Feeding Ecology of the Arctic Ice-Amphipod *Gammarus wilkitzkii.* Physiological, Morphological and Ecological Studies

Die Nahrungsökologie des arktischen Eis-Amphipoden *Gammarus wilkitzkii.* Physiologische, morphologische und ökologische Studien

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Die vorliegende Arbeit ist die im wesentlichen unveränderte Fassung einer Diplomarbeit, die in der Sektion Arctic Biology der University Courses on Svalbard (UNIS) bei Dr. Ole Jørgen Lønne angefertigt und im Mai 2001 dem Fachbereich Biologie der Universität Hamburg Prof. Angelika Brandt und Prof. Hartmut Kausch vorgelegt wurde.

TABLE OF CONTENTS

SUMMARY

Gammarus wilkitzkii is a presumed omnivorous amphipod that lives in high densities in close association with Arctic pack-ice. To illuminate the complexity of food ecology in more detail *G. wilkitzkii* was examined in terms of food detection, food localisation, food preference, feeding mechanism, ingestion and digestion. The present study combines several experiments, in field and laboratory, with special emphasise on physiology, behaviour and morphology.

Sampling took place in September 2000 in the pack-ice north of Svalbard. At three ice stations of each 24 hours duration eight traps baited with different food types were fixed at the ice edge and below the ice. The total number of amphipods caught at all locations was 15. Most of the specimens were attracted by those traps attached at the under-ice surface and baited with "rotten polar cod". They belonged to the genera *Onisimus*. Even though abundance (and biomass) was recorded highest for *G. wilkitzkii* at all three stations this amphipod was only seldom attracted by baited traps. Compared to previous studies the density and biomass data at this sampling side was remarkably reduced, probably due to recent melting and re-freezing processes and the specific re-colonisation abilities of sympagic amphipods.

Since bait experiments resulted in extremely low numbers of attracted amphipods food preference studies were carried out in the laboratory with specimens sampled by SCUBA divers. The most preferred food type was deduced from oxygen consumption rates after exposing the amphipod to homogenates made of plant, animal or detrital material. Fourteen adults (of both sexes) and thirteen juveniles were incubated in a closed bottle set-up for 18 hours.
The oxygen consumption rates showed no sexual but significant ontogenetic differences in both, standard respiration and respiration in "stimulated mode" when exposed to different food types. The respiration of juveniles was 15% higher than of adults reflecting the basically elevated metabolic rate of the young fraction. Compared to adults, intensity and quality of the respiration after stimulating with food was much more pronounced for juveniles. In the laboratory juveniles preferred most detritus since the oxygen consumption rate was highest and constant throughout three replicates for this food type. For the same reason "rotten polar cod" was the most likely food item for adults during the experiment.
The respiration rates show high individual variability. All data should be considered with regard to variable activity modes, since the more active specimens consumed more oxygen than individuals that tend to rest during incubation.

Other experimental set-ups with a wide spectrum of food types including conspecific living and dead amphipods revealed, that *G. wilkitzkii* rejected none of the food types primarily and ingested even foreign material of no nutritive value. The amphipod grasped every object with the gnathopods and held it close to the mouthparts for examinations and ingestion. The affinity was highest

to animal derived, rotten tissue, resulting in increased activity. Macroalgae was pushed away after some "analytical bites".
Visual or chemical cues played a minor role in detection and localisation of food. Grasping the object was initiated after contacting it. *G. wilkitzkii* is assumed to be not capable to orientat along scent gradients towards the food source. Morphological SEM studies on selected setae emphasise their presumed functioning as contact chemosensory hairs.
The ingestion rate of animal derived tissues was highest for juveniles feeding on "rotten polar cod". Microscopic analysis of the fecal pellets support greedy and undiscriminating ingestion behaviour and the lack of distinct enzymes such as cellulase and chitinase. Studies on grooming behaviour and the fact that dye was defecated suggest supplementary filter feeding.
Floating or suspended material is attracted from short distance by the pleopods activity. The resulting small scale circulation ventilates gills (and brood in females) and moves water masses through the filtrating and sensory organs of the oral region. The reaction time to inserted food seems to depend on the individual activity mode and therefore the frequency of pleopod beating.

In nature sea ice provides not only food supply, grid and nursery ground but also shelter for the young fraction of *G. wilkitzkii* and other sympagic amphipods. The predation pressure is high since adult *G. wilkitzkii* also preys on their own juveniles. *G. wilkitzkii* is characterised as a casual rather than a visual predator.

Morphological studies on mouthparts and accessory feeding appendages by means of SEM confirm a more unspecific food ecology of *G. wilkitzkii.*
The frequent utilisation and morphology of the gnathopods, the observed positive tactile responding and the sharp cutting edges on the mandibles suggest carnivorous or necrophageous behaviour. Gnathopods and mandibles were also used to loosen ice encrusted material, such as diatoms. The hard shells were crushed by triturative molars. Scraping on the ice was only observed after food contact took place. While resting collected suspended material served as supplementary food source. Strong setation on the mouthparts, frequent grooming of the setose appendages and the mentioned defecation of dye postulate filter feeding behaviour.

ZUSAMMENFASSUNG

Gammarus wilkitzkii ist ein omnivorer Amphipode, der in hohen Dichten in Assoziation mit dem arktischen Packeis vorkommt. Um Aufschluß über die Komplexität seiner Nahrungsökologie zu erhalten, wurde *G. wilkitzkii* in Hinblick auf die Wahrnehmung und Lokalisierung des Futters, seine Nahrungspräferenz, Nahrungsaufnahmemechanismen, Ingestion und Digestion untersucht. Die vorliegende Studie zieht dafür Feld- und Laborexperimente heran, die die Physiologie, Morphologie und das Verhalten berücksichtigen.
Die Probennahme fand im September 2000 im Packeis nördlich von Spitzbergen statt. An drei 24-stündigen Eisstationen wurden je acht Reusen, die

mit unterschiedlichen Ködern bestückt waren, an der Eiskante und unter dem Eis befestigt. Insgesamt lockten die Reusen 15 Amphipoden an. Die meisten der Individuen wurden von den Untereis-Reusen gefangen, die mit verwestem Dorsch beködert waren. Sie gehörten zur Gattung *Onisimus*. Trotz der für *G. wilkitzkii* festgestellten hohen Abundanzen (und Biomassen) kam diese Art nur selten in den Reusen vor. Dichte und Biomasse waren im Vergleich zu früheren Arbeiten in diesem Untersuchungsgebiet deutlich geringer. Dies wird zurückgeführt auf Schmelz- und Gefrierprozesse und die Fähigkeit der einzelnen Eis-Amphipoden, Meereis neu zu besiedeln.

Da die Reusen nur eine geringe Anzahl Amphipoden anlockten, wurden weitere Studien zur Nahrungsökologie im Labor an Tieren vorgenommen, die von Tauchern gesammelt worden waren. Das bevorzugte Futter wurde mit Respirationsmessungen ermittelt. Die Tiere wurden dabei Homogenaten aus pflanzlichem, tierischem oder Detritus-Material ausgesetzt. Die Inkubationszeit für 14 Adulte beiden Geschlechts und 13 Juvenile betrug in den sauerstoffundurchlässigen Flaschen 18 Stunden.
Der Sauerstoffverbrauch wies keine sexuellen aber signifikante ontogenetische Unterschiede sowohl hinsichtlich der Standardrespiration als auch der Respiration im "stimulierten" Zustand auf. Bei Jungtieren war die Respiration aufgrund ihrer höheren Stoffwechselrate um 15% höher als bei Adulten. Im Vergleich zu den Adulttieren, waren bei Juvenilen Intensität und Qualität der Respiration nach der Stimulation mit Futter ausgeprägter. Jungtiere bevorzugten im Labor Detritus, da bei diesem Futter der Sauerstoffverbrauch am höchsten und bei allen drei Replikaten konstant war. Aus dem selben Grund war verwester Polardorsch das von den Adulttieren bevorzugte Futter.
Die Respirationsraten zeigen hohe individuelle Variabilität. Alle Ergebnisse sollten jedoch auch den Aktivitätsmodus berücksichtigen. Überwiegend aktive Tiere verbrauchten während der Inkubationszeit mehr Sauerstoff als ruhende.

Experimente, in denen ein breites Spektrum verschiedener Futtertypen angeboten wurde, die auch lebende und tote Tiere der selben Art mit einschlossen, machten deutlich, daß *G. wilkitzkii* keines der Futter primär ablehnte. Der Amphipode ingestierte sogar Fremdmaterial. Jedes der Objekte wurde mit den Gnathopoden gepackt und an die Mundwerkzeuge geführt, wo es untersucht und schließlich gefressen wurde. Die Affinität war am größten für tierisches, insbesondere verwestes Material, auf das *G. wilkitzkii* mit einer erhöhten Aktivität reagierte. Von den Makroalgen ließ der Amphipode nach dem "Probieren" ab.
Visuelle oder chemische Reize spielen bei der Wahrnehmung und Lokalisierung von Futter eine untergeordnete Rolle. Es wird vermutet, daß sich *G. wilkitzkii* nicht zielgerichtet an Konzentrationsgradienten orientieren kann. Das Objekt wurde nach dem Körperkontakt gegriffen. REM-Studien zur Morphologie einzelner Setae lassen ihre Funktion als Kontaktchemorezeptoren vermuten.
Die Ingestionsrate von Fleisch war für Juvenile, die verwesten Dorsch fraßen, am höchsten. Mikroskopische Untersuchungen an den Fecal Pellets bestätigen die "gierige", undifferenzierte Ernährungsweise von *G. wilkitzkii.* Vermutlich verfügt der Amphipode nicht über bestimmte Verdauungsenzyme wie z.B.

Cellulase und Chitinase. Das ausgeprägte Putzverhalten und die Defäkation von Lebensmittelfarbe belegen die Existenz von Filtermechanismen.
Driftendes oder supendiertes Material wird durch die Aktivität der Pleopoden angezogen. Die resultierende, kleinräumige Zirkulation fächert den Kiemen und – bei Weibchen – der Brut Sauerstoff zu und passiert die filtrierenden und sensorischen Organe der Mundregion. Die Reaktionszeit auf Futter hängt vom individuellen Aktivitätszustand und damit von der Schlagfrequenz der Pleopoden ab.

In der Natur dient Meereis nicht nur dem Nahrungserwerb, als fester Halt und "Kinderstube", sondern für juvenile *G. wilkitzkii* und andere Eis-Amphipoden auch als Schutz vor Prädatoren. Der Prädationsdruck ist sehr hoch, da adulte *G. wilkitzkii* auch ihre eigenen Jungen erbeuten. Der Amphipode ist eher ein "Gelegenheitsjäger" als ein visueller Prädator.

Die Morphologie der Mundwerkzeuge und der anderen, beim Nahrunserwerb involvierten Extremitäten bestätigt die eher unspezifische Nahrungsökologie von *G. wilkitzkii.*
Der häufige Einsatz und die Morphologie der Gnathopoden, das beobachtete positiv thigmotaktische Verhalten und die scharfen Schneiden der Mandibeln sprechen für eine carnivore oder necrophage Lebensweise. Die Gnathopoden und Mandibeln wurden zudem dazu benutzt, Futter aus dem Eis herauszulösen. Die auf diese Weise freigelegten Diatomeen konnten von den Molaren zermahlen werden. Weiden wurde nur nach Futterkontakt am Eis beobachtet. Während der Ruhephasen am Eis diente suspendiertes Material als zusätzliche Futterquelle. Die starke Behaarung der Mundwerkzeuge, das häufige Putzen der behaarten Extremitäten und die bereits erwähnte Defäkation der Farbpartikel deuten auf den ergänzenden filtrierenden Nahrungserwerb hin.

1. INTRODUCTION

Large areas of the Arctic Ocean are permanently covered by sea ice. The extent of this coverage varies remarkably with the seasons, fluctuating between 7 and 14 x 10^6 km^2, annually [Maykut 1985]. At maximum extent, sea ice covers 5% of the Northern Hemisphere. Sea ice is in continuous motion, driven by winds and currents [Maykut 1985]. It is therefore subjected to permanent environmental changes, such as physical forces, freezing and melting processes [Melnikov 1997].

Apart from its significance for climatic, hydrographic, and geological processes, sea ice plays an important role in the biology and ecology of polar marine systems, since it provides a unique habitat for a diverse flora and fauna [e.g. Horner *et al.* 1992, Melnikov 1997]. The ice-water interface is a particular compartment of this habitat, characterised by several species from both, the sea ice and the pelagic and benthic realm [Carey 1985, Gradinger 1996, Gulliksen & Lønne 1991, Horner *et al.* 1992, Melnikov 1997]. The second main important micro-habitat within sea ice is the brine channel system, which is formed during ice growth between ice crystals by exclusion and concentration of the seawater salts [Maykut 1985, Weissenberger 1992].

Sea ice is defined as either first-year ice (FYI), which is the result of not more than one winters ice growth , or multi-year ice (MYI), when it has survived at least the melting periods of two summers [WMO 1970]. FYI is characterised by flat, smooth and compact lower surfaces with small and narrow brine channels, that offer only few possibilities for shelter, and provide less food supply. Melting modifies the submerged parts of the ice: it becomes spongy and the brine channels widen into pockets and caverns which make the sea ice even more suitable for macrofauna settling [Hempel 1991]. They serve as refuge and allow the accumulation of floating detritus-algae-aggregations, an important food source below the ice [Poltermann 1997]. The MYI is characterised by heterogeneity. It is encompassed by cheese-like, porous surfaces and structures such as edges, ridges, domes, flat areas, crevices, holes and channels [Hop *et al.* 2000, Maykut 1985].

Physiologically, organisms inhabiting brine channels and melting holes within the sea ice are subjected to extreme conditions, such as water temperatures close to the freezing point and high salinities during winter freezing periods. During summer melt the crustaceans encounter low salinities at the ice-water interface [Aarset 1992, Melnikov 1997].
Moreover, high seasonal variations occur in light conditions and availability of nutrients [Grainger 1977], thus certain food sources such as ice algae and phytoplankton are limited to brief periods of the year [Carey 1985, Melnikov 1997].

Nevertheless, sea ice has been successfully colonised by various groups of ice-associated, sympagic organisms which are considered temporary inhabitants of this environment (allochthonous) or spend their entire life cycle, including both sexes and all developmental stages in close association with the ice (autochthonous) [Gulliksen & Lønne 1991, Horner *et al.* 1992, Melnikov & Kulikov 1980].

The dominating species inhabiting the ice belong to the crustaceans. The micro-distribution of crustaceans in the under-ice habitats varies from species to species [Carey 1985]. Individuals have been observed living in brine channels [Cross 1982] and partially or fully embedded in the ice [Gulliksen 1984].

The taxonomic range of the ice micro- and meiofauna includes bacteria, flagellates, algae and protozoans, as well as multi-cellular organisms, such as rotatorians, turbellarians, nematodes, polychaetes and copepods [e.g. Grainger & Hsiao 1990, Friedrich 1997].

The ice-associated fauna inhabiting the upper centimetres below the ice surface consists of ctenophores, chaetognaths, pteropods and copepods [Poltermann 1997].

Larger organisms (> 5 mm) permanently inhabiting the Arctic ice are four species of gammaridean amphipods:

- *Gammarus wilkitzkii* Birula 1897, Gammaridae
- *Apherusa glacialis* Hansen 1887, Calliopiidae
- *Onisimus nanseni* Sars 1900, Lysianassidae
- *Onisimus glacialis* Sars 1900, Lysianassidae

[Lønne & Gulliksen 1991a, c, Melnikov 1997, Poltermann 1997, Werner 1997b].

These species are known as autochthonous [Gulliksen & Lønne 1991]. They use the ice as substrate for food supply, grid, shelter and reproduction [Carey 1985].

Earlier studies documented that sympagic amphipods are physiologically well adapted to the extreme environmental conditions under Arctic sea ice [Aarset 1992]. The most abundant species are *G. wilkitzkii* and *A. glacialis* [Gulliksen & Lønne 1991, Poltermann 1997]. Their distribution depends on various factors: ice type and ice history, content of organic matter, under-ice topography with regards to mesoscale structures and different requirements of the species, with respect to food, shelter and physiological conditions [e.g. Gulliksen & Lønne 1991, Grainger & Hsiao 1990, Cross 1982, Carey 1985, Melnikov 1997, Maykut 1985, Aarset 1992, Poltermann 1997, Hop *et al.* 2000].

The Arctic food web is believed to base on the primary productivity of micro-algae [Bradstreet & Cross 1982, Carey 1985, Cross 1982, Grainger *et al.* 1985, Horner 1989, 1990, Maykut 1985]. But not only the diverse flora and ice-associated meio-and macrofauna represent main food sources in the ice habitat. Their living or remaining material – the latter contributes to detrital assemblages – often accumulate in the lower surface of the ice or are even flushed further into the three-dimensional brine channel system [Poltermann 1997].

Sea ice presents a highly concentrated source of available food [Grainger & Hsiao 1990]. Sympagic amphipods are assumed to use all these food sources available under the sea ice. They also represent important food items for other ice-associated organisms such as pelagic fish, sea birds and seals [Bradstreet

1980, Bradstreet & Cross 1982, Cross 1982, Lønne & Gabrielsen 1992, Lønne & Gulliksen 1989, Poltermann 1997, Werner 1997b]. The sympagic fauna in the Arctic is therefore considered a significant link from lower to higher trophic levels in the Arctic marine food web [Bradstreet & Cross 1982].

Every year about 1.4 x 10^6 km^2 of sea ice is exported from the Arctic Ocean, mainly through the Fram Strait (1.3 x 10^6 km^2). This export is generated by the Transpolar Drift [Nansen 1902]. Since most of the polar perennial sea ice melts in the North Atlantic, the released organisms give a significant input to these biologically rich surface waters [Lønne & Gabrielsen 1992]. The estimated annual loss of sympagic fauna ranges in the order of 7 x 10^5 tons for the perennial sea ice zone [Lønne & Gulliksen 1991c]. The high mortality rate due to melting processes and predation is probably compensated by various adaptations in view of reproduction [Poltermann 2000].

1.1. *Gammarus wilkitzkii*

Morphologically and physiologically *G. wilkitzkii* is well adapted to continuous changes in the physical and chemical environment.

Several studies documented *G. wilkitzkii* being the dominant amphipod species that permanently inhabits the lower surface of Arctic sea ice in the Svalbard and Franz Josef Land area [Carey 1985, Hop *et al.* 2000, Lønne & Gulliksen 1991b, Melnikov 1997, Poltermann 1997, Werner 1997b]. In the Canadian sector of the Arctic, this species is frequent, but of secondary importance [Barnard 1959, Cross 1982, Steele & Steele 1974].

G. wilkitzkii has a circumpolar distribution. Apart from sea ice, the species has been found in the vicinity of coasts, inhabiting the littoral and sub-littoral zone down to 100 m in depth, and penetrating into the large Siberian rivers [Poltermann 1997]. Recent observations of *G. wilkitzkii* in the open ocean off the marginal ice zone indicate, that the species is able to survive in the water column when sea ice is absent [Werner *et al.* 1999].

G. wilkitzkii appears to be mainly associated with MYI [Steele & Steele 1974], with corresponding biomass values of 10 to 100 times higher than values recorded in FYI areas [Lønne & Gulliksen 1991a, c]. Compared to other mesoscale under-ice structures, the species is consistently abundant on ridges [Hop *et al.* 2000]. According to *in situ* observations, *G. wilkitzkii* inhabits the cracks and small holes on the submerged surface of sea-ice [Lønne & Gulliksen 1991a]. The young fraction is able to penetrate into the smaller brine channels of the flat and smooth subsurface of FYI, where it hides from larger individuals as well as from predators, while the large individuals seem to prefer the porous subsurfaces of MYI [Beuchel 2000, Maykut 1985].

The biomass values of *G. wilkitzkii* can reach 10.12 g m^{-2} with an abundance of 368 n m^{-2} [Poltermann 1998]. *G. wilkitzkii* exhibits a low growth rate, needing 5 to 6 years to reach its maximum size [Poltermann 2000]. This is strongly supported by the fact that the oxygen consumption rates of this species are the lowest measured among Arctic and subarctic benthic amphipods [Werner *et al.*

1999]. Although *G. wilkitzkii* is characterised by high fecundity, this species is a presumed K-strategist [Poltermann *et al.* 2000].

G. wilkitzkii is an excellent euryhaline osmoregulator, displaying regulation of haemolymph concentrations of sodium and chloride. This enables the species to lower the melting point of the body fluids, thus preventing internal ice formation at low temperatures. *G. wilkitzkii* is able to survive during sea ice growth in the vicinity of ice by conforming the ambient brine in a salinity range of 34 to 60 [Aarset 1991, Aarset & Aunaas 1987a, b, 1990a]. Being an osmoconformer, the species can occupy brine channels and melting holes open to the lower surface of sea ice, sometimes penetrating up to 30 cm into the ice [Cross 1982, Poltermann 1998].
G. wilkitzkii is described as a cold-tolerant but freeze-sensitive amphipod, that stays away from the advancing ice front [Aarset & Aunaas 1987b]. The general response to increasing temperature and osmotic stress is an increased metabolic rate, indicated by raised oxygen consumption rates [Aarset & Aunaas 1990a, b].

G. wilkitzkii is known as an omnivorous species exhibiting predatory, detritivorous and necrophagous behaviour [Poltermann 1997, Scott *et al.* 1999, Werner 1997a]. This species therefore uses a wide spectrum of food sources, including conspecific amphipods [Poltermann 1997, Werner 1997b] and probably filtered material [Poltermann 1997]. Previous experiments with baited traps below sea ice suggested, that *G. wilkitzkii* prefers most animal derived material [Barnard 1959, Poltermann 1997].
In the laboratory, investigations focussed on feeding experiments with micro-algae or examined gut contents, fecal pellets and lipids.
Gut content analysis of specimens sampled in different seasons assume detritus as a main food source throughout the year [Poltermann 1997]. Detritus consists of plant and animal remains, fungi and bacteria, and is not only considered to be of variable energy content and easy to digest, but is also available all year round [Poltermann 2001]. Hence, food limitation may be less important for *G. wilkitzkii* than for many other polar organisms [Poltermann 2000]. However, *G. wilkitzkii* is able to survive starvation periods of up to 10 months [Poltermann 1997].
Studies on fecal pellets documented that animal remains, especially crustacean parts, contribute only little to ingested food but were found regularly [Bradstreet & Cross 1982]. *In situ* observations noted *G. wilkitzkii* feeding also on pteropods [Gulliksen & Lønne 1989].
Diatom remains were frequently found in fecal pellets as well [Horner 1985b]. The amount of ingested micro-algae was negligible in the studies of Poltermann [1997]. In contrast, diatoms were of remarkable importance in the diet of those *G. wilkitzkii*, sampled along the Pond Inlet ice edge, Canada [Bradstreet & Cross 1982]. Feeding experiments with ice algae revealed the lowest ingestion rates compared to other sympagic amphipods [Werner 1997a].
Lipid analysis recorded conspicuous levels of herbivore-specific (diatom-derived) fatty acids. In addition, copepod-derived fatty acids were found but in less concentration, emphasising a more herbivorous-omnivorous feeding ecology of this species [Scott *et al.* 1999].

In turn, *G. wilkitzkii* represents an important food item for marine mammals and several seabirds [Bradstreet 1982, Bradstreet & Cross 1982, Lønne & Gabrielsen 1992]. The young fraction constitutes a major part of the diet of pelagic predators such as polar cod (*Boreogadus saida*) while the large *G. wilkitzkii* in particular is avoided by polar cod, probably due to the "spiny" morphology of this amphipod [Barnard 1959, Lønne & Gulliksen 1989]. However, *G. wilkitzkii* is considered a key species in the ice based Arctic food web [Poltermann 1997, 1998, Werner 1997a].

1.2. Purpose of this study

Basic for maintaining the energetic machinery of organisms is the necessity for them to obtain energy and vital chemical compounds in form of food or dissolved substances in seawater. Due to the diversity of habitats interior and below sea ice and the multiplicity of species occupying these habitats, several adaptations with respect to mechanisms for gathering, processing certain sorts of food and behavioural responses took place in the evolution of sympagic amphipods, to ensure the optimal result that maximises fitness.

Since sea ice provides a food source for the pelagic and benthic fauna in the Arctic, the quality and quantity of the downward transport of organic detritus, fecal pellets, crustacean molts and other animal and plant remains depend on food ecology of the sympagic biota.

As already figured out, several authors contributed to a better understanding of the food ecology of sympagic amphipods. Various studies concentrated on *G. wilkitzkii* for the following reasons: 1. this amphipod is quite abundant below Arctic sea ice; 2. it is easy to keep alive in the laboratory; and 3. it can be handled easily because of its large body size.

The information on the food ecology of this species is contradictory and often relies on assumptions. Only little information was deduced from *in situ* observations. Generally, conclusions were drawn from gut content and fecal pellet analysis or restricted to experiments in the laboratory.

There remains no doubt *G. wilkitzkii* is an omnivorous species, but up to now, little is known in detail about feeding ecology. Therefore, this study focussed on the following investigations:

- food detection
- food localisation
- food preference
- feeding mechanism
- ingestion
- digestion

The present study intends to combine the results of different methods to illuminate the feeding ecology of *G. wilkitzkii* from various perspectives:

1. field work: baited traps
2. physiological study: oxygen consumption rates when exposed to different food sources
3. behavioural observations: interactions with the abiotic and biotic environment
4. morphological study: mouth parts and feeding appendages

ad 1. Field experiments with baited traps assume the capability of amphipods to sense chemical compounds, and also active foraging behaviour when orientating towards the source of scent.

ad 2. Respiration measurements in the context of feeding ecology are based on the results of Smith & Baldwin [1982]. The hypothesis formulated for this method is: the food preference is deducible from the quality (increased or reduced O_2-consumption) and the intensity (deviation from the standard O_2-consumption) of the respiration rate while exposed to different food types.

ad 3. Distinct behavioural patterns such as grooming or pleopod beating may play an important role in food acquisition. Ethological observations on single specimens and the analysis of their interactions with the biotic and abiotic environment therefore add valuable information on feeding ecology.

ad 4. Morphological peculiarities reflect evolutionary adaptations to certain food types and feeding mechanisms. The correlation of food type, feeding mechanism and morphological variations of the mouth parts and accessory feeding appendages that are involved in the capture, manipulation and sorting of food allow conclusions concerning food preference only by analysing the morphology and their presumed functioning [Agrawal 1965].

2. MATERIAL AND METHODS

2.I. Field work

Sampling area

The samples examined in this study were collected in September 2000 during a scientific cruise with the research vessel JAN MAYEN. As the cruise was part of the course AB-310 „Marine zooplankton and sympagic fauna (= ice fauna)" at the University Courses on Svalbard (UNIS) the stations were located at three distinct longitudes of about 15°E, 31°E and 7.3°E (Fig. 1, Tab. 1) in order to compare the data with those obtained in 1998. At each longitude, the vessel steamed as far north as the ice conditions allowed. When denser drift and multi-year ice was encountered, an ice station was erected on a suitable ice floe, providing working facilities for 24 hours.

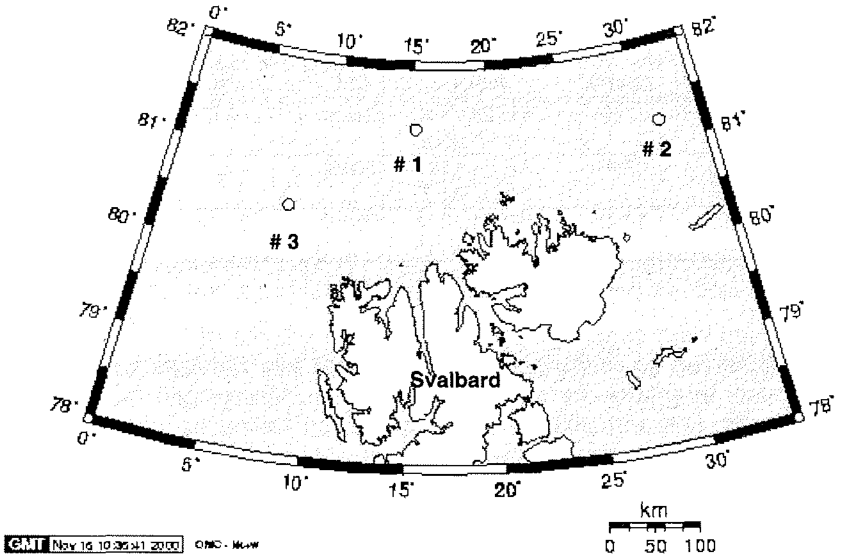


Fig. 1: Map of ice stations in the Arctic Ocean north of Svalbard during expedition on RV JAN MAYEN (September 2000).

Sampling methods

The material used for the abundance and biomass analysis in the course [Arndt *et al.* 2000] and the morphological studies on mouth parts and feeding appendages examined in this study was collected by a SCUBA diver operated electric suction sampler [Lønne 1988]. The mesh size of the filter retaining the organisms was 350 µm. The samples were labelled and stored in 4%

formaldehyde. The species were identified according to Barnard [1959] and Poltermann [1997].
The qualitative material for the laboratory work on living amphipods was collected by SCUBA divers using hand-held dip nets (mesh size 180 µm) with a rectangular frame [Gulliksen 1984]. Immediately after collection, the amphipods were sorted into species and stored in running sea-water tanks. Adults and juveniles of *G. wilkitzkii* were kept separately.
In addition, different food items like polar cod (*Boreogadus saida*) and copepods (*Calanus* sp.) were collected by means of pelagic shrimp trawl or multinet. Aggregates of detritus or ice algae were sampled with the suction sampler (mesh size 180 µm). Microscopic analysis of the detritus-sample yielded inorganic and organic particles such as sediment and aggregations of ice algae, micro-organisms, crustacean exuvies, fecal pellets and other items. The ice algae-sample consisted mainly of fragments of several solitary species of the genera *Nitzschia* spp. and *Navicula* spp. [pers. comm. v. Quillfeldt] and already fermented, amorphous material. All food samples were stored in the freezer.

Tab. 1: Positions and ice characteristics of the three ice stations. FYI: first-year ice, MYI: multi-year ice.

Station #	**date**	**GMT time (start)**	**position (start)**	**floe size (m)**	**floe thickness (m)**	**FYI/MYI (%)**
1	22.09.	17:34	81° 23.77 N 15° 07.95 E	50x30	2,5	50/50
2	25.09.	08:47	81° 14.14 N 31° 17.81 E	150x50	2	80/20
3	27.09.	14:45	80° 31.32 N 07° 33.44 E	60x50	3 - 12	70/30

The traps used were simple plastic bottles with a volume of 5 l. Two holes cut into the top served as entrances, and below that two windows were covered with fine mesh to ensure the release of bait scent. Macroalgae (mainly *Fucus* sp.), copepods, krill and polar cod that had been rotting for one week were offered as bait. At each station, two bait types were tested in four bottles each, two attached directly along the ice edge at 2 m below the surface, and the other two fixed under the ice by means of ice screws (distance to the edge: approx. 4 m). One bottle contained no bait and thus served as control. The traps were always placed at that side of the floe which was exposed to wind and currents, to allow the optimal distribution of the bait scent below the ice.
The traps were controlled every three or four hours in order to prevent the escape of attracted amphipods, while keeping disturbances at a minimum. During night no control was possible due to safety regulations. Total exposure time per station was approx. 24 hours. Animals found in traps were preserved in 4% buffered formaldehyde solution immediately after collection.
Due to the small sampling size the results will be presented without statistical analysis.

Ice conditions and hydrography

In order to classify the ice, ice observations were taken every two hours from the bridge as the vessel was steaming towards the ice station, beginning at first ice contact [Appendix 7 in: Arndt *et al.* 2000]. The observations focused on the proportion of FYI to MYI, average floe size, ice cover, ice thickness, and the presence of melt ponds, rafting and ridging. The ice underside of the floe was characterised by divers. Special attention was paid to brine channels, signs of melting or re-freezing, weathering, ice keels or indications of floe rafting.

At each station, CTD profiles were taken from the upper 300 m (Station # 1 and # 2) or 550 m (Station # 3) depending on the penetration depth of convective water movements, by using a Seabird 911 plus [Appendix 4-6 in: Arndt *et al.* 2000].

2. II. Laboratory work

Juveniles and adults were kept separately in plastic tanks filled with 100 l unfiltered sea-water taken from the Adventfjord. The water derived from 30 m below surface. Half of the volume was exchanged by fresh water twice a week. The average salinity ranged from 33.9 to 34.1, the average temperature was 3.5 to 4.5°C. The animals were kept under dim-light in a temperature controlled cooling room.

All specimens used for physiological and behavioural observations were not fed for at least one month but were cultivated in fresh sea-water taken from the fjord. As the production of fecal pellets continued and no dead specimen nor fragments had to be removed from the tanks during three months, it is reasonable to believe that the fjord water contained enough nutritive substances to ensure the survival of all amphipods.

As *G. wilkitzkii* reaches sexual maturation at a length of 2.3 cm [Poltermann 2000] adults are considered to be those specimens > 2 cm, corresponding to an age of about 2 years [Poltermann 2000]; juveniles were called the smallest fraction (body length: ± 1cm).

Unless stated otherwise all food types were freshly melted before use, except „rotten polar cod" which was kept under more or less anaerobic conditions for 10 days for decomposing purpose.

2.II.1. Physiological study

Oxygen consumption

The oxygen consumption was determined in a closed-bottle set-up (Fig. 2) with single animals incubating for 18 hours in 100 ml (adults) or 50 ml (juveniles) WINKLER glass bottles filled with filtered (WHATMAN® Filter GF/F 0.2 µm) sea-water. Only amphipods without "black-spot"-disease were used: 14 adult of both sexes and 14 juvenile specimens. Among the juveniles, the data of one specimen were eventually expelled because it died soon after the experiment was terminated. The data showed high deviation implying ongoing morbidity. Therefore, only data of 13 juveniles were evaluated. During incubation the amphipods were stored in the darkness at temperatures ranging from 3.5 to 4.5°C. After obtaining a respiration-series of non-stimulated amphipods (series 1) the experiment was repeated with food homogenate which was inserted by means of an EPPENDORF®-pipette. Control bottles without animals but with food homogenate were incubated simultaneously to consider microbial activity. Two bottles containing only water served for calibration. The remaining oxygen content after the incubation time in these bottles, was considered as 100%, the difference to the bottles containing food and/or amphipods was defined as the amount of oxygen consumed.

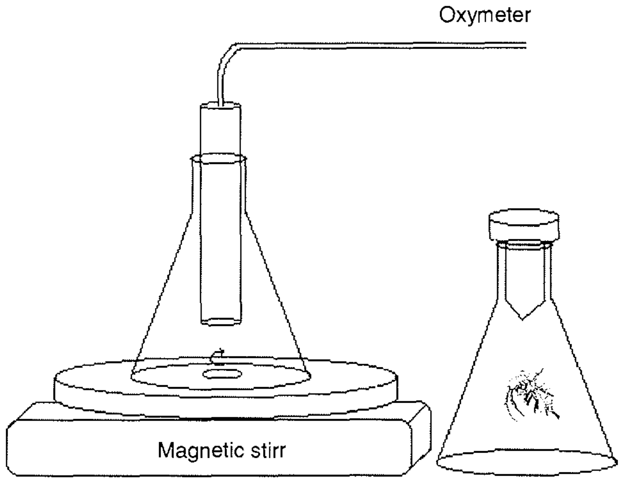
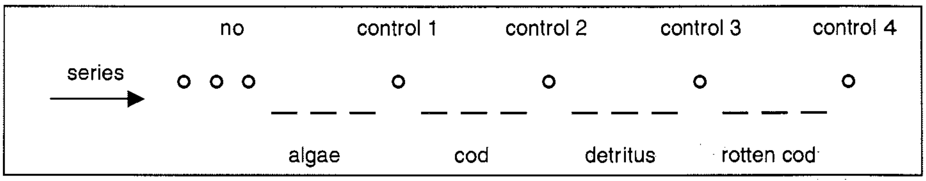


Fig. 2: Experimental set-up for measuring the oxygen consumption by *G. wilkitzkii*.

The concentration of oxygen was measured by means of the OXYGEN SENSOR TRIOXMATIC® 300 with a precision of 0.01 mg l^{-1}. The impact of salinity was controlled but assumed to be negligible. Each specimen was exposed during three successive experimental days ("replicates") to homogenates of macroalgae (*Ulva lactuca*), polar cod (*Boreogadus saida*), detritus or partly decayed "rotten polar cod". Before testing the next food item, the oxygen consumption was controlled in set-ups without food ("control") and compared to the values obtained primarily of the non-stimulated specimens (Tab. 2). All data will be presented as consumed oxygen per dry weight and hour (mg (g DW x $h)^{-1}$). As suggested by Handy & Depledge [1999], all measurements were started at the same time each day to minimise daily variability in oxygen consumption.

The distribution of the experimental results was tested for normal distribution using the KOLMOGOROV-SMIRNOV one-sample test. Since all experimental data were normally distributed, mean values and standard errors (SE) were calculated. A simple regression model was fitted to the "no food-" data points by the method of least squares (SPEARMAN), where the correlation coefficient describes the degree of model fit. To reveal possible heterogeneity in the data a one-way analysis of variance (ANOVA) using F-statistics was preferred. Resulting in significant differences ($p < 0.05$), a univariate analysis of variance (GLM, module SPSS) was chosen for further characterisation of interactions within the regression model. Differences between food types ("series") were tested by means of a factorial analysis of variance (ANOVA). Differences between the size classes and sex were analysed by an unpaired STUDENT´S t-test.

Tab. 2: Experimental design for measuring the oxygen consumption of adults and juveniles. ind.: individual.



	series	food	replicate (ind.)$^{-1}$	no food	replicate (ind.)$^{-1}$
adult	1			no	3
N = 14	2	algae	3		
sex:	3			control 1	1
7 x female	4	cod	3		
7 x male	5			control 2	1
	6	detritus	3		
juvenile	7			control 3	1
N = 13	8	rotten cod	3		
	9			control 4	1

2.II.2. Behavioural observations

The amphipods were introduced into the experimental vials and left for at least one hour before start of experiment. In some experiments a cm-rule was laid alongside the vial, so that the position of the amphipod could be defined in casual observations.

Food detection, seeking behaviour, and localisation

In order to analyse the reaction time to inserted food items the switch of behaviour from "resting" to "responding" (active) was observed. The focus lied on the pleopod beating and its resulting water movements. 11 adults of *G.*

wilkitzkii were kept separately in glass vials, filled with 1.5 l filtered sea-water. Notes were taken from only absolutely resting specimens. The oxygen content of the water at 4°C ranged from 1.65 to 1.69 mg l^{-1} which was assumed to be not limiting. Pieces of polar cod (*Boreogadus saida*) in homogenated form and dyed with food colour served as stimulus that allows the analysis of the pathways taken. One drop was delivered from a micro-pipette after the specimen had terminated a "pleopod active period" and the water movements had calmed down. The tip of the micro-pipette was positioned in a distance of 3 cm from the rostrum directly above the bottom. It is examined, whether a correlation exists between the pleopod beat frequency and the time interval from detection to localisation of the food source. Four of the specimens were observed more closely to describe behaviour and pleopod beating in detail. In addition, the behaviour was recorded on video. The observation time of each specimen was 20 minutes. Due to the discontinuity of the "resting mode" only 5 minute intervals were analysed.

Food type and quantity

Various food types were offered to 10 adult specimens: macroalgae (*Ulva lactuca)*, ice algae, detritus, copepods (*Calanus* sp.), chaetognaths (*Sagitta* sp.), polar cod (*Boreogadus saida)*, rotten polar cod, amphipods (*Themisto* sp., *A. glacialis* and *Onisimus* sp., conspecies). The reaction and food up-take was studied. Between the experiments the amphipods were not fed for three days. In order to investigate whether *G. wilkitzkii* was capable of filtering suspended material from the water, in one experiment only food colour was inserted. The evidence for the existence of filter feeding mechanisms was given when the fecal pellets showed incorporated dye particles.

To determine ingestion rates, pieces of fresh and rotten polar cod and hyperiid amphipods (*Themisto* sp.) were dried for 12 hours at 70°C for dry-weight measurements and afterwards hydrated for 12 hours before inserting. One control with only food in water was incubated for the same time to consider resolving processes of each food item. Every 30 minutes the active feeding of seven or eight adult and juvenile *G. wilkitzkii* was controlled. After 6 hours the amphipods were forced to return the food. The completeness of food removal was controlled before taking again the dry-weight. The measurements were conducted using a METTLER® AE 200 scale, with a precision of 0.1mg.

The fecal pellets of every feeding experiment were collected and stored in 90% ethanol for microscopic analysis. As the food types were known, the analysis concentrated on suspected peculiarities of the digestive canal. From the experiment with food colour only those fecal pellets were taken that were produced after a change of water to exclude dyeing by the water.

Grooming behaviour

As *G. wilkitzkii* is presumed to add its food supply by filter feeding [Poltermann 1997, 2001], the grooming and cleansing behaviour was studied. Several specimens of grown-up *G. wilkitzkii* were kept separately in glass vials filled with 1.5 l filtered sea-water. Primarily, the amphipods were observed during complete rest and than after the stimulation by means of one drop of particle-free "rotten cod-water", water which contained polar cod for 10 days. The behaviour was recorded on video. The observation time for the five males presented was 10 minutes per individual.

Interactions with the abiotic and biotic environment

All observations were made on amphipods which already got used to the glass aquarium filled with 15 l unfiltered sea-water. The aquarium was stored in a black styrofoam box in order to maintain the temperature between 2 and 3°C and to exclude disturbing factors like vibration or light. The animals were kept under dim-light. Visual observations and video-recordings were used to analyse their behaviour.

abiotic:

The behaviour of three grown-up specimens was observed below crushed sea ice and in ice-free waters. In addition, experiments were carried out with ice obtaining real food items like frozen conspecies or ice algae. To test the specimens for visual stimulation, an ice encrusted frozen piece of black paper was offered pretending a food source within the ice. Furthermore, the specimens were mechanically stimulated by means of a fine needle or the water flow generated by a PASTEUR-pipette.
The observation time every 30 minutes was 10 minutes, the experiment was terminated after 3 hours.

biotic:

In order to describe intraspecific interactions males, females and juveniles were combined "pair-wise" in a series of experiments. Each run of 30 minutes duration was conducted twice with new specimens (total number of runs: 12). In selected cases, long-term experiments terminated after 12 hours. In additional experiments, crushed sea ice or polar cod meat in different amounts was offered in order to observe aggressive behaviour between the specimens.
The aquarium equipped with crushed sea ice served for interspecific observations on three adult specimens of *G. wilkitzkii*, four *A. glacialis* and four *Onisimus* sp. The experiment terminated after 6 hours, 3 hours after the ice had melted.

2.II.3. Morphological study

Mouth parts and accessory feeding appendages

The mouth parts, both pairs of antennae and gnathopods of preserved (70% ethanol) *G. wilkitzkii* males were dissected out. Some appendages were placed in an ultrasonic cleaner first, depending on the amount of debris clinging to the amphipod. For scanning electron microscopy (SEM: LEO® 15 25) the appendages were dehydrated through an alcohol series and dried using liquid

carbon dioxide as the exchange medium, then critical point dried and sputter-coated with gold.
The description of the mouth parts and accessory feeding appendages follows the natural order of insertion on the body, starting from rostral to caudal. For the correct determination Barnard & Karaman [1991], Lincoln [1979], Ledoyer [1982] and Kaestner [1993] were used.

Sensory apparatus

The behavioural studies suggested the existence of a sensory apparatus especially in the oral region and on those appendages that get in touch with food. The cuticular surface and setal assemblages of these areas were investigated more closely under high magnification.
The technique of SEM is time-consuming and expensive. The present survey is therefore limited to three specimens only. This procedure did not permit a complete description appendage by appendage, nor the analyse of peculiarities due to sex, intermolt stage or individual variability, nor a blanked coverage of the cuticular surface.

The morphological study did not claim completeness nor accuracy, but concentrated on selected peculiarities that add information to the question of feeding ecology.

3. RESULTS

3.I. Field work

Ice conditions and hydrography

Station # 1

The ice transect north of Wijdefjorden was mainly characterised by FYI of an average floe size of 15 m across and 1.5 m thickness [Appendix 7 in: Arndt *et al.* 2000]. The surface ice structures like ridges and melt ponds were small and scarce. Between the small floes the extended water areas were covered by newly formed frazil and pancake ice. The ice coverage as well as the percentage of MYI increased with increasing latitudes. The station was located at 81°23.59'N 15°08.97'E, about 1° north of the ice edge. The samples were taken at a MYI floe of 50×30 m size and 2-3 m thickness (Tab. 1). Ridges structured the upper surface; the snow cover of about 30 cm was recently frozen. The under-ice surface showed arm-sized holes, crevices, keels and bulges.

Station # 1 was located in the deep water Nansen Basin (stations depth: 1828 m). The CTD cast [Appendix 4 in: Arndt *et al.* 2000] showed a 20 m thick, cold, fresh water layer. The average temperature in this layer and at the surface was –1.71°C, the average salinity was 32.1. The higher density of the stratum below the distinct halocline is due to the increasing influence of Atlantic water. The Atlantic water typified by salinities > 34.8 was recorded at 136 m. The temperature data revealed recent or still ongoing convective motion in the upper 100 m, which typically occur in open drift ice due to cooling and freezing processes.

Station # 2

Similar to the previous transect (Station # 1) this transect was characterised mainly by FYI with open water covered by frazil and grease ice [Appendix 7 in: Arndt *et al.* 2000]. The floe size seldom reached 2 m in diameter except at the ice station, and the ice thickness ranged from 0.5 to 3 m. Ridges and melt ponds were scarce, rafting was not observed. The percentage of MYI always remained below 20%.

The water masses on this location (stations depth: 313 m) were characterised by a distinct stratification with a thermo- and halocline located at 25 m [Appendix 5 in: Arndt *et al.* 2000]. The Atlantic water reached the upper stratum at only 35 m. The average surface temperature was –1.53° C, the average salinity 32.8.

A MYI floe at 81°27.03'N 30°01.15'E served as ice station. The floe size had an estimated size of 150×50 m and was about 2 m thick (Tab. 1). The under-ice structures, including crevices and wide brine channels, indicate similar melting processes as occurred to the ice at Station # 1. During station time the floe drifted south-east (to 81°14.13'N 31°18.30'E) with velocities up to 1 sm h^{-1} due to south-westerly winds of up to 12 m s^{-1}. Ice conditions, physical and hydrographic conditions therefore changed permanently.

Station # 3

The westernmost station was located north-west of Svalbard at 80°31.32'N 07°33.44'E. The distance to the ice edge was about 12 sm. The transect was characterised by an ice coverage of 9/10 [Appendix 7 in: Arndt *et al.* 2000]. Among the dominating FYI the average floe size was 30 m, the thickness mainly ranged between 1-2 m and reached its maximum at the ice station (Tab. 1). Leads were often covered by dense frazil and smashed pancake ice.

The study site consisted of MYI with mainly straight vertical ice edges indicating that the ice had been recently broken. Considering under-ice ridges down to more than 12 m and the large variation in surface structures like high ridges, rafting and melt ponds, the floe was assumed to be older than three years. The under-ice structures confirm the impression of a long history of melting and re-freezing. Divers found a coarse subsurface with bumps and depressions and often wide brine channels of up to 0.3 m.

Similar to Station # 2, the stratification under this ice floe (total depth: 758 m) was interrupted by continual convective motion down to 100 m [Appendix 6 in: Arndt *et al.* 2000]. The Atlantic water was recorded at 78 m. The average temperature of the upper stratum (thermocline at 20 m) was –1.51° C. As the stations floe was in some locations more than 6 m thick, the physical properties up to 12 m were considered. The salinity ranged from 32.8 at the surface to 32.4 at 12 m.

Ice maps

The ice floes at all three stations were exposed to long periods of melting and re-freezing. The study of ice maps [Appendix 9 in: Arndt *et al.* 2000] from the past three months emphasise the assumption that the ice had drifted to the warmer Atlantic water known as West Spitsbergen Current.

In July the ice coverage increased with increasing latitude and formed close drift ice north of 80°N. At the beginning of August the ice north of Svalbard opened, leads got wider and characterised the ice as open and close drift ice far north. From the beginning of September the ice cover suddenly disappeared around 80°N, and an extensive area of open water north of Svalbard, the main island, and north-west of Nordaustlandet was recorded. At that time the ice edge followed a diagonal line from 80°N 10°E northwest of Svalbard to 81°20' N 24°E north of Nordaustlandet causing an extensive open water area north of Svalbard.

Considering the prevailing wind speeds of >12 m s^{-1} from south-west (240°), it can be assumed that the ice already started melting in warm Atlantic waters but was pushed backwards to the north. When transported across the polar front, recorded at 80°55' N on the transect to Station # 1, the ice was yet again exposed to cold Arctic waters and low air temperatures. At all three ice stations the CTD data showed a conspicuous stratified water column with a cold fresh water lens at the surface and denser warm water down to the modified Atlantic water below. This stratification is typical for ice covered polar regions.

3.I.1. Traps

The total number of amphipods attracted by bait was 15 for all ice stations (Tab. 3). More than ¾ of the amphipods were caught at the easternmost station (# 2) by rotten polar cod and belong to the genera *Onisimus*. No amphipod was attracted at Station # 3. The traps baited with crustaceans attracted three specimens of *G. wilkitzkii*. Nearly 67% of the total number entered those traps below the ice.
As the total number is low the data were not analysed statistically.

Tab. 3: Number of attracted sympagic amphipods by different bait types.

Station #	**bait**	**catch side**	***A.glacialis***	***G.wilkitzkii* *ad***	***juv***	***O.nansensi***	***O.glacialis***	
1	macroalgae	edge			1			
		below	1					
1	krill	edge						
		below		2				
1	no (control)	edge						
2	rotten cod	edge			1	2		
		below				5	2	
2	copepods	edge		1				
		below						
2	no (control)	edge						
3	macroalgae	edge						
		below						
3	copepods	edge						
		below						
3	no (control)	edge						
				3	2			**sum**
			1	5		7	2	**(n = 15)**

3.II. Laboratory work

3.II.1. Physiological study

Standard respiration

The standard O_2-consumption was calculated by taking the average of the pooled data achieved from all series without food (Appendix 1). This method considered the presumed change in the physiological stage from starved, non-stimulated (series 1) to stimulated (series 3, 5, 7, 9).

Adults:

A simple regression model was fitted to the points (Fig. 3). The slope of the regression line was slightly negative (y = -0.0017x + 0.332 with $R^2 = 0.0033 \pm 0.091$ SE). The correlation coefficient (SPEARMAN, $R_s = 0.265$, $p > 0.05$) indicated no significant differences between the series. The differences between the three replicates of series 1 were assumed to be negligible (ANOVA: F = 3.008, $p > 0.05$).

The average standard oxygen consumption for all non-stimulated adults was 0.3258 ± 0.090 mg O_2 (g DW x h $)^{-1}$) SE at ± 4°C. The consumption rates did not differ between male and female (ANOVA: F = 0.0, $p > 0.05$, df = 4).

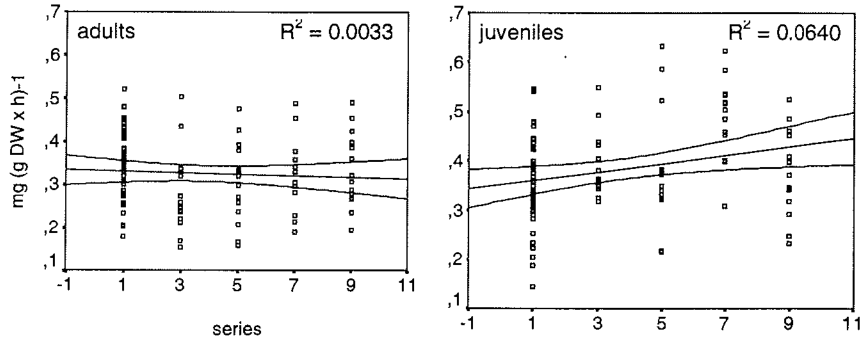


Fig. 3: Standard oxygen consumption (mg (g DW x h$)^{-1}$) for adults and juveniles. Regression line and confidence intervals (95%) are shown. Note that series 1 includes 3 replicates, while series 3, 5, 7, and 9 are the controls.

Juveniles:

In contrast to the regression model demonstrated for adults, the regression line for the standard oxygen consumption of juveniles indicated an increase of the respiration in the course of series (Fig. 3). The slope was positive (y = 0 0.0086x + 0.352 with $R^2 = 0.0064 \pm 0.099$ SE). The correlation coefficient (SPEARMAN, $R_s = 0.265$, $p > 0.01$) indicated significant differences among the individuals as well as the series. The univariate variance analysis (GLM module SPSS) demonstrated highly significant differences between the series ($p < 0.001$, F = 10.161, df = 4) and the individuals ($p < 0.001$, F = 5.248, df = 12). Further analysis revealed, that especially series 7 (= control 3, see Tab. 2) differed significantly from the others (POST-HOC: comparison of series 7 & 1: p = 0.000, 7 & 3: p = 0.029, 7 & 5: p = 0.012, 7 & 9: p = 0.006).

The three replicates of series 1 did not differ (ANOVA: F = 0.077, $p > 0.05$).

Among the individuals the values of individual 5, 6, 10 and 13 deviated remarkably from the average respiration rate (POST-HOC: ind. 6 & 10, p = 0.018, ind. 10 & 13, p = 0.005, ind. 5 & 13, p = 0.05).

The standard O_2-consumption for juveniles was 0.3855 ± 0.102 mg O_2 (g DW x h $)^{-1}$) SE at ± 4°C.

Respiration after stimulation with food

Adults:

The oxygen consumption rates differed remarkably from the standard O_2-consumption when the amphipods were stimulated by food (Fig. 4). The rates were significantly decreased when exposed to algae (t-test, $p < 0.05$, df = 128), fresh polar cod (t-test, $p < 0.001$) and detritus (t-test, $p < 0.05$). In contrast, the stimulation with rotten polar cod resulted in an increased oxygen consumption rate (t-test, $p < 0.001$). The differences between the sexes were negligible for all food types. Only during the exposure to algae, males responded with a slightly decreased respiration rate compared with females (Fig. 4).

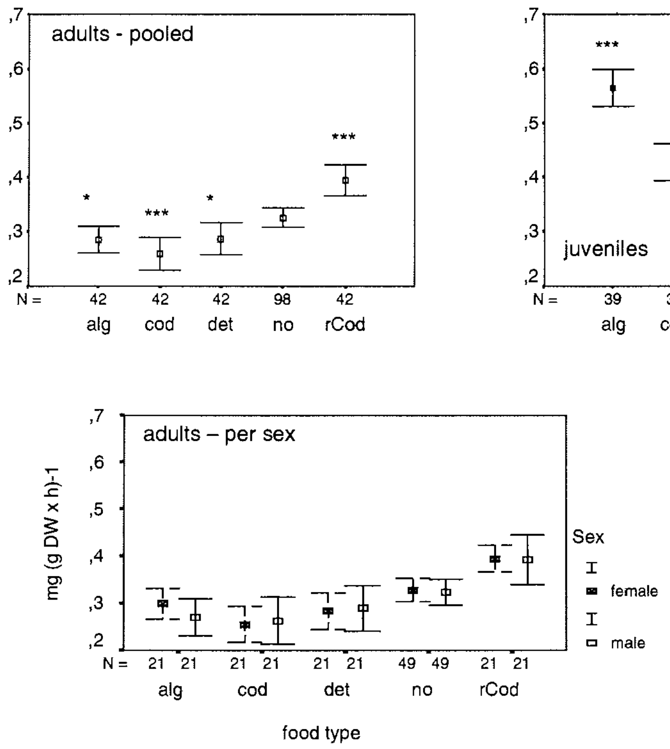


Fig. 4: Average oxygen consumption (mg (g DW x h)$^{-1}$ ± SE) for adults (pooled and subdivided into sex) and juveniles. Note that N is changing. Food types: no food (no), algae (alg), cod, detritus (det) and rotten cod (rCod). Significant difference of the food types from „no food" indicated by: · $p < 0.05$, ··· $p < 0.001$.

Tab. 4: F-test values for the comparison of the three replicates of each food type (ANOVA: df = 2).

food type	adults		juveniles	
	F	p	F	p
algae	3.008	> 0.05	0.109	> 0.05
cod	137.126	< 0.001	24.759	< 0.001
detritus	54.842	< 0.001	42.750	< 0.001
rotten cod	7.719	< 0.001	203.283	< 0.001

The differences between the O_2-consumption rates of the three replicates were significant for the experiment with polar cod, detritus and rotten polar cod (Fig. 5). Especially the third replicate differed remarkably from the previous ones (Tab. 4).

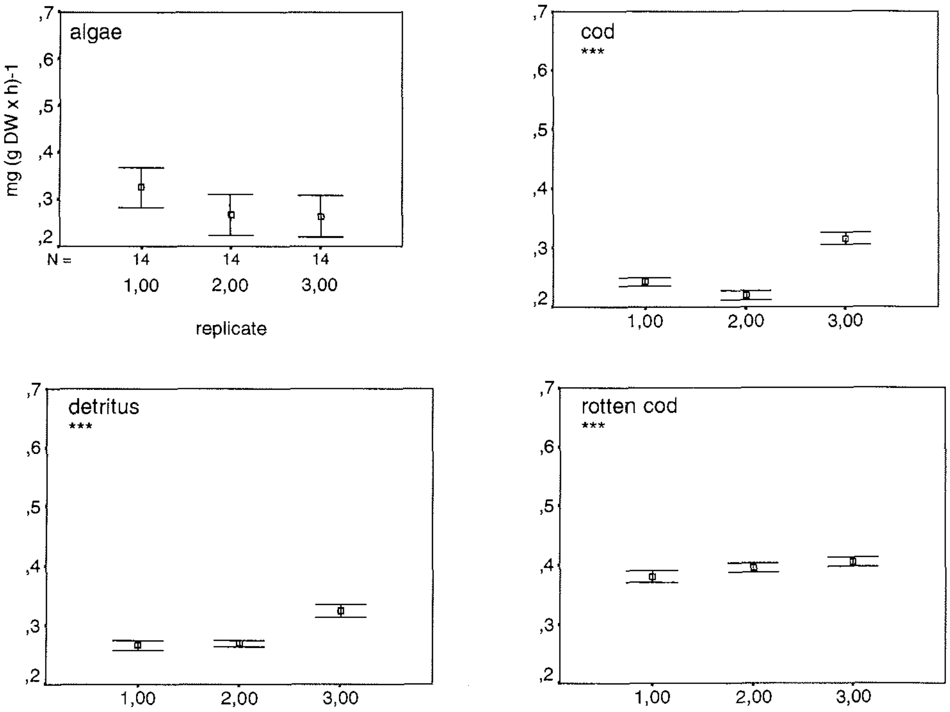


Fig. 5: Oxygen consumption (mg (g DW x h)$^{-1}$ ± SE) for adults of the three replicates per food type. Degree of significance between replicates indicated by: *** $p < 0.001$.

Juveniles:

In contrast to the adult *G. wilkitzkii*, the juveniles responded to all inserted food types with increased oxygen consumption rates (Fig. 4). All differences showed high significance. The highest deviation from the standard O_2-consumption was noted for rotten polar cod, algae and detritus, the lowest for polar cod (t-test: rotten polar cod $p < 0.001$, algae $p < 0.001$, detritus $p < 0.001$, polar cod $p < 0.05$).

Similar to the adults, the O_2-consumption of the three replicates differed significantly for the experimental series with polar cod, detritus and rotten polar cod (Fig. 6, Tab. 4).

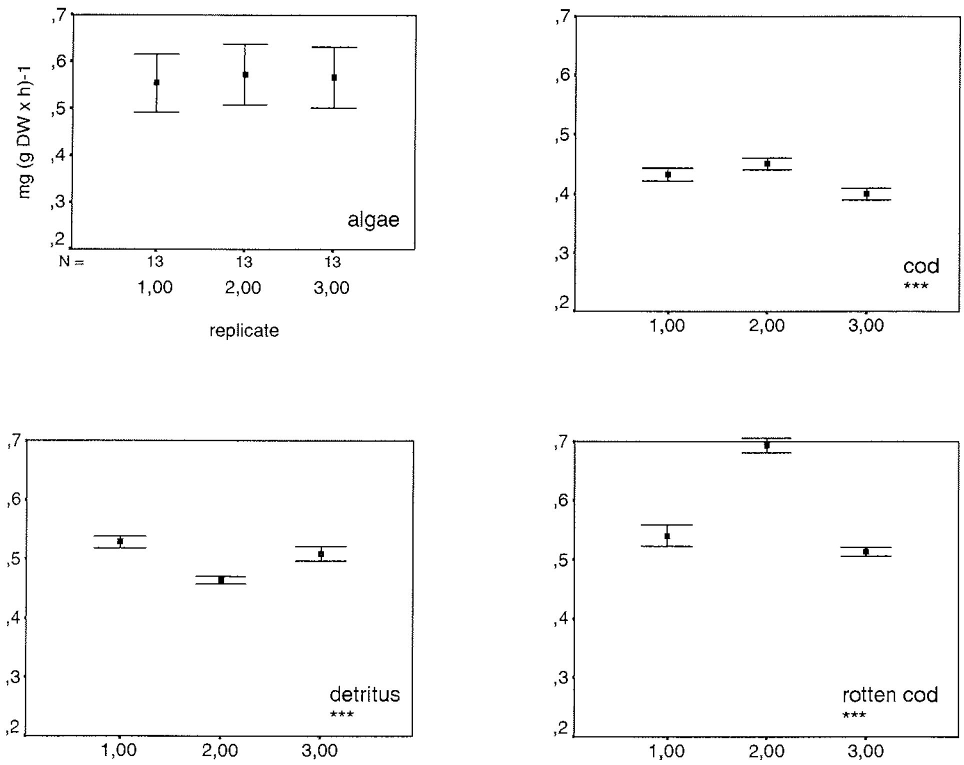


Fig. 6: Oxygen consumption (mg (g DW x h)$^{-1}$ ± SE) for juveniles of the three replicates per food type. Degree of significance between replicates indicated by: *** $p < 0.001$.

Comparison between size classes and individual variability

The average oxygen consumption rates of the adults differed significantly from those of the juveniles (Fig. 7). The standard O_2-consumption was 15% higher for the juveniles. The divergence of the standard respiration rate and the responses to inserted food were even more remarkable (higher values for juveniles to inserted algae: 49%, polar cod: 39%, detritus: 43%, rotten polar cod: 32%).

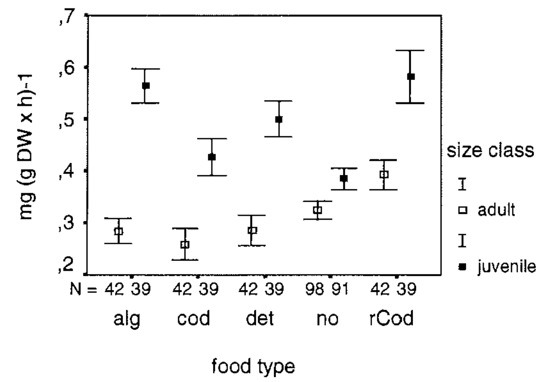


Fig. 7: Comparison of the average oxygen consumption rates (mg (g DW x h)-1 ± SE) per food type between adults and juveniles. Note that N is changing. Food types: no food (no), algae (alg), cod, detritus (det) and rotten cod (rCod). For significant differences see Fig. 4.

The results imply differences in 1. the quality (increased or reduced respiration) and 2. the intensity (deviation from standard O_2-consumption) of the responses to various food types for both size classes. Fig. 7 also demonstrates the range of differences between the replicates indicated by the standard error bars.
The respiration showed high individual variability (Fig. 8). The comparison of size classes revealed various intersections of the consumption values from adults and juveniles (Fig. 8).

3.II.2. Behavioural observations

Food detection, seeking behaviour, and localisation

A specimen which has not been stimulated by food usually either kept its resting position or swam slowly along the vials boundaries. The detection of food resulted in an abrupt change of behaviour. The stimulated amphipod "woke up" and showed food seeking activity: the locomotory activity was initiated or its speed increased, the mouth parts vibrated and moved more intensively and the antennae passed over the mouth parts with higher frequency. The food seeking behaviour in response to a stimulus was usually unmistakable and readily distinguishable from non-stimulated food searching.
Examinations of the paths taken by stimulated amphipods showed that there was no tendency for the direction of movement to be related to the position of the stimulus, or for the amphipod to remain longer in the vicinity of food than elsewhere in the tank.

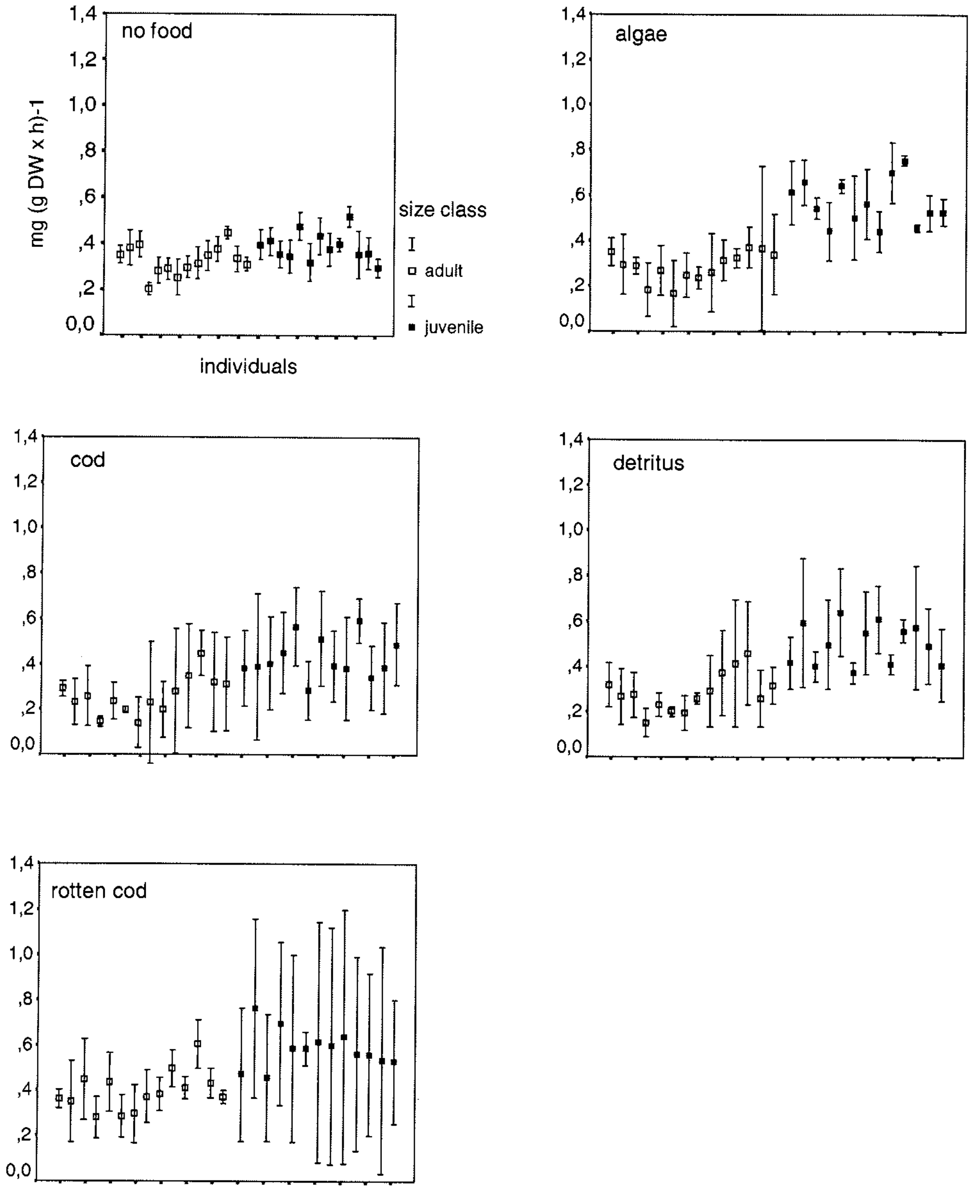


Fig. 8: Individual variability in the oxygen consumption (mg (g DW x h)$^{-1}$ ± SE) of adults and juveniles per food type. Note: N (no food) = 7, N (food types) = 3.

It is inferred from these results that vision is not primarily important for the detection or localisation of food by *G. wilkitzkii*. Chemical stimulation initiated food seeking behaviour, even though it did not guarantee exact localisation.

Several observations suggest that the detection of remote food items depends on the **beating activity of the pleopods**. The resulting water movements are known as respiratory currents, that are a characteristic feature of gammaridean amphipods [e.g. Dahl 1977]. The use of food colour allowed a more detailed description of the circulation patterns.
While resting, *G. wilkitzkii* lied on one side or clung to various objects by means of its powerful pereopods in a curled-up position. The cephalon and anterior segments curved slightly ventral, the pleon being more distinctly arched. Antenna I was raised, pointing dorso-laterally, antenna II was directed forwards and somewhat ventral diverging slightly.
The pleopods showed activity in irregular intervals. The fast and regular beating of the pleopods made their tips swing in a wide arc, posteriorly reaching towards the bases of the uropods and anteriorly into the ventral furrow between the branchiae up to the level of gnathopod II. The current system set in motion by the pleopods affected an area with a radius several times the body length of the specimen and converge upon it from all directions except the ventro-posterior one (Fig. 9). Particularly strong currents were drawn into the chamber which is formed laterally by the coxae from the anterior and antero-ventral directions.

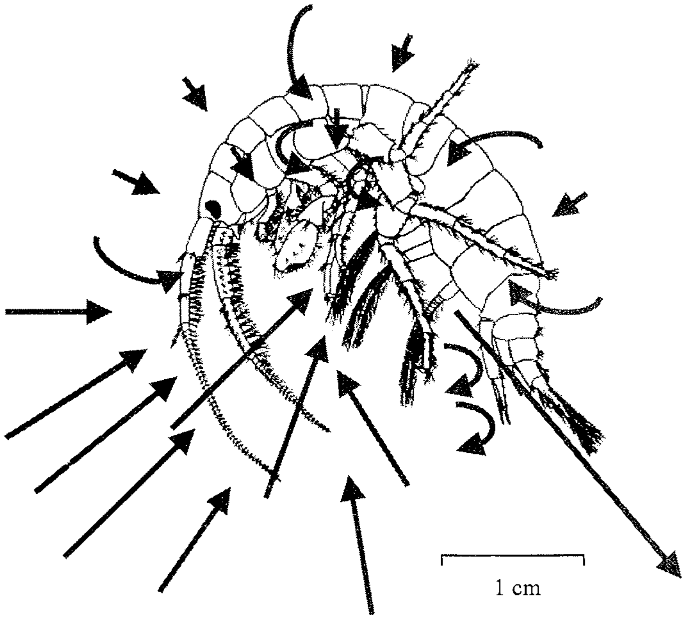
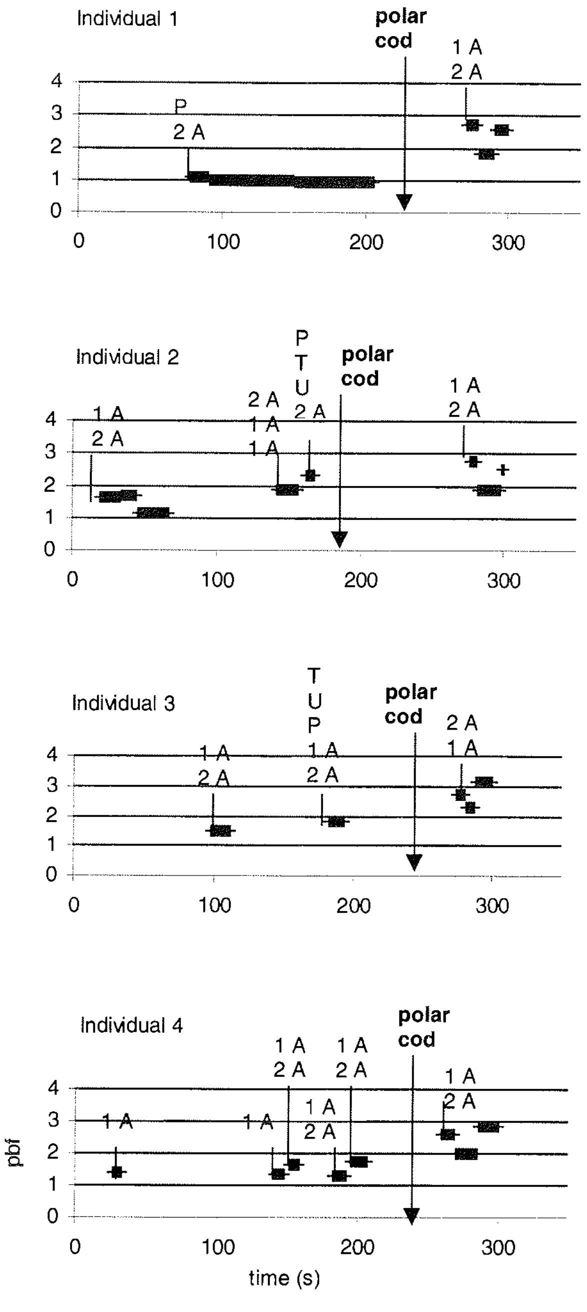


Fig 9: *G. wilkitzkii* in resting position [Poltermann 1997], showing water movements generated by pleopod activity. Length of arrows is roughly proportional to current velocity.

The anterior current swept over the antennary flagellae and mouth parts and entered the branchial region between and around the gnathopods. In contrast, the postero-dorsal and -ventral afferent currents entered the region of the actual pleopod swing between the pereopods. The slow but steady dorsal and postero-dorsal currents flew over the sides of the body and entered the turbulent area caused by the forceful action of the pleopods. The efferent current had the greatest velocity of all. It swept backwards between and below the uropods.

While resting the pleopod beating was interrupted irregularly by intervals of absolute immobility. Therefore, the study of the **reaction time** to inserted polar cod homogenate implied to be correlated to 1. the pleopod activity patterns and 2. the general grooming behaviour (Fig. 10). Usually the "reaction time" is defined as the time from the insertion of food until the first sign of detection (reaction). In this study, this interval was not considered but the time from detection until localisation, because the findings indicated no comparable conditions for all specimens.
Apart from a high individual variability the following conclusions can be drawn (Fig. 10):

- Every "pleopod active period" was initiated by grooming of at least one body part. Generally the antennae passed over the mouth parts or gnathopods.
- The insertion of polar cod homogenate initiated the increase of the pleopod beat frequency (pbf). The pbf of non-stimulated specimens ranged from < 1 and ± 2 beats s^{-1}. A stimulated amphipod showed in general > 2 beats s^{-1} (Fig. 11). The difference in pbf (for casual observations) between resting and active (stimulated) amphipods was pronounced.
- The stimulation resulted in a peculiar response which consisted of four stages (in Fig. 10, the three bars to the right of the insertion of polar cod demonstrate stage 1-3) :
    1. food detection
    2. seeking
    3. localisation of the food source
    4. food up-take and ingestion
- While seeking (stage 2) the pbf was slightly reduced compared with the stages 1 and 3.
- The time from detection until localisation was correlated to the average pbf (Fig. 12). The higher the average pbf of a stimulated amphipod the quicker the food source was found.



Individual 1:
cod → detection: 32 s
→ seeking: 42 s
→ localis.: 53 s

detect. → localis.: 23 s
average pbf: 2.28 s^{-1}

Individual 2:
cod → detection: 88 s
→ seeking: 102 s
→ localis.: 110 s

detect. → localis.: 24 s
average pbf: 2.16 s^{-1}

Individual 3:
cod → detection: 32 s
→ seeking: 39 s
→ localis.: 47 s

detect. → localis.: 17 s
average pbf: 2.61 s^{-1}

Individual 4:
cod → detection: 20 s
→ seeking: 30 s
→ localis.: 46 s

detect. → localis.: 28 s
average pbf: 2.30 s^{-1}

legend:	P: pereopods
→: insert cod	T: telson
A: antennas	U: uropods

Fig. 10: Activity pattern of four individuals considering the pleopod beat frequency (pbf: beats s^{-1}) and grooming behaviour. Each bar indicates an „pleopod-active period“.

When the amphipod became active, the body was straightened and the animal propelled forward. When the pleon was extended the pleopods beating pushed it forward. Due to the straightened position, the pleopods swung at an angle of up to 180°. The resulting water movements effected an area even bigger than while resting thus generating more turbulence.

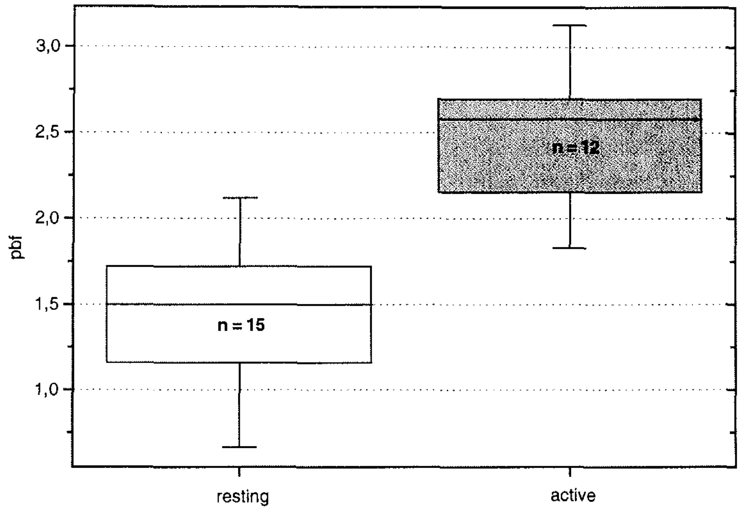


Fig: 11: Pleopod beat frequency (pbf: beats s^{-1}) at casual counts (n) of the 4 selected individuals while resting or active (incl. detection, seeking, localisation); only one value is taken from each „pleopod active period".

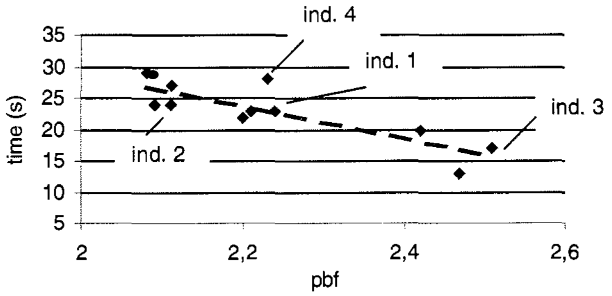


Fig. 12: Correlation between average pleopod beat frequency (pbf: beats s^{-1}) of 11 specimens and the time interval from detection until localisation (first 2 s). ind.: individual.

Food type and quantity

Generally, every food type was grasped by *G. wilkitzkii* with the gnathopods and examined by the mouth parts (Tab. 5). All amphipods showed the highest affinity to animal derived food. These food items were eaten-up completely. Only the less fleshy appendages of crustaceans remained from time to time. From suspended material such as fine remains of ice algae or detritus the amphipod formed bigger aggregations before ingesting it. Close observations revealed, that *G. wilkitzkii* combed the particles together by means of the long antennal setae. Antenna II passed the mouth parts repeatedly for cleansing while the latter formed fluffy aggregations from the material. The mandible palps seemed mostly accessory in examining, holding and rejecting or supplying food particles.

	adult average DW (n=8): 0,066 g ± 0,015		**juvenile** average DW (n=8): 0,007 g ± 0,002	
food type	ingested mg (h^{-1} g^{-1} DW)	±SD (mg)	ingested mg (h^{-1} g^{-1} DW)	±SD (mg)
cod meat (n=8)	10,06	4,21	22,11	5,68
rotten cod meat (n=7)	18,21	3,40	47,49	8,13
Themisto sp. (n=7)	24,62	8,07		

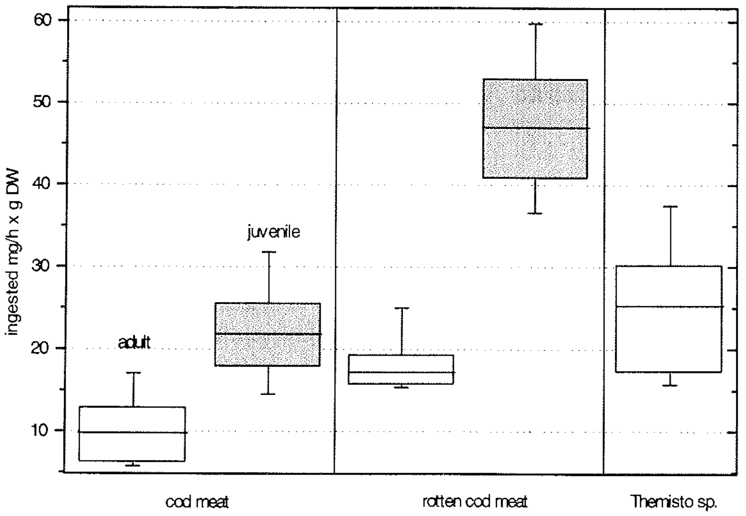


Fig. 13: Ingestion rates of different food types for adults and juveniles of *G. wilkitzkii.*

Tab. 5: Qualitative study on various food types.

food preference			**fecal pellets**				
food type	**up-take**	**comments**	**No examined**	**colour**	**habitus**	**inner structures**	**spec. characteristics**
macroalgae *Ulva lactuca*	x	soon rejected	20	green-brown	thin, fragile	amorphous (coarse)/ fibrious	big pieces of phytal tissue; incl. foreign material (sedim., fluff etc.)
ice algae	x	aggregations formed	0	—	—	—	—
detritus	x	aggregations formed	10	brown	thick, fragile	amorphous (coarse)/ little fibrious	algae fragments; incl. foreign material (sedim., fluff etc.)
copepod *Calanus* sp.	x	often appendages remained	20	red-brown	thick, compact	amorphous (fine)/ fibrious	big oil aggreg.(colour!); many crustacean parts (whole antennes, setae etc.)
chaetognath *Sagitta* sp.	x	eaten up completely	0	—	—	—	—
polar cod *Boreogadus saida (meat)*	x	eaten up completely	15	dark brown	thick, fragile	amorphous (fine)/ little fibrious	soft tissue; few foreign material (fluff)
rotten polar cod (meat)	x	eaten up completely	0	—	—	—	—
amphipod *Themisto* sp.	x	often appendages remained	10	grey-brown	thick, fragile	amorphous (fine)/ little fibrious	few crustacean parts (antennes, setae etc.)
amphipod *Gammarus wilkitzkii*	x	eaten up completely	10	grey-brown	thick, compact	amorphous (fine)/ fibrious	many crustacean parts (setae, feeding appendages, dactyli of gnathopods etc.)
amphipod *Apherusa glacialis*	x	eaten up completely	10	grey-brown	thick, compact	amorphous (fine)/ fibrious	big oil aggreg.; many crustacean parts (setae, feeding appendages etc.)
amphipod *Onisimus* sp.	x	eaten up completely					
food colour	x	—	5	—	—	—	red dots of dye internal/external, distributed over the whole fecal pellet

In order to find out whether *G. wilkitzkii* ingests the material cleaned off the body surface [Poltermann 2001], the water was coloured by red dye. The defecation of red fecal pellets confirmed the existence of any filter feeding mechanism as supplementary food acquisition (Tab. 5).
Macroalgae was closely examined by *G. wilkitzkii* but was soon rejected. Microscopic analysis revealed a regular zig-zag trace of approx. 100 µm size produced by the mouth parts. Traces were found randomly but indicated only "analytical bites" before abandoning the food item.
Among the specimens no individual differences in the behaviour was observed.

The quantitative study showed higher ingestion rates for juveniles than adults (Fig. 13). Juveniles ingested more than twice as much per hour and g DW than adults. The highest rate was found for both size classes for rotten polar cod. In contrast to polar cod meat, the ingestion rate for rotten polar cod was 45% or 55% higher for adults and juveniles, respectively. The adults ingested fastest the amphipod *Themisto* sp. compared to polar cod meat. All data was normally distributed but allowed no statistical analysis (t-test) due to the insufficient number of observations.

Microscopic analysis of the fecal pellets showed that their habitus and morphology varied according to food type (Tab. 5). The colour ranged from greenish (algae), reddish (copepods), greyish (fed amphipods or polar cod) to brown (detritus). A correlation existed between habitus and tissue characteristics of the food. Fecal pellets that include fine amorphous material (e.g. amphipod meat besides crustacean parts such as setae, antennae and other appendages) apart from fibrous, were thick and compact. The less fibrous fecal pellets which were composed of coarse material like those from detrital food were more fragile and thinner. Often the adhesion was given by the incorporation of foreign material. Fluffy, hair-like particles or dust that had erroneously fallen into the experimental vials were later found incorporated within the fecal pellets. Moreover, some fecal pellets contained unfermented pieces of plant tissue, fleshless crustacean appendages and oil aggregations.

Grooming behaviour

When crawling along the substrate, *G. wilkitzkii* constantly probed or "tested" the water and occasionally the substrate with antenna I while antenna II probed the substrate and served for food up-take.

Generally, cleansing of the body took place while resting. Only antenna I and functional feeding appendages were passed over the mouth parts and gnathopods while swimming.
While resting in the curled-up position the amphipod bent in both pairs of antennae from time to time and passed them rapidly over the mouth parts or pinched them in by the subchela of the gnathopods. The remainder of the body was a function of gnathopod II, various parts being cleansed by the grasping margins of either the propodus or dactylus. At irregular intervals the pleon was extremely arched until the telson nearly reached the cephalon in order to clean the postero-dorsal part of the body. This movement generally terminated by

passing the gnathopods from proximal to distal over uropods and telson. Subsequently, the pleopods were combed intensively. As the pereopods bear several spines and setae it is not clear whether the gnathopods cleaned the pereopods or vice versa. The pereopods were cleaned less frequently than the antennae and only for a short time. While resting, the mouth parts were mostly immobile but the maxilliped and maxillulary palps vibrated at irregular intervals. Females, having oostegites while reproductive, used additional cleansing methods when cleaning the thorax. The body was bent 90° or more between pereonites one and three, allowing gnathopod I to make contact with the brood pouch.

No distinct cleansing pattern of the body parts was observed (Fig. 14). Antenna II was cleansed together with antenna I while antenna I often passed the mouth parts or gnathopods alone. Antenna I was cleansed between 25% and 60% more often than antenna II (Fig. 14). In most of the observations, cleansing behaviour was introduced and terminated by vibrating mouth parts and grooming of the antennae.

After inserting one drop of "rotten cod water", the cleansing frequency of the antennae increased remarkably (Fig. 14). Compared to the resting mode, the stimulated amphipods cleaned antenna I up to six times more often. The specimens straightened themselves from the curled-up resting position and started crawling around. Antenna II bent in repeatedly to the mouth parts as soon as the drop was found. The long antennal setae served for the up-take of small particles. The remainder of the body was cleaned only occasionally.

Interactions with the abiotic and biotic environment

abiotic:

aquarium without ice: Generally, *G. wilkitzkii* preferred to crawl with one lateral side towards the substrate (aquarium boundaries). In contrast to the juveniles, the adults lost contact to the substrate from time to time and swam short distances within the water column. No specimen showed any special strategies or path way patterns while crawling around.

aquarium with ice: As the ice provides a bottom-up substrate *G. wilkitzkii* showed the typical lateral positioning to the ice while crawling along or resting. It preferred to cling to the substrate with all five pereopods the way that the head bent down into the water column. This position permitted higher probabilities to "catch" stimuli. The substrate was not treated with any of the antennae, nor gnathopods or other appendages. Several times, *G. wilkitzkii* was observed to bump into ice fragments or – in experiments described below – even other amphipods.

encrusted black paper: The black spot produced by the piece of paper did not attract the amphipods. As soon as the ice had melted and the paper reached the ice-water interface the object was inspected with the mouth parts while held and rotated by means of the gnathopods and antennae, but was then rejected.

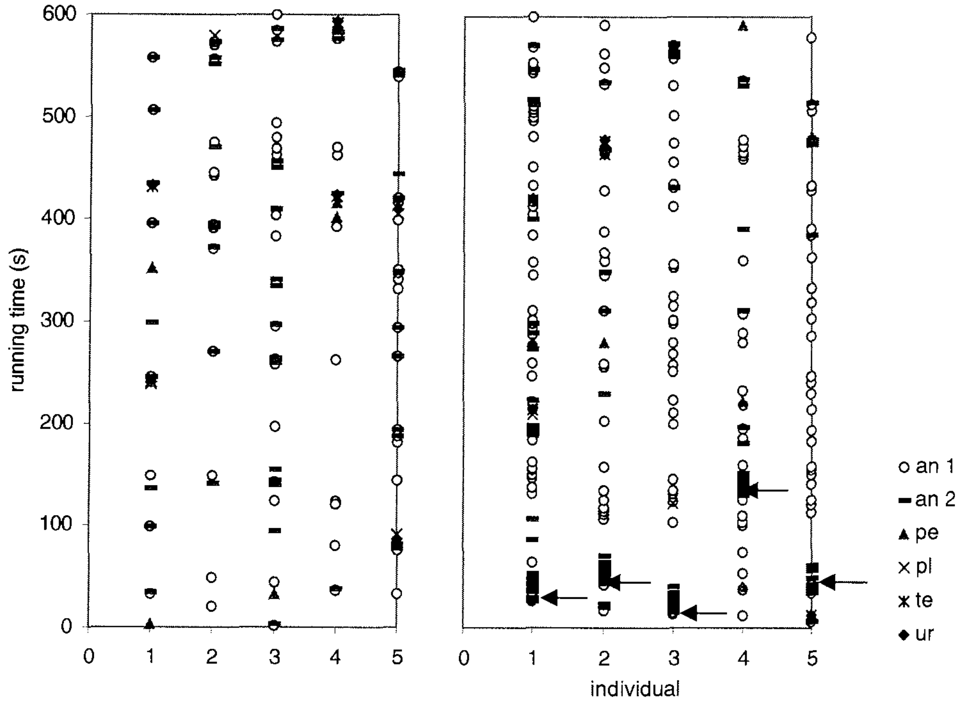


Fig. 14: Cleansing pattern of five specimens of *G. wilkitzkii*. Observation time: 10 minutes. Left: non-stimulated (in resting mode), right: stimulated by one drop of rotten cod water (active). ◄— : food up-take commenced; an: antenna, pe: pereopods, pl: pleopods, te: telson, ur: uropods.

mechanical stimulation: Both pairs of antennae and gnathopods, the pereopods, urosome and telson were stimulated by a gentle touch with a needle or a soft current produced by a pipette. Every stimulation caused an immediate positive, thigmotactical response: *G. wilkitzkii* turned towards the stimulus and grasped the disturbing object with the gnathopods. No reaction was observed stimulating the pereon or pleon.

biotic:

ice-encrusted crustacean carcasses or ice algae: The detection of ice-encrusted objects commenced after they reached the ice-water interface. No remote sensing was observed. But as soon as *G. wilkitzkii* got in touch with the object, it showed increasing physical activity. The frequency of the pleopods beat raised and the positioning to the ice substrate switched from lateral to frontal to facilitate a better inspection. Especially the dactyli of the gnathopods (but probably supported by the propodi) and the antennae started treating the ice or object mechanically. In addition, the mouth parts worked on the ice. Antenna I played only a secondary role in either the food up-take or the mechanical treatment. When the amphipod was disturbed the locality was not found again, not even after long searches. The encrusted crustacean showed some typical zig-zag-lined traces caused by the mouth parts.

intraspecific behaviour: Several observations suggest, that the optical sense is of less importance for food detection and localisation. *G. wilkitzkii* often noticed objects only after colliding with them. Objects that drifted in minimal distance without touching the species were not detected. A series of contacts of two grown-up specimens ended up peacefully in 23% of the encounters (Tab. 6). The first contact generally caused grasping the object with the gnathopods. In some cases this behaviour was repeated at the next contact, in other cases the specimens kept distance but used their antennae for a quick scan and than turned away. Furthermore, ignorance of other specimens but also the maintenance of antennal touch during resting was observed. No correlation was found between sex and behaviour.

Tab. 6: Percentage (%) and relative number of grasps per total number of contacts (/) between different size-classes and sexes. Observation time: 30 minutes.

	males	**females**	**juveniles**
males	89% (8/9) 0% (0/6)	43% (3/7) 33% (2/6)	90% (9/10) 100% (5/5)
females		0% (0/3) 20% (1/5)	100% (4/4) 100% (7/7)
juveniles			0% (0/12) 0% (0/9)

Grasping with the gnathopods in some cases ended up in hard struggles that include jerky body bending. A successful grasp seemed to be a function of rapid and agile movements, and tended to position the caught specimen praecopula-like between the gnathopods. Brought into this position the caught specimen was totally defenceless. Rostral the antennae, latero-ventral the pereopods and caudal the bent telson acted like the bares of a cage.

Cannibalism among adults was never observed.

In contrast to the adult specimens, juveniles never demonstrated aggressive behaviour. Each contact with adults caused the juvenile to flee immediately while the adult commenced chasing. Experiments of 12 hours duration ended up **lethally** for all juveniles.

Casual observations on swimming adults recorded maximum speeds of non-stimulated amphipods ranging from 1.5 – 2.5 cm s^{-1}, but when stimulated (by food or disturbances) speeds of 5 cm s^{-1} could be attained. Juveniles showed only little variability in speed. They generally maintained speeds around 2 – 2.5 cm s^{-1}, irrespective of the degree of stimulation.

In long-term experiments the survival of the juveniles increased with the presence of **sea ice**. Then, no dead or invalid juvenile was recorded.
Small pieces of **meat** caused an intensive defence apart from the preying specimen. As the two pairs of gnathopods were occupied with holding the bait, approaching rivals were chased away by means of a series of blows with the telson. In contrast, big pieces of meat were colonised by several feeding specimens that showed no aggressive behaviour.

Interspecific behaviour: The presence of crushed ice prevented *A. glacialis* and *Onisimus* sp. from being eaten by *G. wilkitzkii*. The lethality increased with the reduction of ice. *A. glacialis* exhibited the best swimming abilities, followed by *Onisimus* sp. while *G. wilkitzkii* had the poorest. The latter swam for relatively short distances and had to rest more often. *Onisimus* sp. exhibited a kind of "avoidance strategy": no encounter was observed since *Onisimus* sp. avoided every contact to *G. wilkitzkii*. In contrast, *A. glacialis* occasionally "bumped" directly into *G. wilkitzkii* but escaped presumably due to its agility and small size. However, all four specimens of *A. glacialis* were preyed first after the ice had melted. *Onisimus* sp. headed forward in a permanent swimming mode but was grasped by *G. wilkitzkii* as soon as exhaustion forced them to rest.
G. wilkitzkii carried the prey in a praecopula-like position. Approaching specimens of the same species were chased away by means of a series of blows with the telson.

3.II.3. Morphological study

Mouth parts and accessory feeding appendages

The mouth parts (Fig. 15), defined as structures which contact food objects while eating, are: labrum (Lb), mandible (Md), paragnath (Pg), maxilla I and II (Mx I and Mx II) and maxilliped (Mxp). Antenna I and II (A I and A II) and gnathopod I and II (Gn I and Gn II) function as accessory feeding appendages that help in capture, manipulation and sorting of the food.

The mouth parts project ventrally beyond the coxal plates. The unpaired labrum is located anterior to the mouth. The mandible, maxillae and maxilliped are paired and located in dorso-ventral layers ventral to the mouth. The paragnaths are situated between mandible and maxilla I. With the mandible as an exception, the left and right sides of the mouth parts are identical. In this study the left side was illustrated. The mouth parts are completely obscured by the maxilliped.

Antenna I (A I)

The first antenna consists of a proximal peduncle of three robust, elongated articles and a distal flagellum. The length of each of the flagellar articles increases from the proximal to the distal articles.

The antennal setae concentrate in assemblages on the medial side. On the flagellum the setae are acutely inclined distally in groups of four to six. The length of setae decreases from the proximal to the distal articles. Only the

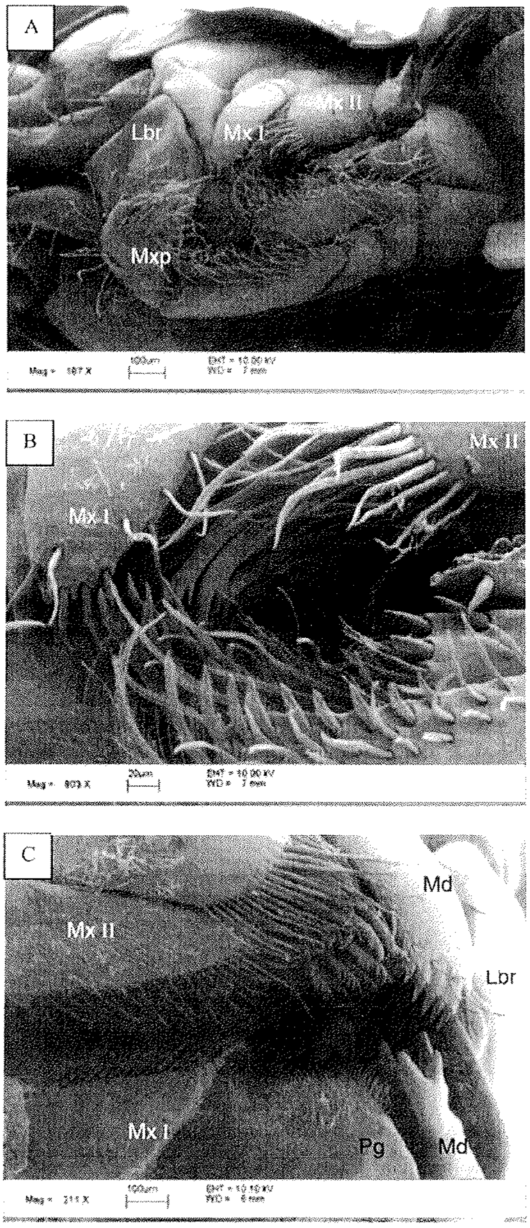


Fig. 15: Oral region in various magnifications and with distinct mouthparts removed. Lbr: labrum, Md: mandible, Pg: paragnath, Mx I & II: maxilla I & II, Mxp: maxilliped. Magnification and scale bar: 187x, 100µm (A); 803x, 20µm (B); 211x, 100µm (C).

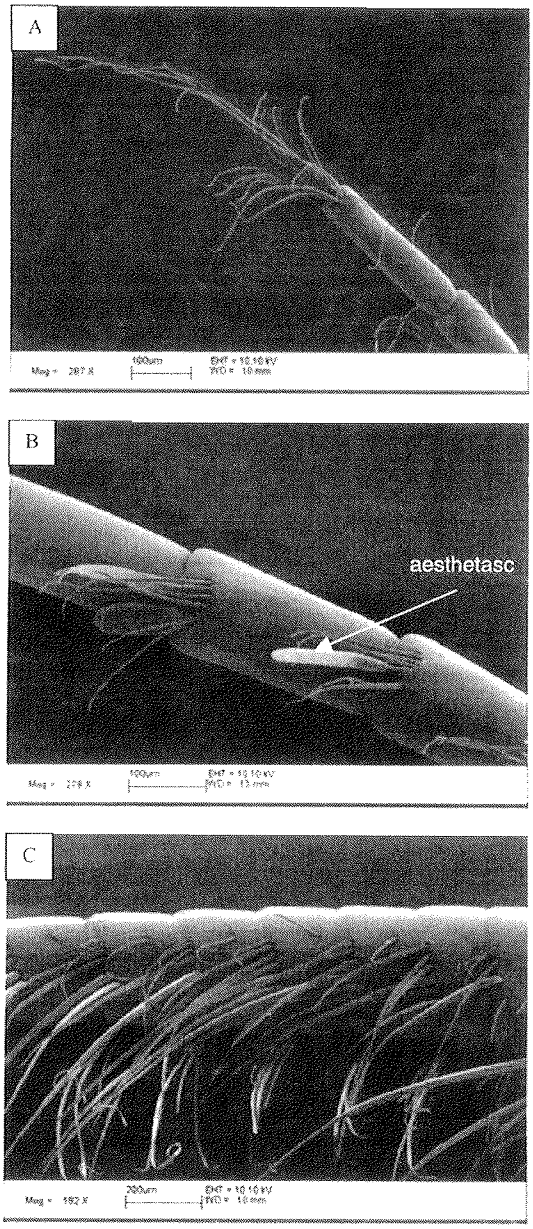


Fig. 16: Apical setae (A) and setation on the basal flagellar articles (C) of antenna II, aesthetasc on the flagellum of antenna I (B). Magnification and scale bar: 287x, 100µm (A); 278x, 100µm (B); 182x, 200µm (C).

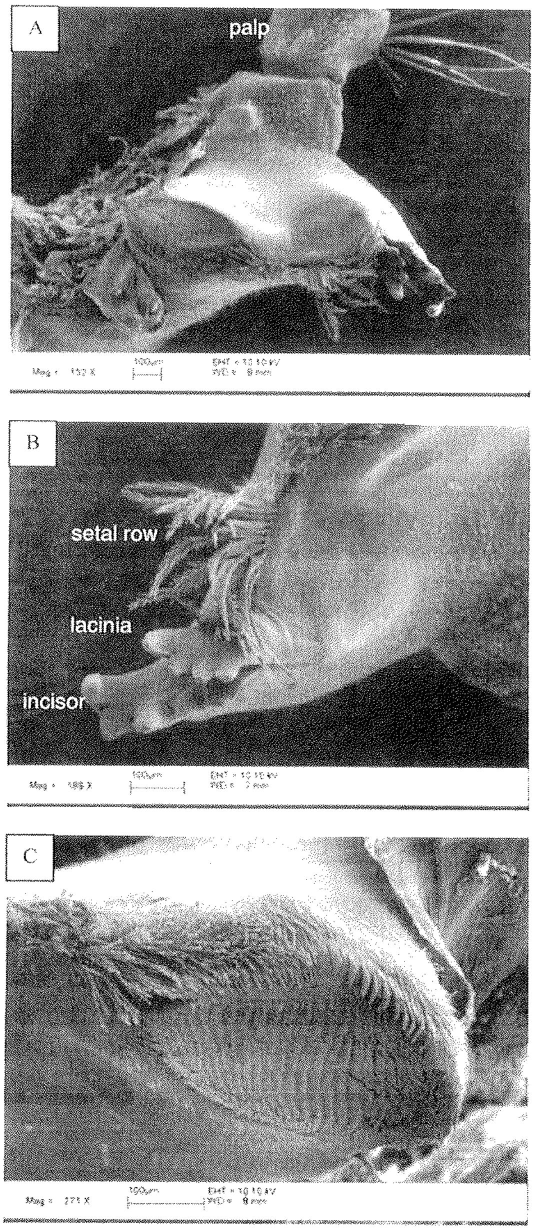


Fig. 17: Left mandible seen from rostrad (A), details: incisor and lacinia mobilis (B), molar (C). Magnification and scale bar: 132x, 100µm (A); 189x, 100µm (B); 271x, 100µm (C).

apical setae (Fig. 16A for antenna II) are again longer. Between two and four aesthetascs contribute to each setae group (Fig. 16B) except on the last and the first proximal articles. The accessory flagellum consists of eight articles which lack aesthetascs.

Antenna II (A II)

The second antenna, approximately as long as antenna I, is characterised by two short proximal articles and one long flagellum. As described for the first antenna, the length of each article increases from proximal to distal. The setation is similar to antenna I but more numerous and denser (Fig. 16C). Apart from the medial setation the peduncles bear groups of long setae to all sides. The setae are up to one third longer than on antenna I.

Labrum, Upper Lip (Lb)

The labrum is nearly circular and weakly sclerotised. It bears dense, short setae on the anterior margin.

Mandible (Md)

The highly calcified mandible (Fig. 17) bears a pronounced three-articulated palp. All articles are extremely setose, especially the elongated terminal article displays long, simple setae on the ventral side and in assemblages along the dorsal margin (Fig. 17B). The incisor is five-toothed, the lacinia mobile four-toothed. The following setal row consists of spines with plumose setae. The setation partly surrounds the molar process where it includes dental rows. The triturative molar (Fig. 17C) comprises a surface of ridges and teeth rows. No morphological differences between the left and the right mandible were found except slight asymmetry due to their gearing working mechanism. There is evidence that both mandibles operate the way described by Coleman [1990]: the cutting edges overlap. Unfortunately, none of the specimens examined showed the normal positioning of the mandibles. This artefact is probably due to the treatment with formaldehyde.

Paragnath, Lower Lip (Pg)

Like the labrum the paragnath is weakly sclerotised. The medial margins are densely setose with short, soft setae. The mandibular lobes are slightly elongated and pointed like alae.

Maxilla I (Mx I)

The first maxilla is five-articulated (Fig. 18). The fourth and fifth articles comprise a palp. The apical and medial part of the palp bear a double ventral row of long simple setae. The third article comprises 11 apical spines that are simple except for the serrations on the distal half of the lateral spines. From the basal article extends the inner endite which bears marginal plumose, long spines and soft setae on the ventro-medial surface.

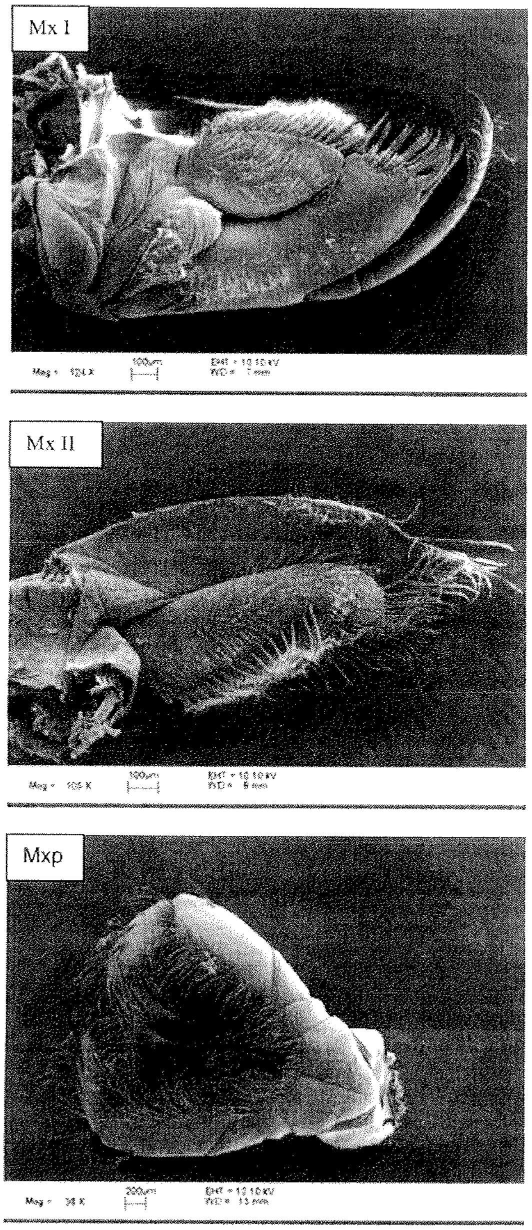


Fig. 18: Maxilla I (mx I: left, from caudad), maxilla II (mx II: left, from rostrad) and maxilliped (mxp: from caudad). Magnification and scale bar: 124x, 100µm (A); 105x, 100µm (B); 36x, 200µm (C).

Maxilla II (Mx II)

The second maxilla (Fig. 18) is three-articulated including endites forming the inner and outer lobes. The inner flashy lobe is densely setose with one row of plumose spines medio-marginally. The outer lobe is similar setose but the setae are serrate.

Maxilliped (Mxp)

The maxilliped (Fig. 18) is a fused pair of appendages. Except for the dactylus all six articles including the inner and outer endites are densely setose on the medial margins. The setae are simple and long and strongly constrict the setae-free aperture between the left and the right maxilliped. Endite three, the outer lobe, is crescent-shaped and densely setose, with a row of spines on the medial and apical margins. Endite two, the inner lobe, is a little bit smaller. The apical portion is simple setose, the medial margin plumose. The propodal setae are as long as the dactylus which lacks setae.

Gnathopod I and II (Gn I and II)

The first and the second gnathopod are morphologically similar. Only the propodus is slightly bigger and apparently stronger of gnathopod II compared to gnathopod I.

The gnathopod is a seven-articulated appendage. The second article, the coxa, is elongated and the next three articles are shorter. The pronounced article is the propodus. Propodus and dactylus form a very oblique subchela (Fig. 19A). The ventral margins of all articles bear groups of long simple setae, the second and third articles have distally a row of spines. The grasping margin on the propodus show a double row of simple setae arranged along the length of palm (Fig. 19B), where they align a lamellar crest (Fig. 19C) below the dactylus. The palmar surface also comprises spines. The dactylus lacks setation and spines.

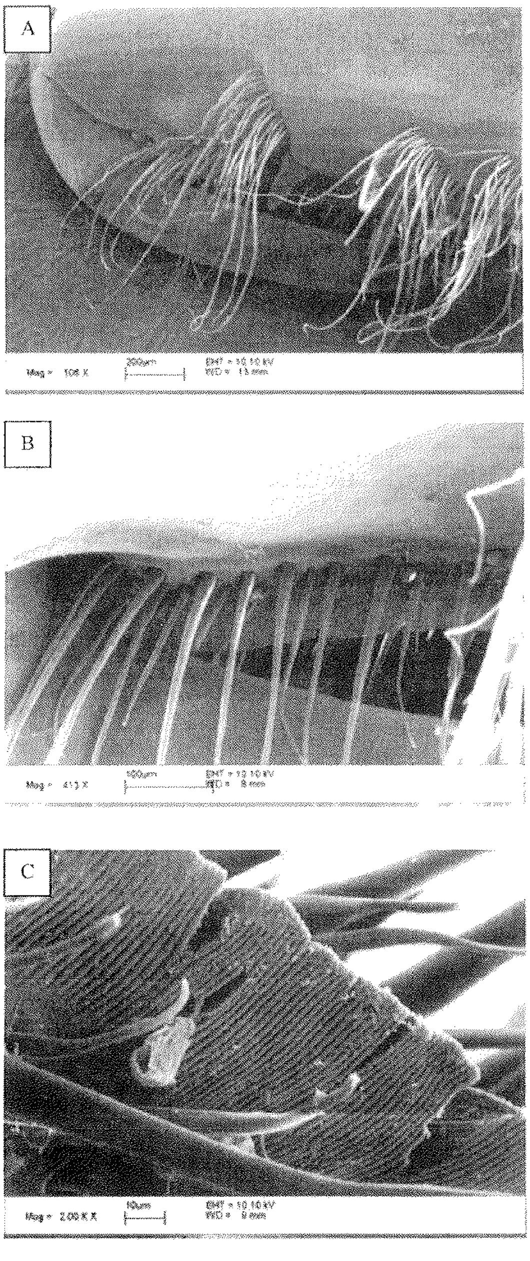


Fig. 19: Propodus and dactylus (A), palmar surface (B) and palmar crest (C) of the left gnathopod I. Magnification and scale bar: 106x, 200µm (A); 413x, 100µm (B); 2.00 K x, 10µm (C).

4. DISCUSSION

4.I. Field work

4.I.1. Number of attracted amphipods and abundances

The low number of amphipods attracted by bait hardly allows any conclusions on food preferences. However, the results may be interpreted in view of the abundance and biomass data achieved simultaneously from the ice stations [Arndt *et al.* 2000]. The trap samples reflect the scarcity of sympagic amphipods on the study site in general (Fig. 20).

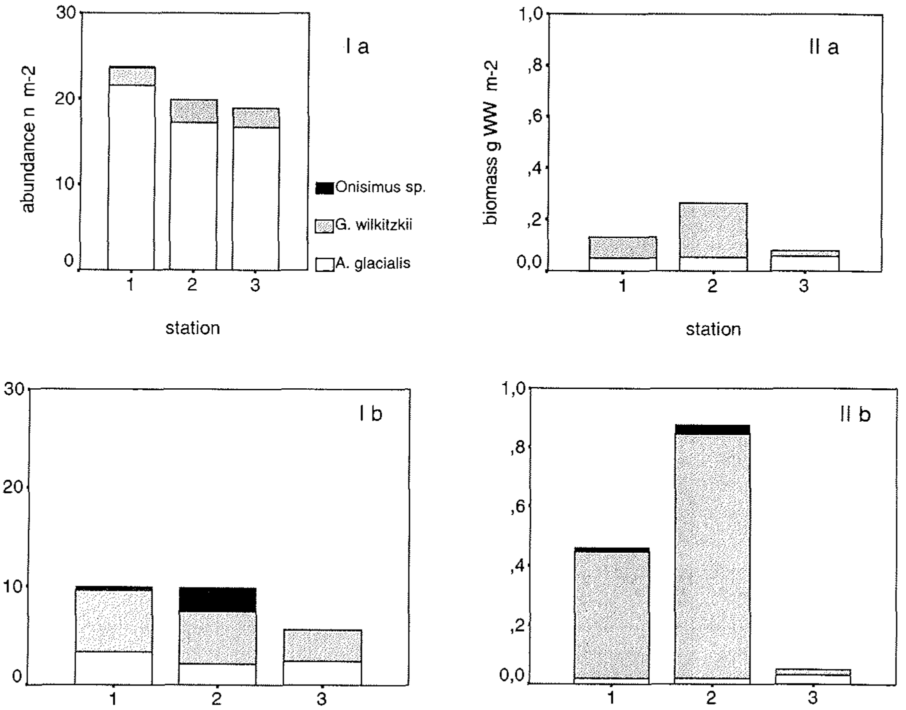


Fig. 20: Abundance (I, n m^{-2}) and biomass (II, g m^{-2}) of the amphipods *G. wilkitzkii*, *A. glacialis* and *Onisimus* sp., sampled from the edge (a) and 4 m (b) below the ice at Stations # 1 - 3 [modified in: Arndt *et al.* 2000].

Abundance and biomass at all three ice stations mainly followed the same pattern as reported earlier [Lønne & Gulliksen 1991a, c, Melnikov 1997] but was reduced remarkably compared to the average values reported in previous studies [e.g. Beuchel *et al.* 1998, Hop *et al.* 2000].
A. glacialis dominated the edge samples at all locations, and *G. wilkitzkii* was the most predominant species in biomass at two of the three stations (Fig. 20).

At Station # 1 the amount of *G. wilkitzkii* found on the edge was very small, both in number and size. At 4 m below the ice *G. wilkitzkii* exceeded *A. glacialis* and contributed 91% of the biomass. Only few *A. glacialis* were found.
The species distribution at Station # 2 followed similar patterns, but the total of biomass was higher. This is mainly due to the much bigger size of *G. wilkitzkii* at this location. Moreover, at this station the highest number of *Onisimus* sp. was observed at 4 m. This species was attracted by those traps baited with rotten polar cod (Tab. 3).
The results at Station # 3, the westernmost station, deviated remarkably from the other stations and also from previous results [e.g. Beuchel *et al.* 1998]. *A. glacialis* totally dominated the entire study site. This species constituted 94% of the abundance at the edge and 60% at 4 m, and made up most of the biomass.

In 1998 a nearly identical study was conducted in the area north of Svalbard [Beuchel *et al.* 1998]. The density numbers had been considered very low. Compared to 1998, the values obtained in 2000 were even lower. However, the main difference between 1998 and 2000 was the scarcity of *G. wilkitzkii* in the latter study. The explanation postulated in Arndt *et al.* [2000] refers to 1. the recent ice history, 2. the specific swimming abilities of the amphipods, and 3. the general distribution of the sympagic fauna below the ice.
The investigated floes were exposed to longer melting periods (see chapter 3.I.). No ecological data is available from the stations floes before the ice was exposed to warmer water. Not only the long-term ice history is unknown, but also the influence of warm water on the sympagic fauna. Therefore, the following interpretations should be considered tentatively.
One possible explanation for the low values found in this study might be that abundance and biomass have been low for the entire year. The drift into the warm Atlantic water might have caused a further loss of sympagic organisms.
The ice in the study area was mainly dominated by FYI. Lønne & Gulliksen [1991a, c] documented for *Onisimus* sp. and *G. wilkitzkii*, that these species were most common in MYI, but when FYI dominated, *A. glacialis* was more abundant since it has the greatest ability for dispersion due to its eigenmotion. The swimming abilities might explain the higher abundance values of *A. glacialis* at Station # 3. In contrast, *G. wilkitzkii* stays very closely to the ice and swims only for short distances [Poltermann 1997, Werner 2000]. The swimming abilities and the reduced predation pressure by *G. wilkitzkii* might have encouraged the re-colonisation of *A. glacialis* at Station # 3. But these processes require a longer time frame than given in this study. Since the duration of both melting events and ice drift across the Polar Front occurred within the scale of weeks, the lack of *G. wilkitzkii* at this station is most likely explained by the inability of this species to stay with the ice during melting [Arndt *et al.* 2000].

The sampling efficiency of baited traps has been discussed in previous studies. Barnard [1959] was the first who sampled seven ice-amphipod species with baited traps. The disadvantage of this method lies in the fact that it attracts only carnivorous, predatory and not herbivorous species [Barnard 1959]. As a consequence, the qualitative composition of the ice fauna may be underestimated. Furthermore, the size of the sampling area remains unclear and hence, the data on the absolute number of animals per m^2 [Barnard 1959]. It is most likely that the single *A.glacialis* caught at Station # 1 was flushed into the trap by advective waters.
Poltermann [1997] sampled a high number of amphipods with baited traps at MYI stations near Svalbard. According to him, traps may selectively attract motile scavengers, such as lysianassid amphipods (e.g. *Onisimus* sp.) with chemoreceptive capabilities to allow them to find and utilise the occasional protein rich source of a carcass [Busdosh *et al.* 1982, Ingram & Hessler 1983, Smith & Baldwin 1982]. The low sampling results might reflect this tendency.

The low abundance values at all three stations indicate a highly reduced possibility to sample amphipods, and even less so by traps. Due to the irregular and rough ice edge in some cases the traps were in very lose contact or even far away from the ice. This might have reduced the number of attracted amphipods as well. With respect to the general findings the efficiency of baited traps still remains uncertain.

4. II. Laboratory work

4. II.1. Physiological study

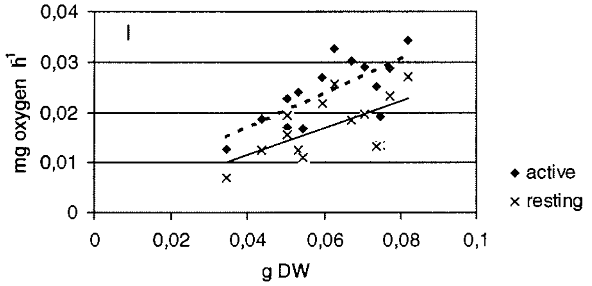
Adult and juvenile *G. wilkitzkii* were exposed to homogenates of four food types to achieve information about the food preference of this species by measuring the oxygen consumption (respiration rate). The results demonstrate no sexual but ontogenetic differences in the standard respiration rate and the intensity and quality of the oxygen consumption when exposed to different food types. In the laboratory, adults are assumed to prefer rotten polar cod, while juveniles prefer detritus.

Based on the hypothesis (see chapter 1.) the results of the respiration measurements infer: The higher the oxygen consumption rate, the more stimulated the amphipod became by the homogenate and thus, the more preferable the food type was assumed to be. In contrast: the lower the O_2-consumption rate, the less stimulating the food item was to *G. wilkitzkii* and therefore, the more reduced were the efforts to seek out the original food source. Furthermore, it was suggested, that the O_2-consumption rate did not only vary with food type but also with size class ("age") and sex. These assumptions were based on the following ideas:

1. the amphipod only responded (e.g. by changing the respiration rate) to those food types it was able to detect with its sensory apparatus,

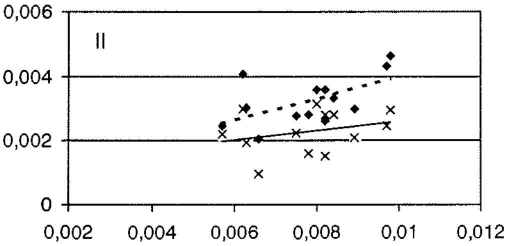
2. since only (particle-free) homogenates were used, the stimulation was considered chemosensory,
3. the stimulation resulted in intense seeking activities and/or physiological preparation for food up-take,
4. the oxygen consumption was a function of the rate of activity and was therefore directly connected to the rate of stimulation.

The latter postulation neglects the natural activity mode of non-stimulated amphipods, which was characterised by permanent switching from resting to being active [Poltermann 1997]. Even though the experimental specimens where kept undisturbed and in the darkness it is very likely that they did not spend the incubation time only resting.



rest y = 0.00105 + 0.264x
R_2 = 0.386
active y = 0.00436 + 0.340x
R_2 = 0.530

PEARSON
r (rest) = 0.621,
p = 0.0089
r (active) = 0.728,
p = 0.0016



rest y = 0.00112 + 0.149x
R_2 = 0.087
active y = 0.00064 + 0.334x
R_2 = 0.325

PEARSON
r (rest) = 0.296,
p = 0.163
r (active) = 0.570,
p = 0.021

Fig. 21: Highest and lowest values selected from series 1 (3 replicates) indicating the standard oxygen consumption (mg O_2 h^{-1} (g DW)$^{-1}$) with respect to the activity mode (resting, active). I: adults (N = 14), II: juveniles (N = 13), solid line: regression line for resting mode, dotted line: regression line for active mode.

The effect of the **activity mode** on the O_2-consumption rate may be one explanation for the individual variability among the replicates of series 1 (Fig. 3). This shall be described in more detail: if the highest respiration rate per individual is assumed to be the value measured while being predominantly active and the lowest is derived from the resting mode, two different regression lines are obtained for each size class (Fig. 21). The average "resting respiration" is up to 25% (adults) or 28% (juveniles) lower than the "active respiration". The demonstrated correlation of the consumed amount of oxygen and the dry weight is high for adults but less pronounced for juveniles (see PEARSON, Fig. 21), possibly due to the smaller range of body mass of the presented grown-up specimens compared to the juveniles. Werner *et al.* [1999] already pointed to this correlation and calculated for resting and swimming specimens O_2-consumption rates ranging from 0.070 mg (g DW x h)$^{-1}$ to 0.154 mg (g DW x h)$^{-1}$, respectively. In contrast to this study, the specimens in Werner *et al.* [1999] consumed 45% less oxygen while resting than while being active. The reason for this discrepancy might be, that the specimens in this study were kept undisturbed in the darkness and the distinct rates were deviated from the variability in the data, while Werner *et al.* [1999] randomly controlled the activity mode during incubation. It is very likely that the latter method caused periodically disturbances that increased the individual activity and thus the oxygen consumption. The incubation under illuminated conditions may also significantly increase the respiration rate [Vernberg 1983].

Therefore, all data gathered in this study for all series include both activity modes, resting and crawling or swimming around.
Unfortunately, Werner *et al.* [1999] did not mention whether the respiration was measured from adult or juvenile specimens. The calculated average O_2-consumption rate (0.112 mg (g DW x h)$^{-1}$) was taken at temperatures around 0°C. Aarset & Aunaas [1990b] found a high temperature sensitivity of (adult ?) *G. wilkitzkii* especially in the range of 0° to 5°C, which is about the range under-ice amphipods would generally experience in the Arctic. At 5°C the amphipods consumed more than twice as much as at 0°C (0.28 ± 0.06 compared to 0.13 ± 0.05 ml (g DW x h)$^{-1}$, after conversion the latter from ml unit to mg [Handy & Depledge 1999]: 0.3998 mg O_2 (g DW x h)$^{-1}$).Therefore, the values achieved at 0°C [Aarset & Aunaas 1990b] correspond to the results in Werner *et al.* [1999] while the rate measured at 5°C approaches the data measured at ± 4°C in this study (0.3258 ± 0.090 for adults or 0.3855 ± 0.102 mg (g DW x h)$^{-1}$ for juveniles).

All "no food series" were pooled to consider the switch in the physiological stage from non-stimulated (starved) to stimulated, assuming a lasting influence of the homogenates in the physiological stage. Thus, the **average standard oxygen consumption** differs more than when calculated only from series 1. Especially the respiration of the juveniles did not oscillate back to the level measured for starved specimens during the control series (series 1). The explanation for the regression line is given by comparing the "food series" with the "no food series" (Fig. 3 and Fig. 7). The adults responded to the majority of food types with a decreased respiration rate, only during exposure to rotten polar cod the oxygen consumption was increased. The diminution ranged from –20% (less consumed O_2 compared to the standard respiration) for polar cod, to –12% for algae and detritus, the elevation is +17% (rotten polar cod). The negative slope of the regression line for the standard respiration (Fig. 3) reflects the discrepancy between the control measurements and the average rate found in series 1. There is no evidence that the average standard respiration of starved specimens differs significantly from the rate measured during the control series, but it is likely that one control day was not enough to allow the respiration rate to "calm down" from the stimulated to the non-stimulated mode of series 1. This impression is supported by the analysis of the course of measurements on juveniles. The positive slope of the regression line (Fig. 3) also demonstrates that during control measurements the respiration has not oscillated back to the average rate calculated for series 1. All food types caused an increase in the O_2-consumption (+10% for polar cod, +23% for detritus, +32% for algae, +34% for rotten polar cod). However, the control series clearly separated the "food series" from one another. The responses to each food type were relatively distinctive, differed remarkably from the standard respiration rate and generally oscillated on one level (Fig. 6).

According to the defined hypothesis, **adult** *G. wilkitzkii* preferred in the laboratory most rotten polar cod as food source thus their respiration was increased indicating stimulation. This assumption is supported since all replicates of the "rotten polar cod series" kept one level and the corresponding error bars were small indicating uniform responses of the whole group (Fig. 5). However, adult *G. wilkitzkii* were observed to feed on all food types (see chapter 3.II.2.).

The respiration rate achieved from the "polar cod-" and "detritus-series" was lowered compared to the standard respiration but it is very likely that the specimens had to become "familiar" with this food type first, since the third replicate was significantly decreased in comparison to replicate 1 and 2. In contrast, macroalgae seemed to be the less adequate food source four adults, since the error bars were high and the respiration rate decreased from replicate 1 to replicate 3 (Fig. 5). Supported by the observations (see chapter 3.II.2.) these results clearly suggest indecisive or refusing behaviour of at least some specimens.

A comparable result was achieved from **juveniles** in the algae series. The standard errors (Fig. 6) demonstrated an indecisive habit even though this series showed the second highest deviation from the standard respiration (Fig. 4). For rotten polar cod the responses were even more unclear. The second replicate differed remarkably from replicate 1 and 3, while replicate 3 kept the lowest level and showed the smallest error bars (Fig. 6), indicating that this rate was most likely after getting familiar with this food type. Polar cod and detritus resulted in O_2-consumption rates which oscillated on more or less one level. Although the juveniles were observed to feed on all food types in the laboratory, detritus seemed to be the most preferable since the responses to inserted detritus (series 6) showed not only high stimulation but also affected series 7 (= control 3) afterwards (Fig. 3). The reaction generated by detritus can be described as intensive as it continued even after removing the stimulus. The same effect was observed on adults in series 9 (= control 4) after the experiment with rotten polar cod (Fig. 3).

The results may indicate that the responses of *G. wilkitzkii* induced by food are immediate but those induced by "no food" after the stimulation are rather low. The time-span from detection and characterisation of the food to reaction and finally localisation and ingestion only lasted some seconds (see chapter 3.II.2.). In contrast, the animal kept a high activity level for hours even after removing the stimulus. This may be either due to neurophysiological [Aarset 1991] or metabolic changes in the internal machinery. According to Aarset [1991], the physiological reasons for the accelerated respiratory rates may be as follows: 1. the preparation of the digestive canal on food up-take; 2. an increase in the locomotory activity as part of the food acquisition; and 3. an increase in catabolic processes. The excretion rate of *G. wilkitzkii* corresponds to some extend with changes in the oxygen consumption [Aarset & Aunaas 1990a]. All results imply that the chemosensory stimulation suggested for *G. wilkitzkii* results in physiological changes inducing the preparation of the body for food up-take.

The results demonstrate no sexual but pronounced **ontogenetic differences**, not only in the food preference but also in the intensity and quality of the response. Ontogenetic differences in diet have already been documented for the genus *Gammarus* [Steele & Steele 1975].
Considering the proven relationship between respiration rate and body size [e.g. Peters 1983, Smith & Baldwin 1982, Vidal 1980a] and thus, the regularly higher standard respiration of young animals (see also chapter 4.II.2.), the juveniles tend to respond more intensely to inserted food and always with an increase in the respiration rate [this study]. Changes in the respiratory rate reflect a number of physiological alterations, including feeding and locomotion [Vernberg 1983] and hence, in the energy requirement [Aarset 1991]. Thus, the oxygen consumption is linked directly to the internal machinery of the amphipod, its metabolic rate [Wilson 1996 in: Handy & Depledge 1999].

The oxygen up-take is not only increased by the locomotory activity (i.e. food seeking behaviour) and the ontogenetic difference in metabolic rate (see chapter 4.II.2.) but also by **feeding** [Vernberg 1983].
Starved animals have a lower rate of O_2-consumption than organisms that were stimulated or fed [Marsden *et al.* 1973]. Starvation may result in a reduction of specific energy reserves and in the change of metabolic substrates used [Vernberg 1983].
Several studies on crustaceans analysed the influence of feeding on the oxygen consumption [e.g. Sellner 1976, Ikeda 1977, Vidal 1980b, Wallace 1973]. Smith & Baldwin [1982] found increased consumption rates of up to 2.5-fold higher than the resting rate for deep-sea Lysianassidae in *in situ* respiration measurements with amphipods exposed to dead fish, assuming special metabolic adaptations for this food limited habitat.
Vidal [1980a] sums up possible reasons for the lower respiration rate of starved copepods, which may result from: 1. a decrease in the respiratory quotient, caused by a shift to oxidation of reserve rather than freshly assimilated material; 2. reduced food searching and feeding activity in the absence of food; and 3. a drop in the energy required for assimilating and processing food materials.
Up to now, there were only few attempts to investigate the influence of different food types and concentrations on the respiration rate. Sellner [1976] found a significant influence on the respiration rate by diet under certain conditions for the benthic harpacticoid copepod *Thompsonula hyaenae.* Females fed the diatom *Navicula pelliculosa* had a higher rate than animals fed different *Navicula* sp., apparently a response which was correlated with the smaller size and lower food energy content of *N. pelliculosa.* The oxygen consumption rate of the calanoid copepod *Calanus pacificus* was directly affected by the

presence or absence of food but not by changes in food concentration implying a simple internal "switch on or off" mechanism [Vidal 1980a]. In contrast, Kersting & van der Leeuw-Leegwater [1976] observed a decrease of the respiration rate at high food concentrations on the anomopod *Daphnia magna*.

Under **natural conditions** the quality and intensity of the respiratory response to each food type probably result from interactions of the following factors: food quality and tissue characteristics, food availability and spatial distribution of the size classes below the ice.
The energetic and nutritive value differs between animal and plant derived food and detritus [Penzlin 1989, Poltermann 2001]. However, detritus is a highly concentrated source of food available in the interior of the ice throughout the year [Grainger & Hsiao 1990] since it is flushed into the brine channel system. Especially apart from late summer, it is the predominant food source for the sympagic fauna. The algae biomass is highest during spring and summer [Horner 1985a], indicating primary production. Encrusted diatoms are the most characteristic algae of pack ice. Macroalgae like *Ulva* sp. only occur occasionally within the ice, for instance, in ice that was formed in shallow coastal areas [Gulliksen & Lønne 1991]. Encrusted animal derived, dead material is also considered to be rare but present. The variability of ice structures such as crevices, holes, channels and pockets function as effective traps for drifting material. Ice micro-organisms modify the organic material.
The smaller juveniles find shelter and hiding places in the three-dimensional system of brine channels, where the fine detrital material accumulates. Because of their larger body size, the low predation pressure of this species due to its "spiny" morphology [Grainger & Hsiao 1990] and the wider spectrum of available food, adult *G. wilkitzkii* inhabit the bigger channels, holes and crevices of the ice subsurface.

Relatively few specimens have been studied. Therefore, conclusions concerning food preferences must be considered tentative. The high interanimal scattering (Fig. 8) may result from the following reasons: 1. individual differences in the physiological stage (e.g. intermolt stage or phase of reproduction etc.); 2. the level of locomotory and other activities; 3. the uncertain gut content assuming that a "starvation period" (in non-filtered water) of more than one month has not emptied the gut completely, thus digestive processes still continued; 4. the (small?) volume of the WINKLER bottles; 5. the duration of the incubation; and 6. the uncertain dependency of the oxygen consumption on food concentration. For instance, in the experimental series with rotten polar cod, single adult specimens had only 5 or 6 mg $O_2\ l^{-1}$ to their disposal before the incubation was terminated. Whether this low oxygen content has any negative effect on this species is not yet proven. Furthermore, the influence of food concentration should also be tested primarily. Since the food concentration factor was not considered in this study, the results concerning food preferences should be handled with special care.
To reduce the interanimal scattering, further studies should increase the number of tested specimens and should primarily control the influence of reduced oxygen contents. To achieve even clearer responses to the distinct food types, each series should be prolonged by more replicates. Besides, other

food items such as different ice algae or crustaceans (copepods, krill) should be investigated. However, considering that respiratory responses are influenced by many exogenous and endogenous, unpredictable factors, the method used in this study to evaluate food preferences of amphipods can be seen as promising.

4.II.2. Behavioural observations

Behavioural observations were conducted as part of the food acquisition and utilisation process. Mechanical stimulation resulted in a positive tactile response [Poltermann 1997, this study]. *G. wilkitzkii* tried to grasp every object it got in contact with the gnathopods and analysed it with the mouth parts. Vision was not found to play an important role in the process of food acquisition. Chemoreception may be important for the short distance detection, localisation and characterisation of food but not for long-distance attraction. It is suggested, that *G. wilkitzkii* responds to the stimulation of contact chemoreceptors.

G. wilkitzkii inhabits the multistructured subsurface and cheese-like interior of the ice, where turbid and calm areas alternate and the light regime is characterised as diffuse. Even with acute vision, it is unlikely that food could be detected by sight at a distance of more than a few centimetres. Visual cues appear to play generally a minor role even for the shallower-living amphipods [Steele & Steele 1999]. Moreover it is considered by Bullock & Horridge [1965], that form **vision** in Crustacea is rudimentary. Most carnivorous amphipods rely on chance encounters for food [von Westernhagen 1976], while visual predators seem to be rare. Sheader & Evans [1975] documented that the hyperiid amphipod *Parathemisto gaudichaudi* hunts moving prey visually.
Since *G. wilkitzkii* is described as an opportunistic omnivorous species [Poltermann 2001, Werner 1997b, this study] it is improbable that food is detected visually because of recognisable features. Moreover, *G. wilkitzkii* was not observed to be a very efficient hunter (see chapter 3.II.2.) and if preying, then only on weak or morbid specimens such as juveniles or exhausted animals. Neither was it attracted by ice encrusted, food source pretending items such as algae, dead amphipods or a piece of black paper. In several experiments, the amphipod passed by potential prey in only cm-distance without detecting it. In some cases it accidentally collided with other specimens which always caused immediate grasping with the gnathopods. These observations demonstrate that visual cues are obviously not involved in detecting food.

Since most of the food of *G. wilkitzkii* is inactive, it is unlikely that food acquisition relies solely on **vibration receptors**, even though the increased cleansing of especially the antennae may imply a response to mechanical stimulation. However, this response was also induced by particle-free homogenates (see chapter 3.II.2., Fig. 14). Grooming was observed on stimulated and non-stimulated, resting specimens and seems to be an important part of the general behaviour of *G. wilkitzkii.*

The **grooming** and cleansing behaviour on crustaceans was examined by several authors [e.g. on amphipods: Colemann 1989, Caine 1976, on decapods: Bauer 1979, Garm & Hoeg 2000]. Most species that show grooming behaviour are regular filter feeders or brush off their body surface for supplementary food supply. Especially cryptic living species are highly setose that use their setae for trapping detrital material. Caine [1976] postulated that filter feeders cleanse their entire body whereas predators primarily cleanse only both pair of antennae. *G. wilkitzkii* showed a combined behaviour of filter feeders and predators, since it cleansed the antennae most frequently but occasionally brushes the entire body surface [Poltermann 1997, this study]. Moreover, grooming behaviour is assumed imperative to prevent epizoic and sediment fouling of the body [Bauer 1979]. As described for *G. wilkitzkii*, also female shrimps use their grasping appendages (chelipeds) for cleansing their brooding eggs, apparently to remove fouling material which enters the ventral furrow by means of the respiratory current.

G. wilkitzkii showed irregular but permanent grooming behaviour that follows stereotype patterns (Fig. 14). Apparently, this behaviour depends on several endogenous and exogenous factors, which allow only tentative interpretations. Grooming results in a transfer of (chemo- and/or mechanosensory) stimulating material from mainly the antennae and the gnathopods to the mouth parts. It is not yet clear for *G. wilkitzkii* which setae types and receptive organs are involved in this process and on which body parts these distinct organs are distributed. Assuming that special chemoreceptors are located on the mouth parts, the detailed characterisation of the food takes place in the oral region. The cleansing rate of antenna I of *G. wilkitzkii* increased remarkably after the insertion of polar cod, emphasising chemoreception either on the antennal appendages or the mouth parts or both.

Antenna I was described as testing organ of the environmental water and occasionally the substrate while antenna II probes the substrate and serves for food up-take. Read & Williams [1991] examined the grooming behaviour of Gammaridae as well and found similar functions of the antennae. They figured out, that the differential use of the antennae and their location on the anterior body end emphasise their chemosensory function. They suggested, that antenna I is specialised in olfactory and antenna II in gustatory reception.

Reports on **chemoreceptor sensitivity** have often been at variance. Up to now, studies on crustaceans have mainly concentrated on the chemosensory apparatus of decapods [e.g. Hindley 1975, Altner *et al.* 1983, Grünert & Ache 1988] and peracarids. Among amphipods, the Lysianassidae are considered specialised on chemical stimuli [Busdosh *et al.* 1982, Dahl 1977, Fuzessery & Childress 1975, Kaufmann 1994, Laverack & Barrientos 1985, Saint-Marie 1992]. Only few papers deal with organs presumed to be chemosensitive and the effect of chemical stimuli on gammaridean amphipods. Many setal types and cuticulary structures on the body or the appendages are considered chemosensory, based on their external and internal morphological peculiarities and neurophysiological features [Read & Williams 1991, Steele 1994, Steele & Steele 1999].

Chemical stimulation was tested on *G. wilkitzkii* by exposing the amphipod to stimuli such as acid, salty or sweet water or water that contained rotten animal tissue [Poltermann 1997, this study]. All tested items resulted in clear positive or negative chemotactical responses.

But, if existent, the chemoreceptive organs of *G. wilkitzkii* do not function as primary receptors. The experiment with ice-encrusted amphipod carcasses demonstrated that the first encounter with this rotten and therefore "smelly" food source occurred accidentally, but when it lost contact with the substrate, the location was not found again, not even after long searches. This demonstrates, that *G. wilkitzkii* is not able to orient along a concentration gradient as described for Lysianassidae [e.g. Busdosh *et al.* 1982, Kaufmann 1994, Saint-Marie 1992, Smith & Baldwin 1982, Ingram & Hessler 1983] and other crustaceans [Grünert & Ache 1988, Hindley 1975].

As *G. wilkitzkii* obviously relies on the occasional encounter of food by colliding with it, there is evidence for the existence of a combined mechanosensory and chemosensory apparatus. Based on neurophysiological and morphological studies using SEM and TEM, several authors found types of so called bimodal or combined receptors, also named "spine setae" [Dahl 1973], "sensory spines" [Brandt 1988], "funnel-canal organs" [Schmidt & Gnatzky 1984] or "**contact chemoreceptors**", analogous the mechano-chemosensory organs found in insects [e.g. Schmidt & Gnatzky 1984, Fuzessery & Childress 1975, Diebel 1992].

The external examination of casual selected single setae on the antennae and gnathopods of *G. wilkitzkii* using SEM demonstrated, that this amphipod possesses setal organs that are assumed to function as "contact chemoreceptors" (Fig. 22). These setae types were found particularly on the antennal flagella and the propodi of gnathopod I and II. One lateral side of the seta appears laminated while the opposite side is not papillose. The distal parts are protected by leaf-like cuticular shields emanating from the external part of the setal wall. Below the shields the seta bears a terminal pore. The setal shaft is supported and protected by a cuticular spine. Therefore, the seta becomes two-pointed, the one point being that of the spine itself, the other one being the more slender and flexible tip of the sensory seta, which in most cases projects a little beyond the end of the spine proper.

Especially the terminal pore and the papillose walls point to chemoreception since the chemical stimuli are assumed to gain access to the chemoreceptors located within the shaft through this porus [Dahl 1973, Diebel 1992, Schmidt 1989]. The projecting spine is considered to be in contact with the sensory neurons of mechanoreceptors. The deflection of the setae-spine complex leads to depolarisation, and thus, the stimulation of the mechanoreceptors [Diebel 1992].

Even though the so called bimodal setae found on *G. wilkitzkii* tend to possess characteristics intermediate between chemosensory and mechanosensory hairs, interpretations based on solely external morphology and the location must be treated with special caution [Diebel 1992] and require further physiological and histological studies.

However, in view of the typical gammaridean **pleopod beating** [Dahl 1977, Barnard 1969, Schellenberg 1942, this study] and the sweeping antennae, pure chemosensory orientation along concentration gradients would provide no real

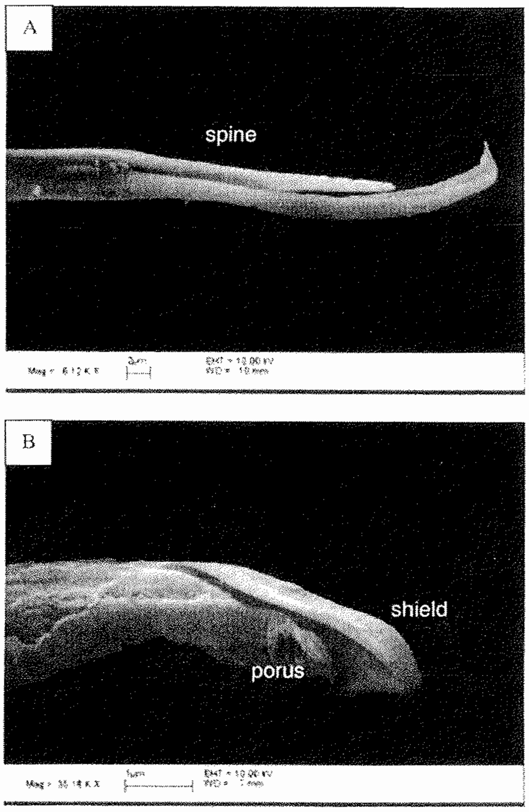


Fig. 22: Spine setae on the peduncle of antenna I. Magnification and scale bar: 6.12 K x, 2 µm (A); 35.18 K x, 1 µm (B).

efficiency. In any case, a small scale circulation is generated that passes over the antennae and through the mouth parts and causes turbulent environmental waters. Chemical gradients are homogenised and concentration peaks smoothed out.

Simultaneously, the chemical stimuli get distributed in an area of the radius several times the body length of the specimen. The advantage of this mechanism is obvious: even food items located three body lengths away from the resting amphipod pass the sensitive apparatus by means of the respiratory current. The flow of water provides the amphipod with information about its chemical environment. As the circulation patterns below the ice are extremely changeable and the subsurface structures are subjected to permanent modifications (melting, freezing, mechanical forces), the habitat of *G. wilkitzkii* is very dynamic and turbulent. Considering the low swimming ability of *G. wilkitzkii* [Lønne & Gulliksen 1991a, Werner *et al.* 1999], it is of practical value to assess at least the surrounding area while resting.

As already established, the pleopod beating never allows an accurate orientation towards the source of stimulation. However, chemotaxis cannot be ruled out completely. It may be important when the animal is within a few centimetres distance off the food.

According to Dahl [1977], the respiratory current (Fig. 9) functions primarily for the ventilation of the branchiae and – in females – the brood. Moreover, it may provide the amphipod with chemosensory information. Kaufmann [1994] believed that the use of respiratory currents may be especially important for deep-sea amphipods living under conditions of energy limitation, since this mechanism increases the volume of water transported across the antennal sensory organs, reducing the need for energetically expensive activities, such as active foraging. Some amphipods generate currents for food acquisition [Dennell 1933, Keith 1969, this study, see also chapter 4.II.3.] or – in reversing the direction from time to time - to prevent fouling [Vuillemin 1967 in: Bauer 1979].

The pleopod beating of *G. wilkitzkii* makes studies concerning the **reaction time** to inserted food items very difficult. The observations reveal, that the reaction time – as defined in this study – apparently depends on the beat frequency (Fig. 10). The latter is remarkably increased when the amphipod becomes stimulated (Fig. 11). The response is stereotypical for every specimen (Fig. 10) but the intensity differs individually. Possible reasons for the individual scattering may be: 1. ongoing water movements in the experimental vials that transport the cod-scent to the amphipod; 2. the unknown spreading capacity of the homogenate by diffusion; 3. the non-uniform resting modes of the individuals; 4. the not exactly standardised method of inserting the drop of homogenate; and 5. the vials boundaries that may influence the natural pathways of the scent plume. However, the results indicate that a relationship exists between the pleopods activity and the chemical stimulation.

Kaufmann [1994] found the same characteristic stages of the reaction as described in this study for Lysianassidae. He suggested, that the first two stages (detection and seeking) primarily involve the olfactory sense ("smell"), while the third, localisation including chemical characterisation of the item, is gustatory in nature ("taste"). The ingestion appears to be largely mechanical, although a chemosensory component may also be involved. Since the homogenate was inserted in only 3 cm distance to the head and is therefore within the radius affected by the respiratory current, it is very likely that *G. wilkitzkii* really "smells" the polar cod.

G. wilkitzkii is able to utilise nearly all **food types** that occur below and within the ice. The amphipod was never observed to discriminate a food item before feeding on it. Every food type was grasped in a greedy manner. However, the amphipod showed the highest affinity to animal derived food (crustacean remains). In contrast, plant tissue was soon rejected. Of fine material, the amphipod apparently formed bigger aggregations after brushing the particles together using the long antennal setae. Combing and brushing is part of the grooming behaviour. The appearance of dye in the fecal pellets underlines that grooming and cleansing serves supplementary for food acquisition. Poltermann [1997] already suggested filtered material as additional food source for *G. wilkitzkii* referring to the intense body setation and the grooming behaviour. In comparison to pure filter feeders such as some caprellids [Caine 1974], *G. wilkitzkii* spends relatively little time (only 21.7%) for grooming [Poltermann 1997]. Hence, filtering as part of the food acquistion is supposed to play a minor role for *G. wilkitzkii* (see chapter 4.II.3.).

The **fecal pellets** verify the results achieved from the qualitative study (see chapter 3.II.2.). *G. wilkitzkii* ingested all food types it was exposed to, including those it rejected after testing. The fecal pellets reflect the tissue characteristics and colour of the original food (Tab. 5). The encrusted inorganic foreign material, unfermented pieces of macroalgae, fleshless crustacean appendages and oil aggregations, may suggest peculiarities in the ingestion mechanism, the treatment by the mouth parts and the digestive canal.

One possible reason for the unfermented pieces of *Ulva lactuca* may be the lack of adequate enzymes in the digestive canal. Since the gut of *Gammarus* is not able to produce cellulase [Agrawal 1965], this amphipod cannot digest plant tissue. A similar explanation may be expressed for the chitinous fragments, that passed through the stomach unaltered except for being mutilated by triturating structures. It is likely that chitinase is not produced by *G. wilkitzkii* as suggested for caprellids [Keith 1969]. It still remains questionable why the fecal pellets produced after feeding on crustaceans still contained oil aggregations since lipids are most energy-conserving and therefore, of best nutritive value. Maybe, the duration in the alimentary canal was too short to ensure complete digestion. The treatment by the mouth parts will be discussed in more detail in chapter 4.II.3. There is evidence, that *G. wilkitzkii* does not distinguish between nutritive and non-nutritive food types but ingests everything of the size of its mouth in a very greedy manner.

The data achieved from the **quantitative study** on the ingestion rate should be handled tentative since the high standard deviations (Fig. 13) may result from the low number of tested specimens. There is no doubt that the juveniles ingested more than twice as much as adults due to their higher metabolic rate [Peters 1983]. However, differences between the food types should be considered with care.

Adults ingested the amphipod *Themisto* sp. fastest, followed by rotten polar cod (Fig. 13). The high standard deviations indicate either high individual variability among the seven specimens or may result from the different tissue characteristics of the three tested food items and their behaviour in water. It is likely that *Themisto* sp. was only torn apart by *G. wilkitzkii* and ingested as big pieces without chewing or cutting it. As the crustaceans possess a chitinous exoskeleton, a high weight-specific ingestion rate was expected. In contrast, *G. wilkitzkii* had to cut the polar cod flesh into accurate pieces before ingesting it. This method is time consuming and takes even longer for fresh than for rotten meat. The fermented flesh (rotten polar cod) is assumed to be softer and more perished. Stored in water, it may get more easily dissolved, which bears another possible error. The special treatment (dehydration and hydration) may have intensified this effect even more.
Werner [1997b] documented for juvenile *G. wilkitzkii* ingestion rates of ice algae two orders of magnitude higher than for adults. The use of diatoms for feeding experiments allows more accurate quantitative analysis by measuring the chlorophyll *a* concentration. The feeding activity is deduced from the clearance rate [Grahame 1983]. However, this method is only useful for herbivorous animals. The ingestion rate of animal derived material by small crustaceans requires other methods. The method applied in this study suggests good results when tested on more specimens and with more "enclosed" food types such as whole crustaceans. Their chitinous skeleton prevents substantial losses during preparative procedures.

The higher ingestion rates for juveniles compared to adults can be explained by the principal relationship between **metabolism and body size**: the specific metabolic rate, and thus the proportion of body energy consumed per day declines with increasing body size within a metabolic group [Peters 1983]. For instance, it has been documented for *Gammarus locusta*, that the specific ingestion rate is always larger for juveniles than adults [Greze 1968]. Studies on copepods and krill also found a decrease in specific carbon ingestion with body size [Atkinson 1994 and Pakhomov & Perissinotto 1996 in: Werner 1997b].
In terms of respiration, it has been demonstrated for subarctic Lysianassidae, that the specific respiration rate declines with rising body mass [Christiansen & Diel-Christiansen 1993]. The same conclusion arises from the comparison of the specific respiration rate, and thus the specific carbon demand, of the individual species of sympagic amphipods [Aarset & Aunaas 1990b].
In general, sympagic amphipods seem to have low metabolic rates [Aarset & Aunaas 1990b], reflecting – from the physiological point of view – a more benthic type with much lower metabolic expenditures than a pelagic type [Clarke & Peck 1991]. Any form of locomotion, like swimming and crawling, costs a relatively high amount of metabolic energy [Peters 1983]. In contrast to pelagic organisms, under-ice amphipods probably do not spend much energy on locomotion, since they are not actively hunting and do not swim for long distances. In addition, sympagic amphipods frequently exhibit long resting phases between phases of activity [Poltermann 1997]. Apart from the ontogenetic differences in the activity rate (see chapter 3.II.1.), juveniles were observed to show higher eigenmotion and migrating capacities [Lønne &

Gulliksen 1991, this study] and hence, an increase in metabolic and respiration rate.

In the laboratory, *G. wilkitzkii* demonstrated a strong **association with the ice**. While resting *G. wilkitzkii* hung down from the ice and bent its head into the water column, so that it formed an angle to the substrate. This position allowed free movements of the head and hence, permitted optimal perception of either chemical or mechanical stimuli.
Under natural conditions, the ice floes permanently change position and directional exposure to the currents. The more variable and sculptured the under ice surface, the higher the variations in the water turbulence.
In this extremely changeable habitat, *G. wilkitzkii* probably prefers calm areas to ensure on the one hand the "sticking" to the ice and to permit on the other hand an optimal position for perceiving information about the environment.
G. wilkitzkii changed the location from time to time but scraping the ice was never observed. The amphipod does not treat the ice in view of reaching ice-encrusted material (see also chapter 4.II.3.). But when touching eatable items, it commenced mechanical treatment of the ice by means of the mouth parts and the feeding appendages. As already demonstrated, this observation emphasises the existence of "contact chemoreceptors".

When ice was present, the juveniles tended to keep contact with the substrate and rather disappeared within the ice, while the adults from time to time loosened the ice and crawled around. In contrast, when no ice was offered the juveniles moved restlessly around until exhaustion forced them to rest. The adults altered between resting and swimming behaviour. This ontogenetic difference may result from the higher predation pressure for juveniles. The ice provides shelter and many hiding places for the smallest fraction. As adult *G. wilkitzkii* prey on juveniles and morbid amphipods irrespective of species [Poltermann 1997, Werner 1997b, Gulliksen & Lønne 1989, this study] the multi-structured, three-dimensional ice is of eminent importance for the survival of potential prey. Moreover, the predation pressure is reduced by the better swimming abilities of other sympagic amphipods [Poltermann 1997, Gulliksen & Lønne 1989, this study] and the avoidance strategy observed on *Onisimus* sp. [this study].
Several studies already documented **cannibalism** among gammarids [e.g. for *G. setosus*: Grainger & Hsiao 1990; for *G. wilkitzkii*: Poltermann 1997, Werner 1997b]. According to Mattson & Cedhagen [1989], cannibalism ensures the survival of the species under limited conditions. However, cannibalism was never observed between specimens of the same size (age) class. The observations imply the existence of micro-habitats (food availability, refuge etc.). The intraspecific aggression might regulate the micro-distribution within the habitat [Hazlett 1975 in: Poltermann 1997].

4.II.3. Morphological study

The correlation of food type, feeding mechanism and morphological variations of the mouth parts and accessory feeding appendages allows conclusions concerning food preference only by analysing the morphology and their presumed functioning [Agrawal 1965].

Grainger & Hsiao [1990], for instance, summarised the relationships between the morphology of the mouth parts and feeding in copepods. Mainly herbivorous (filter-) feeders had long and plumose setae on antenna II, mandible, maxilla I and II and maxilliped. At the opposite extreme was the group comprising raptorial carnivorous (large-particle) feeders. In these, setae on mouth parts were reduced in number and simplified, and certain appendages were modified into grasping and holding structures.
For Mysidacea Kaestner [1993] stated, that the mouth parts of filter feeders, which grind their food, were characterised by a stout molar process, while predators, which bite big pieces from their prey had a sharp and elongated incisor. He schematically demonstrated the importance of a pronounced setation along the medial margins of the mandible (setal row), maxilla I and II and maxilliped on the filter feeder *Hemimysis lamornae.* In contrast, the mouth parts of the more predatory species *Lophogaster typicus* bore strong spiny apical setae and instead of a mandibulary setal row stout teeth.
Amphipods show four methods of food acquisition [Caine 1974]: predation, scavenging, scraping and filter feeding. Combined with behavioural observations, the morphological study suggests a more generalised feeding apparatus that enables *G. wilkitzkii* to various methods of food acquisition. Depending on the casual encounter with food, the amphipod applies predation, scraping and filter feeding. Scavenging is not very likely.
Each of these methods will be discussed for *G. wilkitzkii* in terms of mouth parts morphology and behavioural observations.

Predation, the feeding on captured prey, is based primarily on the interaction of an effective sensory apparatus (e.g. the antennae) and the prey capturing appendages (e.g. the gnathopods) [Caine 1974].
With reference to the observations of this study, it is very likely that predation is an important feeding mechanism for *G. wilkitzkii.* The antennae and gnathopods are primarily involved. However, *G. wilkitzkii* lacks some predatory specialisations, such as an efficient sensory apparatus, that ensures successful hunting and the co-ordinated operation of antennae and gnathopods, and sharp cutting edges.
Among caprellids, only the **first antenna** functions as prey catching appendage, while gnathopod II traps the prey and forces it towards the oral region [Caine 1974]. Even though the caprellids differ remarkably in habitus and behaviour from *G. wilkitzkii,* the first antenna (Fig. 16) in both groups functions as a sensory receptor. While *Caprella* sp., for example, holds antenna I immobile in erected posture until it is stimulated (mechanically?), this long appendage was never observed to be kept in stationary position on *G. wilkitzkii.* It permanently sweeps through the water which prevents directional sensing. But similar to the observations on caprellids [Caine 1974, Keith 1969], gammarids [Agrawal 1965, this study] employ the antennae frequently as accessory food gathering appendages. Whether this is part of the grooming behaviour (endogenous) or is induced by chemical or mechanical stimulation (exogenous) still remains questionable.

The more numerous, denser and longer setae on the **second antenna** (Fig. 16) imply a higher efficiency in taking up small food particles. The setation suggests a supplementary filter-feeding mechanism. The antennae of the amphipod *Anamixis hanseni* push the food into the mouth [Thomas & Taylor 1981]. Such behaviour was never observed for *G. wilkitzkii.*

The mouth parts of *G. wilkitzkii* are interpreted to be able to cope with firm body walls. The incisors of the **mandibles** are facing each other in a cutting position with the laciniae mobiles. Thus, the four cutting edges of the left and the right mandible overlap with each other. The roughly toothed cutting edges imply that the food item is rather torn apart than cut. In contrast to the mandibles of *G. wilkitzkii,* the multi-toothed incisors and laciniae mobiles of the mandibles of the scavengers which cut the food item into accurate pieces differ remarkably (see below). The shape of the zig-zag lined trace on plant tissue, for instance, corresponds exactly with the shape and distance (± 100 µm) of the mandibulary cutting edges.

The mandibles of *G. wilkitzkii* bear triturative molars that appear to work like millstones. They enable *G. wilkitzkii* to reduce the food morsels to small pieces and to crack and grind even hard particles such as the shells of diatoms. Coleman [1987] suggested, that the setal row between lacinia mobile and molar does not only function as ventral lit but also transfers food particles into the oesophagus.

The setation and frequent beating of the mandible palps imply an accessory function in transporting captured or escaping material to the oral region.

The **labrum** functions as an anterior margin to the escape of food particles. It may also have some stabilizing function for the four cutting blades of the mandibles [Coleman 1990].

Posteriorly, the oesophagus is enclosed by the lower lip, the **paragnath.** It prevents the escape of food from the oesophagus. The smooth setation on the medial margins suggests that this process may also subserve a limited grooming function for the mandibles.

The proximal endite of **maxilla I** is folded around the distal endite forming a lateral concave excavation (Fig. 18). The endites of **maxilla II** overlap with each other to a great extent (Fig. 18). Distinct setation composed by different types of setae (plumose, simple, spiny) and various distances separating them on the anterior face and medial margins of the maxillae might not only prevent the escape of food but may also subserve a grooming function. The almost permanently vibrating anterior and posterior mouth parts and the maxillipeds perform on the one hand brushing and combing, and on the other hand sieving and sorting activities by the maxillae.

Coleman [1987] postulated also a cutting function of the strong apical spines on the maxillae. Maxilla I of *G. wilkitzkii* bears such strong spines (Fig. 18), which may co-operate with the cutting blades and setal row of the mandible in treating the food item mechanically. In contrast to the mandibles, the maxillae handle the smaller fraction, the bigger food morsels are transported to the mandibles by the median setal row [Coleman 1987].

The **maxilliped** bears a remarkably setose palp (Fig. 18) protecting the mouth parts (Fig. 15), preventing the escape of small food particles postero-ventrally, and functioning as accessory for cleansing the gnathopods and antennae. Coleman [1987, 1990] documented for Antarctic amphipods that the distal

endites of the maxilliped, in co-operation with the distal article of the maxillulary palp, squeezes food morsels during feeding and both move them oral to the cutting and grinding apparatus. The antennae and lateral faces of the mouth parts are cleansed by means of the medio-marginal setation on the maxillilulary palps. On *G. wilkitzkii* the articulated distal parts of the maxillulary palps and the pointed, non-setose dactyli emphasise a predatory function.
Most amphipods use their **gnathopods** for food acquisition [Coleman 1987]. In most cases the gnathopods are subchelate, that function in trapping and forcing the selected material against the mouth parts. *G. wilkitzkii* clings to the substrate with its pereopods which enables the amphipod to use the head appendages and gnathopods only for food acquisition and grooming. Every grasped object is jammed between dactylus and propodus or either between the propodi of two gnathopods, similar to the observations on e.g. *Caprella linearis* [Caine 1974]. The crested and setose palmar surface of the gnathopods of *G. wilkitzkii* (Fig. 19) suggests a very effective collection of material that sticks to the body surface. The long gnathopods of Lysianassidae reach the whole body surface while cleansing [pers. comm. Andres].
The importance of the gnathopods for predation may only be suggested. Caine [1974] postulated for caprellids, that species with a simple grasping spine on the palmar surface tend to be more predatory, while those which rely on scraping tend to have a bi- or trifurcate spine. Therefore, *G. wilkitzkii* should be considered as a more predatory species although scraping was also observed in this study. The relative size of the gnathopods also correlates with the degree of emphasis on predation [Caine 1974]: increased size of the gnathopods enables the amphipod to capture prey over a great area and to cope with strong prey and – during reproduction – with the partner. According to Caine [1974], the reduction in length and increased stoutness of the gnathopods are related to the emphasis on scraping and the grasping of the substratum. The gnathopods of *G. wilkitzkii* were characterised as long and stout, which suggests a more diverse use for food acquisition.

Scavenging is defined as the grasping of non-living material, usually dead organisms or pieces of detritus [Caine 1977].
The mandibles of *G. wilkitzkii* show none of the characteristic features summarised for scavenging Lysianassidae [Dahl 1979, Saint-Marie 1992, Thurston 1979]: they bear no long sharp cutting blades, nor a bowl-shaped corpus or a reduced molar. But referring to the behavioural observations, scavenging cannot be ruled out as supplementary mechanism for food acquisition. Flesh was not cut into accurate small pieces which minimises the loss of nutritional material, but was rather torn apart in a greedy manner. The clouding of the environmental waters while feeding pieces of flesh suggests no specialised handling and therefore, no maximised utilisation of the food source.

The **scraping** of diatoms and ice encrusted material is the third mode of feeding. Similar to the observations on the caprellid *Leptogorgia* [Caine 1974], *G. wilkitzkii* bites into the substratum while capturing nutritional material. Gnathopod II is used to hold the oral area of the amphipod against the substratum by grasping it while the dactyli of gnathopod I, the maxilliped and apparently antenna II treat the ice. The exact mechanism of loosening the material is not yet clear. McGrouther [1983] observed on the grazing amphipod *Hyale rupicola*, that this is achieved by moving the distal endites of the maxillipeds while treating the substratum with the medial setae. *Caprella penantis* is supposed to use not only the maxilliped but also the mandible and maxillae for scraping [Caine 1974]. This caprellid obviously uses a restraining chamber which is formed by the bases and endites of the maxilliped and the lateral edges by maxilla II. The chamber retains the loosened material and transfers it to the crushing molar process of the mandible. The dense setation of the maxillae and maxilliped of *G. wilkitzkii* in particular, as well as the relatively sharp anterior margins of the mandible (incisor) and strong apical spines of maxilla I suggest food acquisition by scraping. Species which lack numerous setae do relatively little scraping [Caine 1974].

Filter-feeding is usually regarded as a process of sieving off either the flowing ambient waters or a generated current which is produced by the crustacean itself [Grahame 1983]. It involves the acquisition of suspended material from the water by the antennae and/or the mouth parts. This mechanism of food acquisition is therefore closely connected with grooming behaviour (see chapters 3.II.2. and 4.II.2.). The long, setose antennae function as the primary filtering structures. A lot of suspended material may be entrapped as the antennae softly sweep through the water while resting. The more numerous, denser and more plumose the setae the greater the trend towards filter-feeding [Caine 1974].

However, from the phylogenetic point of view, the setation of the mouth parts allows no conclusions concerning their functioning. Seta type and its location on the body may be considered evolutionary artefact [Brandt 1988]. Therefore, the following interpretations are very speculative that require further studies.

To clean the antennae, *G. wilkitzkii* brings them ventrally into the mouth parts area or primarily into the grasp of the gnathopods. A simple extension of the antennae anteriorly pulls them through the grasp, and the material is transferred to the setae on the palmar surface of the propodus. Gnathopod II is cleansed by gnathopod I or directly by the marginal setae along the maxilliped. The material is then passed into the mandibular region by the maxillae. The antennae are probably groomed by the serrate and plumose setation on the mandible and maxillae. Garm & Hoeg [2000] found some correlation between seta type (defined by external morphology) and function. Serrate setae (like those on maxilla I and II, Fig. 18) often serve in grooming but may also be involved in the collection and transfer of food objects. Plumose setae (on the maxillae and mandible, Fig. 17) serve as filters.

Numerous setae and spines on the palp and endites of the maxilliped of *G. wilkitzkii* reflect an emphasis not only on scraping but also on filter-feeding. Coarse material is closely allied to the setae on the palp, fine material is retained by the maxillae [Caine 1974]. True filter feeders such as the amphipod *Haustorius arenarius*, depend on an extremely setose caudal apparatus [Dennell 1933]. The pleopod beating described for *Gammarus* [Dahl 1977, this study] generates a caudal respiratory current which passes the setose sieves of the mouth parts. In contrast to *G. wilkitzkii, H. arenarius* generates the stream of water that passes the mouth parts by the mouth parts proper by means of a kind of "maxillulary suction pump" [Dennell 1933].

Bathyporeira sp. generates a respiratory current similarly to *G. wilkitzkii*, but in contrast to the latter, it was never observed to filter particles from the resulting currents [Nicolaisen & Kanneworff 1969], even though the setation implied any filter feeding mechanism.

The extensive setation and the occurrence of different setae types on the maxilliped and maxillae of *G. wilkitzkii* strongly suggest a filtering of suspended material from the respiratory current. The defecation of food colour verified the existence of any filter feeding mechanism.

5. CONCLUSIONS

Gammarus wilkitzkii successfully colonised the entire sea ice covered Arctic area since this amphipod is physiologically and morphologically well adapted to this highly variable environment.

Sea ice as a "bottom-up substrate" provides shelter, grid, nursery ground and a diverse spectrum of food. Food supply varies with season, origin and history of the ice. The study on respiration revealed ontogenetic differences in food acquisition: adult *G. wilkitzkii* use all food sources available below and within sea ice but prefer most animal derived tissue, whereas juveniles feed more on detritus. The results of the physiological study are strongly supported by behavioural observations and a close examination of the mouth parts and feeding appendages. *G. wilkitzkii* is a highly generalised, opportunistic sympagic amphipod. The amphipod is able to loosen encrusted material, preys on living and dead animals and is capable to filter suspended material from the waters. The principal organs involved in detecting and localising food are bimodal setae which enable *G. wilkitzkii* – in combination with the respiratory current – to assess the surrounding environmental waters in view of mechano-chemical stimuli. In case it is necessary, the amphipod may survive starvation periods for nearly a year.

Whether *G. wilkitzkii* and other ice associated species are able to cope with environmental changes caused by the human being remains an open question. Pollution is a major topic of concern today. An area in the Arctic where major oil drilling operations are being planned is a productive one in terms of ice associated flora and fauna. If, as is thought, the ice community is of main importance for the Arctic food web, what happens if an oil spill is trapped under the ice?

Further studies should concentrate on the effects of pollution such as oil, heavy metals or pesticides on ice organisms. Measuring the oxygen consumption rates – as described in this study – may serve as an promising indicator for metabolic changes and far-reaching impairments.

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APPENDIX

Average oxygen consumption rates (mg (g DW x h)$^{-1}$ ± SD) of adults and juveniles depending on food type.

adults

no food	series		N	average	SD
	1	replicates 1-3	42	0,3452	0,086
	3	control	14	0,2805	0,097
	5	control	14	0,3039	0,095
	7	control	14	0,3263	0,084
	9	control	14	0,3342	0,087
				0,3258	0,090

food type	series		N	average	SD
algae	2	replicates 1-3	42	0,2852	0,078
cod	4	replicates 1-3	42	0,2595	0,097
detritus	6	replicates 1-3	42	0,2865	0,095
rotten cod	8	replicates 1-3	42	0,3936	0,092

juveniles

no food	series		N	average	SD
	1	replicates 1-3	39	0,3528	0,093
	3	control	13	0,3941	0,068
	5	control	13	0,3833	0,126
	7	control	13	0,4872	0,083
	9	control	13	0,3754	0,091
				0,3855	0,102

food type	series		N	average	SD
algae	2	replicates 1-3	39	0,5647	0,1033
cod	4	replicates 1-3	39	0,4277	0,1075
detritus	6	replicates 1-3	39	0,5004	0,1048
rotten cod	8	replicates 1-3	39	0,5823	0,1577

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