



# Food fall-specific scavenging response to experimental medium-sized carcasses in the deep sea

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**ABSTRACT:** In the deep sea, benthic communities largely depend on organic material from the overlying water column for food. The remains of organisms on the seafloor (food falls) create areas of organic enrichment that attract scavengers. The scavenging rates and communities of food falls of medium-sized squid, fish and jellyfish (1–100 cm) are poorly known. To test our hypothesis that scavenging responses are specific for different food falls, we deployed camera landers baited with squid, jellyfish and fish for 9 to 25 h at 1360 to 1440 m in the southern Norwegian Sea. Image analysis of 8 deployments showed rapid food fall consumption ( $20.3 \pm 1.4$  [SD] to  $31.6 \pm 3.7$  g h<sup>-1</sup>) by an amphipod-dominated scavenging community that was significantly different between the food fall types. Fish and squid carcasses were mostly attended by amphipods of the genus *Eurythenes*. Smaller unidentified amphipods dominated the jellyfish experiments together with brittle stars (cf. *Ophiecten gracilis*) and decapod shrimps (cf. *Bythocaris* spp.); the latter only occurred on jellyfish carcasses. The removal time for jellyfish (~17 h) was almost twice as long as that for squid and fish (9–10 h). The maximum scavenger abundance was significantly higher on fish carcasses than on jellyfish and squid. The times at which abundances peaked were similar for jellyfish and fish (after 8–9 h) but significantly sooner for squid ( $3.00 \pm 0.35$  h). Our results, although based on a small number of experiments, demonstrate differences in scavenging responses between food fall species, suggesting tight coupling between the diversity and ecology of benthic scavenging communities in the Norwegian Sea.

**KEY WORDS:** Food fall · Scavenger · Carcasses · Benthic community · Benthic–pelagic coupling · Population dynamics · Deep sea · *Eurythenes*

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## 1. INTRODUCTION

Deep-sea benthic and demersal communities (except chemosynthetic communities) rely on organic input from the overlying water column. Changes in biological communities in the upper water column are thus mirrored in the energy and nutrient fluxes to the seafloor and subsequently the dynamics in the abundance, growth and diversity of deep-sea communities (Billet et al. 1983, Tyler 1988, Gage & Tyler 1991, Wassmann et al. 1991, Smith & Baco 2003, Drzen et al. 2012). However, the exact response and

adaptation of deep-sea benthic organisms to sporadic and intermittent food pulses is poorly understood (Danovaro et al. 2017). Considering that the supply of organic matter decreases with depth both in quality and in quantity (Lee et al. 2004 and references therein), analysing the response of deep-sea communities to these fluxes is crucial for our understanding of deep-sea ecosystems. Organic matter may be deposited on the seafloor as marine snow, which consists of conglomerates of detrital material including dead algal cells, crustacean moults and carcasses of mesozooplankton (e.g. Robinson et al.

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2010). Another vector of organic material to the seafloor is the deposition of dead plant material and carcasses, which is also known as a food fall (Stockton & DeLaca 1982).

Food falls in the deep sea create temporary areas of high organic enrichment set against a typically oligotrophic background (Stockton & DeLaca 1982, Higgs et al. 2014) and are measured to be a major component in the downward carbon flux in deep-sea habitats (Agassiz 1888, Bailey et al. 2007, Sweetman & Chapman 2015, Lalonde et al. 2020). Megafauna food falls such as whale carcasses can locally contribute to a flux of particulate organic carbon (POC) that equals up to 2000 yr of average background POC flux to the deep seafloor (Smith 2006). Observations of medium-sized carcasses (1–100 cm) of fish, squid and gelatinous zooplankton, and their associated scavenging communities, are rare (Soltwedel et al. 2003, Sweetman & Chapman 2015, Hoving et al. 2017), which is likely caused by the rapid consumption of the smaller carcasses and the absence of conspicuous bones (e.g. Soltwedel et al. 2003, Sweetman et al. 2014, Sweetman & Chapman 2015). However, the presence of scavenged fish and squid carcasses in the stomachs of abundant benthic and benthopelagic fauna indicates an important role of these food falls in subsidising deep-sea food webs (Priede et al. 1991, Martin & Christiansen 1997, Drazen et al. 2001, 2012). Experiments with medium-sized food falls of fish and jellyfish show differences in scavenging rates and communities that also vary with depth (Premke et al. 2006, Sweetman et al. 2014, Dunlop et al. 2018). To compare scavenging communities between regions and food fall types, experiments with more than 2 food fall species in 1 region are needed to understand food fall-specific scavenging responses.

Gelatinous macro- and megazooplankton show high diversity and abundance in the epi- and mesopelagic zones (Robison 2004) and are important players in the oceanic food web (Madin & Harbison 2001, Hays et al. 2018). Deposition events of carcasses of jellyfish and other gelatinous macrozooplankton may contribute substantially to the local carbon pump and fueling deep-sea benthic food webs (Billett et al. 2006, Lebrato & Jones 2009, Sweetman & Chapman 2011, 2015, Henschke et al. 2013, Smith et al. 2014, Sweetman et al. 2014, 2016). In Norwegian fjords, the carbon flux associated with jellyfish food falls may be regionally approximately equal to the phytodetrital flux (Sweetman & Chapman 2015). Mesopelagic medium-sized nekton, such as fishes and squid, may also occur in large populations and constitute a considerable portion of the ocean's biomass

(Irigoiien et al. 2014, Doubleday et al. 2016), with global estimates for neritic and oceanic squid at 150 to 300 million metric tonne (t) (Nesis 1985) and mesopelagic fish estimated at far over 1000 million t (Irigoiien et al. 2014). Squids have a single reproductive cycle, which may be followed by mass die-off events and carcass deposition (Boyle & Rodhouse 2005, Hoving et al. 2017). Quantification of carcasses of spent female squids suggested a significant contribution to the local carbon flux in the deep sea in the Gulf of California (Hoving et al. 2017). Recent studies have indicated that as a result of a changing climate and growing anthropogenic pressures, cephalopods as well as gelatinous organisms are increasing in biomass and expanding their range in different marine habitats (Lynam et al. 2006, Doubleday et al. 2016). This suggests that these pelagic invertebrates have some degree of ecological plasticity that may allow them to benefit from a changing ocean environment (Madin & Harbison 2001, Lynam et al. 2006, Purcell 2012, Doubleday et al. 2016). The discussion remains whether reported rising numbers of gelatinous zooplankton (Richardson et al. 2009, Geoffroy et al. 2018, Knutsen et al. 2018) are recurring population fluctuations or if abundances of, for example, jellyfish have been truly rising steadily (Condon et al. 2012, 2013, Sanz-Martín et al. 2016). The potential reasons for the proliferation of these invertebrates are (1) the removal of competition with fishes as a result of commercial fishing (Lynam et al. 2006, Purcell 2012, Doubleday et al. 2016), (2) an increased life cycle pace in response to ocean warming (Pecl & Jackson 2008, Hoving et al. 2013) and (3) flexibility in maturation under low food supply (Madin & Harbison 2001, Hoving et al. 2013). Considering the potential of these invertebrates to outcompete fishes (Lynam et al. 2006, Purcell 2012, Doubleday et al. 2016), it will be important to understand the role of the carcasses of pelagic invertebrates as a food source for deep-sea benthic and demersal fauna to predict their impact in future ocean scenarios with altered pelagic community compositions.

The Norwegian Sea has been classified as one of the most productive areas of the world's oceans (Blindheim 1985). As a meeting point for water masses from the Atlantic as well as the Arctic Ocean, the Norwegian Sea has fauna that includes boreal and Arctic species, but it is relatively poor in overall species richness (Blindheim 1985). Several parts of the Norwegian Sea are spawning areas of the squid *Gonatus fabricii* (Arkhipkin & Bjørke 1999), which is the most abundant squid in the NE Atlantic. Top predators migrate annually to specific locations in

the NE Atlantic to hunt for this squid, and it is estimated that as much as 1.5 million t of *G. fabricii* are consumed annually by sperm whales alone (Bjørke 2001). It is hypothesised that the whales hunt for aggregations of squids, including egg-carrying females (Arkhipkin & Bjørke 1999). Squid carcass deposition may thus be an important vector for carbon transport to the seafloor in the Norwegian Sea, as it is in the Gulf of California (Hoving et al. 2017). The helmet jellyfish *Periphylla periphylla* is a conspicuous member of Norwegian waters (Fosså 1992, Youngbluth & Båmstedt 2001). The species is known in the Norwegian Sea and well established in the sea's coastal fjords, with documented evidence of population expansion to northern fjords (Fosså 1992, Geoffroy et al. 2018). *P. periphylla* is an important vector for carbon transfer to the seafloor (Sweetman & Chapman 2015).

In this study, we compared the scavenging rates and communities of experimental squid, fish and jellyfish food falls. Previous experiments have identified similar scavenging rates and biodiversity for jellyfish and fish food falls (Sweetman et al. 2014). However, other natural jellyfish food falls have shown comparably low scavenger abundances and the absence of typical scavengers such as fish and isopods (Lebrato et al. 2012 and references therein). The scavenging community associated with squid carcasses has only been studied once in an experimental setup (Collins et al. 1999), but a range of scavengers were found associated with natural squid falls (Hoving et al. 2017). Scavengers may have a preference for squid (Premke et al. 2006, Eastman & Thiel 2015), but comparative experiments are lacking. While obligate scavengers are likely rare (Stockton & DeLaca 1982, Smith 1985, Britton & Morton 1994), scavengers may have preference for certain body parts (e.g. Jones et al. 1998, Sweetman et al. 2014) or prey morphology (round fish versus flat fish) (Premke et al. 2006). Scavenging communities and rates may be related to the chemical composition and nutritional value of food falls. For example, mackerel has a higher carbon, lipid and fatty acid content than squid and jellyfish (Clarke et al. 1994, Youngbluth & Båmstedt 2001, Jennings & Cogan 2016, Romotowska et al. 2016, Parzanini et al. 2018). Lipids and fatty acids of the food fall are responsible for the odour plume and hence may impact first arrival times and scavenging response and communities. Finally, scavenging communities differ regionally; hence, experiments should be performed in areas where the flux of medium-sized food falls is expected to be relatively high (i.e. Norwegian Sea).

To follow up on the experiments of Sweetman et al. (2014) in the coastal deep sea off Norway (1250 m), we tested the hypothesis that the composition, abundance and successional stages as well as consumption rates of the scavenging community differed between medium-sized food fall species in an oceanic deep-sea region. To test this hypothesis, we deployed landers with 3 different food fall species (fish: *Scomber scombrus*, squid: *Illex coindetii*, jellyfish: *P. periphylla*) to elucidate the role of medium-sized food falls in the deep seas of the Norwegian Sea.

## 2. MATERIALS AND METHODS

### 2.1. Study site, food fall lander experiments and ocean floor observation system seafloor surveys

To mimic natural food falls, we performed 8 deployments with 2 deep-sea free-fall landers at depths of 1360 to 1440 m in the southern Norwegian Sea during a cruise on the RV 'Heincke' (cruise HE518) in September 2018 (Fig. 1, Table 1). The lander type was based on a KUM lander as in Dunlop et al. (2017, 2018). The size of the bait plate, its design and the amount of bait were similar to the bait plates used by Sweetman et al. (2014) and Dunlop et al. (2017, 2018). The bait plate was positioned 150 cm below an Ocean Imaging Systems camera system enclosing a Nikon D7100 camera (24 megapixel, set to ISO 200, 1/25 s exposure time and f-stop 8), programmed to take 1 image every 2.5 min. A flashlight was triggered simultaneously with the camera for the duration of the photo. Constant lights were not equipped to minimise the impact of the lander features on the scavenging results. In addition, the lander was equipped with a CTD (SBE 37), an acoustic Doppler current profiler (Teledyne RDI Workhorse Sentinel) and a point velocity current meter (Nortek, Aquadopp 6000).

The 3 bait types were offered in standardised amounts of 300 g wet weight (defrosted) and included squid (*Illex coindetii* as a substitute for *Gonatus fabricii*), jellyfish (*Periphylla periphylla*) and fish (*Scomber scombrus*). We did not have access to *G. fabricii* for our experiments. To mimic a squid food fall of *G. fabricii*, we used *I. coindetii* instead, a squid species we expect to have similar nutritional characteristics as *G. fabricii*. Fish and squid were bought at a fish market in Bergen (Norway), while the jellyfish were collected on a cruise to Lurefjorden (Norway) in August 2018. The fish were caught locally, while the squid was imported from Portuguese waters. For a more natural and even distribution of the odour

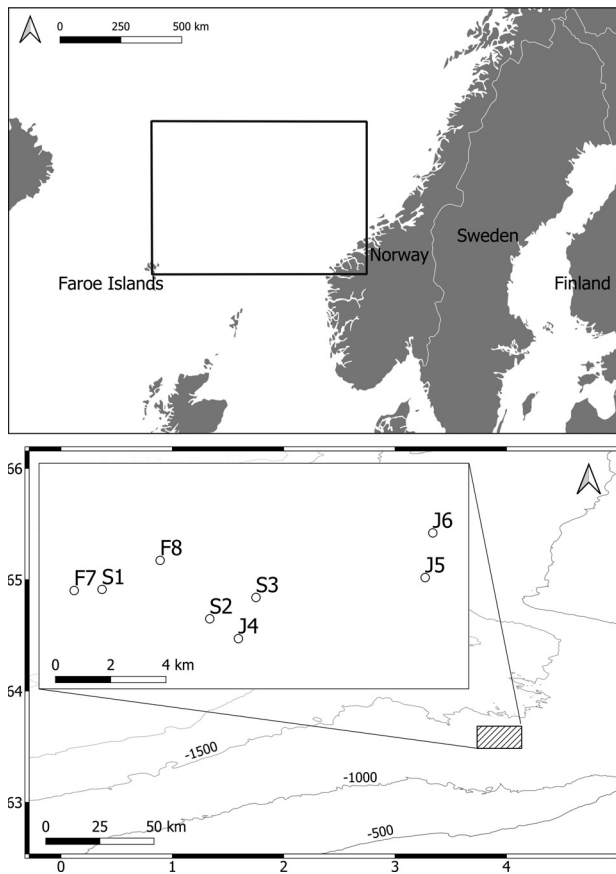


Fig. 1. Study site for lander deployments during cruise HE518. (a) General study site and (b) specific sites for lander deployments and bathymetry. Abbreviations refer to the lander deployment, with specific baits as specified in Table 1

plume, the bait was cut into similar-sized pieces (~10 × 10 cm). To protect the bait from being lost during descent, it was wrapped in nets (mesh size: 150 mm), and zip ties were used to attach it to the bait plate. We also analysed the images during descent and ascent to assure that no loss of bait would obscure the results.

Two landers were deployed simultaneously each day. To ensure a random sampling design, maximum longitude and latitude boundaries of the work area were first defined. To determine the position of the first lander deployment, the length and width (in nautical miles) of the resulting square were multiplied with 1 random number each (generated with the random number generator function in Microsoft Excel). By defining the upper left corner of the work area square as the origin, the 2 numbers were then used to define the deployment location within the square. To determine the position of the second deployment, another random number was generated and multiplied by 360° to define the direction of the

Table 1. Lander deployments. See also Fig. 1 for locations. Deployment (depl.) time was measured as the time the lander hit the water and began descending. Recovery (rec.) time was measured as the time the lander released the weights and began ascending from the seafloor

Depl. no.	Bait type	Depl. duration (h:min)	Depl. date (dd.mm.yy)	Depl. time (h:min UTC)	Rec. date (dd.mm.yy)	Rec. time (h:min UTC)	Depth (m)	Position	Current velocity (cm s <sup>-1</sup> )	Temp. (°C)
S1	<i>Illex coindetii</i>	24:50	09.09.18	10:00	10.09.18	11:18	1372	63° 35.23' N, 3° 50.06' E	9 E	-0.67
S2 <sup>a</sup>	<i>Illex coindetii</i>	23:03	09.09.18	10:35	10.09.18	10:31	1372	63° 34.06' N, 3° 54.48' E	6 E	-0.77
S3	<i>Illex coindetii</i>	16:07	10.09.18	15:49	11.09.18	08:17	1383	63° 34.62' N, 3° 56.49' E	7 NE	-0.67
J4 <sup>a</sup>	<i>Periphylla periphylla</i>	16:57	10.09.18	16:12	11.09.18	09:30	1360	63° 32.74' N, 3° 55.63' E	6 E	-0.78
J5	<i>Periphylla periphylla</i>	17:59	11.09.18	15:41	12.09.18	10:00	1422	63° 35.54' N, 4° 03.72' E	1 NE	-0.77
J6	<i>Periphylla periphylla</i>	17:23	11.09.18	16:05	12.09.18	08:44	1438	63° 37.51' N, 4° 04.32' E	3 N	-0.67
F7	<i>Scomber scombrus</i>	08:51	14.09.18	04:51	14.09.18	14:00	1369	63° 34.80' N, 3° 48.53' E	6 S	-0.67
F8	<i>Scomber scombrus</i>	09:17	14.09.18	05:23	14.09.18	15:00	1383	63° 35.99' N, 3° 51.98' E	3 SE	-0.67

<sup>a</sup>Only used for consumption rate and removal time analysis



second deployment position relative to the first. The second deployment position was then positioned at least 2 km along this random bearing from the first deployment site, which minimised overlap of odour plumes from the baits on each lander (current velocity provided in Table 1). This sampling design resulted in the deployment locations in Fig. 1, with 2 of the 8 deployments (J5 and J6) 6 to 13 km (min. distance S3 to J5 = 6.21 km, max. distance F7 to J6 = 13.32 km) away from the other 6. The deployment duration ranged from 9 to 25 h and was also dependant on weather conditions. The total scavenging rate was quantified by using the initial wet weight of the bait minus the wet weight of the carcass after lander recovery and dividing this weight by the time it took for the bait to be consumed.

To inspect the seafloor before lander deployments and to document seafloor communities in the experimental areas, we performed seafloor observations with the ocean floor observation system (OFOS) at 5 of the 8 deployment locations (S1, S3, J5, J6 and F7). Here, we refer to S1, S3 and F7 as Site 1 and J5 and J6 as Site 2. OFOS is a steel frame equipped with a downward-looking high-definition camera (SubC Imaging), lasers pointing at the seafloor for size reference (25 cm apart) and a deep-sea telemetry (Sea and Sun Technology DTS-6). The OFOS is deployed over the side of the ship and connects via a CTD conducting cable. Towing speed is approximately 0.5 m s<sup>-1</sup> over ground. The telemetry allows for a live, reduced-quality preview and monitoring of the video that is collected by the camera and stored in the camera's internal memory. A weight is attached on a rope and visible in the camera view. When the weight hits the sediment, the length of the conducting cable is adjusted via communication with the winchperson. Survey time ranged from 50 to 150 min. The starting positions of the OFOS tracks are provided in Table S1 in the Supplement at [www.int-res.com/articles/suppl/m685p031\\_supp.pdf](http://www.int-res.com/articles/suppl/m685p031_supp.pdf).

## 2.2. Image analysis

Post processing of the photographs from the lander time-lapse camera was done using ImageJ software with the cell counter plugin (v.1.8.0, National Institutes of Health). We identified and quantified the scavengers that attended the bait by counting the number of individuals of each taxon in each image. Deployments 2 and 4 (Table 1) had to be excluded from the image analysis because extreme overexposure could not be corrected through post processing,

which made it impossible to count the amphipods. Bait-attending individuals were defined as fauna that had their head (or their disk in the case of brittle stars) on the bait plate. Larger scavengers, i.e. fish, that were not on the bait plate were noted separately but not included in the count. We recorded the time of the first arrival of scavengers for each deployment as well as the bait removal time and the maximum observed number (Max<sub>N</sub>) of scavengers (Dunlop et al. 2018).

Framegrab images from the OFOS videos were extracted in a VLC media player (v.3.0.11 Vetinari) using the snapshot tool. Framegrabs were taken every 1.5 min and additionally as close to the seafloor as possible to have the highest possible resolution. Because of variable image quality, the images were classified into good, medium and poor quality. In each collected image, organisms were identified to the highest possible taxonomic unit and counted with the multi-point tool in ImageJ (ImageJ v.1.53g). Image quality did not allow quantification of amphipods. The annotated area in each image was calculated by setting the scale in ImageJ and then calculating the area with the measure tool. The total area surveyed was calculated by the sum of the analysed images. This resulted in a total surveyed area ranging from 8 to 53 m<sup>2</sup> per study region (Table S1). For images with bad quality, the area was not calculated, since OFOS was not parallel to the seafloor and the distances between the 3 lasers were very different. For images with good and medium quality, the distances between the 3 lasers did not differ significantly (Table S1).

## 2.3. Scavenger taxonomy

Fish, brittle stars and other clearly visible and distinguishable taxa such as shrimps and Pantopoda were identified from the images. Amphipods, the major taxonomic group that was present at the bait in all deployments, were identified using amphipod morphological features and genetic analysis of the specimens collected from the carcass remains (e.g. fish skeletons). All 354 collected amphipods were fixed in 4% buffered formaldehyde and later transferred to 70% ethanol for long-term storage. The amphipods were sorted and identified to the lowest possible taxonomic level by using a stereo microscope (Nikon SMZ18 with attached Nikon DS-Fi3 camera). Pereopod 6 (of 59 individuals) was dissected and fixed separately in 96 to 100% ethanol to isolate for future DNA barcoding (e.g. Havermans et al. 2013). Taxonomic names were checked against the

World Register of Marine Species ([www.marine-species.org](http://www.marine-species.org)). The difficulty in identifying *Eurythenes* from only external characteristics visible on images, e.g. pigmentation (Thoen et al. 2011), was the reason to group all amphipods for the statistical analyses. DNA barcoding was applied to verify our amphipod identifications. DNA was extracted from the collected tissue using the Chelex-based InstaGene Matrix (BioRad), following the manufacturer's protocol. PCR amplifications of the mitochondrial cytochrome oxidase subunit 1 gene fragment were carried out using specific degenerate crustacean primers UCOIF and UCOIR (Costa et al. 2009) and AccuStart II PCR SuperMix (QuantaBio). After purification of the PCR products, they were sent to an external service provider for sequencing. Sequences were assembled with CodonCode Aligner v.9.0.1 (CodonCode), queried using BLAST (Altschul et al. 1990) and checked against results in GenBank (NCBI Resource Coordinators 2018).

#### 2.4. Statistical analyses

All statistical analyses were carried out using the free statistical computing software R (R v.4.0.3, R Core Team 2020) in the RStudio environment (v.1.4.1103, RStudio Team 2021) and visualised using the ggplot2 (Wickham 2016) and the RColorBrewer (Neuwirth 2014) packages. Statistical differences in the composition of scavenger assemblages between food fall species were analysed with an ANOSIM based on scavenger  $\text{Max}_N$  in a Bray-Curtis resemblance matrix using the package 'vegan' (Oksanen et al. 2019). The Bray-Curtis similarity coefficient was calculated using the 4<sup>th</sup> root transformed  $\text{Max}_N$  of each taxon to lower the influence of dominant species on the analysis. The R-value reflects the degree to which species composition differed between food fall species. While a high R-value indicates dissimilarity between food fall species, an R-value close to 0 suggests similarity between them. Negative R-values reflect greater dissimilarities within than between groups (Clarke & Gorley 2001). SIMPER (package 'vegan', Oksanen et al. 2019) was used to identify the average contribution of taxa to the overall Bray-Curtis dissimilarity between scavenger assemblages (Clarke 1993). A threshold of 70% was used to identify the most important species contributing to differences between sites (Clarke 1993). Generalised linear models (GLMs) were used to analyse for differences in the maximum abundance of scavengers between baits (fixed categorical variable) based on  $\text{Max}_N$  count data as well as

differences in the time at which the maximum abundance peaked ( $t\text{Max}_N$ ). The models were produced using the basic package (R Core Team 2020). Additionally, depth and current speed were added as covariates to the models (fixed continuous variables). Since we have count data, we based the GLMs on the Poisson distribution to exclude the prediction of negative values. Quasi-Poisson was used in cases of under- or overdispersion (a lower or higher variance than the mean). Models were tested with Shapiro-Wilkox for normal distribution and Fligner-Killeen for homogeneity of variances. Both assumptions were met for all our models. However, reliable testing of these requirements is difficult with small datasets, which needs to be taken into account when interpreting results. Models were selected based on their explanatory power and simplicity. If the explanatory power differed between models, the deviance of residuals of the models is compared. Model results were summarised with the Anova function (package 'car', Fox & Weisberg, 2019). Pairwise comparisons between different baits were assessed using the glht function (general linear hypotheses and multiple comparisons for parametric models, including GLMs) of the package 'multcomp' (Hothorn et al. 2008), with a specification on Tukey's all-pair comparisons. For all 8 deployments, consumption rates—calculated from the consumed wet weight and the bait removal time—were also compared between baits using GLMs due to heteroscedasticity within the dataset. An alpha level of 0.05 was chosen as the basis for assuming statistical significance. To test for differences in benthic background community composition from the OFOS results, background communities were grouped in the 2 sites: fish and squid deployments (S1, S3, F7) for Site 1 and jellyfish deployments (J5, J6) for Site 2. With the taxa density found at the 2 sites, statistical differences in the biodiversity of benthic background taxa were analysed with ANOSIM based on a Bray-Curtis resemblance matrix with Jaccard distances (package 'vegan', Oksanen et al. 2019). SIMPER (package 'vegan', Oksanen et al. 2019) was then used to identify important taxa and their contribution to the overall Bray-Curtis dissimilarity.

### 3. RESULTS

#### 3.1. Benthic community of the research area

Image analysis of the framegrabs from the video taken by OFOS in the areas where we deployed our

landers showed Asteroidea and ophiuroids to be most abundant, followed by shrimp, mysids and gastropods. *Lycodes frigidus*, *Amblyraja hyperborea* and *Cleippides quadricuspis* were observed occasionally (Table S1). The ANOSIM showed no differences in benthic background communities at the 2 different sites ( $R = 0.06$ ,  $p = 0.01$ ), indicating that the benthic background communities within Sites 1 and 2 vary just as much as those between the 2 sites. SIMPER results showed ophiuroids as one of the most contributing taxa to the overall Bray-Curtis dissimilarity, with 54.31%, but no taxon contributed over 70% (threshold).

### 3.2. Scavenging community of the experimental food falls

Amphipods dominated the scavenging community at all bait types, with large lysianassids being the first taxa to arrive at the bait (Figs. 2 & 3 and see Fig. 5). After lander touchdown, these amphipods arrived at squid and fish food falls after 5 to 10 min and after 12 to 22 min at the jellyfish food falls. The scavenger composition in the fish experiments consisted only of amphipods and zoarcid fish (*L. frigidus*), while we additionally observed ophiuroids of the species cf. *Ophiopleura borealis* and occasionally a Pantopoda in the squid experiments (Figs. 2–5). Additionally, 1 ling (*Molva molva*) and a skate (*A. hyperborea*) were observed near the bait plate, though they were never observed feeding on the bait during the squid deployments. In the jellyfish experiments, the community was different, and we found almost exclusively smaller amphipods and decapod shrimps (cf. *Bythocaris* spp.) that did not occur on the other food falls, as well as a smaller brittle star species (cf. *Ophiosten gracilis*). However, we could not identify the smaller amphipod species from the images alone, and we did not collect any specimens.

Morphological examination of 354 amphipods suggests that the dominant amphipod is *Eurythenes gryllus*. Barcoding confirmed this, and the collected lysianassid amphipods from the fish remains belonged to the genus *Eurythenes* (1 individual with >99% sequence coverage in Genbank with *E. gryllus* and 1 individual with >95% sequence coverage with the genus *Eurythenes* sp.). We observed at least 2 more potentially different species of lysianassid amphipods in the images (grouped as Amphipoda spp., Fig. 3). Other amphipod taxa from the families Stegocephalidae and Pardaliscidae were present at all bait types, but in lower numbers (Fig. 5). How-

ever, these taxa were not collected, and their identities could thus not be fully established. Single individuals of the amphipod cf. *C. quadricuspis* (family Calliopidae) were seen in 2 of the squid experiments and in 1 jellyfish experiment, though they were never observed actively feeding.

Image analysis of time-lapse photos from the experiments indicated a succession of larger amphipods followed by smaller ones in both squid and fish deployments, with a more obvious shift in the latter being observed after 3 to 3.5 h. It was not possible to confirm if the smaller amphipods in the jellyfish experiments were the same species as those in the fish and squid food falls. In addition, the presence of ophiuroids and larger amphipods seemed to be inversely correlated in the squid experiments. A slight increase in the abundance of ophiuroids (increasing from 2 to 4 individuals on the bait plate) was visible when amphipods were absent, particularly towards the end of the deployments (a maximum of 4 individuals was reached in deployment 3 after 13 h on the seafloor) when little to no visible parts of the carcasses were left. The numbers of amphipods slightly declined (1 to 3 individuals) after the arrival of a zoarcid on or close to the bait plate, indicating a possible negative correlation between the abundances of these taxa.

### 3.3. Consumption rates and maximum abundance of scavengers

The soft tissue of the baits was completely consumed (see removal times in Table 2) except for *Periphylla periphylla* at deployment 4, where 30 g (8.6%) remained on the bait plate after 16 h. For deployments 7 and 8 with *S. scombrus*, only bones remained on the bait plate, making up 36 g (10.6%) and 28 g (9.5%) of the deployed bait weight, respectively. The remaining bait was considered when calculating the consumption rates.

Squid and fish food falls were consumed in shorter times (squid:  $9.8 \pm 0.3$  h, mean  $\pm$  SD; fish:  $9.1 \pm 0.3$  h) than jellyfish food falls ( $16.8 \pm 0.9$  h), resulting in significantly higher consumption rates for squid ( $30.2 \pm 0.4$  g h<sup>-1</sup>) and fish ( $31.6 \pm 3.7$  g h<sup>-1</sup>) than for jellyfish ( $20.3 \pm 1.4$  g h<sup>-1</sup>) (GLM [Poisson],  $\chi^2 = 7.96$ ; df = 2;  $p = 0.02$ ) (Table 2, Table S2). Multiple comparisons between food fall consumption rates revealed small significant differences between jellyfish and squid bait ( $p = 0.045$ ) as well as between jellyfish and fish bait ( $p = 0.04$ ) (see model results in Table S2). However, no significant difference was found for the consump-



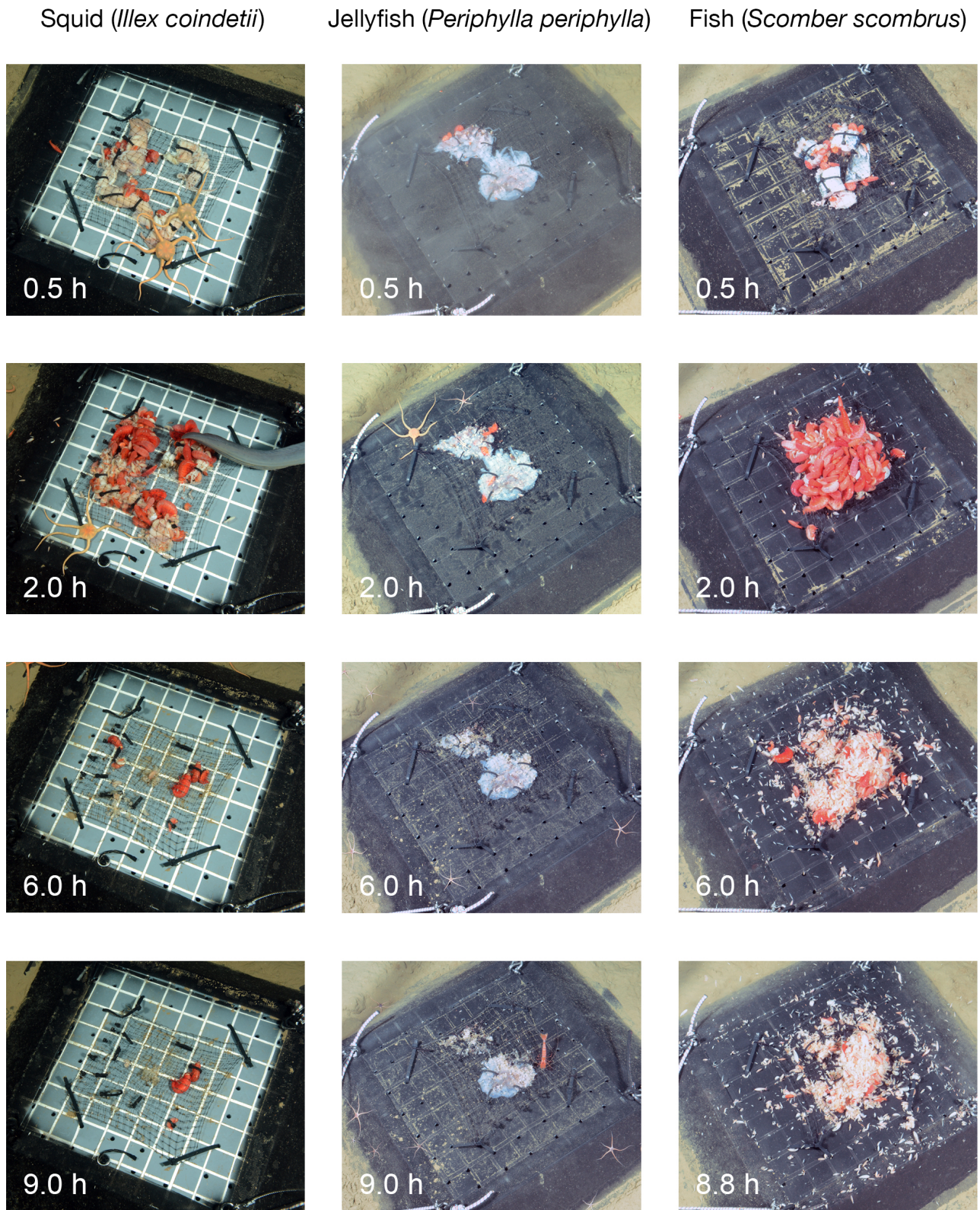


Fig. 2. Scavenger assemblages at deployments S3 (squid), J5 (jellyfish) and F7 (fish) after specific time intervals. Note that the 9.0 h interval for fish is replaced by 8.8 h due to shorter deployment. Hours indicate time at seafloor

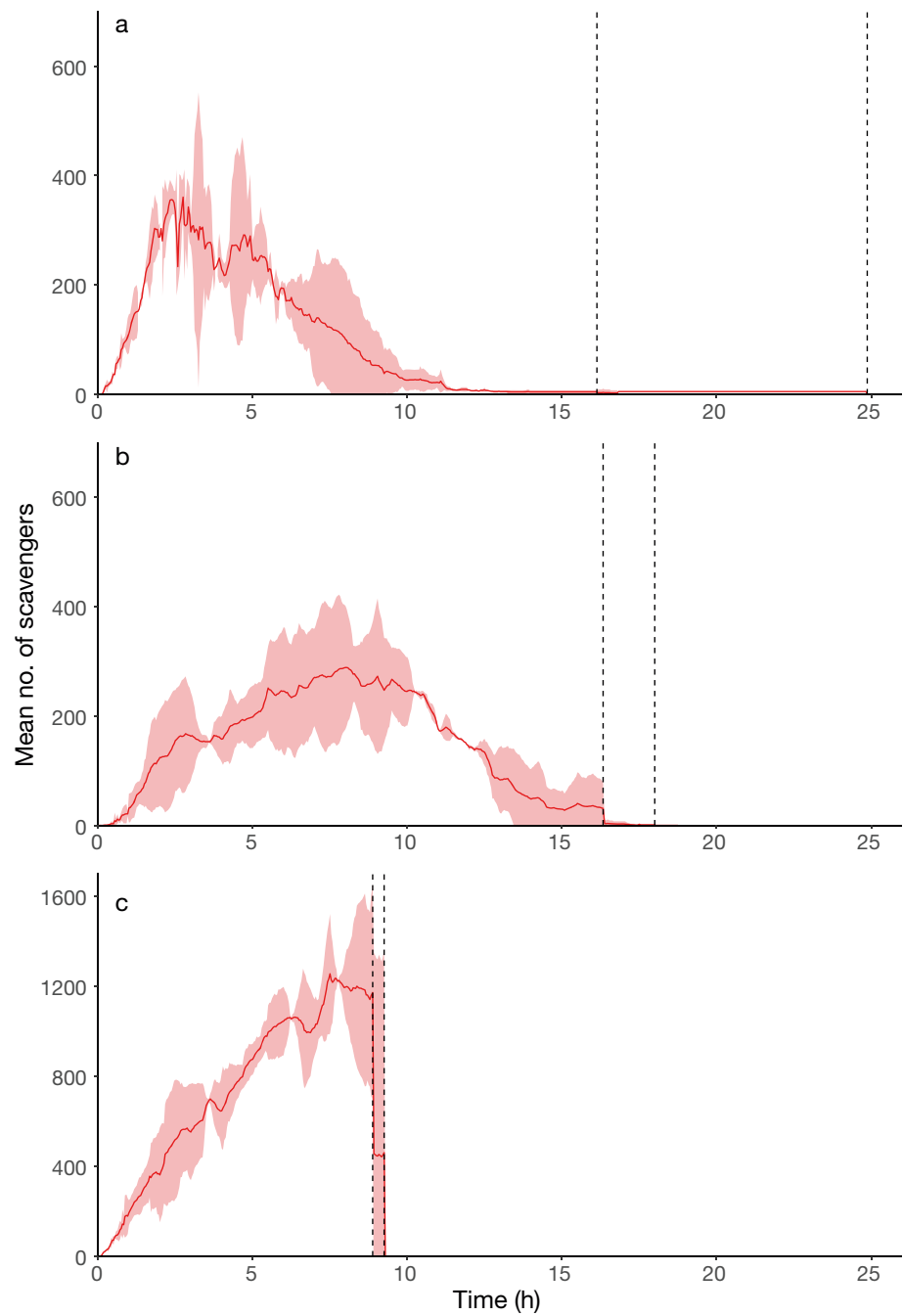


Fig. 3. Mean number of amphipods observed in the food fall experiments with baits (a) *Illex coindetii*, (b) *Periphylla periphylla* and (c) *Scomber scombrus*, as a function of time at the seafloor. Shading shows 95 % CIs. Note the different scales on the y-axes. The end of the experiments is indicated by vertical dotted lines

Table 2. Removal time, consumption rate, maximum number ( $\text{Max}_N$ ) of scavengers and time at which the maximum numbers were reached, given as mean  $\pm$  SD. Number of replicates totals 2 for all experiments

Food fall species	Removal time (h)	Consumption rate ( $\text{g h}^{-1}$ )	$\text{Max}_N$ of scavengers	Time of $\text{Max}_N$ of scavengers (h)
<i>Illex coindetii</i>	$9.80 \pm 0.29$	$30.21 \pm 0.38$	$382 \pm 53.74$	$3.00 \pm 0.35$
<i>Periphylla periphylla</i>	$16.82 \pm 0.92$	$20.34 \pm 1.44$	$303 \pm 73.54$	$8.04 \pm 0.35$
<i>Scomber scombrus</i>	$9.07 \pm 0.26$	$31.60 \pm 3.72$	$1403.5 \pm 17.68$	$8.19 \pm 0.97$





Fig. 4. Representative images of bait-attending species that occurred on or in the vicinity of the bait plate. (a) *Eurythenes gryllus* (sampled organism from squid deployment), (b) *Eurythenes gryllus*, (c,d) Stegocephalidae spp., (e) Pardaliscidae spp. (indicated with arrows), (f) cf. *Cleippides quadricuspis*, (g) cf. *Bythocaris* spp., (h) Pantopoda spp., (i,j) Asteroidea spp., (k) cf. *Ophiopleura borealis*, (l) cf. *Ophiocten gracilis*, (m) *Amblyraja hyperborea*, (n) *Lycodes frigidus*, (o) *Molva molva*

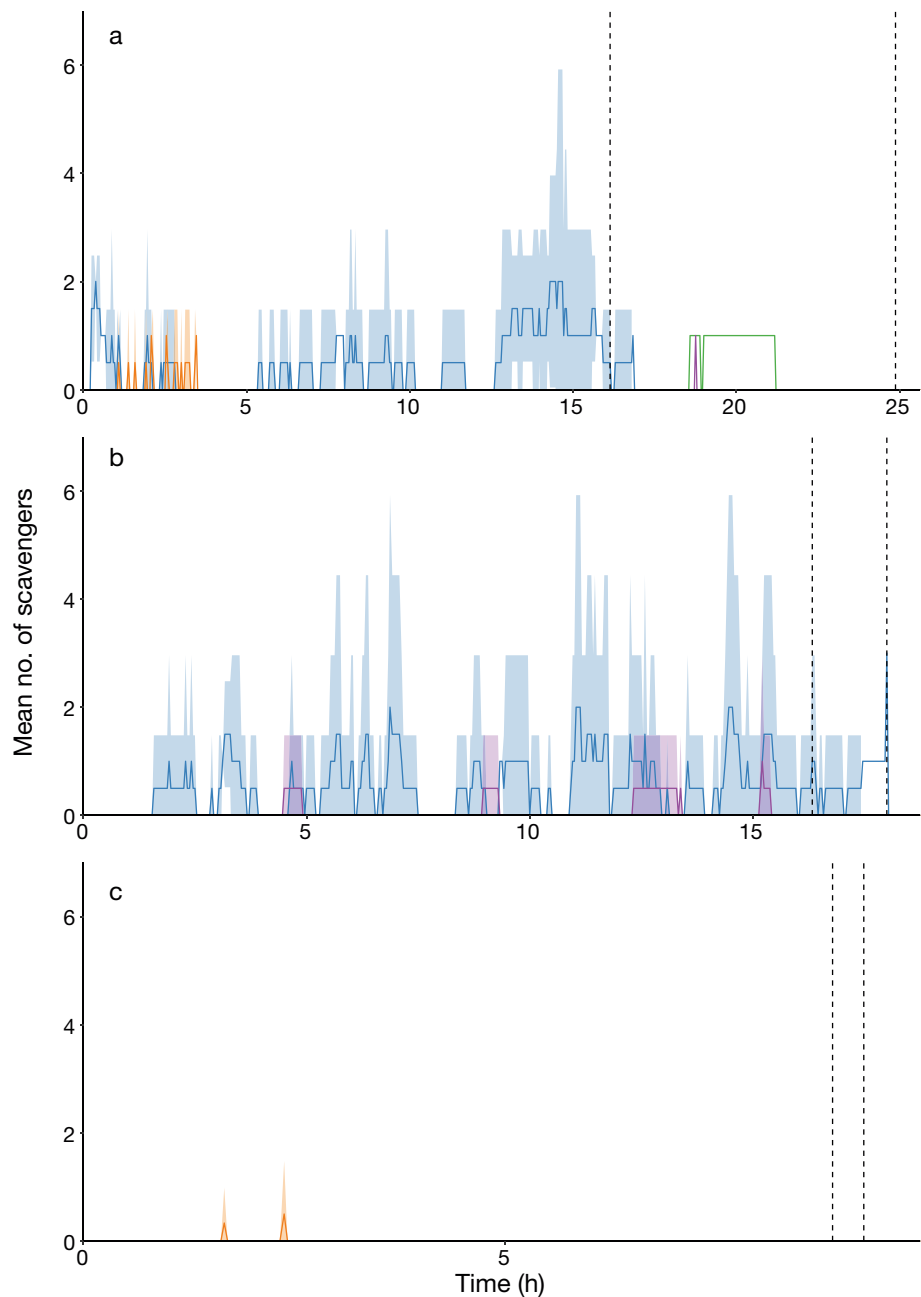


Fig. 5. Mean number of other scavengers observed in the food fall experiments with baits (a) *Illex coindetii*, (b) *Periphylla periphylla* and (c) *Scomber scombrus*, as a function of time at the seafloor. Dark blue: cf. *Ophiopleura borealis*; light blue: cf. *Ophiocten gracilis*; green: Pantopoda spp.; purple: cf. *Bythocaris* spp.; orange: *Lycodes frigidus*. Shading shows 95% CIs. Note different y-axis scales in comparison to Fig. 3 and different x-axis for (a), (b) and (c)

tion rates between fish and squid bait ( $p = 0.96$ ). The  $\text{Max}_N$  of scavengers was significantly higher on the fish food falls ( $1403.5 \pm 17.7$ ) (GLM,  $\chi^2 = 246.87$ ;  $\text{df} = 2$ ;  $p = <0.001$ ) (Table S2) than on the jellyfish ( $316 \pm 83.4$ ) and squid food falls ( $386.5 \pm 54.5$ ). The results were the same when not considering zoarcid fish in the maximum abundance of scavengers (GLM,  $\chi^2 = 246.62$ ;  $\text{df} = 2$ ;  $p = <0.001$ ) (Table S2).  $t\text{Max}_N$  values were significantly different between bait types (GLM [quasi-Poisson],  $\chi^2 = 107.28$ ;  $\text{df} = 2$ ;  $p = <0.001$ ) with the covariates bait ( $\chi^2 = 5301.4$ ,  $\text{df} = 2$ ,  $p = <0.001$ ) and depth ( $\chi^2 = 164.7$ ,  $\text{df} = 1$ ,  $p = <0.001$ ). Statistically

similar results were found with multiple comparisons between  $t\text{Max}_N$  of jellyfish ( $t = 8.04 \pm 0.35$  h) and fish ( $t = 8.19 \pm 0.97$  h), but  $t\text{Max}_N$  was reached significantly faster for squid ( $t = 3.00 \pm 0.35$  h). ANOSIM, which is based on maximum abundances of scavenging taxa (Table S3), revealed differences in community composition between the 3 bait types tested ( $R = 0.78$ ,  $p = 0.2$ ), indicating that the dissimilarity between the scavenger communities on the different baits is greater than the dissimilarity within the scavenger communities on the different baits. SIMPER revealed that the scavenger community found at the squid bait

differed 11.64% from that at the jellyfish bait and 32.46% from that at the fish bait. The overall dissimilarity between the communities found on jellyfish and fish bait was 39.59%. Amphipods were the main driver for the differences between squid and fish scavenger communities (89.14%) and between jellyfish and fish scavenger communities (86.25%) (Table S4). For differences between squid and jellyfish scavenger communities, amphipods, zoarcid fish and shrimps contributed 80.57% (Table S4).

#### 4. DISCUSSION

This study is one of the few experiments that have compared differences in deep-sea scavenging activities and communities associated with different medium-sized food falls. Despite the relatively small number of lander deployments, our study revealed rapid scavenging for all bait types, with differences between the baits regarding scavenger composition and abundances. Differences in consumption rates between bait types were overall significant, but pairwise comparisons revealed no significant difference between consumption rates of fish and squid. Our multi-taxon approach resulted in new regional information about bait-specific scavenging responses.

##### 4.1. Scavenger diversity

Typically, analyses of  $\text{Max}_N$  are made per species, rarely giving insight into the total abundances of scavengers. Some studies exclusively focus on specific scavenger taxa, e.g. fish or amphipods (Priede et al. 1990, Henriques et al. 2002, Jamieson et al. 2017), and omit other scavengers in their analyses. The overall low scavenger diversity observed in our study (minimum of 4 species on fish and maximum of 7 species on squid) seems to be typical for smaller food falls (e.g. Premke et al. 2006, Sweetman et al. 2014). It stands in contrast to the high diversity (species richness 407 species) on large marine mammal falls such as whales (Smith & Baco 2003). This is caused by the long residence time of megafauna food falls, giving opportunity for more complex successional patterns as well as the arrival of detritivores and microbivores.

Although our random sampling design led to the 2 jellyfish stations being further away (~6–13 km) from the other deployment sites, no differences in background community composition were found between the 2 sites. Thus, it can be assumed that the back-

ground composition is similar at all stations. Similarity was further confirmed when investigating the taxa that contributed the most to the differences between the sites. This resulted in a rather low similarity percentage (54.31%), as generally 70% is seen as the threshold when aiming to identify the most important species contributing to differences between sites (Clarke 1993). However, other factors not included in our analyses such as food availability, topography or diel and seasonal rhythms might impact the scavenging communities and rates.

The image-based identification of the amphipods alone did not allow us to readily differentiate between species. The larger amphipods were identified as *Eurythenes gryllus* or *Eurythenes* sp. using barcoding and morphological characteristics. However, we had a low success rate with DNA barcoding. These results fit with the high genetic variance yet very low morphological variation within the genus *Eurythenes* (d'Udekem d'Acoz & Havermans 2015). The presence of amphipods of the family Stegocephalidae on all our food falls is particularly interesting, as they are generally described as micro-predators associated mostly with sessile invertebrates such as cnidarians. Only the stegocephalid genus *Andaniotes* has so far been frequently captured in baited traps and is thus considered to be at least a facultative scavenger (Berge & Vader 2001).

Despite a similar experimental design and a comparable depth (1250 m), Sweetman et al. (2014) found a completely different scavenging community associated with experimental food falls of *Periphylla periphylla* and *Scomber scombrus* in the Sognefjorden, which is around 290 km southeast from our sampling location. In that study, scavenger abundances between the fish and jellyfish food falls differed, but the scavenger diversity and scavenging rates were similar. The most abundant scavenger was a lysianassid amphipod, *Orchomenella obtusa*, which occurred in similar numbers on both food fall types (jellyfish  $\text{Max}_N$ :  $1609.5 \pm 273.5$ , fish  $\text{Max}_N$ :  $2024.7 \pm 1135.9$ ). In contrast to our findings, which showed distinct taxa on the nekton food falls that were absent on the jellyfish food falls, Sweetman et al. (2014) found that both bait types attracted the same scavenger composition consisting of *O. obtusa*, a hagfish (*Myxine glutinosa*), a galatheid crab species (*Munida tenuimana*) and an unidentified decapod shrimp. Similarities were found in the abundances of the decapod shrimp in the fjord (jellyfish  $\text{Max}_N$ :  $9.0 \pm 3.1$ , fish  $\text{Max}_N$ :  $1.3 \pm 0.6$ ) and *Bythocaris* spp. in our samples, which were almost exclusively found in the jellyfish experiments. The scavenging community observed on mixed fish



bait in the Arctic (Fram Strait, 1500–2600 m depth, Premke et al. 2006) was relatively similar to the scavengers we observed on the mackerel. The dominant amphipod species in the Fram Strait study of Premke et al. (2006) were *E. gryllus*, the smaller amphipod *Tmetonyx norbiensis* and a stegocephalid species that only occurred occasionally as well as zoarcid fish and chaetiliid isopods. However, the maximum abundances of scavengers were considerably lower ( $\text{Max}_N$ : 305–800) compared to our fish deployments ( $\text{Max}_N$ :  $1403.5 \pm 17.68$ ) despite the larger bait parcels (2–5 kg) used in Premke et al. (2006). The only other food fall experiment with only squid carcasses (*Illex argentinus*) was carried out on the Patagonian slope between 900 and 1750 m (Collins et al. 1999). Hagfish were the dominant scavengers in experiments down to 1100 m, and crabs and grenadiers consumed most of the bait at 1179 and 1442 m. The bait on 4 other deployments (1100–1740 m) remained largely unconsumed.

#### 4.2. Scavenger abundance and arrival times

The large number of amphipods attracted to food falls as well as their scavenging behaviour likely leads to frequent underestimations of scavenger abundances (e.g. Premke et al. 2006, Sweetman et al. 2014). Large numbers of amphipods may prevent identification and quantification of other scavenging fauna including the ones that are covered by other amphipods on the images. Additionally, some amphipods may be completely out of view, since they also feed on the inner parts of the carcass (Hessler et al. 1978). Due to the limited number of specimens we collected, combined with the difficulty to differentiate between the species using images alone, we may also have underestimated the total amphipod diversity and abundance. However, such possible underestimations were consistent between the experiments, and amphipods could nevertheless be identified as the crucial taxa contributing to the differences between the scavenger community of the different bait types, especially between fish and invertebrates.

Amphipods also arrived first at the food falls and in a matter of minutes at the fish and squid, with only a slightly slower reaction for the jellyfish carcasses. This short first arrival time of amphipods is in agreement with previous studies. We hypothesise that the slight difference seen in the jellyfish experiments is due to the smaller or less intense odour plume released by the jellyfish carcasses. Also, the carbon and nitrogen content of *P. periphylla* is lower (20% C

dry weight, 3% N dry weight; Youngbluth & Båmstedt 2001) than that of *S. scombrus* (56% C dry weight, 10% N dry weight; Jennings & Cogan 2016) and *Illex* sp. (42–58% C dry weight, 5–13% N dry weight; both varying between sex and tissue; Clarke et al. 1994). Generally, there are 3 strategies found in scavengers for the location of food: chemoreception, mechanoreception and photoreception (Eastman & Thiel 2015). Since light decreases with depth (except for bioluminescence), photoreception is unlikely to be a dominant strategy for carcass detection in the deep sea. Long-range mechanoreception by sensing the impact of the carcass when it hits the seafloor has been suggested as a possible strategy (Dahl 1979, Klages et al. 2002) and may be relevant to our experiments, since the impact of the landers on the seafloor is likely large. However, in a natural situation, chemoreception seems to be the most likely way for amphipods to locate the relatively light medium-sized food falls (Premke et al. 2003). Taxonomic differences in chemoreceptive abilities might also be the cause for some of the observed food fall-specific scavenging responses and scavenger assemblages. Scavengers may have species-specific responses to amino acids released by the different carcasses (Meador 1989).

#### 4.3. Food fall attendance time and consumption rates

The first arrival times at fish food falls in the Fram Strait were slower (9–24 min) than those in our fish deployments (5–10 min), while the successional stages between different-sized amphipods were similar to our findings (Premke et al. 2006). Scavengers occurred in lower abundances at the Fram Strait food falls, but the consumption rates were 3 to 4 times higher than those in our study. These findings might indicate that the frequency and abundance of food falls in the Fram Strait are reduced in comparison to those in the southern Norwegian Sea, resulting in a more rapid food uptake. Optimal foraging theory considers scavengers as organisms that utilise patches of food that are randomly distributed (MacArthur & Pianka 1966, Prins & van Langevelde 2008). Scavengers probably have an optimum time spent at the food fall, as the intake of carrion and thus energy decreases over time as the food fall gets smaller (Charnov 1976). Food fall attendance is not related to satiation but is correlated with the expectation to have access to additional food falls (Stephens & Krebs 1987). Therefore, the time that a

scavenging organism spends at the food fall comes at the expense of travel time to the next food fall (Charnov 1976 from Priede et al. 1990). In a food-rich environment, the distance to the next food fall is relatively close, and therefore the bait attendance time will be relatively short. Observations on bait-attending macrourid fishes in the Pacific confirmed this hypothesis (Priede et al. 1990). Experiments in the Fram Strait with squid and jellyfish food falls would be needed to further investigate these differences in attendance time of scavengers at a food fall. Experimental squid food falls on the Patagonian slope showed large variation in bait consumption, with barely any activity shown in 4 of the deeper deployments (Collins et al. 1999). However, when scavengers attended and consumed the carcass (at depths between 900 and 1100 m), the removal time was about 4 h with a consumption rate of  $200 \text{ g h}^{-1}$ , which is 2 times faster than in our deployments and with an almost 7-fold higher consumption rate. In baited camera studies with mackerel in the NW Atlantic (Hargrave 1985) at a depth of 5830 m, *Eurythenes* amphipods arrived first and after 3 h. The consumption rate was much lower ( $100 \text{ g}$  in  $\sim 33 \text{ h}$ ) compared to our study ( $31.6 \text{ g h}^{-1}$ ) and that of Sweetman et al. (2014) ( $57.8 \text{ g h}^{-1}$ ). Overall, this comparison suggests that depth is an important factor in scavenging responses that need further study.

We observed small statistical differences between consumption rates of the different baits. There was also no significant difference between consumption rates of fish and jellyfish food falls in Sognefjorden (Sweetman et al. 2014). The food fall consumption rates in Sognefjorden (Sweetman et al. 2014) were 2 to 4 times higher than those in our study. These results are congruent with the higher (0.2–6.5 times) amphipod abundances reported for both food fall species in comparison to our study. Another study using *P. periphylla* as bait and carried out in the same fjord (Dunlop et al. 2018) found only around 2 times higher consumption rates at 1250 m depth. However, this was arguably due to the missing lysianassid amphipods in these deployments, which were dominant in the other fjord experiments (Sweetman et al. 2014) as well as in our own study. The differences in consumption rate between the fjord study and our study is likely related to 2 scavenging species, the hagfish *M. glutinosa* and the galatheid crab *M. tenuimana*. These 2 species were less abundant than lysianassids in our study but were larger and thus also contributed more towards the overall scavenging rate. Temperature also likely plays a role, as it is one of the dominant abiotic factors that regulate the

metabolic and feeding rates of scavengers (Gillooly et al. 2001, Brown et al. 2004). Bottom temperatures in our experiments were between 0 and  $-1^\circ\text{C}$  at all our stations (Table 1), while the temperature in the fjord was  $8^\circ\text{C}$  (Sweetman et al. 2014). Therefore, temperature is likely another factor that contributes to the lower consumption rates in our experiments compared to the fjord experiments (Sweetman et al. 2014).

#### 4.4. Successional stages

With food supply being a major limiting factor in the deep sea, food falls are important energy sources (Higgs et al. 2014) that shape behaviour and the detection of food falls (see also above, Priede et al. 1990) and hence result in successional stages in food fall consumption (e.g. Smith & Baco 2003, Premke et al. 2006, Soltwedel et al. 2018). Although not as conspicuous compared to megafaunal food falls, such successional stages have been observed on medium-sized food falls before (e.g. Premke et al. 2006, Sweetman et al. 2014, Harbour et al. 2020), and we show them here. Despite our observations being based on relatively few deployments, we found a clear succession between amphipods on both squid and fish carcasses. Larger lysianassids arrived much faster than smaller amphipods, and the latter actually dominated the fish carcass after approximately 3 h. We also observed a minor inverse relationship between ophiuroids and amphipods on the squid food falls. This relationship became more clear when also considering the ophiuroids surrounding the bait plate. The observed succession between larger and smaller amphipods on our squid and fish carcasses is consistent with food fall-associated fauna in the Fram Strait (Premke et al. 2006). This pattern might be due to smaller individuals (1) having reduced motility or (2) avoiding predation by the larger amphipods (Hessler et al. 1978, Ingram & Hessler 1983). Avoidance of larger amphipods may also explain the absence of fish on the *S. scombrus* deployments. The inverse relationship between ophiuroids and amphipods might be an indirect effect of the ophiuroids not being able to process big chunks of the carcass. Instead of directly feeding on the food fall, ophiuroids might feed for longer periods of time on small remains left over from sloppy feeding by other scavengers (Smith 1985). However, other ophiuroid species have been previously observed to actively feed off fish carcasses *in situ* as well as *ex situ* (Nagabhushanam & Colman 1959, Smith 1985). Thus, another



possible explanation would be the slower movement of ophiuroids, resulting in later arrival at the food fall location. The fishes *Lycodes frigidus* and *Amblyraja hyperborea* were not observed consuming the bait. *L. frigidus* instead may prey on the scavenging amphipods, which is supported by slightly declining numbers of amphipods after the arrival of a fish on or close to the bait plate in our experiments. This behavior was also observed in previous studies (e.g. Collins et al. 1999, Premke et al. 2006) and is supported by stomach content analyses of zoarcid species, which revealed lysianassids and other crustaceans as a common dietary component (e.g. Smirnova et al. 2019, Bjelland et al. 2000). However, significant differences between consumption rates of our food fall species did not change when excluding fishes as scavengers (Table S2). In comparison, the ling *Molva molva* likely used the lander as shelter, as it stayed close to one of the attached weights over an extended period of time, suggesting an artificial reef effect (Jamieson et al. 2006, Gates et al. 2019).

#### 4.5. Outlook

Here, we provide a multi-species perspective on food fall-specific scavenging responses in the Norwegian Sea. Die-offs related to squid reproduction or jellyfish blooming can lead to mass deposition of carcasses. Natural observations of large jellyfish food falls suggest that higher concentrations of gelatinous material on the bottom might create local anoxic zones and subsequently less scavenging activity (e.g. Billett et al. 2006, Lebrato & Jones 2009, Sweetman et al. 2014, 2016). Therefore, the effect of multiple carcasses and mass deposition should be analysed in future studies, as has been started by Dunlop et al. (2018). One paradigm in the study on deep-sea food webs is that opportunism is a key strategy, and as a result, obligate scavengers are rare (Stockton & DeLaca 1982, Smith 1985, Britton & Morton 1994). Our data suggest that species-specific preferences for different carrion types do exist in deep-sea scavenging communities, but more research is needed that includes other factors such as the availability of other food sources for non-obligate scavengers, carcass deposition frequency, seafloor structure and bathymetry. Such information will help to better understand deep-sea benthic scavenger behaviour and the role of scavengers in deep-sea food webs and eventually will aid to predict the consequences of altered fluxes of organic material to the seafloor in ocean systems under climate change.

**Data availability.** Data from the experiments are available under <https://doi.pangaea.de/10.1594/PANGAEA.935210> and <https://doi.pangaea.de/10.1594/PANGAEA.935215>.

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