



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

# Vulnerability of megabenthic species to trawling in the Barents Sea

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The development of ecosystem-based fisheries management over the last two decades has increased attention on the protection of vulnerable resources that are of little or no economic significance including bycatch of benthos in bottom trawling. Current knowledge on the response of benthic communities to the impact of trawling is still rudimentary. In the present study, we used data collected in the Barents Sea during 2011 to assess the vulnerability of benthic species to trawling, based on the risk of being caught or damaged by a bottom trawl. Using trait table analysis, we identified 23 “high-risk” benthic species, which include “large weight and upraised” taxa as “easily caught” by a bottom trawl. We further identified a “low-risk” category containing 245 taxa/species and a “medium-risk” category with 80 species. A clear decline in biomass was noted for all three categories when comparing trawled vs. untrawled areas. This suggests that trawling significantly affects the biomass of all species, but predominantly the “high-risk” taxa. Some Barents Sea regions were particularly susceptible to trawling due to the dominance of the “high-risk” species, including *Geodia* sponges in the southwestern Barents Sea, basket stars (*Gorgonocephalus*) in the northern Barents Sea, sea pen (*Umbellula encrinus*) on the shelf facing the Arctic Ocean, and sea cucumber (*Cucumaria frondosa*) in shallow southern areas. These findings can guide management decisions to meet targets set by the United Nations Convention of Biological Diversity and the OSPAR Commission (“Protecting and Conserving the North-East Atlantic and its Resources”). We specifically recommend management action in the southwestern and the northwestern Barents Sea and on the Arctic shelf facing the Arctic Ocean.

**Keywords:** Arctic benthos, fish trawl, management action, shrimp trawl, trawling impact, vulnerable species.

## Introduction

Fisheries research and management have traditionally focused on economically important fish stocks, while resources of minor economic significance have received less attention. Fisheries policy objectives have gradually shifted towards a stronger emphasis on both ecological and economic sustainability, and a complex set of regulatory measures have been developed and put into force (Anonymous, 2002a, 2011; Hoel *et al.*, 2013). Following the World Summit on Sustainable Development (Anonymous, 2002b), ecosystem-based fisheries management has received increased attention over the last two decades (Browman and Stergiou, 2004; Levin *et al.*, 2009), including the protection of vulnerable resources that have a little or no direct economic value (Gullestad *et al.*, 2014). This has been accompanied by increased efforts towards integrated assessments of marine ecosystems that explicitly consider species that are not commercially exploited,

environmental conditions, and human pressures (Link and Browman, 2014).

One of the most widespread, yet manageable, pressures imposed on the seabed is the disturbance of substrate by towed demersal fishing gear (Collie *et al.*, 2000; Kaiser *et al.*, 2002; Eastwood *et al.*, 2007). However, our knowledge of how bottom trawls affect the seabed is still rudimentary, and few general conclusions have been drawn regarding the response of benthic communities to the impact of trawling (Kutti *et al.*, 2005; Løkkeborg, 2005). The effects of trawling on structurally complex habitats and fauna have been compared with the effects of forest clear-cutting (Watling and Norse, 1999). Generally, bottom trawling can have a wide range of effects on the structure of marine ecosystems depending on gear, intensity, spatial area, and the nature of the seabed habitats (Hall, 1999; Kaiser and de Groot, 2000; Tillin *et al.*, 2006). Bottom trawling can remove benthic species that characterize particular

benthic habitat, are used as refuge from predation, or function as food for a wide variety of fish and invertebrates (Malecha *et al.*, 2005; Tissot *et al.*, 2006; Puig *et al.*, 2012). Species removal can result in a significant reduction in the abundance of large invertebrates because of their slow recovery time and high catchability (Jennings *et al.*, 2001a, b), which can then shift the size spectrum to favour an abundance of small invertebrates (Duplisea *et al.*, 2002). Understanding the impact of fishing on the seabed and the associated fauna is a central element in the development of sustainable ecosystem-based marine resource management. It is, therefore, necessary to monitor the status and trends of benthic biota, but it is also critical to take a larger view and understand the structure and dynamics of benthic habitats, how they contribute to the functioning of marine ecosystems, how fishing can alter them, and ultimately how to manage human activity while minimizing the risks of serious or irreversible harm to the ecosystem. Although there is no absolute measure of seabed vulnerability, it can be best defined as the degree of change integrated over time: that is, the time after trawling ceases, and times of active trawling.

Determining the vulnerability of individual species to a given pressure can be achieved by *trait analysis*, which focuses on form and function of the biota (Bolam and Eggleton, 2014; Bolam *et al.*, 2014). If a conceptual link can be made between a given trait and robustness or vulnerability to a given pressure, trait analysis can also be employed in a vulnerability assessment (Certain *et al.*, 2015). The selection of traits to be used will depend on the specific question to be addressed (Petchey and Gaston, 2006) and the availability of biological trait information for the region and communities of interest (see, e.g. <http://www.marlin.ac.uk/biotic/>). Trait information such as “lifespan”, “larval development strategy”, or “fecundity”, although crucial to evaluating sensitivity to pressure and recovery potential can be difficult to obtain for lesser-known species (Tyler *et al.*, 2012), while morphological traits like “body size”, “shape”, and “sediment position” are readily available. Morphological traits can be used to assess vulnerability to trawling, based on the assumption that large-bodied individuals with limited mobility and a fragile body tend to be most affected by trawling (Bergman and Hup, 1992; Thrush *et al.*, 1995; Auster *et al.*, 1996; Blanchard *et al.*, 2004, de Juan *et al.*, 2007).

Recently, Certain *et al.* (2015) proposed a methodology for the quantitative evaluation of vulnerability of communities to various pressures and applied it to the benthic megafauna of the Barents Sea. The approach combines community data with trait analysis to map the vulnerability of the benthic community to trawling. In this study, we expand this work by providing a detailed assessment at the species level to (i) identify the benthic species that are most vulnerable to trawling in the Barents Sea, (ii) provide detailed information on their spatial distribution, and (iii) relate our assessment of regional information to known fishing pressure, as extracted from the Norwegian vessel monitoring system (VMS), to quantify the effect of trawling on the biomass of various benthic species groups.

## Material and methods

### Study area

The Barents Sea is a continental shelf sea located north of Norway and western Russia covering ca. 1.6 million km<sup>2</sup> with an average depth of 230 m (Figure 1; Jakobsson *et al.*, 2004). The region is characterized by intense commercial fishing (Shevelev *et al.*, 2011), a long history of assessment and management of the primary commercially important species (Kovalev and Bogstad, 2011), and the

recent development of integrated assessments and management plans (Anonymous, 2006). Bottom trawling for fish and northern shrimp (*Pandalus borealis*) impacts sediments and benthic fauna over a wide area of the Barents Sea because trawl doors, sweeps, and groundgear all come in contact with the seabed. This effect increases with the use of multirig trawling, which involves two or three trawls tied together, so that they can be dragged side by side. There has been a steady increase in the use of double and triple trawls in the shrimp fishery in the Barents Sea. Whereas in 2000 when ca. 80% of the shrimp fishing effort was with single trawls, this gear type was used <10% of the time in 2010, while the use of triple and double trawls rose to ~40 and 50%, respectively (Hvingel and Thangstad, 2010).

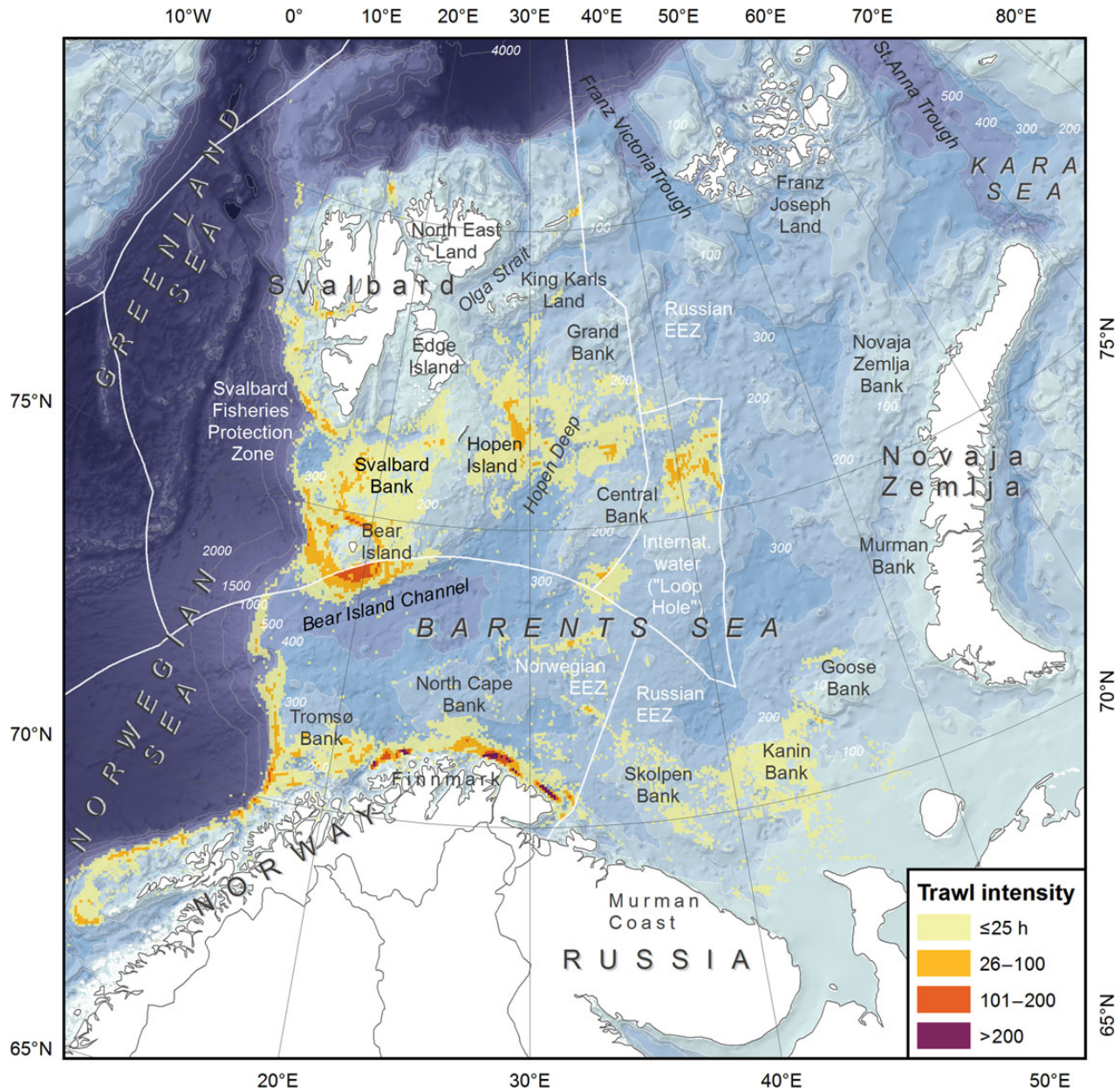
The Hopen Deep and Svalbard shelf have traditionally been considered the most important fishing grounds for shrimp in the Barents Sea (Hvingel and Thangstad, 2010). While trawling for demersal fish species like cod (*Gadus morhua*) occurs in the southern parts of the Barents Sea, both in the Norwegian and the Russian EEZs and in the Svalbard fishery protection zone north to Svalbard, the fisheries for fish and shrimp do not mix. Logbook data from 2009 and 2010 do, however, show decreased shrimp fishing activity on the traditional Hopen fishing grounds, which appears coupled with increased effort farther east in international waters in the so-called Loop Hole. Information from the industry points to high densities of shrimp in this area and to area closures in the Hopen Deep as the main reasons for this change in fishing pattern (Hvingel and Thangstad, 2010).

### Trawling intensity

Trawling intensity was estimated based on VMS data for the period 2007–2010. VMS or satellite tracking equipment is mandatory on-board for all Norwegian fishing vessels over 15 m (since 2009). For the Barents Sea, only small vessels operating close to the coast and in the fjords of northern Norway are exempt from this requirement. Vessels are required to transmit their position by satellite every hour. Transmissions include information on ship call sign, date, time, GPS position, heading, and speed in knots.

To this study, we only used data from vessels where the corresponding commercial logbooks by call sign reported bottom trawl use in the Norwegian and Russian economic zones in the Barents Sea or the Svalbard fisheries protection zone during the above period. Only Norwegian VMS data were used.

Norwegian VMS data do not indicate if the vessel is engaged in fishing at the time of transmission. Vessel speed was, therefore, used as a proxy for trawling, which is usually carried out at a speed of <5 knots, well below the speed for transit. Merging VMS data from two factory trawlers in the Norwegian Reference Fleet with detailed logbook information, Salthaug (2006) found that 70–80% of the VMS observations <5 knots represented trawling. Based on the speed variable in the VMS dataset, we filtered for positions where ship speeds of 2–5 knots (3.7–9.3 km h<sup>-1</sup>, respectively) indicated trawling. We constructed (by the use of Esri ArcGIS software) a 10 × 10 km grid covering the entire Barents Sea and determined the number of identified trawling positions within each grid cell. Assuming a constant towing speed for the 1-h time increment between transmissions, we calculated the total bottom trawl duration for each grid cell. We did not include data from scientific bottom trawls in the Barents Sea because the estimated (assuming an average towing speed of 3.5 knots and a mean door spread of 100 m in the period 2007–2010) total area covered by the scientific bottom trawl (936 km<sup>2</sup>) was considered negligible (6%) compared



**Figure 1.** Bottom trawl intensity in the Barents Sea (h per  $10 \times 10$  km grid cell in the period 2007–2010) estimated from Norwegian VMS data from vessels with reported bottom trawl catches, using an assumed towing speed of 2–5 knots. An estimate of the Russian bottom trawl intensity in the area was not available for inclusion in the analysis [But see Lyubin *et al.* (2011), page 772, Figure 14.6.3].

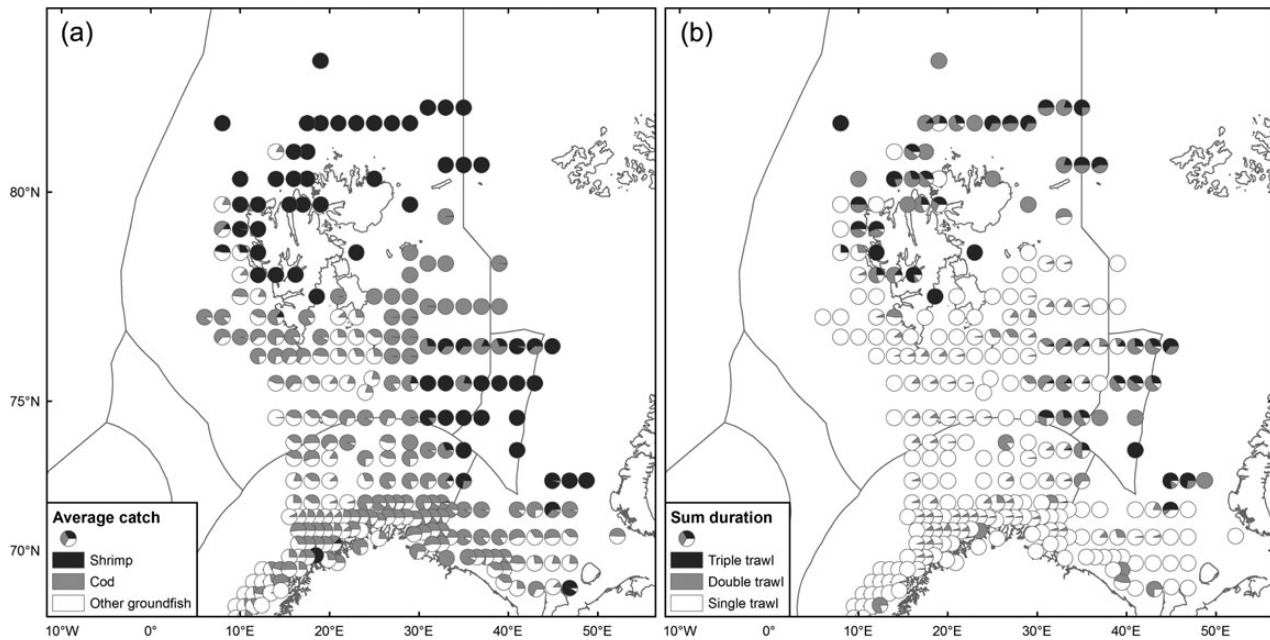
with commercial bottom trawling (16 236 km<sup>2</sup>). The resulting estimates for trawl duration were used as proxies for bottom trawl intensity (Figure 1).

VMS counts from Russian vessels were not available and are not included in Figure 1. Recently published figures (Lyubin *et al.*, 2011, page 772, Figures 14.6.3) show that Russian trawling activity concentrates on the same areas as the Norwegian fishery and, additionally, in a large area of the central and the southeastern parts of the Russian Barents Sea, as well as along the peninsula of Novaya Zemlja. The Russian EEZ was excluded from the analysis.

Data from logbooks show that fisheries for northern shrimp are segregated from fisheries for cod and other groundfish by both area and type of trawling gear (Figures 1 and 2a and b).

**Biological sampling**

Collection and taxonomic identification of benthic megafauna is routinely conducted during the joint annual Norwegian–Russian Ecosystem Surveys, which monitor the environment, pollution, and ecosystem components of the Barents Sea (Michalsen *et al.*, 2013 and [http://www.imr.no/tokt/okosystemtokt\\_i\\_barentshavet/nb-no](http://www.imr.no/tokt/okosystemtokt_i_barentshavet/nb-no)). Benthic samples are collected by bottom trawling (15-min tows at 3 knots, which is equivalent to a towing distance of 0.75 nautical miles or 1.4 km; Anisimova *et al.*, 2010; Jørgensen *et al.*, 2015). A total of 377 stations were sampled in August and September 2011 using four research vessels. The sampling design includes a fixed regular station grid (35 nautical miles or 65 km between each station) spanning ~1.5 million km<sup>2</sup>. The benthic megafauna were



**Figure 2.** Distribution of catches reported by statistical rectangle in commercial logbooks during 2007–2010 by (a) average catch of shrimp, cod, and other groundfish and by (b) sum of trawl duration for each of three bottom trawl gears, i.e. single, double, and triple trawls.

**Table 1.** The two trait and associated modalities used to score species ability for being captured by a bottom trawl.

Trait	Modalities	Why
Mean body weight (biomass/abundance)	1. 0.05–4 g	Maximum size of individuals. Smaller individual is more likely to pass through the nets of the trawling gear or escaping below the trawl gear.
	2. 4–50 g	
	3. 50–3000 g	
Height above sediment surface	1. 1–5 cm	Indicate the height above the sediment surface and possibility to be caught by a trawl. Height means either an upraised body standing at a substrate or a benthic species swimming above.
	2. 5–10 cm	
	3. > 10 cm	

sampled with a Campelen 1800 bottom trawl rigged with rock-hopper groundgear and towed on double warps (Engås and Godø, 1989). The mesh size was 80 mm (stretched) in the front and 16–22 mm in the codend, allowing the capture and retention of smaller fish and the largest benthos from the seabed. The horizontal opening was 11.7 m, and the vertical opening was 4–5 m (Teigsmark and Øynes, 1982). The trawl configuration and bottom contact were monitored remotely by SCANMAR trawl sensors.

The benthic megafauna were separated from the fish and shrimp catch, washed, and sorted to the lowest possible taxonomic level, usually to species, on-board the vessel. The taxonomic identification procedure was quality controlled during dedicated workshops, and taxon names were standardized according to the World Register of Marine Species (Boxshall et al., 2014). Wet-weight biomass was recorded on-board for each taxon using electronic scales (Marel series 1100). All individual data were included in subsequent numerical analysis whether individuals were identified to species or to a higher taxonomic level.

### Species vulnerability to trawling

Several studies have reported that “large individuals” have been reduced in density in trawled areas (Kaiser et al., 1999, 2000; Moran and Stephenson, 2000; Pitcher et al., 2000), meaning that “size” (biomass/abundance) of a benthic animal might be a trait

for a species “vulnerability”. The maximum height above the sediment surface was evaluated as another trait for vulnerability, leading to the hypothesis that a large-bodied specimen standing upraised from the seabed, or swimming above, has a higher risk of being caught by a trawl, compared with a small-bodied specimen below, or staying close to, the seabed. The two traits “individual mean weight” and “height above sediment” were, therefore, selected for this work and classified according to three modalities: 1 = easy to catch, 2 = intermediate, and 3 = difficult to catch by a trawl. The overall score for a species (Supplementary material) was calculated as the arithmetic mean of the two individual trait modalities (Table 1). We considered all species with scores of 2.5 or 3 as having a “high risk”, all species with scores of 2 as having a “medium risk”, and all species <2 as having a “low risk” of being caught by a trawl. This means that large-bodied species extending above the seabed could be considered “highly vulnerable”. This group includes species with a physical contact to the bottom substrate as well as swimming species such as cephalopods.

### Mapping of vulnerable species

Individual taxa or taxon groups with a *high risk of being caught by a trawl* were mapped across the Barents Sea. Groups of taxa were formed based on morphologically similar species, i.e. species having the same likelihood of being caught by a trawl. This set of

maps constitutes a detailed assessment of the locations of vulnerable benthic taxa to the trawling pressure.

### Benthic biomass in trawled vs. untrawled areas

The total biomass of “low-risk”, “medium-risk”, and “high-risk” species was calculated for each station in the Norwegian EEZ, the Svalbard Fisheries Protection Zone, and the Loop Hole (Figure 1), and the biomass values were compared between trawled and untrawled stations. A station was considered *trawled* if it was located in a 10 × 10 km grid cell in which we had identified commercial trawling (Figure 1). No distinction was made between single, double, and/or triple trawls, and the cumulated duration of trawling was not used in the analysis. A station was considered *untrawled* if it was located in a 10 × 10 km grid cell with no recorded commercial trawling.

## Results

### Trawling intensity

Trawling intensity was medium to high ( $\geq 200$  trawl h, Figure 1) mainly due to the use of single bottom trawls for cod and other groundfish (Figure 2a and b) in (i) areas of Tromsø Bank, (ii) farther north along the continental slope up to the area around Bear Island, (iii) Svalbard Bank, and (iv) farther north to King Karls Land. A belt of relatively high trawling intensity extended along the banks off the coast of Finnmark, eastwards towards the Russian EEZ.

Farther north, up to 80°N west, north and east of Svalbard, the northern part of the Hopen Deep, the area between the Great Bank and the Central Bank, and in the “Loop Hole”, shrimp trawls were used (up to 100 trawl h), including both single, double, and triple trawls (Figure 2b).

### Identification of vulnerable species

A total of 354 taxa/taxon groups (Supplementary material) were scored for their vulnerability to being caught by a bottom trawl. According to size (Table 1), 25 taxa/groups had a large, 117 had a mean, and 207 had a small mean body size, while relative to height above sediment, 30 taxa/groups were grouped as high, 165 as medium, and 158 as low above the sediment surface.

When combining information, 21 taxa/taxon groups were classified as having a *large mean body size* and *height* above the sediment, and consequently with “high risk” of being caught by a trawl. These species belonged to the Anomura and Brachyura (Arthropoda), Alcyonacea and Pennatulacea (Cnidaria), the Crinoidea, Holothuroidea, and Ophiuroidea (Echinodermata), Cephalopoda (Mollusca), and Porifera (Table 2). A total of 79 were classified as “medium risk” (large body size, but low above the sediment or *vice versa*) and 245 as “low risk” (small body size, low height above the sediment surface) (Supplementary material) and representing all groups except Pennatulacea, Crinoidea, and Cephalopoda (Table 2). The “high-risk” species (Table 3) included three Arthropods: red king crab (*Paralithodes camtschaticus*) up to 22 cm in carapace length (Powell and Nickerson, 1965) and 549.81 g mean body wet weight “MBWW”; snow crab (*Chionoecetes opilio*) with leg span up to 90 cm ([www.animaldiversity.or](http://www.animaldiversity.or)) and MBWW of 24.5 g; and sea spider (*Colossendeis* spp.) with legs up to 75 cm (Barnes, 1987) and MBWW of 4 g.

The “high-risk” group also included the three Cnidarian species: sea pen (*Umbellula encrinus*) up to 2.1 m (Lis L. Jørgensen pers. obs.) and an MBWW of 4.1 g; and the two Nephtheidae soft

**Table 2.** The amount of species (given as %) within each higher taxonomic group with high risk, medium risk, and low risk of being caught by a trawl (see also Supplementary material).

Phylum	Group	High risk (%)	Medium risk (%)	Low risk (%)	
Arthropoda	Amphipoda	0	0	100	
	Anomura	20	80	0	
	Brachyura	50	50	0	
	Cirripedia	0	33	67	
	Cumacea	0	0	100	
	Isopoda	0	17	83	
	Mysidae	0	0	100	
	Natantia	0	7	93	
	Pycnogonida	7	0	93	
	Cnidaria	Actiniaria	0	100	0
		Alcyonacea	40	60	0
		Anthozoa	0	100	0
		Ceriantharia	0	100	0
		Hydroidea	0	50	50
Pennatulacea		100	0	0	
Zoantharia		0	0	100	
Echinodermata	Asteroidea	0	14	86	
	Crinoidea	100	0	0	
	Echinoidea	0	50	50	
	Holothuroidea	17	25	58	
	Ophiuroidea	27	0	73	
Echiura	Echiura	0	0	100	
Lophophorata	Brachiopoda	0	0	100	
	Bryozoa	0	33	67	
Mollusca	Aplacophora	0	0	100	
	Bivalvia	0	10	90	
	Cephalopoda	100	0	0	
	Gastropoda	2	33	65	
	Polyplacophora	0	0	100	
Nemertini	Nemertini	0	0	100	
Polychaeta	Polychaeta	0	5	95	
Porifera	Porifera	12	52	36	
Priapulida	Priapulida	0	0	100	
Sipunculida	Sipuncula	0	0	100	
Tunicata	Ascidacea	0	45	55	
Turbellaria	Turbellaria	0	0	100	

corals (*Gersemia* spp. and *Drifa glomerata*) up to 20 cm height (pers. obs.) and an MBWW of 5.5–5.9 g.

The Echinoderms contained seven “high-risk” species: basket stars (*Gorgonocephalus arcticus*, 196 g MBWW; *G. eucnemis*, 202 g MBWW; and *G. lamarcki*, 127 g MBWW) with a voluminous body up to 0.5 m in diameter (pers. obs.); sea cucumbers (*Cucumaria frondosa*, up to 30 cm long, Hamel and Mercier, 1996, and 430 g MBWW; and *Parastichopus tremulus* up to 20 cm long, pers. obs., and 67 g MBWW); and two species of sea lilies (*Heliometra glacialis*, 13 g MBWW and *Poliometra prolix*, 2 g MBWW), with five arms, up to 20 cm in length (Dyer et al., 1984) extended upwards. The MBWWs of the sea lilies were most likely strongly underestimated, as they were fragmented while being sieved through the meshes of the trawl, and only parts of the body were available for weighing.

The Molluscs included five “high-risk” species: the cephalopods (*Bathypolypus arcticus*, 40 g MBWW; *Benthoctopus* spp., 39 g MBWW; *Rossia moelleri*, 36 g MBWW; and *R. palpebrosa*, 19 g MBWW), which all might rise above the seabed to avoid capture in the bottom trawl. The sea whelk (*Neptunea ventricosa*, 101 g MBWW) grows up to 16 cm in length and 11 cm in height ([www.arcodiv.org/seabottom](http://www.arcodiv.org/seabottom)).

**Table 3.** The megabenthic species or taxon groups used for examining spatial distribution of the Barents Sea.

Phylum	Group	Category	Species	Body size	Height	Mean
Echinodermata	Ophiuroidea	Globular basket star	<i>G. arcticus</i> , <i>G. eucnemis</i> , <i>G. lamarcki</i>	3	3	3
Cnidarians	Pennatulacea	Erect sea pen	<i>U. encrinus</i>	3	3	3
Porifera	Porifera	Large globular sponges	<i>Geodia barretti</i> , <i>G. macandrewii</i>	3	3	3
Arthropods	Anomura	Large crabs	<i>P. camtschaticus</i> , <i>C. opilio</i>	3	2	2.5
Mollusc	Gastropoda	Large snails	<i>N. ventricosa</i>	3	2	2.5
Echinodermata	Holothuroidea	Large surface sea cucumber	<i>C. frondosa</i> , <i>P. tremulus</i>	3	2	2.5
Cnidarians	Alcyonacea	Upraised corals	<i>D. glomerata</i> , <i>Gersemia</i> spp.	2	3	2.5
Mollusc	Cephalopoda	Mobile cephalopods	<i>B. arcticus</i> , <i>Benthoctopus</i> spp., <i>R. moelleri</i> , <i>R. palpebrosa</i>	2	3	2.5
Porifera	Porifera	Erect stalk sponges	<i>C. gigantean</i>	2	3	2.5
Echinodermata	Crinoidea	Branched sea lilies	<i>H. glacialis</i> <sup>a</sup> , <i>P. prolux</i> <sup>a</sup>	2	3	2.5
Arthropods	Pycnogonida	Large sea spider	<i>Colossendeis</i> spp.	2	3	2.5

These species are selected due to their *high risk* of being caught with a bottom trawl because of their large body size and height over the seabed (see more details in Table 1). For a full species list with traits, see Supplementary material. Literature used for height of species: Powell and Nickerson (1965); Patent (1970); Dyer et al. (1984); Emson et al. (1991); Hamel and Mercier (1996), [www.arcodiv.org/seabottom](http://www.arcodiv.org/seabottom), <http://www.marlin.ac.uk/>.

<sup>a</sup>*H. glacialis* and *P. prolux* are always fragmented when caught by the trawl and are most likely underrepresented in biomass. These two species might, therefore, be more correctly categorized as a “3”, rather than a “2” body size.

Within the Porifera, the globular, surface-dwelling sponge species [*Geodia barrette* and *G. macandrewii*, total trawl haul of 4 tonnes, up to 15 kg per individual, and diameter of 40 cm, (Lis L. Jørgensen, pers. obs.)] were identified as “high-risk” species. Other sponges, such as *Phakellia* spp., *Haliclona* spp., and *Suberites* spp., were also identified with large body weight and length, but were excluded from the list because they generally are lumped into “Porifera indet” due to fragmentation and difficult species identification.

### Geographic distribution of stations dominated by vulnerable species

Of the 391 sampled stations (Figure 3), biomass of 89 was dominated (>50%) by “high-risk” species or species groups. These 89 “high-risk” stations occurred in the following eight areas: Southwest (1), Svalbard Bank (2), Southeast banks (3), Pechora Sea (4), Northern Shelf (5), Northwest (6), Central–Grand banks (7), and Arctic Northeast (8) (Table 4).

In Area 1 (Figure 3), 23 stations covered a large area in the “southwestern” Barents Sea north of the Norwegian coast [for more information on environment and fauna, see Jørgensen et al. (2015)]. While the areas around these stations were exposed to high intensity fish trawling (Figures 1 and 2a and b), only 3 of the 23 stations fell into a grid cell where commercial trawling activity is reported. Species with “high risk” of being caught by a trawl were the sponge (*Geodia* spp.), which contributed on average 94% of the faunal biomass. Sponge species, *G. barrette* and *G. macandrewii*, were also recorded along the western shelf, west and north of Svalbard, eastward to the northern Kara Sea, and along the shelf facing the Arctic Ocean (Figure 4a); occasional observations were also made along the coast in the southern Barents Sea. “Area 1” was also dominated by the sea cucumber (*P. tremulus*) with a strictly limited distribution in the southwestern Barents Sea (Figure 4b; see Table 4 for the five top dominant species and the Supplementary material for the full species list of Area 1 and the areas described in the text below).

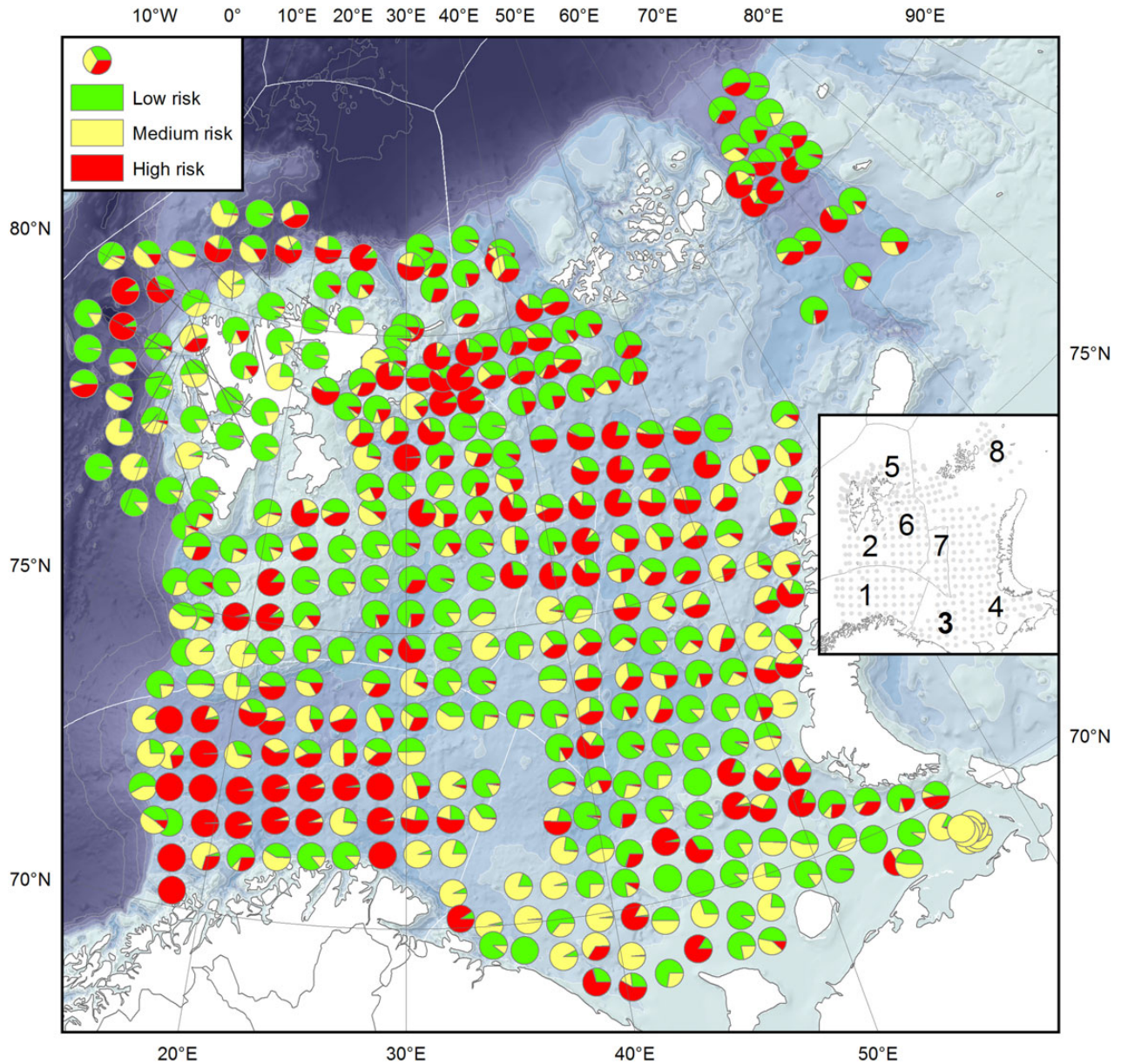
At Svalbard Bank (Area 2), trawling frequency was moderate and mainly limited to fish, rather than shrimp, trawls (Figure 2a and b). The fauna were dominated by the *high-risk* sea cucumber (*C. frondosa*), making up 87% of the fauna biomass, and the basket star (*G. eucnemis*). *Cucumaria frondosa* (Figure 4c) also dominated the

intensely fished (Lyubin et al., 2011, page 772, Figure 14.6.3) south-eastern banks (Area 3) and the moderately fished Pechora Sea (Area 4), where it represented 67% of the total faunal biomass. High-risk species in Area 3 also included the king crab (*P. camtschaticus*), distributed along the coast in the southern Barents Sea, and mainly in the Russian EEZ (Figure 4d), and *Geodia* sponges. The snow crab (*C. opilio*), occurring in the eastern and central Barents Sea (Figure 4b), dominated together with *G. arcticus* in Area 4.

Along the “Northern Shelf” (Area 5) north of Svalbard, Kvitøya, and Franz Victoria Trough facing towards the Arctic Ocean, a group of 11 stations was almost completely dominated by “vulnerable” species (Figures 3 and 4a–f). This included the Nephtheidae soft coral (*Gersemia fruticosa*, *Gersemia rubiformis*, *D. glomerata*, and *Duva florida*) widely distributed throughout the entire Barents Sea, but with the highest biomass in the northeastern Barents Sea outside trawled areas (Figure 4d), the basket star (*G. arcticus*), the sponges (*Geodia* spp.), and the Pennatulacean sea pen (*U. encrinus*; Table 4). These stations were located in a region with a commercial fishing fleet using double and triple trawl gear for the shrimp fishery (Figure 2b). This same fauna were also recorded farther east in the “Northeast Arctic” located in the St Anna Trough (Area 8) outside trawl areas, where the Pennatulacea sea pen was particular dominant on the soft sediment along the shelf and in the channels and trenches facing the Arctic Ocean (Figure 4b).

Ten stations in the northwestern part of the Barents Sea (east of Svalbard, Area 6) were dominated by the echinoderm basket star (*Gorgonocephalus* spp.; 71% of the biomass) and sea lily (*H. glacialis*). Trawling activity, mainly single trawls for cod, was not intense. *Gorgonocephalus* spp. (*G. arcticus*, *G. eucnemis*, and *G. lamarcki*) were widely distributed, with highest biomasses in the northern and eastern Barents Sea, west and north of Svalbard, and consequently outside the most intensely trawled areas (Figure 4a). The sea lily (*H. glacialis*) was distributed in the north, but also in the eastern Barents Sea and the shelf facing the Arctic Ocean, and with highest biomass in the northeastern Barents Sea outside the trawled areas (Figure 4c).

In the central part of the Barents Sea in the international “Loop Hole” area (outside Norwegian and Russian EEZ) between Central Bank and Grand Bank (Area 7), both Russian (Lyubin et al., 2011, page 772, Figure 14.6.3) and Norwegian registered fisheries occur. The Norwegian registered fishery was mixed between shrimp and fish trawls, using single, double, and triple trawls (Figure 2a and b).



**Figure 3.** Stations in the Barents Sea sampled during August–September 2011, each showing the biomass distribution of “high-risk” (red), “medium-risk” (orange), and “low-risk” (green) species being taken by a bottom fish trawl. Area: Southwest (1), Svalbard Bank (2), Southeast banks (3), Pechora Sea (4), Northern Shelf (5), Northwest (6), Central–Grand banks (7), and Arctic Northeast (8) (Table 4).

The seven stations within this area were dominated in biomass (67%) by “vulnerable” species, including the basket star (*Gorgonocephalus* spp.) and the snow crab (*C. opilio*).

Some of the identified “high-risk” species were not dominating in the areas described above. The giant club sponge (*Chondrocladia gigantean*) and other stalked sponges extending from the soft sediment, including *Stylocordyla borealis*, *Cladohriza* spp., and *Asbestopluma* spp., occurred in the western part of the Barents Sea, with the highest biomass on the shelf facing the Arctic Ocean outside the trawled areas (Figure 4e).

The giant sea spider (*Colossendeis* spp.) was recorded in the eastern Barents Sea, with the largest biomasses outside the trawled areas (Figure 4e).

The sea whelk (*N. ventricosa*, *N. communis*, *N. despecta*, and *N. denselirata*) had their main distribution and biomass in the trawled Russian southern Barents Sea (Figure 4e).

The largest cephalopod biomass occurred on the northern shelf facing the Arctic Ocean. *Rossia* spp. and *B. arcticus* were evenly distributed throughout the Barents Sea, with only a slight increase in biomass in the northeast. *Benthoctopus* spp. was mainly recorded in the northern part of the Barents Sea, while only occasionally recorded in the south with low biomass (Figure 4f).

**Benthic biomass in trawled vs. untrawled areas**

The cumulative biomass of “low-risk”, “medium-risk”, and “high-risk” taxa can vary greatly for each category among individual

**Table 4.** The selected vulnerable areas of the Barents Sea with the mean trawl counts and biomass [given in percentage (%) and cumulative % (Cum%) of total biomass per area] of the top five most dominant species, with the *high-risk* species (Table 2) indicated in bold.

Area	Species	Percentage	Cum%
Southwest (1) Twenty-three stations	<b><i>Geodia</i> spp.</b>	94	94
	<i>Thenea muricata</i>	1	95
	<i>Porifera</i> spp.	1	96
	<b><i>P. tremulus</i></b>	0	97
Svalbard Bank (2) Four stations	<i>Molpadia borealis</i>	0	98
	<b><i>C. frondosa</i></b>	80	80
	<b><i>G. eucnemis</i></b>	7	87
	<i>Porifera</i> spp.	5	92
	<i>Strongylocentrotus</i> spp.	3	95
Southeast banks (3) Seven stations	<i>Balanus</i> spp.	1	96
	<b><i>C. frondosa</i></b>	67	67
	<b><i>P. camtschaticus</i></b>	19	86
	<i>Porifera</i> spp.	8	94
	<b><i>Geodia</i> spp.</b>	2	96
Pechora Sea (4) Eight stations	<i>Urasterias linckii</i>	1	97
	<b><i>C. frondosa</i></b>	67	67
	<i>Porifera</i> spp.	12	79
	<b><i>C. opilio</i></b>	8	87
	<b><i>G. arcticus</i></b>	4	91
Northern Shelf (5) Eleven stations	<i>Solaster</i> spp.	1	93
	<b><i>Gersemia</i> spp.</b>	22	22
	<b><i>G. arcticus</i></b>	10	32
	<i>Haliclona</i> spp.	9	41
	<b><i>U. encrinus</i></b>	8	49
Northwest (6) Ten stations	<b><i>G. barretti</i></b>	6	55
	<b><i>Gorgonocephalus</i> spp.</b>	77	77
	<i>Ctenodiscus crispatus</i>	3	3
	<b><i>H. glacialis</i></b>	3	3
	<i>M. borealis</i>	2	2
Central–Grand banks (7) Seven stations	<i>Icasterias panopla</i>	2	2
	<b><i>Gorgonocephalus</i> spp.</b>	48	48
	<b><i>C. opilio</i></b>	19	67
	<i>Sabinea septemcarinata</i>	7	74
	<i>M. borealis</i>	5	79
Arctic Northeast (8) Five stations	<i>C. crispatus</i>	2	81
	<b><i>U. encrinus</i></b>	43	43
	<i>Actinaria</i> spp.	11	54
	<b><i>G. arcticus</i></b>	16	70
	<b><i>Geodia</i> spp.</b>	8	78
	<i>Ophiopleura borealis</i>	5	84

stations, often by several orders of magnitude (Figure 5). Variability in biomass among stations was greatest for the vulnerable taxa. In untrawled areas, there was little difference in the median biomass for species with low, intermediate, or high vulnerability to trawling. There was a distinct decline in biomass for all three categories when moving from untrawled to trawled areas, and the decline was strongest for the most vulnerable taxa by almost one order of magnitude, suggesting that trawling significantly affects the biomass of all species and predominantly the biomass of the most vulnerable ones.

## Discussion

The southern part of the Barents Sea is subjected to high intensity of trawling, and Russian activity is three- to four-fold here, compared with the northwest, and very low in the northeastern part of the Barents Sea (Lyubin *et al.*, 2011). Trawling is also farther north along the continental slope, around islands, banks, in channels,

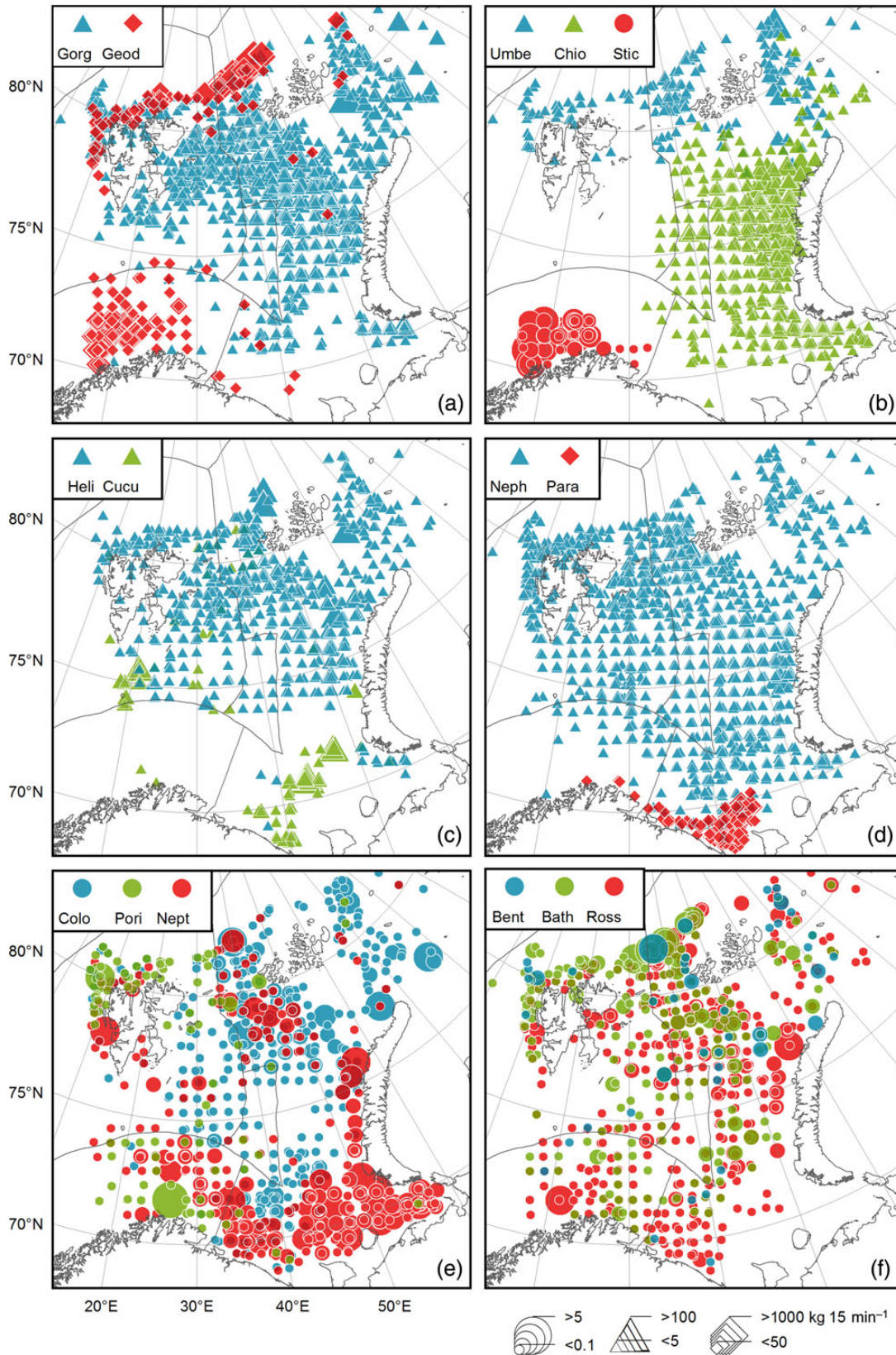
and north and east of Svalbard. Both shrimp and fish trawls are used, including both single, double, and triple trawls. Barents Sea trawling for fish and shrimp is causing a reduction in total benthic biomass (Prena *et al.*, 1999) by as much as 70% (Denisenko, 2001; Wassmann *et al.*, 2006; Denisenko *et al.*, 2007). The reduction in biomass is correlated with trawling intensity (Lyubin *et al.*, 2011). Our study supports these findings and shows that trawling affects the biomass of all species, but predominantly the biomass of those species easily caught by a trawl (being large bodied and upraised from the seabed, i.e. vulnerable species). The highest biomass of vulnerable species was recorded in the northern Barents Sea, outside commercial trawl activity, but surprisingly also in the most intensively trawled southwestern areas of the Barents Sea. It should be noted that biomass in this study is not an absolute value, but only indicative of the total biomass because some easily fragmented species, e.g. cup coral (*Caryophyllia smithii*), hydroid (*Corymorpha* spp.), borrowing sea anemones (*Liponema multicornis*) and Cerianthidae indet, and the sea pen (*Radicipes* spp.) are sieved through the mesh and are most likely underreported. The bottom trawl used is not a traditional quantitative benthic sampling device; the total seabed area covered and the catchability for benthic species are unknown. Nevertheless, the trawl effectively collects larger organisms such as corals, sea pens, sponges, sea stars, and crabs that are patchily distributed on the seabed.

## Southern Barents Sea

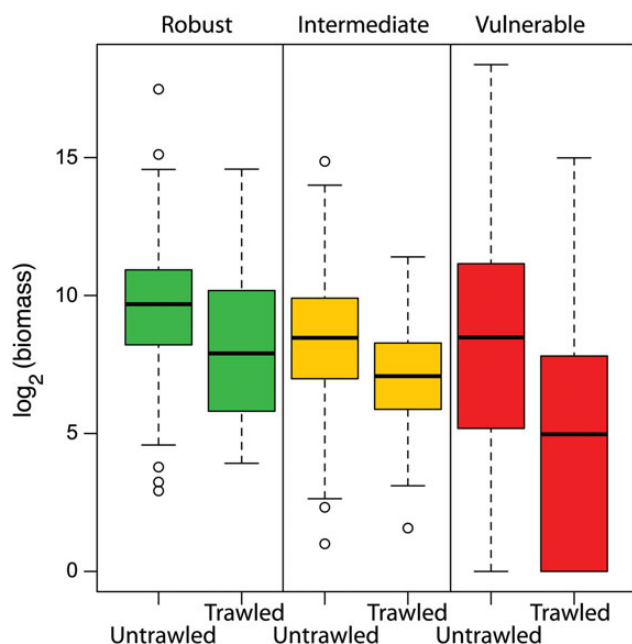
The deep (>250 m) southwestern Barents Sea was characterized by a sponge community dominated by several *Geodia* species. This sponge community represents the second highest biomass per unit area and was only surpassed by the northeastern Barents Sea (Jørgensen *et al.*, 2015). The fauna associated with sponge communities were estimated to be at least twice as rich as that of the surrounding gravel or soft bottom (Bett and Rice, 1992; Klitgaard, 1995), and the increase in associated species richness has been related to increased host volume (Frith, 1976; Westinga and Hoetjes, 1981; Villamizar and Laughlin, 1991; Duarte and Nalesso, 1996; Cinar *et al.*, 2002). Sponge grounds may, therefore, have functions similar to those of coral reefs (Løkkeborg and Fosså, 2011), providing justification for conservation in accordance with the Biodiversity Convention (<http://www.cbd.int/convention/text/>). The number of area-based megafaunal species in the Barents Sea varies from 7 to 39, with the *Geodia* sponge community having 14–19 species (Jørgensen *et al.*, 2015). The *Geodia* sponges form dense populations in the Barents Sea and are effectively caught by bottom trawling; even short trawl hauls can contain several tonnes (Løkkeborg and Fosså, 2011; Lis L. Jørgensen, pers. obs.). A decrease in *Geodia* biomass and distribution areas in the southeast have been observed (Lyubin *et al.*, 2011), but dedicated studies following fluctuations of *Geodia* sponges in other areas of the Barents Sea are lacking.

The coastal waters of northern Russia and Norway are the most intensively trawled areas in the Barents Sea, with trawl marks on the seabed often <1 m apart (Aibulatov *et al.*, 2005) and observations of one trawl mark per 10 m along transects ([www.mareano.no/en/news/news\\_2013](http://www.mareano.no/en/news/news_2013)). This indicates that the *Geodia* species can survive damage due to physical contact with the trawl gear, the handling on the ship deck, and are able to become re-established on the seabed. Løkkeborg and Fosså (2011) comment that *Geodia* sponges left damaged by the trawl on the seabed are vulnerable because they may have their filter-feeding system clogged by non-food particles. However, tissue regeneration in sponges is a well-known phenomenon (Pronzato *et al.*, 1999; Corriero *et al.*, 2004)





**Figure 4.** Distribution (wet weight biomass  $15 \text{ min}^{-1}$  trawling) of identified high-risk species being caught by trawl: (a) *Gorgonocephalus* spp. (Gorg) and *Geodia* spp. (Geod); (b) *U. encrinus* (Umbe), *C. opilio* (Chio), and *Parastycopus* spp. (Stic); (c) *H. glacialis* (Heli) and *C. frondosa* (Cucu); (d) Nephtheidae (Neph) and *P. camtschaticus* (Para); (e) *Colossendeis* spp. (Colo), stalked Porifera including *C. gigantean*, *S. borealis*, *Cladohriza* spp., *Asbestopluma* spp. (Pori), and *Neptunea* spp. including *N. communis*, *N. despecta*, *N. ventricosa*, and *N. denselirata* (Nept); and (f) *Benthocarpus* spp. (Bent), *B. arcticus* (Bath), and *Rossia* spp. including *R. moelleri* and *R. palpebrosa* (Ross). Species mapping data are from Norwegian – Russian Ecosystem Surveys during August – September 2007 – 2013.



**Figure 5.** Biomass of “low-risk” (green), “medium-risk” (orange), and “high-risk” (red) species for trawled (54 stations) and untrawled (160 stations) stations in the Norwegian EEZ.

and suggests that *Geodia* sponges may be robust and repair rapidly after being damaged (Simpson, 1984). *Geodia barretti* is able to continue its reproductive cycle despite manipulation and a reduction in size (Hovmann *et al.*, 2003). Evidence for trawl-induced mortality of the *Geodia* sponges is, therefore, equivocal. An alternative explanation is that fishers try to circumvent sponge areas to avoid clearing large amounts of sponges from the deck and trawl codends, but also because sponges may damage the fish catch in the trawl. They achieve this by directing their bottom trawling to corridors that have been cleared of *Geodia* sponges (John H. Johnsen, Captain R/V GOS, pers. comm.). This implies that local fishers contribute to the conservation of the large sponge beds in the southwestern Barents Sea.

On the shallow plateaus (<200 m) of Svalbard Bank, the banks off the Russian coast, and the Pechora Sea, the sea cucumber (*C. frondosa*) dominated. *Cucumaria frondosa* contributed up to 26 kg (Svalbard Bank), 59 kg (Russian banks), and 61 kg (Pechora Sea) of the biomass after 15 min trawling. Intense trawling could, therefore, result in the depletion of this species because its distribution is relatively restricted to the trawled southern areas of the Barents Sea, and commercial fishing pressure on this species might lead to a population collapse (So *et al.*, 2010).

Other species easily caught by a fish trawl and among the top dominant species were the basket star (*G. arcticus*) and snow crab (*C. opilio*) in the Pechora Sea, king crab (*P. camtschaticus*) on the banks outside the Russian coast, and *Gorgonocephalus euemnis* on Svalbard Bank. Industrial fishing in the southern part of the Russian Barents Sea, removing tonnes of benthos as bycatch (Denisenko *et al.*, 2007), and that on Svalbard Bank (25–100 h during 2007–2011), might have a large impact on the almost immobile population of sea cucumbers and basket stars, whereas snow crab and king crab are highly mobile, and possible fluctuations in their populations might be due to factors other than trawling. Comparisons between species must, therefore, be considered with caution, especially if bycatch is used as a biological indicator.

## Northern Barents Sea

The basket star (*Gorgonocephalus* spp.) dominated the fauna in the intensively trawled “Loop Hole” between Central Bank and Grand Bank (up to 11 kg 15 min<sup>-1</sup> trawl haul) and in the moderately trawled northwestern Barents Sea (up to 244 kg 15 min<sup>-1</sup> trawl haul). These areas are subjected to both shrimp and fish trawling, including single, double, and triple demersal trawls. In the northwest, relatively lower trawl intensity might be the reason that the delicate and fragile long-armed sea lily (*H. glacialis*) dominated, although fragmented when caught by a trawl and most likely with underreported biomass in this study. The body of the basket star and fragments of its arms are frequently entangled in the trawlnetting or caught inside the trawl (Lis L. Jørgensen, pers. obs.). Echinoderms are generally recognized for their ability to regenerate following sublethal disturbance (Emson and Wilkie, 1980; Lawrence and Vasquez, 1996), but specific information on sea lilies and the basket star’s ability to recover after being trawled, handled on deck, and returned back into the sea remains unavailable.

Farther north, the Northern Shelf facing towards the Arctic Ocean is covered by sea ice for >200 d year<sup>-1</sup> (Jørgensen *et al.*, 2015). Here, the cnidarian soft coral (*Gesmeria* spp.) and the octocoral sea pen (*U. encrinus*) dominate together with the basket star and the *Geodia* spp. sponges. This shelf, dominated by corals, sponges, and basket stars, has been protected because it is outside the current range of industrial fishing, which might change as exploitation moves northward (Lynghammar *et al.*, 2013). Industrial fisheries are beginning to harvest the Arctic shelves around Svalbard for the boreal Atlantic cod (*G. morhua*), which has become abundant north in the Barents Sea (Kovalev and Bogstad, 2011; ICES, 2013; Johansen *et al.*, 2013). The biomass of *Gesmeria* spp. is highest in untrawled areas (McConnaughey *et al.*, 2000), but these species are also known to regenerate well from acute localized injuries, which, along with the ability to temporarily retract and survive repeated crushing, may benefit the soft coral in heavily trawled habitats (Henry *et al.*, 2003). *Gesmeria* spp. can be considered as a habitat-structuring species, because the embryonic development of the basket star may occur inside the soft coral itself, with young specimens clinging to the outside of the specimens for feeding (Patent, 1970) and settling to grow to maturity in the surrounding area. Evidence of trawl-induced direct mortality of the *Gesmeria* spp. and a possible indirect effect on basket star juveniles is, therefore, unclear.

The easternmost part of the shelf might remain untrawled due to the long distance to the nearest fishing harbour, which offers a possible reason for the high abundance of *U. encrinus* (up to 5000 individuals 15 min trawling<sup>-1</sup>). This remote part of the Arctic Barents Sea is not generally affected by direct human activity. For such areas, appropriate conservation measures are feasible and should be instituted and enforced (Caro *et al.*, 2012). The megafauna of the northern shelf can serve as an example of undisturbed shelf fauna. The ecological objectives (Skjoldal and Misund, 2008; Arctic Council, 2013) for biodiversity, population size, and individual length must be developed and integrated into a management plan. Extensive aggregations formed by *U. encrinus* (sea pen fields) up to of 50 years of age (Wilson *et al.*, 2002) and sizes of 2.3 m (Lis L. Jørgensen, pers. obs.) in height are recognized as ecological and biologically significant habitats for both fish and invertebrates (DFO, 2005) and belong to the OSPAR List of Threatened and/or Declining Species and Habitats (<http://www.ospar.org/>). Together with the fact that baseline time-series and diagnostic data

on functional biodiversity represent the most severe shortcoming for credible conservation actions and a legitimate management of Arctic species (Christiansen et al., 2014), we recommend tailored conservation actions to counteract specific human activities.

### Barents Sea generally

The above-mentioned large and easily caught species are all among the top biomass contributors in the areas described. But, other identified “high-risk” species were less prominent. This includes the sea whelk (*N. ventricosa*). Whelks were significantly more abundant in unfished areas and were identified as vulnerable due to the lack of a pelagic larval stage, a lifespan of  $\geq 10$  years, and a slow post-impact recovery (McConnaughey et al., 2000). It was, therefore, surprising to find relatively large biomasses of *Neptunea* species (*N. communis*, *N. despecta*, and *N. denselirata*) in the southern Barents Sea within the trawled Russian EEZ. This might indicate a lifestyle similar to the sea whelk (*Buccinum* spp.), which is a predatory scavenger more abundant in trawled areas (McConnaughey et al., 2000). Change in the populations of large-bodied whelks may, therefore, be attributed to a reduction or an increase in trawling activity, and population fluctuations must, therefore, be viewed with caution if trying to access biologically induced population changes.

The giant club sponge (*C. gigantean*) and other stalked sponges (*S. borealis*, *Cladohriza* spp., *C. gigantean*, and *Asbestopluma* spp.) are easily broken or caught by bottom trawls. These stalked sponges are fragmented, sieved through the netting, difficult to identify, and possibly strongly underreported. Nevertheless, the species records showed a western distribution in the Barents Sea with the highest biomass in the north outside trawled areas. Low biomass was also recorded in trawled areas in the southern Barents Sea. Here, a non-destructive mapping (i.e. video recording) is needed to provide a true picture of the quantitative distribution of the stalked soft-bottom sponges in the Barents Sea, together with trawl-vulnerability studies and establishment of ecosystem objectives.

Another species identified as “high risk of being caught by a trawl” is the giant Pycnogonida sea spider (*Colossendeis* spp.) found primarily in the eastern part of the Barents Sea. Little is known about the vulnerability of this species or the other smaller species of sea spiders (*Boreonymphon abyssorum*, *Cordylochele* spp., *Nymphon brevisrostre*, *N. elegans*, *N. gracilipes*, *N. grossipes*, *N. hirtipes*, *N. hirtum*, *N. spinosum*, *N. stroemi*, and *Pseudopallene* spp.). Up to 6000 sea spiders ( $\geq 4.5$  kg wet weight 15 min<sup>-1</sup> trawl haul in 2005–2013) were recorded in the untrawled northeastern Barents Sea ( $>75^\circ\text{N}$ ,  $>40^\circ\text{E}$ ), having a mean biomass three-fold higher than the value in comparable trawled areas.

A similar conundrum exists for the “easily caught” Cephalopoda (*Benthoctopus* spp., *B. arcticus*, *R. moelleri*, and *R. palpebrosa*), which are widely distributed, but with their highest biomass occurring in the untrawled northeastern areas. The cephalopods might rise above the seabed to avoid capture in the bottom trawl, a behaviour which might make them more vulnerable.

The mapping of regional and local Barents Sea fauna (Jørgensen et al., 2015), the identification of areas vulnerable to trawling (Certain et al., 2015), and species easily caught by bottom trawl, together with their distributional information as reported here, are important steps in a management process. But, if the impact of trawling on benthos needed to be minimized for effective management, investigations should also consider trawling impact on diversity and structural heterogeneity (e.g. Kutti et al., 2005; Løkkeborg and Fosså, 2011), mortality, growth, and recruitment rates on benthic species, as well as the ecological implications of these

factors [e.g. Arctic fish, Christiansen et al., 2014; demersal fish such as haddock (*Melanogrammus aeglefinus*), plaice (*Pleuronectes platessa*), and cod; and benthic feeders such as walrus (*Odobenus rosmarus*), seals (Phocidae), whales (Cetacea), and birds] for local areas in the Barents Sea.

### Conclusions

Commercially important fish stocks are migrating north- and eastward in the Barents Sea, and an international commercial fishing fleet is expected to follow. This fishing activity might enter areas with large biomasses of species easily caught by a bottom trawl. This work identified 23 species with large body weight and upraised and consequently “easily caught” by a bottom trawl.

In the southwestern part of the Barents Sea, *Geodia* sponges may have functions similar to those of coral reefs due to an increase in the richness of associated species. Awareness of this region is, therefore, recommended. Intense trawling is recorded here, but the commercial fishing fleet may have generated trawling corridors to avoid filling trawls with sponges and may consequently have “protected” this area. This type of “trawling in corridors” should be applied northward to avoid possible damping or local eradication of the basket star, sea pen, soft coral, and sea lily fields with their associated fauna in the northern Barents Sea.

North of  $80^\circ\text{N}$ , the highly vulnerable cnidarian sea pen (*U. encrinus*) needs particularly high awareness due to the lack of mapping and knowledge of its vulnerability. Sea pens are recognized as habitats for both fish and invertebrates and belong to the OSPAR List of Threatened and/or Declining Species and Habitats.

We recommend vulnerability studies on species such as the Pycnogonida (*Colossendeis* spp., *B. abyssorum*, *Cordylochele* spp., *N. brevisrostre*, *N. elegans*, *N. gracilipes*, *N. grossipes*, *N. hirtipes*, *N. hirtum*, *N. spinosum*, *N. stroemi*, and *Pseudopallene* spp.), stalked sponges (*C. gigantean*, *S. borealis*, *Cladohriza* spp., and *Asbestopluma* spp.), Cephalopoda (*Benthoctopus* spp., *R. moelleri*, and *R. palpebrosa*), the solitary coral (*C. smithii*), the solitary hydroid (*Corymorpha* spp.), the delicate soft-sediment sea anemones (*L. multicornis* and Cerianthidae indet), and the sea pen (*Radicipes* spp.).

### Supplementary material

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

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