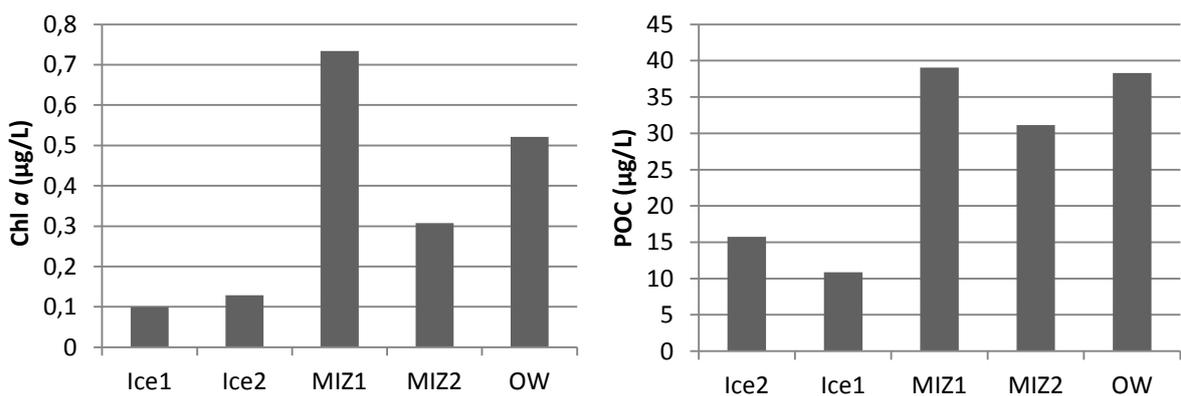
Sea ice extension in the study area varied between 57 °S and 59 °S (**Fig. 2**). According to the ice observations from the bridge, in the MIZ on the way into the pack ice (MIZ1), the mean ice concentration was 67.5 % (range 30-100 %) and in the MIZ, on the way out of the pack ice (MIZ2), the mean ice concentration was 63.48 % (range 0-100%). The MIZ region is characterised by mostly small ice floes and pancake ice (**Fig. 3**). The pack ice region is characterised by a large solid ice cover and large ice floes, 1 to 4 m thick, which can be interrupted by leads i.e. open water areas (**Fig. 3**). In this region the mean sea ice concentration of Ice Camp1 was 90 % (range 70-100 %) and of Ice Camp2 95 % (range 80-100 %). In all ice-covered regions a couple of yellow to brown-coloured undersides of ice floes were observed, caused by phytoplankton assemblages which grow underneath the ice. In the pack ice regions larval krill were observed by scientific divers closely associated to the underside of these ice floes, especially at current sheltered sides.



**Fig. 3** Various sea ice forms. Top left: closed pack ice. Top right: pack ice with leads. Bottom left: over-rafted ice floes in the marginal ice zone. Bottom right: pancake ice in the marginal ice zone.

### 3.2 Analyses of Chl *a* and POC

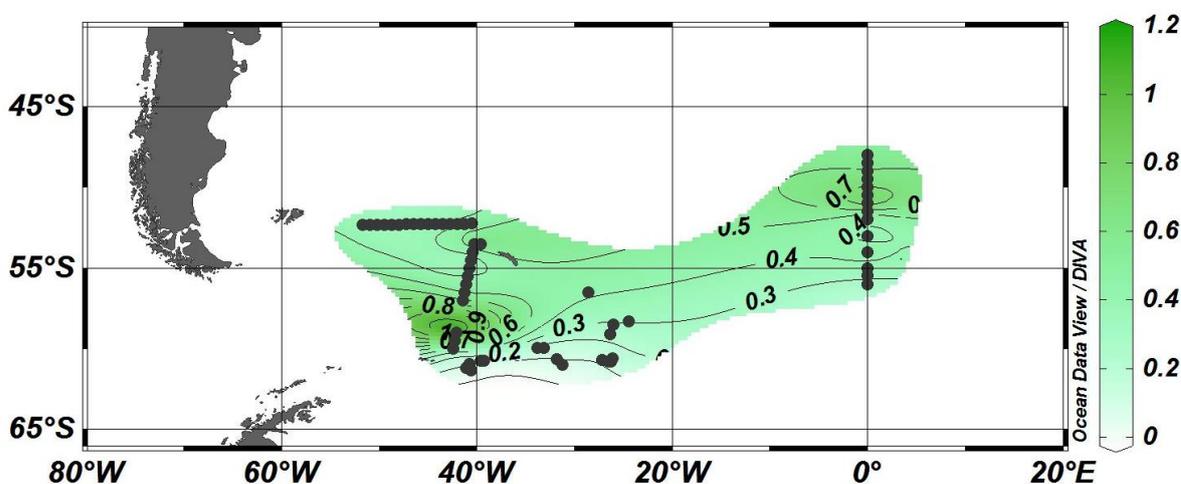
*Chl a and POC concentrations in the water column*



**Fig. 4** Mean Chlorophyll *a* (Chl *a*) and particulate organic carbon (POC) concentrations (µg L<sup>-1</sup>) in 10 m depth at open water (OW), the marginal ice zones (MIZ1 and 2) and in pack ice regions (Ice Camp1 and 2). Samples were taken by a rosette water sampler with an attached CTD probe.

Chl *a* and POC concentrations were highly variable in OW regions and in ice associated regions (Fig. 4+5). The most elevated Chl *a* and POC concentrations measured for all

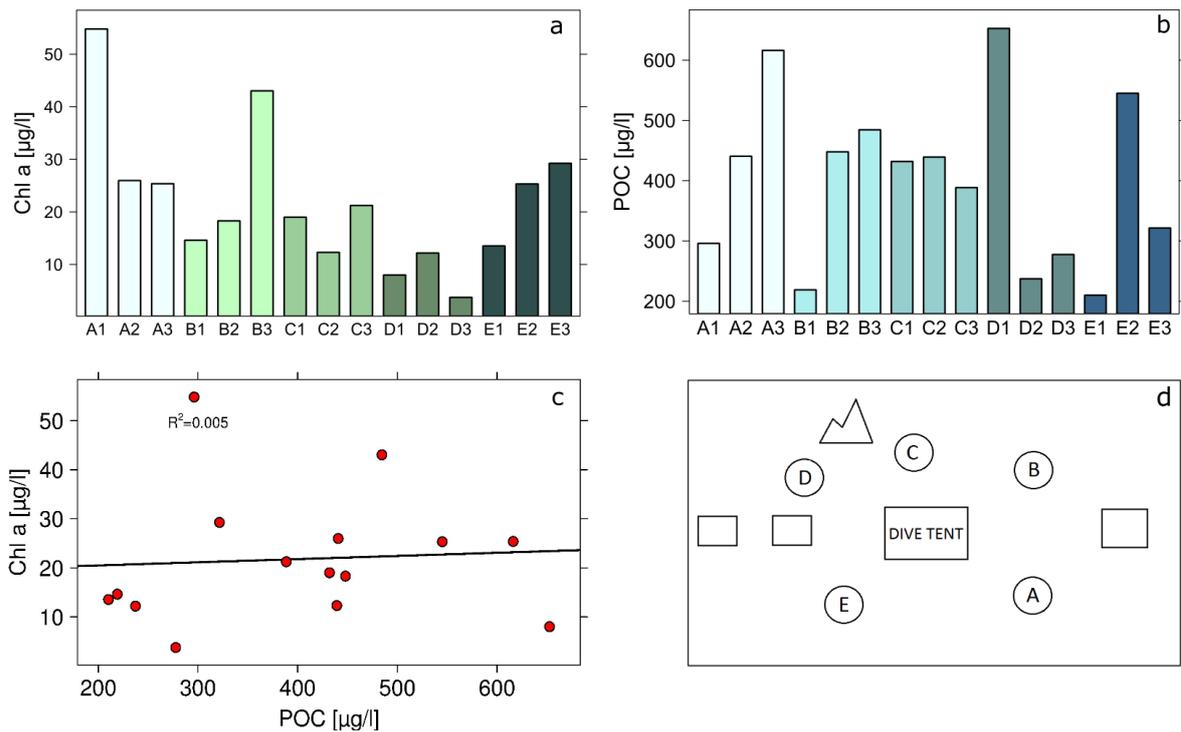
stations were in the MIZ1 with  $0.73 \mu\text{g L}^{-1}$  Chl *a* (range  $0.23\text{-}1.17 \mu\text{g L}^{-1}$ ) and  $39.06 \mu\text{g L}^{-1}$  POC (range  $23.23\text{-}52.40 \mu\text{g L}^{-1}$ ). The mean Chl *a* concentration at 10 m depth in OW areas was  $0.52 \mu\text{g L}^{-1}$  (range  $0.22\text{-}0.99 \mu\text{g L}^{-1}$ ) and the mean POC concentration was  $38.3 \mu\text{g L}^{-1}$  ( $28.59\text{-}47.38 \mu\text{g L}^{-1}$ ). In the MIZ2 the Chl *a* concentration was  $0.30 \mu\text{g L}^{-1}$  (range  $0.29\text{-}0.31 \mu\text{g L}^{-1}$ ) and the POC concentration  $31.13 \mu\text{g L}^{-1}$  ( $25.79\text{-}36.48 \mu\text{g L}^{-1}$ ). Chl *a* and POC concentrations were low at both Ice Camps. The mean Chl *a* concentration was  $0.10$  at Ice Camp1 and  $0.13 \mu\text{g L}^{-1}$  Chl *a* at Ice Camp2 (range  $0.08\text{-}0.11$  and  $0.07\text{-}0.18 \mu\text{g L}^{-1}$ , respectively). The mean POC concentration was  $10.89 \mu\text{g L}^{-1}$  at Ice Camp1 and  $15.74 \mu\text{g L}^{-1}$  at Ice Camp2 (range  $10.39\text{-}19.61$  and  $14.51\text{-}17.46 \mu\text{g L}^{-1}$ , respectively).



**Fig. 5** Mean Chlorophyll *a* concentrations ( $\mu\text{g L}^{-1}$ ) in the water column at 10 m depth. Black, filled circles mark CTD station casts. (Cantzler et al. 2014)

#### *Chl a and POC concentrations in ice cores at Ice Camp1*

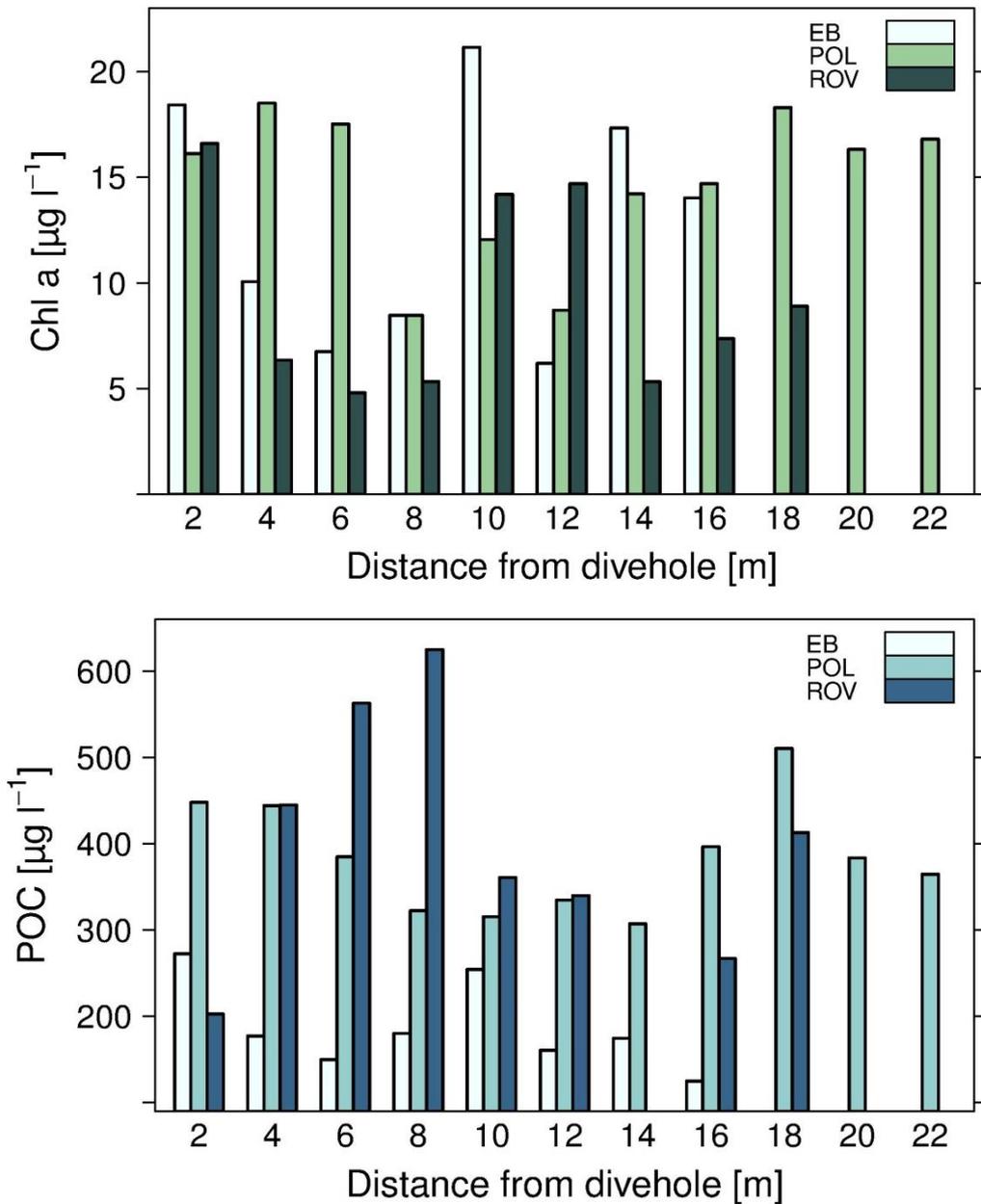
Both Chl *a* and POC concentrations in ice cores at Ice camp1 showed a high variability between and within sampling sides (Fig. 6). The mean Chl *a* concentration was  $21.78 \mu\text{g L}^{-1}$  (range  $3.75\text{-}54.8 \mu\text{g L}^{-1}$ ) and the concentrations varied up to 3 times within sample side D. The mean POC concentration was  $400.55 \mu\text{g L}^{-1}$  (range  $210.17\text{-}652.64 \mu\text{g L}^{-1}$ ), while the concentrations varied up to two times within sample side D. Further, Fig. 6c shows that the correlation between Chl *a* and POC concentrations was very low (Spearman's Ranks correlation coefficient  $R=0.005$ ), suggesting that a minor part of POC derived from autotrophic algae and hence that more heterotrophic food sources were abundant.



**Fig. 6** Comparisons of Chlorophyll *a* (Chl *a*, a) and particulate organic carbon (POC, b) concentrations ( $\mu\text{g L}^{-1}$ ) between ice cores at different sample sites of Ice Camp1 and their correlation (c). Ice cores were taken at five sample sites (A,B,C,D,E) around the dive hole (d). At each site three squares were chosen (no. 1,2 and 3), respectively and in each one, three ice cores were taken. The last 10 cm segments of three ice cores per square were pooled (e.g. A1 bars represents last 10 cm of three pooled ice cores).

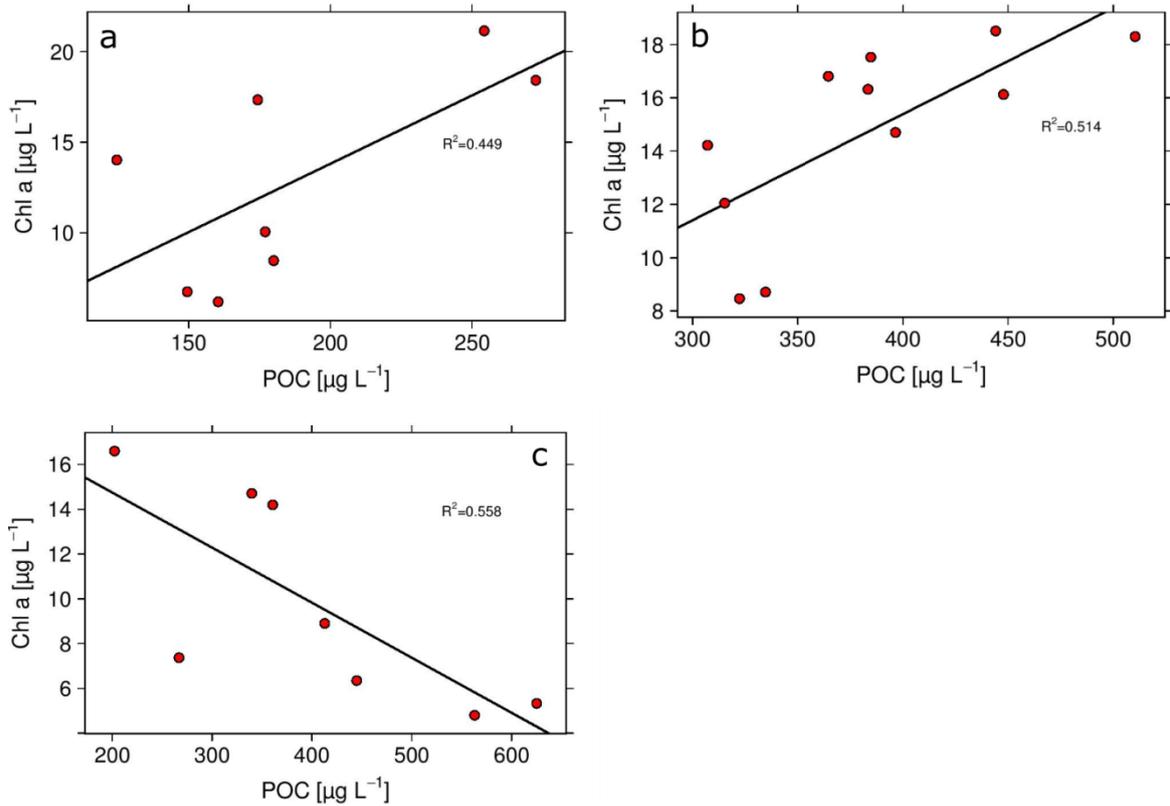
### *Chlorophyll a and particulate organic carbon concentrations in ice cores at Ice Camp2*

At Ice Camp2, Chl *a*- and POC concentrations showed also a high variability between and within different sampling transects (Fig. 7). The mean Chl *a* concentration was  $12.42 \mu\text{g L}^{-1}$  (range  $4.8\text{-}21.15 \mu\text{g L}^{-1}$ ) and the mean POC concentration  $330.31 \mu\text{g L}^{-1}$  (range  $124.6\text{-}625.09 \mu\text{g L}^{-1}$ ). Chl *a* concentrations varied up to three times within ROV- and EB transects and POC concentrations varied also up to three times within ROV transect.



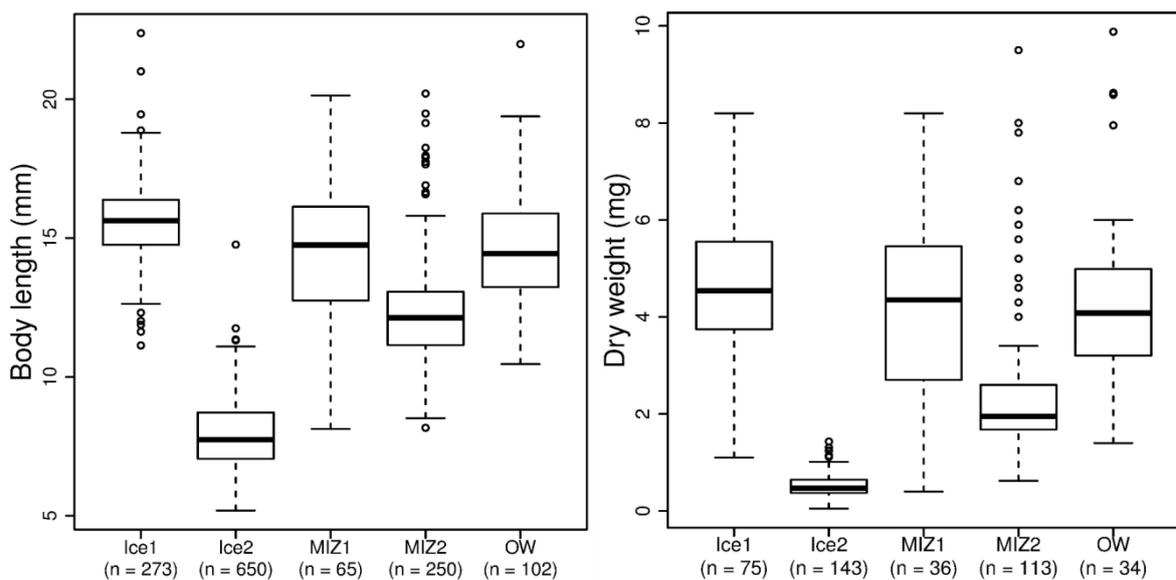
**Fig. 7** Chlorophyll *a* (Chl *a*) and particulate organic carbon (POC) concentrations ( $\mu\text{g L}^{-1}$ ) from ice cores of three transects (EB, POL, ROV) at Ice Camp2, taken in different distances towards the divehole. Each bar represents the last 10 cm segment of 2-3 pooled ice cores.

Statistically significant correlations were found between Chl *a* and POC measured on all three transects (Fig. 8). A positive correlation was found on EB and POL transect (Fig. 8a+b; Spearman's Ranks correlation coefficient  $R=0.449$  and  $R=0.514$ , respectively) and a negative on the ROV transect (Spearman's Ranks correlation coefficient  $R=0.558$ ). The results indicate that on the EB and POL transect the POC values derived mainly from autotrophic material, whereas on the ROV transect the highest percentage of the POC results from heterotrophic material.



**Fig. 8** Correlation between Chlorophyll *a* (Chl *a*) and particulate organic carbon (POC) concentrations ( $\mu\text{g L}^{-1}$ ) in ice cores from Ice Camp2. (a) EB-, (b) POL- and (c) ROV transect.

### 3.3 Larval stages, body lengths and dry weights



**Fig. 9** Dry weights and body lengths of larval krill caught in the open water (OW), marginal ice zones (MIZ1+2) and in pack ice regions (Ice Camp1+2). Different larval stages were pooled. For details see Table 1.

Among larval krill populations caught at different regions body length, dry weight and larval stage composition varied. Fig. 9 shows body lengths and dry weights summarized for all larval stages, whereas body lengths and dry weights per stage per region as well as stage compositions are shown in Table 1.

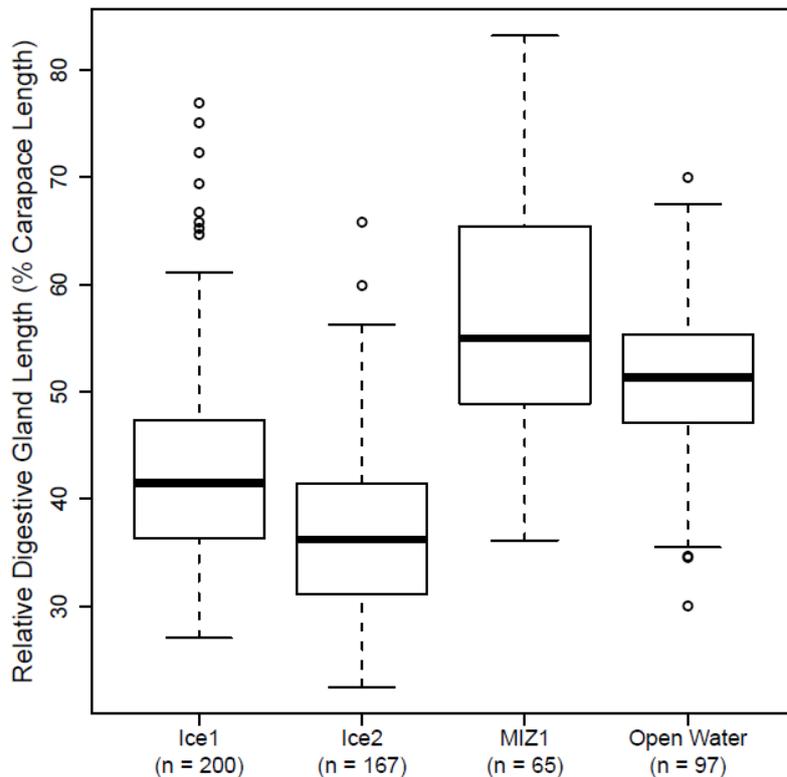
Significant differences for body lengths were found between all regions (ANOVA:  $F_{3,4,5}=1046.544$ ,  $P=8.827^{-7}$ ), while significant differences for dry weights (ANOVA:  $F_{3,2,96}=892.3655$ ,  $P=7.027^{-5}$ ) were only found between Ice Camp2 and MIZ1 as well as between Ice Camp1 and 2. Krill larvae caught in Ice Camp1 had the largest body lengths (mean  $15.69 \pm 1.44$  SD) and highest dry weights (mean  $4.59 \pm 1.38$  SD), while smallest body lengths (mean  $7.96 \pm 1.22$ ) and dry weights (mean  $0.50 \pm 0.25$  SD) were found at Ice Camp2. MIZ1 and OW had larger body lengths ( $14.37 \pm 0.33$  SD;  $14.25 \pm 2.02$  SD, respectively) and higher dry weights ( $4.21 \pm 1.95$  SD;  $4.41 \pm 1.94$  SD, respectively) than MIZ2 (mean bodylength:  $12.33 \pm 0.33$  SD; mean dryweight:  $2.49 \pm 1.51$  SD).

At Ice Camp1 and OW stage composition ranged from F6 to juveniles and at MIZ1 and 2 from F5 to juveniles. At Ice Camp2 F3 to F6 stages were caught.

**Table 1** Comparison of body lengths (BL, mm) and dry weights (DW, mg) of furcilia (F) and juvenile (J) stages caught in the open water (OW), marginal ice zone (MIZ1 and 2) and pack ice zone (Ice Camp1 and 2). Data are given as arithmetic mean with data ranges in parentheses. N: Number of replicates used for dry weight analyses of all caught animals (Total numbers).

Region	Stages	Total numbers	BL (mm)	DW (mg)	n (DW)
OW	F6	3	11.99 (10.92-14.12)	1.4	1
	J	98	14.59 (10.46-21.98)	4.41 ( 1.4-9.88)	34
MIZ1	F5	1	8.13		
	F6	19	11.44 (8.13-20.13)	2.59 (0.4-5.9)	9
	J	46	15.33 (11.39-18.73)	4.7 (2.1-8.2)	27
MIZ2	F5	2	9.84 (9.13-10.4)		
	F6	235	11.16 (5.94-15.18)	2.14(1.28-5.6)	52
	J	54	14.09 (10.76-20.2)	4.63 (1.7-9.5)	20
Ice1	F6	28	14.30 (11.13-17.59)	3.59 (2.2-7.1)	11
	J	244	15.75 (12.01-24.88)	4.94 (1.1-17.09)	64
Ice2	F3	4	5.89 (5.19-6.8)		
	F4	81	6.74 (5.57-10.75)	0.33 (0.21-0.62)	23
	F4-5	12	6.57 (6.01-7.16)		
	F5	111	7.37 (6.25-10.65)	0.44 (0.24-1.24)	45
	F5-6	13	7.55 (6.97-8.97)		
	F6	175	8.63 (6.2-11.09)	0.69 (0.24-2.02)	74

### 3.4 Feeding activity



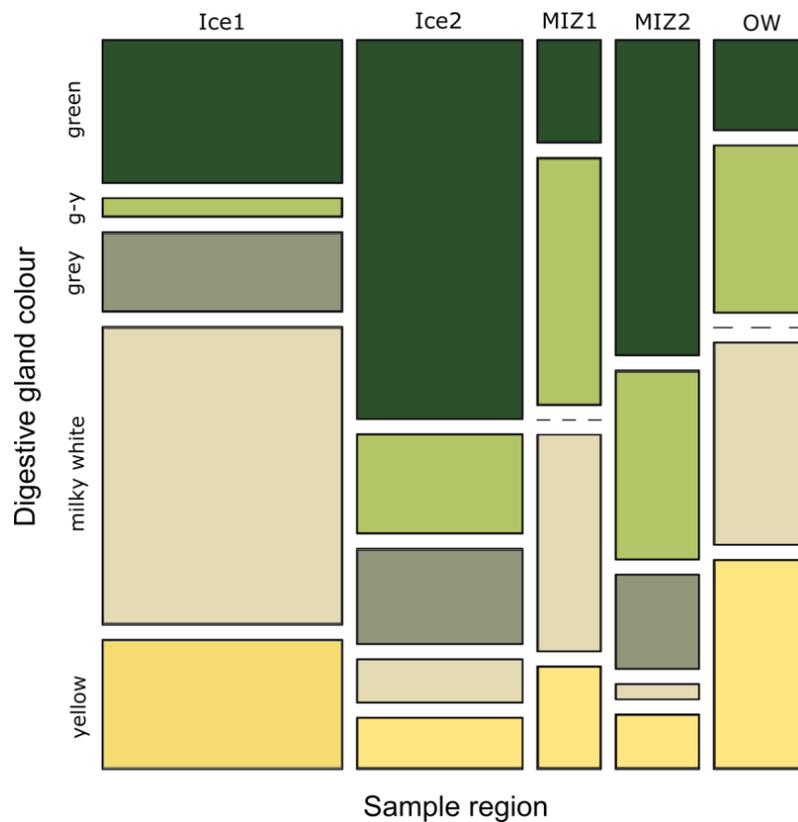
**Fig. 10** Relative digestive gland length (in % of carapace length) of Krill larvae caught in pack ice regions (Ice1 and Ice2), in the marginal ice zone (MIZ1) and in open water.

The analysis of DG length (relative to carapace length) provides in contrast to stomach content analyses information about recent feeding histories of krill over longer timescales (Nicol et al. 2004; O'Brien et al. 2010; Shin 2000). High amounts of ingested food result in a longer DG (Shin 2000). According to Shin (2000) the relative DG length is a reliable indication for the recent feeding history from a few days to a week.

Feeding activities were highly variable between sampling sites (ANOVA:  $F_{3,7.4}=4.39$ ,  $P=0.04566$ , Fig. 10) suggesting large differences in food availabilities between pack ice regions and MIZ1 and OW. Results of feeding activities are reflected by Chl  $a$  and POC concentrations in water samples.

Krill collected in the MIZ1 had the largest DGs with a mean of 56.94 % ( $\pm 11.68$  SD), followed by krill from the OW, which had smaller sizes with a mean of 51.21 % ( $\pm 6.86$  SD). Compare to these two regions, krill sampled in in Ice Camp1 and Ice Camp2 had the smallest mean DGs (42.76 %  $\pm 9.43$  SD and 37.14 %  $\pm 8.04$  SD, respectively). MIZ1 shows significant differences between Ice Camp1 and Ice Camp2 (Posthoc test  $P < 0.05$ ).

### 3.5 Digestive gland colour



**Fig. 11** Varying proportions of DG colours (as percentage of all analysed larvae per region). g-y: green to yellow; OW: Open water; MIZ: Marginal ice zone; Ice1+2: Pack ice regions Ice Camp 1+2. Cell width corresponds to the amount of analysed larvae (OW: 97, MIZ1: 65, Ice Camp1:243, Ice Camp2: 198, MIZ2: 85)

The DG has been reported to serve as major organ for food assimilation and enzyme secretion in crustacean species (Dall and Moriarty 1986). The coloration of the DG of krill indicates feeding preferences on different food sources (Kawaguchi et al. 1986, 1999; Nicol et al. 2004). According to Kawaguchi et al. (1986) a green DG reflects the concentration of different phytoplankton sizes consumed by adult krill. Other studies suggested relationships between additional colourations, e.g. a milky-white DG should indicate a high amount of zooplankton as diet part (Atkinson et al. 2002), but these relations have not been quantitatively examined (Shin 2000). Moreover, all studies are restricted to adult krill, while the colouration of the DG has not yet been examined for larval krill.

The DG colours showed in general a high variability within krill populations caught at different regions (Fig. 11), suggesting the utilisation of various food sources. Through

visual analyses we could determine five main colouration types: green, green to yellow, grey, milky white and yellow. All colours were found in Ice Camp1 and 2 and in MIZ2, while in MIZ1 and OW grey DGs were missing. Although colour proportions varied, the occurrence of almost all colouration types in all regions shows that the food selection differs between individual larval krill and implies an omnivore feeding behaviour of krill larvae. At Ice Camp1, a large part of krill larvae had a milky white colouration, while yellow, green, green to yellow and grey colours were observed in fewer larvae. This suggests that krill larvae from Ice Camp1 had ingested zooplankton at highest rates, which was underlined by stomach content analyses. At Ice Camp2 and MIZ2, the majority of DGs with green and green to yellow colourations, indicating that autotrophic food sources were consumed at higher rates than other food sources. However, stomach content analyses showed that phytoplankton was no dominant food source in these areas. At MIZ1, most larvae had green to yellow and milky white colours, while green and yellow colours were found in fewer larvae, suggesting that autotrophic and heterotrophic food sources were consumed in equal proportions. Although a high amount of phytoplankton was found in stomachs from OW, the colourations of the DGs show that phytoplankton was not the primary food source. Moreover, no relationship of a grey DG was found with certain food types at Ice Camp1 and 2 or at MIZ2. Also, no relation could be identified between dominant food sources and individual examined larval stomachs of selected animals with certain DG colours (see also Table 2, appendix).

Overall, the comparison between the DG colour and stomach content analyses yielded partly inconsistent results. Studies including quantitative assessments of stomach contents in relation to certain colour types could give useful additional information. Colour ranges should be clearly defined through picture scales. How sensitive certain colouration types respond to varying food conditions and further which food quantities result in certain visible colours, is still unclear. However, analyses of the DG colours provide easy and fast accessible information about feeding trends within krill populations and should therefore be further examined.

## 3.6 Stomach content analyses

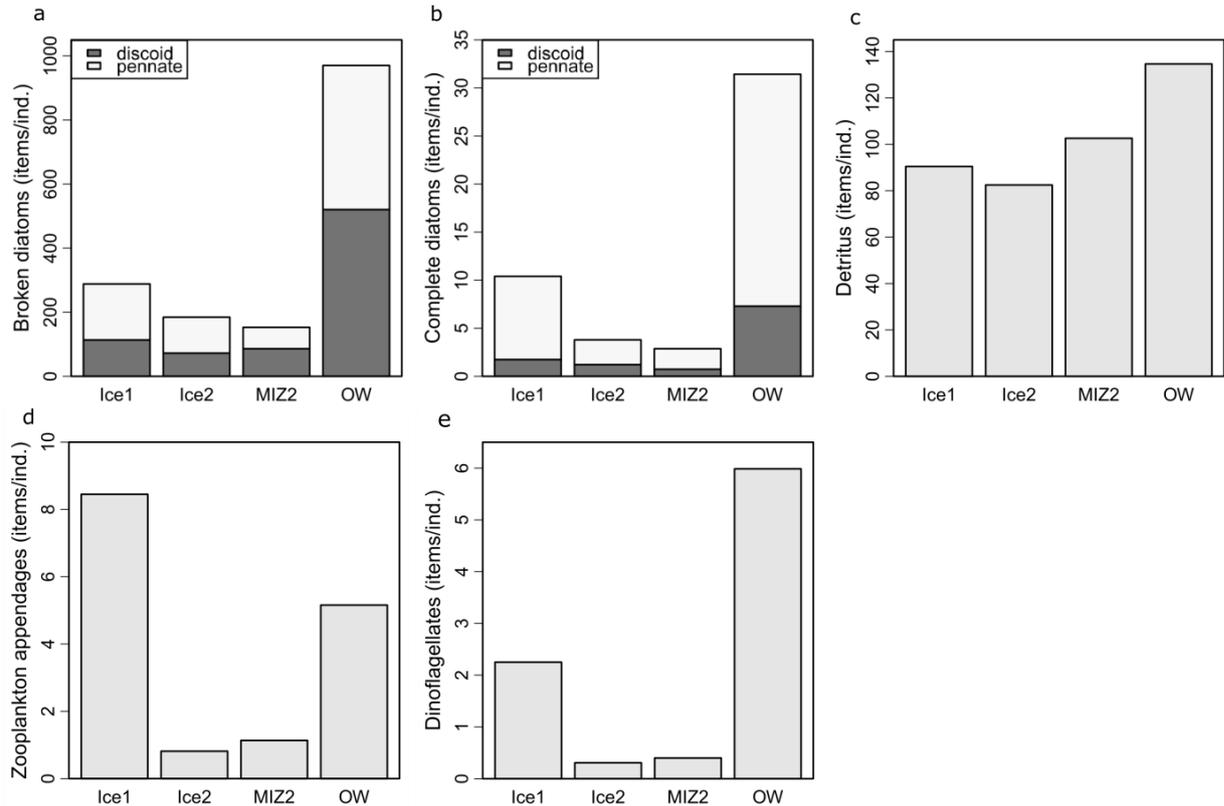
### 3.6.1 In regions with different ice coverage during the day

Numbers of all identified items are shown in Table 2 (appendix), whereas numbers of items that predominate in the total stomach content are shown in Fig. 12. (Note that volumes were not calculated. Therefore, the real proportions of various food items in the total stomach content could differ from counted data. Rare and larger items such as zooplankton pieces or big detritus pieces might be underestimated, common and small items such as broken diatoms might be overestimated.)

All samples contained regularly several zooplankton antennae fragments and bristles, but no further categorisation was possible and hence no quantification of the amount of ingested zooplankton based on the number of antennae fragments and bristles. The highest amount of zooplankton appendages was observed in areas where larval stomachs contained also copepod mandibles. Therefore counted zooplankton appendages underline the possible importance of zooplankton as prey, although some can be mistaken from crustacean molts instead of the remains of digested animals.

Exemplary species for diatoms were *Fragilariopsis* spp. (e.g. *Fragilariopsis kerguelensis*, *Fragilariopsis rhombica*, *Fragilariopsis curta*), *Thalassiosira* spp., *Entemoneis* spp., *Gyrosigma* sp., *Nitzschia* spp. and *Actinocyclus* spp..

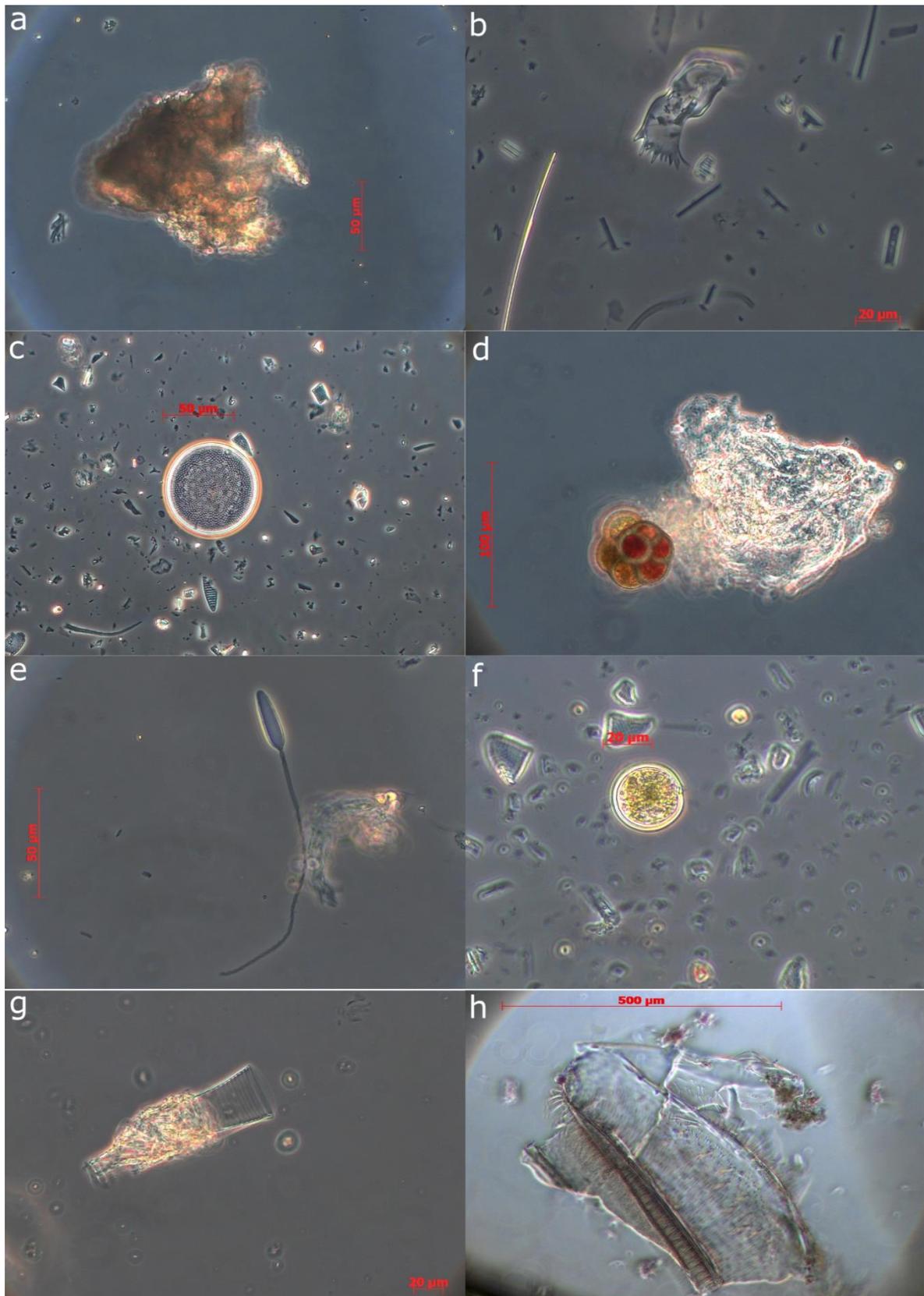
The total number of all identifiable items (Table 2, appendix) demonstrate that larval krill in OW had the fullest stomachs (1283.55 items/stomach), followed by larvae from Ice1 with relative full to empty stomachs (394.6 items/stomach) and relatively empty stomachs of larvae from the MIZ2 and Ice Camp2 (314.1 and 299.48 items/stomach, respectively). Overall, diatoms, in particular, but also detritus and zooplankton appendages were major parts of ingested food items by larval krill.



**Fig. 12** Mean numbers of counted food items (averaged per individual (ind.) per chamber) in krill stomachs pack ice regions (Ice1+2), the maginal ice zone (MIZ2) and open water (OW). (a) Broken diatom pieces with discooid and pennate shapes. (b) Complete diatoms with discooid and pennate shapes. (c) Counted detritus pieces. (d) Zooplankton appendages. (e) Dinoflagellates.

The stomachs of larvae from OW were filled with the highest amount of complete and broken diatoms as well as detritus, which pieces had a mean diameter of 31.66  $\mu\text{m}$  (Fig. 12). Numbers of both fractions were more than twice as high as the regions associated with ice. Also several zooplankton pieces in conjunction with some copepod mandibles, which were usually rare in other regions, (Table 2, appendix) and some autotrophic flagellates were found. At MIZ2 lowest numbers of broken and complete diatoms were found and in addition from all ice areas the most and longest detritus pieces with a mean diameter of 33.02  $\mu\text{m}$ . Further, at MIZ2, larval stomach content showed only few indications that zooplankton was ingested, since no copepod mandibles and only a few zooplankton appendages were found. Protists were also rare in larval stomachs at MIZ2. Larval stomachs at Ice Camp1 were characterised by the highest numbers of complete diatoms of all ice associated regions and in comparison to Ice Camp2 and OW, by fewer broken diatoms. In larval stomachs of Ice Camp1, the number of detritus pieces was relatively low and had a mean diameter of 30.41  $\mu\text{m}$ . Moreover,

stomachs from Ice Camp1 contained the highest amount of zooplankton appendages, combined with a few copepod mandibles and several dinoflagellates. Larval stomachs from Ice Camp2 had more broken diatoms than Ice Camp1 and MIZ2 and low numbers of complete diatoms. Stomachs from this region showed also the lowest number of detritus with the smallest diameter of 28.74  $\mu\text{m}$  and fewest zooplankton appendages of all regions.



**Fig. 13** Exemplary items found in stomachs of krill using a stereomicroscope. (a) big detritus piece. (b) small copepod mandible. (c) Diatom (*Actinocyclus* sp.). (d) Foraminifera. (e) Nematocyst. (f) Dinoflagellate (*Prorocentrum* sp.). (g) tintinnid (*Laackmaniella naviculaefera*). (h) Internal walls of a krill stomach with specialised appendages like setae filters for separation and grinding of food particles.

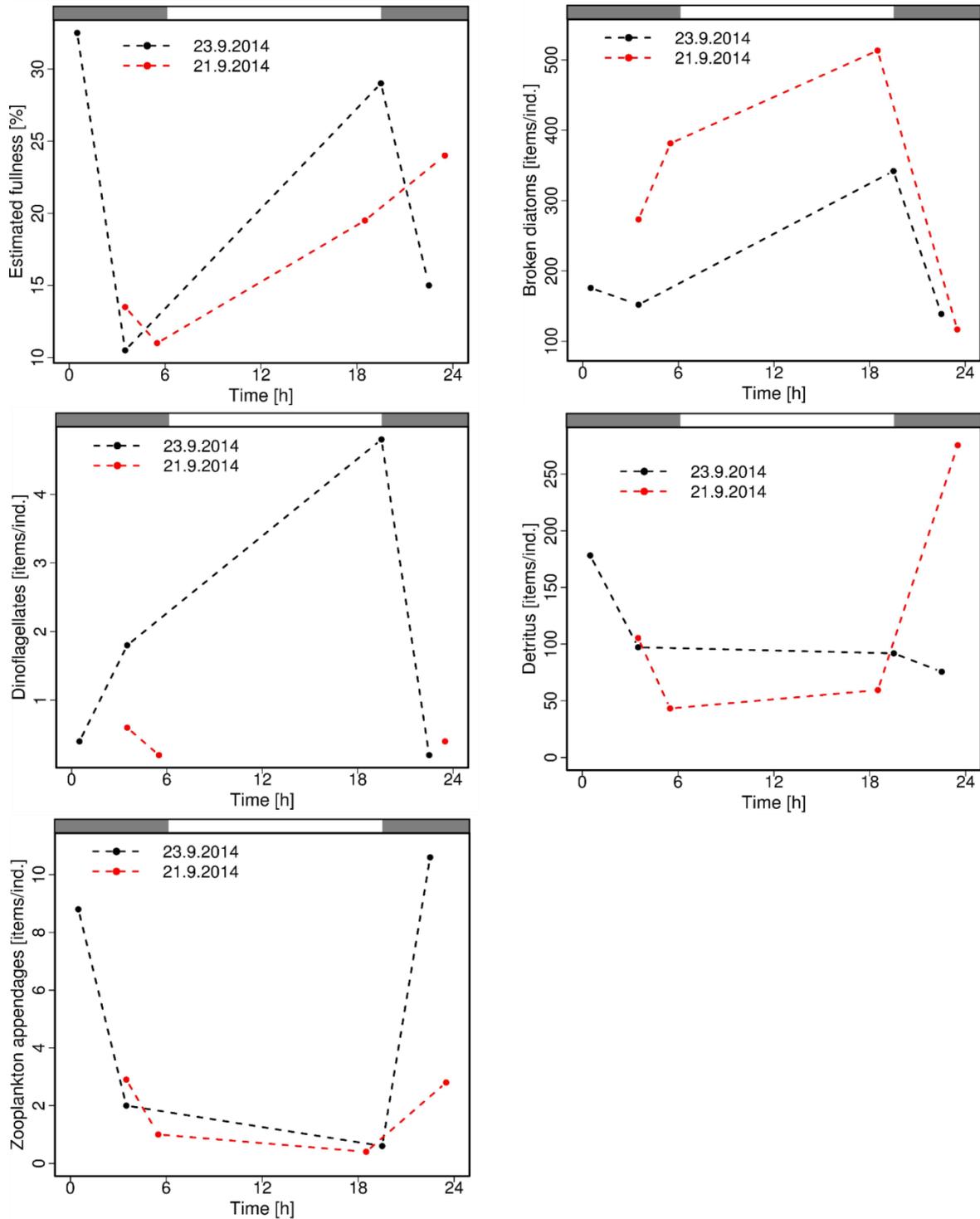
### 3.6.2 Stomach content in a 24 hrs time series

According to the fishpump results, larval krill showed a distinct vertical migration behaviour over 24 hrs. During ten consecutive days, highest amounts of larval krill were caught (at 11 m depth) during the night around 8 pm and 2 am, while only very few larvae were caught during the day. In combination with observations by the scientific dive team, the results demonstrate that larval krill feeds under the sea ice during the day and leaves the sea ice after sun set and migrate into the upper 20 m of the water column.

In order to assess the food sources consumed by larval krill during the night stomach contents of larvae caught by the fishpump during the 21th and 23th September were analysed. The stomach content of larvae from both sampling days showed similar trends.

We observed that larval stomachs were fullest at the end of the day and during midnight (Fig. 14 & Table 3, appendix), suggesting that larval krill was eating during the day under the sea ice and before midnight in the water column. The amount of broken diatoms and dinoflagellates in larval stomachs increased parallel with sunrise, while maximum counted numbers were found on sunset at the evening, followed by decreasing amounts with the onset of night. In contrast, detritus and zooplankton appendages showed increasing amounts during midnight with lowest counted numbers at the end of night and day. Hence, these food sources seem to account for the observed full stomachs around midnight, representing an additional food supply in the water column, while diatoms and dinoflagellates are consumed to higher extents during the day. Consequently, different food sources were consumed by larval krill during the day under the sea ice and during the night in the water column.

Since no copepod mandibles were found in any analysed stomach of larval krill caught by the fishpump (Table 3, appendix), it must be taken into account that parts of the zooplankton appendages could have been derived from molts. However, a positive relationship between zooplankton appendages and copepod mandibles in larval stomachs was shown in chapter 4.2.3. Results of stomach contents of larval krill caught by the fishpump at Ice Camp2 during the night (shown in Fig. 14 where data points at daytime are missing) and results of stomach analyses from Ice Camp2 during the day shown in chapter 3.5.1 complement each other.



**Fig. 14** Mean numbers of counted food items (averaged per individual (ind.) per chamber) of krill caught with the fishpump at Ice Camp2 during the 21th and 23th September. Each point represents 5 analysed animals, which were caught during one hour (e.g. catches between 5 and 6 am are plotted at 5.30 am). Grey bar indicates night time.

### 3.6.3 Critical evaluation of stomach content analyses

Microscopic stomach content analyses are an easy and fast way to get an overview of the dietary intake by organisms. However, a problematic point is that the recognition of the ingested food items depend on their digestibility (Schmidt et al. 2006). Food items, such as diatoms which silica shells are slowly digested, are easy to identify, whereas soft shelled organisms, such as naked ciliates can be fast digested and are not identifiable in the stomachs of organisms. In addition, the gastric mill in crustacean species can grind food items to a level that they are also not visible by microscopic observations of stomach contents (Nemoto 1967). The limited identification of various food particles and hence the omitting of potentially important food sources is probably the major disadvantage of visual stomach content analyses.

Different approaches exist for recording the amount and sizes of food items. One common procedure is to count food items through scanning the whole counting chamber with the stomach content for rare and larger items such as tintinnids or zooplankton appendages and to perform two transects, horizontally and vertically, across the whole diameter of the chamber to count common and small items such as diatom pieces (see chapter 2.6.2., Schmidt et al. 2006). Then, numbers are extrapolated for the whole chamber. Cell counts can be split into various size and species categories (Meyer and El-Sayed 1983). The classification into different numbers of food dimensions will result in more or less precise results of the mean dimension of a particular food item. These values can be used to calculate further biovolumes of e.g. diatoms, dinoflagellates or tintinnids (Schmidt et al. 2006). Diatoms for example are divided into pennate and discoid forms, which represent the main difference in used formulas for volume calculations. Kang and Park (2001) used different geometrical shapes for volume calculations from linear dimensions (as just diameters are measurable), a rectangular shape is usually used for pennate diatoms and a cylindrical for discoid diatoms. But depending on the species the cell height can range from 1/2 to 1/10 of the diameter (Katrin Schmidt, personal communication), so simplified assessments must be used. Therefore, resulting volumes are very imprecise, which is why volumes were not calculated in the present study. For 'non-geometric' forms like detritus pieces or zooplankton appendages volumes cannot be

calculated at all. Hence they are left out in further stomach content comparisons (e.g. Schmidt et al. 2006), leading to a slightly different impression of the total stomach content. Sizes and shapes of copepod mandibles can be used for species identifications and volume calculations for copepods (Lass et al. 2001), thus providing relatively precise results for this animal group.

Gradinger and Bluhm (2010) made use of a different counting method. They calculated relative frequencies (%) at which certain food items were found in 20 randomly chosen fields. In the present study, this method was slightly modified and partly used for stomachs of the fishpump time series (for method see 2.6.2). It revealed a practical and quick approach for visual analyses of stomach contents. A detailed comparison of both counting methods should be made in future studies. Other semi quantitative methods can be used to estimate stomach fullness. Daly (1990) classifies stomach fullness into empty,  $<1/2$ ,  $>1/2$  or full, while Atkinson et al. (2002) scored fullness into 0 (empty) to 10 (full), which enables a quick overview on the amount of ingested food. The study of Perissinotto et al. (2000) suggests a different approach to measure carbon and organic proportions in krill stomachs. They filtered suspended stomach contents onto GF/C glass-fibre filters, which yielded fast results on autotrophic and heterotrophic carbon contents. However, important information about exact food sources is missing in this method. Whether this method can be used with small larval stomachs is unclear.

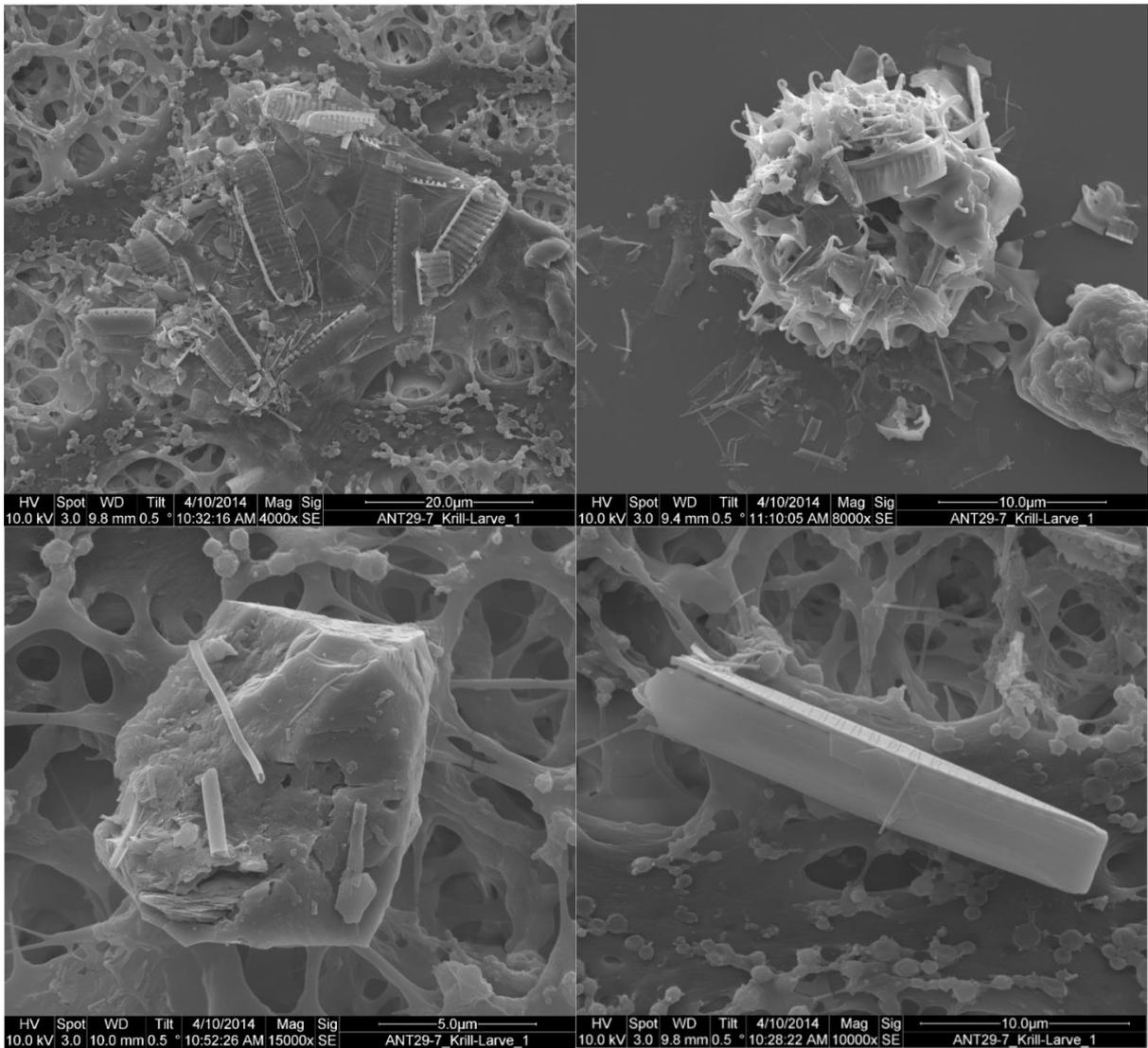
Another important aspect influencing stomach contents is cod-end feeding. Lass et al. (2001) gave evidence that stomach fullness of the northern krill, *Meganyctiphanes norvegica*, was affected by cod-end feeding in one of their used net, which derived from a smaller meshed size (330  $\mu\text{m}$ ) compared to other nets. This influence cannot be easily considered due to logistical difficulties on expeditions but should be examined in other studies to exclude this factor. Since food digestion will continue once krill is caught, the time until krill is further processed is a critical factor for stomach content analyses. Gut evacuation time is quite short (3.7 to 6.3 h for juvenile krill (Atkinson and Snyder 1997)) and may alter significantly stomach fullness with longer processing times. Unfortunately, this impact could not be examined on the expedition and time periods over which krill was stored in tanks were not noted, but should be done in future studies. Also the time when krill was caught should be noted as migration behaviour might influence the amount and composition of the food. Through visual inspection, stomachs which were

dissected of living krill contained fewer food items than stomachs of krill which were immediately frozen. Therefore, krill should get frozen as soon as possible and stomachs dissected on frozen animals.

Stomach content analyses enable a quick snapshot of the ingested food sources of organisms. Although, the method is often described as 'time-consuming' (e.g. Perissinotto et al. 2000), different methods to count and estimate food items make stomach content analyses easier and quicker. The time period, krill is stored in tanks until processing seem to be the most critical factor influencing stomach content and should be considered in future studies. Incubating krill in tanks with a known food concentration for defined times and then analysing the stomach content could help assessing the effects of storage time.

#### 3.6.4 Analyses from scanning electron microscopy pictures

The SEM showed details in the stomach content of krill (Fig. 15). Aggregations of digested material often covered with silica skeletons of diatom remains and detritus were found. With the SEM species were found, which could not been identified by light microscopy of stomach content, such as the dinoflagellate *Polarella glacialis* and the diatom *Gyrosigma* sp.. Furthermore, we observed differences in the digestibility of food items.



**Fig. 15** Top left: overview of a stomach content with several pieces of broken diatoms. Top right: dinoflagellate *Polarella glacialis*. Bottom left: possible detritus piece. Bottom right: broken pennate diatom.

## 4 Discussion

The Scotia Sea and the northern Weddell Sea are characterised by high seasonal variations in solar irradiance and high fluctuations in sea ice cover (Ackley and Sullivan 1994; Okada and Yamanouchi 2002). When the advance of sea ice starts in the Weddell Sea with the beginning of austral winter, large areas of krill larvae habitat become covered with ice (Nicol 2006). Several studies have shown that a greater sea ice extent in winter is linked to a high recruitment success and hence population size of krill in the following summer (Kawaguchi and Satake 1994; Siegel and Loeb 1995; Atkinson 2004). However, the benefit of winter sea ice for a successful larval development of krill remains unclear. The sea ice can serve as a substratum for organisms (bacteria, algae and protists e.g. Garrison 1991), which can be an alternative food source for krill larvae during winter (Daly 1990; Kottmeier and Sullivan 1990; Meyer et al. 2002), but data about the feeding behaviour of krill larvae especially in winter time are scarce (Siegel 2005).

Due to the described correlation between the sea ice extent and the population recruitment success of krill (Kawaguchi and Satake 1994; Siegel and Loeb 1995; Atkinson 2004), we expected larvae from ice covered regions to be in a better condition than those from OW. Therefore, the sea ice biota should provide a profitable feeding ground for the larvae.

In view of the presented results, it can be concluded that krill larvae from pack ice regions were not in better condition than in OW or the MIZ in terms of dry weight, feeding activity, stomach content and growth rates (see Cantzler et al. (2014)). In addition, we found that more food was available for larval krill in OW and in the MIZ1 than in the pack ice regions and MIZ2.

### 4.1 Food availability for larval krill in regions with different degrees of ice coverage

The investigated areas of the OW, MIZ and pack ice regions showed large differences in the food availability for larval krill.

At both Ice Camps, the low Chl *a* and POC concentrations in water under the sea ice show that the food availability in the water beneath the sea ice was low. The autotrophic and heterotrophic food sources in the water seem to be insufficient for krill larvae to survive the winter months in pack ice regions. In contrast, the highest concentrations of Chl *a* and POC within the sea ice suggest that extensive food sources do exist. As scientific divers observed larval krill foraging under sea ice during the expedition, it was suggested that the larval krill feed on organisms associated with the ice as reported in previous studies (Daly 1990; Quetin and Ross 1991; Frazer et al. 2002). However, stomach content analyses and feeding activities showed that, in pack ice regions, the sea ice biota was consumed only to a minor extent by the krill larvae.

Firstly, the amount of diatoms and detritus particles (which had the smallest diameter) was low in larval stomachs in pack ice regions. Secondly, larval krill had the lowest feeding activities at Ice Camp1 and 2. Thus, it can be suggested that low food quantities were not only ingested recently, but for longer time. Consequently, sea ice microalgae (of which diatoms (Bacillariophyceae) are the most abundant microalgal taxa (Arrigo 2014)) and in addition detritus, were ingested only in small amounts by larvae from the pack ice regions. This is despite the fact that Chl *a* and POC concentrations in the sea ice at Ice Camp1 and 2 were far greater than in water of the other regions. In this respect, it is questionable to what extent the food sources within sea ice are accessible for larval krill at the water/ice interface and if Chl *a* and POC concentrations in the bottom section of ice cores are reasonable proxies for the available food for larval krill (Daly 2004). Nevertheless at Ice Camp1, increased concentrations of Chl *a* and POC in sea ice corresponded with observed higher amounts of ingested food items and higher feeding activities compared to Ice Camp2. Thus, at both Ice Camps, the amount of food items in larval stomachs, as well as feeding activities during the day, seem closely related to the food availability in the sea ice rather than to the food available in the water column. Although not quantified, the ice melting observed at Ice Camp1 would be expected to release ice biota into the water column (Legendre et al. 1992; Meyer et al. 2009; Meyer 2011) leading to enhanced food availability for larval krill at Ice Camp1 compared with Ice Camp2. Contrary to this expectation, Chl *a* and POC concentrations in the water at 10 m

depth were lower at Ice Camp1 than at Ice Camp2. Therefore at Ice Camp1, melting processes would seem to have led only to a minor degree to an additional food release from the sea ice during sampling time. Measurements of Chl *a* and POC in water depths closer to the sea ice surface could yield more precise results about the release of ice biota into the water column.

Dinoflagellates and zooplankton can be an additional food source for larval krill in the pack ice regions. Although, Schmidt et al. (2006) suggested that molts could serve as an extra nutrient budget when other food sources are rare, their nutritional benefit is difficult to assess and they probably cannot meet essential food demands over a longer time scale. Therefore, molts, which were regularly found in larval stomachs, were not regarded as an important food source for larval krill. Protists, especially naked ciliates, cannot be excluded as a possible food source due to fast digestion processes in the larval stomachs.

In contrast to the pack ice regions, food supply was high for krill larvae at MIZ1. This is indicated by the highest concentrations of Chl *a* and POC in water and also the highest feeding activities of krill larvae at MIZ1. However, at MIZ2 Chl *a* and POC concentrations in water were lower and larval krill had emptier stomachs. The observed differences in the food availability between MIZ1 and 2 could be explained by the large geographical distance between the sampling sites. Varying melting processes may have led to an additional food release in the water at MIZ1 at the time of sampling. Alternatively, a high feeding rate combined with short gut passage times could be the reason why larval stomachs were emptier at MIZ2. Since larvae from MIZ2 could not be measured for their relative DG length, information about food ingestion over longer timescales are missing. Thus, it must be taken into account that krill larvae from MIZ2 could have just recently ingested low food quantities, due to the patchy food abundance in the sea ice.

Detritus particles in larval stomachs from MIZ2 were more abundant and larger than at the other ice regions, suggesting that detritus was the more important food source. Moreover, the smaller amount of diatoms in stomachs of MIZ2 than in stomachs from pack ice regions, together with higher POC than Chl *a* concentrations in water samples, rather suggest the minor importance of phytoplankton compared to detritus at this site during the study period.

At the OW, a high food supply was observed for larval krill. This is represented by higher Chl *a* and POC concentrations than in the pack ice regions and at MIZ2, higher feeding activities than in the pack ice regions and the highest stomach content. The far higher amount of diatoms, dinoflagellates and detritus in larval stomachs from OW than in pack ice regions, also underlines that food sources within the water column are more readily accessible for larval krill than food sources trapped in the sea ice.

In conclusion, the food availability for larval krill was high in the OW and in the MIZ1. In the pack ice regions, larval krill could not benefit from the high biomass within the sea ice due to limited physical access. Therefore, ice melting processes, releasing sea ice organisms together with detritus into the water column, can be of major importance for larval krill to survive the winter in ice covered regions. Zooplankton and dinoflagellates could account for an additional food supply in the pack ice regions and help to ensure larval survival. Nutritional benefits of different food types could provide additional information about their relative importance across the region.

## 4.2 Larval krill daily migration behaviour: a strategy to exploit new food resources in a patchy environment?

Daily vertical migration patterns can be found in many small pelagic animals (Van Hoffelen and Herman 2006). Most euphausiids are known to migrate to deeper waters during the day for predator avoidance and to return to surface layers during the night to feed (Ritz 1994; Van Hoffelen and Herman 2006). However, information about migration patterns of larval krill in pack ice regions are scarce (Everson 2000). On the ANT 29/7 expedition, the daily migration behaviour of larval krill at Ice Camp2 was observed by scientific divers and from the fishpump, which pumped water and hence larvae from underneath the ship continuously over ten consecutive days.

The analyses of the stomach fullness of larval krill caught by the fishpump suggest that the animals were eating during the day and before midnight. Dinoflagellates and in particular diatoms, were present in larval stomachs primarily during daytime when the larvae were observed in close association with the sea ice. This suggests a greater

ingestion of these food taxa under the sea ice than when the larvae are dispersed in the first 20 m of the water column at night. Mainly detritus and zooplankton were found in stomachs of larval krill collected at night while they were in the first 20 m of the water column. Hence, it can be suggested that larval krill are opportunistic and switch their food source together with their position in the water column. The origin of detritus and zooplankton appendages found in larval stomachs during nighttime could point to interactions with other species, e.g. copepods. Vertical migration patterns of other prey and predator species of larval krill could be important to understand krill's diel vertical migration (DVM) as a whole.

One reason for the DVM of larval krill in terms of food supply could be the enhanced access to the heterogeneously distributed food in sea ice. Since krill larvae are able to swim only to a moderate extent against the current, it is difficult for them to reach new feeding grounds on their own. According to Meyer et al. (2009), krill larvae are drifting passively with the current in the upper 10-15 m of the water column, while above, larvae were sheltered from currents in refuges of over-raftered ice floes, drifting mainly with the sea ice by wind. Sinking down in the water column at the end of the day positions them in stronger flows and hence results in intensified transportation of larval krill by currents. Speed and directions of currents and ice floes can be different, so when krill larvae ascent to the sea ice again in the morning, they may encounter a habitat which provides possible new and rich food sources.

As food availabilities were lower and heterogeneously distributed in pack ice regions than in OW or in MIZ1 (see chapter 4.1), the DVM could serve as a trade-off between the predator-avoidance during the day under the sea-ice, the additional nocturnal food supply in the water column and the daily exploration of new feeding grounds in pack ice regions.

### 4.3 Larval condition in relation to food availability

Evaluating the condition of krill larvae in one region might depend on how different parameters are related. The large differences in the condition of krill larvae between Ice Camp1 and 2 as well as between MIZ1 and 2 challenge it to determine the overall larval condition in these areas.

Overall, larval krill from the pack ice region were not in better condition than larvae from OW. These data are in agreement with an associated study of Cantzler et al. (2014) using primarily lipid content and growth as condition parameters for larval krill and another study of O'Brien et al. (2010) using primarily feeding activity and growth as proxies of condition.

Krill larvae caught at Ice Camp1 had the largest body lengths and highest dry weights, but significant differences were only found in the bodylength between Ice Camp1 and OW. In addition, the stage composition (with mostly juveniles) and growth rates (see Cantzler et al. 2014) were similar between OW and Ice Camp1. In contrast to Ice Camp1, krill larvae at Ice Camp2 had the smallest bodylengths and dry weights as well as a different stage composition (larval stages F3-F6). This suggests great regional differences between Ice Camp1 and 2 and demonstrating that the presence of sea ice does not guarantee a better body condition. The different larval stage compositions of krill at Ice Camp1 and Ice Camp2 also suggest that spawning time could have varied. Larvae of Ice Camp2 could have been derived from late spawning krill, which would explain why larvae are younger and had less time to develop than larvae from Ice Camp1. Alternatively, the rate of development may have been higher at Ice Camp1 due to a better food supply as indicated by Chl *a* and POC concentrations in the sea ice, as well as stomach contents and feeding activities of krill larvae. Therefore, both spawning date and adverse food conditions could have influenced larval condition at Ice Camp2.

Regional differences in the body condition of larval krill were also found between MIZ1 and 2. At MIZ2, larval krill had the highest growth rates and lipid content (Cantzler et al. 2014) although they had smaller body lengths and less dry weight than at MIZ1, OW and Ice Camp1. However, our data suggest that the MIZ habitat provides favourable conditions for larval krill to survive the winter considering that larval krill at MIZ1 had higher body lengths and dry weights than at OW plus the high food supply (see chapter 4.3). Due to the location further north than the pack ice regions, the MIZ is generally characterised by longer daylight, favouring the growth of ice algae, and an enhanced release of ice biota into the water column by swell and movements of ice floes (Daly 1990; Buesseler et al. 2003; Meyer et al. 2009). Melting processes during the end of

winter and start of spring can create a shallow, mixed layer, which significantly enhances primary production (Eicken 1992; Arrigo et al. 1997) and hence allow larval krill access to food sources that were trapped in the sea ice before (Daly 2004). The primary production can often be greater in the MIZ than in the OW (Kang and Park 2001). In addition, the high amount of detritus in the stomachs of krill larvae at MIZ2 suggests enhanced particle fluxes from the sea ice into the water below. The POC level in MIZ2, at 10 m depth, demonstrates that the detritus was of high nutritional value compare to the POC level in the pack ice region.

Therefore, the MIZ can be seen as a trade-off zone for larval krill. On the one hand, they have a sufficient amount of food to grow and on the other hand the MIZ provides areas of physical shelter as protection from predators and currents.

#### 4.4 Conclusion

Due to the described close correlation between the winter sea ice extent and the recruitment success of krill (Kawaguchi and Satake 1994; Siegel and Loeb 1995; Atkinson 2004), we expected larvae from pack ice regions to be in a better condition in terms of feeding activity and food supply than from OW.

However, it can be concluded that larvae from pack ice regions were not in better condition than larvae from OW. The food availability for larval krill was high in OW and MIZ1. In the pack ice regions, larval krill could not benefit from the high biomass found within the last 10 cm of the sea ice, probably due to limited physical access. Therefore, the movements of ice floes as well as ice melting processes that can lead to an enhanced release of food items from the sea ice into the water, might be of major importance for larval krill to survive the winter. The observed DVM of larval krill with resulting differences in the speed and direction of currents and ice floes could serve as a strategy to maximise the chances of encountering potential new feeding grounds in the pack ice region, where food abundance is patchy. Overall, it was seen that larval krill are opportunistic and have the flexibility to use alternative food sources other than phytoplankton, such as zooplankton and detritus.

The MIZ may be a beneficial nursery area for larval krill. Longer daylight favours primary production and also food export from the sea ice into the water can be intensified

through melting processes and movements of ice floes. Moreover, the MIZ provides sheltered areas as protection from predators and currents. The highest amount and largest diameter of detritus pieces found in larval stomachs at MIZ2 suggest detritus as an important food source in this zone.

## 4.5 Outlook

Results of this study indicate that the employed methods are not reasonable proxies for quantifying accessible food sources in the sea ice for larval krill. This is underlined by the discrepancy between the high biomass found within the last 10 cm of the sea ice and relatively empty stomachs as well as the low feeding activities of the larval krill in the pack ice regions. Analyses of Chl *a* and POC in the last 10 cm of ice cores could indicate different properties of available food sources for larval krill in the pack ice regions, but do not allow precise comparisons with concentrations measured in the water column. Thus, there is need for improved methods to quantify the food sources that can be exploited at the ice/water interface by larval krill.

Meiners et al. (2011) suggested that the brine volume of the sea is a crucial factor determining the formation of ice algal communities. In this study, most of the Chl *a* was restricted to sea ice with a brine volume of more than 10 %. Large brine volume fractions seem to be indicative for a high permeability in sea ice, influencing the particle flux from the sea ice into the water column (Becquevort et al. 2009; Meiners et al. 2011). Therefore, the porosity of sea ice could be an important parameter in order to assess the amount of accessible food for larval krill.

Alternatively, the use of less than the last 10 cm fractions of sea ice for Chl *a* and POC analyses could be tested. Since larval krill was observed under the sea ice especially in association with over-rafted ice floes, the under-ice topography could be of major importance for the feeding behaviour of larval krill (Meyer et al. 2009). Meyer et al. (2009) suggests that over-rafted ice refuges allow both aggregations of planktonic organisms that drift passively with the current, and secondly, sedimentation of ice biota released from brine channels. Hence, it should be further investigated to what extent upward facing ice surfaces are utilized as feeding grounds in comparison to downward

facing surfaces. Analyses of Chl  $a$  and POC in these two aspects of the sea ice, sampled by scientific divers, could provide new ways to assess the available food sources.

Therefore, additional studies are needed, which test new methods to quantify the accessible food for larval krill and also evaluate the effect of various sea ice properties on the development of larval krill during winter.

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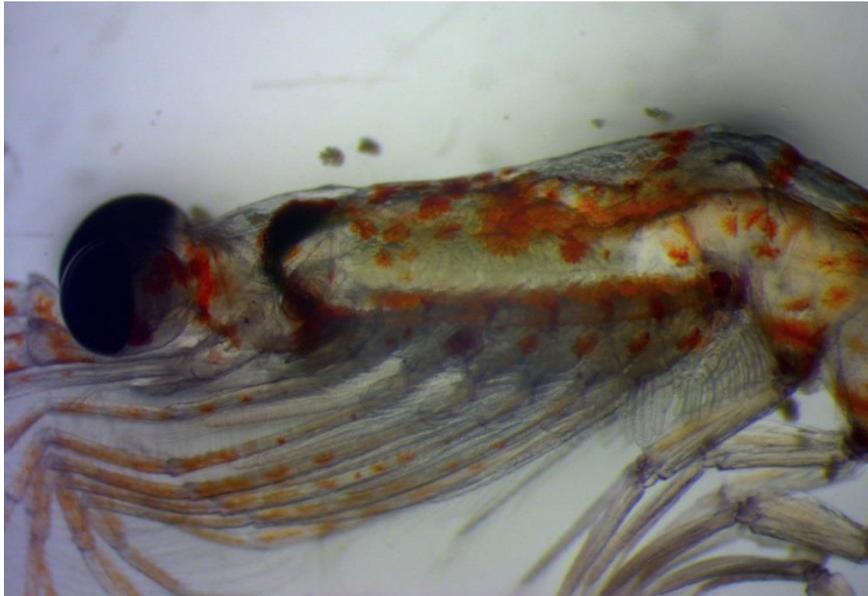
## Appendix

**Table 2** Mean numbers of identified food items in stomachs of larval krill (items/ind.) caught in different regions during the day. Averaged per individual per chamber with 5 stomachs in each. OW: open water, Ice Camp1+2: Pack ice regions, MIZ: Marginal ice zone, r: randomly chosen.

Area	OW						Ice1				Ice2				MIZ2								
Station	540-1	540-1	540-1	540-1	541-3	541-3	555	555	555	555	566	566	566	566	566	566	566	566	586-1	586-1	586-1		
Stage	J	J	J	J	J	J	J	J	J	J	FIV-VI	FVI	FVI	FVI									
DG Colour	r	r	r	r	my	mw	r	r	r	r	r	r	r	r	r	r	r	r	green	grey	grey	gy	gw
Stomachs/analyses	(n=5)	(n=5)	(n=5)	(n=5)	(n=2)	(n=2)	(n=5)	(n=5)	(n=5)	(n=5)	(n=5)	(n=5)	(n=5)	(n=5)	(n=5)	(n=5)	(n=5)	(n=5)	(n=4)	(n=5)	(n=5)	(n=5)	
<b>Diatoms</b>																							
discoid (complete)	5	9,2	10,2	2,6	182	6	0,8	0,8	3,8	1,6	1,6	1	0,4	0,4	1,6	3	0,5	0,2	1	1			
(broken)	556,2	1253	847,8	145,8	284,5	27	162,2	135,6	217,8	183,6	91,8	130,2	32,4	38,2	59,8	309,4	122,3	59,4	124,4	16,6			
pennate (complete)	0,6	31,6	26	2	18	8,5	1,4	4,2	4,6	3,6	1,4	1,2	1,2	0,8	2	6,6	2,25	1,8	2,4	0,6			
(broken)	32,4	378	253,8	50,2	851	759,5	39,8	116,4	110	52,6	16,2	16,2	3,6	18,4	27	281	83,75	5,4	129,6	74,8			
Fragilariopsis spp. (complete)	28	6,8	17	3,8	37	3,5	2,4	7	6,8	4,6	0,2	0,2	1,6	0	0	0,6	0	0,8	0,8	0			
(broken)	259,2	351	297	43,2	243	54	21,6	54	27	32,4	5,4	5,4	10,8			32,4	6,75	5,4	27	16,2			
<b>Protist shell</b>																							
<b>Dinoflagellates</b>																							
Dinoflagellate remains		3,2	1	3,8	18	27,5	2	11	2,8	4,2	0,2	1	1,4	1,4	1,4	22,6	32,5	1	2,8	0,8			
Dinophysis spp.																							
Prorocentrum spp.	5,6	11,8	15,2	4,4	1,5	1	1,8	2,4	1,8	3		0,2	0,4			0,75	0,6	0,6					
<b>Silicoflagellates</b>																							
broken shell	1,4	4	1,6			0,5			2		1	1,6		0,8				3					
Dictyocha spec.	0,4			0,2	3,5											0,2							
Dictyocha spec. naked					3	0,5										1							
<b>Zooplankton</b>																							
zooplankton pieces	0,8	1	1,2	6,8	13,5	11	14,4	1,2	9,6	8,6	0,4	0,2	0,4		0,2	1	3,5	0,8	0,4	2,2			
copepod mandibles		0,2		0,2	2,5	1			0,4	0,2													
zooplankton antennae	4	72,2	3,8	26,8	88	38	11,8	5	15,8	4,6	1,4	1,6	3	2,2	1	6,8	64	37,2	54	48,8			
carapace			3,8		13,5	7,5	1,2		0,4	1,2					5	8,5	0,4	1	0,2				
exuvia	0,2						0,2	0,4	2	0,4					0,2			0,2	0,6	0,8			
<b>Other items</b>																							
<b>Detritus</b>																							
average diameter [µm]	167,4	156,6	59,4	91,8	243	202	48,6	59,4	86,4	167,4	91,8	75,8	64,8	32,4	43,2	87	182,3	43,2	135	129,6			
	36,13	31,72	27,27	24,7	31,11	30,67	33,33	23,63	35	29,68	24,7	25,33	25	30	37,5	31,25	27,41	45,25	28,8	25			
<b>Tintinnids</b>																							
		0,2	0,2	0,2		1	0,4								0,2	0,2	0,252						
<b>Nematocysts</b>																							
				0,5	0,5				0,2	0,2	0,4	0,2	0,4	0,6	0,2	0,2		0,4	1	1,8			
<b>Foraminifera</b>																							
	0,6	0,8	1	0,2	1	1		0,2		0,4			0,2	0,6	0,2	0,6	0,5	0,4					
<b>Parasite</b>																							
							0,2		0,4						0,2								
<b>Total count pieces</b>	1062	2280	1539	382	2006	1171	323,4	403,2	491,4	471,8	211,8	234,8	120,6	95,8	137	771,4	437,3	157,2	491,4	293,8			
Mean/region	1407						422				287							314					

**Table 3** Mean numbers of identified food items in stomachs of larval krill (items/ind.) caught by the fishpump during the nights on the 21.9. and 23.9.2013. Averaged per individual per chamber with 5 stomachs in each. r: randomly chosen

Area	Ice2									
Date	21.9.					23.9.				
Time	8-9 pm	11-0 pm	3-4am	3-4am 2	5-6am	7-8pm	10-11 pm	0-1 am	3-4 am	
Stage	FIV-VI	FIV-VI	FIV-VI	FIV-VI	FIV-VI	FIV-VI	FIV-VI	FIV-VI	FIV-VI	FIV-VI
DG Colour	r	r	r	r	r	r	r	r	r	r
Stomachs/analyses	(n=5)	(n=5)	(n=5)	(n=5)	(n=5)	(n=5)	(n=5)	(n=5)	(n=5)	(n=5)
<b>Diatoms</b>										
discoïd (complete)	1	3,4	0,6	0,8	1,6	1,2	0,8	0,6	1,6	
(broken)	313,2	70,2	102,6	205,2	232,2	131,4	7,4	91,8	118,8	
pennate (complete)	5,2	3,2	3,8	1,2	1	4	1,4	3,4	15,6	
(broken)	194,8	46,6	60,2	124,6	149,2	205,2	131,4	78,6	27,8	
Fragilariopsis spp. (complete)	3,8	1,6	4,8	0	0,2	0,4	0,8	0	0,8	
(broken)	5,4	0	54	0	0	5,4	0	5,4	5,4	
<b>Protist shell</b>	0,8	2		0,2	0,8		0,6			
<b>Dinoflagellates</b>										
Dinoflagellate remains	15,8	7,8	10,8	2,2	4	39,4	0,8	24,6	5,8	
Dinophysis spp.		0,2				0,6		0,2	0,2	
Prorocentrum spp.		0,2	0,6		0,2	4,2	0,2	0,2	1,6	
<b>Silicoflagellates</b>										
broken shell	2,4			1,6	3,2		1,6	0,4	0,4	
Dictyocha spec.										
Dictyocha spec. naked	3,4	10,2				0,2	5,4	0,8	0,2	
<b>Zooplankton</b>										
zooplankton pieces	0,4	2,8	4,2	1,6	1	0,6	10,6	8,8	2	
copepod mandibles										
zooplankton antennae	2,2	27,4	10,6	6	0,4	5,8	8,2	9	6,4	
carapace	3,4	3,2	4,2	2,2	1,6	4	3,4		1,6	
exuvia	0,4		0	0	0,8			7,8	0,4	
<b>Other items</b>										
<b>Detritus</b>	59,4	275,4	135	75,6	43,2	91,8	75,6	179,2	97,2	
average length [µm]	40	32,16	26,4	57,14	35	30,59	41,43	30,3	34,4	
<b>Tintinnids</b>	0,6	0,2	0,4	0,4	0,2		0,2		0,2	
<b>Nematocysts</b>					0					
<b>Foraminifera</b>	0,6	0,2	0,6		0,6		0,2	0,2	0,2	
<b>Parasite</b>										
<b>Fullness estimation [%]</b>	19,5	24	13,5	13,5	11	29	19,5	32,5	10,5	
<b>Identifiable items [% of visible items]</b>	23,5	29,5	20	33,5	14	36,5	30	15	24,5	



**Fig. 16** *Euphausia superba* under the microscope.

**Table 4** Ice observations from the ship's bridge during the expedition

Date	Region	Hour	Minutes	Latitude	Longitude	Ice coverage (%)
2013-08-28T15	MIZ1	1	0	-59,15	-42,117	40
2013-08-28T16	MIZ1	6	0	-59,333	-42,183	70
2013-08-28T17	MIZ1	1	0	-59,467	-42,217	30
2013-08-28T18	MIZ1	0	0	-59,5	-42,233	50
2013-08-28T19	MIZ1	10	0	-59,5	-42,267	60
2013-08-28T20	MIZ1	0	0	-59,617	-42,267	50
2013-08-29T11	MIZ1	7	0	-61,217	-42,059	90
2013-08-29T12	MIZ1	4	0	-61,25	-42,067	100
2013-08-29T13	MIZ1	2	0	-61,233	-42,067	80
2013-08-29T14	MIZ1	3	0	-61,25	-42,083	30
2013-08-29T15	MIZ1	10	0	-61,267	-41,883	70
2013-08-29T16	MIZ1	14	0	-61,25	-41,7	60
2013-08-29T17	MIZ1	0	0	-61,2	-41,45	90
2013-08-29T18	MIZ1	4	0	-61,217	-41,317	90
2013-08-29T19	MIZ1	21	0	-61,183	-41,183	90
2013-08-29T20	MIZ1	0	0	-61,2	-41,233	80
2013-09-01T10	Camp1	5	0	-61,2	-40,967	90
2013-09-01T13	Camp1	33	0	-61,2	-41,05	90
2013-09-01T13	Camp1	53	0	-61,183	-41,05	90
2013-09-02T13	Camp1	8	0	-61,05	-40,933	80
2013-09-05T13	Camp1	22	0	-60,8	-39,15	100
2013-09-09T11	Camp1	19	0	-60,817	-40,167	70
2013-09-09T12	Camp1	0	0	-60,8	-40,583	90
2013-09-09T14	Camp1	5	0	-60,783	-39,117	90
2013-09-09T16	Camp1	0	0	-60,767	-38,967	90
2013-09-09T17	Camp1	0	0	-60,767	-38,85	90
2013-09-09T19	Camp1	0	0	-60,733	-38,617	90
2013-09-10T10	Camp1	0	0	-59,967	-34,533	90
2013-09-10T11	Camp1	3	0	-59,967	-34,267	100
2013-09-10T12	Camp1	0	0	-59,967	-34,2	90
2013-09-10T13	Camp1	0	0	-59,967	-34,083	100
2013-09-10T14	Camp1	49	0	-59,967	-33,833	90
2013-09-10T16	Camp1	4	0	-59,95	-33,85	90

2013-09-10T17	Camp1	0	0	-59,95	-33,85	90
2013-09-16T10	Camp2	58	0	-60,733	-27,133	100
2013-09-17T09	Camp2	0	0	-60,6	-27,15	100
2013-09-17T10	Camp2	8	0	-60,6	-27,15	100
2013-09-17T13	Camp2	15	0	-60,6	-27,133	100
2013-09-17T16	Camp2	1	0	-60,6	-27,1	100
2013-09-20T12	Camp2	14	0	-60,567	-26,55	100
2013-09-29T09	Camp2	5	0	-59,767	-25,6	100
2013-09-29T10	Camp2	2	0	-59,733	-25,567	100
2013-09-29T10	Camp2	58	0	-59,717	-25,583	100
2013-09-29T12	Camp2	5	0	-59,617	-25,6	90
2013-09-29T13	Camp2	10	0	-59,517	-25,75	90
2013-09-29T15	Camp2	1	0	-59,383	-25,95	90
2013-09-29T15	Camp2	54	0	-59,367	-25,967	100
2013-09-29T18	Camp2	1	0	-60,567	-26,217	80
2013-09-30T09	Camp2	0	0	-58,417	-26,117	80
2013-09-30T15	Camp2	0	0	-58,15	-26,183	90
2013-09-30T16	Camp2	2	0	-59,35	-26,2	90
2013-09-30T18	Camp2	0	0	-58,933	-26,383	100
2013-10-01T09	MIZ2	0	0	-56,717	-28,5	80
2013-10-01T10	MIZ2	16	0	-56,55	-28,7	100
2013-10-01T14	MIZ2	56	0	-56,5	-28,7	90
2013-10-01T16	MIZ2	23	0	-56,517	-28,633	80
2013-10-01T18	MIZ2	4	0	-56,517	-28,6	80
2013-10-02T09	MIZ2	0	0	-58,217	-26,433	70
2013-10-02T10	MIZ2	10	0	-58,383	-26,2	10
2013-10-02T11	MIZ2	0	0	-58,4	-26,133	0
2013-10-02T12	MIZ2	0	0	-58,417	-26,15	10
2013-10-02T15	MIZ2	0	0	-58,433	-26,2	0
2013-10-02T16	MIZ2	1	0	-58,483	-26,133	50
2013-10-02T17	MIZ2	0	0	-58,433	-26,133	0
2013-10-03T09	MIZ2	0	0	-58,433	-25,983	100
2013-10-03T10	MIZ2	0	0	-58,433	-25,983	100
2013-10-03T11	MIZ2	0	0	-58,45	-26,017	90
2013-10-03T12	MIZ2	0	0	-58,417	-26	90
2013-10-03T15	MIZ2	0	0	-58,383	-26,233	0
2013-10-03T16	MIZ2	6	0	-58,45	-26,183	80
2013-10-04T09	MIZ2	0	0	-58,4	-25,05	90
2013-10-04T09	MIZ2	59	0	-58,35	-24,967	100
2013-10-04T11	MIZ2	0	0	-58,333	-24,733	90
2013-10-04T15	MIZ2	3	0	-58,3	-24,35	90
2013-10-04T16	MIZ2	4	0	-58,317	-24,35	60

**Table 5** POC ( $\mu\text{g L}^{-1}$ ) and Chl *a* ( $\mu\text{g L}^{-1}$ ) concentrations in ice cores taken on three transects (EB, POL, ROV) in different distances towards the divehole at Ice Camp2. Each bar represents the last 10 cm segment of 2-3 pooled ice cores.

EB 1	16	124,6005	14,0222807
EB 2	14	174,3105	17,34
EB 3	12	160,3705	6,196666667
EB 4	10	254,2205	21,15
EB 5	8	179,9705	8,466666667
EB 6	6	149,4605	6,75
EB 7	4	176,9705	10,06090909
EB 8	2	272,42575	18,42
POL 1	22	364,52575	16,80928571
POL 2	20	383,37575	16,32
POL 3	18	510,3990833	18,3
POL 4	16	396,45575	14,7
POL 5	14	307,07575	14,22
POL 6	12	334,64575	8,71

POL 7	10	315,25575	12,05
POL 8	8	322,26575	8,466111111
POL 9	6	384,71575	17,525
POL 10	4	444,11575	18,511111111
POL 11	2	447,80575	16,125
ROV 1	18	412,8005	8,9
ROV 2	16	266,8705	7,370672269
ROV 3	14		5,331818182
ROV 4	12	339,7505	14,7059322
ROV 5	10	360,7505	14,1959633
ROV 6	8	625,0905	5,331818182
ROV 7	6	562,9805	4,8
ROV 8	4	444,8605	6,35
ROV 9	2	202,3005	16,59818182
mean		330,3099938	12,41883632

**Table 6** POC ( $\mu\text{g L}^{-1}$ ) and Chl a ( $\mu\text{g L}^{-1}$ ) concentrations in Ice Cores at Ice Camp1. The last 10 cm segments of three ice cores per square were pooled (e.g. A1 bars represents last 10 cm of three pooled ice cores).

Core site	Core name	Chla ( $\mu\text{g/L}$ )	POC ( $\mu\text{g/L}$ )
A	A1	54,8	280,8805
A	A2	25,97	425,4105
A	A3	25,37	600,9605
B	B1	14,62	203,8205
B	B2	18,3	432,7005
B	B3	43,03	469,2505
C	C1	19	416,7105
C	C2	12,31	424,0005
C	C3	21,23	373,3705
D	D1	8	637,4305
D	D2	12,19	222,0705
D	D3	3,75	262,4105
E	E1	13,54	194,9605
E	E2	25,32	529,8705
E	E3	29,25	306,3605
mean		21,77866667	385,3471667

**Table 7** Chlorophyll *a* (Chl *a*) ( $\mu\text{g L}^{-1}$ ) and particulate organic carbon (C) ( $\mu\text{g L}^{-1}$ ) concentrations in the water at 10 m depth (measured with CTD). (Data by Christine Klaas)

Region	station Nr	cast(prior)	Day	Month	Year	hour	minute	Long decimal	Lat decimal	depth	Av. Chla	C $\mu\text{g/l}$
OW	537	2	26	8	2013	6	29	-39,5815	-53,545	10	0,65359746	37,20014925
OW	538	2	26	8	2013	12	41	-40,30666667	-53,50116667	10	0,577239644	44,48411314
OW	539	2	26	8	2013	18	29	-40,4665	-54,00083333	10	0,332894629	28,5907215
OW	540	2	27	8	2013	0	25	-40,63166667	-54,4985	10	0,369376697	33,02377457
OW	541	2	27	8	2013	6	15	-40,78183333	-54,9985	10	0,340428601	30,85006907
OW	542	2	27	8	2013	12	30	-40,94916667	-55,49683333	10	0,453692696	41,16406307
OW	543	1	27	8	2013	16	40	-41,11	-56,00166667	10	0,407029585	47,37664832
OW	544	1	27	8	2013	20	58	-41,26166667	-56,50033333	10	0,513082109	47,14693946
MIZ1	545	1	28	8	2013	1	12	-41,43733333	-57,00316667	10	0,593682027	51,16357621
MIZ1	546	1	28	8	2013	13	21	-42,08283333	-59,004	10	1,170204755	50,32795114
MIZ1	547	1	28	8	2013	17	49	-42,2325	-59,50566667	10	0,792657771	52,40092096
MIZ1	548	1	28	8	2013	22	56	-42,392	-59,9975	10	0,239487809	23,23481996
Camp1	555	16	3	9	2013	23	15	-40,80683333	-60,94883333	10	0,112012675	10,39405714
Camp1	555	37	6	9	2013	20	17	-39,62466667	-60,76466667	10	0,078970951	11,55271543
Camp1	555	45	8	9	2013	17	41	-39,318	-60,74566667	10	0,106981544	nan
Camp1	556	1	10	9	2013	16	0	-33,8515	-59,95733333	10	0,176598662	19,60983493
Camp1	557	2	11	9	2013	1	55	-33,153	-59,94583333	10	0,133753443	nan
Ice2	565	3	16	9	2013	14	49	-27,161	-60,71283333	10	0,086411596	0
Ice2	566	5	22	9	2013	12	35	-26,54316667	-60,80283333	10	0,079369709	15,24917943
Ice2	566	16	24	9	2013	12	2	-26,29783333	-60,78733333	10	0,172059614	14,51417143
Ice2	566	28	26	9	2013	10	56	-26,0865	-60,61766667	10	0,177998556	17,45749943
MIZ2	582	2	3	10	2013	20	47	-26,06383333	-58,49366667	10	0,291262651	25,79012132
MIZ2	587	5	5	10	2013	11	23	-24,42933333	-58,28433333	10	0,30763716	36,47812886

## Eidesstattliche Erklärung

Hiermit versichere ich, Laura Halbach, dass ich die vorliegende Bachelorarbeit selbstständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Marburg, den 25.7.2015