Contribution to the Supplement: 'Effects of Fishing on Benthic Fauna, Habitat and Ecosystem Function'

Original Article

Trawling disturbance on megabenthos and sediment in the Barents Sea: chronic effects on density, diversity, and composition

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Bottom-trawl fisheries are expanding into deeper habitats and higher latitudes, but our understanding of their effects in these areas is limited. The ecological importance of habitat-forming megabenthos and their vulnerability to trawling is acknowledged, but studies on effects are few. Our objective was to investigate chronic effects of otter trawl fishery on substratum and megabenthos on the shelf (50–400 m) and slope (400–2000 m) in the southern Barents Sea. The study area represents a wide range in the history of fishing intensity (FI). Physical impact of trawling, density of trawl marks (TMs), was quantified on 250 video transects from shelf and slope, and megabenthos (>2 cm) composition was studied on 149 video transects from the shelf. The number of satellite-recorded vessels within grid cells 5 × 5 km was used as a proxy for FI in the TM analysis and for the megabenthos records within a 2-km radius around the transects. The effects of using different search area sizes were tested. Patterns in the density of TMs and megabenthos composition were compared with FI using linear regression and correspondence analysis. Occurrence of TMs was not directly related to FI but to bottom type, whereas megabenthos density and diversity showed a negative relation. For 79 of the 97 most common taxa, density was negatively correlated with FI. The sponges *Craniella zetlandica* and *Phakellia/Axinella* were particularly vulnerable, but also *Flabellum macandrewi* (Scleractinia), *Ditrupa arietina* (Polychaeta), *Funiculina quadrangularis* (Pennatulacea), and *Spatangus purpureus* (Echinoidea) were negatively correlated with FI, whereas asteroids, lamp shells, and small sponges showed a positive trend. Our results are an important step towards the understanding of chronic effects of bottom trawling and are discussed in relation to the descriptors "Biological diversity" and "Seafloor integrity" in the EU Marine strategic framework directive.

Keywords: Barents Sea, fishing pressure, management, megabenthos, sponges, trawling impact, video transects, VMS.

Introduction

Bottom trawling is one of the most widespread sources of physical disturbance on habitats and organisms on the continental shelves throughout the world (Jackson, 2001; Kaiser *et al.*, 2002). This is reflected by the intensive research effort to address these issues during the past two decades (Collie *et al.*, 2000; Kaiser *et al.*, 2006). Bottom-trawl fisheries are expanding into ever deeper habitats, where trawling impacts have also been documented recently (e.g. on continental slopes and seamounts: Morato and Pauli, 2004; Mortensen *et al.*, 2005; Althaus *et al.*, 2009; Clark, 2009;

Clark *et al.*, 2016). However, as of yet, investigations of deeper ecosystems have been few. The direct physical impact of towed bottom trawls alters seabed complexity, crushing, burying, killing, and removing biota (e.g. Watling and Norse, 1998). This can lead to chronic effects on ecosystem functions including reduced benthic production (e.g. Jennings *et al.*, 2001), reduced biodiversity and habitat homogenization (e.g. Dayton *et al.*, 1995), and changes in community composition (Hinz *et al.*, 2009). Large vulnerable species (e.g. corals and sponges) are lost, because they grow too slow to recover between disturbance events (Dayton *et al.*, 1995;

Pitcher *et al.*, 2000; Clark, 2009; Clark *et al.*, 2016; Pitcher *et al.*, 2016). Since these are often ecological "engineering species", this affects their role in nutrient turnover, and the provision of highly structured habitats that hosts a rich associated fauna (Buhl-Mortensen and Mortensen, 2004); in addition, they often act as refuges for commercially important fish (e.g. Coleman and Williams, 2002; Buhl-Mortensen *et al.*, 2010).

The evidence of these effects is considerable (e.g. Kaiser *et al.*, 2002; however, there is a high level of context-dependence in individual studies (e.g. Thrush and Dayton, 2002). The physical disturbance created by a trawl on the bottom depends on sediment composition, topography, trawling speed, construction, and weight of trawling equipment (e.g. Gray and Elliott, 2009; O'Neill and Ivanović 2016). Moreover, the magnitude of the ecosystem response to trawling disturbance depends on the number and identity of the species present in the area, their biological traits, and ecological functions (e.g. de Juan *et al.*, 2007). Potential recovery time-scales for different parts of benthic communities have been quantified, but such results are mainly derived from small-scale experimental studies (Kaiser *et al.*, 2006). There are few studies that document the long-term impacts of ongoing bottom trawling on large benthic fauna. It must be emphasized to study the long-term effects if we wish to understand the changes caused by bottom trawling at the ecosystem level (Hinz *et al.*, 2009). Recently, there has been a move towards an ecosystem-based approach in fisheries management (Bianchi and Skjoldal, 2008; Siron *et al.*, 2008). However, with regard to the implementation of ecosystem-based management, an extension of effect studies to represent all habitats, including polar areas, is needed (Thrush and Dayton, 2010). Here, we include high-latitude ecosystems (i.e. north of the Arctic Circle) in the Barents Sea and areas off Lofoten in the Norwegian Sea (68−71.3°N), from the shelf to deeper waters. The Norwegian fishing industry is a major socio-economic pillar in Norwegian coastal communities, and the export of seafood is substantial and constitutes a national export value of ∼1.53 billion USD (11.8 billion NOK for 2013; Directorate of Fisheries).

In the Barents Sea and off Lofoten, there is fishing activity to depths of at least 900 m and the predominant gear is otter trawl (Buhl-Mortensen *et al.*, 2013). However, these areas have also been considered as ecologically valuable and vulnerable (Anon, 2009, 2010) and include cold-water coral reefs (i.e. *Lophelia pertusa*) and sponge aggregations (Buhl-Mortensen *et al.*, 2015a). These large benthic organisms are often scattered and patchily distributed (Buhl-Mortensen *et al.*, 2010), and therefore poorly quantifiable with common or classical benthic sampling techniques. Quantitative video observations, therefore, provide the best information about the vulnerability of megabenthos to bottom trawling (Buhl-Mortensen *et al.*, 2014a). In addition to recording distribution and density of megabenthos, video is also suitable for collecting information about the composition of seabed substrates and indications of trawling activity (e.g. trawl marks, TMs; Buhl-Mortensen *et al.*, 2013).

Demersal fishing is so intensive and pervasive that the use of reference areas (pristine sites) to identify effects of fisheries on natural communities is often not possible (Dayton *et al.*, 1995). However, areas (of comparable environmental settings) that differ in intensity of trawling activity, as indicated by information from vessel monitoring systems (VMSs; e.g. Dinmore *et al.*, 2003; Hiddink *et al.*, 2006a, b; Piet *et al.*, 2007), combined with visual inspection of effects on the substratum and bottom fauna, can provide a way to detect the impact of fishing. Hinz *et al.* (2009) suggests that results

of subtle cumulative effects may only become apparent when fishing disturbances are examined over larger spatial and temporal scales.

In this study, we examined the impacts of otter trawling on substratum and megabenthos at the continental shelf and slope off Norway in the southern part of the Barents Sea in an area that was video-surveyed by the MAREANO programme in the period 2006–2008 (Buhl-Mortensen *et al.*, 2015a). This material allowed for a comparison of observed impact to the seabed and benthos in areas that had experienced different levels of bottom trawling activity. Density of TMs and megabenthos (organisms >2 cm) composition along video transects was compared for areas with a wide range in fishing intensity (FI) as estimated from VMS records. The TM analysis included 250 (700 m long) video transects and the fauna analysis was performed only on 151 of these. The main objectives of this study were to: (i) examine the relationship between density of TMs and FI, in different seabed environments; (ii) examine the impacts of bottom trawling on megabenthos from the shelf to deeper waters; and (iii) develop meaningful biodiversity indicators related to fisheries suited for a sustainable and ecosystem-based management of these ecosystems.

Material and methods
Study area
The impacts of bottom trawling on megabenthos were examined in the southwestern part of the Barents Sea and off Lofoten (Figure 1). This offshore area is commercially important for fisheries and potential exploitation of hydrocarbon. The area has a varied seabed topography including large low-relief areas and steep areas of sloping terrain (Buhl-Mortensen *et al.*, 2012). Water depth on the shelf ranges from 50 m (banks) down to 400 m in troughs between banks. The bottom types vary from 100% mud to gravel and boulders (Buhl-Mortensen *et al.*, 2009). The oceanography of the area is influenced by two major water masses (Hansen and Østerhus, 2000). The northward flowing Norwegian Coastal Current comprises the low salinity Norwegian Coastal Water with variable temperature. This water overlies the Norwegian Atlantic Current (with Norwegian Atlantic Water) like a wedge thickest towards the coast. Between 600 and 900 m, there is a transition zone of cold Norwegian Sea Arctic Intermediary Water (between 0.5 and −0.5°C). Below 900 m, Norwegian Sea Deep Water (less than −0.5°C) is dominating.

The main demersal fishing activity in this part of the Barents Sea is conducted by stern trawlers targeting gadoids. The fishery operates throughout the year, but with variable intensity in different areas due to seasonal immigrations of fish stocks. The fleet consists of 40 vessels ranging in size from 24 to 69 m, of which 90% are larger than 40 m and 25% larger than 60 m. The study area was mapped for bathymetry, geology, benthos, and pollutants in the period 2006–2008 by the MAREANO mapping programme (www.mareano.no) covering an area of 20 000 km². Five surveys were conducted in this period; one with RV Håkon Mosby in June 2006, and four with RV G. O. Sars including March/April and October in 2007, and June and October in 2008. The video survey locations were selected using a stratified semi-random method, to provide a representative distribution of samples with respect to marine landscapes, different depth ranges, and bottom types (Buhl-Mortensen *et al.*, 2015b). Megabenthos, bottom substratum, and TMs observed along video transects were quantified. For an analysis of the correlation between densities of observed TMs and FI, 250 video transects
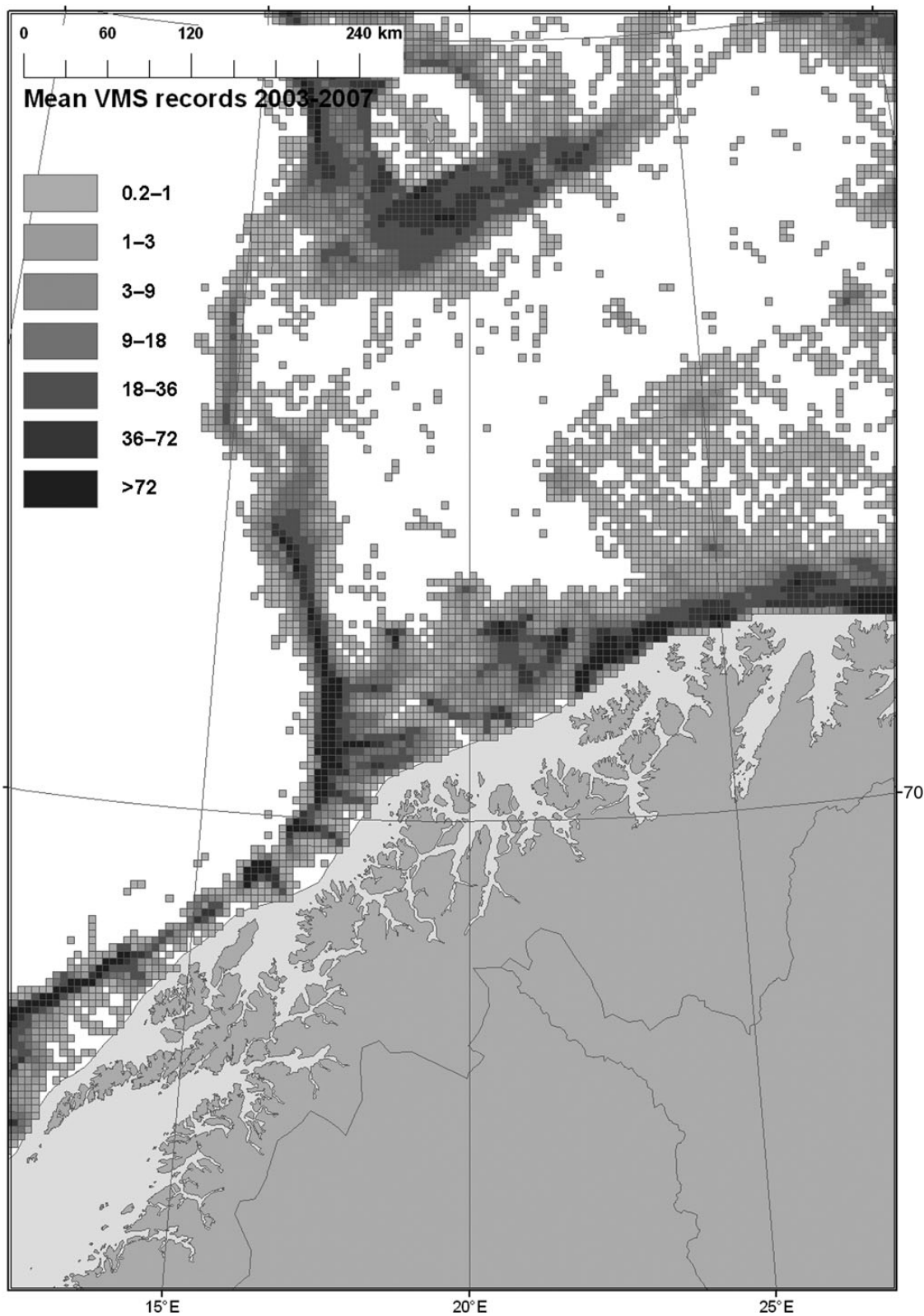
Figure 1. The distribution of FI in the study area scaled to a grid size of 5 × 5 km. FI is based on year mean number of VMS records, data from 2003 to 2007, and records are sorted to represent trawling (see the Methodology section). The grey scale refers to eight FI levels with white areas having no records of trawling.

conducted in the period 2006–2008 from 50 to 2000 m depth on the continental shelf and slope were used. The megabenthos analysis

included 151 of these transects from 55 to 399 m depth on the continental shelf that provided a good coverage of different history of FI

from a variety of substrates ranging from hard bottom to mud. Video transects from deeper locations were not included in the fauna analyses; for this analysis, we focus on the depth range where most fishing takes place and most data were available. This analysis was conducted on 149 transects after having excluded two sites with extreme FI levels.

Quantification of FI from VMS data

In Norway, VMS was introduced on all Norwegian fishing vessels of length >24 m in July 2000. Since then, the Norwegian Directorate of Fisheries has received information about time (minute resolution), vessel position, permit number, heading, and speed approximately every 60 min. We included only data from Norwegian vessels due to the quality of position information (VMS records every second hour). There are occasionally a couple of non-Norwegian vessels inside the study area and this will represent a minor source of error in the estimate of FI. VMS records before 2003 were not used, because earlier data had a higher frequency of missed records due to a less stable tracking system (Salthaug, 2006). The effects of the physical disturbance from trawling on bottom and benthos may last for several years depending on substratum and longevity of the fauna. Our study of megabenthos includes species with a lifespan of several years. In an attempt to account for temporal variability of the fisheries, as well as any long-lasting effects, we used the VMS records from the available 3 years before the video surveys to estimate FI (e.g. results from surveys conducted in 2006 were related to FI estimates based on 2003–2005 records).

VMS records are not discriminating between vessels that are actively fishing or not, and this represents a challenge when using it as a proxy for FI [see, e.g., Dinmore *et al.* (2003); Mills *et al.* (2007); Witt and Godley (2007); Hintzen *et al.* (2010); Lee *et al.* (2010); Skaar *et al.* (2011)]. To identify trawling vessels, we adopted a speed rule of 2–5 knots based on results from Skaar *et al.* (2011). Mapping FI, using VMS data as a proxy, depends on several assumptions related to the distribution of trawling activity. The time interval between vessel positions limits the spatial resolution that can be obtained, because the position of a vessel is not known between the records, which could be a distance of 3.6–9 km when trawling. Fishing vessels in the study area are known to change direction during trawling and track lines are often curved (Skaar *et al.*, 2011). Assuming straight lines between records is likely to provide a false representation [but see Rijnsdorp *et al.* (1998), Hintzen *et al.* (2010), and Lambert *et al.* (2012) for other fisheries]. We have used the number of VMS point records to estimate FI to avoid a set of assumptions.

The scale used to aggregate the data has differed among fisheries effect studies: Witt and Godley (2007) scaled fishing activity to 3 × 3 km, whereas Mills *et al.* (2007) used a grid size of 1 km. Defining an appropriate spatial scale for FI analysis is not straightforward. There is a spatial mismatch between the VMS recorded vessel position and the position of the trawl which is in physical contact with the seabed (Skaar *et al.*, 2011), a mismatch that is likely to increase with depth and topographic complexity. The warp length to depth ratio for otter trawl is depth-dependent and in the study area, it is in general 2–3 times the water depth. The trawl is then at a distance from 200 m to 1 km behind the vessel, but in a steep terrain there is an additional deviation to the sides of the vessel that may be considerable. The width of an otter trawl track, the distance between the otter doors, is 40–200 m and a trawl tow, which normally lasts >3 h (equivalent of three VMS records), will be ~30 km long and pass over several 5 × 5 km grid cells and could affect up to 24% of grid cell area (Skaar *et al.*, 2011; Buhl-Mortensen *et al.*, 2013). In contrast,

bottom and fauna data for impact analysis are collected from a 700-m long video transect. For the analysis of the correlation between observed TMs and FI, we used the 5 × 5 km gridded VMS records (Figure 1). Whereas, for the analysis of the relations between FI and megabenthos composition, we used a search radius of 2 km (12.6 km^2) around the centroid of each video transect (Figure 2) to generate FI estimates, and the two approaches were compared and results were consistent (see Discussion).

Video recording and analyses

The seabed was inspected with the tethered video platform CAMPOD, equipped with a high definition colour video camera (SonyHDC-X300) tilted forward at an angle of ~45°. It also has a standard definition video camera for navigation purposes, lights (2 × 400 W HMI), depth sensor, CTD, current meter, turbidity sensor, and an altimeter. Video transects were ~700 m long, a sufficient length for documentation of diversity of megabenthos (Buhl-Mortensen *et al.*, 2015a). CAMPOD was towed behind the survey vessel at a speed of 0.7 knots at a near-constant altitude of 1.5 m above the seabed controlled by a winch operator, providing a field view of ca. 2 m. To achieve the best view, the video was towed uphill in steep terrain. Geo-positioning of the video data was provided by a hydroacoustic positioning system (Simrad HIPAP and Eiva Navipac software) with a transponder mounted on CAMPOD, giving a position accuracy of ~2% of water depth. Navigational data (date, UTC time, positions, and depth) were recorded automatically at 10-s intervals using the software CampodLogger (IMR), and also used to annotate fauna, bottom types, signs of fishing impact, occurrence of litter, and local geological seabed features during video recording.

In the laboratory, a detailed video analysis was undertaken where all organisms were identified to the lowest possible taxonomic level and counted, or quantified as % seabed coverage for encrusting organisms (sponges, bryozoans, and colonial tunicates) using the custom-made software, VideoNavigator (IMR). Bottom TMs were counted and the percentage cover of six classes of bottom substrata (mud, sand, pebbles, cobbles, boulders, and outcrops) was estimated subjectively on a scale of 5% intervals at regular intervals within video sequences. These estimates were converted to bottom type classes following the Folk scale (Folk, 1954), and later grouped into three classes dominated by: (i) mud, (ii) sand, and (iii) hard. The area covered by a video transect was calculated based on travelled distance (calculated from "cleaned" geographical positions where noise was removed) and average field width (estimated from two laser scales, 10 cm apart). Density data (the number of organisms counted divided by the area observed) for solitary organisms were standardized as the number of individuals per 100 m^2. For this study, the relative composition of substrates was translated to three bottom types (mud, sand, and hard) and data from the video analyses were pooled for whole video transects.

Data analyses

TMs are one of the few clear signs of physical impact from bottom trawling on the seabed. All marks on the seabed that were clearly related to trawling were quantified during video analysis. To investigate substrate-specific responses to FI, all analyses were performed both on pooled data and on the three main bottom types (mud, sand, and hard bottom). We used linear regression analysis to study the relation between FI and observed physical disturbance of the seabed (TMs) and megabenthos composition (density and diversity). This allows both for parameterization in a statistical model and provides a detailed quantitative description of the linear relation. For the analysis of the relation between FI and density of
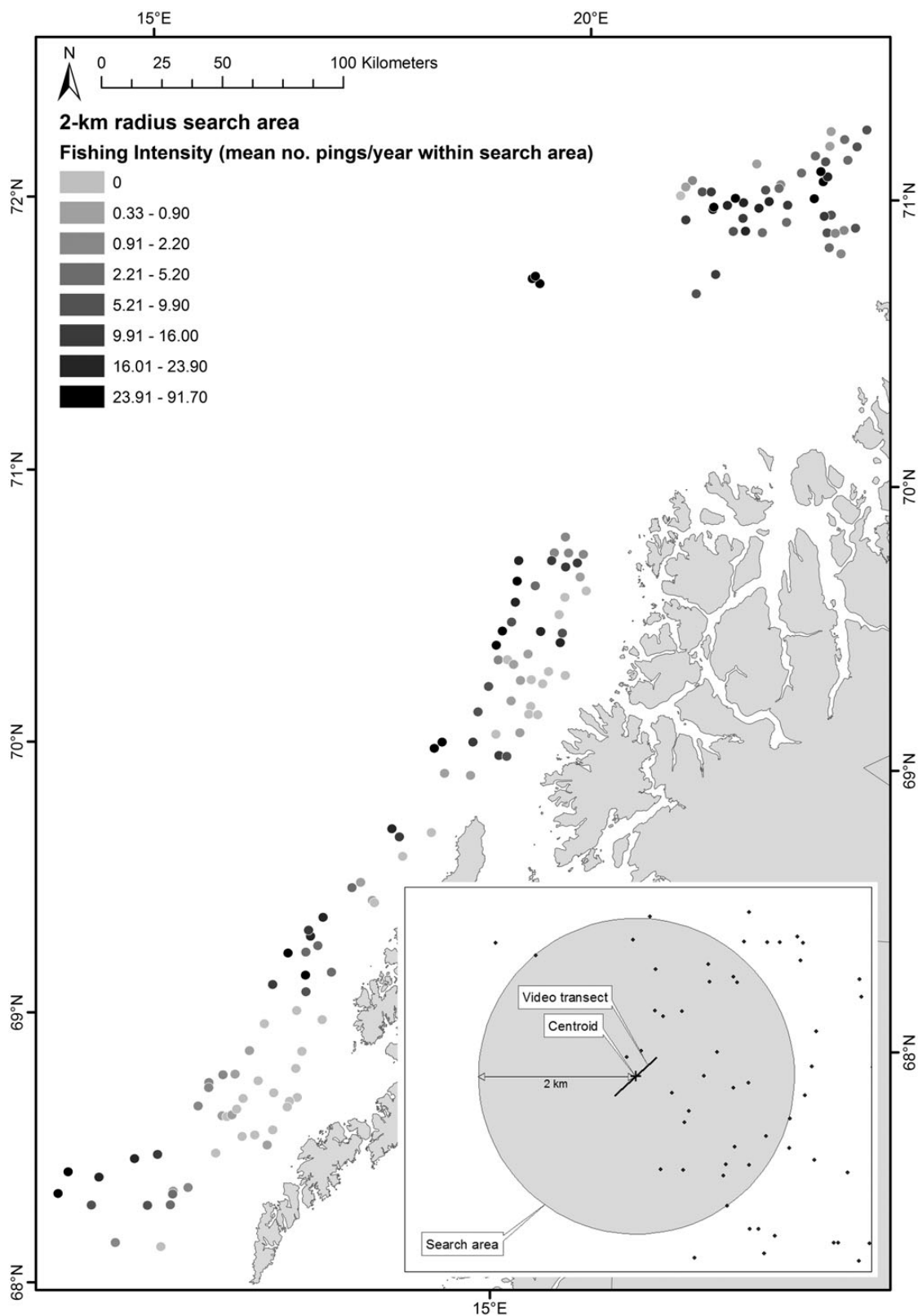
Figure 2. The distribution of 151 video transects used in the megabenthos analysis. The localities are marked with circles ($R = 2$ km) the area used to count VMS records to estimate FI. FI is based on the mean number of VMS records per year from the 3 years before megabenthos mapping. The grey scale refers to eight FI levels. Inserted illustration shows how VMS records were selected to estimate FI. The straight line represents the video transect and its centroid is marked with a cross. VMS records ("VMS pings") that fell inside the area defined by a search radius of 2 km around the centroid were counted.
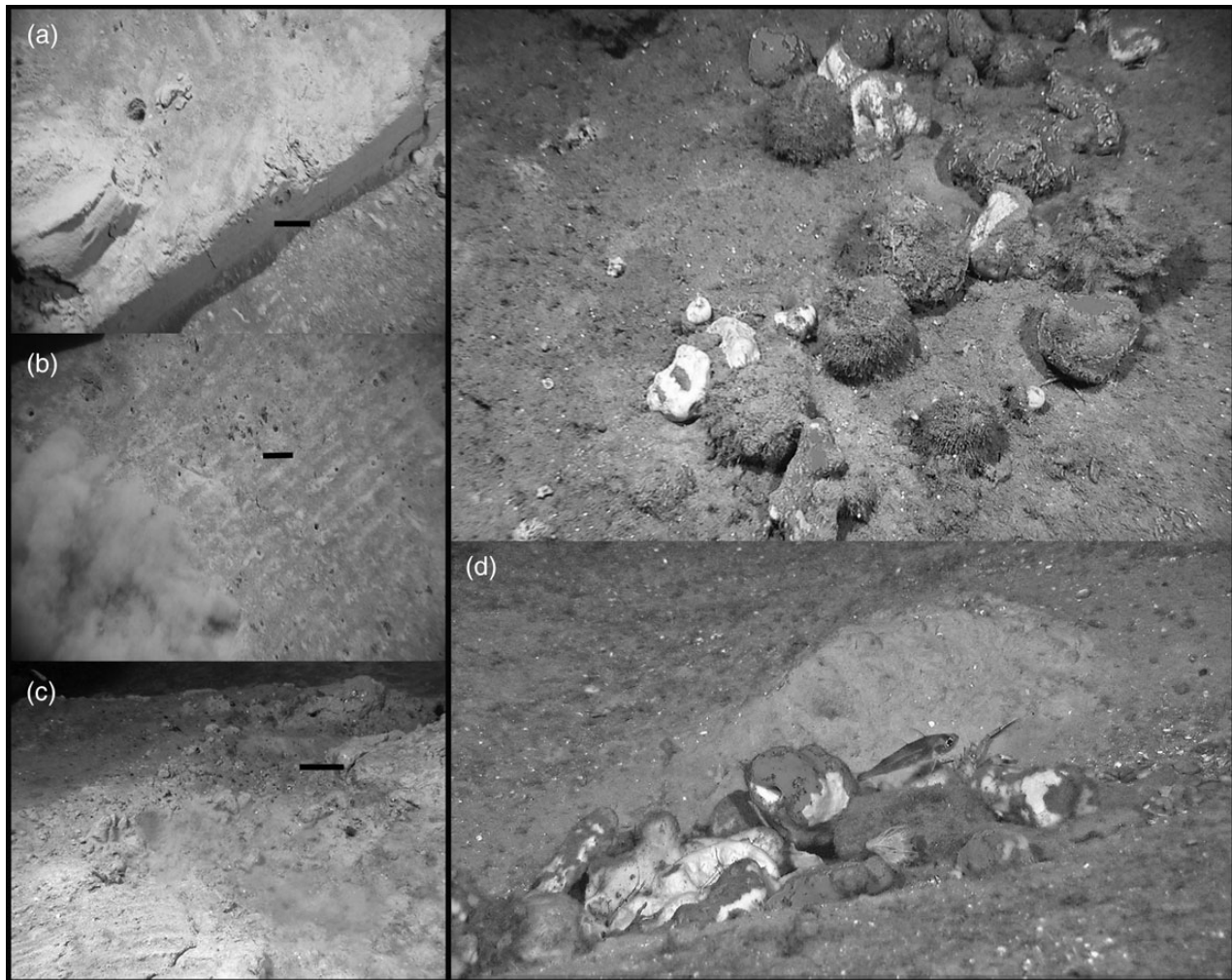
Figure 3. Physical impact on the substratum from otter trawl photos from video records. (a) Cut in sediment from trawl door. (b) Marks after chain in trawl opening. (c) Sediment turned over by a trawl. Black line in a-c shows 10 cm scale based on two laser points from the video platform CAMPOD. (d) Signs of physical impact on large sponges. *Geodia* (the white potato sponge) and *Steletta* (the round and furry looking sponge) are two large species that are dragged along by the trawl and are often found shuffled together or accumulated in ditches and/or lines behind the trawl. Typically they are covered with sediment probably from silting created by the trawling activity (photo courtesy to MAREANO/IMR).

TMs, we used both separate FI estimates for each year and pooled datasets (mean, maximum, and sum) for the last 3 years before video observations. For the analysis of the response of specific fauna groups and taxa to FI, we used linear correlation analysis as an indication of a positive or negative relation between observed densities and FI. To investigate similarities in fauna composition and to relate patterns with environmental factors focusing on FI and TMs, detrended correspondence analysis (DCA; Hill and Gauch 1980) was conducted. DCA is an ordination technique based on reciprocal averaging (Hill, 1973). It is an indirect gradient analysis, where environmental data are overlain on the ordination plot based on the species data. The environmental variables can then be correlated with variation covered by the axes in a multidimensional space. The environmental variables contained five numerical variables (depth, FI mean, FI min, FI max, and TMs) and two categorical variables (FI and bottom type). The categorical FI variable refers to the same eight levels of FI as presented in Figures 1 and 2. Only the 111 species occurring in at least five video transects were used for the analyses. DCA was performed using the software PC-Ord, with rescaling of axes and no downscaling of

rare species (McCune and Mefford, 2006). Four datasets were analysed: 149 transects (all bottom types); 29 from mud localities; 70 from sand; and 50 video transects from hard bottom (sandy gravel, gravel, and boulder).

Results
FI and seabed environment

FI was not randomly distributed in the study area (Figure 1) but concentrated to near the shelf break, flank of banks, and the more level areas of certain banks, and it was also related to bottom types (Supplementary Table S1). VMS records from the different years were strongly correlated (r values between 0.78 and 0.87), indicating that the spatial distribution of fisheries is relatively stable from year to year in the period covered by this study. Most of the VMS records (57%) were from mixed bottom dominated by sand; least records are from hard substrates (10%) whereas mud substrates were second most common (33%).

TMs were the main sign of physical impact from trawling that was observable on video records. TMs vary in severity, due to the bottom
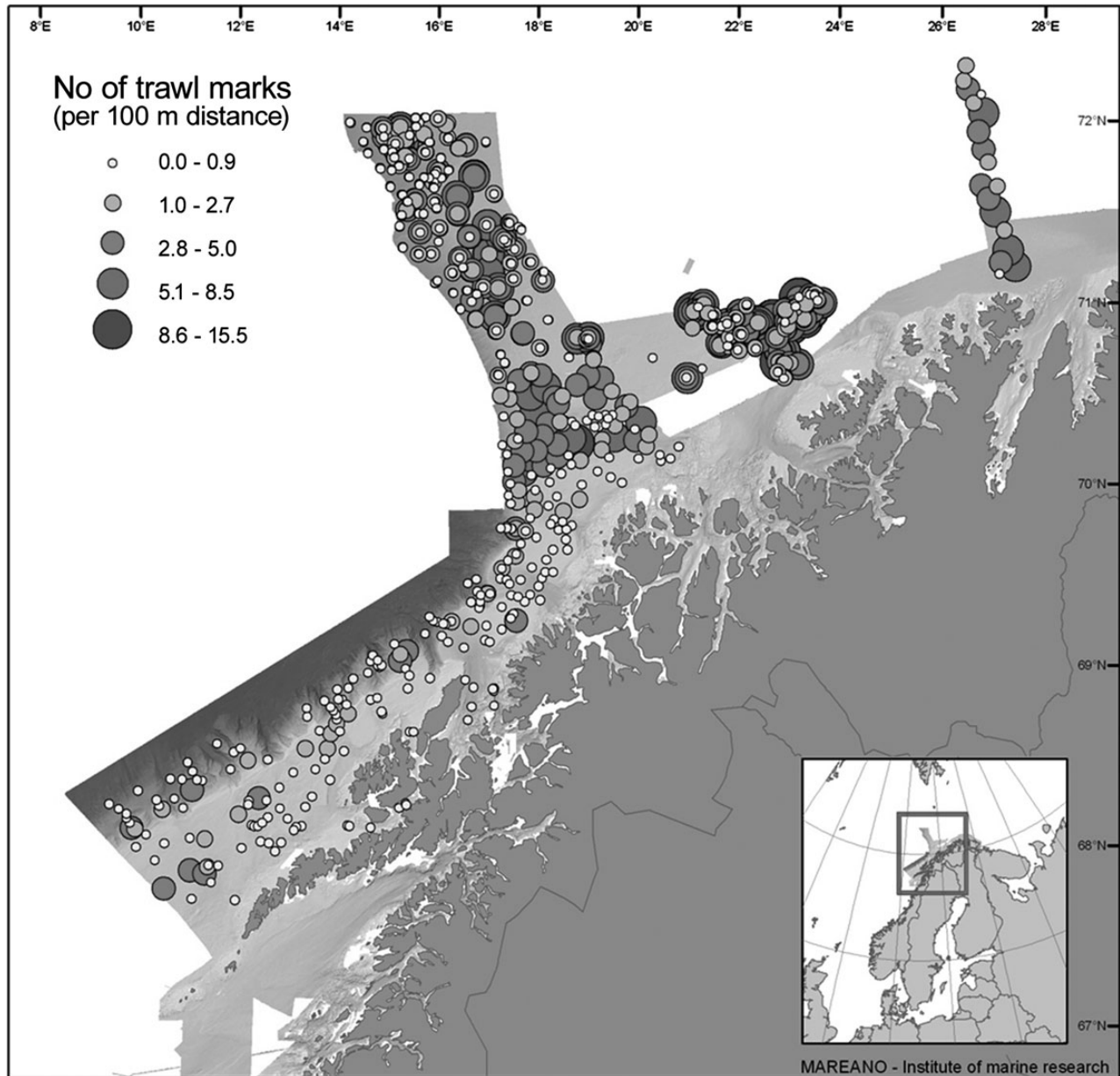
Figure 4. Density of TMs in the areas mapped by the MAREANO programme [from Buhl-Mortensen *et al.* (2013)].

type and the gear component from which they originate (Figure 3a−c). Figure 4 shows the abundance of TMs in the area mapped by MAREANO. In total, 266 TMs were observed. Depth distribution of observed TMs is shown in Supplementary Figure S2. An average of 1.06 marks per 100 m (2.18 when excluding zero values) and a maximum of 8.9 was observed. Thus, it was not uncommon to find TMs every 25 m and in some places every 10 m. The bi-modal depth distribution appears related to two main fisheries, a peak at 100−400 m reflects whitefish fisheries, and one deeper at 600−700 m reflects the fisheries on Greenland halibut. TMs were observed down to 873 m.

In some areas, TMs are combined with dislocation of large megabenthos species. The sponges *Geodia* and *Steletta* appear to have been displaced by trawls or shuffled together in trenches made by the trawl doors and are redistributed into well-defined lines (Figure 3d). To investigate if VMS data can indicate that the longevity of TMs based on the correlation between FI for different years before the observation of TMs and the number of TMs per 100 m was investigated (Supplementary Table S2). The correlation between TM and FI was in general low (Supplementary Table S1), with a maximum *r* value of 0.26 for TM observed in 2007 vs. FI for 2006. Twice as many TMs were observed on mud and on sand compared with on hard bottom, both for the mean TM for the three bottom types and for the total number of observations. This pattern was contrasting what was found for FI where the mean values for hard substrates were close to the mean for sand, and five times higher than mud (Table 1). The number of TMs per 100 m was not significantly correlated with FI (Supplementary Figure S2). TMs were included as an environmental variable in the DCA analyses, and results revealed stronger correlations between ordination axes and FI and TMs than the analyses of the whole dataset (Figure 5 and Table 2). The percentage of the variance explained by the three first ordination axes was between 20 and 22% for the analysis of hard, sand, and all substrates

pooled, whereas 30% of the variation was explained for the DCA of mud substrates (Table 2). Mean FI was most strongly correlated with the first DCA axis for the analysis of videos from hard bottom ($R = -0.50$), and the correlation was weakest for videos from sand ($R = -0.12$). Observed TMs were most strongly correlated with the first ordination axis for videos from sand ($R = -0.61$) and weakest for hard bottom ($R = -0.45$; Table 2).

FI and megabenthos

The variability in megabenthos density and diversity was large and results from the correlation analysis showed a positive and significant ($p < 0.01$) co-correlation, except for mud substrates (Table 3). Linear correlation (Table 3) and regression analysis (Figure 6) showed a negative and significant trend in density and diversity with increased FI with exception for mud substrates. The equations resulting from the linear regression analysis indicate that an increase in FI from 0 to 50 could decrease megafauna density from 44 to 12 individuals per 100 m^2 and diversity from 26 to 18 taxa per video.

Table 1. FI (year mean VMS records in a 5 × 5 km grid cell) and TMs observed per 100 m video (from the same grid cells) for all bottom types (250 video transects) and divided.

Bottom types	All	Hard	Sand	Mud
Fishing intensity				
FI mean	27.0	36.7	40.3	7.4
FI min	0.0	0.0	0.0	0.0
FI max	398.0	340.3	398.0	172.7
Trawl marks				
No video	250	61	95	94
TM mean	1.1	0.8	1.2	1.1
TM max	8.9	6.8	8.9	8.4
TM min	0.0	0.0	0.0	0.0

FI values provided as mean, minimum, and maximum values of yearly mean for the period 2003–2007 are listed (see Figure 1 for FI in the area). The number of video transects observed for TMs is listed.

Table 2. Correlation of environment matrix with ordination axes (Pearson and Kendall correlations) for DCA of video transects (see plots in Figures 5 and 7–9).

Axis	1	2	3	Sum
All substrates				
Eigen value	0.3407	0.2729	0.1344	3.4582
% variance explained	9.85	7.89	3.89	21.63
Depth	0.05	**0.46**	**−0.56**	
FI mean	−0.14	0.09	0.14	
FI min	−0.17	0.11	0.15	
FI max	−0.11	0.05	0.12	
Trawl marks	**−0.44**	0.26	−0.4	
Hard bottom				
Eigen value	0.30452	0.15876	0.1117	2.6152
% variance explained	11.64	6.07	4.27	21.99
Depth	**−0.54**	**0.3**	−0.09	
FI mean	−0.5	0.04	0.08	
FI min	−0.51	0.05	0.09	
FI max	−0.45	0.03	0.06	
Trawl marks	−0.45	0.06	−0.03	
Sand				
Eigen value	0.3572	0.2010	0.1423	3.4731
% variance explained	10.29	5.79	4.10	20.17
Depth	−0.13	**0.22**	**−0.26**	
FI mean	−0.12	0.14	0.16	
FI min	−0.16	0.18	0.15	
FI max	−0.08	0.08	0.16	
Trawl marks	**−0.61**	0.04	−0.11	
Mud				
Eigen value	0.4843	0.2307	0.1137	2.7436
% variance explained	17.65	8.41	4.14	30.20
Depth	0.08	**0.7**	−0.14	
FI mean	−0.26	0.09	−0.1	
FI min	−0.29	−0.06	−0.06	
FI max	−0.23	0.21	−0.19	
Trawl marks	**−0.51**	0.37	0.18	

Strongest correlations for the axis related to the different substrates are marked in bold.
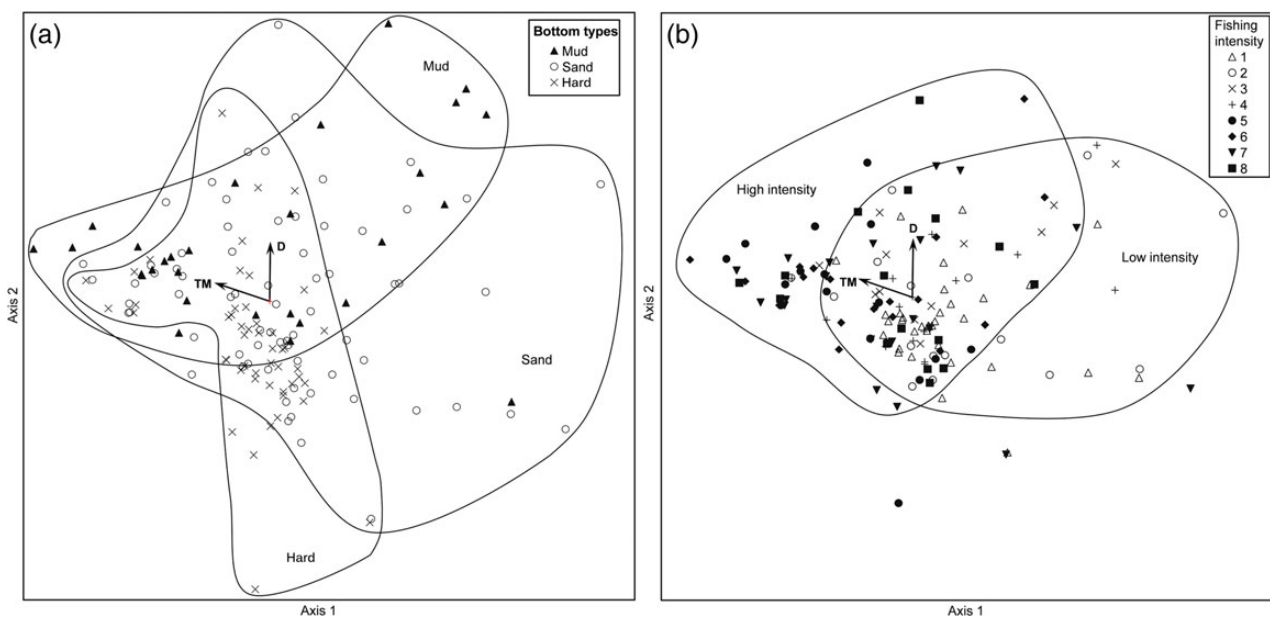

Figure 5. DCA plot of 149 video transects used in the megabenthos analysis, with bottom types indicated as different symbols (a) and FI classes see Figure 1 (b). The influence of the density of observed TMs and depth (D) is indicated with arrows.

Table 3. Pearson's correlation coefficients for the linear relation between FI, based on VMS records, and depth, mega fauna density, and diversity.

Substratum	FI	Depth	Density
All (d.f. 148)			
Density (no × 100 m^{-2})	−0.26**		
Diversity (no × taxa video^{-1})	−0.28**	−0.1	0.52**
Hard (d.f. 49)			
Density (no × 100 m^{-2})	−0.29*		
Diversity (no × taxa video^{-1})	−0.36**	0.1	0.66**
Sand (d.f. 69)			
Density (no × 100 m^{-2})	−0.29**		
Diversity (no × taxa video^{-1})	−0.30**	0.11	0.57**
Mud (d.f. 28)			
Density (no × 100 m^{-2})	0.12	−0.38*	
Diversity (no × taxa video^{-1})	−0.22	−0.61**	0.19

Pearson's correlation coefficients that are 0.1 or larger are listed and statistical significance is indicated by **$p < 0.01$, *$p < 0.05$.

Results from DCA with 149 video transects and 111 taxa had a total variance ("inertia") in species data of 10.07 (Figure 5). Depth was strongly correlated with the second and third axes (Table 2). The density of observed TMs was strongly correlated with first and third axes, whereas FI indices were weakly correlated with the DCA axes. The DCA plot of all 149 video transects did not demonstrate clear patterns with separate groups of video transects with respect to bottom types and FI. However, it was possible to identify groups based on combined categories of bottom types and FI (Figure 5). To study the effect of FI on different bottom types, DCA was performed separately for the three bottom types such as hard bottom, sand, and mud. For the analysis of transects from mud, 29 transects and 62 taxa had a variance ("inertia") in the species data of 4.7. Depth was strongly correlated with the second axis (Table 2 and Figure 7). The density of TMs was strongly correlated with the first axis, whereas FI was moderately correlated with the first and second DCA axes. The results from the analysis of observations on sand (70 transects and 98 taxa) had a variance ("inertia") in the species data of 7.53. Depth was weakly correlated with the axes. The density of observed TMs was strongly correlated with the first DCA axis, whereas the FI indices were poorly correlated with the first and second axes (Table 2). Results from the DCA analysis of observations from hard bottom (50 transects and 86 taxa) had a total "inertia" in the species data of 4.92. All variables (depth, TMs, and FI indices) were strongly correlated with the first axis.

The correlations between the FI indicator variables and ordination axes were stronger for the analyses of bottom types separately than the analysis of all video transects together. The strongest correlations of the FI variables were found for video transects from hard bottom (Table 2). The density of observed TMs was most strongly correlated with ordination axes for the analysis of soft bottom video transects from mud (Table 2).

The location of taxa in the ordination plots (Figures 7–9) indicates their association to areas with different FI. This indication was consistent for several of the species for two or more of the four different DCA analyses. The five taxa that were most typical for areas with low FI and low density of TMs were: *Flabellum macandrewi* (Scleractinia), Zooanthidae, *Ditrupa arietina* (Polychaeta), *Funiculina quadrangularis* (Pennatulacea), and *Spatangus purpureus* (Echinoidea). These species may be regarded as highly sensitive to bottom trawling. The five taxa that were most typical for areas with high FI were: *Actinostola callosa* (Actiniaria), and the sponges

Hyalonema sp., *Porifera* sp. B., *Steletta* sp., and *Stylocordyla borealis*. For hard substrates, the DCA plot (Figure 8) indicates that encrusting organisms (Bryozoa and Porifera) are not associated with locations with high FI.

Linear correlation analysis showed that density decreased within-creasing FI for 80% of the 97 most common taxa (Table 4). Out of 25 sponge taxa (many of these were morphospecies), 21 showed a negative correlation with FI. The fan-shaped Axinellidae (*Phakellia/Axinella*), the round *Craniella* (photo of the species is provided in Supplementary Figure S4), and encrusting sponges showed the strongest negative correlation ($p < 0.01$). No clear trend was found for the large sponges *Geodia* and *Steletta*. Four small sponge taxa showed a positive pattern in relation to FI, and of these, an unidentified species and *S. borealis* showed the strongest positive trend (Table 4). All crustacean taxa were mobile and showed a negative relation to FI, a trend that was most prominent for the hermit crabs (Paguridae). Among Cnidaria, 11 taxa showed a negative relation to FI, and these were mainly anemones, sea pens, and the cup coral *F. macandrewi*. Five taxa with a positive response included broccoli corals (Nephtheidae), *Bolocera*, and *Actinostola*. Tunicata showed a mixed and week response, and among Polychaeta, four taxa showed a negative relation to FI (e.g. Serpulidae and *Ditrupa*).

Six Echinoderm taxa showed a negative trend [i.e. Ophiuroidea, Antedonacea (feather stars), and Echinoidea including *S. purpureus*]. Of the four taxa with a positive trend, three were Asteroidea (i.e. *Ceramaster granularis*, Poranidae, and a small white unidentified Asteroidea). The common red sea cucumber *Parastichopus* showed a clear trend (positive and significant) only on hard bottom. Among the molluscs, Bivalvia showed a negative relation to FI and gastropods a positive. Brachiopoda showed a positive relation, whereas the echiuroid *Bonellia* and bryozoans were negatively related to FI.

Discussion
Estimating FI

Quantifying the impacts of bottom trawling under realistic conditions has remained challenging, and the spatial and temporal scale of disturbance generated by the entire fishing fleet in a given area is unfeasible in an experimental context (Hinz *et al.*, 2009). In addition to designed experiments, comparison among areas with different fishing history at one point in time and comparisons of single areas over time are the main approaches for studies of the impacts of bottom trawling on benthic communities; each approach has its own strengths and weaknesses (e.g. Kenchington *et al.*, 2007). The introduction of satellite tracking data for vessels (VMS) has provided a unique opportunity to examine the response of benthic organisms to a gradient of fishing activity at appropriate spatial scales under realistic conditions (Hinz *et al.*, 2009). However, it still relies on the interpretation of what fishing vessel activities represent trawling, a mismatch in scale and position of the impacted area by a trawl, and the information gathered on fauna response.

In this study, we have examined the relationship between fishing activity with otter trawl using VMS records (FI) and observed density of TMs on the shelf and slope (50–2000 m) and the chronic effects on megabenthos composition on the shelf (50–400 m) off Northern Norway in the southern part of the Barents Sea using video observations. The main goal has been to quantify impact of bottom trawling in these areas. In the study area, FI was not evenly distributed over different habitats and thus, there is a risk that environmental differences could be masking effects from
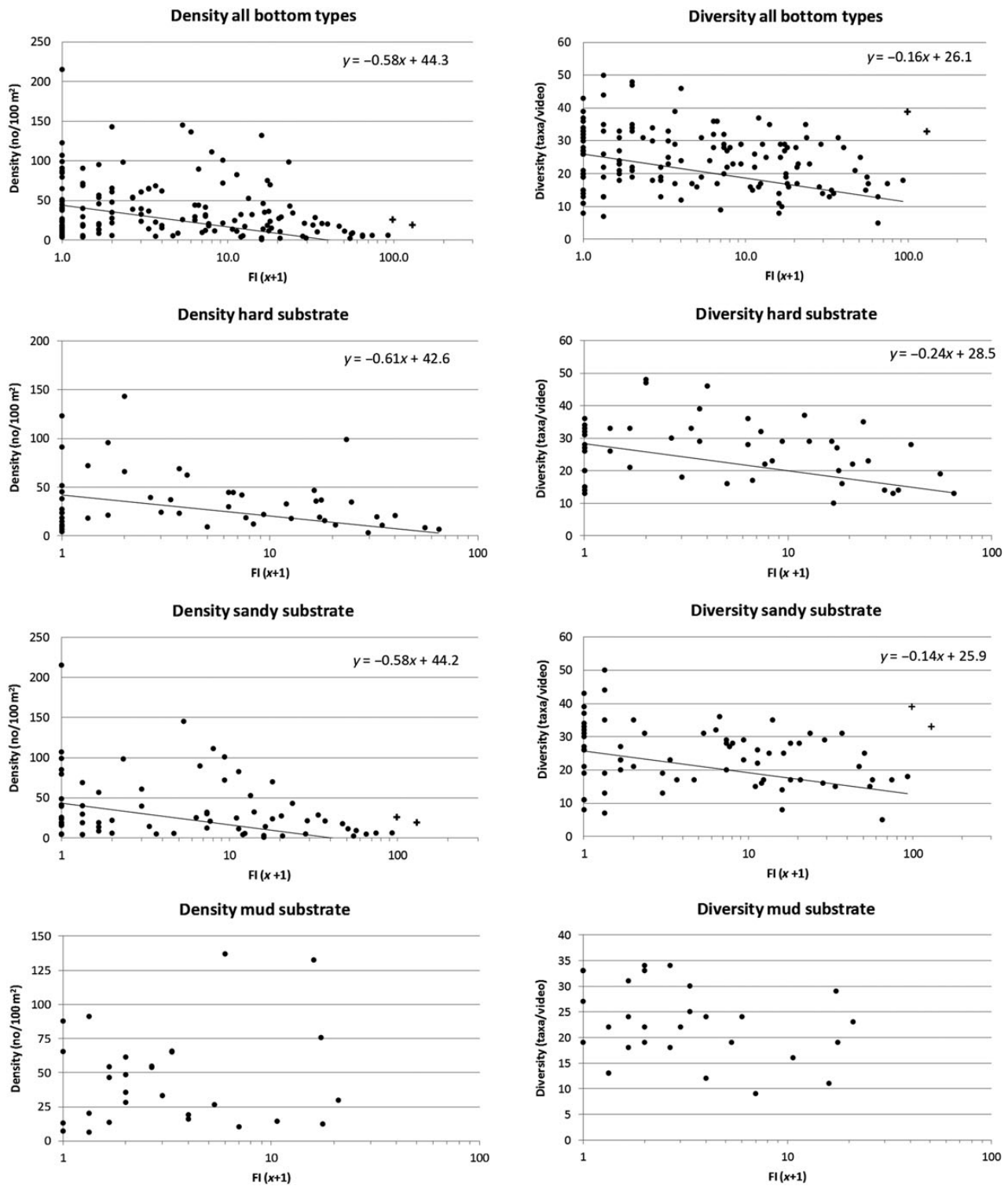
Figure 6. Megabenthos density (left) and diversity (right) on different substrates plotted against FI two points are not visible due to close values. Linear equation is provided where the correlation is significant ($p < 0.05$; for details see Table 3). $+$: two excluded data point (see text for further explanation).

fisheries. However, FI was not co-correlated with depth and sediment composition, although a wide range in depth and substrates were included in the dataset. We compared the two FI estimates used in this study: one based on 5×5 km^2 grid cells (used in the TMs

analysis) and the other on records from a circle ($R = 2$ km) with a video transect at its centre. The estimates showed a strong linear correlation ($r = 0.95$ and $p < 0.001$) and fauna FI relation was only slightly different for the two FI estimates. Both the area affected by
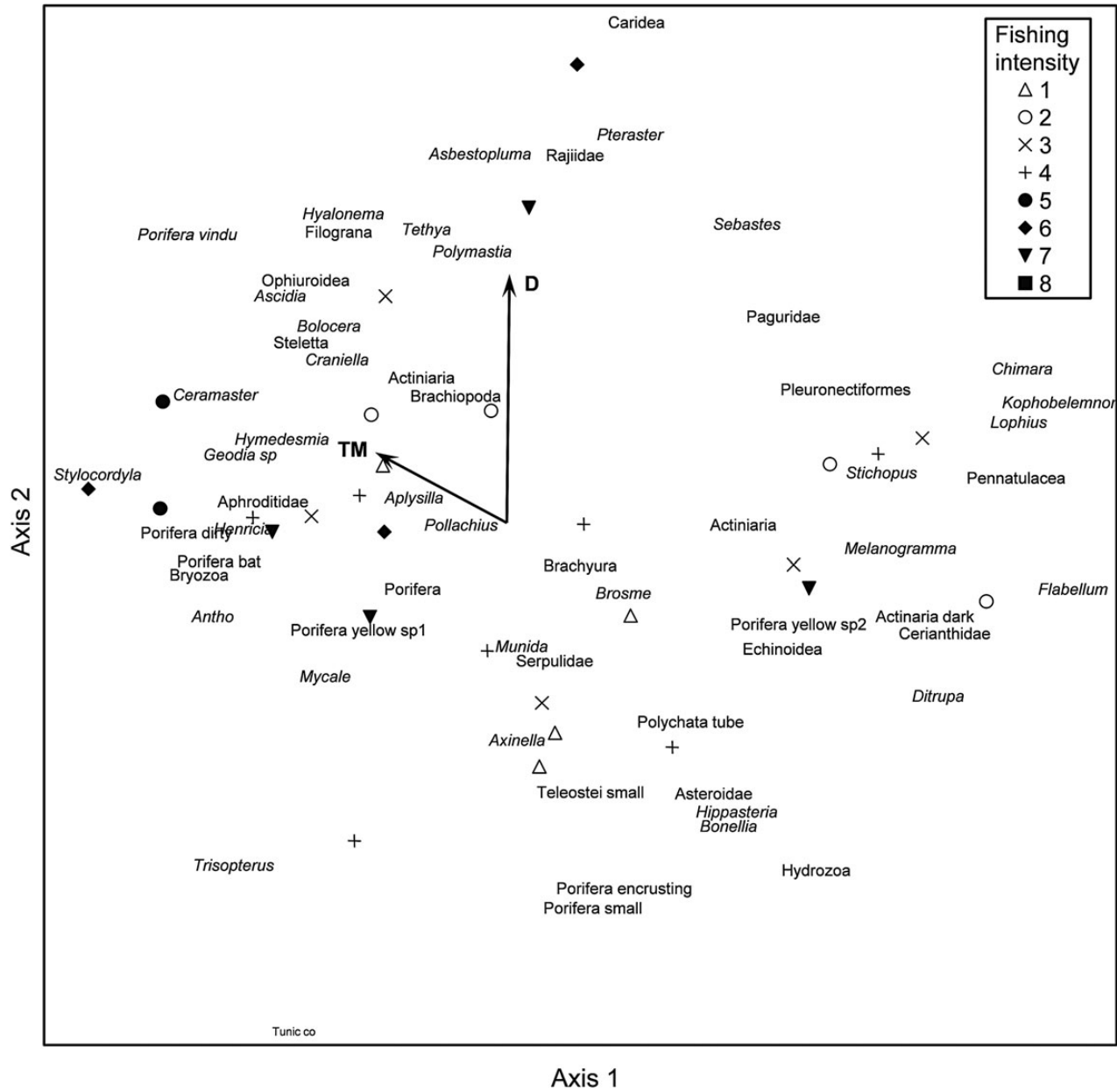
Figure 7. DCA plot of video transects analysed for megabenthos composition, from soft bottoms (mud and sandy mud) with fishery intensity indicated as different symbols. The influence of the density of observed TMs and depth (D) is indicated with arrows.

a trawl haul (5.92 km²) and the uncertainty of where the seabed has been trawled are large in contrast to the 700-m long video transect used to record megabenthos and TMs. This difference in scale, the large gradient in FI (0 to >90 recorded vessels per year) at the study sites, and the uncertainty of trawl position can probably explain the small difference between the approaches.

FI and seabed environment

Physical disturbance from trawling occurs chronically over large spatial scales and therefore can be expected to lead to more severe effects and much slower recovery rates than assumed from experimental studies (Hinz *et al.,* 2009). In this study, we used VMS records from the last 3 years preceding our fauna observations as a proxy for FI. Many of the megabenthos taxa recorded on video are

long-lived and effects from fisheries will probably persist for long periods (i.e. >10 years) as indicated by previous studies on megabenthos (Pitcher *et al.,* 2000, 2016; Clark 2009; Clark *et al.,* 2016). Thus, relevant FI estimates should preferably include VMS records 5–10 years back in time; unfortunately, reliable records from the study area are not available before 2003. To relate the fauna observation from 2006 to 2008 to the same time in fisheries history, FI estimate was based on VMS records from 2003 to 2005 to cover the 3 years immediately preceding the fauna observations. Using a longer time frame would most likely have increased our ability to find relationships between FI and organisms with long lifespans. Our observations of physical impact on the seabed have revealed the presence of large tracks that, in areas with high FI, can occur every 10 m. Our observations of 30–40 cm deep cuts
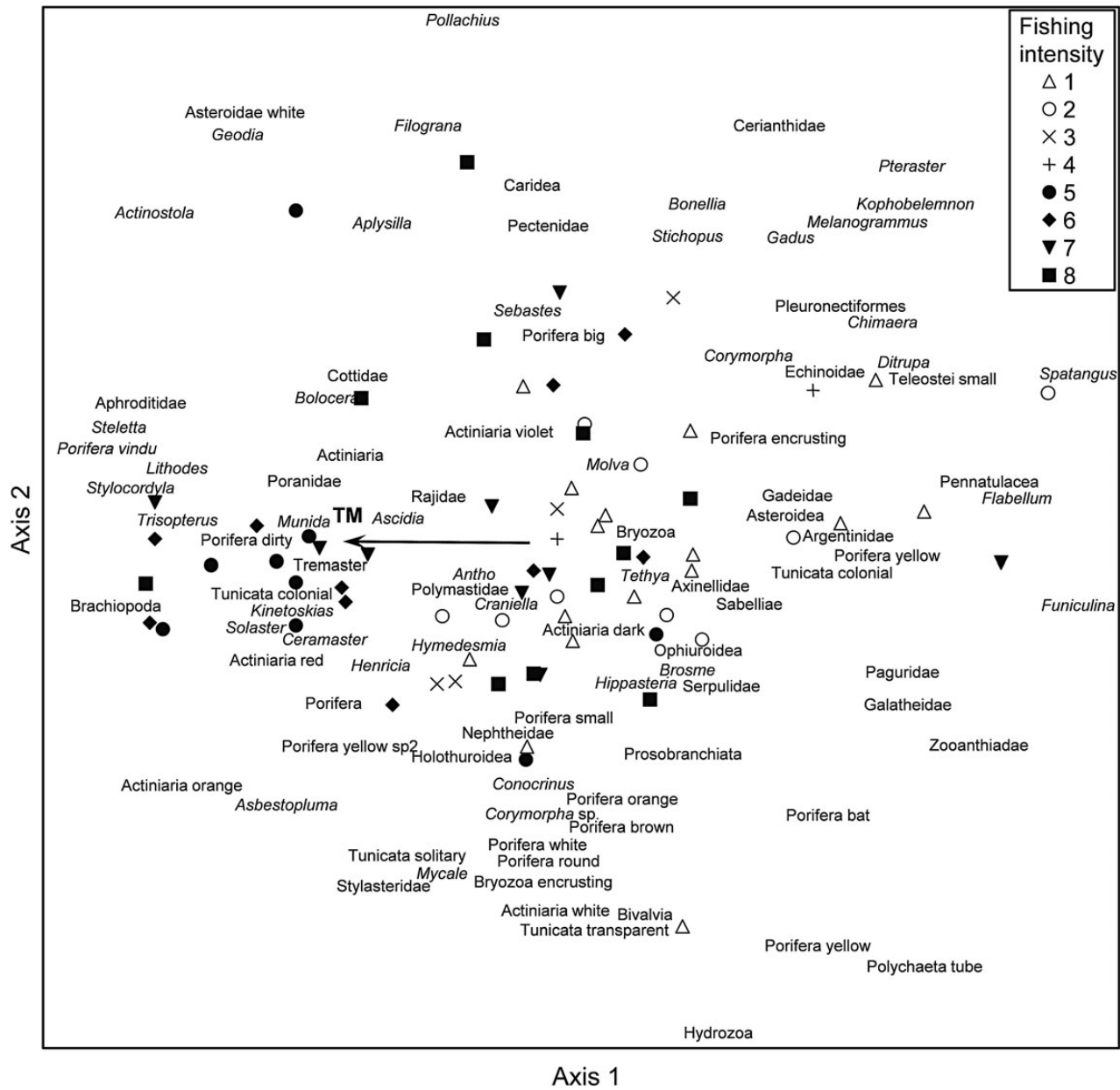
Figure 8. DCA plot of video transects analysed for megabenthos composition, from sand bottoms with FI indicated as different symbols. The influence of the density of observed TMs is indicated with an arrow.

from trawl doors in compact morainic clay indicated that tracks may prevail for long time in this kind of substratum. Depending on depth and sediment type, these tracks can probably last for several years, which are supported by observations of organisms that seem to adjust to the presence of such tracks (Johansen, 2012). This is the most likely explanation for the lack of a clear relationship between FI and the density of TMs, and that TMs in an area were mainly related to sediment type. Sediment composition is probably decisive for the rate of their accumulation at different FI levels; in addition, their persistence will depend on erosion and sediment deposition.

FI and megabenthos

The lack of clear patterns for observation on mud is likely due to a combination of factors; the number of observations from mud was relatively few ($N = 29$), larger epifauna were in general scarce,

and infauna are the main benthos component on mud bottoms and these organisms, living in the sediment, are not well documented by video surveys.

The community analysis (DCA) showed that the general pattern of specific communities was related to the different bottom types (Figures 7–9). Fisheries will probably not change the type of community that populate a specific habitat but the relative composition; thus, the pattern of benthos related to depth and bottom type will most likely shine through in any study dealing with a variety of bottom types and depths. However, the change in dominance of taxa related to FI will favour resilient or robust taxa and vulnerable parts of the fauna will decrease or disappear. The associations of taxa to areas exposed to high or low FI could be explained in two ways: (i) the effect of physical disturbance of fishing together with the tolerance of the taxa controls the taxa distribution and (ii) the distribution of
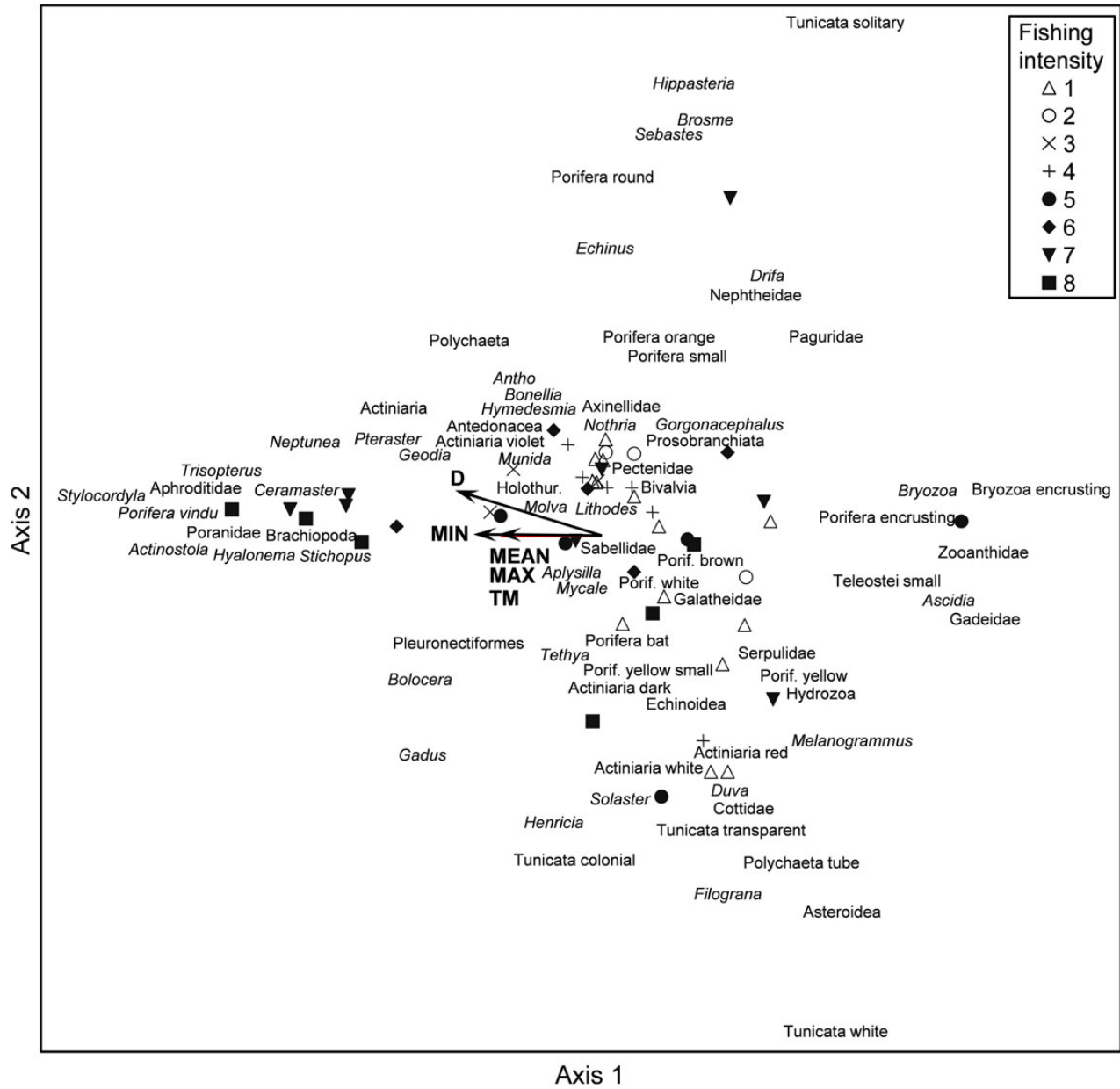
Figure 9. DCA plot of video transects analysed for megabenthos composition, from hard bottoms with FI indicated as different symbols. The influence of the density of observed TMs, depth (D), as well as min, mean, and max FI is indicated with arrows.

taxa is correlated with environmental variables that direct the distribution of fisheries (i.e. fish distribution). We tried to eliminate the effect of the latter by analysing the different bottom types separately. Except for the DCA of video transects from hard substrates, the FI indices were poorly correlated with the ordination axes (Table 3). TM density, however, was strongly correlated with the first ordination axis for all datasets (Table 3). This indicates that there is a clear effect on the fauna composition related to density of trawlmarks, and that the VMS records may be too broad scaled to reflect local effects of physical disturbance from individual trawl hauls.

Out of the 97 most common taxa, 79 showed a negative trend in density with increased FI. Of the nine taxa showing a statistically significant ($p < 0.05$) negative response, five were sponges. That most sponge taxa show a negative trend in density related to

increased FI is not unexpected and it is generally accepted that large sessile fauna will take years to decades to recover from bottom trawling (Pitcher *et al.*, 2016). Indirect evidence (Sainsbury *et al.*, 1997; Pitcher *et al.*, 2000) suggests that large sponges probably take more than 15 years to recover. Repeated trawl experiments has shown that the removal rate for epibenthic species can vary between 5 and 20% of the biomass (Pitcher *et al.*, 2000; Burridge *et al.*, 2003). The removal rates for sea whips (gorgonians), sea fans (gorgonians), and large sponges (porifera) are 5, 10 and 20%, respectively. An experiment with repeated trawling showed that each trawl removed roughly 5–20% of the biomass of sessile epifauna and 13 trawls removed 70–90% of the estimated initial biomass (Pitcher *et al.*, 2000, 2016; Burridge *et al.*, 2003). The fan-shaped Axinellidae sponges (*Phakellia/Axinella*) and the

Table 4. Pearson's correlation coefficients for the linear relation between density of megabenthos taxa (No 100^{-2}) and fishing intensity (mean VMS registrations per year, see text for explanation) on different substratum.

FI	Substratum / Megafauna taxa	All d.f. 148	Hard d.f. 49	Sand d.f. 69	Mud d.f. 28	FI	Substratum / Megafauna taxa	All d.f. 148	Hard d.f. 49	Sand d.f. 69	Mud d.f. 28
	Porirera					−	*Kophobelemnon stelliferum*			−0.13	−0.18
−	Axinellidae	−0.21**	−0.30*	−0.21**	−0.25	−	Hydrozoa	−0.1		−0.11	−0.21
−	Porifera small	−0.18*	−0.28*	−0.16*		−	*Paragorgia arborea*			−0.1	
−	Porifera encrusting	−0.17*	−0.35**	−0.15		−	*Flabellum macandrewi*			−0.11	−0.14
−	*Craniella zetlandica*	−0.16*	−0.16	−0.22**	−0.18	+	*Tubularia* sp.	0.13		0.14	
−	Porifera yellow	−0.15*	−0.22	−0.23**		+	Nephtheidae		−0.13	0.21*	
−	Porifera white	−0.14*	−0.25*	−0.12		+	*Bolocera tuediea*		0.29*		
−	*Hymedesmia* spp.	−0.13	−0.1	−0.20**	−0.13	+	Actiniaria sp. 2		0.39**		
−	*Tethya cranium*	−0.12	−0.14	−0.15	−0.13	+	*Actinostola callosa*		0.46**		−0.15
−	*Antho dicotoma*	−0.13	−0.15	−0.17*	0.13		Tunicata				
−	*Aplysilla sulfurea*	−0.12		−0.14		−	Tunicata white		−0.12		
−	Porifera orange	−0.11	−0.14	−0.12		−	Tunicata		−0.1		
−	Porifera brown		−0.17			+	Tunicata solitary		0.12		
−	*Mycale lingua*			−0.13	−0.23	+	*Ascidia* sp.				0.12
−	*Polymastia* sp.				−0.14		Polychaeta				
−	Porifera white small				−0.15	−	Polychaeta tube	−0.14*	−0.16	−0.14	−0.21
−	Porifera bat	−0.1	−0.12	−0.11		−	Serpulidae	−0.11	−0.24*		0.15
−	Porifera dirtyyellow		−0.11		−0.11	−	*Nothria* spp.		−0.11		
−	Porifera yellow white			−0.13		−	*Ditrupa arietina*	−0.1		−0.14	
−	Porifera round	−0.1		−0.14			*Filograna implexa*	0.1	−0.15	0.19	−0.22
−	*Geodia* spp.		−0.1				Echinodermata				
−	*Steletta*				−0.11	−	Ophiuroidea	−0.11	−0.1	−0.15	
+	Porifera indet.		−0.16	−0.12	0.27		*Parastichopus tremulus*	−0.11	0.31*	−0.12	−0.14
+	Porifera yellow small			−0.1	0.35*	−	Antedonacea	−0.11			
+	Porifera sp. B		0.19			−	Echinoidea	−0.1		−0.14	−0.11
+	*Stylocordyla borealis*		0.24*		0.41*	−	*Echinus* spp.		−0.1		
	Crustacea					−	*Spatangus purpureus*			−0.12	
−	Caridea		−0.17			−	Asteroidea		−0.14	−0.13	−0.15
−	Paguridae	−0.13	−0.20	−0.13	−0.28	+	*Henricia* sp.				0.16
−	Galatheidae		−0.12			+	*Ceramaster granularis*			0.26	0.45**
−	*Munida sarsi*				−0.17	+	Poranidae	0.20*	0.47**		
	Cnidaria					+	Asteroidea White	0.24**			
−	Actiniaria sp. 1		−0.14				Mollusca				
−	Actiniaria red		−0.14			−	Bivalvia	−0.12			
−	Actiniaria dark		−0.12			+	Gastropoda	0.11			
−	Actiniaria violet		−0.11			+	Brachiopoda		0.17		−0.1
−	Zooanthidae			−0.13			Echiuroidea				
−	Cerianthidae	−0.11			−0.19	−	*Bonellia viridis*			−0.11	
−	Pennatulacea	−0.1		−0.14	−0.14	−	Bryozoa	−0.1	−0.17		

Only correlations that are 0.1 or larger are listed. Statistical significance is indicated by **$p < 0.01$, *$p < 0.05$.
FI, the general relation to fishing intensity is indicated; −, negative; +, positive.

round *Craniella* were among the sponges with the strongest negative response. Axinellidae are vulnerable to dislodging because of their relatively large fans and a small attachment hold-fast. No strong negative relationship was found between FI and density of the large sponges *Geodia*, *Stryphnus*, and *Steletta*. Our study of TMs showed that large sponges often pile up in mounds or in trenches created by trawl doors in areas of high FI (Figure 3d). Clearly, this physical stress of displacement together with resuspension of sediments is negative for the exposed sponges. The explanation for the lack of trend related to FI could be that these sponges have been discarded from trawlers in the same area where they were caught and thus pile up with locally high abundances. This assumes that they can survive the physical stress this handling represents. Ophiuroids, Antedonacea (feather stars), and Echinoidea, including *S. purpureus*, showed a negative relation to FI. The brittle arms and exposed position on the seabed of feather stars probably make them particularly vulnerable to the physical impact by trawling. In

a study by Olsgard *et al.* (2008), a decline in bioturbators, including Ophiuroids and Echinoidea, was documented. Our study showed that a positive trend related to FI was indicated for asteroids, of which most are known to be scavengers and could be aggregated do to the generation of dead/dying organisms by trawling. Also, a group of small sponges, including *S. borealis*, showed a positive relation to FI. The stalked *S. borealis* might sustain trawling by bending down and/or the ability to regenerate the upper body parts.

Management implications

Norway's waters in the Barents Sea and off Lofoten have considerable areas classified as particularly valuable and vulnerable (Anon, 2006), and it is of international interest that these areas are managed in a sustainable way. It is therefore important to increase our knowledge of the cumulative disturbance and resilience of the Barents Sea ecosystems [see also Thrush *et al.* (2016)]. Fishing impacts to the seabed represent a key impediment to the implementation of government

policy for the Barents Sea and areas off Lofoten (Anon, 2010; White Paper, 2006). Maintaining the value of fish stocks while ensuring their ecologically sustainable management requires the enforcement of a more ecosystem-based approach to marine resource management; to date, there is no simple readily applicable solution. The Norwegian Government has set ambitious goals to ensure that activities in the valuable and vulnerable areas identified in the Barents Sea management plan are conducted in a way that does not threaten ecological functions or biodiversity (White Paper, 2006). In this context, the changes in megabenthos related to trawling that are documented in this study from these areas are highly relevant and important.

In accordance with the procedure for evaluation of spatially managed areas suggested by Steltzenmüller *et al.* (2013), the information required for marine spatial planning must correspond to management goals and operational objectives. Requirements of the European Marine Strategy Framework Directive (MSFD; EC, 2008) encompass the distribution and composition of bottom fauna on all scales as well as human pressures and related impacts. The goal for biodiversity management (MSFD, descriptor 1) is that "biological diversity is maintained". The quality and occurrence of habitats and the distribution and density of species are in line with prevailing physiographic, geographic, and climatic conditions. Good environmental status (GES) is achieved if there is no further loss of the diversity of genes, species, and habitats/communities at ecologically relevant scales and when deteriorated components are restored to "target levels". Our results indicate that trawling is decreasing abundance and diversity of megabenthos in the study area, and that some sponge taxa are particularly sensitive to this pressure. Another management goal in the MSFD that is highly relevant to fisheries management relates to "seafloor integrity", stating that it should be "at a level that ensures that the structure and functions of the ecosystems are safeguarded and benthic ecosystems, in particular, are not adversely affected". According to the MSFD, this means that diversity and productivity are maintained and that human activities do not cause serious adverse impacts to the natural ecosystem structure and functioning in both space and time, and recovery should be rapid and secure if a use ceases (EC, 2008). We have shown that deep TMs frequently occur in the study area and that some large sponges seem to be displaced by trawling. The effects on functionality of the ecosystem by the changes in abundance of the larger organisms belonging to the benthic community are hard to estimate, but many of these are bioturbators and filter-feeders and thus important both for remineraliztion and the benthic pelagic coupling.

According to Hinz *et al.* (2009), "studies that quantify the effects of trawl disturbance are critical if we are to inform fisheries managers and policy makers as to the potential outcome of different fishing effort management scenarios". Here, we have shown a decrease in density for most megabenthos taxa with increased trawling intensity. The Norwegian "Law for the Management of Marine Living Resources" (Norwegian Government, 2008) states that management of marine resources should follow the precautionary and the ecosystem approach. The precautionary approach calls for avoidance of potentially irreversible changes and identification of undesirable outcomes (Frid *et al.*, 2000). The ecosystem approach calls for management on large spatial scales, with a breadth in terms of structure, functions, and services (e.g. Bianchi and Skjoldal 2008; De Young *et al.*, 2008). Impact on biodiversity relates to both approaches, since biodiversity loss can be irreversible, higher diversity can mean higher productivity and stability (e.g. Tilman *et al.*, 1996; McCann 2000), and diversity results from the interaction between local

processes such as competition and predation and immigration from regional species pools (e.g. Gaston, 2003). Cooperation biodiversity and ecosystem function (BEF) is linked to ecosystem services (ES). The diversity, particularly connected to functions, is directly connected to resilience of ecosystem function (e.g. habitat provision, productivity, and carbon flux) that, in turn, will secure ES provided to man (e.g. food security and human wellbeing). Although the relationship between BEF and ES has been documented for terrestrial ecosystems for marine ecosystems, present knowledge of this relationship is poor for open oceans and the deep sea environment (Naeem, 2012). A loss in biodiversity and changes in benthic community structure will most likely have negative feedback effects on marine services and goods such as sustaining commercially important fish populations (e.g. Loreau *et al.*, 2001; Worm *et al.*, 2006). This is particularly the case for habitat-forming organisms in the deep water and low temperature area studied here (Buhl-Mortensen *et al.*, 2010). The MAREANO mapping down to 2000 m has registered TMs down to 873 m and damage to fauna including vulnerable habitats of epi- and infauna (Buhl-Mortensen *et al.*, 2013), but in the area covered by this study corals were not an important part of the megabenthos.

In this study, we hope to have contributed to a better understanding of the effects of bottom trawling on the benthic community in the Barents Sea, and that this can support a sustainable and ecosystem-based management of these ecosystems. The observed general decrease in density and diversity and responses of specific taxa will provide important information for knowledge-based indicator development for GES related to descriptors 1 and 6 of the MSFD.

Conclusion

Dense occurrences of TMs were observed, but no direct relation with FI was documented. The number of TMs was highest on mud, although FI was larger in sandy mixed bottoms. This indicates that the longevity of TMs on the seabed depends on the softness of the sediment.

A clear and negative relationship between FI and density and diversity of megabenthos was found in the study area that, in general, was significant but not on mud substrates. Most megabenthos taxa decreased in density with increased FI exceptions were a few scavenging taxa.

In the study area, sponges are a vulnerable group, and *Craniella zetlandica* and *Phakellia/Axinella* appear particularly sensitive. However, a few small sponges, e.g. *S. borealis*, appear resilient.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

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