

# 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 6 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 depths between 1500 and 2600 m. All amphipods, both on photographs and captured, belonged 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 those in other reported deep-sea areas in arrival time at bait, abundance and length distribution of individuals sampled. The giant amphipod *Eurythenes gryllus* dominated in our bait experiments; it exceeded numbers counted by other workers by >13-fold, and the first individuals appeared up to 20 times faster than in other reported experiments. Specimen attraction and abundance seem 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 in the Pacific and Atlantic Oceans.

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

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## INTRODUCTION

Studies with baited time-lapse cameras and traps have revealed large, motile, scavenging fauna attracted to carrion in the deep sea all over the world (Dayton & Hessler 1972, Smith 1985, Witte 1999). Comparing the bait-attending fauna of different areas within the North Atlantic, Mediterranean Sea and Pacific, the scavenger communities have been found to differ in terms of species composition and the numbers of individuals attracted (Priede et al. 1990, Thurston et al. 1995, Christiansen 1996, Priede & Merrett 1998, Janssen et al. 2000, Legezynska et al. 2000). 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 scaveng-

ing 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 benthic-pelagic 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 in which baited time-lapse camera experi-

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ments 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 11 700 km<sup>2</sup> 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).

## MATERIALS 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 3 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 the 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 h. 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 m<sup>2</sup>. Pictures (Kodak Ektachrome 200, 35 mm × 35 mm × 30 m) were taken at 3 min intervals. Six experiments were carried out with this configuration during 2 Arctic expeditions of the German RV 'Polarstern' in the summers of 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 3 of them were partitioned into 2 chambers. While bait was only available in 1 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; 3 others were placed at 1.20, and another 3, at 1.50 m above the seafloor.

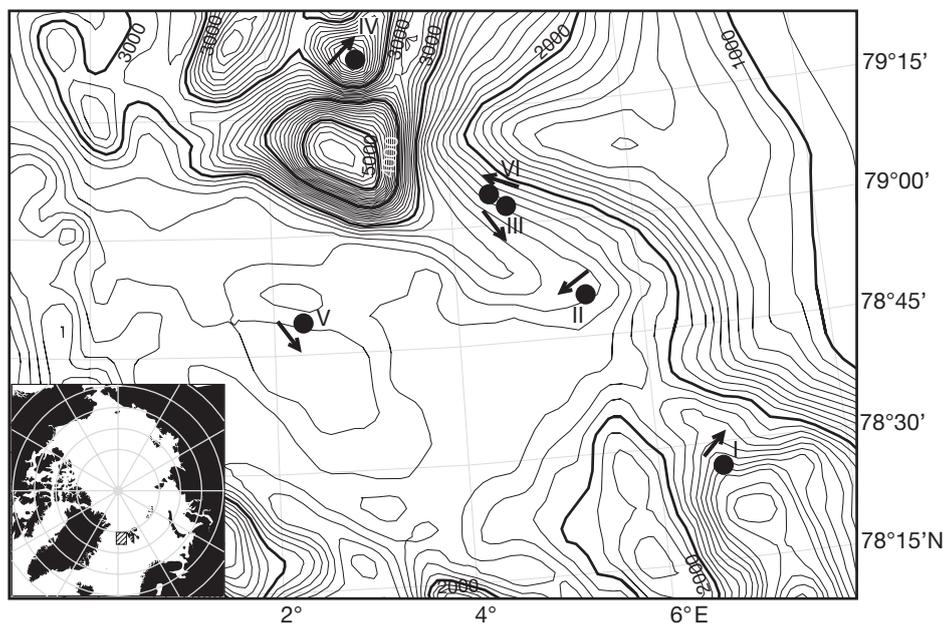


Fig. 1. Locations of Stns I to VI in the Fram Strait, Arctic Ocean. Arrows indicate the main bottom current direction from 1997 to 2002 (Premke et al. 2003, Schauer et al. unpubl. data)

Table 1. Compilation of published data on results of baited camera experiments in the deep sea, considering amphipods the most abundant scavengers (\*: no data available)

Most abundant scavenger type	Area	Depth (m)	Photo-interval	Total time of deployment	First arrival	Max. no. of ind. image <sup>-1</sup>	Bait type	Bait weight (kg)	Consumption rate (g d <sup>-1</sup> )	Current speed (cm s <sup>-1</sup> )	Calculated abundances (ind. km <sup>-2</sup> )	Source
<i>Eurythenes</i>	Arabian Sea	4040	20 min	129 h	0.7 h	9 (21 h)	Shark	29	500	3	216	Witte (1999)
<i>Eurythenes</i>	Arabian Sea	3190	5.2 min	57.7 h	3.5 h	34 (23.5 h)	Tuna	3.2	2690	2.7	6	Janssen et al. (2000)
<i>Eurythenes</i>	Arabian Sea	3950	9.6 min	104.3 h	0.7 h	47 (13.2 h)	Tuna	5.1	4320	2.9	140	Janssen et al. (2000)
<i>Eurythenes</i>	NW Atlantic	5830	10 min	5 d	3.9 h	5	Mackerel	0.1	*	*	*	Hargrave (1985)
<i>Eurythenes</i>	NE Atlantic	4009	4 min	24 h	12 min	6	Grenadier fish	*	*	2–7	*	Lampitt et al. (1983)
<i>Orchomene</i> , <i>Paralicella</i>	NE Atlantic	4855	8 min	26 h	81 min	38 (13.5 h)	Squid, kippers	*	*	*	*	Thurston (1979)
<i>Hirondellea</i>	Philippine Trench	9605	5 min	16–29 h	20 min	*	Fish	1–3	*	7.5	*	Hessler et al. (1978)
Amphipods & fish	North Atlantic	4850	2 min	16.9 h	*	*	Tuna	2	*	2.5	*	Rowe et al. (1986)
<i>Orchomene</i> , <i>Paralicella</i>	St. Catalina Basin	1310	1–4 h	4–56 d	*	*	Yellowtail mackerel	2–40	*	*	*	Smith (1985)
Fish & amphipods	NE Atlantic	4000–4800	10–15 min	36–276 h	40 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	Video: 3 min every 30 min	*	150 min	*	*	*	*	*	*	Laver et al. (1985)
<i>Eurythenes</i> , <i>Tmetonyx</i>	Arctic Ocean (I)	2644	3 min	25.5 h	15 min	740 (9.75 h)	4 trout, 1 turbot, 1 mackerel	2.7	2600	1.5–8.2 (5.8)	454	Present study
<i>Eurythenes</i>	Arctic Ocean (II)	2524	3 min	17.5 h	12 min	605 (14.75 h)	2 sole, 4 mackerel	2.7	3800	4.3–6.4 (4.8)	885	Present study
<i>Eurythenes</i>	Arctic Ocean (III)	2377	3 min	19.5 h	24 min	305 (4.75 h)	4 trout, 1 plaice, 1 shrimp	2	5600	5.3–8.9 (7.6)	134	Present study
<i>Eurythenes</i> , <i>Tmetonyx</i>	Arctic Ocean (IV)	1468	3 min	24.8 h	21 min	630 (10 h)	2 trout, 1 ling	5	5500	0.8–8.3 (4)	363	Present study
<i>Eurythenes</i>	Arctic Ocean (V)	2504	3 min	28.5 h	21 min	620 (4.5 h)	3 sole, 3 garfish	2.5	5000	1.7–7.6 (4.6)	304	Present study
<i>Eurythenes</i>	Arctic Ocean (VI)	2341	3 min	30.5 h	9 min	800 (14.45)	1 sole, 5 cod-heads	4	3500	2.8–13.5 (7.9)	917	Present study

Freshly thawed fishes and a crustacean were used as bait at comparable mass, but in different compositions (Table 1). Aiming to identify food preferences by analyses of the time-lapse photographs, we used the fish species trout *Salmo trutta* or sole *Solea solea* as standard bait. Additionally, other species used were turbot *Psetta maxima*, mackerel *Scomber scombrus*, plaice *Pleuronectus platessa*, ling *Molva molva*, garfish *Belone belone* and heads of cod *Gadus morhua*, 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 stereomicroscope (Olympus, 10 × 6.3 magnification) to identify and quantify all visible organisms. Individuals were counted on each slide at the beginning of observation, then on every tenth slide and, finally, on every fifth slide during dense population structures. 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 cases of juvenile *E. gryllus* and adult, but smaller-sized, *Tmetonyx norbiensis*. This situation affected data analysis of the photographs. Clearly, the obtained counts of amphipod numbers 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 h, 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 *Eurythenes gryllus* and amphipods belonging to the species *Tmetonyx norbiensis* (Oleröd, 1987) we counted all amphipods <10 mm together and used the proportion from captured amphipods

of *E. gryllus* and *T. norbiensis* obtained in each experiment to calculate the theoretical respective numbers of these 2 species.

Abundances in the vicinity of the station were also calculated by applying the relationship  $n = Ct_{arr}^{-2}$  (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 an average of 3 readings. All specimens were blotted dry, and their wet weight was measured individually on a microbalance. Because traps were lost during Expt 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 characteristics were considered to be juveniles. In our study, females and males of *Eurythenes gryllus* were identified at a minimum length of 15.5 and 17 mm, respectively. It is likely that some individuals within the juvenile category (15.5 to 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'  $\geq 15.5$  mm were unrecognised females.

## RESULTS

### Lengths and abundances of amphipods

Lander Deployments I to V collected 4200 amphipod individuals belonging to 3 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 8 individuals of *Stegocephalus* sp.

Table 2. *Eurythenes gryllus* and *Tmetonyx norbiensis*. Mean length, SD and length range, all experiments combined for females, males, juveniles  $< 15.5$  mm and juveniles  $\geq 15.5$  mm

	Area	N	Length (mm)		
			Mean	SD	Range
<b><i>Eurythenes gryllus</i></b>					
Female	Expt I–V	485	34.51	12.05	15.5–75
Juvenile $\geq 15.5$ mm	Expt I–V	539	19.95	3.48	15.5–33
Juvenile $< 15.5$ mm	Expt I, II, IV	328	11.26	2.51	4–15.5
Male	Expt I–V	651	34.30	9.42	17–56
<b><i>Tmetonyx norbiensis</i></b>					
Female	Expt I, III, IV	142	22.03	4.93	8–34
Ovigerous female	Expt I, III, IV	929	28.67	3.52	11–38
Juvenile	Expt I	4	10.00	3.94	7–15
Male	Expt I, III, IV	408	24.33	3.65	10–31

### *Eurythenes gryllus*

The mean lengths of males, females, females plus juveniles and juveniles were calculated for all experiments (Table 2). Comparing mean length of adult females (34.1 mm) from all 5 stations to mean length of adult males (34.3 mm), there were no significant differences (ANOVA,  $p > 0.05$ ). Considering those juveniles  $\geq 15.5$  mm to be females, statistical differences become significant. Among the stations, significant differences were found in Expt IV, where females are larger than males, and in Expt V, where males are larger than females.

Comparisons were also made for the length range of adult females and males at all of the 5 locations sampled. Despite similar mean body length of the 2 sexes, it is obvious that females grow to be larger, with the largest female collected 75 mm and the largest male 56 mm long (Fig. 2, Table 2).

The mean body lengths are about 17 and 11 mm for all juveniles and without juveniles  $\geq 15.5$  mm, respectively (Fig. 3). Juveniles  $< 15.5$  mm were found in Expts I, II and IV. No juveniles  $< 15.5$  mm were found at Stns II and V (Table 2).

In Expts III and V fewer amphipods were caught than in Expts 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 (Figs. 2 & 3). The low number of captured amphipods (of both sexes) was also reflected in the photographic data, where the lowest number of amphipods occurred (Fig. 4).

### *Tmetonyx norbiensis*

The mean sizes of males, females, ovigerous females and juveniles were determined (Table 2). High num-

bers of *T. norbiensis* were captured only in Expts I and IV (see Table 3). Samples from Expt III contained only 5 individuals: 3 females (2 of them ovigerous) and 2 males, with a mean body length of 26.3 mm (females) and 25.5 mm (males).

The smallest females and males identified were 8 and 10 mm, respectively. Because of a lack of external characters, 4 ind. were considered to be juveniles.

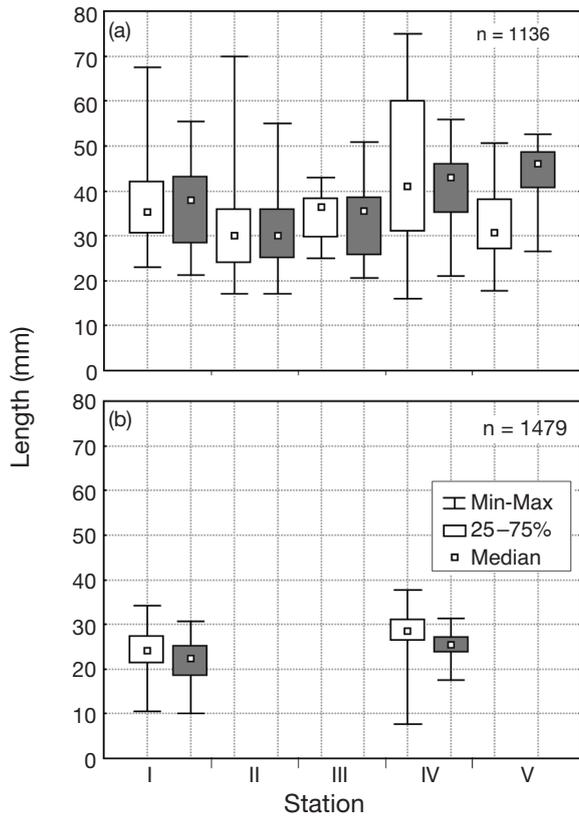


Fig. 2. (a) *Eurythenes gryllus* and (b) *Tmetonyx norbiensis*. Box and whisker plot of lengths (mm) of mature females excluding juveniles (white boxes) and males (grey boxes)

Table 3. *Eurythenes gryllus* and *Tmetonyx norbiensis*. Sex ratio of specimens in each experiment. N indicates the total number of males and females. Numbers in parentheses are total numbers and sex ratios for *E. gryllus* when juveniles  $\geq 15.5$  mm (assumed to be unidentified females) were included. -: no individuals caught

	<i>Eurythenes gryllus</i>		<i>Tmetonyx norbiensis</i>	
	N	M:F	N	M:F
Expt I	191 (430)	1:0.45 (1:2.26)	257	1:1.54
Expt II	583 (799)	1:0.86 (1:1.54)	-	-
Expt III	44 (57)	1:0.46 (1:0.90)	5	1:1.50
Expt IV	264 (330)	1:0.74 (1:1.18)	1217	1:2.99
Expt V	54 (59)	1:1.25 (1:1.45)	-	-
Total	1136 (1675)	1:0.75 (1:1.58)	1479	1:2.63

Females grew to be larger than males, with the largest female captured 38 mm, and the largest male, 31 mm (Fig. 5).

### Spatial distribution and aggregation dynamics of the scavenger community on bait

Scavengers captured with traps or determined on photographs belonged to 5 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. A third amphipod species, *Stegocephalus* sp., appeared rarely (single individuals). Other organisms detected on the photographs were zoarcid fish and chaetiliid isopods.

In 5 of our experiments the amphipod *Eurythenes gryllus* was the most abundant species, both in traps and on photographs. In the traps of Expt IV the number of *Tmetonyx norbiensis* individuals exceeded those of *E. gryllus* by a factor of close to 4 (Figs. 3 & 5). Although *T. norbiensis* was captured frequently in 2 of the 6 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 6 individuals per photograph (Table 1). During 1 experiment 2 fish entered 1 of our traps that was oriented towards the camera. The bait inside the trap had, at this point, been nearly consumed, and most of the trapped *Eurythenes gryllus* had escaped (the funnel opening was obviously too large). One fish specimen left the trap after a while, but the remaining fish was finally (after 8 h) attacked by the few *E. gryllus* that were still inside the trap. The subsequent release of body fluids of the wounded fish attracted 100s of new amphipods, and the fish was skeletonised within 11 h.

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 h, leaving clean skeletons only (Table 1).

First arrivals of single individuals of *Eurythenes gryllus* were recorded after a 15, 12, 24, 21, 21 and 9 min time at bottom (tab) (Expts I–VI, respectively; Table 1). The maximum number of individuals differed from experiment to experiment (Fig. 4), but we also recorded differences in the time of arrival of individuals that are considered to show 2 patterns of feeding aggregations:

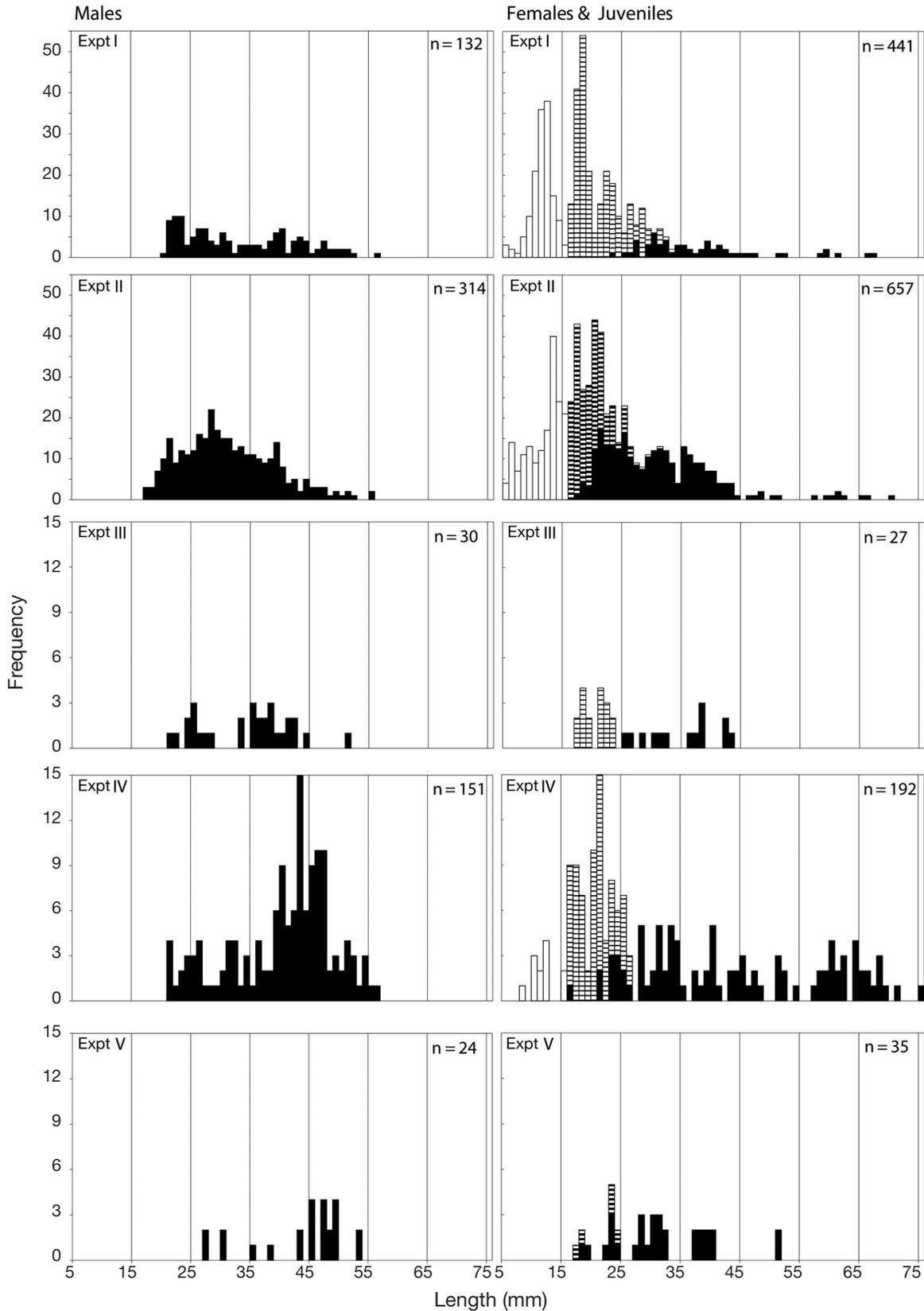


Fig. 3. *Eurythenes gryllus*. Length-frequency distributions from 5 stations in Fram Strait based on total body length. Left panels: males (black); right panels: females (black), juveniles  $\geq 15.5$  mm (striped) and juveniles  $< 15.5$  mm (white). Note the different scales on the y-axis

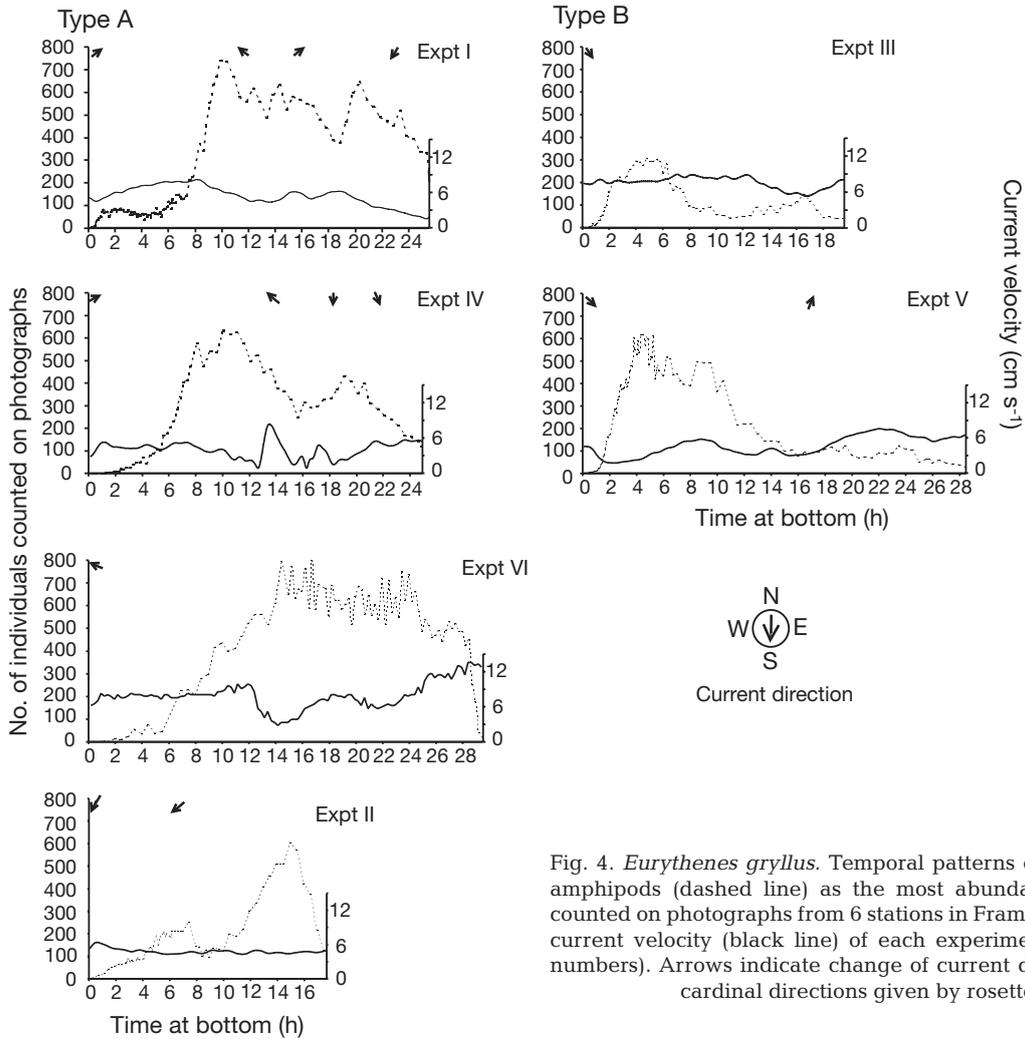


Fig. 4. *Eurythenes gryllus*. Temporal patterns of numbers of amphipods (dashed line) as the most abundant scavenger counted on photographs from 6 stations in Fram Strait and the current velocity (black line) of each experiment (right axis numbers). Arrows indicate change of current direction, with cardinal directions given by rosette

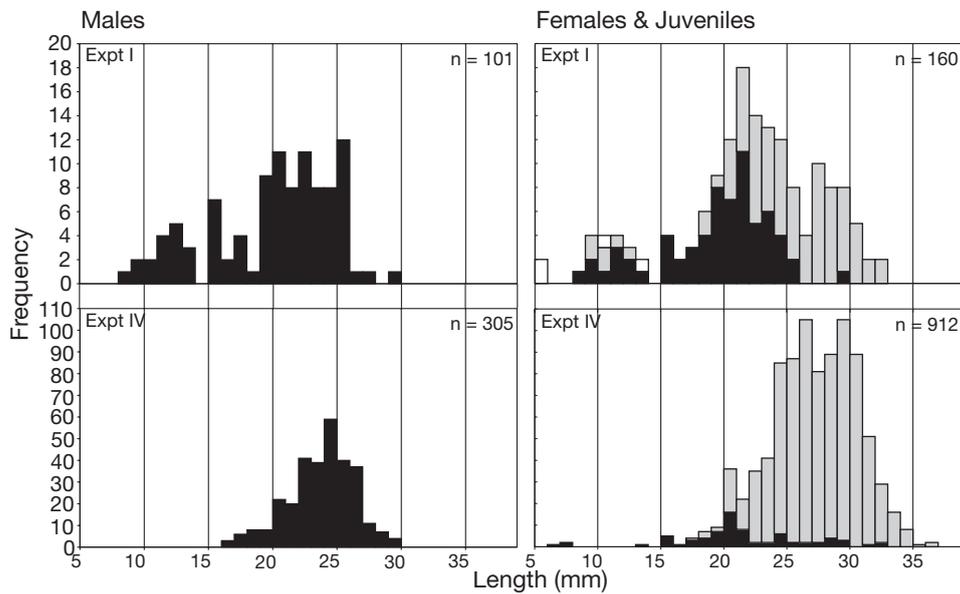


Fig. 5. *Tmetonyx norbiensis*. Length-frequency distributions based on total body length. Left panels: males (black); right panels: females without eggs (black), ovigerous females (grey) and juveniles (white). Note the different scales on the y-axis

Type A—maximum numbers of individuals present between 10 and 24 h tab, with a maximum number of 600 to 800 ind.  $0.7 \text{ m}^{-2}$  (Fig. 4, Expts I, II, IV, VI);

Type B—maximum numbers of individuals present between 3 and 6 h tab, with a maximum number of 300 to 600 ind.  $0.7 \text{ m}^{-2}$  (Fig. 4, Expts 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 4 h after the arrival of bait deployments 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 repeated visits by single specimens.

Generally, large amphipods appeared first, followed by a second peak of smaller individuals. The Type A aggregation is shown by Expt II, in which large individuals primarily dominated during the first 4 h. About 10 h later, the maximum peak of amphipods (600 ind.  $0.7 \text{ m}^{-2}$ ) consisted mainly of smaller individuals (Fig. 4, Expt IV). The current flow during the first 4 h ( $5.4 \text{ cm s}^{-1}$  on average) was only slightly higher than later ( $4.8 \text{ cm s}^{-1}$  on average). The opposite is illustrated in Fig. 4 (Expt III showed a Type B aggregation). Current speed was fairly constant throughout the experiment ( $7.6 \text{ cm s}^{-1}$  on average), and the number of amphipods reached a maximum of 300 (mostly larger) ind.  $0.7 \text{ m}^{-2}$  after 4.75 h tab. After 6 h tab, the abundance declined to a few individuals, but then increased again to 150 (mostly smaller) ind.  $0.7 \text{ m}^{-2}$  by 16.5 h tab. In contrast to Expt II, the majority of small individuals attending Expt III did not account for the maximum abundance during this experiment (Fig. 4, Expt III).

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

### 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 is preferred over ling, and other round fish species are attacked with equal facility. In Expt IV, the first scavenging amphipods fed on trout, those following 30 min later fed on ling and, about 1 h later, new arrivals at the bait started to feed on sole. Amphipods consumed the trout within 8.5 h tab, and 4 h later the sole was

skeletonised. The species that served longest as bait was the ling, the total consumption of which required 22 h (Fig. 6).

The consumption rate differed among stations, and ranged from 2500 to  $5500 \text{ g d}^{-1}$ . Consumption at Stn III was divided into 2 rates: for the entire experiment, including the relatively tiny and light shrimp, it amounted to about  $2500 \text{ g d}^{-1}$ , but it amounted to a rate of  $5600 \text{ g d}^{-1}$  if only fish were considered.

As illustrated in Fig. 4 (Expts III and V), the number of amphipods increased quickly after deployment of the lander at the seafloor during these 2 experiments, and rapid consumption of the bait followed, so that most of the bait was consumed within 10 h. This rapid bait consumption at Stns III and V is related to the early peak abundance of *Eurythenes gryllus* (Type B). Although, in contrast to other deployments, the bait wet weight was lower in Expts III and V, i.e. 2 and 2.5 kg, respectively, the consumption rate was high in Expt V (with  $5000 \text{ g d}^{-1}$ ) and even the highest calculated in Expt III ( $5600 \text{ g d}^{-1}$ , excluding the small shrimp). With bait wet weight ranging between 2.7 and 5 kg in the other experiments, consumption rates in experiments of Type A were relatively low ( $2600$  to  $3800 \text{ g d}^{-1}$ ), except at Stn IV ( $5500 \text{ g d}^{-1}$ ).

### 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 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, Stn III was not considered. Generally, ovigerous females were more frequent than females without eggs.

### *Eurythenes gryllus*

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

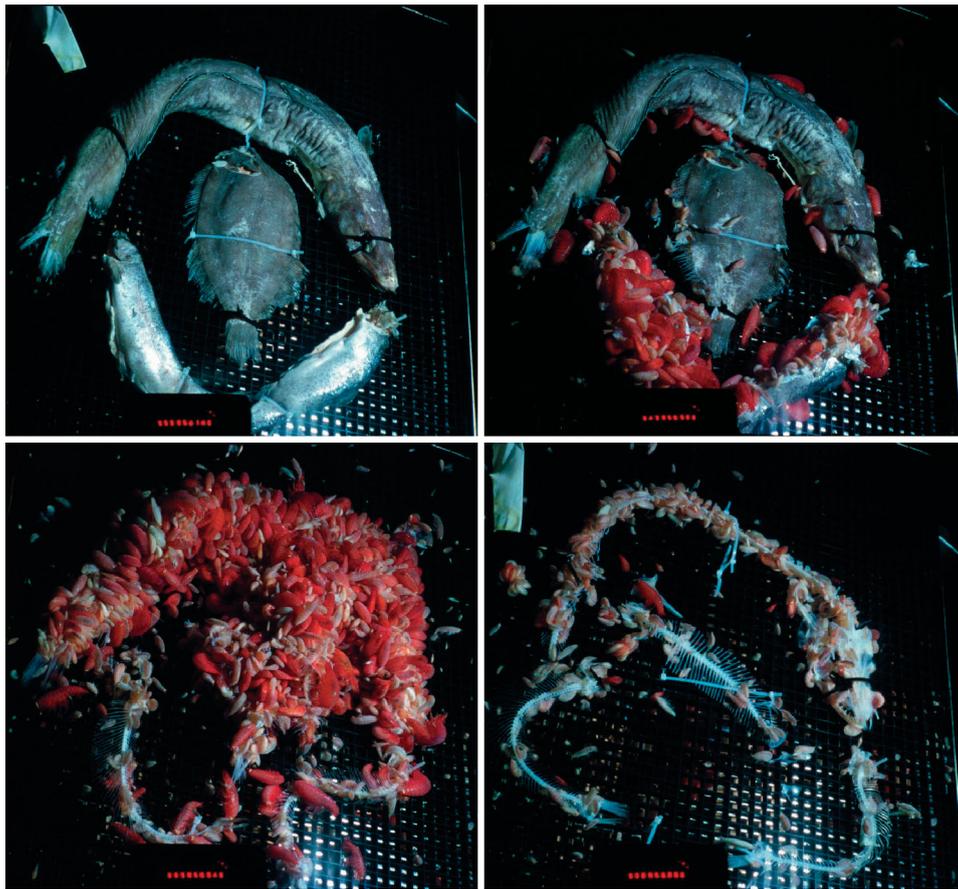


Fig. 6. Example of a scavenger aggregation at Stn IV. Time-lapse photographic sequence at time intervals of 0, 6, 10 and 22.5 h (time at bottom). Red, white and pink organisms were amphipods

### *Tmetonyx norbiensis*

There is also a length–sex correlation between the stations. Females and males of *T. norbiensis* at Stn I were smaller than those at Stn 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).

## DISCUSSION

For a long time the seafloor of the deep sea was considered to be a monotonous, desert-like environment colonised by only a 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 eco-

system (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 temporally or spatially receive 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 north-eastern Atlantic revealed that macroaggregates settling from the euphotic zone at a rate of 100 to 150 m d<sup>-1</sup> lead to a deposit of phytodetritus on the sediment surface. Time-lapse camera experiments in different regions of the world's oceans demonstrated that the deep-sea benthic community responds rather quickly to such food supply (Rice et al. 1994). Phytodetrital material is colonised 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 form 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 kinds and masses 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 an 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 with 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 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, pers. comm.). 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 rapidly consume bait, 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*. To analyse 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 abundance 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 such abundances by applying the equation of Priede & Merrett (1996). These authors 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 bottom current speed for each experiment and the mean amphipod swimming speed ( $7.3 \text{ cm s}^{-1}$ ; Laver et al. 1985) enable us to calculate abundances of *Eurythenes gryllus* in the vicinity of the lander (Table 1); these calculations assume that the amphipods are not static, but swim continuously (Bregazzi 1973), so that the narrow odour plume never passes between the 2 nearest amphipods, but that one or the other will intercept the plume and move towards the bait. Given that at Stns 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  $>1 \text{ km}$ .

## 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) reported on a video transect close to our area of investigation prepared with a towed system. Along the 17.5 km transect covering an area of about  $13\,500 \text{ m}^2$ , a single fish skeleton (length 36 cm and biomass approximately 0.5 kg wet weight) was identified on 1 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 *Eurythenes gryllus* feeds rapidly on available food sources. The probability of locating a scavenger in an ongoing feeding process or of finding 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 covered with ice for several months of the year. The population density of bears in our area of investigation during the winter months is unknown, but bears occur frequently on the 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 were discovered during our video transects.

Many lysianassoid amphipods are marine cold-water inhabitants and some of them contribute significantly to the Antarctic and Arctic benthos (Arntz et al. 1994, De Broyer & Jazdzewski 1993). 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 compared to oligotrophic waters like the open Pacific was also observed by other authors (e.g. Thurston 1990, Christiansen 1996).

### Aggregation dynamics

Two categories (Types 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), as we noted in 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, in that area, amphipods were not the only organisms in the scavenger community and carcass 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, the total consumption of which required 22 h tab; however, this can be simply explained by the differences in wet weight of trout and sole as compared to ling, which was 4 times heavier (Fig. 6). The same was observed in Expt 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 those of flat fish, but no preferences within round fish.

Table 4. Grouping of all stations (except Stn VI) in 2 different types, based on camera, trap and current meter data analysis

Type A	Type B
High maxima (600–800 ind. 0.7 m <sup>-2</sup> )	Low maxima (300–600 ind. 0.7 m <sup>-2</sup> )
High calculated abundances (454–885 km <sup>-2</sup> )	Low calculated abundances (134–304 km <sup>-2</sup> )
Slow increase of scavengers to maximum (10–24 h)	Fast increase of scavengers to maximum (3–6 h)
Low consumption rate (2600–3800 g d <sup>-1</sup> )	High consumption rate (5000–5300 g d <sup>-1</sup> )
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

### 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 predation by fish. It could also be a function of size and evolution. Hargrave (1985) also observed that amphipods arriving during the first 12 h 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* do not seem to be neutrally buoyant. Neutral buoyancy gives *E. gryllus* an advantage over *T. norbiensis*, as it can therefore swim continuously with comparatively little effort, actively search for food falls, and once an odour trail is tracked, arrive earlier at the carcass (Smith & Baldwin 1982, Sainte-Marie & Hargrave 1987). The deep-sea lysianassoids can be divided into 2 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-triturative 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*, etc.) 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), processing food in a more or less continuous way as small and triturated bites, and can survive 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 3 stations versus the infrequent occurrence of *T. 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 in the south-eastern Pacific at a depth of 7800 m (Thurston et al. 2002), where females dominate. In our collections only Stn 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 of 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 abysso-pelagic rather than a benthic lifestyle (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 have been detected over the past years, some of which circulate in the 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 10s or even 100s 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, residence at depths >1000 m above the sea bed could remove brooding females from the foraging range of predatory abyssal fish.

Adult red females are at less risk from pelagic predators because these mostly use photoreception for foraging, as opposed to abyssal predators which 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 assume that individuals grouped in the 'juveniles  $\geq 15.5$  mm' category are unidentified females. The largest females caught measured 75 mm in 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 were 154 and 122 mm, respectively (Baldwin & Smith 1987). All the above-mentioned studies were based on traps deployed on the sea floor and 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. Sizes similar to those we found were mentioned only from the upwelling area in the south-eastern Pacific (Thurston et al. 2002). Significant data are available on the size structure of *Eurythenes* populations from various widely separated localities (Bowmann & Manning 1972, Thurston 1979, Baldwin & Smith 1987, Charmasson & Calmet 1987, Ingram & Hessler 1987, Christiansen et al. 1990, Thurston & Bett 1995, Christiansen 1996, Thurston et al. 2002). A comparison of size at the 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 (1995) data suggest a minimum hatching 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 probability that speciation of *E. gryllus* in the Arctic is incipient (see Thurston et al. 2002).

Ingram & Hessler (1983) found a size range of 3 to 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.

### CONCLUSIONS

Scavenger aggregation dynamics and behaviour in connection with carcasses in the Arctic Ocean differed from observations reported for other deep-sea areas, with regards to the species attracted, their succession, their abundances and lengths. Scavengers are 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 2 proposed categories.

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