

ORIGINAL RESEARCH ARTICLE

Epibenthic diversity and productivity on a heavily trawled Barents Sea bank (Tromsøflaket)

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Summary Shallow Arctic banks have been observed to harbour rich communities of epifaunal organisms, but have not been well-studied with respect to composition or function due to sampling challenges. In order to determine how these banks function in the Barents Sea ecosystem, we used a combination of video and trawl/dredge sampling at several locations on a heavily trawled bank, Tromsøflaket – located at the southwestern entrance to the Barents Sea. We describe components of the benthic community, and calculate secondary production of dominant epifaunal organisms. Forty-six epibenthic taxa were identified, and sponges were a significant part of the surveyed benthic communities. There were differences in diversity and production among areas, mainly related to the intensity of trawling activities. Gamma was the most diverse and productive area, with highest species abundance and biomass. Trawled areas had considerably lower species numbers, and significant differences in epifaunal abundance and biomass were found between all trawled and untrawled areas. Trawling seems to have an impact on the sponge communities: mean individual poriferan biomass was higher in untrawled areas, and, although poriferans were observed in areas subjected to more intensive trawling, they were at least five times less frequent than in untrawled areas.

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1. Introduction

The Barents Sea is one of the most productive marginal seas of the world's oceans (Carmack and Wassmann, 2006; Sakshaug, 1997; Sakshaug and Slagstad, 1991). The estimated average annual primary productivity in the Barents Sea is about $100 \text{ g C m}^{-2} \text{ y}^{-1}$, but can be up to three times higher on the shallow banks (Sakshaug et al., 2009). Those shallow water regions make up more than one-third of the Barents Sea area (Jakobsson, 2002) and are characterized by strong depth gradients and dynamic physical processes, including turbulent currents which interact to generate seasonally high productivity. Shallow depths encourage rapid settlement of newly fixed organic carbon to the sea floor, and together with strong near-bottom currents, support rich filter-feeding communities (Kędra et al., 2013). Shallow banks are significant biodiversity hot spots in the larger ecosystem, and their ecosystem functioning may be particularly significant since carbon cycling, benthic secondary production, and food-web subsidies are enhanced (Grebmeier et al., 2006; Piepenburg et al., 1997; Piepenburg and Schmid, 1996, 1997).

Tromsøflaket, located at the southern entrance of the Barents Sea, is similar to other Barents Sea banks as it supports rich communities of epifaunal organisms, including long-lived and potentially vulnerable sponges and corals (Buhl-Mortensen et al., 2012; Jørgensen et al., 2011; Zenkevich, 1963). It is also an important spawning and harvesting area for some species of commercial fish (Loeng and Drinkwater, 2007; Olsen et al., 2010; Winsnes and Skjoldal, 2009). Benthic secondary productivity in this region has recently been estimated, and high values have been suggested for some biotopes (Buhl-Mortensen et al., 2012). Some areas are heavily fished, with bottom trawls being one of the most common gears employed, but potential impacts on ecological function, including future fisheries, have not been assessed.

Dredging and trawling activities can have serious impacts on the bottom communities, and marine ecosystems in general (Callaway et al., 2007; De Juan et al., 2011; Handley et al., 2014; Hiddink et al., 2006; Hinz et al., 2009; Kaiser et al., 2006; Olsgaard et al., 2008). These effects include habitat alteration (Mangano et al., 2013) and shifts in benthic communities towards smaller, short-lived and fast-growing species, which can cause system shifts from high to low diversity and from a high biomass – low turnover to a low biomass – high turnover system (Dannheim et al., 2014). This has wider ecosystem implications: affecting marine food webs by altering the quality of food available to commercially important species as well as affecting their size (Hinz et al., 2009; Shephard et al., 2014; Smith et al., 2013).

Despite their potential for having high ecosystem value, many shallow areas represent a challenge for researchers. The coarse substrate and strong currents make the use of traditional quantitative sampling gears (grabs) difficult or impossible. However, an underwater video has been used effectively to assess epifaunal community structure and function in a variety of shallow water habitats, and can identify areas with evidence of trawling activities (Buhl-Mortensen et al., 2009, 2012; Lindholm et al., 2004). Moreover, since it is a non-destructive sampling methodology, visual surveys are valuable for examining potentially vulnerable or sensitive seabed areas (Kilgour et al., 2014).

We, therefore, use underwater video to investigate epibenthic communities in the Tromsøflaket area. We ask what the characteristic values for diversity, biomass, and secondary production of epibenthic fauna on this Arctic bank are, and discuss how trawling may affect those parameters. These results provide important data for future studies of benthic fauna and ecosystem functioning.

2. Material and methods

2.1. Study area

Tromsøflaket is located in the southwestern Barents Sea with a depth plateau between 150–200 m (Buhl-Mortensen et al., 2009). The oceanography here is influenced by two major current systems. The southern part is dominated by the north-flowing Norwegian Coastal Current, with relatively cold, low-salinity coastal water while the rest of the bank is influenced by the Norwegian Atlantic Current, bringing relatively warm, saline water to the north (Bellec et al., 2008; Dijkstra et al., 2013; Skarðhamar and Svendsen, 2005). Bottom temperature and salinity average are 4.8°C (± 1.5 standard deviation) and 35.1‰ (± 0.3), respectively (Jørgensen et al., 2015). Most of the bank sediments are glacially derived. Coarse sediments are found on ridges and shallow parts of the bank while finer sediments concentrate in depressions, on the slopes, and in the deeper areas (Bellec et al., 2008). The bank is ecologically and economically important since it supports vulnerable sponge habitats which account for about 90% of the benthic biomass (Buhl-Mortensen et al., 2009; Jørgensen et al., 2015), and is a spawning area for commercial fish. In addition, it is a retention area for eggs and larvae (Olsen et al., 2010), which are then preyed upon by breeding and overwintering seabirds. Long-line, Danish seine, and bottom-trawling fishers are highly active on the east side of the bank (Jørgensen et al., 2016; Olsen et al., 2010; Winsnes and Skjoldal, 2009).

2.2. Sampling and data analysis

A combination of video and trawl/dredge sampling was used to describe components of the benthic community, and to calculate secondary production of dominant epifaunal organisms. The sea-bed conditions and epifauna were recorded and photographed in summer 2008 using a SUB-fighter 4500 ROV equipped with zoom- and wide-angle video cameras (Fig. 1). Lasers on the ROV permitted the size estimation of objects detected. Differential GPS (in relation to the support ship *Olympic Poseidon*) was used for positioning. A transponder mounted on the ROV confirmed $\pm 5 \text{ m}$ accuracy in the depth and positioning. Videos were taken at the depths of: 177–213 m in Alke Nord, 160–173 m in Alke Sør, and about 190 m in the Gamma areas. The video survey was conducted under contract to the oil and gas company ENI, and raw video files were provided for the purposes of these analyses.

Five to ten-minute-long video transects were taken in each area. In all, 24 video transects from Alke Nord, 21 from Alke Sør, and 23 from Gamma were analyzed in detail using frame captures approximately every 30 s ($n = 10\text{--}20$ frames per transect). To complement underwater video information, epifauna were collected at several locations (7 from Alke and

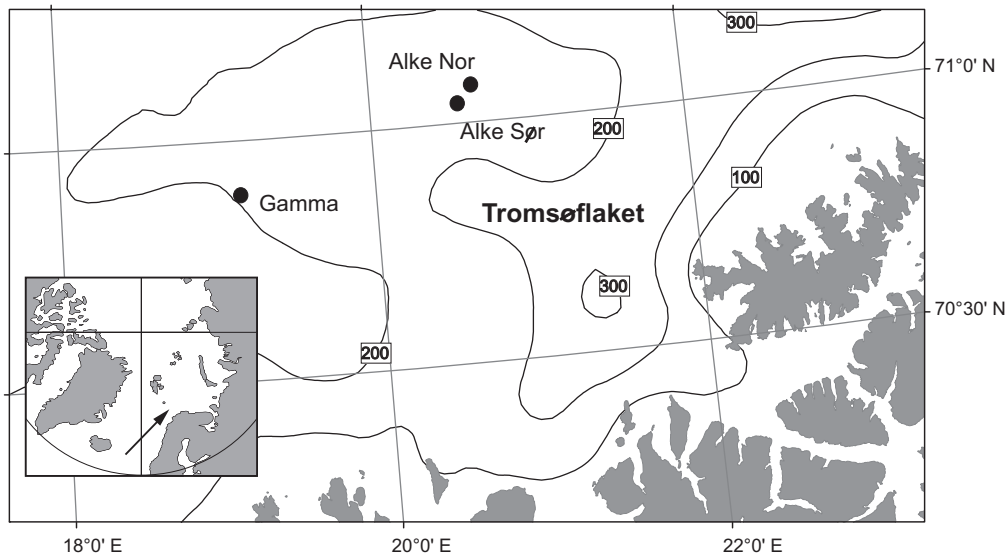


Figure 1 Map indicating the location of Tromsøflaket and positions of sampling sites.

6 from Gamma fields) with dredges and trawls in August 2008 aboard the r/v Oceania. Benthic epifaunal organisms collected by dredge were sorted onboard and fixed in buffered 10% formalin. Later in the laboratory, material was identified to the lowest possible taxonomic level, dried and weighed (dry weight; a selection of different sizes of organisms was made). For each species, the size–biomass relationship was established. On the basis of this information, species (or lowest identifiable taxonomic level) identities observed on the video were confirmed, counted from each snapshot and measured. Biomass (dry weight) was determined using the empirical relationships calculated from dredge samples. Secondary production was calculated according to Brey (2001). In order to convert biomass [$\text{g dry weight m}^{-2}$] into energy [kJ] and thereafter to production values [kJ y^{-1}], data were first transformed using published conversion factors (Brey, 2001). Subsequently, production/biomass ($P B^{-1}$) ratios were calculated for up to three size categories (large, medium and small, depending upon how much the $P B^{-1}$ ratio varied with organism size) for each species by employing a multiple regression model incorporating habitat (e.g., water temperature, depth) and taxon-specific (e.g., phylum level, motility) data (Bolam et al., 2010; Brey, 2001). To calculate secondary production, the biomass per area of each

organism/size class was multiplied by the respective $P B^{-1}$ ratio. Total production values for each replicate were then calculated as the sum of production values for each individual, and thereafter aggregated at the phylum level. Production at each area was represented as the average of the replicates but one individual transect outlier was excluded from further analysis. Finally, average production values were transformed to carbon using the conversion factor $45.7 \text{ J} = 1 \text{ mg C}$ (Salonen et al., 1976), and all the calculated values were standardized to a per m^2 basis.

For each snapshot, the presence of trawling tracks was noted (Photo 1) and, later, those results were used to contrast the effects of trawling on biodiversity, total abundance, total biomass, and poriferan biomass. Mean values are given with standard errors. Differences in taxonomic richness, abundance, and biomass among sampling areas (Alke Nord, Alke Sør and Gamma) were tested using the nonparametric Kruskal–Wallis test and Dunn's post hoc multiple comparisons test while differences between trawled and untrawled areas were tested with the corrected Mann–Whitney U test (sample size larger than 20 and ties occurred across both samples; Sokal and Rohlf, 1981). Nonparametric tests were chosen since normality could not be obtained even after data transformation. The number of taxa observed and estimated total

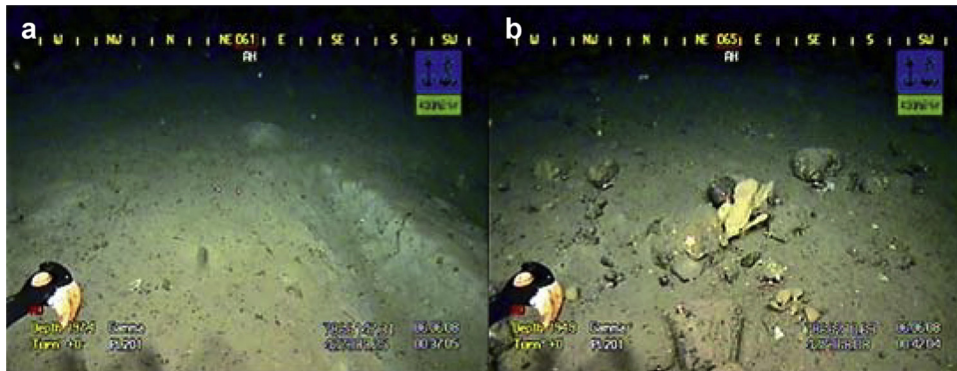


Photo 1 Snapshots of underwater video showing trawled areas (a) versus untrawled areas (b).

richness [Chao2] with 95% confidence intervals for each area were computed according to Colwell et al. (2004). Data analyses were performed using the Excel, EstimateS (Colwell, 2009) and Statsoft software STATISTICA v. 6.

3. Results

3.1. Diversity

Altogether, 46 epibenthic taxa and 7 fish taxa were identified across all surveyed areas (Fig. 2, Table 1). Estimated richness [Chao2] was 88 species with 95% confidence intervals from 46 to 106. In Alke Nord the mean number of observed taxa was 26 while Chao2 gave the estimate of 38 species (95% CI 29–79). In Alke Sør the mean number of observed taxa was 21, with Chao2 of 27 (95% CI 22–51), and in Gamma the mean number of observed taxa was 28, with Chao2 of 40 (95% CI 30–96). Mean number of taxa per snapshot was 0.5 ± 0.03 in Alke Nord, 0.3 ± 0.03 in Alke Sør and 1.5 ± 0.1 in Gamma. Alke Nord and Alke Sør were characterized by a gravel and soft sediment bottom; and Gamma had muddy and sandy sediments, with some crushed stones. In areas with heterogeneous bottoms, i.e. with both soft and hard substrate, more taxa were found.

3.2. Productivity, abundance and biomass

Gamma was the most productive area, with total production of $0.5 \text{ g C m}^{-2} \text{ y}^{-1} \pm 0.44$, Alke Nord's total production was $0.33 \text{ g C m}^{-2} \text{ y}^{-1} \pm 0.77$ (with an exception of one video transect, where production of mainly poriferans and echinoderms reached $5.6 \text{ g C m}^{-2} \text{ y}^{-1}$; however, this video was excluded from further analysis as an outlier) and Alke Sør had the lowest total production of only $0.07 \text{ g C m}^{-2} \text{ y}^{-1} \pm 0.12$ (Fig. 3). Poriferans contributed the most to the total production in all areas, followed by echinoderms (Fig. 3).

In Alke Nord and Alke Sør there were no organisms present on most of the snapshots (60–67%), while in Gamma only 10% of the photographs showed no macroscopic organisms. Mean epifaunal total abundance in Alke Nord reached $0.7 \text{ ind. m}^{-2} \pm 0.3$, $1.6 \text{ ind. m}^{-2} \pm 0.8$ in Gamma and only $0.1 \text{ ind. m}^{-2} \pm 0.02$ in Alke Sør (Fig. 4A). There were significant

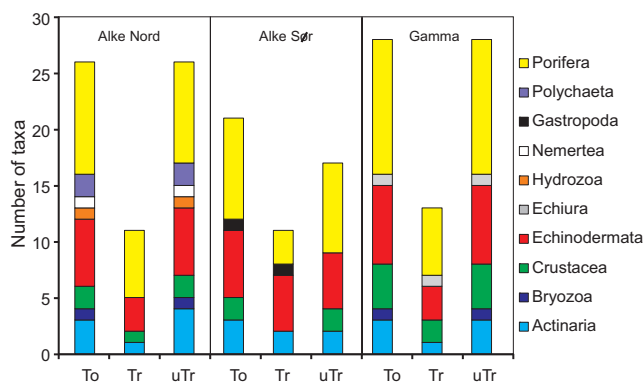


Figure 2 Total (To) taxa number in different taxonomic groups in trawled (Tr) and untrawled (uTr): Alke Nord, Alke Sør and Gamma.

Table 1 Most common taxa arranged in biomass (per m^2) order for trawled and untrawled areas in Alke Nord, Alke Sør and Gamma. A – Actinaria, B – Bryozoa, C – Crustacea, E – Echinodermata, Ec – Echiura, H – Hydrozoa, P – Porifera. Poriferan species that occurred only once are marked with *. Taxa identified to higher level than family and single taxa other than poriferans are not included.

Trawled	Untrawled
Alke Nord	
<i>Ceramaster granularis</i> (E)	<i>Geodia barretti</i> (P)
* <i>Phakellia ventilabrum</i> (P)	Chalinidae indet. (P)
* <i>Geodia barretti</i> (P)	<i>Ceramaster granularis</i> (E)
<i>Leptychaster arcticus</i> (E)	<i>Crisia eburnea</i> (B)
<i>Stylocordyla borealis</i> (P)	<i>Bolocera tuediae</i> (A)
<i>Polymastia</i> sp. (P)	<i>Phakellia ventilabrum</i> (P)
<i>Stichastrella</i> sp. (E)	<i>Actinostola callosa</i> (A)
<i>Bolocera tuediae</i> (A)	<i>Stylocordyla borealis</i> (P)
* <i>Asbestopluma pennatula</i> (P)	<i>Cerianthus</i> sp. (A)
<i>Munida</i> sp. (C)	<i>Leptychaster arcticus</i> (E)
	<i>Henricia</i> sp. (E)
	Hexactinellida (P)
	<i>Axinella infundibuliformis</i> (P)
	* <i>Asbestopluma pennatula</i> (P)
	<i>Munida</i> sp. (C)
	* <i>Mycale lingua</i> (P)
Alke Sør	
<i>Phakellia ventilabrum</i> (P)	<i>Phakellia ventilabrum</i> (P)
<i>Stichastrella</i> sp. (E)	<i>Geodia barretti</i> (P)
<i>Ceramaster granularis</i> (E)	<i>Ceramaster granularis</i> (E)
<i>Hippasteria phrygiana</i> (E)	* <i>Aplysilla sulfurea</i> (P)
<i>Poraniomorpha</i> sp. (E)	<i>Stichastrella</i> sp. (E)
* <i>Antho dichotoma</i> (P)	<i>Leptychaster arcticus</i> (E)
	<i>Bolocera tuediae</i> (A)
	<i>Axinella infundibuliformis</i> (P)
	<i>Poraniomorpha</i> sp. (E)
	<i>Asbestopluma pennatula</i> (P)
	<i>Hyas</i> sp. (C)
	* <i>Polymastia</i> sp. (P)
	* <i>Stylocordyla borealis</i> (P)
	<i>Munida</i> sp. (C)
Gamma	
<i>Geodia barretti</i> (P)	<i>Geodia barretti</i> (P)
<i>Parastichopus tremulus</i> (E)	<i>Parastichopus tremulus</i> (E)
<i>Geodia macandrewii</i> (P)	<i>Geodia macandrewii</i> (P)
* <i>Phakellia ventilabrum</i> (P)	<i>Phakellia ventilabrum</i> (P)
<i>Ceramaster granularis</i> (E)	<i>Aplysilla sulfurea</i> (P)
<i>Munida</i> sp. (C)	<i>Mesothuria intestinalis</i> (E)
* <i>Hymedesmia</i> sp. (P)	<i>Lithodes maja</i> (C)
<i>Bonellia viridis</i> (Ec)	<i>Axinella infundibuliformis</i> (P)
* <i>Mycale lingua</i> (P)	<i>Bolocera tuediae</i> (A)
	<i>Stichastrella</i> sp. (E)
	<i>Hymedesmia</i> sp. (P)
	<i>Ceramaster granularis</i> (E)
	<i>Reniera</i> sp. (P)
	<i>Bonellia viridis</i> (Ec)
	<i>Munida</i> sp. (C)
	<i>Henricia</i> sp. (E)
	* <i>Chalinidae</i> indet. (P)

Table 1 (Continued)

Trawled	Untrawled
	<i>Hyas</i> sp. (C)
	<i>Mycale lingua</i> (P)
	*Hexactinellida (P)
	<i>Stylocordyla borealis</i> (P)

differences in epifaunal total abundance among those three areas (Kruskal–Wallis test: $p < 0.05$; Dunn's test: $p < 0.05$; Table 2). Mean epifaunal total biomass (dry weight) in Alke Nord reached $10.1 \text{ g m}^{-2} \pm 4.0$, $20.8 \text{ g m}^{-2} \pm 5.3$ in Gamma and only $1.1 \text{ g m}^{-2} \pm 0.3$ in Alke Sør (Fig. 4B). There were significant differences in epifaunal total biomass among areas (Kruskal–Wallis test: $p < 0.05$; Dunn's test: $p < 0.05$; Table 2).

3.3. Trawled versus untrawled areas

Tracks from trawling were registered at all surveyed areas. Trawled areas had considerably lower taxonomic richness: in Alke Nord 26 taxa were found in untrawled areas versus 11 taxa noted in trawled areas. In Alke Sør 17 taxa and 11 taxa were found in untrawled and trawled areas, respectively. In the Gamma 28 taxa were found in untrawled versus 13 taxa found in trawled areas (Fig. 2). Mean number of taxa per snapshot reached in Alke Nord: 0.5 ± 0.04 and 0.2 ± 0.05 , in Alke Sør: 0.4 ± 0.04 and 0.2 ± 0.05 and in Gamma: 1.5 ± 0.1 and 0.9 ± 0.1 in untrawled and trawled areas, respectively. There were significant differences in taxonomic richness per photograph between trawled and untrawled area at each study site (Mann–Whitney U test, $p < 0.01$; Table 2). Poriferans dominated in terms of the number of taxa, production, and biomass in all regions (Figs. 2 and 3). Hydrozoans, bryozoans and annelids (filtering feeding Sabeliidae) were only present in untrawled areas. Actinarians, echinoderms, crustaceans and poriferans were present in both trawled and untrawled areas, but each group was more diverse in untrawled areas (Table 1). Gastropods were recorded only in trawled sites of Alke Sør. Sponge diversity was higher in untrawled areas (porifera *Axinella infundibuliformis* only present there).

Mean epifaunal abundance reached $0.9 \pm 0.4 \text{ ind. m}^{-2}$ and $0.1 \pm 0.03 \text{ ind. m}^{-2}$ in Alke Nord, $1.8 \pm 0.9 \text{ ind. m}^{-2}$ and $0.6 \pm 0.2 \text{ ind. m}^{-2}$ in Gamma, and only $0.1 \pm 0.02 \text{ ind. m}^{-2}$

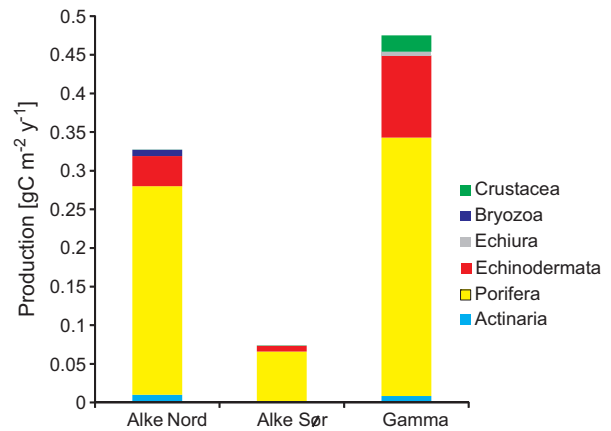


Figure 3 Total epibenthic production [$\text{g C m}^{-2} \text{ y}^{-1}$] per dominating taxa in areas: Alke Nord, Alke Sør and Gamma.

m^{-2} and $0.06 \pm 0.02 \text{ ind. m}^{-2}$ in Alke Sør, in untrawled and trawled areas, respectively (Fig. 4A). Mean epifaunal biomass in Alke Nord reached: $13.0 \pm 5.2 \text{ g m}^{-2}$ and $0.5 \pm 0.16 \text{ g m}^{-2}$, in Alke Sør: $1.4 \pm 0.4 \text{ g m}^{-2}$ and $0.3 \pm 0.09 \text{ g m}^{-2}$ and in Gamma: $23.3 \pm 6.3 \text{ g m}^{-2}$ and $6.3 \pm 2.5 \text{ g m}^{-2}$ in untrawled and trawled areas, respectively (Fig. 4B). There were significant differences in epifaunal abundance and biomass between all untrawled and trawled areas (Mann–Whitney U test, $p < 0.05$; Table 2; Fig. 4A and B). Sponges mean individual biomass in untrawled areas was higher: $32.2 \pm 57.0 \text{ g m}^{-2}$ and $19.1 \pm 54.7 \text{ g m}^{-2}$ in Alke Nord, $18.5 \pm 31.8 \text{ g m}^{-2}$ and $8.2 \pm 8.6 \text{ g m}^{-2}$ in Alke Sør and $53.5 \pm 59.8 \text{ g m}^{-2}$ and $46.2 \pm 49.1 \text{ g m}^{-2}$ in Gamma, untrawled and trawled areas respectively. Although poriferans were also observed in areas subjected to more intensive trawling they were at least five times less frequent (and 18 times less in Gamma) than in untrawled areas.

4. Discussion

In the Barents Sea, banks are recognized as important diversity and productivity “hot spots” (Cochrane et al., 2012; Kędra et al., 2013). Indeed, 46 taxa were found in this study in Tromsøflaket, which was equal to the lower *Chao2* 95% confidence interval. Nevertheless, this value is lower than other findings for this bank: Buhl-Mortensen et al. (2012)

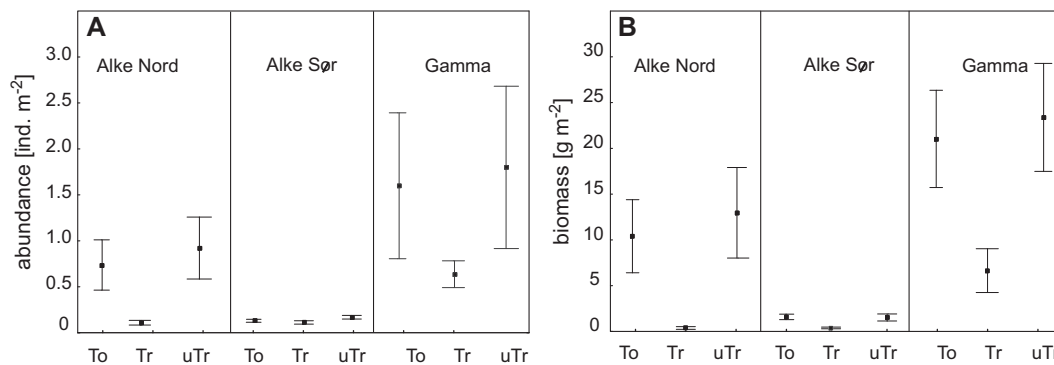


Figure 4 (A) Mean abundance [ind. m^{-2}] and (B) mean total epibenthic biomass [g m^{-2}] (dry weight) with standard error for Alke Nord, Alke Sør and Gamma per total area (To) and in trawled (T) and untrawled (uTr) areas.

Table 2 Results of statistical tests: K-W – Kruskal–Wallis, D – Dunn's post hoc multiple comparisons, U – corrected Mann–Whitney U, used to assess differences in abundance, biomass and taxonomic richness (number of taxa), among sampling areas (Alke Nord, Alke Sør and Gamma) and between trawled and untrawled areas. Test results are given (stat) and significance level (p). Significant differences are marked with *.

	Test		Abundance		Biomass		Taxonomic richness	
			stat	p	stat	p	stat	p
Area	K-W	H	249.77*	<0.01	216.27*	<0.01	293.32*	<0.01
Alke Nord vs. Alke Sør	D	z	4.03*	<0.05	2.90*	<0.05	1.13	>0.05
Alke Nord vs. Gamma	D	z	11.07*	<0.05	10.83*	<0.05	13.50*	<0.05
Alke Sør vs. Gamma	D	z	14.15*	<0.05	12.87*	<0.05	13.73*	<0.05
Trawled vs. untrawled								
Alke Nord	U	Z_{cor}	-4.31*	<0.01	-4.10*	<0.01	-3.95*	<0.01
Alke Sør	U	Z_{cor}	-2.08*	0.037	-1.97*	0.048	-1.98*	0.047
Gamma	U	Z_{cor}	-2.95*	<0.01	-4.06*	<0.01	-3.55*	<0.01

reported about 180 taxa; another study showed over 100 taxa in Tromsøflaket area (Buhl-Mortensen et al., 2009). Our values were lower; however, those two studies were conducted on a larger area, in a wider range of habitats, and with higher sampling effort than in the current study. Also, the reported average number of taxa was only about 30 for depths under 200 m in Tromsøflaket (Buhl-Mortensen et al., 2012). Where the same sediment types were sampled, Buhl-Mortensen et al. (2009) reported many of the same dominant poriferan (*Asbestopluma pennatula*, *Geodia* spp., *Stylacordyla borealis*, *Phakellia* sp., *Axinella* sp. and *Polymastia* sp.) and asteroidean taxa (*Ceramaster granularis* and *Poraniomorpha* spp.) as found here. Buhl-Mortensen et al. (2012) reported higher diversity and production in regions with heterogeneous bottom sediments, where gravel and/or stones were present.

In general, Arctic shallow banks are characterized by high biomass of epifaunal communities, especially when compared to deeper areas (Grebmeier et al., 2006; Kędra et al., 2013; Piepenburg et al., 1997; Piepenburg and Schmid, 1996, 1997). Although Tromsøflaket epifaunal diversity was relatively high, its biomass (less than 20 g m⁻² dry weight in all fields on average) and production (below 0.5 g C m⁻² y⁻¹, but above 5 g C m⁻² y⁻¹ in one Alke Nord location) were lower compared to epibenthos in other parts of the Barents Sea. However, the biomass and production estimation in this study might be biased due to the chosen method (video analysis) and more extensive dredge sampling may reveal higher values. In deep parts of the Barents Sea, benthic biomass is on average about 100 g m⁻² wet weight (Gulliksen et al., 2009), while on the most productive bank (Svalbard Bank) it averages about 600 g m⁻² (Idelson, 1930; Kędra et al., 2013). Buhl-Mortensen et al. (2012) reported similar or lower (to our results) epifaunal production values for some biotopes. Lower primary production and greater depths at Tromsøflaket (compared to Svalbard Bank) likely result in lower organic matter input to the sea floor, and may be reflected by the lower epifaunal biomass there. However, this pattern is not necessary reflected for epifauna at all deeper (about 200 m) banks in the Barents Sea (Jørgensen et al., 2016). Moreover, Tromsøflaket is subjected to intensive fishing through its whole area (Jørgensen et al., 2016), influencing standing stocks of benthic epifauna. Epifaunal

contribution to benthic productivity at other sites of approximately 200 m in the Barents Sea is believed to be minor (about 4%; Piepenburg, 2005), but since we only focused on the epifauna and no infaunal samples were taken, we cannot estimate the bank's total benthic production.

In our study trawling tracks were registered at all surveyed regions. Fishing intensity at Tromsøflaket is high, particularly in both Alke fields (<http://kart.fiskeridir.no/>; Jørgensen et al., 2016). This is reflected in significantly lower biomass and productivity in those fields compared to Gamma, where fishing pressure is lower. Although we designated particular fields in each snapshot as trawled or untrawled, lack of trawling marks on analyzed videos at Gamma (and other areas) does not preclude their presence nearby and their influence on epifauna there. Bottom trawling is known to have direct influence on bottom communities through dislocation, damage and mortality of benthic organisms (Bergman and Hup, 1992; Bergman and van Santbrink, 2000; Collie et al., 2016; Jennings and Kaiser, 1998), but also indirect effects through sediment disturbance and resuspension (Jennings et al., 2001; Watling et al., 2001). Sessile filter-feeders and large-bodied animals, such as sponges (dominant taxa in this study), hydroids, soft corals and bryozoans, are more sensitive to such disturbance but can survive in lightly trawled areas (Boulcott and Howell, 2011; Kaiser et al., 2002, 2006; Løkkeborg, 2005; Tillin et al., 2006). Heavily trawled areas in our study were less diverse, but all functional groups were present, including the sessile poriferans (although filter-feeding hydrozoans, bryozoans and polychaetes were absent). Intensively trawled areas are often characterized by a higher relative biomass of mobile animals and scavenging invertebrates (Collie et al., 1997; Rumohr and Kujawski, 2000; Tillin et al., 2006) which might have been the case of gastropods presence in Alke Sør. The high abundance of the opportunist crustaceans *Munida* sp. and *Hyas* sp. was also noted in the Gamma and Alke Sør, but in both trawled and untrawled areas.

Trawling impacts on sessile organisms are particularly high, and in the case of large sponges, the removal rate is estimated to reach about 20% of initial biomass per single trawl (Pitcher et al., 2000). Although the removal process is fast and effective, the time needed for recovery is long and the success of recovery uncertain. Studies on the recovery

rate of benthic populations in fished areas suggest a steady recovery of the benthic megafauna within at least 5 years after cessation of trawling and dredging activities (Hermsen et al., 2003). Benthic infaunal communities are reported to need at least 18 months to recover (Desprez, 2000; Sarda et al., 2000; Tuck et al., 1998), but the recovery of large sessile fauna will more likely take years to decades (Ragnarsson et al., 2015). Sponges, in particular, needed 8 years to recover (based on meta-analysis of about 100 different fishing impact manipulations, mainly from north Europe and northeast America; Kaiser et al., 2006), but there are some indications that large sponges and corals recovery might take even more than 15 years (on tropical shelves in Australia, Pitcher et al., 2000). Islandic scallop needed about 20 years to initiate population recovery, after heavy fishing on the Svalbard Bank was ceased due to stock depletion; yet, the current densities and biomass are still lower than in the 1920s, before the fisheries had started (Idelson, 1930; Kędra et al., 2013). In this study, sponge diversity was lower in trawled areas and specimens observed in trawled areas had lower individual biomass than ones outside the trawling tracks. Although some, even large, sponges were found in this study in old trawling tracks, it is more likely that those individuals were dislocated and moved by recent fishing activities, so it is questionable whether they survived.

The impact of chronic bottom trawling on benthic fauna depends on the natural disturbance levels to which benthic communities are adapted. In general, biomass and production of fauna on poorly-sorted, gravelly or muddy sediments, as found in our study, were more sensitive to chronic trawling than well-sorted sandy habitat substrates (Bolam et al., 2014; Queiros et al., 2006). Removal or disturbance of habitat-forming species like corals and sponges can have a serious effect on biodiversity and ecosystem functioning. For example, lower benthic production in regions of high importance for fisheries may reduce fish growth and reproduction since bottom fishing may affect diet composition and prey quality (Collie et al., 2016; Johnson et al., 2015; Shephard et al., 2014; Smith et al., 2013). It is important to note, however, that we only evaluated epibenthic megafauna in this study, and we cannot be certain to what extent these results are mirrored in other community components.

5. Conclusions

Our results suggest some impact of trawling on the epifaunal biomass and productivity in Tromsøflaket that are not unequivocal. More unambiguous results could be obtained if large areas with no trawling impacts were sampled. Increasing anthropogenic pressure in the area, including continued trawling and potential oil drilling, as well as accelerating climate change, will strongly affect vulnerable epifauna and habitats of Tromsøflaket. Thus, further studies on diversity and productivity of epifauna, and their links with infaunal components, in this area are required.

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