Meta bolism and physiological traits of the deep sea amphipod Eurythenes gryllus

K. Premke, M. Graeve

VIE ET MILIEU - LIFE AND ENVIRONMENT, 2009, 59 (3/4): 251-260

METABOLISM AND PHYSIOLOGICAL TRAITS OF THE DEEP SEA AMPHIPOD *EURYTHENES GRYLLUS*

K. PREMKE[1,2,], M. GRAEVE[2]*

[1] Present address: Uppsala Universitet, Limnology, Department of Ecology and Evolution, Husargatan 3, 75 123 Uppsala, Sweden
[2] Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany
** Corresponding author: Katrin.premke@ebc.uu.se*

METABOLIC RATE
OXYGEN CONSUMPTION
LIPID
DEEP SEA
AMPHIPOD
EURYTHENES GRYLLUS

ABSTRACT. – Laboratory experiments were carried out to measure standard (starved animals) and active (animals exposed to food odour) metabolic rates of the deep-sea amphipod *Eurythenes gryllus*. Six individuals could be kept alive and in good condition in the lab for several months and were used for measuring respiration rates. A considerable increase in oxygen consumption was observed following the addition of food odour. Mean specific oxygen consumption rate ranged from 0.11 to 2.05 ml O_2 g^{-1} AFDW h^{-1} for standard animals and 0.45 to 1.51 ml O_2 g^{-1} AFDW h^{-1} for active animals. Amphipods are adapted to a sporadic food source in a food limited environment by having two levels of metabolism: a standard (minimal) rate much like a state of dormancy and an active rate for optimal utilisation of food fall. The active rate was three times higher than the standard rate. Total lipid content (ranging from 22.1 to 37.6 % DW) of individuals collected from the Arctic Fram Strait was measured to calculate food energy stores. Oxygen consumption rates can be combined with lipid content 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 d for an active rate and for up to 203 d at standard rate of metabolism.

INTRODUCTION

One of the most important scavenging amphipods in the deep sea 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 other benthic or bentho-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 low input rates of other organic matter to the deep sea (Smith 1985). 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 mostly within 30 min and occurred in high numbers (Witte 1999, Janssen *et al*. 2000, Premke *et al*. 2003). Additionally, the marked seasonality of high latitude marine ecosystems implies that the relationship between nutrition and metabolism is of specific significance for many polar organisms, since they must survive long periods without major food supply (e.g. Clarke 1983, Sainte-Marie 1984).

Lipids are important, since they have the capability to store energy in a very efficient way. As a storage fuel lipids are advantageous, because they can be stored in anhydrous form and represent more energy for less bulk (Gurr & Harwood 1991). In the Arctic marine food web lipids play an important role to buffer the seasonality of food availability (Graeve *et al*. 1997, 2001).

The arctic deep-sea scavenging amphipod community is an important energy mediator from carcasses to other organisms of all trophic levels (Jones *et al*. 1998). Therefore, this study focused on the conjunction of deep-sea and high-latitude conditions and its effect on the metabolic rates and energy storage capacities of scavengers. It aims to answer questions related especially to *Eurythenes gryllus* as a main scavenging consumer in the Arctic deep-sea ecosystem; providing additional data to the limited amount of information of the energetics of deep-sea communities.

MATERIAL AND METHODS

Sampling and experimental set-up: The amphipods were collected in summer 2001 in the Fram Strait, off Spitsbergen, (79°21'N, 02°59'E) (Fahrbach 2002) with baited traps fixed on a free falling tripod lander at 1468 m water depth where temperature varied between –0.5 and 1.5°C and salinity was close to 34 ‰. Surface water temperature was cold enough (1.5-2.5°C) to recover animals in good condition.

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 extremely stenothermic animal which is difficult to handle (George 1979). Therefore, only six animals 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 animals studied survived up to five months in a cooled circular tank.

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

Body mass, length and lipid content: All animals used for length-weight measurements (n = 948) were fixed on board in 4 % buffered formaldehyde and 96 % filtered sea water. In the laboratory, the animals were identified to species level. Sex was determined by external characters. Specimens with oostegites visible under a stero 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. 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 (Christiansen *et al*. 1990). Presented values are averages of three readings. All individuals were blotted dry and their wet weight measured individually on a micro balance.

The animals used for lipid analyses originated from the same geographical area (same stations) 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 dry body mass, followed by extraction in a solution of dichloromethane: methanol (2:1) after Folch *et al*. (1957) and Bligh & Dyer (1959). The total lipid content was measured gravimetrically after Hagen (2000). For the presentation of the results, total lipid content was calculated as percentage of individual dry weight (% DW). Lipid values were converted to energy content using the caloric equivalent of 39.58 kJ g^{-1} (Gnaiger & Bitterlich 1984).

Metabolic rate: 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 %. Animals were kept under reduced red light conditions in tanks and were provided with pieces of 10 x 5 x 5 cm artificial viscose sponges as substratum.

The amphipods spent most of the time motionless, burrowed into sponges. In order to measure oxygen consumption of standard metabolism rather than stress metabolism it was necessary to keep individuals for a period of several weeks in aquaria. During starvation (70 to 148 d) and acclimatisation metabolism of amphipods were going into standard rate.

The standard metabolism is defined as a time when amphipods were unexposed to bait scent (in a state of dormancy, Smith & Baldwin 1982) whereas the active metabolism reflects exercising activity (exposed to food odour) up to the maximum possible level of maximum metabolic rate (Willmer *et al*. 2000).

For each individual *Eurythenes gryllus* the calculated mean of oxygen consumption rate (ml O_2 h^{-1}) and specific oxygen consumption rate (O_2 g^{-1} AFDW h^{-1}) (three to five measurements) was determined from the decrease of oxygen concentration. Oxygen consumption was measured by oxygen microoptodes (PreSens). The sensor consisted of a fiber optic cable supplied with a standard glass fiber plug to a one-channel optode array (Microx TX3). The sensor end, trapped in a syringe, was kept in a sensor block. Air and water tightness of syringe in the block were ensured by double o-rings. The sensor block as well as the specifically designed respiration chambers for amphipods was connected to a closed recirculating flow system. The respiration chamber was immersed in a water bath to maintain stable temperature. All data (oxygen saturation, time, phase angle, sensor number, and control for background lighting) were transmitted directly to a computer for quasi continuous (every 30 sec) data registration. Further, technical details and backgrounds can be found in Holst *et al*. (1997), Klimant *et al*. (1995, 1997) and Gatti *et al*. (2002). Two-point calibration of the optode 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.

Twenty hours before experimental measurements started amphipods were individually kept for acclimatisation in 175 ml respiration chambers. For every amphipod, three to five repeated cycles of oxygen measurements were done. Respiration chambers were opened when the oxygen concentration was below 60 %. Thus, none of the amphipods was exposed to significant lower oxygen concentrations than reported for in situ concentrations of the bottom water at the sampled stations. Therefore, a physiological stress due to unusual low oxygen concentration can be excluded.

Due to technical problems three amphipods in the experiments could only be taken for measuring standard metabolism

Table I. – Wet and dry weights of analyzed specimens, lipid content in the dry weight [%] and energy content of lipids calculated based on the caloric equivalent 39.58 kJ. Values are expressed as the mean ± SD. [a] lengths were measured from formaldehyde samples, divided into four subclasses and compared with the lipid content per WW of organisms measured.

Length[a] [mm]	Wet weight [g]	Dry weight [g]	Lipid [g]	Lipid [% DW]	Lipid energy content [kJ]	N
up 16 mm	0.13 ± 0.05	0.03 ± 0.02	0.01 ± 0.002	22.1 ± 7.85	0.25	5
30 to 41 mm	0.64 ± 0.27	0.14 ± 0.07	0.04 ± 0.028	29.5 ± 5.52	1.71	7
42 to 53 mm	2.01 ± 0.59	0.50 ± 0.04	0.19 ± 0.032	37.6 ± 7.91	7.45	4
54 to 80 mm	3.40 ± 0.75	0.68 ± 0.13	0.20 ± 0.078	29.6 ± 9.21	8.10	5

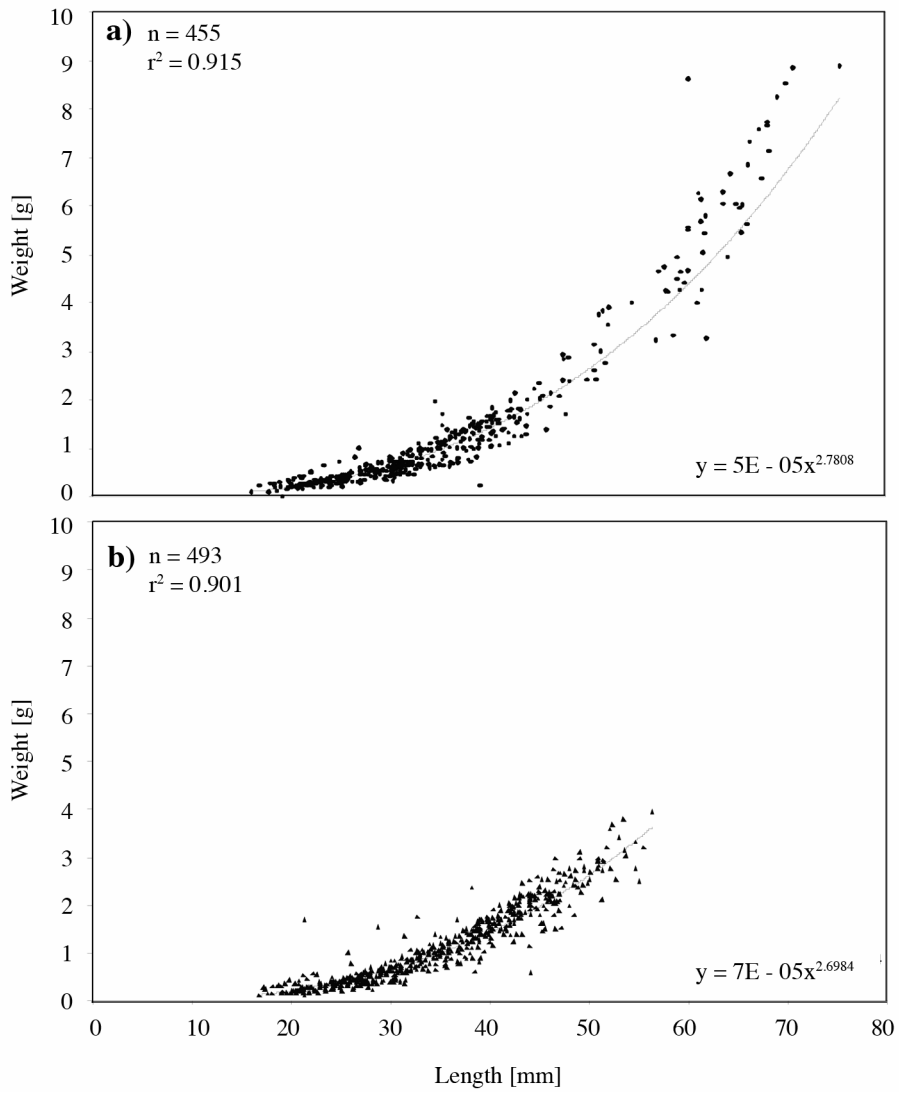

Fig. 1. – Relationship between wet weight [g] and length [mm] of a) female ($y = 5E - 05x^{2.7808}$) and b) male ($y = 7E - 05x^{2.6984}$) individuals of *Eurythenes gryllus*. Correlation coefficient (r^2) and individual number (n) were given.

(no food odour added) whereas experiments with the other three individuals were run on standard metabolism and active metabolism (food odour added). At least 20 h after the transfer of amphipods into the chamber when they were in standard metabolism, a short pulse (3 minutes) of food odour (1 ml food odour to individual II, 5 ml to individual III and 2 ml to individual V) was delivered into the water circuit. The food odour comprised a 70 % water solution of fresh mackerel extraction, made from *Scomber scombrus*.

The measurements of metabolic rate in the absence of food odour were performed days before measurements with food odour were run. During the experiments, the chambers were submerged in a water bath, which maintained the temperature at 0°C ± 0.1°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 immediate and usually oxygen levels were back to 100 % air saturation after 10 min. At the end of each experiment ammonium concentrations were measured in all respiration chambers to control for waste products using a test kit provided 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 weight (AFDW) of each individual.

RESULTS

Length weight measurements and lipid content

It is difficult to estimate the length of lipid analyzed organisms, given that the animals should be processed directly after being taken out of the freezer. Therefore, we used the length–weight relationship of the formaldehyde fixed samples to get an idea of the size classes (Fig. 1 a, b, Table I).

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

Table II. – Body length, wet weight (WW) and ash free dry weight (AFDW) of six individuals of *Eurythenes gryllus* used for oxygen consumption measurements. Oxygen consumption rates of both, starved (standard rate, SR) and exposed to bait (active rate, A) refer to: (i) individual rate, (ii) mass specific rate per gram wet weight, (iii) mass specific rate per gram ash free dry weight and (iv) energy losses in metabolism in Joules per day converted based on the oxycaloric equivalent of 20.08 J ml^{-1} O_2 (Gnaiger 1983).

Individual		**Lenght**	**Weight [g]**		**Oxygen consumption**			
Number		[mm]	WW	AFDW	(ml O_2 Ind^{-1} h^{-1})	(ml O_2 g^{-1}WW h^{-1})	(ml O_2 g^{-1}AFDW h^{-1})	(J d^{-1})
I	SR	34	0.83	0.03	0.06 ± 0.003	0.07 ± 0.01	2.05 ± 0.14	29.83
II	SR	42	1.93	0.07	0.01 ± 0.00	0.004 ± 0.00	0.11 ± 0.00	3.60
	A				0.03 ± 0.008	0.02 ± 0.01	0.46 ± 0.15	15.56
III	SR	43	1.93	0.06	0.02 ± 0.00	0.01 ± 0.01	0.46 ± 0.35	11.84
	A				0.09 ± 0.01	0.05 ± 0.01	1.51 ± 0.31	43.26
IV	SR	43	2.19	0.07	0.03 ± 0.007	0.01 ± 0.00	0.37 ± 0.01	12.76
V	SR	45	2.21	0.08	0.03 ± 0.01	0.01 ± 0.001	0.39 ± 0.03	15.19
	A				0.09 ± 0.008	0.04 ± 0.00	1.08 ± 0.00	42.17
VI	SR	66	7.43	0.22	0.07 ± 0.007	0.01 ± 0.001	0.37 ± 0.04	35.23

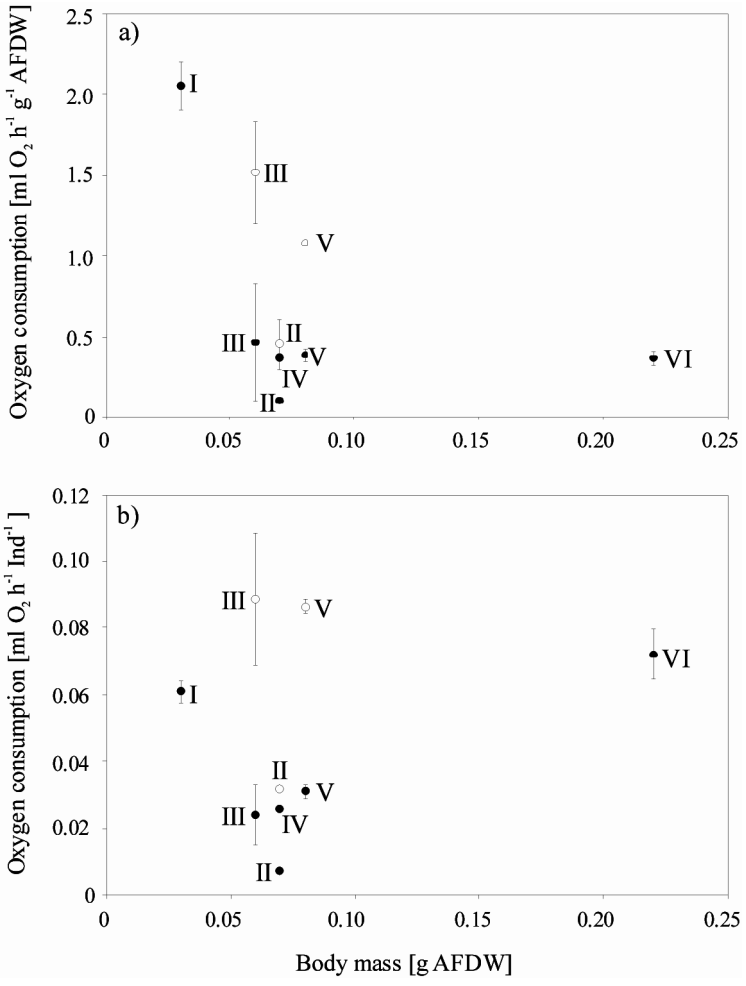

Fig. 2. – Oxygen consumption rate versus body mass of *Eurythenes gryllus*: a) mass specific oxygen consumption rates [ml O2 h^{-1} g^{-1} AFDW] versus body weight and b) oxygen consumption rates of individuals [ml O2 h^{-1} Ind^{-1}] versus body weight. Latin numbers indicate order of individual numbers. ○ Organisms exposed to food odour, ● Organisms unexposed to food odour.

to 75 mm and 8.89 g for females ($r^2 = 0.92$; $y = 5E - 05x^{2.7808}$) and 16 mm and 0.13 g to 56 mm and 3.95 g for males ($r^2 = 0.9$; $y = 7E - 05x^{2.6984}$) (Fig. 1 a, b). Values of weight (w) and length (L) are provided in the form of a conventional allometric equation: $w = a \times L^b$, where *a* (estimate of intercept) and *b* (estimate of slope) are constants.

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 (Table II).

Depending on their different wet weight and estimated size of individuals, individuals were classified into four subclasses: individuals (1) up to 16 mm, (2) 30 to 41 mm, (3) 42 to 53 mm and (4) 54 to 80 mm length (Table I). Lipid content of the 21 individuals was highly variable, ranging from 22.1 to 37.6 % DW with the mean value of 29.3 ± 8.6 % DW.

Oxygen consumption

For all six individuals the mean of oxygen consumption rates versus the body mass is shown (Fig. 2 a, b). The mean specific oxygen consumption rate ranged from 0.11 to 2.05 ml O_2 g^{-1} AFDW h^{-1} for standard specimens (no food odour) and 0.45 to 1.51 ml O_2 g^{-1} AFDW h^{-1} for active specimens (exposed to food odour, Table II). Individual oxygen consumption of amphipods unexposed to bait scents increased with the size of specimen, except for the smallest individual which had a very high consumption rate and the largest that had a very small consumption rate (Fig. 2 b). Whereas this is not true for organisms exposed to bait scents.

Exemplary three data sets are shown on oxygen consumption with and without food odour (Fig. 3). During the standard metabolism, amphipods showed no swimming activity. While the measurement cycle was closed, decrease of oxygen content within the respiration chambers was continuous and uniform (Fig. 3). The decrease of oxygen saturation was uniform within single experiments and is caused by respiration. After restarting the circulation, flushing of the chamber was quick. After adding the food odour the amphipods responded with a high swimming activity and an increase in oxygen consumption, exceeding the standard consumption rates (0.01 to 0.04 ml O_2 ind^{-1} h^{-1}) about threefold (0.03 to 0.08 ml O_2 ind^{-1} h^{-1}; Fig. 2 a-c). These experiments suggest that the total amount of substance (1, 2 or 5 ml of food odour) appeared not to be of influence on the activity of amphipods (Fig. 3 a-c). Generally the animals exposed to food odour kept their higher activity until the end of the experiment. However, we have to interpret the results carefully because we did not use artificial substrate in the respiration chamber to reduce amphipods stress, thus the data could also reflect physical or/and physiological stress.

DISCUSSION

Collection, maintenance and experimentation with arctic deep-sea animals are challenging. This study showed an influence of food odour on oxygen consumption of arctic deep-sea amphipods, given that respiration rates of *E. gryllus* not exposed to bait odour were about three times less than in exposed specimens. However, these results have to be viewed with care because only six individuals could be taken for measurements, thus, we can only speculate with the available data as to the mechanism underlying the results.

Deep-sea metabolic rate data have a particularly important role to play in this contentious area, perhaps determining the metabolic rates of animals will allow us to understand the relative importance of ecological and physical factors.

Deep-sea scavengers, such as *Eurythenes gryllus*, are attracted within 10 to 30 minutes to bait after it has reached the seafloor (Hessler *et al*. 1978, Lampitt *et al*. 1983, Premke *et al*. 2006). This corroborates the theory that amphipods are able to sense nutrients almost immediately and can switch rather promptly into an active metabolic mode to approach the food source rapidly (Sainte-Marie 1992, Hargrave *et al*. 1994). 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 crustaceans emphasized that bait attraction was a major factor in influencing oxygen consumption (Carr 1988, Weissburg 1997, Atema 1998, Takeuchi & Watanabe 1998). The metabolic rate is largely controlled amongst others by the temperature dependence of biochemical processes (Gillooly *et al*. 2001). Furthermore, Peck (2002) showed that polar cold-blood animals have a low standard metabolism, influenced by two interacting processes: a low aerobic scope (which could be related to mitochondrial function at low temperature) and the body size. Also, the largest individuals of *E. gryllus* in the Arctic Ocean are much smaller than those found in the North Atlantic and central North Pacific, but the smallest individuals are about the same size (Fig. 4).

The mean oxygen consumption rate for *Eurythenes gryllus in situ* ranged from 0.004 to 0.07 ml O_2 g^{-1} WW h^{-1} for standard rate and 0.01 to 0.05 ml O_2 g^{-1} WW h^{-1} for active rate (Table II). Similar results were found for *E. gryllus* of the Arctic Ocean at a depth of 1850 m (0.006 – 0.06 ml O_2 g^{-1} h^{-1}) (George 1979). For Antarctic *E. gryllus*, trapped at 580 m, a slightly higher oxygen consumption of 0.09 ml O_2 g^{-1} WW h^{-1} was measured (Opalinski & 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 & Jazdzewski 1978).

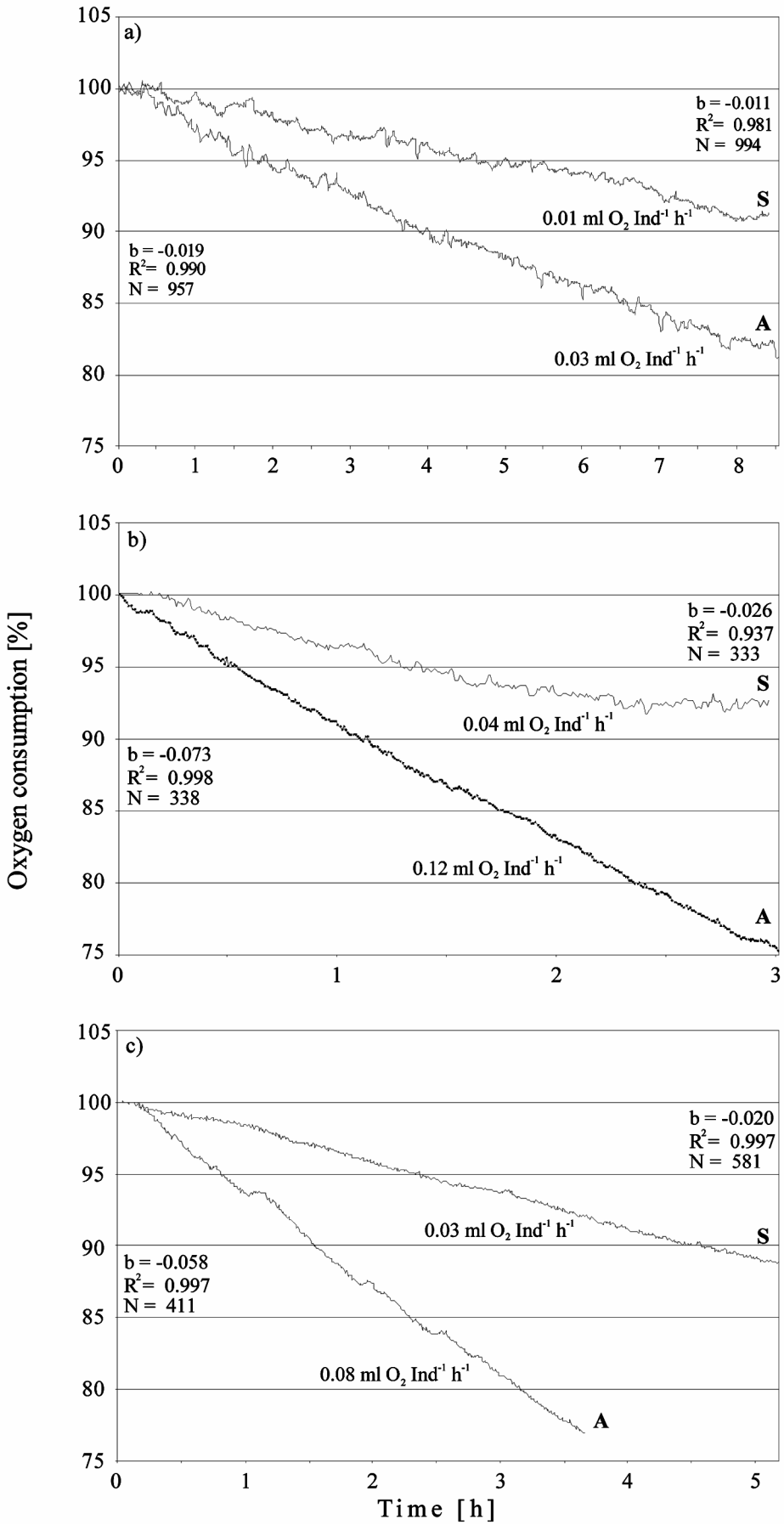

Fig. 3. – Effects of food odour on the metabolism of a) individual II, b) individual III and c) individual V of *Eurythenes gryllus*. Bold line: individuals exposed to bait odour (**A**ctive rate), thin line: individuals unexposed to bait odour (**S**tandard rate). For every cycle, oxygen concentration per individuum, slope (b) of linear regression, correlation coefficient (r^2), and number of single measurements (N) included the linear regression, are given.

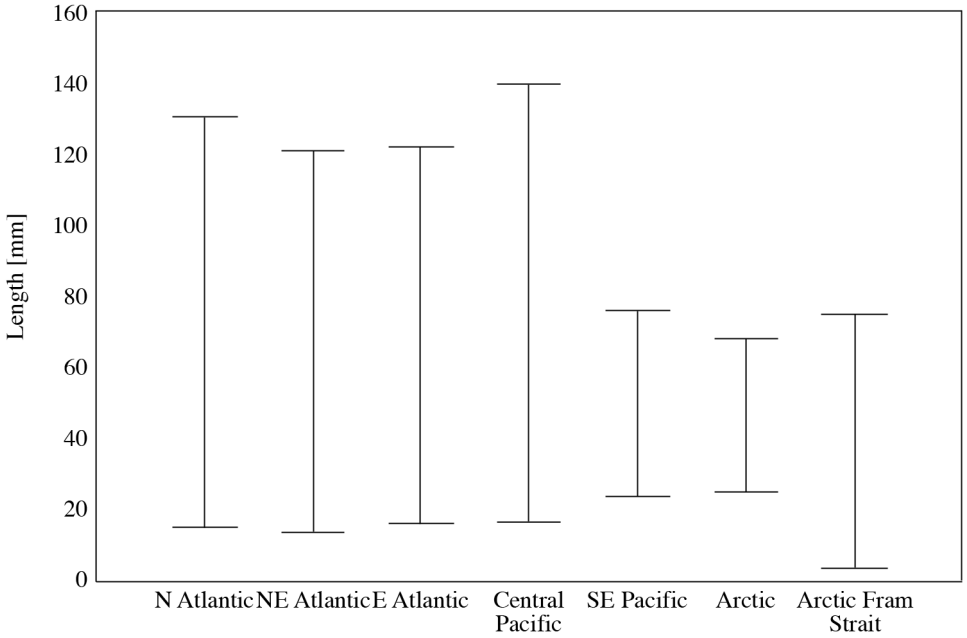

Fig. 4. – Length range of *Eurythenes gryllus* of different areas. Minima and maxima are given. Source, in the order of areas: Christiansen *et al*. 1990, Charmasson & Camlet 1987, Wickins 1983, Ingram & Hessler 1983, Thurston *et al*. 2002, Bowman & Manning 1972, Premke *et al*. 2006.

An active rate of metabolism was shown by a rapid increase in respiration rates of *Eurythenes gryllus* when exposed to bait (Fig. 3 a-c). Smith & Baldwin (1982) ascertained an active and a standard metabolism phase of *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 reticulates* (Crisp *et al*. 1978). In the standard metabolism 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 standard oxygen consumption rates of amphipods, without exposure to bait odour, are in a state of torpor or dormancy (Smith & Baldwin 1982). When food supply is low, torpor will also be used by terrestrial animals such as bumblebees, their metabolic rate is three orders of magnitude less during torpor than during active foraging (Heinrich 1975).

Odour plumes emanating from food falls may contain information about the quality and quantity of food at the source (Ritschoff 1980, Zimmer-Faust & Case 1982) as well as its distance from the food source (Moore & 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; as this ratio decreases, the food odour characteristics in a circuit changes and can lead to a termination of searching (Zimmer-Faust 1987).

Smith & 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 to the scavenging amphipod *Eurythenes gryllus* in the Arctic Ocean. As these and other results showed, amphipods can 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 & Weslawski 1989). These animals have a similar way of life and locomotor activity, but there are 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 & Jazdzewski 1978, Opalinski & Weslawski 1989, Schmid 1996). Moreover, respiration rates of intertidal and pelagic amphipods were about 50-times lower than those from deep-sea amphipods (e.g. Busdosh & 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 & Jazdzewski 1978) a similar ratio was found. Such active scavengers as *Eurythenes gryllus* may have higher growth and metabolic rates than either deep-living species that

are lethargic (George 1979, Ingram & Hessler 1987).

Compared to the active scavenger *E. gryllus*, the lysianassoid amphipod *Waldeckia obesa* is relatively inactive. *W. obesa* has a standard metabolism of 0.01 ml O_2 g^{-1} WW h^{-1} (Chapelle & Peck 1995) whereas the mean metabolism of *E. gryllus* is three times (0.02 ml O_2 g^{-1} WW h^{-1}, standard rate), to nearly five times higher (0.04 ml O_2 g^{-1} WW h^{-1}, active rate), respectively. Also the active Antarctic and Arctic amphipod scavengers *Abyssorchomene plebs* (0.056 ml O_2 g^{-1} WW h^{-1}, Rakusa-Suszczewski 1990) and *Anonyx nugax* (0.1 ml O_2 g^{-1} WW h^{-1}, Schmid 1996) show higher metabolic rates than the inactive Arctic amphipod *Stegocephalus inflatus* (0.01 ml O_2 g^{-1} 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 the mean lipid content of 6.8% of wet weight (Table I) are slightly higher than those reported for other investigations on *E. gryllus* (2.1 to 4.8 %, Opalinski & Jazdzewski 1978, George 1979, Smith & Baldwin 1982, Clarke 1983, Hargrave *et al*. 1994, 1995, Bühring & Christiansen 2001). This high lipid content resulted in the unusually high mean caloric content of 3.96 kJ ind^{-1} (Table I) and is sufficient to maintain *E. gryllus* at the standard rate of respiration for an average of 409 d (range between 56 to 626 d) and at the active rate for an average of 152 d (range between 109 to 176 d). 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 standard period for 203 d and an active period for 76 d without food. It is clear that *E. gryllus* can survive several months without food because of its low standard metabolic rate. Also starvation periods as long as 18 months have been reported for Antarctic amphipods (Coleman 1991). A lower sustenance time (4.5 d for active and 96 d for standard rate) was estimated for the smaller amphipod *Paralicella capresca* (Smith & Baldwin 1982). These data obviously show that sustenance times are higher for large, compared to small individuals, because of their higher lipid reserves (Table I, Dahl 1979, Bohé-Lafrique 1985). On the other hand, interspecific comparisons of chemical composition must be viewed 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 33.7 J d^{-1} by having an active respiration rate of 1.65 ml O_2 ind^{-1} d^{-1} (individual of 35 mm length) and a total lipid content of 6.1 % (Table I and II). Meanwhile they consume 0.12 % of their lipid energy (assuming only 50% of total lipids represent energy storage).

However, further experiments are needed to clarify if the findings of this study hold true keeping in mind that the study based on a small number of samples. Nevertheless, they amplify and confirm previous studies that metabolic rates of *E. gryllus* increased while exposed to fish odour.

Furthermore, the study reveals that deep-sea scavenging amphipods in high-latitudes could survive for a longer time without food than other deep-sea amphipods, even though they have smaller overall body size. These might then be adaptations to the highly seasonal high-latitude environment.

ACKNOWLEDGEMENTS. – The authors are grateful to colleagues who helped on board, and especially to officers and crew of RV "Polarstern" for their cooperation. For help during lipid analysis we would like to thank V Harberts and M Premke-Kraus for help during oxygen consumption measurements. We are also grateful to M Klages and to K v Juterzenka, for her valuable comments on an earlier version of this manuscript and Martina Rudy, National Water Research Institute, Canada for improving the English.

REFERENCES

Ansell AD 1972. Distribution, growth and seasonal changes in biochemical composition for the bivalve *Donax vittatus* (da Costa) from Kames Bay, Millport. *J Exp Mar Biol Ecol* 10: 137-150.

Armitage KB 1962. Temperature and oxygen consumption of *Orchomonella chilensis* (Heller) (Amphipoda: Gammaeroidea). *Biol Bull* 123: 225-232.

Atema J 1998. Tracking turbulence: Processing the bimodal signals that define an odor plume. Introduction to the featured articles. *Biol Bull Mar Biol Labour, Woods Hole* 2: 179-180.

Bligh EG, Dyer WJ 1959. A Rapid Method of Total Lipid Extraction and Purification. *Can J Biochem Physiol* 37: 911-917.

Bohé-Lafrique S 1985. Les équarisseurs épibenthiques dans l'Atlantique nord-est profond. Thesis, Univ Aix-Marseille II, 67 p.

Bowman TE, Manning RB 1972. Two Arctic bathyl crustaceans: the shrimp *Bythocaris cryonesus* new species and the amphipod *Eurythenes gryllus*, with *in situ* photographs from Ice Island T-3. *Crustaceana* 23: 187-201.

Bühring SI, Christiansen B 2001. Lipids in selected abyssal benthopelagic animals: links to the epipelagic zone? *Prog Ocean* 50: 369-382.

Busdosh M, Atlas RM 1975. Response of two Arctic amphipods. *Gammarus zaddachi* and *Boeckosimus* (*Onisimus*) *affinis*, to variations in temperature and salinity. *J Fish Res Can* 32: 2564-2568.

Carr WES 1988. The molecular structure of chemical stimuli in the aquatic environment. *In* Atema J, Fay RR, Popper AN, Tavolga WN eds, Sensory biology of aquatic animals. Springer Verlag, New York: 3-27.

Chapelle G, Peck LS 1995. The influence of acclimation and substratum on the metabolism of the Antarctic amphipods *Waldeckia obesa* (Chevreux 1905) and *Bovallia gigantea* (Pfeffer 1808). *Polar Biol* 15: 225-232.

Charmasson SS, Calmet DP 1987. Distribution of scavenging Lysianassidae Amphipods *Eurythenes-Gryllus* in the North-east Atlantic - Comparison with studies held in the Pacific. *Deep-Sea Res* 34: 1509-1523.

Childress JJ 1975. The respiratory rates of midwater crustaceans as a function of a depth of occurrence and relation to the O_2 minimum layer off southern California. *Comp Biochem Physiol* 50: 787-799.

Christiansen B, Pfannkuche O, Thiel H 1990. Vertical distribution and populations structure of the necrophagous amphipod *Eurythenes gryllus* in West European Basin. *Mar Ecol Prog Ser* 66: 35-45.

Clarke A 1983. Life in cold water: the physiological ecolgy of polar marine ectotherms. *Oceanogr Mar Biol Ann Rev* 21: 341-453.

Coleman RM 1991. Measuring parental investment in nonspherical eggs. *Copeia* 4: 1092-1098.

Crisp M, Davenport J, Shumway SE 1978. Effects of feeding and of chemical stimulation on the O_2 uptake of *Nassarius reticulates* (Gastropoda: Prosobranchia). *J Mar Biol Ass UK* 58: 387-399.

Dahl E 1979. Deep-sea carrion feeding amphipods: evolutionary patterns in niche adaptation. *Oikos* 33: 167-175.

Desbruyères D, Geistdoerfer P, Ingram CL, Khripounoff A, Lagardère JP 1985. Répartition des populations de l'épibenthos carnivore. *In* Laubier L, Monniot Cl Eds, Peuplements profondes du Golfe de Gascogne, IFREMER: 233-242.

Fahrbach E 2002. The Expedition ARKTIS XVII/1 of the Research Vessel "Polarstern" in 2001. *Ber Polarforsch* 33: 1-43.

Folch J, Lees M, Stanley GHS 1957. A simple methode for the purification of total lipids from animal tissues. *J Biol Chem* 226: 497-509.

Gatti S, Brey T, Müller WEG, Heilmayer O, Holst G 2002. Oxygen microoptodes: a new tool for oxygen measurements in aquatic animal ecology. *Mar Biol* 140: 1075-1085.

George RY 1979. What adaptive strategies promote immigration and speciation in deep-sea enviroment. *Sarsia* 64: 61-65.

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL 2001. Effects of size and temperature on metabolic rate, *Science* 293: 48-2251.

Gnaiger E 1983. Heat Dissipation and Energetic Efficiency in Animal Anoxibiosis - Economy Contra Power. *J Exp Zool* 228: 471-490.

Gnaiger E, Bitterlich G 1984. Proximate biochemical composition and caloric content calculated from elemental CHN analysis: a stoichiometric concept. *Oecologia* 62: 289-298.

Graeve M, Kattner G, Piepenburg D 1997. Lipids in Arctic benthos: does the fatty acid and alcohol composition reflect feeding and trophic interactions? *Polar Biol* 18: 53-61.

Graeve M, Dauby P, Scailteur Y 2001. Combined lipid, fatty acid and digestive tract content analyses: a penetrating approach to estimate feeding modes of Antarctic amphipods. *Polar Biol* 24: 853-862.

Gurr MI, Harwood JL 1991. Lipid Biochemistry. 4th edn, Chapman and Hall, London.

Hagen W 2000. Lipids. *In* Harris RP, Wiebe PH, Lenz J, Skjoldal HR, Huntley M eds, ICES zooplankton methodology manuel, Academic, London: 113-119.

Hargrave BT, Prouse NJ, Phillips GA, Cranford PJ 1994. Meal size and sustenance time in the deep-sea amphipod *Eurythenes gryllus* collected from the Arctic Ocean. *Deep-Sea Res* 41: 1489-1508.

Hargrave BT, NJ Phillips, Prouse GA, Cranford PJ 1995. Rapid digestion and assimialation of bait by the deep-sea amphipod *Eurythenes gryllus*. *Deep-Sea Res* 42: 1905-1921.

Heinrich B 1975. Energetics of pollination. *Ann Rev Ecol Systemat* 6: 139-170.

Hessler RR, Ingram CL, Yayanos AA, Burnett BR 1978. Scavenging amphipods from the floor of the Philippine Trench. *Deep-Sea Res* 25: 1029-1047.

Holst G, Glud RN, Kühl M, Klimant I 1997. A microoptode array for fine-scale measurements of oxygen distribution. *Sensors Actuators* 38/39: 122-129.

Ingram CI, Hessler RR 1983. Distribution and behaviour of scavenging amphipods from the central north Pacific. *Deep-Sea Res* 30:683-706.

Ingram CI, Hessler RR 1987. Population biology of the deep-sea amphipod *Eurythenes gryllus*: inferences from instar analyses. *Deep-Sea Res* 34:1889-1910.

Janssen F, Treude T, Witte U 2000. Scavenger assemblages under differing trophic conditions: a case study in the deep Arabian Sea. *Deep-Sea Res II* 47: 2999-3026.

Jones EG, Collins MA, Bagley PM, Addison S, Priede IG 1998. The fate of cetacean carcasses in the deep sea: observations on consumption rates and succession of scavenging species in the abyssal north-east Atlantic Ocean. *Proc R Soc B*, 265: 1471-2954.

Klimant I, Meyer V, Kühl M 1995. Fiberoptic oxygen microsensors, a new tool in aquatic biology. *Limnol Oceanogr* 40: 1159-1165.

Klimant I, Kühl M, Glud RN 1997. Optical measurements of oxygen and temperature in microscale: strategies and biological implications. *Sensors Actuators* 38: 29-37.

Lampitt RS, Merrett NR, Thurston MH 1983. Inter-relations of necrophagous amphipods, a fish predator, and tidal currents in the deep sea. *Mar Biol* 74: 73-78.

Laver MB, Olsson MS, Edelman JL, Smith KL 1985. Swimming rates of scavenging deep-sea amphipods recorded with a free-vehicle video camera. *Deep-Sea Res* 32: 1135-1142

Moore P, Atema J 1988. A model of a temporal filter in chemoreception to extract directional information from a turbulent odor plume. *Biol Bull* 174: 355-363.

Moore PA, Scholz N, Atema J 1991. Chemical orientation of lobsters, *Homarus americanus,* in turbulent odor plumes. *J Chem Ecol* 17: 1293-1307.

Morris RJ 1973. Changes in the lipid composition of *Acanthephyra purpurea* Milne Edwards (Crustacea: Decapoda) during its diurnal migration: a preliminary investigation. *J Exp Mar Biol Ecol* 13: 55-61.

Opalinski KW 1974. Standard, routine, and active metabolism of the Antarctic amphipod - *Paramoera walkeri* (Stebbing). *Pol Arch Hydrobiol* 21: 423-429.

Opalinski KW, Jazdzewski K 1978. Respiration of some Antarctic amphipods. *Pol Arch Hydrobiol* 25: 643-655.

Opalinski KW, Weslawski JM 1989. Ecology, metabolic rate and metabolic adaptations in Spitsbergen amphipods. *Pol Arch Hydrobiol* 36: 33-350.

Peck LS 2002. Ecophysiology of Antarctic marine ectotherms: limits to life. *Polar Biol* 25: 31-40.

Premke K, Muyakshin S, Klages M, Wegner J 2003. Evidence for long-range chemoreceptive tracking of food odour in deep-sea scavengers by scanning sonar data. *J Exp Mar Biol Ecol* 285/286: 283-294.

Premke K, Klages M, Arntz W 2006. Aggregations of Arctic deep-sea scavengers at large food falls: temporal distribution, consumption rates and population structure. *Mar Ecol Prog Ser* 325:121-135.

Rakusa-Suszczewski S 1990. Respiration of *Orchomene plebs* (Hurley 1965) and *Waldeckia obesa* (Chevreux 1905) from Admiralty Bay (South Shetland Islands, Antarctica). *Pol Arch Hydrobiol* 37: 297-303.

Ritschoff D 1980. Enzymatic production of small molecules attracting hermit crabs to simulated gastropod predation sites. *J Chem Ecol* 6: 665-675.

Sainte-Marie B 1992. Foraging of scavenging deep-sea lysianassid amphipods. *In* Rowe GT, Pariente V eds, Deep-Sea Food Chains and the Global Carbon Cycle, Kluwer Academic Publishers: 105-124.

Sainte-Marie B 1984. Morpghological adaptations for carrion feeding in four species of littoral or cicalittoral lysianassid amphipods. *Can J Zool* 62: 1668-1674.

Schmid MK 1996. Zur Verbreitung und Respiration ökologisch wichtiger Bodentiere in den Gewässern um Svalbard (Arktis). *Ber Polarforsch* 202: 1-92.

Smith KL, Baldwin RJ 1982. Scavenging deep-sea amphipods: effects of food odor on oxygen consumption and a proposed metabolic strategy. *Mar Biol* 68: 287-298.

Smith CR 1985. Food for the deep-Sea: utilization, dispersal, and flux of nekton falls at the Santa-Catalina basin floor. *Deep-Sea Res* 32. 417-442.

Takeuchi I, Watanabe K 1998. Respiration rate and swimming speed of the necrophagous amphipod *Eurythenes gryllus* from Antarctic deep waters. *Mar Ecol Prog* Ser 163: 285-288.

Thurston MH, Petrillo M, Della Croce N 2002. Population structure of the necrophagous amphipod *Eurythenes gryllus* (Amphipoda: Gammaridea) from the Atacama Trench (southeast Pacific Ocean). *J Mar Biol Ass UK* 82: 205-211.

Weissburg MJ 1997. Chemo- and mechanosensory orientation by crustaceans in laminar and turbulent flows: From odor trails to vortex streets. *In* Lehrer M ed, Orientation and Communication in Arthropods, Birkhäuser Verlag, Basel: 215-246.

Wickins JF 1983. Catches of large Lysianassid Amphipods in baited traps at the nuclear-energy-authority dump site during June 1979. *Deep-Sea Res* 30: 83-86.

Willmer P, Stone G, Johnston I 2000. Environmental Physiology of Animals. Chapter 6 Metabolism and Energy supply. Blackwell Science.

Witte U 1999. Consumption of large carcasses by scavenger assemblages in the deep Arabian Sea: observation by baited camera. *Mar Ecol Prog Ser* 183: 139-174.

Zimmer-Faust RK, Case JF 1982. Odors influencing foraging behaviour of the California spiny lobster, *Panulirus interruptus*, and other decapod Crustacea. *Mar Behav Physiol* 9: 35-58.

Zimmer-Faust RK 1987. Crustacean chemical perception: towards a theory on optimal chemoreception. *Biol Bull* 172: 10-29.

Received February 2, 2009
Accepted October 29, 2009
Associate Editor: G Tita