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The role of sympagic meiofauna in Arctic and Antarctic sea-ice food webs

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Abstract

Sympagic meiofauna—proto- and metazoans $\geq 20\,\mu$m inhabiting the brine channels in sea ice—may play an important role in polar marine food webs, since they recycle part of the ice-algae production within the sea-ice system. The few studies conducted on the feeding ecology of sympagic meiofauna have indicated herbivorous feeding and a generally low grazing impact based on theoretical maximum potential ingestion rates (I_{max}). I combined meiofauna community studies, biochemical analyses and feeding experiments to test my hypotheses that (1) due to carnivorous, cilivorous and omnivorous sympagic meiofauna the sea-ice food webs are more complex than previously assumed, (2) the feeding impact of sympagic meiofauna is more diverse and may have been underestimated, (3) sympagic meiofauna plays an important role in cryo-pelagic coupling and (4) global warming may affect Arctic sympagic meiofauna composition and feeding strategies, with possible consequences for the entire Arctic marine food web.

Sea-ice samples were taken in the Antarctic (western Weddell Sea and southern Indian Ocean, winter) and Arctic (Central Arctic, summer; Canadian Arctic and Spitsbergen fjords, spring). Additionally, brackish meltponds on summer sea ice in the Central Arctic were sampled. Antarctic sympagic meiofauna comprised, besides the commonly reported taxa, also radiolarians, the ctenophore *Euplokamis* sp., the nudibranch *Tergipes antarcticus*, cyclopoid copepods and rhabdocoel platyhelminthes. Diversity, abundance and biomass of metazoan meiofauna were significantly higher in the perennially ice-covered western Weddell Sea than in the seasonally ice-covered southern Indian Ocean. Arctic sympagic meiofauna likewise included taxa new to sea ice: the cnidarian *Sympagohydra tuuli*, the calanoid copepod *Eurytemora richingsi*, nemerteans and white-rose acoel platyhelminthes. Brackish meltponds hosted various proto- and metazoans: particularly ciliates, rotifers, red acoels and nematodes in new ice covering the pond surfaces as well as the foraminifer *Neogloboquadrina pachyderma*, rotifers and the under-ice amphipod *Apherusa glacialis* in and on the very porous ice at the pond bottoms.

Stable isotope and fatty acid analyses served to gain information on *in situ* feeding of sympagic meiofauna. I developed a two-source model to estimate trophic positions and identify feeding grounds based on stable isotopes. In order to identify diets, to determine ingestion rates and to assess selectivity, I conducted grazing and predation experiments with various Arctic and Antarctic sympagic meiofauna taxa, for which I specifically developed new methods and modified established ones. The biochemical analyses and feeding experiments showed in good agreement that most metazoan meiofauna taxa prey on ciliates: Arctic cyclopoids, indetermined harpacticoids, rotifers, nauplii, acoels, the

calanoid *Eurytemora richingsi* and nematodes as well as Antarctic *Euplokamis* sp., rhabdocoels and acoels. Some taxa even prey on metazoans, as observed in the Arctic cnidarian *S. tuuli* and indetermined harpacticoids as well as Antarctic *Euplokamis* sp.. Many of these taxa are omnivores which supplement their diets with algae, bacteria and detritus. A few meiofauna taxa are mainly herbivorous, but can additionally prey on ciliates or cannibalistically feed on their nauplii (as the Arctic harpacticoids *Halectinosoma* spp. and *Tisbe* spp., respectively). Ingestion rates were influenced by food density (functional response) and predator density (competition). Grazing rates of *Tisbe* spp. were 1–36 % of grazer body carbon per day and generally lower than I_{max}. The experimentally derived grazing impact of the meiofauna community was always below 2 % of the ice-algae standing stock per day and by one order of magnitude lower than estimates from I_{max}. Predation rates, in contrast, were very high in some metazoan meiofauna taxa (e. g. 191 % of predator body carbon per day in *Euplokamis* sp. preying on copepods), in part exceeding I_{max}. The experimentally derived predation impact of the meiofauna community was accordingly high, at single stations > 200 % of the ciliate or 37 % of the nauplii standing stock per hour.

I draw the following conclusions: (1) As hypothesised, sea-ice food webs are more complex than previously assumed. This can be attributed in part to the discovery of new sympagic meiofauna taxa. The Arctic sea-ice food web seems to be more complex than the Antarctic one and might be based to a higher degree on bacteria and detritus. (2) The results confirm a diverse feeding impact of sympagic meiofauna on algae, ciliates and metazoan meiofauna. The hypothesis of a high feeding impact is confirmed for predation on ciliates and copepods, but not for grazing on algae. The predation impact is probably constrained by regulating factors, including competition and diet switches. Predation by meiofauna may nevertheless change the meiofauna community structure. (3) Cryo-pelagic coupling is influenced by meiofauna predation, which can diminish the amount of meiofauna released from the ice and available to under-ice and sub-ice predators. New pathways in cryo-pelagic coupling are feeding migrations of meiofauna between the sea ice, meltponds and the pelagic realm, which can enhance interactions with under-ice and sub-ice fauna. (4) The gradual loss of perennial sea ice in the Arctic in consequence of global warming probably causes a decrease in sympagic meiofauna diversity, abundance and biomass. Consequently, the sea-ice food web may become less complex and more vulnerable. Under-ice and sub-ice predators may be affected by the shift in potential prey taxa. Over the next decades, an increase in brackish meltponds might locally enhance cryo-pelagic coupling in late summer. The expected long-term changes in the quantity and quality of cryo-pelagic coupling deserve further investigation.

Zusammenfassung

Als sympagische Meiofauna werden die Proto- und Metazoen $\geq 20\,\mu$m bezeichnet, die in den Solekanälen im Meereis leben. Diese Organismen spielen möglicherweise eine wichtige Rolle in polaren marinen Nahrungsnetzen, da sie einen Teil der Eisalgenproduktion innerhalb des Meereissystems recyceln. Die wenigen Studien, die bislang zur Nahrungsökologie sympagischer Meiofauna durchgeführt worden sind, haben Hinweise auf eine herbivore Ernährungsweise und einen allgemein niedrigen Grazingdruck (basierend auf theoretischen maximalen potentiellen Ingestionsraten I_{max}) gegeben. Ich habe Studien zu Meiofauna-Gemeinschaften mit biochemischen Analysen und Fraßexperimenten kombiniert, um meine Hypothesen zu prüfen, dass (1) aufgrund von carnivorer, cilivorer und herbivorer sympagischer Meiofauna die Meereis-Nahrungsnetze komplexer sind als bislang angenommen, (2) der Fraßdruck der sympagischen Meiofauna vielfältiger ist als bislang angenommen und sein Umfang möglicherweise unterschätzt wurde, (3) sympagische Meiofauna eine wichtige Rolle in der cryo-pelagischen Kopplung spielt und (4) der Klimawandel die Zusammensetzung der arktischen sympagischen Meiofauna und deren Ernährungsstrategien beeinflussen kann, was Folgen für das gesamte arktische marine Nahrungsnetz haben kann.

Meereisproben wurden in der Antarktis (westliches Weddellmeer und südlicher Indischer Ozean, Winter) und Arktis (Zentrale Arktis, Sommer; Kanadische Arktis und Fjorde auf Spitzbergen, Frühling) genommen. Außerdem wurden brackige Schmelztümpel auf dem sommerlichen Meereis der Zentralen Arktis beprobt. Die antarktische sympagische Meiofauna umfasste, neben den üblicherweise in der Literatur angeführten Taxa, auch Radiolarien, die Ctenophore *Euplokamis* sp., die Nudibranchie *Tergipes antarcticus*, cyclopoide Copepoden und rhabdocoele Plathelminthen. Im ganzjährig eisbedeckten westlichen Weddellmeer waren Diversität, Abundanz und Biomasse der Metazoen-Meiofauna signifikant höher als im saisonal eisbedeckten südlichen Indischen Ozean. Die arktische sympagische Meiofauna schloss ebenfalls einige neue Meereis-Taxa ein: den Cnidarier *Sympagohydra tuuli*, den calanoiden Copepoden *Eurytemora richingsi*, Nemertinen und weiß-rosa acoele Plathelminthen. Brackige Schmelztümpel beherbergten etliche Proto- und Metazoen, v. a. Ciliaten, Rotatorien, rote Acoele und Nematoden in der neuen Eisdecke auf den Tümpeln sowie die Foraminifere *Neogloboquadrina pachyderma*, Rotatorien und den Untereis-Amphipoden *Apherusa glacialis* in und auf dem sehr porösen Eis am Grund der Tümpel.

Mittels Analysen stabiler Isotope und Fettsäuren konnte ich Informationen über die Ernährung von sympagischer Meiofauna *in situ* gewinnen. Ich entwickelte ein Zwei-

Quellen-Modell, um auf Grundlage der Isotopendaten die trophischen Ebenen abzuschätzen und auf die Herkunft der Nahrung zu schließen. Zur Identifikation von Nahrungsquellen, Bestimmung von Ingestionsraten und Erfassung von Selektivität führte ich außerdem Grazing- und Prädationsexperimente mit verschiedenen arktischen und antarktischen sympagischen Meiofauna-Taxa durch, für die ich spezifisch Methoden neu entwickelte oder modifizierte. Die biochemischen Analysen und Fraßexperimente haben übereinstimmend gezeigt, dass die meisten Metazoen-Meiofauna-Taxa Ciliaten fressen: arktische Cyclopoide, unbestimmte Harpacticoide, Rotatorien, Nauplien, Acoele, der Calanoide *Eurytemora richingsi* und Nematoden sowie die antarktischen *Euplokamis* sp., Rhabdocoele und Acoele. Einige Taxa ernähren sich sogar räuberisch von Metazoen, wie ich für die arktischen *S. tuuli* und unbestimmte Harpacticoide sowie für die antarktischen *Euplokamis* sp. beobachtet habe. Viele dieser Taxa sind omnivor und ergänzen ihre Nahrung mit Algen, Bakterien und Detritus. Wenige Meiofauna-Taxa sind vorrangig herbivor, können sich aber zusätzlich von Ciliaten ernähren (so die arktischen Harpacticoiden *Halectinosoma* spp.) oder kannibalistisch ihre Nauplien fressen (so die arktischen Harpacticoiden *Tisbe* spp.). Die Ingestionsraten wurden durch Futterdichte (funktionelle Reaktion) und Räuberdichte (Konkurrenz) beeinflusst. Die Grazingraten von *Tisbe* spp. lagen bei 1–36 % des Grazer-Kohlenstoffgehaltes pro Tag und im Allgemeinen unterhalb von I_{max}. Der aus Experimenten abgeleitete Grazingdruck der Meiofauna-Gemeinschaft war stets niedriger als 2 % des Eisalgenbestandes pro Tag und um eine Größenordnung kleiner als Abschätzungen auf Grundlage von I_{max}. Die Prädationsraten hingegen waren für einige Metazoen-Meiofauna-Taxa sehr hoch (z. B. 191 % des Räuber-Kohlenstoffgehaltes pro Tag für Copepoden fressende *Euplokamis* sp.) und teils höher als I_{max}. Der aus Experimenten abgeleitete Prädationsdruck der Meiofauna-Gemeinschaft war entsprechend hoch, an einzelnen Stationen > 200 % des Ciliatenbestandes oder 37 % des Nauplienbestandes pro Stunde.

Aus meiner Studie ergeben sich folgende Schlussfolgerungen: (1) Meiner Hypothese entsprechend sind Meereis-Nahrungsnetze komplexer als bislang angenommen, was zum Teil auf die Entdeckung neuer sympagischer Meiofauna-Taxa zurück zu führen ist. Das arktische Meereis-Nahrungsnetz scheint komplexer zu sein als das antarktische und basiert möglicherweise zu einem größeren Anteil auf Bakterien und Detritus. (2) Die Ergebnisse bestätigen einen vielseitigen Fraßdruck der sympagischen Meiofauna auf Algen, Ciliaten und Metazoen-Meiofauna. Die Hypothese eines hohen Fraßdruckes bestätigt sich für den Prädationsdruck auf Ciliaten und Copepoden, nicht jedoch für den Grazingdruck auf Algen. Der Prädationsdruck wird wahrscheinlich durch regulierende Faktoren wie Konkurrenz und Wechsel der Nahrungsquellen beschränkt. Dennoch kann Präda-

tion durch Meiofauna die Struktur der Meiofauna-Gemeinschaft verändern. (3) Die cryo-pelagische Kopplung wird durch Meiofaunaprädation beeinflusst, die bewirken kann, dass weniger Meiofauna aus dem Eis freigesetzt wird und Untereis-Räubern zur Verfügung steht. Neue Verbindungswege in der cryo-pelagischen Kopplung bestehen in Fraßmigrationen der Meiofauna zwischen Meereis, Schmelztümpeln und Pelagial, die zu verstärkten Interaktionen mit der Untereis-Fauna führen können. (4) Der graduelle Verlust der ganzjährigen Eisbedeckung in der Arktis in Folge des Klimawandels führt wahrscheinlich zu einer Abnahme der Diversität, Abundanz und Biomasse der sympagischen Meiofauna. Dadurch kann das Meereis-Nahrungsnetz an Komplexität verlieren und störungsanfälliger werden. Untereis-Prädatoren können durch Veränderungen in der Zusammensetzung der potentiellen Beutetaxa betroffen sein. Über die kommenden Jahrzehnte kann ein vermehrtes Auftreten brackiger Schmelztümpel möglicherweise lokal zu einer Verstärkung der cryo-pelagischen Kopplung im Spätsommer führen. Die zu erwartenden langfristigen Veränderungen in der Quantität und Qualität der cryo-pelagischen Kopplung sollten in Zukunft näher untersucht werden.

1 Introduction: The role of sympagic meiofauna in sea-ice food webs—a three-method approach

1.1 Motivation and overview of my thesis

Large parts of the polar oceans are covered with sea ice. Ice algae, inhabiting the brine channels in sea ice (Fig. 1.1), contribute substantially to total primary production in ice-covered regions—up to 28 % in certain parts of the Southern Ocean (Arrigo and Thomas 2004) and up to 57 % in the Central Arctic (Gosselin et al. 1997). They thus constitute an important base of the polar marine food webs (Legendre et al. 1992, Arrigo et al. 2010). It is still unknown, however, to what extent this primary production is available to under-ice grazers and, after release from the ice, to zooplankton and zoobenthos. One influencing factor in this respect is the feeding activity of sympagic meiofauna, i. e. proto- and metazoans $\geq 20\,\mu$m inhabiting the brine channels (Gradinger 1999a). Little is known about the diets of these organisms, and only rough estimates of their grazing impact exist so far (Bluhm et al. 2010).

This study aims to investigate the diets and feeding strategies of sympagic metazoan meiofauna, assess its feeding impact and give new insights into its role in cryo-pelagic coupling. It also covers regional and seasonal differences in both polar regions and considers possible consequences of global warming. The study is based on a three-method approach, combining analyses of Arctic and Antarctic meiofauna communities with biochemical and experimental methods.

In the following, I give an overview of the sea-ice environment and habitat (Section 1.2) and describe the current state of knowledge of the feeding ecology of sympagic meiofauna (Section 1.3). I then give details on the approach of this study (Section 1.4) and list the respective publications (Section 1.5). The following Chapters 2–5 comprise accepted or submitted manuscripts, which tackle the problem according to the three-method approach. I close with a synopsis (Chapter 6), in which I interpret the results from Chapters 2–5 in conjunction, draw more general conclusions and give an outlook to requirements of future research.

1.2 Sea ice and sympagic communities

Sea ice is a characteristic feature of both the Arctic and the Antarctic, but the sea-ice regimes differ, reflecting the geographic, oceanographic and atmospheric differences between the polar regions (Comiso 2010).

The Arctic Ocean is situated at high latitudes (51–90 °N, mainly north of 70 °N; Haas 2010). It is surrounded by continents, with connections to the world oceans only by few passages (Brandon et al. 2010), and is characterised by mainly convergent drift patterns of sea ice (Haas 2010). Due to freshwater inflow from large rivers resulting in a stable layer of cold surface water (Brandon et al. 2010), oceanic heat flux to the ice is low (Haas 2010). These features lead to high proportions of multi-year sea ice, which persists throughout the summer. The ice can grow 2–3 meters thick by thermodynamic growth (Weeks 2001), but it can become considerably thicker by ridging and rafting, as observed particularly north of Greenland (Haas 2010). In summer, vast areas on the Arctic sea ice are covered with meltponds (Lu et al. 2010). The northern hemisphere sea-ice extent ranges between 5–8 $\times 10^6\,\mathrm{km}^2$ in August or September and 15–16 $\times 10^6\,\mathrm{km}^2$ in March (1978–2006 satellite records, Comiso 2010). Due to feedback mechanisms related to the high albedo of sea ice compared to open water (Petrich and Eicken 2010), the recently observed global warming trend is particularly pronounced in the Arctic (Holland and Bitz 2003, IPCC 2007) and has caused a dramatic decrease in Arctic sea-ice extent particularly in summer (Comiso et al. 2008, Stroeve et al. 2008a), in the thickness of first-year ice (Haas et al. 2008b) and possibly also multi-year ice (Maslanik et al. 2007) as well as in the ice age (Maslanik et al. 2007, Nghiem et al. 2007, Drobot et al. 2008). A record minimum in sea-ice extent of $4.3 \times 10^6\,\mathrm{km}^2$ was observed in September 2007 (Stroeve et al. 2008b). The summer sea-ice cover, and thus the perennial sea ice, is expected to be lost completely within the next few decades (Stroeve et al. 2007, Wang and Overland 2009).

The Southern Ocean is a ring ocean surrounding the Antarctic continent, confined to the north by the southern polar front (Brandon et al. 2010). It is thus situated mostly at lower latitudes than the Arctic Ocean (45–85 °S, mainly north of 70 °S) and characterised by mainly divergent sea-ice drift patterns (Haas 2010). Furthermore, due to weak stratification, the oceanic heat flux is much higher than in the Arctic (Haas 2010). In consequence, the sea ice in most parts of the Southern Ocean is seasonal and comparatively thin (Worby et al. 2008). As an exception, some embayments, such as the Weddell Sea with more convergent drift patterns, have a perennial sea-ice cover and high amounts of deformed ice (Haas 2010). The Antarctic sea-ice extent ranges between 2–4 $\times 10^6\,\mathrm{km}^2$ in Febuary and

18–20 $\times$ 10^6 km^2 in September (1978–2009 satellite records, Comiso 2010). Due to atmospheric patterns related to the ozone hole and to the high influence of the albedo of the Antarctic inland ice sheet, the Antarctic seems to be less influenced by global warming than the Arctic (IPCC 2007, Mayewski et al. 2009). A significant decrease in sea-ice extent has been observed only west of the Antarctic Peninsula (Stammerjohn et al. 2008, Comiso 2010), but recently a warming trend has also been reported from other parts of Antarctica (Steig et al. 2009).

Sea ice in both polar regions hosts diverse communities of sympagic (ice-associated) organisms, ranging from unicellular algae to mammals such as seals and the polar bear (Horner et al. 1992, Tynan et al. 2010). Sea ice is permeated with a system of brine channels, which form due to the exclusion of salt ions from the ice crystal matrix during freeze-up (Fig. 1.1) (Weeks 2001). The brine channels make up the habitat for sympagic viruses, bacteria, fungi, algae and proto- and metazoan meiofauna (Deming 2010, Arrigo et al. 2010, Caron and Gast 2010, Bluhm et al. 2010). These organisms can colonise the entire ice column (Horner et al. 1992). In the Arctic, however, the by far largest part of

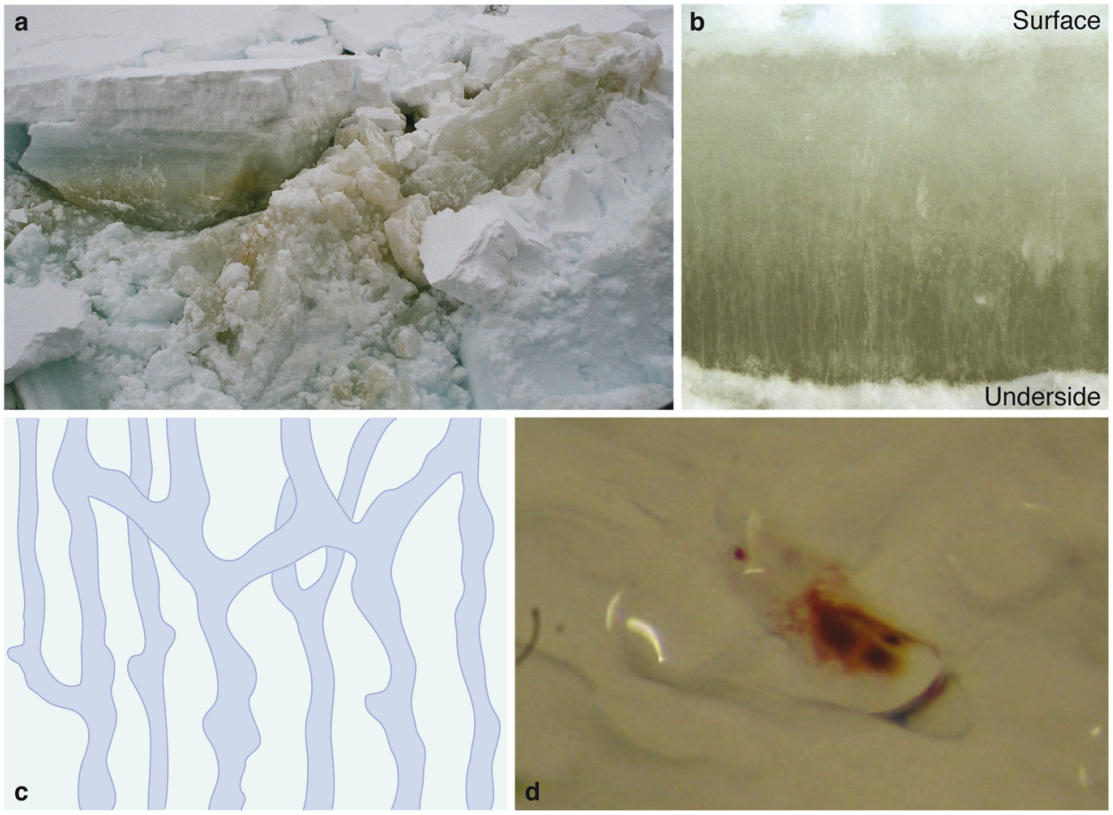

Figure 1.1: Brine channels in sea ice. **a** Chunks of sea ice. The brown colouration is caused by ice algae inhabiting the brine channels in the ice. **b** Block of sea ice (30 cm thick) viewed from the side. Larger brine channels from which the brine has drained are visible as vertical lines in lighter colour. **c** Schematic drawing of brine channels (dark colour). **d** The harpacticoid copepod *Idomene antarctica* inside a brine channel at the ice underside (photo courtesy by Rainer Kiko).

organisms is concentrated in the lowermost few centimeters of the ice, whereas in the Antarctic high densities of sympagic organisms also occur in the interior and upper parts of the ice (Arrigo et al. 2010, Bluhm et al. 2010). They can also colonise platelet layers underneath Antarctic fast ice (Dieckmann et al. 1992, Günther et al. 1999) and surface layers, which can occur at the snow-ice interface of Antarctic sea ice in summer (Garrison and Buck 1991, Kiko et al. 2008b). The protozoan meiofauna ($\geq 20\,\mu$m) consists of ciliates, foraminifers, radiolarians, acantharians, heliozoans and big heterotrophic flagellates in both polar regions (Caron and Gast 2010). The metazoan meiofauna comprises mainly harpacticoid copepods and acoel turbellarians (in both polar regions), calanoid copepods (only in the Antarctic), cyclopoid copepods, rotifers, nematodes and larvae of benthic polychaetes and molluscs (all mainly or only in the Arctic) (Schnack-Schiel 2003, Bluhm et al. 2010). In addition, cnidarians (Bluhm et al. 2007, Piraino et al. 2008) have been reported from Arctic and nudibranches (Pelseneer 1903, Kiko et al. 2008b) and ctenophores (Dahms et al. 1990, Kiko et al. 2008b) from Antarctic sea ice. Besides the organisms inhabiting the brine channels, also under-ice amphipods are part of the sympagic communities in both Arctic (Lønne and Gulliksen 1991) and Antarctic (Krapp et al. 2008). Furthermore, some pelagic and sub-ice organisms live in close association with sea ice, including krill in the Antarctic as well as amphipods, pelagic copepods and fishes in both polar regions (Bluhm et al. 2010).

1.3 Sympagic meiofauna in sea-ice food webs

The potential importance of sympagic meiofauna as grazers which may recycle part of the ice-algae production within the brine-channel system has long been recognised (Gradinger 1999a). Nevertheless, information on the feeding ecology of these organisms is still rather limited (Bluhm et al. 2010).

Sympagic meiofauna has been generally assumed to be herbivorous (Gradinger 1995, Brierley and Thomas 2002, Arrigo and Thomas 2004). This assumption is based on two gut-content studies with Arctic sympagic meiofauna (Grainger and Hsiao 1990) and the Antarctic sympagic calanoid *Paralabidocera antarctica* (Hoshiai et al. 1987), few feeding experiments and lipid analyses with Antarctic sympagic calanoids (Schnack-Schiel et al. 1995, Swadling et al. 1997b, 2000) as well as rare occasional observations (Chengalath 1985, Tchesunov and Riemann 1995, Friedrich and Hendelberg 2001). Only recently has the potential of carnivorous meiofauna received some attention (Bluhm et al. 2007, Piraino et al. 2008, Bluhm et al. 2010).

Grazing rates of sympagic metazoan meiofauna have been determined experimentally only for Antarctic calanoids (Schnack-Schiel et al. 1995, Swadling et al. 1997b). In con-

sequence, the grazing impact of sympagic meiofauna communities has up to now only been estimated from maximum potential ingestion rates, calculated from allometric equations which had originally been developed for filter-feeding zooplankton (Moloney and Field 1989). Estimates are highly variable, usually indicating that the grazing impact is negligible (Gradinger 1999a, Nozais et al. 2001, Michel et al. 2002, Gradinger et al. 2005), but sometimes suggesting that meiofauna may under certain conditions control the accumulation of ice algae (Gradinger et al. 1999). The predation impact of potentially carnivorous meiofauna such as the Arctic cnidarian *Sympagohydra tuuli* (Bluhm et al. 2007, Piraino et al. 2008) on other meiofauna taxa has not been estimated as yet.

Knowledge on the food sources of sympagic meiofauna and good estimates of the grazing and predation impact are essential for understanding to what extent meiofauna competes with under-ice grazers and predators for sympagic food sources. Sea-ice algae are consumed by krill in the Antarctic (Meyer et al. 2002), by under-ice amphipods (Richardson and Whitaker 1979, Werner 1997, Werner and Auel 2005) and planktonic copepods (Pasternak and Schnack-Schiel 2007, Falk-Petersen et al. 2009) in both the Arctic and Antarctic. Sympagic meiofauna in the Arctic are preyed on by carnivorous under-ice amphipods (Werner et al. 2002), in the Antarctic possibly by amphipods (Krapp et al. 2008) and krill (Wickham and Berninger 2007). Such feeding activities contribute strongly to the transfer of organic matter and energy from the sympagic to the pelagic realm and are thus important factors in cryo-pelagic coupling (Werner 2006a). In consequence, competitive feeding activity by sympagic meiofauna would influence the magnitude and pathways of cryo-pelagic coupling.

1.4 The three-method approach of this study

In order to improve our understanding of sympagic meiofauna feeding ecology and its role in cryo-pelagic coupling, I combined three different methods.

As a first approach of my study, I investigated sympagic meiofauna communities in different regions of the Antarctic and Arctic (Fig. 1.2) with respect to diversity, abundance and biomass (Chapter 2, Kramer et al. in press; Chapter 3, Kramer and Kiko 2010; Chapter 5, Kramer and Prowe in preparation; see also Kiko et al. under revision, Marquardt et al. under revision). The biomass data was required to calculate *in situ* ingestion rates and to assess the grazing and predation impact of sympagic meiofauna. Furthermore, abundance and biomass were needed to determine realistic densities of organisms to be applied in feeding experiments. Additionally, knowledge on meiofauna diversity in general and specific taxa in particular (Kiko et al. 2008a, Siebert et al. 2009) contributed to the

development of hypotheses on the sympagic food web and served for the interpretation of the results from biochemical analyses and experiments.

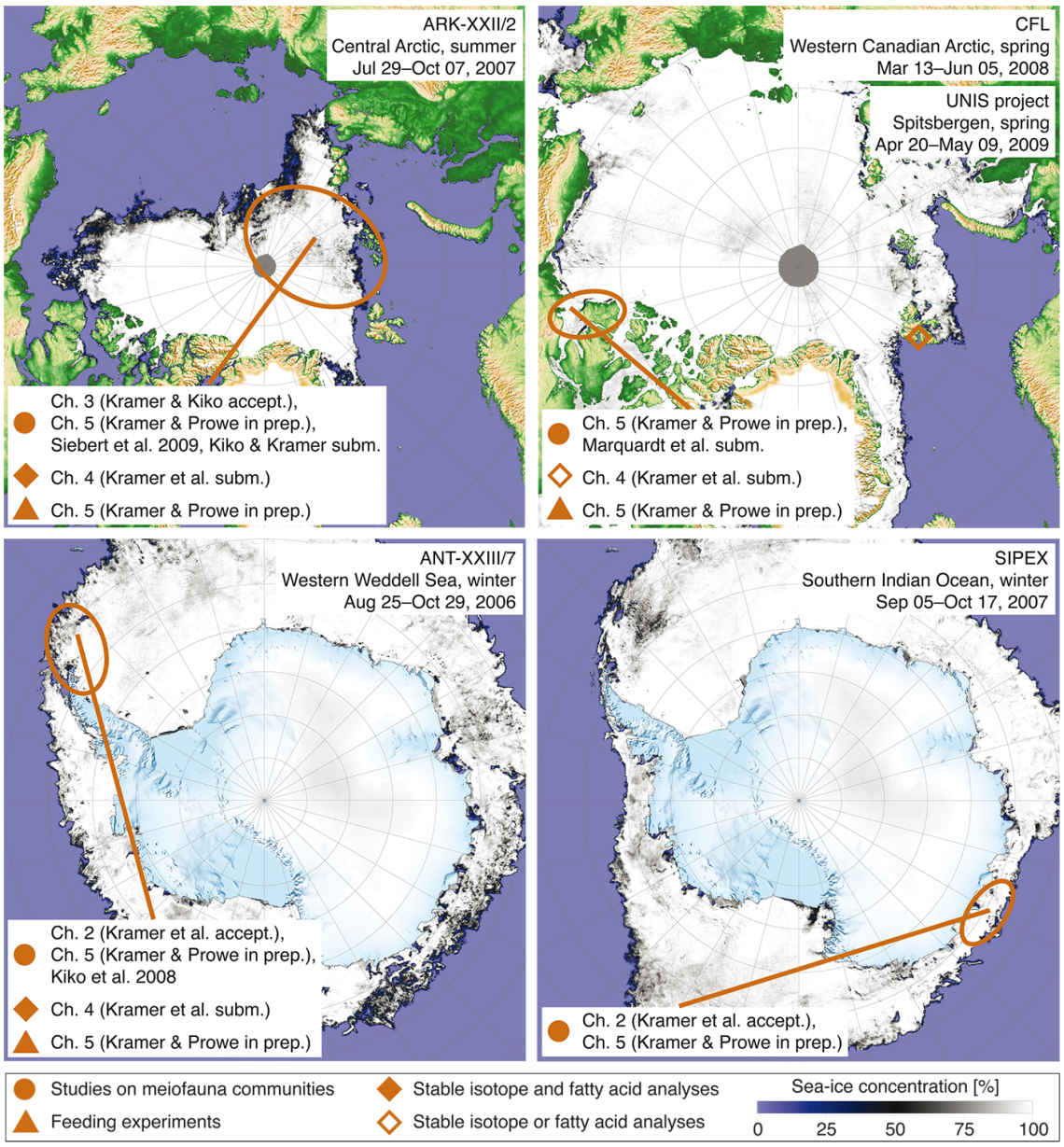

Figure 1.2: Sampling regions in the Arctic (top) and Antarctic (bottom). AMSR-E sea-ice concentrations in the middle of the respective sampling periods are shown in the maps, obtained from www.seaice.de. The symbols indicate the methods applied. The thesis chapters and publications or manuscripts presenting the respective results are also listed. The feeding impact (Chapter 5, Kramer and Prowe in preparation) was calculated for all expeditions except for Spitsbergen.

As a second approach, I analysed stable carbon and nitrogen isotopes and fatty acids in Arctic and Antarctic sympagic metazoan meiofauna (Fig. 1.2; Chapter 4, Kramer et al. under revision) to investigate trophic positions, diets and feeding strategies. Stable isotopes also served to gain information on feeding grounds, which are important in the context of cryo-pelagic coupling. The power of these methods lies in their potential to

reveal *in situ* information on feeding ecology. However, they allow to trace only some specific diets and they do not give any information on ingestion rates. Since the analyses require sufficient amounts of material and thus many meiofauna specimens per sample, they cannot easily be applied to rare taxa.

As a third approach, I therefore conducted feeding experiments with several taxa of Arctic and Antarctic sympagic metazoan meiofauna (Fig. 1.2), which were offered different algae food and meiofauna prey (Chapter 5, Kramer and Prowe in preparation; see also Siebert et al. 2009). The experiments served to confirm the analytical results, to reveal specific diets not traced by the biochemical approach, to observe feeding strategies including selectivity and to gain insights into the feeding ecology also of rare meiofauna taxa. In addition, the experiments allowed to measure grazing and predation rates and to determine functional relationships with food density (functional response) and grazer / predator density (competition). Ultimately, I aimed to calculate the grazing and predation impact based on experimental ingestion rates and biomass data.

Viewed in conjunction, these three methods should provide a comprehensive insight into the role of sympagic meiofauna in sea-ice food webs. My hypotheses have been:

1. The sea-ice food webs are more complex than previously thought, since carnivorous, cilivorous and omnivorous feeding are common amongst sympagic meiofauna.
2. The feeding impact of sympagic meiofauna is more diverse than commonly assumed and may have been underestimated.
3. Sympagic meiofauna plays an important role in cryo-pelagic coupling.
4. Global warming may change the community composition and feeding strategies of Arctic sympagic meiofauna, which might have consequences for the entire Arctic marine food web.

1.5 Publications included in or related to my thesis

Chapters 2–4 of this thesis have been accepted or submitted for publication in peer-reviewed journals:

- **Kramer M**, Swadling KM, Meiners KM, Kiko R, Scheltz A, Nicolaus M, Werner I (in press) Antarctic sympagic meiofauna in winter: comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions. *Deep-Sea Res II*. doi: 10.1016/j.dsr2.2010.10.029—Chapter 2
- **Kramer M**, Kiko R (2010) Brackish meltponds on Arctic sea ice—a new habitat for marine metazoans. *Polar Biol*. doi: 10.1007/s00300-010-0911-z—Chapter 3

- **Kramer M**, Struck U, Schukat A, Kiko R, Werner I (under revision) Trophic positions of Arctic and Antarctic sympagic meiofauna and its role in cryo-pelagic coupling identified by stable isotopes and fatty acids. *Mar Ecol Prog Ser*—Chapter 4

In addition, other papers and manuscripts to which I made important contributions are included in the interpretations given in the synopsis and partly served as a base for the calculation of the feeding impact (Chapter 5, Kramer and Prowe in preparation):

- Marquardt M, **Kramer M**, Werner I (under revision) Vertical distribution patterns of sympagic meiofauna in fast and pack ice in the Canadian Beaufort Sea. *Polar Biol*
- Kiko R, Kern S, **Kramer M**, Mütze H (under revision) Colonization of newly forming Arctic sea ice by meiofauna – a case study for the future Arctic? *Mar Ecol Prog Ser*
- Siebert S, Anton-Erxleben F, Kiko R, **Kramer M** (2009) *Sympagohydra tuuli*: first report from sea ice of the central Arctic Ocean and insights into histology, reproduction and locomotion. *Marine Biol* 156:541–554
- Kiko R, **Kramer M**, Spindler M, Wägele H (2008) *Tergipes antarcticus* (Gastropoda, Nudibranchia): distribution, life cycle, morphology, anatomy and adaptation of the first mollusc known to live in Antarctic sea ice. *Polar Biol* 31:1383–1395

2 Antarctic sympagic meiofauna in winter: comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions

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2.1 Abstract

This study of Antarctic sympagic meiofauna in pack ice during late winter compares communities between the perennially ice-covered western Weddell Sea and the seasonally ice-covered southern Indian Ocean. Sympagic meiofauna (proto- and metazoans $> 20\,\mu$m) and eggs $> 20\,\mu$m were studied in terms of diversity, abundance and carbon biomass, and with respect to vertical distribution. Metazoan meiofauna had significantly higher abundance and biomass in the western Weddell Sea (medians: $31.1 \times 10^3\,\mathrm{m}^{-2}$ and $6.53\,\mathrm{mg\,m}^{-2}$, respectively) than in the southern Indian Ocean (medians: $1.0 \times 10^3\,\mathrm{m}^{-2}$ and $0.06\,\mathrm{mg\,m}^{-2}$, respectively). Metazoan diversity was also significantly higher in the western Weddell Sea. Furthermore, the two regions differed significantly in terms of meiofauna community composition, as revealed through multivariate analyses. The overall diversity of sympagic meiofauna was high, and integrated abundance and biomass of total meiofauna were also high in both regions (0.6–$178.6 \times 10^3\,\mathrm{m}^{-2}$ and 0.02–$89.70\,\mathrm{mg\,m}^{-2}$, respectively), mostly exceeding values reported earlier from the northern Weddell Sea in winter. We attribute the differences in meiofauna communities between the two regions to the older first-year ice and multi-year ice that is present in the western Weddell Sea, but not in the southern Indian Ocean. Our study indicates the significance of perennially ice-covered regions for the establishment of diverse and abundant meiofauna communities. Furthermore, it highlights the potential importance of sympagic meiofauna for the organic matter pool and trophic interactions in sea ice.

2.2 Introduction

The Southern Ocean is characterised by two profoundly different types of pack ice: first- and multi-year ice. The mainly divergent drift patterns of sea ice in the Southern Ocean cause large portions of the ice to be exported (Gow and Tucker III 1990), and this results in strong seasonality in sea-ice cover: in winter, up to $19 \times 10^6\,\mathrm{km}^2$ of the Southern Ocean is covered by sea ice, while the ice-covered area in summer can be as low as $2 \times 10^6\,\mathrm{km}^2$ (Comiso and Nishio 2008). Seasonally ice-covered areas thus make up the major part of the Antarctic sea-ice zone, and 90 % of the Antarctic sea-ice cover is first-year ice (Brierley and Thomas 2002). A typical example of a seasonally ice-covered region is the southern Indian Ocean, where sea ice is confined to a narrow band that extends to a maximum of no more than 300 km from the continent in some locations (Worby et al. 1998). Sea ice in this area is highly dynamic, characterised by a divergent net drift, and it is generally thinner than sea ice in the Weddell Sea (Worby et al. 1998). The Weddell Sea, in contrast, is one of the few Antarctic regions where geographic, oceanographic and meteorological conditions cause convergent sea-ice drift patterns, resulting in a perennial sea-ice cover (Brierley and Thomas 2002). Ice concentrations in the Weddell Sea are high, large proportions of thick multi-year ice and deformed ice are found (Gordon 1993, Haas et al. 2008a, 2009), and the snow cover is comparatively thick (Massom et al. 2001, Haas et al. 2008a, Nicolaus et al. 2009), particularly in the western regions (Willmes et al. in press). We hypothesise that these different sea-ice regimes—seasonal ice cover with young and first-year ice on one hand, perennial ice cover with multi-year ice on the other—host different communities of sympagic (sea-ice associated) organisms.

Sea ice is permeated with a system of brine channels that develops during its formation and growth when salt ions are rejected from the crystal lattice of water molecules; brine thus collects in between the ice crystals (Weissenberger et al. 1992, Cottier et al. 1999). These brine channels are inhabited by viruses, bacteria, fungi, microalgae, protozoans and metazoans, which, together with under-ice organisms, constitute the sympagic community (Brierley and Thomas 2002, Schnack-Schiel 2003). The metazoans and larger protozoans ($> 20\,\mu$m) living inside the brine channels of sea ice are referred to as sympagic meiofauna (Gradinger 1999a).

Protozoan meiofauna in Antarctic sea ice comprises mainly foraminiferans and ciliates (Garrison and Buck 1989, Gradinger 1999a, Schnack-Schiel et al. 2001), with heliozoans being reported only once (Garrison and Buck 1989). Metazoan meiofauna comprises mainly harpacticoid and calanoid copepods and acoel platyhelminthes (commonly referred to as "turbellarians") (Gradinger 1999a, Schnack-Schiel et al. 2001, Guglielmo

et al. 2007). Ctenophores (Dahms et al. 1990, Kiko et al. 2008b) and nudibranchs (Kiko et al. 2008a,b) have been reported in very few studies from the Weddell Sea, and never from the eastern part of the southern Indian Ocean.

In comparison to sea-ice algae, sympagic meiofauna has received only little attention, and studies during winter are particularly scarce. Antarctic sympagic meiofauna studies have usually focused on copepods (Swadling 2001, Guglielmo et al. 2007, Kiko et al. 2008b, Schnack-Schiel et al. 2008), with few publications dealing with other specific taxa (Janssen and Gradinger 1999, Kiko et al. 2008a). The only two general studies on Antarctic sympagic meiofauna communities by Gradinger (1999a) and Schnack-Schiel et al. (2001) focus on integrated abundance and biomass and summarise results from several cruises to the Weddell Sea, including one expedition in late winter. The present study aims to expand our knowledge of Antarctic sympagic meiofauna diversity, abundance, carbon biomass and vertical distribution patterns in late winter.

Given the large proportion of seasonally ice-covered regions in the Southern Ocean (Brierley and Thomas 2002), knowledge of the sympagic communities in these regions is of central importance for understanding the Antarctic sympagic ecosystem. Sympagic communities in seasonally and perennially ice-covered regions obviously have different options to colonise sea ice and are likely characterised by different successional histories. We therefore hypothesised that substantial differences exist between sympagic meiofauna communities in seasonally and perennially ice-covered regions. To test this hypothesis, we compare meiofauna communities between the seasonally ice-covered southern Indian Ocean and the perennially ice-covered western Weddell Sea.

2.3 Materials and methods

2.3.1 Field work

Analyses of Antarctic sympagic meiofauna communities in late winter were based on samples from the perennially ice-covered western Weddell Sea and the seasonally ice-covered southern Indian Ocean (Fig. 2.1, Supplement 2.S1). Samples in the western Weddell Sea were taken during the RV *Polarstern* cruise ANT–XXIII / 7 ("WWOS", August 24 to October 29, 2006), while sea ice in the southern Indian Ocean was sampled during the SIPEX expedition on RSV *Aurora Australis* (voyage 1, September 5 to October 17, 2007). Due to logistic constraints, and since winter cruises are scarce, sampling had to be conducted in two consecutive years, but took place during the same season.

In the western Weddell Sea, sea ice was sampled near the South Orkney Islands and east of the tip of the Antarctic Peninsula. Air temperatures during the study period were usu-

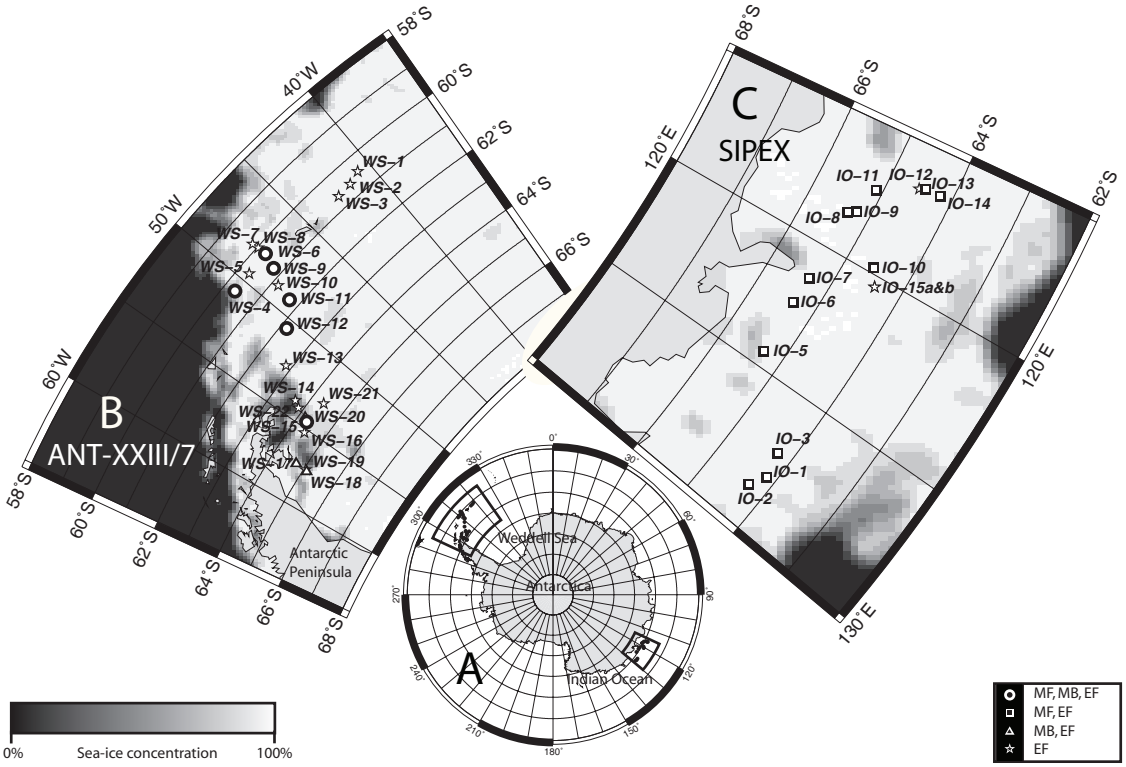

Figure 2.1: Stations sampled for community analyses of Antarctic sympagic meiofauna during SIPEX and ANT–XXIII / 7. **A** Overview with all stations from both cruises; areas for enlarged station maps (B) and (C) are highlighted. **B** Stations sampled in the western Weddell Sea during ANT–XXIII / 7 (August 24 to October 29, 2006) with sea-ice concentration from September 20, 2006. **C** Stations sampled in the southern Indian Ocean during SIPEX (September 5 to October 17, 2007) with sea-ice concentration from September 20, 2007. All sea-ice concentration data are based on AMSR-E data and were re-plotted in grey scale from www.seaice.de (Spreen et al. 2008). The legend refers to both (B) and (C); MF: meiofauna full cores, MB: meiofauna bottom-ice sections, EF: environmental full cores. Note the different scales in (B) and (C).

ally between -10 °C and -2 °C (Willmes et al. in press). The ice edge retreated southward during the period of the cruise, from 58–60 °S on August 24 to 59–65 °S on October 29 (cf. AMSR-E sea-ice maps from www.seaice.de, data not shown here). Ice concentration in most parts of the study area was above 9 / 10 (Haas et al. 2009). Modal ice thickness (from electro-magnetics) was 1.2–1.4 m (first-year ice), with secondary modes between 2.5 m and 3.0 m (multi-year ice); mean ice thickness was 2.1 m due to large amounts of ice thicker than 3 m (Haas et al. 2009). Modal snow thickness (from ground-penetrating radar) was 5–10 cm, with secondary modes between 30 cm and 45 cm (Haas et al. 2009) indicating second-year snow (Nicolaus et al. 2009). While thin and medium first-year ice with thin snow cover prevailed in the southern part of the study area, the northern part was characterised by deformed first- and second-year ice with thick snow cover (Haas et al. 2009, Willmes et al. in press). The sampling stations in the western Weddell Sea (Fig. 2.1 A, Supplement 2.S1) were pack ice, most of which probably originated from the

Larsen and Ronne polynyas (Haas et al. 2009). The samples from stations WS–4, WS–7, WS–11 and WS–21 were multi-year ice covered with second-year snow, whereas the samples from all other stations were first-year ice (Haas et al. 2009, Willmes et al. in press). Snow stratigraphies, sea-ice textures and bulk salinity profiles are shown in Willmes et al. (in press); information about biogeochemical conditions and ice algal photosynthetical parameters are given in Meiners et al. (2009).

In the southern Indian Ocean, sea ice was sampled in the 115–130 °E sector off Wilkes Land, East Antarctica. Air temperatures during the study period usually remained between -16 °C and -9 °C (Meiners et al. in press). The ice edge was located at 62–64 °S and retreated southward only slightly during the period of the cruise (cf. AMSR-E sea-ice maps from www.seaice.de, data not shown here). Ice concentration was usually between 8 / 10 and 9 / 10 (Worby et al. accepted). Modal ice thickness (from laser altimetry) was about 0.8 m with no strong secondary modes; mean ice thickness was 2.0 m due to the high percentage of surface ridging (Worby et al. accepted). The eastern part of the study area was characterised by high proportions of new and young ice with no or little snow cover, the northwestern part by thin first-year ice, while thicker first-year ice, thicker snow cover and strong deformation were recorded in the southwestern part (Worby et al. accepted). Sampled sea ice (Fig. 2.1 B, Supplement 2.S1) was drifting pack ice except for station IO–5, which was offshore fast ice hemmed in by large icebergs. All sampled ice was first-year ice, which was often rafted (Meiners et al. in press, Worby et al. accepted). The ice close to the coast had probably formed east of the study region, while ice floes close to the ice edge were from different origin (T. Worby, pers. comm.). Information about ice physics, biogeochemical parameters and ice algal biomass and composition are given in Meiners et al. (in press) and Worby et al. (accepted).

Level ice was sampled with an engine-powered KOVACS ice corer (inner diameter 9 cm) at 21 stations in the western Weddell Sea and 14 stations in the southern Indian Ocean (Fig. 2.1, Supplement 2.S1). At each station, snow thickness, ice thickness and freeboard were determined, air and snow temperatures were measured, and at least one full ice core (environmental full core EF) was taken for determination of ice *in situ* temperature, bulk salinity, brine salinity, relative brine volume, concentration of chlorophyll *a* (chl *a*) and phaeopigment *a* (phaeo), and ratio phaeo / chl *a* over the entire ice column. Another full core (meiofauna full core MF) was taken at six stations during ANT–XXIII / 7 and 12 stations during SIPEX for determination of abundance and carbon biomass of sympagic meiofauna taxa and eggs over the entire ice column on fixed samples. During ANT–XXIII / 7, an additional three bottom-ice sections of 5 cm length (meiofauna

bottom-ice sections MB) were taken at nine stations for live counts of sympagic metazoan meiofauna.

2.3.2 Determination of environmental parameters

At each sampling station, snow and ice thickness as well as freeboard at the coring site were determined as the median of up to 10 measurements. Air temperature close to the snow surface, snow temperature above the snow-ice interface and ice *in situ* temperatures were measured using a handhold thermometer (Testotherm 720, Pt 100 sensor, accuracy 0.2 °C). Ice temperature was measured on full core EF in intervals of 5–10 cm by inserting the temperature probe into small holes drilled with an electric drill. Subsequently, core EF was cut into sections of usually 5–10 cm length directly in the field. The sections were melted in the dark at +4 °C, and bulk salinity was measured with a conductivity meter (WTW microprocessor conductivity meter LF 196, accuracy 0.2). Brine salinity (accuracy better than 4) was calculated from ice temperature according to Assur (1958) and Frankenstein and Garner (1967). Relative brine volume (accuracy better than 4%) was calculated from ice temperature and bulk salinity according to Frankenstein and Garner (1967), the ice temperature for the calculation being adjusted to the values expected for the middle point of each section by calculating the weighted average of the two nearest measurements.

For chl *a* and phaeo measurements, subsamples of at least 250 mL of the melted sections of core EF were filtered on Whatman GF/F filters within 24 h after melting. Pigments were extracted in 90 % acetone for 6–12 h at -25 °C (Gradinger 1999b) after ultrasonic cell disruption during ANT–XXIII/7 or in 100 % methanol for 24 h at 0 °C (McMinn et al. 2007) without cell disruption during SIPEX. Pigment concentrations were determined by fluorometric measurements (Turner 10-AU fluorometer, detection limit 0.1 μg L^{-1}) before and after acidification with 0.1 N HCl. The different methodologies, particularly the use of different extraction agents, might have slightly impacted the data, but the effect is assumed to be small (Buffan-Dubau and Carman 2000).

2.3.3 Meiofauna community analyses

Sample processing and species identification

Core MF was cut into sections of usually 5–10 cm length directly after coring. The ice samples for meiofauna analyses (MF and MB) were melted in the dark at +4 °C in a surplus of 0.2 μm filtered seawater (200 ml per 1 cm core length, Gradinger 1999a). This method considerably reduces osmotic stress for the organisms during melting (Garrison and Buck 1986); although very delicate organisms, such as aloricate ciliates and acoel

platyhelminthes, may be disrupted even under moderate osmotic stress, this method is generally accepted (Horner et al. 1992) and commonly applied in studies on sympagic organisms (Nozais et al. 2001, Schnack-Schiel et al. 2001, Gradinger et al. 2005, Schünemann and Werner 2005), so that our data are readily comparable with the previous literature. Within 24 h after complete melting of the ice, organisms were enriched over a 20 μm gauze. MB samples were transferred into petri dishes for live counts of metazoan meiofauna performed immediately at 0 °C. MF samples were fixed with borax-buffered formaldehyde (2 % in sea water). These samples were later rinsed with water (MilliQ : tap water, v:v = 1:1) and transferred into petri dishes for abundance and biomass analyses.

Meiofauna and eggs were sorted and counted using a stereomicroscope equipped with transmitted and impinging light (Leica WILD MZ 12.5, 20–100× magnification; Leica MZ 16 F, 20–115× magnification). For identification and further characterisation of specific taxa and eggs, light and electron microscopes were also used (see Supplement 2.S4 for details). Protozoans were grouped into ciliates, foraminiferans and radiolarians; other protozoans, such as heterotrophic flagellates, were not considered. Within ciliates, the tintinnids were distinguished; foraminiferans were identified to species level whenever possible. Copepods were identified to species level as far as possible. For the platyhelminthes acoels and rhabditophors were distinguished. Nudibranchs (juveniles and adults) were identified to species level. Eggs and veliger larvae of *Tergipes antarcticus* were identified using the description given by Kiko et al. (2008a); eggs and veligers were assessed together, since late egg stages and early veliger stages could not be distinguished from one another in some of the fixed samples. Eggs of acoel platyhelminthes were identified by morphological comparison of the fixed eggs with (i) eggs from specimens collected during ANT–XXIII / 7 which reproduced in culture and (ii) eggs observed in the bodies of fixed sympagic acoels from ANT–XXIII / 7 (scanning electron microscopic images, see Supplement 2.S4 Fig. 2.S4.2 for details).

Assessment of abundance, carbon biomass and diversity

Abundance and carbon biomass of protozoans, metazoans and eggs were determined as bulk values (i. e. in relation to volume of melted ice) for each ice-core section. Integrated abundance and carbon biomass of the full cores MF (i. e. in relation to ice area) were also calculated in order to compare the stations and regions.

For calculation of carbon biomass, the carbon contents of meiofauna and eggs were determined from length and width principally according to Gradinger et al. (1999)—see Supplement 2.S2 Table 2.S2.1 for details.

For the assessment of metazoan diversity, the absolute number of species $\hat{S}$, Margalef's species richness d, Pielou's evenness J', Shannon–Wiener diversity H' and the expected species number in a sample of 100 individuals ES_{100} were calculated from integrated abundance (Clarke and Warwick 2001). For these calculations, it was assumed that the ctenophores, the acoel and rhabditophor platyhelminthes, the cyclopoid copepods and the harpacticoid copepods *Drescheriella* spp., *Ectinosoma* sp., *Diarthrodes* cf. *lilacinus*, *Harpacticus* sp. and "harpacticoid species 1" represented only one species each. Eggs and larvae were not included in the calculations. The data are thus conservative estimates.

2.3.4 Comparison of the two study areas

Two-tailed Mann–Whitney U-tests were performed to test for differences between the two regions in terms of (1) integrated abundance and carbon biomass of protozoans, metazoans and eggs and (2) metazoan diversity measures.

Integrated abundance of meiofauna, including eggs, was further analysed by means of non-parametric multivariate statistics to investigate patterns in the meiofauna community structure. To test for differences between the two regions, a global one-way analysis of similarities (ANOSIM, Clarke and Warwick 2001) was applied. Meiofauna taxa discriminating between the two regions and typifying taxa for each region were identified by the one-way similarity percentages method (SIMPER; Clarke and Warwick 2001). To visualize and further investigate grouping patterns of the stations, hierarchical agglomerative clustering with group-average linkage was performed, and significance of clustering was tested with a similarity profile test (SIMPROF, Clarke and Warwick 2001). Furthermore, non-metric multi-dimensional scaling (MDS) to two dimensions was conducted (Clarke and Warwick 2001).

Comparison of vertical meiofauna abundance profiles between stations and regions was complicated by the inherent differences in ice thicknesses as well as by the different cutting schemes applied during the two expeditions. To overcome these problems, each core was divided into five theoretical sections of 1 / 5 of the total core length, and the average bulk abundance was calculated for each theoretical section (as weighted arithmetic means of the abundances in the comprised sections). These were used in second-stage analyses (Clarke and Warwick 2001), defining the theoretical sections as inner factors and the stations as outer factors, thus investigating similarities and differences between stations in terms of vertical meiofauna distribution. A second-stage ANOSIM (ANOSIM2) and also a second-stage cluster analysis and MDS (Clarke and Warwick 2001) were conducted.

Environmental variables were investigated with the focus on relationships to patterns seen in meiofauna communities. In a first approach, vertical profiles of sea-ice parameters

were disregarded, using integrated pigment concentrations as well as average values of ice temperature, bulk salinity and derived measures. To investigate whether inter-regional differences in terms of integrated meiofauna communities were also reflected by environmental variables, two-tailed Mann–Whitney U-tests were applied to each environmental variable. Subsets of environmental variables best matching the grouping of stations based on meiofauna data were identified using the BIO-ENV procedure (Clarke and Warwick 2001), which was applied to similarity matrices from analysis of both integrated meiofauna communities and vertical meiofauna profiles. The environmental variables entered in the procedure were ice and snow thickness, bulk salinity, ice temperature, brine volume and chl *a* concentration; the variables excluded were considered to be either of minor relevance to integrated meiofauna abundance or highly correlated with the above-mentioned variables. In a second approach, vertical profiles of environmental sea-ice parameters were analysed: average values were calculated for theoretical core sections as described for the meiofauna analyses. Dissimilarities of stations in terms of profiles of different sub-sets of environmental sea-ice variables were calculated using the above-mentioned second-stage routine. The sub-sets analysed included (i) the full set, (ii) all abiotic variables, (iii) all biotic variables, (iv)–(x) all possible sub-sets of the set sea-ice temperature, relative brine volume and chl *a* concentration. Correlations with the pattern based on vertical meiofauna profiles were calculated using the RELATE procedure (Clarke and Warwick 2001).

All multivariate analyses were based on Bray–Curtis similarities or dissimilarities (Bray and Curtis 1957) calculated from fourth-root transformed abundance data, or on euclidean distances of z-standardised environmental variables. The significance level for all statistical tests was 5 %. Details of the statistical procedures are given in Supplement 2.S3.

2.4 Results

All data sets from this study are available online, doi:10.1594/PANGAEA.734773.

2.4.1 Environmental parameters

Level-ice thickness, snow thickness and freeboard on the sampling stations were significantly higher in the western Weddell Sea than in the southern Indian Ocean (Table 2.1). Negative freeboard was measured at stations WS–1, IO–3 and IO–10. Air and snow temperatures during sampling were significantly higher in the western Weddell Sea than in the southern Indian Ocean (Table 2.1).

Table 2.1: Medians and ranges of environmental parameters measured at the sampling stations in the western Weddell Sea and southern Indian Ocean. In case of sea-ice parameters, medians and ranges of point values calculated for each station (i. e. values averaged or integrated over full cores) as well as ranges of bulk values measured for each ice-core section are given—note the different units for integrated and bulk values in case of pigment concentrations ($mg\,m^{-2}$ and $\mu g\,L^{-1}$, respectively). Overall medians of point values are given where no significant difference between the regions was detected; significant differences in point values are marked with $\star$ (U-test, significance level 5 %). n denotes the number of stations where the respective parameter was measured. The full data sets, including vertical profiles, are available online, doi:10.1594/PANGAEA.734773.

	Medians and ranges of point values for stations (i. e. average or integrated values for full ice cores)							Ranges of bulk values for ice-core sections	
	Weddell Sea			Southern Indian Ocean			Overall	Weddell Sea	Southern Indian Ocean
Parameter	Med	Range	n	Med	Range	n	Med	Range	Range
Level-ice thickness [cm]	125	63–244	22	81	37–210	15	$\star$	—	—
Snow thickness [cm]	17	0–105	22	5	0–9	15	$\star$	—	—
Freeboard [cm]	+8	-2 to +23	22	3	-4 to +8	15	$\star$	—	—
Air temperature [°C]	-6.0	-16.0 to +6.1	22	-11.1	-20.1 to -5.6	15	$\star$	—	—
Snow temperature [°C]	-6.5	-10.9 to -0.3	22	-9.6	-15.7 to -5.5	11	$\star$	—	—
Sea-ice temperature [°C]	-4.5	-6.3 to -2.8	22	-4.5	-6.9 to -2.8	13	-4.5	-10.5 to -1.8	-11.9 to -1.7
Brine salinity	76.0	49.0–102.3	22	75.6	48.8–111.2	13	75.6	32.2–162.5	30.5–180.3
Bulk salinity	5.1	1.1–6.5	22	7.2	5.0–10.0	15	$\star$	0.0–14.0	2.1–18.7
Relative brine volume [%]	6.3	2.0–9.9	22	9.8	6.6–13.7	13	$\star$	0.0–33.6	2.2–29.5
Chl *a* [$mg\,m^{-2}$] or [$\mu g\,L^{-1}$]	8.0	1.2–70.8	19	1.2	0.1–13.6	15	$\star$	0.0–1339.8	0.0–74.8
Phaeo [$mg\,m^{-2}$] or [$\mu g\,L^{-1}$]	1.5	0.1–11.3	19	0.5	0.0–3.9	15	$\star$	0.0–192.5	0.0–36.8
Phaeo / chl *a*	0.2	0.1–0.5	19	0.3	0.2–0.5	15	0.3	0.0–1.0	0.0–0.6

Sea-ice temperature and, consequently, brine salinity (averaged over the full cores) did not differ significantly between the study regions (Table 2.1). Also the vertical profiles were generally similar in both regions, with temperatures usually increasing from the ice surface to the bottom-ice layer, where temperatures were at the freezing point of sea water. At a few stations in the western Weddell Sea there was also a slight increase in temperature near the ice surface, and at two stations the temperature was almost constant throughout the ice column. Bulk salinity and brine volume of the full cores were significantly lower in the western Weddell Sea than in the southern Indian Ocean (Table 2.1). Also the shapes of the bulk salinity profiles were different. In the southern Indian Ocean, all bulk salinity profiles were generally C-shaped; at most stations, the profiles were very smooth. In the western Weddell Sea, C-shaped profiles prevailed, but at most stations the profiles were irregular and the C-shape less distinct. Stations WS–4, WS–7, WS–11 and WS–21 exhibited I-shaped (linear) bulk salinity profiles.

Integrated concentrations of chl *a* and phaeo in the ice were significantly higher in the western Weddell Sea than in the southern Indian Ocean (Table 2.1). The ratio phaeo / chl *a*, in contrast, did not differ significantly between the two regions (Table 2.1).

2.4.2 Meiofauna communities

Taxonomic composition

In total 20 sympagic meiofauna taxa were recorded in this study, and different types of eggs were distinguished (Table 2.2). The eggs and several meiofauna taxa occurred frequently in the ice in both the western Weddell Sea and the southern Indian Ocean (Table 2.2), including acoel platyhelminthes and an unidentified ctenophore (see Supplement 2.S4 Fig. 2.S4.4 for photographs and further information). Others occurred mainly or exclusively in one of the two regions (Table 2.2): tintinnid ciliates, the foraminiferan *Turborotalita quinqueloba*, radiolarians and the harpacticoid copepod *Microsetella rosea* in the southern Indian Ocean; rhabditophor platyhelminthes (see Supplement 2.S4 Fig. 2.S4.1–2.S4.3 for photographs and further information), the nudibranch *Tergipes antarcticus*, several harpacticoid copepod species, the calanoid copepod *Stephos longipes* and cyclopoid copepods in the western Weddell Sea.

Table 2.2: Qualitative information on taxonomic composition of sympagic meiofauna and eggs in the western Weddell Sea and southern Indian Ocean (+++ abundant, ++ not abundant but frequent, + occasional occurrence, — not recorded) and on vertical distribution (x occurrence in internal or surface layers, o occurrence only in bottom layers, i. e. lowermost 20 cm).

Taxon	Occurrence		Vertical distribution
	Weddell Sea	Southern Indian Ocean	
Ciliata	+++	+++	
Tintinnida indet.	+	+++	x
Other Ciliata	+++	+++	x
Foraminifera	++	+++	
Neogloboquadrina pachyderma	++	+++	x
Turborotalita quinqueloba	—	+	x
Radiolaria	+	++	x
Ctenophora	++	++	x
Plathelminthes	+++	++	
Acoela indet.	+++	++	x
Rhabditophora indet.	++	—	o
Nudibranchia	++	+	
Tergipes antarcticus ad.	+[a]	—	
T. antarcticus juv.	++	+	x
Harpacticoida	+++	++	
Drescheriella glacialis, *D. racovitzai*	+++	—	x
Drescheriella spp. nauplii	+++		x
Ectinosoma sp.	+	—	o
Idomene antarctica	++	—	x
Diarthrodes cf. *lilacinus*	+	—	o
Nitokra gracilimana	+++	+	x
Microsetella rosea	—	+	x
Harpacticus sp.	+++	+	x
"Harpacticoida species 1"	+	—	x
Calanoida	++	+	
Paralabidocera antarctica	+	+	o
P. antarctica nauplii		+	o
Stephos longipes	++	—	x
S. longipes nauplii		+	o
Cyclopoida	+	—	x
Eggs	+++	+++	
Eggs and veliger larvae of *T. antarcticus*	+++	+++	x
Eggs of Acoela	+++	+++	x
Other eggs	+++	+++	x

[a] in non-quantitative large-volume samples only

Integrated abundance and carbon biomass, metazoan diversity

For most meiofauna taxa and eggs, individuals from the western Weddell Sea were generally bigger than individuals from the southern Indian Ocean, resulting in higher individual carbon contents for animals from the western Weddell Sea (Supplement 2.S2 Table 2.S2.2).

Abundance of sympagic meiofauna in total did not differ significantly between the western Weddell Sea and the southern Indian Ocean (Mann–Whitney U-test, significance level 5 %), whereas total meiofauna carbon biomass was significantly higher in the western Weddell Sea than in the southern Indian Ocean (Table 2.3). Protozoans usually dom-

Table 2.3: Medians and ranges of integrated abundance and carbon biomass of sympagic meiofauna and eggs from six full cores from the western Weddell Sea and ten full cores from the southern Indian Ocean. Overall medians are given where no significant difference between the regions was detected; significant differences are marked with ⋆ (U-test, significance level 5 %). The full data sets, including vertical profiles, are available online, doi:10.1594/PANGAEA.734773.

Taxon	Abundance in $10^3\,m^{-2}$					Carbon biomass in $mg\,m^{-2}$				
	Weddell Sea		Southern Indian Ocean		Overall	Weddell Sea		Southern Indian Ocean		Overall
	Med	Range	Med	Range	Med	Med	Range	Med	Range	Med
Meiofauna total	62.6	12.7–178.6	15.0	0.6–163.4	31.0	10.90	3.99–89.70	1.89	0.02–28.28	⋆
Protozoa total	20.7	2.5–85.0	14.0	0.2–139.2	14.0	3.91	2.76–8.47	1.85	0.00–28.23	3.53
Ciliata	20.0	1.4–84.9	6.1	0.2–63.7	9.2	2.38	0.13–6.27	0.18	0.00–4.49	0.48
Foraminifera	0.7	0.2–3.1	8.8	0.0–117.8	2.0	1.14	0.02–2.62	1.06	0.00–26.83	1.14
Radiolaria	0.2	0.0–0.9	0.3	0.0–9.9	0.2	0.01	0.00–2.20	0.04	0.00–2.17	0.01
Metazoa total	31.1	10.2–146.0	1.0	0.0–53.4	⋆	6.53	1.23–81.23	0.06	0.00–1.10	⋆
Copepoda CI–CVI	8.0	3.0–16.7	0.0	0.0–0.3	⋆	3.01	0.32–4.98	0.00	0.00–0.21	⋆
Copepoda NI–NVI	2.8	0.8–19.3	0.5	0.0–49.6	0.9	0.19	0.03–1.83	0.04	0.00–1.04	0.05
Plathelminthes	10.5	6.3–132.7	0.4	0.0–4.5	⋆	1.83	0.26–76.22	0.02	0.00–0.21	⋆
Eggs total	253.1	7.2–7064.3	20.1	6.6–217.7	31.5	35.90	0.50–5089.23	0.63	0.13–9.00	⋆
Eggs and veliger larvae of *Tergipes antarcticus*	4.9	0.0–17.4	3.1	0.2–32.8	4.5	0.07	0.00–0.52	0.03	0.00–0.44	0.04
Eggs of Acoela	225.3	0.0–7000.5	4.2	0.9–148.5	6.7	32.38	0.00–5083.09	0.18	0.03–6.67	0.27
Other eggs	13.7	0.3–46.4	9.6	3.4–36.4	10.6	2.48	0.06–5.62	0.41	0.08–2.48	0.98

Table 2.4: Contributions by several meiofauna taxa to integrated abundance and carbon biomass of total protozoans, metazoans or meiofauna, given in %. The full data sets are available online, doi:10.1594/PANGAEA.734773.

Contribution in terms of	Abundance				Carbon biomass			
	Weddell Sea		Southern Indian Ocean		Weddell Sea		Southern Indian Ocean	
Contribution by	Med	Range	Med	Range	Med	Range	Med	Range
Protozoa to meiofauna	28	18–71	92	32–100	40	9–69	96	3–100
Metazoa to meiofauna	72	29–82	8	0–68	60	31–91	4	0–97
Ciliata to Protozoa	95	52–100	50	1–100	63	5–100	25	0–100
Ciliata to meiofauna	26	11–71	39	1–73	9	3–47	12	0–63
Foraminifera to Protozoa	4	0–44	46	0–99	30	0–95	62	0–100
Foraminifera to meiofauna	2	0–9	43	0–94	10	0–66	59	0–98
Radiolaria to Protozoa	0	0–6	1	0–10	0	0–45	1	0–42
Radiolaria to meiofauna	0	0–1	1	0–9	0	0–18	0	0–41
Copepoda to Metazoa	52	9–73	50	15–93	46	6–94	65	35–95
Copepoda to meiofauna	23	7–58	3	0–34	24	6–49	2	0–63
Nauplii to Copepoda	23	8–84	100	77–100	11	1–40	100	30–100
Plathelminthes to Metazoa	48	25–91	50	6–85	53	6–94	35	5–65
Plathelminthes to meiofauna	33	10–74	3	0–34	22	3–85	1	0–34
Tergipes antarcticus to Metazoa	0	0–1	0	0–0	0	0–3	0	0–0
Tergipes antarcticus to meiofauna	0	0–1	0	0–0	0	0–3	0	0–0
Ctenophora to Metazoa	1	0–2	0	0–1	0	0–4	0	0–0
Ctenophora to meiofauna	0	0–1	0	0–0	0	0–2	0	0–0

inated the meiofauna communities in the southern Indian Ocean, while in the western Weddell Sea metazoans were usually dominant in terms of both abundance and biomass (Table 2.4).

Abundance and carbon biomass of protozoans in total, as well as of ciliates, foraminiferans and radiolarians separately did not differ significantly between the two regions (Fig. 2.2, Table 2.3). In the western Weddell Sea, ciliates dominated the protozoan community in terms of abundance and usually also in terms of biomass, followed by foraminiferans (Fig. 2.3, Table 2.4). In the southern Indian Ocean, abundance contributions from ciliates and foraminiferans were almost equal, and foraminiferans were usually dominant in terms of biomass. Radiolarian contribution to total protozoan abundance was always low, but they could contribute substantially to protozoan biomass.

Metazoan abundance and carbon biomass were significantly higher in the western Weddell Sea than in the southern Indian Ocean (Table 2.3). This trend was found for platyhelminthes as well as for copepodids (Fig. 2.2, Table 2.3). Abundance and biomass of copepod nauplii did not differ significantly between the two regions (Fig. 2.2, Table 2.3). Ctenophores appeared to be more abundant in the western Weddell Sea than in the south-

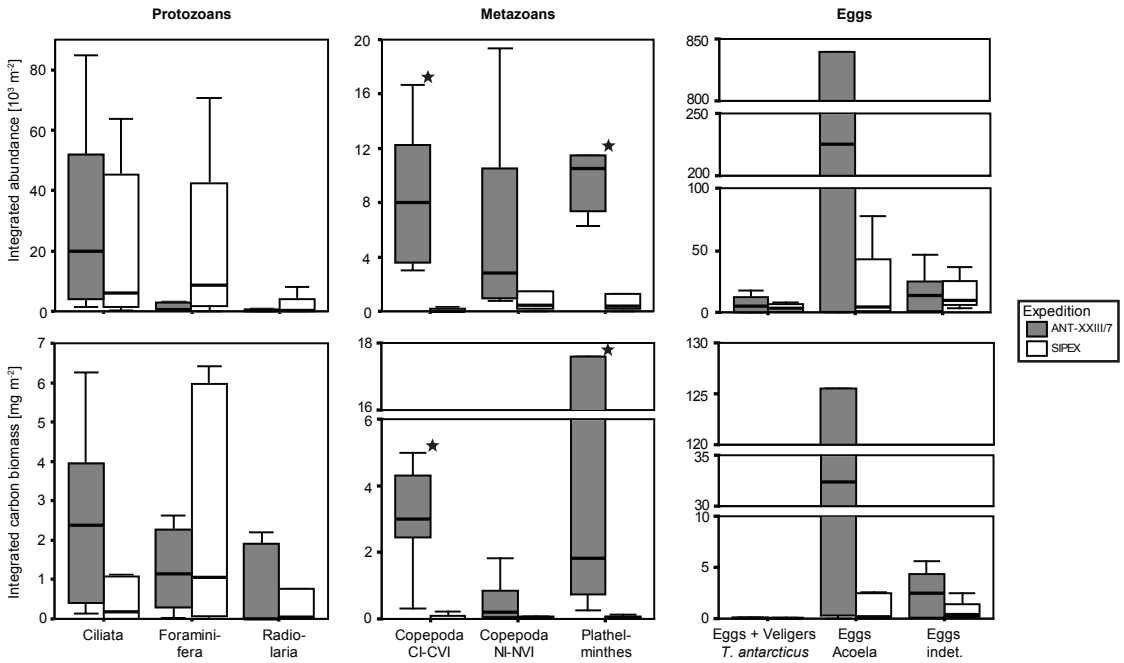

Figure 2.2: Boxplots of integrated abundance (top) and carbon biomass (bottom) of sympagic protozoan meiofauna, metazoan meiofauna and eggs in the two study regions, showing medians, quartiles and ranges from six stations in the western Weddell Sea (ANT–XXIII / 7) and 10 stations in the southern Indian Ocean (SIPEX). Outliers (with distance from quartiles being more than 1.5 times the interquartile distance) are not displayed. The metazoan taxa with very low abundance and biomass (ctenophores and juvenile *Tergipes antarcticus*) are not included. Significant differences between the regions are marked with ⋆. Note the different scaling of abundance and biomass axes.

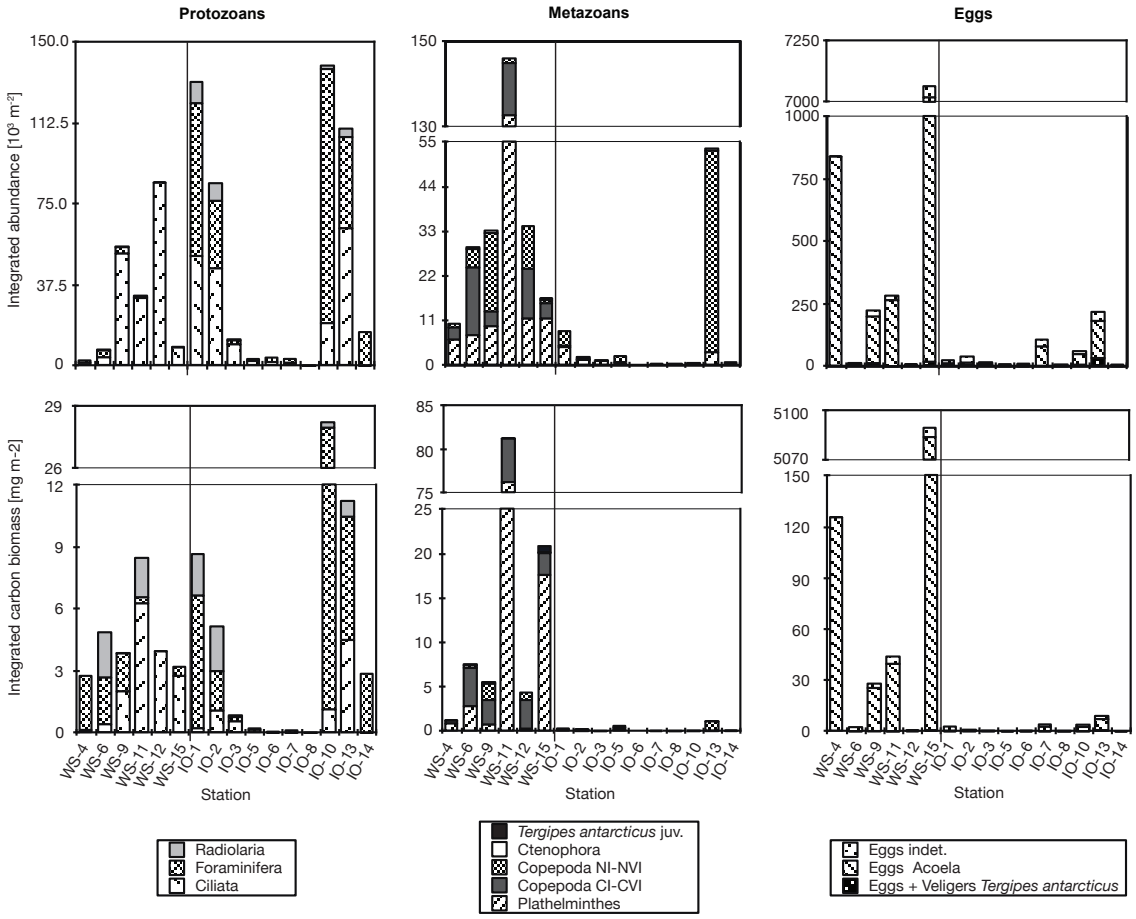

Figure 2.3: Integrated abundance (top) and carbon biomass (bottom) of sympagic protozoan meiofauna, metazoan meiofauna and eggs at each station, with contributions by the major taxa. Note the different scaling of abundance and biomass axes.

ern Indian Ocean (up to four individuals in three out of six full cores and 11 out of 23 bottom-ice sections in the western Weddell Sea; up to three individuals in two out of 12 full cores in the southern Indian Ocean). Juveniles of *Tergipes antarcticus* were found in very low numbers in both regions (one individual in one full core and two bottom-ice sections from the western Weddell Sea and in one full core from the southern Indian Ocean). In both regions, metazoans were always dominated by either copepods or platyhelminthes, in terms of both abundance and biomass (Fig. 2.3, Table 2.4). In the western Weddell Sea, platyhelminthes usually made lower contributions to abundance than copepods, but higher contributions to biomass. Contributions of both *Tergipes antarcticus* and ctenophores to metazoan abundance and biomass were always low.

The total abundance of eggs (including nudibranch veliger larvae) did not differ significantly between the two regions, whereas carbon biomass was significantly higher in the western Weddell Sea than in the southern Indian Ocean (Table 2.3). Neither abundance nor biomass of nudibranch eggs and veligers, acoel eggs or unidentified eggs differed sig-

nificantly between the two regions (Fig. 2.2, Table 2.3). In the western Weddell Sea, in particular, eggs were often considerably more abundant than meiofauna, and egg biomass could be more than 200 times higher than meiofauna biomass (Fig. 2.2, Table 2.3).

Table 2.5: Medians and ranges of metazoan diversity and evenness measures calculated from abundances in six full cores from the western Weddell Sea and 10 full cores from the southern Indian Ocean. Overall medians are given where no significant difference between the regions was detected; significant differences are marked with $\star$ (U-test, significance level 5 %).

Diversity measure	Metazoan diversity and evenness				
	Weddell Sea		Southern Indian Ocean		Overall
	Med	Range	Med	Range	Med
Species number $\hat{S}$	8.5	3.0–10.0	1.0	0.0–3.0	$\star$
Margalef's index d	0.7	0.2–0.9	0.0	0.0–0.2	$\star$
Expected species number ES_{100}	6.5	2.8–8.7	1.0	0.0–2.9	$\star$
Shannon–Wiener diversity H'	1.0	0.4–1.7	0.0	0.0–0.6	$\star$
Pielou's index J'	0.6	0.2–0.7	0.6	0.3–0.8	0.6

Metazoan diversity in the ice was significantly higher in the western Weddell Sea than in the southern Indian Ocean (Mann–Whitney U-test) in terms of several measures (species number $\hat{S}$, Margalef's index d, expected species number in a sample of 100 individuals ES_{100} and Shannon–Wiener diversity H'; Table 2.5). Evenness in distribution of individuals across the species present was not significantly different between the two regions (Pielou's index J'; Table 2.5).

The two study regions further differed significantly in terms of the meiofauna community composition including eggs (global one-way ANOSIM). This pattern was also clearly seen in cluster analyses (Fig. 2.4 A), revealing similarities of only 44 % between the regions, and illustrated by MDS (Fig. 2.4 B). The best discriminating taxa (SIMPER; average contribution to between-group dissimilarity > 5 % and average divided by standard deviation > 2) were *Drescheriella* spp. and unidentified harpacticoid copepods, both of which were abundant in the western Weddell Sea but absent or extremely rare in the southern Indian Ocean, as well as tintinnid ciliates, which showed an opposite pattern. Acoel platyhelminthes and unidentified ciliates were the most typifying for the western Weddell Sea, while unidentified eggs, eggs of acoels, eggs and veliger larvae of *Tergipes antarcticus* and tintinnid ciliates typified the community in the southern Indian Ocean (SIMPER; average contribution to within-group similarity > 10 % and average divided by standard deviation > 2).

Clustering and MDS (Fig. 2.4 A, B) further revealed that the meiofauna community at stations IO–1, IO–2, IO–10 and IO–13 (cluster α) differed from the six other stations (cluster β) in the southern Indian Ocean (significant differences, SIMPROF), with similarities of only 59 %. The α stations were generally characterised by intermediate total abundance and were usually dominated by protozoans (mainly foraminiferans), with high contributions from eggs. The β stations, in contrast, were characterised by low total

abundance, with eggs being dominant and protozoans (mainly ciliates) also contributing considerably to total abundance. The discriminating taxa between the two clusters (SIMPER; average contribution to between-group dissimilarity $> 10\,\%$ and average divided by standard deviation > 2) were tintinnids and radiolarians, both of which were abundant at the α stations, but absent or rare at the β stations. Also within the western Weddell Sea, two groups could be discerned: station WS–4 (cluster γ), characterised by high total abundance, pronounced dominance of eggs, low contribution from metazoans

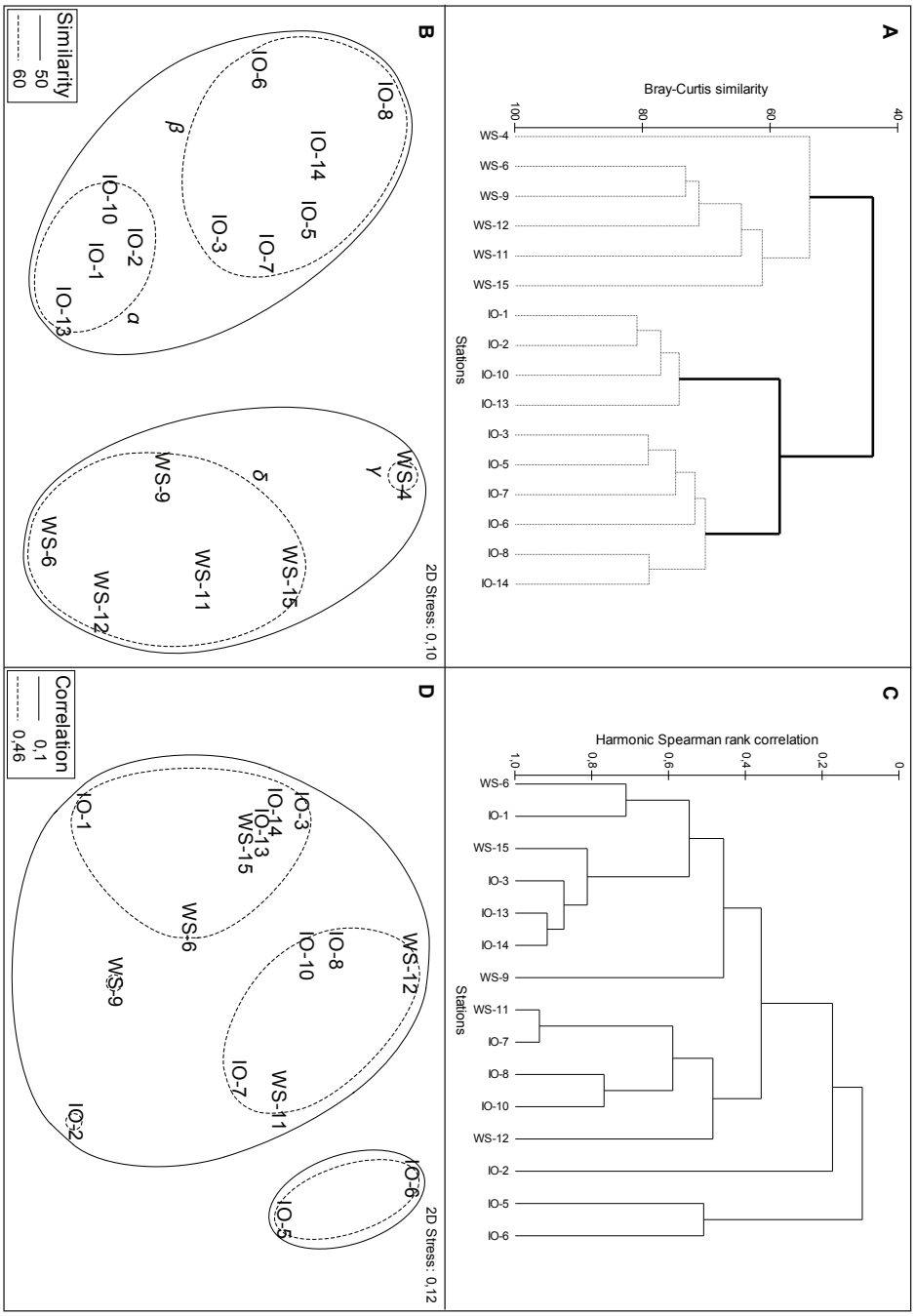

Figure 2.4: Grouping patterns of stations in terms of integrated abundance (**A**, **B**) and vertical abundance profiles (**C**, **D**) of sympagic meiofauna, including eggs. Cluster dendograms (**A**, **C**): hierarchical agglomerative; bold lines in (A) indicating significant clusters (SIMPROF, significance level 5 %). MDS plots (**B**, **D**): non-metric, with similarity levels from clustering (lines). See Supplement 2.S3 for details on statistical procedures.

and very low contribution from protozoans as well as low metazoan diversity; and stations WS–6, WS–9, WS–12, WS–11 and WS–15 (cluster δ) with intermediate or high total abundance, higher contributions from proto- and metazoans and comparatively high metazoan diversity. The groups within the regions did not seem to be related to the geographic position (cf. Fig.2.1).

Several subsets of sea-ice environmental variables (averaged or integrated over the full cores) matched well with the grouping patterns of stations based on meiofauna communities, with correlation coefficients for similarity matrices above 0.50 (BIO-ENV). Amongst these best-matching subsets, none contained the sea-ice temperature. The best-matching subset of three variables, with a correlation coefficient of 0.57, comprised snow thickness, ice thickness and bulk salinity.

Vertical distribution

Meiofauna in both regions was not restricted to the bottom-ice layer. Internal and surface communities were found at many stations, at times exceeding the abundance in bottom layers at the respective station (Fig. 2.5, Supplement 2.S5). Occurrence in internal or surface layers was most obvious for protozoans, but was also observed for several metazoan taxa, while other metazoans occurred exclusively in bottom layers (Table 2.2, Fig. 2.5, Supplement 2.S5).

Maximum bulk abundance of protozoans was found in a surface layer (uppermost 20 cm) in the western Weddell Sea and in bottom ice (lowermost 20 cm) in the southern Indian Ocean. Maximum metazoan and egg abundance was found in bottom ice in both regions.

Vertical carbon biomass profiles generally followed abundance profiles; only at some stations, biomass profiles were distinctly different from abundance profiles, mainly due to the relatively low biomass contributions of ciliates and of eggs and veliger larvae of *Tergipes antarcticus*. Highest bulk biomass of protozoans, metazoans and eggs was recorded in bottom layers in both the western Weddell Sea and the southern Indian Ocean.

Vertical meiofauna abundance profiles did not differ significantly between the two regions (ANOSIM2). Second-stage cluster analyses and MDS revealed five clusters, reflecting different types of vertical profiles (Fig. 2.4 c, d). The grouping patterns were not related to the geographic positions of the stations (cf. Fig. 2.1). The environmental variables assessed during this study matched the grouping of vertical meiofauna profiles very poorly (BIO-ENV, RELATE), with the exception of the subset of vertical pigment profiles (RELATE).

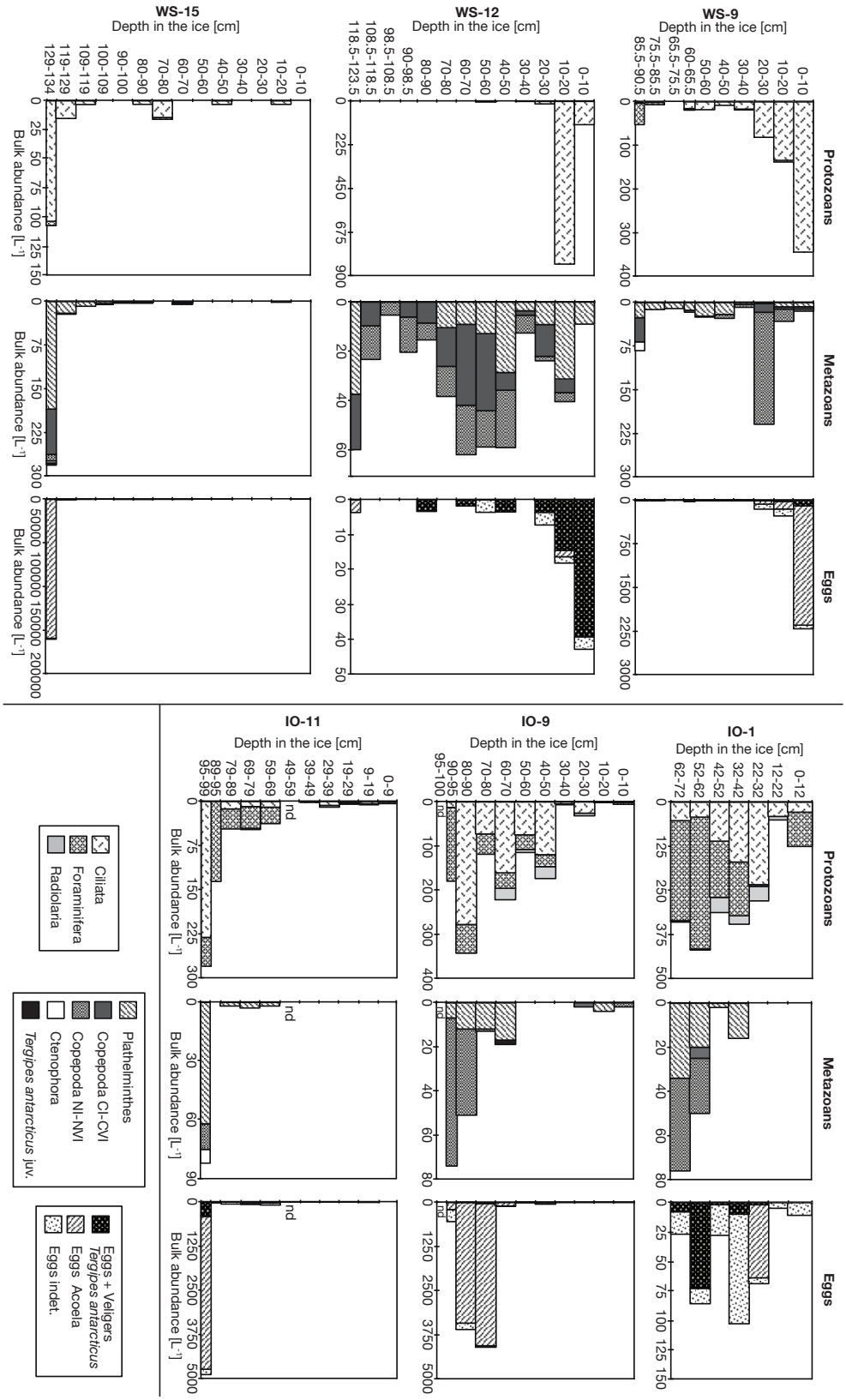

Figure 2.5: Examples of vertical bulk abundance profiles of sympagic protozoan meiofauna, metazoan meiofauna and eggs in sea ice in the western Weddell Sea (left) and the southern Indian Ocean (right). Note the different scaling of abundance axes. Vertical bulk abundance profiles of all stations are shown in Supplement 2.S5.

2.5 Discussion

We have found significant differences in sympagic meiofauna communities between the perennially sea-ice-covered western Weddell Sea and the seasonally sea-ice-covered southern Indian Ocean, which we attribute mainly to the presence of older ice in the western Weddell Sea, thus supporting our hypothesis. Our study has further revealed that in both regions sympagic meiofauna diversity, abundance and carbon biomass were higher than expected from the literature (Gradinger 1999a, Schnack-Schiel et al. 2001). The study indicates the significance of regions with perennial ice cover and old ice for the development of abundant and diverse sympagic communities and highlights the potential importance of meiofauna in the sympagic ecosystem.

2.5.1 Significance of old ice and perennial ice cover to sympagic metazoan meiofauna

Significant differences between sympagic meiofauna communities in the western Weddell Sea and the southern Indian Ocean were particularly obvious in metazoans, which were more diverse and abundant and had accordingly higher carbon biomass in the western Weddell Sea. We attribute these differences to the different sea-ice regimes of the two regions, the western Weddell Sea being characterised by perennial ice cover (Brierley and Thomas 2002) and older ice, the southern Indian Ocean by seasonal ice cover (Worby et al. 1998) and younger ice.

Generally, differences in abundance and biomass of sympagic meiofauna can be seasonal (Schünemann and Werner 2005) or spacial (Swadling et al. 1997a). In this study, samples from both regions were taken during the same months of two consecutive years and at quite similar latitudes. Although the lower air and snow temperatures in the southern Indian Ocean might indicate more hibernal conditions during sampling than in the western Weddell Sea, sea-ice temperature profiles were generally similar and average temperatures of full cores did not differ significantly between the two regions. We thus assume that sympagic organisms were not exposed to more hibernal conditions in the southern Indian Ocean than in the western Weddell Sea, and consequently that the observed differences were spacial rather than seasonal.

The significantly higher ice and snow thickness and lower bulk salinity in the western Weddell Sea compared to the southern Indian Ocean, as well as the irregularly C-shaped and I-shaped bulk salinity profiles in the former region compared to the distinctly C-shaped profiles in the latter, indicate that the ice sampled in the western Weddell Sea was generally older (Weeks 2001, Nicolaus et al. 2009). Also the significantly higher brine volumes in the southern Indian Ocean are related to the younger age of the ice,

since brine volume is positively correlated with bulk salinity if temperatures are constant (Frankenstein and Garner 1967). Hence, although most of the ice sampled for meiofauna analyses in the western Weddell Sea was first-year ice, it was older than the ice sampled in the southern Indian Ocean—a difference that can be attributed to the fact that most of the pack ice in the western Weddell Sea is formed in polynyas much further to the south (Haas et al. 2009, Willmes et al. in press), where the onset of ice formation is earlier in autumn.

Space limitation due to low relative brine volumes obviously did not strongly affect meiofauna, since the bigger metazoan meiofauna was more abundant in the western Weddell Sea in spite of smaller brine volume fractions. Freeboard, which can affect the development of surface communities (Horner et al. 1992), is also considered to be of minor significance for integrated meiofauna communities in winter. Given the good match between integrated meiofauna communities and the environmental parameters indicating sea-ice age, we suggest that the different age of the ice sampled is one of the main reasons for the observed differences in meiofauna communities. Communities in older ice have had more time to colonise the habitat and to further develop than communities in younger ice. The observed differences might partly be features of a succession in first-year ice, with a shift from communities characterised by protozoans, acoels and harpacticoids to communities with lower protozoan contributions and a more diverse metazoan fauna. To further investigate this issue, future studies should include time series in growing first-year ice as well as comparisons of first- and multi-year ice sampled within one region.

Besides the age of the actual ice floes, we suggest that general differences in the sea-ice regimes give additional explanation to the observed differences in meiofauna communities: perennial ice cover and high proportions of multi-year ice in the Weddell Sea (more than 40 % of the total sea-ice cover, S. Schwegmann, pers. comm.), particularly in its western regions (Brierley and Thomas 2002), standing in contrast to seasonal ice cover and almost exclusively young and first-year ice in the southern Indian Ocean (Worby et al. 1998), as observed also during the present study (Haas et al. 2009, Worby et al. accepted). In seasonally ice-covered regions, the ice needs to be newly colonised each winter when formed and is accessible only to species that can, at least during part of their life cycle, survive longer periods in the water column. In perennially ice-covered regions, in contrast, the large amounts of multi-year ice provide a stable habitat particularly to species that spend all phases of their life cycle in the ice and cannot survive longer periods in the water column. We consider it probable that this multi-year ice serves as a refuge during summer from which newly forming sea ice can be colonised in winter, as suggested for sympagic copepods by Schnack-Schiel et al. (1998). To further address this issue, future

studies should compare areas with different amounts of multi-year ice (e. g. western and eastern Weddell Sea) and experimentally investigate swimming ability and colonisation mechanisms of sympagic meiofauna.

Generalising our results, we suggest that at least sympagic metazoan meiofauna is more diverse and abundant in perennially ice-covered regions (even in first-year ice). Rhabditophores as well as several copepod species presumably rely on perennial ice cover—particularly some harpacticoids, which were amongst the discriminating taxa. Furthermore, platyhelminthes, copepods and ctenophores seem to reach higher abundance in older sea ice or perennially ice-covered regions. Sympagic protozoans, in contrast, appear to be less influenced by the age of the ice and sea-ice regime, at least in terms of total abundance; however, species-level analyses of ciliates may reveal differences also in protozoan communities.

2.5.2 High meiofauna diversity, abundance and biomass in winter

Our study has revealed that Antarctic sympagic meiofauna communities are more diverse than previously reported, reflected by the high number of different taxa found in both regions. Our study is the first to report sympagic occurrence of rhabditophor platyhelminthes and the harpacticoid copepod *Microsetella rosea*. Rhabditophors seem to be an important component of the sympagic meiofauna community in perennially ice-covered regions: in spite of low abundance, they can, due to their high individual carbon content, reach similarly high biomass to the acoels (this study, data not shown). Judging from morphology and anatomy, the rhabditophors were probably rhabdocoels (see Supplement 2.S4 Fig. 2.S4.3 for details). Several other taxa we found in sea ice have rarely been reported from this habitat before. The frequent occurrence of ctenophores and of the nudibranch *Tergipes antarcticus* in sea ice is particularly interesting regarding the functioning of the sympagic ecosystem: both ctenophores (Ju et al. 2004, Scolardi et al. 2006) and nudibranchs (Kiko et al. 2008a) are probably carnivores and might thus, in spite of low abundance and biomass, play a particularly important role in the sympagic food web. Sympagic ctenophores can obviously colonise different porous ice habitats in winter, such as bottom ice and slush layers. Judging from general morphological features, we assume that the ctenophores we found were not of the species *Callianira antarctica* reported from summer sea ice by Kiko et al. (2008b), but rather *Euplokamis* sp. (see Supplement 2.S4 Fig. 2.S4.4 for details).

Abundance and carbon biomass of Antarctic sympagic meiofauna in winter have been underestimated so far, since previous studies, based on principally similar methods, reported substantially lower abundance and biomass from a winter expedition to the north-

ern Weddell Sea (Gradinger 1999a, Schnack-Schiel et al. 2001) than found in our study for both the western Weddell Sea and the southern Indian Ocean. Meiofauna abundance in our study mostly exceeded abundance reported earlier from the northern Weddell Sea in winter (Gradinger 1999a) (median 14-fold higher in the western Weddell Sea, threefold higher in the southern Indian Ocean). The difference was even more distinct for meiofauna biomass (Gradinger 1999a) (median 27-fold higher in the wester Weddell Sea, fivefold higher in the southern Indian Ocean). For the western Weddell Sea, these findings can be attributed particularly to the high abundance and biomass of ciliates (medians 11-fold and 119-fold higher, respectively, than in the previous study (Schnack-Schiel et al. 2001)), but also to the high abundance of platyhelminthes (median threefold higher) and copepods (median twofold higher). For the southern Indian Ocean, the differences from the previous study were particularly due to high ciliate abundance and biomass (medians fourfold and ninefold higher, respectively), but also due to high foraminiferan biomass (median twofold higher). In the western Weddell Sea, we further found contributions of ciliates to total meiofauna abundance and biomass to be generally higher than previously reported from winter (twofold and fourfold higher contributions, respectively, regarding median abundance and biomass), while foraminiferan contributions to meiofauna abundance and biomass were substantially lower compared to the previous study (44-fold lower and fourfold lower, respectively) (Gradinger 1999a). Metazoan contribution to total meiofauna abundance was distinctly higher than in the previous study (twofold higher for total metazoans as well as for platyhelminthes and copepods) (Gradinger 1999a). In terms of biomass, total metazoan and platyhelminth contributions were slightly higher during the previous expedition (Gradinger 1999a); this is probably due to the fact that biomass calculations in the previous study were mainly based on carbon content data of Arctic sympagic meiofauna (Gradinger 1999a) instead of size measurements of the actual individuals studied.

There are many possible explanations for the differences between our data and those from the previous studies, including differences in sea-ice conditions between western and northern Weddell Sea (Eicken 1992, Schnack-Schiel et al. 2008) and inter-annual variability (Eicken 1992) as well as the generally observed heterogeneity of sympagic communities (Swadling et al. 1997a, Schnack-Schiel et al. 2008). Regardless of the reason for differences, our study indicates that the role of Antarctic sympagic meiofauna in the sympagic ecosystem has been underestimated so far. Both contribution of meiofauna to sea-ice particulate organic carbon (POC) and feeding impact of meiofauna are essentially functions of carbon biomass. The high meiofauna biomass we report thus implies an accordingly high POC contribution and feeding impact, questioning previous findings

by Gradinger (1999a), according to which Antarctic sympagic meiofauna does not control the accumulation of ice algae.

2.5.3 Occurrence of meiofauna internal and surface communities in winter

Our study contradicts previous observations that sympagic meiofauna is mainly restricted to the bottom ice in winter (Schnack-Schiel et al. 2001), since we found sympagic meiofauna to frequently occur in internal and surface layers. A restriction to bottom ice was only found for some metazoan taxa and is thus probably related to physiological limitations and life-cycle strategies of specific taxa, as has been proposed in recent studies from summer (Kiko et al. 2008b, Kiko 2010, Schnack-Schiel et al. 2008).

Our data suggest that, other than integrated abundance, vertical distribution of sympagic meiofauna is not strongly influenced by the age of the ice or the sea-ice regime, but rather controlled by other factors. Vertical distribution of meiofauna was correlated with vertical pigment profiles, which might either be an indication of trophic relationships, or a consequence of common factors controlling vertical distribution of both ice algae and sympagic meiofauna. However, vertical meiofauna distribution was not correlated with any of the abiotic variables measured, nor was it related to geographic positions. It does not seem to be related to ice textures, either (cf. Meiners et al. in press). It is therefore still a matter of question which factors control vertical distribution of sympagic organisms.

2.5.4 Conclusions

Multi-year ice and old first-year ice are probably of central importance for the establishment of diverse and abundant sympagic communities, at least in the case of metazoan meiofauna. If the observed warming in the region of the Antarctic Peninsula (IPCC 2007) results in a loss of multi-year ice in the western Weddell Sea, this may drive sympagic meiofauna communities into a state more similar to that in the southern Indian Ocean. In the Arctic Ocean, a reduction in sea-ice age has already been observed (Rigor and Wallace 2004, Maslanik et al. 2007, Nghiem et al. 2007), and the complete loss of multi-year ice has been predicted to occur before the middle of this century (Stroeve et al. 2007, Wang and Overland 2009). We assume that this development will result in a loss in diversity, abundance and biomass of sympagic meiofauna.

Diversity, abundance and biomass of Antarctic sympagic meiofauna have been underestimated so far. The high meiofauna diversity implies that interactions within the sympagic community, such as feeding and competition, are probably more complex than previously expected and ought to be taken into account in future ecological studies. Due to their high carbon biomass and potentially high contributions to the total sea-ice POC, sympagic

meiofauna and eggs are a potentially important food source for under-ice organisms such as krill. On the other hand, these may also have to compete with meiofauna for food, particularly since meiofauna ingestion rates are likely to be higher than previously assumed. Our study thus highlights the importance of sympagic meiofauna in sympagic and adjacent ecosystems. Hence, if a reduction in sea-ice age and loss of multi-year sea ice due to global warming result in reduced abundance and diversity of sympagic meiofauna, this will probably affect other components of the polar marine ecosystems.

2.6 Acknowledgments

We thank all those who helped us in the field and lab during ANT–XXIII / 7 and SIPEX, particularly Erika Allhusen (Alfred Wegener Institute, Bremerhaven) and Dai Fang-Fang (University of Zhejiang Wanli), who did most of the chlorophyll sampling and measurements during ANT–XXIII / 7. We thank Heike Wägele (University of Bonn) for identification of the nudibranch *Tergipes antarcticus*, Sigrid Schiel (Alfred Wegener Institute, Bremerhaven) for her help with harpacticoid taxonomy, Ole Riemann (University of Würzburg Graduate School), Alexander Kieneke (German Center for Marine Biodiversity Research, Wilhelmshaven) and Wilko Ahlrichs (University of Oldenburg) as well as Bart Tessens (University of Hasselt) for their help with platyhelminth taxonomy and electron microscopy. Kerri Scolardi (Mote Marine Laboratory, Sarasota, Florida) is thanked for giving her opinion on the unidentified ctenophore and for providing information about Antarctic planktonic ctenophores. We thank Dieter Piepenburg (Institute for Polar Ecology, Kiel) for his advice concerning statistics. We further acknowledge the effort of two anonymous reviewers, whose constructive comments helped to improve the manuscript. The constant support by captains, officers and crews of RV *Polarstern* and RSV *Aurora Australis* during the expeditions ANT–XXIII / 7 and SIPEX is gratefully acknowledged. This research was supported by the Deutsche Forschungsgesellschaft WE 2536 / 11–1 (to IW, MK, AS) as well as by the Australian Government through the Antarctic Climate and Ecosystems Cooperative Research Centre (ACE CRC) and Australian Antarctic Science Project 2767 (to KM) and 1358 (to KS).

2.S Supplementary material

2.S1 Stations and samples

Table 2.S1: Stations and ice-core samples taken during the cruises ANT–XXIII / 7 to the western Weddell Sea (WS–1, WS–2, etc.) with RV *Polarstern* and SIPEX to the southern Indian Ocean (IO–1, IO–2, etc.) with RSV *Aurora Australis*. FYI := first-year ice, MYI := multi-year ice; MF := meiofauna full core, MB := meiofauna bottom-ice section, EF := environmental full core.

Station		Date (yymmdd)	Coordinates		Ice type	Cores taken
			Lat	Long		
WS–1	PS 69 / 542	060908	60°27.86' S	40°48.61' W	FYI	EF
WS–2	PS 69 / 543	060909	60°35.92' S	41°38.38' W	FYI	EF
WS–3	PS 69 / 546	060910	60°37.83' S	42°36.38' W	FYI	EF
WS–4	PS 69 / 549	060919	60°19.71' S	50°47.91' W	MYI	MF, MB, EF
WS–5	PS 69 / 551	060920	60°19.71' S	49°29.63' W	FYI	EF
WS–6	PS 69 / 554	060921	60°17.55' S	48°00.15' W	FYI	MF, MB, EF
WS–7	PS 69 / 556	060922	59°50.10' S	48°05.05' W	MYI	EF
WS–8	PS 69 / 558	060923	60°01.93' S	48°01.25' W	FYI	EF
WS–9	PS 69 / 562	060924	60°44.93' S	48°19.53' W	FYI	MF, MB, EF
WS–10	PS 69 / 564	060926	61°11.07' S	48°54.11' W	FYI	EF
WS–11	PS 69 / 565	060928	61°41.94' S	49°06.80' W	MYI	MF, MB, EF
WS–12	PS 69 / 567	060930	62°10.20' S	50°34.30' W	FYI	MF, MB, EF
WS–13	PS 69 / 568	061001	62°49.75' S	52°25.33' W	FYI	EF
WS–14	PS 69 / 572	061002	63°39.71' S	53°51.89' W	FYI	EF
WS–15	PS 69 / 574	061003	64°17.61' S	54°34.61' W	FYI	MF, MB, EF
WS–16	PS 69 / 576	061004	64°24.95' S	55°16.06' W	FYI	EF
WS–17	PS 69 / 577	061005	64°43.55' S	57°19.86' W	FYI	MB, EF
WS–18	PS 69 / 578	061008	65°06.57' S	57°24.04' W	FYI	MB, EF
WS–19	PS 69 / 579	061009	65°03.13' S	57°20.63' W	FYI	EF
WS–20	PS 69 / 581	061011	64°11.25' S	54°23.77' W	FYI	MB, EF
WS–21	PS 69 / 584	061012	64°22.84' S	52°53.52' W	MYI	EF
WS–22	PS 69 / 585	061013	63°51.42' S	54°08.79' W	FYI	EF
IO–1		070911	64°08.40'S	128°00.00'E	FYI	MF, EF
IO–2		070912	64°17.40'S	128°36.00'E	FYI	MF, EF
IO–3		070914	64°13.80'S	127°06.60'E	FYI	MF, EF
IO–5		070918	65°18.60'S	124°27.00'E	FYI	MF, EF
IO–6		070920	65°21.00'S	122°21.00'E	FYI	MF, EF
IO–7		070922	65°20.40'S	121°18.00'E	FYI	MF, EF
IO–8		070925	65°19.80'S	118°31.20'E	FYI	MF, EF
IO–9		070928	65°12.60'S	118°20.40'E	FYI	MF, EF
IO–10		070929	64°34.20'S	119°48.00'E	FYI	MF, EF
IO–11		071002	65°06.00'S	117°19.20'E	FYI	MF, EF
IO–12		071005	64°31.80'S	116°34.80'E	FYI	EF
IO–13		071006	64°26.40'S	116°29.40'E	FYI	MF, EF
IO–14		071007	64°11.40'S	116°29.40'E	FYI	MF, EF
IO–15a		071010	64°24.60'S	120°22.20'E	FYI	EF
IO–15b		071010	64°24.60'S	120°22.20'E	FYI	EF

2.S2 Meiofauna carbon content

Table 2.S2.1: Equations for determination of indvidual carbon contents of sympagic meiofauna and eggs along with the literature references. Modifications and assumptions are specified. C:= carbon content in μg, L:= length in μm, W:= width in μm. For samples from SIPEX, measurements were performed on specimens from all sections, and carbon contents were calculated separately for each section from median values of length and width (medians from full cores being used if no measurements were available for the specific section); for samples from ANT–XXIII / 7, measurements were performed on specimens from bottom sections (specimens from other sections being measured only if less than 10 specimens from a bottom section of a specific core could be measured), and carbon contents were calculated separately for each core using median values of length and width. Length and width measurements were performed by image analyses (Gradinger et al. 1999) using a stereomicroscope (Leica MZ 16 F) equipped with a digital camera (Leica DC 200) and image analyses software (Leica IM 1000).

Taxon	Equation	References (and modifications and assumptions)
Tintinnida (Loricata)	$C = 2.2005\ L^{0.841}\ W^{1.682} \cdot 10^{-7}$	Volume according to Friedrich (1997) without correction factor, carbon content according to Menden-Deuer and Lessard (2000)
Other Ciliata (Aloricata)	$C = 1.5131\ L^{0.984}\ W^{1.968} \cdot 10^{-7}$	Volume according to Friedrich (1997), carbon content according to Menden-Deuer and Lessard (2000)
Neogloboquadrina pachyderma, *Turborotalita quinqueloba*, other Foraminifera	$C = 1.8640\ L\,W^2 \cdot 10^{-7}$	Volume assuming an ellipsoid with height = 0.5 width, carbon content according to Michaels et al. (1995)
Radiolaria	$C = 3.1416\ L\,W^2 \cdot 10^{-7}$	Volume assuming an ellipsoid with height = 0.75 width (median from 11 measurements), carbon content according to Michaels et al. (1995)
Ctenophora	$C = 5.0928\ L^{2.49} \cdot 10^{-8}$	According to Scolardi et al. (2006) for *Callianira antarctica* (winter values)
Acoela (Plathelminthes)	$C = 5.5935\ L\,W^2 \cdot 10^{-8}$	According to Friedrich (1997)
Rhabditophora (Plathelminthes)	$C = 7.1887\ L\,W^2 \cdot 10^{-8}$	According to Friedrich (1997) for Nematoda
Tergipes antarcticus (Nudibranchia)	$C = 7.1887\ L\,W^2 \cdot 10^{-8}$	According to Friedrich (1997) for Nematoda
Nitokra gracilimana (semi-cylindrical copepods)	$C = 5.8689\ L\,W^2 \cdot 10^{-8}$	Volume according to Warwick and Gee (1984), dry weight according to Friedrich (1997), carbon content according to Baguley et al. (2004)
Microsetella rosea (semi-cylindrical compressed copepods)	$C = 6.6025\ L\,W^2 \cdot 10^{-8}$	Volume according to Warwick and Gee (1984), dry weight according to Friedrich (1997), carbon content according to Baguley et al. (2004)
Ectinosoma sp., *Idomene antarctica*, *Diarthrodes* cf. *lilacinus* (pyriform copepods)	$C = 4.1921\ L\,W^2 \cdot 10^{-8}$	Volume according to Warwick and Gee (1984), dry weight according to Friedrich (1997), carbon content according to Baguley et al. (2004)
Drescheriella spp., *Harpacticus* sp., "harpacticoid species 1", Harpacticoida indet., Cyclopoida indet. (pyriform depressed copepods)	$C = 2.7248\ L\,W^2 \cdot 10^{-8}$	Volume according to Warwick and Gee (1984), dry weight according to Friedrich (1997), carbon content according to Baguley et al. (2004)
Stephos longipes, *Paralabidocera antarctica* (calanoid copepods)	$C = 2.1\ L^{3.4333} \cdot 10^{-10}$	Dry weight according to Mumm (1991) for *Calanus finmarchicus*, carbon content according to Båmstedt (1986)
Copepod nauplii	$C = 3.7098\ L\,W^2 \cdot 10^{-8}$	Dry weight according to Friedrich (1997), carbon content according to Baguley et al. (2004)
Eggs / veliger larvae of *Tergipes antarcticus*	$C = 3.06\ L^{2.88} \cdot 10^{-8}$	According to Fotel et al. (1999) for veliger larvae of *Mytilus edulis*
Other eggs	$C = 6.2724\ L\,W^2 \cdot 10^{-7}$	Volume assuming an ellipsoid with height = width, carbon content for eggs of calanoids according to Huntley and Lopez (1992)

Table 2.S2.2: Medians and ranges of length and width measurements and individual carbon contents (calculated from these values) for all meiofauna taxa and eggs, separately for each region. The number of individuals measured is also given. Some *Tergipes antarcticus* were measured alive, all other measurements are from fixed individuals.

Taxon	Length in μm						Width in μm						Individual carbon content in ng			
	Weddell Sea			Southern Indian Ocean			Weddell Sea			Southern Indian Ocean			Weddell Sea		Southern Indian Ocean	
	Med	Range	N	Med	Range	N	Med	Range	N	Med	Range	N	Med	Range	Med	Range
Ciliata																
Tintinnida	—	—	—	53	33–296	254	—	—	—	40	28–121	254	—	—	3.1	1.1–83.9
Other Ciliata	119	46–541	83	104	31–248	164	72	34–201	83	71	22–146	164	75	6.8–2520	63	1.9–622
Foraminifera																
Neogloboquadrina pachyderma	250	249–251	2	97	33–249	479	216	200–232	2	80	29–214	475	2180	1860–2520	120	5.3–2130
Turborotalita quinqueloba	—	—	—	123	118–129	2	—	—	—	109	106–111	2	—	—	271	248–295
Foraminifera indet.	179	81–275	15	56	33–95	91	139	61–237	15	48	30–89	86	643	56–2880	24	5.5–140
Radiolaria	213	58–289	7	85	52–129	103	234	54–270	7	78	49–114	102	3650	53–6610	160	39–530
Ctenophora	497	105–756	4	158	97–196	5	349	72–358	4	92	67–106	5	264	5.5–749	15	4.5–26.0
Plathelminthes																
Acoela	173	47–665	133	85	37–592	88	103	36–334	133	58	32–254	88	104	3.3–4140	16	2.1–2130
Rhabditophora	1450	474–1501	3	—	—	—	313	273–325	3	—	—	—	10200	2550–11400	—	—
Nudibranchia																
Tergipes antarcticus ad.	2916	2795–3038	2	—	—	—	485	—	1	—	—	—	49300	47300–51400	—	—
Tergipes antarcticus juv.	868	778–974	4	347	—	1	204	127–281	2		25 % of length		2590	903–5510	190	—
Harpacticoida																
Drescheriella spp.	469	247–864	87	—	—	—	143	77–246	88	—	—	—	262	40–1420	—	—
Ectinosoma sp.	485	400–531	3	—	—	—	157	115–177	3	—	—	—	500	222–694	—	—
Idomene antarctica	306	211–433	5	—	—	—	106	91–130	5	—	—	—	145	73–309	—	—
Diarthrodes cf. *lilacinus*	587	559–615	2	—	—	—	184	155–214	2	—	—	—	836	561–1180	—	—
Nitokra gracilimana	404	204–772	30	333	—	1	146	80–247	30	134	—	1	506	77–2770	349	—
Microsetella rosea	—	—	—	561	—	1	—	—	—	121	—	1	—	—	541	—
Harpacticus sp.	571	440–873	18	511	—	1	163	115–267	18	124	—	1	415	157–1690	213	—
"Harpacticoida species 1"	417	—	1	—	—	—	177	—	1	—	—	—	357	—	—	—
Harpacticoida indet.	404	218–948	45	—	—	—	122	91–251	45	—	—	—	164	49–1630	—	—
Calanoida																
Paralabidocera antarctica	611	597–624	2	685	—	1	168	165–172	2	222	—	1	770	713–829	1140	—
Stephos longipes	624	338–921	8	549	461–636	2	223	189–326	8	179	133–225	2	829	101–3160	533	294–886
Cyclopoida	479	102–850	8	—	—	—	249	144-341	8	—	—	—	806	57.8–2700	—	—
Copepoda nauplii	142	70–213	97	124	48–375	116	91	37–189	97	70	45–227	116	43	3.5–283	23	3.6–715
Eggs																
Eggs and veliger larvae of *Tergipes antarcticus*	80	40–180	93	89	36–148	187	60	30–88	51	60	25–105	189	9.3	1.3–96	12	0.92–54.0
Eggs of Acoela	65	20–165	56	40	24–100	431	61	20–160	56	36	20–79	431	140	4.7–2480	30	5.8–361
Other eggs	70	15–180	227	40	12–135	514	60	15–180	226	37	11–111	514	148	2.0–3420	32	0.78–976

2.S3 Details on statistical procedures

Table 2.S3: Details on statistical procedures used for the comparison of the two study regions.

Procedure	Specification	Parameters	Software	Used for
Mann-Whitney U-test	Two-tailed		SPSS (SPSS 2001)	Integrated abundance and carbon biomass; metazoan diversity; environmental parameters (for full cores)
ANOSIM	Global one-way	Max. 999 permutations for calculating the distribution of the test statistics	PRIMER v6 (Clarke and Gorley 2006)	Integrated abundance; vertical abundance profiles (with second-stage routine)
SIMPER	One-way		PRIMER v6 (Clarke and Gorley 2006)	Integrated abundance
Cluster analysis	Hierarchical agglomerative, group-average linkage		PRIMER v6 (Clarke and Gorley 2006)	Integrated abundance; vertical abundance profiles (with second-stage routine)
SIMPROF		1000 permutations for obtaining the mean similarity profile expected under the null hypothesis; 999 simulated profiles for calculating the distribution of the test statistics	PRIMER v6 (Clarke and Gorley 2006)	Integrated abundance
MDS	Non-metric, to two dimensions	Starting configuration based on result of MDS to three dimensions; numerical optimisation based on method of steepest descent and Kruskal fit scheme 1; iteration until improvement of stress (defined according to Clarke and Warwick (2001)) < 0.01 25 restarts	PRIMER v6 (Clarke and Gorley 2006)	Integrated abundance; vertical abundance profiles (with second-stage routine)
BIO-ENV		Harmonic Spearman rank correlation coefficient (defined according to Clarke and Ainsworth (1993)) for matrix comparison	PRIMER v6 (Clarke and Gorley 2006)	Environmental parameters (for full cores) vs. integrated meiofauna abundance; environmental parameters (for full cores) vs. vertical meiofauna abundance profiles (with second-stage routine)
RELATE		Harmonic Spearman rank correlation coefficient (defined according to Clarke and Ainsworth (1993)) for matrix comparison; max. 999 permutations for calculating the distribution of the test statistics	PRIMER v6 (Clarke and Gorley 2006)	Subsets of environmental parameters vs. meiofauna abundance (vertical profiles, with second-stage routine)
Second-stage routine	Inner factors: sections, outer factors: stations	Harmonic Spearman rank correlation coefficient (defined according to Clarke and Ainsworth (1993)) for matrix comparison	PRIMER v6 (Clarke and Gorley 2006)	Vertical abundance profiles; vertical profiles of environmental parameters
Transformation, standardisation	Overall transformation	Fourth-root transformation	PRIMER v6 (Clarke and Gorley 2006)	Abundance (for multivariate analyses)
	Individual transformation to approximate normality	Logarithmic, root or power transformation; substraction of mean, division by variance	PRIMER v6 (Clarke and Gorley 2006)	Environmental parameters (for multivariate analyses)

2.S4 Morphology and taxonomy

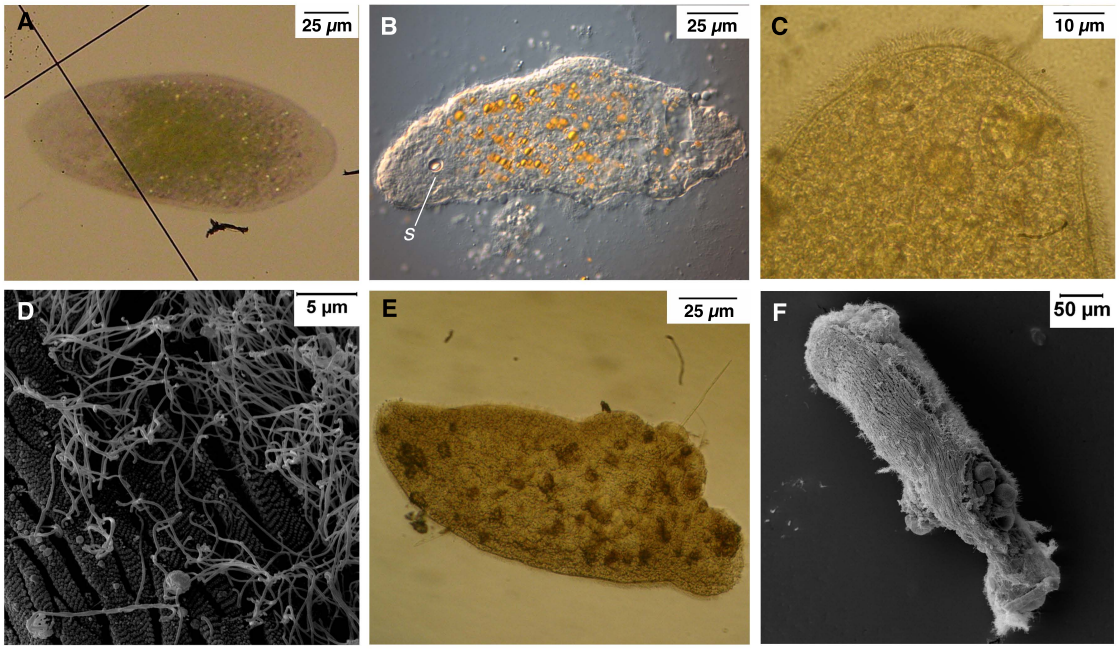

Figure 2.S4.1: Acoel platyhelminthes from Antarctic sea ice. The animals showed most of the characteristics Janssen and Gradinger (1999) describe for a "whitish species" of Antarctic sympagic acoels. The acoels were white in color and oval in shape, usually without deformations, swellings, protuberances or ruptures when observed alive at 0 °C (**A**, Leica WILD MZ 12.5 stereomicroscope). A globular tail was not noted in any of the specimens observed alive. The statocyst *s* with one statolith, characteristic of acoels, was evidently seen in the anterior part of the body; high temperatures (> 10 °C) during microscopy of live animals caused swellings and disintegration (**B**, Leica DMLB light microscope, 200×). The epidermis was evenly ciliated (**C**, Leitz Dialux 20 light microscope, 400×) and had characteristic longitudinal furrows (**D**, Zeiss DSM 940 digital scanning electron microscope, 20 kV, distance between lense and stub 7 mm, 3000×, software Orion 6.60.3). Formaldehyde-fixed acoels were often deformed (**E**, Leitz Dialux 20, 100×). Also acoels fixed with PAF (sodium cacodylate buffered isosmotic picric acid formaldehyde) were usually deformed, sometimes with ruptures, and had lost part of their cilia (**F**, Zeiss DSM 940, 20 kV, distance 10 mm, 200×). We assume that the swellings and ruptures were caused by high temperatures, osmolarity stress and mechanical strain during sample processing rather than being related to reproduction.

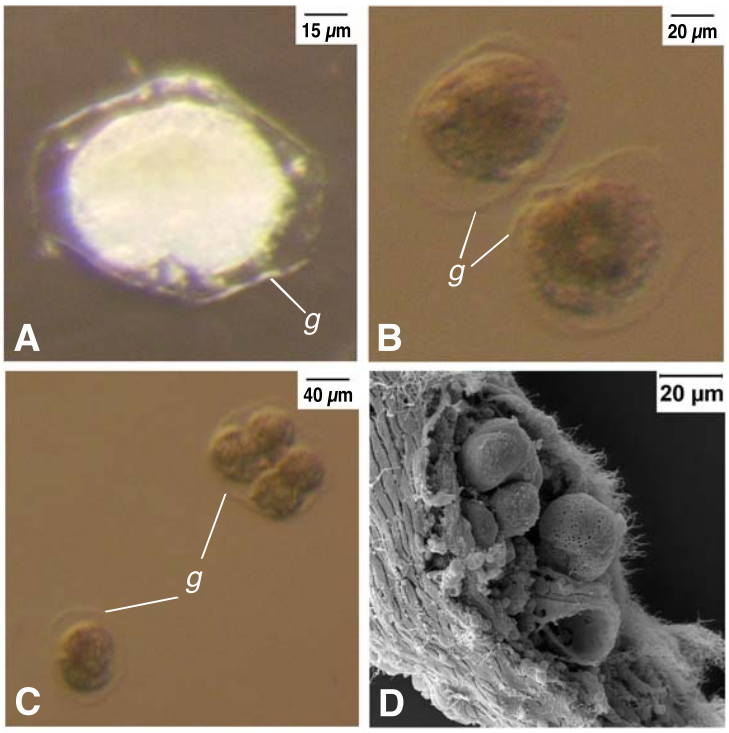

Figure 2.S4.2: Eggs of acoel platyhelminthes from Antarctic sea ice. The eggs were milky in colour and irregular in shape, roughly roundish or oval. They occurred either solitarily or in pairs or quartets, sometimes also in clutches of up to 20 eggs. Single eggs or clutches were usually surrounded by a gallert *g* and often attached to diatoms. The formaldehyde-fixed eggs (**A–C**, Leica MZ 16 F stereomicroscope, 100×) were morphologically similar to eggs of Antarctic sympagic acoels reproducing in culture (not shown) and to eggs observed inside the body of PAF-fixed acoels (**D**, Zeiss DSM 940, 20 kV, distance 7 mm, 775×).

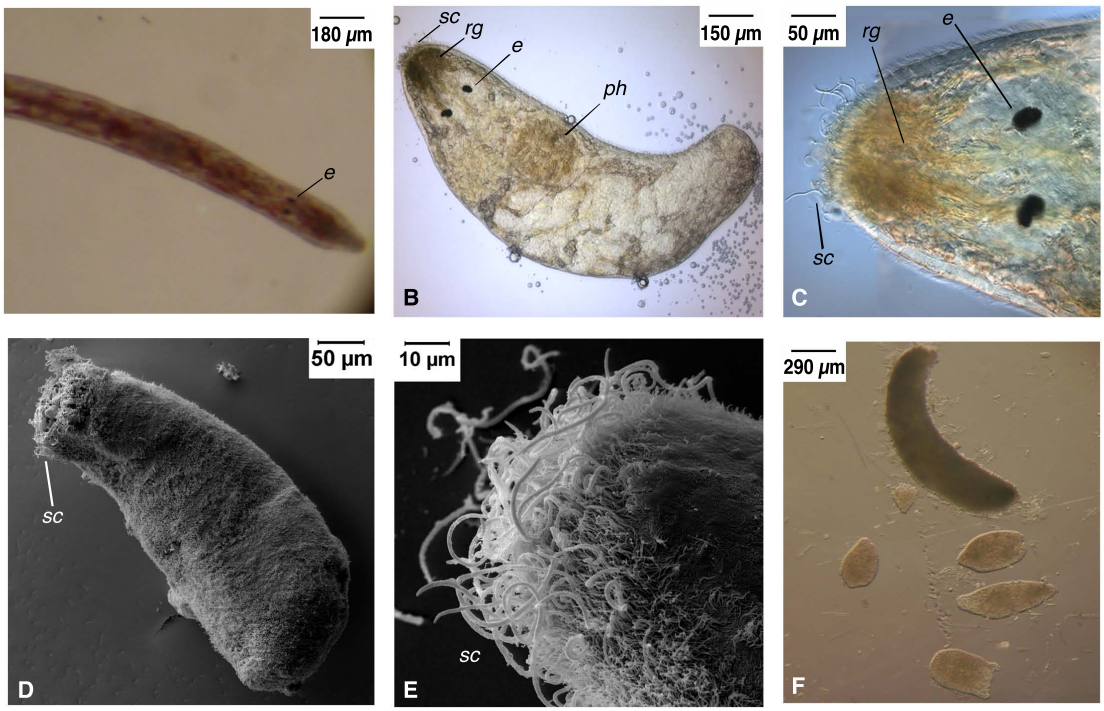

Figure 2.S4.3: Rhabditophor platyhelminthes from Antarctic sea ice. The rhabditophors had a very slender, elongated body with red pigment blots on the otherwise transparent epidermis and two prominent cerebral eyes *e* in the head region (**A**, Leica WILD MZ 12.5). The rhabdite gland *rg* characteristic of rhabditophores was observed in the anterior pole of the body in PAF fixed specimens (**B**, Leica DMLB, 100×; **C**, Leica DMLB, 400×). The pharynx *ph* situated on the right side of the body (**B**) is characteristic of rhabdocoels (B. Tessens, pers. comm.). The body was evenly ciliated, with particularly long sensorical cilia *sc* on the anterior pole of the body (**C**; **D**, Zeiss DSM 940, 10 kV, distance 10 mm, 200×; **E**, Zeiss DSM 940, 20 kV, distance 11 mm, 1000×). Some of the characteristic features were not possible to observe in formaldehyde-fixed specimens using a stereomicroscope: fixation caused loss of pigmentation and shrinkage of the body, and the cerebral eyes were hard to discern. The rhabditophores were nevertheless easy to distinguish from acoels, since the rhabditophores were less transparent and their body surface appeared more irregular due to the longer cilia (**F** showing acoels (bottom) and one rhabditophor (top), Leica MZ 16 F, 32×).

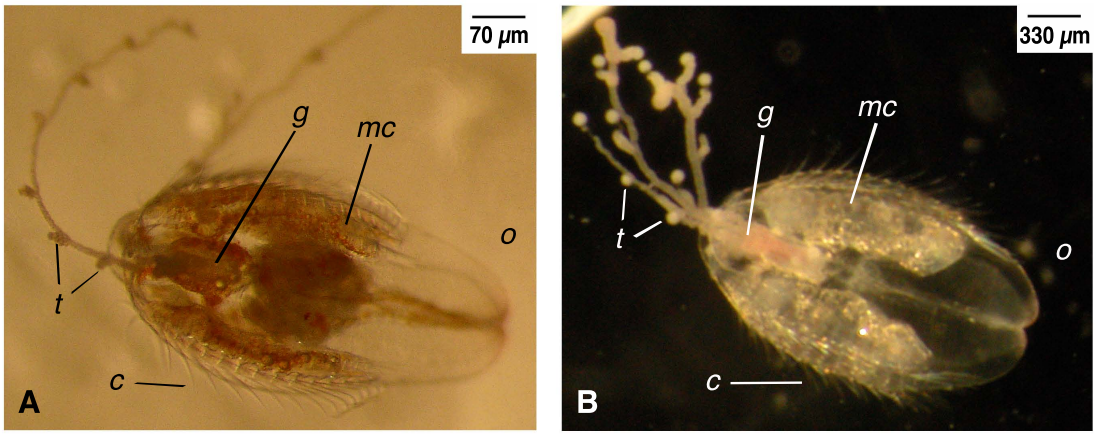

Figure 2.S4.4: A A ctenophore from Antarctic sea ice (Leica WILD MZ 12.5). The ctenophores were of ellipsoid shape with a slightly tapered oral end *o*, and without aboral projections. Their gut *g* had large meridional canals *mc*. The long tentacles (up to 5 times the body length) exited from the aboral end of the body; they had widely spaced, tightly coiled tentilla *t*. The comb rows *c* with remarkably long cilia stretched from the aboral end to about 3/4 towards the oral end of the body. The animals thus differed distinctly from *Callianira antarctica* Chun, 1898, which is more slender with aboral projections; *C. antarctica* also has smaller meridional cannals of different shape, its comb rows extend all the way from the aboral to the oral end, and the tentilla do not appear to be tightly coiled (Chun 1898; K. Scolardi, pers. comm.). Small individuals (100–800 μm) occurred regularly in the bottom ice in both Weddell Sea and southern Indian Ocean; small and larger (2–3 mm) individuals were found in a slush layer between rafted floes in the Weddell Sea. **B** A ctenophore from a surface water sample taken west of the Antarctic peninsula in September, in a region with high pack-ice concentration (photo by K. Scolardi). The animals are supposed to be a species of Pleurobrachiidae, possibly *Euplokamis* sp. (K. Scolardi and G. Matsumoto, pers. comm.), and might be the same species as the ctenophores from sea-ice samples.

2.S5 Vertical distribution

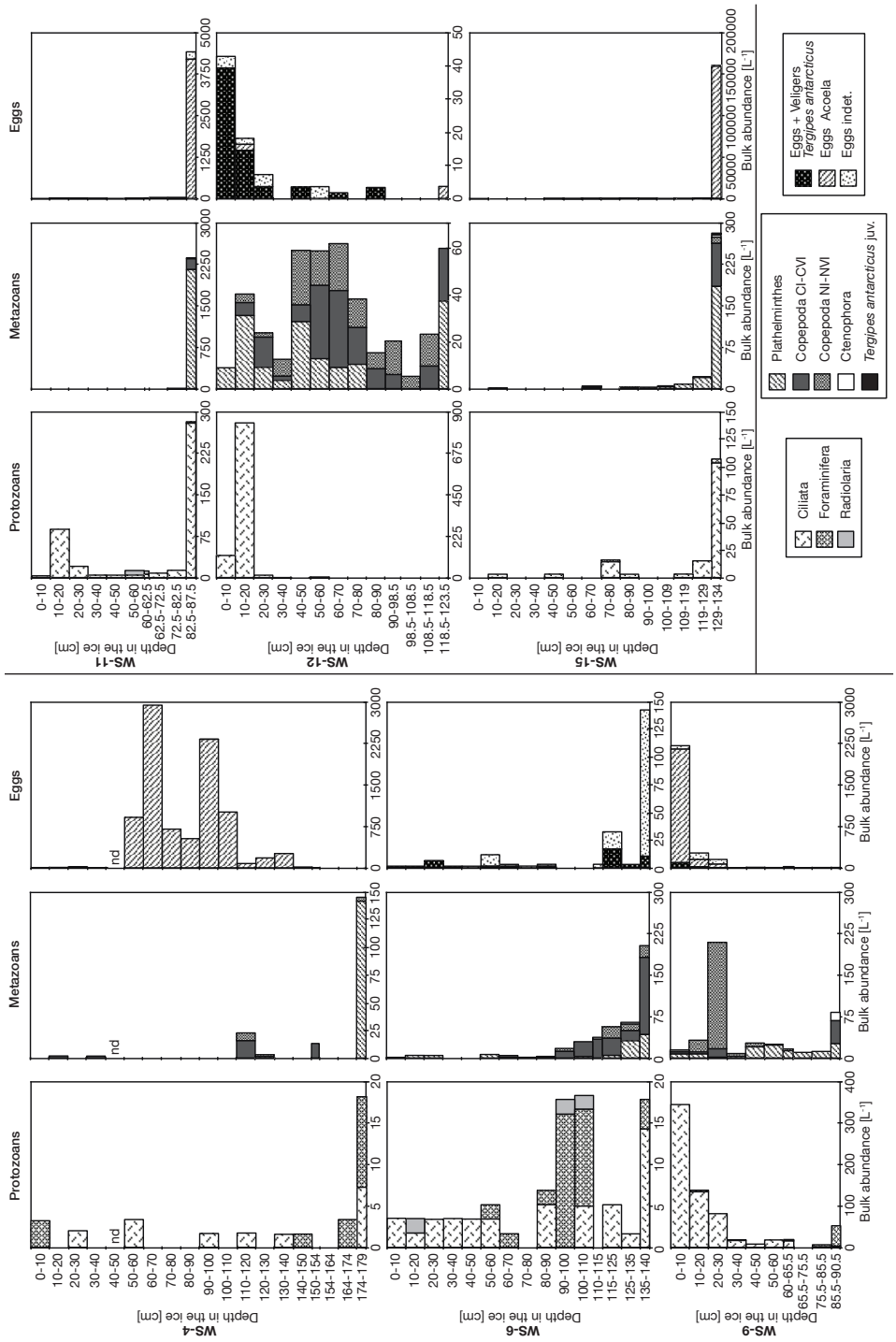

Figure 2.S5.1: Vertical bulk abundance profiles of sympagic protozoan meiofauna, metazoan meiofauna and eggs from sea ice in the western Weddell Sea. Note different scaling of abundance axes. Vertical carbon biomass profiles generally followed abundance profiles, with exception of protozoans at WS–4, WS–6, WS–9 and WS–1 and eggs at WS–12. Highest bulk biomass of metazoans, protozoans and eggs was recorded in bottom layers (1319 μgL^{-1}, 60 μgL^{-1} and 115739 μgL^{-1}, respectively).

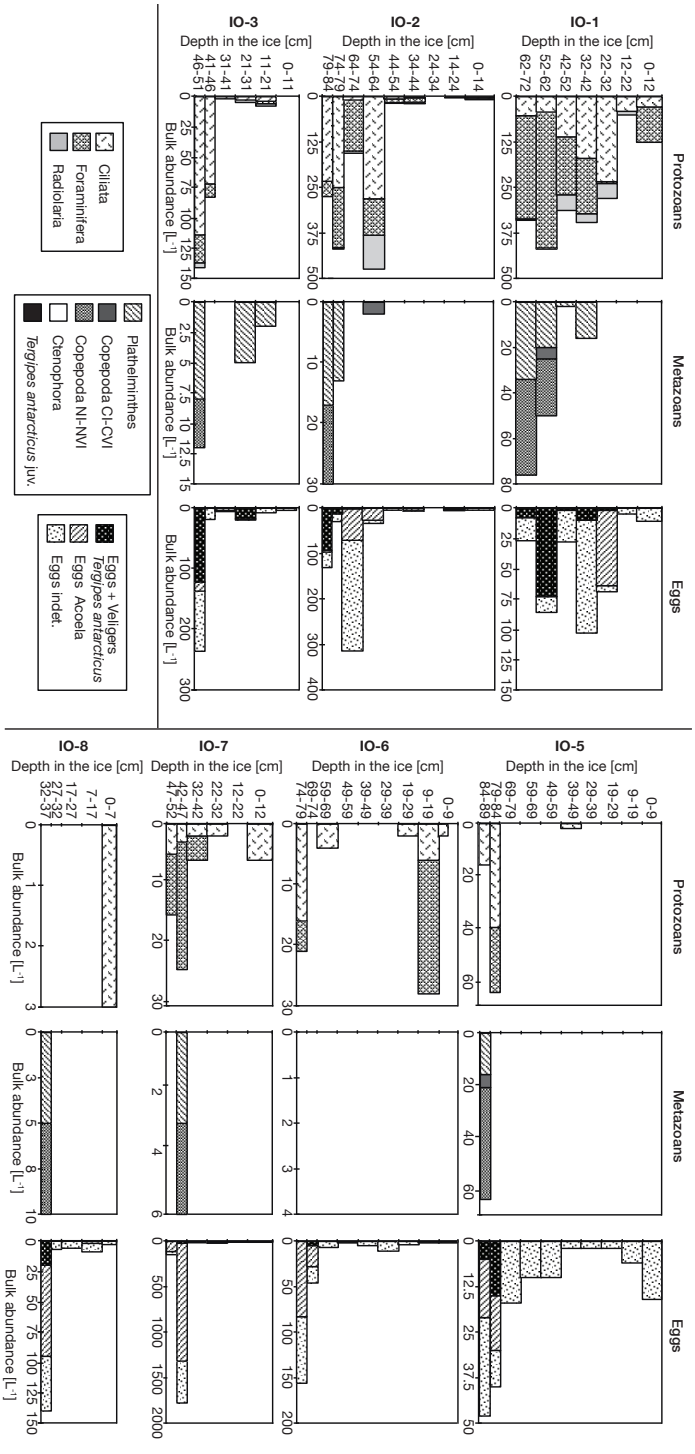

Figure 2.S5.2: Vertical bulk abundance profiles of sympagic protozoan meiofauna, metazoan meiofauna and eggs from sea ice in the southern Indian Ocean. Note different scaling of abundance axes. Vertical carbon biomass profiles generally followed abundance profiles, with exception of metazoans at IO–9, protozoans at IO–7, IO–9 and IO–11 and eggs at IO–9. Highest bulk biomass of metazoans, protozoans and eggs was recorded in bottom layers (17 μgL^{-1}, 254 μgL^{-1} and 209 μgL^{-1}, respectively).

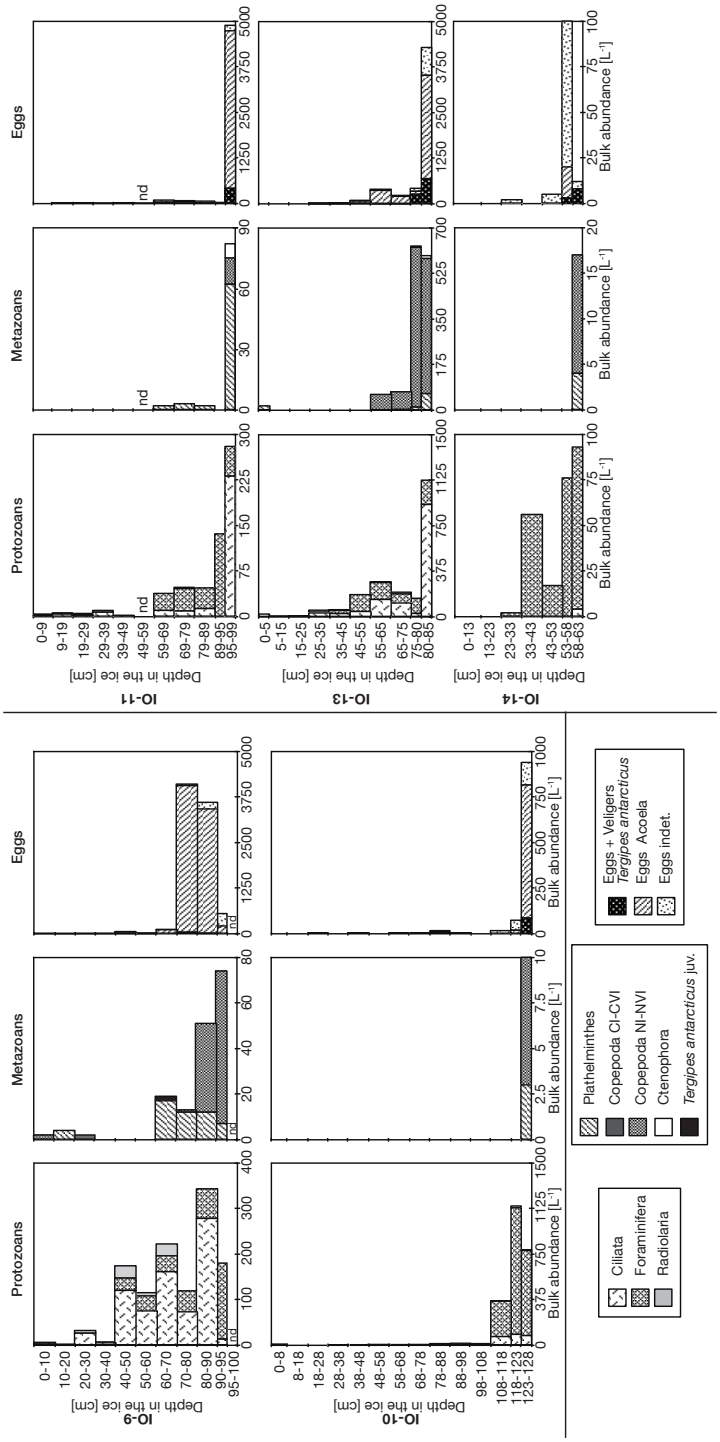

Figure 2.S5.2 (continued)

3 Brackish meltponds on Arctic sea ice—a new habitat for marine metazoans

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3.1 Abstract

Meltponds on Arctic sea ice have previously been reported to be devoid of marine metazoans due to fresh-water conditions. The predominantly dark frequently also green and brownish meltponds observed in the Central Arctic in summer 2007 hinted to brackish conditions and considerable amounts of algae, possibly making the habitat suitable for marine metazoans. Environmental conditions in meltponds as well as sympagic meiofauna in new ice covering pond surfaces and in rotten ice on the bottom of ponds were studied, applying modified techniques from sea-ice and under-ice research. Due to the very porous structure of the rotten ice, the meltponds were usually brackish to saline, providing living conditions very similar to sub-ice water. The new ice cover on the surface had similar characteristics as the bottom layer of level ice. The ponds were thus accessible to and inhabitable by metazoans. The new ice cover and the rotten ice were inhabited by various sympagic meiofauna taxa, predominantly ciliates, rotifers, acoels, nematodes and foraminiferans. Also, sympagic amphipods were found on the bottom of meltponds. We suggest that, in consequence of global warming, brackish and saline meltponds are becoming more frequent in the Arctic, providing a new habitat to marine metazoans.

3.2 Introduction

In summer, vast areas of the Arctic sea ice are covered with meltponds. Meltponds strongly affect the heat and mass balance of the sea ice cover through their low albedo, which is of particular interest in the context of global warming and has thus received considerable attention recently (Eicken et al. 2004, Flocco and Feltham 2007, Flocco et al. 2010). Moreover, meltponds have been proposed to play a very particular role in Arctic ecosystems, providing freshwater habitats for specific microbial communities amidst the saline marine environment (Gradinger and Nürnberg 1996, Ikävalko et al.

1996, Brinkmeyer et al. 2004). Little is known about these particular habitats, but they are reported to be devoid of metazoans due to harsh living conditions, and since specifically marine species are excluded by the fresh-water conditions (Ikävalko et al. 1996, Carstens 2001).

During the expedition ARK–XXII / 2 to the Central Arctic in late summer 2007, the ice at the bottom of meltponds was often strongly deteriorated, and meltponds were predominantly dark rather than blue (Fig 3.1), suggesting brackish conditions (Gradinger 1998, Carstens 2001). Furthermore, the frequently observed green and brownish colouration

Figure 3.1: Top Photographs of meltpond-covered sea ice taken from the bridge during ARK–XXII / 2, on Aug 3, 2007 (left) and Sep 8, 2007 (right). From mid August on, a cover of new ice formed on the meltpond surfaces (right). **Bottom** The rotten ice on the bottom of most meltponds had a honeycomb structure, i. e. was very porous, often with large thaw holes (photo courtesy by Stefan Kern).

hinted to considerable amounts of algae. These observations gave rise to the hypothesis that the meltponds might be inhabitable by metazoans. To address this hypothesis, we studied environmental conditions in meltponds and analysed the new ice covering the surface of meltponds as well as the rotten ice at the meltpond bottom for sympagic meiofauna (meta- and protozoans $> 20\,\mu$m inhabiting the brine channels of sea ice). For reference, also sub-ice water and the bottom layer of level ice were sampled.

3.3 Materials and methods

During the ARK–XXII / 2 cruise to the Central Arctic in Aug–Sep 2007 (Schauer 2008), visual sea ice observations from the bridge were conducted hourly (Aug 1–Sep 25; 75.6–89.6°N, 33.7°E–134.9°W), including estimation of the fraction of sea ice covered with meltponds (meltpond fraction).

During the second half of the expedition, when meltponds had frozen over, 15 meltponds were sampled at seven stations (84–88°N, 102°E–135°W; Supplement 3.S1). The water column of the ponds, the new ice on the surface and the rotten ice at the bottom of the ponds were sampled to obtain information on living conditions as well as on sympagic meiofauna inhabiting the ice and amphipods living on the pond bottom. For comparison, also samples of level ice (bottommost 5 cm) and sub-ice water (0 m and 5 m below the ice) were taken adjacent to the ponds at some stations (Supplement 3.S1).

Cores of new, rotten and level ice for environmental parameters and meiofauna counts were taken with an engine-powered KOVACS ice corer (inner diameter 9 cm). Additional non-quantitative ice samples for meiofauna analyses were obtained by scraping or cutting the underside of blocks of ice. Samples from the pond water column as well as water samples from the interstices and thaw holes of the rotten ice (interstitial water) for environmental parameters were taken with a hand pump. Sub-ice water samples for the analysis of environmental parameters and sub-ice fauna were taken with a hose (Schünemann and Werner 2005) and an under-ice pump (Werner and Martinez Arbizu 1999), respectively. Amphipods were caught from meltponds using a suction tube.

The pond depth at the coring site (from the pond bottom to the water surface) and the length of ice cores were measured with a ruler. The temperature of the new ice and rotten ice cores for the analysis of environmental parameters was measured according to Horner et al. (1992) (Testotherm 720, Pt 100 sensor, accuracy 0.2 °C). The temperature and salinity profiles of the pond water column were recorded before sampling the water and the rotten ice (WTW microprocessor conductivity meter LF 196, accuracy 0.2). Cores of new ice and rotten ice for environmental parameters were melted separately in the dark at $+4$ °C, and the bulk salinity of the melted ice was measured. Brine salinity and brine

volume fraction of the ice were calculated according to Assur (1958) and Frankenstein and Garner (1967), respectively. In case of rotten ice, the calculated brine volume fraction probably strongly underestimates the actually inhabitable space due to the drainage of interstitial water from the larger pores, and brine salinity probably reflects conditions in narrow brine channels only.

Subsamples of melted ice and water samples were filtered onto Whatman GF/F filters, pigments were extracted in acetone, and chlorophyll *a* concentrations were determined fluorometrically (Turner 10-AU fluorometer, detection limit 0.1 $\mu g L^{-1}$) (Gradinger 1999b, Kramer et al. in press). Concentrations in ice are given as bulk concentrations (i. e. in relation to the volume of melted ice, not of brine)—actual concentrations in brine would be higher, depending on the brine volume fraction.

Ice samples for sympagic meiofauna analyses were melted in the dark at $+4\,°C$ in a surplus of 0.2 μm filtered seawater to reduce osmotic stress for the organisms (Garrison and Buck 1986), and meiofauna was enriched over a 20 μm gauze. Meiofauna and sub-ice fauna were sorted alive for assessment of taxa and rough estimation of contributions. Meiofauna abundance was determined in one new-ice sample and four level-ice samples (Supplement 3.S1).

3.4 Results

The meltpond fraction was usually 20–40 % of the ice cover.

Details on environmental conditions in meltponds are given in Supplement 3.S2. Meltpond depth ranged between 30 cm and 60 cm, which was about 1/3 of the level-ice thickness. The ice at the bottom of the meltponds (rotten ice) had a honeycomb structure, i. e. extremely porous with large brine channels and often with thaw holes (Fig. 3.1). The meltponds were usually brackish to saline throughout the water column: salinities at the pond bottom were mostly similar to sub-ice water salinities, while higher up in the pond water column as well as in interstitial water (from the rotten ice) salinities were usually markedly lower. In terms of algal pigments, the water column of meltponds was similar to sub-ice water, while the interstitial water had elevated values more similar to bottom level ice.

Both the rotten ice at the pond bottoms and the new ice cover on the pond surfaces had similar characteristics as bottom level ice in terms of bulk salinity and calculated brine volume fraction (in case of rotten ice probably underestimated due to drainage of interstitial water during sampling). Calculated brine salinity in both ice habitats (for rotten ice reflecting conditions in narrow brine channels) was intermediate between that of bottom level ice and pond water. In general, pigment bulk concentrations in new ice were lower

Table 3.1: Sympagic meiofauna and amphipods inhabiting the meltponds in the Central Arctic sampled during ARK–XXII / 2. For reference, meiofauna from level ice (bottom 5 cm) adjacent to the meltponds and sub-ice fauna at meltpond stations (from 0 m below the ice) are also listed. Taxa found in meltponds are in bold letters. +++ abundant and dominant, ++ abundant, + present in low abundance, — not observed, nd = no data. For meltpond MP–1, also abundance in new ice (from one core) is given. For level ice, the abundance range (from four stations with triplicate samples) is given. Some important environmental parameters are also displayed (S = salinity, chl a as bulk concentration for ice).

	Meltponds								Level ice		Sub-ice layer
	New ice					Rotten ice			Bottom 5 cm		0 m
	MP–1	MP–5	MP–6(a–c)	MP–8a	MP–8(b–c)	MP–1	MP–2b	MP–5			
Ciliata indet.	+++ 218 L^{-1}	nd	+	+++	+++	++	nd	++	+ to +++	147–740 L^{-1}	nd
Neogloboquadrina pachyderma	++ —	—	+	+		+++	nd	+	— to +	0–3 L^{-1}	++
Radiolaria indet.	— —	—	—	—	—	—	nd	—	— to +	—	— to +
Acoela red	+ —	+++	+	—	—	—	nd	—	— to +++	0–77 L^{-1}	—
Acoela white	— —	—	—	—	—	—	nd	—	— to +	0–9 L^{-1}	—
Acoela white-rose	— —	—	—	—	—	—	nd	—	— to +	0–5 L^{-1}	—
Nemertea indet.	— —	—	—	—	—	—	nd	—	— to +	—	—
Nematoda indet.	+ —	++	—	—	—	—	nd	—	— to ++	0–59 L^{-1}	—
Rotifera indet.	++ 9 L^{-1}	++	+++	++	+++	—	nd	+++	+ to +++	3–54 L^{-1}	+
***Halectinosoma* spp.**	— —	+	—	—	—	—	nd	+	+ to ++	0–30 L^{-1}	+
***Tisbe* spp.**	— —	+	+		+	—	nd	+	— to ++	0–7 L^{-1}	+
Calanus spp.	— —	—	—	—	—	—	nd	—	— to +	—	— to +
Metridia longa	— —	—	—	—	—	—	nd	—	—	—	— to +
Eurytemora richingsi	— —	—	—	+	—	—	nd	—	—	—	—
Calanoida indet.	— —	—	—	—	—	—	nd	—	—	—	+
Oithona* cf. *similis	— —	—	—		+	—	nd	—	— to +	—	++ to +++
Cyclopoida indet.	— —	—	—	—	—	—	nd	+	— to +	0–7 L^{-1}	— to +
Nauplii Copepoda indet.	+ —	—	—		+	—	nd	+	— to ++	0–32 L^{-1}	++ to +++
Apherusa glacialis	nd —	nd	nd	nd	nd	+	++	nd	—	—	nd
Eggs Metazoa indet.	— —	—	—	—	—	+	nd	—	nd	38–3359 L^{-1}	nd
S_{water} (pond water column or sub-ice water)	nd	29.1–29.3	a: 23.8–31.2 b: 11.9–31.2 c: 29.9–31.1	nd	nd	nd	nd	29.1–29.3	—		20.6–31.2
S_{bulk}	10.4	7.3	nd	nd	nd	4.5	nd	4.9	2.4–4.7		—
chl a [$\mu g\,L^{-1}$]	4.8	3.6	nd	nd	nd	1.0	nd	40.6	0.2–17.9		0.4–0.5
Remarks	brown edges	green; large thaw holes	rotten ice very porous; platelet-like ice underlying new ice	green	black; large thaw holes	brown edges	—	green; large thaw holes	—		—

than in bottom level ice and similar to concentrations in the pond water column (implying intermediate concentrations in the brine), while in rotten ice they were closer to bottom level ice values. Maximum concentrations in new ice were well within the range of bottom level ice values and in rotten ice by far exceeded these.

All ponds where sympagic meiofauna and amphipods were sampled were dark or green in colour, with extremely porous rotten ice at the bottom. They were saline or brackish to saline, both new and rotten ice had high bulk salinities, and pigment concentrations in new and rotten ice were moderate to extremely high (Table 3.1). Various sympagic meiofauna taxa were recorded in new ice on meltpond surfaces and in rotten ice at meltpond bottoms (Table 3.1). In new ice, ciliates, red acoels and rotifers were dominant and nematodes were also common, similar as in level ice. In rotten ice, the foraminifer *Neogloboquadrina pachyderma* (otherwise common in sub-ice water rather than in level ice) and rotifers were abundant, ciliates were also common. Harpacticoids and nauplii, though partly abundant in bottom level ice, were scarce in both meltpond ice types. The cyclopoid *Oithona* cf. *similis*, dominant in sub-ice water, was rare in meltpond ice. Sub-ice calanoids were not found in meltpond ice samples. Several specimens of the under-ice amphipod *Apherusa glacialis* were sampled from the rotten ice at the bottom of two meltponds.

3.5 Discussion

We give the first record of metazoans inhabiting Arctic sea-ice meltponds: a large variety of sympagic meiofauna was found to inhabit the new ice on the surface and the rotten ice at the bottom of brackish and saline meltponds, and under-ice amphipods of the species *Apherusa glacialis* were found on top of the rotten ice. We attribute the occurrence of these metazoans to the characteristics of meltponds in the Central Arctic in summer 2007, which differed distinctly from those reported previously (Eicken et al. 1994, Ikävalko et al. 1996, v. Juterzenka et al. 1997, Gradinger 1998, Carstens 2001, Eicken et al. 2002, Brinkmeyer et al. 2004). We suggest that, due to global warming, meltponds will become increasingly inhabitable by metazoans.

The meltponds examined in detail during our expedition were usually deeper (this study; S. Hendricks, personal communication) than reported previously (Supplement 3.S3). Due to the honeycomb structure of the rotten ice at the bottom, the ponds were mostly brackish to saline and generally similar to sub-ice water in terms of environmental conditions. This stands in contrast with previous studies, according to which meltponds used to be predominantly shallow and fresh to oligohaline (Ikävalko et al. 1996, v. Juterzenka et al. 1997, Gradinger 1998, Carstens 2001, Brinkmeyer et al. 2004),

even at the end of the melt season and beginning of freeze-up (Eicken et al. 1994, Carstens 2001, Eicken et al. 2002). The prevailing dark and green colours of meltponds during our expedition (own observations) indicate a preponderance of brackish and saline meltponds also on the large scale, since green or dark colours are generally characteristic of brackish meltponds, whereas freshwater or oligohaline meltponds are usually blue (Carstens 2001). In consequence of the brackish to saline pond water, the new ice forming on the meltpond surface towards the end of summer had typical sea-ice characteristics with environmental conditions intermediate between the meltpond water column and bottom sea ice.

Due to these environmental conditions in the pond water column and the new ice cover, combined with the high porosity of the rotten ice at the pond bottom, the meltponds were accessible to and inhabitable by sympagic organisms. We suggest that sympagic meiofauna migrates laterally from the bottom layer of the sea ice into the rotten ice on the bottom of the meltponds and into the ponds themselves, from where they can enter the new ice cover on top of the ponds. The low distances between the old ice (adjacent to the ponds and at the pond bottom) and the new ice on the pond surface probably facilitate its colonisation by sympagic meiofauna, compared to the slow colonisation of new ice forming in open water (Kiko et al. under revision). Under-ice amphipods probably enter the meltponds through the large brine channels and thaw holes in the rotten ice at the bottom of the ponds. Sub-ice fauna might likewise be able to access the meltponds through the rotten ice (Kramer et al. under revision) and thrive in the water column of the ponds, since they need to cope with similarly brackish conditions and variable salinities in the sub-ice water (Werner 2006b). As chlorophyll *a* concentrations in the meltponds were often similarly high as in bottom level ice during the same time, the meltponds supplied ample food sources to the animals entering the ponds (Kramer et al. under revision).

In consequence of global warming, the meltpond fraction in the Arctic is most likely increasing (Flocco and Feltham 2007, Flocco et al. 2010), since the proportion of seasonal ice is increasing (Maslanik et al. 2007, Nghiem et al. 2007, Drobot et al. 2008, Kwok et al. 2009) and meltpond fractions are generally higher on first-year ice than on multi-year ice (Eicken et al. 2002, 2004). At the same time, an extended melt season (Markus et al. 2009) certainly causes an elongated meltpond season, which might cause the meltponds to become deeper. An increase in meltpond depth over the last decades is already indicated by literature data (Supplement 3.S3). Furthermore, meltponds are likely to become more porous, since meltpond permeability increases over the melt season (Eicken et al. 2004). As a consequence of an increased meltpond depth and porosity in conjunction with the recently observed thinning of the Arctic sea-ice cover (Haas et al. 2008b),

brackish and saline meltponds are probably becoming more frequent even at very high latitudes, as already indicated by the observations of mainly black and green meltponds during ARK–XXII / 2. A strong decay of meltponds with development of melt holes, as observed during ARK–XXII / 2, has also been reported from the Beaufort Sea recently (Barber et al. 2009).

We conclude that, with the probable increase in saline and brackish meltponds in the Arctic, a new habitat is becoming accessible to both sympagic and sub-ice fauna, which might play an important role in cryo-pelagic coupling (Kramer et al. under revision).

3.6 Acknowledgments

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3.S Supplementary material

3.S1 Meltpond sampling stations

Table 3.S1: Meltpond sampling stations during ARK–XXII / 2, with sampling date (yymmdd), latitude (Lat) and longitude (Lon), meltpond identifier (MP–ID) and types of samples taken (+). Water col. = pond water column, New ice = new ice on pond surface, Rotten ice = rotten ice at pond bottom, Interst. water = interstitial water from rotten ice, Env = environmental parameters, Amph = amphipod samples, Meio = meiofauna samples, Fauna = sub-ice fauna samples. q denotes quantitative fauna samples with determination of abundance.

Station	Date	Location		Meltponds								Level ice		Sub-ice water	
				MP–ID	Environmental parameters				Meiofauna		Amph	Env	Meio	Env	Fauna
		Lat	Lon		Water col.	New ice	Rotten ice	Interst. water	New ice	Rotten ice					
PS 70 / 322	070831	88°08'N	150°05'E	MP–1	—	+	+	+	q	+	+	+	q	+	—
PS 70 / 328	070902	87°49'N	170°36'W	MP–2a	+	+	+	+	—	—	—	+	—	—	—
PS 70 / 328	070902	87°49'N	170°36'W	MP–2b	—	—	—	—	—	—	+				
PS 70 / 338	070905	85°42'N	135°02'W	MP–3a	+	—	—	—	—	—	—	+	+	—	—
PS 70 / 338	070905	85°42'N	135°02'W	MP–3b	+	—	—	—	—	—	—				
PS 70 / 342	070907	84°30'N	138°22'W	MP–4	+	+	+	—	—	—	—	+	+	—	—
PS 70 / 352	070910	86°38'N	177°33'E	MP–5	+	+	+	+	+	+	—	+	q	+	—
PS 70 / 363	070912	86°24'N	135°49'E	MP–6a	+	—	—	—	+	—	—	+	q	+	+
PS 70 / 363	070912	86°24'N	135°49'E	MP–6b	+	—	—	—	+	—	—				
PS 70 / 363	070912	86°24'N	135°49'E	MP–6c	+	—	—	—	+	—	—				
PS 70 / 363	070913	86°28'N	134°59'E	MP–7	+	+	+	+	—	—	—				
PS 70 / 371	070916	84°39'N	102°44'E	MP–8a	—	—	—	—	+	—	—	+	q	+	+
PS 70 / 371	070916	84°39'N	102°44'E	MP–8b	—	—	—	—	+	—	—				
PS 70 / 371	070916	84°39'N	102°44'E	MP–8c	—	—	—	—	+	—	—				
PS 70 / 371	070916	84°39'N	102°44'E	MP–8d	+	+	+	+	—	—	—				

3.S2 Environmental conditions in meltponds

Table 3.S2: Environmental conditions in meltpond habitats, level ice (bottom 5 cm) and sub-ice water (0 m and 5 m under the ice) during ARK–XXII / 2. Water col. = pond water column, New ice = new ice on pond surface, Rotten ice = rotten ice at pond bottom, Interst. water = interstitial water from rotten ice. H = meltpond depth or ice thickness, T = temperature, S = salinity, δV = brine volume fraction. nd = not determined. For ice, concentrations are given as bulk values (i. e. in relation to the volume of melted ice, not of brine). Medians (ranges) are given. n is the number of ponds, level-ice sites or sub-ice sites for which the respective parameter was determined.

	Meltponds				Level ice	Sub-ice water	
	Water col.	New ice	Rotten ice	Intersts. water	Bottom 5 cm	0m	5m
H [m]	40 (30–60) $n = 10$	11.3 (3.7–16.0) $n = 6$	16.0 (4.5–53.0) $n = 5$	—	125.5 (106.0–190.0) $n = 8$	—	—
T [°C]	Mean -0.9 (-1.7 to +0.5) $n = 10$ Surface -0.5 (-1.9 to -0.1) $n = 10$ Bottom -1.5 (-1.7 to +1.3) $n = 10$	-1.2 (-1.9 to -0.7) $n = 4$	-1.4 (-1.9 to -0.9) $n = 4$	nd	-1.5 (-2.2 to -1.3) $n = 5$	-1.6 (-1.7 to -1.3) $n = 4$	-1.7 (-1.8 to -1.7) $n = 4$
S_{water} or S_{brine}	Mean 21.0 (2.9–30.7) $n = 10$ Surface 11.2 (1.7–29.9) $n = 10$ Bottom 28.5 (5.6–31.2) $n = 10$	21.1 (12.4–33.9) $n = 4$	25.2 (16.4–33.9) $n = 4$	16.4 (4.1–28.7) $n = 4$	27.6 (23.5–39.1) $n = 5$	29.8 (20.6–31.2) $n = 4$	30.9 (29.3–32.2) $n = 4$
S_{bulk}	—	3.4 (0.3–10.4) $n = 6$	4.4 (2.9–10.5) $n = 6$	—	3.2 (1.9–4.7) $n = 8$	—	—
δV [%]	—	14.0 (9.0–19.1) $n = 4$	13.5 (8.3–24.1) $n = 4$	—	10.6 (4.4–18.0) $n = 5$	—	—
chl a [μg L^{-1}]	0.3 (0.1–1.1) $n = 4$	0.5 (0.0–4.8) $n = 6$	1.4 (0.1–40.6) $n = 6$	1.4 (0.1–54.6) $n = 5$	2.7 (0.2–17.9) $n = 8$	0.5 (0.2–1.7) $n = 4$	0.3 (0.1–2.1) $n = 4$
phaeo [μg L^{-1}]	0.1 (0.0–0.2) $n = 4$	0.2 (0.0–0.5) $n = 6$	0.8 (0.1–34.7) $n = 6$	0.4 (0.0–10.2) $n = 5$	0.2 (0.0–2.7) $n = 8$	0.2 (0.1–0.3) $n = 4$	0.3 (0.0–0.4) $n = 4$

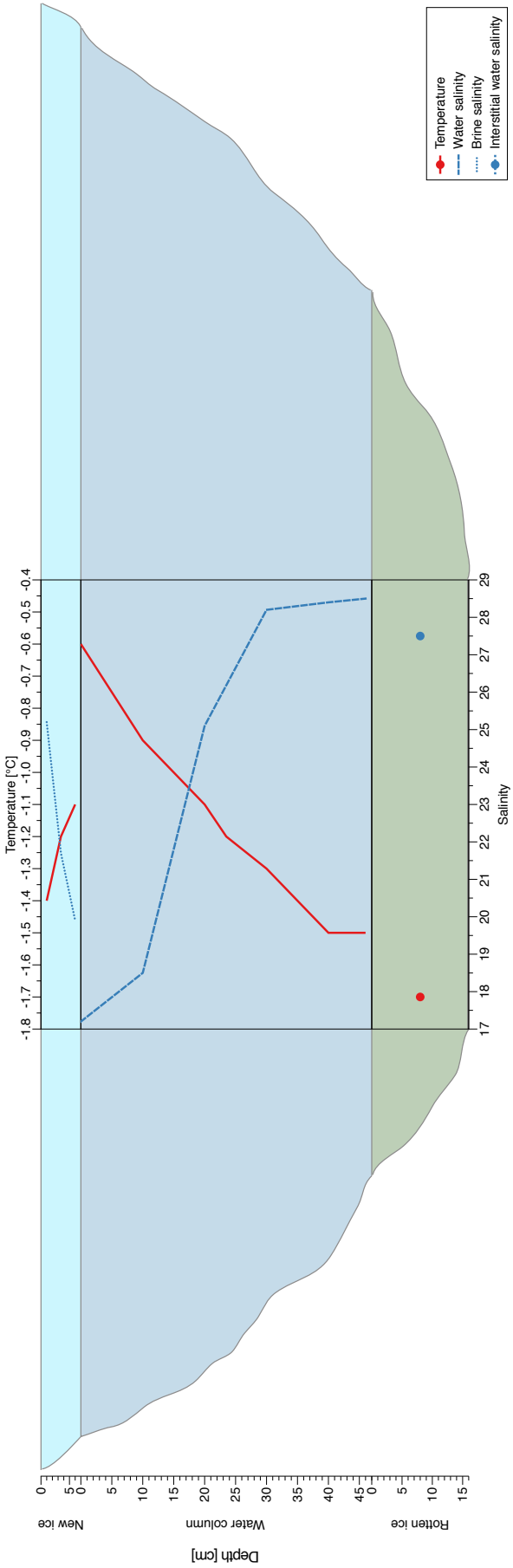

Figure 3.S2: Schematic drawing of meltpond MP-2a with temperature and salinity profiles.

3.S3 Meltpond depth from literature

Table 3.S3: Meltpond depth in different regions of the Arctic from 1958 to date, retrieved from literature.

Year	Region	Meltpond depth (range) [cm]	Reference
1958	Central Arctic	26	Untersteiner 1961
1972	Canadian Arctic	5	Grenfell and Maykut 1977
1974	Canadian Arctic	(10–30)	Grenfell and Maykut 1977
1982	Canadian Arctic	(3–5)	Holt and Digby 1985, Perovich 1994
1990	Greenland Sea	(4–45)	Garrity et al. 1991
1991	Canadian Arctic	(3–5)	Holt and Digby 1985, Perovich 1994
1991	Central Arctic	≤ 20	Eicken et al. 1995
1993	Fram Strait / Western Greenland Sea	14 (3–63)	Carstens 2001
1993	NW of Franz Joseph Land	(20–50)	Ivanov and Alexandrov 1994
1993	Barents Sea	(2–35)	Makshtas and Podgorny 1996
1993	East Siberian Sea	25	Zatchek and Darovskikh 1997
1993	Eurasian Arctic	26	Eicken et al. 1996
1994	Canadian Arctic	26 (0–86)	Morassutti and LeDrew 1995, 1996
1994	Central Arctic	35 (20–60)	Tucker et al. 1999
1994	Fram Strait / Western Greenland Sea	14 (3–63)	Carstens 2001
1995	Canadian Arctic		Perovich et al. 1998
1995	Laptev / East Siberian Sea	27	Haas 1997
1995	Laptev / East Siberian Sea	(10–40)	Kolatschek and Zatchek 1997
1997	Eurasian Arctic	16 (10–42)	v. Juterzenka et al. 1997
1997	Central Arctic	70 (–120)	Melnikov 1997
1998	Beaufort / Chukchi Sea	(10–50)	Skyllingstad et al. 2009
1999	Arctic Ocean	(25–30)	Brinkmeyer et al. 2004
2000	Arctic Ocean	(25–30)	Brinkmeyer et al. 2004
2002	Resolute	(3–6)	Scharien and Yackel 2005
2007	Central Arctic / Laptev Sea	102 (20–175)	Hendricks et al. unpubl.
2007	Central Arctic / Laptev Sea	40 (30–60)	this study

4 Trophic positions of Arctic and Antarctic sympagic meiofauna and its role in cryo-pelagic coupling identified by stable isotopes and fatty acids

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4.1 Abstract

The importance of sea ice in polar marine food webs is recognised, but little is known about the role of sympagic metazoan meiofauna (animals $> 20\,\mu$m inhabiting the brine channels of sea ice). We aimed to identify trophic positions and feeding strategies of Arctic and Antarctic sympagic meiofauna and to investigate its role in cryo-pelagic coupling by combining analyses of stable isotopes of carbon and nitrogen on one hand, of fatty acids and alcohols on the other. We developed a two-source model for calculation of trophic levels and proportions of sea-ice derived carbon from stable isotope data. To validate our methods, we included analyses of Arctic sub-ice fauna and under-ice amphipods. Our study reveals that sympagic meiofauna is not primarily herbivorous, but carnivory, cilivory, omnivory, bacteriovory and detritivory are common. Flexible feeding strategies are in our view adaptations to the dynamic sea-ice habitat. Utilisation of pelagic food sources by several sympagic meiofauna taxa probably plays an important role in cryo-pelagic coupling. Porous, brackish meltponds on Arctic sea ice constitute further feeding grounds for sympagic and sub-ice fauna and might temporarily and locally enhance cryo-pelagic coupling in times of climate change. Stable isotopes and fatty acids are very suitable tools in sympagic meiofauna studies and ought to be further developed.

4.2 Introduction

Sea ice plays an important role in polar marine food webs. Ice algae, inhabiting the brine channels of sea ice, contribute up to 25 % of the total primary production in ice-covered areas of the Southern Ocean (Arrigo et al. 1997), and up to 60 % in the Arctic Ocean (Gosselin et al. 1997). These microalgae constitute important food sources for under-

ice and sub-ice fauna such as Antarctic krill (Daly 1990), Arctic under-ice amphipods (Werner 1997) and Arctic species of the calanoid copepods *Calanus* and *Pseudocalanus* (Runge and Ingram 1988, 1991, Falk-Petersen et al. 2009). Under-ice grazing has been recognised as an important pathway for energy and organic matter from the sympagic to the pelagic realm, referred to as cryo-pelagic coupling (Scott et al. 1999, Søreide et al. 2006, Werner 2006a). Recently, the potential impact of the decline of the Arctic sea ice cover on Arctic food webs has received considerable attention (Grebmeier et al. 2006, Falk-Petersen et al. 2007, 2009).

Little is known about the role of sympagic metazoan meiofauna in the food web and in cryo-pelagic coupling. These small animals ($> 20\,\mu$m) inhabiting the brine channels of sea ice are generally assumed to graze on sea-ice algae (Gradinger 1995, Brierley and Thomas 2002, Arrigo and Thomas 2004) and may thus compete for this food source with under-ice grazers (Kramer et al. in press). On the other hand, sympagic meiofauna may also constitute a food source for carnivorous or omnivorous under-ice and sub-ice fauna (Werner et al. 2002, Werner and Auel 2005) and may thus play an important role in cryo-pelagic coupling. In spite of this, only few studies have investigated diets of sympagic meiofauna by means of gut content analyses (Hoshiai et al. 1987, Grainger and Hsiao 1990) or for single taxa by means of fatty acid analyses (Swadling et al. 2000) or feeding experiments (Schnack-Schiel et al. 1995, Siebert et al. 2009). The potential importance of carnivorous meiofauna has been recognised only recently (Siebert et al. 2009, Kramer et al. in press). The role of sympagic meiofauna in cryo-pelagic coupling has been investigated indirectly through studies on the population dynamics of sub-ice fauna (Werner 2006b, Kiko et al. 2008b).

In this study, we combine two methods to identify trophic positions and feeding strategies of Arctic and Antarctic sympagic meiofauna and to elucidate its role in cryo-pelagic coupling: analyses of C:N ratios and stable isotopes (SI) of carbon and nitrogen on one hand, of lipid and wax ester (WE) content, fatty acid (FA) and fatty alcohol (FAlc) composition on the other. Both methods are well-established in feeding studies of pelagic and benthic animals (Kattner and Fricke 1986, Jacob et al. 2006, Cornils et al. 2007). Our study is the first to apply both methods in combination to a large variety of Arctic and Antarctic sympagic meiofauna. Sub-ice fauna $> 50\,\mu$m, under-ice and sub-ice amphipods and particulate organic matter (POM) were analysed as well for complementary data and baselines.

We aimed at

- Testing our hypothesis that carnivory, cilivory and omnivory as well as flexible feeding strategies are common in sympagic meiofauna
- Studying aspects of cryo-pelagic coupling by (1) investigating the contributions of sympagic and pelagic food sources to meiofauna diets and (2) identifying the role of brackish and saline meltponds as potential feeding grounds for sympagic meiofauna, sub-ice fauna and under-ice amphipods

4.3 Materials and methods

4.3.1 Sampling and sample processing

Samples from Arctic and Antarctic sea ice were collected in different regions and seasons (Table 4.1, Supplement 4.S1).

POM samples

Sea-ice POM was obtained from sea-ice cores taken with an engine-powered KOVACS ice corer (inner diameter 9 cm) on level ice (Horner et al. 1992). The bottommost 10 cm of the cores were cut into sections of 1–5 cm length, which were processed separately. Pelagic and sub-ice POM were obtained from sub-ice water samples taken with a hose at 5 m and 0 m depth under the ice, respectively (Schünemann and Werner 2005). Meltpond POM was obtained from (i) new ice covering meltponds, (ii) strongly deteriorated (rotten) ice on the bottom of meltponds, (iii) water in meltponds and (iv) water from the interstices and thaw holes of the rotten ice (interstitial water). Cores of new and rotten ice were taken with an ice corer, samples from the pond water column and interstitial water were taken with a hand pump. Due to the deteriorated nature of the ice on the bottom, the ponds were connected to the underlying water column and were thus brackish to saline (Kramer and Kiko 2010). Since both inorganic carbon (from carbonates) and nitrogen (from clay minerals) are assumed to be negligable in these ice and water samples, the particulate fraction is considered as POM, consisting mainly of algae (Müller 1977).

The ice samples were melted in the dark at $+4\,^{\circ}$C. Sub-samples of melted ice, sub-ice water and pelagic water and meltpond water were filtered onto Whatman GF/F filters (pre-combusted: 520 °C, 12 h), which were frozen at -80 °C until further analyses.

Fauna samples

Sympagic meiofauna was obtained (i) from bottom-ice sections (up to 10 cm long) of sea-ice cores, (ii) from bottom-ice samples scraped or sawn off from blocks of sea ice

which were cut from ice floes or from new ice on meltponds, and (iii) from sea-ice chunks picked up from the water beside the ship using a cage attached to the ship's crane. Sub-ice fauna was sampled from directly under the ice using an under-ice pump equipped with a 50 μm gauze (Werner and Martinez Arbizu 1999). Under-ice and sub-ice amphipods were obtained (i) from under-ice pump samples, (ii) from the underside of ice chunks picked from the water or (iii) from meltponds.

Table 4.1: Sampling campaigns for sampling of sympagic meiofauna, sub-ice fauna, under-ice and sub-ice amphipods (Amph) and particulate organic matter (POM) for analyses of stable isotopes (SI) of nitrogen and carbon, C:N ratio (C:N), fatty acids (FA) and fatty alcohols (FAlc). + sample type taken, — sample type not taken.

Region	Coverage		Time		Campaign	Samples									
	Latitudes	Longitudes	Season	Dates		Sympagic meiofauna			Sub-ice fauna			Amph		POM	
						SI	C:N	FA, FAlc	SI	C:N	FA, FAlc	SI	C:N	SI	C:N
Central Arctic	82°01' N–88°09' N	33°58' E–134°55' W	Summer	Jul 29–Oct 7 2007	ARK–XXII/2 (RV *Polarstern*)	+	+	+	+	+	+	+	+	+	+
Western Canadian Arctic: Beaufort Sea, Amundsen Gulf	69°57' N–71°34' N	119°36' W–126°10' W	Spring	Mar 13–Jun 5 2008	CFL legs 7–8 (CCGS *Amundsen*)	—	—	+	—	—	—	—	—	—	—
Arctic: Spitsbergen: Tempelfjorden/Billefjorden	78° N	17° E	Spring	Apr 20–May 9 2009	UNIS sampling campaign	+	+	—	—	—	—	—	—	+	+
Antarctic: Southern Ocean: Western Weddell Sea	59°50' S–65°07' S	40°47' W–57°24' W	Winter	Aug 24–Oct 29 2006	ANT–XXIII/7 (RV *Polarstern*)	+	+	+	—	—	—	—	—	—	—

The ice samples for sympagic meiofauna were melted in the dark at $+4\,^{\circ}$C in a surplus of 0.2 μm filtered seawater to reduce osmotic stress (Garrison and Buck 1986, Gradinger 1999a). Sympagic meiofauna was enriched over a 20 μm gauze and transferred into filtered sea water. Sub-ice fauna samples were enriched over a 50 μm gauze and transferred into filtered sea water, and amphipods were placed separately into large beakers with filtered sea water directly after sampling. All animals were kept in the dark at $0\,^{\circ}$C until further processing.

Sympagic meiofauna and sub-ice fauna were sorted alive at $0\,^{\circ}$C according to taxonomic groups (species, genus or higher taxonomic level) and, when applicable, further to size classes or stages. Identification of sympagic meiofauna to species level was usually not possible, since taxonomic knowledge on sympagic meiofauna is sketchy, identification of live specimens is often impossible and even identification of fixed specimens partly requires sophisticated preparation (Friedrich 1997). After sorting, the animals were placed into clean filtered sea water several times to remove algae and detritus. In case algae or detritus were abundant in the samples, this process was repeated after starving the animals for 1–2 days to allow gut evacuation.

Amphipods and larger sub-ice fauna were rinsed with MilliQ water and frozen individually at -80 °C until further analyses. In case of sympagic meiofauna and smaller sub-ice fauna, multiple specimens of each taxonomic group had to be pooled for analyses (up to 1000 specimens per sample, depending on biomass; Supplement 4.S2). Since direct rinsing with MilliQ water was not feasable for sympagic meiofauna and small sub-ice fauna (Supplement 4.S2), the animals were transferred onto pre-combusted Whatman GF / F filters on a small filtration unit, the sea water was removed, the samples were quickly rinsed with a few mL of MilliQ water and the filters with the animals were frozen at -80 °C.

4.3.2 Stable isotope analyses and carbon and nitrogen contents

Measurement and data analysis

Samples for carbon and nitrogen stable isotopes (SI) and content were oven-dried (45 °C, 24 h). The samples were measured without acidification, since the carbonate content was assumed to be negligable, and without lipid extraction, since this procedure would require larger samples. Furthermore, both acidification and lipid extraction might bias the nitrogen isotope value (Jacob et al. 2005, Mintenbeck et al. 2008).

Measurements of nitrogen and carbon SI and contents were performed simultaneously (Fry et al. 1992) with a THERMO / Finnigan MAT V isotope ratio mass spectrometer, coupled to a THERMO Flash EA 1112 elemental analyser via a THERMO / Finnigan Conflo III interface (Museum für Naturkunde, Berlin). The elemental analyser was equipped with a special sample holder facilitating analyses of filter samples. A blank run was performed after each measurement run to lower the background noise, thus allowing for measurement of very small samples.

SI ratios are expressed as δ^{13}C and δ^{15}N, relative to atmospheric nitrogen (Mariotti 1983) and VPDB (Vienna PeeDee Belemnite standard), respectively.

Standard deviation for repeated measurements of our lab standard material (peptone) is generally smaller than 0.15 ‰ for both nitrogen and carbon. Standard deviations of concentration measurements of replicates of our lab standard are < 3 % of the concentration analysed.

Nitrogen SI values were corrected for the air blank effect according to Fry et al. (1992) (Supplement 4.S3). The blank effect on carbon SI values was assumed to be negligible, since δ^{13}C values of blank filters were close to values of the samples. For blank correction of nitrogen and carbon contents, the respective filter blank—1 μg for nitrogen and 24 μg for carbon—was subtracted from the measured value. In case of amphipods and larger sub-ice fauna, which were measured without filter, only the nitrogen content was corrected by subtracting the air blank (1 μg).

A two-tailed Mann-Whitney U-test (significance level 5 %) was applied to test for differences between sample types in terms of C:N ratios, using the software SPSS 11.0 (SPSS 2001).

Two-source model for trophic level calculation

For estimating the trophic levels of the fauna as well as the proportions of carbon ultimately derived from sea ice, we essentially followed the approach by Post (2002), accounting for both mixing of pelagic and sympagic material and trophic fractionation at the same time. We reformulated the equations, thus correcting an inaccuracy in the equation for proportions given by Post (2002) (p. 714, left column, second paragraph)—see Supplement 4.S4 for derivation, specifically equation 4.S4.4 for comparison with Post (2002). Our equations also account for differences in C:N between sea-ice algae and phytoplankton.

Assuming that the herbivorous fauna feeds on sea-ice algae and phytoplankton, and combining equations for mixing (Fry 2006) and fractionation (Waser et al. 1998), the isotope value δ_f^X of a consumer is

$$\delta_f^X = \underbrace{a^X \cdot \delta_i^X + \left(1 - a^X\right) \cdot \delta_w^X}_{mixing} + \underbrace{D^X \cdot (\lambda - 1)}_{fractionation} \ , \tag{4.1}$$

where subscripts i and w denote algae from sea-ice and water, respectively, and superscript X denotes the element C or N, δ^X is δ^{13}C or δ^{15}N, a^X is the proportion of element X derived from sea-ice algae, λ is the trophic level of the fauna (the trophic level of algae being 1) and D^X is the trophic enrichment factor for element X per trophic level (assumed to be constant). In case of great differences in C:N between sea-ice algae and phytoplankton, a^C and a^N cannot be assumed to be equal, but rather

$$a^C = \frac{a^N \cdot (C/N)_i}{a^N \cdot (C/N)_i + (1 - a^N) \cdot (C/N)_w} \ , \tag{4.2}$$

where $(C/N)_i$ and $(C/N)_w$ are the mass-based C:N ratios of sea-ice algae and phytoplankton, respectively. The proportions of sea-ice derived carbon and nitrogen and the trophic level are calculated by solving the system of equations 4.1 and 4.2 for a^C, a^N and λ, respectively (Supplement 4.S4).

We calculated the proportions of sea-ice derived carbon and nitrogen and the trophic level for each fauna sample from the Central Arctic, using the δ^{13}C and δ^{15}N values of the respective fauna sample and median δ^{13}C, δ^{15}N and C:N values of all sea-ice and pelagic POM samples. Medians were used to account for the small-scale variability in sea ice (Steffens et al. 2006). We further assumed $D^C = 0.3$ ‰ and $D^N = 2.2$ ‰ (McCutchan

et al. 2003). Most studies found or assumed higher values for trophic enrichment (e. g. $D^C = 0.6\,‰$, $D^N = 3.4\,‰$, Søreide et al. 2006). However, for the small meiofauna, which is in the focus of this study, trophic enrichment is presumably smaller, since it is negatively related to growth rate (Fry 2006), which in turn decreases with size (Moloney and Field 1989).

Remarks on the two-source model

The model is based on the assumptions that (i) the SI values of POM reflect those of algae reasonably well, (ii) there are no more than two algal food sources at the base of the food web (sea-ice algae and phytoplankton), (iii) the SI values of these algae do not vary much in space or time (i. e. the algae sampled for baselines have the same isotope values as those the herbivores actually consumed), and (iv) the trophic enrichment is equal for all members of the food web.

If (i) POM contains a considerable non-algae fraction, such as heterotrophic protists, the SI values of POM are higher than those of algae. The trophic levels of meiofauna taxa preying mainly on heterotrophic protists may be underestimated accordingly.

If (ii) additional algal food sources with different isotope values are consumed by the herbivores (e. g. algae from meltponds), the model does not give exact results. The additional food sources then need to be taken into consideration when interpreting the results, specifically if calculated trophic levels are unreasonably high or low or if the calculated proportions of sea-ice derived carbon are far beyond the range 0–1.

If (iii) baseline isotope values vary strongly in space or time, the baseline values entered in the model may be different from those of the algae actually consumed by herbivores (specifically if tissue turnover rates are low), which can again result in unreasonably high or low calculated trophic levels or in proportions of sea-ice derived carbon beyond the range 0–1.

If (iv) the trophic enrichment depends, for example, on feeding types, as proposed by McCutchan et al. (2003), specifically the calculated trophic levels may be correct only for certain taxa. In case of our data, trophic levels varied by usually ± 1 to ± 2 when D^N was altered between 1.4 and 3.4 (as proposed for carnivores feeding on invertebrates by McCutchan et al. 2003 and for sub-ice fauna by Søreide et al. 2006, respectively).

The model results therefore need to be interpreted with caution and in the light of the scatter of algal isotope values. If little is known about the variability of baseline values in relation to tissue turnover rates and about trophic enrichment (as it is the case for sympagic meiofauna), the absolute values of calculated trophic levels and the proportions of sea-ice derived carbon should not be taken too strictly. Nevertheless, they can be good indicators

of higher or lower trophic level, and of stronger or weaker association with sympagic food sources.

4.3.3 Lipid, fatty acid and fatty alcohol analyses

Lyophilised fauna samples were treated with ultrasound for disruption and incubated in 4 mL dichloromethane : methanol (2:1 v / v) with an internal standard (23:0) for 120 h. Lipids were then extracted (Folch et al. 1957, modified after Hagen 2000), and extracts were frozen at -80 °C in 1 mL solvent until further analyses.

Fatty acids (FA) and fatty alcohols (FAlc) were analysed in 500 μL subsamples of total lipid extracts. FA were converted to their methyl ester derivates (FAMEs) (Kattner and Fricke 1986) and analysed together with FAlc using a gas chromatograph (Agilent Technologies 7890A) equipped with a cold injection system (KAS 4), a DB-FFAP column (30 m length, 0.25 mm inner diameter, 0.25 μm film thickness), helium as carrier gas, temperature programming (80–240 °C) and a flame ionisation detector.

FA and FAlc data analyses were performed with Agilent ChemStation (Rev. B04.01). Filter samples were corrected for filter peaks determined on six blank filters. Only peaks with a blank-corrected area over 1 % were considered in further analyses.

Total lipid content was determined from the known amount of internal standard. For estimation of the lipid fraction of dry mass, the dry mass for each fauna sample was calculated from measured carbon contents (Supplement 4.S5). This method can result in under- or overestimations of lipid fractions, and values > 100 % of dry mass may occur, indicating that either the specimens measured for dry mass were smaller than those measured for lipid content, or the equations for conversion of carbon to dry mass are inaccurate for the respective taxon. The wax ester (WE) proportion was calculated as twice the FAlc proportion assuming equal masses for the FAlc and FA chains of each WE molecule. A two-tailed Mann-Whitney U-test was applied to test for differences between sample types in terms of WE contents.

Principal component analysis (PCA), performed with PRIMER v6 (Clarke and Gorley 2006), was applied to arcsine square-root transformed FA proportions in order to visualise groups of samples and to identify those FA contributing most to the differences between samples. For the sake of clarity, and in order to minimise bias from contamination, only those FA were included which exceeded 10 % of total FA abundance in at least one sample. FA 24:1(n-9) was excluded, since this peak in the chromatograms had shown to be uncertain.

The ratio of the metazoan / detritus marker 18:1(n-9) and the diatom marker 18:1(n-7) (Sargent et al. 1987, Falk-Petersen et al. 1990) and the ratio of polyunsaturated and sat-

urated FA (PUFA / SFA) were calculated to estimate the dietary importance of diatoms relative to metazoans and detritus (Graeve et al. 1997). The ratio of the diatom marker 16:1(n-7) and its saturated counterpart 16:0 as well as the ratio of the diatom marker 20:5(n-3) and the flagellate marker 22:6(n-3) (Sargent et al. 1987) were determined to assess the dietary importance of diatoms relative to flagellates (St. John and Lund 1996). The sum of the odd-numbered FA 15:0, 17:0 and 17:1, indicating feeding on bacteria (Rezanka and Sigler 2009), was also calculated.

Marker FA for specific taxonomic groups with coincident functions as biomembrane components should be used with caution, e. g. 20:5(n-3) and 22:6(n-3). These FA are very conservative and losses via catabolism are low (Sargent and Whittle 1981, Sargent and Henderson 1995). FA ratios that strongly depend on the total lipid content of the specimen (e. g. PUFA / SFA, Stübing and Hagen 2003) are only of limited use as trophic indices, since total lipid content may vary greatly with various factors that are unrelated to specific feeding preferences. Since the sample sizes in this study were not big enough to test for relationship between total lipid content and FA ratios, the ratios need to be interpreted with caution and in conjunction with the other data.

4.4 Results

4.4.1 C:N ratios and stable isotopes

Molar C:N ratios of POM differed substantially between the different realms (sea ice, sub-ice water, pelagic realm, meltponds) and between different regions (Central Arctic, Spitsbergen fjords). C:N ratios of sympagic meiofauna (Supplement 4.S6 Table 4.S6) did not differ significantly between Central Arctic and Antarctic taxa (medians both 4.7). In the Central Arctic, sympagic meiofauna and sub-ice fauna did not differ significantly in C:N ratios (medians 4.7 and 6.1, respectively), while under-ice and sub-ice amphipods had significantly higher C:N (median 10.8).

Both carbon and nitrogen stable isotope (SI) values were generally higher in sea-ice than in pelagic and sub-ice POM in the Central Arctic in late summer (Fig. 4.1 A and Supplement 4.S6 Fig. 4.S6.1). In POM from meltponds (water column, new ice, rotten ice and interstitial water), carbon isotope values were generally similar to those of pelagic POM, while nitrogen isotope values were generally higher. The general relationship between pelagic and sea-ice POM was opposite in fjords in Spitsbergen in spring, where isotope values were lower in sea-ice than in pelagic and sub-ice POM (Supplement 4.S6 Fig. 4.S6.1).

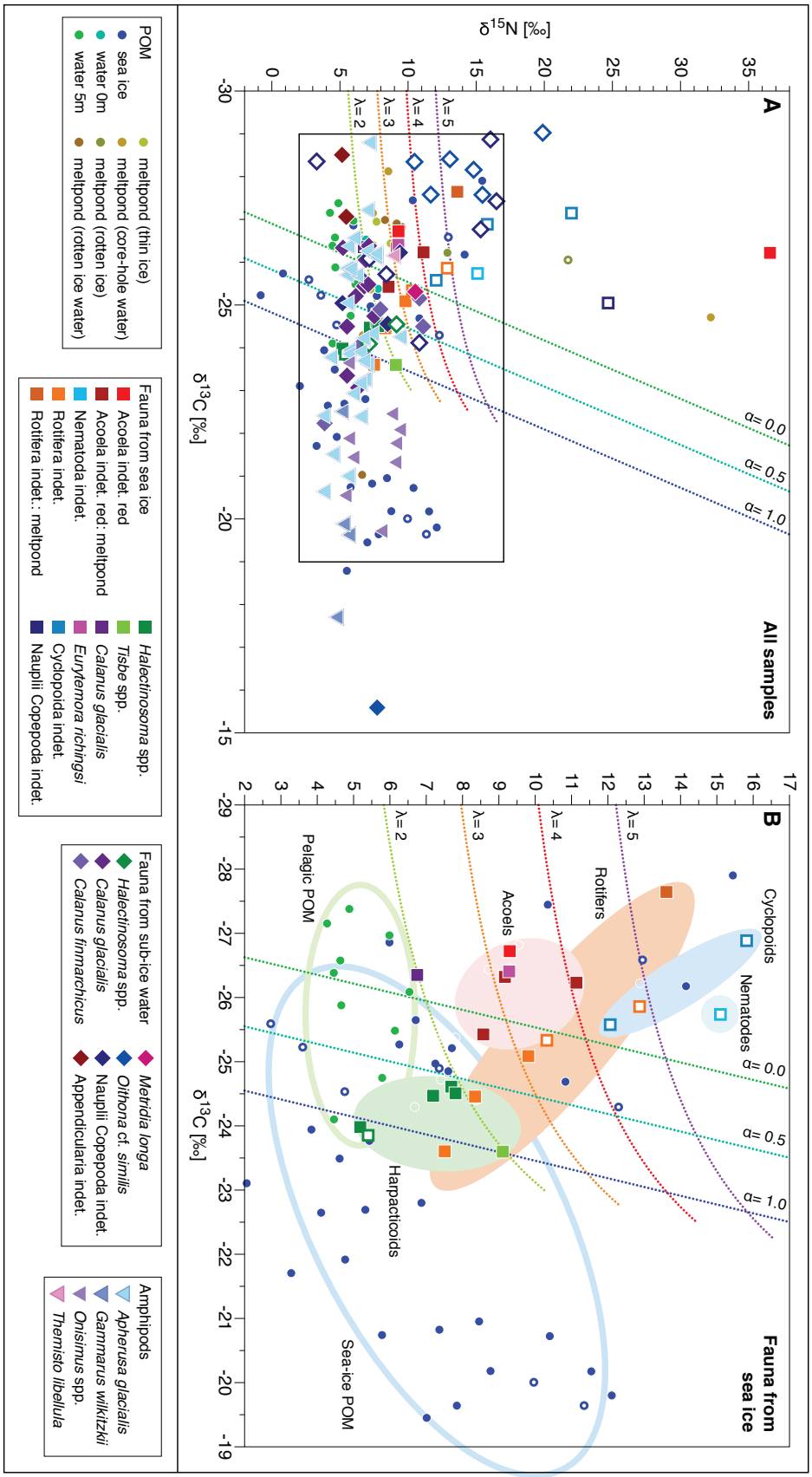

Figure 4.1: A Stable carbon (δ^{13}C) and nitrogen isotopes (δ^{15}N) of POM from sea ice, sub-ice water and meltponds (circles), fauna from sea ice (squares), fauna from sub-ice water (diamonds) and amphipods (triangles), sampled in the Central Arctic in summer. Samples smaller than the largest filter blank are depicted as open symbols. Isolines of proportions of trophic levels λ and of sea-ice derived carbon α (dotted lines) were calculated using a two-source model with sea-ice algae and phytoplankton as sources (Supplement 4.S4). **B** Enlarged boxed area from A: δ^{13}C and δ^{15}N of sympagic meiofauna, sea-ice and pelagic POM.—Circles and shaded areas qualitatively illustrate POM types and faunal groups, respectively.

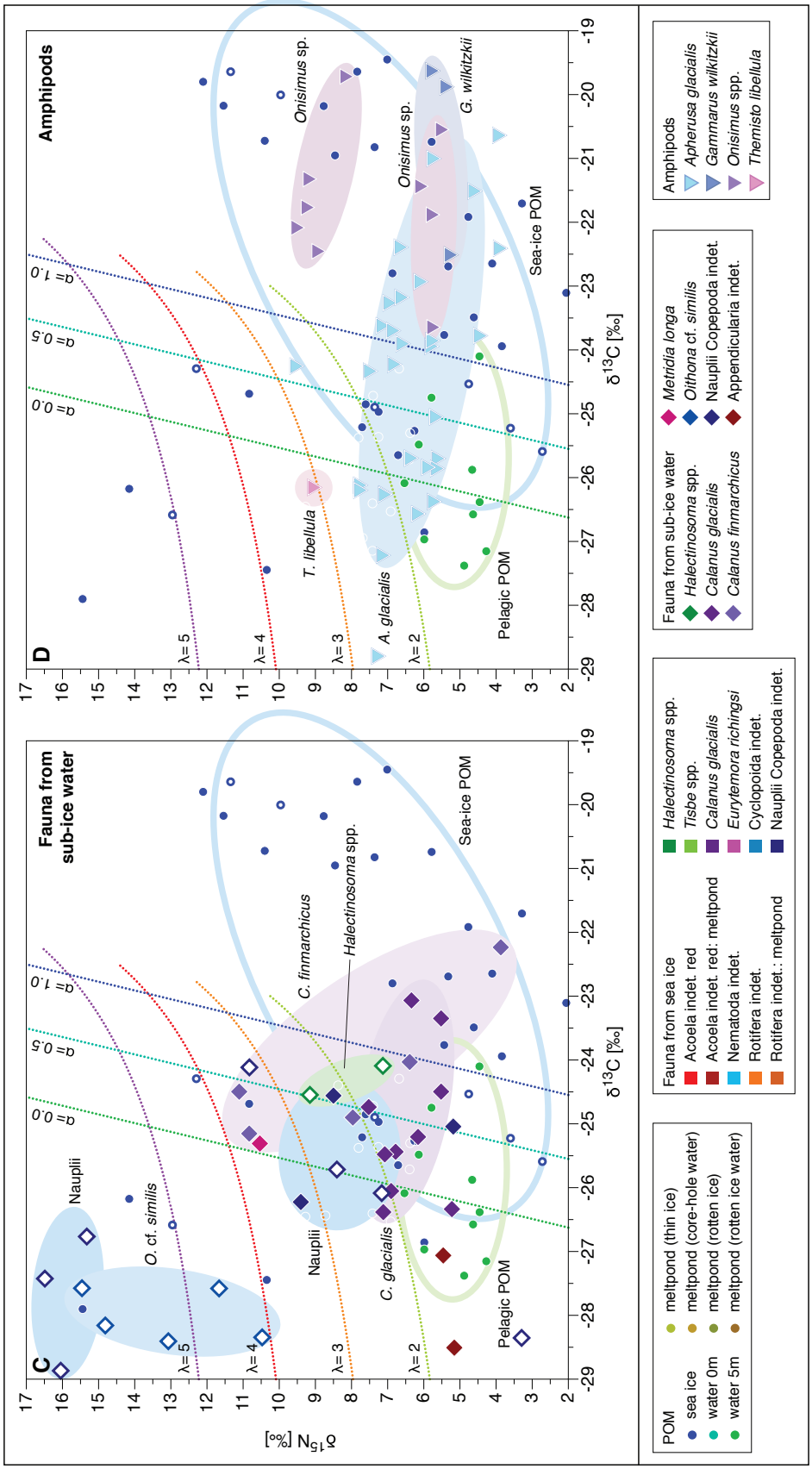

Figure 4.1 (continued): **C** Enlarged boxed area from A: $\delta^{13}C$ and $\delta^{15}N$ of fauna from sub-ice water, sea-ice and pelagic POM. **D** Enlarged boxed area from A: $\delta^{13}C$ and $\delta^{15}N$ of amphipods, sea-ice and pelagic POM.—Circles and shaded areas qualitatively illustrate POM types and faunal groups, respectively.

In general, nitrogen SI values of sympagic meiofauna, sub-ice fauna and under-ice and sub-ice amphipods in the Central Arctic were within the range of values of POM or slightly elevated (Fig. 4.1 B–D and Supplement 4.S6 Table 4.S6). Values of amphipods (Fig. 4.1 D) were within the lower range of sympagic meiofauna and sub-ice fauna (Fig. 4.1 B and C, respectively). Amongst sympagic meiofauna, generally low nitrogen isotope values were recorded for harpacticoids, while high values were measured in cyclopoids, nematodes and sometimes rotifers. Amongst amphipods, nitrogen isotope values were low in *Gammarus wilkitzkii*, *Apherusa glacialis* and some of the *Onisimus* spp. and high in *Themisto libellula* and some of the *Onisimus* spp.. Exceptionally high nitrogen isotope values > 20 ‰ were measured in single samples of sympagic red acoels (described by Friedrich and Hendelberg 2001), nauplii and cyclopoids, and of sub-ice *Oithona* cf. *similis* (Fig. 4.1 A).

Carbon SI values of animals in the Central Arctic were usually in the range of values of POM (Fig. 4.1 B–D and Supplement 4.S6 Table 4.S6). Values of sympagic meiofauna and sub-ice fauna (Fig. 4.1 B and C, respectively) were usually in the lower range, values of under-ice and sub-ice amphipods (Fig. 4.1 D) were often higher. Amongst sympagic meiofauna, harpacticoids had comparatively high carbon isotope values, while values of red acoels, nematodes, the calanoid *Eurytemora richingsi*, cyclopoids and nauplii were generally low. Amongst amphipods, generally high values were found in the sympagic species *Gammarus wilkitzkii* and *Onisimus* spp., low values in the pelagic species *Themisto libellula*.

For Antarctic sympagic meiofauna, lowest nitrogen SI values were found in white acoels, intermediate values in rhabdocoels and highest values in the ctenophore *Euplokamis* sp. (Supplement 4.S6 Table 4.S6).

Calculated trophic levels (Fig. 4.2 and Supplement 4.S6 Table 4.S6) of sympagic meiofauna and sub-ice fauna from the Central Arctic had wide ranges from sub-zero values to values > 10. Amongst sympagic meiofauna, highest median values were obtained by red acoels, nauplii, cyclopoids, nematodes (from bottom sea-ice) and rotifers (sampled from new ice on meltpond surfaces). Lowest median values were found for the sympagic harpacticoids *Tisbe* spp. and *Halectinosoma* spp.. In the amphipods *Onisimus* spp. and *Gammarus wilkitzkii*, calculated trophic levels were highly variable and often negative. In the other two amphipod species, trophic levels were less variable and usually positive, with a lower median in *Apherusa glacialis* than in *Themisto libellula*.

Calculated proportions of sea-ice derived carbon of Central Arctic fauna (Fig. 4.2 and Supplement 4.S6 Table 4.S6) were often beyond the theoretically expected range of 0–1. Proportions > 0.5 were found amongst sympagic meiofauna in harpacticoids and

sometimes rotifers, amongst amphipods in the under-ice species *Gammarus wilkitzkii*, *Onisimus* spp. and most of the *Apherusa glacialis*. Extremely negative values were obtained by sympagic rotifers (sampled from new ice on meltponds), red acoels, cyclopoids, nauplii and nematodes (sampled from sea ice) as well as by sub-ice *Oithona* cf. *similis* and sometimes nauplii.

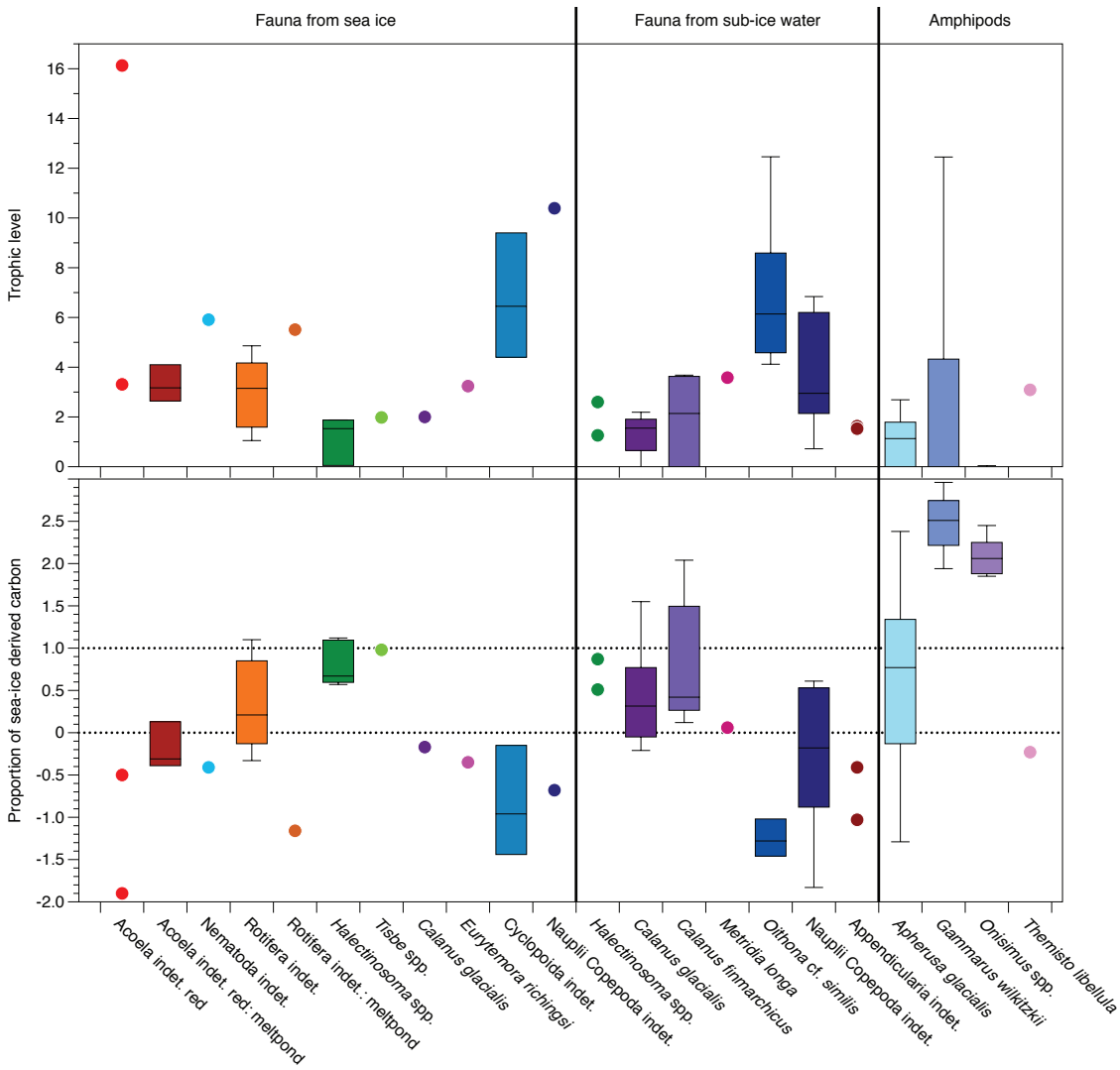

Figure 4.2: Boxplots of trophic levels (upper panel) and proportions of sea-ice derived carbon (lower panel) calculated for sympagic meiofauna, sub-ice fauna and under-ice and sub-ice amphipods from the Central Arctic. Calculations are based on a two-source model with sea-ice algae and phytoplankton as sources (Supplement 4.S4). Boxplots show medians, quartiles and ranges; outliers are not displayed. Only trophic levels > 0 are shown. Colours in the online version are the same as in Fig. 4.1.

4.4.2 Lipid and wax ester contents and fatty acids

Total lipid contents (Supplement 4.S6 Table 4.S6), expressed in % of dry mass, were moderate to low in both sympagic meiofauna (irrespective of regions and seasons) and sub-ice fauna (median 29 %, quartiles 20 % and 48 %), with no significant differences

between sympagic meiofauna from the Central Arctic and the Weddell Sea (no dry-mass data available for the Canadian Arctic) nor between sympagic meiofauna and sub-ice fauna in the Central Arctic (U-test, significance level 5 %).

Wax ester (WE) contents (Fig. 4.3 and Supplement 4.S6 Table 4.S6) were significantly lower in sympagic meiofauna (< 22 %) than in sub-ice fauna in the Central Arctic (16–92 % in copepods); WE contents in sympagic meiofauna did not differ significantly between different regions and seasons (U-test). No WE were detected in sympagic rhabdocoels and sub-ice appendicularians.

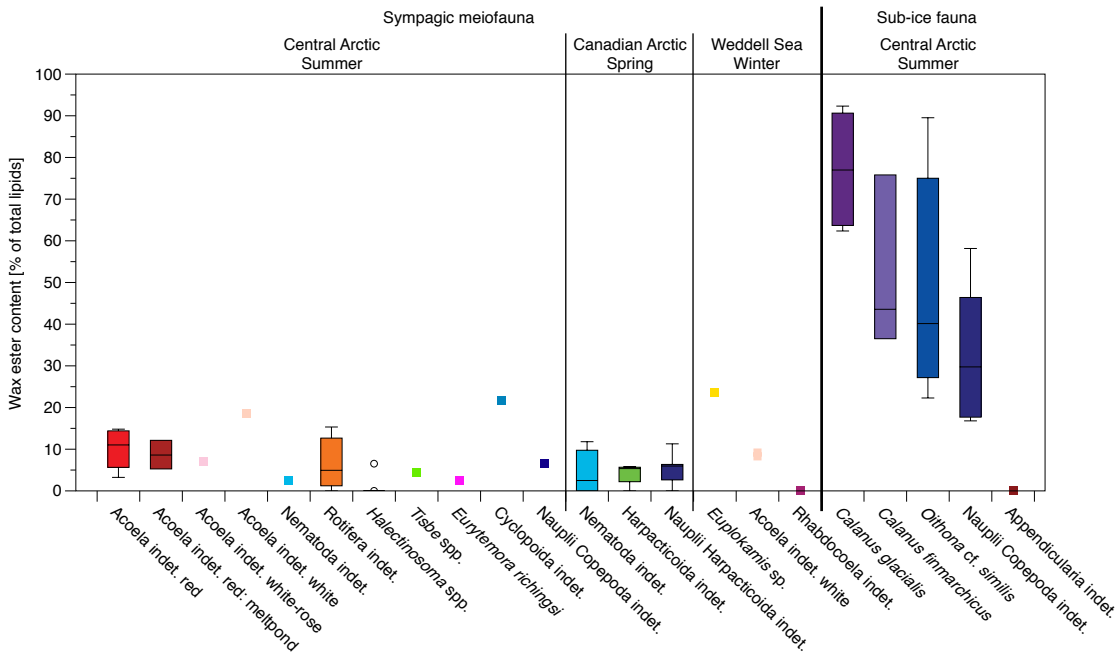

Figure 4.3: Boxplots of wax-ester contents (calculated from fatty alcohol fractions) relative to total lipid content for sympagic meiofauna from the Central Arctic, Canadian Arctic and the Weddell Sea as well as for sub-ice fauna from the Central Arctic. Boxplots show medians, quartiles and ranges; outliers and extreme outliers are displayed as filled and open circles, respectively. Colours in the online version are the same as in Fig. 4.1.

Principal component analysis of fatty acid (FA) composition of sympagic meiofauna and sub-ice fauna revealed three principal components (PC) together accounting for 59 % of the total variability (Fig. 4.4 and Supplement 4.S6 Fig. 4.S6.2). PC 1 separated the diatom markers 16:1(n-7), 18:1(n-7) and 20:5(n-3) (positive loadings) from the metazoan / detritus marker 18:1(n-9) (negative loading). PC 2 separated the diatom markers 16:1(n-7) and 18:1(n-7) (positive loadings) from the flagellate markers 22:6(n-3) and 18:4(n-3) and the calanid markers 20:1(n-9) and 22:1(n-11) (negative loadings). PC 3 separated the diatom marker 18:1(n-7) and the flagellate marker 22:6(n-3) (positive loadings) from the calanid markers 20:1(n-9) and 22:1(n-11), the diatom marker 16:1(n-7) and

the metazoan / detritus marker 18:1(n-9) (negative loadings). Sub-ice fauna and sympagic meiofauna were best separated by PC 2.

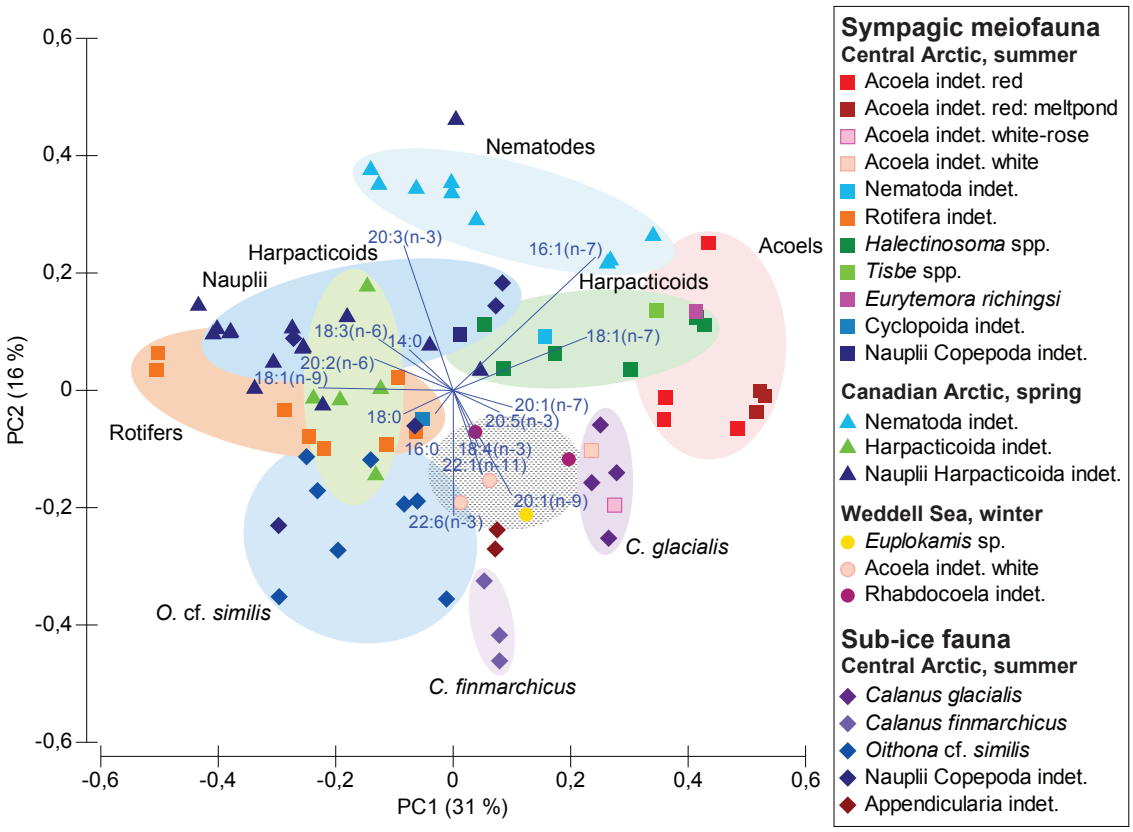

Figure 4.4: Results of principal component analysis (PCA) of fatty acid composition of sympagic meiofauna and sub-ice fauna, including the 15 most important fatty acids as variables (exceeding 10 % of total fatty acids in at least one sample). The first two principal components (PC1, PC2) are shown, accounting for 31 % and 16 % of the total variability, respectively. PC3 is shown in Supplement 4.S6 Fig. 4.S6.2. Sympagic meiofauna from the Central Arctic in summer (squares), Canadian Arctic in spring (triangles) and Weddell Sea in winter (circles) as well as sub-ice fauna from the Central Arctic in summer (diamonds) are shown. Shaded areas qualitatively illustrate faunal groups, the hatched area illustrates samples from the Weddell Sea. Colours are the same as in Fig. 4.1.

Amongst sympagic meiofauna from the Central Arctic in summer (Fig. 4.4 and Supplement 4.S6 Table 4.S6, Fig. 4.S6.2 and Fig. 4.S6.3), rotifers and cyclopoids were generally associated with the negative PC 1 axis. They were characterised by very high proportions of metazoan / detritus markers relative to diatom markers (also high 18:1(n-9) / 18:1(n-7) and intermediate to low PUFA / SFA ratios) and comparatively low amounts of diatom markers relative to flagellate markers (also low or intermediate 16:1(n-7) / 16:0 and 20:5(n-3) / 22:6(n-3) ratios). Rotifers sometimes also had high amounts of bacteria markers (odd-numbered FA). Acoels, in contrast, were associated with the positive PC 1 axis, and diatom markers were of accordingly greater importance relatively to both metazoan / detritus and flagellate markers, specifically in the red acoel taxon with highest PC 1 values. Considerable amounts of calanid markers were also present, specifically

in the white and white-rose acoels with negative PC 2 values. The calanoid *Eurytemora richingsi* was very similar to the red acoels in terms of FA composition, except for the lack of calanid markers. Harpacticoids and nematodes were likewise associated with the positive PC 1 axis and had slightly positive PC 2 values. They were characterised by high proportions of diatom markers and minor importance of flagellate or metazoan / detritus markers. Nematodes also had bacteria markers. Copepod nauplii differed from copepodids by association with positive PC 2 and negative PC 3 rather than positive PC 1 axes. Accordingly, diatom markers were less important and proportions of metazoan / detritus markers were higher; they also had comparatively high proportions of bacteria markers.

Sympagic harpacticoid copepodids and nauplii from the Canadian Arctic in spring differed from those from the Central Arctic in summer by negative PC 1 values, accordingly greater importance of metazoan / detritus markers (specifically in nauplii) and flagellate markers (specifically in copepodids) relative to diatom markers and generally higher proportions of bacteria markers. Nematodes in spring had generally lower PC 1 values than in summer, along with distinctly higher PC 2 and mostly higher PC 3 values, with similarly greater importance of metazoan / detritus and bacteria markers, but minor importance of flagellate markers.

The Antarctic sympagic ctenophore *Euplokamis* sp., rhabdocoels and white acoels were associated with negative PC 2 and positive PC 3 axes and characterised by minor importance of diatom relative to flagellate markers, intermediate importance of metazoan / detritus markers and absence of bacteria markers. The Antarctic acoels differed from the Arctic ones by lower PC 1 values, lower proportions of diatom and higher proportions of flagellate markers and very low amounts of calanid markers.

Seasonal trends were observed in harpacticoids and nematodes from the Canadian Arctic (data not shown). Harpacticoids (from early naupliar stages in mid-March to late copepodid stages in the end of April) showed an increase in proportions of diatom markers as well as PUFA, associated with a decrease in metazoan / detritus markers and MUFA or SFA. Also a switch from low to higher proportions of flagellate markers at the transition from naupliar to copepodid stages was observed. In nematodes, an increase in PUFA and a decrease in MUFA and diatom markers was observed from early to late May.

4.5 Discussion

4.5.1 Complexity of the sympagic food web

We provide first detailed information on the feeding ecology of several Arctic and Antarctic sympagic meiofauna taxa. Based on very few studies (Hoshiai et al. 1987, Grainger

and Hsiao 1990, Schnack-Schiel et al. 1995, Swadling et al. 2000), it has previously been assumed that sympagic meiofauna is primarily herbivorous (Gradinger 1995, Brierley and Thomas 2002, Arrigo and Thomas 2004). In contrast, our results of stable isotope (SI) and fatty acid (FA) analyses strongly suggest that omnivorous, detritivorous and even carnivorous feeding of sympagic meiofauna are rather common (Table 4.2), confirming our hypothesis. The sympagic food web is thus more complex than generally assumed.

We interpret the results from SI and FA analyses in conjunction to conclude on trophic positions and diets of sympagic meiofauna (Table 4.2). Observations of feeding in the lab are also included. In general, a meiofauna taxon is considered carnivorous if calculated trophic levels were high ($\lambda \approx 4$–5) or δ^{15}N values were high in comparison with other taxa from the respective expedition, if proportions of metazoan or calanid markers were likewise high (ideally with high 18:1(n-9) / 18:1(n-7) and low PUFA / SFA ratios) and the animals could (based on their phylogeny and morphology) be expected to feed on metazoans. Animals with similar characteristics in SI and FA, but obviously not adapted to ingest metazoans are considered to feed on fecal pellets, carrion and eggs and classified as detritivorous. No specific FA biomarkers for ciliates have been identified as yet; however, intermediate to high trophic levels ($\lambda \approx 3$–5) or δ^{15}N in combination with generally low proportions of metazoan and calanid markers (often also low 18:1(n-9) / 18:1(n-7) and intermediate to high PUFA / SFA ratios) indicate cilivorous feeding. Animals with such characteristics are thus classified as cilivores, particularly if we additionally observed feeding on ciliates in the lab for the same or related taxa (Kramer and Prowe in preparation), or if morphological characteristics of these taxa and knowledge on feeding habits of higher taxa pointed to cilivorous feeding. Taxa with low trophic level ($\lambda \approx 2$) or low δ^{15}N, high proportions of diatom markers and low proportions of metazoan and calanid markers (ideally with low 18:1(n-9) / 18:1(n-7) and high PUFA / SFA ratios) are considered herbivorous. Bacterivory is indicated by the presence of odd-numbered FA (Rezanka and Sigler 2009) and possibly by high variability in SI values.

We suggest that the sympagic ctenophore *Euplokamis* sp. with its high δ^{15}N values is the top predator in Antarctic sea ice, preying on copepods and ciliates (Kramer and Prowe in preparation), thus occupying a trophic position comparable to that of the Arctic sympagic cnidarian *Sympagohydra tuuli* (Siebert et al. 2009).

We consider Arctic sympagic cyclopoids as carnivorous–omnivorous–detritivorous, feeding on small metazoan meiofauna, ciliates, fecal pellets, carrion, eggs, flagellates and diatoms, as indicated by both our SI and FA data and confirmed by gut content analyses (Grainger and Hsiao 1990). Meiofauna also seems to play an important role in the diets of some sympagic harpacticoids particularly in early spring, i. e. during the growth phase,

Table 4.2: Qualitative overview of results and conclusions for sympagic meiofauna: calculated trophic level (λ) or δ^{15}N, principal components (PC), FA markers, FA ratios, sum of odd-numbered FA; proposed diets and feeding types based on these results in conjunction with observations and literature information (if available); proposed feeding grounds based on SI. Taxa are sorted according to diets. HH very high, H high, I intermediate, L low, LL very low. -PC1 or +PC1 association with negative or positive PC1 axis, respectively—accordingly for PC2 and PC3. Diat = diatoms, Flag = flagellates, Cil = ciliates, Meta = metazoans, Meio = meiofauna, Cop = copepods, Cala = calanids, Bac = bacteria, CE = carrion and eggs, FP = fecal pellets. carniv = carnivorous, ciliv = cilivorous, omniv = omnivorous, herbiv = herbivorous, bacteriv = bacterivorous, detritiv = detritivorous. i = sea ice, mp = meltponds, w = sub-ice water.

Taxon (region, season)	λ or δ^{15}N	PC	FA markers	18:1(n-9)/ 18:1(n-7)	PUFA/ SFA	16:1(n-7)/ 16:00	20:5(n-3)/ 22:6(n-3)	Odd-numbered FA	Proposed diets	Proposed feeding type	Feeding grounds
Euplokamis sp. (Weddell Sea, winter)	H	-PC2, +PC3	Diat, Flag (Meta)	I	I–H	L	L	LL	Cop (Cil)	carniv	
Cyclopoida indet. (Central Arctic, summer)	H–HH	-PC1, -PC2, +PC3	Diat, Meta (Flag, Cala)	H	L	L	L	LL	Small Meio, Cil, FP, CE, Flag, Diat	carniv-omniv-detritiv	mp, w
Harpacticoida indet. (Canadian Arctic, spring)		-PC1	Diat, Flag, Meta (Cala)		I	L	L	L–H	Small Meio, Cil, Flag, Diat, Bac	carniv-omniv-bacteriv	
Rhabdocoela indet. (Weddell Sea, winter)	I	-PC2, +PC3	Diat, Flag (Meta)	I	I–H	L	L	LL	Cil, small Meio, Flag, Diat	ciliv-omniv	
Rotifera indet. (Central Arctic, summer)	L–HH	-PC1	Meta, Diat (Flag, Cala)	H	L–I	L	L–I	L–H	Cil, FP, CE, Flag, Diat, Bac	ciliv-omniv-bacteriv-detritiv	i, mp, w
Nauplii Harpacticoida indet. (Canadian Arctic, spring)		-PC1	Diat, Meta (Flag)	I	L–I	L	L–I	H	Cil, FP, CE, Flag, Diat, Bac	ciliv-omniv-bacteriv-detritiv	
Nauplii Copepoda indet. (Central Arctic, summer)	HH	+PC2, -PC3	Diat (Flag, Meta)		L	I	L	H	Cil, FP, CE, Diat, Flag, Bac	ciliv-omniv-bacteriv-detritiv	mp
Nematoda indet. (Canadian Arctic, spring)		+PC2	Diat, Meta (Flag)	I	L–I	H	I–H	L–I	Cil, FP, CE, Diat, Bac (Flag)	ciliv-omniv-bacteriv-detritiv	
Acoela indet. white (Central Arctic, summer)		+PC1, -PC2, +PC3	Diat, Cala (Flag, Meta)	LL	I	L	L	LL	Diat, Flag, FP, CE (Cil, small Meio)	herbiv-detritiv	
Acoele indet. white-rose (Central Arctic, summer)		+PC1, -PC2	Diat, Flag, Cala (Meta)	L	H	I	L	LL	Diat, Flag, FP, CE (Cil, small Meio)	herbiv-detritiv	
Acoela indet. white (Weddell Sea, winter)	L	-PC2, +PC3	Flag, Diat (Meta, Cala)	I	I–H	L	L	LL	Flag, Diat, Cil (small Meio, FP, CE)	herbiv-ciliv	
Acoela indet. red (Central Arctic, summer)	L–I (HH)	+PC1	Diat (Flag, Cala, Meta)	LL	L	I	L	LL	Diat, Flag, Cil (small Meio, FP, CE)	herbiv-ciliv	mp, w
E. richingsi (Central Arctic, summer)	I	+PC1, +PC2	Diat (Flag)	LL	L	I	L	LL	Diat, Flag, Cil	herbiv-ciliv	w
Nematoda indet. (Central Arctic, summer)	HH	+PC1, +PC2	Diat, Flag (Meta)	L	H	H	L	I	Diat, Flag, Bac (Cil, small Meio, FP, CE)	herbiv-bacteriv	m
Halectinosoma spp. (Central Arctic, summer)	L	+PC1, +PC2, +PC3	Diat (Flag, Meta, Cala)	L	I	I	L	L	Diat, Flag (Cil, small Meio)	herbiv	i
Tisbe spp. (Central Arctic, summer)	L	+PC1, +PC2	Diat (Flag, Meta)	L	HH		I	LL	Diat (Flag, Nau, FP)	herbiv	i

as indicated by FA and observations of cannibalisms and cilivory (Kramer and Prowe in preparation). These harpacticoids, also feeding on flagellates, diatoms and bacteria, are classified as carnivorous–omnivorous–bacterivorous. In Antarctic sea ice, the calanoid *Stephos longipes* has been suggested to occupy a similar trophic position (Michels and Schnack-Schiel 2005).

A rather ciliate-based diet is obviously consumed by Arctic sympagic rotifers, copepod nauplii and some nematodes (the latter only in spring). In addition, these meiofauna taxa also seem to feed on bacteria, flagellates and diatoms as well as on fecal pellets, carrion and eggs, as concluded from FA data. They are thus classified as cilivorous–omnivorous–bacterivorous–detritivorous. We suggest that rhabdocoels, classified here as cilivorous–omnivorous, occupy a comparable or slightly higher trophic position in Antarctic sea ice, as indicated by intermediate δ^{15}N and FA markers.

Other sympagic meiofauna seem to rely more on algae, but supplement their diet with fecal pellets, carrion, eggs, ciliates, small meiofauna or bacteria. Based on FA, we suggest that fecal pellets, carrion or eggs are the main dietary supplements for Arctic white and white-rose acoels, categorised as herbivorous–detritivorous. Red acoels and the calanoid *Eurytemora richingsi* seem to feed less on fecal pellets, carrion and eggs and are considered herbivorous–cilivorous. Nematodes in summer are obviously rather herbivorous–bacterivorous. We suggest that Antarctic white acoels are herbivorous–cilivorous (similar to Arctic red acoels), as indicated by comparatively low δ^{15}N, FA markers and feeding observations (Kramer and Prowe in preparation).

Only few meiofauna taxa can be characterised as almost exclusively herbivorous, including the Arctic harpacticoids *Tisbe* spp. and *Halectinosoma* spp.. In these taxa, predominantly herbivorous feeding was evident from SI, FA and feeding experiments (Kramer and Prowe in preparation) and has also been suggested in literature (Grainger and Hsiao 1990, Arndt and Swadling 2006). The harpacticoid *Drescheriella glacialis* and the calanoid *Paralabidocera antarctica* have been suggested to play a similar role in the Antarctic sympagic ecosystem (Arndt and Swadling 2006).

The persistently low wax ester (WE) proportions and the generally low to moderate lipid contents (also confirmed by low C:N ratios) in sympagic meiofauna—particularly when compared to sub-ice fauna—indicate a more continuous feeding rather than intensive energy storage during all seasons (Sargent et al. 1981), implying that sympagic meiofauna can explore various food sources. Seasonal switches in food sources, as observed in under-ice amphipods (Werner and Auel 2005), seem to occur also in sympagic meiofauna. Based on FA proportions, metazoans seem to be an important diet for nematodes, harpacticoid copepodids and nauplii specifically in spring, which seems to be the growth

phase at least of the harpacticoids (own observations, unpublished). In summer, diatoms obviously become more important as a diet for these taxa. Short-term switches in feeding strategies of sympagic meiofauna are indicated by the high variability in both SI values and FA proportions in several taxa. Furthermore, sympagic meiofauna seems to adapt its feeding strategies to the specific conditions, as indicated by two observations. Firstly, flagellates are obviously more important in the diets in winter (prior to the diatom bloom in the ice) than in spring and summer (when diatoms are more abundant). Secondly, animals from cultures, which were reared on mixed ice algae containing mainly diatoms, had higher proportions of diatom markers than animals from nature (Supplement 4.S6 Table 4.S6). Sympagic meiofauna is thus characterised by flexible feeding strategies. Short-term and seasonal switches are probably adaptations to the highly dynamic sea-ice habitat, which is characterised by high short-term and small-scale variability as well as strong seasonality (Schünemann and Werner 2005, Steffens et al. 2006).

Carnivorous feeding has been reported only twice for Arctic sympagic acoels (Friedrich and Hendelberg 2001) and the cnidarian *Sympagohydra tuuli* (Siebert et al. 2009) and has been discussed for the Antarctic sympagic calanoid *Stephos longipes* (Michels and Schnack-Schiel 2005) and the nudibranch *Tergipes antarcticus* (Kiko et al. 2008a). Based on our data, we suggest that carnivory, cilivory and omnivory are much more common in sympagic meiofauna. This certainly influences cycling of energy and matter in sea ice. The feeding impact of sympagic meiofauna—so far calculated under the assumption that meiofauna feeds primarily or exclusively on sea-ice algae (Gradinger 1999a, Gradinger et al. 1999, Nozais et al. 2001, Michel et al. 2002, Gradinger et al. 2005), based on allometric equations for mainly herbivorous zooplankton (Moloney and Field 1989)—needs to be revisited in the light of carnivorous and omnivorous feeding.

4.5.2 Distinction of feeding grounds based on the stable isotope data

Sympagic and sub-ice fauna can obtain food from at least two feeding grounds: the sea ice and the pelagic realm. In the Arctic, also saline or brackish meltponds need to be considered as a potential feeding ground nowadays: the pond water column and the new ice on top of such ponds provide favourable living conditions, may supply ample algae food and are, due to the honeycomb structure of the rotten ice on the bottom, accessible to sympagic meiofauna, sub-ice fauna and under-ice amphipods (Kramer and Kiko 2010).

Algae from these three habitats differ in SI values (as reflected by POM SI values in this study) due to nutrient and carbon cycling conditions, which differ between closed systems (such as the brine channel system in sea ice and, to some extent, probably also

meltponds) and open systems (such as the pelagic realm). Such differences can be traced in the consumers throughout the food web (Post 2002).

Feeding on pelagic food sources is indicated by relatively low carbon SI values in animals, since carbon isotope values of pelagic POM were generally lower than those of sea-ice POM in the Central Arctic during our study. However, also POM from the different meltpond habitats (water column, new ice on top, rotten ice at the bottom) had generally low carbon isotope values (usually in the lower range of those of pelagic POM), which came along with relatively high nitrogen isotope values. Low carbon isotope values in animals therefore might also indicate food sources from meltponds, particularly when in the same time nitrogen isotope values were high. According to the two-source model applied in this study, feeding on primarily pelagic food sources is indicated by low levels of sea-ice derived carbon a (ideally 0–0.5), whereas higher a (ideally 0.5–1) indicate feeding on primarily sympagic food sources. However, meltponds as a third possible feeding ground are not included in the model, and feeding on POM from meltponds may likely result in low a. In such case, trophic levels λ calculated by the model would be elevated due to the high nitrogen isotope values of meltpond POM. This is seen clearly in samples of rotifers from new ice on meltponds, which had lower median a and higher median λ than samples of the respective taxon from sea ice, probably related to the fact that animals from meltpond samples had been feeding extensively in this habitat. We therefore interpret our carbon isotope data and the calculated proportions of sea-ice derived carbon in conjunction with the nitrogen isotope data and the calculated trophic levels, generally assuming feeding on primarily sympagic food sources when δ^{13}C and a were high, primarily pelagic food sources when δ^{13}C and a were low and δ^{15}N and λ were not extraordinarily high, and primarily meltpond food sources when δ^{13}C and a were low and δ^{15}N and λ were extraordinarily high.

Our SI data indicate feeding of several sub-ice fauna taxa and under-ice amphipods on sympagic food sources, thus confirming previous studies (Scott et al. 1999, Werner and Auel 2005, Falk-Petersen et al. 2009). On the other hand, they give first evidence that some taxa of sympagic meiofauna feed substantially on pelagic food sources rather than grazing primarily or exclusively on sea-ice algae, as generally assumed (Gradinger 1995, Brierley and Thomas 2002, Arrigo and Thomas 2004). Furthermore, our data indicate that meltponds play an important role as an additional feeding ground for both sympagic meiofauna and sub-ice fauna in the Arctic. Our study thus reveals new pathways in cryo-pelagic coupling processes.

4.5.3 Cryo-pelagic coupling and the role of meltponds

Our data indicate that sympagic cyclopoids, rotifers, acoels and the calanoid *Eurytemora richingsi* feed substantially on pelagic food sources (Table 4.2). Sympagic cyclopoids, rotifers and acoels are common members of the Arctic sympagic community (Gradinger 1999a, Gradinger et al. 1999, Nozais et al. 2001, Schünemann and Werner 2005) and often found in the sub-ice water, specifically in summer (Werner and Martinez Arbizu 1999, Werner 2006a,b). *E. richingsi* was first described as an Arctic deep-water species (Heron and Damkaer 1976), but it also occurs in upper water layers in the vicinity of sea ice (Kosobokova et al. 1998) and in sub-ice water (Werner and Martinez Arbizu 1999). It has not been reported from sea ice itself before, but since many specimens and different developmental stages were found in the ice at various locations of the Central Arctic during ARK–XXII / 2 (own data, unpubl.), we suggest that this species is a regular part of the Arctic sympagic community. All sympagic taxa proposed to utilise pelagic food sources have good or moderate swimming capability (Friedrich 1997; own observations). The sympagic harpacticoids *Halectinosoma* spp. and *Tisbe* spp. obviously rely primarily on sympagic food sources. These harpacticoids are common members of the sympagic community (Arndt and Swadling 2006), which are also found in the sub-ice water in summer (Werner and Martinez Arbizu 1999, Werner 2006a,b), but have poor swimming capability (own observations). For amphipods, our data indicate utilisation of primarily sympagic food in the under-ice species *Gammarus wilkitzkii* and *Onisimus* spp., while *Apherusa glacialis* seems to feed not only on sea ice algae, as previously reported (Werner 1997, Scott et al. 1999, Werner and Auel 2005), but also on phytoplankton. The pelagic amphipod species *Themisto libellula* frequently found in the vicinity of sea ice (Auel and Werner 2003) obviously relies on pelagic rather than on sympagic food. Our data thus give new insight into the feeding ecology of *A. glacialis*, while confirming previous conclusions based on experimental and FA studies for *G. wilkitzkii*, *Onisimus* spp. and *T. libellula* (Werner 1997, Scott et al. 1999, 2001, Werner et al. 2002, Auel and Werner 2003, Werner and Auel 2005).

It is generally assumed that sympagic meiofauna profits particularly from the ample food supply in the ice (Gradinger 1995, Brierley and Thomas 2002, Arrigo and Thomas 2004). In contrast to this, our findings suggest that only meiofauna taxa with poor swimming capability, specifically harpacticoid copepods, rely almost exclusively on sympagic food sources and probably do not actively migrate between the sea ice and the pelagic realm. Sympagic taxa with better swimming capabilities, specifically calanoid and cyclopoid copepods, rotifers and acoels, do not seem to depend on sympagic food sources, but rather feed on pelagic food in the sub-ice water layer, at least during summer. The

role of Arctic and Antarctic sympagic meiofauna for cryo-pelagic coupling, specifically as a pathway from the sea ice to the pelagic realm, has been recognised before, since sympagic meiofauna is abundant in the sub-ice water specifically during summer (Werner 2006b, Kiko et al. 2008b). In contrast, the potential significance of sympagic meiofauna re-entering the ice remained unclear: the possibility of such active migration has been discussed (Werner 2006a, Kiko et al. 2008b), but there was no evidence of this pathway in cryo-pelagic coupling as yet. Our data emphasise the importance of sympagic meiofauna for the transport of organic matter from the sea ice to the pelagic realm, suggesting that meiofauna might leave the ice not only due to meltwater flushing (Werner 2006b, Kiko et al. 2008b), but also actively for feeding in sub-ice layers. Here they may constitute an important food source for carnivorous and omnivorous under-ice amphipods, sub-ice fauna and pelagic animals (Werner et al. 2002, Werner and Auel 2005). On the other hand, our data give first evidence of sympagic meiofauna re-entering the ice after feeding in the sub-ice water, since meiofauna with SI values indicating pelagic feeding were sampled from inside the sea ice. Sympagic meiofauna thus needs to be considered a link not only from sea ice to the pelagic realm, but also from the pelagic realm back to sea ice, providing additional supply of energy and organic matter to the sympagic community.

According to our SI data, food sources from meltponds are probably utilised by sympagic acoels, cyclpoids, rotifers, nauplii and nematodes (Table 4.2)—even by specimens in samples from sea-ice bottom layers, not from meltponds, implying again active migration between the two habitats. Specifically rotifers, acoels and nematodes were often found in the new ice cover on meltponds during our expedition to the Central Arctic, occasionally also sympagic cyclopoids and nauplii (Kramer and Kiko 2010). Rotifers have good swimming capability, acoels moderate, nematodes and sympagic nauplii rather poor (Friedrich 1997; own observations). We previously suggested that these meiofauna taxa migrate laterally from the bottom layer of the sea ice into the rotten ice on the bottom of the meltponds and into the ponds themselves, from where they can enter the new ice cover on top of the ponds (Kramer and Kiko 2010). Our SI data indicate that they feed in these habitats and are able to migrate back into the brine channels of the surrounding ice thereafter. Amongst sub-ice fauna, the cyclopoid *Oithona* cf. *similis* and nauplii probably utilise food sources from meltponds. The under-ice amphipods, in contrast, obviously do not rely on food sources originating from melt ponds, although *Apherusa glacialis* were often found in this habitat during our expedition (Kramer and Kiko 2010). Both under-ice amphipods and sub-ice fauna probably enter the meltponds through the large brine channels and thaw holes in the rotten ice at the bottom of the ponds (Kramer and Kiko 2010). In conclusion, both sympagic meiofauna and sub-ice fauna can profit from the sometimes

ample food supply in brackish and saline meltponds. Furthermore, it can be suspected that interactions between sympagic meiofauna, sub-ice fauna and possibly under-ice amphipods take place in meltponds, and therefore cryo-pelagic coupling might be enhanced in these particular habitats.

4.5.4 Suitability of stable isotope and fatty acid analyses to sympagic meiofauna studies

This is the first study applying SI and FA analyses to a wide range of sympagic meiofauna taxa from both Arctic and Antarctic. The only sympagic meiofauna where FA and lipids have been measured previously is the comparatively large Antarctic calanoid copepod *Paralabidocera antarctica* (Swadling et al. 2000). We specifically developed methods for sample preparation and partly modified the measurement procedures for adoption of SI and FA analyses to sympagic meiofauna, accounting for their small size and delicate nature. With these specific arrangements—particularly including a filtration procedure for sample preparation and a data correction for filter blanks—the methods prove well suitable to sympagic meiofauna studies. We further developed a two-source model for calculation of trophic levels and proportions of sea-ice derived carbon from SI data, following the approach by Post (2002). If interpreted with the necessary caution, the model results give valuable information on feeding habits.

In order to validate our procedures, we included analyses of Arctic sub-ice fauna (SI and FA) as well as under-ice and sub-ice amphipods (SI). Our results are in general accordance with previous studies, confirming e. g. exploitation of sympagic algal food sources by under-ice amphipods (Werner 1997, Scott et al. 1999, Werner and Auel 2005) as well as by the pelagic calanoids *Calanus* spp. (Falk-Petersen et al. 2009), preference of pelagic food sources by the sub-ice amphipod *Themisto libellula* (Auel and Werner 2003) and distinct feeding strategies of the different under-ice amphipod species (Werner 1997, Scott et al. 1999) including species-specific feeding in *Onisimus* spp. (Werner and Auel 2005). They also confirm omnivorous or carnivorous feeding in the pelagic cyclopoid *Oithona* cf. *similis* (Lischka and Hagen 2007) contrasted with mainly herbivorous feeding in *Calanus* spp. with slight species-specific differences (Falk-Petersen et al. 2009) as well as energy storage strategies in the epipelagic copepods (Scott et al. 2000, Lischka and Hagen 2007, Narcy et al. 2009).

The good agreement with literature concerning food sources of the pelagic copepods (Lischka and Hagen 2007, Falk-Petersen et al. 2009) particularly supports the validity of our two-source SI model. Unreasonably high calculated trophic levels and negative calculated proportions of sea-ice derived carbon could be explained by the existence of

a third feeding ground (meltponds). In case of amphipods, carbon isotope values were often beyond the range of median POM values making them insuitable for evaluating the model, but in those cases where carbon isotope values were within the range of median POM values model results were in good agreement with literature, indicating carnivorous feeding in *T. libellula* (Auel and Werner 2003) and herbivorous feeding in *A. glacialis* (Werner 1997, Scott et al. 1999, Werner and Auel 2005). Possible additional feeding grounds and variability of baseline isotope values thus need to be borne in mind when interpreting results from the model.

Concerning sympagic meiofauna, interpretation of the single results would be difficult. Sample sizes were often close to the detection limit, enhancing the risk of inaccuracy and contamination in both SI and FA measurements. Since dry mass could not be measured directly but needed to be calculated from carbon contents, the derived lipid content is accordingly inaccurate; as FA composition is strongly influenced by the total lipid content (Hagen et al. 2001), interpretation of FA data was difficult. This was further complicated by the fact that little is known about the FA composition of several potential diets of sympagic meiofauna (e. g. ciliates) and about FA metabolism of most sympagic meiofauna taxa (*de novo* synthesis, chain elongation etc.).

Nonetheless, if SI data, results of the two-source model, lipid and WE contents, FA proportions and FA ratios are viewed in conjunction, they give a consistent picture of the trophic positions of sympagic meiofauna (Table 4.2), which are also in general accordance with experimental feeding studies (Kramer and Prowe in preparation). We thus suggest that future studies in feeding ecology should likewise combine different methods, particularly if little is known on the system or taxa studied.

4.5.5 Conclusions and outlook

The sympagic food web is more complex than previously expected, including, besides herbivorous, also omnivorous, cilivorous and carnivorous meiofauna species. The structure of the food web probably undergoes seasonal changes caused by dietary switches in several sympagic meiofauna taxa. Experimental studies are required to investigate the implications of carnivory and omnivory for the feeding impact of sympagic meiofauna.

Sympagic meiofauna feeding on pelagic food sources and actively migrating between the sea-ice and pelagic realms, as reported here for the first time, probably plays an important role in cryo-pelagic coupling. In the Arctic, meltponds nowadays provide additional food sources not only to sympagic meiofauna, but also to sub-ice fauna. It is probable that during the next decades, in consequence of global warming, an increasing proportion of the Arctic sea ice will be covered with brackish or saline meltponds over an extended

summer season (Kramer and Kiko 2010), providing a feeding ground for and enabling enhanced interactions between sympagic and pelagic organisms. We thus hypothesise that climate change will temporarily enhance cryo-pelagic coupling in those areas of the Arctic still covered by sea ice in summer.

SI and FA analyses are very suitable tools in the study of trophic positions and feeding strategies also of sympagic meiofauna. SI are particularly useful, since they can reveal interactions between sympagic and pelagic organisms due to SI differences between algae from sea ice, meltponds and pelagic realm. In order to obtain more reliable information from SI about trophic levels and the dietary importance of sea-ice algae, tissue turnover rates and trophic enrichment in sympagic meiofauna need to be determined experimentally. SI measurements of a third element (e. g. sulphur) would allow the application of a three-source model and therefore a better distinction between food sources from sea ice, meltponds and the pelagic realm along with a more certain estimation of trophic levels. For further interpretation of FA data, particularly analyses of sympagic ciliates in conjunction with experimental studies are required to identify specific ciliate markers.

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4.S Supplementary material

4.S1 Stations and samples

Table 4.S1: Sampling stations during four expeditions to obtain POM (ice = from sea ice, water = from sub-ice water 0 m and 5 m below the ice, mp = from meltponds) and fauna (Meio = sympagic meiofauna, Sub-ice = sub-ice fauna, Amph = under-ice and sub-ice amphipods) for stable isotope (SI) and fatty acid (FA) analyses. + sample type taken, — sample type not taken.

Region	Campaign	Station	Date	Location		Sample types taken for SI or FA					
				Lat	Lon	POM			Fauna		
						ice	water	mp	Meio	Sub-ice	Amph
Central Arctic	ARK–XXII/2	PS 70/248	070802	81°57' N	34°02' E	+	+	—	+	—	—
Central Arctic	ARK–XXII/2	Heli 1	070803	82°48' N	33°45' E	—	—	—	+	+	—
Central Arctic	ARK–XXII/2	PS 70/257	070805	83°30' N	33°57' E	—	—	—	+	+	+
Central Arctic	ARK–XXII/2	PS 70/259	070806	84°07' N	34°41' E	—	—	—	+	+	—
Central Arctic	ARK–XXII/2	PS 70/260	070807	84°29' N	36°08' E	+	+	—	—	+	+
Central Arctic	ARK–XXII/2	PS 70/262	070811	84°32' N	60°37' E	—	—	—	+	—	+
Central Arctic	ARK–XXII/2	PS 70/264	070812	83°38' N	60°23' E	+	+	—	—	+	+
Central Arctic	ARK–XXII/2	PS 70/271	070815	82°30' N	60°48' E	+	+	—	+	+	—
Central Arctic	ARK–XXII/2	PS 70/276	070817	82°08' N	69°12' E	—	—	—	+	—	—
Central Arctic	ARK–XXII/2	PS 70/285	070820	82°09' N	86°20' E	+	+	—	—	+	—
Central Arctic	ARK–XXII/2	PS 70/301	070824	84°35' N	89°50' E	+	+	—	—	—	—
Central Arctic	ARK–XXII/2	PS 70/309	070827	87°03' N	104°48' E	—	+	—	+	—	—
Central Arctic	ARK–XXII/2	PS 70/317	070830	88°21' N	142°51' E	—	—	—	+	—	—
Central Arctic	ARK–XXII/2	PS 70/322	070831	88°08' N	150°05' E	—	—	+	+	—	+
Central Arctic	ARK–XXII/2	PS 70/328	070902	87°49' N	170°36' W	+	—	+	—	—	+
Central Arctic	ARK–XXII/2	PS 70/338	070905	85°42' N	135°02' W	+	—	—	+	—	—
Central Arctic	ARK–XXII/2	PS 70/342	070907	84°30' N	138°22' W	+	—	+	—	—	—
Central Arctic	ARK–XXII/2	PS 70/352	070910	86°38' N	177°33' E	—	+	+	+	—	—
Central Arctic	ARK–XXII/2	PS 70/363	070912	86°24' N	135°49' E	—	—	—	+	—	—
Central Arctic	ARK–XXII/2	PS 70/363	070913	86°28' N	134°59' E	+	+	+	—	+	—
Central Arctic	ARK–XXII/2	PS 70/371	070916	84°39' N	102°44' E	—	+	+	+	+	—
Central Arctic	ARK–XXII/2	PS 70/373	070917	84°11' N	108°56' E	—	—	—	+	—	—
Canadian Arctic	CFL	D29–L	080317	70°54' N	123°29' W	—	—	—	+	—	—
Canadian Arctic	CFL	D32	080322	71°03' N	121°46' W	—	—	—	+	—	—
Canadian Arctic	CFL	D33	080325	71°04' N	121°47' W	—	—	—	+	—	—
Canadian Arctic	CFL	D33–L,–M,–H	080328	71°03' N	121°47' W	—	—	—	+	—	—
Canadian Arctic	CFL	D33–L,–M	080329	71°04' N	121°47' W	—	—	—	+	—	—
Canadian Arctic	CFL	D33–M	080331	71°04' N	121°47' W	—	—	—	+	—	—
Canadian Arctic	CFL	D33–L,–M	080403	71°04' N	121°47' W	—	—	—	+	—	—
Canadian Arctic	CFL	D36–L,–M	080406	71°14' N	124°13' W	—	—	—	+	—	—
Canadian Arctic	CFL	D38–L,–H	080411	71°16' N	124°37' W	—	—	—	+	—	—
Canadian Arctic	CFL	D38	080413	71°16' N	124°46' W	—	—	—	+	—	—
Canadian Arctic	CFL	D41–M	080416	70°47' N	122°14' W	—	—	—	+	—	—
Canadian Arctic	CFL	D43–M	080429	70°45' N	123°42' W	—	—	—	+	—	—
Canadian Arctic	CFL	F1–L+M	080508	70°11' N	124°50' W	—	—	—	+	—	—
Canadian Arctic	CFL	F2–H	080513	69°57' N	126°10' W	—	—	—	+	—	—
Canadian Arctic	CFL	F2–L	080516	69°57' N	126°10' W	—	—	—	+	—	—
Canadian Arctic	CFL	F3–M	080520	71°34' N	119°36' W	—	—	—	+	—	—
Spitsbergen	UNIS campaign	Billef. 3	090504	78° N	17° E	+	+	—	—	—	—
Spitsbergen	UNIS campaign	Tempelf. 3	090504	78° N	17° E	+	+	—	+	—	—
Weddell Sea	ANT–XXIII/7			59°50' S–65°07' S	40°47' W–57°24' W	—	—	—	+	—	—

4.S2 Required sample size

Table 4.S2: Sizes of samples required in stable isotope and fatty acid analyses for the different fauna taxa, along with C, N and lipid contents of the samples analysed. For taxa marked with ⋆, the filtration method was applied (i. e. animals were placed onto filters, rinsed and frozen). In taxa marked with ∗, part of the samples had been prepared without filters (i. e. the animals were rinsed in petri dishes filled with cold MilliQ water and transferred into small vials with little MilliQ water, which was then withdrawn with a capillary tube before freezing the samples), and since the respective samples were often contaminated with remaining salt and difficult to handle, the salts had to be removed and (in case of SI samples) the animals to be placed on filters later on. ice = sea ice (5 cm bottom layer), water = sub-ice water (0 m), mp = new ice on surface of meltponds.

Taxon	Habitat	Region	Required sample size SI (number of individuals)	C content per sample [μg]	N content per sample [μg]	Required sample size FA (number of individuals)	Lipid content per sample [μg]
Ctenophora							
Euplokamis sp. ∗	ice	Weddell Sea	50	4	4	85	35
Plathelminthes							
Acoela indet. white ∗	ice	Weddell Sea	110–150	13–38	4–8	90–150	12
Acoela indet. red ⋆	ice, mp	Central Arctic	34–50	34–50	5–7	18–80	16–73
Acoela indet. white ⋆	ice	Central Arctic	nd	nd	nd	50	14
Acoela indet. white-rose ∗	ice	Central Arctic	nd	nd	nd	45	14
Rhabdocoela indet. ∗	ice	Weddell Sea	10–20	14–32	4–6	20	28–29
Rotifera							
Rotifera indet. ⋆	ice, mp	Central / Canadian Arctic	600–1000	8–37	3–8	500–1000	4–11
Nematoda							
Nematoda indet. ∗	ice	Central / Canadian Arctic	50–150	4–27	1–3	50–250	10–25
Polychaeta							
Trochophora Polychaeta indet. ⋆	ice	Spitsbergen	140	3	2	nd	nd
Polychaeta indet. juv. ⋆	ice	Spitsbergen	> 6	nd	nd	nd	nd
Copepoda							
Halectinosoma spp. ∗	ice, water	Central Arctic	29–60	9–46	4–11	26–30	11–44
Tisbe spp. ∗	ice	Central Arctic	50	25	7	50	62
Harpacticoida indet. ⋆	ice	Canadian Arctic	nd	nd	nd	78–100	6–17
Calanus glacialis CV–CVI ∗	water, ice	Central Arctic	1	38–476	6–50	1	159–361
Calanus finmarchicus CIV–CVI ∗	water	Central Arctic	1	44–128	8–27	1	8–28
Eurytemora richingsi ⋆	water	Central Arctic	30	42	8	30	10
Metridia longa ⋆	water	Central Arctic	1	73	11	nd	nd
Oithona cf. similis ∗	water	Central Arctic	50–70	3–20	2–4	45–70	1–18
Cyclopoida indet. ⋆	ice	Central Arctic	50-67	1–4	2–3	50	13
Nauplii Harpacticoida indet. ⋆	ice	Canadian Arctic	nd	nd	nd	47–103	7–16
Nauplii Copepoda indet. ⋆	ice	Central Arctic	> 85	nd	1	100	9
Nauplii Copepoda indet. ⋆	water	Central Arctic	70–100	2–41	2–5	70–100	5–11
Amphipoda							
Apherusa glacialis	water, mp	Central Arctic	1	20–700	3–66	nd	nd
Onisimus spp.	water	Central Arctic	1	127–619	19–81	nd	nd
Gammarus wilkitzkii	water	Central Arctic	1–2	193–768	31–112	nd	nd
Themisto libellula	water	Central Arctic	1	770	82	nd	nd
Appendicularia							
Appendicularia indet. ∗	water	Central Arctic	nd	166–297	31–50	nd	46–52

4.S3 Blank correction

Nitrogen stable isotope values were corrected for the air blank effect according to Fry et al. (1992), using a peptone standard. For 32 different concentrations of the standard, we calculated the nitrogen content (m_{st}) and measured the δ^{15}N ($\delta_{st,m}$), shown in table beside. We assumed the δ^{15}N of the air blank (δ_{air}) to be 0.000 ‰. We could thus determine the true δ^{15}N of peptone ($\delta_{st,t} = 7.621$ ‰) and the air blank size ($m_{air} = 1\ \mu$g) from linear regression of $\delta_{st,m}$ against $\frac{1}{m_{st}}$:

$$\delta_{st,m} = \delta_{st,t} + (\delta_{air} - \delta_{st,t}) \cdot m_{air} \cdot \frac{1}{m_{st}} \qquad (4.S3.1)$$

The blank-corrected δ^{15}N of a sample (δ_t) can then be calculated from the measured value (δ_m) and nitrogen content (m) of the sample by re-arranging equation 4.S3.1 (with $\delta_{st,t} = \delta_t$, $\delta_{st,m} = \delta_m$ and $m_{st} = m$):

$$\delta_t = \frac{\delta_m \cdot m - \delta_{air} \cdot m_{air}}{m - m_{air}} \qquad (4.S3.2)$$

Table 4.S3: Concentrations of peptone standard used for blank correction, calculated nitrogen contents (m_{st}) and measured δ^{15}N ($\delta_{st,m}$).

Peptone [mg]	m_{st}	$\frac{1}{m_{st}}$	($\delta_{st,m}$)
0.023	0.003	395.257	4.132
0.026	0.003	349.650	3.391
0.030	0.003	303.030	3.245
0.032	0.004	284.091	6.044
0.041	0.005	221.729	5.573
0.050	0.006	181.818	5.976
0.057	0.006	159.490	5.222
0.058	0.006	156.740	5.446
0.063	0.007	144.300	4.693
0.064	0.007	142.045	6.108
0.074	0.008	122.850	5.953
0.078	0.009	116.550	6.032
0.086	0.009	105.708	6.679
0.099	0.011	91.827	6.132
0.107	0.012	84.962	6.820
0.127	0.014	71.582	6.601
0.210	0.023	43.290	7.177
0.305	0.034	29.806	7.189
0.372	0.041	24.438	7.399
0.410	0.045	22.173	7.612
0.432	0.048	21.044	7.550
0.467	0.051	19.467	7.602
0.528	0.058	17.218	7.556
0.549	0.060	16.559	7.566
0.625	0.069	14.545	7.543
0.631	0.069	14.407	7.532
0.686	0.075	13.252	7.645
0.776	0.085	11.715	7.639
0.835	0.092	10.887	7.601
0.926	0.102	9.817	7.662
0.928	0.102	9.796	7.683
1.053	0.116	8.633	7.689

4.S4 Derivation of equations for trophic levels and for proportions of sea-ice derived carbon (two-source model)

For estimating the trophic levels of the fauna as well as the proportions of carbon ultimately derived from sea ice, we essentially followed the approach by Post (2002), accounting for both mixing of pelagic and sympagic material and trophic fractionation at the same time. We reformulated the equations, thus correcting an inaccuracy in the equation for proportions given by Post (2002)—see equation 4.S4.4 and remark below. Our equations also account for differences in C:N between sea-ice algae and phytoplankton.

If the herbivorous fauna feeds on sea-ice algae and phytoplankton, the isotope value δ^X_{alg} of the food mix will be, according to the general mixing equation (Fry 2006):

$$\delta^X_{alg} = a^X \cdot \delta^X_i + \left(1 - a^X\right) \cdot \delta^X_w \quad , \tag{4.S4.1}$$

where subscripts i and w denote algae from sea-ice and water, respectively, and superscript X denotes the element C or N, $\delta^X := \delta^H X$ (i. e. the stable isotope ratio of element X in delta notation), a^X is the proportion of element X derived from sea-ice algae. Due to trophic fractionation (Waser et al. 1998), the isotope value δ^X_f of a faunal consumer is:

$$\delta^X_f = \delta^X_{alg} + D^X \cdot (\lambda - 1) \quad , \tag{4.S4.2}$$

where λ is the trophic level of the fauna (the trophic level of algae being 1) and D^X is the trophic enrichment factor for element X per trophic level (assumed to be constant). Combining equations 4.S4.1 and 4.S4.2 gives

$$\delta^X_f = \underbrace{a^X \cdot \delta^X_i + \left(1 - a^X\right) \cdot \delta^X_w}_{mixing} + \underbrace{D^X \cdot (\lambda - 1)}_{fractionation} \quad . \tag{4.S4.3}$$

Note that rearranging equation 4.S4.3 with $X = \mathrm{C}$ gives

$$a^C = \frac{\delta^C_w - \left(\delta^C_f - D^C \cdot (\lambda - 1)\right)}{\delta^C_w - \delta^C_i} \quad , \tag{4.S4.4}$$

which differs from the equation given by Post (2002) (p. 714, left column, second paragraph) in the minus sign before D^C and in the trophic level of algae, 1, that is subtracted from λ.

In case of great differences in C:N between sea-ice algae and phytoplankton, a^C and a^N cannot be assumed to be equal, but rather

$$\begin{aligned} a^C &= \frac{m_i^C}{m_i^C+m_w^C} &&= \frac{m_i^N\cdot(C/N)_i}{m_i^N\cdot(C/N)_i+m_w^N\cdot(C/N)_w} \\ &= \frac{\frac{a^N}{1-a^N}\cdot m_w^N\cdot(C/N)_i}{\frac{a^N}{1-a^N}\cdot m_w^N\cdot(C/N)_i+m_w^N\cdot(C/N)_w} &&= \frac{a^N\cdot(C/N)_i}{a^N\cdot(C/N)_i+(1-a^N)\cdot(C/N)_w} \quad , \end{aligned} \tag{4.S4.5}$$

where m_i^X and m_w^X denote the amount (mass) of element X derived from sea-ice algae and phytoplankton, respectively, and $(C/N)_i$ and $(C/N)_w$ are the mass-based C:N ratios of sea-ice algae and phytoplankton, respectively.

The proportions of sea-ice derived carbon and nitrogen and the trophic level are calculated by solving the equation system 4.S4.3 and 4.S4.5 for a^C, a^N and λ, respectively. Rearranging equation 4.S4.3 with $X = \mathrm{N}$ and equation 4.S4.5, one gets

$$\lambda = \frac{\delta_f^N - \delta_w^N - a^N\cdot\left(\delta_i^N - \delta_w^N\right)}{D^N} + 1 \quad , \tag{4.S4.6}$$

$$a^N = \frac{a^C\cdot(C/N)_w}{a^C\cdot(C/N)_w + (1-a^C)\cdot(C/N)_i} \quad . \tag{4.S4.7}$$

Substituting equations 4.S4.6 and 4.S4.7 into equation 4.S4.3 with $X = \mathrm{C}$ and rearranging, one gets

$$\begin{aligned} 0 = \quad & \left(a^C\right)^2\cdot\left[\left((C/N)_w-(C/N)_i\right)\cdot D^N\cdot\left(\delta_i^C-\delta_w^C\right)\right] \\ & -a^C\cdot\left[\left((C/N)_w-(C/N)_i\right)\cdot D^N\cdot\left(\delta_f^C-\delta_w^C\right)-\left((C/N)_w-(C/N)_i\right)\cdot D^C\cdot\left(\delta_f^N-\delta_w^N\right)\right] \\ & -a^C\cdot\left[(C/N)_w\cdot D^C\cdot\left(\delta_i^N-\delta_w^N\right)-(C/N)_i\cdot D^N\cdot\left(\delta_i^C-\delta_w^C\right)\right] \\ & -\left[(C/N)_i\cdot D^N\cdot\left(\delta_f^C-\delta_w^C\right)-(C/N)_i\cdot D^C\cdot\left(\delta_f^N-\delta_w^N\right)\right] \quad . \end{aligned} \tag{4.S4.8}$$

If $(C/N)_w \neq (C/N)_i$, the solution of equation 4.S4.8 for which $0 \leq a^C \leq 1$ in case of ideal data is

$$\begin{aligned} a^C = \quad & -\tfrac{p}{2} - \sqrt{\left(\tfrac{p}{2}\right)^2 - q} \quad \text{, where} \\ p = \quad & -\left(\frac{\delta_f^C-\delta_w^C}{\delta_i^C-\delta_w^C} - \frac{D^C}{D^N}\cdot\frac{\delta_f^N-\delta_w^N}{\delta_i^C-\delta_w^C} + \frac{(C/N)_w}{(C/N)_w-(C/N)_i}\cdot\frac{D^C}{D^N}\cdot\frac{\delta_i^N-\delta_w^N}{\delta_i^C-\delta_w^C} - \frac{(C/N)_i}{(C/N)_w-(C/N)_i}\right) \\ q = \quad & -\left(\frac{(C/N)_i}{(C/N)_w-(C/N)_i}\cdot\frac{\delta_f^C-\delta_w^C}{\delta_i^C-\delta_w^C} - \frac{(C/N)_i}{(C/N)_w-(C/N)_i}\cdot\frac{D^C}{D^N}\cdot\frac{\delta_f^N-\delta_w^N}{\delta_i^C-\delta_w^C}\right) \quad . \end{aligned} \tag{4.S4.9}$$

In case of $(C/N)_w = (C/N)_i$ the solution of equation 4.S4.8 is simply

$$a^C = \frac{D^N\cdot\left(\delta_f^C-\delta_w^C\right) - D^C\cdot\left(\delta_f^N-\delta_w^N\right)}{D^N\cdot\left(\delta_i^C-\delta_w^C\right) - D^C\cdot\left(\delta_i^N-\delta_w^N\right)} \quad . \tag{4.S4.10}$$

In some cases, $\left(\frac{p}{2}\right)^2 - q$ (equation 4.S4.9) was just slightly below zero, supposably due to limited measurement accuracy; in these cases we assumed $\left(\frac{p}{2}\right)^2 - q = 0$.

To calculate isolines of trophic levels λ, we substituted equation 4.S4.4 into equation 4.S4.7, which in turn was substituted into equation 4.S4.3 with $X = \mathrm{N}$:

$$\begin{aligned}\delta_f^N = \; & \frac{(C/N)_w \cdot \left(\delta_i^N - \delta_w^N\right) \cdot \delta_f^C - (C/N)_w \cdot D^C \cdot \left(\delta_i^N - \delta_w^N\right) \cdot \lambda + (C/N)_w \cdot \left(D^C - \delta_w^C\right) \cdot \left(\delta_i^N - \delta_w^N\right)}{((C/N)_w - (C/N)_i) \cdot \delta_f^C - ((C/N)_w - (C/N)_i) \cdot D^C \cdot \lambda + ((C/N)_w - (C/N)_i) \cdot \left(D^C - \delta_w^C\right) + (C/N)_i \cdot \left(\delta_i^C - \delta_w^C\right)} \\ & + D^N \cdot \lambda + \delta_w^N - D^N \quad .\end{aligned} \tag{4.S4.11}$$

To calculate isolines of proportions of sea-ice derived carbon $a := a^C$, we solved equation 4.S4.3 with $X = \mathrm{C}$ for $(\lambda - 1)$ and substituted this equation as well as equation 4.S4.7 into equation 4.S4.3 with $X = \mathrm{N}$:

$$\begin{aligned}\delta_f^N = \; & \frac{D^N}{D^C} \cdot \delta_f^C - \frac{D^N}{D^C} \cdot \left(\delta_i^C - \delta_w^C\right) \cdot a^C - \frac{D^N}{D^C} \cdot \delta_w^C + \delta_w^N \\ & + \frac{(C/N)_w \cdot \left(\delta_i^N - \delta_w^N\right) \cdot a^C}{(C/N)_i + ((C/N)_w - (C/N)_i) \cdot a^C} \quad .\end{aligned} \tag{4.S4.12}$$

We then substituted median δ^{13}C, δ^{15}N and C:N values of sea-ice and pelagic POM as well as the assumed trophic enrichment factors $D^C = 0.3$ and $D^N = 2.2$:

$$\delta_f^N = \frac{18.65\,\delta_f^C - 5.59\,\lambda + 494.84}{-5.36\,\delta_f^C + 1.60\,\lambda - 109.64} + 2.2\,\lambda + 2.6 \tag{4.S4.13}$$

$$\delta_f^N = 7.33\,\delta_f^C - 17.47\,a^C + 197.17 - \frac{18.65\,a^C}{5.36\,a^C - 13.69} \tag{4.S4.14}$$

4.S5 Calculation of dry mass

For calculation of the lipid fraction of dry mass, the dry mass for each fauna sample was calculated from measured carbon contents (see table below) whenever possible, specifically from medians of replicates from the same station (if available) or from medians of all samples of the respective taxon and stage (only non-negative values included).

Table 4.S5: Equations for calculation of individual dry mass *DM* from measured carbon content *C* or from length *L* and width *W* for the different meiofauna and sub-ice fauna taxa.

Taxon	Habitat	Region	*DM* [μg] calculated from *C* [μg]	Reference	DM [μg] calculated from *L* [μm] and *W* [μm]	Reference
Ctenophora						
Euplokamis sp.	ice	Weddell Sea	$DM = 11.9760 \cdot C$	Scolardi et al. (2006) for planktonic *Callianira antarctica* in winter	$DM = 6.0992 \cdot L^{2.49} \cdot 10^{-7}$	Scolardi et al. (2006) for planktonic *Callianira antarctica* in winter
Plathelminthes						
Acoela	ice, mp	Central Arctic, Weddell Sea	$DM = 2.5 \cdot C$	Feller and Warwick (1988)	$DM = 1.3984 \cdot L \cdot W^2 \cdot 10^{-7}$	Friedrich (1997)
Rhabdocoela	ice	Weddell Sea	$DM = 2.5 \cdot C$	Feller and Warwick (1988)	$DM = 1.7972 \cdot L \cdot W^2 \cdot 10^{-7}$	Friedrich (1997) for Arctic sympagic Nematoda
Rotifera		Central / Canadian Arctic	$DM = 1.285 \cdot C$	Friedrich (1997)	$DM = 0.2673 \cdot L \cdot W^2 \cdot 10^{-7}$	Friedrich (1997)
Nematoda	ice	Central / Canadian Arctic	$DM = 1.9455 \cdot C$	Baguley et al. (2004)	$DM = 1.7972 \cdot L \cdot W^2 \cdot 10^{-7}$	Friedrich (1997)
Polychaeta						
Trochophora Polychaeta	ice	Spitsbergen	$DM = 2.5 \cdot C$	Feller and Warwick (1988)	$DM = 1.3475 \cdot L \cdot W^2 \cdot 10^{-7}$	Nozais et al. (2005)
Polychaeta juv.	ice	Spitsbergen	$DM = 2.5 \cdot C$	Feller and Warwick (1988)	$DM = 1.3475 \cdot L \cdot W^2 \cdot 10^{-7}$	Nozais et al. (2005)
Copepoda						
Halectinosoma spp.	ice, water	Central Arctic	$DM = 2.1834 \cdot C$	Baguley et al. (2004)	$DM = 1.2814 \cdot L \cdot W^2 \cdot 10^{-7}$	Warwick and Gee (1984) for semi-cylindrical Harpacticoida (V from L and W), Friedrich (1997) (DM from V)
Tisbe spp.	ice	Central Arctic	$DM = 2.1834 \cdot C$	Baguley et al. (2004)	$DM = 0.5949 \cdot L \cdot W^2 \cdot 10^{-7}$	Warwick and Gee (1984) for pyriform-depressed Harpacticoida (V from L and W), Friedrich (1997) (DM from V)
Harpacticoida indet.	ice	Canadian Arctic	$DM = 2.1834 \cdot C$	Baguley et al. (2004)	$DM = 0.9153 \cdot L \cdot W^2 \cdot 10^{-7}$	Warwick and Gee (1984) for pyriform Harpacticoida (V from L and W), Friedrich (1997) (DM from V)
Calanus glacialis	water, ice	Central Arctic	$DM = 2 \cdot C$	Båmstedt (1986)	$DM = 4.2 \cdot L^{3.4333} \cdot 10^{-10}$	Mumm (1991)
Calanus finmarchicus	water	Central Arctic	$DM = 2 \cdot C$	Båmstedt (1986)	$DM = 4.2 \cdot L^{3.4333} \cdot 10^{-10}$	Mumm (1991)
Eurytemora richingsi	water	Central Arctic	$DM = 2 \cdot C$	Båmstedt (1986)	$DM = 4.2 \cdot L^{3.4333} \cdot 10^{-10}$	Mumm (1991) for *C. glacialis*, *C. finmarchicus*
Metridia longa	water	Central Arctic	$DM = 2 \cdot C$	Båmstedt (1986)	$DM = 4.2 \cdot L^{3.4333} \cdot 10^{-10}$	Mumm (1991) for *C. glacialis*, *C. finmarchicus*
Oithona cf. similis	water	Central Arctic	$DM = 2.1834 \cdot C$	Baguley et al. (2004)	$DM = 0.5949 \cdot L \cdot W^2 \cdot 10^{-7}$	Warwick and Gee (1984) for pyriform-depressed Harpacticoida (V from L and W), Friedrich (1997) (DM from V)
Cyclopoida indet.	ice	Central Arctic	$DM = 2.1834 \cdot C$	Baguley et al. (2004)	$DM = 0.5949 \cdot L \cdot W^2 \cdot 10^{-7}$	Warwick and Gee (1984) for pyriform-depressed Harpacticoida (V from L and W), Friedrich (1997) (DM from V)
Nauplii Harpacticoida indet.	ice	Canadian Arctic	$DM = 2.1834 \cdot C$	Baguley et al. (2004)	$DM = 0.81 \cdot L \cdot W^2 \cdot 10^{-7}$	Friedrich (1997)
Nauplii Copepoda indet.	ice	Central Arctic	$DM = 2.1834 \cdot C$	Baguley et al. (2004)	$DM = 0.81 \cdot L \cdot W^2 \cdot 10^{-7}$	Friedrich (1997)
Nauplii Copepoda indet.	water	Central Arctic	$DM = 2.1834 \cdot C$	Baguley et al. (2004)	$DM = 0.81 \cdot L \cdot W^2 \cdot 10^{-7}$	Friedrich (1997)

4.S6 Details on results from SI and FA

Table 4.S6: Parameters from stable isotope (SI) and fatty acid (FA) analyses for sympagic meiofauna, sub-ice fauna and under-ice and sub-ice amphipod taxa. Either median (minimum / maximum) or arithmetic mean ± standard deviation from all samples of one taxon are given. n_{SI} and n_{FA} are the numbers of samples for SI and FA analyses, respectively. Ind C content = individual C content, Ind DM = individual dry mass, Tot Lip = total lipid content, WE = wax ester fraction of total lipids, Tot FA = total fatty acid fraction of total lipids, Tot FAlc = total fatty alcohol fraction of total lipids, Unknowns = total unknown fraction (i. e. indetermined GC peaks) of total lipids, FA = proportions of the different fatty acids, Diat = diatom, Meta = metazoan, Cala = calanid, Flag = flagellate, PUFA = polyunsaturated FA, SFA = saturated FA. Acoela r = Acoela red, Acoe wr = Acoela white-rose, Acoe w = Acoela white, Roti = Rotifera, *C. glac.* = *Calanus glacialis*, *E. rich.* = *Eurytemora richingsi*, Naup C = Nauplii Copepoda, Naup H = Nauplii Harpacticoida, Troch Poly = Trochophora Polychaeta, Poly juv. = Polychaeta juvenile. c = sample from cultures, mp = sample from new ice on meltpond surface.

Table 4.S6.1: Parameters from SI and FA analyses for sympagic meiofauna taxa from the Central Arctic. See above for abbreviations.

	Fauna from sea ice/-Central Arctic. summer												
	Acoela r	**Acoela r (mp)**	**Acoe wr**	**Acoe w**	**Nematoda**	**Rotifera**	**Roti (mp)**	***Halectinosoma* spp.**	***Tisbe* spp.**	***C. glac.***	***E. rich.***	**Cyclopoida**	**Naup C**
n_{SI}	2	3	0	0	2	6	1	7	2	1	1	3	1
n_{FA}	4	3	1	1	1	8	0	6	1	0	1	1	1
Ind C content [μg]	1.50 (1.12/1.87)	0.97 (0.67/1.01)	nd	nd	-0.04 (-0.15/0.07)	0.03 (0.01/0.28)	0.03	0.16 (-0.15/1.52)	0.23 (-0.04/0.50)	346.02	1.39	0.02 (0.01/0.09)	-0.10
Ind DM [μg]	3.74 (2.81/4.66)	2.41 (1.68/2.52)	nd	nd	-0.08 (-0.30/0.14)	0.04 (0.01/0.36)	0.04	0.34 (-0.33/3.33)	0.50 (-0.09/1.09)	692.05	2.78	0.04 (0.02/0.19)	-0.22
Molar C:N	10.71 (8.32/13.10)	7.64 (7.61/8.73)	nd	nd	2.19 (2.19/2.19)	5.07 (3.56/5.77)	6.09	2.28 (-0.30/5.01)	4.44 (4.44/4.44)	11.05	5.88	0.39 (0.22/2.29)	-9.50
δ^{15}**N**	22.93 (9.30/36.57)	9.17 (8.57/11.13)	nd	nd	15.10 (15.10/15.10)	9.81 (7.51/12.87)	13.61	7.19 (5.18/7.81)	9.11 (9.11/9.11)	6.75	9.28	15.82 (12.07/22.00)	24.69
δ^{13}**C**	-26.47 (-26.72/-26.22)	-26.23 (-26.32/-25.43)	nd	nd	-24.90 (-25.74/-24.06)	-25.09 (-25.86/-23.60)	-27.64	-24.47 (-25.06/-22.50)	-23.61 (-23.63/-23.60)	-26.35	-26.41	-26.89 (-27.15/-25.58)	-25.05
λ	9.72 (3.31/16.13)	3.17 (2.64/4.10)	nd	nd	5.91 (5.91/5.91)	3.15 (1.05/4.86)	5.51	1.53 (0.05/1.88)	1.98 (1.98/1.98)	2.00	3.24	6.45 (4.40/9.40)	10.39
a^C	-1.20 (-1.90/-0.50)	-0.31 (-0.39/0.13)	nd	nd	-0.41 (-0.41/-0.41)	0.21 (-0.33/1.10)	-1.16	0.67 (0.57/1.12)	0.98 (0.98/0.98)	-0.17	-0.35	-0.96 (-1.44/-0.15)	-0.68
a^N	-0.46 (-0.66/-0.25)	-0.17 (-0.21/0.09)	nd	nd	-0.21 (-0.21/-0.21)	0.14 (-0.18/1.17)	-0.49	0.56 (0.45/1.22)	0.97 (0.97/0.97)	-0.10	-0.19	-0.42 (-0.56/-0.09)	-0.33
Tot Lip [% of DM]	31.80 (7.19/74.35)	24.43 (19.99/28.67)	nd	nd	68.58	24.18 (15.87/46.09)	nd	99.13 (38.92/133.70)	93.43	nd	10.81	211.80	nd
WE [% of tot Lip]	11.02 (3.24/14.81)	8.60 (5.27/12.13)	7.00	18.48	2.51	4.94 (0.00/15.33)	nd	0.00 (0.00/6.53)	4.33	nd	2.45	21.67	6.49
Tot FA [% of tot Lip]	81.86 ± 12.67	79.63 ± 10.78	86.82	66.53	81.59	64.25 ± 9.22	nd	94.40 ± 8.38	71.46	nd	76.27	70.10	75.66
Tot FAlc [% of tot Lip]	5.01 ± 2.72	4.33 ± 1.71	3.50	9.24	1.25	3.31 ± 3.06	nd	0.54 ± 1.33	2.17	nd	1.23	10.83	3.24
Unknowns [% of tot Lip]	13.13 ± 9.98	16.04 ± 12.30	9.68	24.23	17.15	32.44 ± 7.45	nd	5.06 ± 7.93	26.38	nd	22.50	19.06	21.10
FA [% of tot FA]													
14:0	4.17 ± 0.60	3.04 ± 0.38	1.59	2.55	3.11	5.71 ± 1.65	nd	2.62 ± 1.13	4.34	nd	4.15	4.04	5.22
15:0	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	0.20 ± 0.57	nd	0.00 ± 0.00	0.00	nd	0.00	0.00	0.00
16:0	13.78 ± 2.84	13.89 ± 1.01	9.98	10.24	8.31	15.80 ± 5.38	nd	13.69 ± 2.40	0.00	nd	15.58	16.72	14.16
17:0	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	2.34	1.95 ± 2.29	nd	0.36 ± 0.89	0.00	nd	0.00	0.00	3.30
18:0	3.43 ± 2.36	0.00 ± 0.00	1.35	7.41	2.29	6.21 ± 6.20	nd	2.05 ± 0.94	4.05	nd	2.37	7.44	2.19
16:1(n-9)	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	0.25 ± 0.70	nd	0.00 ± 0.00	0.00	nd	0.00	0.00	0.00
16:1(n-7) Diat marker	24.62 ± 10.39	23.60 ± 1.11	13.08	6.36	24.99	6.29 ± 4.86	nd	21.09 ± 6.27	36.55	nd	32.46	12.97	24.98
16:1(n-5)	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.00	nd	0.00	0.00	0.00
17:1	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	1.34 ± 1.43	nd	0.00 ± 0.00	0.00	nd	0.00	0.00	1.79
18:1(n-9) Meta marker	2.12 ± 1.83	0.00 ± 0.00	6.90	2.25	4.85	21.14 ± 8.86	nd	6.09 ± 2.40	4.78	nd	0.00	13.15	9.24
18:1(n-7) Diat marker	13.63 ± 1.46	15.95 ± 1.52	7.94	13.47	5.16	1.21 ± 1.68	nd	14.87 ± 7.91	6.59	nd	14.05	3.04	0.00
18:1(n-5)	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	0.33 ± 0.93	nd	0.00 ± 0.00	0.00	nd	0.00	0.00	0.00
20:1(n-9) Cala marker	3.10 ± 2.43	5.32 ± 1.73	9.84	5.52	0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.00	nd	0.00	0.00	0.00
20:1(n-7)	5.09 ± 2.39	5.63 ± 0.22	4.65	4.09	0.00	0.00 ± 0.00	nd	1.67 ± 1.52	0.00	nd	0.00	0.00	0.00
22:1(n-11) Cala marker	2.19 ± 1.59	3.36 ± 1.54	0.00	4.59	0.00	1.92 ± 2.00	nd	0.50 ± 1.21	0.00	nd	0.00	2.10	0.00
22:1(n-9)	2.76 ± 1.06	3.15 ± 0.37	0.00	4.06	0.00	0.56 ± 1.58	nd	1.03 ± 2.52	0.00	nd	0.00	0.00	1.75
22:1(n-7)	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.00	nd	0.00	0.00	0.00
24:1(n-9)	0.51 ± 1.02	0.64 ± 1.10	0.00	2.57	0.00	1.68 ± 2.42	nd	0.54 ± 0.86	0.00	nd	3.13	3.41	2.88
16:2(n-4)	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	0.56 ± 1.10	nd	0.00 ± 0.00	0.00	nd	0.00	0.00	0.00
18:2(n-6)	0.60 ± 0.70	0.00 ± 0.00	1.33	1.91	1.56	1.39 ± 1.59	nd	1.97 ± 1.16	7.07	nd	0.00	1.59	0.00
18:2(n-4)	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.00	nd	0.00	0.00	0.00
20:2(n-6)	0.00 ± 0.00	0.00 ± 0.00	1.39	0.00	2.85	5.78 ± 3.52	nd	1.69 ± 1.87	0.00	nd	0.00	4.56	0.00
22:2(n-6)	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	0.00 ± 0.00	nd	0.00 ± 0.00	4.66	nd	0.00	2.03	2.39
16:3(n-4)	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.00	nd	0.00	0.00	0.00
18:3(n-6)	0.40 ± 0.80	1.88 ± 0.21	0.00	2.84	2.01	6.41 ± 2.51	nd	2.49 ± 2.89	0.00	nd	1.89	3.34	4.16
18:3(n-4)	0.00 ± 0.00	0.00 ± 0.00	0.00	1.94	0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.00	nd	1.70	0.00	0.00
18:3(n-3)	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.00	nd	0.00	0.00	0.00
20:3(n-3)	0.86 ± 0.99	0.00 ± 0.00	0.00	3.01	1.99	0.57 ± 1.61	nd	0.40 ± 0.98	0.00	nd	0.00	0.00	1.71
16:4(n-1)	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.00	nd	0.00	0.00	0.00
18:4(n-3) Flag marker	1.45 ± 1.94	1.03 ± 0.96	2.16	1.97	3.25	0.82 ± 1.16	nd	0.59 ± 0.92	8.83	nd	1.50	2.20	1.56
18:4(n-1)	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	0.26 ± 0.74	nd	0.00 ± 0.00	0.00	nd	0.00	0.00	0.00
20:4(n-6)	0.00 ± 0.00	0.00 ± 0.00	0.00	0.00	0.00	0.66 ± 1.23	nd	0.46 ± 0.71	0.00	nd	0.00	0.00	0.00
20:4(n-3)	0.00 ± 0.00	0.00 ± 0.00	1.89	1.96	0.00	0.20 ± 0.56	nd	1.64 ± 1.05	0.00	nd	0.00	0.00	0.00
20:5(n-3) Diat marker	13.41 ± 3.79	15.37 ± 0.38	16.47	13.64	18.01	9.58 ± 8.32	nd	14.76 ± 1.79	15.06	nd	13.13	9.42	12.16
22:5(n-3)	0.00 ± 0.00	0.00 ± 0.00	1.56	0.00	0.00	0.21 ± 0.58	nd	0.00 ± 0.00	2.39	nd	0.00	1.39	0.00
22:6(n-3) Flag marker	7.89 ± 3.49	7.15 ± 0.36	19.85	9.62	19.28	8.98 ± 5.93	nd	11.50 ± 2.03	5.69	nd	10.04	12.61	12.53
FA ratios													
18:1(n-9)/18:1(n-7)	0.16 (0.00/0.31)	0.00 (0.00/0.00)	0.87	0.17	0.94	6.44 (3.85/9.42)	nd	0.42 (0.15/3.95)	0.73	nd	0.00	4.32	nd
PUFA/SFA	1.32 (0.57/1.43)	1.54 (1.43/1.54)	3.45	1.83	3.05	1.17 (0.54/2.20)	nd	1.96 (1.76/2.17)	5.21	nd	1.28	1.32	1.39
16:1(n-7)/16:0	1.61 (1.47/2.26)	1.73 (1.60/1.78)	1.31	0.62	3.01	0.41 (0.00/1.43)	nd	1.24 (1.15/1.34)	nd	nd	2.08	0.78	1.76
20:5(n-3)/22:6(n-3)	1.61 (1.52/2.88)	2.12 (2.09/2.25)	0.83	1.42	0.93	0.96 (0.00/3.65)	nd	1.29 (1.25/1.33)	2.65	nd	1.31	0.75	0.97

Table 4.S6.2: Parameters from SI and FA analyses for sympagic meiofauna taxa from Canadian Arctic, Spitsbergen and Weddell Sea. See above for abbreviations.

	Fauna from sea ice—Canadian Arctic. spring				Fauna from sea ice—Spitsbergen. spring			Fauna from sea ice—Weddell Sea. winter			
	Nematoda	**Nematoda (c)**	**Harpacticoida**	**Naup H**	**Nematoda**	**Troch Poly**	**Poly juv.**	***Euplokamis* sp.**	**Acoela w**	**Acoela w (c)**	**Rhabdocoela**
n_{SI}	0	8	0	0	3	1	1	1	2	0	3
n_{FA}	9	6	5	15	0	0	0	1	2	2	2
Ind C content [μg]	nd	0.14 (-0.02 / 0.20)	nd	nd	-0.02 (-0.02 / -0.01)	0.02	-0.99	0.07	0.19 (0.12 / 0.26)	nd	1.41 (1.41 / 1.58)
Ind DM [μg]	nd	0.28 (-0.03 / 0.38)	nd	nd	-0.04 (-0.05 / -0.02)	0.05	-2.16	0.84	0.47 (0.30 / 0.64)	nd	3.53 (3.52 / 3.95)
Molar C:N	nd	8.15 (-1.56 / 9.52)	nd	nd	nd	2.58	nd	1.17	4.63 (3.54 / 5.72)	nd	5.33 (4.04 / 5.68)
δ^{15}**N**	nd	17.41 (14.54 / 54.98)	nd	nd	nd	20.29	nd	10.51	7.54 (7.31 / 7.77)	nd	8.88 (8.69 / 8.90)
δ^{13}**C**	nd	-19.81 (-24.56 / -19.03)	nd	nd	-26.64 (-27.15 / -25.76)	-25.07	-21.15	-20.10	-19.06 (-19.43 / -18.70)	nd	-19.20 (-19.59 / -19.08)
λ	nd	nd	nd	nd	nd	-63.56	nd	nd	nd	nd	nd
a^C	nd	nd	nd	nd	nd	-5.23	nd	nd	nd	nd	nd
a^N	nd	nd	nd	nd	nd	-27.79	nd	nd	nd	nd	nd
Tot Lip [% of DM]	nd	54.86 (39.99 / 65.32)	nd	nd	nd	nd	nd	48.40	19.67 (14.93 / 24.41)	nd	34.77 (33.93 / 35.62)
WE [% of tot Lip]	2.49 (0.00 / 11.80)	0.00 (0.00 / 6.00)	5.35 (0.00 / 5.79)	5.96 (0.00 / 11.29)	nd	nd	nd	23.52	8.74 (8.28 / 9.20)	nd	0.00 (0.00 / 0.00)
Tot FA [% of tot Lip]	72.41 ± 6.98	91.70 ± 6.07	77.73 ± 3.82	64.05 ± 7.13	nd	nd	nd	88.24	90.27 ± 1.00	nd	93.99 ± 3.62
Tot FAlc [% of tot Lip]	2.09 ± 2.45	0.50 ± 1.22	2.11 ± 1.21	2.62 ± 1.52	nd	nd	nd	11.76	4.37 ± 0.32	nd	0.00 ± 0.00
Unknowns [% of tot Lip]	25.49 ± 6.63	7.80 ± 5.29	20.16 ± 4.30	33.33 ± 7.02	nd	nd	nd	0.00	5.36 ± 1.32	nd	6.01 ± 3.62
FA [% of tot FA]											
14:0	7.09 ± 1.13	3.46 ± 0.41	6.37 ± 1.77	12.88 ± 6.76	nd	nd	nd	5.94	3.56 ± 0.44	2.10 ± 0.45	1.81 ± 0.27
15:0	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	nd	nd	nd	0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
16:0	11.64 ± 1.42	15.47 ± 0.63	16.32 ± 1.98	11.39 ± 4.12	nd	nd	nd	14.66	12.07 ± 0.23	10.33 ± 0.03	15.17 ± 2.00
17:0	0.84 ± 1.30	0.64 ± 1.00	2.42 ± 2.65	3.76 ± 2.66	nd	nd	nd	0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
18:0	1.25 ± 1.50	1.84 ± 0.79	2.05 ± 1.21	3.43 ± 1.40	nd	nd	nd	3.53	6.44 ± 0.06	5.25 ± 0.05	3.21 ± 0.05
16:1(n-9)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	nd	nd	nd	0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
16:1(n-7) Diat marker	28.43 ± 5.60	44.27 ± 5.06	6.67 ± 2.83	3.79 ± 2.09	nd	nd	nd	4.28	4.78 ± 0.89	4.74 ± 1.67	10.53 ± 1.96
16:1(n-5)	0.21 ± 0.63	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	nd	nd	nd	0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
17:1	0.00 ± 0.00	0.24 ± 0.59	0.95 ± 1.31	2.01 ± 1.55	nd	nd	nd	0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
18:1(n-9) Meta marker	10.29 ± 4.87	2.78 ± 1.92	11.60 ± 5.14	16.89 ± 7.35	nd	nd	nd	3.69	7.42 ± 0.61	4.36 ± 1.31	9.04 ± 1.55
18:1(n-7) Diat marker	3.70 ± 5.50	6.91 ± 3.46	0.00 ± 0.00	2.35 ± 6.04	nd	nd	nd	2.82	4.54 ± 0.70	4.74 ± 1.17	6.67 ± 0.75
18:1(n-5)	0.56 ± 0.84	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	nd	nd	nd	1.25	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
20:1(n-9) Cala marker	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	nd	nd	nd	0.00	0.70 ± 1.00	0.75 ± 1.06	0.00 ± 0.00
20:1(n-7)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	nd	nd	nd	4.74	6.25 ± 0.78	9.58 ± 1.03	3.47 ± 0.72
22:1(n-11) Cala marker	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.74	0.00 ± 0.00	nd	nd	nd	0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
22:1(n-9)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.54 ± 1.13	nd	nd	nd	0.00	2.27 ± 0.14	4.07 ± 0.90	0.00 ± 0.00
22:1(n-7)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	nd	nd	nd	0.00	0.00 ± 0.00	4.96 ± 0.19	0.00 ± 0.00
24:1(n-9)	0.92 ± 0.91	0.74 ± 1.81	1.58 ± 1.59	3.26 ± 2.59	nd	nd	nd	0.00	0.00 ± 0.00	0.00 ± 0.00	0.74 ± 1.05
16:2(n-4)	1.43 ± 0.95	0.66 ± 1.61	0.37 ± 0.82	0.31 ± 0.82	nd	nd	nd	0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
18:2(n-6)	0.29 ± 0.86	0.00 ± 0.00	0.81 ± 1.11	0.46 ± 0.98	nd	nd	nd	0.00	1.55 ± 0.38	0.59 ± 0.84	3.22 ± 1.28
18:2(n-4)	0.00 ± 0.00	0.41 ± 1.02	0.00 ± 0.00	0.00 ± 0.00	nd	nd	nd	0.00	1.52 ± 0.35	0.63 ± 0.89	0.00 ± 0.00
20:2(n-6)	1.57 ± 1.24	0.27 ± 0.67	2.30 ± 2.29	4.73 ± 4.05	nd	nd	nd	0.00	2.43 ± 0.97	1.40 ± 0.14	1.83 ± 2.59
22:2(n-6)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	nd	nd	nd	0.00	0.00 ± 0.00	1.75 ± 0.13	0.00 ± 0.00
16:3(n-4)	0.63 ± 0.94	0.00 ± 0.00	0.38 ± 0.84	0.00 ± 0.00	nd	nd	nd	0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
18:3(n-6)	2.95 ± 1.73	0.73 ± 0.81	4.60 ± 1.86	4.80 ± 1.36	nd	nd	nd	0.00	2.71 ± 1.47	0.00 ± 0.00	2.17 ± 3.07
18:3(n-4)	0.27 ± 0.81	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	nd	nd	nd	0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
18:3(n-3)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	nd	nd	nd	0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
20:3(n-3)	7.48 ± 7.11	0.00 ± 0.00	4.52 ± 4.34	5.74 ± 7.00	nd	nd	nd	0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
16:4(n-1)	0.52 ± 1.03	0.00 ± 0.00	0.00 ± 0.00	1.04 ± 1.43	nd	nd	nd	0.00	1.70 ± 0.35	0.00 ± 0.00	0.00 ± 0.00
18:4(n-3) Flag marker	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	nd	nd	nd	0.00	2.39 ± 0.31	0.69 ± 0.98	3.86 ± 0.88
18:4(n-1)	0.00 ± 0.00	0.00 ± 0.00	0.63 ± 0.87	0.00 ± 0.00	nd	nd	nd	0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
20:4(n-6)	1.10 ± 1.09	0.67 ± 0.74	0.41 ± 0.63	0.00 ± 0.00	nd	nd	nd	0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
20:4(n-3)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	nd	nd	nd	0.00	0.00 ± 0.00	0.00 ± 0.00	1.59 ± 0.17
20:5(n-3) Diat marker	15.85 ± 4.55	17.00 ± 1.20	20.56 ± 1.90	14.56 ± 8.85	nd	nd	nd	30.74	17.83 ± 1.84	17.86 ± 0.38	13.96 ± 2.03
22:5(n-3)	0.17 ± 0.51	0.00 ± 0.00	0.37 ± 0.82	0.34 ± 0.65	nd	nd	nd	0.00	0.00 ± 0.00	0.00 ± 0.00	4.62 ± 0.78
22:6(n-3) Flag marker	2.81 ± 1.04	3.90 ± 0.22	16.76 ± 2.77	7.74 ± 3.16	nd	nd	nd	28.35	21.84 ± 0.41	26.20 ± 0.64	18.11 ± 1.68
FA ratios											
18:1(n-9) / 18:1(n-7)	1.15 (0.00 / 3.21)	0.32 (0.00 / 0.75)	nd	1.89 (0.00 / 6.14)	nd	nd	nd	1.31	1.66 (1.39 / 1.94)	0.98 (0.62 / 1.35)	1.38 (1.10 / 1.65)
PUFA / SFA	1.68 (0.94 / 2.74)	1.08 (1.03 / 1.23)	1.92 (1.45 / 2.75)	1.40 (0.28 / 3.40)	nd	nd	nd	2.45	2.36 (2.31 / 2.41)	2.78 (2.73 / 2.83)	2.47 (2.16 / 2.78)
16:1(n-7) / 16:0	2.64 (1.90 / 2.88)	2.95 (2.49 / 3.12)	0.31 (0.29 / 0.84)	0.27 (0.14 / 0.52)	nd	nd	nd	0.29	0.40 (0.34 / 0.45)	0.46 (0.34 / 0.57)	0.69 (0.67 / 0.72)
20:5(n-3) / 22:6(n-3)	5.34 (2.12 / 12.95)	4.27 (3.83 / 5.37)	1.15 (1.05 / 1.67)	1.62 (1.03 / 4.60)	nd	nd	nd	1.08	0.82 (0.77 / 0.86)	0.68 (0.68 / 0.68)	0.77 (0.74 / 0.80)

Table 4.S6.3: Parameters from SI and FA analyses for sub-ice fauna taxa from the Central Arctic. See above for abbreviations.

	Sub-ice fauna—Central Arctic. summer						
	***Halectinosoma* spp.**	***C. glacialis***	***C. finmarchicus***	***M. longa***	***O.* cf. *similis***	**Naup C**	**Appendicularia**
n_{SI}	2	10	5	1	9	10	2
n_{FA}	0	4	3	0	8	5	2
Ind C content [μg]	-0.02 (-0.02/-0.02)	235.49 (38.18/475.71)	104.04 (43.51/127.76)	72.51	0.23 (-0.10/7.69)	0.10 (-0.07/0.41)	nd
Ind DM [μg]	-0.05 (-0.05/-0.05)	470.98 (76.37/951.42)	208.09 (87.01/255.51)	145.02	0.51 (-0.22/16.79)	0.21 (-0.16/0.88)	nd
Molar C:N	0.13 (-0.29/0.54)	8.42 (5.85/11.85)	6.43 (5.45/8.98)	7.84	5.30 (2.12/6.43)	3.59 (-4.85/9.16)	6.58 (6.22/6.93)
δ^{15}**N**	8.14 (7.13/9.15)	6.56 (5.22/7.53)	7.96 (3.87/11.11)	10.54	13.07 (7.73/19.88)	8.95 (3.29/16.49)	5.31 (5.16/5.46)
δ^{13}**C**	-24.32 (-24.55/-24.09)	-25.32 (-26.38/-23.07)	-24.50 (-25.15/-22.24)	-25.31	-27.58 (-29.03/-15.59)	-26.16 (-28.87/-24.12)	-27.78 (-28.51/-27.06)
λ	1.93 (1.26/2.60)	1.55 (-0.72/2.19)	2.14 (-5.74/3.68)	3.58	6.14 (4.12/12.46)	2.95 (0.72/6.84)	1.58 (1.53/1.63)
a^C	0.69 (0.51/0.87)	0.31 (-0.21/1.55)	0.42 (0.12/2.04)	0.06	-1.28 (-2.13/3.03)	-0.18 (-1.83/0.61)	-0.72 (-1.03/-0.41)
a^N	0.59 (0.39/0.80)	0.22 (-0.12/2.39)	0.30 (0.07/6.22)	0.04	-0.56 (-9.93/-0.44)	-0.10 (-0.65/0.48)	-0.33 (-0.45/-0.22)
Tot Lip [% of DM]	nd	30.28 (24.70/57.36)	4.90 (3.37/15.74)	nd	26.46 (3.55/48.56)	41.40 (27.48/59.01)	nd
WE [% of tot Lip]	nd	76.99 (62.36/92.32)	43.57 (36.51/75.81)	nd	59.41 (27.18/89.53)	29.75 (16.80/58.16)	0.00 (0.00/0.00)
Tot FA [% of tot Lip]	nd	60.59 ± 7.79	71.71 ± 8.93	nd	62.55 ± 12.30	52.78 ± 18.29	94.30 ± 6.64
Tot FAlc [% of tot Lip]	nd	38.58 ± 7.83	25.98 ± 10.48	nd	28.92 ± 12.80	15.79 ± 8.32	0.00 ± 0.00
Unknowns [% of tot Lip]	nd	0.83 ± 0.96	2.31 ± 1.55	nd	8.53 ± 4.73	31.43 ± 12.55	5.70 ± 6.64
FA [% of tot FA]							
14:0	nd	9.34 ± 1.50	5.25 ± 9.10	nd	6.18 ± 2.34	4.24 ± 1.18	7.30 ± 0.79
15:0	nd	0.00 ± 0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.32 ± 0.72	0.00 ± 0.00
16:0	nd	6.82 ± 0.74	10.54 ± 1.75	nd	18.57 ± 3.77	15.27 ± 4.73	10.83 ± 0.71
17:0	nd	0.00 ± 0.00	0.00 ± 0.00	nd	3.50 ± 3.61	1.64 ± 2.43	0.00 ± 0.00
18:0	nd	0.00 ± 0.00	0.00 ± 0.00	nd	5.70 ± 5.29	7.36 ± 6.04	0.00 ± 0.00
16:1(n-9)	nd	0.00 ± 0.00	0.00 ± 0.00	nd	0.43 ± 1.05	0.00 ± 0.00	0.00 ± 0.00
16:1(n-7) Diat marker	nd	24.06 ± 4.99	3.31 ± 2.01	nd	2.00 ± 2.05	3.53 ± 2.60	3.60 ± 1.45
16:1(n-5)	nd	0.00 ± 0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
17:1	nd	0.00 ± 0.00	0.00 ± 0.00	nd	0.85 ± 1.32	0.81 ± 1.82	0.00 ± 0.00
18:1(n-9) Meta marker	nd	5.70 ± 2.94	6.77 ± 1.61	nd	11.86 ± 5.93	6.28 ± 8.80	2.61 ± 1.09
18:1(n-7) Diat marker	nd	0.34 ± 0.67	0.52 ± 0.91	nd	0.74 ± 1.15	6.71 ± 8.31	0.00 ± 0.00
18:1(n-5)	nd	0.00 ± 0.00	2.00 ± 0.08	nd	0.00 ± 0.00	0.59 ± 1.31	0.00 ± 0.00
20:1(n-9) Cala marker	nd	17.91 ± 3.96	12.98 ± 5.61	nd	3.07 ± 3.21	1.37 ± 1.35	0.00 ± 0.00
20:1(n-7)	nd	0.00 ± 0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
22:1(n-11) Cala marker	nd	6.71 ± 3.30	13.08 ± 3.00	nd	0.97 ± 1.50	0.53 ± 1.18	0.00 ± 0.00
22:1(n-9)	nd	1.32 ± 1.57	2.88 ± 2.61	nd	0.62 ± 1.53	1.38 ± 1.91	0.00 ± 0.00
22:1(n-7)	nd	0.00 ± 0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
24:1(n-9)	nd	0.86 ± 1.08	3.89 ± 0.78	nd	0.00 ± 0.00	5.99 ± 4.91	0.00 ± 0.00
16:2(n-4)	nd	0.00 ± 0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.37 ± 0.82	0.00 ± 0.00
18:2(n-6)	nd	0.42 ± 0.85	2.18 ± 2.24	nd	0.00 ± 0.00	0.66 ± 1.47	3.56 ± 0.60
18:2(n-4)	nd	0.00 ± 0.00	0.00 ± 0.00	nd	0.39 ± 0.95	0.00 ± 0.00	0.00 ± 0.00
20:2(n-6)	nd	0.14 ± 0.27	2.23 ± 1.96	nd	2.81 ± 3.14	3.36 ± 3.13	0.00 ± 0.00
22:2(n-6)	nd	0.00 ± 0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
16:3(n-4)	nd	0.00 ± 0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
18:3(n-6)	nd	0.14 ± 0.29	0.00 ± 0.00	nd	3.58 ± 1.80	4.46 ± 1.57	0.00 ± 0.00
18:3(n-4)	nd	0.00 ± 0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
18:3(n-3)	nd	0.00 ± 0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.00 ± 0.00	3.27 ± 0.32
20:3(n-3)	nd	0.00 ± 0.00	0.00 ± 0.00	nd	0.55 ± 1.34	10.78 ± 8.78	0.00 ± 0.00
16:4(n-1)	nd	2.90 ± 1.95	0.00 ± 0.00	nd	0.36 ± 0.88	0.00 ± 0.00	0.00 ± 0.00
18:4(n-3) Flag marker	nd	2.36 ± 1.68	0.00 ± 0.00	nd	5.31 ± 4.72	2.49 ± 1.56	5.81 ± 0.74
18:4(n-1)	nd	0.00 ± 0.00	0.00 ± 0.00	nd	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
20:4(n-6)	nd	0.00 ± 0.00	0.00 ± 0.00	nd	0.60 ± 1.48	0.32 ± 0.71	0.00 ± 0.00
20:4(n-3)	nd	0.00 ± 0.00	0.00 ± 0.00	nd	1.13 ± 1.84	0.86 ± 1.18	0.00 ± 0.00
20:5(n-3) Diat marker	nd	14.91 ± 2.54	13.18 ± 1.08	nd	9.12 ± 5.28	9.82 ± 13.56	37.65 ± 2.30
22:5(n-3)	nd	0.00 ± 0.00	0.00 ± 0.00	nd	2.19 ± 2.54	0.00 ± 0.00	0.00 ± 0.00
22:6(n-3) Flag marker	nd	6.05 ± 1.16	21.18 ± 1.79	nd	19.48 ± 5.51	10.88 ± 1.64	25.38 ± 1.84
FA ratios							
18:1(n-9)/18:1(n-7)	nd	7.43 (7.43/7.43)	5.36 (5.36/5.36)	nd	5.36 (2.97/7.75)	0.00 (0.00/10.31)	nd
PUFA/SFA	nd	1.66 (1.47/1.86)	3.54 (1.31/4.83)	nd	1.59 (0.65/1.97)	2.88 (0.55/3.10)	4.17 (4.09/4.26)
16:1(n-7)/16:0	nd	3.50 (2.69/4.48)	0.23 (0.22/0.45)	nd	0.09 (0.00/0.27)	0.31 (0.00/0.42)	0.33 (0.25/0.41)
20:5(n-3)/22:6(n-3)	nd	2.38 (2.30/2.84)	0.62 (0.62/0.62)	nd	0.51 (0.00/0.77)	0.51 (0.00/2.61)	1.48 (1.47/1.50)

Table 4.S6.4: Parameters from SI analyses for under-ice and sub-ice amphipod taxa from the Central Arctic. See above for abbreviations.

	Amphipods—Central Arctic. summer			
	A. glacialis	***G. wilkitzkii***	***Onisimus* spp.**	***T. libellula***
n_{SI}	32	4	9	1
n_{FA}	0	0	0	0
Ind C content [μg]	512.80 (19.82 / 700.36)	306.01 (192.81 / 384.01)	501.55 (127.44 / 618.64)	770.11
Ind DM [μg]	nd	nd	nd	nd
Molar C:N	11.31 (6.29 / 19.67)	7.58 (5.58 / 8.20)	8.91 (7.88 / 13.78)	11.00
δ^{15}**N**	6.52 (3.94 / 9.58)	5.36 (4.90 / 5.81)	8.20 (5.55 / 9.55)	9.09
δ^{13}**C**	-24.24 (-28.80 / -20.64)	-19.75 (-22.51 / -17.70)	-21.77 (-23.65 / -19.72)	-26.15
λ	1.13 (-20.45 / 2.69)	-33.93 (-211.71 / 12.45)	-3.95 (-34.08 / 0.04)	3.09
a^C	0.77 (-1.29 / 2.38)	2.51 (1.94 / 2.96)	2.06 (1.21 / 2.45)	-0.23
a^N	0.67 (-0.52 / 20.71)	34.57 (-11.19 / 209.37)	6.51 (1.40 / 35.98)	-0.13
Tot Lip [% of DM]	nd	nd	nd	nd
WE [% of tot Lip]	nd	nd	nd	nd
Tot FA [% of tot Lip]	nd	nd	nd	nd
Tot FAlc [% of tot Lip]	nd	nd	nd	nd
Unknowns [% of tot Lip]	nd	nd	nd	nd
FA [% of tot FA]				
14:0	nd	nd	nd	nd
15:0	nd	nd	nd	nd
16:0	nd	nd	nd	nd
17:0	nd	nd	nd	nd
18:0	nd	nd	nd	nd
16:1(n-9)	nd	nd	nd	nd
16:1(n-7) Diat marker	nd	nd	nd	nd
16:1(n-5)	nd	nd	nd	nd
17:1	nd	nd	nd	nd
18:1(n-9) Meta marker	nd	nd	nd	nd
18:1(n-7) Diat marker	nd	nd	nd	nd
18:1(n-5)	nd	nd	nd	nd
20:1(n-9) Cala marker	nd	nd	nd	nd
20:1(n-7)	nd	nd	nd	nd
22:1(n-11) Cala marker	nd	nd	nd	nd
22:1(n-9)	nd	nd	nd	nd
22:1(n-7)	nd	nd	nd	nd
24:1(n-9)	nd	nd	nd	nd
16:2(n-4)	nd	nd	nd	nd
18:2(n-6)	nd	nd	nd	nd
18:2(n-4)	nd	nd	nd	nd
20:2(n-6)	nd	nd	nd	nd
22:2(n-6)	nd	nd	nd	nd
16:3(n-4)	nd	nd	nd	nd
18:3(n-6)	nd	nd	nd	nd
18:3(n-4)	nd	nd	nd	nd
18:3(n-3)	nd	nd	nd	nd
20:3(n-3)	nd	nd	nd	nd
16:4(n-1)	nd	nd	nd	nd
18:4(n-3) Flag marker	nd	nd	nd	nd
18:4(n-1)	nd	nd	nd	nd
20:4(n-6)	nd	nd	nd	nd
20:4(n-3)	nd	nd	nd	nd
20:5(n-3) Diat marker	nd	nd	nd	nd
22:5(n-3)	nd	nd	nd	nd
22:6(n-3) Flag marker	nd	nd	nd	nd
FA ratios				
18:1(n-9) / 18:1(n-7)	nd	nd	nd	nd
PUFA / SFA	nd	nd	nd	nd
16:1(n-7) / 16:0	nd	nd	nd	nd
20:5(n-3) / 22:6(n-3)	nd	nd	nd	nd

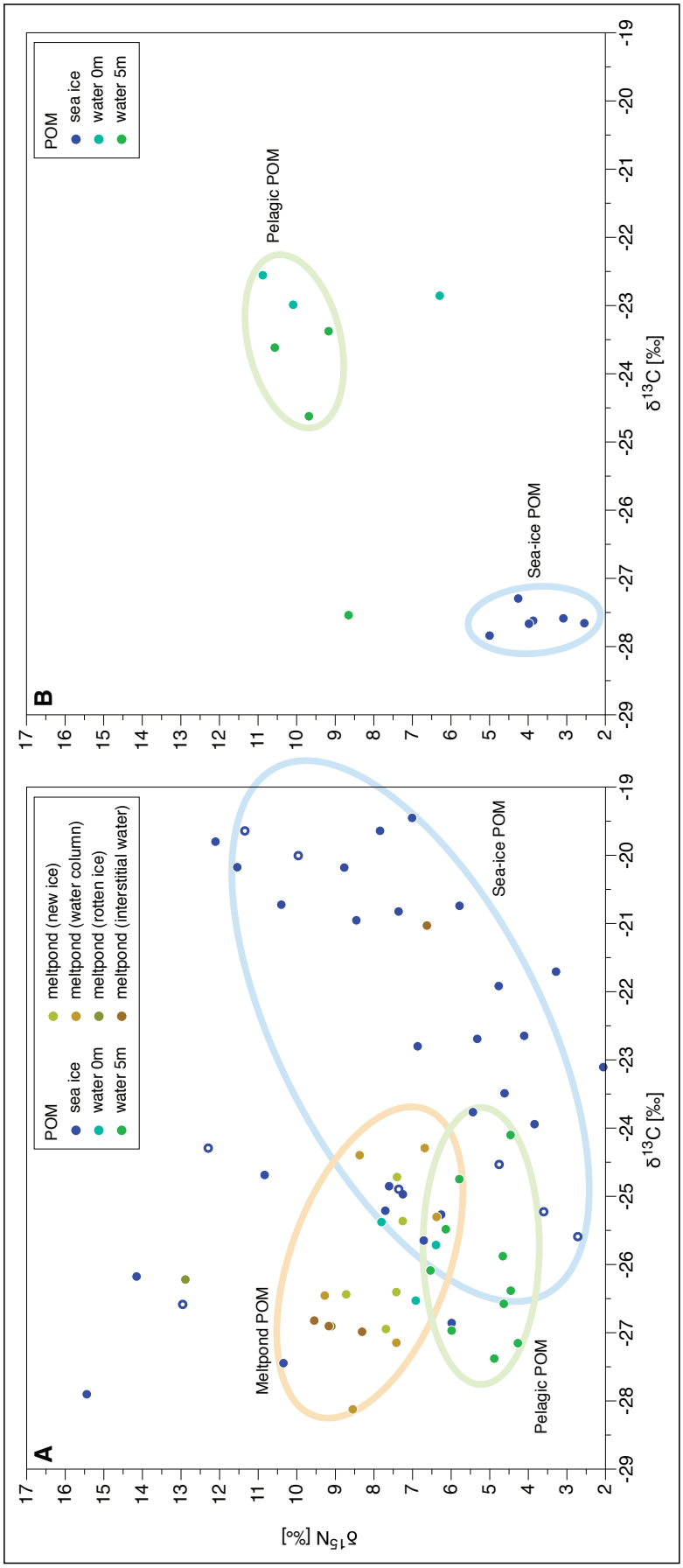

Figure 4.S6.1: A Stable carbon ($\delta^{13}C$) and nitrogen isotopes ($\delta^{15}N$) of POM from sea ice, sub-ice water and meltponds in the Central Arctic in summer (enlarged boxed area from Fig. 4.1 A). **B** $\delta^{13}C$ and $\delta^{15}N$ of POM from sea ice and sub-ice water in two fjords in Spitsbergen in spring. — Samples smaller than the largest filter blank are depicted as open symbols. Circles qualitatively illustrate POM types.

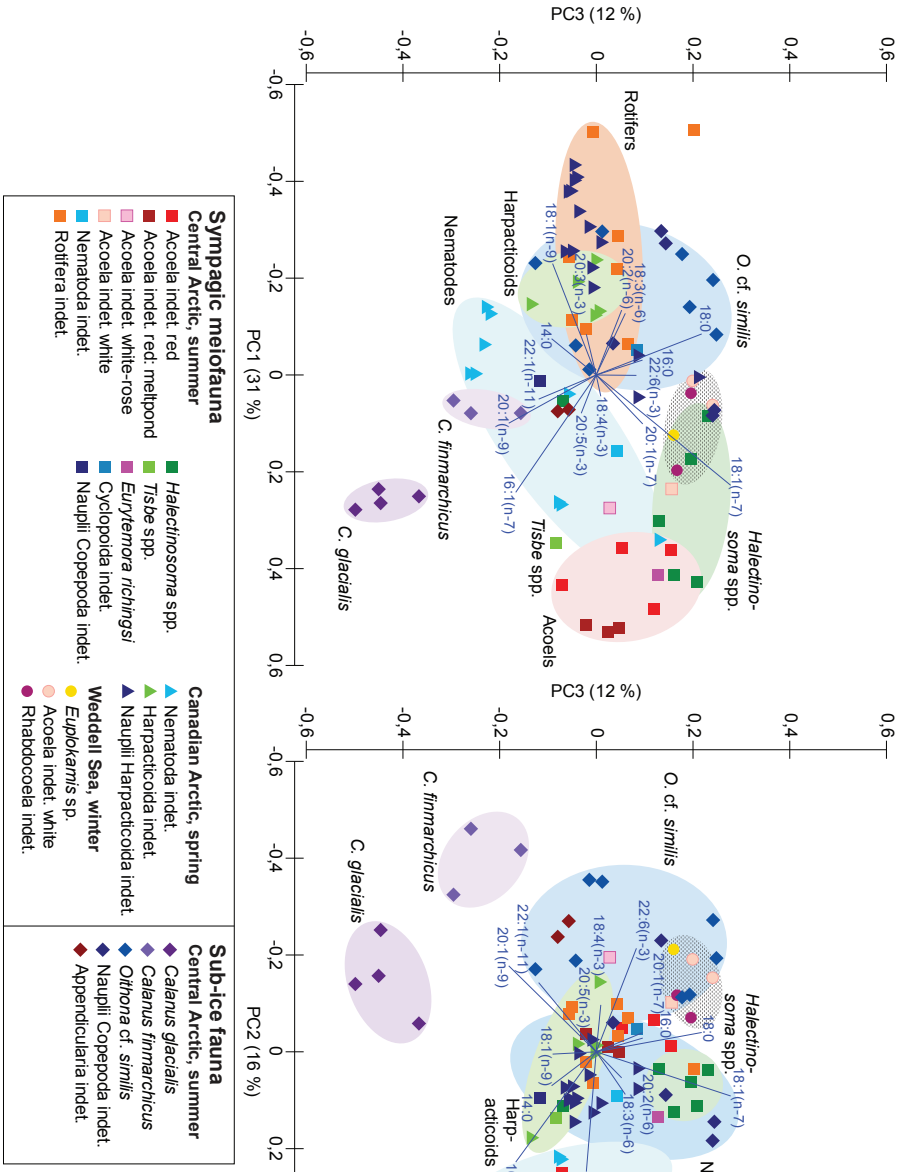

Figure 4.S6.2: Results of principal component analysis of fatty acid composition of sympagic meiofauna and sub-ice fauna, including the 15 most important fatty acids as variables (exceeding 10 % of total fatty acids in at least one sample). The first three principal components (PC1 vs. PC3, PC2 vs. PC3) are shown, accounting for 31 %, 16 % and 12 % of the total variability, respectively. PC1 vs. PC2 is shown in Fig. 4.4. Sympagic meiofauna from the Central Arctic in summer (squares), Canadian Arctic in spring (triangles) and Weddell Sea in winter (circles) as well as sub-ice fauna from the Central Arctic in summer (diamonds) are shown. Shaded areas qualitatively illustrate faunal groups, the hatched area illustrates samples from the Weddell Sea. Colours are the same as in Fig. 4.1 and 4.4.

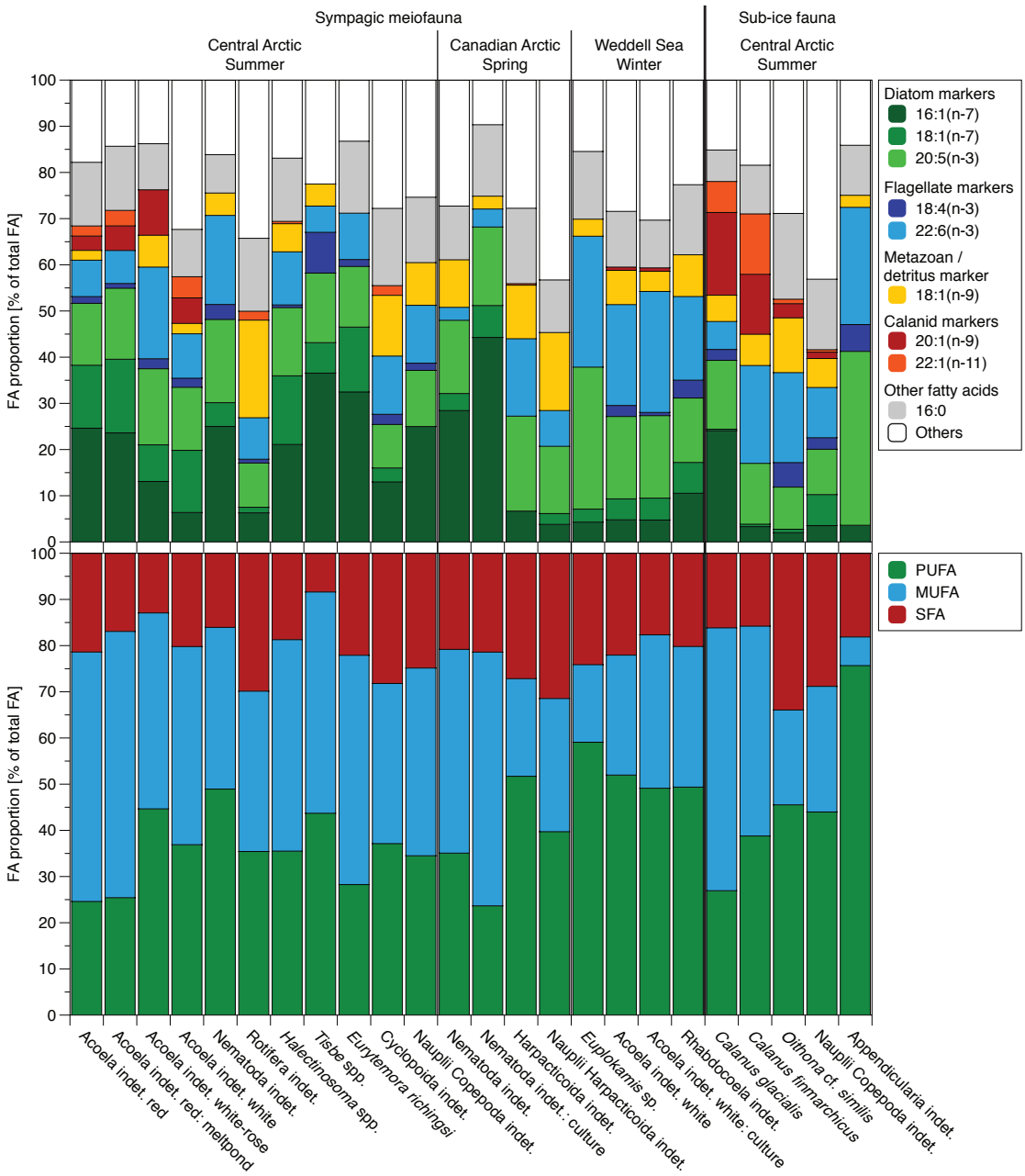

Figure 4.S6.3: Bar chart of proportions of different fatty acids (upper panel) and of polyunsaturated (PUFA), monounsaturated (MUFA) and saturated (SFA) fatty acids (lower panel) for sympagic meiofauna from the Central Arctic, Canadian Arctic and the Weddell Sea as well as for sub-ice fauna from the Central Arctic.

5 Diets, ingestion rates and feeding impact of sympagic meiofauna based on experiments

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Manuscript in preparation

5.1 Abstract

Sea-ice algae contribute substantially to primary production in ice-covered regions, but it is still unknown to what extent their production is available to under-ice, pelagic and benthic grazers. Sympagic meiofauna (proto- and metazoans $\geq 20\,\mu$m inhabiting the brine channels in sea ice) are assumed to recycle part of the ice-algae production within the system, but estimates of their grazing impact are rough due to the lack of experimental studies. Furthermore, the predation impact within the meiofauna community has not been assessed so far. We conducted grazing and predation experiments with Arctic and Antarctic sympagic meiofauna to investigate diets and to determine ingestion rates with respect to functional response and competition. From these rates, combined with biomass data from different Arctic and Antarctic regions obtained during four expeditions, we determined the feeding impact of sympagic meiofauna. Several meiofauna taxa fed on both ciliates and algae. Predation on metazoans was observed in the Arctic cnidarian *Sympagohydra tuuli* and the Antarctic ctenophore *Euplokamis* sp., cannibalism was recorded in Arctic harpacticoid copepods (*Tisbe* spp. and indetermined species). Carbon-based grazing rates of *Tisbe* spp. of 1–36 $\%\,d^{-1}$ were lower than maximum potential ingestion rates from allometric equations and could be described by a rectilinear functional response. Predation rates of meiofauna depended on predator and prey taxa, with highest rates in *Euplokamis* sp. preying on copepods (191 $\%\,d^{-1}$). In the Arctic harpacticoids *Halectinosoma* spp. preying on ciliates and in *S. tuuli* preying on nauplii, a decrease of predation rates with predator density indicated competition. The experimentally derived grazing impact on the ice-algae standing stock ($< 2\,\%\,d^{-1}$) was by one order of magnitude lower than estimates from allometric equations. The predation impact on ciliates and on nauplii was considerably high at some stations (up to $> 200\,\%\,h^{-1}$ and 37 $\%\,h^{-1}$, respectively). We conclude that cilivorous and carnivorous feeding as well as flexible feeding strategies enable sympagic meiofauna to survive periods of low ice-algae pro-

duction. Threshold food densities and competition might be important factors in sea ice, constraining the grazing and predation impact. Meiofauna grazing is unlikely to limit food availability to under-ice and sub-ice grazers. Carnivorous feeding by meiofauna, in contrast, probably constitutes competition to under-ice and sub-ice predators and is thus likely to influence cryo-pelagic coupling.

5.2 Introduction

Large parts of the polar oceans are covered with sea ice: the sea-ice area ranges between $2 \times 10^6\,\mathrm{km}^2$ and $17 \times 10^6\,\mathrm{km}^2$ in the southern hemisphere (5–45 % of the total Southern Ocean area of $38 \times 10^6\,\mathrm{km}^2$), in the northern hemisphere it is $4–15 \times 10^6\,\mathrm{km}^2$ (29–100 % of the total Arctic Ocean area of $14 \times 10^6\,\mathrm{km}^2$) (Comiso 2010). Ice algae, inhabiting the brine channels in sea ice, contribute substantially to total primary production in ice-covered regions—up to 28 % in certain parts of the Southern Ocean (Arrigo and Thomas 2004) and up to 57 % in the Central Arctic (Gosselin et al. 1997)—and thus constitute an important base of the polar marine food webs (Legendre et al. 1992). However, it is still unknown to what extent this primary production is available to under-ice grazers and, after release from the ice, to zooplankton and zoobenthos. Since sympagic meiofauna—proto- and metazoans $\geq 20\,\mu$m inhabiting the brine channels—are assumed to also utilise ice algae as a food source (Gradinger 1995, Arrigo and Thomas 2004), part of the primary production may be recycled within the system.

Estimates of the extent of such recycling are still very rough, though. Due to the lack of experimental studies, the feeding impact of sympagic meiofauna on ice algae has up to now only been estimated using ingestion rates from allometric equations, which had originally been developed for filter-feeding zooplankton (Moloney and Field 1989). In most cases, these estimates indicate a low feeding impact (Gradinger 1999a, Nozais et al. 2001, Michel et al. 2002, Gradinger et al. 2005), but some studies suggest that sympagic meiofauna may in certain situations control accumulation of ice algae and compete with under-ice grazers for this food source (Gradinger et al. 1999, Kramer et al. in press).

Besides lacking experimental support of ingestion rates, these estimates of the feeding impact neglect the fact that most sympagic meiofauna taxa are not strictly herbivorous, but rather omnivorous, detritivorous, cilivorous or carnivorous (Kramer et al. under revision). Cilivorous or carnivorous feeding and flexible feeding strategies (such as omnivory, diet switches, starvation periods) may substantially reduce the grazing pressure on ice algae. At the same time, predation by sympagic meiofauna may alter the composition of the meiofauna community and limit the availability of certain prey species to carnivorous sub-

ice and under-ice fauna, such as the Arctic amphipods *Themisto libellula* and *Gammarus wilkitzkii* (Werner et al. 2002, Auel and Werner 2003).

We conducted feeding experiments with various Arctic and Antarctic sympagic meiofauna taxa to

- confirm the cilivorous and carnivorous feeding in certain meiofauna taxa which Kramer et al. (under revision) deduced from fatty acid and stable isotope analyses,
- determine grazing and predation rates,
- investigate and quantify factors influencing ingestion rates (food composition, food density, grazer / predator density) by means of statistics and linear modelling,
- obtain more realistic estimates of the grazing impact on ice algae as well as first estimates of the predation impact on sympagic ciliates and metazoan meiofauna.

5.3 Materials and methods

5.3.1 Sampling and sample processing

Sea ice was sampled during four expeditions to different Arctic and Antarctic regions in summer, spring and winter (Table 5.1). Ice cores for determination of biomass of ice algae and abundance and biomass of sympagic meiofauna were taken and cut according to Kramer et al. (in press). Sympagic meiofauna and ice-algae for experiments were gained from non-quantitative sea-ice samples—i. e. from chunks of ice sampled with the aid of

Table 5.1: Expeditions with sea-ice sampling to obtain sympagic meiofauna for feeding experiments (Exp), and to determine abundance and biomass of sympagic meiofauna taxa (Abun, Biom) as well as chlorophyll *a* concentration and ice-algae biomass (Chl) for estimation of the feeding impact. + samples taken for this study; (+)[1] meiofauna abundance already published in Marquardt et al. (under revision) and Marquardt (2010); (+)[2] temperature, salinity, chl *a*, meiofauna abundance / biomass already published in Kramer et al. (in press); (+)[3] temperature, salinity provided by G. Carnat, B. Delille, N.-X. Geilfus and G. Song, chl *a* provided by B. Philippe, C. J. Mundy and M. Gosselin; — samples not taken.

Region	Coverage		Time		Campaign	Samples			
						Symp meiofauna		Algae	
	Latitudes	Longitudes	Season	Dates		Exp	Abun, Biom	Exp	Chl
Central Arctic	82°01' N–88°09' N	33°58' E–134°55' W	Summer	Jul 29–Oct 7 2007	ARK–XXII / 2 (RV *Polarstern*)	+	+	+	+
Western Canadian Arctic: Beaufort Sea, Amundsen Gulf	69°57' N–71°34' N	119°36' W–126°10' W	Spring	Mar 13–Jun 5 2008	CFL legs 7–8 (CCGS *Amundsen*)	+	(+)[1]	+	(+)[3]
Antarctic: Southern Ocean: Western Weddell Sea	59°50' S–65°07' S	40°47' W–57°24' W	Winter	Aug 24–Oct 29 2006	ANT–XXIII / 7 (RV *Polarstern*)	+	(+)[2]	+	(+)[2]
Antarctic: Southern Indian Ocean	64°08' S–65°21' S	116°29' E–128°36' E	Winter	Sep 5–Oct 17 2007	SIPEX voyage 1 (RSV *Aurora Australis*)	—	(+)[2]	—	(+)[2]

a cage on the ship's crane (Kiko et al. 2008a) or sawn from ice floes, or from pooled bottom-ice sections from cores.

All ice samples were melted in the dark at $+4\,^{\circ}$C (Gradinger 1999a), for meiofauna samples after addition of filtered sea water (Garrison and Buck 1986, Gradinger 1999a). Melted algae core sections were processed for chlorophyll *a* (chl *a*) analyses according to Gradinger (1999b) and Kramer et al. (in press). Organisms from melted meiofauna core sections were enriched over a 20 μm gauze and fixed with formaldehyde for abundance and biomass determination (Gradinger 1999a). Organisms from non-quantitative samples were enriched likewise and transferred into petri dishes or beakers. Metazoan meiofauna and larger ciliates for feeding experiments were sorted from these samples and either used directly, or kept in the dark at $0\,^{\circ}$C and reared on a mixed sympagic protist diet until the start of the experiments. Parts of the samples from which metazoan meiofauna and larger ciliates had been withdrawn completely were used as stocks for mixed protist cultures, reared on F / 2 culture media.

In addition, ice *in situ* temperature and bulk salinity were determined as described in Horner et al. (1992) and Kramer et al. (in press) for calculation of the brine volume fraction according to Frankenstein and Garner (1967).

5.3.2 Determination of ice-algae biomass and abundance and biomass of sympagic meiofauna

Biomass of ice algae and abundance and biomass of sympagic meiofauna in the brine were determined to adjust densities in feeding experiments to natural conditions and to calculate ingestion rates from experimentally-derived functional response equations. Integrated biomass of ice algae and sympagic meiofauna were determined for estimation of the feeding impact.

Bulk concentration of chl *a* in the algae core sections (chl_{bulk}, chlorophyll mass per volume melted ice) was determined fluorometrically according to Gradinger (1999b) and converted to integrated concentration (chl_{int}, mass per area). Furthermore, chl *a* concentration in the brine (chl_{br}, mass per volume brine) was calculated as

$$chl_{br} = \frac{chl_{bulk} \cdot V_{ice_m}}{V_{ice_s} \cdot \delta V_{brine}} \quad , \tag{5.1}$$

where V_{ice_m} is the volume of melted ice, V_{ice_s} is the respective volume of solid ice (core area times section length), and δV_{brine} is the brine volume fraction. Chl *a* concentrations were converted to carbon biomass of ice algae assuming a conversion factor of 52 for the Antarctic in winter (Meiners et al. in press), of 44 for the Canadian Arctic in spring (B. Philippe, pers. comm.) and 470 for the Central Arctic in summer (own data from

ARK–XXII / 2 based on chl *a* and POC measurements, unpubl.; the high ratio might have been caused by high proportions of dinoflagellates and heterotrophic flagellates, Landry et al. 2000).

Bulk abundance and integrated abundance of sympagic meiofauna taxa was determined according to Gradinger (1999a). Meiofauna abundance in the brine was calculated as for chlorophyll. Meiofauna abundance was converted to biomass on the base of length and width measurements (Gradinger et al. 1999, Kramer et al. in press).

5.3.3 Setup of feeding experiments

We modified established methods of grazing experiments (Frost 1972) and developed set-up and evaluation of predation experiments specifically for application to sympagic meiofauna, as described in the following.

Quantitative grazing experiments were conducted with the Arctic sympagic harpacticoid copepods *Tisbe* spp. as grazer and mixed cultures of sea-ice protists as food. Non-quantitative grazing experiments were conducted also with Arctic sympagic red and white acoel platyhelminthes, nematodes, harpacticoid copepods (*Halectinosoma* spp. and an unidentified species) and cyclopoid copepods, as well as with Antarctic sympagic white acoels as grazers. The 13 treatments in the quantitative experiments differed in initial protist composition and biomass (Supplement 5.S5 Fig. 5.S5.1). Each treatment was run with triplicate grazer setups *g* and triplicate protist-only setups *p*. The well-mixed suspensions of protist cultures for each treatment were distributed into 6-well plates (5 mL per well). 10 grazers were added to three of the wells *g* without prior starvation, while no grazers were added to the remaining three wells *p*. To simulate *in-situ* conditions inside the ice, experiments were not conducted in a plankton wheel, but in well-plates which were kept still. Thus protists were allowed to settle, and meiofauna could graze on surfaces. By the end of the experiments, the grazers were removed, the protists from grazer triplicates and protist-only triplicates were re-suspended from the bottom of the wells, fixed in formaldehyde or Lugol solution, identified based on Tomas (1997) and counted according to Utermöhl (1958).

Quantitative predation experiments were conducted with several different combinations of metazoan meiofauna taxa as predators and metazoan meiofauna or ciliates as prey, and with different predator and prey densities, which were within the range of densities determined for sea-ice brine (Table 5.2). These 43 treatments were run in predator triplicates or duplicates (with predators) whenever possible. In 14 cases, replication was not possible due to limited ressources. In all but 19 cases, one to three prey-only setups (without predators) were run for each treatment to assess prey reproduction and losses due to handling.

Table 5.2: Predator and prey taxa used in predation experiments, number of individuals (Ind), number of replicates with predators (Pd repl. = predetor replicates) and without predators (Py repl. = prey-only replicates), duration and experiment identity label (ID).

Region	Predator (Pd)		Prey (Py)		Pd	Py	Duration	Predation
	Taxon	Ind	Taxon	Ind	repl.	repl.		experiment ID
Arctic	Cnidaria: *Sympagohydra tuuli*	1	Ciliata	30	3	0	11 d	Sym-Cil-a
		1	Rotifera	15	3	1	8 d	Sym-Rot-a
		1		20	3	1	14 d	Sym-Rot-b
		2		30	3	1	13 d	Sym-Rot-c
		2		60	3	1	13 d	Sym-Rot-d
		1	Nauplii	15	3	0	9 d	Sym-Nau-a
	Plathelminthes: Acoela indet. red	1	Ciliata	40	3	1	9 d	Aco_r-Cil-a
		1		45	3	1	21 d	Aco_r-Cil-b
		2		6	3	1	10 d	Aco_r-Cil-c
		2		10	3	1	10 d	Aco_r-Cil-d
		2		20	3	1	10 d	Aco_r-Cil-e
		2		50	3	1	10 d	Aco_r-Cil-f
	Harpacticoida: *Tisbe spp.* copepodides	7	*Tisbe spp.* nauplii	77	1	0	9 h	Tis-Nau-a
		8		24	1	0	46 h	Tis-Nau-b
		8		104	1	0	19 h	Tis-Nau-c
		9		114	1	0	46 h	Tis-Nau-d
		15		160	1	0	22 h	Tis-Nau-e
		18		120	1	0	18 h	Tis-Nau-f
	Harpacticoida: *Halectinosoma spp.*	1	Ciliata	65	3	1	8 d	Hal-Cil-a
		2		65	3	1	8 d	Hal-Cil-b
		5		65	3	1	20 d	Hal-Cil-c
		11		55	3	1	9 d	Hal-Cil-d
		11		65	3	1	21 d	Hal-Cil-e
		20		65	3	1	22 d	Hal-Cil-f
	Harpacticoida indet.	5	Ciliata	65	3	1	26 d	Harp-Cil-a
		5		80	3	1	9 d	Harp-Cil-b
		5		100	3	1	19 d	Harp-Cil-c
		5		700	1	1	47 h	Harp-Cil-d
Antarctic	Ctenophora: *Euplokamis sp.*	4	Ciliata	20	1	0	6 d	Eup-Cil-a
		4		40	2	0	17 d	Eup-Cil-b
		4	Ciliata red	40	2	0	10 d	Eup-Cil-c
		4	Acoela indet. white	40	2	0	23 d	Eup-Aco-a
		3	Nauplii	33	1	0	3 d	Eup-Nau-a
		3		60	2	0	4 d	Eup-Nau-b
		4	Harpacticoida	40	1	0	3 d	Eup-Harp-a
		4	Calanoida: *Stephos longipes*	26	1	0	5 h	Eup-Ste-a
		4		40	1	0	9 h	Eup-Ste-b
	Plathelminthes: Acoela indet. white	1	Ciliata	10	3	3	17 d	Aco_w-Cil-a
		2		10	3	3	17 d	Aco_w-Cil-b
		2		20	3	3	17 d	Aco_w-Cil-c
		6		10	3	3	17 d	Aco_w-Cil-d
		10		10	1	0	19 d	Aco_w-Cil-e
		10		20	1	0	10 d	Aco_w-Cil-f

For each treatment, a 6-well plate was filled with filtered sea water (5 mL per well), a certain number of prey items were placed into each well, and a certain number of predators were added to the wells of predator setups without prior starvation. Prey items and predators were counted in regular intervals (usually 5 hours to 5 days, depending on predator taxa), thus giving initial and intermediate conditions and revealing predation rates with respect to temporal variability. Consumed or dead prey as well as dead predators were

replaced to enable continuous (and near-constant) predation also at low prey density and in spite of predator and prey mortality.

All experiments were run in the dark at 0 °C for usually 5–83 days; only 12 predation experiments were run shorter (Table 5.2). The long duration enabled us to measure grazing rates in spite of the low individual ingestion rates, to observe temporal variabilities in predation rates and to obtain robust estimates of average ingestion rates.

After each experiment, grazers / predators were photographed for determination of volumes and calculation of carbon contents from length and width (Gradinger et al. 1999, Kramer et al. in press). In few grazing experiments, *Tisbe* spp. grazers reproduced during the experiments; in these cases nauplii were included in carbon content determination and further evaluations. The carbon content of all prey as well as of predators in few cases where the size was not measured for the individual experiments were estimated from carbon contents of the respective taxon from the respective expedition. Carbon contents of protists in grazing experiments were likewise determined from size measurements (Hillebrand et al. 1999), which, for each treatment, were conducted for at least one of the grazer triplicates and one of the protist-only triplicates. The carbon content determination, particularly for metazoan meiofauna, is based on many assumptions (Gradinger et al. 1999) and therefore inaccurate by at least 10 %. Due to error propagation this probably caused bias in the calculated feeding impact. However, it is the best estimate possible since direct measurements are not available.

5.3.4 Evaluation of feeding experiments

Grazing rates of *Tisbe* spp.

Grazing rates were calculated from the decrease of protist biomass in each of the 13 treatments, determined as the biomass difference between protist-only and grazer setups at the end of the experiments, assuming that this difference had been ingested and that grazing rates were constant over time. Total carbon-based grazing rates were determined from total protist biomass by linear regression (see Supplement 5.S1 for details). Likewise, taxon-specific carbon-based grazing rates as well as abundance-based grazing rates were calculated for 16 different protist taxa (Supplement 5.S1 Table 5.S1), the latter needed for determination of selectivity.

The treatments were grouped according to protist composition identified by cluster analysis and SIMPROF test (see Supplement 5.S1 for details; significance level of all statistic tests in this study 5 %). To test whether total and taxon-specific grazing rates were significantly positive, a one-tailed test was applied, using the t statistic of the respective

regression coefficient as test statistic. All following analyses were performed with only the eight treatments with significantly positive total grazing rates.

We applied a one-way ANOVA to test whether total grazing rates were influenced by protist composition, using the composition groups from cluster analysis. A one-tailed Spearman rank correlation test was performed to test for a positive monotonic relationship between the total grazing rates and the estimated initial total protist biomass. We assumed a rectilinear functional response (Frost 1972) and thus performed a linear regression of total grazing rates on initial total protist biomass.

A two-way ANOVA was performed on taxon-specific grazing rates to test for the influence of taxon (16 taxa as levels) and protist biomass composition (three groups from cluster analysis as levels). Out of the potential number of grazing rates for 16 taxa in eight treatments, 28 were significantly positive and thus used in the ANOVA. One-tailed Spearman rank correlation tests were performed to test for a positive monotonic relationship between the taxon-specific grazing rates and the estimated initial biomass of the respective taxon.

Grazing selectivity of *Tisbe* spp.

Selectivity for each protist taxon j in each treatment is presented as electivity index ε ranging from -1 to +1 with 0 representing no preference for the respective taxon (Chesson 1983). For calculation, we used estimates of protist abundance at the beginning and end of the experiments, which were based on the linear regression applied to determine grazing rates (see Supplement 5.S2 for details).

To examine whether selectivity in these mixed-protist grazing experiments differed between the protist taxa or was influenced by protist composition, a two-way ANOVA was performed on the electivity indices. The two factors specified for which of the 16 protist taxa the index had been calculated and which of the three biomass composition clusters the treatment had been assigned to. For each protist taxon, two-tailed Spearman rank correlation tests were performed to test for monotonic relationships of electivity vs. initial abundance and electivity vs. initial biomass of the respective taxon.

Predation rates of Arctic and Antarctic sympagic meiofauna

Gains and losses in prey attributed to reproduction and handling in predation experiments ΔB_{py} were determined from prey-only replicates (see Supplement 5.S3 for details). To obtain carbon-based predation rates for each predator replicate and time step, the change in prey biomass per time was corrected with the respective ΔB_{py} and divided

by the predator biomass (averaged over the respective time step). For *Halectinosoma* spp. preying on ciliates, abundance-based predation rates were calculated likewise.

Since changes in predation rates over time did not seem to be systematic for any predator-prey combination (Supplement 5.S6 Fig. 5.S6.1 and 5.S6.2), all time steps of all predator setups within each predator-prey combination were regarded as independent replicates. The influence of prey and predator biomass on predation rates was then investigated for each predator-prey combination.

In two cases where two- and three-dimensional plots clearly indicated a trend in predation rates with prey and predator biomass, two-dimensional functions were fitted to the data. For *Sympagohydra tuuli* preying on nauplii, a linear function (i. e. a plain) was fitted. For *Halectinosoma* spp. preying on ciliates, we applied an empirical model originally derived for microzooplankton grazing (Peters 1994), which takes into account both prey and predator abundance. The original equation, which assumes power laws of prey and predator abundance and body volume, was transformed using a base-10 logarithm and fitted to the abundance-based predation rates by multiple linear regression. The exponents for temperature and ciliate body volume were taken from Peters (1994) since ciliate body volumes were estimated as the median from the respective expedition and all experiments were performed at the same temperature, and therefore no range of values was covered in the experiments.

In predator-prey combinations where a relationship between predation rates and prey or predator biomass was not obvious due to large scatter in the data or an insufficient number of data points, the replicates (i. e. the different time steps in each predator replicate) were grouped according to predator and prey biomass by cluster analysis and SIMPROF test (see Supplement 5.S3 for details). An average predation rate was then calculated for each cluster, and a t-test was applied to test whether it was significantly positive.

Maximum potential ingestion rates

For both grazing and predation experiments, the individual maximum potential carbon-based ingestion rate I_{max} was calculated according to Moloney and Field (1989) for the respective range of grazer / predator carbon content to compare with experimental ingestion rates. Temperature correction was performed assuming a Q_{10} value of 2 (Gradinger et al. 1999).

5.3.5 Assessment of feeding impact

To estimate *in situ* ingestion rates, functional response and competition equations were derived from the experiments for various combinations of grazers / predators and food / prey.

Since grazing experiments were conducted with one grazer taxon only, we applied the respective equation to all proto- and metazoan meiofauna, assuming that it represented the grazing behaviour of the different taxa sufficiently well. For predation on ciliates, we applied the equations derived for certain predator taxa to other predator taxa which we assumed to have similar feeding modes. For predation on metazoans, we assumed that predation took place only for those predator-prey combinations where feeding had actually been observed in quantitative or non-quantitative experiments and, in case of non-quantitative experiments, applied equations of similar taxa. An exponential term for temperature correction was included in all equations. Based on these equations, individual *in situ* ingestion rates $I_{ijk,ind}$ were calculated for each pair of grazer or predator i and food type (algae or prey taxon) j, and for each ice-core section k, using the median carbon content of grazer / predator i in section k, the abundance or biomass of predator i and food type j in the brine and the sea-ice temperature of section k. For comparison, maximum potential ingestion rates I_{max} were calculated according to the temperature-corrected allometric equation (Moloney and Field 1989).

Based on these individual *in situ* ingestion rates and maximun potential ingestion rates, we calculated integrated community ingestion rates for each station and food type. From these, we derived the feeding impact of meiofauna on the standing stock of each food type for each station (see Supplement 5.S4 for details).

Community ingestion rates and feeding impact for each food type were tested for differences between the expeditions by pairwise application of two-tailed U-tests. For integrated community grazing rates and grazing impact within each region, two-tailed U-tests were applied to test for differences between results from maximum potential ingestion rates and measured grazing rates.

5.4 Results

5.4.1 Ice-algae biomass and meiofauna abundance and biomass

Taxonomic composition of sympagic meiofauna, abundance and biomass of most taxa as well as ice-algae biomass differed between the four regions and seasons investigated (Table 5.3, 5.4). Thus a range of different communities was covered in this study. It should be noted that some taxa (e. g. the cnidarian *Sympagohydra tuuli* and nemerteans) occurred in bottom-ice sections (Table 5.3) or non-quantitative samples, but not in full cores (Table 5.4), and are thus not included in the estimates of feeding impact given below.

Table 5.3: Ice-algae and meiofauna abundance and biomass in the brine channels of sea ice for different regions and seasons (including amphipods from melted ice cores). Medians (ranges) are given. — taxon not observed in any sea-ice samples from the respective expedition, *nd* no data. For the western Canadian Arctic, the values were calculated from chl *a* concentration provided by B. Philippe et al., meiofauna bulk abundance obtained from Marquardt (2010) and Marquardt et al. (under revision) and sea-ice temperature and bulk salinity provided by G. Carnat et al.. For the Antarctic, the values were calculated from chl *a* concentration, meiofauna bulk abundance and biomass and brine volume fraction obtained from Kramer et al. (in press). Incomplete ice cores (with missing sections) as well as additional bottom-ice sections (meiofauna counted alive) are included.

	Arctic		Antarctic	
	Central Arctic Summer	Western Canadian Arctic Spring	Western Weddell Sea Winter	Southern Indian Ocean Winter
Abundance in brine [mL^{-1}]				
Algae	*nd*	*nd*	*nd*	*nd*
Ciliata	1.71 (0.00–26243.54)	0.16 (0.00–230.17)	0.05 (0.00–22.69)	0.07 (0.00–3.23)
Foraminifera	0.00 (0.00–180.38)	—	0.00 (0.00–0.65)	0.03 (0.00–5.75)
Radiolaria	0.00 (0.00–36.88)	—	0.00 (0.00–0.11)	0.00 (0.00–0.89)
Zooflagellata	*nd*	0.00 (0.00–1.17)	*nd*	*nd*
Cnidaria	0.00	0.00 (0.00–0.07)	—	—
Ctenophora	—	—	0.00 (0.00–0.06)	0.00 (0.00–0.05)
Nematoda	0.00 (0.00–445.98)	0.00 (0.00–16.56)	—	—
Acoela	0.00 (0.00–651.81)	0.00 (0.00–1.23)	0.04 (0.00–9.16)	0.00 (0.00–0.47)
Rhabditophora	—	—	0.00 (0.00–0.05)	—
Rotifera	0.04 (0.00–2119.12)	0.04 (0.00–23.89)	—	—
Nemertea	0.00	0.00 (0.00–0.04)	—	—
Nudibranchia juv.	—	—	0.00 (0.00–0.02)	0.00 (0.00–0.02)
Other Mollusca juv.	—	0.00 (0.00–0.19)	—	—
Polychaeta larv. / juv.	—	0.00 (0.00–0.20)	—	—
Cirripedia Nauplii	—	0.00 (0.00–0.01)	—	—
Harpacticoida CI-CVI	0.00 (0.00–1800.62)	0.00 (0.00–0.38)	0.03 (0.00–2.40)	0.00 (0.00–0.04)
Calanoida CI-CVI	0.00	—	0.00 (0.00–0.34)	0.00 (0.00–0.02)
Cyclopoida CI-CVI	0.00 (0.00–52.87)	0.00 (0.00–0.22)	0.00 (0.00–0.04)	—
Copepoda indet. CI-CVI	—	0.00 (0.00–0.03)	—	—
Copepoda Nauplii	0.00 (0.00–240.14)	0.02 (0.00–1.93)	0.00 (0.00–34.64)	0.00 (0.00–1.65)
Amphipoda	0.00	0.00 (0.00–0.03)	—	—
Biomass in brine [μgL^{-1}]				
Algae (from chl *a*) [$\times 10^3$]	6.14 (0.37–157.00)	3.55 (0.02–4001.53)	2.21 (0.06–241.58)	0.40 (0.00–13.04)
Ciliata	21.82 (0.00–532.11)	4.56 (0.00–8891.98)	5.59 (0.00–1053.59)	0.29 (0.00–397.93)
Foraminifera	0.00 (0.00–98.56)	—	0.00 (0.00–1640.02)	1.56 (0.00–1343.73)
Radiolaria	0.00 (0.00–149.11)	—	0.00 (0.00–214.39)	0.00 (0.00–214.62)
Zooflagellata	*nd*	0.00 (0.00–21.85)	*nd*	*nd*
Cnidaria	0.00	0.00 (0.00–30.62)	—	—
Ctenophora	—	—	0.00 (0.00–19.88)	0.00 (0.00–0.81)
Nematoda	0.00 (0.00–75.96)	0.00 (0.00–1475.74)	—	—
Acoela	0.00 (0.00–295.18)	0.00 (0.00–161.44)	3.99 (0.00–5047.85)	0.00 (0.00–21.31)
Rhabditophora	—	—	0.00 (0.00–496.38)	—
Rotifera	0.29 (0.00–37.56)	0.56 (0.00–402.32)	—	—
Nemertea	0.00	0.00 (0.00–1221.98)	—	—
Nudibranchia	—	—	0.00 (0.00–53.70)	0.00 (0.00–3.25)
Gastropoda / Bivalvia juv.	—	0.00 (0.00–181.10)	—	—
Polychaeta larv. / juv.	—	0.00 (0.00–113.06)	—	—
Cirripedia Nauplii	—	0.00 (0.00–9.53)	—	—
Harpacticoida CI-CVI	0.00 (0.00–1901.61)	0.00 (0.00–573.72)	4.49 (0.00–1309.99)	0.00 (0.00–12.02)
Calanoida CI-CVI	0.00	—	0.00 (0.00–1084.83)	0.00 (0.00–21.79)
Cyclopoida CI-CVI	0.00 (0.00–41.44)	0.00 (0.00–140.63)	0.00 (0.00–23.04)	—
Copepoda indet. CI-CVI	—	0.00 (0.00–22.83)	—	—
Copepoda Nauplii	0.00 (0.00–31.56)	1.65 (0.00–685.98)	0.00 (0.00–3676.59)	0.00 (0.00–34.71)
Amphipoda	0.00	0.00 (0.00–636.56)	—	—
n	99	108	104	105

Table 5.4: Integrated ice-algae and meiofauna abundance and biomass (in the whole ice column, expressed in relation to ice area) for different regions and seasons (including amphipods from melted ice cores). Medians (ranges) are given. — taxon not observed in any sea-ice samples from the respective expedition, *nd* no data. For the western Canadian Arctic, chl *a* concentration for calculation of algae biomass was provided by B. Philippe et al.; meiofauna integrated abundance was obtained from Marquardt (2010) and Marquardt et al. (under revision). For the Antarctic, chl *a* concentration for calculation of algae biomass as well as integrated meiofauna abundance and biomass were obtained from Kramer et al. (in press). Incomplete ice cores (with missing sections) are included, additional bottom-ice sections (meiofauna counted alive) are excluded.

	Arctic		Antarctic	
	Central Arctic Summer	Western Canadian Arctic Spring	Western Weddell Sea Winter	Southern Indian Ocean Winter
Abundance integrated [$\times 10^3\,m^{-2}$]				
Algae	*nd*	*nd*	*nd*	*nd*
Ciliata	39.30 (22.79–76.08)	27.74 (1.73–208.43)	19.96 (1.41–84.88)	14.58 (0.18–65.56)
Foraminifera	0.16 (0.00–1.89)	—	0.71 (0.16–3.14)	18.43 (0.00–117.83)
Radiolaria	0.94 (0.00–159.23)	—	0.16 (0.00–0.94)	0.69 (0.00–9.90)
Zooflagellata	*nd*	0.00 (0.00–7.55)	*nd*	*nd*
Cnidaria	0.00	0.00	—	—
Ctenophora	—	—	0.16 (0.00–0.63)	0.00 (0.00–0.56)
Nematoda	0.00 (0.00–0.16)	0.39 (0.00–94.79)	—	—
Acoela	0.94 (0.47–1.41)	1.18 (0.31–11.47)	10.53 (6.29–132.35)	0.81 (0.00–4.46)
Rhabditophora	—	—	0.00 (0.00–0.47)	—
Rotifera	1.89 (1.26–3.77)	2.36 (0.47–153.89)	—	—
Nemertea	0.00	0.00	—	—
Nudibranchia juv.	—	—	0.00 (0.00–0.16)	0.00 (0.00–0.17)
Other Mollusca juv.	—	0.16 (0.00–1.10)	—	—
Polychaeta larv. / juv.	—	0.00 (0.00–0.16)	—	—
Cirripedia Nauplii	—	0.00 (0.00–0.16)	—	—
Harpacticoida CI-CVI	0.79 (0.47–27.19)	0.24 (0.00–2.52)	7.15 (2.67–16.35)	0.00 (0.00–0.34)
Calanoida CI-CVI	0.00	—	0.31 (0.00–0.63)	0.00 (0.00–0.19)
Cyclopoida CI-CVI	0.00 (0.00–0.16)	0.31 (0.00–2.20)	0.00 (0.00–0.63)	—
Copepoda indet. CI-CVI	—	0.00 (0.00–0.16)	—	—
Copepoda Nauplii	0.16 (0.00–0.16)	2.44 (0.16–6.60)	2.83 (0.79–19.33)	0.56 (0.00–49.63)
Amphipoda	0.00	0.00 (0.00–0.16)	—	—
Biomass integrated [$mg\,m^{-2}$]				
Algae (from chl *a*) [$\times 10^3$]	0.19 (0.12–0.82)	2.07 (0.01–24.63)	0.26 (0.18–0.48)	0.05 (0.00–0.44)
Ciliata	1.29 (0.33–2.25)	0.75 (0.12–11.30)	2.38 (0.13–6.27)	0.31 (0.00–4.49)
Foraminifera	0.01 (0.00–0.32)	—	1.14 (0.02–2.62)	2.13 (0.00–26.83)
Radiolaria	0.01 (0.00–1.08)	—	0.01 (0.00–2.20)	0.09 (0.00–2.17)
Zooflagellata	*nd*	0.00 (0.00–0.14)	*nd*	*nd*
Cnidaria	0.00	0.00	—	—
Ctenophora	—	—	0.00 (0.00–0.20)	0.00 (0.00–0.01)
Nematoda	0.00 (0.00–0.03)	0.20 (0.00–8.60)	—	—
Acoela	0.22 (0.02–4.06)	0.08 (0.01–0.99)	1.23 (0.26–72.96)	0.04 (0.00–0.21)
Rhabditophora	—	—	0.00 (0.00–3.26)	—
Rotifera	0.03 (0.01–0.06)	0.06 (0.00–2.51)	—	—
Nemertea	0.00	0.00	—	—
Nudibranchia	—	—	0.00 (0.00–0.69)	0.00 (0.00–0.03)
Gastropoda / Bivalvia juv.	—	0.11 (0.00–0.41)	—	—
Polychaeta larv. / juv.	—	0.00 (0.00–0.22)	—	—
Cirripedia Nauplii	—	0.00 (0.00–0.13)	—	—
Harpacticoida CI-CVI	0.59 (0.43–25.03)	0.27 (0.00–5.76)	2.52 (0.32–4.25)	0.00 (0.00–0.10)
Calanoida CI-CVI	0.00	—	0.22 (0.00–0.99)	0.00 (0.00–0.21)
Cyclopoida CI-CVI	0.00 (0.00–0.06)	0.10 (0.00–0.90)	0.00 (0.00–0.33)	—
Copepoda indet. CI-CVI	—	0.00 (0.00–0.10)	—	—
Copepoda Nauplii	0.01 (0.00–0.03)	0.26 (0.02–2.18)	0.19 (0.03–1.83)	0.04 (0.00–1.04)
Amphipoda	0.00	0.00 (0.00–3.25)	—	—
n	5	6	6	12

5.4.2 Experimental diets and non-quantitative observations

Diets of Arctic and Antarctic sympagic meiofauna in feeding experiments differed between meiofauna taxa and included sea-ice algae, sympagic ciliates, rotifers, copepodids, copepod nauplii and polychaet larvae (Table 5.5). In nauplii, feeding was not observed, but it was noted that the guts were brown-coloured even in early naupliar stages of the Arctic harpacticoids *Tisbe* spp.. The nauplii of these species were often observed on fecal pellets. Grazing effects were not apparent in qualitative grazing experiments with Arctic cyclopoids and nematodes.

Table 5.5: Diets of Arctic and Antarctic sympagic meiofauna in feeding experiments. + feeding observed, +* probably cannibalistic feeding (observed in cultures where nauplii were presumably of the same species), ++ diet obviously preferred (the respective prey was reduced more efficiently than alternative prey, or predation rates for the respective prey were much higher than those for alternative prey), — feeding not observed, *nd* not determined (no experiments conducted with this predator-prey combination).

	Observations of feeding on						
	Algae	Ciliata	Rotifera	Polychaeta Trochophora	Copepoda NI-NVI	Harpacticoida CI-CVI	Calanoida CI-CVI
Arctic							
Cnidaria: *Sympagohydra tuuli*	—	—	+	+	++	*nd*	*nd*
Plathelminthes: Acoela (red, white)	—	+	*nd*	*nd*	*nd*	*nd*	*nd*
Harpacticoida indet.	+	++	*nd*	*nd*	+*	*nd*	*nd*
Harpacticoida: *Halectinosoma* spp.	+	+	*nd*	*nd*	*nd*	*nd*	*nd*
Harpacticoida: *Tisbe* spp.	+	—	*nd*	*nd*	+*	*nd*	*nd*
Antarctic							
Ctenophora: *Euplokamis* sp.	—	+	*nd*	*nd*	++	++	++
Plathelminthes: Acoela (white)	+	+	*nd*	*nd*	*nd*	*nd*	*nd*

Tisbe spp. and indetermined Arctic harpacticoids as well as Antarctic acoels efficiently grazed on the bottom and in the edges of the experimental vials: at the end of the experiments generally more algae were sticking to the bottom and edges of the vials in protist-only setups than in grazer setups.

In the Arctic cnidarian *Sympagohydra tuuli*, budding was often observed shortly after feeding. Also the Arctic harpacticoids *Tisbe* spp. and *Halectinosoma* spp. as well as Antarctic acoels reproduced during feeding experiments. *Tisbe* spp. also moulted in grazing experiments.

5.4.3 Grazing rates and selectivity of *Tisbe* spp.

Replicates in grazing experiments (both grazer setups and protist-only setups) showed a high variability in protist abundance, biomass and, partly, composition. Initial protist biomass (Supplement 5.S5 Fig. 5.S5.1), determined from linear regressions, ranged between $1\,\mathrm{mg\,L^{-1}}$ and $18\,\mathrm{mg\,L^{-1}}$ in total and was thus within the range of algae biomass in sea-ice brine (Table 5.3). The 13 treatments grouped into three significantly different

clusters (SIMPROF) according to initial protist biomass compositions (Supplement 5.S5 Fig. 5.S5.1).

Total carbon-based grazing rates of the Arctic sympagic harpacticoids *Tisbe* spp. were significantly positive in eight out of 13 treatments (Supplement 5.S5 Fig. 5.S5.1; one-tailed test with t statistics of regression coefficients). In these treatments, *Tisbe* spp. ingested between 1 % and 36 % of their body carbon content per day (Fig. 5.1). All experimentally derived grazing rates were below the curve of maximum potential ingestion rates, calculated for the respective range of grazer carbon content using an allometric equation (Moloney and Field 1989); only for the highest experimental value, the confidence interval overlapped with the curve (Fig. 5.1 A). The total grazing rate was not significantly influenced by protist composition (one-way ANOVA), but there was a significant positive monotonic relationship between total grazing rate and initial total protist biomass (one-tailed Spearman rank correlation test, correlation coefficient 0.69). Furthermore, there was a significant linear relationship (F statistics) between grazing rate I [$\%\,\mathrm{d}^{-1}$] and initial total protist biomass P_p [$\mathrm{mg\,L}^{-1}$] (functional response) with a significantly positive slope and a non-significant offset (t statistics two-tailed) (Fig. 5.1 B):

$$I = -1.533 + 1.917 P_p \quad (\mathrm{R}^2 = 0.92, p < 0.05) \ . \tag{5.2}$$

Taxon-specific grazing rates (Supplement 5.S5 Fig. 5.S5.2) were highly variable within each protist taxon. They did not differ significantly among the taxa, nor were they significantly influenced by protist biomass composition (2-way ANOVA). A significant positive monotonic relationship with the biomass of the respective taxon was detected only for *Thalassiosira bioculata* (one-tailed Spearman rank correlation test; correlation coefficient 1.0).

Feeding selectivity, measured by Chesson's electivity index (Fig. 5.2), was significantly different between the various protist taxa, but was not significantly influenced by protist composition (two-way ANOVA). Furthermore, there was no significant monotonic relationship between the electivity index and the initial abundance or biomass of the respective taxon for any of the protist taxa (two-tailed Spearman rank correlation tests). *Tisbe* spp. positively selected the big centric diatom *Thalassiosira angulata* and the pennate diatom *Pseudonitzschia* cf. *seriata*, while negatively selecting cyanobacteria, big flagellates, indetermined pennate diatoms and ciliates (Fig. 5.2).

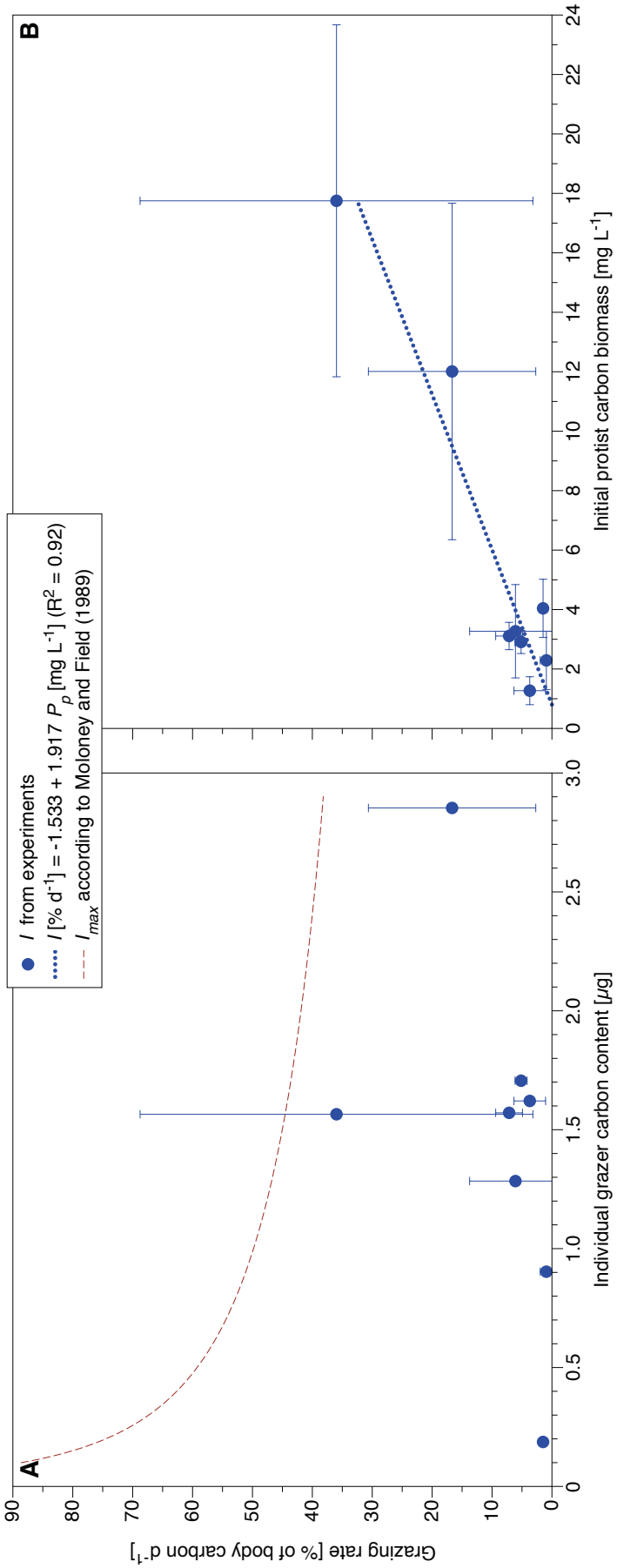

Figure 5.1: Experimentally derived carbon-based grazing rates of *Tisbe* spp. plottet against **A** the individual grazer carbon content and **B** the initial protist carbon biomass in the respective treatment (blue dots). Grazer carbon contents are means of triplicate grazer setups (inaccuracy estimated to be at least 10 %). Both grazing rate and initial protist biomass were estimated from linear regressions. Error bars show the 95 % confidence intervals of the regression coefficients. Only significantly positive grazing rates are shown (one-tailed test with *t* statistics of regression coefficients). For comparison, the maximum potential ingestion rate I_{max}, calculated from an allometric equation (Moloney and Field 1989), is shown as a dashed red curve (A). The dotted blue line (B) shows a linear regression of experimentally derived grazing rates on the initial carbon biomass (functional response) used for calculation of the grazing impact.

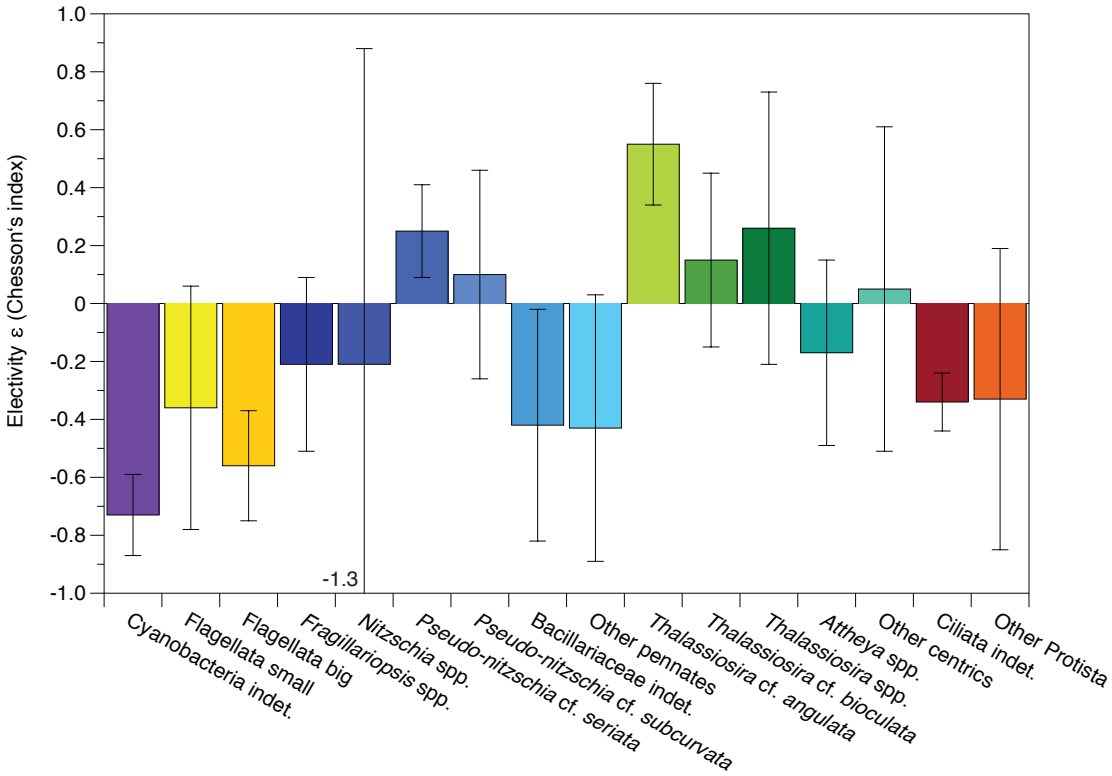

Figure 5.2: Grazing selectivity of *Tisbe* spp. from the electivity index ε (Chesson 1983) for each protist taxon (mean from 13 treatments, error bars denote standard deviations). Only the range from -1.0 to +1.0 is shown, minima of error bars beyond this range are displayed as numbers.

5.4.4 Predation rates of Arctic and Antarctic sympagic meiofauna

Predation rates varied notably over time within each setup, but no consistent trend or systematic temporal change was observed for any combination of predator and prey taxa (Supplement 5.S6 Fig. 5.S6.1 and 5.S6.2).

For *Sympagohydra tuuli* preying on ciliates and for Antarctic white acoels preying on ciliates, calculated predation rates exhibited an extreme scatter around zero and were often extremely negative (Supplement 5.S6 Fig. 5.S6.1, 5.S6.3 and 5.S6.4). Some distinctly negative values occured also in *Euplokamis* sp. preying on acoels or ciliates, in *S. tuuli* preying on rotifers or nauplii and in Arctic red acoels preying on ciliates (Supplement 5.S6 Fig. 5.S6.1–5.S6.4 and 5.S6.6–5.S6.7). Apart from counting errors, these negative values could be caused either by higher prey losses in prey-only setups than in predator setups, or by (faster) prey reproduction in predator setups.

For *Sympagohydra tuuli* preying on copepod nauplii, calculated predation rates distinctly decreased with both predator and prey biomass (Supplement 5.S6 Fig. 5.S6.7).

The relationship was well described by a two-dimensional linear function:

$$I = 241.836 - 1.06136 B_{py} - 0.114801 B_{pd} \quad (\mathrm{R}^2 = 0.73,\ p < 0.05)\ , \tag{5.3}$$

where I is the carbon-based ingestion rate [$\%\,\mathrm{d}^{-1}$] and B_{py} and B_{pd} are the biomass [$\mu\mathrm{g\,L}^{-1}$] of prey and predator, respectively. The fit was significant (F statistics), and all coefficients were significantly different from zero (t statistics).

For *Halectinosoma* spp. preying on ciliates, predation rates likewise decreased with predator biomass, while an influence of prey biomass was not obvious (Fig. 5.3). The relationship could be approximated by a two-dimensional power function according to Peters (1994) fitted to the data:

$$I_{ab} = V_{py}^{-0.344} \cdot V_{pd}^{-0.121} \cdot A_{py}^{-1.750} \cdot A_{pd}^{-0.366} \cdot 10^{0.033T} \cdot 10^{3.602} - 0.1 \quad \begin{array}{l}(\mathrm{R}^2 = 0.482,\ p < 0.05 \\ \text{for linear regression on} \\ \text{log-transformed data})\ ,\end{array} \tag{5.4}$$

where I_{ab} is the abundance-based ingestion rate [h^{-1}], V_{py} and V_{pd} are the body volumes [$\mu\mathrm{m}^3$] of prey and predator, respectively, A_{py} and A_{pd} are the abundance [mL^{-1}] of prey and predator, respectively, and T is the temperature (0 °C in this case). The fit was significant (F statistics), and the regression coefficients for offset, prey and predator abundance were significantly different from zero, while the coefficient for predator volume was not.

No trend in predation rates with predator or prey biomass could be identified for the following predator-prey combinations: *Sympagohydra tuuli* preying on ciliates, Antarctic white acoels preying on ciliates, *S. tuuli* preying on rotifers, *Euplokamis* sp. preying on acoels, copepodids of *Tisbe* spp. preying on nauplii of the same species (Supplement 5.S6 Fig. 5.S6.3, 5.S6.4, 5.S6.6 and 5.S6.8). This was due to large scatter and, partly, too few data points or many negative values. Since no significant clusters in predator and prey biomass could be identified (SIMPROF), one average predation rate was calculated for each of these predator-prey combinations. Only in case of *Tisbe* spp., the predation rate was significantly positive (average 13 $\%\,\mathrm{d}^{-1}$).

Identification of a trend in predation rates with prey or predator biomass was likewise impossible for the following predator-prey combinations: *Euplokamis* sp. preying on ciliates, Arctic red acoels preying on ciliates, indetermined Arctic harpacticoids preying on ciliates, *Euplokamis* sp. preying on copepods (nauplii, copepodids of harpacticoids and copepodids of the calanoid *Stephos longipes* in separate treatments merged for analyses) (Supplement 5.S6 Fig. 5.S6.3–5.S6.5 and 5.S6.8). Again, this was due to large scatter and as no sufficient range of predator or prey biomass concentrations was covered. For each of these predator-prey combinations, average predation rates were calculated for two or three

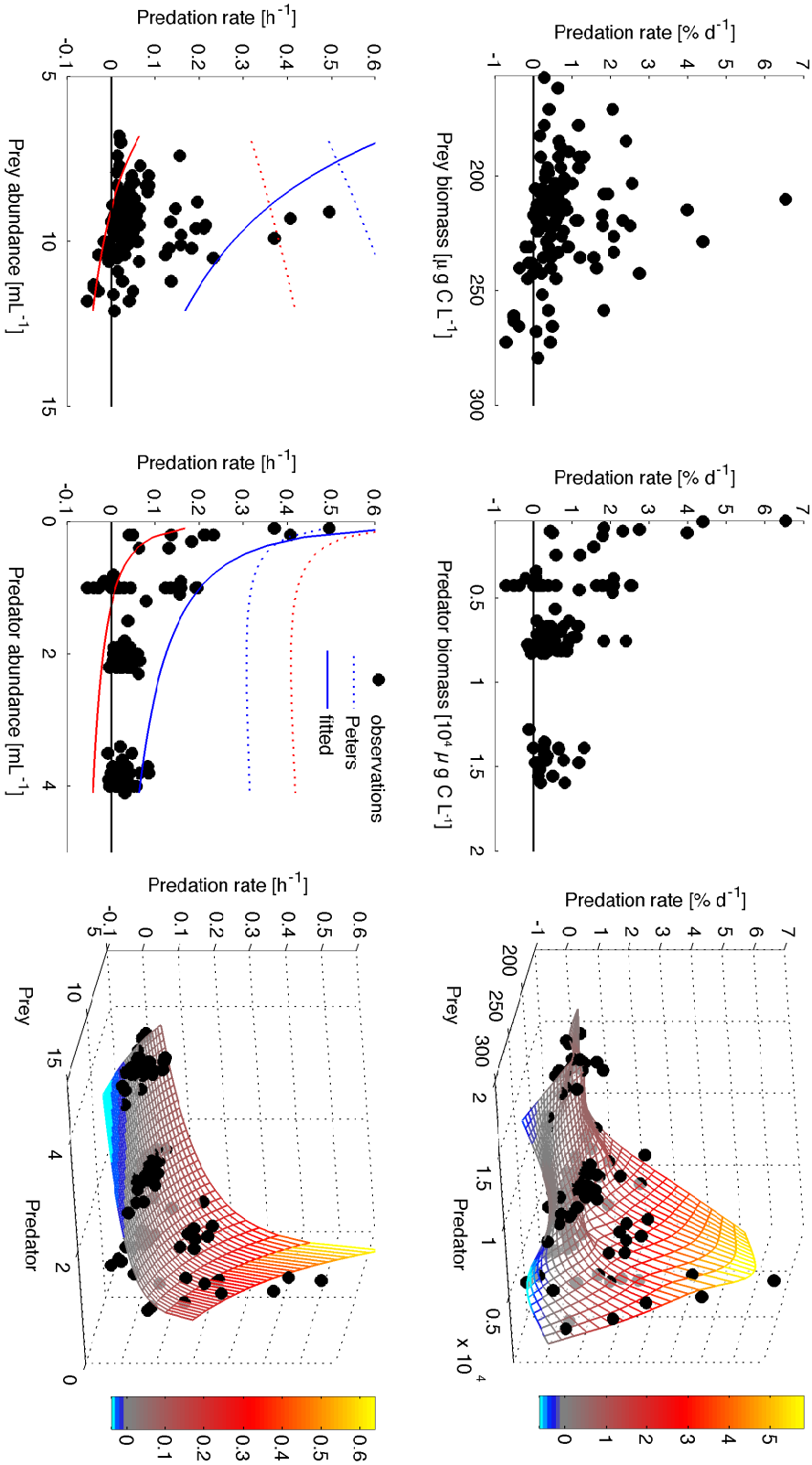

Figure 5.3: Top Carbon-based predation rates of the Arctic harpacticoids *Halectinosoma* spp. preying on ciliates, plotted against prey biomass (left), predator biomass (middle) and both prey and predator biomass (right). The mesh in the 3D plot was interpolated using the Matlab gridfit routine (release 2.0, May 23, 2006). **Bottom** Individual-based predation rates of *Halectinosoma* spp. preying on ciliates, plotted against prey abundance (left), predator abundance (middle) and both prey and predator abundance (right). The surface in the 3D plot shows the fitted Peters model (Eq. 5.4). The blue and red lines in the 2D plots show the upper and lower border of the surface within the data range; dotted lines illustrate the original model with the parameters suggested by Peters (1994).

significant clusters of predator and prey biomass (Table 5.6). For Arctic red acoels preying on ciliates, predation rates were significantly positive for high prey and low predator biomass, while for low prey or high predator biomass they were not significantly positive. For the indetermined harpacticoids preying on ciliates, predation rates were significantly positive for low, but not for intermediate or high prey biomass, irrespective of predator biomass. For *Euplokamis* sp. preying on ciliates, predation rates were significantly positive for high, but not for low prey biomass. For *Euplokamis* sp. preying on copepods, predation rates were significantly positive for low, but not for high predator biomass.

Table 5.6: Predation rates for predator-prey combinations where significant clusters of predator and prey biomass could be distinguished. B_{pd} = predator biomass range, B_{py} = prey biomass range, I = predation rate (average; marked with $\star$ if significantly positive, t-test, significance level 5 %), n = number of measurements.

Predator—prey	Cluster	B_{pd} [μg L^{-1}]	B_{py} [μg L^{-1}]	I [% d^{-1}]	n
Acoela red—Ciliata	A	0.156–0.874	0.018–0.095	-0.11	27
	B	0.165–1.048	0.141–0.219	2.46 $\star$	44
	C	3.464–4.619	0.173–0.189	0.18	3
Harpacticoida—Ciliata	A	2.278–3.579	0.389–0.656	0.83 $\star$	30
	B	1.365–2.276	0.668–0.786	0.46	15
	C	2.440	5.535	0.34	1
Euplokamis sp.—Ciliata	A	0.085–0.128	0.196–0.204	-20.34	2
	B	0.255–0.340	0.204–0.247	15.18	2
	C	0.255–0.340	0.436–0.611	12.99 $\star$	20
Euplokamis sp.—Copepoda	A	0.255	0.141–0.473	191.22 $\star$	9
	B	0.340	0.690–1.666	503.59	6

Predation rates were generally enveloped by the curve of maximum potential ingestion rates (Moloney and Field 1989; Fig. 5.4). However, for predators with very low individual carbon content (*Euplokamis* sp. and white acoels), measured predation rates partly exceeded the calculated maximum potential ingestion rates. For predators with very high individual carbon content, in contrast (big harpacticoids and red acoels), measured predation rates were substantially lower than calculated maximum potential ingestion rates.

5.4.5 Feeding impact

In situ ingestion rates were determined according to experimentally derived equations (Table 5.7) and, for comparison, as maximum potential ingestion rates from an allometric equation (Moloney and Field 1989). The rectilinear functional response for calculation of grazing rates (Table 5.7) is based on Eq. 5.2 in combination with the assumptions that grazing rates are zero at low algal concentrations (below the x intercept of the linear function) and constant at I_{max} for high algal concentrations (beyond the intercept of the linear function with I_{max}). Since the grazing experiments did not allow deduction of competition, grazer biomass was not included in the equation. For predation, different equations were applied to different predator-prey combinations (Table 5.7). In two cases, predation rates could be calculated using fitted functions (Eqs. 5.3 and 5.4) describing both functional response and competition. Predation rates were set to zero when the fitted

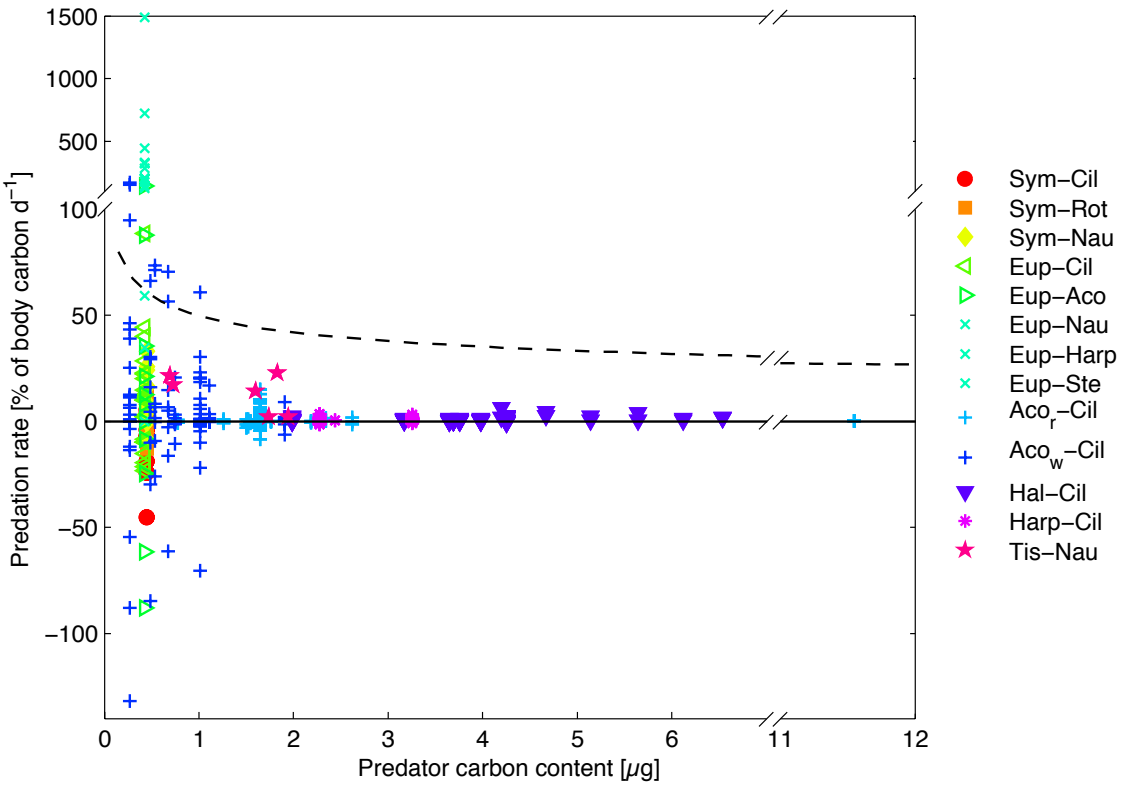

Figure 5.4: Experimentally derived carbon-based predation rates plottet against the median individual predator carbon content in the respective setup. For comparison, the maximum potential ingestion rate I_{max}, calculated from an allometric equation (Moloney and Field 1989), is shown as a dashed curve.

functions returned negative values and set to the maximum measured if the fitted functions exceeded this value. In other cases, based on Table 5.6 and the text above, predation rates were assumed to be constant over certain ranges of predator and prey biomass; predation rates were assumed to be zero if the average predation rate within the respective range was not significantly positive (t test). In case of white acoels, predation rates were not assumed to be zero (as suggested by the experiments) but the equation for red acoels was applied, since feeding of white acoels on ciliates had actually been observed. For temperature correction we assumed a Q_{10} value of 2 with exception of the equation derived from Eq. 5.4, where a Q_{10} of 1.16 is inherent to the original model (Peters 1994).

Experimentally derived community grazing / predation rates and grazing / predation impact (in the following termed ingestion rates and feeding impact when referring to both grazing and predation) showed some differences (U-test) between the expeditions (Fig. 5.5), which may be regional and / or seasonal. Within the Arctic, community ingestion rates and feeding impact did not differ significantly between the Central Arctic (summer) and the Canadian Arctic (spring), irrespective of the food type. Within the

Table 5.7: Equations for calculation of carbon-based grazing and predation rates I [$\%\,\mathrm{d}^{-1}$] from algae biomass B_{alg} [$\mathrm{mg\,L^{-1}}$], prey biomass B_{py} [$\mu\mathrm{g\,L^{-1}}$] or prey abundance A_{py} [$\mathrm{mL^{-1}}$], predator biomass B_{pd} [$\mu\mathrm{g\,L^{-1}}$] or predator abundance A_{pd} [$\mathrm{mL^{-1}}$], prey body volume V_{py} [$\mu\mathrm{m}^3$] and carbon content C_{py} [$\mu\mathrm{g}$] and predator body volume V_{pd} [$\mu\mathrm{m}^3$] and carbon content C_{pd} [$\mu\mathrm{g}$]. All variables were determined for each meiofauna taxon and ice-core section separately, except for body volumes, were medians of the respective taxon and expedition were used. Since our experiments did not allow conclusions on interspecific competition, we used B_{pd} and A_{pd} of the respective predator taxon, not total meiofauna.

Food / Prey	**Grazer / Predator**	**Ingestion rate** [$\%\,\mathrm{d}^{-1}$]	**Determined for pred—prey**
Algae	All protozoan and metazoan meiofauna	$I = \begin{cases} 0 \quad \text{for } B_{alg} < \frac{1.533}{1.917} \\ I_{max} \quad \text{for } B_{alg} > \frac{I_{max} \cdot exp(-0.0693T)+1.533}{1.917} \\ (-1.533 + 1.917 B_{alg}) \cdot exp(0.0693T) \quad \text{otherwise} \end{cases}$	*Tisbe* spp.— mixed protists
Ciliata	Cnidaria	$I = 0$	*Sympagohydra tuuli*— Ciliata
Ciliata	Ctenophora	$I = \begin{cases} 0 \quad \text{for } B_{py} \leq 0.43 \\ 12.99 \cdot exp(0.0693T) \quad \text{for } B_{py} > 0.43 \end{cases}$	*Euplokamis* sp.— Ciliata
Ciliata	Nematoda, Plathelminthes, Nemertea, Gastropoda	$I = \begin{cases} 0 \quad \text{for } B_{py} \leq 0.14 \text{ or } B_{pd} \geq 1.05 \\ 2.46 \cdot exp(0.0693T) \quad \text{for } B_{py} > 0.14 \text{ and } B_{pd} < 1.05 \end{cases}$	Acoela red— Ciliata
Ciliata	*Halectinosoma* spp. (all regions), other Harpacticoida (Antarctic, Central Arctic), Cyclopoida, Calanoida, Amphipoda	$I = \begin{cases} 0 \quad \text{for } V_{py}^{-0.344} \cdot V_{pd}^{-0.121} \cdot A_{py}^{-1.750} \cdot A_{pd}^{-0.366} \cdot 10^{0.033T} \cdot 10^{3.602} < 0.1 \\ 0.5 \cdot \frac{C_{py}}{C_{pd}} \cdot 2400 \quad \text{for } V_{py}^{-0.344} \cdot V_{pd}^{-0.121} \cdot A_{py}^{-1.750} \cdot A_{pd}^{-0.366} \cdot 10^{0.033T} \cdot 10^{3.602} > 0.6 \\ (V_{py}^{-0.344} \cdot V_{pd}^{-0.121} \cdot A_{py}^{-1.750} \cdot A_{pd}^{-0.366} \cdot 10^{0.033T} \cdot 10^{3.602} - 0.1) \cdot \frac{C_{py}}{C_{pd}} \cdot 2400 \quad \text{otherwise} \end{cases}$	*Halectinosoma* spp.— Ciliata
Ciliata	Harpacticoida (Canadian Arctic, except for *Halectinosoma* spp.)	$I = \begin{cases} 0.83 \cdot exp(0.0693T) \quad \text{for } B_{py} < 0.66 \\ 0 \quad \text{for } B_{py} \geq 0.66 \end{cases}$	Harpacticoida (CFL)— Ciliata
Ciliata	Other meiofauna	$I = 0$	No experiments
Acoela	Ctenophora	$I = 0$	*Euplokamis* sp.— Acoela white
Acoela	Other meiofauna	$I = 0$	No experiments
Rotifera	Cnidaria	$I = 0$	*Sympagohydra tuuli*— Rotifera
Rotifera	Other meiofauna	$I = 0$	No experiments
Nauplii	Cnidaria	$I = \begin{cases} 0 \quad \text{for } 1.06B_{py} + 0.11B_{pd} > 241.84 \\ 33.18 \quad \text{for } 1.06B_{py} + 0.11B_{pd} < 275.02 \\ (241.84 - 1.06B_{py} - 0.11B_{pd}) \cdot exp(0.0693T) \quad \text{otherwise} \end{cases}$	*Sympagohydra tuuli*— Nauplii
Nauplii	*Tisbe* spp., other Harpacticoida (Canadian Arctic, except for *Halectinosoma* spp.)	$I = 13.34 \cdot exp(0.0693T)$	*Tisbe* spp. Copepodides— Nauplii
Copepoda	Ctenophora	$I = \begin{cases} 191.22 \cdot exp(0.0693T) \quad \text{for } B_{pd} < 0.26 \\ 0 \quad \text{for } B_{pd} \geq 0.26 \end{cases}$	*Euplokamis* sp.— Copepoda
Copepoda	*Themisto libellula*	$I = 1.93 \cdot exp(0.0693T)$	*Themisto libellula*— *Calanus* spp. (Auel and Werner 2003)
Copepoda	Other meiofauna	$I = 0$	No experiments
Other meiofauna	All protozoan and metazoan meiofauna	$I = 0$	No experiments

Antarctic, community ingestion rates and feeding impact on ice algae and ciliates were significantly higher in the western Weddell Sea (winter) than in the southern Indian Ocean (winter), but no significant differences were found for predation on copepods.

Comparing Arctic to Antarctic regions, community grazing rates were significantly higher in the Canadian Arctic than in the southern Indian Ocean, but the grazing impact did not differ significantly between any of the Arctic versus Antarctic regions. It never

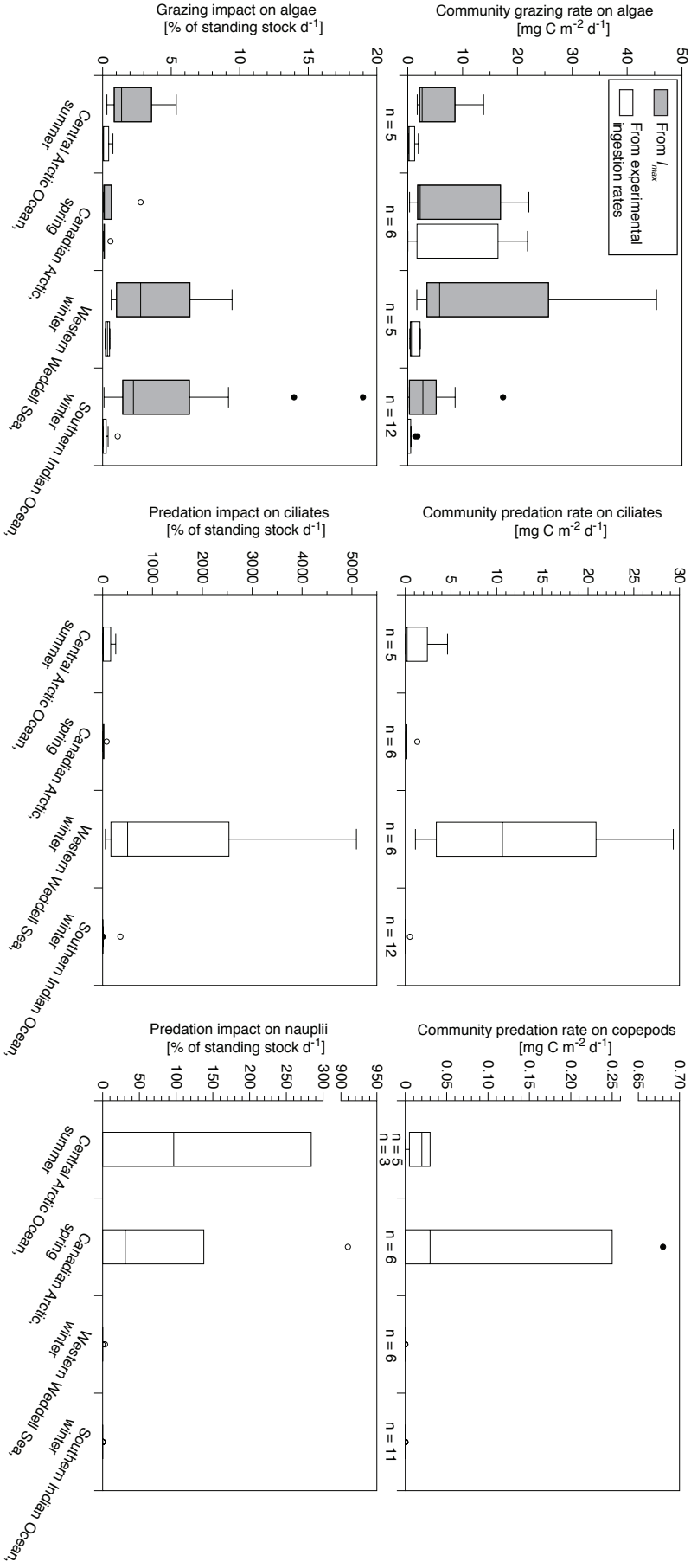

Figure 5.5: Areal ingestion rate (top) of sympagic meiofauna communities and feeding impact on the standing stock of food organisms (bottom) for ice algae (left), sympagic ciliates (middle) and sympagic copepods (right) as food organisms, based on data from four expeditions (different regions and seasons) and experimentally-derived equations (Table 5.7, white boxes). Grazing rates were also calculated as I_{max} from an allometric equation (Moloney and Field 1989, grey boxes). Boxplots show medians, quartiles (boxes), ranges (whiskers), outliers (filled circles) and extreme outliers (open circles).

exceeded 2 % of the ice-algae standing stock per day (Fig. 5.5, left panel). Community predation rates and predation impact on ciliates (Fig. 5.5, middle panel) were significantly higher in the western Weddell Sea than in the Central and Canadian Arctic. The predation impact in the western Weddell Sea often exceeded 500 % of the ciliate standing stock per day (20 % per hour) with extremes above 5000 % per day (200 % per hour). In the other regions, extremes were still as high as 80–350 % of the standing stock per day (3–15 % per hour) at some stations. Community predation rates and predation impact on copepods in both Arctic regions were significantly higher than in the southern Indian Ocean. The predation impact in the Arctic sometimes exceeded 10 % of the copepod standing stock per day, while in the Antarctic it was always below 1 % per day. Assuming only nauplii were ingested, the predation impact on the nauplii standing stock in the Canadian and Central Arctic could exceed 280 % and 900 % per day (11 % and 37 % per hour), respectively (Fig. 5.5, right panel).

Experimentally derived community grazing rates were significantly lower (U-test) than estimates based on calculated maximum potential ingestion rates, with exception of the Canadian Arctic in spring, where ice-algae biomass was high and feeding close to satiation (Fig. 5.5, left panel). The experimentally derived grazing impact was significantly lower in all regions than estimates from maximum potential ingestion rates, the difference being one order of magnitude.

5.5 Discussion

5.5.1 Predation and flexible feeding strategies in sea ice

Our study gives evidence of cilivorous and carnivorous feeding in several Arctic and Antarctic sympagic meiofauna taxa. It is the first experimental study investigating both grazing and predation of various sympagic metazoan meiofauna taxa from both polar regions. Previously, only grazing rates of the Antarctic sympagic calanoids *Paralabidocera antarctica* (Swadling et al. 1997b) and *Stephos longipes* (Schnack-Schiel et al. 1995, Swadling et al. 1997b) were measured in experiments, and predation was investigated only qualitatively in a recent study on the Arctic sympagic cnidarian *Sympagohydra tuuli* (Siebert et al. 2009). Other experimental feeding studies focused on sympagic protozoans (Caron and Gast 2010). Our study confirms the findings by Kramer et al. (under revision), who deduced from stable isotope and fatty acid data that carnivorous feeding of sympagic metazoan meiofauna *in situ* is rather common and that the sympagic food web is therefore more complex than generally assumed. In particular, our experiments confirm the existence of top predators amongst both Arctic and Antarctic sympagic meiofauna (the

cnidarian *S. tuuli* and the ctenophore *Euplokamis* sp., respectively), as suggested in recent papers (Bluhm et al. 2007, Piraino et al. 2008, Siebert et al. 2009, Kramer et al. in press, Kramer et al. under revision).

Furthermore, our study shows that sympagic meiofauna can exploit several different food sources: Arctic harpacticoids and Antarctic acoels feed on both algae and ciliates, some Arctic harpacticoids additionally feed cannibalistically on their own nauplii, the cnidarian *Sympagohydra tuuli* preys on nauplii as well as on rotifers and polychaete larvae, and the ctenophore *Euplokamis* sp. preys on ciliates in addition to nauplii and copepodids of different taxa. In grazing experiments, the Arctic harpacticoid *Tisbe* spp. ingested various protist taxa, the grazing being independent of protist composition; selectivity was not very pronounced and observed only for few protist taxa. Also in these respects our observations support a recent study suggesting that omnivorous feeding and flexible feeding strategies are common in sympagic meiofauna (Kramer et al. under revision). Similar observations of omnivory and flexibility have been reported for various sympagic protozoans (Caron and Gast 2010) and for the under-ice amphipods *Onisimus* spp. and *Gammarus wilkitzkii* (Werner and Auel 2005).

This view of flexible feeding strategies is further supported by the temporal variability in predation rates, as observed directly in experiments and suggested by the fluctuations of predation rates over time. Sympagic meiofauna appears to often feed in pulses, followed by periods of starvation. This seems to be particularly pronounced in *Sympagohydra tuuli*, *Euplokamis* sp. and Antarctic white acoels. In planktonic copepods, high ingestion rates following starvation periods have been interpreted as strategies attributed to predator avoidance (Tiselius 1998). This explanation is unlikely at least for the sympagic top predators *S. tuuli* and *Euplokamis* sp., but it supports the view that pulse feeding might be a strategy enhancing flexibility.

Since most sympagic meiofauna taxa apparently do not depend on ice algae as food source, they can survive also periods of low ice-algae production by switching to alternative diets, as previously reported for the under-ice amphipods *Onisimus glacialis* and *Gammarus wilkitzkii* (Werner and Auel 2005). During these periods, bacterial production probably becomes the most important base of the food web due to bacterivorous feeding of ciliates and some meiofauna (Kramer et al. under revision), which in turn are preyed on by other meiofauna. Furthermore, the ability of meiofauna to utilise different food sources enables them to live in a habitat with patchy distribution of algae and prey organisms and with high temporal fluctuations, both of which are typical for sea ice (Eicken 1992, Swadling et al. 1997a). Also the habit to feed in pulses followed by starvation periods can be advantageous in this respect, as previously proposed for the under-ice am-

phipod *Gammarus wilkitzkii* (Werner et al. 2002). The observed feeding strategies are thus probably adaptations to the sea-ice habitat (Kramer et al. under revision) and hence natural consequences of selection.

5.5.2 Factors influencing ingestion rates: functional response, competition, size and taxa

Grazing rates of the harpacticoids *Tisbe* spp. are influenced by food biomass, and the relationship can be described by a rectilinear functional response, as previously proposed for various grazers (Frost 1972, Rothhaupt 1990). Since the offset in the linear function was not significant, it is uncertain whether there is a threshold food concentration below which the animals do not graze. Such a threshold, possibly related to a switch to ciliate or animal prey, might be an important factor, constraining the grazing impact and preventing the ice-algae stock from exhaustion (Strom et al. 2000). Previous grazing experiments with the Antarctic sympagic calanoid *Stephos longipes* did not indicate a functional response nor a threshold food concentration (Schnack-Schiel et al. 1995), which suggests differences in grazing behaviour between these taxa. However, due to different methods, that study is not directly comparable to ours. Additional grazing experiments with various meiofauna taxa are thus required to investigate these issues.

For predation rates, the influence of prey density was less evident. For the ctenophore *Euplokamis* sp. or red acoels preying on ciliates, predation rates were significantly positive only at high prey biomass, suggesting there might be a functional response which was not evident in our data because of large scatter and because it was possibly concealed by other factors. For other predator-prey combinations, an opposite effect was observed, i. e. a significant decrease in predation rates with prey density (for the harpacticoids *Halectinosoma* spp. preying on ciliates and the cnidarian *Sympagohydra tuuli* preying on nauplii) or significantly positive predation rates only at low prey biomass (for indetermined harpacticoids preying on ciliates). This observation should not be seen as an evidence of decreasing food uptake by predators with prey density, but rather as an indicator of intraguild predation amongst the prey organisms (Lonsdale et al. 1979, Wu et al. 2010). This intraguild predation might be more pronounced in prey-only setups than in predator setups due to predator avoidance strategies of the ciliates (Lima 1998, Jakobsen 2002) and thus cause the observed density effect. Besides, it might also be an artifact, caused by a too narrow range of prey densities.

The influence of predator density on predation rates was more evident, suggesting that predation rates are more strongly influenced by predator than by prey density: for both *Halectinosoma* spp. preying on ciliates and *Sympagohydra tuuli* preying on nauplii, preda-

tion rates showed a significant decrease with predator density, and for red acoels preying on ciliates as well as for *Euplokamis* sp. preying on copepods predation rates were significantly positive only at low predator density. This relationship can indicate intraspecific competition. Although intraspecific competition is part of ecological theory (Begon et al. 2006), it is rarely observed in experiments, therefore generally considered to occur only at extremely high densities beyond the natural range (Fussmann et al. 2005) and not often included in models (Skalski and Gilliam 2001). In the sea-ice habitat, however, meiofauna densities in the brine channels are subject to fluctuating temperatures (which controle the brine volume fraction) and can temporarily be extremely high (Table 5.3), which might cause intraspecific and possibly also interspecific competition. Such competition might be an important factor constraining the feeding impact at high meiofauna densities. On the other hand, the brine channel geometry might enable meiofauna predators to avoid each other (Krembs et al. 2000) and thus reduce the effect of competition.

Besides food and grazer / predator density, also the size of both grazer / predator and food particles / prey can influence the ingestion rate (Hansen et al. 1994, 1997). In grazing experiments with *Tisbe* spp., such a relationship was not obvious. As measured grazing rates usually remained significantly below the size-dependent maximum potential ingestion rates I_{max} according to Moloney and Field (1989), the respective equation was neither confirmed nor contradicted. In predation experiments with *Halectinosoma* spp. preying on ciliates, the decrease of ingestion rates with predator size suggested by the fit of the Peters model was not significant, probably due to the insufficient range in predator size. Possibly because of this insufficient range a relationship between predation rate and predator size was not obvious for any other predator-prey combination, either. Viewing all predation experiments with different predator-prey combinations (Fig. 5.4), a decrease of predation rates with predator carbon content was indicated by the data. At low predator carbon content, the highest measured predation rates distinctly exceeded I_{max}, while at high predator carbon content all measured predation rates were far below I_{max}. This observation indicates that the slope of I_{max} for predation rates might be steeper than suggested by Moloney and Field (1989), provided the measured predation rates were maximum rates, as expected due to the high prey densities applied. In some treatments, however, high predator densities may have prevented in some cases that maximum rates were reached. The influence of food particle / prey size was not studied in any of the experiments.

As obvious from the above discussion, ingestion rates and functional relationships with grazer / predator and food density differed amongst grazer / predator taxa. This might indicate that different meiofauna taxa apply different capture strategies, as known from

planktonic copepods (Tiselius and Jonsson 1990), which could contribute in shaping different ecological niches in spite of the generally observed omnivory. This may be an important factor in sustaining high meiofauna diversity in sea ice. Furthermore, also the food type influenced ingestion rates and functional relationships, indicating different capture strategies for different food types, as previously reported from the under-ice amphipod *Gammarus wilkitzkii* (Werner et al. 2002) and a planktonic copepod (Kiørboe et al. 1996). Variable capture strategies are again an example of the flexibility of sympagic meiofauna in terms of feeding.

5.5.3 Low grazing and high predation impact

For the first time we were able to give estimates of both grazing and predation impact based on experimental ingestion rates, including the influence of grazer / predator and algae / prey density. Previous studies (Gradinger 1999a, Gradinger et al. 1999, Nozais et al. 2001, Michel et al. 2002, Gradinger et al. 2005) calculated the grazing impact of sympagic meiofauna exclusively from allometric equations accounting only for the influence of grazer carbon content (Moloney and Field 1989). Two grazing studies with Antarctic calanoid copepods (Schnack-Schiel et al. 1995, Swadling et al. 1997b) do not provide estimates of the grazing impact on ice algae.

According to our data, the grazing impact on the ice-algae standing stock was extremely low in all regions and during all seasons studied. Since the grazing impact calculated from experimental grazing rates was by about one order of magnitude lower than estimates applying allometric equations (Moloney and Field 1989), previous studies using this method (Gradinger 1999a, Gradinger et al. 1999, Nozais et al. 2001, Michel et al. 2002, Gradinger et al. 2005) have substantially overestimated the grazing impact of sympagic meiofauna.

In contrast, the predation impact on the ciliate standing stock was often extremely high: our data suggests that in some cases the ciliate standing stock could be grazed down completely within a few hours or even less than one hour, if predation rates were not restricted. The predation impact on ciliates was highly variable with no obvious seasonal or regional differences, but the highest impact was determined for the western Weddell Sea in winter. The estimated predation impact on the copepod standing stock was extremely low for the Antarctic in winter, of the same order of magnitude as the grazing impact, whereas it was notably higher in the Arctic in spring and summer. When related to the nauplii standing stock only, the predation impact in the Arctic was considerably higher, of the same order of magnitude as the impact on ciliates, suggesting that the standing stock of nauplii could be preyed down completely within a few hours in the absence of constraining factors.

The predation impact on both ciliates and copepods may—at least temporarily or locally—be even higher than we estimated, since even more taxa might feed on ciliates and copepods than we assumed in our calculations. Additionally, also other meiofauna taxa than ciliates and copepods may be preyed on, e. g. rotifers (Siebert et al. 2009). On the other hand, the brine channel geometry might reduce the predation impact, since small meiofauna prey can probably better avoid predators in the brine channels than in the experimental vials (Krembs et al. 2000). Furthermore, most meiofauna taxa are likely to cover part of their energy demand by grazing on algae at least during times of high ice-algae standing stocks, which probably also lowers the predation impact. We thus hypothesise that the actual predation impact can be particularly high during autumn and winter, when the ice-algae standing stock is low. However, meiofauna predators probably can alter the meiofauna community structure on the small scale throughout the year, given the temporal variability of predation rates observed in experiments and the patchy distribution of sympagic meiofauna in the ice (Swadling et al. 1997a).

We conclude that grazing activity by sympagic meiofauna is generally unlikely to restrict the accumulation of ice algae or to limit the availability of ice algae to under-ice and sub-ice grazers. Predation activity by meiofauna, in contrast, can substantially influence the meiofauna community composition. Furthermore, it is probable that carnivorous meiofauna compete with under-ice and sub-ice predators, such as carnivorous amphipods (Werner et al. 2002, Auel and Werner 2003) and krill (Wickham and Berninger 2007), for prey organisms. Carnivorous and omnivorous meiofauna is thus likely to influence the quantity and quality of cryo-pelagic coupling through predation activity within the ice. Carnivorous feeding by sympagic meiofauna should therefore explicitely be included in future investigations and theoretical considerations concerning the role of sea ice in polar marine ecosystems.

5.5.4 Potential of feeding experiments and modelling in sympagic meiofauna studies

The methods we applied in grazing and predation experiments proved well feasible for meiofauna, and future studies using similar methods can help to resolve some of the issues that still remained unclear in this study. The influence of grazer / predator and food particle / prey sizes on ingestion rates should be investigated and the respective parameters better constrained by applying a wide range of grazer / predator and food particle / prey sizes. Likewise, functional response and competition should be further investigated by applying a wide range of grazer / predator and protist / prey densities. Since ingestion rates are likely to be influenced by the geometry of the brine channel system, future studies

should also aim to mimic this geometry following the approach by Krembs et al. (2000) or to assess ingestion rates *in situ* as described for benthic meiofauna by Decho (1988).

Extended modelling effort is required to better describe and understand the response of ingestion rates to grazer / predator and protist / prey density and size. We used the model by Peters (1994) for the harpacticoids *Halectinosoma* spp. preying on ciliates. Mechanistic models including predator density (Jost 2000) are based on additional assumptions about the underlying predation process and fitting these models would have been beyond the scope of this work. Both the function fitted to our data and the original model (Peters 1994) estimated a similar effect of the predator density on predation rates, indicating that the model describes the intraspecific predator behaviour in sea ice pretty well. The influence of prey density, in contrast, differed substantially (in magnitude and sign) compared to the original model. This model was derived predominantly from ingestion rates of zooplankton feeding on algae and bacteria, and thus does not take into account effects of intraguild predation. Development of a new model specifically for sympagic meiofauna, including intraguild predation besides competition and functional response, is therefore desirable.

5.6 Acknowledgements

We first of all thank Iris Werner (Institute for Polar Ecology IPÖ, University of Kiel, Germany) for her constant support during all phases of this study, including constructive comments on the manuscript. Great thanks are also due to Rainer Kiko (IFM-GEOMAR, Kiel, Germany) for excellent collaboration and great support in the field and lab during ANT–XXIII / 7 and ARK–XXII / 2. We further thank Markus Pahlow (IFM-GEOMAR), Dieter Piepenburg (IPÖ) and Wolfgang Ebenhöh (Institute for Chemistry and Biology of the Marine Environment ICBM, University of Oldenburg, Germany) for advice concerning data evaluation, statistics and modelling. Miriam Marquardt, Verena Lieb, Claudia Wittwer and Christin Kleinelanghorst (IPÖ) are thanked for conducting the protist counts in grazing experiments and the carbon content assessment of sympagic meiofauna and algae. We also thank our colleagues for kindly providing unpublished data, particularly Gauthier Carnat (Centre for Earth Observation Science, University of Manitoba, Winnipeg, Canada), Bruno Delille and Nicolas-Xavier Geilfus (Chemical Oceanography Unit, University of Liège, Belgium), Guisheng Song (Institut des sciences de la mer de Rimouski ISMER, University of Quebec at Rimouski, Canada) and Thomas Brown (University of Plymouth, UK) for temperature and salinity data from CFL as well as Benoit Philippe, Christopher John Mundy and Michel Gosselin (ISMER) for chl *a* data from CFL.

5.7 Role of the funding source

This research was supported by the Deutsche Forschungsgesellschaft WE 2536 / 11–1,–2 (to MK) and by the Kiel Cluster of Excellence "The Future Ocean" (to FP). The funding sources had no involvement in study design, data collection, analysis and interpretation, writing of the report or the decision to submit the paper for publication.

5.S Supplementary material

5.S1 Details on the determination of grazing rates

The carbon-based grazing rate I ([μg μg^{-1} d^{-1}] or [d^{-1}]) was assumed to be

$$I = \frac{P_p - P_g}{G \cdot t} \quad , \tag{5.S1.1}$$

where P_p and P_g are the protist biomass in protist-only setups and grazer setups, respectively, G is the grazer biomass and t is the duration of the experiment. Eq. 5.S1.1 was rearranged to calculate one grazing rate for each treatment based on protist biomass from the protist-only triplicates (P_{p_r}, $r = 1,2,3$) and the grazer triplicates (P_{g_q}, $q = 1,2,3$; Eq. 5.S1.2). Linear regression of P_{g_q} against $-G_q \cdot t$ yielded the grazing rate as slope I and an estimated initial protist biomass as intercept P_p

$$\begin{pmatrix} P_{p1} \\ P_{p2} \\ P_{p3} \\ P_{g1} \\ P_{g2} \\ P_{g3} \end{pmatrix} = -I \begin{pmatrix} 0 \\ 0 \\ 0 \\ G_{g1} \\ G_{g2} \\ G_{g3} \end{pmatrix} \begin{pmatrix} 0 \\ 0 \\ 0 \\ t_1 \\ t_1 \\ t_1 \end{pmatrix} + P_p \quad . \tag{5.S1.2}$$

In this way, one protist biomass and one grazing rate per treatment could be calculated without previously averaging between the replicates.

According to Eq. 5.S1.2 total grazing rates (I_{tot}) were calculated for each of the 13 treatments using total protist biomass in protist-only setups and grazer setups. In addition, taxon-specific grazing rates (I_j) for 16 different protist taxa j (listed in the Table 5.S1) were calculated from the biomass of the respective taxa. Likewise, taxon-specific grazing rates were calculated based on the protist abundances of the 16 taxa for calculating the selectivity index.

Groups of treatments with similar protist composition were identified by cluster analysis (hierarchical agglomerative, group-average linkage) with similarity profile test (SIMPROF, Clarke and Warwick 2001; 1000 permutations, 999 simulated profiles; significance level of all statistic tests in this study 5 %) applied to the estimated relative initial biomass of the 16 protist taxa in the 13 treatments. In few cases estimates of initial biomass were just slightly negative; these values had to be set to zero prior to analysis.

Table 5.S1: List of protist taxa in grazing experiments and groups used in plots and calculations.

Protist groups	**Taxa included**	**Remarks**
Cyanobacteria indet.	Cyanobacteria indet.	
Flagellata small	Flagellata indet. 1	small
Flagellata big	*Cryptomonas* spp.	
	Dinoflagellata indet.	
	Chlamydomonas spp.	
	Flagellata indet. 2	big
Fragillariopsis spp.	*Fragillariopsis* species 1	
	Fragillariopsis species 2	similar to *Nitzschia* spp.
Nitzschia spp.	*Nitzschia frigidia*	
	Nitzschia spp.	
Pseudo-nitzschia cf. *seriata*	*Pseudo-nitzschia* cf. *seriata*	
Pseudo-nitzschia cf. *subcurvata*	*Pseudo-nitzschia* cf. *subcurvata*	
Bacillariaceae indet.	Bacillariaceae indet.	
Other pennates	Achnanthaceae indet.	
	Navicula spp.	
	Navicula transistans var. *Derasa f. delicatula*	
	Cylindrotheca closterium	
	Bacillariales indet.	
	Entomoneidaceae indet.	*Entomoneis kjellmannii* or *Amphiprora hyperborea*
Thalassiosira cf. *angulata*	*Thalassiosira* cf. *angulata*	
Thalassiosira cf. *bioculata*	*Thalassiosira* cf. *bioculata*	
Thalassiosira spp.	*Thalassiosira* spp.	
Attheya spp.	*Attheya longicornis*	
	Attheya cf. *longicornis*	
	Attheya septentrionalis	
Other centrics	*Bacteriosira bathymophala*	
	Chaetoceros spp.	
	Coscinodiscineae indet.	similar to *Leptocylindricus* spp.
	Biddulphiales indet.	
Ciliata indet.	Ciliata indet.	
Other Protista	Heliozoa indet.	
	Protista indet. 1	possibly *Phaeocystis pouchetii*
	Protista indet. 2	
	Protista indet. 3	centric shape

5.S2 Details on the determination of grazing selectivity

A selectivity index α_j was calculated for each protist taxon and treatment according to Chesson (1983) assuming that the abundance of a taxon j ($j = 1, ..., 16$, Supplement 5.S1 Table 5.S1) was reduced by grazing (Manly et al. 1972):

$$\alpha_j = \frac{ln((P_{p,j} - P_{g,j})/P_{p,j})}{\sum_{l=1}^{m} ln((P_{p,l} - P_{g,l})/P_{p,l})} \ , \ j = 1, ..., m = 16 \ . \tag{5.S2.1}$$

The initial abundance of taxon j, $P_{p,j}$, was approximated by the estimated initial protist abundance (Eq. 5.S1.2). Using taxon-specific grazing rates I_j and estimated initial protist abundance $P_{p,j}$, an estimate of the abundance $P_{g,j}$ of taxon j at the end of the experiment was calculated

$$P_{g,j} = -I_j \cdot \bar{G} \cdot t + P_{p,j} \ , \tag{5.S2.2}$$

where $\bar{G}$ is the abundance of the grazer *Tisbe* spp. averaged over the triplicates. Only those taxa were considered for Eq. 5.S2.1 for which the taxon-specific grazing rate in the particular treatment was significantly positive.

The electivity index ε was calculated according to Chesson (1983):

$$\varepsilon_j = \frac{m \cdot \alpha_j - 1}{(m-2) \cdot \alpha_j + 1} \ , \ j = 1, ..., m = 16 \ . \tag{5.S2.3}$$

5.S3 Details on the determination of predation rates

Gains and losses in prey attributed to reproduction and handling in predation experiments were determined from the average change in prey carbon biomass per time ΔB_{py} in prey-only replicates for each time step in each treatment. For treatments with ciliate prey which were lacking prey-only setups, ΔB_{py} was estimated as average from all prey-only setups with ciliate prey. For experiments with rotifers, nauplii and copepodide prey which were lacking prey-only setups, ΔB_{py} was set to zero, since for these taxa individuals are not likely to be lost during counting and reproduction rates are low compared to those for ciliates.

To identify groups of replicates according to predator and prey biomass, a cluster analyses (hierarchical agglomerative clustering based on Bray-Curtis similarity) and a SIMPROF test (1000 permutations, 999 simulated profiles) were applied to fourth-root transformed biomass data.

5.S4 Details on the assessment of the feeding impact

Based on individual *in situ* ingestion rates $I_{ijk,ind}$, bulk ingestion rates $I_{ijk,bulk}$ were calculated for each pair of predator / grazer i and food type j, and for each ice-core section k, according to the equation

$$I_{ijk,bulk} = I_{ijk,ind} \cdot B_{ik,bulk} \quad , \tag{5.S4.1}$$

where $B_{ik,bulk}$ is the bulk carbon biomass of predator or grazer taxon i in section k—i. e. $I_{ij,bulk}$ is the carbon biomass of a certain food type ingested by a certain predator or grazer taxon per time and volume of melted ice. The bulk community ingestion rate $I_{comm,jk,bulk}$ of total sympagic meiofauna was then calculated for each ice-core section and food type as

$$I_{comm,jk,bulk} = \sum_i I_{ijk,bulk} \quad , \tag{5.S4.2}$$

and the integrated community ingestion rate $I_{comm,j,int}$ was calculated for each station and food type as

$$I_{comm,j,int} = \frac{\sum_k (I_{comm,jk,bulk} \cdot V_{ice_m,k})}{A} \quad , \tag{5.S4.3}$$

where $V_{ice_m,k}$ is the volume of melted ice-core section k and A is the ice-core cross-sectional area—i. e. $I_{comm,j,int}$ is the carbon biomass of a certain food type ingested by sympagic meiofauna per time and ice area.

The feeding impact $F_{j,st}$ of meiofauna on the standing stock of each food type was then calculated for each station as

$$F_{j,st} = \frac{I_{comm,j,int}}{B_{j,int}} \quad , \tag{5.S4.4}$$

where $B_{j,int}$ is the integrated carbon biomass of food type j—i. e. $F_{j,st}$ is the fraction of the standing stock of a certain food type ingested by sympagic meiofauna per time.

5.S5 Details on the results of grazing experiments

Initial protist composition in grazing experiments

The 13 treatments grouped into three significantly different clusters (SIMPROF) according to initial protist biomass compositions determined by linear regressions. Treatments 1, 3 and 4 (cluster A) were dominated by the large centric diatoms *Thalassiosira* spp. and *T. bioculata* as well as ciliates, with low contributions of small centric diatoms and other protists (i. e. protists other than flagellates, diatoms and ciliates) and very low contribu-

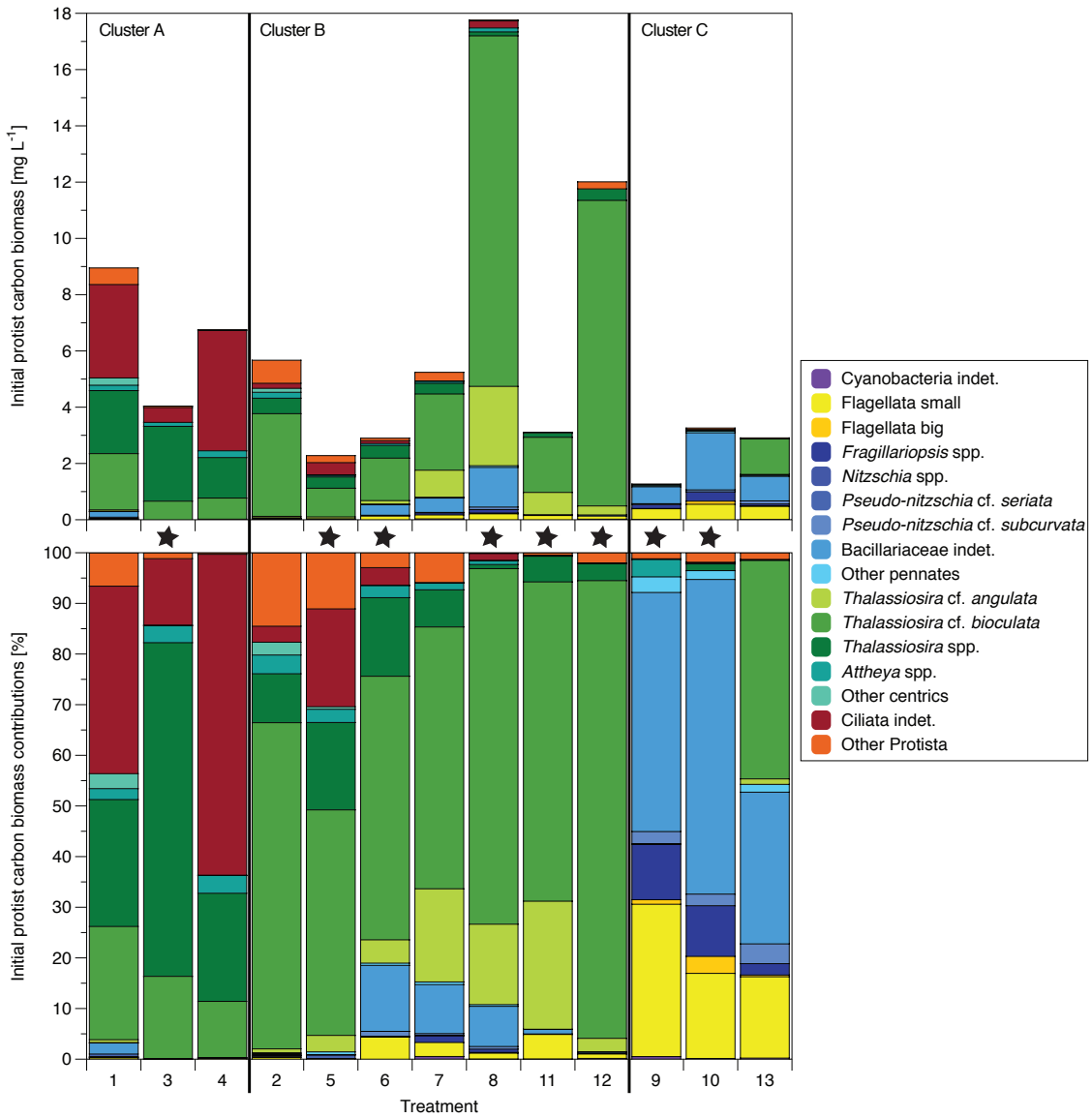

Figure 5.S5.1: Initial protist composition in the 13 treatments of grazing experiments, estimated from linear regressions, with absolute biomass (upper panel) and biomass contributions (lower panel) of the different protist taxa. The treatments are grouped into three significantly different clusters (SIMPROF). Treatments where grazing rates were significantly positive are marked ⋆ (one-tailed test with t statistics of regression coefficients).

tions of pennate diatoms. Treatments 2, 5, 6, 7, 8, 11 and 12 (cluster B) were dominated by *T. bioculata*, with in part remarkably high contributions of *T. angulata*, *Thalassiosira* spp. or pennate diatoms, usually low contributions of ciliates and other protists and always low contributions of small centric diatoms and small flagellates. Treatments 9, 10 and 13 (cluster C) were dominated by pennate diatoms, with remarkably high contributions of small flagellates, usually low contributions of centric diatoms and very low contributions of big flagellates and other protists. Biomass contributions of cyanobacteria were low in all treatments.

Taxon-specific grazing rates

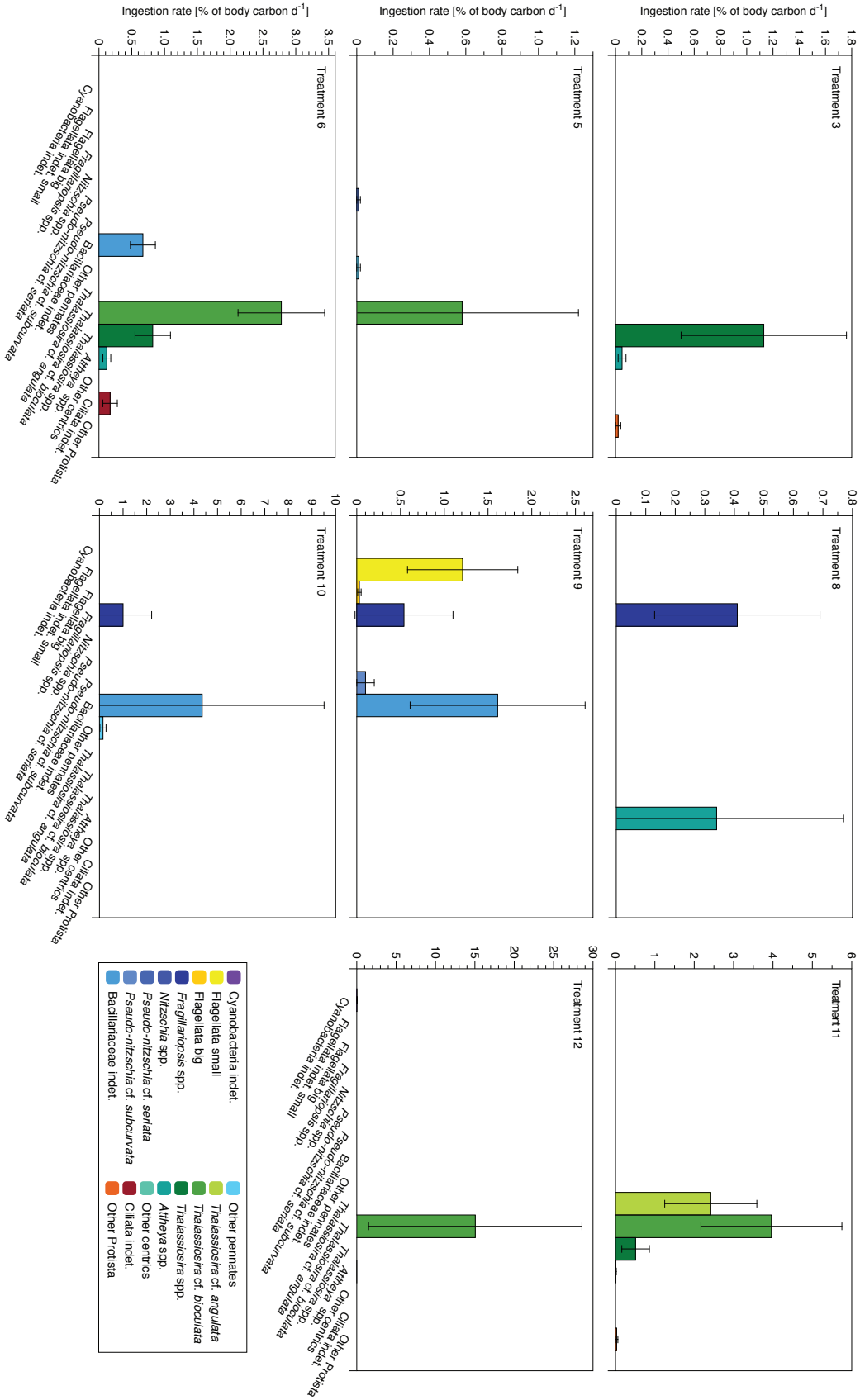

Figure 5.S5.2: Taxon-specific grazing rates of *Tisbe* spp. in the eight treatments with significantly positive total ingestion rates. Only significantly positive taxon-specific grazing rates are shown. Error bars denote 90 % confidence intervals of the regression coefficients.

5.S6 Details on the results of predation experiments

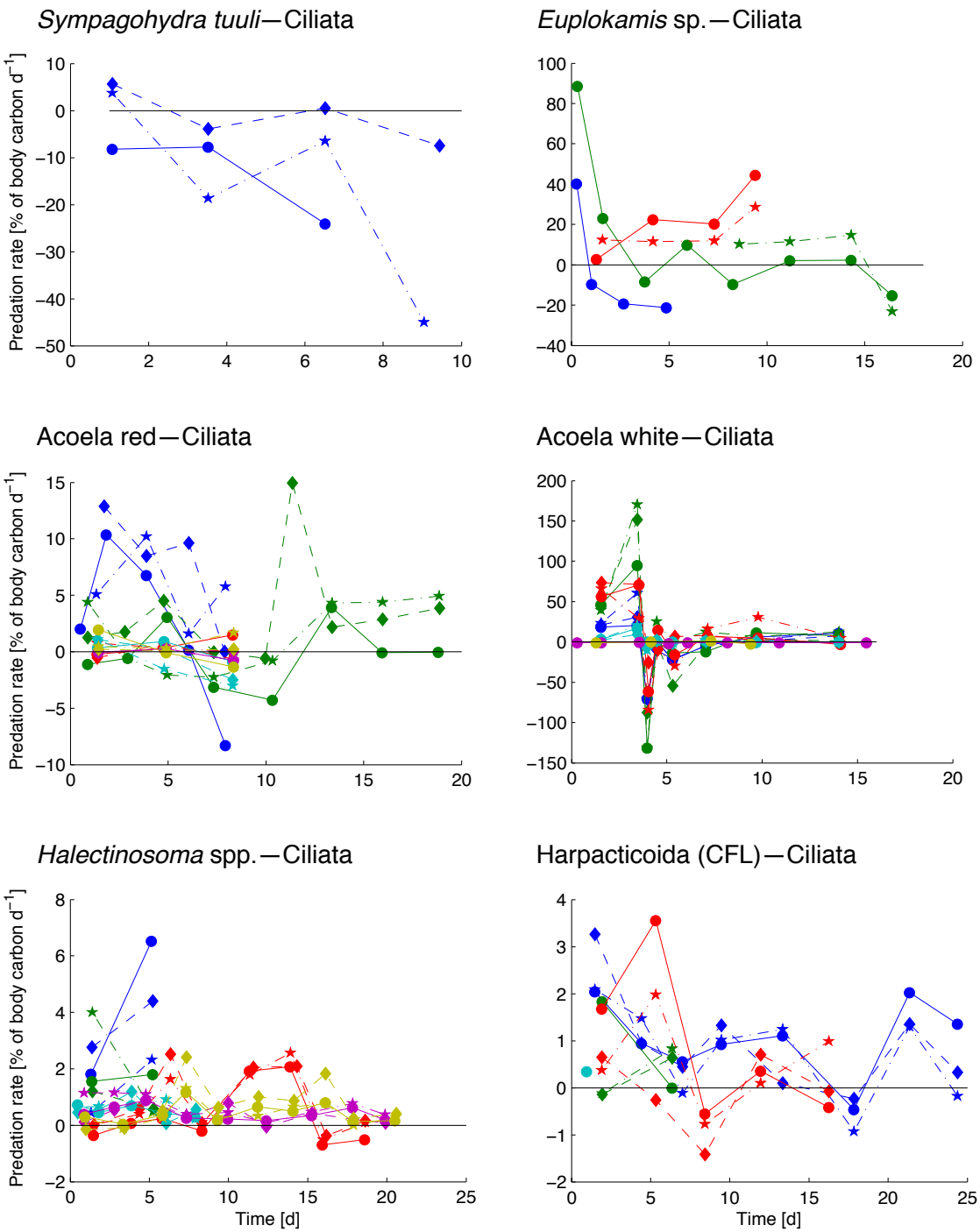

Figure 5.S6.1: Predation rates of different metazoan meiofauna predators on ciliate prey, plotted over the time from the beginning of the experiment. Replicate predator setups (run simultanously under similar conditions) are indicated by similar colours but different symbols.

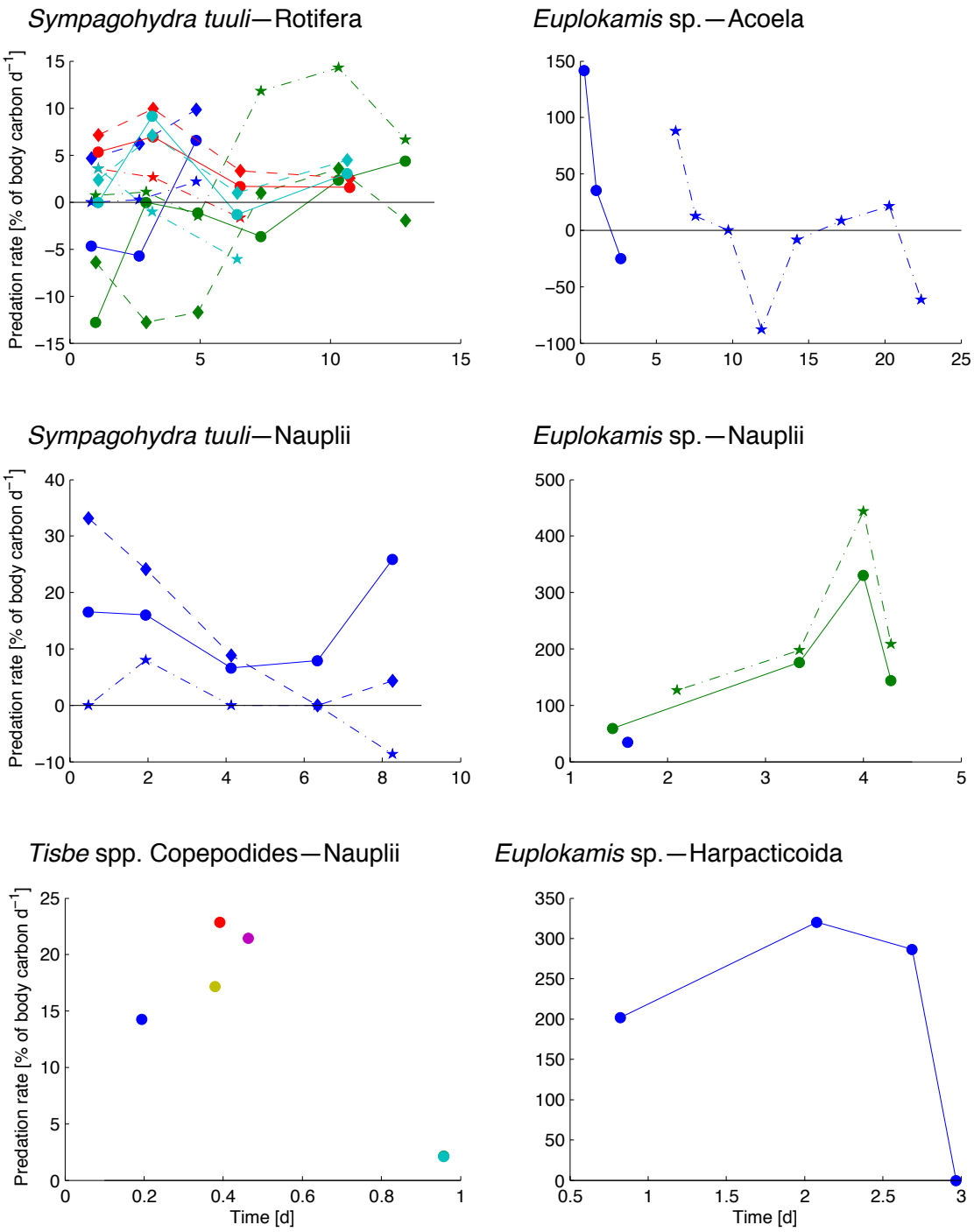

Figure 5.S6.2: Predation rates of different metazoan meiofauna predators on metazoan prey, plotted over the time from the beginning of the experiment. Replicate predator setups (run simultanously under similar conditions) are indicated by similar colours but different symbols. *Euplokamis* sp. preying on *Stephos longipes* are not shown.

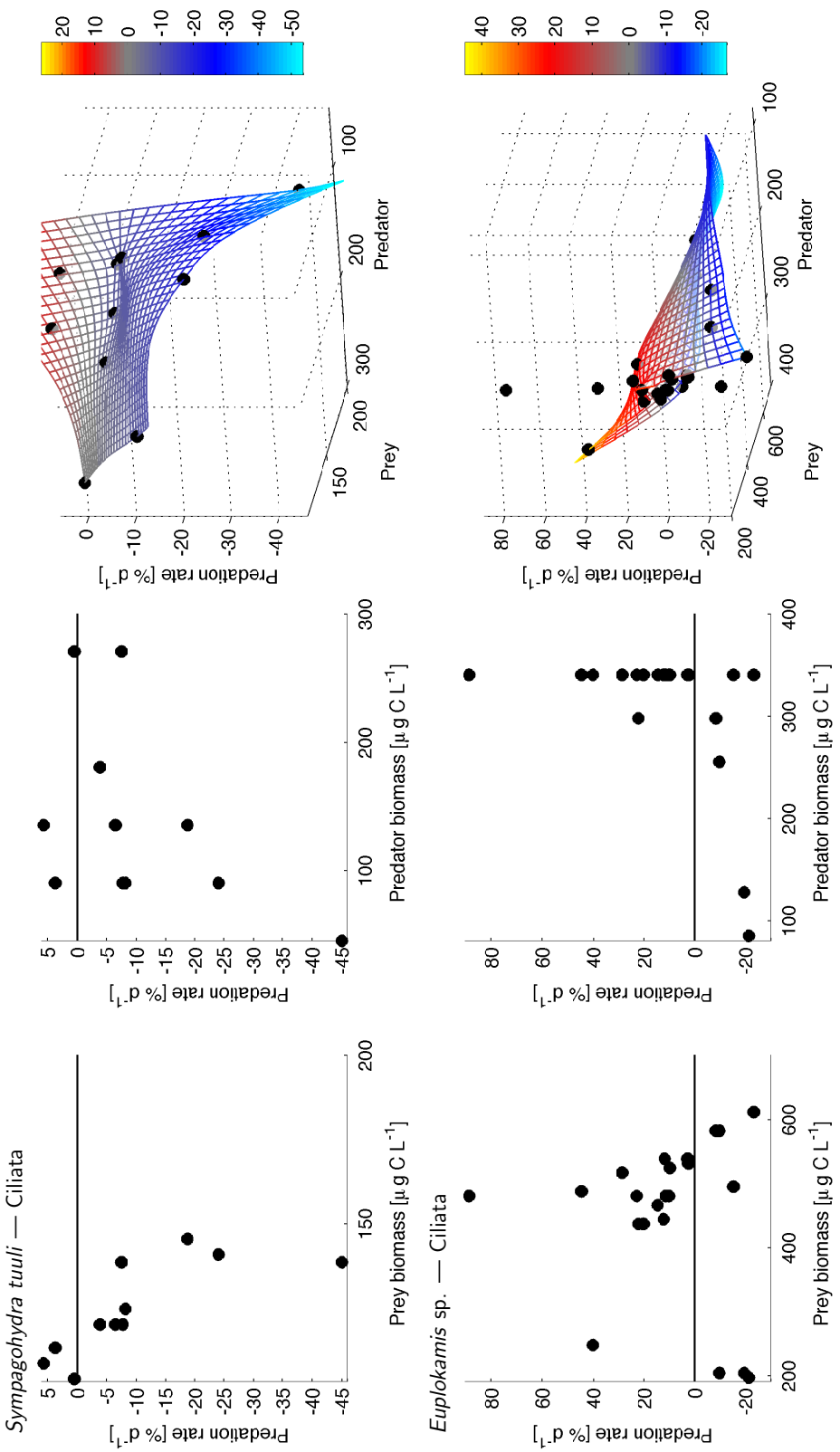

Figure 5.S6.3: Carbon-based predation rates of the Arctic cnidarian *Sympagohydra tuuli* (top) and the Antarctic ctenophore *Euplokamis* sp. (bottom) preying on ciliates, plotted against prey biomass (left), predator biomass (middle) and both prey and predator biomass (right). The mesh in the 3D plots was interpolated using the Matlab gridfit routine (release 2.0, May 23, 2006).

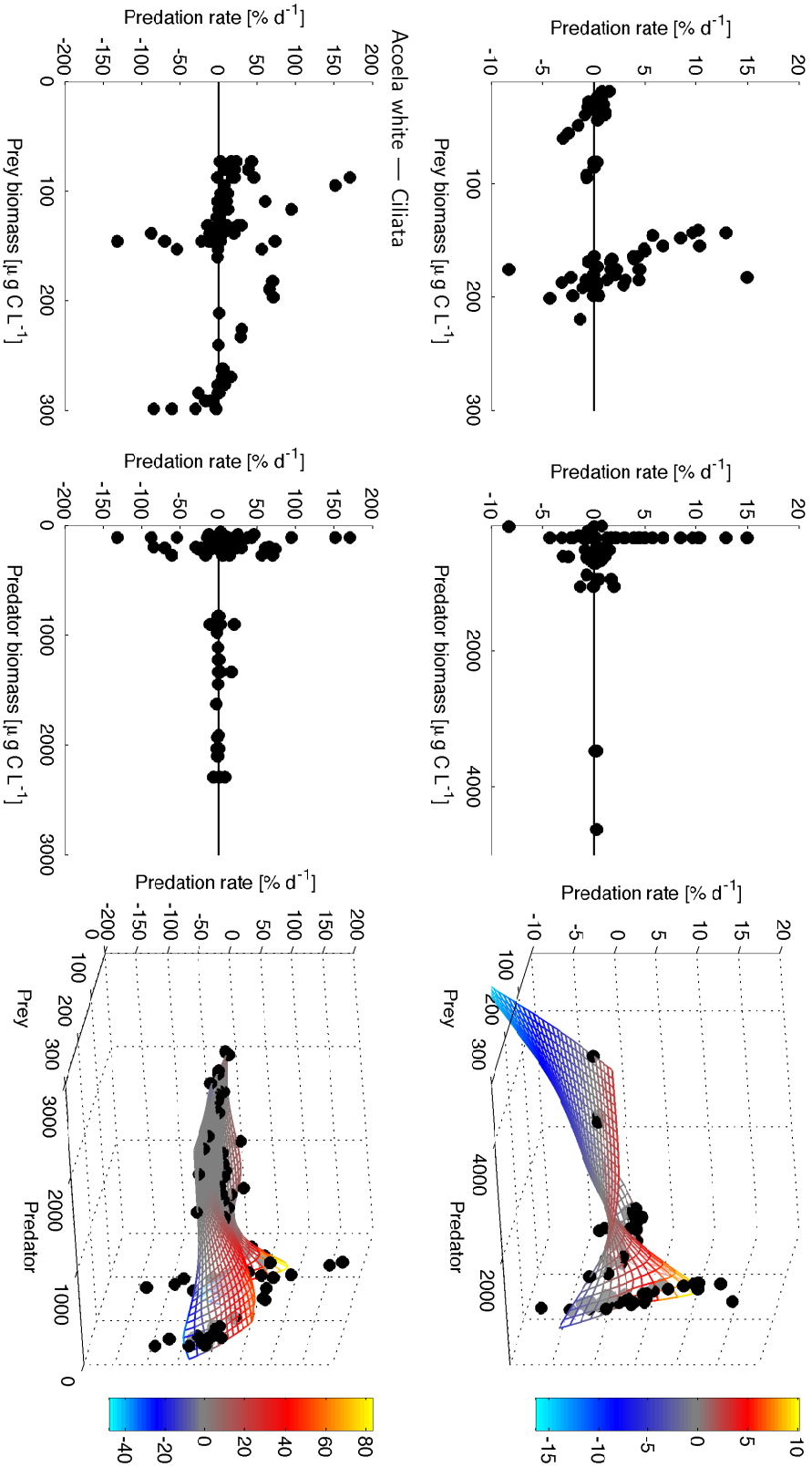

Figure 5.S6.4: Carbon-based predation rates of Arctic red (top) and Antarctic white (bottom) acoels preying on ciliates, plotted against prey biomass (left), predator biomass (middle) and both prey and predator biomass (right). The mesh in the 3D plots was interpolated using the Matlab gridfit routine (release 2.0, May 23, 2006).

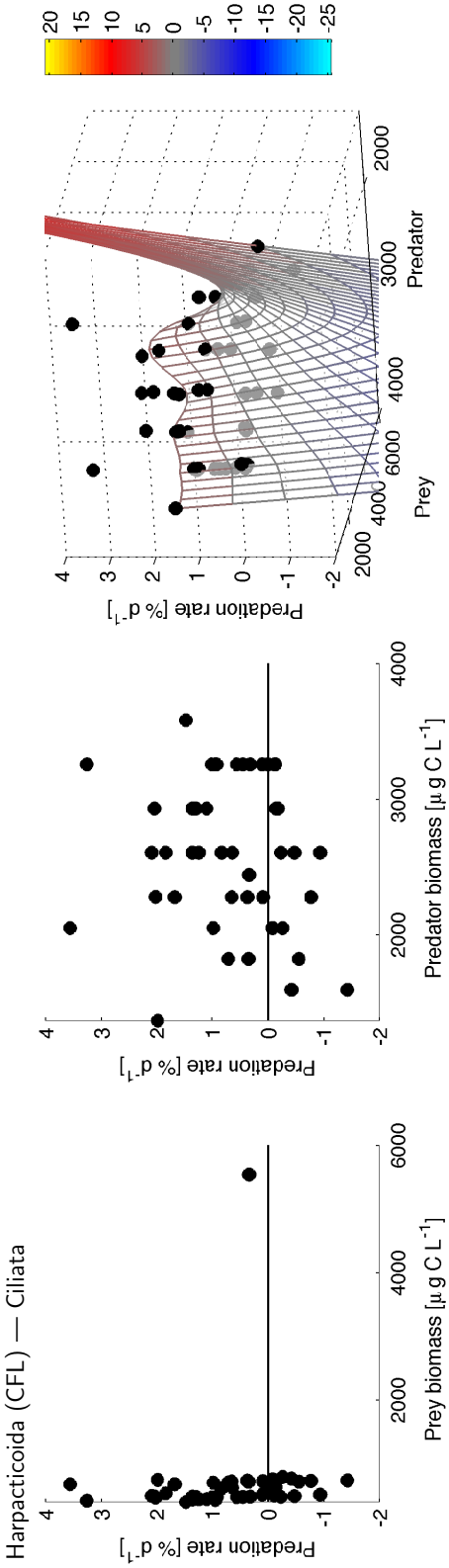

Figure 5.S6.5: Carbon-based predation rates of indeterminated harpacticoids from the Canadian Arctic preying on ciliates, plotted against prey biomass (left), predator biomass (middle) and both prey and predator biomass (right). The mesh in the 3D plots was interpolated using the Matlab gridfit routine (release 2.0, May 23, 2006).

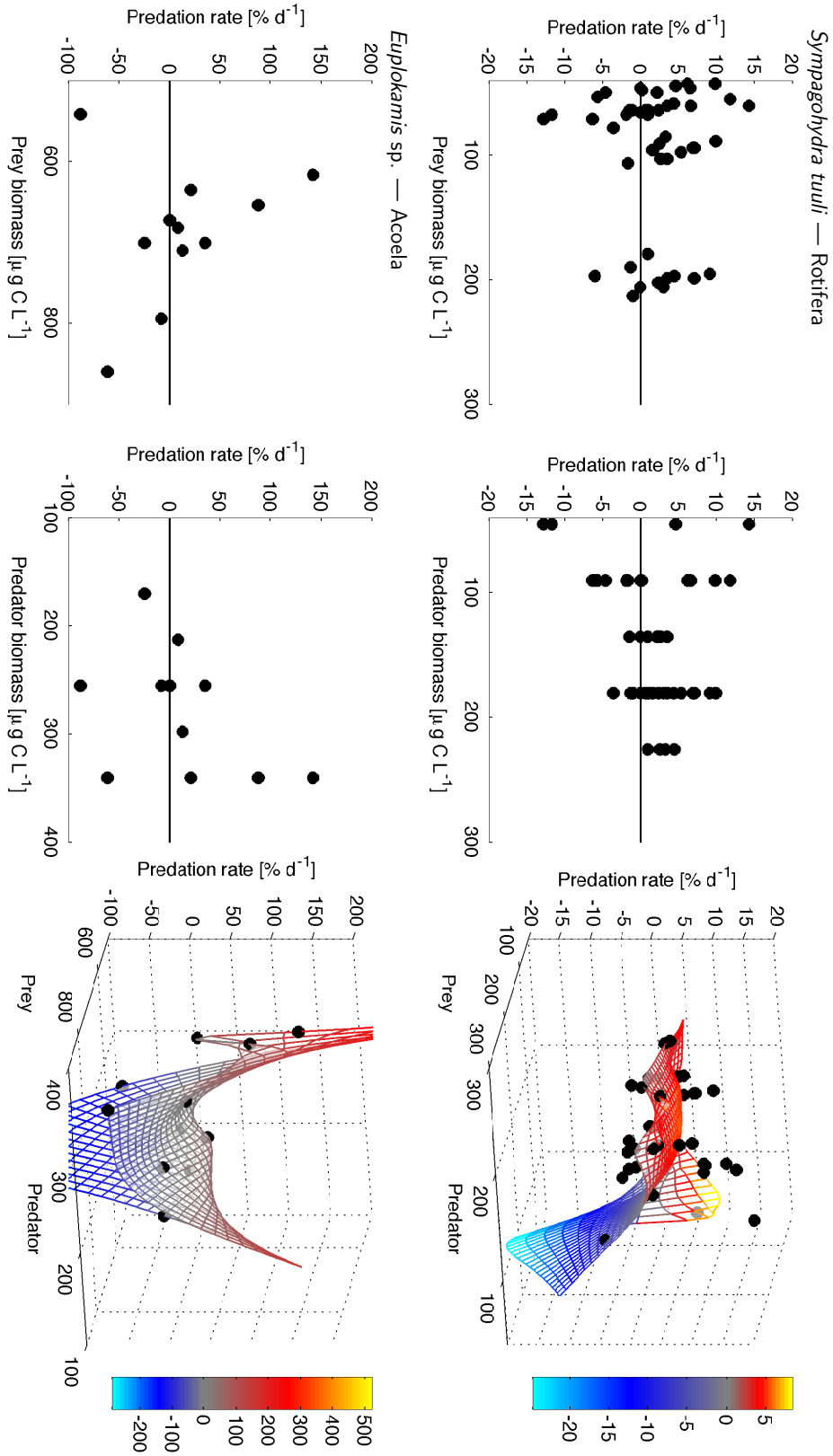

Figure 5.S6.6: Carbon-based predation rates of the Arctic cnidarian *Sympagohydra tuuli* preying on rotifers (top) and the Antarctic ctenophore *Euplokamis* sp. preying on white acoels (bottom), plotted against prey biomass (left), predator biomass (middle) and both prey and predator biomass (right). The mesh in the 3D plots was interpolated using the Matlab gridfit routine (release 2.0, May 23, 2006).

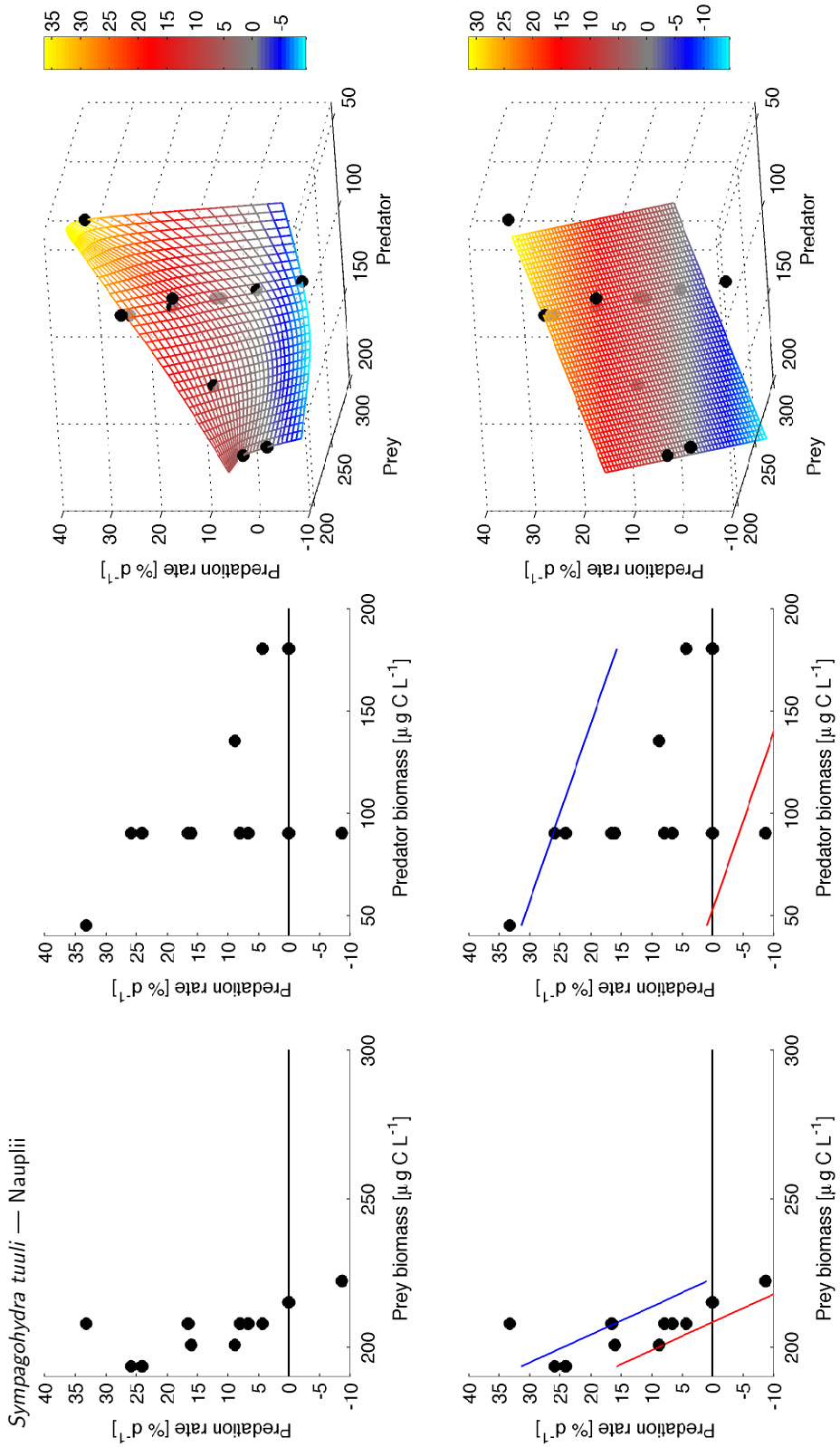

Figure 5.S6.7: Top Carbon-based predation rates of the Arctic cnidarian *Sympagohydra tuuli* preying on nauplii, plotted against prey biomass (left), predator biomass (middle) and both prey and predator biomass (right). The mesh in the 3D plot was interpolated using the Matlab gridfit routine (release 2.0, May 23, 2006). **Bottom** Same as above, the surface in the 3D plot showing a plain fitted to the data (Eq. 5.3) and the red and blue lines in the 2D plots showing the upper and lower borders of the plain within the data range.

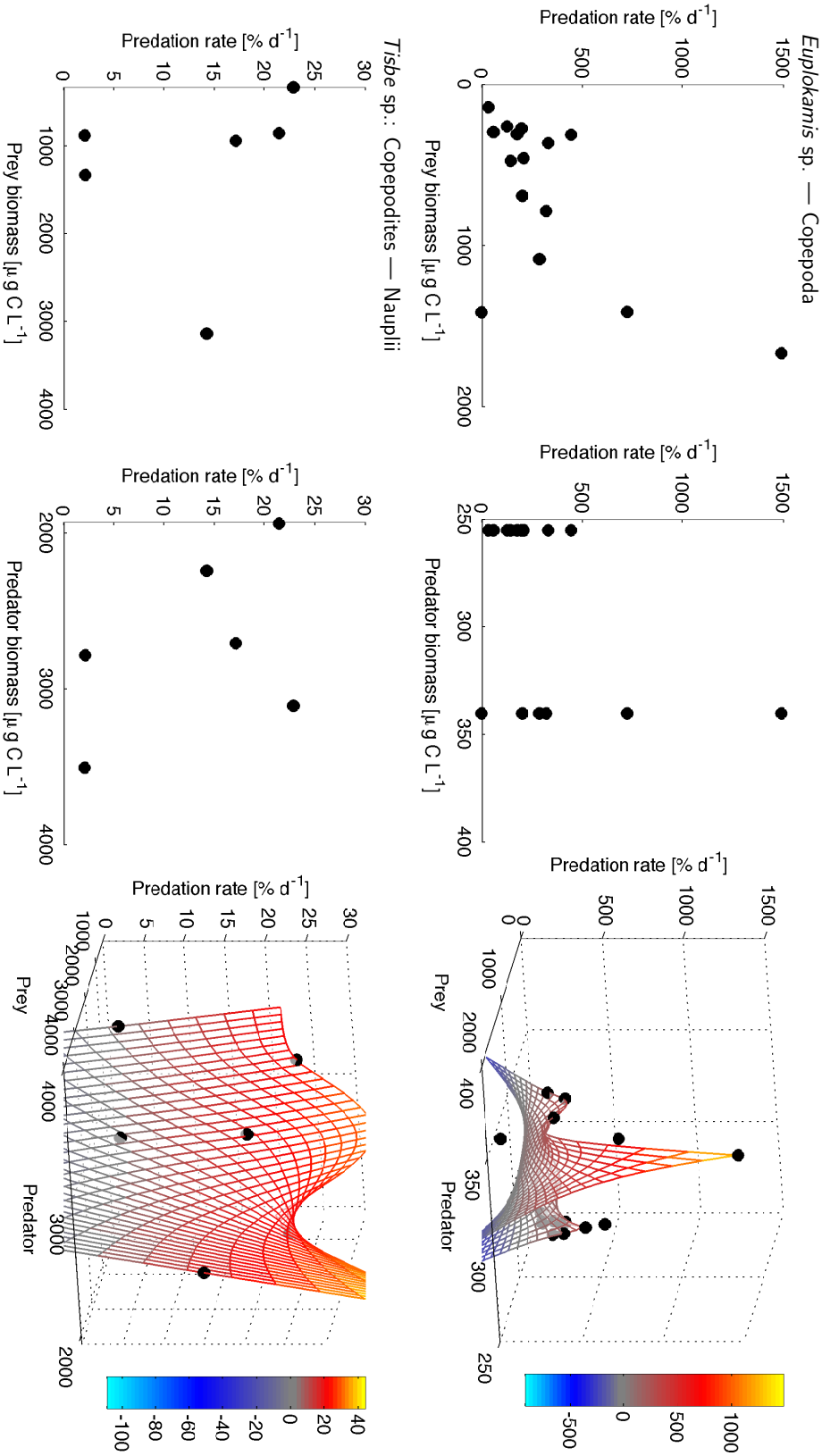

Figure 5.S6.8: Carbon-based predation rates of the Antarctic ctenophore *Euplokamis* sp. preying on copepods (merged from separate setups with nauplii, harpacticoid copepodides and calanoid copepodides of *Stephos longipes* as prey; top) and of copepodides of the Arctic harpacticoid *Tisbe* spp. preying on nauplii of the same species (bottom), plotted against prey biomass (left), predator biomass (middle) and both prey and predator biomass (right). The mesh in the 3D plots was interpolated using the Matlab gridfit routine (release 2.0, May 23, 2006).

6 Synopsis

6.1 Complexity of sea-ice food webs

My study has confirmed my hypothesis that the sea-ice food webs in both Arctic (Fig. 6.1) and Antarctic (Fig. 6.2) are much more complex than previously assumed. The results of biochemical analyses (Chapter 4) and experimental studies (Chapter 5) show in good agreement that sympagic metazoan meiofauna is not strictly herbivorous, but can exploit various food sources, including ciliates, metazoans, bacteria and detritus. Omnivorous feeding seems to be a common strategy in sympagic metazoan meiofauna.

Earlier studies on meiofauna feeding ecology provided evidence of herbivorous feeding (Hoshiai et al. 1987, Grainger and Hsiao 1990, Schnack-Schiel et al. 1995, Swadling et al. 1997b, 2000), resulting in the generalisation that sympagic meiofauna feeds mainly or exclusively on sea-ice algae (Gradinger 1995, Brierley and Thomas 2002, Arrigo and Thomas 2004). Following this assumption, the sea-ice food webs would be accordingly simple: ice algae would be grazed on by meiofauna, sub-ice fauna and under-ice fauna, and higher trophic levels would be found exclusively outside the ice. In fact this represents a food chain rather than a food web. In contrast, my study has shown that predators, feeding on ciliates or metazoan meiofauna, are common in both Arctic and Antarctic sea ice (Chapters 4 and 5). My data additionally indicate bacterivory in several sympagic metazoan meiofauna taxa (Chapter 4), as also reported from sympagic protozoan meiofauna (Laurion et al. 1995, Sime-Ngando et al. 1999, Caron and Gast 2010). The omnivorous feeding strategies in most sympagic metazoan meiofauna taxa, as evident from my results, are in agreement with observations for protozoan meiofauna (Caron and Gast 2010) and studies on under-ice amphipods (Werner and Auel 2005), which likewise indicate omnivorous feeding in several taxa. Predation, bacterivory and omnivory imply highly complex food-web structures with various trophic links (Fig. 6.1 and 6.2).

The findings of carnivorous sympagic meiofauna and complex food webs can in part be attributed to several sympagic meiofauna taxa which sea-ice biologists were unaware of until recently. The Arctic cnidarian *Sympagohydra tuuli*, which was first reported from sea ice a few years ago (Bluhm et al. 2007, Piraino et al. 2008) and which we studied in more detail (Siebert et al. 2009), is a top predator in Arctic sea ice (Chapters 4 and 5). Antarctic ctenophores, reported from sea ice only by Dahms et al. (1990) and

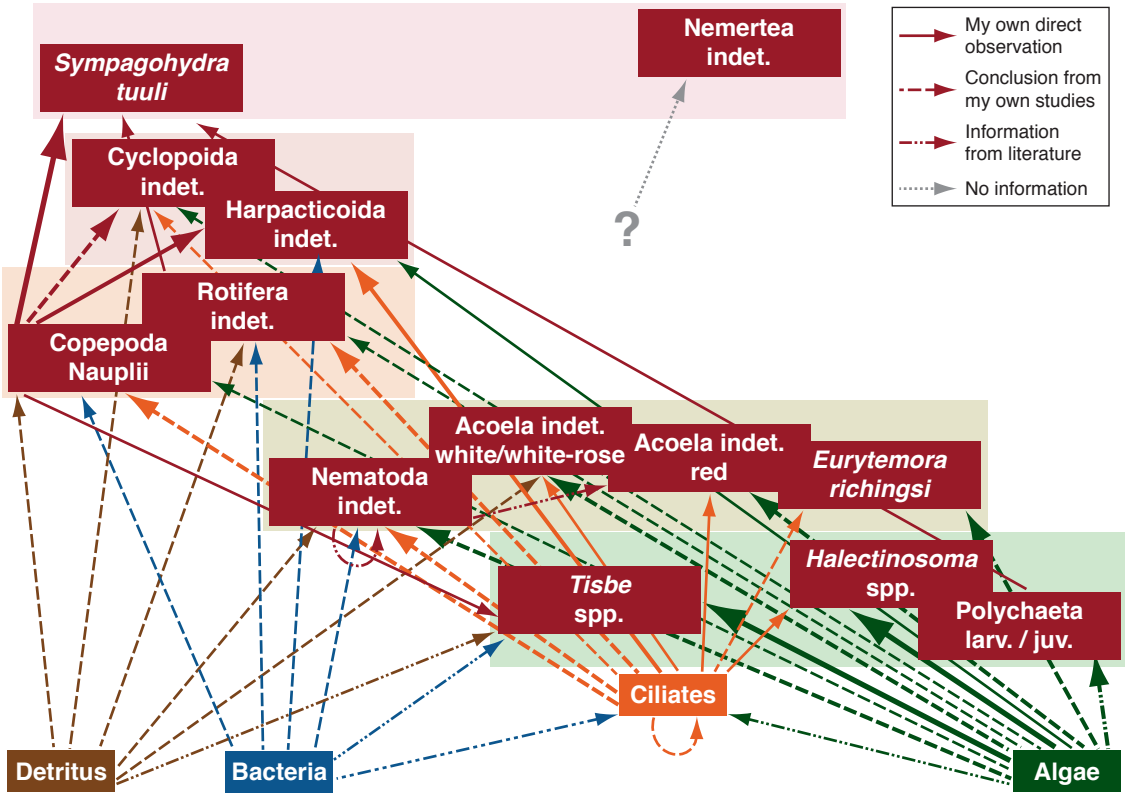

Figure 6.1: Schematic drawing illustrating the structure of the food web in Arctic sea ice. Arrows illustrate prey-predator relations, the colour illustrating the food type (algae, bacteria, detritus, ciliates or metazoan meiofauna). The arrow style indicates the source of information: besides my own direct observations in feeding experiments (solid line) and conclusions from my own stable isotope and fatty acid data or ingestion rates combined with models (dashed line), information from literature is included as well (dash-dotted line; Grainger and Hsiao 1990, Tchesunov and Riemann 1995, Friedrich and Hendelberg 2001, Arndt and Swadling 2006, Caron and Gast 2010). The stroke weight indicates possible dietary preferences indicated by stable isotope and fatty acid data or by observations in feeding experiments. For the sake of clarity, the microbial loop is not depicted.

Kiko et al. (2008b) and indentified in this study as *Euplokamis* (Chapter 2), are top predators in Antarctic sea ice (Chapters 4 and 5). The Antarctic rhabdocoels which we first reported from sea ice (Chapter 2) probably also prey on other meiofauna (Chapter 4). I assume that the Arctic nemerteans (Marquardt et al. under revision) and the Antarctic nudibranch *Tergipes antarcticus* (Kiko et al. 2008a), which we recently reported on, are further top predators. Nemerteans are generally carnivorous, with typical diets including polychaetes, copepods, molluscs and nematodes (McDermott and Roe 1985). Nemerteans in sea ice might thus feed on small metazoan meiofauna, e. g. polychaete larvae, nauplii and nematodes. Nudibranches typically feed on cnidarians (Clark 1975). Since these have never been reported from Antarctic sea ice, *T. antarcticus* might instead prey on the ctenophore *Euplokamis* sp. and additionally feed on algae (Kiko et al. 2008a) and possibly ciliates. Other taxa new to sea ice, including white-rose acoels and the calanoid *Eurytemora richingsi* in the Arctic, obviously do not prey on metazoans, but nevertheless

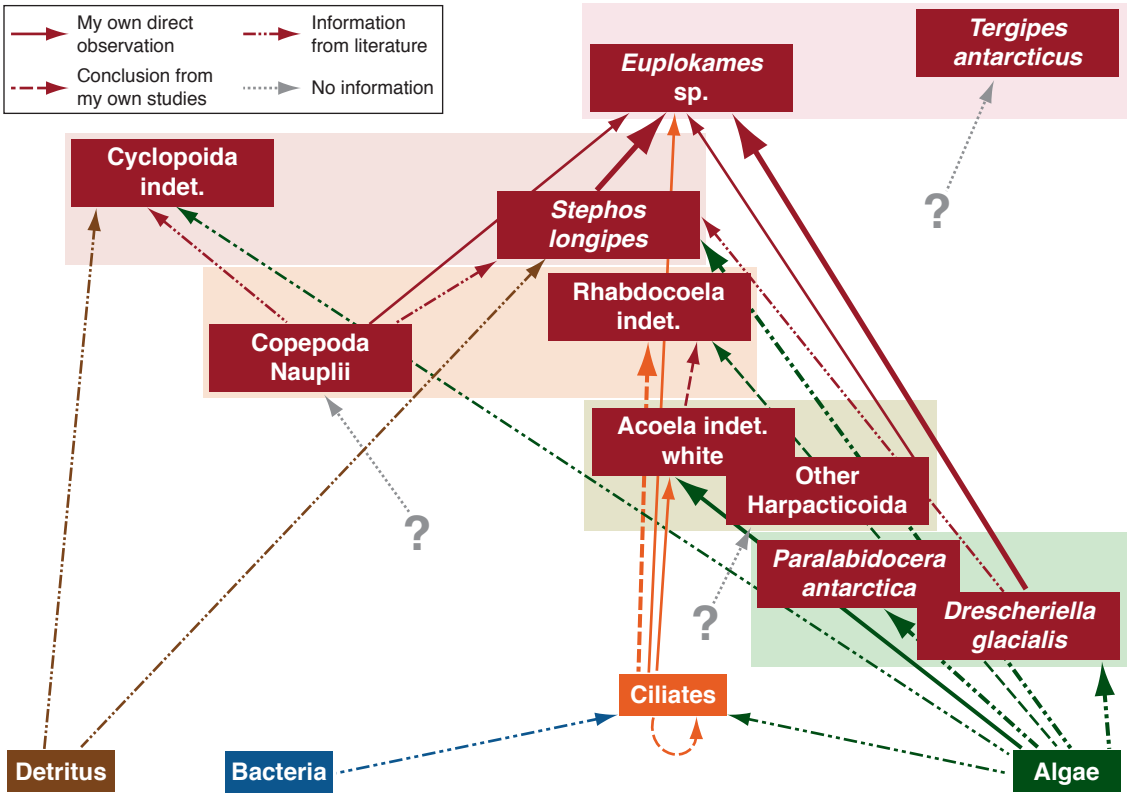

Figure 6.2: Schematic drawing illustrating the structure of the food web in Antarctic sea ice. Arrows illustrate prey-predator relations, the colour illustrating the food type (algae, bacteria, detritus, ciliates or metazoan meiofauna). The arrow style indicates the source of information: besides my own direct observations in feeding experiments (solid line) and conclusions from my own stable isotope and fatty acid data or ingestion rates combined with models (dashed line), information from literature is included as well (dash-dotted line; Hoshiai et al. 1987, Schnack-Schiel et al. 1995, Swadling et al. 1997b, 2000, Michels and Schnack-Schiel 2005, Arndt and Swadling 2006, Caron and Gast 2010). The stroke weight indicates possible dietary preferences indicated by stable isotope and fatty acid data or by observations in feeding experiments. For the sake of clarity, the microbial loop is not depicted.

contribute to the complexity of the food web by omnivorous feeding on algae, ciliates, bacteria and detritus (Chapter 4). The same might be true for several harpacticoid species recently reported from Antarctic sea ice (Kiko et al. 2008b, Schnack-Schiel et al. 2008), but studies on their feeding ecology are required for confirmation. In summary, findings about these additional sympagic meiofauna taxa contribute substantially to a better understanding of the sea-ice food webs.

Furthermore, the approach of this study enabled me to gain diverse insights into sympagic meiofauna feeding ecology and thus to resolve the complexity of the food webs. I combined different methods—stable isotope and fatty acid analyses (Chapter 4), grazing and predation experiments (Chapter 5)—allowing for a differentiated identification of feeding types and diets, whereas earlier investigations relied on just one method each—gut content studies (Hoshiai et al. 1987, Grainger and Hsiao 1990), grazing experiments (Schnack-Schiel et al. 1995, Swadling et al. 1997b) or lipid analyses (Swadling et al.

2000). I also included various sympagic meiofauna taxa in my study, allowing for a comprehensive picture, whereas previous feeding studies often focused on specific copepod taxa (Hoshiai et al. 1987, Schnack-Schiel et al. 1995, Swadling et al. 1997b, 2000). By studying Arctic and Antarctic taxa, I could show that the findings of carnivorous and cilivorous feeding and complex sea-ice food webs hold for both polar regions.

In spite of the generally similar patterns in Arctic and Antarctic sea-ice food webs, there are also some differences.

- My study indicates that intermediate trophic levels in Arctic sympagic metazoan meiofauna substantially feed on detritus and bacteria (Fig. 6.1; Chapter 4). This might be different in Antarctic sympagic meiofauna, where detritus and bacteria seem to play a minor role in meiofauna diets (Fig. 6.2). However, further feeding studies on Antarctic sympagic meiofauna including copepods are required for confirmation.
- Since the number of sympagic metazoan meiofauna species reported from the Arctic is higher than that from the Antarctic (Bluhm et al. 2010), the sea-ice food web has an inherent potential to be more complex in the Arctic (Fig. 6.1) than in the Antarctic (Fig. 6.2). To confirm this, species-level analyses of feeding ecology are needed, which will require substantial taxonomical effort.
- Arctic and Antarctic sea-ice food webs differ in the under-ice and sub-ice grazers and predators. The under-ice amphipods *Apherusa glacialis*, *Onisimus* spp. and *Gammarus wilkitzkii* as well as the planktonic copepods *Calanus* spp. play a key role as grazers under Arctic sea ice (Werner 1997, 2006a, Falk-Petersen et al. 2009), and *G. wilkitzkii* and the pelagic amphipod *Themisto libellula* are probably the most important meiofauna predators in this region (Werner et al. 2002, Auel and Werner 2003). In the Antarctic, in contrast, the krill species *Euphausia superba* is the main under-ice grazer (Meyer et al. 2002), while both *E. superba* and the under-ice amphipods *Eusirus* spp. can feed on planktonic copepods (Wickham and Berninger 2007, Krapp et al. 2008) and might thus also prey on sympagic meiofauna.

In conclusion, some general aspects of sea-ice food webs apply to both the Arctic and the Antarctic, but details in the food-web structure, particularly including quantitative information, are certainly not directly transferable.

6.2 Feeding impact of sympagic meiofauna

My study has shown that feeding of sympagic meiofauna impacts not just ice algae, but also ciliates and metazoan meiofauna. The feeding impact is thus more diverse than previously assumed. Based on experimentally determined ingestion rates, the grazing

impact of meiofauna on ice algae is very low, but the predation impact on ciliates and metazoan meiofauna can be extremely high (Chapter 5).

The grazing impact based on experimental grazing rates was consistently low in my study: it never exceeded 2 % of the ice-algae standing stock per day in any of the four regions and was by one order of magnitude lower than estimates based on allometric calculations of maximum potential ingestion rates (Chapter 5). Sympagic meiofauna is thus unlikely to control the accumulation of ice algae or to restrict their availability to under-ice grazers at least during the productive seasons. Previous studies, based on allometric calculations of maximum potential ingestion rates, have come to similar conclusions (Gradinger 1999a, Nozais et al. 2001, Michel et al. 2002, Gradinger et al. 2005). The remarkable grazing impact by sympagic meiofauna reported in one study (in the same order of magnitude as ice-algae primary production, Gradinger et al. 1999) was probably due to a substantial overestimation caused by the application of maximum potential ingestion rates (Chapter 5). Unpublished grazing experiments with the Antarctic sympagic copepods *Stephos longipes* and *Drescheriella glacialis* indicate that the copepod grazing impact can be very high in Antarctic surface layers in summer (up to 31 % of the ice-algae standing stock per day, Michels and Schnack-Schiel unpublished, reported in Bluhm et al. 2010). Since the authors report only a maximum value, I consider this rather an exception related to the very specific surface layer habitat.

The generally low grazing impact is in direct contrast to a remarkably high predation impact. The high predation rates I measured for some sympagic meiofauna taxa in experiments (for some predator-prey combinations almost 200 % of the predator body carbon per day) lead to very high estimates of the predation impact *in situ*, partly exceeding 20 % of the ciliate standing stock per hour and 10 % of the nauplii standing stock per hour (Chapter 5). This has several interesting implications.

- It is probable that the predation impact of metazoan meiofauna on other members of the community is constrained by several regulating factors. These probably include intra-specific and possibly inter-specific competition at high predator densities as well as the option of dietary switches at low prey densities (Chapter 5). Furthermore, the three-dimensional structure of the brine-channel system is likely to play an important role in this context, since it provides refuges for small meiofauna prey from larger meiofauna predators (Krembs et al. 2000).
- In spite of such constraining factors, predation by some sympagic meiofauna species on other meiofauna is probably an important structuring element within the meiofauna community, influencing the community composition at least on small spatial and temporal scales (Chapter 5). This may concern, besides ciliates and copepods,

other small metazoan meiofauna, e. g. rotifers in the Arctic, which are amongst the preys of *Sympagohydra tuuli* (Siebert et al. 2009).

- Carnivorous meiofauna most likely competes for prey with under-ice and sub-ice predators such as carnivorous amphipods and krill. It is probable that predation by sympagic meiofauna can limit the release of organisms from the ice and constrain the availability of meiofauna prey to under-ice and sub-ice predators, thus influencing cryo-pelagic coupling.

6.3 Sympagic meiofauna feeding ecology and cryo-pelagic coupling

My study has revealed several new aspects of cryo-pelagic coupling related to feeding activity by sympagic meiofauna (Fig. 6.3). These include new aspects of established theories as well as completely new pathways.

Several pathways of cryo-pelagic and cryo-benthic coupling have been described previously, some of which also consider the role of sympagic meiofauna.

- Incorporation of organisms into sea ice is a pathway from the pelagic and benthic realms to the sea-ice realm. It has been studied to some extent for algae (Garrison et al. 1983, Gradinger and Ikävalko 1998, Weissenberger 1998, Niimura et al. 2000, Krembs et al. 2002) and discussed for meiofauna (Carey Jr and Montagna 1982, Dieckmann et al. 1986, Riemann and Sime-Ngando 1997). Our recent study (Kiko et al. under revision) provides new insights into the colonisation of new ice by meiofauna in the context of global warming.
- A two-way link between sea ice and the pelagic and benthic realms is through migrations of cryo-pelagic and cryo-benthic meiofauna species related to their life cycles, as previously described for several Antarctic (Kurbjeweit et al. 1993, Schnack-Schiel et al. 1995, Tanimura et al. 1996, Swadling et al. 2004) and Arctic taxa (Gradinger et al. 2009). Such migrations have been suggested to be related in part to the ample food supply in sea ice (Carey Jr 1992, Kurbjeweit et al. 1993, Tanimura et al. 1996, Gradinger et al. 2009).
- The release of algae and meiofauna from sea ice, particularly during meltwater flushing, constitutes important pathways from the ice to the sub-ice, pelagic and benthic realms (Werner 2006a,b, Tamelander et al. 2008, 2009), providing food sources to these ecosystems (Søreide et al. 2006, Bluhm and Gradinger 2008, Morata et al. 2010).
- Feeding activity of under-ice and sub-ice fauna directly at the ice underside is another important aspect in this context (Werner 2006a), since at least under-ice am-

phipods and krill are able to obtain sympagic food organisms directly from the ice without their previous release to the sub-ice realm (Marschall 1988, Stretch et al. 1988, Werner 1997).

Feeding activity of sympagic meiofauna is an important influencing factor in the latter two aspects, which has barely been discussed so far. Particularly predation by carnivorous meiofauna can have substantial impact on the meiofauna community and thus diminish the amount of meiofauna released from the ice or available as prey to under-ice and sub-ice predators (Chapter 5). The effect of meiofauna grazing on the release and availability of ice algae, in contrast, is probably very low (Chapter 5).

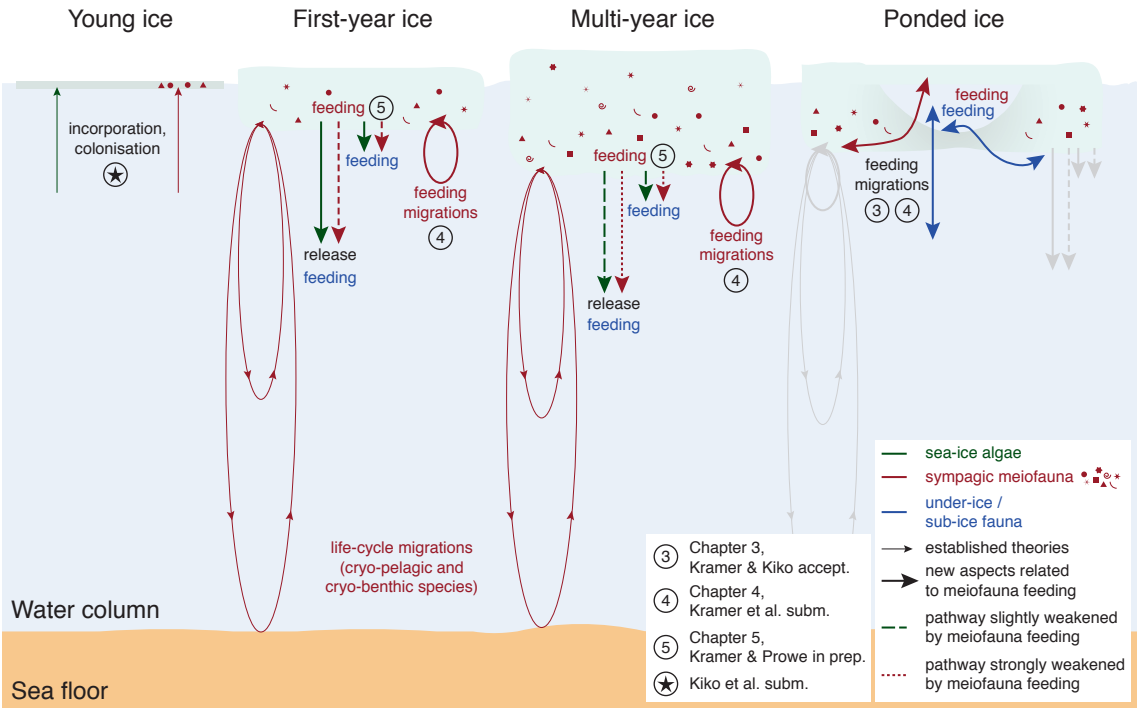

Figure 6.3: Schematic drawing illustrating the role of sympagic meiofauna in cryo-pelagic coupling in regions covered by young ice, first-year ice, multi-year ice and meltpond-covered ice. New aspects related to meiofauna feeding, which are based on the results of my study, are depicted as thick arrows, while established theories from literature are indicated by thin arrows. The weakening of pathways by meiofauna feeding, indicated by dashed or dotted arrows, is concluded from the feeding impact of meiofauna on ice algae and certain meiofauna taxa. Differences between first- and multi-year ice in this respect are based on differences in the feeding impact between the regions studied and are discussed in detail in Section 6.4. Differences between meiofauna diversity and abundance between young, first-year and multi-year ice, indicated by the read symbols, are based on Kiko et al. (under revision) and Chapter 2.

Completely new pathways in cryo-pelagic coupling lie in migrations of sympagic meiofauna related directly to feeding activity. My study has shown that several sympagic meiofauna taxa enter the pelagic realm in late summer to feed in this habitat and then migrate

back into the brine channels of sea ice (Chapter 4), which constitutes a pathway in two directions: on the one hand, it increases the availability of sympagic meiofauna prey to under-ice and sub-ice predators, while on the other hand, it supplies organic matter of pelagic origin to the sympagic community. Similarly, many sympagic meiofauna taxa migrate into brackish surface meltponds on Arctic summer sea ice (Chapter 3). Here they exploit the food sources and migrate back into the sea ice adjacent to the ponds (Chapter 4). Sub-ice fauna and under-ice amphipods can likewise enter the brackish meltponds (Chapter 3). It is thus probable that feeding interactions between sympagic meiofauna, sub-ice fauna and under-ice amphipods are enhanced in this specific habitat (Chapter 4).

The food-web structure in both Arctic and Antarctic sea ice, and in consequence the pathways of cryo-pelagic coupling, are very likely to undergo seasonal changes. These are not only related to the seasonality in meiofauna community composition (Schünemann and Werner 2005, Werner 2006a), but also to the availability of algal food to meiofauna during different seasons and possibly to dietary preferences during certain phases of their life cycles (Chapter 4). A seasonality in diets and feeding strategies has likewise been described for under-ice amphipods (Werner and Auel 2005) and krill (Meyer et al. 2010). I suggest the following seasonal cycle for the feeding of sympagic meiofauna and the related cryo-pelagic coupling:

- In spring, when ice-algae production is high, commonly leading to a vernal ice-algae bloom (Hsiao 1992, Günther and Dieckmann 1999, Mock and Gradinger 1999, Fiala et al. 2006), sympagic metazoan meiofauna makes use of the ample food supply by diatoms (Chapter 4). Some taxa, however, substantially supplement their diets by small meiofauna, ciliates and detritus to meet their energy requirements during their growth phases, as observed in meiofauna from the Canadian Arctic (Chapter 4). As a consequence of carnivorous feeding by meiofauna and high ice-algae standing stocks, cryo-pelagic coupling in spring is likely to occur almost exclusively through the release of and under-ice grazing on sea-ice algae.
- In summer, the proportion of diatoms in the diets of sympagic meiofauna increases and carnivorous feeding decreases (Chapter 4). Consequently, the release of meiofauna from the ice and their availability to under-ice predators gain importance in cryo-pelagic coupling. In late summer, the feeding migrations of sympagic meiofauna into the pelagic realm and into brackish meltponds (in the Arctic) presumably result in enhanced interactions with under-ice and sub-ice fauna (Chapter 4). Therefore, the coupling pathways through meiofauna are even strengthened. This in in general accordance with a study by Werner (2006b), who reported that abundance of sympagic meiofauna in sub-ice water under Arctic pack ice was highest in

summer. The author attributes this observation mainly to meltwater flushing. My results do not contradict this assumption, but point to the additional importance of the reduced predation impact by meiofauna and of enhanced migrations.

- In autumn, when the ice-algae biomass can obtain another maximum (Hoshiai 1981, Watanabe and Satoh 1987, Fiala et al. 2006), sympagic meiofauna is likely to continue primarily herbivorous feeding, and the predation impact is likely to remain low. Meiofauna thus remains available to under-ice predators, but release of meiofauna from the ice and thus its availability to sub-ice predators probably decreases due to new ice formation at the ice underside (Werner 2006b) and reduced migration activity.
- Later in autumn, when the ice-algae biomass decreases towards a winter minimum (Hoshiai 1981, Dieckmann et al. 1998, Günther and Dieckmann 1999, Fiala et al. 2006), the diatom-based diets of sympagic meiofauna are probably supplemented by flagellates, but also by ciliates, metazoans, bacteria and detritus. The latter four are likely to be the main energy sources for sympagic meiofauna in the dark midwinter. Due to the predominantly carnivorous diets of meiofauna and low ice-algae standing stocks, cryo-pelagic coupling through sympagic organisms is likely to be rather limited during late autumn and winter. This is in accordance with the study by Werner (2006b), who reported that sympagic meiofauna was virtually absent in sub-ice water in winter and chl *a* concentrations were extremely low. The under-ice amphipods *Gammarus wilkitzkii* and *Onisimus glacialis*, which rely on a rather carnivorous diet during this period (Werner and Auel 2005), may to some extent be able to avoid competition with sympagic meiofauna by feeding on planktonic sub-ice fauna, as observed in experiments with *G. wilkitzkii* (Werner et al. 2002). However, abundance of this alternative prey is also low in winter (Werner 2006b), and it is uncertain whether the amphipods are able to capture motile planktonic prey *in situ* (I. Werner pers. comm.). I therefore assume that competition between sympagic meiofauna and under-ice amphipods is particularly strong in winter.
- In late winter, under the influence of daylight and subsequent algae growth (Dieckmann et al. 1998, Günther and Dieckmann 1999, Fiala et al. 2006, Riedel et al. 2008), flagellates again become more important parts of the meiofauna diets, as observed in Antarctic sympagic meiofauna (Chapter 4). Accordingly, the importance of meiofauna as a pathway of organic matter from the sea ice to the pelagic realm probably increases again.

6.4 Sympagic meiofauna under global warming: impacts on the Arctic marine food web

The recently observed global warming has dramatic effects on the Arctic sea-ice cover (IPCC 2007, Perovich and Richter-Menge 2009). In particular, it causes a regime shift from a perennial to a seasonal sea-ice cover in the Central Arctic (Maslanik et al. 2007, Nghiem et al. 2007) with large amounts of young ice formed over deep basins (Kiko et al. under revision). Expected consequences for the Arctic marine food web have been discussed with focus on algae, sub-ice grazers, benthic grazers and mammals (Falk-Petersen et al. 2007, Arrigo et al. 2008, Bluhm and Gradinger 2008, Sun et al. 2009). My study indicates that changes in meiofauna communities and feeding strategies in consequence of global warming will have additional impacts on the Arctic marine food web.

The shift in the Arctic sea-ice regime will probably influence the composition of sympagic meiofauna communities. Meiofauna diversity, abundance and biomass are likely to decrease (Chapter 2), and the communities will probably become dominated by species with a pelagic life style, which can survive the ice-free summer and easily colonise the ice from the pelagic realm (Kiko et al. under revision). The decrease in meiofauna diversity will certainly reduce the complexity of the meiofauna food web, since food-web complexity is related to diversity. Such decrease in complexity may cause a higher vulnerability of the system (Kondoh 2003, Worm et al. 2006, Kartascheff et al. 2009). It is thus possible that the sea-ice food web in a seasonally ice-covered Arctic will be less robust: e. g. some food sources may more easily become depleted, and the lack of certain food sources may have more drastic consequences on higher trophic levels. The expected shift in sympagic meiofauna communities may also have dramatic consequences for the under-ice predators. Although Arctic under-ice amphipods are rather generalistic feeders (Werner and Auel 2005), they might not be well adapted to feed on the rather small and motile meiofauna taxa with a pelagic life style such as rotifers and cyclopoids (I. Werner pers. comm.).

Furthermore, a regime shift in the Arctic sea-ice cover alters the quality and quantity of cryo-pelagic coupling and thus impacts the entire Arctic marine food web (Falk-Petersen et al. 2007, Bluhm and Gradinger 2008). Changes in meiofauna feeding interactions and feeding impact, related to the regime shift, may cause further changes in cryo-pelagic coupling (Fig. 6.3):

- Over the next decades, when summer sea-ice will still persist in parts of the Arctic Ocean, brackish meltponds may become increasingly frequent (Chapter 3). Due to feeding interactions of sympagic meiofauna with sub-ice and under-ice fauna in

such meltponds, cryo-pelagic coupling is likely to be particularly strong in sea-ice regimes with high proportions of brackish meltponds. It is thus likely that, over the next decades, cryo-pelagic coupling in summer will be enhanced in areas still covered with ice during that season (Chapter 4).

- In the long term and on a large scale, this seasonal and local increase in cryo-pelagic coupling will be overlaid by changes caused by the shift from a perennially towards a seasonally ice-covered Arctic. The feeding impact of sympagic meiofauna is a function of diets, ingestion rates and biomass. My results indicate that meiofauna communities are more diverse and abundant in perennially than in seasonally ice-covered regions (Chapter 2) and show that diets and ingestion rates differ between meiofauna taxa (Chapter 5). In conclusion, it is highly probable that the grazing and predation impact differ in both quality and quantity between perennially and seasonally ice-covered regions, and that the pathways and magnitude of cryo-pelagic coupling differ accordingly. My results indicate that both the grazing and the predation impacts of sympagic meiofauna might be lower in seasonally than in perennially ice-covered regions. This is indicated by the fact that the calculated grazing and predation impacts were significantly lower in the seasonally ice-covered southern Indian Ocean than in the perennially ice-covered western Weddell Sea (Chapter 5). In consequence, cryo-pelagic coupling might be stronger in regions with seasonal sea-ice cover (Fig. 6.3). However, it must be kept in mind that results from the Antarctic might not be directly applicable to the Arctic due to differences in the food-web structure. Furthermore, observations of carnivorous feeding in additional taxa as well as further measurements of ingestion rates may alter the estimates of feeding impact and possibly result in a different picture. Besides, the lower meiofauna biomass in seasonally ice-covered regions (Chapter 2) may partly compensate the effect of a possibly lower predation impact and might even reduce cryo-pelagic coupling in these regimes.

Further comparative meiofauna studies between perennially and seasonally ice-covered regions are thus required. These may enable us to foresee whether a change in meiofauna communities and feeding strategies due to the decline of the perennial Arctic sea-ice cover will enhance or reduce cryo-pelagic coupling during the ice-covered season. Regarding the complete annual cycle, an overall decrease in cryo-pelagic coupling is, in my view, most probable.

6.5 Outlook

The particular strength of this study lies in the combination of stable isotope and fatty acid analyses with grazing and predation experiments, all of which have proven well feasable in application to sympagic meiofauna. Stable isotopes and fatty acids revealed information on *in situ* feeding, including trophic positions and feeding grounds as well as some specific diets. Feeding experiments confirmed the results from the biochemical analyses and additionally provided ingestion rates as well as information on functional response and competition. Ultimately, in combination with quantitative meiofauna community studies, I was able to estimate the grazing and predation impact of sympagic meiofauna, to draw conclusions on its role in cryo-pelagic coupling and to discuss possible consequences of global warming.

Future studies on the feeding ecology of sympagic meiofauna should thus likewise combine analytical and experimental methods. The most important issues to study are, in my view:

1. Identification of the diets of taxa which were not investigated in the present study, including particularly Antarctic harpacticoids and the nudibranch *Tergipes antarcticus* as well as Arctic polychaetes and nemerteans
2. Quantification of the role of bacterivory for different sympagic meiofauna taxa
3. Detailed investigation of the seasonality of dietary preferences and ingestion rates
4. Better quantification of various factors influencing ingestion rates, including—besides food (prey) and grazer (predator) density—also food particle (prey) and grazer (predator) size as well as ambient temperature
5. Investigation of the role of brine channel geometry for grazer / predator and prey behaviour and thus for ingestion rates
6. Analyses of the feeding impact of sympagic meiofauna on various components of the sympagic community (algae, bacteria, ciliates, specific meiofauna taxa) under different conditions (community composition, prey spectra, selectivity)

In addition to the methods applied in my study, I see a high potential in studies on enzyme activity (Green et al. 2006, Meyer et al. 2010), DNA analyses of gut contents (Töbe et al. 2010) and feeding experiments using fluorescent dyes (Sherr and Sherr 1993, Laurion et al. 1995) or radioactive labels (Carman 1990, Swadling et al. 1997b). Furthermore, mathematical modeling will be essential to tackle the issues 4–6. Models need to be developed which describe the influence of several factors on ingestion rates (4) as exactly as possible. The behaviour of meiofauna grazers / predators and prey in brine channels (5) can be addressed with spacially explicit individual-based models (Grimm and Railsback

2005) combined with experiments (Krembs et al. 2000). A simple conceptual food-web model could be developed to investigate the feeding impact of sympagic meiofauna in different scenarios (i. e. under different conditions) (6). This might also help to estimate possible influences of global warming on the Arctic sea-ice food web and to foresee some of the consequences for the Arctic marine food web.

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Curriculum vitae

Maike Kramer
Born: 30 June, 1982, Bottrop
Nationality: German
Family status: unmarried

Postgraduate education and scientific work

Since Oct 07	**Research associate (until Oct 14, 2010) and doctoral candidate at the Institute for Polar Ecology, Christian-Albrechts Universität zu Kiel** Topic: The Role of sympagic meiofauna in Arctic and Antarctic sea-ice food webs
Since Aug 09	Member of the Integrated School of Ocean Sciences, Graduate School in the Cluster of Excellence "Future Ocean"

Graduate and under-graduate education

Sep 02–Oct 07	**Studies of Marine Environmental Sciences (Marine Umweltwissenschaften) at the Carl von Ossietzky Universität Oldenburg; Degree: Diplom** • Subjects: environmental sciences (compulsory), mathematics/physics (major), biology and chemistry/geology (minor), environmental law (compulsory optional), languages and politics (elective) • Scholarship of the Studienstiftung des deutschen Volkes
Mar 07–Oct 07	Diploma thesis at the Institute for Polar Ecology, Kiel; Topic: Sympagic meiofauna in the Antarctic pack ice in winter
Jan 05–Aug 05	Semester abroad at the University of Helsinki, Finland
Sep 04–Nov 04	Internship at the Marine Biology Laboratory, Trieste, Italy
Mar 04	Internship at Lammi Biological Station, Finland

Voluntary service, secondary and primary education

Jul 01–Jul 02	**European Voluntary Service at the 4H association Juuka, Finland**
1992–2001	**Christian-Dietrich-Grabbe-Gymnasium Detmold; Degree: Abitur**
1988–1992	**Primary school: Ferdinand-Weerth-Schule Detmold**

Research expeditions

Apr 09–May 09	UNIS project (Spitsbergen, Arctic)
Mar 08–Jun 08	CFL (CCGS *Amundsen*, Canadian Arctic)
Jul 07–Oct 07	ARK-XXII/2 (RV *Polarstern*, Central Arctic)
Aug 06–Oct 06	ANT-XXIII/7 (RV *Polarstern*, Weddell Sea, Antarctic)

Publications

- **Kramer M**, Struck U, Schukat A, Kiko R, Werner I (under revision) Trophic positions of Arctic and Antarctic sympagic meiofauna and its role in cryo-pelagic coupling identified by stable isotopes and fatty acids. *Mar Ecol Prog Ser*
- Marquardt M, **Kramer M**, Werner I (under revision) Vertical distribution patterns of sympagic meiofauna in fast and pack ice in the Canadian Beaufort Sea. *Polar Biol*
- Kiko R, Kern S, **Kramer M**, Mütze H (under revision) Colonization of newly forming Arctic sea ice by meiofauna – a case study for the future Arctic? *Mar Ecol Prog Ser*
- **Kramer M**, Swadling KM, Meiners KM, Kiko R, Scheltz A, Nicolaus M, Werner I (in press) Antarctic sympagic meiofauna in winter: comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions. *Deep-Sea Res II*. doi: 10.1016/j.dsr2.2010.10.029
- **Kramer M**, Kiko R (2010) Brackish meltponds on Arctic sea ice—a new habitat for marine metazoans. *Polar Biol*. doi: 10.1007/s00300-010-0911-z
- Siebert S, Anton-Erxleben F, Kiko R, **Kramer M** (2009) *Sympagohydra tuuli*: first report from sea ice of the central Arctic Ocean and insights into histology, reproduction and locomotion. *Marine Biol* 156:541–554
- Kiko R, **Kramer M**, Spindler M, Wägele H (2008) *Tergipes antarcticus* (Gastropoda, Nudibranchia): distribution, life cycle, morphology, anatomy and adaptation of the first mollusc known to live in Antarctic sea ice. *Polar Biol* 31:1383–1395

Conference contributions

- **Kramer M**, Schukat A, Struck U, Prowe F, Kiko R, Werner I (2010) Complexity of sea-ice food webs: the role of sympagic meiofauna. Oral presentation. IGS International Symposium on Sea Ice in the Physical and Biogeochemical System, Tromsø (Norway), June 2010
- **Kramer M**, Kiko R, Kern S, Schünemann H (2010) Colonisation of newly forming sea ice by meiofauna in the Central Arctic. Poster. ASLO Ocean Sciences Meeting, Portland (UK), February 2010
- Kiko R, John U, **Kramer M**, Lucassen M (2010) Adaptation to environmental extremes – insights from a doomed ecosystem: sea ice. Oral presentation. ASLO Ocean Sciences Meeting, Portland (UK), February 2010
- **Kramer M**, Schukat A, Struck U, Werner I (2009) Feeding ecology of Arctic sympagic meiofauna during CFL and ARK-XXII/2. Poster. CFL All-Hands Meeting, Winnipeg (Canada), November 2009
- Marquardt M, **Kramer M**, Werner I (2009) Vertical and horizontal distribution of sympagic meiofauna in fast and pack ice during CFL in the Canadian Arctic. Poster. CFL All-Hands Meeting, Winnipeg (Canada), November 2009
- **Kramer M**, Kiko R, Siebert S, Struck U, Werner I (2008) The role of sympagic meiofauna for the flow of organic matter in Arctic sea-ice food webs. Oral presentation. Arctic Net, Arctic Change Conference, Quebec City (Canada), December 2008

- Kiko R, **Kramer M**, Lucassen M, Schnack-Schiel S (2008) Ecophysiology of metazoans living inside sea ice. Oral presentation. 15th International Symposium on Polar Sciences, Incheon (Korea), September 2008
- **Kramer M**, Kiko R, Siebert S, Werner I (2008) Diversity, abundance and feeding ecology of Arctic and Antarctic sympagic meiofauna. Poster. SCAR/IASC IPY Open Science Conference, St. Petersburg (Russia), July 2008
- Kiko R, **Kramer M**, Lucassen M, Schnack-Schiel SB, Werner I (2008) Antarctic sea ice: habitat characteristics, metazoan fauna, and adaptations to low temperature. Oral presentation. SCAR/IASC IPY Open Science Conference, St. Petersburg (Russia), July 2008
- Werner I, Ershova A, Kiko R, **Kramer M**, Krapp R, Preobrazhenskaya O, Schünemann H, Siebert S (2008) News from the sea-ice biological research in the Arctic and Antarctic. Oral presentation. Deutsche Gesellschaft für Polarforschung, 23. International Polar Meeting, Münster (Germany), March 2008

Lebenslauf

Maike Kramer
Geboren: 30. Juni 1982, Bottrop
Nationalität: deutsch
Familienstand: ledig

Promotion und wissenschaftliche Arbeit

Seit 10.07	**Wissenschaftliche Mitarbeiterin (bis 14.10.10) und Doktorandin am Institut für Polarökologie, Christian-Albrechts Universität zu Kiel** Thema: Die Rolle der sympagischen Meiofauna in arktischen und antarktischen Meereis-Nahrungsnetzen
Seit 08.09	Mitglied der Integrated School of Ocean Sciences, Graduiertenkolleg im Exzellenzcluster „Ozean der Zukunft“

Studium

09.02–10.07	**Studium der Marinen Umweltwissenschaften an der Carl von Ossietzky Universität Oldenburg; Abschluss: Diplom** • Fächer: Umweltwissenschaften (Pflichtfach), Mathematik/Physik (Hauptfach), Biologie und Chemie/Geologie (Nebenfächer), Umweltrecht (Wahlpflichtfach), Sprachen und Politik (Wahlfächer) • Stipendium der Studienstiftung des deutschen Volkes
03.07–10.07	Diplomarbeit am Institut für Polarökologie, Kiel; Thema: Sympagische Meiofauna im antarktischen Packeis im Winter
01.05–08.05	Auslandssemester an der Universität Helsinki, Finnland
09.04–11.04	Praktikum am Meeresbiologischen Laboratorium, Triest, Italien
03.04	Praktikum an der Biologischen Station Lammi, Finnland

Freiwilligendienst, Schulbildung

07.01–07.02	**Europäischer Freiwilligendienst beim 4H-Verein Juuka, Finnland**
1992–2001	**Christian-Dietrich-Grabbe-Gymnasium Detmold; Abschluss: Abitur**
1988–1992	**Grundschule: Ferdinand-Weerth-Schule Detmold**

Forschungsexpeditionen

04.09–05.09	UNIS-Projekt (Spitzbergen, Arktis)
03.08–06.08	CFL (CCGS *Amundsen*, Kanadische Arktis)
07.07–10.07	ARK-XXII/2 (RV *Polarstern*, Zentrale Arktis)
08.06–10.06	ANT-XXIII/7 (RV *Polarstern*, Weddellmeer, Antarktis)

Veröffentlichungen

- **Kramer M**, Struck U, Schukat A, Kiko R, Werner I (in Revision) Trophic positions of Arctic and Antarctic sympagic meiofauna and its role in cryo-pelagic coupling identified by stable isotopes and fatty acids. *Mar Ecol Prog Ser*
- Marquardt M, **Kramer M**, Werner I (in Revision) Vertical distribution patterns of sympagic meiofauna in fast and pack ice in the Canadian Beaufort Sea. *Polar Biol*
- Kiko R, Kern S, **Kramer M**, Mütze H (in Revision) Colonization of newly forming Arctic sea ice by meiofauna – a case study for the future Arctic? *Mar Ecol Prog Ser*
- **Kramer M**, Swadling KM, Meiners KM, Kiko R, Scheltz A, Nicolaus M, Werner I (im Druck) Antarctic sympagic meiofauna in winter: comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions. *Deep-Sea Res II*. doi: 10.1016/j.dsr2.2010.10.029
- **Kramer M**, Kiko R (2010) Brackish meltponds on Arctic sea ice—a new habitat for marine metazoans. *Polar Biol*. doi: 10.1007/s00300-010-0911-z
- Siebert S, Anton-Erxleben F, Kiko R, **Kramer M** (2009) *Sympagohydra tuuli*: first report from sea ice of the central Arctic Ocean and insights into histology, reproduction and locomotion. *Marine Biol* 156:541–554
- Kiko R, **Kramer M**, Spindler M, Wägele H (2008) *Tergipes antarcticus* (Gastropoda, Nudibranchia): distribution, life cycle, morphology, anatomy and adaptation of the first mollusc known to live in Antarctic sea ice. *Polar Biol* 31:1383–1395

Konferenzbeiträge

- **Kramer M**, Schukat A, Struck U, Prowe F, Kiko R, Werner I (2010) Complexity of sea-ice food webs: the role of sympagic meiofauna. Vortrag. IGS International Symposium on Sea Ice in the Physical and Biogeochemical System, Tromsø (Norwegen), Juni 2010
- **Kramer M**, Kiko R, Kern S, Schünemann H (2010) Colonisation of newly forming sea ice by meiofauna in the Central Arctic. Poster. ASLO Ocean Sciences Meeting, Portland (UK), Februar 2010
- Kiko R, John U, **Kramer M**, Lucassen M (2010) Adaptation to environmental extremes – insights from a doomed ecosystem: sea ice. Vortrag. ASLO Ocean Sciences Meeting, Portland (UK), Februar 2010
- **Kramer M**, Schukat A, Struck U, Werner I (2009) Feeding ecology of Arctic sympagic meiofauna during CFL and ARK-XXII/2. Poster. CFL All-Hands Meeting, Winnipeg (Kanada), November 2009
- Marquardt M, **Kramer M**, Werner I (2009) Vertical and horizontal distribution of sympagic meiofauna in fast and pack ice during CFL in the Canadian Arctic. Poster. CFL All-Hands Meeting, Winnipeg (Kanada), November 2009
- **Kramer M**, Kiko R, Siebert S, Struck U, Werner I (2008) The role of sympagic meiofauna for the flow of organic matter in Arctic sea-ice food webs. Vortrag. Arctic Net, Arctic Change Conference, Quebec Stadt (Kanada), Dezember 2008
- Kiko R, **Kramer M**, Lucassen M, Schnack-Schiel S (2008) Ecophysiology of metazoans living inside sea ice. Vortrag. 15th International Symposium on Polar Sciences, Incheon (Korea), September 2008

- **Kramer M**, Kiko R, Siebert S, Werner I (2008) Diversity, abundance and feeding ecology of Arctic and Antarctic sympagic meiofauna. Poster. SCAR/IASC IPY Open Science Conference, St. Petersburg (Russland), Juli 2008
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- Werner I, Ershova A, Kiko R, **Kramer M**, Krapp R, Preobrazhenskaya O, Schünemann H, Siebert S (2008) News from the sea-ice biological research in the Arctic and Antarctic. Vortrag. Deutsche Gesellschaft für Polarforschung, 23. International Polar Meeting, Münster (Deutschland), März 2008

Erklärung

Diese Abhandlung ist – abgesehen von der Beratung durch die Betreuerin – nach Inhalt und Form meine eigene Arbeit. Die Arbeit hat bisher weder ganz noch teilweise einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegen. Die Arbeit ist unter Einhaltung der Regeln guter wissenschaftlicher Praxis der Deutschen Forschungsgemeinschaft entstanden.

Kapitel 2 ist im Druck zur Veröffentlichung in Deep-Sea Research II, Kapitel 3 ist in Polar Biology veröffentlicht, Kapitel 4 ist in Revision zur Veröffentlichung in Marine Ecology Progress Series.

Kiel, den 30. November 2010

Maike Kramer