

**Aggregations of Arctic deep-sea scavenging amphipods
at large food falls**

**Ökologische Untersuchungen nekrophager Amphipoden in
der arktischen Tiefsee**

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Glossary

| | |
|-------|---|
| tab | Time at bottom |
| ROV | Remotely operated vehicle |
| SSS | Scanning sonar system |
| IBE | Integrated backscattered energy |
| S6 | Sector 6 (Area of polar projection of SSS-data) |
| S7 | Sector 7 (Area of polar projection of SSS-data) |
| F | Female |
| M | Male |
| J | Juvenile |
| Cs | Current speed |
| Cd | Current direction |
| WS | Weighted sum |
| kJ | Kilojoule |
| POM | Particular organic matter |
| WW | Wet weight |
| DM | Dry mass |
| AFDM | Ash free dry mass |
| BBL | Benthic boundary layer |
| EL | Ekman layer |
| r^2 | Correlation coefficient |
| A | Active oxygen consumption rate |
| R | Resting oxygen consumption rate |

Summary

The energy flow in the deep-sea benthic ecosystem is partly driven by sinking carcasses of larger pelagic organisms and mammals (food falls), which act as a local and highly concentrated organic input, given the low input rates of other organic matter to the deep sea. For benthic or benthopelagic scavengers the impact of any food fall is unpredictable both in space and in time. Due to the high number of individuals aggregating at food falls and their feeding efficiency mobile deep-sea scavengers such as the cosmopolitan amphipod *Eurythenes gryllus* have to be considered as an important component of the deep-sea food web. Deep-sea scavenging amphipods evolved towards a highly motile feeding guild, characterized by efficient metabolism and suitable receptor systems enabling fast localization of potential food sources in competition to others. However, information on the spatio-temporal attraction of these scavengers to food falls and on their food finding strategies is still scarce.

The aim of the present study is to elucidate the feeding ecology of *Eurythenes gryllus* in the Arctic deep sea. Literature data show that this species occurs frequently and in high numbers at food falls, so it was likely to obtain data on its food finding strategies and, its aggregation dynamics at food falls, which could be combined with information on its metabolism under controlled conditions in aquaria experiments. Six large food fall experiments were carried out during expeditions with the RV 'Polarstern' in the Arctic summer seasons 2000 and 2001 (ARK XVI/2 and ARK XVII/1) between 1400 and 2600 m water depth. For *in situ* investigations a tripod lander was used equipped with a baited time-lapse camera, a scanning sonar system (SSS), an acoustic doppler current profiler and baited traps. This combination of optical and acoustical measurements allowed to scan an area of about 8000 m² around the lander for approaching amphipods.

A total of 3490 invertebrate scavengers were sampled during these experiments which were dominated by *Eurythenes gryllus* (accompanied in some experiments by *Tmetonyx norbiensis*).

The length-frequency analysis of all individuals measured indicates that the females (16 to 75 mm length) of *Eurythenes gryllus* have a larger maximum size compared to males (17 to 56 mm length), whereas the sex ratio slightly favoured males 1:0.7.

Two kind of scavenger aggregations were distinguished: One category consisting of a slow responding community (10 to 24 h) with high numbers of amphipods (600 to 800 Ind. 0.7m⁻²) and low consumption rate (2600 to 3800 g d⁻¹) (Type I). A second type arrived earlier (3 to 6

h) with lower numbers of individuals (300 to 600 Ind. 0.7 m^{-2}) and high consumption rate (5000 to 5300 g d^{-1}) (Type II).

As a basic difference to other studies, the maximum number of *Eurythenes gryllus* was not only 13 times higher than those found in other studies, the individuals also appeared up to 20 times faster.

Scanning sonar data demonstrate that the amphipods swim upstream along a narrow path towards the bait. Thus, in combination with current measurements (direction and speed) and time-lapse photography this study shows that chemoreception serves for food fall localization in the scavenging amphipod *Eurythenes gryllus* over relatively large distances (tenths of metres). Further analysis of the SSS data indicates that individuals once they disappeared did not stay in close vicinity to the lander but swam away with the current. This supports the assumption that *E. gryllus* is a temporary invader instead of being a local inhabitant.

The findings of the investigations *in situ* were supported by results of respiration rate measurements in *E. gryllus* indicating an increase in oxygen consumption after exposure to food odour in laboratory experiments. *E. gryllus* was found to be adapted to the sporadic food supply by two states of metabolisms: a resting rate ($0.02 \text{ ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$) much like a state of dormancy and an active rate ($0.04 \text{ ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$) for optimal utilisation of food fall when available. Based on total lipids (6.1 % of wet weight) and metabolic rates, sustenance times have been calculated. *E. gryllus* may survive 76 days at an active level of metabolism and about 203 days in the more energy saving resting mode up to the next ingestion.

The results of this study are encourage future use of these acoustic and optical combined instruments. *Eurythenes gryllus* must be regarded as an important component of the deep-sea food web due to their feeding efficiency, their large number attracted and their role in the consumption. To get a more detailed idea of the deep-sea community it could be useful to apply this methodological approach also in other latitudes.

Zusammenfassung

Das Benthos der Tiefsee wird neben hohem hydrostatischen Druck und konstant niedriger Temperatur und Dunkelheit insbesondere durch den geringen Nahrungseintrag in Form von partikulärem organischem Kohlenstoff aus der euphotischen Zone geprägt. Verendete Tiere, die entweder aus der Wassersäule auf den Boden sinken oder selbst bodenlebend waren, stellen daher eine wichtige Komponente im Nahrungsnetz des Tiefseebenthos dar. In Konkurrenz zu anderen stellt das Aufspüren und Finden dieser lokal begrenzten "food falls" besondere Anforderungen an Rezeptorsysteme, Mobilität und Stoffwechselphysiologie aasfressender Organismen.

Im Rahmen dieser Arbeit wurden insgesamt sechs "food fall" - Experimente von Bord des Forschungsschiffs "Polarstern" (ARK XVI/2, ARK XVII/1) in 1400 bis 2600 m Wassertiefe in der Framstrasse (Arktis) durchgeführt und ausgewertet. Im Mittelpunkt der Untersuchungen stand dabei der kosmopolitisch verbreitete, aasfressende Tiefseeamphipode *Eurythenes gryllus* (Lichtenstein 1822), von dem zu Beginn der Arbeit bekannt war, dass er im Untersuchungsgebiet vorkommt.

Ziel der Arbeit war es, erstmalig Informationen zur raum-zeitlichen Attraktion dieses Tiefseebewohners mit Hilfe ausgelegter Köder zu gewinnen, und dabei die Wahrnehmung und Lokalisierung von "food falls" über große Distanzen zu bestimmen. Darüber hinaus wurde die Aggregationsdynamik der angelockten nekrophagen Organismen untersucht und Unterschiede oder Ähnlichkeiten sowohl innerhalb des Untersuchungsgebietes als auch im Vergleich zu Untersuchungen in anderen Meeresgebieten herausgearbeitet.

Dazu wurden *in situ* - Beobachtungen mit Freifallsystemen („Ländern“) und experimentelle Untersuchungen zum Metabolismus mit gehälterten Individuen von *Eurythenes gryllus* durchgeführt. Die Länder waren mit einer beköderten Kamera, einem akustischen Strömungsmesser, einem Scanning Sonar System (SSS) sowie einer ebenfalls beköderten Reuse ausgestattet. Erstmals konnte durch die Kombination von akustischen und optischen Instrumenten an den Ländern das erfasste Areal im Vergleich zu anderen Untersuchungen um ein Vielfaches, von bislang maximal 4 m² auf 8000 m², vergrößert werden.

Die Analyse der Reusenproben ergab, dass es sich bei den insgesamt 3490 gewonnenen Individuen um nur drei Amphipodenarten (*Eurythenes gryllus*, *Tmetonyx norbiensis* und *Stegocephalus* sp.) handelt, wobei *E. gryllus* in allen sechs Experimenten am häufigsten vorkam.

Die raum-zeitliche Attraktion nekrophager Amphipoden wurde in zwei Aggregationstypen differenziert: Typ I zeichnet sich durch langsames (10-24 h) Erreichen des Maximums, verbunden mit hoher Individuenzahl (600 – 800 Ind. 0.7 m^{-2}), geringer Fraßrate (2600 – 3800 g d^{-1}) und wechselnder Strömungsrichtung (aus SSW, SE, NNE) aus. Typ II dagegen wird durch ein schnelles (3 - 6 Stunden) Erreichen der maximalen Anzahl der Aasfresser am Köder mit verhältnismäßig geringer Individuenzahl (300 – 600 Ind. 0.7 m^{-2}), großer Fraßrate (5000 – 5300 g d^{-1}) und konstanter Strömungsrichtung (aus NNW) an vier Stationen charakterisiert.

Das Geschlechterverhältnis der Art *Eurythenes gryllus* verhielt sich von Männchen zu Weibchen 1:0.7, wobei die Weibchen (Größenbereich von 16 – 75 mm) größer waren als die Männchen (17- 56 mm). Die in der Framstrasse gefangenen Organismen erreichen damit bei weitem nicht die Maximallängen, die in anderen Untersuchungen in niederen Breiten nachgewiesen wurden. Ähnliche Größen wurden nur noch in Auftriebsgebieten gefunden. Es wurden keine eitragenden Weibchen bei *E. gryllus* festgestellt.

Ein auffälliges Ergebnis dieser Arbeit ist, dass *Eurythenes gryllus* im Untersuchungsgebiet durch ausgelegte Köder zahlenmäßig viel häufiger angelockt wird, als in vergleichbaren Studien anderer Breitengrade (Individuenzahlen um bis zu 20-fach höher).

Die sonar-gestützten Ergebnisse zeigen, dass Chemorezeption ein wichtiges Element in der Lokalisierung der Nahrungsquelle über größere Distanzen sein muss. Es wurde nachgewiesen, dass *Eurythenes gryllus* in Gruppen erscheint und die letzten Dutzend Meter auf einem schmalen Pfad gegen die Strömung in Richtung Köder schwimmt. Durch die Auswertung von 1430 Zeitrafferfotografien konnte belegt werden, dass es sich bei den vom SSS erfassten Objekten tatsächlich um *E. gryllus* oder andere vagile Organismen handelt. Dabei wurde eine signifikante zeitliche Korrelation zwischen den kameragestützten und SSS auf basierenden Daten festgestellt.

Die *in situ* verzeichnet chemorezeptive Wahrnehmung eines "food falls" wurde durch Ergebnisse experimenteller Untersuchungen zum Metabolismus der Aasfresser unterstützt. Dazu wurden Individuen von *Eurythenes gryllus* über mehrere Monate gehältert und Sauerstoffverbrauchsmessungen unter kontrollierten Bedingungen im Kühlabor durchgeführt. Es wurde gezeigt, dass *E. gryllus* zwei Aktivitätszustände einnehmen kann, die als Anpassung an den sporadischen Nahrungseintrag in die Tiefsee interpretiert werden können: Ohne Zugabe von Beuteduftstoffen befinden sich die Amphipoden in einer Phase, die als "Ruhezustand" interpretiert wurde. Dabei wird der Sauerstoffverbrauch im Vergleich zum aktiven Zustand bis um die Hälfte reduziert ($0.019 \text{ ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$). Nach Zugabe von Beuteduftstoff fangen die sonst ruhenden Organismen an aufzuschwimmen und gehen in

eine "aktive" Phase des Metabolismus über, bei der ein erhöhter Sauerstoffverbrauch ($0.04 \text{ ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$) gemessen wurde. Die in diesem Zusammenhang ebenfalls durchgeführten Lipidanalysen zeigen, dass *E. gryllus* bei einem totalen Lipidgehalt von 6.1 % in der "ruhenden" Phase durchschnittlich bis zu 203 Tage sowie in der aktiven Phase bis zu 76 Tage hungern und auf der Basis seiner Lipidspeicher bis zur nächsten Nahrungsaufnahme überdauern kann.

Die methodischen Ansätze dieser Arbeit erweist sich als sehr geeignet hinsichtlich der zukünftigen Nutzung von akustisch und optisch kombinierten Instrumenten. Die Ergebnisse zeigen, dass *Eurythenes gryllus* aufgrund seiner Effizienz der Nahrungsverwertung sowie seiner hohen Abundanz an "food falls" eine wichtige Rolle im Nahrungsnetz der arktischen Tiefsee spielt. Untersuchungen in anderen Breitengraden, unter besonderer Berücksichtigung der Schwerpunkte dieser Arbeit und mit dem gleichen methodischen Ansätzen, könnten die Schlussfolgerungen dieser Arbeit hinsichtlich nekrophager Tiefseegemeinschaften erweitern.

1. Introduction

The deep-sea biosphere is an extensive and voluminous environment that includes the ocean floor and the water column from the continental slope to the abyssal plains 80 % of this region are deeper than 1000 m (Figure 1; Tardent 1993). The abyss of the ocean is one of the least understood segments of Earth's biosphere, particularly in relation to life strategies and functional adaptation of the biota (Gage and Tyler 1991). For a long time the seafloor of the deep sea was considered as a monotonous, desert like environment colonized by only few organisms because of the harsh environmental

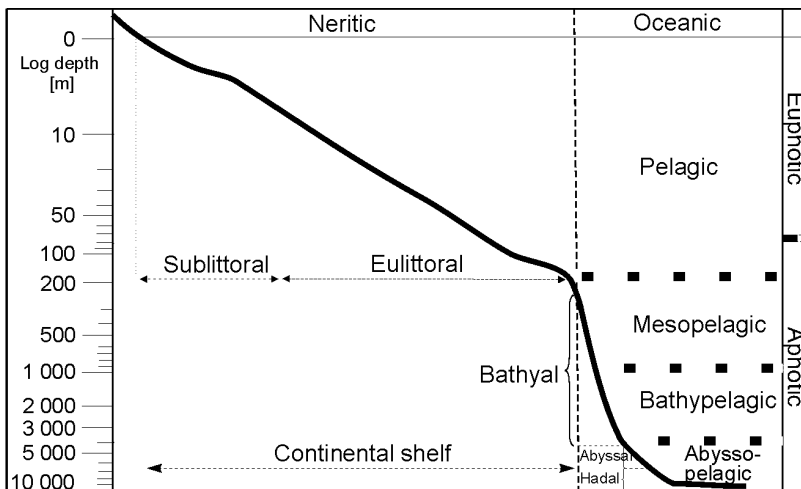


Figure 1: Ecological classification of marine depth zones (acc. to Tardent 1993, and others).

conditions such as low temperature, high hydrostatic pressure, absence of light, and limited food supply (Dayton and Hessler 1972). Results of the first exploratory deep-sea expeditions which started in the middle of the 19th

century already led to a shift in the understanding of the deep-sea communities since invertebrates and fish were caught even at the greatest depths sampled. During the second half of the last century, employments of deep-diving submersibles, remotely operated vehicles, lander systems and moorings led to further advances in the understanding of the deep-sea ecosystem. Formerly believed to be remote, strongly decoupled from processes in the upper water column like, for example, primary and secondary production in the euphotic zone, thus sluggish in its reaction we know today that the deep-sea benthos is often coupled to primary production by fast sinking phytodetritus ('marine snow') and may receive quite large amounts of even relatively fresh organic material through this kind of aggregated phytoplankton (Thiel et al. 1989, Pfannkuche et al. 1999). Primary production is the major food and energy source for marine benthic organisms. Because of the utilisation and transformation of this matter during its passage through the water column, only a part of the primarily produced matter reaches the deep-sea floor (Figure 2 b; Murray 1998), ranging for different regions of the world ocean between 1 to 3 % of the total primary production within the

euphotic zone (Klages et al. 2003). Time-lapse camera experiments in different regions of the world ocean demonstrated that the deep-sea benthic community may respond quite fast to this kind of food supply (Rice et al. 1994). Such phytodetrital material is rapidly colonised by Bacteria and Protozoa (flagellates and foraminifers), while large deposit feeding animals ingest it (Gooday and Turley 1990). Furthermore, modern sampling and *in situ* labelling techniques allowed to study the response of Bacteria and meiofauna organisms to fresh food supply indicating quite fast reaction (Soltwedel and Schewe 1998, Schewe 2002, Witte et al. 2003).

Nonetheless, one of the most important limiting factors in deep-sea ecology seems to be food availability. All production in the deep sea is fuelled either indirectly or directly by the import of organic matter to the seafloor, and the major part is derived from carbon production by photosynthesis in the euphotic zone (Figure 2; Rowe and Staresinic 1976). This dependency on organic import determines the allochthonous nature of the deep-sea ecosystem. Other quite important contributions to the energy supply into the deep sea are food falls. These include the bodies of large vertebrates such as marine mammals and fish, and large energy rich invertebrates such as cephalopods and crustaceans. Already in an article almost fifty years ago the importance of sinking whale and shark remains as a food source was suggested (Bruun 1957). The first direct evidence was reported by Isaacs and Schwartzlose (1975) using dead fish as bait anchored at the seafloor and observed by a camera showing the fast response of the large mobile deep-sea scavenger community to carcasses. During the last decade carcasses of medium and large sized invertebrates and vertebrates were found to serve as spot like food supply for the deep-sea benthos of yet unknown quantity (Smith et al. 1989, Britton and Morton 1994, Klages et al. 2001).

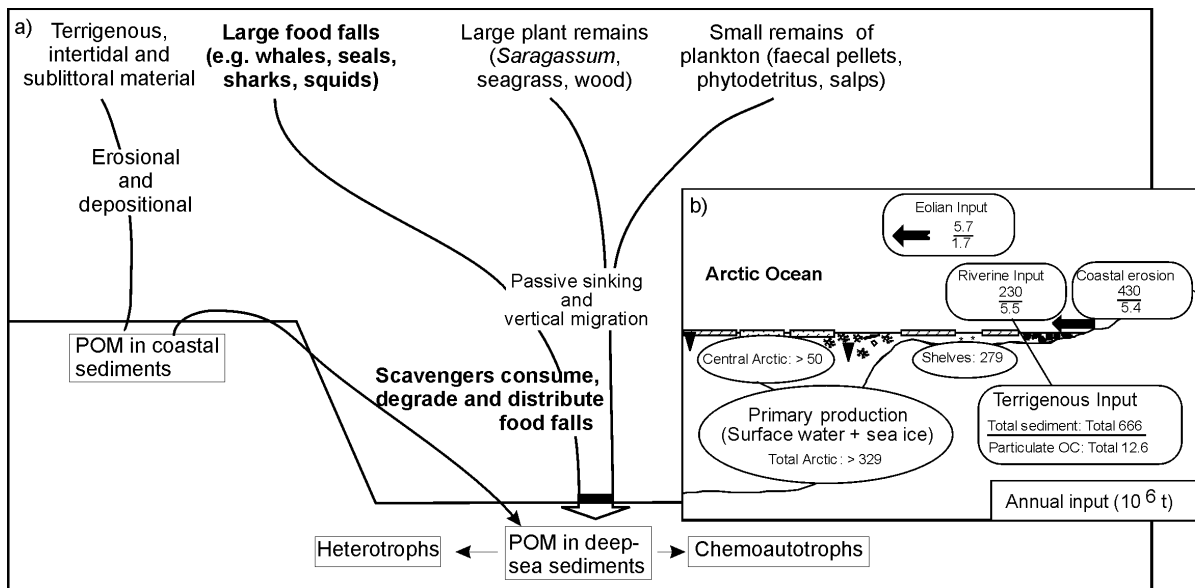


Figure 2: a) Conceptual model of the potential sources, transport, sinks and utilisation for organic matter in the deep sea. POM: Particular organic matter (slightly modified from Rowe and Staresinic 1976). b) Modern total sediment and terrigenous and marine organic carbon input in the Arctic Ocean (10^6 t y^{-1}) (from Stein and Macdonald 2003; based on Rachold et al. 2003 and Sakshaug 2003).

Because of the difficulties in assessing the quantity of carcasses reaching the seafloor during a given period their role for the transfer of organic matter into the deep-sea benthos is still under discussion. Smith et al. (1989, and references cited therein) discussed the migratory routes of grey whales (*Eschrichtius robustus*) along the west coast of North America and concluded that the random distribution of whale carcasses due to natural mortality would lead to an average distance between nearest neighbours of about 9 km only. This kind of calculation caused the speculation whether or not whale carcasses in the deep-sea may serve as stepping stones for organisms depending upon such form of organic material (Butman et al. 1994). In another study Smith (1985) calculated contrarily that large nekton falls (weighing between 2 and 40 kg) contribute only about 4 % of the energy needs of the scavenging ophiuroid *Ophiophthalmus normani* in the Santa Catalina Basin at about 1300 m water depth. The discrepancy and the problem of such calculations is that they are mostly based on remains detected along video surveys. As the highly motile scavenger community detects and consumes such food parcels fast, the probability to detect ongoing feeding processes or remains is low (Klages et al. 2001, publication IV). In a recent study Soltwedel et al. (2003a) reported their results obtained along a video survey with a towed video and still camera system. Along the transect covering an area of about 10 000 m² of seafloor at water depths between 1250 and 5600 m only a single fish skeleton was found. In contrast to this low number of small sized carcasses more large food falls were reported in the literature (Naganuma et al. 1996, Deming et al. 1997,

Smith et al. 1998). Still, the general rarity of observed remains of natural food falls on underwater photographs suggests that this kind of energy transfer into the deep sea is seldom (Stockton and DeLaca 1982). However, own observations carried out with baited time-lapse cameras demonstrated that the mobile deep-sea scavenger community at the locations sampled in the Fram Strait responds so fast to the deployed bait that, in case of natural events, the probability to detect them by means of manned or unmanned submersibles may decrease very soon after a carcass reaches the seabed.

A tendency of scavengers to occur in higher numbers in more productive waters was observed in the North Pacific and the Atlantic Ocean. Along a transect extending from eutrophic waters of California to the central North Pacific, higher catch rates in productive waters at the western boundary of the California Current compared to the oligotrophic open Pacific were found (Smith and Baldwin 1984). A similar pattern has been reported from the eastern North Atlantic, comparing the temperate West European Basin with the subtropical Madeira abyssal plain where the deep-sea receives less organic input. Also, in the deep western Arabian Sea amphipods were rare, being completely absent at 1900 m and occurring in low numbers only at 4040 m depth (Witte 1999). Generally, in the above mentioned areas scavenger abundances were much lower than in polar regions (Thurston 1979, Smith and Baldwin 1984, Charmasson and Camlet 1987, Janssen et al. 2000). Despite the strong seasonality in surface primary production, deep-sea areas in the Arctic and Antarctic impress by their richness in terms of scavenger abundance and biomass, compared to other regions like the central Pacific Ocean, the Arabian Sea or the North Atlantic (e.g. Presler 1986).

Many genera of lysianassoid amphipods (Figure 3) are marine cold-water scavengers some of whom contribute significantly to the species number of the Antarctic and Arctic benthos. Lysianassoids, forming the largest amphipod family with > 500 species in 112 genera world wide (Barnard and Karaman 1991), are one

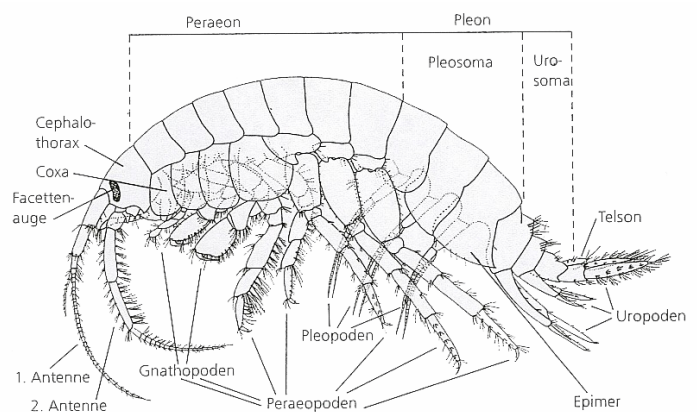


Figure 3: Lateral view of a typical Gammaridae (Amphipoda). Slightly modified after Westheide and Rieger (1996).

of the most abundant and widespread macro-invertebrate scavenger group in the World Ocean (Slattery and Oliver 1986). For an understanding of the function of deep-sea scavenging communities and ecosystems and their sensitivity to influences of the

food input as well as environmental and anthropogenic changes, we need to understand their energy flow patterns and trophic connections.

The Arctic scavenging amphipod community may be an important energy mediator from carcasses to other organisms of all trophic levels. Therefore, this study aims answering questions related especially to *Eurythenes gryllus* as a main scavenging consumer in the deep-sea ecosystem. It will concentrate on their food finding strategy, their aggregation dynamics at food falls, and their metabolic strategy in the food limited environment of the deep sea.

1.1. Biology of scavenging crustaceans of the deep sea

Mobile deep-sea scavengers such as the cosmopolitan amphipod *Eurythenes gryllus* (Lichtenstein 1822) are considered as an important component of the deep-sea food web. Both, the high number in which they are usually caught with baited traps and their remarkable food consumption rates suggest a significant role in the benthic food web (Hargrave 1985, Christiansen 1996, Witte 1999). However, there are still considerable gaps in our understanding of consumption, degradation and distribution of organic matter by scavenging crustaceans in the deep ocean (Isaacs 1969, Dayton and Hessler 1972, Haedrich and Rowe 1976).

Table 1: Data of respiration rate ($\text{ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$) and lipid content (% total WW) of benthic scavenging amphipods in comparison in bathyal, abyssal and shallow water.

| Species | Respiration [ml O ₂ g ⁻¹ WW h ⁻¹] | Lipid [% total, WW] | Location | Reference |
|------------------------------|--|------------------------|-------------------------|-----------------------------|
| Bathyal & abyssal | | | | |
| <i>Eurythenes gryllus</i> | - | 2.1 | NE Atlantic | Bühring & Christiansen 2001 |
| <i>Eurythenes gryllus</i> | - | 2.6 | Antarctic Ocean | Clarke 1984 |
| <i>Eurythenes gryllus</i> | 0.06 | - | Arctic Ocean | George 1979 |
| <i>Eurythenes gryllus</i> | 0.08 - 0.10 | - | Antarctic Ocean | Opalinski & Jazdzewski 1978 |
| <i>Eurythenes gryllus</i> | 0.004 - 0.07 | 6.8 | Arctic Ocean | Premke & Graeve submitted |
| <i>Eurythenes gryllus</i> | - | 4.8 | Central N Pacific Ocean | Smith & Baldwin 1982 |
| <i>Eurythenes gryllus</i> | 0.025 | - | Antarctic Ocean | Takeuchi & Watanabe 1998 |
| <i>Orchomene sp.</i> | 0.21 - 0.98 | 2.5 | Santa Catalina Basin | Smith & Baldwin 1982 |
| <i>Paralicella caperesca</i> | - | 3.7 | NE Atlantic | Bühring & Christiansen 2001 |
| <i>Paralicella caperesca</i> | 0.02 - 0.66 | 1.9 | NW Atlantic | Smith & Baldwin 1982 |
| Shallow water | | | | |
| <i>Abyssorchomene plebs</i> | 0.056 | - | Antarctic Ocean | Rakusa-Suszczewski 1990 |
| <i>Anonyx nugax</i> | 0.03 - 0.12 | - | Arctic Ocean | George 1979 |
| <i>Anonyx nugax</i> | - | 5.0 - 6.9 | Arctic Ocean | Percy & Fife 1981 |
| <i>Anonyx sarsi</i> | - | 3.7 | Atlantic Ocean | Sainte-Marie 1986 |
| <i>Orchomene sp.</i> | - | 3.5 | Antarctic Ocean | Kolakowska 1987 |
| <i>Paramoera walkeri</i> | 0.03 - 0.06 | - | Antarctic Ocean | Opalinski 1974 |
| <i>Waldeckia obesa</i> | 0.009 | - | Antarctic Ocean | Chapell & Peck 1995 |

From an evolutionary point of view, crustaceans represent a successful group of invertebrates that show strikingly wide adaptive radiation in the aquatic environment, as

insects do in the terrestrial realm (George 1979, Hay et al. 1987, Duffy and Hay 1991). The systematic branch of the Malacostraca, for example, includes with the Peracarida and the Eucarida two important suborders. In both polar oceans and in the deep sea peracarids are the most successful crustaceans in terms of their species number, which outnumbers decapods, for example, by far in the Arctic and Antarctic (Maxwell 1977, Arntz et al. 1997). Among the peracarids the amphipod superfamily Lysianassoidea is a typical cold-water group which separated during its evolution into many species (Barnard and Karaman 1991). Many of them, especially the polar and deep-sea inhabitants, adapted to a scavenging mode of life attending food falls in high individual numbers. Lysianassoid amphipods like the cosmopolitan *Eurythenes gryllus* are characterised by morphological, anatomical and physiological adaptations linked to their scavenging mode of life (Dahl 1979, Smith and Baldwin 1982). When a carcass has been localized by them they start to feed to satiation increasing their body size by three to five times (Figure 4; Shulenberg and Hessler 1974, Dahl 1979). In contrast to *Eurythenes gryllus* other scavengers such as species of the genus *Orchomene* and other closely related genera are less efficient and more generalist feeders (Sainte-Marie 1984, Sainte-Marie et al. 1989). On the basis of morphological and physiological criteria these two types of deep-sea lysianassoids were divided into two functional groups by Sainte-Marie (1992). Individuals of the first group (*E. gryllus*) are supposed

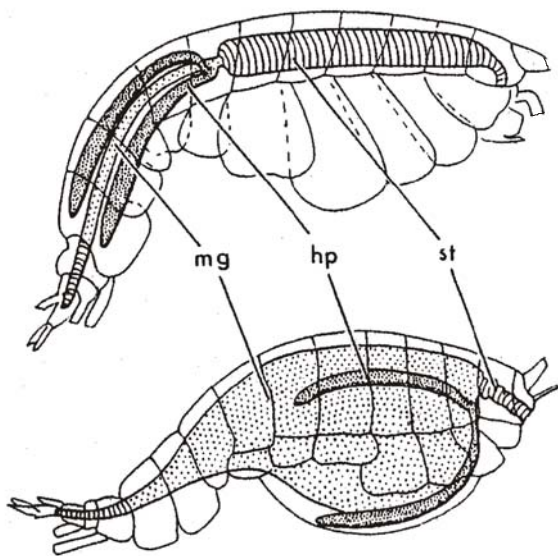


Figure 4: Diagrammatic sketch of modification of the intestinal tract for food storage in lysianassoid amphipods. Above stomodaeal storage in *Orchomene*, below extrem magnification of midgut storage in *Eurythenes*, *Parallicella* and *Hirondellea*. mg-midgut, hp-hepatopancreatic caeca. st-stomodaeum (slightly modified from Dahl 1979).

to have low metabolic rates, they have shearing mandibles (a broad, shearing incisor with a large *corpus mandibulae*) and guts modified to keep large amounts of food (Figure 4; Shulenberg and Hessler 1974, Dahl 1979). These characters help them to survive even long periods without feeding (Dahl 1979, Thurston 1979). Individuals of the second group (*Orchomene*) are assumed to have higher metabolic rates (Table 1), mandibles which do not appear to be suited for the rapid ingestion of bait (a blunt

incisor, a narrow, flat *corpus mandibulae* and a triturative molar), and rather small guts. They process food in a more or less continuous way as small and ground bites and may sustain only short periods of starvation (Dahl 1979, Thurston 1979, Sainte-Marie 1984). In order to sustain starvation periods energy reserves are converted in lysianassoids from ingested food into lipid storage products (Wirsen and Jannasch 1983). *Eurythenes gryllus* stores lipid in the hepatopancreas and, for reproduction purposes, in the gonads (Bohé-Lafrique 1985). Principally, lipids are present in lysianassoids as phospholipids (structural lipids) and triglycerids (stock lipids), but free fatty acids, lower glyceride and small quantities of glycogen were also identified (Yayanos et al. 1978, Kolakowska 1987, Sainte-Marie 1992).

The largest individual of *Eurythenes gryllus* being caught had a length of 140 mm (Ingram and Hessler 1987). According to literature data and own unpublished visual observations made with a Remotely Operated Vehicle in the Fram Strait this species is a good swimmer and a mean swimming speed of 7 cm sec^{-1} was calculated by Laver et al. (1985). The wide vertical range of occurrence in this species which has been collected between 0 and 7800 m indicates extraordinary barotolerance (Figure 5; Ingram and Hessler 1983, Desbruyères et al. 1985, Thurston et al. 2002). Concerning its temperature tolerance *E. gryllus* must be considered as stenotherm. Thus, as long as water temperature is kept below 4°C it can be retrieved and decompressed from

deeper water layers.

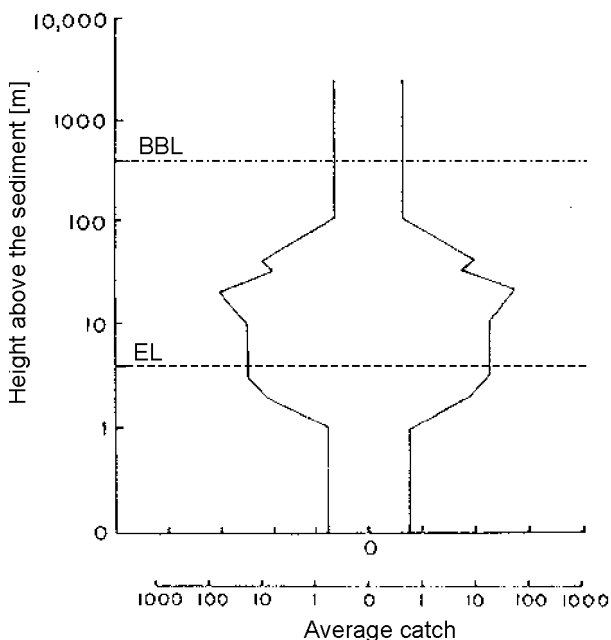


Figure 5: Vertical distribution of *Eurythenes gryllus*. The average catch with height (m) above the sediment for *E. gryllus*, plotted on a log10 scale. 1800 m is the largest distance above sediment traps have been set.

----- Benthic boundary layer (BBL, 400 m),
 ----- Ekman layer (EL, 4 m). Slightly modified from Ingram & Hessler 1983.

The ontogenetic migration postulated for *Eurythenes gryllus* by Christiansen et al. (1990) seems to be quite complex. With increasing size, immature *E. gryllus* move up into the water column adopting to an abysso-pelagic mode of life rather than a benthic mode of existence (Ingram and Hessler 1983, Smith and Baldwin 1984, Charmasson and Camlet 1987,

Christiansen et al. 1990). However, based on the few and spot like experiments and measurements carried out on *E. gryllus* the entire life cycle of this species remains still poorly understood.

Brooding females, which are believed to have multiple broods, have never been captured with baited traps, presumably because they are not actively foraging for food while their marsupium (the brood pouch) is either filled with fertilised eggs or juveniles. Two reasons are most likely for their absence at food falls: (i) an increase in stomach volume would cause a loss of the brood and (ii) cannibalism might be of a certain risk at sites where high numbers of scavengers are concentrated.

The eyes of *Eurythenes gryllus* are of normal size but lacking dark pigments. The tapetum appears to be well developed, enabling the eye to receive even low light intensities, generated, for example, by bioluminescent organisms in the deep sea (Bowman and Manning 1972).

Various structures have been identified as possible sites for chemo- or mechanoreception in amphipods, and specifically in the Lysianassoidea: a bundle of setae on the antennular flagellum (i.e., the callynophore) which are presumably chemoreceptors (Dahl 1979, Lowry 1986), and the antennal calceoli which may be chemoreceptors (Dahl et al. 1970) or mechanoreceptors (Lincoln and Hurley 1981). Also some lysianassoids possess cuticular sensilla of various types which may be both types of receptors as well (Mauchline and Ballatyne 1975).

In summing up this brief overview on the biology of *Eurythenes gryllus* and some other lysianassoids, together with the peculiarities of their environment some of the basic assumptions published by Smith and Baldwin (1982) concerning the demands of scavengers are considered particularly important for the understanding of my thesis:

- (i) the deep-sea environment is food-energy limited,
- (ii) large organic food falls represent the prime source of food for scavengers,
- (iii) the occurrence of food falls is aperiodic and unpredictable.

The most important adaptations to thrive under these conditions are:

- (i) fast detection and localisation of any potential food fall,
- (ii) consumption within short periods of time of large quantities of food and their storage for gradual utilisation during a long time interval and,
- (iii) keeping the metabolism at a low rate until the next event.

1.2. Location of food

In a food-limited environment the impact of any food fall is, as outlined above, unpredictable both in space and in time for benthic or benthic-pelagic scavengers. Therefore, there is a strong need for scavenging amphipods to have suitable receptors for the localisation of potential food sources. In principal, three different kinds of receptor systems may enable them to realise food falls: (i) mechanoreceptors (Dahl 1979), (ii) chemoreceptors (Smith and Baldwin 1984) and (iii) photoreceptors (Hallberg et al. 1980).

Because of some fundamental physical laws all three possible senses are suitable for different spatial ranges of detection. Depending on intensity and frequency acoustic signals reach long distances of hundreds or even thousands of metres, whereas chemical solutes being transported by currents and diffusion processes reach medium distances and light only some metres.

In order to detect sound, animals require at least one kind of receptor transducing the forces of particle motion or pressure changes into neural signals (Hopp et al. 1998). Hydroacoustic stimuli have a long range penetration. These stimuli will either arise when a food fall hits the sea floor (Klages et al. 2002) or during food consumption of scavengers producing feeding noises (Smith and Baldwin 1984). At a first glance it might be assumed that detection and localisation of food by mechanoreception implies no preferential direction of arriving individuals at the carcass because of the omnidirectional propagation of sound in water. But actually there is little information whether or not scavenging crustaceans possess any mechanoreceptor enabling them to identify the direction from where the sound originated. Therefore, it might be possible that mechanoreception is one, probably the first, step in a cascading process followed by chemoreception.

Chemoreception is another, well studied mechanism in crustaceans (Atema 1986, van Leeuwen and Maly 1991, Yen et al. 1996) to realize potential food sources via perceiving food odour of carcasses transported by bottom currents. Due to their size and ability to track odour cues from potential prey, lobsters, for example, have been used as model organisms in laboratory experiments to study principles in their chemosensory orientation (Derby and Atema 1982, Carr 1988, Weissburg 1997, Atema 1998). Because of the nature of odour dispersal it is commonly accepted that local fluid conditions determine to a certain extent the dispersal of odour molecules in the environment giving organisms a chance to track the food odour towards the source (Vickers 2000).

Detection but at least localisation of food by chemoreception would imply a distinct direction of arrival to bait against the current. In turbulent odour plumes, typical orientation manoeuvres consist of slow upstream walking.

There are several reports in the literature that deep-sea scavenging amphipods appeared at the bait between 10 to 30 minutes after deployment (Hessler et al. 1978, Lampitt et al. 1983, Jones et al. 1998, Janssen et al. 2000). Already the first of these reports supported the assumption that chemoreception must be involved in scavenging amphipods tracking bait exposed at the seafloor. Odour emanating from food falls may also contain some information about the quality (perhaps even about the quantity) of a potential food source (Ritschoff 1980, Zimmer-Faust and Case 1982). As the odour concentration decreases with distance from the source the animals follow a gradient in concentration which indicates the distance to the source (Moore and Atema 1988, Moore et al. 1991). Whether or not this kind of information is used by scavengers to decide after a given period of unsuccessful search to abort further energy expenditure in food finding is difficult to assess. However, in another publication Smith and Baldwin (1982) reported about their findings in an *in situ* study where single individuals of deep-sea scavengers exposed to food odour in a respiration chamber switched at a certain period after capture from high metabolic activity to very low respiration rates. This was explained by the authors as going back into a dormancy state to save energy for the next food fall event since in the actual one they did not succeed to localise it.

With the exception of bioluminescence there is no light in the deep sea. Nonetheless, many deep-sea invertebrates and fish do have eyes, even those which do not enter the pelagic realm. There are some indications that bioluminescent organisms (Bacteria) also attend food falls which might serve as additional information for animals such as *Eurythenes gryllus*. Actually there is no information in the literature that photoreception might be involved in the food finding strategy of scavenging deep-sea organisms. However, this aspect will be raised again in the discussion of this thesis.

1.3. Aims of this study

The intention of the present study was basically to determine the spatio-temporal attraction of the cosmopolitan deep-sea scavenging amphipod *Eurythenes gryllus* by bait at a polar deep-sea location. In a broader context the results are assumed to contribute to answer the question why there are so many species in the deep sea. Especially the sediment-inhabiting fauna was found during the past decades to be highly diverse, e.g. many more individuals and species than formerly assumed were

found in quantitative sediment samples. The activity of infaunal organisms such as Bacteria, nematodes, polychaetes and crustaceans is relevant for transformation and exchange processes of organic and other matter at the sediment-water interface. However, there are still gaps in our understanding about the factors promoting high biodiversity in the deep sea.

Patches of organic carbon deposited at the seafloor have a direct influence on the activity, biomass and species composition of the sediment fauna. Reasons for this kind of patchiness in carbon deposition are manifold. Dead marine organisms sinking into the benthos are of course one example for patchy food supply. Such kind of gradual difference in organic carbon supply should govern differences in the structure and activity of the sediment community. Regarding motile scavengers as one component of the variety of organisms structuring the sediment surface, baited time-lapse camera experiments are a good measure because they simulate naturally occurring situations under controlled conditions.

The major aims of this thesis are:

- (i) To clarify the question, how does the abundant deep-sea amphipod *Eurythenes gryllus* localise food falls over medium to long distances (tenths to hundreds of metres), or in other words, is there an omnidirectional or directional pattern in approach discernible?
- (ii) To assess the aggregation dynamics of this deep-sea scavenger (and possibly other abundant species at large food falls), its population structure, density and distribution patterns (temporal and spatial).
- (iii) To investigate the role of the scavenging amphipod *Eurythenes gryllus* in the Arctic deep-sea in summer discussing the similarities and differences to other latitudes.
- (iv) To determine the energy budget of *Eurythenes gryllus* relating to the scarce and unpredictable impact of food in space and time, and to assess the duration of a potential starvation phase.

2. Material and Methods

The first section of this chapter gives a brief synopsis of the study area. The second part summarises how the scavenging amphipods were sampled and processed. Figure 6 serves as an overview of the methods used, but more comprehensive descriptions of the methods applied are given in the various publications of this thesis, and are therefore only shortly outlined herein with reference to the respective publications.

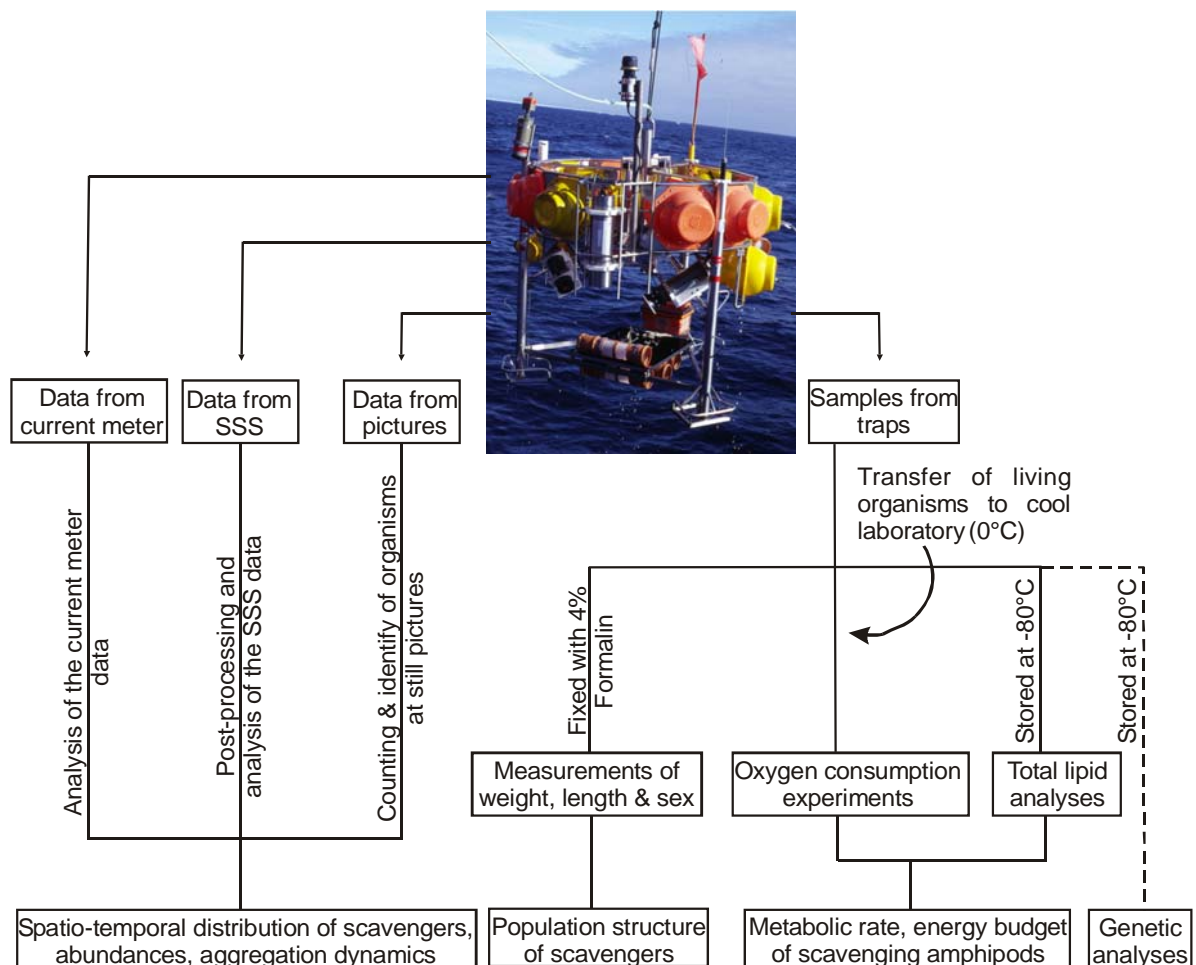


Figure 6: Summary of the sample treatment for the different studies. All samples taken by a tripod lander (picture). Details are given in the 'Material and Methods' chapter of each publication. SSS: Scanning Sonar System.

2.1. Study area

The field studies presented here were carried out in the Fram Strait (Arctic Ocean) during Nordic summer seasons 2000 and 2001. The main sampling area was in the vicinity of the deep-sea long-term observatory ("Hausgarten") of the Alfred Wegener Institute for Polar and

Marine Research west of Svalbard at about 79°04' N, 04°19' E (2600 m water depth; Figure 7).

The Fram Strait is the only deep connection between the North Atlantic and the Arctic Ocean and plays a significant role for global water mass exchange. The various topographic structures of the Fram Strait lead to a splitting of the warm and nutrient-rich West Spitsbergen Current, carrying Atlantic water northward, spreading into at least three branches. Basically, one part enters the Arctic Ocean north of Svalbard (33 %), a second branch flows northward along the northwestern slope of the Yermak Plateau (45 %), and the third part (22 %), which for our experiments is the most relevant, recirculates immediately into the Fram Strait at about 79° N (Manley 1995, Rudels et al. 2000). This region is characterised by strong annual fluctuations in ice-coverage, whereas the eastern part of the Fram Strait is generally ice free during the summer months (Rudels et al. 2000). Furthermore, the Fram Strait exhibits a complex topography which has an influence on the mesoscale current regime. A number of eddies were measured over the past years in our area of investigation some of which are circulating in opposite direction to others close by (Schauer et al. submitted).

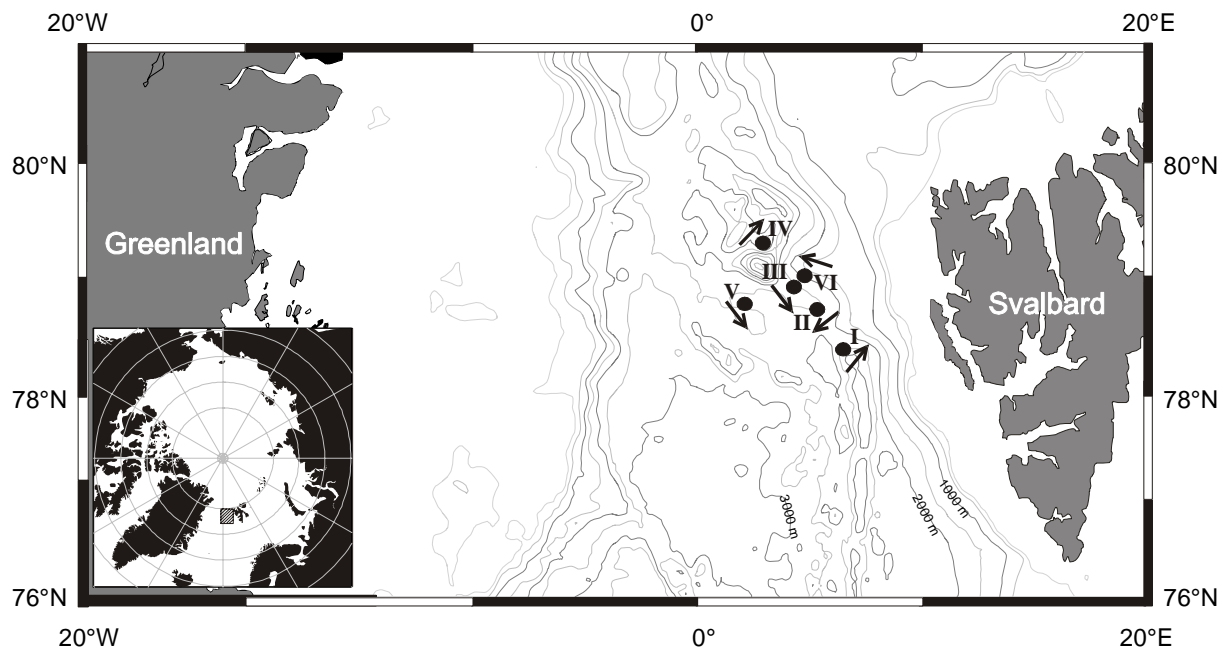


Figure 7: Locations of stations I to VI in the Fram Strait, Arctic Ocean. Arrows indicates the main bottom current direction during 1997 to 2002 (Schauer et al. submitted, Premke et al. 2003).

2.2. Sampling

Aiming at a better understanding of the spatio-temporal attraction of scavenging amphipods in the deep sea by bait a total of six *in situ* experiments were carried out during two Arctic expeditions of the German RV "Polarstern" in summer 2000 and 2001 (for details see the respective cruise reports; Krause and Schauer 2001, Fahrbach 2002). All stations were situated in the Fram Strait, Arctic Ocean (Figure 7), at nearly the same water depth of about 2500 m (Table 2). Main platform for a variety of instruments was a tripod lander (see Figure 6) equipped with a baited time-lapse camera (model Simrad Mesotech Photosea 5000), a Photosea 1500SX flash, a Simrad Mesotech MS1000 scanning sonar system (SSS) adapted to an autonomous mode of operation, an acoustic doppler current profiler (Anderaa Instruments RCM11), traps, glass spheres for buoyancy and ballast weight. Two acoustic releasers allowed for calling the system back to surface after deployment periods lasting between 17.5 and 29.5 hours.

The camera view was centred on bait exposed on a grid which was attached to the lander about 15 cm above the seafloor covering an area of 0.7 m². Pictures (Kodak Ektachrome

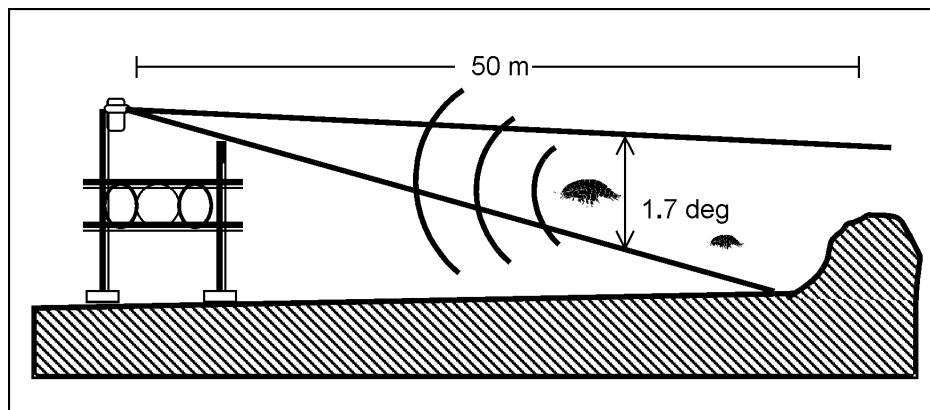


Figure 8: Schematically drawn of the scanning sonar system fixed on the bottom lander. Scattering objects were detected in the horizontal plane of the acoustical 'pencil beam' at distances of ≥ 50 m.

200, 35 mm x 35 mm x 30 m) were taken at 3 minutes intervals. The SSS (consisting of a sonar head ('Simrad' 1071 Series) working at 675 KHz rotating in a horizontal plane at pre-set steps and speed

was configured to detect scattering objects in the plane of an acoustical 'pencil beam' rotation at distances of ≥ 50 m (Figure 8). As no calibration of the backscatter characteristics of the main amphipod species recorded in the experiments was possible the visual observation made by the time-lapse camera was used instead for correlation between recorded backscatter energy and amphipod abundance on single pictures.

Table 2: Deployment data: station number, geographic positions, depth, total time of deployment and current speed.

| Station | Geographic positions | Depth [m] | Total time of deployment | Current speed [cm sec ⁻¹] |
|---------|----------------------|-----------|--------------------------|---------------------------------------|
| I | 78°30' N, 06°36' E | 2644 | 25.5 h | 1.5-8.2 (5.8) |
| II | 78°50' N, 05°52' E | 2524 | 17.5 h | 4.3-6.4 (4.8) |
| III | 79°04' N, 04°19' E | 2377 | 19.5 h | 5.3-8.9 (7.6) |
| IV | 79°21' N, 02°59' E | 1468 | 24.8 h | 0.8-8.3 (4) |
| V | 78°50' N, 02°42' E | 2504 | 28.5 h | 1.7-7.6 (4.6) |
| VI | 79°06' N, 04°19' E | 2341 | 30.5 h | 2.8-13.5 (7.9) |

2.3. Sample treatment

Five different methods were applied for the treatment of samples and materials:

Food falls in the Arctic Ocean

Food falls in the deep sea are rare and difficult to find. Rapid utilisation of the bait might partly explain the extreme rarity of such events. Publication IV describes the first observation of a fish carcass at about 1280 m water depth, west of Svalbard. Residence time of such food fall events was estimated.

Location of food

To elucidate one of the assumed mechanisms in food source localization in more detail and to provide a description of the spatio-temporal distribution of scavengers in the vicinity of the lander see technical aspects and details of scanning sonar, time-lapse camera and current data in publication I.

Aggregation dynamic studies

To investigate differences of aggregation dynamics of scavengers at large food falls, as well as the density and temporal distribution patterns within the study area on the basis of photographs, photos taken by the time-lapse camera were analysed according to species identification and temporal variability in abundance. They have been processed following the methodology described in publications I and II.

Population structure of scavenging amphipods

Organisms collected with traps attached to the lander were fixed on board in 4 % buffered formaldehyde and were later on identified to get data on the abundances and species composition of scavenging amphipod aggregations in the study area. Thus, they gave an indication whether these organisms have to be considered as temporary immigrants or members of a local population. For detailed information as species identification, determination of sex and lengths see publication II.

Laboratory metabolic rate measurements of *Eurythenes gryllus*

About 50 collected organisms were kept alive in a cooled laboratory container on board and later on at the institute for further experiments under controlled conditions. In order to measure oxygen consumption of routine metabolism rather than stress metabolism it was necessary to keep individuals for a period of several weeks in aquaria. However, mortality was high during the first days after capture. Only amphipods in good physical condition were selected for respiration measurements. For oxygen consumption aspects and lipid analyses see the 'Material and Methods' chapter of publication III.

3. General Discussion

In this section an overview of the main published and some unpublished results will be presented and discussed. Specific topics are discussed in more detail in the separate publications. The first two chapters will focus on the strategy for finding a food source in the deep sea and on the metabolism of necrophagous amphipods, while the third part concentrates on the aggregation dynamics of Arctic scavengers at food falls. Finally, some future perspectives will be pointed out.

Diversity in the deep sea

One of the most striking findings in biological oceanography of the past decades was the discovery of a much greater species diversity at deep-sea sediments than previously thought. One issue of current deep-sea research concerns the improvement of our basic understanding of the largely unknown reasons for this high diversity. Sanders (1968) introduced the stability-time hypothesis in order to explain the (at that time) unexpected high diversity of deep-sea soft bottoms. This hypothesis emphasises the role of environmental parameters in permitting diversity. The basic assumption in this theory was that high species diversity in the deep sea and in the tropics reflects long-term climatic stability (Hessler and Sanders 1967). Sanders (1979) believed benthic communities to be biologically accommodated, because the constancy of conditions gave evolution sufficient time for diversification and the development of species interactions. Basic to his view is the idea that each species must occupy an increasingly narrow, specialised niche. In other marine systems, so the argumentation of Sanders (*loc. cit.*), the communities are controlled by strongly oscillating physical conditions which do not permit a similar tendency towards high biodiversity. However, Dayton and Hessler (1972) argue that the maintenance of high species diversity in the deep sea is more a result of continued biological disturbance than of high specialised competitive niche diversification. As food falls represent an episodic, but locally significant supply of organic matter for benthic deep-sea organisms, this impact has to be considered as a natural disturbance (Dayton and Hessler 1972, Smith 1986, Soltwedel et al. 2003b). Carcasses are often localised quite fast by the motile deep-sea scavengers such as fishes, amphipods, isopods and brittle stars, which attend such food falls with hundreds and even thousands of individuals, rapidly consuming most of the organic matter (Priede et al. 1991, Jones et al. 1998, Janssen et al. 2000, Premke et al. 2003). Due to their activity these scavengers contribute to natural disturbance, by creating physical, chemical and biological gradients at relatively small scales. The resulting small-scale heterogeneity at the seafloor might contribute to the high diversity of the smallest biota inhabiting the deep-sea

floor. Only few calculations have been published on the significance and long-term effects of food falls (e.g. Smith 1986).

In this study the deep-sea amphipod *Eurythenes gryllus* was used as a key species to investigate the spatio-temporal attraction of scavenging amphipods by food falls. With this kind of studies on key species it is possible to develop models to simulate deep-sea processes. Thus, we get an improvement of our understanding of the unknown reasons for this high diversity.

3.1. Food finding strategies of the scavenging crustaceans under study

Deep-sea scavenging communities are dominated mostly by lysianassoid amphipods and large fish, both highly efficient necrophages (Smith 1985, Christiansen et al. 1990, Priede et al. 1991, Jones et al. 1998, Witte 1999). One of the most abundant scavenging amphipods attracted to food falls is the cosmopolitan lysianassoid amphipod *Eurythenes gryllus*, which accordingly might be of relevance for some biological processes associated with food fall utilisation in the deep sea.

The purpose designed lander experiments, e.g. the combined use of current meter, baited time-lapse camera and scanning sonar system (SSS) clearly demonstrated that the scavenging amphipod *Eurythenes gryllus* use chemoreception to localise the carcasses. They swim at least the last tenths of metres against the current to reach the bait. A significant temporal correlation between integrated backscattered energy (IBE) based on measurements of the scanning sonar system and amphipod individuals counted on photographs was found (Figure 9 a). The interpretation of long-range chemoreception given in this study is also supported by the current meter data indicating current direction opposite to the direction of approaching individuals (Figure 9 b).

In a food-limited environment the impact of any food fall for benthic or benthopelagic scavengers is unpredictable both in space and in time. For this reason scavenging amphipods would be expected to optimise the food finding strategy and the resource yield while limiting the risk of predation (Covich 1976). Chemoreception is the most probable method by which amphipods detect and locate food falls (e.g. Rowe et al. 1986, Sainte-Marie and Hargrave 1987, Atema 1998).

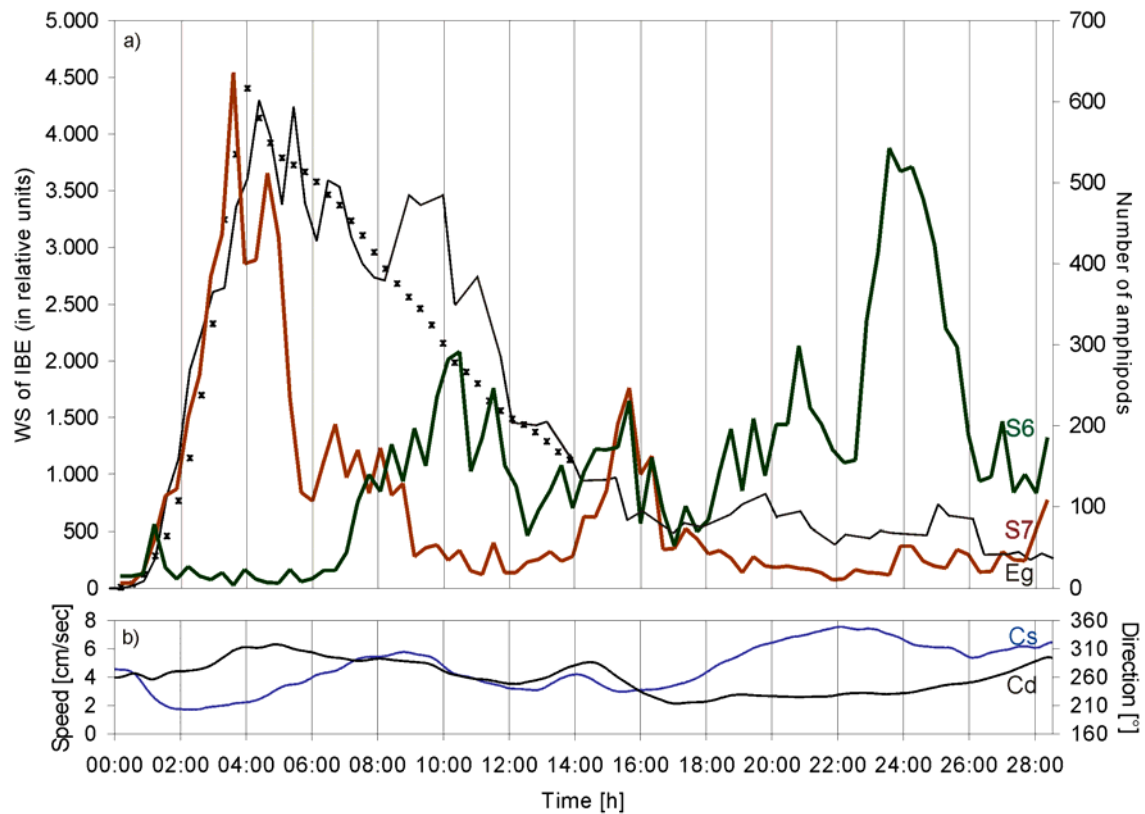


Figure 9: (a) The spatio-temporal patterns of WS of IBE together with the number of arrived amphipods vs. bottom time of experiment V. (b) Current speed and direction vs. bottom time, 2 m above the sea bottom. Abbreviations: WS, weighted sum; IBE integrated backscattered energy; S6, sector six; S7, sector seven; Eg, *Eurythenes gryllus*; Cs, current speed; Cd, current direction; cross symbols indicate cumulative sum.

Mechanoreception and photoreception may also be used by these animals, but no conclusive evidence for either of these sensory modes is available (see chapter 1.2.; Smith and Baldwin 1984, Hallberg et al. 1980, Klages et al. 2002). Mechanoreception, which was discussed by Dahl (1979) and Smith and Baldwin (1984) has recently been introduced again as another potential source of information for deep-sea scavengers (Klages et al. 2002), but more in the terms of fast long-range transmission of information about food falls, unlikely to assist in tracking the source. Given that detection and localisation of food by mechanoreception of carcass impact on the seafloor or feeding noise would imply that there is no preferential direction of arrival to bait (Wilson and Smith 1984).

Based on chemoreception as a major sense to localise the source a spiral foraging pattern would be the most energy efficient per unit-area covered, with the lowest risk of predation, compared to meandering and linear foraging patterns (Kitchell 1979). Smaller amphipods would restrict such foraging pattern closer to the sediment, while larger organisms could forage with less risk from predation further above the sediment surface and take advantage of possible vertical diffusion of chemical cues from food falls (Jumars and Gallagher 1982). In the Fram Strait there were also several eddies described by Cisewski (2001), which should

have an effect on the dispersal of the odour plumes of carcasses. The horizontal extent and the rate of dispersion of an odour trace would increase with distance from the bottom because current velocity and horizontal eddy diffusion rates normally increase from the bottom to the top of the Ekman layer. This layer benefits the amphipods in the water column in comparison to epibenthic scavengers (Ingram and Hessler 1983).

The data of SSS of approaching amphipods at station V show, that the movement of organisms was concentrated in only two sectors, namely sector six (S6) and seven (S7) (Figure 10). Focussing on S6 at about ten minutes after bait deployment, the curves in Figure 9 are still close to zero. The plot of SSS data in polar projection (Figure 11 a) indicates no

IBE at this time of deployment and, as to be expected, there were no individuals in the view field of the time-lapse camera attached to the lander. Four hours later, IBE and the number of amphipods counted on the photographs at this

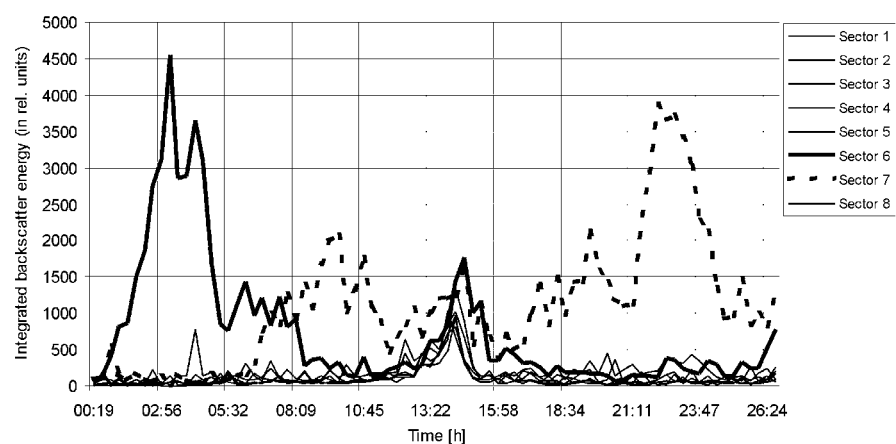


Figure 10: The spatio-temporal patterns of weighted sum of integrated backscattered energy of all eight sectors (experiment V).

time, increased compared to the beginning of the experiment. Amphipods heading towards the lander were also well seen in the polar projection of IBE data (Figure 11 b). The backscatter data also clearly demonstrate that the amphipods swim upstream along a narrow path towards the bait (Figure 9 b; Figure 11 b,c).

Scanning sonar data in combination with current measurement (direction, speed) and time-lapse photography give evidence that chemoreception must be involved in food fall localisation of the scavenging amphipod *Eurythenes gryllus*.

Further analysis of the SSS data (see sonar data at about 10 h in Figure 9 a) indicates that disappearing individuals of *Eurythenes gryllus* did not stay in close vicinity to the lander but did swim with the current at least 50 m away, e.g. further than the detection range of the sonar head. This supports the assumption that *E. gryllus* is a temporary invader instead of being a local inhabitant.

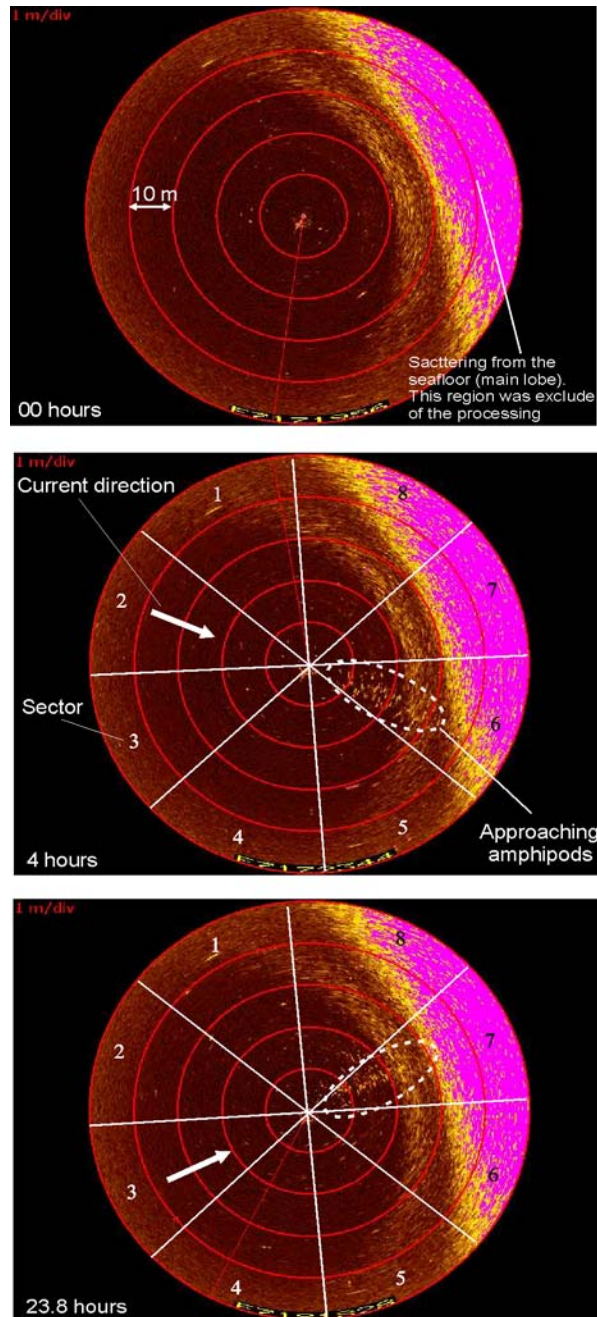


Figure 11: Temporal patterns of amphipods arrival. Sonar data plotted in polar projection at different time intervals (0, 4, 23.8 hours, at bottom time). The pink area is a persistent region of strong backscattering induced by bottom intersection. The yellow spots are signals induced by organisms.

Another rise of IBE in sector 7 between 22 and 26 h after deployment in experiment number V was not accompanied by an increase in amphipod number counted on the photographs (Figure 9 a). This could be either explained by higher current speed prevailing, with the result that individuals needed more time to cover the same distance so that the sonar system detected them more often at a given time interval. Or it could be explained by reduced amount of food which did no longer attract the later coming individual very much. In addition, Zimmer-Faust (1987) found that the ratio of amino acids and ammonia decreases with increasing carrion age and decomposition, consequently a corresponding reduction in predatory feeding might be expected (Kjosbakken et al. 1983). High IBE values between 13 and 16 hours after deployment were noted in experiment V in all sectors (Figure 10), without a correlated increase in amphipod number on the photographs. It is supposed that these values were caused by zooplankton drifting near the bottom. Epibenthic sled samples (500 and 300 μm mesh size) taken in the same area at 30 and 100 cm above the seafloor in August 2000, respectively, contained numerous individuals of the calanoid copepod *Calanus hyperboreus* (Auel et al. 2003).

By analysing SSS data in detail for S6 and S7, the data also suggest that some of the amphipods appeared in groups approaching the food source (Figure 11 b,c). There is also evidence of clumping or aggregation of amphipods in leaving the site of the food fall. Wolff (1971) observed large aggregations of swimming amphipods just above the bottom from a submersible at 4160 m. In the animal kingdom aggregation occurs at all sizes from bacteria to whales and across a range of temporal stability from the transient assemblages of midges to the obligatory school of herring (Allee 1931).

It is difficult to explain how aggregation of *Eurythenes gryllus* may have developed, but perhaps in response to external cues such as our food fall. Food finding is enhanced in aggregations that act as an interacting array of sensors, gathering and analysing more information about a system than a single individual could achieve (Parrish and Edelstein-Keshet 1999). Such sensory integration system could transduce physical signals into social cues, which amplify group response (Norris and Schilt 1988, Grunbaum 1997).

The backscatter SSS data clearly demonstrate that the amphipods swim upstream along a narrow path towards the bait, which corroborates the theory that food sources are detected by chemoreception. If the food source was realised by mechanoreception we would expect an arrival from all directions.

3.2. Oxygen consumption and lipid analyses of *Eurythenes gryllus*

One aim of this investigation was to measure the energy budget of *Eurythenes gryllus*. This prompted me to address the question of the metabolic requirements of these scavengers to get an idea of their energy strategy, and how they could survive in such food limited environments as the deep sea, on the basis of oxygen consumption and lipid resources.

Generally, polar marine habitats are characterized by low but relatively constant water temperatures, seasonal or permanent ice cover as well as seasonally variable food input from the water column (Hempel 1985, Clarke et al. 1988, Arntz et al. 1994). All factors combined are thought to be responsible for the low metabolism and productivity in most benthic taxa investigated (Arntz et al. 1994, Brey et al. 1995, Chapelle and Peck 1995).

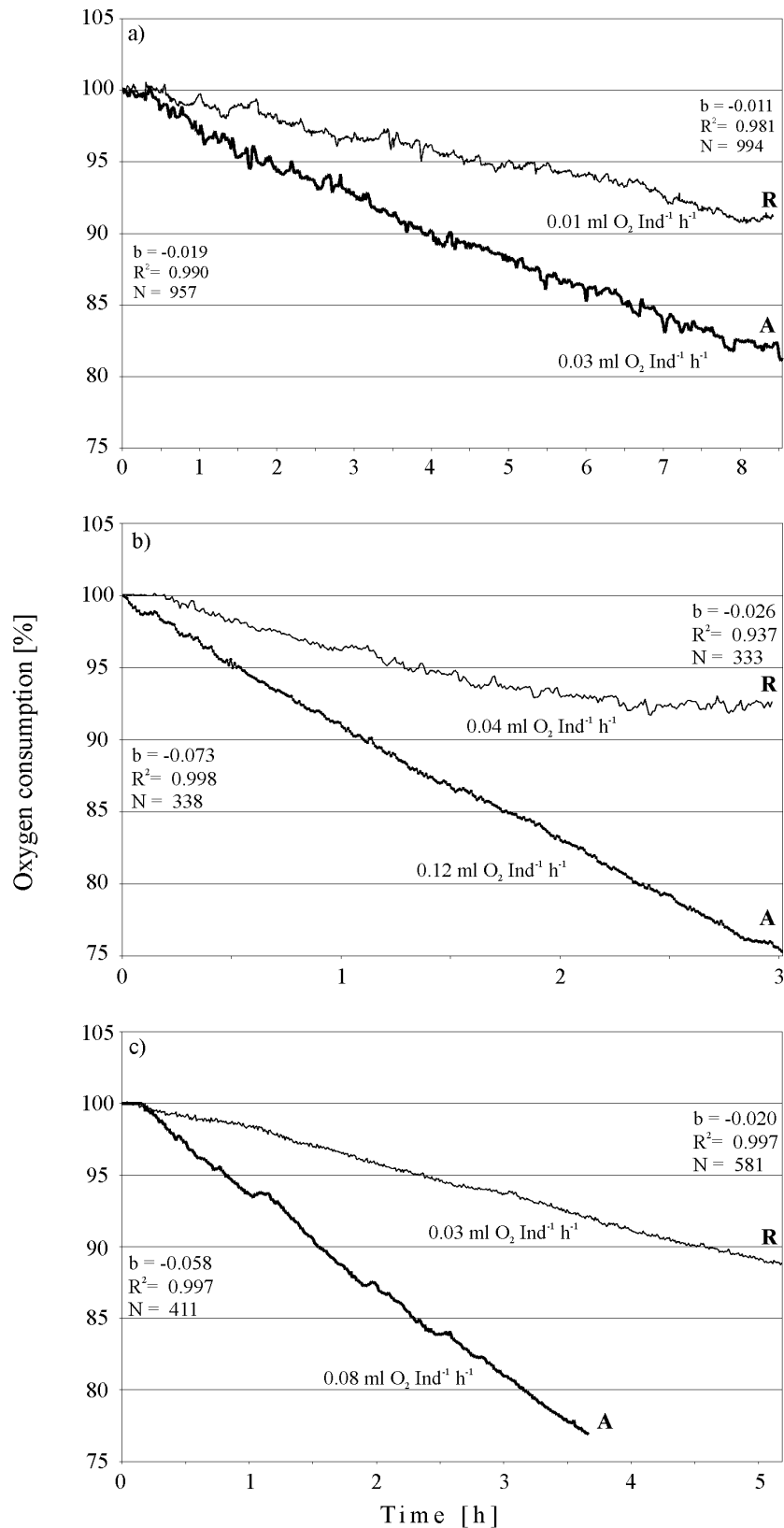


Figure 12: Effects of food odour on the metabolism of a) individual II, b) individual III and c) individual V of *Eurythenes gryllus*. Bold line: individuals exposed to bait odour (Active rate), fine line: individuals unexposed to bait odour (Resting rate).

For every cycle, oxygen concentration per individuuum, slope (b) of linear regression, correlation coefficient (R^2), and number of single measurements (N) included in the linear regression are given.

Smith and Baldwin (1982) proposed three assumptions for deep-sea scavengers, that (i) the deep sea is an oligotrophic food-energy limited environment, (ii) there is a selective advantage for those animals that optimally utilise the available food energy and (iii) that large food falls are the main food source for scavengers. These assumptions could also apply to the scavenging amphipod *Eurythenes gryllus*. As results showed, it can withstand long starvation periods, quickly respond and optimally utilise a once localised food fall, and it has a high assimilation efficiency.

In accordance with the literature it was shown in this study that the deep-sea scavenger *Eurythenes gryllus* may appear quite fast after deployment of bait, in this study even very fast, between 10 to 30 minutes after bait deployment (see publication I and II).

The *in situ* investigations (see chapter 1.2. and 3.1.) strongly suggest that chemoreception is an important, if not the main sense involved in food fall localisation by *Eurythenes gryllus*. This is further supported by results of respiration rate measurements on *E. gryllus* indicating an increase in oxygen consumption after exposure to food odour in laboratory experiments (Figure 12). Also previous laboratory investigations using other crustaceans including scavenging amphipods emphasised that bait odour influences oxygen consumption (Carr 1988, Weissburg 1997, Atema 1998). In this study, respiration rates of *E. gryllus* individuals which were not exposed to bait odour were about three orders of magnitude lower than those of specimens being exposed. It is therefore reasonable to conclude that the scavenging deep-sea amphipod *Eurythenes gryllus* might exhibit two metabolic conditions: a resting stage resembling the kind of dormancy stage described by Smith and Baldwin (1982) for other deep-sea amphipods, and the active stage in which they search for food falls.

The mean oxygen consumption rate ranged from 0.003 to 0.074 ml O₂ g⁻¹ WW h⁻¹ for resting and from 0.01 to 0.05 ml O₂ g⁻¹ WW h⁻¹ during activity (Table 1). Similar results were found by George (1979) for *Eurythenes gryllus* at a depth of 1850 m (0.06 – 0.064 ml O₂ g⁻¹ h⁻¹). For Antarctic specimens of *E. gryllus*, trapped at 580 m, slightly higher oxygen consumption rates of 0.09 ml O₂ g⁻¹ WW h⁻¹ were measured by Opalinski and Jazdzewski (1978). However, methodological differences may be responsible for the latter difference, because much more sensitive oxygen optodes were used in my experiments compared to the electrodes being used twenty five years ago.

During starvation (lasting between 7 to 148 days) and acclimatisation periods (at least 20 hours), the oxygen consumption in *Eurythenes gryllus* was found to decrease. The metabolic activity increased fast measured by respiration rates in *E. gryllus* soon after exposure to bait (Figure 12 a-c). Smith and Baldwin (1982) also discriminated from *in situ* respiration measurements an active and a resting phase of the deep-sea scavenging amphipods

Paralicella capresca and *Orchomene* sp.. Increased oxygen consumption rates related to food odour have also been noted for the gastropod *Nassarius reticulatus* (Crisp et al. 1978). In the “resting” period amphipods have lower oxygen consumption and depend on their storage of lipid reserves (Chapelle et al. 1994). *In situ* long-term investigations showed that resting oxygen consumption rates of amphipods, without exposure to bait odour, to be such a state of torpor (Smith and Baldwin 1982). In this investigation, bait odour was also accompanied by an increase in oxygen consumption, exceeding the resting rates about threefold. When food supply is low, torpor will also be used by terrestrial animals such as bumblebees, whose metabolic rate is three orders of magnitude lower during torpor than during active foraging (Heinrich 1975). The alternation between high and low metabolism in some scavenging lysianassoid deep-sea amphipods investigated by Smith and Baldwin (1982) was used to explain this as an energy-conserving strategy in obligatory scavengers to cope with their unpredictable and scarce food source.

Some scavenging deep-sea amphipods were found to be adapted to the sporadic food supply in form of carcasses in their otherwise food limited environment by two states of metabolism: a resting rate much like a state of dormancy and an active rate for optimal utilisation of food falls when available.

Metabolic rates of cold water benthic lysianassoid amphipods (-1° to 6° C) from deep and shallow water show no obvious differences with bathymetry (Table 1).

Active foraging scavengers such as *Eurythenes gryllus* may have higher growth and metabolic rates than deep-living species that are lethargic (George 1979). Compared with the active scavenger *E. gryllus*, the lysianassoid amphipod *Waldeckia obesa* is relatively inactive. *W. obesa* has a standard metabolism of $0.009 \text{ ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$ (Chapelle and Peck 1995) whereas mean metabolism of *E. gryllus* is three times ($0.02 \text{ ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$, resting rate), and nearly five times higher ($0.04 \text{ ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$, active rate), respectively. Also the active Antarctic and Arctic scavengers *Abyssorchomene plebs* ($0.056 \text{ ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$; Rakusa-Suszczewski 1990) and *Anonyx nugax* ($0.1 \text{ ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$; Schmid 1996) show higher metabolic rates than the inactive Arctic species *Stegocephalus inflatus* ($0.01 \text{ ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$; Schmid 1996).

Based on total lipids and metabolic rates, sustenance times have been calculated for *Eurythenes gryllus*. Own measurements of lipids with mean lipid weight of 0.1 g and mean lipid content of 6.8 % of wet weight (Table 1) are slightly higher than those found in other investigations of *E. gryllus* (2.1 to 4.8 % lipid of wet weight; Opalinski and Jazdzewski 1978, George 1979, Smith and Baldwin 1982, Clarke 1984, Bühring and Christiansen 2001). This

comparatively high lipid content resulted in a mean caloric content of 946.6 cal (n = 21) which was calculated to be sufficient to maintain *E. gryllus* at a resting rate of respiration for 409 days, on average (ranging from 56 to 626 days) and at the active rate for 152 days, on average (ranging from 109 to 176 days). In reality not all lipids are available as energy reserves, so that under the conservative assumption that only 50 % of lipids become used as energy reserves, this would lead to sustenance periods of 203 days (resting), and 76 days (active). If *E. gryllus* would follow the strategy to switch into a state of dormancy after attending a food fall, which is not yet proven, this species might survive several months without food. Such kind of long starvation capability lasting even longer (18 months) has been reported for Antarctic benthic amphipods (Coleman 1991). A lower sustenance time (4.5 days assuming activity versus 96 days during resting) was estimated for the smaller, compared to *E. gryllus*, deep-sea amphipods *Paralicella capresca* (Smith and Baldwin 1982) and *Orchomene cf. abyssorum* (24 days and 59 days, respectively; Kaufmann 1992). Published sustenance time for species where metabolic rates and energy reserves have been measured indicate a strong relationship between sustenance time and body size, with larger species exhibiting much longer sustenance times than smaller ones (Smith and Baldwin 1982, Hargrave 1985, Sainte-Marie 1986). This size-based relationship results from the larger gut capacity found in larger species (Figure 4; Kaufmann 1992, Sainte-Marie 1992). Generally, interspecific comparisons of chemical composition must be made with care due to variations in physiological states such as growth, sex and reproduction (Ansell 1972, Morris 1973).

Scavenging amphipods such as *Eurythenes gryllus* are able to produce lipid stores enabling them to survive long-term starvation. Under certain assumptions it can be calculated that *E. gryllus* may survive 76 days at an active level of metabolism and about 203 days in the more energy saving resting mode.

3.3. Scavenger aggregation dynamics at food falls in the Fram Strait, Arctic Ocean

Baited time-lapse camera experiments are useful approaches in studying the deep-sea scavenger community because they allow for a precise simulation of a naturally occurring event in the deep sea. Among some of the studies summarised in Table 3 other authors using baited traps (Christiansen 1990, Thurston et al. 2002) worked on single experiment data sets, with different kind and mass of bait which might have been masked any differences in composition and succession of the motile scavenger community.



Figure 13: Aggregations of *Lycodes cf. frigidus* in the 'Hausgarten' area at deployed bait. Video observation of a ROV (IFREMER).

The invertebrate scavenger community sampled in the Fram Strait was dominated by *Eurythenes gryllus* (accompanied in some experiments by *Tmetonyx norbiensis*) which, as a basic difference to other studies on this species in different regions of the world ocean, responded much faster to the bait deployment (Table 3; Hessler et al. 1978, Lampitt et al. 1983, Laver et al. 1985, Smith 1985, Rowe et al. 1986, Baldwin and Smith 1987). Aiming at analysing still photographs taken with the time-lapse camera for species identification and individual counting a grid was used in all experiments some 15 cm above the seafloor instead of deploying the fish bait directly on the bottom. The latter approach was generally used by others but was not considered in this study because any quantitative analysis would have been more

difficult. This implies that the number of individuals counted on each photograph is a minimum value, because some amphipods were certainly covered by others, were feeding inside the body cavity of the carcass or on smaller remains below the grid. Nonetheless, the maximum numbers of individuals of *E. gryllus* counted on the pictures were very high compared to other studies (Figure 14).

The maximum number of *Eurythenes gryllus* was not only 13 times higher than found previously in other experiments, the individuals also appeared up to 20 times faster (e.g. Lampitt et al. 1983, Hargrave 1985, Janssen et al. 2000).

Although difficult to assess on the actual data basis the aggregation dynamics described in publication II suggests that natural food falls are quite common in the area of investigation. This assumption is not only supported by the fast attraction and the high number of individuals being attracted but also by the many demersal fish (mainly *Lycodes* cf. *frigidus*; Zoarcidae) attending the baited experiments. Individuals of this species were observed not only with the time-lapse camera used but also by means of video cameras of a Remotely Operated Vehicle (ROV) which was used for other bait experiments in the 'Hausgarten' area in 2001 and 2003. Dozens if not hundreds of *L. cf. frigidus* individuals concentrated around the fish bait (Figure 13; M. Klages, pers. comm.) The video observations demonstrated that these eelpouts do not feed primarily on the bait (which occasionally also happened) but preyed upon arriving motile scavengers. In a manner of sit-and-wait predator they, as recorded on video tapes which were analysed, snapped for *Eurythenes gryllus* if they passed by closely to the mouth of a fish. By putting all these single observations and findings together it seems likely that food falls occur at a sufficient frequency because otherwise the fish behaviour and the abundance of scavengers are difficult to explain. A recent study (Soltwedel et al. 2003a; see publication IV) reported results obtained by a video transect with a towed system.

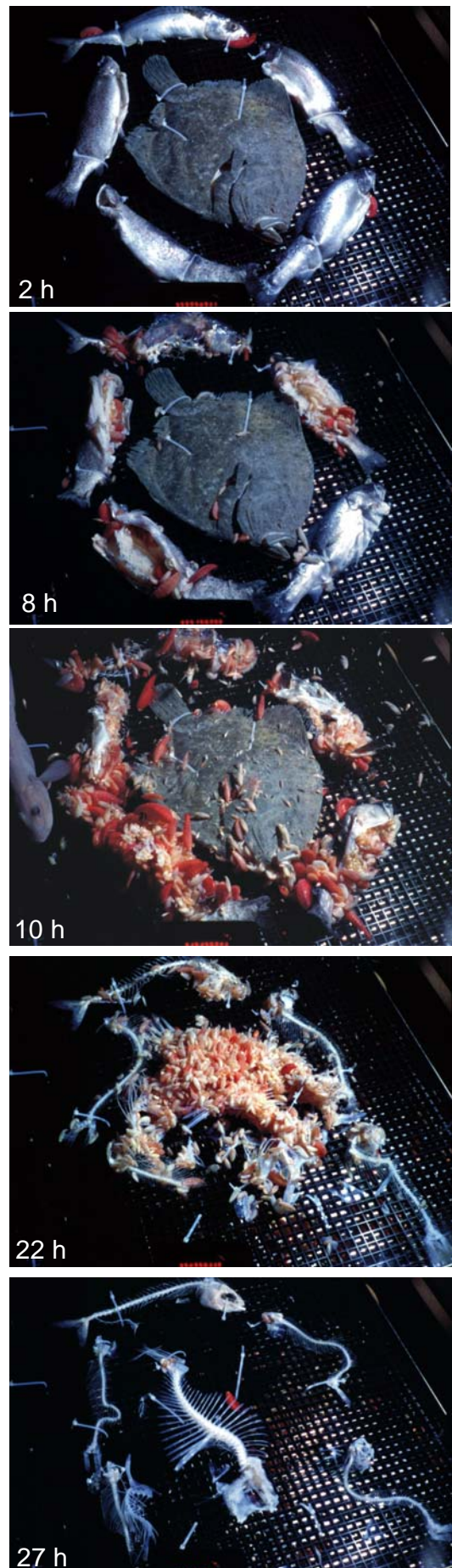


Figure 14: Example of scavenger aggregation at station I. Time-lapse photograph sequences were shown at different time intervals from the beginning to only bones remaining (2, 8, 10, 22 and 27 hours, time at bottom). As bait 2.7 kg of fish (turbot, trout and mackerel) were used. Red, white and pink organisms were the necrophagous amphipods, *Eurythenes gryllus*.

Along a transect of 17.5 km length, which was close to the site of investigation where the lander experiments of this thesis were carried out, covering an area of about 13,500 m² a single fish skeleton (length of 36 cm and a biomass of approx. 0.5 kg wet weight) was identified on a single underwater still picture at 1280 m water depth. Although Klages et al. (2001) also found the carcass of a deep-sea decapod in the Molloy Deep at 5551 m water depths, there are only very few reports on natural food falls detected in the literature. The two cited publications are the only ones for the Fram Strait. This finding seems to be in contrast to the assumption of frequent events. One explanation for the rarity of such findings is that the opportunity to observe an ongoing feeding process of a scavenger aggregation in the deep sea is first of all difficult to achieve because there are not so many cabled or autonomous underwater vehicles available, and second the probability to find the remains of a fish or invertebrate decreases with time (Rowe et al. 1986).

Large carcasses such as whale skeletons were found in different regions of the ocean over the past years (Naganuma et al. 1996, Smith et al. 1998) but surprisingly no such observation has been reported for the Arctic. The polar bear (*Ursus maritimus*) as the top predator in the Arctic ecosystem is hunting for seals in the Fram Strait seasonally when ice cover permits his hunting strategy. The population density of *U. maritimus* in the area of investigation during winter is unknown, but they occur, for example, frequently on Svalbard (1700 to 2200 Ind.; IUCN/ SSC 2003) which is only about 150 km east of our study site. The remains of mammals attacked by polar bears are expected to settle to the seafloor but no bones have as yet been discovered during video transects.

Many of the genera of lysianassoid amphipods are marine cold-water inhabitants and some of them contribute significantly to the species number of the Antarctic and Arctic benthos (DeBroyer and Jazdzewski 1993, Arntz et al. 1994). In the Antarctic other top predators such as leopard seals (*Hydrurga leptonyx*) and killer whales (*Orcinus orca*) hunt for penguins and seals and their remains certainly also serve as food for scavengers. The ice as resting site for birds and mammals together with the seasonally high productivity of polar oceans supported the higher trophic level organisation of polar ecosystems compared to more oligotrophic regions like the central Pacific Ocean, the Arabian Sea or the North Atlantic. Although difficult to verify, this evolutionary development may have led to the frequent occurrence of scavengers in both polar regions.

The higher trophic level organisation of polar ecosystems with more abundant mammals could help to explain the high abundances of scavengers especially, but not exclusively, at high latitudes.

Table 3: Compilation of published results of baited camera experiments in the deep sea regarding amphipods as the most abundant scavenger types. Asterisk indicates no data available.

| Most abundant scavenger type | Area | Depth [m] | Total time of deployment | First arrival | Max. no. image ⁻¹ | Bait weight [kg] | Consumption rate [g d ⁻¹] | Current speed [cm sec ⁻¹] | Author |
|-------------------------------|--------------------|-------------|--------------------------|---------------|------------------------------|------------------|---------------------------------------|---------------------------------------|-------------------------|
| <i>Eurythenes</i> | Arabian sea | 4040 | 129 h | 0.7 h | 9 (21 h) | 29 kg | 500 | 3 | Witte 1999 |
| <i>Eurythenes</i> | Arabian sea | 3190 | 57.7 h | 3.5 h | 34 (23.5 h) | 3.2 | 2690 | 2.7 | Janssen et al. 2000 |
| <i>Eurythenes</i> | Arabian sea | 3950 | 104.3 h | 0.7 h | 47 (13.2 h) | 5.1 | 4320 | 2.9 | Janssen et al. 2000 |
| <i>Eurythenes</i> | NW Atlantic | 5830 | 5 days | 3.9 h | 5 | 0.1 | * | * | Hargrave 1985 |
| <i>Eurythenes</i> | NE Atlantic | 4009 | 24 h | 12 min. | 6 | * | * | 2 - 7 | Lampitt et al. 1983 |
| <i>Orchomene, Paralicella</i> | NE Atlantic | 4855 | 26 h | 81 min. | 38 (13.5 h) | * | * | * | Thurston 1979 |
| <i>Hirondellea</i> | Philippine Trench | 9605 | 16 - 29 h | 20 min. | * | 1 - 3 | * | 7.5 | Hessler et al. 1978 |
| Amphipods, fish | North Atlantic | 4850 | 16.9 h | * | * | 2 | * | 2.5 | Rowe et al. 1986 |
| <i>Orchomene, Paralicella</i> | St Catalina Basin | 1310 | 4 - 56 days | * | * | 2 - 40 | * | * | Smith 1985 |
| Fish & amphipods | NE Atlantic | 4000 - 4800 | 36 - 276 h | 40 min. | * | 50 - 100 | 1200 - 9600 | * | Jones et al. 1998 |
| <i>Eurythenes</i> | NE Pacific | 4900-5900 | * | 150 min. | * | * | * | * | Laver et al. 1985 |
| <i>Eurythenes, Tmetonyx</i> | Arctic Ocean (I) | 2644 | 25.5 h | 15 min. | 740 (9.75 h) | 2.7 | 2600 | 1.5-8.2 (5.8) | Premke et al. submitted |
| <i>Eurythenes</i> | Arctic Ocean (II) | 2524 | 17.5 h | 12 min. | 605 (14.75 h) | 2.7 | 3800 | 4.3-6.4 (4.8) | Premke et al. submitted |
| <i>Eurythenes</i> | Arctic Ocean (III) | 2377 | 19.5 h | 24 min. | 305 (4.75 h) | 2 | 5600 | 5.3-8.9 (7.6) | Premke et al. submitted |
| <i>Eurythenes, Tmetonyx</i> | Arctic Ocean (IV) | 1468 | 24.8 h | 21 min. | 630 (10 h) | 5 | 5500 | 0.8-8.3 (4) | Premke et al. submitted |
| <i>Eurythenes</i> | Arctic Ocean (V) | 2504 | 28.5 h | 21 min. | 620 (4.5 h) | 2.5 | 5000 | 1.7-7.6 (4.6) | Premke et al. submitted |
| <i>Eurythenes</i> | Arctic Ocean (VI) | 2341 | 30.5 h | 9 min. | 800 (14.45) | 4 | 3500 | 2.8-13.5 (7.9) | Premke et al. submitted |

Two categories (Type I & II) of scavenger aggregations were introduced in this study (Table 4), one describing a fast responding community with larger individuals appearing and leaving first, and a second one arriving later with lower numbers of individuals (see publication II).

Table 4: Grouping of all stations (except station IV) in two different types, based on camera, trap and current meter data analysis.

| Type I | Type II |
|--|---|
| High scavenger maxima (600 – 800 Ind. 0.7 m ⁻²) | Low scavenger maxima (300 - 600 Ind. 0.7 m ⁻²) |
| High calculated abundances (454 – 885 km ⁻²) | Low calculated abundances (134 – 304 km ⁻²) |
| Slow increase of scavengers to maximum (10 – 24 hours) | Fast increase of scavengers to maximum (3 – 6 hours) |
| Low consumption rate (2600 – 3800 g d ⁻¹) | High consumption rate (5000 - 5300 g d ⁻¹) |
| Inconstant current direction (SSW, SE, NNE) | Constant NNW current direction |
| Juveniles caught | No juveniles caught |
| <i>Tmetonyx norbiensis</i> caught | No <i>Tmetonyx norbiensis</i> caught |

The reasons for this difference are difficult to assess. Attending food falls is of a certain risk to the individuals because cannibalism might occur, an argument that has been introduced to explain the absence of ovigerous females at such sites (Ingram and Hessler 1987). Even predatory fish are endangered if voracious scavengers are abundant and food decreases in quantity (Rakusa-Suszczewski 1982). This has been confirmed during my experiments. During one lander deployment two zoarcid fish entered a baited trap which was in the view field of the time-lapse camera. One individual escaped after several minutes whereas the other became attacked by some individuals of *Eurythenes gryllus*, starting at the abdominal body parts. After the first amphipods were clinging to the still living fish more and more amphipod specimens became attracted and started to feed on the fish, which died during the following hours and was totally fed up (own unpublished time-lapse photography observations). Other reasons for ovigerous females to avoid food falls might be that developing gonads or eggs being laid in the marsupium prevent gut expansion or shallow the body cavity, thus limiting food intake (Hargrave et al. 1994).

Two kind of scavenger aggregations were distinguished: One category describing a fast responding community with low maxima in specimens number (Type I) and a second type coming later with higher numbers of individuals (Type II).

The ontogenetic migration postulated for *Eurythenes gryllus* by Christiansen et al. (1990) is apparently quite complex. With increasing size, immature *E. gryllus* move up into the water column adopting to an abyssopelagic lifestyle rather than a benthic mode of existence (Ingram and Hessler 1983, Smith and Baldwin 1984, Charmasson and Camlet 1987, Christiansen et al. 1990). Smith et al. (1979) found less developed stages of *E. gryllus* females at 5 m above the seafloor and more mature stages at 400 m above the seafloor, and attributed this to a vertical ontogenetic distribution. The area of investigation where the

measurements for this study were carried out exhibits a rather complex topography which has an influence on the not yet fully understood physical conditions, hence the mesoscale current regime. A number of eddies were detected over the past years, some of which circulate in opposite direction to others close by (Cisewski 2001, Schauer et al. submitted). Such current

conditions will also have an effect on the dispersal of food odour (see chapter 3.1.). As chemoreception is the main sense involved in food fall localization at distances of tens or even hundreds of metres in scavenging individuals of *Eurythenes gryllus* (see publication I), the hydrography of the Fram Strait with its eddies might favour a scavenger mode of life.

The length-frequency analysis of all individuals measured indicates that the females of *Eurythenes gryllus* have a larger mean size compared to males. The largest female caught measured 75 mm body length while the largest male was 56 mm long (Figure 15). These sizes are considerably smaller than those found for individuals collected in the North Atlantic and in the central North Pacific, where the largest female measured 130 resp. 139 mm and the largest male 90 resp. 109 mm (Christiansen et al. 1990, Ingram and Hessler 1987, Baldwin and Smith 1987; Figure 16). All studies were based on traps deployed either on the sea floor or in the water column at 500 m above bottom or more. In all of these studies small and juvenile individuals were captured almost exclusively close to or above the sea floor, whereas larger specimens were distributed throughout the water column (Figure 5).

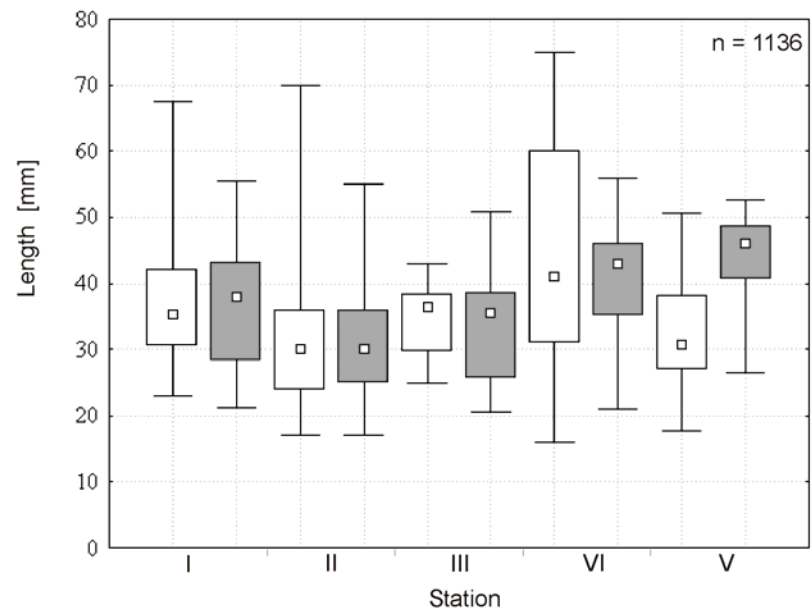


Figure 15: Lengths [mm] of adult females (white boxes) and males (grey boxes) of *Eurythenes gryllus*, median, minimum and maximum illustrated as a Box and Whisker Plot.

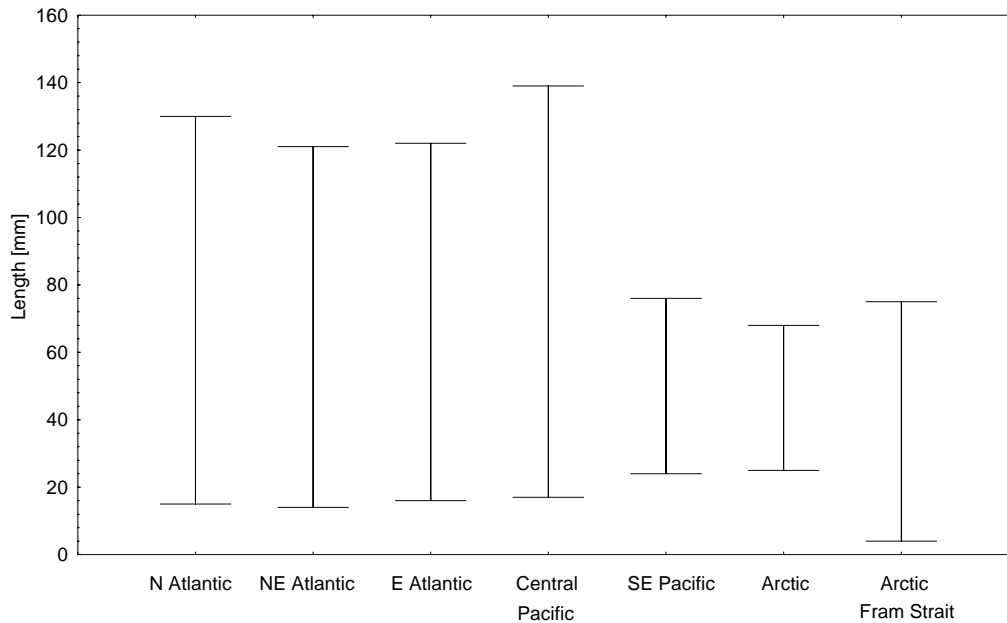


Figure 16: Lengths of *Eurythenes gryllus* of different areas. Mean of Maxima are given. Source, in order of areas: Christiansen et al. 1990, Charmasson and Camlet 1987, Wickins 1983, Ingram and Hessler 1983, Thurston et al. 2002, Bowman and Manning 1972, Premke et al. submitted.

The largest specimens (immature females) collected in the Antarctic measured respectively 114 mm for the Weddell Sea specimens and for Admiralty Bay 92 mm (De Broyer pers. comm.). Similar sizes to those found during this study were only recorded from the upwelling area in the south-east Pacific (Thurston et al. 2002) and in the Antarctic (De Broyer pers. comm.; Figure 16).

The Arctic scavengers studied seem to present differences concerning the species attracted, their succession, their abundances and lengths compared with scavengers from other latitudes. However, scavengers attracted and their abundances seem to be directly linked to the organic input of food fall in the area.

Due to their efficiency mobile deep-sea scavengers such as the cosmopolitan amphipod *Eurythenes gryllus* must be regarded as an important component of the deep-sea food web considering their large number and their role in the consumption, conversion and distribution of organic matter at the benthic-pelagic interface.

3.4. Future perspectives

The present findings give evidence of a long-range chemoreceptive tracking of food odour by scavenging amphipods. The application of a scanning sonar system attached to a lander frame in combination with a baited-time lapse camera and acoustic doppler current profiler allowed for the first time to identify the direction of arrival together with temporal information. Faster arrival and higher individual numbers than in all other studies cited in the literature were found at the location sampled in the Fram Strait. However, further experiments in the Arctic Ocean are needed to clarify if the findings of this study hold true for other areas and other seasons in the Arctic Ocean, and whether the same scavenger community is attracted.

Despite the darkness in the deep sea lysianassoid amphipods such as *Eurythenes gryllus* have well-developed eyes. However, this study did not aim at elucidating if photoreception might be involved in food finding at short distances. This factor should be considered in future studies on food finding strategies in deep-sea scavengers. There are some indications that food falls are also attended by bioluminescent organisms, which might serve as additional information for animals such as *E. gryllus*.

In addition, genetic investigations of intra-specific aggregations would be interesting. This could clarify whether an aggregation is a unit population or consists of different populations and if there are temporary invaders instead of stationary habitants. There is evidence that individuals of *Eurythenes gryllus* in the Arctic and Antarctic oceans belong genetically to the same species (Held, pers. comm.). In cooperation with the working groups on molecular genetics at the institutes in Bochum and Brüssel, genetic analyses are in preparation to clarify whether individuals of *E. gryllus* of the Arctic, Antarctic, Pacific and Atlantic oceans belong to one species or if they have to be considered as subspecies.

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5. Publications

The below listed publications are part of this thesis and my share of each publication is explained.

Publication I

Katrin Premke, Sergej Muyakshin, Michael Klages, Jan Wegner

Evidence for long range chemoreceptive tracking of food odour in deep sea scavengers by scanning sonar data. *J Exp Mar Biol Ecol* 285/286, 2003, pp 283-294

The third and the second author initiated the study and formulated the idea to use a scanning sonar system to investigate the food finding localization of scavengers. The fourth author developed the technical details of the sonar system. I designed the experimental concept, performed the laboratory work and wrote the first version of the manuscript which was improved in cooperation with the co-authors. The scanning sonar data analysed procedure was developed in close cooperation with the second author.

Publication II

Katrin Premke, Michael Klages, Wolf E. Arntz

Aggregations of Arctic deep-sea scavengers at large food falls: temporal distribution, consumption rates and population structure. *Mar Ecol Prog Ser*, accepted

I further developed, adjusted and designed the experimental concept, conduct the laboratory work. The procedure for subsequent result analysis and my first version of the manuscript were refined in cooperation with the co-author.

Publication III

Katrin Premke, Martin Graeve

The effects of bait scents and starvation on the metabolic rate of the necrophagous deep-sea amphipod *Eurythenes gryllus* (Lichtenstein, 1822). *Polar Biology*, submitted

The concept and the initial idea for this paper was elaborated by the first author. I also developed the conceptual and methodological approach for the respiration experiments. Lipid measurements were carried out by the second author. The data processing was conduct by the first author, as well as writing the first draft of the manuscript. The revision of the first version, was made in cooperation with the second.

Publication IV

Thomas Soltwedel, Karen von Juterzenka, Katrin Premke & Michael Klages

What a lucky shot ! Photographic evidence for a medium-sized natural food-fall at the deep seafloor. *Oceanologica Acta*, in press

The original concept was elaborated by the first author, who wrote also the first version. I conduct a part of the data analyses and wrote this for the draft. The last version was the results of the comments of all authors on the first draft.

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Evidence for long range chemoreceptive tracking of food odour in deep sea scavengers by scanning sonar data

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Abstract

There is much speculation about chemoreception being involved in food finding strategies of deep-sea scavengers in the literature (Dahl, 1979; Meador, 1981; Busdosh et al., 1982, Sainte-Marie, 1992). Most of these ideas have emerged from analysing time-lapse photographs and video recordings of bait deployments in the deep sea (Thurston, 1979; Lampitt et al., 1983; Hargrave, 1985; Priede et al., 1990). However, optical instruments have considerable restrictions in spatial coverage, thus all past efforts in determining any directionality in the appearance of scavengers have been limited from 0.9 to 4 m² only (Smith, 1985; Wilson and Smith 1984). Here we present data obtained by using a scanning sonar system (SSS) which allows detection of single objects larger than 2 cm at a maximum distance of 50 m in a horizontal plane. Together with the SSS a baited time-lapse camera attached to a free falling lander was used in the Arctic deep sea at two locations in the Fram Strait at about 2500 m water depths. We would like to point out that this combination of optical and acoustical measurements allowed for the first time the long range detection of approaching scavenging amphipods in the deep sea. *Eurythenes gryllus* (Lichtenstein, 1822), a cosmopolitan deep-sea scavenging amphipod, was recorded to attend our bait experiments with a maximum of 618 individuals with first arrival 12 min. after deployment which is one of the fastest arrivals ever observed. We found a significant temporal correlation between integrated backscatter energy (IBE) based on measurements of the SSS and amphipod individuals counted on photographs.

Keywords: Chemoreception *Eurythenes gryllus* Spatio-temporal attraction Deep Sea

1. Introduction

The energy flow in the deep-sea benthic ecosystem is partly driven by sinking carcasses of larger pelagic organisms and mammals (“food fall”), which act as a local and highly concentrated organic input (Stockton and DeLaca, 1982). Various investigations with baited purpose designed time-lapse cameras have discovered a large motile fauna attracted to carrion in the deep sea (Dayton and Hessler, 1972; Smith, 1985; Witte et al., 1999). Klages et al. (2001) reported an observation with a remotely operated vehicle of an ongoing feeding process of scavengers on a natural food fall in the Arctic deep sea. Although being difficult to estimate how much and how often organic carbon enters the deep sea by food falls, it is obvious that these single events are unpredictable for individuals depending on this kind of energy supply. In response, lysianassoid amphipods like *Eurythenes gryllus* are characterized not only by their voracity but also by morphological, anatomical and physiological adaptations linked to their scavenging mode of life (Dahl, 1979; Smith and Baldwin, 1982). This is certainly remarkable regarding the aspect that for benthic or benthopelagic scavengers the impact of any food fall is unpredictable as well in space and time. After the first underwater photographs had shown the fast response of the deep-sea community to bait, the hypothesis that chemoreception must be the major sense involved in food localization came up (Issac, 1969; Dayton and Hessler, 1972). Because the food odour of a carcass is transported by bottom currents, which are usually very low in the deep sea ($< 10 \text{ cm s}^{-1}$) (Rowe et al., 1986; Witte, 1999; Sauter et al., 2002), the high number of individuals being attracted is surprising. At the deep-sea scavenging communities are dominated mostly by lysianassoid amphipods and large fishes, both highly efficient necrophages (Christiansen et al., 1990; Priede et al., 1991). There is much speculation about chemoreception being involved in food finding strategies of deep-sea scavengers in the literature (e.g. Meador 1981; Busdosh et al., 1982; Sainte-Marie, 1992). Most of these ideas about chemoreception have emerged from analysing time-lapse photographs and video recordings of bait deployments in the deep sea (Thurston, 1979; Lampitt et al., 1983; Hargrave, 1985; Priede et al., 1990). However, optical instruments have considerable restrictions in spatial coverage, thus all past efforts in determining any directionality in the appearance of scavengers were limited to an area of 0.9 to 4 m² only (e.g. Wilson and Smith, 1984; Smith, 1985). In this study we used in addition to a time-lapse camera a scanning sonar system (SSS), which allows detection of single objects larger than 2 cm at a maximum distance of 50 m in a horizontal plane.

2. Methods

Our study area was in the Fram Strait (Fig. 1). Two experiments were carried out during the expedition PS ARK XVII/1 of the German RV 'Polarstern' in summer 2001 (Fahrbach et al., in press).

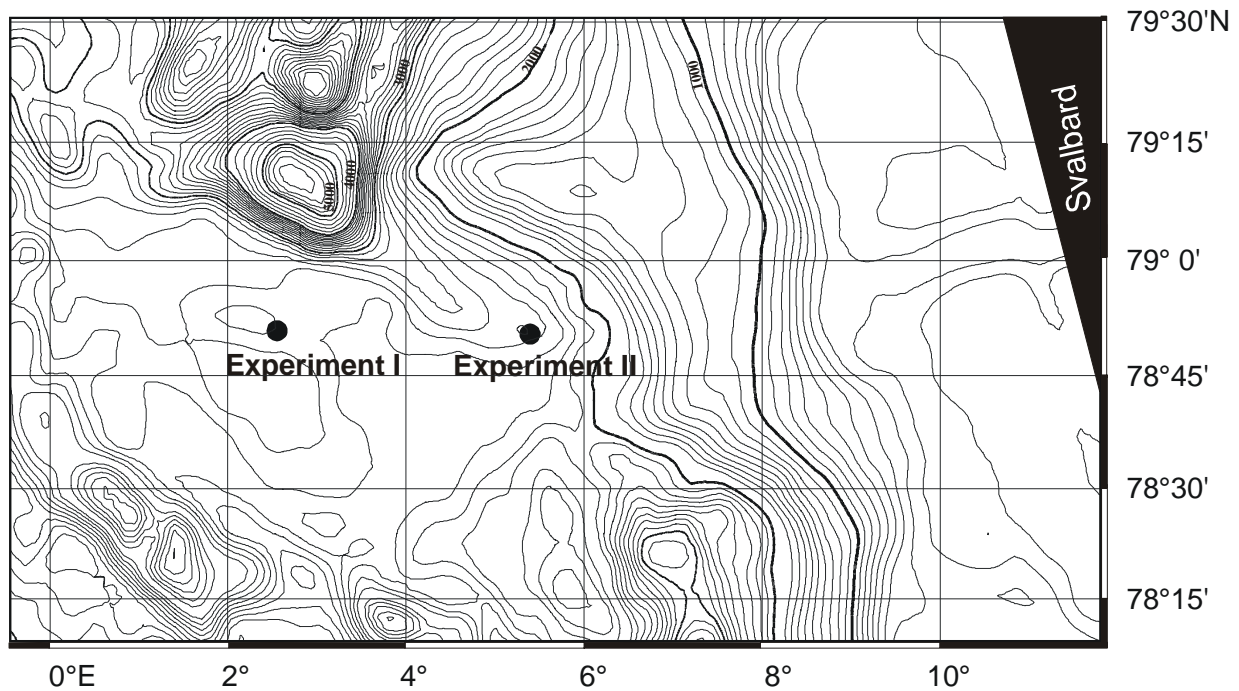


Figure 1: Location of stations in the Arctic Ocean

2.1. Experimental set-up

A tripod lander was used equipped with a baited time-lapse camera (model Simrad Mesotech Photosea 5000), Photosea 1500SX flash, the Simrad Mesotech MS1000 scanning sonar system adapted to autonomous mode of operation, an acoustic Doppler current profiler (Aanderaa Instruments RCM11), traps, glass spheres for buoyancy and ballast weight. The camera view was centered to fish bait exposed on a grid 15 cm above the seafloor. Pictures (Kodak Ektachrome 200, 35 mm x 35 mm x 30 m) were taken at 3 min. intervals for a period of about 29 hours and 18 hours respectively. The SSS (containing of sonar-head "Simrad" 1071 Series) was configured to detect scattering objects in the plane of the acoustical beam rotation at distances of 50 m with range sampling resolution of 0.1 m during a 5 min. rotation period at 0.9° steps. To achieve high angle resolution and to decrease the bottom reverberation, a transducer with a rather narrow 2.7° conical beam was used.

At the end of each experiment the lander was acoustically called back to surface. All organisms caught/ collected with the traps attached to the lander were sampled and stored in 4 % buffered formaldehyde for species identification, determination of sex and lengths.

2.2. Post processing of photographs

Slides were examined by eye with a binocular microscope to identify and quantify all species and individuals visible. Counted amphipods (almost only *Eurythenes gryllus*) were easily identified by characteristics like body form, colour (red, white and pink) and eye shape. Photographs were compared with fixed specimens caught with traps during the respective lander deployments.

2.3. Post processing of sonar data

In order to obtain the description of spatio-temporal distribution of scattering objects in the vicinity of the lander we used the echo integration procedure similar to those described in MacLennan (1990). The integrated backscatter energy (IBE) was calculated by formula (1):

$$e(\Delta r, \Delta \varphi) = \sum_{r_k \in \Delta r} \sum_{\varphi_j \in \Delta \varphi} u^2(r_k, \varphi_j) r_k^2 10^{2\alpha r_k} \quad (1)$$

where: $u(\dots)r_k^2$ – output signal amplitude (r_k^2 – intrinsic multiplier of the sonar-head, so called 20logR TVG-function), α – sound absorption coefficient, $10^{2\alpha r}$ – post processing multiplier for absorption compensation, r_k, φ_j – fixed points (nodes) of the angle-range plane, $\Delta \varphi \Delta r$ – integration domain of this plane.

Using the following model of the received signal (2),

$$u^2(r_k, \varphi_j, m) = a^2 I_0 r_0^2 \frac{\sigma_m(r_k, \varphi_j)}{r_m^4} 10^{-2\alpha r_k} A^4(r_k - r_m) D^4(\varphi_j - \varphi_m) \quad (2)$$

where: I_0 – sound intensity at r_0 , r_m – distance from the scatter, σ_m – backscattering crosssection, φ_m – direction on the scatter, $A(\dots)$ – pulse envelope, $D(\dots)$ – directivity pattern, a – device dependent coefficient together with reasonable assumptions about statistic properties of signals, it can be shown, that average values calculated by formula (1) are proportional to mean concentration of the scattering objects and their mean backscattering section in the space domain, from which the integrated signals were received:

$$\langle e(\Delta r, \Delta \varphi) \rangle = \left\langle a^2 I_0 r_0^2 \sum_{m(r_m \in \Delta r, \varphi_m \in \Delta \varphi)} \frac{\sigma_m(r_m, \varphi_m)}{r_m^2} n_r n_\varphi \right\rangle \sim \langle \sigma \rangle_{\Delta r, \Delta \varphi} \frac{\langle N \rangle_{\Delta r, \Delta \varphi}}{r_{\Delta r}^2 \Delta r} = \langle \sigma \rangle_{\Delta r, \Delta \varphi} \langle n \rangle_{\Delta r, \Delta \varphi} \quad (3)$$

where: n_r and n_φ - width of the of $A(\dots)$ and $D(\dots)$ correspondingly; $m(r_m \in \Delta r, \varphi_m \in \Delta \varphi)$ mean that object with number m is found in the domain $\Delta \varphi \Delta r$.

Average IBE values of four SSS rotations were calculated for each of the eight 45°- sectors at consecutive 5 m range intervals. The region with obvious bottom reverberation was not considered in the calculation.

Finally, the weighted sum (WS) of IBE values for each sector was calculated by using (4)

$$E(\Delta\varphi) = \sum_l e(\Delta r_l, \Delta\varphi) r_{\Delta r_l}^2 \Delta r \sim \sum_l \langle \sigma \rangle_{\Delta r_l, \Delta\varphi} \frac{\langle N \rangle_{\Delta r_l, \Delta\varphi}}{r_{\Delta r_l}^2 \Delta r} r_{\Delta r_l}^2 \Delta r = \langle \sigma \rangle_{\Delta\varphi} \langle N \rangle_{\Delta\varphi} \quad (4)$$

As follows from (4) WS of IBE is proportional to the whole number of scattering objects in the corresponding sector.

3. Results

During both lander experiments (Tab. 1) the scavenging fauna was dominated by the lysianassoid amphipod *Eurythenes gryllus* that was attracted by fish bait. The only fish species that was observed around and on the bait was the zoarcids *Lycodes cf. frigidus*. Further on their were observed on the bait isopods (*Saduria sabinii*) and an other species of amphipods (*Stegocephalus* sp).

First arrivals of single individuals of *E. gryllus* were recorded after 12 and 21 min, respectively. Large individuals dominated the feeding community during the first hours after deployment (Fig. 2c & 3c) and in the first experiments, the majority of large individuals left the food fall already four hours after bait deployment, leaving the remains for smaller relatives.

Due to differences in current speed regime during both lander deployments (see Fig. 2d & 3d), we accordingly recorded differences in the temporal arrival of individuals. The maximum number of individuals counted on photographs in experiment I were 618 after 4.5 hours and in experiment II, where the current speed was higher, it was nearly the same individual number, but 10 hours later (Fig 2b, 2d & 3b, 3d).

In experiment I three garfishes and one of the sole were totally skeletonized after 7 ½ h. 3 h later the second sole was completely consumed by scavengers. During experiment II no other animals except *E. gryllus* and the fishes were observed around the bait. After 8 h all mackerels were skeletonized. Not until after 16½ h the soles were totally consumed.

Amphipods of both experiments were on the surface on the bait and burrow partly with the fore into it. At least all bait was completely consumed, with only bone remaining.

Table 1: Deployment data, occurrence of scavengers and bait weight of both experiments

| | Experiment I | Experiment II |
|---|---|---|
| Position | 78°50' N 02°42' E | 78°50' N 05°52' E |
| Date/ time of deployment | 17.07.01/ 18:42 p.m. | 13.07.01/ 19:53 p.m. |
| Depth | 2504 m | 2524 m |
| Bottom time | 28.5 h | 17.5 h |
| Current velocity | 1.7 – 7.6 cm s ⁻¹ | 4.3 – 6.4 cm s ⁻¹ |
| Bait species | 3 soles * 3 garfishes † | 2 soles * 4 mackerels ‡ |
| Bait weight | 2500 g | 2700 g |
| First occurrence of <i>Eurythenes gryllus</i> (after bottom contact of the lander) | 21 min. | 12 min. |
| Max. no. of individuals (at time after bottom contact of the lander) | 618 (4,5 h) | 605 (14,75 h) |
| Other individuals actively feeding on bait** | <i>Lycodes cf. frigidus</i> (5/ 0.5 h) <i>Stegocephalus</i> (6/ 2.4h) <i>Saduria sabini</i> (5/ 25 h) | <i>Lycodes cf. frigidus</i> (4/ 1h) |
| Bait consumption with only bone remaining | 3 garfishes after 7.5 h 3 soles after 12 h | 4 mackerels after 8 h 2 soles after 17 h |

* *Pleuronectus platessa*

† *Belone belone*

‡ *Scomber scombrus* (all fish species kept frozen until used)

** Maximal number of individuals per slide/ time of occurrence

To identify any directionality in the arrival of amphipods, we analysed the spatio-temporal correlation between weighed sum (WS) of IBE in eight 45° sectors (see Fig. 2a & 3a), and number of amphipods counted on the photographs. As illustrated in Fig. 2b, there is a constant energy increase in WS in sector 6 in experiment I during the first 4 hours after deployment, corresponding with an increase of amphipod individuals on the photographs. The number $M(t)$ of *E. gryllus* individuals attracted by bait is mathematically described by the “particle conservation law” in the formula:

$$M(t) = \int_0^t \int_S v_n(t', r) c(t', r) dS dt' \quad (5)$$

where: $M(t)$ - number of individuals inside the area S surrounding the bait, $v_n(t, r)$ – projection of swimming speed on the perpendicular to S , $c(t, r)$ – volume concentration of individuals on the surface S .

Replacing $v_n(t,r)$, to distinguish time ΔT and surface ΔS domains with certain mean speed projection U and $c(t,r)$ with $N(t)/V$ ($N(t)$ – the whole number of individuals in the sonar observation volume V corresponding to the selected surface domain), it follows:

$$M(t) \approx U \frac{\Delta S}{V} \int_0^t N(t') dt' \quad \text{for } t' \in \Delta T \quad (5a)$$

High values of IBE and WS during the arrival phase (first 4 hours) in experiment I were observed in sector 6 only. If the proportionality between $E(\Delta\varphi)$ and N according to formula (3) (see 21 hours) is considered and integration replaced by cumulative summation, we obtain finally:

$$M(t_i) \approx \gamma U_a \sum_{j=1}^i E(\Delta\varphi_{6,t_j}) \quad \text{for } i \leq 12 \quad (5b)$$

where: γ - scaling coefficient, U_a – projection of the mean swimming speed on the perpendicular to ΔS .

This means that we here examine sector 6 as domain ΔS and the time interval 0-4 h as ΔT .

It is noteworthy that in both experiments, the lander had a declination in its horizontal position visible in all sonar panoramas (see the pink region in Fig. 2a and 3a, respectively) by a persistent region of strong backscattering induced by bottom intersection of the rotation plane of the beam. However, in experiment I this was of advantage because the SSS beam in sector 6 and 7 covered the first meters above the seafloor where most amphipods had to pass through to reach the bait. The opposite was the case in experiment II (pulse transmission in current direction into the water column), thus explaining the discrepancy in numbers of amphipods counted on photographs and detected by SSS (Fig. 3b).

Using least square methodology, we calculated the product γU_a providing the minimum root mean square (RMS) difference between sonar data based estimates and counted individuals arriving. The graphs in Fig. 2b illustrate the correlation of both measurements in first 4 hours, indicating that arriving amphipods contribute to most of the IBE during arrival phase in sector 6.

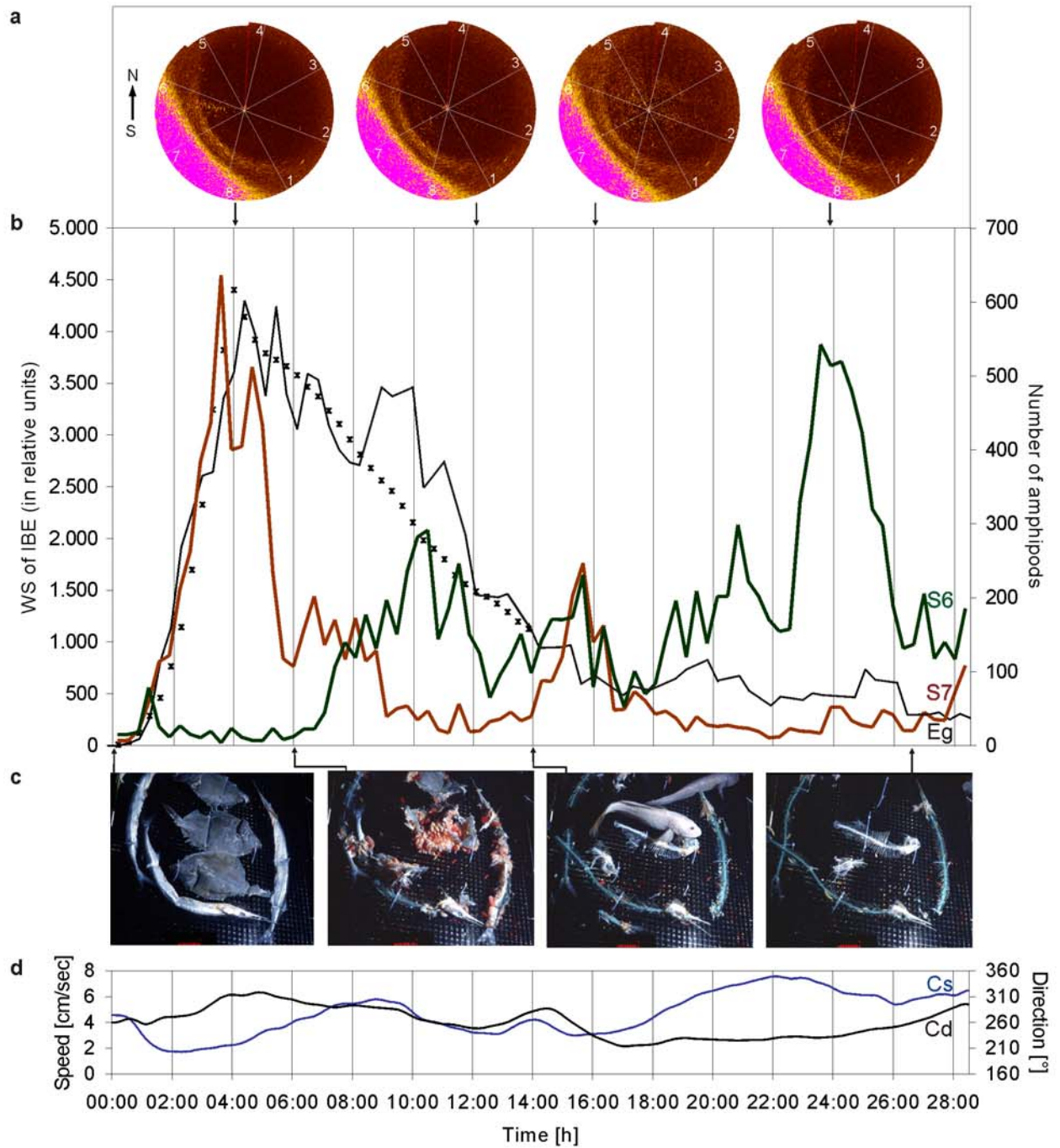


Figure 2: Temporal patterns of amphipods arrival (a-c) during **experiment I**: (a) Sonar data plotted in polar projection at different time intervals (4, 12.17, 16 and 23.8 hours bottom time). The pink area is a persistent region of strong backscattering induced by bottom intersection. The other yellow spots are signals induced by organisms (b) The spatio-temporal patterns of WS of IBE together with the number of amphipods vs bottom time. (c) Time-lapse photograph sequence of bait deployment at different time intervals (0.25, 6, 14 and 26.5 hours bottom time). Red, white and pink organisms are amphipods, yellow organisms (c4) are isopods. (d) Current speed and direction vs bottom time, 2 m above sea bottom. Abbreviations: WS, weighted sum; IBE, Integrated Backscatter Energy; S6, sector six; S7, sector seven; Eg, *Eurythenes gryllus*; Cs, Current speed; Cd, Current direction; cross symbols indicate cumulative sum.

Further integrating with a negative coefficient $-\gamma U_d$ give us possibility to calculate the number of individuals during the departure phase between 4 and 13 hours. In formula this is calculated for sectors 6 and 7 together because the WS has comparable values in both cases (see time interval 4 – 13 h on the Fig.2b):

$$M(t_i) \approx \gamma U_a \sum_{j=1}^{12} E(\Delta\phi_{6,t_j}) - \gamma U_d \left[\sum_{j=13}^i (E(\Delta\phi_{6,t_j}) + E(\Delta\phi_{7,t_j})) \right] \quad (5c)$$

if $13 \leq i \leq 40$. Considering sector 6 (and 7) in experiment I, there is again a close temporal correlation between counted animals on photographs (decreasing 4 hours after start of the experiment) and number of leaving individuals estimated by analysing the constantly decreasing WS of IBE. A slight deviation between measured and calculated data during the departure phase is most likely explained by further arrivals of smaller individuals. The minimum RMS difference between calculated and counted data is reached at $U_d = 0.35 U_a$. This implies that the number of individuals leaving first in current direction is partially compensated by the arrival of new groups of individuals (see time interval 8-11 h in Fig. 2b) thus both these process together gives the average departure speed U_d equal to $0.35 U_a$.

4. Discussion

As reported for other deep-sea areas scavengers arrived not only fast but also in high numbers after bait deployment ingesting large amount of bait within short period of time (e.g. Isaacs and Hessler, 1983; Jones et al., 1998). We counted extraordinary many individuals of *Eurythenes gryllus* on our pictures exceeding numbers of individuals counted by others not only more than 13 fold but appeared up to 20 times faster as in other experiments (e.g. Lampitt et al. 1983; Hargrave 1985; Janssen et al. 2000).

In many textbooks chemoreception is introduced as one of the main sense in crustaceans for food finding. Lysianassoids are assumed to approach carcasses against the current (Thurston 1979; Busdosh et al. 1982) but this is documented with considerably restricted data based on optical instruments. By using acoustical instruments we achieved a better spatial coverage in our data which correlates with optical information of the time-lapse camera. We found a significant temporal correlation between IBE based on measurements of the SSS and amphipod individuals counted on photographs. Our interpretation of long-range chemoreception is also supported by our current meter data indicating current direction at the beginning of the deployment in westward direction, with a shift to south westerly direction about 15 hours after the start of experiment I (Fig. 2d).

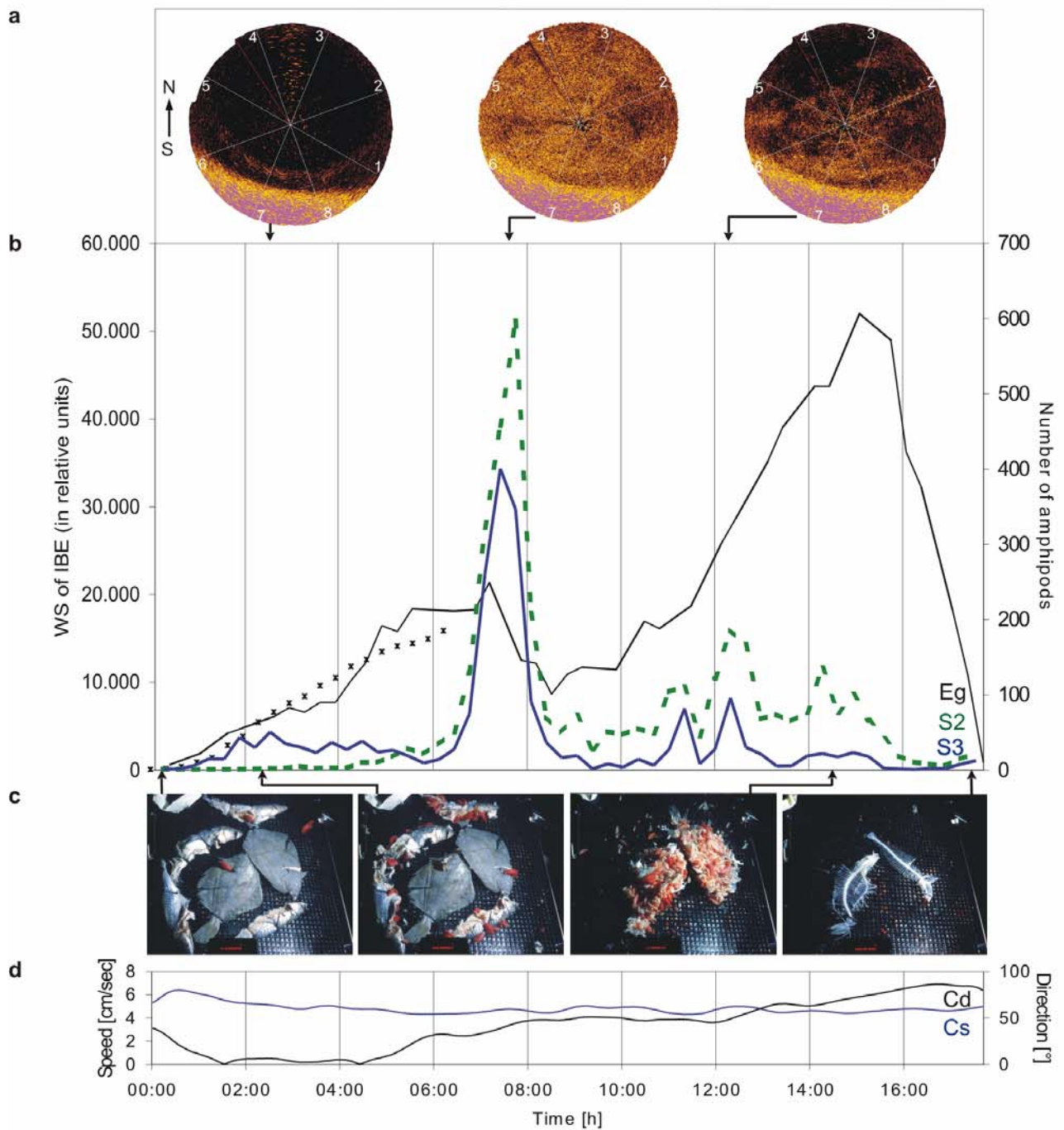


Figure 3: Temporal patterns of amphipods arrival (a-c) during **experiment II**: (a) Sonar data plotted in polar projection at different time intervals (2.5, 7.5 and 12.5 hours bottom time). The pink area is a persistent region of strong backscattering induced by bottom intersection. The other yellow spots are signals induced by organisms (b) The spatio-temporal patterns of WS of IBE together with the number of amphipods vs bottom time. (c) Time-lapse photograph sequence of bait deployment at different time intervals (0.28, 2.25, 14.6 and 17.4 hours bottom time). Red, white and pink organisms are amphipods.

The backscatter data recorded by SSS and analysed in detail for sector 6 and 7 suggest that some of the amphipods appeared in groups swimming upstream along a narrow path towards the bait (Fig. 2a). It is difficult to explain how this animal aggregation may have been

formed, but perhaps in response to the external cue of our food fall (Parrish and Edelstein-Keshet 1999). Food finding is enhanced in aggregations that act as an interacting array of sensors, gathering and analysing more information about the system than a single individual could achieve. Such sensory integration system could transduce physical signals into social cues, which amplify group response (Grunbaum, 1997). In this case long range mechanoreception about the lander impact may have led the group formation of single individual while swimming towards the lander/ bait.

Mechanoreception has recently been introduced again as another potential source of information for deep sea scavengers (Klages et al. 2002), but more in the terms of fast long range transmission of information about food falls, unlikely to assist in tracking the source.

Further analysis of the SSS data (see sonar data at about 10h in Fig. 2a & 2b) indicates that disappearing individuals of *Eurythenes gryllus* did not stay in close vicinity to the lander but swam with the current at least 50 m away, e.g. further than the detection limit of the SSS. This supports the assumption that *E. gryllus* is a temporary invader instead of being a local inhabitant. Sainte-Marie and Hargrave (1987) suggest a gradient of necrophagy among deep-sea species, with *E. gryllus* rallying to bait from greater distances than the fish *Coryphaenoides* sp., which in turn, is attracted from much greater distances than smaller lysianassoids such as *Orchomene* spp. and *Paralicella caperesca*.

Another rise of the WS in sector 7 (experiment I) between 21 and 24 h after deployment was not accompanied by an increase in amphipod number counted on the photographs (Fig. 2b). This could be either explained by higher current speed prevailing with the result that individuals needed more time to cover the same distance so that the sonar system detected them more often at a given time interval or by reduced amount of food which did not attract the late coming individual very much (see Fig. 2d).

We observed high WS values between 13 and 16 hours after deployment in experiment I in all sectors, without a correlated increase in amphipod number at our photographs. We suppose that these WS values were caused by zooplankton drifting near the bottom. High WS values in experiment II observed in all sectors about 6 hours after lander deployment until ballast release (Fig 3b) are also assumed to be caused by drifting clouds of zooplankton. Epibenthic sled samples (300 and 500 μm mesh size) taken in August 2000 in the same area about 1-1.5 m above the seafloor contained numerous individuals of the calanoid copepod *Calanus hyperboreus*.

The purpose designed lander experiments, e.g. the combined use of current meter, baited time-lapse camera and scanning sonar system clearly demonstrated that the scavenging amphipod *Eurythenes gryllus* swims at least the last tenth of meters against the current to localize the bait. Chemoreception must be the major sense to follow the odour. The fast

arrival and rapid bait consumption we observed in our Fram Strait experiments implies a feeding strategy of *E. gryllus* where high energetic expenditures for locomotion is outweighed by ingestion of large amounts of carrion.

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**Aggregations of Arctic deep-sea scavengers at large food falls: temporal
distribution, consumption rates and population structure**

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ABSTRACT: Scavenging amphipods were studied at six locations in the Fram Strait (Arctic Ocean). At each location a tripod lander equipped with a time-lapse camera, acoustic doppler current profiler and baited traps was deployed at water depth between 1500 and 2600 m. All amphipods, both on photographs and captured, belong to the superfamily Lysianassoidea or Stegocephaloidea. Differences between the stations occurred in time and number of amphipod maxima, consumption rates, taxonomic composition, size structure and current direction. Scavenger aggregation dynamics and behaviour on carcasses in the Arctic Ocean differ from other reported deep-sea areas in arrival time at bait, abundance and length distribution of individuals sampled. The giant amphipod *Eurythenes gryllus*, dominated at our bait experiments, exceeded numbers counted by other workers more than 13 fold, and first individuals appeared up to 20 times faster than in other reported experiments. Specimen attraction and abundance seems to be directly linked to the organic input of food falls, in the area. Relations between scavenger aggregations and trophic conditions are discussed with respect to results obtained under different trophic regimes in the Arabian Sea, and the Pacific and Atlantic Oceans.

KEY WORDS: Deep sea Arctic Ocean · *Eurythenes gryllus* · scavengers population dynamics

INTRODUCTION

Studies with baited time-lapse cameras and traps have revealed a large motile scavenging fauna attracted to carrion in the deep sea all over the world (Dayton & Hessler, 1972, Smith 1985, Witte 1999). In comparing the bait-attending fauna of different areas within the North Atlantic, Mediterranean Sea and the Pacific, the scavenger communities have been found to differ in terms of species composition and the numbers of individuals attracted (Christiansen 1996, Janssen et al. 2000, Legezynska et al. 2000, Priede & Merrett 1998, Priede et al. 1990, Thurston et al. 1995). In the deep-sea scavenging communities are dominated mostly by lysianassoid amphipods and large fish, both highly efficient necrophages (Christiansen et al. 1990, Priede et al. 1991). One of the most important scavenging amphipods attracted to food falls in the deep sea is the cosmopolitan lysianassoid *Eurythenes gryllus* (Lichtenstein 1822), which seems to play an important role in biological processes in deep water (Charmasson & Calmet 1990). For benthic or benthopelagic scavengers the impact of any food fall is unpredictable both in space and in time. Food falls are extremely large local organic carbon enrichments, given the low input rates of other organic matter to the deep sea. Differences are related to differences in surface productivity and the resulting export flux to the deep sea. This link, including availability of food falls, affects population densities and species composition of scavengers (e.g. Smith & Baldwin 1984, Thurston et al. 1995, Christiansen 1996).

The Fram Strait differs considerably from most other localities where baited time-lapse camera experiments have been conducted. It is a seasonally ice covered area where a cryopelagic fish and invertebrate fauna exists beneath the ice (Gradinger 1998, Poltermann 2001) and seals being prey organisms of the Arctic top predator *Ursus maritimus* rest on the ice. Oceanographic features such as eddies are thought to result in a wider dispersal of the odour plume than in other regions.

Six large food fall experiments distributed over an area of about 11700 km² were performed in the Fram Strait in order to investigate the scavenger community, its spatial and temporal distribution and its composition (species, sex ratio, length-frequency distribution).

MATERIAL AND METHODS

Study sites

The Fram Strait is the only deep connection between the North Atlantic and the Arctic Ocean and plays a significant role in global water mass exchange (Fig. 1). The various topographical structures of the Fram Strait lead to a splitting of the warm and nutrient-rich West Spitsbergen Current, carrying Atlantic water northward, into at least three parts. One part enters the Arctic Ocean north of Svalbard (33%), a second branch flows northward along the north western slope of the Yermak Plateau (45%), and the third part (22%), which for our experiments is the most relevant, recirculates immediately in Fram Strait at about 79° N (Manley 1995, Rudels et al. 2000). This region is characterised by strong annual fluctuations in ice-coverage, although the eastern part of the Fram Strait is generally ice free during the summer months (Rudels et al. 2000).

Experimental set-up

A tripod lander equipped with a baited time-lapse camera (model Simrad Mesotech Photosea 5000), a Photosea 1500SX flash, an acoustic Doppler current profiler (Aanderaa Instruments RCM11), baited traps, glass spheres for buoyancy and ballast weight was used. Two acoustic releases allowed the retrieval of the system after deployment periods lasting between 17.5 and 29.5 hours. The camera view was

centred on bait exposed on a grid which was attached to the lander about 15 cm above the seafloor covering an area of 0.7 m². Pictures (Kodak Ektachrome 200, 35 mm x 35 mm x 30 m) were taken at 3 minutes intervals. Six experiments were carried out with this configuration during two Arctic expeditions of the German RV "Polarstern" in summer 2000 and 2001 (for details see the respective cruise reports; Krause & Schauer 2001, Fahrbach 2002). All stations were situated in the Fram Strait, Arctic Ocean (Fig. 1, Table 1).

All traps were made of plastic pipes of 65 cm length with a funnel opening of 15 cm (3.5 cm at the end) and three of them were partitioned into two chambers. While bait was only in one of the chambers, bait odour could penetrate into the neighbouring chamber. About 50 g of fish was used as bait in each trap. Three traps were fixed horizontally below the grid, three others 1.20 m and 1.50 m above the seafloor, respectively.

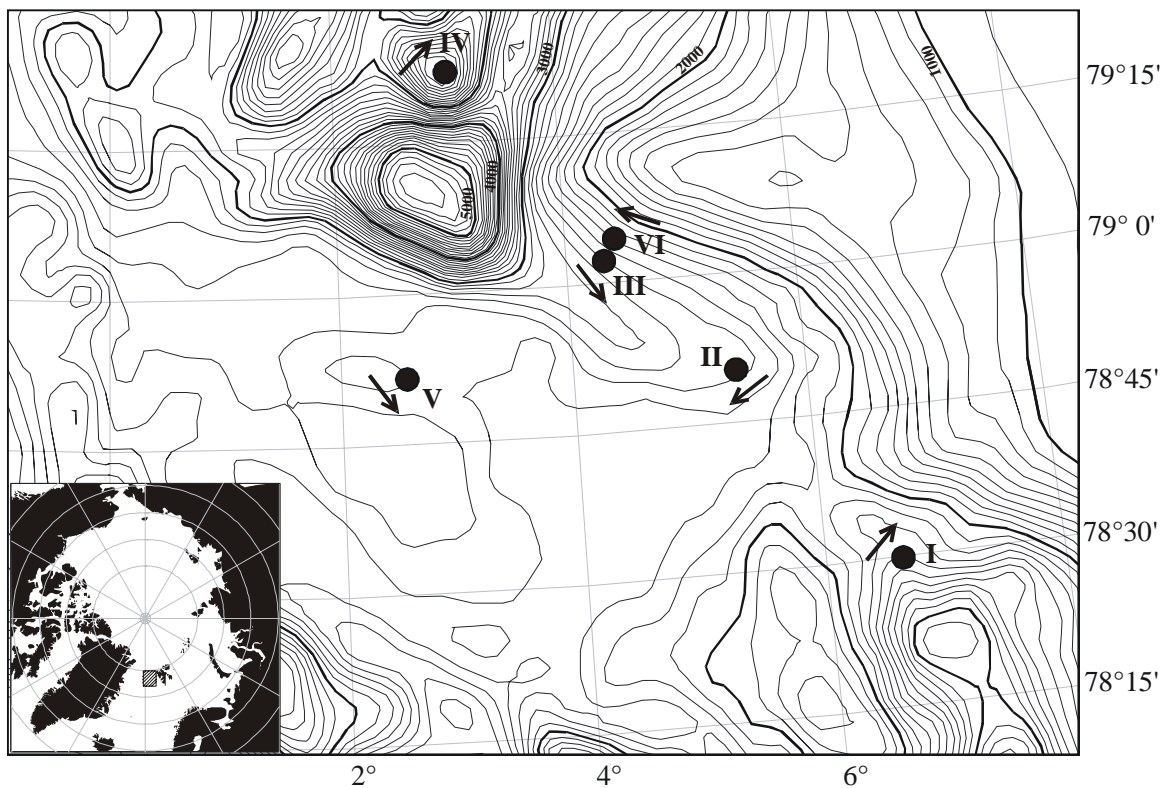


Figure 1: Locations of stations I to VI in the Fram Strait, Arctic Ocean. Arrows indicate the main bottom current direction during 1997 to 2002 (Schauer et al. submitted, Premke et al. 2003).

Freshly thawed fishes and a crustacean were used as bait at comparable mass but in different composition (Table 1). Aiming to identify food preferences by analyses of the time-lapse photographs we used as standard bait the fish species *Salmo trutta* (trout) or *Solea solea* (sole).

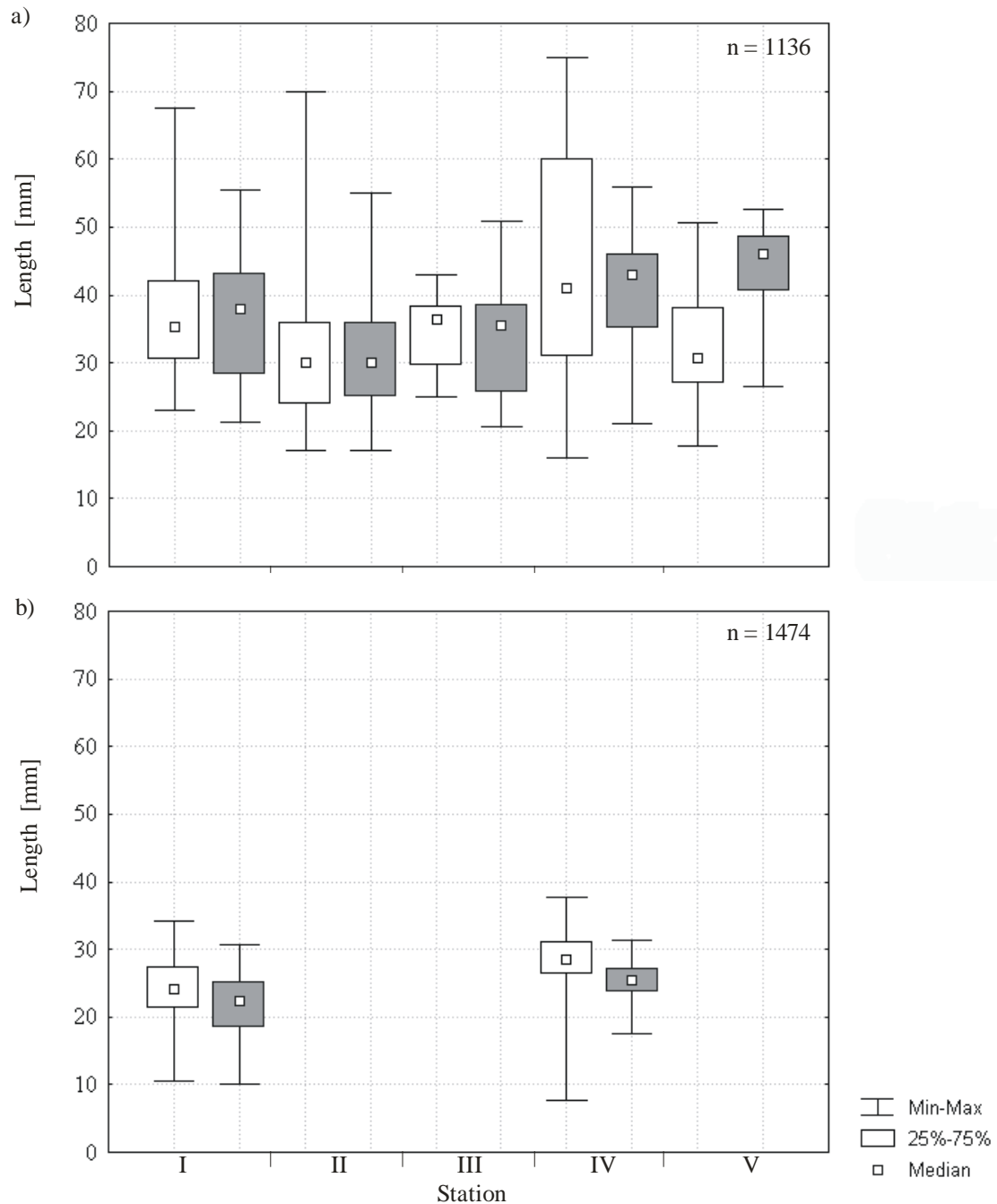


Figure 2: Box and Whisker Plot of lengths [mm] of mature females excluding juveniles (white boxes) and males (grey boxes). a) *Eurythenes gryllus*, b) *Tmetonyx norbiensis*.

Additionally, other species were used: *Psetta maxima* (turbot), *Scomber scombrus* (mackerel), *Pleuronectus platessa* (plaice), *Molva molva* (ling), *Belone belone* (garfish) and heads of *Gadus morhua* (cod), and in one case a non-fish-bait, a natant decapod (with a wet weight of ~50 g).

Post processing of photographs

Slides were examined with a stereo microscope (Olympus, 10 x 6.3 magnification) to identify and quantify all visible organisms. Individuals were counted on each slide at the beginning, then on every tenth slide and on every fifth slide during dense population structures, respectively. Amphipods visible on the slides, almost exclusively *Eurythenes gryllus* were easily identified by characteristics such as body shape, colour (red, white and pink) and eye shape. Photographic identification of individuals was difficult, especially in the case of juvenile *Eurythenes gryllus* and the adult but smaller sized *Tmetonyx norbiensis*. This will affect data analysis of photographs. Clearly, the counts of amphipod numbers obtained have to be regarded as a crude minimum estimate. The large number of amphipods attracted in our experiments, as well as their overlapping arrivals and departures after about 4 hours also impeded the determination of the number of frames over which a single individual was present.

The identification was verified by analysis of preserved individuals sampled with the baited traps on the lander. As it was difficult to distinguish between small, presumably juvenile amphipods (< 10 mm) of *E. gryllus* and amphipods belonging to the genus *Tmetonyx norbiensis* Oleröd 1987, we counted all amphipods < 10 mm together and used the proportion from captured amphipods of *E. gryllus* and *Tmetonyx norbiensis* obtained in each experiment to calculate the respective numbers of these two species. Abundances in the vicinity of the station were also calculated by applying the relationship $n = C t_{arr}^{-2}$ (after Priede & Merrett 1996), where C is a constant (for each

experiment) depending on amphipod swimming speed and current speed, and t_{arr} is the arrival time of the first amphipod after the lander reached the sea floor.

Post processing of trap material

All organisms collected with traps were fixed onboard in 4 % buffered formaldehyde. In the laboratory, animals were rinsed in fresh water and identified to species or genus level. Sex was determined by external characters, the length of each individual was measured to the nearest millimetre from the apex of the head to the tip of the telson under a stereo microscope while gently straightening the animal. Final measurements were based on average of three readings. All specimens were blotted dry and their wet weight measured individually on a micro balance. Because traps were lost during experiment VI there was no fixed material available from this experiment.

Specimens with oostegites visible under a stereo microscope were considered to be females. Presence of genital papillae between pereonite 7 and pleonite 1 identified males. Individuals without external sexual characters were considered to be juveniles. In our study, females and males of *Eurythenes gryllus* were identified at a minimum length of 16 and 17 mm, respectively. It is likely that some individuals within the juvenile category (16 - 30 mm) were unrecognised females because oostegites are difficult to detect in the very early stage of development. They were included in a second category comprising the female and larger juvenile specimens, assuming that all "juveniles" over 15 mm were unrecognised females.

Table 1: Compilation of published data on results of baited camera experiments in the deep sea regarding amphipods as the most abundant scavenger types. Asterisk indicates no data available.

| Most abundant scavenger type | Area | Depth [m] | Total time of deployment | First arrival | Photo-interval | Bait type | Calculated abundances [Ind. km ⁻²] | Max. no. image ⁻¹ | Bait weight [kg] | Consumption rate [g d ⁻¹] | Current speed [cm sec ⁻¹] | References |
|------------------------------|--------------------|-------------|--------------------------|---------------|--------------------------------|--------------------------------------|--|------------------------------|------------------|---------------------------------------|---------------------------------------|---------------------|
| <i>Eurythenes</i> | Arabian Sea | 4040 | 129 h | 0.7 h | 20 min. | shark | 216 | 9 (21 h) | 29 kg | 500 | 3 | Witte 1999 |
| <i>Eurythenes</i> | Arabian Sea | 3190 | 57.7 h | 3.5 h | 5.2 min. | tuna | 6 | 34 (23.5 h) | 3.2 | 2890 | 2.7 | Janssen et al. 2000 |
| <i>Eurythenes</i> | Arabian Sea | 3950 | 104.3 h | 0.7 h | 9.6 min. | tuna | 140 | 47 (13.2 h) | 5.1 | 4320 | 2.9 | Janssen et al. 2001 |
| <i>Eurythenes</i> | NW Atlantic | 5830 | 5 days | 3.9 h | 10 min. | mackerel | * | 5 | 0.1 | * | * | Hargrave 1985 |
| <i>Eurythenes</i> | NE Atlantic | 4009 | 24 h | 12 min. | 4 min. | grenadier fish | * | 6 | * | * | 2 - 7 | Lampitt et al. 1983 |
| <i>Ochomene, Paralicella</i> | NE Atlantic | 4855 | 26 h | 81 min. | 8 min. | squid, kippers | * | 38 (13.5 h) | * | * | * | Thurston 1979 |
| <i>Hirondellea</i> | Philippine Trench | 9605 | 16 - 29 h | 20 min. | 5 min. | fish | * | * | 1 - 3 | * | 7.5 | Hessler et al. 1978 |
| Amphipods, fish | North Atlantic | 4850 | 16.9 h | * | 2 min. | tuna | * | * | 2 | * | 2.5 | Rowe et al. 1986 |
| <i>Ochomene, Paralicella</i> | St Catalina Basin | 1310 | 4 - 56 days | * | 1 to 4 h | yellowtail mackerel | * | * | 2 - 40 | * | * | Smith 1985 |
| Fish & amphipods | NE Atlantic | 4000 - 4800 | 36 - 276 h | 40 min. | 10 to 15 min. | dolphin | * | * | 50 - 100 | 1200 - 9600 | * | Jones et al. 1998 |
| Grenadier fish | N Pacific | 4400 - 5900 | * | * | * | * | * | 5 (60 min) 12 (400 min.) | * | * | * | Priede et al. 1990 |
| <i>Eurythenes</i> | NE Pacific | 4900-5900 | * | 150 min. | video: 3 min. every 30 min. | * | * | * | * | * | * | Laver et al. 1985 |
| <i>Eurythenes, Tmetonyx</i> | Arctic Ocean (I) | 2644 | 25.5 h | 15 min. | 3 min. | 4 trouts, 1 turbot, 1 mackerel | 454 | 740 (9.75 h) | 2.7 | 2600 | 1.5-8.2 (5.8) | Premke et al. 2003 |
| <i>Eurythenes</i> | Arctic Ocean (II) | 2524 | 17.5 h | 12 min. | 3 min. | 2 soles, mackerel | 885 | 605 (14.75 h) | 2.7 | 3800 | 4.3-8.4 (4.8) | Premke et al. 2003 |
| <i>Eurythenes</i> | Arctic Ocean (III) | 2377 | 19.5 h | 24 min. | 3 min. | 4 trouts, 1 plaice, 1 shrimp | 134 | 305 (4.75 h) | 2 | 5600 | 5.3-8.9 (7.6) | Premke et al. 2003 |
| <i>Eurythenes, Tmetonyx</i> | Arctic Ocean (IV) | 1468 | 24.8 h | 21 min. | 3 min. | 2 trouts, 1 sole, 1 ling | 363 | 630 (10 h) | 5 | 5500 | 0.8-8.3 (4) | Premke et al. 2003 |
| <i>Eurythenes</i> | Arctic Ocean (V) | 2504 | 28.5 h | 21 min. | 3 min. | 3 soles, garfish | 304 | 620 (4.5 h) | 2.5 | 5000 | 1.7-7.6 (4.6) | Premke et al. 2003 |
| <i>Eurythenes</i> | Arctic Ocean (VI) | 2341 | 30.5 h | 9 min. | 3 min. | 1 sole, 5 cod-heads | 917 | 800 (14.45) | 4 | 3500 | 2.8-13.5 (7.9) | Premke et al. 2003 |

RESULTS

Lengths and abundances of amphipods

Lander deployments I to V collected 4200 amphipod individuals belonging to three species. About 700 specimens were taken randomly from the total sample for further genetic and lipid analyses, resulting in 3494 amphipods for this study, including 2003 individuals of *Eurythenes gryllus*, 1483 individuals of *Tmetonyx norbiensis* and eight individuals of *Stegocephalus* sp..

Table 2: Mean length, standard deviation and length range of *Eurythenes gryllus* and *Tmetonyx norbiensis*, all experiments combined for females, males, juveniles < 16mm and juveniles > 15 mm.

| <i>Eurythenes gryllus</i> | | Length [mm] | | | |
|---------------------------|----------------------|-------------|-------|-------|-------|
| | | N | Mean | S.d. | Range |
| Female | Experiment I-V | 491 | 34.51 | 12.05 | 16-75 |
| Juvenile > 15mm | Experiment I-V | 539 | 19.95 | 3.48 | 16-33 |
| Juvenile < 16mm | Experiment I, II, IV | 328 | 11.26 | 2,51 | 4-15 |
| Male | Experiment I-V | 645 | 34.30 | 9.42 | 17-56 |

Tmetonyx norbiensis

| | | | | | |
|------------------|-----------------------|-----|-------|------|-------|
| Female | Experiment I, III, IV | 142 | 22.03 | 4.93 | 8-34 |
| Ovigerous female | Experiment I, III, IV | 929 | 28.67 | 3.52 | 11-38 |
| Juvenile | Experiment I | 4 | 10.00 | 3.94 | 7-15 |
| Male | Experiment I, III, IV | 408 | 24.33 | 3.65 | 10-31 |

***Eurythenes gryllus*.** The mean lengths of males, females, females and juveniles and juveniles were calculated for all experiments (Table 2). Comparing mean length of adult females (34.1 mm) of all five stations to mean length of adult males (34.3 mm) there were no significant differences (ANOVA, $p > 0.05$). Considering those juveniles larger than 15 mm to be females statistical differences become significant. Among the stations significant differences were found in experiment IV, where females are larger than males and in experiment V, where males are larger than females.

Comparisons were also made for the length range of adult females and males at all of the five locations sampled. Despite similar mean body-length of the two sexes it is

obvious that females grow larger with the largest female collected being 75 mm long and the largest male 56 mm (Fig. 2, Table 2).

The mean body length of all juveniles is about 17 mm and 11 mm without juveniles > 15 mm, respectively (Fig. 3). Juveniles < 16 mm were found in experiments I, II and IV. No juveniles < 16 mm were found at station II and V (Table 2).

Experiments III and V caught fewer amphipods than I, II and IV. Mean length of females at both stations was similar (34 mm/ 31.6 mm) but the mean length of males (33.8 mm/ 43.2 mm) was significantly different (Fig. 2 and 3). The low number of captured amphipods (of both sexes) was also reflected in the photographic data where also the lowest number of amphipod occurred (Fig. 4).

Tmetonyx norbiensis. The mean sizes of males, females, ovigerous females and juveniles were determined (Table 2). High numbers of *T. norbiensis* were captured only in experiments I and IV (Table 3). Samples from experiment III contained only five individuals; three females (two of them ovigerous) and two males, with a mean body length of 26.3 mm (females) and 25.5 mm (males).

The smallest females and males identified were to 8 and 10 mm respectively. Because of a lack of external characters, four individuals were considered as juveniles. Females grow larger than males, with the largest female captured of 38 mm and the largest male of 31 mm (Fig. 5).

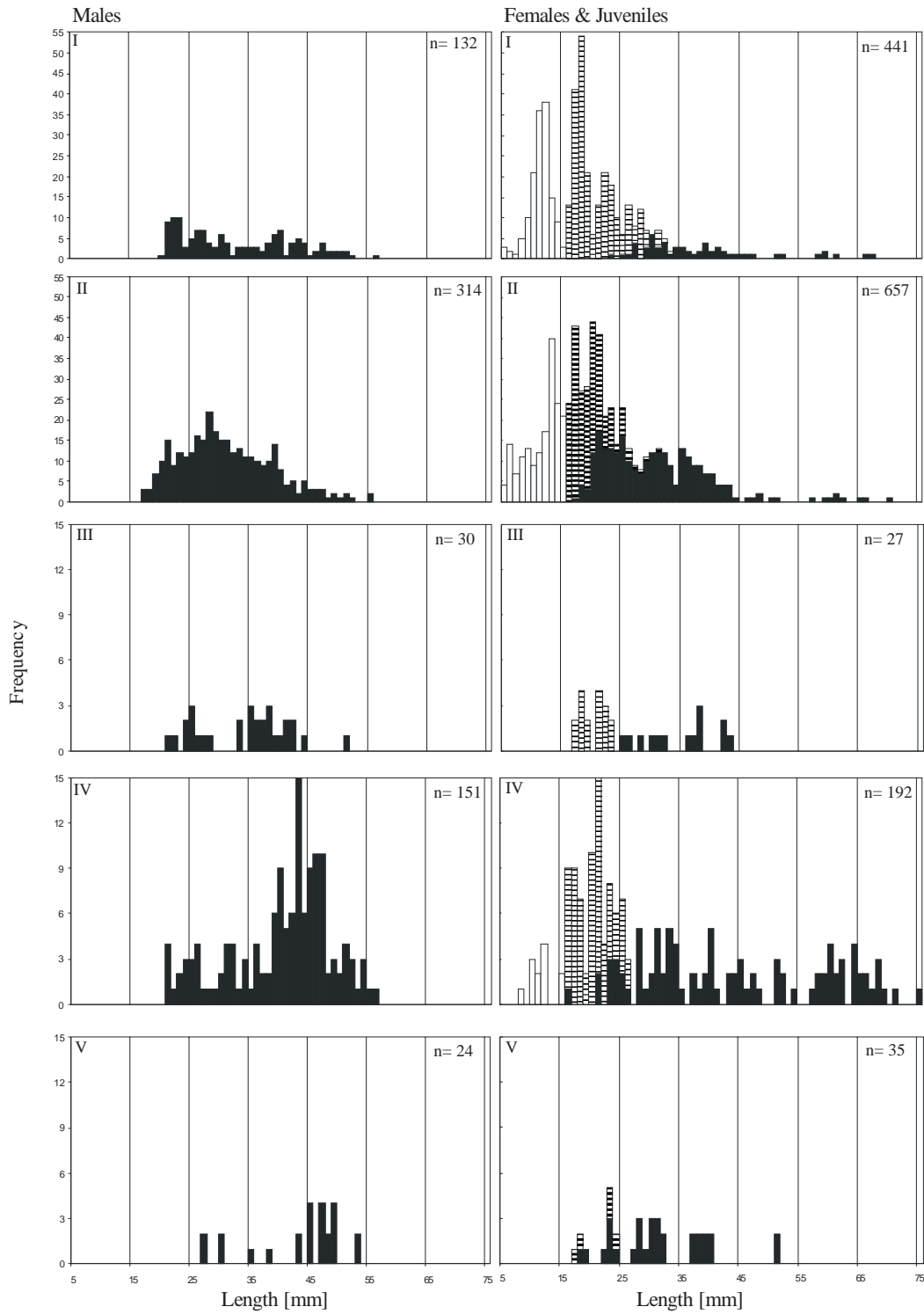


Figure 3: Length-frequency distributions of *Eurythenes gryllus* from five stations in Fram Strait based on total body length. Males (black, left figures), females (black, right figures), juveniles >16 mm (shaded) and juveniles <15 mm (white). Note the different scales of the y-axis.

Spatial distribution and aggregation dynamics of the scavenger community on bait

Scavengers captured with traps or determined on photographs belonged to five taxa (Table 1). The scavenger community on our photographs was dominated numerically by the lysianassoid amphipod *Eurythenes gryllus* followed by *Tmetonyx norbiensis*, the latter in considerably lower abundance. The third amphipod species, *Stegocephalus* sp., appeared rarely (single individuals). Other organisms which were detected on the photographs were zoarcid fish and chaetiliid isopods.

Table 3: Sex ratio of *Eurythenes gryllus* and *Tmetonyx norbiensis* for each experiment. N indicates the total number of males and females. The total number of males plus females including juveniles > 16mm and the sex ratio of males and females with juveniles > 15 mm are indicated in brackets.

| | <i>Eurythenes gryllus</i> | | <i>Tmetonyx norbiensis</i> | |
|----------------|---------------------------|-----------------|----------------------------|--------|
| | N* | ♂:♀♀* | N | ♂:♀♀ |
| Experiment I | 191 (430) | 1:0.45 (1:2.26) | 257 | 1:1.54 |
| Experiment II | 575 (799) | 1:0.83 (1:1.54) | -- | -- |
| Experiment III | 44 (57) | 1:0.46 (1:0.90) | 5 | 1:1.50 |
| Experiment IV | 264 (330) | 1:0.74 (1:1.18) | 1217 | 1:2.99 |
| Experiment V | 54 (59) | 1:1.25 (1:1.45) | -- | -- |
| Total | 1128 (1675) | 1:0.73 (1:1.57) | 1474 | 1:2.63 |

* in brackets: including juveniles > 16 mm
 -- no individuals caught

In five of our experiments the amphipod *Eurythenes gryllus* was the most abundant species, both in traps and on photographs. In the traps of experiment IV the number of *Tmetonyx norbiensis* individuals exceeded those of *E. gryllus* by a factor close to four (Figs. 3 and 5). Although *T. norbiensis* was captured frequently in two of the six experiments, this species was identified on photographs in much lower abundances.

The zoarcid fish *Lycodes* cf. *frigidus* appeared occasionally on photographs in all experiments with a maximum of six individuals per photograph (Table 1). During one experiment two fish entered one of our traps that was oriented towards the camera.

The bait inside the trap was at this point nearly consumed and only a few *Eurythenes gryllus* were still in the trap (the funnel opening was obviously too large). One fish specimen left the trap after a while but the remaining one was finally (after 8 hours) attacked by the few *E. gryllus* which were still inside the trap. The subsequent release of body fluids of the wounded fish attracted hundreds of new arriving amphipods and the fish was than skeletonized within 11 hours.

The isopod *Saduria sabina* and the amphipod *Stegocephalus* sp. were identified only occasionally on the photographs and only a single individual of *Stegocephalus* sp. was captured. In all of the experiments amphipods were found on the surface of the bait. Bait was consumed completely, after a minimum of 12 and a maximum of 28 hours leaving clean skeletons only (Table 1).

First arrivals of single individuals of *Eurythenes gryllus* were recorded after 15, 12, 24, 21, 21, and 9 minutes, respectively (experiments I - VI, minutes given are tab (time at bottom, Table 1). The maximum number of individuals differed from experiment to experiment (Fig. 4) but we also recorded differences in temporal arrival of individuals which are considered to show two types of feeding aggregations:

Type A: maximum numbers of individuals present between 10 to 24 hours tab with a maximum number of 600 – 800 individuals 0.7 m^{-2} (Fig. 4 I, II, IV, VI)

Type B: maximum numbers of individuals present between 3 to 6 hours tab with a maximum number of 300 – 600 individuals 0.7 m^{-2} (Fig. 4 III, V)

In both Types the feeding communities were dominated by large individuals during the first hours of tab and the majority of large individuals had left the food fall four hours after bait deployment arrival at the sea floor. A permanent coming and going of individuals suggested a rather short retention period at food falls, but we were unable to identify repeat visits by single specimens.

Generally, large amphipods appeared first followed by a second peak of smaller individuals. The type A aggregation is shown by experiment II in which mainly large individuals dominated the first four hours. About 10 hours later the maximum peak of

amphipods (600 individuals per 0.7 m^{-2}) consisted mainly of smaller individuals (Fig. 4 IV). The current flow during the first four hours (5.4 cm s^{-1} on average) was only slightly higher than later (4.8 cm s^{-1} on average). The opposite is illustrated in Fig. 4, experiment III type B aggregation. Current speed was rather constant throughout the experiment (7.6 cm s^{-1} on average) and the number of amphipods reached a maximum of 300 mostly larger individuals per 0.7 m^{-2} after 4.75 hours tab. After 6 hour tab the abundance declined to few individuals but than increased again to 150 mostly smaller individuals 0.7 m^{-2} by 16.5 hours tab. In contrast to experiment II, the majority of small individuals attending experiment III did not account for the maximum abundance during this experiment (Fig. 4 III).

Abundances for *Eurythenes gryllus* calculated from the time of first arrival were 454 km^{-2} (station I), 885 km^{-2} (station II), 134 km^{-2} (station III), 363 km^{-2} (station IV), 304 km^{-2} (station V) and 917 km^{-2} (station VI), respectively. The stations with high abundances of *E. gryllus* (station I, II, IV and VI) are Type A aggregations while those with low abundances (III and V) belong to Type B.

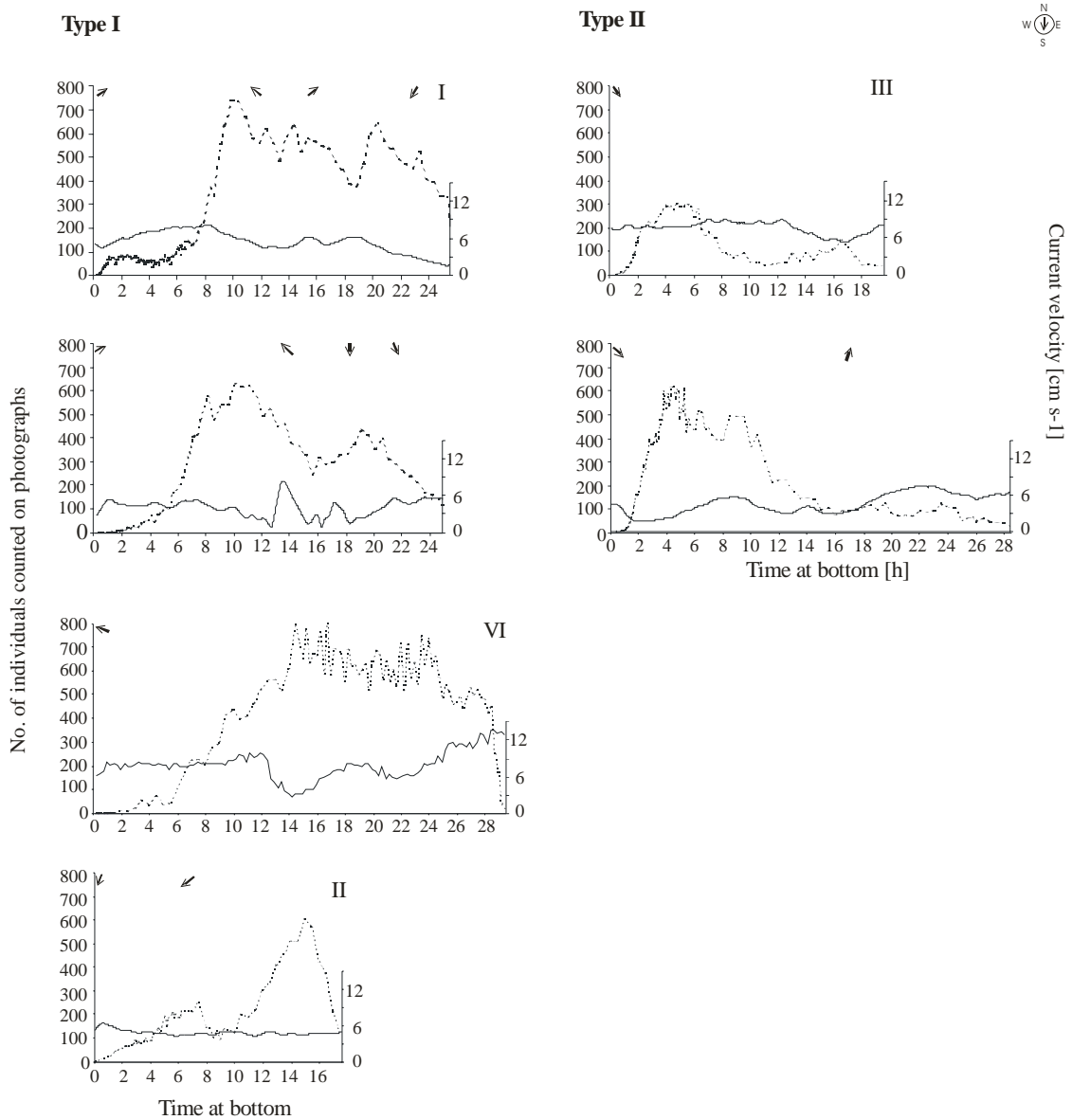


Figure 4: Temporal patterns of numbers of individuals of *Eurythenes gryllus* (dashed line) as the most abundant scavenger counted on photographs from six stations in Fram Strait and the current velocity (black line) of each experiment (right numbers). Arrows indicate change of current direction.

Food preferences and consumption rate

By counting individuals at bait species over time we identified a pronounced preference for round fish species over flat fish species in *Eurythenes gryllus*. Among the round species trout will be preferred before ling and other round fish species are attacked with equal facility. In experiment IV the first scavenging amphipods fed on trout, those

following 30 minutes later on ling and about one hour later new individuals arriving at the bait started to feed on sole. Amphipods consumed the trout within 8.5 hours tab, and four hours later the sole was skeletonized. The species which served longest as bait was the ling which needed 22 hours for total consumption (Fig. 6).

The consumption rate differed among stations and ranged from 2500 to 5500 g d⁻¹. Consumption rate at station III was divided into two rates: for the entire experiment including the relatively tiny and light shrimp it amounted to about 2500 g d⁻¹, but to a rate of 5600 g d⁻¹ if only the fish are considered.

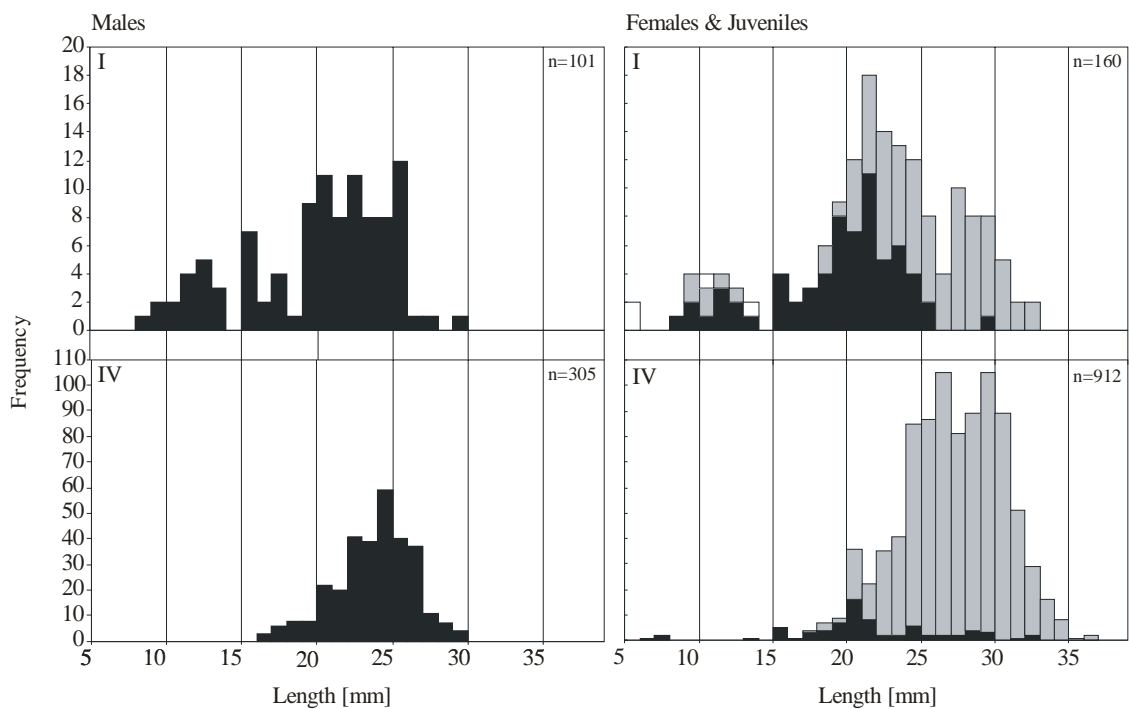


Figure 5: Length-frequency distributions of *Tmetonyx norbiensis* based on total body length for males (black, left figures), females without eggs (black, right figures), ovigerous females (grey, right figures) and juveniles (white, right figures). Note the different scales of the y-axis.

As illustrated in Fig. 4 III and V the number of amphipods increased quickly after deployment of the lander at the seafloor during these two experiments, and rapid consumption of the bait followed so that most of the bait was consumed within 10 hours. This rapid bait consumption at station III and V is related to early peak

abundance of *Eurythenes gryllus* (Type B). Although in contrast to other deployments the bait wet weight was lower in experiments III and V, i.e. 2 and 2.5 kg, respectively, the consumption rate was high with 5000 g d⁻¹ (experiment V) and even the highest calculated (5600 g d⁻¹ excluding the small shrimp) in experiment III. With bait wet weight ranging between 2.7 to 5 kg in the other experiments, consumption rates in experiments of type A were relatively low (2600 g d⁻¹ up to 3800 g d⁻¹) except station IV (5500 g d⁻¹).

Sex ratio

The ratio of males to females was determined for each location (experiment), and for all stations combined. From a reproductive point of view the most important sexual ratio is the number of mature males to mature females. For *Eurythenes gryllus* this comparison favours the mature males 1:0.7, all experiments combined (Table 3). Females of *E. gryllus* carrying eggs were never captured. The sex ratios of *Tmetonyx norbiensis* strongly favoured females 2.6:1, all experiments combined (Table 3). Because of low abundances station III was not considered. Generally, ovigerous females were more frequent than the females without eggs.

There is also a length-sex correlation between the stations, which looks approximately similar. Female body lengths of *Eurythenes gryllus* of station II, which were relatively small at the 25-75 % level (Box & Whisker Plot) compared to other stations, coincide with small body lengths for males at this station. Both, males and females at station IV contained the largest individuals (Fig. 2). There was, however, a considerable difference between the sexes at station V.

Tmetonyx norbiensis: there is also a length-sex correlation within the stations. Females and males of *T. norbiensis* at station I were smaller than those at station IV. For both species there is a correlation between photographic abundances and

numbers of amphipods captured. Fewer amphipods of *Eurythenes gryllus* on photographs correspond to fewer amphipods captured in traps (Fig. 4).

Table 4: Grouping of all stations (except station IV) in two different types, based on camera, trap and current meter data analysis.

| Type A | Type B |
|--|---|
| High maxima (600 – 800 Ind. 0.7 m ⁻²) | Low maxima (300 - 600 Ind. 0.7 m ⁻²) |
| High calculated abundances (454 – 885 km ⁻²) | Low calculated abundances (134 – 304 km ⁻²) |
| Slow increase of scavengers to maximum (10 – 24 hours) | Fast increase of scavengers to maximum (3 – 6 hours) |
| Low consumption rate (2600 – 3800 g d ⁻¹) | High consumption rate (5000 - 5300 g d ⁻¹) |
| Inconstant current direction (SSW, SE, NNE) | Constant NNW current direction |
| Juveniles caught | No juveniles caught |
| <i>Tmetonyx norbiensis</i> caught | No <i>Tmetonyx norbiensis</i> caught |

DISCUSSION

For a long time the seafloor of the deep sea was considered as a monotonous, desert-like environment colonised by only few organisms because of the high hydrostatic pressure, low temperature, absence of light and limited food supply (Svedrup et al. 1942, Dayton & Hessler 1972, Somero et al. 1983). Scientific results obtained during the second half of the last century led to a shift in the understanding of the deep-sea ecosystem (Sanders 1968). The deep-sea benthos was thought to be common and decoupled from processes such as primary and secondary production in the water column. We know today that this is only partly true and that the deep-sea benthos may receive temporarily or spatially relatively larger amounts of organic material from either aggregated phytoplankton (Thiel et al. 1989, Pfannkuche et al. 1999) or carcasses of medium and large sized invertebrates and vertebrates (Smith et al. 1989, Britton & Morton 1994, Klages et al. 2001) than previously assumed. Studies in the northeastern Atlantic revealed that macroaggregates settling from the euphotic zone at a rate of 100

– 150 m per day lead to a deposit of phytodetritus on the sediment surface. Time-lapse camera experiments in different regions of the world ocean demonstrated that the deep-sea benthic community responds rather quickly to such food supply (Rice et al. 1994). Phytodetrital material is colonized rapidly by Bacteria and Protozoa (flagellates and foraminifers), and is ingested by large deposit feeding animals (Gooday & Turley 1990).

Methodology

Baited time-lapse camera experiments from a useful approach to studying the deep-sea scavenger community because they allow a precise simulation of a naturally occurring event in the deep sea. Most of the studies summarised in Table 1 using baited traps (Thurston et al. 2002) worked on single experiment data sets, with different kind and mass of bait so any differences in composition and succession of the motile scavenger community might have been masked. It should be kept in mind that in our experiments captured organisms permitted reliable species or genus identification.

Natural food falls

The role of carcasses as a mechanism for the transfer of organic matter into the deep sea is still under discussion. Smith et al. (1989, and references cited therein) discussed the migratory routes of grey whales (*Eschrichtius robustus*) along the west coast of North America and concluded that the random distribution of whale carcasses due to natural mortality would lead to on average distance between falls of about 9 km. In another study Smith (1985) calculated that large nekton falls (2 to 40 kg) contribute only about 4 % of the energy needs of the scavenging ophiuroid *Ophiophthalmus normani* in the Santa Catalina Basin at about 1300 m water depth. The problem of such calculations is that they are based mostly on remains detected along video surveys. As

the highly motile scavenger community detects and consumes food parcels very rapidly, the probability of detecting active feeding or evidence of such parcels remains is rather low (Klages et al. 2001, Soltwedel et al. 2003). Ocean bottom seismometers, record infrequent micro-seismic events of unknown origin which may be related to the impact of falling carcasses (W. Jokat (AWI), personal communication). This kind of impact may be detected by scavenging invertebrates even at distances far beyond 100 m (Klages et al. 2002).

Abundances

The scavenging community of the deep Arctic Ocean was found to quickly discover and consume bait rapidly, as has been reported from other deep-sea areas (Hessler et al. 1978, Lampitt et al. 1983, Laver et al. 1985, Smith 1985, Rowe et al. 1986, Vinogradov & Vinogradov 1991). It was dominated by *Eurythenes gryllus* and *Tmetonyx norbiensis*. Aiming at analysing still photographs from the time-lapse camera we used a grid some 15 cm above the seafloor instead of deploying the fish bait directly on the bottom. This implies that the number of individuals being counted on each photograph is a minimum value because we cannot rule out the possibility that some amphipods are concealed by others, and that even more individuals may be below the grid. Nonetheless, we counted an extraordinary amount of individuals of *E. gryllus* on our pictures.

As the number of amphipods on pictures gives no indication of the abundances in the vicinity of the stations, we calculated them by applying the equation of Priede & Merrett (1996). They have found, that times of first arrivals of abyssal macrourids, *Coryphaenoides armatus*, correlated well with data of trawled fish density. By using this equation the average of the bottom current speed of each experiment, and a mean amphipod swimming speed (7.3 cm s^{-1} , Laver et al. 1985) enable us to calculate

abundances of *Eurythenes gryllus* in the vicinity of the lander (Table 1); it implies that the amphipods are not static but are swimming permanently (Bregazzi, 1973), so that the narrow odour plume never passes between two nearest amphipods but that one or the other will intercept the plume and move towards the bait. Given that at station I, III, IV and V the maximum of counted individuals on pictures was twice that of calculated abundances (Table 1), we could assume that the radius of approaching amphipods is more than one kilometre.

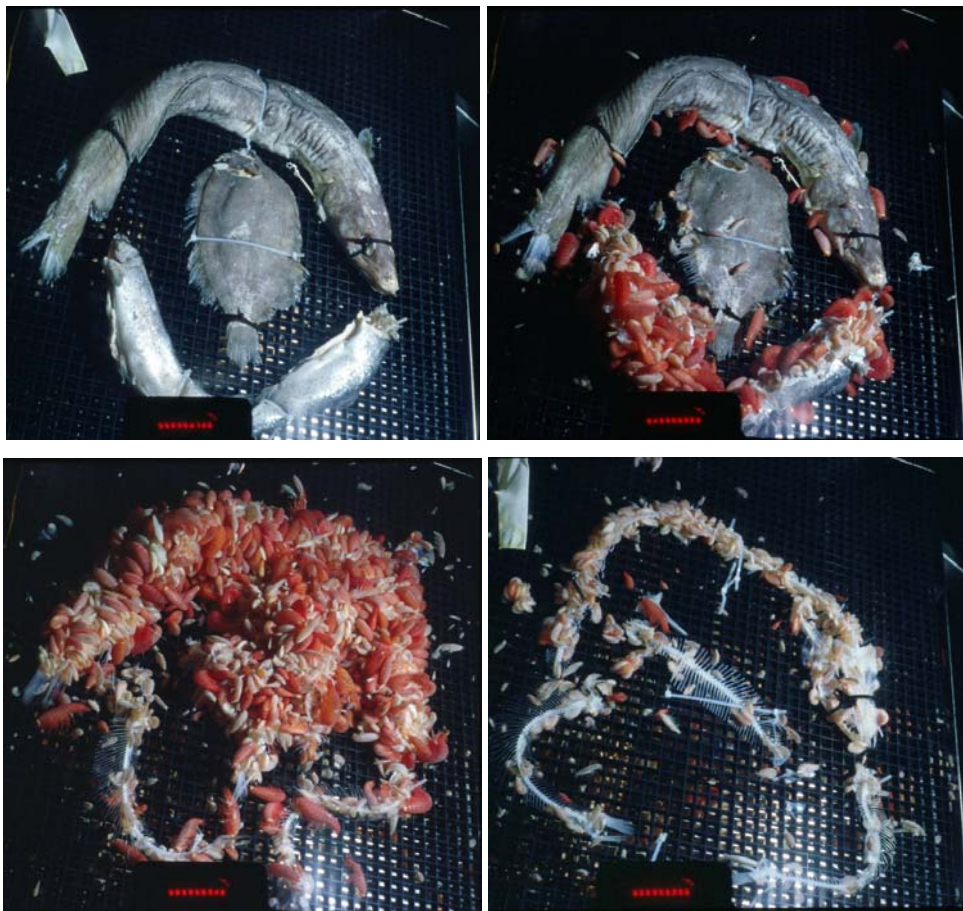


Figure 6: Example of a scavenger aggregation at station IV. Time-lapse photograph sequences at different time intervals (0, 6, 10 and 22.5 hours, time at bottom). Red, white and pink organisms were amphipods.

Frequency of occurrence

Aggregation dynamics suggest that natural food falls are quite common in the area of investigation; otherwise the population density would be lower. In a recent study Soltwedel et al. (2003) report by a video transect with a towed system close to our area of investigation. Along the 17.5 km transect covering an area of about 13500 m² a single fish skeleton (length 36 cm and biomass approx. 0.5 kg wet weight) was identified on one underwater photograph at 1280 m water depth. This scarcity of observed remains of natural food falls on underwater photographs seems to be in contrast to the assumption of frequent events. On the other hand our time-lapse camera experiments, as do those of others, clearly demonstrate that *E. gryllus* feeds rapidly on available food sources. The probability of locating an ongoing scavenger feeding process or to find the remains of a food fall decreases with time (Rowe et al. 1986). Whale skeletons have been found in different regions of the ocean (Naganuma et al. 1996, Smith et al. 1998), but surprisingly no such observation has been made for the Arctic. Polar bears (*Ursus maritimus*) hunting for seals live in the Fram Strait which is ice-covered for several months of the year. The population density of bears in our area of investigation during the winter months is unknown, but they occur frequently on Svalbard which is only about 150 km east of our study site. Wounded or dead seals attacked by polar bears are expected to settle to the seafloor but no bones have been discovered during our video transects.

Many lysianassoid amphipods are marine cold-water inhabitants and some of them contribute significantly to Antarctic and Arctic benthos (Arntz et al. 1994, De Broyer & Jazdzewski 1996). In the Antarctic other top predators such as leopard seals (*Hydrurga leptonyx*) and killer whales (*Orcinus orca*) hunt for penguins whose remains certainly also serve as food for scavengers. The higher trophic level organisation of polar ecosystems compared to more oligotrophic regions like the central Pacific Ocean, the Arabian Sea or the North Atlantic with less abundant mammals could explain the high

number of *Eurythenes gryllus* (and other scavenging amphipod species) attending our bait experiments. A tendency for *E. gryllus* to occur in higher numbers in more productive waters such as the North Pacific and Atlantic Ocean than in the oligotrophic waters like the open Pacific was also observed by other authors (e.g. Thurston 1990, Christiansen 1996).

Aggregation dynamics

Two categories (Type A & B, Table 4) of scavenger aggregations were introduced in this study, one describing a fast responding community with larger individuals appearing and leaving first, and a second one arriving later with lower numbers of individuals. The reasons for this difference are difficult to assess. Attending food falls is a risk to the individuals because cannibalism can occur, an argument that has been used to explain the absence of ovigerous females at such sites (Ingram & Hessler 1987). Amphipods are at risk of predation by attendant fish (e.g. Lampitt et al. 1983). Furthermore, developing gonads or eggs laid in the marsupium prevent gut expansion or risk the loss of the brood, thus limiting food intake (Hargrave et al. 1994). Even predatory fish are endangered when confined in the presence of voracious scavengers when food decreases in quantity (Walker 1907, Rakusa-Suszczewski 1982), our unpublished time-lapse photography observation of a zoarcid fish being killed by *Eurythenes gryllus* while captured in a trap.

The strategy of “tank-topping”, a behaviour describing feeding at a carcass until the stomach is filled, resting close by and feeding again after defecation, can be rejected for most of the large individuals of the Type A category because the size spectra clearly show that smaller individuals dominate the aggregation towards the end of the experiments.

Consumption rates

Rates of bait consumption were similar to those found in the deep Arabian Sea (Janssen et al. 2000). In the North-Atlantic bait consumption rates were considerably faster, however, there not only amphipods belonged to the scavenger community and carcasses wet weights were up to 100 kg of dolphin (Jones et al. 1998, Table 1).

The influence of different kinds of food offered has been studied and striking differences in the consumption of tuna and shark have been found (e.g. Jannasch 1978). In our experiments, the species which lasted longest as bait was the ling which needed 22 hours to become totally consumed, however this is simply explained by the difference in wet weight of trout and sole as compared to ling which was four times heavier (Fig. 6). The same was observed in experiment V, where the cod heads were preferred but finally devoured later as a result of their larger size. Due to the robust skin of flat fish we observed food preferences for round fish as compared to flat fish but no preferences within round fish.

Functional groups in scavengers

There are differences in the dominance and behaviour of *Eurythenes gryllus* and *Tmetonyx norbiensis*. Large individuals of *E. gryllus* arrived first, in high numbers, at freshly exposed bait and ingested large amounts within a short period of time, which may be a way of avoiding either competition with or being preyed upon by fish. It could also be a function of size and evolution. Hargrave (1985) also observed that amphipods arriving during the first twelve hours were larger than those arriving subsequently. *Eurythenes* stores food reserves as lipids, resulting in individuals attaining a state close to neutral buoyancy. In contrast, bathyal species of *Tmetonyx* seem not to be neutrally buoyant. Taking this advantage as early arrival relies on an active search for a carcass and once an odour trail is tracked, on high swimming speed

of larger amphipod individuals (Smith & Baldwin 1982, Sainte-Marie & Hargrave 1987). The deep-sea lysianassoids can be divided into two functional groups on the basis of morphological and physiological criteria (Sainte-Marie 1992). Individuals in the first group, including *E. gryllus* are characterised not only by their voracity but also by morphological, anatomical and physiological adaptations linked to their scavenging mode of life (Dahl 1979, Smith & Baldwin 1982). They have low metabolic rates, mandibles with a broad, shearing incisor a large corpus mandibulae, and a non-tritulative molar process and capacious guts modified for rapid batch-process feeding. They process food in large pieces passed into the oesophagus without trituration and may survive long periods without feeding (Dahl 1979, Thurston 1979). These species are assumed to utilise food at high assimilation efficiencies (Hargrave 1985, De Broyer & Thurston 1987). Individuals in the second group (*Orchomene* (s.l.) spp. *T. norbiensis* ect.) have higher metabolic rates (Smith & Baldwin 1982), less specialised mandibles with a narrow, flat corpus mandibulae and grinding molar and rather small guts. They appear to be generalist feeders (Sainte-Marie et al. 1989) process food in a more or less continuous way as small and triturated bites, and can sustain only short periods of starvation (Dahl 1979, Thurston 1979, Sainte-Marie 1984). This could explain the high abundances of the obligate scavenging amphipod *E. gryllus* at three stations vs. the infrequent occurrence of *Tmetonyx norbiensis*.

Sex ratio

For *Eurythenes gryllus* the sex ratio of mature males to mature females was almost equivalent; all experiments combined (Table 3). An equal sex ratio confirms the expectations of a continuously breeding population. This sex ratio coincides with that found in the North Atlantic Ocean (Charmasson & Calmet 1987, Christiansen et al. 1990) but is markedly different from that found in the north-eastern Pacific (Baldwin & Smith 1987), in the central North Pacific (Ingram & Hessler 1987) and south-east

Pacific at a depth of 7800 m (Thurston et al. 2002), where females dominate. In our collections only station V showed preponderance of females.

The sex ratio of *Tmetonyx norbiensis* strongly favoured females (1:2.6, all experiments combined; Table 3). Also in the eastern North Atlantic at a depth of 4855 m males of *Orchomene gerulicorbis* and *O. cavimanus* were outnumbered by females (Thurston 1979). Generally, ovigerous females of *T. norbiensis* were found more frequently than females without eggs. Breeding females of *Eurythenes gryllus* have been reported only once (Thurston & Bett 1995), which might be an indication for a different way of life compared to *T. norbiensis*.

Vertical migration

The ontogenetic migration postulated for *Eurythenes gryllus* (Christiansen et al. 1990) may be complex. With increasing size, immature *E. gryllus* move up into the water column adopting an abyssopelagic lifestyle rather than a benthic mode of existence (Ingram & Hessler 1983, Smith & Baldwin 1984, Charmasson & Calmet 1987, Christiansen et al. 1990). Our area of investigation exhibits a complex topography which has an influence on the mesoscale current regime. A number of eddies were detected over the past years, some of which circulate in opposite direction to others close by (Schauer et al. 2004). Such current conditions have an effect on the dispersal of the food odour. The horizontal extent and the rate of dispersion of an odour trace should increase with distance from the bottom because current velocity and horizontal eddy diffusion rates normally increase from the bottom to the top of the Ekman layer, thus benefiting the amphipods in the water column relative to epibenthic scavengers (Ingram & Hessler 1983). As chemoreception is the main sense involved in food fall localisation at distances of tens or even hundreds of metres in scavenging crustaceans (Premke et al. 2003), the current conditions of the Fram Strait might favour a scavenger mode of life. If brooding takes place high in the water column and the

offspring is released near the sea bed, it might be considered an iteroparous species (Ingram & Hessler 1987). Also, a residence at heights of more than 1000 m above the sea bed could remove brooding females from a foraging range of predatory abyssal fish. Pelagic predators are less risky for adult red females because they mostly use photoreception for foraging contrary to abyssal predators which rather use mechanoreception. Furthermore, ovigerous females may not feed on or actively avoid carcasses to reduce predation (Hessler et al. 1978, Baldwin & Smith 1987).

Length frequency distribution

In all our investigations combined, females of *Eurythenes gryllus* have a larger mean size compared to males. This difference is not statistically significant if we consider that individuals grouped in the “juveniles” category are females. The largest females caught measured 75 mm length while the largest male was 56 mm long. These sizes are much smaller than those found in the North Atlantic, where the largest female measured 130 mm and the largest male 90 mm (Christiansen et al. 1990) and in the central North Pacific, where the largest recorded female and male 154 mm and 122 mm respectively (Baldwin & Smith 1987). All those studies were based on traps deployed on the sea floor and up in the water column to 500 m above bottom or more. In all of these studies small individuals were captured almost exclusively on or near the sea floor, but larger organisms were distributed throughout the water column. Similar sizes to those we found were mentioned only from the upwelling area in the south-east Pacific (Thurston et al. 2002). Significant data is available on the size structure of *Eurythenes* populations from various widely separated localities (Bowmann & Manning 1972, Thurston 1979, Wickens 1983, Baldwin & Smith 1987, Charmasson & Calmet 1987, & Hessler 1987, Christiansen et al. 1990, Thurston & Bett 1995, Christiansen 1996, Thurston et al. 2002). Comparison of size at onset of maturity with earlier results would be appropriate. Also, in the light of the findings of Thurston & Bett (1995), a juvenile

specimen of 4 mm is most unexpected. Allowing for the smaller size of individuals in the Arctic populations, the Thurston & Bett data suggest a minimum hatchling size of 7 to 8 mm. Specimens of 4 mm suggest that the Arctic population differs significantly from those in other oceans, and adds weight to the possibility of the incipient speciation in '*Eurythenes gryllus*' (see Thurston et al. 2002).

Ingram & Hessler (1983) found a size range of 3-12 mm for *Orchomene gerulicorbis*. The absence of small (< 7 mm) *Tmetonyx norbiensis* individuals in our catches contrasts with previous findings. The absence of smaller *T. norbiensis* may indicate that the population is not of local origin, but results from an active immigration of older amphipods that hatched over adjacent depths. Alternative explanations might include an ontogenetic diet change – *Tmetonyx* species are adventitious necrophages at most – or seasonality of breeding, or a combination.

CONCLUSION

Scavenger aggregation dynamics and behaviour on carcasses in the Arctic Ocean differed from other reported deep-sea areas concerning the species attracted, their succession, their abundances and lengths. Scavengers attracted and their abundances seem to be directly linked to the frequency of food falls in the area. Mobile deep-sea scavengers such as the cosmopolitan amphipod *Eurythenes gryllus* must be regarded as an important component of the deep-sea food web considering their abundance and their role in the consumption, conversion and distribution of organic matter at the benthic-pelagic interface.

Further experiments in the Arctic Ocean are needed to determine if the findings of this study hold true for other areas and other seasons in this specific region, whether the same scavenger community is attracted and if we can differentiate scavenger aggregations into the two proposed categories.

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The effects of bait scents and starvation on the metabolic rate of the necrophagous deep-sea amphipod *Eurythenes gryllus* (Lichtenstein 1822)

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Abstract

In high latitude marine ecosystems the relationship between nutrition and metabolism is of particular interest for many polar organisms, since they must survive long periods without food supply. When a food fall is available, scavengers must be able to sense its presence almost immediately. These prompted us to raise the question of the metabolic requirements of these scavengers to get an idea about their energy strategy on the basis of metabolic rate and lipid resources, and how they could survive in such food-energy limited environments like the deep sea.

Laboratory experiments were carried out to measure metabolic rates of the necrophagous deep-sea amphipod *Eurythenes gryllus*. Without showing any abnormal behaviour amphipods could be successfully at atmospheric pressure kept over five month in tanks with recirculating seawater. Respiration rates of *E. gryllus* showed clearly the influence of food odour on oxygen consumption. Animals are adapted to a sporadic food source in a food limited environment by having two states of metabolism: a resting rate much like a state of dormancy and an active rate for optimal utilisation of food fall. The “active” rate exceeded the “resting” rate by approximate three times. Total lipid content of individual’s collection from the Arctic Fram Strait was measured to determine food energy storages. Oxygen consumption rates can be combined with lipid analyses to estimate the energy reserves. We calculated that scavenging amphipods such as *Eurythenes gryllus* have energy storage capabilities for long term sustenance, up to 76 days for an active rate and for up to 203 days at resting rate of metabolism.

Keywords: oxygen consumption, deep sea, *Eurythenes gryllus*, lipid, metabolic rate

Introduction

Deep-sea scavenging communities are mostly dominated by lysianassoid amphipods and large fish, both highly efficient necrophages (Christiansen et al., 1990; Priede et al., 1991). One of the most important scavenging amphipods in the deep sea attracted to food falls is the cosmopolitan lysianassoid *Eurythenes gryllus* (Lichtenstein, 1822), which seems to play an important role in biological processes in the deep-sea ecosystem (Desbruyères et al., 1985). As for benthic or benthic-pelagic scavengers the impact of any large food fall is unpredictable both in space and in time. Food falls in the deep sea represent extremely large local energy enrichment, given mostly the low input rates of other organic matter to the deep sea (Sokolova, 2000). When a food fall is

available, scavengers must be able to sense its presence almost immediately and locate the food fall directionally and efficiently. Previous studies showed that the scavenging amphipod *E. gryllus* approached a food fall within 30 minutes and occurred in high numbers (Witte, 1999; Janssen et al., 2000; Premke et al. 2003). Additionally, the marked seasonality of high latitude marine ecosystems means that the relationship between nutrition and metabolism is of specific significance also for many polar organisms, since they must survive long periods without major food supply (e.g. Clarke, 1983). Lipids are important, since they have the capability to store energy in a very efficient way. As a storage fuel they have the advantage that they can be stored in anhydrous form and represent more energy for less bulk (Gurr and Harwood, 1991). On average, carbohydrates contain about 17 kJ/g and proteins 24 kJ/g, whereas lipids have twice as much energy content (39 kJ/g) (Brody, 1945; Winberg, 1971). In the marine food web lipids play an important role to buffer the seasonality of food availability. Especially the marine zooplankton contains large amounts of lipids, particularly in copepods from Polar Regions (e.g. Lee and Hirota, 1973; Sargent and Whittle, 1981). Benthic organisms are generally less rich in lipids compared to zooplankton (Clarke, 1983; Graeve et al., 1997). However Bühring and Christiansen (2001) reported on high amounts of lipids in *Eurythenes gryllus* from the Northeast Atlantic. Considerable amounts of lipids were also found in benthic amphipods from the Weddell Sea (Graeve et al., 2001).

The Arctic deep-sea scavenging amphipod community may be an important energy mediator from carcasses to other organisms of all trophic levels. Therefore, this study aims at answering questions related especially to *Eurythenes gryllus* as a main scavenging consumer in the Arctic deep-sea ecosystem. It will concentrate on their energy budget relating it to the scarce and unpredictable impact of food in space and time, and also to assess the duration of a potential starvation phase. Determination of lipids and oxygen consumption of *E. gryllus* were performed with and without food odour.

Material and Methods

Sampling and experimental set-up

The organisms were collected in summer 2001 in the Fram Strait, Arctic Ocean (Fahrbach, 2002) (Figure 1) with baited traps fixed on a free falling tripod lander at 1468 m water depth (79°21'N, 02°59'E).

The deep-sea benthic habitat of the study area west of Svalbard is a stable environment: temperature varies between -0.5 and 1.5 °C and salinity is close to 34 ‰.

Generally it is difficult to keep deep-sea organisms in aquaria at surface pressure and temperature. *Eurythenes gryllus* is a very eurybathic but also an extreme stenothermic organism which is difficult to handle (George, 1979). Therefore, only six organisms could be used for measuring oxygen consumption rates of *Eurythenes gryllus*. Other individuals collected alive died in the aquarium or were not in good condition for measurements. The six specimens studied survived up to five months in a cooled circular tank, showing normal behaviour.

Other specimens collected from the traps were used for length-weight measurements ($n = 948$) and lipid analyses ($n = 21$).



Figure 1: Study area. Location of the station in the Fram Strait, Arctic Ocean.

Body mass, length and lipid content

All organisms used for length-weight measurements ($n = 948$) were fixed on board in 4 % buffered formaldehyde. In the laboratory, the animals were rinsed in freshwater and identified to species or genus level. Sex was determined by external characters, the length of each individual was measured to the nearest millimetre from the apex of the head to the tip of the telson under a stereo-microscope while gently straightening the dorsal curvature of the animal. Final measurements were based on an average of three readings. All specimens were blotted dry and their wet weight measured individually on a micro balance.

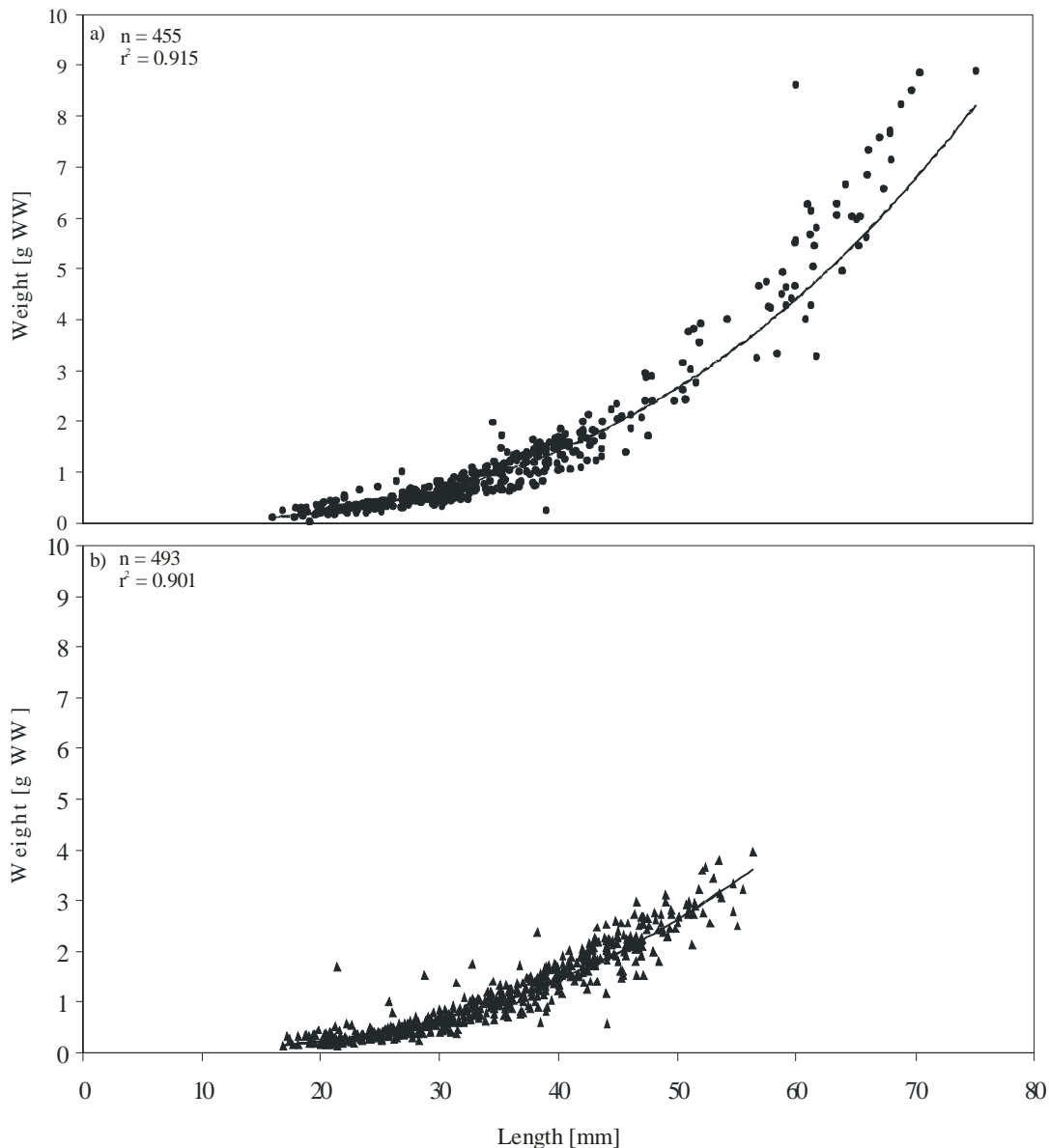


Figure 2: Wet weight [g] and length [mm] of a) female and b) male organisms of *Eurythenes gryllus*. Correlation coefficient (r^2) and individual number (n) were given.

The animals used for lipid analyses originated from the same geographical area and belonged to similar size-classes as those in the respiration studies. Twenty-one individuals of *Eurythenes gryllus* were lyophilized for 48 h in order to determine their body dry mass, followed by extraction in a solution of dichloromethane: methanol (2:1) after Folch et al. (1957) and Bligh and Dyer (1959). The total lipid content was measured gravimetrically after Hagen (2000). Lipid values were converted to energy content using caloric equivalent of 39.58 kJ g⁻¹, 9.42 cal mg⁻¹, respectively (Gnaiger and Bitterlich, 1984).

Metabolic rate

After sampling, amphipods for measuring oxygen consumption were kept in circular tanks in a cool container on board. However, mortality was high during the first days after capture. Only amphipods in good physical conditions were selected for respiration measurements. The transport of live specimens to the lab was carried out in refrigerated boxes by plane and animals were subsequently held in black circular tanks with circulating sea water at 0°C in a cool laboratory and with an oxygen saturation of 100 %. Organisms were kept under reduced red light conditions in tanks where animals were provided with pieces of 10 x 5 x 5 cm sponges as substratum.

The amphipods spent most of the time motionless, burrowed into sponges. Only three individuals (in the following named I, IV and V) were fed small pieces of shrimps one week before starting experimental run. The other organisms not fed for about five months. In order to measure oxygen consumption of routine metabolism rather than stress metabolism it was necessary to keep individuals for a period of several weeks in aquaria.

The oxygen consumption rate of *Eurythenes gryllus* was determined from the decrease of oxygen concentration in a closed recirculating flow system. It was measured by oxygen microoptodes where oxygen acts as a dynamic fluorescence quencher of a luminophore, which is immobilized in a polymer matrix. Intensity, lifetime and modulation of phase angle of the fluorescence signal are influenced by the number of oxygen molecules present and can be measured. In contrast to the original Winkler method (Winkler, 1888), oxygen microoptodes do not consume oxygen during the measurements procedure (Klimant et al., 1995). Technical details and backgrounds can be found in Holst et al. (1997), Klimant et al. (1997) and Gatti et al. (2002). Sensors consist of a fiber optical cable supplied with a standard glass fiber plug to connect it to the optode array. All data (oxygen saturation, time, phase angle, sensor number, control for background lighting) were transmitted directly to a computer for continuous data registration. Two-point calibration was performed with all microoptodes connected to the same water reservoir. Nitrogen bubbling and air bubbling were used to calibrate the 0 % and 100 % air saturation points, respectively.

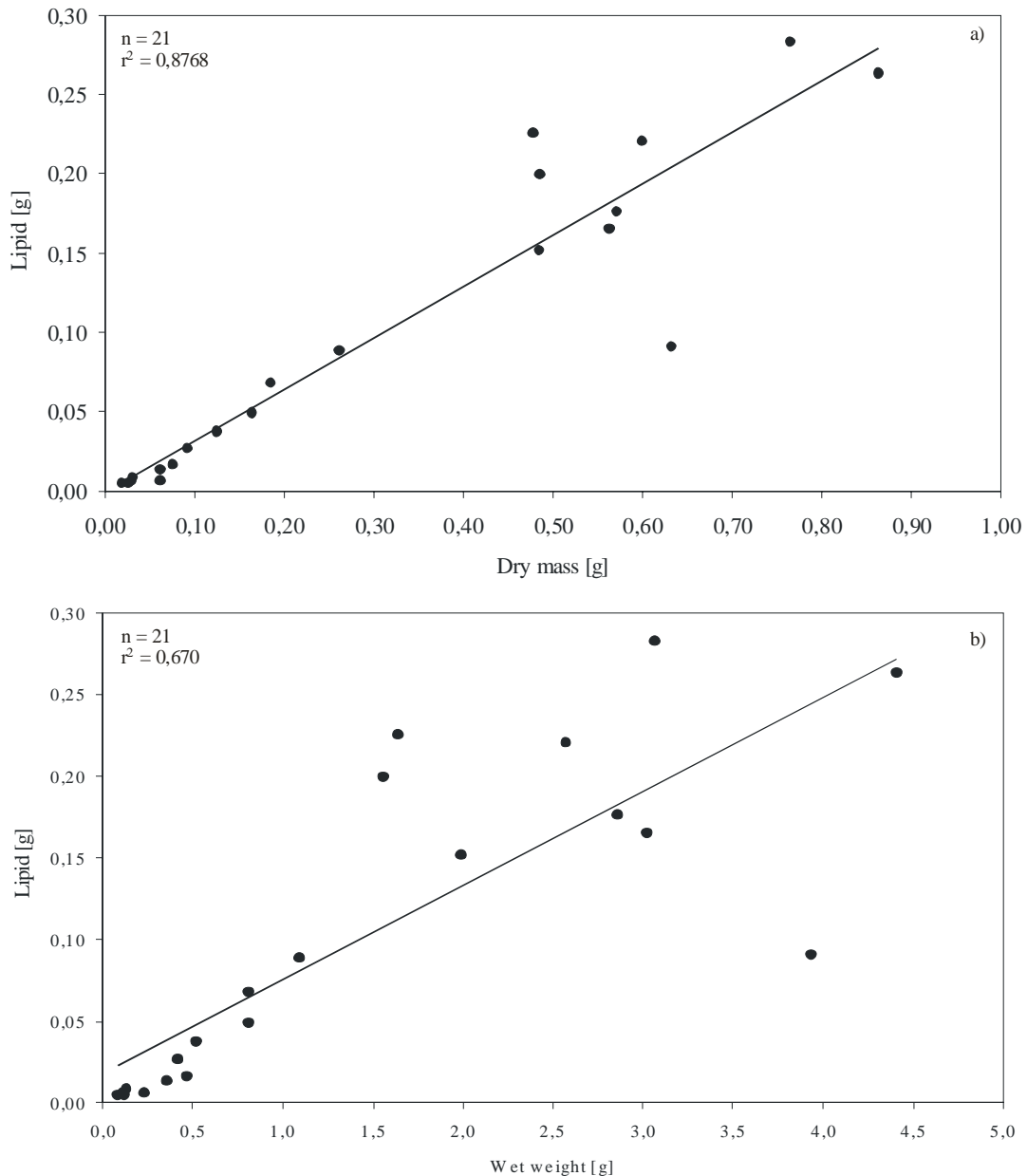


Figure 3: a) Lipid content [g] and dry mass g of the 21 organisms measured. b) Lipid content [g] and wet weight [g] of the 21 organisms measured

Amphipods were individually kept in 175 ml respiration chambers, to prevent them from swimming freely. Measurements started 20 hours (time of acclimatisation) after the transfer of amphipods into the chamber. Depending on amphipods, every individual was allowed to go through 3 to 5 repeated cycles of opening and closing of the system. Only three amphipods serving to acquire data both on resting metabolism (no food odour) and active metabolism (food odour). After a period of acclimatisation a short pulse (3 minutes) of 1 to 5 ml of food odour (1 ml food odour to individual II, 5 ml to individual III and 2 ml to individual V) was given into the water circuit. The food odour

comprised 70 percent water solution of fresh mackerele extraction. During the experiments, the chambers were submerged in a water bath, which maintained the temperature at $0^{\circ}\text{C} \pm 0.1^{\circ}\text{C}$. The circulation was closed during measurements and was open at the end of the experiment. After opening of circulation flushing of chamber was quick, optode response was immediately and usually oxygen levels were back to 100% air saturation after 10 minutes. Recordings of the dissolved oxygen concentration at three second intervals were contained only one amphipod whereas each control chamber, containing seawater. At the end of each experiment ammonium concentrations were measured in all respiration chambers to control for waste products using a test kit by Merck (Merckoquant for ammonium). In all experiments ammonium concentrations were below detection limits.

Wet weight and body length of each individual were measured immediately after the end of the experiments. Excess surface water was removed carefully with soft tissues. Amphipods were deep-frozen at -80°C for subsequent measuring of ash free dry mass (AFDM) of each individual.

Table 1: Overview of lipid analyses: wet weight, dry mass, lipid weight [g] and total lipid [%] of 21 individuals measured. Lipid values were converted to caloric equivalents using 39.58 kJ g^{-1} .

| Length^a [mm] | Wet weight [g] | Dry weight [g] | Lipid [g] | Lipid [%] | Lipid [kJ] |
|--------------------------------|-----------------------|-----------------------|------------------|------------------|-------------------|
| < 16 mm | 0.13 | 0.03 | 0.006 | 5.4 | 0.25 |
| 30 to 42 mm | 0.64 | 0.14 | 0.04 | 6.1 | 1.71 |
| 42 to 54 mm | 2.01 | 0.5 | 0.19 | 9.9 | 7.45 |
| 54 to 80 mm | 3.40 | 0.68 | 0.20 | 6.5 | 8.10 |

^a length were measured from formaldehyde samples, divided into four subclasses and compared with WW of lipid organisms measured.

Results

Length weight measurements and lipid content

It is difficult to estimate the length of organismen which may used for lipid analyses, given that animals should directly processes after taking out of the freezer. Therefore we used the length–weight relationship of formaldehyde samples to get an idea of the size classes (Figure 2 a,b, Table 1).

The body lengths of amphipods, only used for length-weight measurements correlated well with the body weight (wet weight) and ranged from 16 mm and 0.11 g to 75 mm

and 8.89 g for females and 16 mm and 0.13 g to 56 mm and 3.95 g for males (Figure 2 a,b).

Lengths of amphipods, used in oxygen experiments ranged from 34 mm to 66 mm, with a wet weight of 0.83 to 7.43 g.

The total lipid content of 21 individuals of *Eurythenes gryllus* (Figure 3) was measured in order to identify their energy reserves with respect to metabolic rate to get an idea of the metabolic requirements and sustenance time of these scavengers. Lipid weight and total lipid content of the 21 organisms were variable, ranging from 0.0053 to 0.2633 g total lipid, and 22.1 to 29.6 % total lipid of dry weight (2.3 to 13.7 % total lipid of wet weight, respectively, Figure 3). Depending on their different wet weight and estimated size of individuals, organisms were classified into for subclasses: organisms (1) up to 16 mm, (2) 30 to 42 mm, (3) 42 to 54 mm and (4) 54 to 80 mm length (Table 1). The length (resp. weight) was measured from formaldehyde samples and compared with wet weight of lipid organisms measured.

Oxygen consumption

For all six individuals the mean of oxygen consumption rates (three to five measurements) versus the body mass is shown (Figure 4 a, b). The mean oxygen consumption rate ranged from 0.11 to 2.051 ml O₂ g⁻¹ AFDM h⁻¹ (Ash Free Dry Mass) for resting specimens (no food odour) and 0.45 to 1.51 ml O₂ g⁻¹ AFDM h⁻¹ for active specimens (exposed to food odour, Table 1). Individual oxygen consumption increased with the size of specimen, except for the smallest individual which had a very high consumption rate and the largest which had a very small consumption rate (Figure 4 b). Mass specific respiration rates, however, showed an inverse relationship; they decreased with increasing specimen size, except the largest animal (Figure 4 a).

Exemplary three data sets are shown, oxygen consumption with and without food odour (Figure 5). During the resting or routine metabolism, amphipods showed no swimming activity. While the measurement cycle was closed, decrease of oxygen content within the respiration chambers was continuous and uniform (Figure 5). The decrease of oxygen saturation was uniform within single experiments and is caused by respiration. After opening of circulation flushing of chamber was quick. At least 20 hours after the transfer of amphipods into the chamber when they were in resting metabolism, a short pulse of food odour was given into the water circuit. The response was a high swimming activity and an increase of oxygen consumption, exceeding the resting consumption rates (0.01 to 0.04 ml O₂ Ind⁻¹ h⁻¹) about threefold (0.03 to 0.08 ml O₂ Ind⁻¹ h⁻¹; Figure 5 a-c). The total amount of substance (1, 2 or 5 ml of food odour) appeared not to be of influence on the activity of amphipods (Figure 5 a-c). Generally

the individuals exposed to food odour kept their higher activity until the end of the experiment.

Table 2: Body weight and length of *Eurythenes gryllus*. Mean oxygen consumption of *E. gryllus* per ind., rate per g ash free dry mass (AFDM) and rate per wet weight (WW), for both unexposed to bait (resting rate, R), exposed to bait (active rate, A). An oxycaloric equivalent of 4.86 cal ml⁻¹ O₂ was used to convert oxygen consumption values into calories.

| Individual Number | Length [mm] | Weight [g] | | Oxygen consumption | | | |
|-------------------|-------------|------------|------|--|---|---|------------------------|
| | | WW | AFDM | (ml O ₂ Ind ⁻¹ h ⁻¹) | (ml O ₂ g ⁻¹ WW h ⁻¹) | (ml O ₂ g ⁻¹ AFDM h ⁻¹) | (cal d ⁻¹) |
| I | 34 | 0,83 | 0,03 | 0,06 (R) | 0,07 (R) | 2,05 (R) | 7,13 (R) |
| II | 42 | 1,93 | 0,07 | 0,01 (R) 0,03 (A) | 0,004 (R) 0,02 (A) | 0,11 (R) 0,46 (A) | 0,86 (R) 3,72 (A) |
| III | 43,2 | 1,93 | 0,06 | 0,02 (R) 0,09 (A) | 0,01 (R) 0,05 (A) | 0,46 (R) 1,51 (A) | 2,83 (R) 10,34 (A) |
| IV | 43,2 | 2,19 | 0,07 | 0,03 (R) | 0,01 (R) | 0,37 (R) | 3,05 (R) |
| V | 44,9 | 2,21 | 0,08 | 0,03 (R) 0,09 (A) | 0,01 (R) 0,04 (A) | 0,39 (R) 1,08 (A) | 3,63 (R) 10,08 (A) |
| VI | 66 | 7,43 | 0,22 | 0,07 (R) | 0,01 (R) | 0,37 (R) | 8,42 (R) |

Discussion

Deep-sea scavengers, such as *Eurythenes gryllus*, are attracted within 10 to 30 minutes at bait after it has reached the seafloor (Hessler et al. 1978; Lampitt et al. 1983). This corroborates the theory that amphipods are able to sense nutrients almost immediately and can switch nearly promptly into an active metabolic mode to approach the food source rapidly. It was confirmed by *in situ* investigations that chemoreception is the main sense involved in food fall localisation in scavenging crustaceans (Premke et al., 2003). Also previous laboratory investigations of other scavenging amphipods or crustacean emphasised that bait attraction was a major factor in influencing oxygen consumption (Carr, 1988; Weissburg, 1997; Atema, 1998, Takeuchi and Watanbe 1998). In this study, the increased respiration rate of *E. gryllus* showed clearly the influence of food odour on oxygen consumption, given that respiration rates of *E. gryllus* not exposed to bait odour were about three times less than exposed specimens.

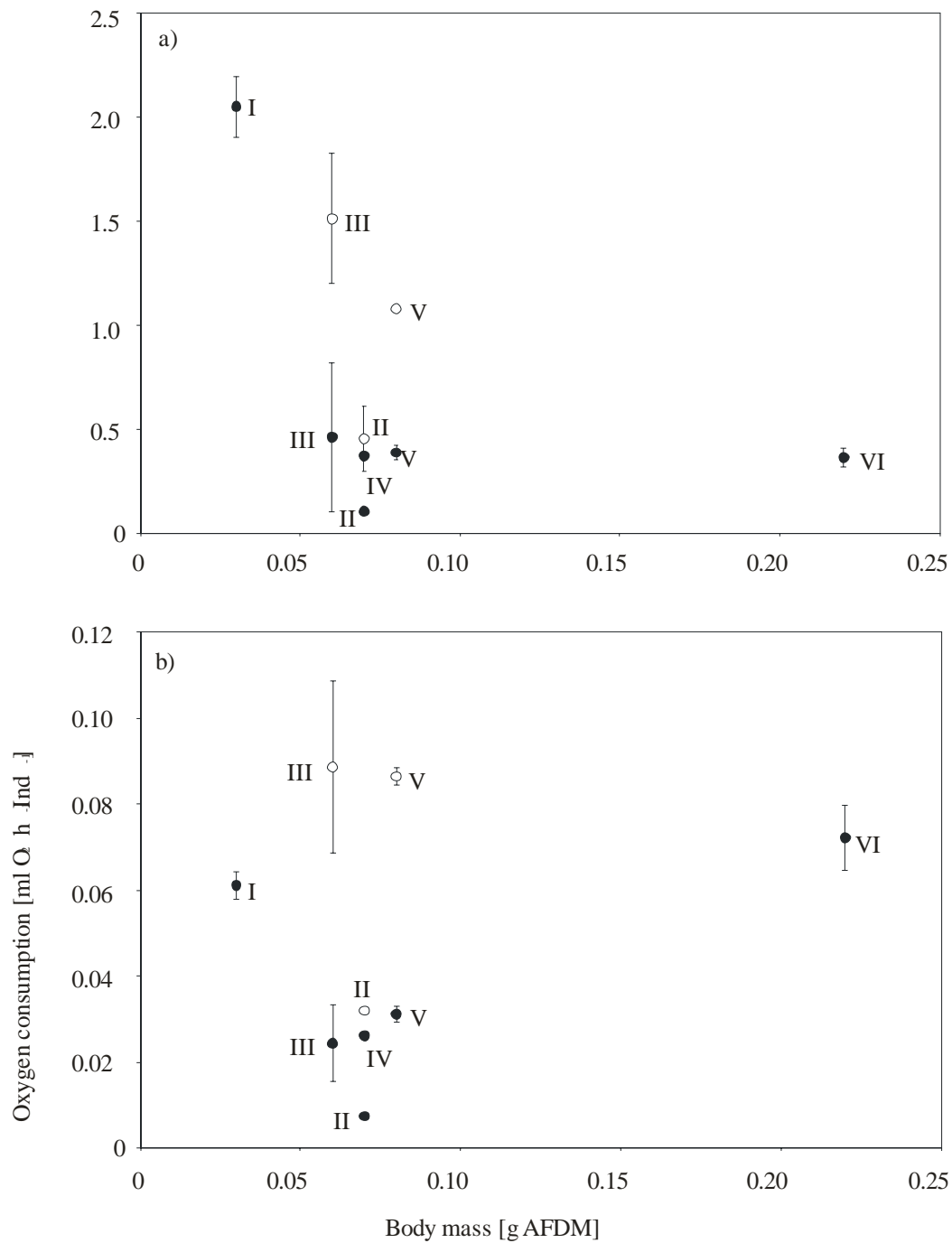


Figure 4: Oxygen consumption rate versus body mass of *Eurythenes gryllus*. a) mass specific oxygen consumption rates [ml O₂ h⁻¹ g⁻¹ AFDM] versus body mass and b) oxygen consumption rates of individuals [ml O₂ h⁻¹ Ind⁻¹] versus body mass. Latin numbers indicate order of individual numbers ○ Organisms exposed to bait, ● Organisms unexposed to bait.

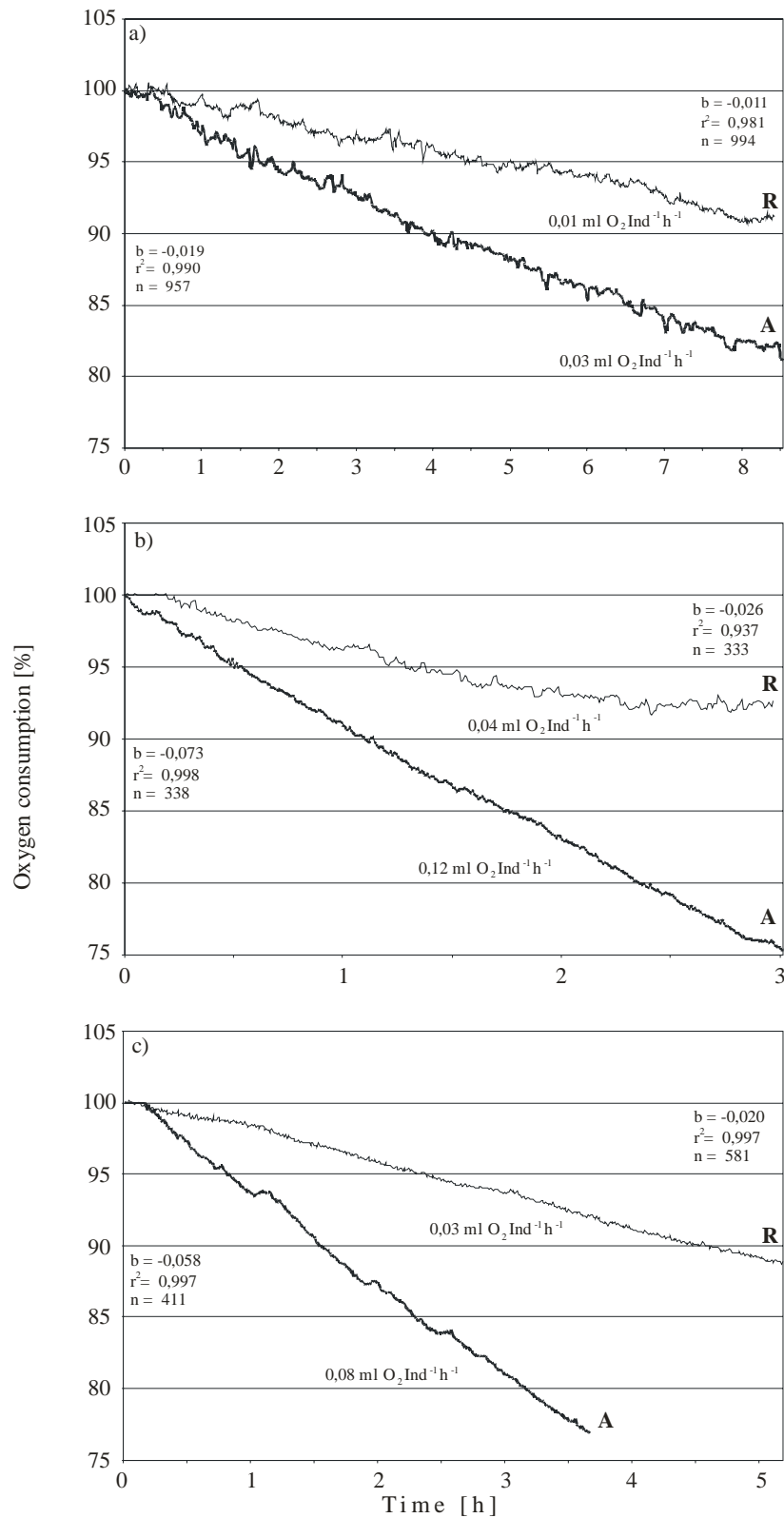


Figure 5: Effects of food odour on the metabolism of a) individual II, b) individual III and c) individual V of *Eurythenes gryllus*. Bold line: individuals exposed to bait odour (**A**ctive rate), fine line: individuals unexposed to bait odour (**R**esting rate). For every cycle, oxygen concentration per individuum, slope (b) of linear regression, correlation coefficient (r²), and number of single measurements (n) included the linear regression, are given.

The mean oxygen consumption rate ranged from 0.003 to 0.074 ml O₂ g⁻¹ WW h⁻¹ for resting and 0.01 to 0.05 ml O₂ g⁻¹ WW h⁻¹ for active rate. Similar results were figured out by George (1979) for *Eurythenes gryllus* of the Arctic Ocean at a depth of 1850 m (0.06 – 0.064 ml O₂ g⁻¹ h⁻¹). For Antarctic *E. gryllus*, trapped at 580 m, a slightly higher oxygen consumption of 0.09 ml O₂ g⁻¹ WW h⁻¹ was measured (Opalinski and Jazdzewski 1978). Differences of oxygen consumption between males and females could not be estimated due to the low number of females and males; however, in other studies no sex-related differences were found (Opalinski and Jazdzewski 1978).

During starvation (7 to 148 days) and acclimatisation time (at least 20 hours) metabolism of amphipods were going into resting rate. An active rate of metabolism was shown by a rapid increase in respiration rates of *Eurythenes gryllus* when exposed to bait (Figure 5 a-c). Smith and Baldwin (1982) ascertained an active and a resting phase of scavenging amphipods *Paralicella capresca* and *Orchomene* sp. from *in situ* respiration measurements. Increased oxygen consumption rates related to food odour have also been noted for the gastropod *Nassarius reticulatus* (Crisp et al. 1978). In the “resting” period amphipods have lower oxygen consumption and subsisted on a high lipid energy reserve.

During this phase the amphipod would maintain an intensive sensitivity to the presence of potential food falls. *In situ* long-term investigation showed that resting oxygen consumption rates of amphipods, without exposing to bait odour, as being such a state of torpor (Smith and Baldwin 1982).

When food supply is low torpor will also be used by terrestrial animals such as bumblebees, and metabolic rate is three orders of magnitude less during torpor than during active foraging (Heinrich 1975).

After the short pulse of food odour was given into the circuit, amphipods showed, besides an increasing of oxygen consumption, a high swimming activity, searching for the food-source, which continued up to the end of the experiment. The opposite was found for Antarctic deep-sea scavenging amphipods, studied *in situ* at 1300 m and 3650 m, respectively, they stopped their search approximately eight hours after capture (Smith and Baldwin 1982). Smith and Baldwin (1982) assume that this could be a metabolic strategy of organisms. However, it is surprising that all organisms stopped their activity at the same time, which could imply that such activity is not a metabolic strategy. If so, we would expect a greater intraspecific variance.

Odour plumes emanating from food falls may contain information about the quality and quantity of food source (Ritschoff 1980; Zimmer-Faust and Case 1982) as well as its distance from food source (Moore and Atema, 1988; Moore et al., 1991), potentially permitting the scavengers to make a decision whether or not to search for the odour

source. Also, the nutritional quality of food may be indicated by the ratio of amino acids to ammonia, by decreasing, the food odour characteristics in circuit changed which could lead to a termination of searching (Zimmer-Faust, 1987).

In *Waldeckia obesa*, which is an important member of the guild of Antarctic necrophagous animals (Presler, 1986; De Broyer and Klages, 1990), the effect of specific dynamic action of feeding has been shown: oxygen consumption raise by a factor of 4, where the post-prandial rise in metabolism took around 8 to 10 days to decay to the pre-feeding level (Chapelle et al., 1994). This could be explain the high respiration rate of individual I, where oxygen consumption raised by a factor of three.

Smith and Baldwin (1982) proposed three assumptions which are generally valid for deep-sea scavengers: (i) the deep sea is an oligotrophic food-energy limited environment, (ii) there is a selective advantage for those animals which optimally utilize the available food energy and (iii) large food falls are the main food source for scavengers. These assumptions could also apply for the scavenging amphipod *Eurythenes gryllus*. As this and other results showed, these amphipods could withstand long starvation periods, respond quickly and have high assimilation efficiency (Bohé-Lafrique, 1985; Sainte-Marie, 1992; Hargrave et al., 1994). Similar behaviour was described for several Arctic and Antarctic scavenging pelagic amphipods (e.g. Opalinski and Weslawski, 1989). These animals have the similar way of life and locomotors activity, but there exists differences in body size and environment.

The present measurements and literature data show that benthic amphipods exhibit a slightly higher oxygen consumption rate as compared with pelagic amphipods (Opalinski and Jazdzewski, 1978; Opalinski and Weslawski, 1989; Schmid, 1996). Respiration rates of intertidal and pelagic amphipods were about 50-times lower than those from deep-sea amphipods (e.g. Busdosh and Atlas, 1975; Childress, 1975; Opalinski, 1974). In some Antarctic species such as e.g. *Orchomenella chilensis* (Armitage, 1962), *Abyssorchomene plebs* (Rakusa-Suszczewski, 1990) or *Eusirus perdentatus* (Opalinski and Jazdzewski, 1978) a similar ratio was found. Probably higher metabolic rate of benthic amphipods as compared with pelagic ones results from higher energy consumption for respiration movements in benthic animals living in a low-oxygen environment and adapted to pumping over big volumes of water through their tube. In addition, active scavengers such as *Eurythenes gryllus* may have higher growth and metabolic rates than either deep-living species that are lethargic (George, 1979; Ingram and Hessler, 1987). Compared to the active scavenger *E. gryllus*, the lysianassoid amphipod *Waldeckia obesa* is relatively inactive. *W. obesa* has a standard metabolism of $0.009 \text{ ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$ (Chapelle and Peck, 1995) whereas mean metabolism of *E. gryllus* is three times ($0.02 \text{ ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$, resting rate), to nearly

five times higher ($0.04 \text{ ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$, active rate), respectively. Also the active Antarctic and Arctic amphipod scavengers *Abyssochomene plebs* ($0.056 \text{ ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$; Rakusa-Suszczewski, 1990) and *Anonyx nugax* ($0.1 \text{ ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$; Schmid, 1996) show higher metabolic rates than the inactive Arctic amphipod *Stegocephalus inflatus* ($0.01 \text{ ml O}_2 \text{ g}^{-1} \text{ WW h}^{-1}$; Schmid, 1996).

Based on total lipids and metabolic rates, sustenance times have been calculated for *Eurythenes gryllus*. Our measurements of total lipids with mean lipid weight of 0.1 g and mean lipid content of 6.8 % of wet weight (Table 1) are a slightly higher than those reported for other investigations of *E. gryllus* (2.1 to 4.8 %; Opalinski and Jazdzewski, 1978; George, 1979; Smith and Baldwin, 1982; Clarke, 1984; Hargrave et al., 1994, 1995; Bühring and Christiansen, 2001). This high lipid content resulted in the unusually high mean caloric content of $946.6 \text{ cal ind}^{-1}$ (Table 1) and is sufficient to maintain *E. gryllus* at the resting rate of respiration for an average of 409 days (range between 56 to 626 days) and at the active rate for an average of 152 days (range between 109 to 176 days). In fact, the net energy of lipids available to the body (metabolizable energy) is rather less than the gross energy because of excretory losses, so that we could conservatively assume that only 50 % of lipids were energy reserves. Thus, the amphipods could sustain a resting period for 203 days and an active period for 76 days without food. It is clear that *E. gryllus* can survive several months without food because of its low resting metabolic rate. Also starvation periods as long as 18 months have been reported for Antarctic amphipods (Coleman, 1991). A lower sustenance time (4.5 days for active and 96 days for resting rate) was estimated for the smaller amphipod *Paralicella capresca* (Smith and Baldwin, 1982). These data show obviously that sustenance times are higher for large than for small individuals, because of their higher lipid reserves (Table 1, Dahl, 1979, Bohé-Lafrique, 1985). On the other hand, interspecific comparisons of chemical composition must be handled with care due to variations in physiological states such as growth, sex and reproduction (Ansell, 1972; Morris, 1973).

Given a mean swimming speed of 7 cm s^{-1} (resp. 4.56 m d^{-1} , Laver et al. 1985) we calculated that amphipods require for an active day an energy expenditure of 8.05 cal d^{-1} by having an active respiration rate of $1.65 \text{ ml O}_2 \text{ ind}^{-1} \text{ d}^{-1}$ (individual of 35 mm length) and a total lipid content of 6.1 % (Table 1 and 2). Meanwhile they consume 0.12 % of their lipid energy (assuming only 50 % of total lipids represent energy storage).

Conclusion

However, further experiments are needed to clarify if the findings of this study hold true. The number of organisms used for oxygen consumption study was low due to the complicity to keep deep-sea amphipods in aquaria. Nevertheless, some clear trends in the data could be found: *Eurythenes gryllus* were found to be adapted to a sporadic food source in a food limited environment by showing two states of metabolisms: a resting rate close to a state of dormancy and an active rate (exceeding the resting rates about thrice) for optimal utilisation of food fall when available. Scavenging amphipods like *E. gryllus* are able to produce lipid stores enabling them to survive long-term starvation, up to 76 days for an active rate and for up to 203 days at a resting rate of metabolism.

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Publication IV

**What a lucky shot ! Photographic evidence for a medium-sized natural food-fall
at the deep seafloor**

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Abstract: Although the use of deep-sea imagery considerably increased during the last decades, reports on nekton falls to the deep seafloor are very scarce. Whereas there are a few reports describing the finding of whale carcasses in the deep north-eastern and south-eastern Pacific, descriptions of invertebrate or vertebrate food-falls at centimetre to metre scale are extremely rare. After four years of extensive work at a deep-sea long-term station in northern polar regions (AWI-"Hausgarten"), including large-scale visual observations with various camera systems covering some 10.000 m² of seafloor at water depths between 1250 and 5600 m, this paper describes the first observation of a fish carcass at about 1280 m water depth, west off Svålbard. The fish skeleton had a total length of 36 cm and an approximated biomass of 0.5 kg wet weight. On the basis of *in situ* experiments, we estimated a very short residence time of this particular carcass of about 7 h at the bottom. The fast response of the motile deep-sea scavenger community to such events and the rapid utilisation of this kind of organic carbon supply might partly explain the extreme rarity of such an observation.

Keywords: Food-falls, carcasses, deep-sea, imagery, scavengers

Introduction

Deep-sea benthic assemblages generally depend on particulate organic matter (POM) settling on the seafloor. Exceptions are chemosynthetic communities around hydrothermal vents and cold seeps, and assemblages of micro-organisms inhabiting the deep biosphere hundreds of meters below the seafloor. A yet undetermined fraction of POM consists of carcasses of dead invertebrates and vertebrates, covering a size range from centimetres to several metres. Whereas there are a few reports documenting whale carcasses and their fate at the deep seafloor (see Smith et al., 1998, and references therein), there is very little information on small- or medium-sized natural food-falls (< 1 m) to be found in the literature. This short note describes the first observation of a medium-sized fish carcass at a deep-sea long-term station in northern polar regions.

Methods

In summer 1999, the German Alfred Wegener Institute for Polar and Marine Research (AWI) established a deep-sea long-term station (AWI-"Hausgarten") west off Svålbard (Fig. 1) to

study causes and effects of physical, chemical and biological gradients in the deep sea within a multidisciplinary approach. Since then, various deep-sea systems equipped with video and still cameras were deployed to carry out visual observations, to supervise various sampling programmes, and to install experiments at the deep seafloor.

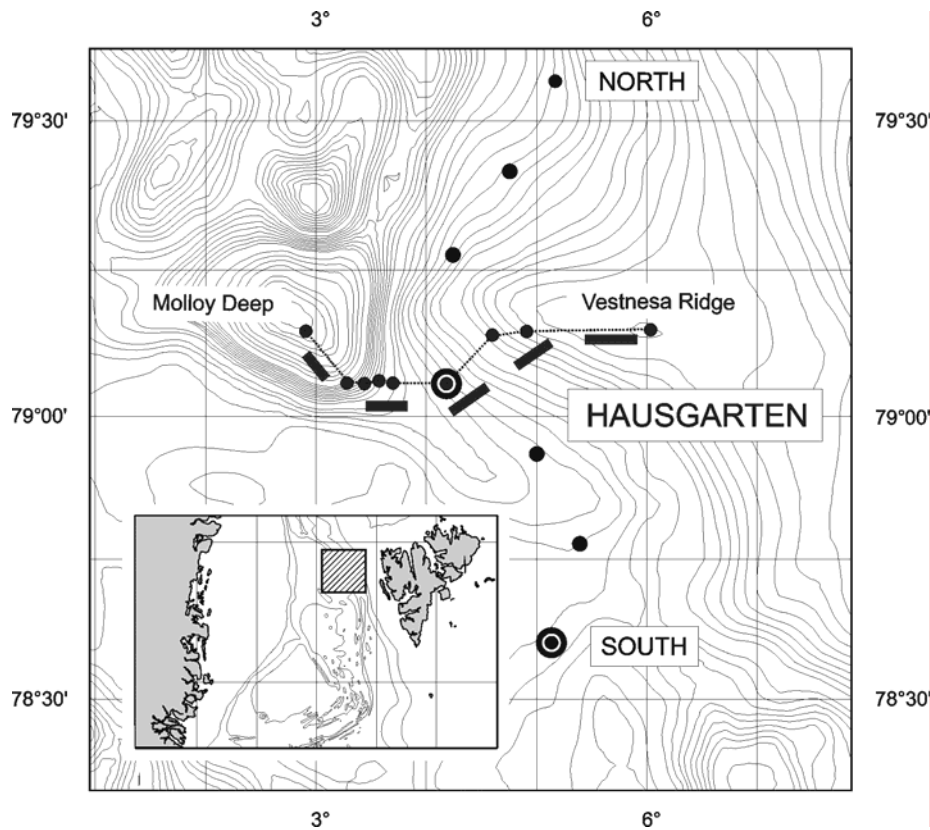


Fig. 1: The deep-sea long-term station "Hausgarten" of the Alfred-Wegener-Institute for Polar and Marine Research (●: permanent sampling sites; —: OFOS transects; ⊙: experimental areas).

An "Ocean Floor Observation System" (OFOS), a metal frame carrying a video- and 'photo-on-command' still camera, was repeatedly used to assess geological and biogenic structures, as well as epifaunal assemblages along a depth transect ranging from 1250 m (Vestnesa Ridge) to 5600 m water depth (Molloy Deep). This system was generally towed approx. 1.5 m above seafloor at an average towing speed of 0.5 kn. A laser scaling device consisting of three laser points at a distance of 50 cm enables to determine the total area covered by still camera images and to measure objects at the seafloor.

The OFOS was deployed once during RV "Polarstern" expedition ARK XIII/2 in summer 1997 at 5330-5400 m, and, recently, 4-times during RV "Polarstern" expedition ARK XVIII/1b in summer 2002 at 1270-1290, 1370-1660, 2360-2580, and 2830-3880 m water depth. Deployments along the AWI-"Hausgarten" transect yielded a total of ~ 40.000 colour slides covering a distance of 17.5 km and an area of approx. 13.500 m². A video-guided multiple

corer (MUC) was deployed for sediment sampling with prior observations of the seafloor at a vast number of sites, and several dives with a Remotely Operated Vehicle (ROV) in summers 1999 and 2001 were used to carry out large-scale surveys and to install experiments at the seafloor. Thus, till today, some hundred hours of video observations covering water depths from 1250 to 5600 m and an unknown, but clearly huge area of the seafloor off Svålbard gives a comprehensive impression of the deep-sea environment at AWI-"Hausgarten".

Results

By now, only one out of 40.000 slides produced during OFOS deployments at AWI-"Hausgarten" (RV "Polarstern" expedition ARK XVIII/1b, Station PS62/191-1, 10.08.2002, 79°08.8' N / 5°47.6' E, ~ 1280 m water depth) showed a medium-sized food-fall (Fig. 2). The skeleton identified on the slide appeared to be the remains of a 36 cm tall fish. Because of the relatively large skull with big eye holes, and due to the place where the picture was taken, the fish most probably belonged to the genus *Sebastes* (Redfish) (Stehmann, pers. comm.). This individual specimen must have had a biomass of approx. 450-500 g wet weight. It should be noted that the observed carcass is most likely a natural food-fall, as RV "Polarstern" definitely did not discard garbage near the OFOS track and boat traffic in the study area is almost zero.

To describe macrofauna communities directly associated with the carcass, a total of 66 seafloor images covering a distance of about 200 m in up-slope (25 frames) and down-slope (40 frames) directions of the food-fall were analysed for abundances and distribution patterns of epifaunal organisms. Small bright organisms with a body length of approx. 1 cm and gammaridean-like shape were considered as amphipods. Unfortunately, the identification could not be confirmed due to the lack of sample material. Since the areas covered by single images vary slightly among each other, abundances are normalised to 10 m².

The epibenthic macro- and megafauna associated with the food-fall consists mainly of

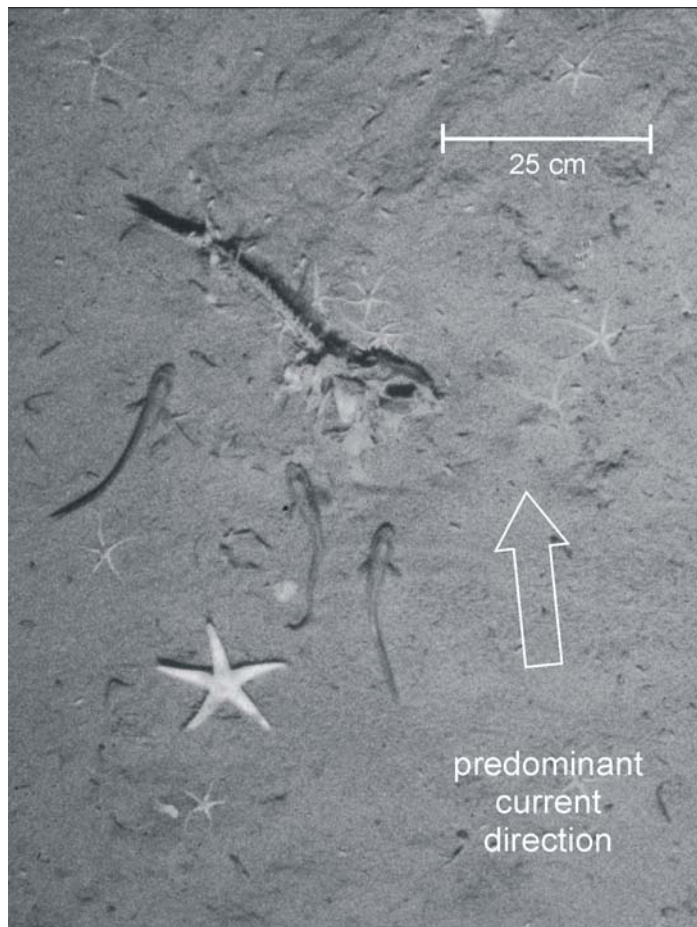


Fig. 2: Close-up of the natural food-fall (fish carcass) observed at 1280 m water depth west of Svålbard (79° 08.8' N / 5° 47,6' E)

of ophiuroids and amphipods. Ophiuroids (*Ophiocten* sp., as confirmed by species identifications out of trawl samples taken in the same area) are the predominant faunal element throughout all images analysed within this study; the mean abundance was 174 ind. / 10 m². Ophiuroid density on the slide showing the carcass (227 ind. / 10 m²) showed no significant difference from abundances analysed from up-slope or down-slope frames (Fig. 3). Nevertheless, single individuals observed on the carcass indicate that ophiuroids are obviously attracted either by the carcass itself, or by excretion products left by (other) scavengers (Fig. 2).

A different distribution pattern was observed for the organisms considered as amphipods. About 23 individuals, approx. 1 cm in length, were either directly attached to the carcass, or covered the surrounding seafloor within a circle of 0.5 m in diameter, i.e. an area of approx. 0.2 m². Additional 21 specimens were found when increasing the circle to 1 m in diameter (approx. 0.8 m²), and further 19 individuals within a circle of 1.5 m in diameter. Outside this area (approx. 1.75 m²), amphipod densities sharply drop to about 10 individuals per m². The entire food-fall slide exhibits a total of 85 amphipod specimens, corresponding to a calculated density of 245 ind. / 10 m². Densities on the other slides analysed within this study range from 18 to 93 ind. / 10 m² (mean density: 50 ind. / m²). The size of individuals fits within the size range of *Uristes* sp., which had been observed at a small food-fall in the neighbouring Molloy Deep (Klages et al., 2001).

There are three asteroids to be found close to the carcass. One specimen is apparently moving towards the carcass (there is some indication from the lifted position of one arm), two other specimens are moving in or out from different directions. On the slides analysed within this study, we observed three further asteroid specimens, but always only single individuals

per image. Other macrofauna elements eventually appearing along the OFOS transect are ceriantharians, gastropods, decapod crustaceans, and pycnogonids.

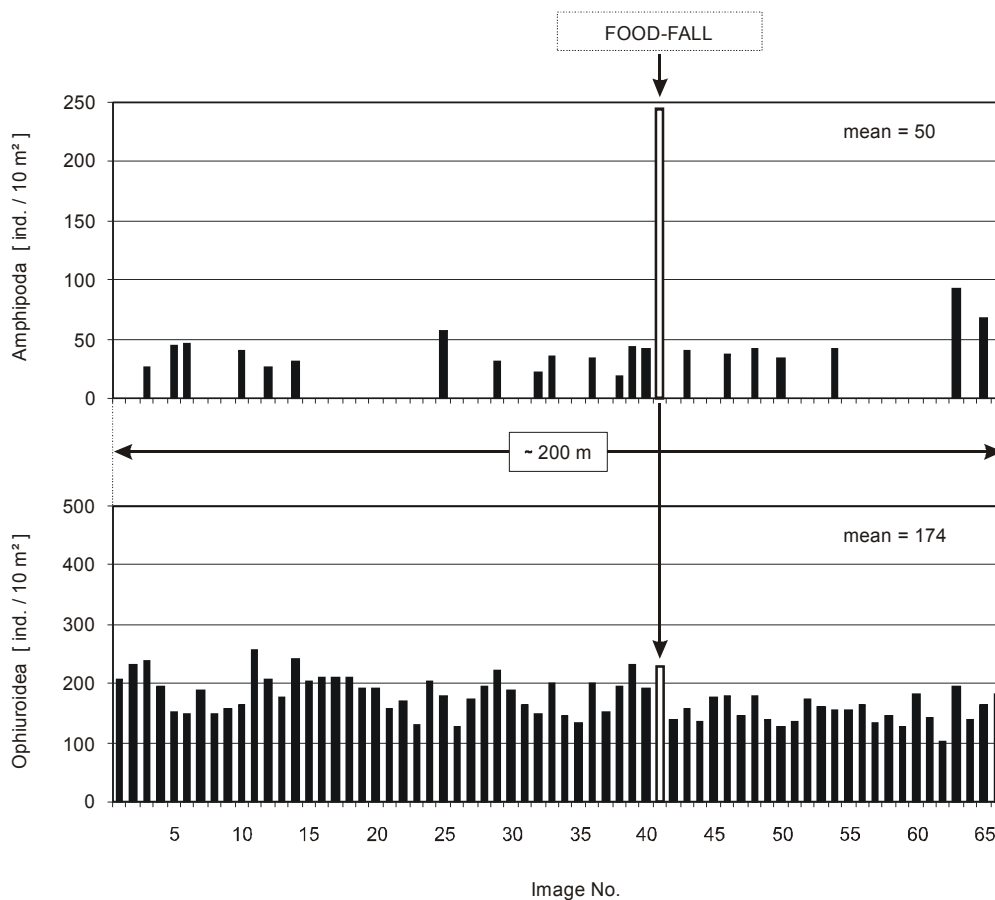


Fig. 3: Abundances and distribution patterns of amphipods and ophiuroids along the OFOS transect. White bars indicate abundances enumerated on the image (no. 41) exhibiting the fish carcass (missing bars = no data).

A total of 18 (partly juvenile?) zoarcid fishes were found evenly distributed on the slides analysed for this study, thus displaying a rather high mean density of 8 specimens per 100 m². The three 18-20 cm tall zoarcid fishes (*Pachycara* ssp.) to be found on the food-fall image, however, show a non-random dispersion in relation to the carcass, which could be specified from the following settings. OFOS aligns in towing direction with its ground distance weight at last. As OFOS was towed in an east-westerly direction and the predominant current direction in the study area is known to be to the North, we may conclude that the orientation of the zoarcid fishes is virtually with the currents (Fig. 2).

Discussion

Direct observations with manned submersibles and underwater photography during the last decades considerably increased our knowledge of the deep-sea realm. The finding of whale carcasses in the deep Pacific Ocean inspired various authors to investigate associated benthic assemblages and to study the fate of such large food-falls to the deep sea (Baco et al., 1996; Naganuma et al., 1996; Deming et al., 1997; Smith et al., 1998). In contrast, descriptions of small- or medium-sized food-falls (centimetre to metre scale) are extremely rare (Christiansen and Boetius, 2000; Klages et al., 2001), sometimes only mentioned casually within a broader context (Heezen and Hollister, 1971; Shepard and Marshall, 1975; Jannasch, 1978; Cacchione et al., 1978; Smith, 1985), and thus hard to find in the literature. By presenting data of stomach content analyses of carnivorous deep-sea invertebrates, where food remains of dead fishes, pelagic crustaceans and pteropods were identified, Sokolova (2000) gives some indirect evidence for the occurrence of smaller food-falls at the deep seafloor.

Klages et al. (2001) described the ongoing feeding process of scavengers on a 30 cm tall bathypelagic shrimp *Pasiphaea tarda* Krøyer, 1845, observed at 5551 m water depth during a ROV dive in summer 1999 in the Molloy Deep (Fram Strait), where extensive sampling and observation took place during the last four years. The recent finding of a fish carcass is actually the second observation of a natural food-fall within the same region, however, it is the first observation after surveying several 10.000 m² of the seafloor with OFOS-, MUC- and ROV-based still and video cameras. Whereas the fish skeleton was found on the upper slope, the shrimp carcass (Klages et al., 2001) was observed at the bottom of the deepest depression of the Arctic Ocean (5551 m), thereby indicating that water depth, i.e. residence time in the water column, is not a decisive factor for the detection of small- or medium-sized food-falls at the deep seafloor.

There are three different hypotheses aiming to explain, why nekton food-falls are not detected in routine deep-sea bottom surveys (Stockton and DeLaca, 1982): I. short residence times at the seafloor (i.e. rapid utilisation of food-falls by scavengers), II. temporal variability of food-fall events (observations in the wrong season?), III. spatial aggregation of food-falls, e.g. at sites with generally higher abundances of fish, or along migratory routes of large marine mammals (wrong place of the observer?). The latter two hypotheses cannot be tested at present, however, a number of *in situ* feeding experiments demonstrated that necrophages rapidly ingest and disperse carcasses efficiently within hours (e.g. Thurston, 1979; Smith, 1985; Jones et al., 1998; Janßen et al., 2000; Premke et al., 2003).

Depending on the local density of highly motile scavengers (e.g. large amphipods, fishes), the bulk of the carrion may be consumed before less motile and, hence, less competitive

organisms (e.g. small amphipods, isopods, ophiuroids) can arrive and obtain their portion of the food-fall (Smith, 1985; Jones et al., 1998). Facultative scavengers might also feed on faecal pellets produced by scavengers, which already left the scene. The fact that there were mainly ophiuroids and small amphipods to be seen on the slide exhibiting the fish skeleton probably provides evidence for a succession of scavenging organisms as depicted above.

Ophiuroids of the genus *Ophiocten*, which are abundant elements of North Atlantic and Greenland Sea deep-sea communities (e.g. Piepenburg and Juterzenka, 1994; Lamont and Gage, 1998) are reported to use deposit-feeding as a main feeding mode (Pearson and Gage, 1984). Since ophiuroids are known for their versatile feeding strategies ("omnivores"), individuals observed in the vicinity of the carcass may still benefit from the leftovers. Scavenging and microphagous feeding strategies are clearly reflected by macrofauna distribution patterns observed along the OFOS transect (Fig. 3).

A comparison of epifauna densities approx. 200 m up-slope and down-slope of the carcass documented a significant aggregation of amphipods and slightly enhanced abundances of ophiuroids and asteroids and fish in the immediate vicinity of the carcass, indicating that a variety of benthic organisms is attracted by medium-sized food-falls. The three zoarcid fishes (*Pachycara* ssp.?) attending the nekton fall most probably did not feed on the carcass, but respond to enhanced concentrations of their potential prey, i.e. the scavenging amphipods. The exploitation of scavenger aggregations by predators (fish feeding on amphipods) was observed before by the first author during feeding experiments with a ROV at the central AWI-"Hausgarten" station at 2500 m water depth in summer 1999. The zoarcid fishes attending the food-fall were oriented with the presumed currents, thereby facing at invading scavenging amphipods, attracted by the carrion odour transported in near-bottom currents.

From a feeding experiment with a baited trap at AWI-"Hausgarten" in summer 2000 we may derive to a rough estimate on how long the fish carcass might have been lying at the seafloor. The trap (20 x 20 x 60 cm) was made out of Perspex™ to allow a visual observation of activities inside the enclosure. A time-lapse camera supervising the experiment documented a large number (up to 400 individuals) of scavenging amphipods (*Eurythenes gryllus*) feeding on the bait, which consisted of 200 g of salmon filet. Nine hours after the deployment, when the bait was almost entirely eaten up by the amphipods, a 45 cm tall zoarcid fish calculated to have a wet weight of approx. 700 g entered the trap. The amphipods immediately attacked the fish, killed and finally skeletonised it within 11 hours.

The 36 cm tall fish carcass observed in summer 2002 was estimated to have had a biomass of 450-500 g wet weight. Assuming similar environmental conditions (e.g. comparable near-bottom currents dispersing the carrion odour) and a similar scavenger community feeding on the carcass, it would have taken about 7 hours between touch down to the seafloor and "converting" the entire fish to what we found on that photograph. This estimate, however,

bases on the assumption that the food-fall was in (fairly) good condition when reaching the seafloor. When considering already ongoing degradation and feeding on the nekton fall during passage through the water column, estimated residence time of the carcass at the seafloor would probably have been even shorter.

There is, to our knowledge, no information to be found in the literature which might help to estimate how long a complete fish skeleton will remain as intact as the one observed on our photograph. The degradation of the fish bones by bacteria is surely a very slow process, however, the bioturbation of larger benthic organisms will probably disintegrate, disperse and bury single bones or fragments within rather short time, that is days or weeks depending on local bioturbation rates.

The frequency of nekton falls to the deep sea is still a matter of debate. The attempt made by Smith (1985), to use animal aggregations at the seafloor exceeding mean abundances in the vicinity as an indicator for food-falls, may serve as a tool for better estimates of POM flux rates to the deep seafloor via nekton falls. The increasing use of deep-sea imagery and future automations in image analysis of both, video and still photographs, will help to refine our knowledge on the importance of POM fluxes consisting of carcasses of dead invertebrates and vertebrates in the deep-sea environment.

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