

Seasonal Dynamics, Cryo-Pelagic Interactions and Metabolic Rates of Arctic Pack-Ice and Under-Ice Fauna – A Review –

by Iris Werner¹

Abstract: Arctic pack-ice and the adjacent under-ice water are unique ecosystems characterized by specific habitat structures (ice cover and thickness, brine-channel-system and morphology of the ice underside) and special environmental conditions (freezing-melting cycle of the ice, variations in the availability of space and substrate, strong gradients in the distribution of biomass and food sources). The ice underside is the only interface in the marine environment at which two habitats (ice and water) only differ in their aggregate state, and merge into each other permanently by the processes of ice growth and decay. In this comparatively thin layer on top of the ocean, a diverse community comprising genuine sympagic species as well as members of the pelagic and of the benthic fauna, all mostly with a clear dominance of small species, has developed in order to colonize this unique ecosystem.

The Arctic pack-ice and sub-ice ecosystems play several important ecological roles for the associated fauna, such as providing a permanent (for autochthonous species) or a temporary (for allochthonous species) habitat to thrive, reproduce and grow in, and a solid substrate to attach to. Due to the permanent motion of the pack ice, it also serves as a spreading vehicle for the inhabiting fauna, leading to a strikingly similar species composition and distribution across the entire Arctic Ocean and its marginal seas. The accumulation of autotrophic and heterotrophic biomass in the ice and at the ice underside provides rich food sources, which are available and abundant during longer periods throughout the year than in the free water column. This favourable food availability, and the special structures of the ice underside protruding into the under-ice layer providing sheltered areas render the under-ice habitat as an ideal nursery ground for young and delicate stages of numerous species.

The sea-ice habitats are connected to adjacent ecosystems, above all with the pelagic realm, by a variety of two-way coupling processes such as the flow of organic matter and energy, as well as by exchange and migration of organisms. Incorporation of particles and organisms from the water column and the sea floor into newly forming sea ice on the one hand, and release and downward flux of particles and organisms from decaying sea ice on the other hand is an exchange process without much active contribution of the organisms themselves, but which connects the food webs on the sea floor, in the water column, and in the sea ice. Members of the sympagic fauna, mainly copepods, migrate through the ice-water interface, pelagic copepods and amphipods migrate between the sub-ice water and deeper waters, and even benthic amphipods can be closely associated with the underside of Arctic pack-ice, connecting the benthic with the sympagic ecosystem by their active migrations. Although some of these migrations are due to reproductive processes, e.g., the release and accumulation of eggs below the ice, most migrations are related to the search for food. Feeding activities play a key role in cryo-pelagic coupling processes and thus in the transfer of matter and energy between sea-ice, water column, and sea floor. Amphipods grazing on ice-produced organic matter such as ice algae, detritus, or ice fauna, release their comparatively large faecal pellets into the underlying water column, thus forming a direct link between the sea ice and the pelagic ecosystem. Several species of Arctic under-ice amphipods also prey on pelagic copepods caught from the water column, thus forming a pathway of organic matter and energy flux from the pelagic to the sea-ice realm. Such diverse feeding habits reflect an adaptation to an environment with a highly variable and sometimes scarce food supply. None of the amphipod species exclusively grazes on ice algae during the whole year, indicating that the sympagic food-web structure is definitely more complex than previously thought.

Despite the extreme seasonality in high-Arctic light regime, air temperature, sea-ice conditions, and marine primary production, the seasonal dynamics of pack-ice and under-ice (or sub-ice) habitats and fauna are comparatively moderate. The ice-associated habitats change with the seasons mainly in

response of two processes: the temperature-dependent freeze–melt cycle of the ice, and the light-dependent primary production of ice algae and sub-ice phytoplankton. Although faunal diversity is lower in winter than in other seasons, Arctic pack-ice habitats are not at all deserted during winter, and major components of the sympagic fauna are present and active all year round. The most pronounced seasonal fluctuations of physical properties occur in the upper and middle parts of the ice, preventing an intense colonization of these habitats by sympagic metazoans. In contrast, environmental conditions in the lower part of the ice, at the ice underside, and in the under-ice water show only moderate to low seasonal variations, favouring the accumulation of sea-ice organisms in the bottom part of Arctic pack ice during all seasons, a permanent colonization of the ice underside by autochthonous amphipods, and a rather stable metazoan biomass in the under-ice water all year round.

Seasonal differences in species and stage composition both in the ice and at the ice underside point to algal biomass as food source with its seasonal fluctuations as the major factor controlling herbivorous grazers in these habitats. For most taxa of the sympagic meiofauna, the overwintering strategies remain not fully understood as yet. The most probable hypothesis appears to be the strategy that low numbers of individuals and mainly non-feeding stages survive the winter in the pack-ice habitat and build up new populations by reproduction in spring, as soon as feeding conditions improve. The different feeding behaviours and overwintering strategies of the four species of autochthonous under-ice amphipods, including seasonal shifts in food preferences as well as the use of storage lipids, present an effective niche separation in this environment, which has been successfully colonized by only these few species. Due to the relatively stable environmental conditions, seasonal adaptations in metabolism, which is generally low due to the energy-saving lifestyle attached to the ice underside, are not required in Arctic under-ice amphipods. In the under-ice habitat, the most conspicuous seasonal phenomenon is the presence of a thin layer of meltwater with reduced salinity below the ice in summer. Most pelagic species of sub-ice fauna show their seasonal abundance minima during summer, pointing to the adverse effect of the low-salinity water layer acting as a barrier, in particular for sensitive juvenile stages. In contrast, all sympagic species show their abundance maxima during this time of the year, implicating that melt-water flushing is the major transport process for these organisms from the ice to the under-ice water.

The shrinking and thinning of the Arctic sea-ice cover, as well as an increase of low-salinity melt-water in the surface waters of the Arctic Ocean, will certainly have tremendous effects on the entire sympagic ecosystem. A decreasing ice cover simply means the loss of a unique habitat for a specialized flora and fauna, the potential regression of perennial sea ice leads to the disappearance of the autochthonous sympagic fauna. The major environmental factors controlling abundances of dominant species and groups in the sympagic habitats are either directly (ice cover, ice thickness, under-ice morphology, under-ice hydrography) or indirectly (primary productivity) influenced by changes due to climate warming in the Arctic. Shifts in species composition and dominance, and thus changes in the specific sea-ice related food-web structures, can be expected in a changing environment. Thus, the effects of global warming will certainly have adverse effects on the Arctic pack-ice and under-ice as well as on adjacent and interconnected ecosystems, leading to the extinction of several endemic species in the worst case.

Zusammenfassung: Das arktische Packeis und das angrenzende Untereis-Wasser sind einzigartige Ökosysteme, die durch spezifische Habitatstrukturen (Eisbedeckungsgrad und Eisdicke, Sole-Kanalsystem, Morphologie der Eisunterseite) und spezielle Umweltbedingungen (Gefrier–Schmelz–Zyklus des Eises, Variationen in der Verfügbarkeit von Raum und Substrat, starke Gradienten in der Verteilung von Biomasse und Nahrungsquellen) charakterisiert sind. Die Eisunterseite ist die einzige Grenzschicht im marinen Milieu, an der zwei Lebensräume (Eis und Wasser) sich nur in ihrem Aggregatzustand unterscheiden und durch die Prozesse von Eisbildung und -aufbruch permanent ineinander übergehen. In dieser vergleichsweise dünnen Schicht auf der Oberfläche des Ozeans hat sich eine diverse Lebensgemeinschaft bestehend aus genuinen sympagischen (= eisassoziierten) Arten sowie aus Vertretern der

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pelagischen und benthischen Fauna, alle mit einer deutlichen Dominanz von kleinen Arten, entwickelt, um dieses einmalige Ökosystem zu besiedeln.

Die arktischen Packeis- und Untereis-Systeme spielen mehrere ökologische Rollen für die assoziierte Fauna, so z.B. indem sie einen permanenten (für autochthone Arten) oder einen temporären (für allochthone Arten) Lebensraum zum Nahrungserwerb, Fortpflanzung und Entwicklung bieten, sowie ein solides Substrat zum Anheften. Das Packeis dient auf Grund seiner permanenten Drift auch als ein Verbreitungsmedium für die es besiedelnde Fauna, was zu einer erstaunlich ähnlichen Artenzusammensetzung und Verteilung im gesamten Arktischen Ozean und seinen Randmeeren führt. Die Ansammlung von autotropher und heterotropher Biomasse im Eis und an der Eisunterseite stellt reichhaltige Nahrungsquellen dar, die während längerer Zeitspannen im Laufe des Jahres verfügbar sind als in der freien Wassersäule. Diese günstige Nahrungsverfügbarkeit und die speziellen Strukturen an der Eisunterseite, die in die Wassersäule hineinragen und somit geschützte Areale bilden, machen das Untereis-Habitat zu einem idealen Aufzucht habitat für junge und empfindliche Stadien zahlreicher Arten.

Die Meereis-Habitats sind über eine Vielzahl von zweiseitigen Kopplungsprozessen, wie z.B. Flüsse von organischem Material und Energie sowie Austausch und Wanderungen von Organismen, mit angrenzenden Ökosystemen verbunden, vor allem mit dem Pelagial. Die Inkorporation von Partikeln und Organismen aus der Wassersäule und vom Meeresboden in sich bildendes Neueis einerseits und die Freisetzung und Sedimentation von Partikeln und Organismen aus dem aufbrechenden Eis andererseits sind Austauschprozesse ohne viel aktive Beteiligung der Organismen selbst, die aber die Nahrungsnetze auf dem Meeresboden, in der Wassersäule und im Eis miteinander verbinden. Vertreter der sympagischen Fauna, v.a. Copepoden, wandern durch die Eis-Wasser-Grenzschicht, pelagische Copepoden und Amphipoden wandern zwischen dem Untereis-Wasser und größeren Tiefen hin und her, und sogar benthische Amphipoden können eng mit der arktischen Eisunterseite assoziiert sein und so das benthische mit dem sympagischen Ökosystem durch ihre aktiven Wanderungen verbinden. Obwohl einige dieser Wanderungen an reproduktive Prozesse gekoppelt sind, z.B. die Freisetzung und Akkumulation von Eiern unter dem Eis, so stehen doch die meisten Wanderungen mit der Nahrungssuche im Zusammenhang. Fressaktivitäten spielen eine Schlüsselrolle in kryo-pelagischen Kopplungsprozessen und damit für den Transfer von Material und Energie zwischen dem Meereis, der Wassersäule und dem Meeresboden. Amphipoden fressen organisches Material aus dem Eis, z.B. Eisalgen, Detritus, Eisfauna, und entlassen ihre relativ großen Kotballen in die darunterliegende Wassersäule, was eine direkte Verbindung zwischen Meereis und Pelagial darstellt. Mehrere Arten von arktischen Untereis-Amphipoden erbeuten auch pelagische Copepoden aus der Wassersäule und formen damit einen Verbindungsweg für organisches Material und einen Energiefluss zwischen dem Pelagial und dem Meereis. Solche diversen Fressgewohnheiten stellen eine Anpassung an eine Umwelt mit einer hochvariablen und manchmal knappen Nahrungsverfügbarkeit dar. Keine Amphipodenart ernährt sich ausschließlich von Eisalgen über das ganze Jahr, was daraufhin deutet, dass das sympagische Nahrungsnetz definitiv komplexer strukturiert ist als bislang angenommen.

Trotz der extremen Saisonalität im hocharktischen Lichtregime, Lufttemperatur, Meereisbedeckung und mariner Primärproduktion ist die saisonale Dynamik der Packeis- und Untereis-Habitats und ihrer Fauna vergleichsweise moderat. Die eisassoziierten Lebensräume verändern sich im Laufe der Jahreszeiten vor allem durch zwei Prozesse: den temperaturabhängigen Gefrier-Schmelz-Zyklus des Eises und die Licht abhängige Primärproduktion der Eisalgen und des Untereis-Phytoplanktons. Obwohl die Diversität der Fauna im Winter niedriger ist als in anderen Jahreszeiten, sind die arktischen Packeis-Habitats keineswegs unbesiedelt während des Winters, und einige Vertreter der sympagischen Fauna sind das ganze Jahr über vorhanden und aktiv. Die am stärksten ausgeprägten saisonalen Fluktuationen der physikalischen Eigenschaften treten in den oberen und mittleren Bereichen des Eises auf und verhindern damit eine intensive Besiedlung dieser Habitats durch sympagische Metazoen. Im Gegensatz dazu zeigen die Umweltbedingungen im unteren Teil des Eises, an der Eisunterseite und im Untereis-Wasser nur moderate oder geringe saisonale Variationen und begünstigen somit eine Anreicherung von Organismen als Bodengemeinschaft im Eis, eine permanente Besiedlung der Eisunterseite durch autochthone Amphipoden und eine ziemlich stabile Metazoenbiomasse im Untereis-Wasser während des ganzen Jahres.

Saisonale Unterschiede in der Zusammensetzung von Arten und Stadien im Eis und an der Eisunterseite weisen auf die Nahrungsquelle Eisalgenbiomasse mit ihren saisonalen Fluktuationen als Hauptkontrollfaktor für die Herbivoren in diesen Lebensräumen hin. Für die meisten Taxa der sympagischen Meiofauna sind die Überwinterungsstrategien bislang noch nicht vollständig aufgeklärt. Als wahrscheinlichste Hypothese wird die Strategie angenommen, dass nur wenige Individuen und hauptsächlich nicht-fressende Stadien den Winter im Packeis überstehen und dann durch Reproduktion neue Populationen im Frühling aufbauen, sobald sich die Nahrungsbedingungen verbessert haben. Die unterschiedlichen Fressverhalten und Überwinterungsstrategien der vier Arten von autochthonen Untereis-Amphipoden, die saisonale Verschiebungen des Nahrungsspektrums sowie den Abbau von Speicherlipiden einschließen, stellt eine effektive Einnischung in diesem Lebensraum dar, der nur von diesen vier Arten erfolgreich besiedelt worden ist. Auf Grund der relativ

stabilen Umweltverhältnisse sind saisonale Adaptationen des Stoffwechsels, der wegen der Energie sparenden Lebensweise – hängend an der Eisunterseite – generell niedrig ist, bei arktischen Untereis-Amphipoden nicht erforderlich. Das auffälligste saisonale Phänomen im Untereis-Habitat ist im Sommer das Auftreten einer dünnen Schmelzwasserschicht mit reduziertem Salzgehalt unter dem Eis. Die meisten pelagischen Arten der Untereis-Fauna haben im Sommer ihr saisonales Abundanzminimum, was auf den ungünstigen Effekt der ausgesüßten Wasserschicht hinweist, die möglicherweise als eine Barriere vor allem für empfindliche Jugendstadien wirkt. Im Gegensatz dazu zeigen alle sympagischen Arten ihr Abundanzmaximum zu dieser Zeit, wohl weil der Schmelzwasserabfluss der wichtigste Transportprozess dieser Organismen vom Eis in das Untereis-Wasser darstellt.

Der Rückgang von Eisbedeckung und Eisdicke sowie die Zunahme von ausgesüßtem Schmelzwasser in der Oberflächenschicht des Arktischen Ozeans werden sicherlich signifikante Effekte auf das gesamte sympagische Ökosystem haben. Der Rückgang des Meereises bedeutet schlicht den Verlust eines einzigartigen Lebensraumes für eine spezialisierte Flora und Fauna, die mögliche Reduzierung von mehrjährigem Eis wird zu einem Verschwinden der autochthonen sympagischen Fauna führen. Die wichtigsten Umweltfaktoren, die die Abundanzen der dominanten Arten und Faunengruppen in den sympagischen Habitats kontrollieren, sind entweder direkt (Eisbedeckungsgrad, Eisdicke, Untereis-Morphologie, Untereis-Hydrographie) oder indirekt (Primärproduktion) von den Klima induzierten Veränderungen in der Arktis beeinflusst. Verschiebungen in den Artenzusammensetzungen und Dominanzen und damit Veränderungen in den spezifischen, Eis assoziierten Nahrungsnetzen können in einer sich verändernden Umwelt erwartet werden. Die Auswirkungen der globalen Erwärmung wird sicherlich ungünstige Effekte auf die arktischen Packeis- und Untereis-Gemeinschaften sowie auf angrenzende und verbundene Ökosysteme haben, bis hin zum Aussterben mehrerer endemischer Arten im schlimmsten Fall.

GENERAL INTRODUCTION

The long-term average sea-ice cover in the Arctic Ocean and its marginal seas ranges between 7×10^6 km² in summer (September) and 14×10^6 km² in winter (March), with the central parts being ice covered all year. Multi-year ice with thicknesses >2 m is the dominant ice type in the Arctic Ocean (MAYKUT 1985), and a prerequisite for the development and maintenance of an autochthonous sympagic (i.e. ice-associated) community. The pack ice is in constant motion, following large- and small-scale circulation patterns, e.g., the Transpolar Drift System from the ice-forming areas on the Siberian shelves throughout the Arctic Ocean, with the major outflow through Fram Strait into the Greenland Sea (COLONY & THORNDIKE 1985, AAGAARD & CARMACK 1989). This mainly multi-year ice will melt on the way south in the Greenland Sea.

Recent studies indicate that the Arctic sea-ice cover is undergoing significant climate-induced changes, regarding both its extent and thickness. Satellite-derived estimates of maximum ice extent show a net reduction between 1978 and 1996 at an average rate of 3 % per decade (PARKINSON et al. 1999), or even of 9 % per decade in the perennial sea-ice cover (COMISO 2002). The sea-ice area for the Arctic shows near-record minima for the summers of 2002-2004. The recent years represent a unique event because they have a year-to-year persistence of minimum ice extents (STROEVE et al. 2005). Data on ice thickness, derived from submarine-based upward looking sonar, also suggest a net thinning of the sea-ice cover since 1958 (ROTHROCK et al. 1999, WADHAMS & DAVIS 2000). The thinning averaged 40 %, representing a decrease from about 3 m to <2 m ice thickness. Climate models are in general agreement that Arctic ice extent and thickness will continue to decline over the next century as the global climate warms (SERREZE et al. 2003).

Sea ice is not only an important factor influencing climate, hydrography, and geology, but also harbours unique and

extreme habitats for a diverse and highly specialized sympagic flora and fauna, including bacteria, fungi, unicellular algae, proto- and metazoans (HORNER et al. 1992). Major primary producers in the ice are pennate diatoms and numerous flagellate taxa (HORNER 1985, IKÁVALKO & GRADINGER 1997), which have been reported to contribute up to 25 % of the total marine primary production in the Arctic (LEGENDRE et al. 1992). For metazoans (meio- and macrofauna) inhabiting the brine-channel system within the sea-ice matrix (WEISSENBARGER 1992) or the ice-water interface, the ice serves either as a temporary breeding, nursery and feeding ground or refuge area (allochthonous sympagic animals), or as a permanent habitat during the entire life-cycle (autochthonous sympagic animals). Abundance and distribution of sympagic fauna is largely controlled by abiotic factors such as ice conditions, temperature, salinity, and space, but also by biological factors such as food availability and predation pressure (see reviews by GRADINGER 2001, SCHNACK-SCHIEL 2003, and references therein).

Dominant taxonomical groups of sympagic metazoan meiofauna in Arctic pack ice are nematodes, turbellarians, rotifers, and copepods (FRIEDRICH 1997, SCHÜNEMANN 2004). They are very well adapted to the extreme and variable conditions in the sea-ice habitat (FRIEDRICH 1997, GRAINGER & MOHAMMED 1990, KREMBS et al. 2000), but also occur in the under-ice water (HORNER & SCHRADER 1982, WERNER & MARTINEZ ARBIZU 1999). Sympagic meiofauna organisms are believed to feed on bacteria, algae, and protists (GRAINGER et al. 1985, GRAINGER & HSIAO 1990) or on dissolved organic matter (TCHESUNOV & RIEMANN 1995) within the ice, and are in turn part of the diet of predators at the ice-water interface or in the under-ice water, such as amphipods, ctenophores, and fish (BRADSTREET & CROSS 1982, CAREY & BOUDRIAS 1987, GRAINGER & HSIAO 1990).

The underside of Arctic pack-ice is a habitat with special abiotic and biotic conditions (WERNER & LINDEMANN 1997, POLTERMANN 1997). The macrofauna at this interface between ice and water comprises almost exclusively gammaridean amphipods. Species composition and abundances mainly varies with age, type, and morphology of the ice (HOP et al. 2000 and references therein). In perennial pack-ice, the most common species are *Apherusa glacialis*, *Onisimus glacialis*, *O. nanseni* and *Gammarus wilkitzkii*, as well as the gadid fish species *Boreogadus saida* (LØNNE & GULLIKSEN 1989, GRADINGER & BLUHM 2004). The amphipod species have a circumpolar distribution and are considered autochthonous, i.e. they occur in the under-ice habitat during all seasons and spend their entire life-cycle here (LØNNE & GULLIKSEN 1991a, POLTERMANN et al. 2000), being well adapted to changes in temperature and salinity regimes at the ice-water interface (AARSET 1991). These under-ice amphipods feed on ice- and under-ice flora and fauna as well as on ice-bound detritus (WERNER 1997, POLTERMANN 2001, SCOTT et al. 1999), and form an important trophic link to the pelagic realm, because they represent an important part in the diet of pelagic predators such as polar cod *Boreogadus saida* (LØNNE & GULLIKSEN 1989) and diving seabirds like black guillemot *Cephus grylle* and little auk *Alle alle* (LØNNE & GABRIELSEN 1992).

The boundary layer between the underside of the ice and the underlying water column is a further particular habitat influenced by both the ice, e.g., freezing-melting cycle, and the

pelagic realm, e.g., supply of nutrients. Animals found in this boundary layer (here defined down to 1 m depth below the ice) have been termed sub-ice fauna (HORNER et al. 1992). In contrast to the under-ice amphipods, they are generally not in physical contact with the ice underside. They are either sympagic (originating from the ice) or pelagic, and they use this habitat for shelter and as a feeding and nursery ground (HORNER & MURPHY 1985, WERNER & MARTINEZ ARBIZU 1999). Major groups of this fauna are calanoid, cyclopoid, and harpacticoid copepods, as well as foraminifera and pteropod gastropods (HORNER & MURPHY 1985, HERMAN & ANDERSEN 1989, WERNER & MARTINEZ ARBIZU 1999). The sub-ice community is also considered an important trophic link between sea-ice derived primary production, on which sub-ice organisms graze, and higher trophic levels in the water column (GRAINGER et al. 1985, CONOVER et al. 1986, RUNGE & INGRAM 1988, GRAINGER & HSIAO 1990). A key macrofaunal species in the sub-ice habitat is the hyperiid amphipod *Themisto libellula* (LØNNE & GULLIKSEN 1991a,b, WESLAWSKI et al. 1993), which connects the sea ice with deeper waters by means of feeding activities and migrations (BRADSTREET & CROSS 1982, AUDEL et al. 2002).

Despite great advances in high-polar pack-ice research, which have become possible due to the operation of powerful research icebreakers during the last 20 years, there have been and still are many open questions about the functioning of the sea-ice ecosystems in general, the ecological roles and adaptations of the sympagic fauna in particular, and thus the possible reactions of the system to environmental changes. The general objective of this review is to summarize mostly recently published data and observations in order to complement and advance our knowledge of the ecology of Arctic pack-ice and under-ice fauna focussing on the following major issues:

- (1) One crucial problem in our understanding of life-cycles and adaptations of sympagic organisms is the paucity of seasonal studies from the high Arctic. Which are the environmental factors controlling diversity, abundance, and distribution of sympagic fauna during different seasons? How do sympagic animals survive the dark and food-limited Arctic winter?
- (2) With regard to the ecological role of the pack-ice for adjacent ecosystems, biologically mediated processes connecting sea-ice and underlying water column come into the focus of interest. By which matter and energy flows are the different ecosystems connected? Can dominant processes of cryo-pelagic coupling be quantified?
- (3) Because energetics are considered a central feature of adaptation to temperature, the study on metabolic rates of sympagic organisms could be a major tool in order to answer the questions about their adaptation and survival strategies in this extreme environment. Do metabolic rates of sympagic species differ from those of pelagic and benthic species?

The research summarized in this review can therefore be divided into three topics, which are, however, connected by their ecological interrelationships. The themes are:

- (1) Seasonal dynamics in the Arctic ice and under-ice habitat and fauna,
- (2) Coupling processes between Arctic pack ice and adjacent ecosystems,
- (3) Respiration rates of amphipods below Arctic pack ice.

Regarding our results summarized here, field data and mate-

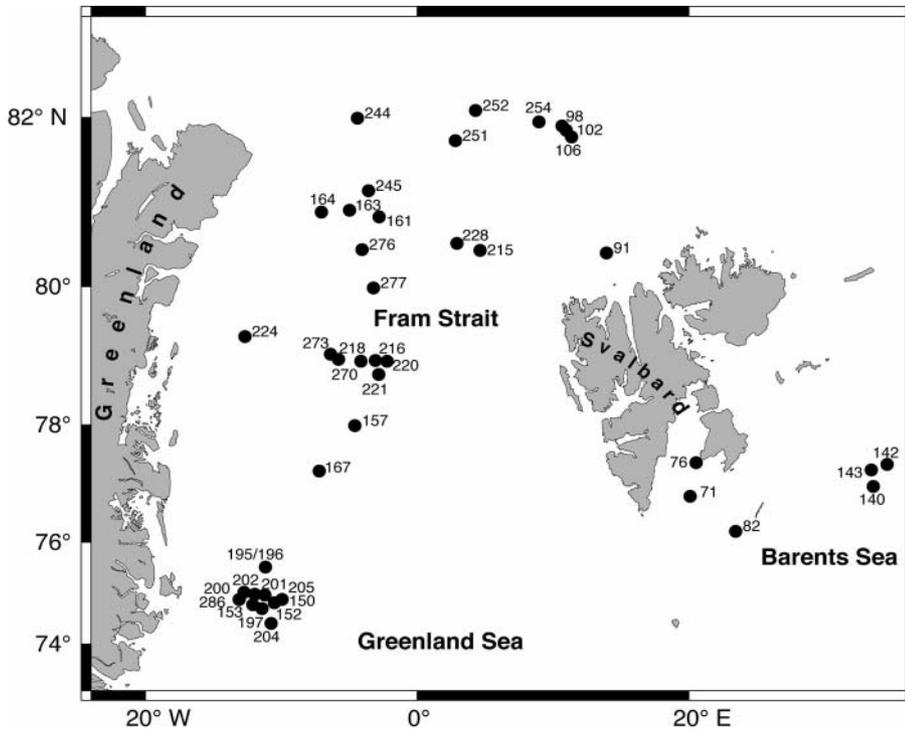


Fig. 1: Pack-ice stations sampled during different expeditions to the Arctic for the research on which this review is based. Station numbers are days of the year.

Abb. 1: Packeisstationen, die während verschiedener Arktis-Expeditionen für die in dieser Übersicht zusammengefassten Untersuchungen beprobt wurden. Die Stationsnummern stellen den Tag des Jahres dar.

rial for experimental and biochemical work were collected at numerous ice stations during several expeditions with the German research icebreaker RV “Polarstern” to the northern Greenland Sea and Fram Strait as well as to the western Barents Sea in different seasons of the years 1994–2003 (Fig. 1). Material and methods of all investigations are extensively described in the respective original papers cited, and will thus not appear in this review.

SEASONAL DYNAMICS IN THE ARCTIC PACK-ICE AND UNDER-ICE HABITAT AND FAUNA

Polar regions are generally characterized by pronounced seasonal variations in air temperature, light regime, and primary production. Furthermore, the polar marine ecosystems are strongly influenced by the seasonally changing sea-ice cover and the related processes of freezing and new-ice production, and melting and sea-ice decay (MAYKUT 1985). Despite this obvious seasonality, the task to define seasons, in particular biological seasons, in the high-Arctic marine ecosystem is not straight-forward. Ecologically defined seasons will not match the calendrical timing very well. For instance, in March, when the calendar spring starts on the northern hemisphere, ice cover is at maximum extension in the Arctic (MAYKUT 1985), and algal biomass both in the ice and in the under-ice water is close to zero (HORNER & SCHRADER 1982, THOMAS et al. 1995, WERNER 2005, SCHÜNEMANN & WERNER 2005). On the other hand, in September, when the calendar autumn starts, ice cover in the Arctic is at its minimum (MAYKUT 1985), and ice-algal biomass in pack ice can reach maximum values or start to decrease again (WERNER & GRADINGER 2002). Seasons are defined in our study area and for our sampling dates as follows:

(a) Winter (March/April) with a very dense pack-ice cover, rapid new ice formation in leads and polynyas, very low air temperatures, a thick snow cover on the ice, freezing at the ice–water interface, and very low concentrations of chloro-

phyll *a* in the ice and under-ice water.

(b) Spring (May/June) with a gradually decreasing ice cover, increasing air temperatures, the onset of snow melt, and increasing chl *a* concentrations.

(c) Summer (July/August/September) with comparatively less dense ice cover, rather melting than freezing at the ice–water interface and between floes, high air temperatures, melt-ponds on the surface of the ice, and high concentrations of chl *a*.

(d) Autumn (September/October) with new-ice formation again, refreezing of surface melt-ponds, decreasing air temperature, and low concentrations of chl *a* in the under-ice water (Tab. 1). These definitions of seasons will be used throughout this review.

A general problem with seasonal studies in the high-Arctic pack-ice, including the present one, is the usual practice of sampling different seasons in different years. Hence, one can not exclude effects of interannual variabilities (LØNNE & GULLIKSEN 1991a,b, GRADINGER 1998, WERNER & GRADINGER 2002, WERNER & AUER 2005, SCHÜNEMANN & WERNER 2005, WERNER 2006). This is, however, an inevitable compromise in high-Arctic off-shore research which has to be accepted until better possibilities for seasonal studies, such as the year-long SHEBA drift-ice station (PEROVICH et al. 1999), become more common and also accessible for biological research. A statistical comparison of our two early summer (July/August) cruises to the same area in 1994 and 2000 do not show any significant differences in species composition, abundance or biomass of the sub-ice fauna (WERNER 2006), indicating that the variations between years may be small as compared to the seasonal patterns observed. Regional variabilities on the scale of the area studied are also believed to be of minor importance, because both in the sea-ice interior (GRADINGER 1999a, SCHÜNEMANN 2004) as well in the upper water column of the Arctic Ocean, species composition and abundance of metazoans are usually strikingly similar (GRAINGER 1965, HOPCROFT et al. 2004). Almost all stations sampled in the present study were in multi-year ice within or from the Trans-

Exped. ARK year	Time	Season	Air temp. (°C)	Ice cover (n/10)	Ice thickness (m)	Temp. ice (°C)	Salinity ice (brine)	Temp. 0-1 m (°C)	Salinity 0-1 m	Chl <i>a</i> ice (mg m ⁻³)	Chl <i>a</i> 0-1 m (µg l ⁻¹)	POC 0-1 m (µg l ⁻¹)
XIX/1 2003	Mar/ Apr	Winter	-28.5 -2.7	7-10	0.8 - 2.5	-21.9 -2.4	42.5-223.7	-1.9 -1.8	34.0-34.6	0.12-0.60	0.02-0.05	150-572
XIII/1 1997	May/ June	Spring	-10.4 +2.1	4-9	1.6 - 3.5	-7.1 -0.2*	7->100*	-1.8 -1.4	31.8-34.6	0.73-2.63	0.01-0.45	nd
X/1 1994	July/ Aug	early summer	-1.7 +2.5	3-9	2.1 - 3.5	-1.6 +0.8*	2-30*	-1.7 -1.0	16.7-32.1	0.13-2.94	0.30-2.65	nd
XVI/2 2000	Aug	early summer	-2.4 +0.5	1-10	2.3 - 3.3	-0.8 -2.1	3.7-37.4	-1.8 -0.3	29.9-33.3	nd	0.03-1.53	234-405
XVIII/2 2002	Sept	late summer	-7.2 -0.5	1-9	1.4 - 3.4	-5.6 -2.0	5.5-42.5	-1.8 -1.6	30.5-32.5	0.25-2.31	0.12-1.42	204-352
XI/2 1995	Sept/ Oct	Autumn	-10.8 -4.5	7-10	1.6 - 3.3	-6.4 +0.1*	3.5-100*	-1.6 -1.5	31.5-32.4	1.43-18.40	0.03-0.33	nd

Tab. 1: Environmental conditions in the pack-ice and under-ice habitat in the northern Greenland Sea and Fram Strait area (Arctic) during different seasons. Ranges of temperatures (temp.), salinities, and concentrations of chlorophyll *a* (chl *a*) are given for the entire ice thickness (ice) and for the under-ice water layer (0-1 m), particulate organic carbon (POC) only for the under-ice water layer, exped. = expedition number with RV "Polarstern", nd = not determined, * data from GRADINGER 1998.

Tab. 1: Umweltbedingungen im Packeis- und Untereis-Habitat in der nördlichen Grönlandsee und Framstraße (Arktis) während verschiedener Jahreszeiten. Die Bereiche von Temperatur (temp.) Salzgehalt, und Konzentrationen von Chlorophyll *a* (chl *a*) sind für die gesamte Eisdicke (ice) und für das Untereis-Wasser (0-1 m) angegeben, partikulärer organischer Kohlenstoff (POC) nur für das Untereis-Wasser, exped. = Expeditionsnummer mit FS "Polarstern", nd = nicht bestimmt, * Daten aus GRADINGER 1998.

polar Drift system and upon Polar Surface Water, so that it is most probable that the observed patterns and variabilities are mainly due to seasonal, and not so much to regional, influences. Unfortunately, the months November through February could not be sampled as yet.

There are only very few seasonal studies on high-Arctic ecosystems or organisms, e.g., on oceanic phytoplankton (GRADINGER & LENZ 1995, STRASS & NÖTHIG 1996), oceanic zooplankton (RICHTER 1994), or benthic macroalgae (MAKAROV et al. 1999, BISCHOF et al. 2002). Most studies on seasonal dynamics and processes in the high Arctic were carried out near-shore in fjords (RYSGAARD et al. 1999), including some seasonal studies on the near-shore fast-ice ecosystems (HORNER & MURPHY 1985, SIFERD et al. 1997). Studies on seasonal properties and dynamics in the Arctic sea-ice and under-ice habitats in off-shore pack-ice are particularly rare (PEROVICH et al. 2003, MELNIKOV et al. 2002) and, when containing biological data, have been mostly restricted to spring, summer and autumn (LØNNE & GULLIKSEN 1991a,b, GRADINGER 1998). Due to technical constraints, biological data on winter conditions in this habitat have been especially scarce (THOMAS et al. 1995, DRUZHKOVA et al. 2001), and, regarding in particular ice and under-ice fauna, mostly of qualitative nature (POLTERMANN 1997, MELNIKOV et al. 2002).

Seasonal variations of environmental conditions and sympagic metazoans in Arctic pack-ice

Inside the pack-ice, seasonal variations in physical properties such as ice temperature, brine salinity, and brine volume are most pronounced in the upper part (25 % of ice thickness), moderate in the middle part (50 % of ice thickness), and only small in the lower part (25 % of ice thickness) of the ice. In winter, minimum temperature measured near the surface were

-22 °C with a corresponding salinity of $S = 223$, and a brine volume of less than 1 % of the ice (SCHÜNEMANN & WERNER 2005). In spring, ice temperature gradually increases first in the upper and then in the middle part of the ice, due to rising air temperatures, causing brine salinities to decrease and brine volumes to increase (GRADINGER 1998). In summer, temperatures in the upper part are mostly high, often close to 0 °C, leading to the accumulation of melt-water in ponds, and to very low brine salinities (down to $S = 0$), with theoretical brine volumes being mostly >5 % of the ice (GRADINGER 1998, WERNER et al. 2002a, SCHÜNEMANN & WERNER 2005). Towards autumn, decreasing air temperatures cause cooling of first the upper and then the middle parts of the ice, with the corresponding increase in brine salinity and decrease in brine volume again (GRADINGER 1998). These partly extreme values and strong seasonal fluctuations of physical properties probably prevent an intense colonization of the upper and middle parts of the ice by sympagic metazoans.

The lower parts of the ice are not very strongly characterized by these seasonal developments of physical parameters, because in thick multi-year ice, the underside of the ice is much more influenced by the under-ice water column, which does not show such strong seasonal fluctuations as the atmosphere. Thus, temperature and brine salinity do not vary much throughout the seasons and are usually close to the conditions of the underlying seawater (GRADINGER 1998, SCHÜNEMANN & WERNER 2005). Even in winter, brine volume in the lower parts of the ice is mostly well above 5 % (SCHÜNEMANN & WERNER 2005). These moderate environmental conditions and small seasonal variations have probably favoured the colonization, growth, and accumulation of sea-ice organisms in the bottom part of Arctic pack-ice (GRADINGER 1999a,b, WERNER et al. 2002a, SCHÜNEMANN & WERNER 2005), and should provide a favourable habitat for sympagic metazoans throughout the year.

The vertical distribution of algal biomass (determined as chl *a*) shows mainly bottom maxima during all seasons, with concentrations ranging between the detection limit in winter to maximum values of 67 $\mu\text{g l}^{-1}$ in summer (SCHÜNEMANN & WERNER 2005). However, the seasonal variation between spring (1.63 mg chl *a* m^{-2}), summer (1.21 and 0.95 mg chl *a* m^{-2}), and autumn (2.60 mg chl *a* m^{-2}) of integrated chl *a* concentration in the pack ice is small, and only the winter value (0.25 mg chl *a* m^{-2}) is significantly lower (WERNER & GRADINGER 2002, SCHÜNEMANN & WERNER 2005). In contrast, integrated abundances of sea-ice metazoans do not vary much between winter (3.7-24.8 10^3 ind. m^{-2}) and summer (0.6-34.1 10^3 ind. m^{-2}). In all seasons, highest abundances of metazoans occur in the bottom layers of the ice with similar maximum values of 251 ind. l^{-1} in winter, and 317 ind. l^{-1} in summer (SCHÜNEMANN & WERNER 2005), and 144 ind. l^{-1} in spring (MOSHKINA 2004). However, regarding taxonomical composition, a distinct difference between the seasons becomes evident (Fig. 2). In winter, the diversity of sea-ice metazoans is clearly the lowest, with copepod nauplii strongly dominating the community with a contribution of 93 %, and all other taxa (rotifers, turbellarians, nematodes, juvenile and adult copepods) occurring only as single specimens. In spring and summer, the different taxa are distributed more evenly to total abundances. For example, juvenile and adult copepods (43 %), rotifers (33 %), nematodes (16 %), copepod nauplii (5 %), and turbellarians (3 %) all form a part of the community during summer (SCHÜNEMANN & WERNER 2005), and the same holds true for spring pack ice from the same area (MOSHKINA 2004).

The only ice property showing significant variations in the lower part of the ice between winter and summer, and thus suggesting an explanation for the differences in faunal composition, is the concentration of algal biomass and therefore of potential food for sympagic metazoans (GRAINGER & HSIAO 1990, JANSSEN & GRADINGER 1999). In many copepod species, the nauplii have non-feeding stages during which they could survive the food-limited season, and they may also use internal lipid reserves as energy resource (WERNER & AUDEL 2004). The most probable hypothesis about overwintering of the other sympagic taxa and stages appears to be the strategy of only low numbers of animals surviving the winter in the pack-ice habitat which build up the new populations by reproduction in spring, as soon as feeding conditions improve (SCHÜNEMANN & WERNER 2005). This hypothesis is supported by the numerous observations on all developmental stages of copepods including egg-carrying females, as well as juvenile nematodes and turbellarians in Arctic pack ice (FRIEDRICH 1997). High abundances of copepod nauplii in Arctic pack-ice in spring are also interpreted as a sign for intense reproductive activity during that season (NOZAIS et al. 2001). A re-colonization of pack-ice above deep water as in our study area by the mainly benthic species and taxa is rather unlikely. Other possible overwintering strategies such as the formation of resting stages, or the migration to the under-ice water layer can be largely ruled out, since neither resting stages in the ice, nor sympagic metazoans in the under-ice water are found in winter (WERNER 2005, SCHÜNEMANN & WERNER 2005).

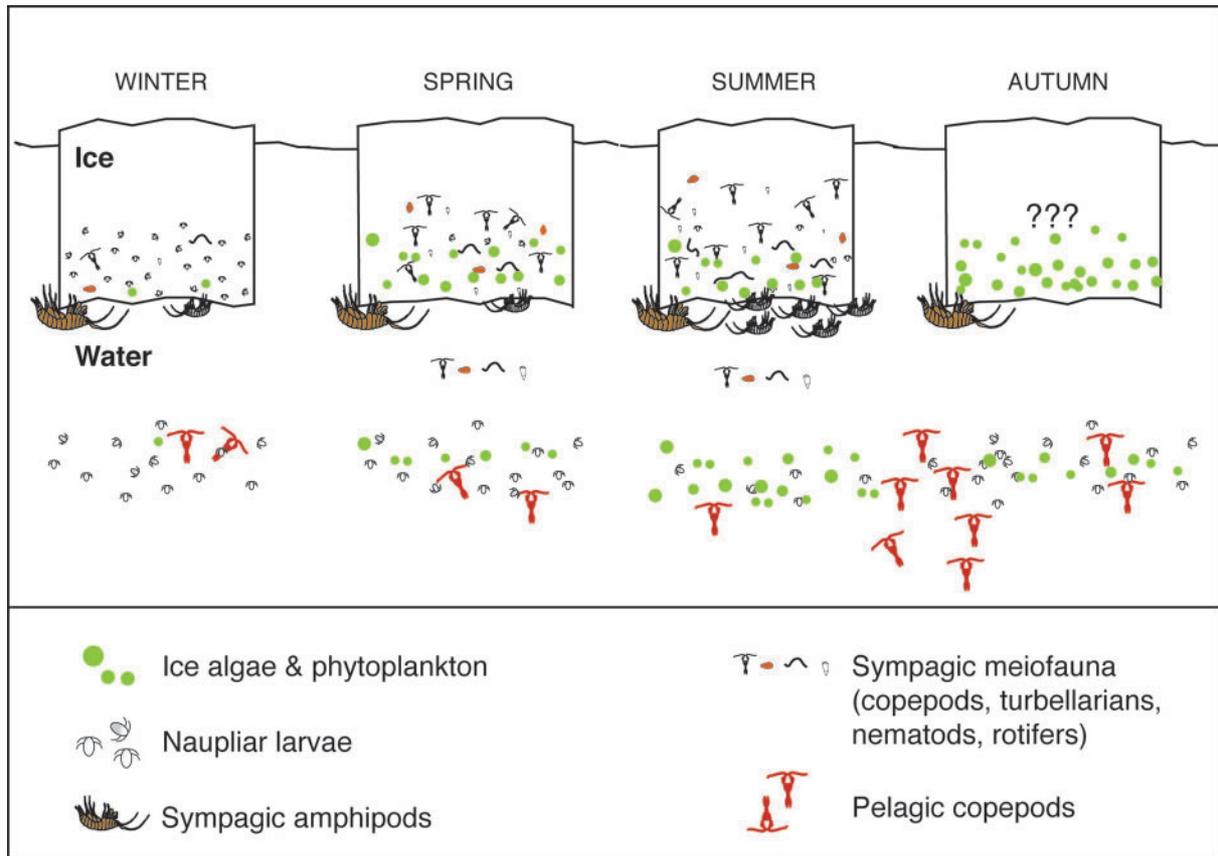


Fig. 2: Schematic illustration of seasonal dynamics of sympagic meiofauna, under-ice amphipods, and sub-ice fauna in and below Arctic pack-ice.

Abb. 2: Schematische Darstellung der saisonalen Dynamik von sympagischer Meiofauna, Untereis-Amphipoden und Untereis-Fauna in und unter arktischem Packeis.

Seasonal patterns, metabolic adaptations and overwintering strategies of amphipods at the ice-water interface

The autochthonous under-ice amphipod species *Apherusa glacialis*, *Onisimus glacialis*, *O. nanseni*, and *Gammarus wilkitzkii* are known to occur in the habitat at the ice-water interface during all seasons and spend their entire life-cycle here (LØNNE & GULLIKSEN 1991a,b, POLTERMANN et al. 2000). Studies on seasonal occurrence of Arctic under-ice amphipods in off-shore pack have been restricted to spring, summer and autumn, and almost all quantitative data on abundance have only covered the summer and early autumn months (HOP et al. 2000, and references therein). Due to technical constraints, observations during winter have been only qualitative until now (POLTERMANN 1997, MELNIKOV et al. 2002). Thus, our studies presented here provide the first seasonal data set on abundances of under-ice amphipods from the high-Arctic multi-year pack-ice, confirming the view that all four species are autochthonous in this habitat.

Summarizing some of our studies (WERNER & GRADINGER 2002, WERNER 2005, WERNER & AUDEL 2005) show a clear seasonal pattern only for one species, *Apherusa glacialis*, with significantly higher abundances in summer than in winter, spring, and autumn (Figs. 2,3). Median values in summer are about one order of magnitude higher than during all other seasons. A factor analysis has revealed that *A. glacialis* is positively related to ice-algal biomass and to melting conditions at the ice underside (WERNER & GRADINGER 2002), probably because melting provides better availability of the major food source ice algae to this herbivorous species (WERNER 1997, SCOTT et al. 1999, WERNER & AUDEL 2005). Both, melting and high ice-algal biomass usually occur in summer, explaining the peak abundances of *A. glacialis* during this season. In order to explain the low autumn and winter values, it has been speculated whether *A. glacialis* leaves the under-ice habitat to overwinter and reproduce in deeper waters (MELNIKOV & KULIKOV 1980), or changes to live under new ice which forms in autumn (LØNNE & GULLIKSEN 1991a,b, WERNER & GRADINGER 2002). However, convincing evidence for either hypothesis is still lacking. Both, egg-bearing females and females with juveniles in the marsupium have been found in the under-ice habitat, reproduction takes place during winter, and juveniles start to be released in March (MELNIKOV 1997, POLTERMANN 1997). A high mortality rate has been calculated for *A. glacialis* in its first year (BEUCHEL & LØNNE 2002), so that probably only a part of the population survives the following winter. These losses, and the shortage of algal food, may explain the lower abundances in autumn, winter and spring; in summer the new recruits born in spring then contribute to higher abundances. Densities of *Onisimus* spp. and *G. wilkitzkii* in winter are at their lower range (WERNER 2005, WERNER & AUDEL 2005), but no significant seasonal differences are found regarding median values (Fig. 3). These species are more omnivorous and therefore not so much depending on primary production (WERNER 1997, SCOTT et al. 1999, POLTERMANN 2001, WERNER et al. 2002b, WERNER & AUDEL 2005). As in *A. glacialis*, reproduction in both *Onisimus* species and in *G. wilkitzkii* mainly takes place during the winter months, and juveniles are released from early spring on (BARNARD 1959, STEELE & STEELE 1975, BEUCHEL & LØNNE 2002), contributing to higher variability and higher maximum values of abundances observed in summer and autumn (Fig. 3).

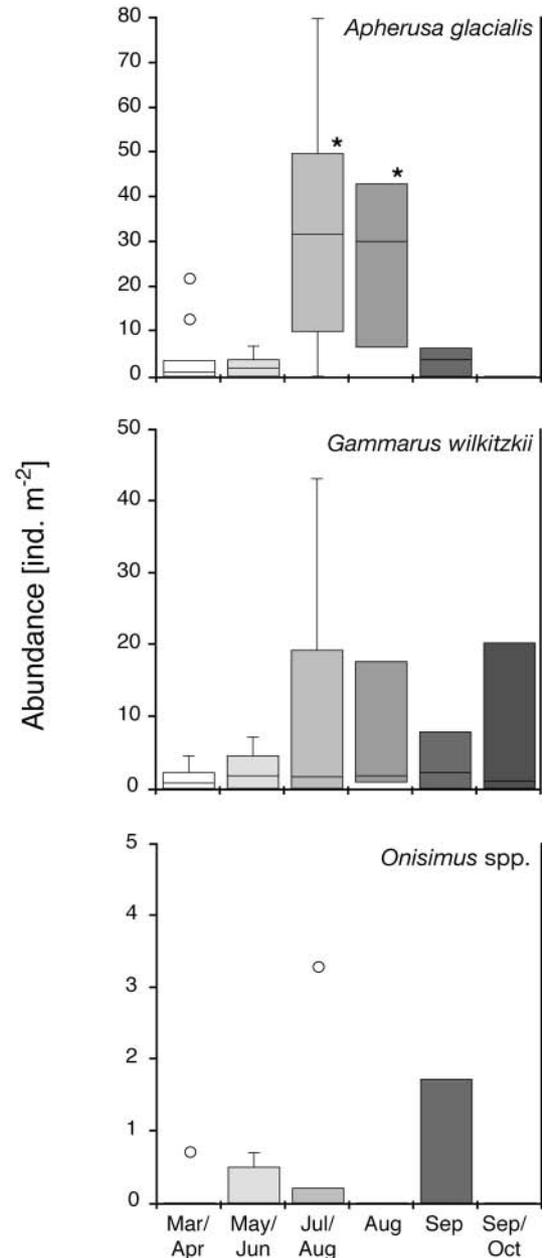


Fig. 3: Abundances of under-ice amphipods below Arctic pack ice during different seasons. * = statistically significant difference.

Abb. 3: Abundanzen von Untereis-Amphipoden unter arktischem Packeis während verschiedener Jahreszeiten. * = statistisch signifikanter Unterschied.

A detailed analysis of total lipids (TL), different lipid classes, and fatty acids (FA) as biomarkers for different food sources has revealed the seasonally varying feeding types and overwintering strategies of the four species (WERNER & AUDEL 2005). *Apherusa glacialis* is a herbivorous species extensively feeding on ice algae, predominantly diatoms, at the underside of the sea ice during the productive season (WERNER 1997, SCOTT et al. 1999). In our summer and autumn data, this is reflected in very high concentrations of the 16:1 (n-7) FA, which is a typical component of diatoms (GRAEVE et al. 1994, FALK-PETERSEN et al. 1998), and low values for the isomer ratio 18:1 (n-9) / 18:1 (n-7), which has been proposed as an index of carnivory (GRAEVE et al. 1997, FALK-PETERSEN et al. 2000, AUDEL et al. 2002). In winter, when ice algae and under-ice phytoplankton are scarce (WERNER 2005, SCHÜNEMANN &

WERNER 2005), *A. glacialis* seems to rely at least partly on the catabolism of stored lipids as energy source, evident in the strong decline of the high TL content in autumn (46 % of dry mass) to a low value in late winter (22 % of dry mass). Additional food sources, such as algal detritus clumps (POLTERMANN 2001), or fresh ice algae (e.g., diatoms and chrysophytes) were present also in the bottom of the winter ice, however, in very low concentrations (Werner, Ikävalko and Schünemann unpubl.) and also very patchily distributed and thus, harder to find for the grazing amphipods. Nonetheless, some individuals of this species analyzed show FA biomarkers, which indicate active herbivorous feeding also during winter (WERNER & AUDEL 2005).

Onisimus glacialis contains biomarker FA for diatoms in high concentrations only in summer and autumn, but accumulates high amounts of indicators for a carnivorous diet including calanoid copepods during winter, such as the fatty acid 18:1 (n-9) and the long-chain monounsaturated FA and alcohols 20:1 (n-9) and 22:1 (n-11). Correspondingly, the carnivory index nearly doubled from summer to winter. This amphipod species is generally referred to as omnivorous (SCOTT et al. 1999, POLTERMANN 2001). Our results reveal that a switch in dominant food sources occurs from ice algae in summer and autumn to metazoan prey in winter. Since calanoid copepods are present in the under-ice habitat also during winter (HORNER & MURPHY 1985, WERNER 2005, 2006), *O. glacialis* will probably find sufficient food resources, so that there is no clear reduction in the moderately high TL content during this period of the year (WERNER & AUDEL 2005).

Onisimus nanseni shows a lipid composition typical of omnivorous feeding with a combination of metazoan (calanoid copepods) markers and diatom markers throughout the year (WERNER & AUDEL 2005). Highest concentrations of metazoan markers and a slightly increased index of carnivory occurs during winter, but seasonal changes in lipid composition and feeding behaviour of *O. nanseni* are less pronounced than those of the congener and sympatric *O. glacialis*. *O. nanseni* generally seems to rely on an opportunistic feeding mode with an omnivorous diet (SCOTT et al. 1999). Although a reduced feeding activity has been observed in this species in winter (POLTERMANN 2001), this amphipod follows a “business as usual” strategy without specific adaptations for overwintering, but with an increased proportion of metazoan prey and detritus as an available food source in winter (WERNER & AUDEL 2005).

Gammarus wilkitzkii is generally considered as omnivorous to carnivorous (WERNER 1997, POLTERMANN 2001). Studies on its FA composition in the Barents Sea (SCOTT et al. 1999), as well as feeding experiments with individuals from the Greenland Sea (WERNER et al. 2002b) reveal that calanoid copepods represent a major diet component for *G. wilkitzkii* during summer. In contrast to most published results, summer individuals contained, however, high amounts (>20 %) of diatom markers, while the typical indicators for calanoid copepods as prey were only present in low levels of 4 %. Correspondingly, the carnivory index showed very low values of <3, hence comparable to those of the herbivorous *Apherusa glacialis*. During winter lower amounts of the diatom markers, slightly elevated concentrations of calanoid markers and an increased carnivory index suggest a change in diet composition from primarily ice algae in summer to metazoan prey in winter, similar to the switch in feeding behaviour of *Onisimus*

glacialis. However, calanoid markers and carnivory index of *G. wilkitzkii* were even in winter substantially lower than those of *O. glacialis* and, in contrast to *O. glacialis*, the TL content of *G. wilkitzkii* decreased in winter (10 % DM) to less than half of the summer (21 % DM) value. Thus, the change to predatory feeding during winter is apparently less profitable for *G. wilkitzkii*, and a considerable proportion of its energetic needs is probably covered by internal lipid reserves, although only very few animals with empty guts have been found in winter (POLTERMANN 2001). *G. wilkitzkii* has apparently realized a highly flexible and opportunistic strategy to cope with changing feeding conditions in the under-ice habitat. This species is able to exploit a wide spectrum of different, locally and seasonally abundant food sources ranging from ice algae, detritus, and ice fauna to predatory feeding on other under-ice amphipods and planktonic copepods (WERNER 1997, SCOTT et al. 1999, POLTERMANN 2001, WERNER et al. 2002b, WERNER & AUDEL 2005). The different feeding behaviours, food preferences and overwintering strategies of the four species of autochthonous under-ice amphipods present an effective development of niche separation in this environment.

In none of the sympagic amphipod species, a significant difference in respiration rates in summer and winter is found, indicating that the under-ice habitat is a comparatively stable habitat in terms of seasonal variations, above all in temperature ($\Delta t = 1.5^\circ\text{C}$, WERNER & AUDEL 2005). Seasonal variations in food availability and sources are thus not reflected in seasonal changes of metabolic rates in Arctic under-ice amphipods, similar to the constant rates measured in Arctic benthic amphipods (*Anonyx* spp., *Gammarus* spp.) during summer and winter (WESLAWSKI & OPALINSKI 1997). Seasonal differences in respiration rates of the Antarctic amphipod *Orchomene plebs* are only related to the different composition of sexes and developmental stages during different seasons (RAKUSA-SUSZCZEWSKI 1982). A metabolic reduction in order to save energy during the winter, as common in herbivorous polar copepod species, e.g., *Calanus* spp. (HIRCHE 1991), or observed as one possible overwintering strategy in Antarctic krill *Euphausia superba* (TORRES et al. 1994), is obviously not an option for neither of the under-ice amphipods, because they have to stay active in the extensive search for patchily distributed food such as algal detritus clumps. In addition, the autochthonous under-ice amphipods can not find refuge from winter-active predators like *Gammarus wilkitzkii* and polar cod *Boreogadus saida* in their habitat (WERNER & AUDEL 2005). Seasonal adaptations in metabolism are thus not required by and not advantageous for the environmental conditions in the Arctic under-ice habitat.

Seasonal dynamics of the sub-ice fauna below the pack ice

The sub-ice water layer directly below the pack ice is strongly influenced by the seasonal freezing-melting cycle of the ice. Organisms found in this boundary layer over deep water are either sympagic (originating from the ice) or pelagic, and they use this habitat for shelter and as feeding and nursery grounds (HORNER & MURPHY 1985, WERNER & MARTINEZ ARBIZU 1999), usually without being in physical contact with the ice underside (HORNER et al. 1992). Major groups of this fauna are calanoid, cyclopoid, and harpacticoid copepods, as well as foraminiferans and pteropod gastropods (HORNER & MURPHY 1985, HERMAN & ANDERSEN 1989, WERNER & MARTINEZ

ARBIZU 1999). Most members of the sub-ice community are considered an important trophic link between sea-ice derived primary production and higher trophic levels in the water column (GRAINGER et al. 1985, GRAINGER & HSIAO 1990). The only seasonal study on this community below Arctic pack ice so far has delivered only some qualitative data (MELNIKOV et al. 2002).

The temperature in the sub-ice water layer (0-1 m depth) is mostly at or close to the freezing point (-1.5 to -1.9 °C) with salinities between 32.4-34.6 in winter, early spring, and late autumn. In late spring and early autumn, but in particular during the summer months, a thin layer of melt-water can develop directly below the pack ice (EICKEN 1994, GRADINGER 1996, WERNER & MARTINEZ ARBIZU 1999, WERNER & GRADINGER 2002), with elevated temperatures of -1.4 to -0.3 °C and lowered salinities of 31.8-16.7 in our study area and during our study period (WERNER & GRADINGER 2002, WERNER 2005, 2006). Concentrations of chl *a* in the sub-ice water are very low in winter (0.02 µg l⁻¹), increase during spring (0.2 µg l⁻¹), reach their seasonal maximum in early summer (1.0 µg l⁻¹), and decrease again in late summer (0.5 µg l⁻¹) and autumn (0.1 µg l⁻¹) (WERNER 2005, 2006). The seasonal development of algal biomass in the sub-ice water is of course depending on seasonally changing light conditions (RYSGAARD et al. 1999), but also on melting of the ice underside (GRADINGER 1996, WERNER & GRADINGER 2002).

In the course of the year, total abundances of the sub-ice fauna show a steep increase from low values at the earliest sampling dates in winter towards the end of winter / beginning of spring reaching maximum numbers then, and a decrease to minimum numbers in early summer. A second peak occurs in late summer, followed by a decrease towards autumn again (Fig. 4). This significant trend is mainly due to the abundances of copepod nauplii, which dominate the sub-ice community during all seasons (Fig. 4), and of the small pelagic copepod *Oithona similis*, which usually ranks next in terms of abundances (WERNER 2006). Abundances of both faunal groups are positively related with denser ice coverage and lower water temperatures in my data set (WERNER 2006). Copepod nauplii are also the dominant metazoan group found inside the ice at the same stations during winter (SCHÜNEMANN & WERNER 2005), indicating that these young, maybe still non-feeding stages of probably mainly harpacticoid and cyclopoid copepods have developed a successful overwintering strategy in both habitats. *O. similis* is capable of feeding on a wide spectrum of food sources including algae, detritus, small crustaceans, and faecal material (GONZALEZ & SMETACEK 1994,

KATTNER et al. 2003), thus possibly using the abundant particulate organic carbon suspended in the sub-ice water (WERNER 2005, 2006) or small nauplii as food sources during all seasons.

Significant seasonal variations are also evident in the sympagic fauna found in the sub-ice water, above all in the ectinosomatid copepods (*Halectinosoma* spp., *Pseudobradya* sp.), in foraminiferans (mostly *Neogloboquadrina pachyderma*), and in the pelagic pteropod *Limacina helicina* (mostly juveniles), but not in the large calanoid copepods *Calanus* spp. and *Pseudocalanus minutus* (WERNER 2006). Sympagic metazoans are virtually absent in the sub-ice water during winter (WERNER 2005) and autumn, and occur in this habitat only in spring and summer (Fig. 2), positively related to the presence of melt-water below the ice, which probably transports the sympagic organisms from the ice to the underlying water layer (GRAINGER & MOHAMMED 1986, WERNER et al. 2002a, WERNER 2006).

Abundances of foraminiferans in the sub-ice water are very low in winter (WERNER 2005), early summer and autumn, and show a high peak in spring and a lower peak in late summer (WERNER 2006). The spring peak may be related to major reproduction of *N. pachyderma* during this season, since mostly juveniles (mean test size 0.13 mm) were found below the pack ice off northeast Greenland in late winter/early spring (HERMAN & ANDERSEN 1989, WERNER 2006).

Limacina helicina juveniles show significantly higher abundances in winter than in early summer, and low numbers during all other seasons (WERNER 2005, 2006). These young stages may profit from the shelter of a dense ice cover, with which they show a positive relation, and from the absence of zooplankton predators during winter, e.g. ctenophores, chaetognaths, and adult *L. helicina* known to feed on their own juveniles and copepod nauplii (GILMER & HARBISON 1991). Juvenile *L. helicina* are believed to feed on small suspended particles such as phytoplankton and protozoans (GILMER & HARBISON 1991), and possibly also on suspended detritus, available in the sub-ice water also during winter (WERNER 2005, 2006).

Although biomass of total sub-ice fauna does not display any significant seasonal trend, some dominant groups and species of the sub-ice fauna do. For example, biomass of *Oithona similis* develops parallel to the abundance values of the species, biomass of copepod nauplii increases together with their mean lengths from spring over summer to autumn, and

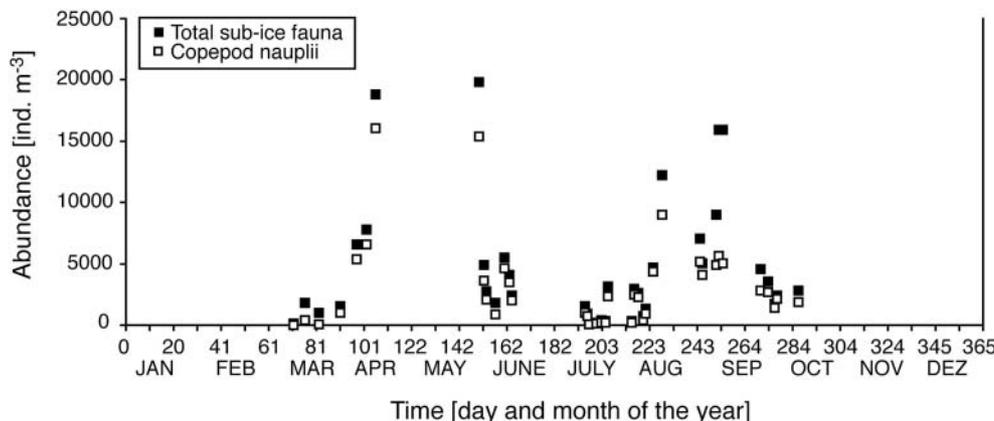


Fig. 4: Abundances of sub-ice fauna below Arctic pack-ice during different seasons.

Abb. 4: Abundanz der Untereis-Fauna unter arktischem Packeis während verschiedener Jahreszeiten.

the sympagic fauna shows a steady increase in biomass from winter to spring, early and late summer, and a decrease again towards late summer. At the majority of sampling dates during the course of the year, there was a sub-ice faunal biomass of 0.5 to 3.5 mg C m⁻³ potentially available for predators below the pack ice (WERNER 2005, 2006).

The calanoid copepods *Pseudocalanus minutus* and *Calanus* spp. are not related to any ice-associated environmental variable and do not show any significant seasonal trends in their abundances below the pack ice. Occasionally dense swarms with exceptionally high biomass values occurred in spring, early and late summer (WERNER 2006). In contrast to the sub-ice habitat below coastal fast ice, which becomes an early feeding ground for calanoid copepods, such as *C. glacialis* and *Pseudocalanus* spp. using the algal bloom at the ice underside during spring (CONOVER et al. 1986, RUNGE & INGRAM 1988), the habitat below pack ice does not appear to play this ecological role for these species. However, in the Storfjord area, the calanoid copepod *P. minutus* occurs in high numbers in winter, and shows indications of active development and growth by a shift in stage composition (WERNER 2005). The overwintering of this generally herbivorous species must be fuelled either by internal lipid reserves, or by a more omnivorous feeding, e.g., on the abundant suspended organic matter in this habitat also in winter (WERNER 2005).

The most conspicuous seasonal phenomenon in the sub-ice habitat is the presence of a thin, but often pronounced layer of melt-water with reduced salinity directly below the ice in summer (GRADINGER 1996, WERNER & MARTINEZ ARBIZU 1999, WERNER & GRADINGER 2002, WERNER 2006). Despite maximum concentrations of chl *a*, resulting probably from melting off the bottom of the ice containing highest biomass of ice algae (GRADINGER 1999b), most species show their abundance minima in the sub-ice water during this time of the year (Figs. 2, 4). This may be due to the desalinated water layer, which could act as a barrier to species without a pronounced salinity tolerance (CONOVER & SIFERD 1993), in particular for sensitive juvenile stages such as copepod nauplii. Even species with the general ability to cope with low salinities like *Oithona similis* (GRAINGER 1988), *Calanus glacialis* and *Pseudocalanus* spp. (GRAINGER & MOHAMMED 1990) may rather avoid these layers in order to save the energy expenditure required for osmoregulation. At several stations during summer, abundances of *Calanus* spp. and *P. minutus* were higher at 5 m depth than in the uppermost first metre of the sub-ice water column (Werner unpubl.). The foraminifer *Neoglobobulina pachyderma* may tolerate a salinity of *S* = 30, but very low salinities like *S* = 5 are lethal to this species (M. Spindler pers. comm.). In contrast, sympagic copepods usually show wide salinity tolerances (GRAINGER & MOHAMMED 1990), and are especially abundant in the sub-ice water during melting periods with reduced salinities (HORNER & MURPHY 1985, WERNER & MARTINEZ ARBIZU 1999, WERNER 2006).

Factor analyses have shown that the major environmental factors controlling seasonal abundances of dominant species and groups at the ice-water interface and in the sub-ice water are all subject to pronounced seasonal variability themselves. Ice cover and ice thickness as the main structures of the habitat, temperature and salinity indicating freezing or melting conditions at the ice underside, and chl *a* as a measure for food

availability for herbivores, depending on seasonally changing light conditions (WERNER & GRADINGER 2002, WERNER 2006). All these factors are either directly (ice conditions, under-ice hydrography) or indirectly (primary productivity) influenced also by the already observed, and believed to continue, changes due to climate warming in the Arctic. Thus, the effects of global change will apparently have tremendous effects on the Arctic sea-ice and under-ice ecosystems as well.

COUPLING PROCESSES BETWEEN ARCTIC PACK-ICE AND ADJACENT ECOSYSTEMS

Sea ice influences adjacent ecosystems, in particular the underlying and adjacent water masses, in various physical, chemical and geological ways. The presence of a sea-ice cover decreases the exchange of heat and gases, as well as the effects of wind stress, between the atmosphere and the upper ocean substantially (MAYKUT 1985, GOW & TUCKER 1990). The surface layer of polar oceans is notably influenced by the freezing-melting cycle of the sea ice. During ice formation, brine of high salinity is expelled from the growing ice sheet, leading to higher density of the seawater and to convective circulation. During melting of the ice, a freshened water layer develops at the surface (GOW & TUCKER 1990, GOLOVIN et al. 1996, EICKEN 2003). In the Arctic, transport of sea-ice sediments by drifting pack ice plays a significant role for the large-scale distribution and overall budgeting of sediment masses (EICKEN et al. 1997, 2000).

The most important direct impacts of a sea-ice cover on the pelagic ecosystem are probably the high albedo and attenuation of light, and thus the hampering of photosynthesis on the one hand (HORNER & SCHRADER 1982, HORNER 1985), and, due to melt-water production, the stabilisation and stratification of the upper water column enhancing primary production on the other hand (RUDELS 1989, PEINERT et al. 2001). Besides these large-scale processes, numerous other physical mechanisms such as the formation of a skeletal layer at the ice underside (WEEKS & GOW 1978, EICKEN 2003), chemical processes such as nutrient and gas fluxes through the ice-water interface (COTA et al. 1987, THOMAS & PAPADIMITRIOU 2003), and biological patterns such as entrainment of biota (SPINDLER 1990, GRADINGER & IKÄVALKO 1998) connect the two ecosystems sea ice and water column on different spatial and temporal scales. Both the under-ice morphology (WERNER & LINDEMANN 1997), as well as under-ice currents appear to have a remarkable influence on porewater fluxes, especially of nutrients, and on the spatial distribution of organisms at the ice-water interface (KREMBS et al. 2002).

Particle flux from the pack-ice to the water column and the sea floor

Vertical particle flux in the ocean controls the transfer of carbon and silica from surface to deeper waters, nutrient regeneration, delivery of food to pelagic and benthic communities, and preservation of sediment records (DUNBAR et al. 1998). In ice-covered polar oceans, flux patterns are not only governed by pelagic production and processes, but also by sea-ice related particle sources and their release mechanisms, which both show a pronounced spatial and temporal variability (PEINERT et al. 2001). The presence of sea ice alters the vertical

particle flux both qualitatively and quantitatively.

Several studies based on satellite-born ice information and sediment-trap data have clearly shown the relationship between the ice coverage and the particle flux in the Arctic. Highest fluxes, both of lithogenic and biogenic particles, have been measured in the marginal ice zone (MIZ), followed by areas of open water. Lowest fluxes occur below a dense and permanent pack-ice cover (RAMSEIER et al. 1999, 2001, PEINERT et al. 2001). However, ice-bound primary and particle production begins early in the season at very low light levels (MOCK & GRADINGER 1999), before the onset of phytoplankton growth in the water column (PEINERT et al. 2001).

Ice-related particle sources can be lithogenic or biogenic. In contrast to the Antarctic, the sediment load of Arctic sea-ice can be very high and is transported and distributed through the Arctic Ocean and its marginal seas by drifting pack-ice (EICKEN et al. 2000). Sea-ice sediments are distributed throughout the entire ice thickness including the ice underside (PFIRMAN et al. 1989, WERNER & LINDEMANN 1997). Particle flux from Arctic sea ice is often dominated by lithogenic material of various grain sizes (HEBBELN 2000, LEVENTER 2003).

Biogenic particle sources from the ice generally comprise all members of the sympagic communities including viruses, bacteria, unicellular algae (diatoms, flagellates), proto- and metazoans including large under-ice amphipods (HORNER et al. 1992, WERNER & GRADINGER 2002), as well as ice-bound detritus (POLTERMANN 2001). The highest concentration of most organisms in Arctic pack-ice is usually found in the lowermost part of the ice (GRADINGER et al. 1999, WERNER et al. 2002a, SCHÜNEMANN & WERNER 2005), which thus can release the bulk of the sympagic biomass upon disintegration (PEINERT et al. 2001). Melting and break-up of the ice are the major processes leading to this release of particles to the water column (LEVENTER 2003). Bottom ablation rates of Arctic multi-year ice during summer vary between 10 and 62 cm, with increasing values observed during recent years (GOLOVIN et al. 1996, PEROVICH et al. 2003 and references therein). Melting at the ice underside is not only caused by elevated insulation in spring and summer, but also takes place when ice floes come into contact with warmer or more saline water masses, for example in the marginal ice zone or on their way south in the Greenland Sea. Release of ice-bound particles is thus not restricted to the summer months, but also occurs in winter (HEBBELN 2000, RAMSEIER et al. 2001, PEROVICH et al. 2003). After break up and complete melting of the floes, large amphipods inhabiting the ice underside are also released to the water column where they represent a major input of organic carbon (LØNNE & GULLIKSEN 1991b, WERNER et al. 1999, PEINERT et al. 2001).

The fate of these heterogenous particles, in particular of the heterotrophic components, and their role in the pelagic ecosystem are not fully understood as yet. Production, release and fate of ice algae appear to depend both on meteorological (air temperature, rain, melt) and biological forcings (under-ice biomass of calanoid copepods) (FORTIER et al. 2002). For autotrophic ice organisms, a seeding effect in the water column has been discussed (HORNER 1976, ALEXANDER 1980, SYVERTSEN 1991, PEINERT et al. 2001). Released ice algae have also been observed to form large aggregates directly below the ice (TREMBLAY et al. 1989, FORTIER et al. 2002, MELNIKOV et

al. 2002, WERNER & GRADINGER 2002). All organic matter released from the sea ice can be an important food source for pelagic grazers, in particular early in the year before the phytoplankton starts to grow (TREMBLAY et al. 1989, MICHEL et al. 1996, FORTIER et al. 2002), undergo microbial degradation in the water column, or serve as a food pulse – depending on sinking velocities and water depth – also for benthic communities (GREBMEIER & BARRY 1991, PEINERT et al. 2001, LEVENTER 2003). Despite their comparatively large body mass and high body density, under-ice amphipods are able to maintain position in the ice-free water column for a period of several days at least, thus representing a potential food source for higher trophic levels such as fish or diving seabirds (WERNER et al. 1999). The food webs on the sea floor, in the water column, and in the sea ice are thus connected by a downward flux of organic particles (and therefore energy) released from melting or disintegrating sea ice.

Migrations of organisms between the ecosystems

Copepods are a major group of the sympagic meiofauna, both in Arctic (GRADINGER 1999a) and in Antarctic (SCHNACK-SCHIEL et al. 2001) pack ice. About 15 species have been described in Arctic sea-ice so far, mainly members of the sub-orders Harpacticoida and Cyclopoida with the most abundant and widespread genera *Halectinosoma* spp., *Tisbe* spp., and *Cyclopina* spp.. Most of these species have also been found in the under-ice water, both below fast ice (HORNER & SCHRADER 1982) and below pack ice (WERNER & MARTINEZ ARBIZU 1999, MELNIKOV et al. 2002, WERNER 2006). The vertical distribution of the copepods in the ice and under-ice water usually shows highest abundances in the lowermost centimetres of the ice and in the uppermost 1-2 m of the under-ice water, with always higher abundances in the ice than in the under-ice water (WERNER et al. 2002a). However, a certain exchange of these organisms through the ice-water interface must take place, which is connected with a change in several environmental variables occurring in the two different habitats, e.g. temperature and salinity (WERNER et al. 2002a). Sympagic copepods can tolerate a wide range of salinities of $S = 20-70$ (GRAINGER & MOHAMMED 1990), so that they could thrive both in the lowermost part of the ice even in winter (SCHÜNEMANN & WERNER 2005), and in the under-ice water layer influenced by meltwater in summer (EICKEN 1994, WERNER et al. 2002a, WERNER 2006). An unsolved question still is whether these organisms migrate actively between sea-ice interior and under-ice water layer, e.g., in the search for food, or whether they are passively transported by physical processes like melt-water flushing through the lowermost part of the ice (GRAINGER & MOHAMMED 1986, EICKEN et al. 2002). With melt-water present, more sympagic copepods are found below the ice than without melt-water (WERNER & MARTINEZ ARBIZU 1999, WERNER et al. 2002a, WERNER 2006), and the timing of their occurrence in the under-ice water (June through September) coincides well with the period of bottom melt (PEROVICH et al. 2003, WERNER 2006), indicating that the latter process is more likely.

Gravity drainage and brine expulsion during freezing at the ice underside (MAYKUT 1985) in early winter are additional potential transport mechanisms from the ice into the water column, because only very low numbers of sympagic copepods have been found inside Arctic pack ice in late winter (SCHÜNEMANN

& WERNER 2005). However, they are also absent from the under-ice water during winter (WERNER 2005, 2006). The sea-ice interior is a habitat offering substrate surfaces similar to the original habitat of these copepod species, the sea floor (MONTAGNA & CAREY 1978), from where they are believed to colonize the sea ice like an "upside-down-benthos" (CAREY & MONTAGNA 1982, GRAINGER 1991). In shallow near-shore areas, several copepod species migrate between the seafloor and the ice underside in the seasonal course of freezing and melting (GRAINGER 1991). This is very unlikely to happen in deep waters where our studies were carried out, so that the copepods have to stay close to the ice underside in order to prevent losing contact to their habitat. Thus, it may be concluded that migrations of sympagic copepods through the ice-water interface of Arctic pack ice take place but represent probably only a small-scale process seasonally limited to the melting period.

Several species of calanoid copepods, above all of the dominant genus *Calanus*, connect the deep waters, where they overwinter (HIRCHE 1991, AUDEL et al. 2003), with the under-ice water layer, where they occur in spring, summer and autumn (HORNER & SCHRADER 1985, WERNER & MARTINEZ ARBIZU 1999, WERNER 2006), by means of their extended vertical migrations and by feeding activities as discussed below. The largest species, *C. hyperboreus*, spawns already in late winter at depth, the buoyant eggs rise to the surface where they arrive in the under-ice habitat. Here, the naupliar larvae hatch from the eggs in spring so that the first-feeding stages can already use the early ice-algal production as food source (CONOVER 1988). Accumulations of eggs of also *C. glacialis* at the ice-water interface have been observed below off-shore pack ice in spring (WERNER & HIRCHE 2001), indicating that the under-ice habitat serves as a nursery ground also for this species. Ice-algal biomass and production were very high in the lowermost part of the ice (MOCK & GRADINGER 1999), but still low in the underlying water column at that time (NÖTHIG et al. 1998). Hence, it is very probable that not only the young stages, but also the spawning females have been profiting from the abundant food source in the ice, similar as reported from the Canadian Arctic (RUNGE & INGRAM 1988). The high abundance of copepod nauplii of different shapes, sizes and stages, as well as the occurrence of juvenile stages of other species (e.g., pteropods *Limacina helicina*, foraminiferans *Neogloboquadrina pachyderma*, hyperiid amphipods *Themisto libellula*) in the under-ice water (HERMAN & ANDERSEN 1989, WERNER & MARTINEZ ARBIZU 1999, WERNER 2006) point to the possibly important role of a nursery ground for several pelagic species, thus forming a link between the ice underside and the water column by ontogenetic or seasonal migrations. In the Antarctic, the life-cycle of the calanoid copepod *Stephos longipes* is closely coupled to the sea-ice habitat, where the young stages develop and feed on ice algae before the older stages and adults return to the water column (SCHNACK-SCHIEL et al. 1995, 2001).

The pelagic hyperiid amphipod *Themisto libellula* often occurs in high densities in the under-ice habitat (GULLIKSEN & LØNNE 1989, LØNNE & GULLIKSEN 1991b, KOSZTEYN et al. 1995), mostly juveniles have been observed close to the ice underside (WESLAWSKI et al. 1993, WERNER 2006). This species can conduct deep vertical migrations from depths of about 1000 m (VINOGRADOV 1999) to the ice-covered surface where it feeds on ice algae (AUDEL et al. 2002) and calanoid

copepods (AUDEL & WERNER 2003) as discussed below in more detail.

In shallow areas under seasonal land-fast ice, a number of epibenthic amphipod species colonize the ice underside during winter and spring, e.g., *Ischyrocerus anguipes*, *Onisimus affinis*, *O. littoralis*, *Halirages mixtus*, *Gammarus setosus*, and *Weyprechtia pinguis* (PIKE & WELCH 1990, WESLAWSKI et al. 1993). These species use the ice underside temporarily as a feeding ground for ice algae, detritus and living prey (NEWBURY 1983, CAREY 1992). It has been hypothesized that the origin of most of the true under-ice amphipods (i.e. *O. nanseni*, *O. glacialis*, *G. wilkitzkii*) also was the benthic environment from where these species departed in their evolutionary development to permanently colonize the ice underside as an "upside down benthos" (CAREY 1992). The observation of the epibenthic amphipod *Anonyx sarsi* below Arctic off-shore pack ice, probably in the search for food in late winter (WERNER et al. 2004), may represent an example how such a process could commence, and indicates that cryo-benthic coupling processes are not confined to near-shore fast ice. In the offshore pack ice of the north-western Weddell Sea (Antarctica) the epibenthic deep-water lysianassid amphipod *Abyssorchomene rossi* was caught in baited traps directly below the ice (KAUFMANN et al. 1995). These observations indicate that epibenthic amphipods can be closely associated with the underside of Arctic and Antarctic pack-ice, connecting the benthic with the sympagic ecosystem by their active migrations and probably feeding activities.

Feeding activities at the ice-water interface and in the under-ice water

Feeding activities play a key role in cryo-pelagic coupling processes and thus in the transfer of organic matter and energy flux between the sea ice and the water column. It has been extensively shown in Arctic coastal areas with land-fast and seasonal ice that sympagic algae are used for food by pelagic calanoid copepods, in particular by *Calanus glacialis* and *Pseudocalanus* spp., and especially early in spring before pelagic production begins (CONOVER et al. 1986, RUNGE & INGRAM 1988). Because these pelagic species are typical suspension-feeders, and probably deterred from the melting ice underside by a low-salinity water layer (RUNGE & INGRAM 1988, WERNER 2006), they probably stay in a certain distance (of several decimetres at least) away from the ice underside, where they await and feed on ice algae melted off and eroded from the ice (CONOVER et al. 1986, TREMBLAY et al. 1989). Related to these feeding activities close to the ice-water interface, diurnal vertical migrations, with ascends to the surface at night, of these copepods have been observed (CONOVER et al. 1988, RUNGE & INGRAM 1988), representing a connection between the sea ice and deeper waters. Although it is not proven as yet that similar feeding activities of pelagic copepods on sympagic algae take place also below Arctic pack-ice, several observations indicate the possibility at least. Very high abundances and egg production rates were measured in *C. glacialis* below first-year pack-ice in the Barents Sea already in May (WERNER & HIRCHE 2001, HIRCHE & KOSOBOKOVA 2003). The reproductive and growth period of this species and of *Pseudocalanus minutus* probably commences already end of March / beginning of April (HIRCHE & KOSOBOKOVA 2003, WERNER 2005), a time when internal lipid reserves or ice algae

are probably the main energy sources for the copepods, because no sufficient phytoplankton biomass is available in ice-covered areas (SØREIDE et al. 2003). During the summer melting period, occasionally very high abundances of *Calanus* spp. and *Pseudocalanus* spp. have been found directly below Arctic pack ice in different regions (WERNER & MARTINEZ ARBIZU 1999, MELNIKOV et al. 2002, WERNER 2006), possibly using melted-off ice-algal biomass as food source in the under-ice habitat.

The pelagic amphipod species *Themisto libellula* is also connected to the sea ice by various feeding activities. Gut content analyses have shown the ingestion of ice algae and sympagic meiofauna (BRADSTREET & CROSS 1982), diving observations have reported of *T. libellula* attacking smaller crustaceans at the ice underside (LØNNE & GULLIKSEN 1991b) and analyses of fatty acid biomarkers have revealed ice algae as a major food item for the species (AUDEL et al. 2002), which also feeds on calanoid copepods below the pack ice (AUDEL & WERNER 2003).

The autochthonous Arctic under-ice amphipods *Apherusa glacialis*, *Onisimus glacialis*, *O. nansenii*, and *Gammarus wilkitzkii* are direct mediators of organic matter and energy fluxes at the ice-water interface where they spend their entire life-cycle (LØNNE & GULLIKSEN 1991b, POLTERMANN et al. 2000), and occur during all seasons (WERNER & GRADINGER 2002, WERNER & AUDEL 2005). In contrast to the pelagic copepods and amphipods mentioned above, these species live in physical contact with the ice underside, where they move around and rest attached, hide in cracks and holes, feed and reproduce. Feeding preferences are species-specific, both feeding experiments (WERNER 1997, WERNER et al. 2002b), and analyses of fatty acid biomarkers (SCOTT et al. 1999, WERNER & AUDEL 2005) have shown that *A. glacialis* is strictly herbivorous, *Onisimus* spp. are omnivorous, and *G. wilkitzkii* is omnivorous with a strong predatory component. Amphipods grazing on ice-produced organic matter release their comparatively large faecal pellets (with an average organic carbon content of about 22 % of dry mass) into the underlying water column, thus forming a direct link between the sea ice and the pelagic ecosystem (WERNER 2000). Faecal pellet production rates are species-specific, and depending on amphipod abundances, this process can lead to a transfer of about 2 % of ice-bound particulate organic carbon per day through the ice-water interface (WERNER 2000). This process will take place everywhere in the ice-covered Arctic and provides a pathway for organic matter flux from the ice to the water independently of melting conditions. There are various possible fates of the amphipod faecal pellets released to the water column. Due to their large size and high sinking velocities (WERNER 2000), they could sink rapidly to greater depth (LAMPITT et al. 1990), or even to the sea floor, especially in shallow areas, representing an important food source for the benthos (CAREY 1992, POLTERMANN 1997). However, they can also be retained in the upper water layer due to hydrographical conditions such as turbulent mixing (CAREY 1987), and be ingested and reworked by coprophagous pelagic copepods such as *Oithona similis* (GONZÁLES & SMETACEK 1994). This species is numerous and abundant in the under-ice habitat year-round (WERNER & MARTINEZ ARBIZU 1997, WERNER 2005, 2006). Pellet sedimentation from copepods (*Calanus glacialis*, *Pseudocalanus* spp.) feeding on ice algae amount to 2.3 % of total standing stock of chl *a* d⁻¹ (TREMBLAY et al.

1989), or 60-70 % of the total carbon flux to deeper layers in spring/summer (MICHEL et al. 1996), emphasizing the pivotal role of grazing and faecal pellet production for the overall cryo-pelagic carbon flux.

Grazing impact of under-ice amphipods on sea-ice algae in the lowermost part of Arctic pack-ice can be 1-3 % of algal standing stock per day during summer (WERNER 1997), so that it would theoretically take the amphipods about 1-3 months to graze up the entire standing stock after primary production in the ice ceases with begin of the dark season, leading to the almost complete absence of ice algae at the end of winter (MELNIKOV et al. 2002, SCHÜNEMANN & WERNER 2005). It is, however, not probable that the ice-algal biomass or algal detritus is still available to the amphipods when freezing during winter leads to ice growth at the ice underside, which can be as high as 0.1-0.8 cm d⁻¹ in high-Arctic pack ice between November and June (PEROVICH et al. 2003), probably sealing off the ice underside to a certain degree.

Several species of Arctic under-ice amphipods also prey on calanoid copepods caught from the water column, thus forming a pathway of organic matter and energy flux from the pelagic ecosystem to the sea-ice realm. Such a predatory behaviour has been shown in particular for *Gammarus wilkitzkii*, but also for *Onisimus* spp., by means of direct feeding experiments (WERNER et al. 2002b) and analyses of fatty acid biomarkers (SCOTT et al. 1999, WERNER & AUDEL 2005), proving that the cryo-pelagic matter flux is indeed a two-way process. Predation pressure of *G. wilkitzkii* on *Calanus* spp. in the under-ice water can be very high (up to 61.5 % of standing stock per day), leading to the speculation that the copepods may avoid the upper layer of the water column in order to escape this effective predation (WERNER et al. 2002b, HIRCHE & KOSOBOKOVA 2003). Abundances of *Calanus* spp. are often higher at 5 m depth than at 1 m depth below the ice (Werner unpubl.).

The Arctic under-ice fauna, in particular the amphipods, form an important link between the sea-ice, where they live attached to and feed from, and higher trophic levels in the water column. They are preyed upon by polar cod *Boreogadus saida* (LØNNE & GULLIKSEN 1989), which is also part of the under-ice fauna at times (GRADINGER & BLUHM 2004), and by diving seabirds like the black guillemot *Cephus grylle* and the little auk *Alle alle* (LØNNE & GABRIELSEN 1992), and even by ringed seals (BRADSTREET & CROSS 1982).

RESPIRATION RATES OF AMPHIPODS BELOW ARCTIC PACK-ICE

The metabolic rate of an aerob organism can be estimated by measuring the oxygen consumption or (external) respiration rate. The respiration rate is the summed energy expenditure for all metabolic processes (PETERS 1983). With respect to the activity of animals, the metabolic rates are defined as follows. Standard (or basal) metabolism is the oxygen consumption rate for maintenance only, routine metabolism is the oxygen consumption rate measured with uncontrolled but minimum activity, and active metabolism is the oxygen consumption rate with enforced activity. In most studies on marine pelagic species, no attempt has been made to define the level of metabolism, on the assumption that the experimental set-up

provides measured rates close to routine metabolism (IKEDA et al. 2000). In our experiments, we have followed this approach and assumption, so that an approximate routine metabolism is meant with the respiration rates given. The conversion of oxygen consumed to carbon dioxide produced by means of the respiratory quotient, which is depending on the metabolic substrate, leads to an estimation of minimum food requirements of the organism (IKEDA et al. 2000). Thus, respiration rates can also be used as an index for feeding and ingestion rates, and can be compared with ingestion rates derived from e.g. feeding experiments (WERNER 1997, WERNER et al. 2002b, AUDEL & WERNER 2003).

We have studied and compared the respiration rates of the truly sympagic amphipod species *Apherusa glacialis*, *Onisimus* spp., and *Gammarus wilkitzkii* (WERNER et al. 2002b, WERNER & AUDEL 2005), of the pelagic amphipod species *Themisto libellula* (AUDEL & WERNER 2003), and of the epibenthic amphipod species *Anonyx sarsi* (WERNER et al. 2004), which all occurred below the Arctic pack-ice. Because experimental set-up (closed-bottle method), ambient temperature and salinity (test animals were acclimated at least for 48 h), as well as measuring techniques (Winkler titration) were the same for all species, direct comparisons of the different respiration rates are possible. Moreover, body sizes of *G. wilkitzkii*, *T. libellula*, and *A. sarsi* used in the experiments were very similar, so that the comparisons between these three species of different forms of life are especially interesting.

It has been a scientific question for a long time, how ectotherm animals survive at very low temperatures, e.g., in polar waters, and the study of their metabolic rates has been a major tool in order to answer this question, because energetics are considered a central feature of adaptation to temperature (PECK 2002). The hypothesis of “metabolic cold adaptation”, i.e. the idea that animals living at low temperatures should have a comparatively elevated metabolism (SCHOLANDER et al. 1953, WOHLISCHLAG 1964), has not been disproved completely, but most recent studies measuring standard or routine metabolism carefully show that metabolic rates in polar species are generally low (e.g., CLARKE 1980, CHAPELLE & PECK 1995, PECK 2002). Metabolism in Antarctic ectotherms is considerably lower than for temperate and tropical counterparts (PECK 2002), as has been shown e.g., for marine molluscs along latitudinal gradients (PECK & CONVEY 2000). These low metabolic rates may be related to mitochondrial function at low temperatures, and are associated with slow growth and development rates (PECK 2002). For some polar species, partial acclimation to short-term temperature changes as well as seasonal acclimation have been observed (PÖRTNER et al. 1998, 1999a,b).

Metabolic rates are of course depending on ambient temperature (IKEDA et al. 2000). Arctic under-ice amphipods live in a habitat with very low, but rather constant temperatures. In the course of a year, temperatures at the ice–water interface may vary between 0 °C and -1.9 °C, with, however, most of the time being at or close to the freezing point (WERNER & MARTINEZ ARBIZU 1999, WERNER 2006). In none of the sympagic amphipod species, a significant difference in respiration rates in summer and winter could be found, indicating that the under-ice habitat is a comparatively stable habitat in terms of seasonal variations, above all in temperature (WERNER & AUDEL 2005). Moreover, the lifestyle attached to

the ice underside appears to be rather energy-saving, despite the comparatively high body density of the amphipods (WERNER et al. 1999), and resembles rather a benthic (although upside-down) than a pelagic form of life. The respiration rates of *Onisimus* spp. and *Gammarus wilkitzkii* (AARSET & AUNAS 1990, WERNER et al. 1999, WERNER et al. 2002b, WERNER & AUDEL 2005) are among the lowest rates measured in polar amphipods. Similarly low rates have been measured, e.g., in the Antarctic benthic and under-ice species *Paramoera walkerii* (KLEKOWSKI et al. 1973), in *Orchomene plebs* (RAKUSA-SUSZCZEWSKI 1982, RAKUSA-SUSZCZEWSKI & LACH 1991), and in *Bovallia gigantea* (OPALINSKI & SICINSKI 1995). Even lower rates are known from the deep-sea amphipod *Eurythenes gryllus* (TAKUCHI & WATANABE 1998), and from the Antarctic benthic *Waldeckia obesa* (RAKUSA-SUSZCZEWSKI & LACH 1991, CHAPELLE & PECK 1995), which is a rather inactive species, resting most of the time and only moving slowly in the search for food (CHAPELLE et al. 1994). A direct comparison of the different studies is unfortunately difficult due to different body sizes, sex, and nutritional conditions of the amphipods used, which all influence respiration rates, however, it can be shown that the metabolic rates of the Arctic under-ice amphipods are generally within the same low range as of the Antarctic benthic amphipods (Tab. 2).

Another important factor influencing respiration rate is the level of activity and mobility. Swimming *Gammarus wilkitzkii* have a more than twice as high energy expenditure than animals attached (WERNER et al. 1999), similar to other crustaceans which have to actively swim in order to prevent sinking (SPAARGAREN 1980, KILS 1981). Since the species is attached to the ice underside most of the time and swims only short distances (POLTERMANN 1997), it can save a large amount of locomotory energy. *Apherusa glacialis* shows significantly (Kruskal-Wallis test, $p < 0.001$) higher specific respiration rates as compared to the other Arctic under-ice amphipods (Fig. 5), which can be attributed to the smaller body size, but also to the comparatively higher mobility of the species. In contrast to the other species, *A. glacialis* is usually moving along the ice underside most of the time, and it is also the best swimmer, known to have the highest spreading capabilities in colonizing new ice areas (LÖNNE & GULLIKSEN 1991a,b,

Species	Lifestyle	Respiration rate
<i>Onisimus</i> spp.	s	1.8 ± 2.2
<i>Gammarus wilkitzkii</i>	s	0.7 ± 0.5
<i>Paramoera walkerii</i>	s/b	1.4 ± 0.6*
<i>Eurythenes gryllus</i>	b	0.4 ± 0.1*
<i>Orchomene plebs</i>	b	1.7 ± 0.3*
<i>Waldeckia obesa</i>	b	0.1 ± 0.0*
<i>Bovallia gigantea</i>	b	1.8 ± 0.7*

Tab. 2: Respiration rates as daily turn-over (% d⁻¹) of different polar amphipod species, measured at T = 0 ± 1 °C. Given are means ± sd. Lifestyles: s = sympagic, b = benthic. * = data reproduced from T. Brey, Respiration in aquatic evertebrates - Unpublished data bank, original references listed in the data bank and mentioned in the text.

Tab. 2: Respirationsraten als täglicher Umsatz (% Tag⁻¹) von verschiedenen polaren Amphipodenarten, gemessen bei T = 0 ± 1 °C. Angegeben sind Mittelwerte ± SD. Lebensformen: s = sympagisch, b = benthisch. * = Daten reproduziert von: T. Brey, Respiration in aquatischen Invertebraten, unveröffentl. Datenbank, Referenzen in Datenbank und im Text erwähnt.

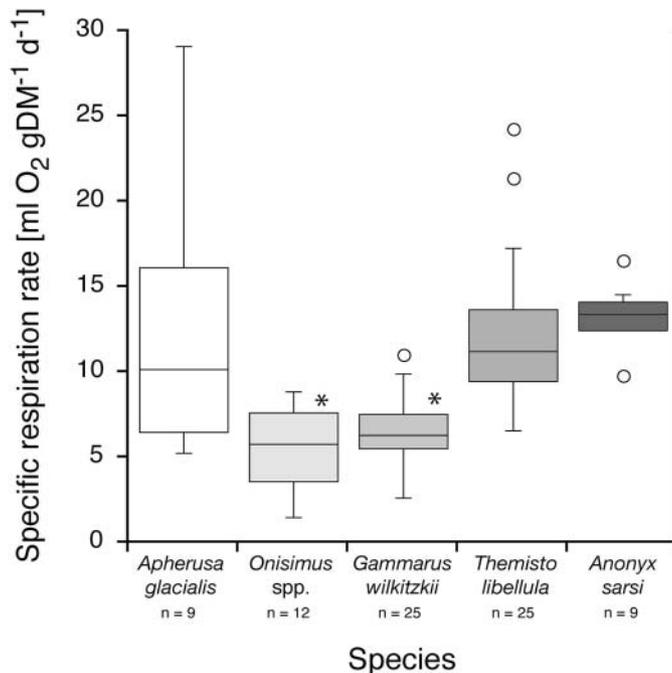


Fig. 5: Specific respiration rates of different amphipod species below Arctic pack ice. * = statistically significant difference.

Abb. 5: Spezifische Respirationsraten von verschiedenen Amphipodenarten unter arktischem Packeis. * = statistisch signifikanter Unterschied.

BEUCHEL & LØNNE 2002). The effect of an active pelagic lifestyle with permanent swimming is best demonstrated by the comparison of the respiration rates of the sympagic *G. wilkitzkii* and the pelagic *Themisto libellula* from the same location and of similar body sizes (WERNER et al. 2002b, AUDEL & WERNER 2003). Respiration rates of *T. libellula* were about twice as high as of the attached *G. wilkitzkii* (Fig. 5). The same holds true when comparing respiration rates of the sympagic *G. wilkitzkii* and the epipelagic amphipod *Anonyx sarsi* of comparable body sizes, again the rates of the actively swimming *A. sarsi* were about twice as high as of the attached *G. wilkitzkii*, both in the epibenthic (WESLAWSKI & OPALINSKI 1997) as well as in the under-ice habitat (WERNER et al. 2004, Fig. 5), demonstrating again the energy-saving lifestyle of the under-ice amphipods. The respiration rates of the sympagic amphipods *Onisimus* spp. and *G. wilkitzkii* are significantly lower than of the pelagic *T. libellula* and the epibenthic *A. sarsi* (Kruskal-Wallis test, $p < 0.001$).

According to an energy budget approach outlined by PAKHOMOV & PERISSINOTTO (1996), oxygen consumption rates can be converted into food consumption or ingestion rates, yielding the minimum energy demand covering routine metabolism. These rates can be compared with the results of direct feeding experiments in order to reveal which food sources could meet the energy demands of the under-ice amphipods (WERNER 1997, WERNER et al. 2002b, AUDEL & WERNER 2003). Summarizing all measurements and experiments on feeding and respiration rates shows that for none of the species, feeding exclusively on fresh ice algae could cover metabolic demands at all times. The predominantly herbivorous species *Apherusa glacialis* exhibits a comparatively high variability in the ingestion rate derived from respiration measurements with a mean turn-over of $2.6 \% d^{-1}$ ($sd = 1.8 \% d^{-1}$), half of which can be covered by feeding on ice algae with $1.3 \pm 0.3 \% d^{-1}$ (WERNER 1997), probably even more during the productive

season. Additional energy sources for this species are phyto-detritus (POLTERMANN 2001), and internal storage lipids during winter (WERNER & AUDEL 2005). In *Onisimus* spp., energy demands derived from respiration rates were the lowest among the Arctic under-ice amphipods with $1.1 \% d^{-1}$ ($sd = 0.5 \% d^{-1}$), only a third of which ($0.3 \pm 0.1 \% d^{-1}$) could be covered on average by grazing on fresh ice algae (WERNER 1997). The remaining energy demand of these two species (*O. glacialis*, *O. nansenii*) is covered by the ingestion of detritus (POLTERMANN 2001) as well as by carnivorous feeding (SCOTT et al. 1999, WERNER & AUDEL 2005). For *Gammarus wilkitzkii*, grazing on ice algae in the experiment covers only a very small part ($0.1 \pm 0.0 \% d^{-1}$, WERNER 1997) of their basic energy demand derived from respiration measurements of $1.3 \% d^{-1}$ ($sd = 0.4 \% d^{-1}$). Another minor food item are sympagic copepods, the ingestion of which can also yield about $0.1 \% d^{-1}$, but the major food source are calanoid copepods from the water column which can deliver an energy input of $8.0 \pm 5.6 \% d^{-1}$ for the predator, much more than actually required to meet basic metabolic demands (WERNER et al. 2002b). Although these experimentally derived data should always be regarded with caution when considering the situation in the field, they nonetheless indicate that *G. wilkitzkii* derives the major amount of its food from the water column, and that such a voracious feeding, when abundant and energy-rich prey is present, reflects an adaptation to a restricted environment with a highly variable and sometimes scarce food supply. This “sit-and-wait-strategy” appears to be advantageous to save energy during times of low prey availability (low respiration rates), to react quickly in the presence of prey, and to ingest food quantities in excess of actual energy demands in order to store internal lipid reserves for the next period of food shortage (SCOTT et al. 1999, WERNER & AUDEL 2005). In contrast, energy demands derived from respiration measurements ($1.9 \pm 0.7 \% d^{-1}$) and from feeding experiments on calanoid copepods ($1.9 \pm 1.5 \% d^{-1}$) were very similar in the amphipod species *Themisto libellula* (AUDEL & WERNER 2003), indicating that *T. libellula* is able to cover its metabolic demands by feeding on calanoid copepods. Different to the sympagic *G. wilkitzkii*, this pelagic species can actively follow its prey and avoid food shortages, and has therefore not developed this voracious feeding behaviour in the presence of prey (AUDEL & WERNER 2003).

OUTLOOK FOR FUTURE RESEARCH

Great advances in our knowledge about the sea-ice ecology in both hemispheres have been achieved during the last 20 years. However, the majority of studies and publications deal with the autotrophic and/or the microbial compartments of the sympagic ecosystems. Despite several studies on the species composition, vertical and horizontal distribution, abundance and biomass, controlling factors and special adaptations, seasonal and interannual variabilities of sea-ice and sub-ice metazoans, there are still gaps in our basic understanding of their functions and roles in the sympagic ecosystem. These issues should be addressed by future research projects. The major open questions are:

- (1) The origin and incorporation mechanism of sympagic metazoans, in particular over deep waters, a task including qualified taxonomical work on the many undescribed species in Arctic pack ice.
- (2) The fate and role of particles and organisms released from decaying sea ice to the water column.

(3) The quantitative role of sympagic meiofauna and sub-ice zooplankton in the complex sympagic food web, which has to be addressed by adequate experimental and biochemical approaches.

(4) The overwintering strategies of sympagic meiofauna and sub-ice zooplankton, a task, which requires year-round studies at a permanent ice station. In particular more data from the dark season are urgently needed.

(5) The physiological adaptations (osmoregulation, enzyme kinetics) of sympagic fauna to the variable factors temperature and salinity in the sea-ice habitat. Very important scientific questions arise from the observation of a changing environment and its potential impacts on the sympagic communities.

(6) The shrinking and thinning of the Arctic pack-ice cover, with a shift from mostly perennial to mostly seasonal ice, will probably have profound effects on species composition and interactions, on the sympagic food web and life cycles related to the formation and decay of sea ice.

(7) The potentially harmful impact of increased UV radiation, due to atmospheric ozone depletion, on Arctic and Antarctic under-ice fauna, as well as possible protection mechanisms should be studied.

Other interesting environmental impact topics include:

(8) The effects of oil pollution on the sympagic habitat and communities, as well as

(9) The accumulation and transfer of pollutants in the sympagic foodwebs.

In order to achieve progress in these future studies, some new technologies for sampling (e.g., scuba diving and automatic underwater vehicles below the ice), in situ measurements (e.g., microelectrodes and endoscopes for deployment inside the brine-channel system), and biochemical approaches (stable isotopes, molecular analyses, oxygen radicals) have been developed and will be increasingly used in the future. In general, multi-disciplinary approaches, combining remote sensing, ice physics and chemistry, oceanography and meteorology, are of overriding importance for both large-scale and process-oriented research on sea-ice ecology.

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