



# Pelagic deep-sea fauna observed on video transects in the southern Norwegian Sea

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## Abstract

Observations of the diversity, distribution and abundance of pelagic fauna are absent for many ocean regions in the Atlantic, but baseline data are required to detect changes in communities as a result of climate change. Gelatinous fauna are increasingly recognized as vital players in oceanic food webs, but sampling these delicate organisms in nets is challenging. Underwater (in situ) observations have provided unprecedented insights into mesopelagic communities in particular for abundance and distribution of gelatinous fauna. In September 2018, we performed horizontal video transects (50–1200 m) using the pelagic in situ observation system during a research cruise in the southern Norwegian Sea. Annotation of the video recordings resulted in 12 abundant and 7 rare taxa. Chaetognaths, the trachymedusa *Aglantha digitale* and appendicularians were the three most abundant taxa. The high numbers of fishes and crustaceans in the upper 100 m was likely the result of vertical migration. Gelatinous zooplankton included ctenophores (lobate ctenophores, *Beroe* spp., *Euplokamis* sp., and an undescribed cydippid) as well as calycophoran and physonect siphonophores. We discuss the distributions of these fauna, some of which represent the first record for the Norwegian Sea.

**Keywords** Norwegian Sea · Zooplankton · Micronekton · Macroplankton · In situ observations · Vertical migration · *Aglantha*

## Introduction

The pelagic ocean is the largest habitat on the planet and houses a high diversity, abundance and biomass of organisms. Up to 25% of the pelagic biomass can consist of gelatinous zooplankton (Robison 2004). Gelatinous organisms mainly consisting of the pelagic Cnidaria, Ctenophora and Tunicata have a variety of different body morphologies and feeding strategies, allowing them to occupy different niches in the oceanic foodweb (Haddock 2004). Pelagic tunicates (thaliaceans and appendicularians) are filter feeders (Holland 2016), while medusae, siphonophores and ctenophores are predators feeding on a wide spectrum of zooplankton including gelatinous organisms and micronekton (Pagès et al.

2006). Another prominent and widely distributed phylum in the oceanic water column are Chaetognatha, semi-gelatinous predators that can be among the numerically dominant plankton members of ocean communities (Bone et al. 1991).

Despite their low protein content, gelatinous zooplankton are common prey of many marine taxa including fishes, crustaceans, turtles and even some cephalopods (Heeger et al. 1992; Cardona et al. 2012; Hoving and Haddock 2017). The complex trophic interconnections of gelatinous zooplankton in the pelagic foodweb mark their central role within the pelagic ecosystem and their potential importance in the biological carbon pump (Alldredge 2004; Lebrato et al. 2012; Henschke et al. 2013; Sweetman and Chapman 2015). Gelatinous organisms have several traits that may give them an advantage in warmer, deoxygenated waters (Thuesen et al. 2005; Ekau et al. 2010). Although blooms of gelatinous organisms have been occurring for millennia, recent observations have drawn scientific and public interest to the question of whether or not the frequency of such blooming events is increasing, e.g. as a result of climate change (Lynam et al. 2011; Brotz et al. 2012; Condon et al. 2012, 2013). Confirming such potential increases requires a

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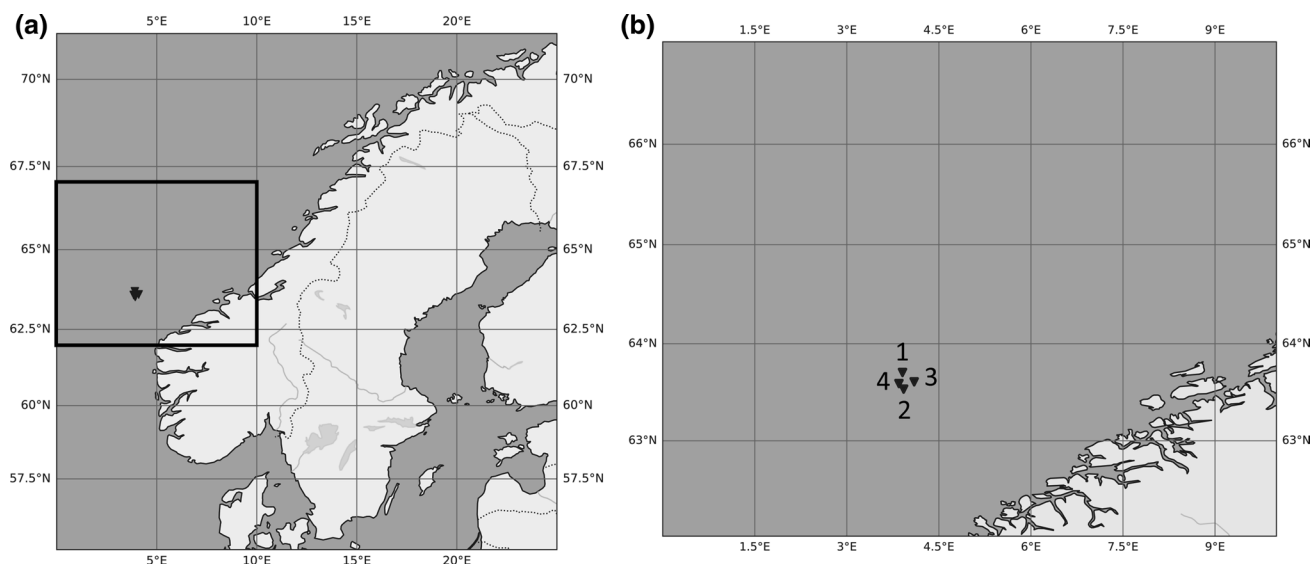
baseline of species diversity, distribution and abundance of gelatinous organisms.

Fragile gelatinous zooplankton is often damaged or destroyed when sampled with nets, which has led to a systematic underestimation of its abundance and diversity in the ocean, in particular in the deep pelagic. The use of in situ observations (with optical sampling systems) has changed our perspective substantially (Haddock 2004; Robison 2004). Manned submersibles and remotely operated vehicles (ROVs) allow the observation of fragile gelatinous zooplankton in their natural habitat. Midwater ocean exploration with these vehicles has led to the discovery of new gelatinous species and records (e.g. Matsumoto and Robison 1992; Hoving et al. 2018), the documentation of their behaviour (Robison et al. 2017) and the provision of novel information on the trophic interactions in the deep-sea ‘jelly web’ (Robison 2004; Choy et al. 2017; Hoving and Haddock 2017). Although submersibles and ROVs can provide detailed images and video material of large deep pelagic fauna and allow faunal collections (Robison 2004), they are also challenging and costly to operate. To allow cost-effective pelagic video transects comparable to ROV video transects, the pelagic in situ observation system (PELAGIOS) was developed (Hoving et al. 2019). The PELAGIOS is a camera platform that collects concomitant environmental data while towed horizontally at desired depths. The annotation of the high definition video results in diversity, distribution and abundance data of slow-swimming pelagic fauna larger than 1 cm. To establish a baseline of pelagic fauna distribution and abundance, and to identify potential important contributors (e.g. medusae, squids, larvaceans) to the biological carbon pump, we performed

deep-sea pelagic video transects with PELAGIOS in the southern Norwegian Sea.

## Material and methods

During a research cruise on R/V Heincke in September 2018 in the southern Norwegian Sea, we deployed the pelagic in situ observation system (PELAGIOS) four times to perform horizontal pelagic video transects (Fig. 1; Table 1). The PELAGIOS is a battery powered towed camera platform with a high definition camera (type 1Cam Alpha, SubC Imaging), forward LED illumination, a CTD (SBE 19 SeaCAT, Sea-Bird Scientific) and a telemetry (DST-6, Sea and Sun Technology; Linke et al. 2015) that transmits data and video preview via the CTD conducting cable to the deck unit (Hoving et al. 2019). The PELAGIOS was towed over the side of the ship on the CTD conducting cable at approximately 1 knot (0.51 m/s) speed over ground. The desired towing depth for the pelagic video transect was reached by paying out CTD wire while monitoring the depth from the CTD. The duration of one complete PELAGIOS deployment was between 3 h 11 min and 3 h 28 min, and at each depth we towed for approximately 6.5–23.3 min (Tables 1 and 2). Horizontal video transects were performed at specific depths between 50 and 1200 m (Table 2) and from 16:00 to 20:00 UTC (Table 1). We started with the deepest transect and ended shallow on Station\_1. At all other stations we started shallow and ended with the deepest transect (Table 2). Hydrography of the water column was reconstructed by performing a vertical cast with an onboard SBE CTD (Fig. 2).



**Fig. 1** **a** The study area in the Norwegian Sea and **b** the four locations where PELAGIOS deployments were performed during HE518 indicated by black triangles

**Table 1** Stations with PELAGIOS deployments during the cruise HE518 in September 2018

| Station                 | Date       | Latitude (N) | Longitude (E) | Start (UTC) | Stop (UTC) | Sunset (UTC + Daylight Saving Time) |
|-------------------------|------------|--------------|---------------|-------------|------------|-------------------------------------|
| Station_1<br>HE518_5-1  | 2018-09-09 | 63.7059      | 3.90709       | 16:07:00    | 19:46:00   | 19:31:00                            |
| Station_2<br>HE518_11-1 | 2018-09-10 | 63.5343      | 3.92559       | 16:28:00    | 19:50:00   | 19:31:00                            |
| Station_3<br>HE518_17_1 | 2018-09-11 | 63.6097      | 4.09736       | 16:37:00    | 19:55:00   | 19:23:00                            |
| Station_4<br>HE518_28-1 | 2018-09-14 | 63.59188     | 3.84858       | 16:19:00    | 19:30:00   | 19:14:00                            |

The HE518\_number refers to the cruise station list

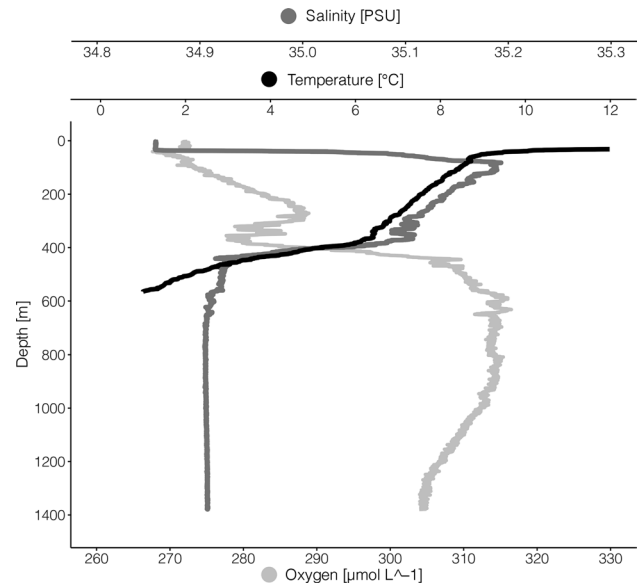
**Table 2** Overview of the transect depths targeted at each station by PELAGIOS

| Depth [m] | Transect length [min:sec] |           |           |           |
|-----------|---------------------------|-----------|-----------|-----------|
|           | Station_1                 | Station_2 | Station_3 | Station_4 |
| 50        | 11:20                     | 15:47     | /         | /         |
| 75        | 9:43                      | /         | /         | /         |
| 100       | /                         | 11:54     | 10:35     | /         |
| 200       | /                         | 12:44     | 13:49     | 11:39     |
| 300       | /                         | 12:52     | 9:41      | 10:01     |
| 400       | /                         | 13:19     | 16:20     | 10:24     |
| 500       | 6:35                      | 10:47     | 17:05     | 10:31     |
| 600       | 7:46                      | 19:27     | 14:44     | 20:29     |
| 700       | 20:34                     | 18:25     | 18:00     | 20:17     |
| 800       | 20:10                     | 17:52     | 15:02     | 20:10     |
| 850       | /                         | /         | /         | 14:29     |
| 900       | 16:59                     | /         | 15:12     | 6:51      |
| 1000      | 15:23                     | /         | /         | 23:20     |
| 1100      | 18:42                     | /         | /         | /         |
| 1200      | 17:59                     | /         | /         | /         |

The '/' marks absence of a pelagic video transect

The HD video was annotated using the Video Annotation and Reference System (VARS) developed by the Monterey Bay Aquarium Research Institute (MBARI) (Schlining and Jacobsen Stout 2006). Recorded organisms larger than 1 cm in diameter were annotated and identified to the lowest possible taxonomic classification. Organisms observed while PELAGIOS was ascending or descending between transects were annotated but not considered in our data analysis. After the analysis of the video material the observation data were matched with the depth data and classified with the corresponding transects. This resulted in 15 abundant taxa (Table 3) and additional rare taxa, as well as groupings of unidentifiable organisms due to poor image conditions (Table 4).

To calculate abundances, we divided the absolute number of counts of each taxon per transect by the

**Fig. 2** Vertical profiles of temperature, salinity, dissolved oxygen and density from the surface to 1350 m depth. The CTD-cast at the 15th of September 2018 at 06:58 UTC at 63°35'24 N and 3°57'26 E. Temperature data below 580 m was not available

corresponding transect duration to obtain the relative abundance of taxa in individuals per time unit. To calculate the number of individuals per unit volume, we used faunal observations from simultaneous deployments of the PELAGIOS and a Underwater Vision Profiler (UVP5) together (Hoving et al. 2019). The UVP5 samples a fixed volume enabling a back calculation of the sampled volume of PELAGIOS during the same transect. This resulted in a conversion factor of 6. This factor is based on pelagic worms of the genus *Poecobius* (0.8–1.5 cm), which are poor swimmers and were observed clearly by both UVP5 and PELAGIOS (Christiansen et al. 2018; Hoving et al. 2019). The conversion factor may change when considering larger animals that can be seen from further away (Reisenbichler

**Table 3** Weighted mean depth (m) of the 12 most abundant taxa and 3 rare taxa (*Beroe*, *Bolinopsis* and white Cydippida) encountered by PELAGIOS, at each station and the overall weighted mean with standard deviation (SD)

| Observation         | Station |       |        |       | Mean  | ± SD    |
|---------------------|---------|-------|--------|-------|-------|---------|
|                     | 1       | 2     | 3      | 4     |       |         |
| Actinopteri         | 80.9    | 122.5 | 239.4  | 320   | 190.7 | ± 94.6  |
| Euphausiacea        | 112.7   | 290.5 | 509.1  | 597.2 | 377.4 | ± 189.3 |
| Decapoda & Mysida   | 989.2   | 665.9 | 797.7  | 840.8 | 823.4 | ± 115.4 |
| Chaetognatha        | 757     | 555.4 | 668.8  | 689.3 | 667.6 | ± 72.6  |
| Appendicularia      | 896.5   | 657.5 | 643.7  | 800   | 749.4 | ± 104.6 |
| <i>Clione</i>       | 69.8    | 50    | Absent | 600   | 239.9 | ± 254.7 |
| <i>Aglantha</i>     | 765.9   | 582.6 | 754.9  | 770.5 | 718.5 | ± 78.6  |
| Diphyidae           | 75      | 99.9  | 108.7  | 200   | 120.9 | ± 47.3  |
| Other Calycophorae  | 598.2   | 391.8 | 516.2  | 496.6 | 500.7 | ± 73.5  |
| Physonect Deep-type | 1036.4  | 777.5 | 900    | 908.1 | 905.5 | ± 91.6  |
| Other Physonectae   | 90.8    | 241.4 | 284.1  | 337   | 238.3 | ± 91.7  |
| <i>Beroe</i>        | 913     | 406.1 | 603.3  | 600   | 630.6 | ± 181.5 |
| <i>Bolinopsis</i>   | 800     | 412.3 | 610    | 650.2 | 618.1 | ± 138.3 |
| <i>Euplokamis</i>   | 187.2   | 360.4 | 448.6  | 485.6 | 370.5 | ± 115.1 |
| White Cydippida     | 1120.1  | 750.8 | 645    | 1000  | 879   | ± 189.7 |

**Table 4** Pooled counts per transect depths of the rare taxa Cirrata, Polychaeta, Pyrosomatida and Salpida

| Observation           | Transect depth (m) |    |     |     |     |     |     |     |     |     |     |     |      |      |      |  |
|-----------------------|--------------------|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|------|------|------|--|
|                       | 50                 | 75 | 100 | 200 | 300 | 400 | 500 | 600 | 700 | 800 | 850 | 900 | 1000 | 1100 | 1200 |  |
| <i>Beroe</i>          |                    |    |     |     | 1   | 2   | 1   | 2   | 2   | 1   |     | 1   |      |      | 1    |  |
| <i>Bolinopsis</i>     |                    |    |     | 1   | 2   | 2   |     | 7   | 2   | 2   |     | 1   |      |      |      |  |
| Cirrata               |                    |    |     |     |     |     |     |     | 1   |     | 1*  |     |      |      |      |  |
| Polychaeta            |                    |    |     |     | 1   |     |     |     | 2   |     |     |     |      |      |      |  |
| Pyrosoma              |                    |    |     |     |     |     |     |     |     |     |     | 1   |      |      |      |  |
| Salpida               | 5                  |    |     |     |     |     |     |     |     |     |     |     |      |      |      |  |
| Unident Cydippida     |                    |    |     |     |     | 3   | 7   |     | 3   | 1   |     |     | 1    |      |      |  |
| Unident Ctenophora    |                    |    |     |     |     |     |     | 1   |     |     |     |     |      |      |      |  |
| Unident Hydromedusae  |                    |    |     |     | 1   | 1   | 1   |     | 1   | 1   |     | 5   | 2    | 1    | 1    |  |
| Unident Lobata        |                    | 1  |     |     |     |     | 1   | 2   | 1   |     | 1   |     | 1    |      |      |  |
| Unident Pteropoda     | 1                  |    |     | 3   |     |     |     |     |     |     |     |     |      |      |      |  |
| Unident Siphonophora  | 1                  |    |     |     | 1   | 2   |     |     | 2   |     |     |     |      |      |      |  |
| Unidentified organism |                    |    |     |     |     |     |     |     | 1   | 2   | 1   | 7   | 5    | 6    | 2    |  |
| White Cydippida       |                    |    |     |     |     |     |     | 1   | 2   | 1   |     |     | 4    | 1    | 2    |  |

Unidentified Hydromedusae other than *Aglantha digitale*, as well as Ctenophora and Siphonophora not identifiable to a lower taxon

1\*The observation of this cirrate octopod was not made during a transect, but during a descend phase in between a 800 and a 900 m transect

et al. 2016) or due to the consistency and transparency of the organisms affecting their visibility.

All graphs besides the map were produced in R version 3.6.1. The map was made with python and the packages matplotlib and cartopy.

Differences between stations were analyzed by calculating the weighted mean depth for each station as well as an overall weighted mean for each of the 15 most abundant taxa (Latasa et al. 2017).

## Results

### Hydrography

The hydrography was typical for the studied region (Blindheim and Rey 2004). The upper < 50 m were influenced by the Norwegian Coastal Current (NCC), with a salinity well below 34.9 and temperatures > 12 °C (Fig. 2). Below

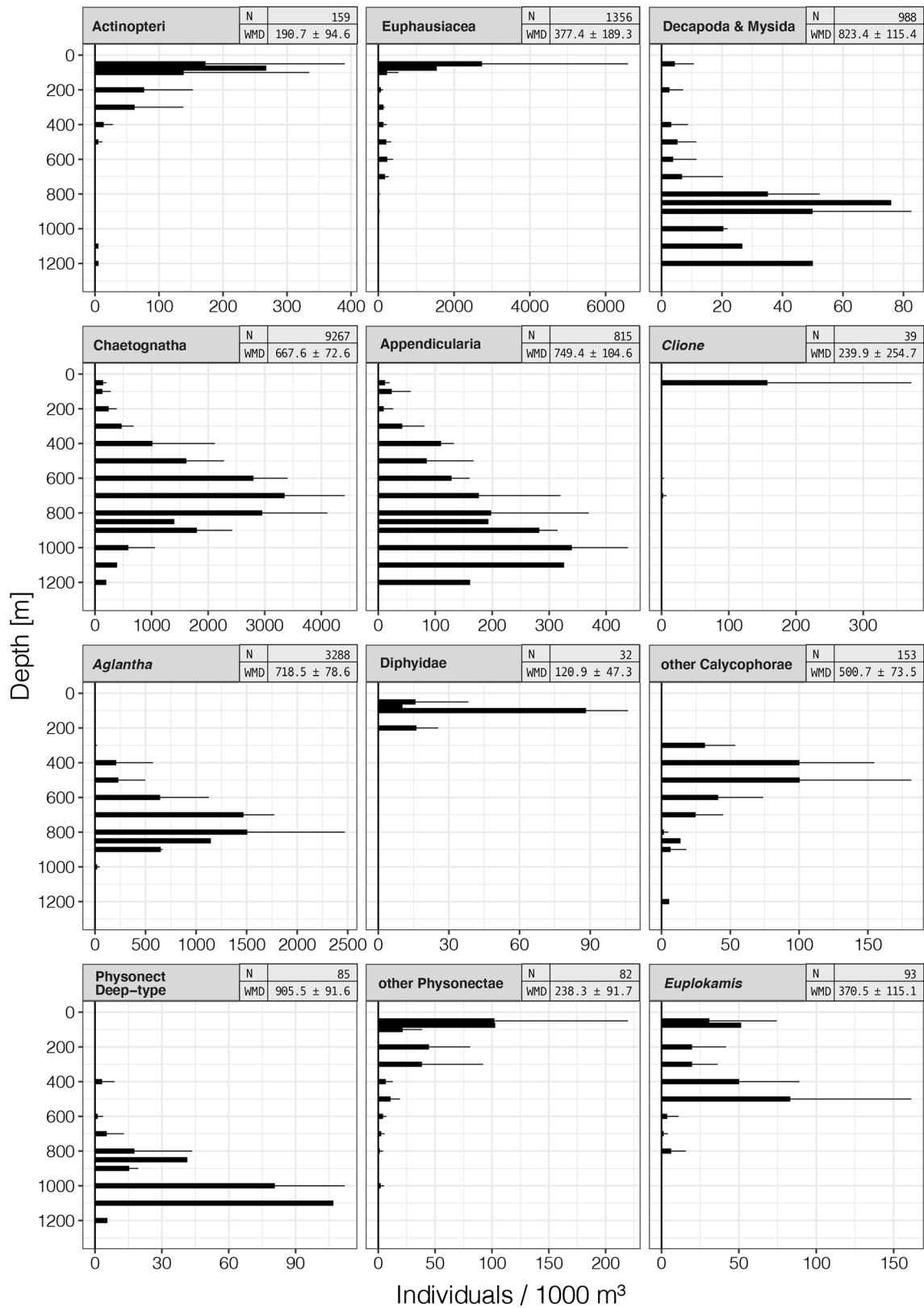
the NCC, the salinity increased to  $> 35$ , indicating a layer of Atlantic Water (AW) extending down to  $\sim 400$  m. At around 400 m, the salinity rapidly dropped to  $\sim 34.92$  with a minor salinity minimum close to 450 m, and there was a simultaneous increase in oxygen concentration moving from AW to intermediate water. Temperature steadily declined from 5 to 0 °C between  $\sim 400$  and 600 m. We expect that below the intermediate water masses and deeper than  $\sim 600$  m Norwegian Sea Deep Water (NSDW) was found. This water mass is characterized by temperatures below 0 °C and a salinity of  $\sim 34.91$ . Unfortunately, temperature data below 580 m were corrupted.

## Fauna

The video transects revealed 26 different taxa; fifteen abundant taxa (Table 3) and seven rare and seven unidentified taxa (Table 4). At all four sampling sites, the transects at 500, 600, 700 and 800 m depth had the highest animal abundances. Chaetognatha, which showed their highest abundances in these depths, dominated all transects with 68.8, 67.0, 63.0, and 64.6% of all annotations (Station\_1 to Station\_4, respectively) (Fig. 3). The small trachymedusa *Aglantha digitale* had its distribution peak between 500 and 800 m (Figs. 3 and 4) and accounted for 25.2, 22.4, 27.6 and 24.7% of all annotations (Station\_1 to Station\_4, respectively) and was the second most abundant taxon encountered in all transects. Appendicularians, crustaceans, ctenophores and siphonophores combined contributed about 10% of the observations between 500 and 800 m at Stations 2, 3 and 4, and less than 6% of the observations at Station\_1.

The 12 most abundant taxa differed in their vertical distribution patterns (Fig. 3). Non-gelatinous taxonomic groups included Actinopteri (ray-finned fishes), Decapoda and Mysida (jointly called shrimps, because distinction between the taxa was not possible on the videos), Euphausiacea (krill) and the semi-gelatinous Chaetognatha (arrow worms). Highest Actinopteri abundances were observed in the upper 100 m with a maximum of 267.6 ind  $1000\text{ m}^{-3}$  at 75 m at Station\_1, and abundances decreased with depth. Shrimps were observed at all stations and throughout the entire sampling depth range, but increased in numbers below 700 m, with a maximum of 76 ind  $1000\text{ m}^{-3}$  at the single transect at 850 m depth at Station\_4. A secondary abundance peak was observed at the deepest transect of 1200 m with 50.1 ind  $1000\text{ m}^{-3}$  at Station\_1. Euphausiacea were also observed at all stations and at every sampled depth, except at 1200 m. Their highest abundances were observed at 50 m depth at Station\_1 with 5461.8 ind  $1000\text{ m}^{-3}$ . Below 100 m, the abundance of Euphausiacea decreased by approximately one order of magnitude, and below 800 m depth by another order of magnitude.

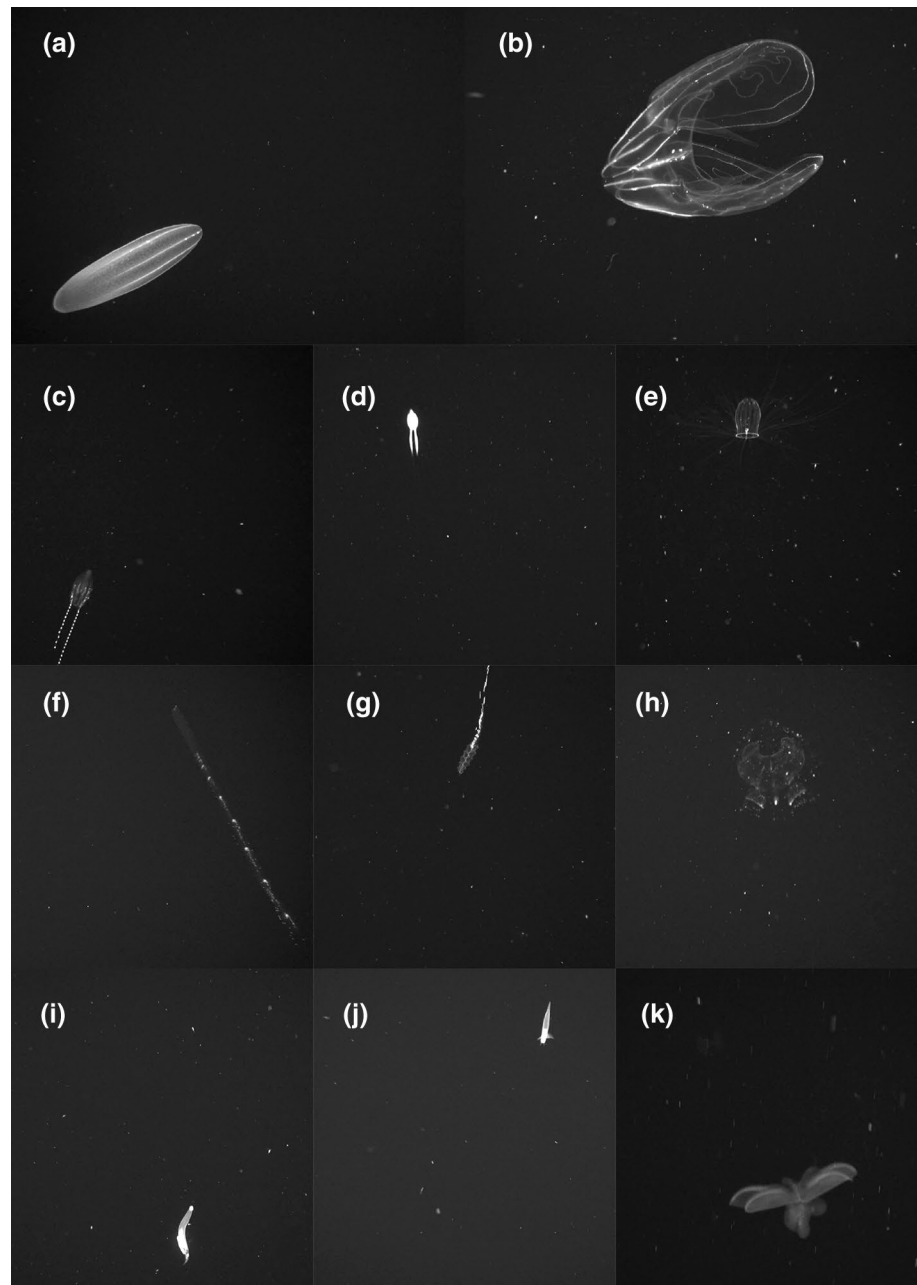
Appendicularians were present throughout the sampled depth range with the exception of the 75 m transect at Station\_1. Their numbers showed a continuous increase with depth, and peaked at 1000 m depth with 339.8 ind  $1000\text{ m}^{-3}$  (mean,  $sd=98.7$ ). Chaetognaths were dominant between 200 and 1000 m. They were observed throughout the whole depth range (Fig. 3), and their vertical distribution pattern showed a normal distribution around an abundance peak at 700 m depth with 3350.5 ind  $1000\text{ m}^{-3}$  (mean,  $sd=1063.3$ ). The highest numbers of pteropods of the genus *Clione* (157.6 ind  $1000\text{ m}^{-3}$ ; mean,  $sd=213.9$ ) occurred at 50 m depth, but these mollusks were also present at 600 and 700 m. The trachymedusa *Aglantha digitale* was present between 50 and 1000 m depth but absent from the 75, 100 and 200 m transects (Figs. 3 and 4). Their highest abundance was observed at 800 m depth with 1507 ind  $1000\text{ m}^{-3}$  (mean,  $sd=963.5$ ), and below 850 m depth the abundance decreased sharply. After chaetognaths, *A. digitale* was the second most abundant taxon. Small, unidentified calycophoran siphonophores were grouped together as ‘other Calycophorae’ and occurred between 300 and 1200 m depth. They were more abundant in the upper half of their distributional range and their peak abundance was 100.5 ind  $1000\text{ m}^{-3}$  (mean,  $sd=81.1$ ) at 500 m depth. Calycophoran siphonophores of the family Diphyidae were restricted in their vertical distribution to the upper 200 m. They had their highest abundance at 100 m depth with 88.2 ind  $1000\text{ m}^{-3}$  (mean,  $sd=17.9$ ). A group of physonect siphonophores with a similar morphology, but which could not be identified to species, were grouped as ‘Physonect Deep-type’ (Fig. 3). These siphonophores occurred from 400 to 1200 m depth, but the majority of specimens were observed at 1100 m depth with 107 ind  $1000\text{ m}^{-3}$  at Station\_1. Physonect siphonophores other than the ‘Physonect Deep-type’ were observed from 50 to 800 m as well as at 1000 m. Their abundance decreased with depth after a peak at 75 m (102.9 ind  $1000\text{ m}^{-3}$ ) at Station\_1. *Beroe* spp. ctenophores were observed in low numbers from 300 to 1200 m depth. The maximum abundance was 6.6 ind  $1000\text{ m}^{-3}$  (mean,  $sd=6.2$ ) at 400 m depth. Some of the observed *Beroe* spp. could be clearly identified as *B. abyssicola* based on the conspicuous red coloration of the stomodaeum (Fig. 4). The habitus of the others points towards the unresolved species complex *Beroe* cf. *cucumis* (Bayha et al. 2004; Mills and Haddock 2007; Johansson et al. 2018), suggesting the presence of at least two species of *Beroe* in the study area. The lobate ctenophore *Bolinopsis* (*Bolinopsis* sp. or *Bolinopsis infundibulum*) was observed from 200 to 900 m depth. The maximum abundance of *Bolinopsis* was at 600 m with 10.1 ind  $1000\text{ m}^{-3}$  (mean,  $sd=8.3$ ). The cydippid ctenophore *Euplokamis* sp. was observed



**Fig. 3** Vertical distribution profiles of the 15 observed major taxa, with the extrapolated number of specimens per 1000 m<sup>3</sup> on the horizontal axes and the water depth on the vertical axes. Columns show the mean abundances across all 4 sampling sites, with the standard

deviation (sd) as error bars. The header of the single plots gives the taxon, the weighted mean depth (WMD) and the total number of counts for each taxon (N). The shallowest transect was conducted at 50 m depth, the deepest at 1200 m depth

**Fig. 4** Frame-grabs of Norwegian pelagic fauna from videos recorded with PELAGIOS. From top left to bottom right the rows show the following taxa: **a** *Beroe abyssicola*. ~40 mm (Johansson et al. 2018); **b** lobate ctenophore *Bolinopsis* sp. 40 mm (Nagabhushanam 1959); **c** cydippid ctenophore *Euplokamis* sp. ~10 mm (Granthag et al. 2012); **d** undescribed white cydippid; **e** *Aglantha digitale* ~10 mm (Hosia and Båmstedt 2007); **f** Physonect siphonophore; **g** Physonect Deep-type; **h** Appendicularian; **i** Chaetognath ~40 mm (Falkenhaug 1991); **j** *Clione* sp. ~20 mm (Satterlie et al. 1985); **k** cirrate octopod



at 50, 75 and from 200 to 800 m depth (Figs. 3 and 4). Their maximum abundance was  $83.2 \text{ ind } 1000 \text{ m}^{-3}$  (mean,  $\text{sd} = 78.2$ ) at 500 m depth. An undescribed white cydippid (Hosia and Båmstedt 2007) was observed from 600 to 800 m and from 1000 to 1200 m depth (Figs. 3 and 4). Their highest abundance of  $11.1 \text{ ind } 1000 \text{ m}^{-3}$  was observed during the deepest transect at 1200 m depth.

Fourteen groups of organisms were observed in low numbers, including unidentifiable ctenophores, siphonophores, and hydromedusae, pelagic tunicates, polychaetes and cirrate octopods (Fig. 4; Table 4).

## Discussion

Our observations included 12 abundant, seven rare, and seven unidentified pelagic taxa. The numerically dominant group were chaetognaths, followed by the small trachymedusa *Aglantha digitale*, both predators on other zooplankton. Filter feeding appendicularians were the third most abundant group. Crustaceans, which we divided into krill (Euphausiacea) and shrimps (Decapoda and Mysida), occurred at high densities at specific depth

layers. Omnivorous krill were the dominant organisms in the uppermost 50, 75 and 100 m transects, whereas larger shrimps were most abundant much deeper, between 800 and 900 m depth.

The major faunal components consisting of ray-finned fishes, euphausiids, shrimps, hydrozoans, ctenophores, chaetognaths and appendicularians, as well as the overall pelagic diversity and abundance, are in line with previous observations in the North Atlantic, where optical sampling was performed using ROV and UVP (Vinogradov 2005; Stemmann et al. 2008).

Our in situ video observations are generally limited to organisms that are  $> \sim 1$  cm in size, and often do not show sufficient taxonomic characteristics required for identification to species level. Pelagic net surveys provide a higher taxonomic resolution for crustaceans and ray-finned fishes (Piatkowski et al. 1994), as well as for the hydrozoan gelatinous fauna (Hosia et al. 2008, 2017), but catch efficiency may be low. On the other hand, optical sampling like performed in our study does reveal fauna poorly sampled by nets, ctenophores and appendicularians in particular, and provides unique data on the detailed vertical and horizontal distribution of fragile organisms (Hosia et al. 2017). The diversity of gelatinous fauna in the Norwegian Sea remains poorly studied, and more detailed faunistic studies would probably reveal new records of hydrozoans and ctenophores for Norwegian waters. In this study, significant numbers of the cydippid ctenophore *Euplokamis* sp. ( $n = 93$ ) were documented for the first time in the southern Norwegian Sea. These ctenophores were readily identified to genus due to the characteristically coiled tentilla, resembling droplets along the tentacles (Fig. 2). There are few published records of *Euplokamis* sp. from Norwegian waters, but it is reported to occur in western Norwegian fjords (Granhag et al. 2012), and has been observed in the Norwegian/Icelandic Sea (Licandro et al. 2015), and near Svalbard (Majaneva and Majaneva 2013). First records of *Euplokamis* sp. in Swedish waters were reported for the Gullmar Fjord on the west coast (Granhag et al. 2012). *Euplokamis* may thus be present throughout the Norwegian shelf from the Skagerrak to Svalbard.

The other, yet undescribed, white cydippid ctenophore, similar to an undescribed horned cydippid with highly extensible tentacles (Hosia and Båmstedt 2007), was only observed below 600 m depth, with highest densities at the 1200 m transect at Station\_1. This suggests that the vertical distribution was not completely sampled, and that the undescribed cydippid is a lower meso- and bathypelagic species with a distribution extending below our sampling range.

Several taxa appeared to be associated with specific water masses. Shrimps were primarily found in NSDW below 600 m. The undescribed white cydippid and the siphonophore that we referred to as the ‘Physonect Deep-type’ also

appeared mostly restricted to these deeper waters. Of the numerically dominant groups, both chaetognaths and *Aglantha digitale* had their peak abundances below 600 m depth, in the NSDW. *A. digitale* was virtually absent from AW, while chaetognaths also extended their distribution to the upper 400 m, perhaps due to this taxon including several species of varying affinity to the different water masses. Euphausiacea, *Clione* and diphyid siphonophores were primarily observed in the upper AW. Other calycophorans and *Euplokamis* sp. were particularly abundant in the intermediate waters, but also occurred, to a lesser extent, in the water masses above and below.

Appendicularians were a common group, increasing in abundance with depth throughout the mesopelagic zone. Abundant appendicularians in mesopelagic waters are also reported from other oceanic regions, but are relatively poorly studied (Stemmann et al. 2008). The role of appendicularians in mesopelagic food webs and in vertical flux is nevertheless of high interest. Not only are appendicularians able to feed on particles down to bacterial size range, thus short circuiting the “normal” pelagic food chain (Robinson et al. 2010), but their discarded houses are a major contributor of marine snow particles and vertical flux of carbon (Robison et al. 2005; De La Rocha and Passow 2007).

For some of the observed taxa, potential diel vertical migration (DVM) must also be considered. While relatively detailed, our vertical distribution data only provide a temporal snapshot. Ray-finned fishes, krill, shrimps and physonect siphonophores are known daily vertical migrators (Barham 1966; Piatkowski et al. 1994; Frank and Widder 2002), and their observed distributions in the upper layers may have been indicative of these taxa migrating towards the surface as sunset was approaching. While our data do not provide information on diel changes in the vertical distribution of the observed taxa, deployments were more or less consistent in their timing with respect to the sunset and, thus, the expected stage of DVM. As DVM of many taxa is likely controlled by the ambient light environment (e.g. Norheim et al. 2016), between-day variation may nevertheless have been caused by differences in cloud cover. However, the significant differences found in the distribution of ray-finned fishes were likely caused by the fact that we started the transects in deep waters during the first station, while we started the later stations in shallow waters.

When considering the observed depth distributions and extrapolated abundances, the total number of observations should be taken into account. These data are much more uncertain for the less frequent taxa. Also, the deepest layers at 1000 m or below only had 1–2 transects per depth, preventing comparisons between sites and general conclusions. Due to the relatively coarse taxonomic resolution of the data, many of the taxa are also likely to contain several species, with potentially different environmental preferences,



ecological niches and behaviour. For example, three species of krill are common and abundant in the Norwegian Sea: *Meganyctiphanes norvegica*, *Thysanoessa inermis* and *Thysanoessa longicaudata* (Melle et al. 2004). In our data, these and other similar organisms were lumped.

Comparing abundance estimates obtained by different studies is challenging, as they may be affected by a variety of factors including e.g. the sampling methods, interannual and geographical variation, as well as diurnal and/or seasonal changes in abundance and distribution of the target taxa. With these caveats in mind, we can make some comparisons to published data for our most abundant groups. Vertical distributions of chaetognaths in the Norwegian and Greenland Seas have been studied in November 1995 using a Multinet, a multiple plankton net (Dale et al. 1999). The results are surprisingly similar to ours, with maximum densities of 3–4 chaetognaths  $\text{m}^{-3}$  observed between 400 and 800 m depth. For *Aglantha digitale*, ROV vertical profiles—a method comparable to ours in that it is limited to observing organisms larger than 1 cm in size—from Norwegian fjords in October and May 2004–2005 show peaks of up to ~3 adult individuals  $\text{m}^{-3}$  at around 300 m depth (Hosia and Båmstedt 2007). These results are also of the same order of magnitude as ours, although the exact depth of the peak abundance differs, perhaps due to local hydrography. The abundance estimates of chaetognaths and *A. digitale* may be realistic because the size of these organisms is similar to the *Poeobius* polychaete that was used for estimating sampling volume of PELAGIOS (Hoving et al. 2019). Estimating abundance of larger fauna requires further calibration efforts of PELAGIOS as larger fauna may be detected when they are further away from the camera compared to smaller organisms (Reisenbichler et al. 2016).

Our results may to a degree be influenced by attraction or avoidance responses elicited by the PELAGIOS. Such responses could result from the hydrodynamic disturbance caused by the gear, as well as the light. It is known that certain taxa such as ray-finned fishes, krill and decapods, respond to underwater instruments (Stoner et al. 2008). Underestimation of observations may influence our estimates of myctophid and other mesopelagic fishes as they are known to avoid lights and trawls (Kaartvedt et al. 2012). On the other hand, overestimation of abundance may be caused by organisms being attracted towards lights or the instrument itself, as has been reported for other organisms including krill and some ray-finned fishes (e.g. Wiebe et al. 2004; Raymond and Widder 2007; Utne-Palm et al. 2018). However, we did not observe highly reactive responses to the lights.

We have noticed the absence of larger nekton. This particularly is relevant to the oegopsid squid *Gonatus fabricii*, which is widely distributed in the North Atlantic and adjacent Arctic seas and is the dominant cephalopod in terms of biomass, and a pivotal component in the

food web (Kristensen 1984; Wiborg et al. 1984). *Gonatus fabricii* is consumed by a variety of apex predators such as various cetaceans and deep-sea fishes (Lick and Piatkowski 1998; Santos et al. 1999; Bergstad et al. 2010). It is estimated that sperm whale populations in the north east Atlantic alone consume as much as 1.5 million tons of *G. fabricii* each year (Bjørke 2001). Our sampling site was chosen because previous studies reported mature and spent females of *G. fabricii* in the area (Arkhipkin and Bjørke 1999; Bjørke 2001). The absence of *G. fabricii* could be caused by an avoidance of PELAGIOS resulting in an escape response before specimens are within the view-field of the camera. It is also possible that the sampling volume of the PELAGIOS system and the transects were not sufficient to document the species. However, it should be noted that *Gonatus steenstrupi* was recorded by ROVs during dives at the northern mid-Atlantic ridge (Vecchione et al. 2010). We furthermore did not observe the coronate medusa *Periphylla periphylla*, which occurs at high densities in several Norwegian fjord systems (e.g. Båmstedt et al. 2003), and which is also common in the Norwegian Sea in depths below 200 m (Dalpadado et al. 1998). The absence of *P. periphylla* could be the result of patchy distribution or by avoidance behaviour.

Our results provide a first overview of the vertical composition, distribution and abundance of macroplankton in the Norwegian Sea. We show that predatory and, to a lesser degree, filter feeding non-crustacean zooplankton dominate the mesopelagic macroplankton community of the study area. The resultant vertical abundance distributions may be useful for modelling trophic pathways and vertical flux in the mesopelagic. More detailed, net- or ROV-based studies are necessary in order to describe the currently poorly known species level diversity of gelatinous zooplankton in this region. Additionally, the absence of observations of the abundant squid *G. fabricii* asks for a more intense sampling program to better understand the biology of this important species.

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## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest to disclose.

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## References

- Allredge A (2004) The contribution of discarded appendicularian houses to the flux of particulate organic carbon from oceanic surface waters. In: Gorsky G, Youngbluth MJ, Deibel D (eds) Response of marine ecosystems to global change: Ecological impact of appendicularians. Éditions des Archives Contemporaines, Paris, pp 309–326
- Arkhypkin AI, Bjørke H (1999) Ontogenetic changes in morphometric and reproductive indices of the squid *Gonatus fabricii* (Oegopsida, Gonatidae) in the Norwegian Sea. *Polar Biol* 22:357–365. <https://doi.org/10.1007/s003000050429>
- Båmstedt U, Kaartvedt S, Youngbluth M (2003) An evaluation of acoustic and video methods to estimate the abundance and vertical distribution of jellyfish. *J Plankton Res* 25:1307–1318. <https://doi.org/10.1093/plankt/fbg084>
- Barham EG (1966) Deep scattering layer migration and composition: observations from a diving saucer. *Science* 151:1399–1403. <https://doi.org/10.1126/science.151.3716.1399>
- Bayha KM, Harbison GR, McDonald JH, Gaffney PM (2004) Preliminary investigation on the molecular systematics of the invasive ctenophore *Beroe ovata*. Aquatic invasions in the Black, Caspian, and Mediterranean Seas. Dumont H. Kluwer Academic Publishers, Dordrecht, pp 167–175
- Bergstad OA, Gjelsvik G, Schander C, Høines ÅS (2010) Feeding ecology of *Coryphaenoides rupestris* from the mid-atlantic ridge. *PLoS ONE* 5:1–10. <https://doi.org/10.1371/journal.pone.0010453>
- Bjørke H (2001) Predators of the squid *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea. *Fish Res* 52:113–120. [https://doi.org/10.1016/S0165-7836\(01\)00235-1](https://doi.org/10.1016/S0165-7836(01)00235-1)
- Blindheim J, Rey F (2004) Water-mass formation and distribution in the Nordic Seas during the 1990s. *ICES J Mar Sci* 61:846–863. <https://doi.org/10.1016/j.icesjms.2004.05.003>
- Bone Q, Kapp H, Perrot-Bults AC (eds) (1991) The biology of chaetognaths. Oxford University Press, Oxford
- Brotz L, Cheung WWL, Kleisner K et al (2012) Increasing jellyfish populations: trends in large marine ecosystems. *Hydrobiologia* 690:3–20. <https://doi.org/10.1007/s10750-012-1039-7>
- Cardona L, de Quevedo IÁ, Borrell A, Aguilar A (2012) Massive consumption of Gelatinous Plankton by Mediterranean Apex Predators. *PLoS ONE* 7:1–14. <https://doi.org/10.1371/journal.pone.0031329>
- Choy CA, Haddock SHD, Robison BH (2017) Deep pelagic food web structure as revealed by in situ feeding observations. *Proc R Soc B Biol Sci* 284:1–10. <https://doi.org/10.1098/rspb.2017.2116>
- Christiansen S, Hoving HJT, Schütte F et al (2018) Particulate matter flux interception in oceanic mesoscale eddies by the polychaete *Poeobius* sp. *Limnol Oceanogr* 63:2093–2109. <https://doi.org/10.1002/lno.10926>
- Condon RH, Graham WM, Duarte CM et al (2012) Questioning the Rise of Gelatinous Zooplankton in the World's Oceans. *Bioscience* 62:160–169. <https://doi.org/10.1525/bio.2012.62.2.9>
- Condon RH, Duarte CM, Pitt KA et al (2013) Recurrent jellyfish blooms are a consequence of global oscillations. *Proc Natl Acad Sci USA* 110:1000–1005. <https://doi.org/10.1073/pnas.1210920110>
- Dale T, Bagøien E, Melle W, Kaartvedt S (1999) Can predator avoidance explain varying overwintering depth of *Calanus* in different oceanic water masses? *Mar Ecol Prog Ser* 179:113–121. <https://doi.org/10.3354/meps179113>
- Dalpadado P, Ellertsen B, Melle W, Skjoldal HR (1998) Summer distribution patterns and biomass estimates of macrozooplankton and micronekton in the nordic seas. *Sarsia* 83:103–116. <https://doi.org/10.1080/00364827.1998.10413676>
- De La Rocha CL, Passow U (2007) Factors influencing the sinking of POC and the efficiency of the biological carbon pump. *Deep Res II* 54:639–658. <https://doi.org/10.1016/j.dsr2.2007.01.004>
- Ekau W, Auel H, Pörtner H-O, Gilbert D (2010) Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosciences* 7:1669–1699. <https://doi.org/10.5194/bg-7-1669-2010>
- Falkenhaus T (1991) Prey composition and feeding rate of *Sagitta elegans* var. *arctica* (chaetognatha) in the Barents Sea in early summer. *Polar Res* 10:487–506. <https://doi.org/10.3402/polar.v10i2.6761>
- Frank TM, Widder EA (2002) Effects of a decrease in downwelling irradiance on the daytime vertical distribution patterns of zooplankton and micronekton. *Mar Biol* 140:1181–1193. <https://doi.org/10.1007/s00227-002-0788-7>
- Granhag L, Majaneva S, Friis Møller L (2012) First recording of the ctenophore *Euplokamis* sp. (Ctenophora, Cydippida) in Swedish coastal waters and molecular identification of this genus. *Aquat Invasions* 7:455–463. <https://doi.org/10.3391/ai.2012.7.4.002>
- Haddock SHD (2004) A golden age of gelata: past and future research on planktonic ctenophores and cnidarians. *Hydrobiologia* 530:549–556. <https://doi.org/10.1007/s10750-004-2653-9>
- Heeger T, Piatkowski U, Möller H (1992) Predation on jellyfish by the cephalopod *Argonauta argo*. *Mar Ecol Prog Ser* 88:293–296. <https://doi.org/10.3354/meps088293>
- Henschke N, Bowden DA, Everett JD et al (2013) Salp-falls in the Tasman Sea: a major food input to deep-sea benthos. *Mar Ecol Prog Ser* 491:165–175. <https://doi.org/10.3354/meps10450>
- Holland LZ (2016) Tunicates. *Curr Biol Mag* 26:146–152. <https://doi.org/10.1016/j.cub.2015.12.024>
- Hosia A, Båmstedt U (2007) Seasonal changes in the gelatinous zooplankton community and hydromedusa abundances in Korsfjord and Fanafjord, western Norway. *Mar Ecol Prog Ser* 351:113–127. <https://doi.org/10.3354/meps07148>
- Hosia A, Stemmann L, Youngbluth M (2008) Distribution of net-collected planktonic cnidarians along the northern Mid-Atlantic Ridge and their associations with the main water masses. *Deep Res Part II* 55:106–118. <https://doi.org/10.1016/j.dsr2.2007.09.007>
- Hosia A, Falkenhaus T, Baxter EJ, Pagès F (2017) Abundance, distribution and diversity of gelatinous predators along the northern Mid-Atlantic Ridge: a comparison of different sampling methodologies. *PLoS ONE* 12:1–18. <https://doi.org/10.1371/journal.pone.0187491>

- Hoving HJT, Haddock SHD (2017) The giant deep-sea octopus *Haliphron atlanticus* forages on gelatinous fauna. *Sci Rep* 7:1–4. <https://doi.org/10.1038/srep44952>
- Hoving HJT, Neitzel P, Robison B (2018) In situ observations lead to the discovery of the large ctenophore *Kiyohimea usagi* (Lobata: Eurhampheidae) in the eastern tropical Atlantic. *Zootaxa* 4526:232–238. <https://doi.org/10.11646/zootaxa.4526.2.8>
- Hoving HJT, Christiansen S, Fabrizius E et al (2019) The Pelagic In situ Observation System (PELAGIOS) to reveal biodiversity, behavior, and ecology of elusive oceanic fauna. *Ocean Sci* 15:1327–1340. <https://doi.org/10.5194/os-15-1327-2019>
- Johansson ML, Shiganova TA, Ringvold H et al (2018) Molecular Insights Into the Ctenophore Genus *Beroe* in Europe: new species, spreading invaders. *J Hered* 109:520–529. <https://doi.org/10.1093/jhered/esy026>
- Kaartvedt S, Staby A, Aksnes DL (2012) Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass. *Mar Ecol Prog Ser* 456:1–6. <https://doi.org/10.3354/meps09785>
- Kristensen TK (1984) Biology of the Squid *Gonatus fabricii* (Lichtenstein, 1818) from West Greenland Waters. *Meddelelser om Grønland. Biosci* 13:2–20
- Latasa M, Cabello AM, Morán XAG et al (2017) Distribution of phytoplankton groups within the deep chlorophyll maximum. *Limnol Oceanogr* 62:665–685. <https://doi.org/10.1002/lno.10452>
- Lebrato M, Pitt KA, Sweetman AK et al (2012) Jelly-falls historic and recent observations: a review to drive future research directions. *Hydrobiologia* 690:227–245. <https://doi.org/10.1007/s10750-012-1046-8>
- Licandro P, Blackett M, Fischer A et al (2015) Biogeography of jellyfish in the North Atlantic, by traditional and genomic methods. *Earth Syst Sci Data* 7:173–191. <https://doi.org/10.5194/essd-7-173-2015>
- Lick R, Piatkowski U (1998) Stomach contents of a Northern Bottlenose Whale (*Hyperoodon ampullatus*) Stranded at Hiddensee, Baltic Sea. *J Mar Biol Assoc UK* 78:643–650. <https://doi.org/10.1017/S0025315400041679>
- Linke P, Schmidt M, Rohleder M et al (2015) Novel online digital video and high-speed data broadcasting via standard coaxial cable onboard marine operating vessels. *Mar Technol Soc J* 49:7–18. <https://doi.org/10.4031/MTSJ.49.1.2>
- Lynam CP, Lilley MKS, Bastian T et al (2011) Have jellyfish in the Irish Sea benefited from climate change and overfishing? *Glob Chang Biol* 17:767–782. <https://doi.org/10.1111/j.1365-2486.2010.02352.x>
- Majaneva S, Majaneva M (2013) Cydippid ctenophores in the coastal waters of Svalbard: is it only *Mertensia ovum*. *Polar Biol* 36:1681–1686. <https://doi.org/10.1007/s00300-013-1377-6>
- Matsumoto GI, Robison BH (1992) *Kiyohimea usagi*, a new species of lobate ctenophore from the Monterey Submarine Canyon. *Bull Mar Sci* 51:19–29
- Melle W, Ellertsen B, Skjoldal HR (2004) Zooplankton: the link to higher trophic levels. In: Skjoldal HR, Saetre R (eds) *The Norwegian Sea Ecosystem*. Tapir Academic Press, Trondheim, pp 137–202
- Mills CE, Haddock SHD (2007) Intertidal invertebrates of the Central California Coast. In: Carlton JT (ed) *The light and smith manual*. University of California Press, Berkeley
- Nagabhushanam AK (1959) Feeding of a Ctenophore, *Bolinopsis infundibulum* (O. F. Müller). *Nature* 184:829. <https://doi.org/10.1038/184829a0>
- Norheim E, Klevjer TA, Aksnes DL (2016) Evidence for light-controlled migration amplitude of a sound scattering layer in the Norwegian Sea. *Mar Ecol Prog Ser* 551:45–52. <https://doi.org/10.3354/meps11731>
- Pagès F, Flood P, Youngbluth M (2006) Gelatinous zooplankton net-collected in the Gulf of Maine and adjacent submarine canyons: new species, new family (Jeanbouillonidae), taxonomic remarks and some parasites. *Sci Mar* 70:363–379. <https://doi.org/10.3989/scimar.2006.70n3363>
- Piatkowski U, Rodhouse PG, White MG et al (1994) Nekton community of the Scotia Sea as sampled by the RMT 25 during austral summer. *Mar Ecol Prog Ser* 112:13–28. <https://doi.org/10.3354/meps112013>
- Raymond EH, Widder EA (2007) Behavioral responses of two deep-sea fish species to red, far-red, and white light. *Mar Ecol Prog Ser* 350:291–298. <https://doi.org/10.3354/meps07196>
- Reisenbichler KR, Chaffey MR, Cazenave F et al (2016) Automating MBARI's midwater time-series video surveys: the transition from ROV to AUV. *OCEANS 2016 MTS/IEEE Monterey*. IEEE, Monterey, pp 1–9
- Robinson C, Steinberg DK, Anderson TR et al (2010) Mesopelagic zone ecology and biogeochemistry—a synthesis. *Deep Res Part II* 57:1504–1518. <https://doi.org/10.1016/j.dsr2.2010.02.018>
- Robison BH (2004) Deep pelagic biology. *J Exp Mar Bio Ecol* 300:253–272. <https://doi.org/10.1016/j.jembe.2004.01.012>
- Robison BH, Reisenbichler KR, Sherlock RE (2005) Giant Larvacean houses: rapid carbon transport to the deep sea floor. *Science* 308:1609–1611. <https://doi.org/10.1126/science.1109104>
- Robison BH, Reisenbichler KR, Sherlock RE (2017) The coevolution of midwater research and ROV technology at MBARI. *Oceanography* 30:26–37. <https://doi.org/10.5670/oceanog.2017.421>
- Santos MB, Pierce GJ, Boyle PR et al (1999) Stomach contents of sperm whales *Physeter macrocephalus* stranded in the North Sea 1990–1996. *Mar Ecol Prog Ser* 183:281–294. <https://doi.org/10.3354/meps183281>
- Satterlie RA, LaBarbera M, Spencer AN (1985) Swimming in the Pteropod Mollusc, *Clione limacina*. *J Exp Biol* 116:189–205
- Schlining BM, Jacobsen Stout N (2006) MBARI's video annotation and reference system. *OCEANS 2006*. IEEE, Boston, pp 1–5
- Stemmann L, Hosia A, Youngbluth MJ et al (2008) Vertical distribution (0–1000 m) of macrozooplankton, estimated using the Underwater Video Profiler, in different hydrographic regimes along the northern portion of the Mid-Atlantic Ridge. *Deep Res Part II* 55:94–105. <https://doi.org/10.1016/j.dsr2.2007.09.019>
- Stoner AW, Ryer CH, Parker SJ et al (2008) Evaluating the role of fish behavior in surveys conducted with underwater vehicles. *Can J Fish Aquat Sci* 65:1230–1243. <https://doi.org/10.1139/F08-032>
- Sweetman AK, Chapman A (2015) First assessment of flux rates of jellyfish carcasses (jelly-falls) to the benthos reveals the importance of gelatinous material for biological C-cycling in jellyfish-dominated ecosystems. *Front Mar Sci* 2:1–7. <https://doi.org/10.3389/fmars.2015.00047>
- Thuesen EV, Rutherford LD, Brommer PL et al (2005) Intragel oxygen promotes hypoxia tolerance of scyphomedusae. *J Exp Biol* 208:2475–2482. <https://doi.org/10.1242/jeb.01655>
- Utne-Palm AC, Breen M, Løkkeborg S, Humborstad O-B (2018) Behavioural responses of krill and cod to artificial light in laboratory experiments. *PLoS ONE* 13:1–17. <https://doi.org/10.1371/journal.pone.0190918> January
- Vecchione M, Young RE, Piatkowski U (2010) Cephalopods of the northern Mid-Atlantic Ridge. *Mar Biol Res* 6:25–52. <https://doi.org/10.1080/17451000902810751>
- Vinogradov GM (2005) Vertical distribution of macroplankton at the Charlie-Gibbs Fracture Zone (North Atlantic), as observed from the manned submersible “Mir-1.” *Mar Biol* 146:325–331. <https://doi.org/10.1007/s00227-004-1436-1>
- Wiborg KF, Gjøsaeter J, Beck IM (1984) The Squid *Gonatus fabricii* (Lichtenstein) Investigations the Norwegian Sea and Western Barents Sea 1982–1983. *ICES C Doc*. pp 1–14

Wiebe PH, Ashjian CJ, Gallager SM et al (2004) Using a high-powered strobe light to increase the catch of Antarctic krill. *Mar Biol* 144:493–502. <https://doi.org/10.1007/s00227-003-1228-z>

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