The impact of trawling on the epibenthic megafauna of the West Greenland shelf

Yesson C.[1*], Fisher J.[1] , Gorham T.[1], Turner C. J.[1], Hammeken Arboe N.[2], Blicher M. E.[2] & Kemp K. M.[1]

[1]Institute of Zoology, Regent's Park, London NW14RY, UK, [2]Greenland Institute of Natural Resources, Box 570, Kivioq 2, 3900 Nuuk, Greenland

Corresponding author: tel +44 20 7449 6267; email: chris.yesson@ioz.ac.uk

Abstract

Benthic habitats are important elements of polar marine environments. They provide valuable ecosystem functions, but can be vulnerable to anthropogenic influences such as the direct impacts of bottom trawl fisheries. Trawling can reduce diversity and dramatically alter communities, although some habitats, notably those exposed to natural disturbance, have shown considerable resilience.

The shrimp trawl fishery of West Greenland has been in operation since the 1950s, using otter trawls to catch the northern shrimp (*Pandalus borealis*). It is a significant part of the Greenlandic economy, accounting for 50% of exports. It operates along the west coast from the narrow, rockier shelf of the south, up to deeper, muddy areas around Disko Bay.

Here we use a benthic drop camera to sample 201 sites subject to a wide range of bottom trawling intensity between latitudes 60-72°N and depths 61-725m. Epibenthic taxa were recorded at the taxonomic rank of class. Measures of environmental conditions (depth, temperature, current speed, iceberg concentration) were collected at all sites. Linear models were used to determine the relationships of environment and trawling intensity with taxon abundance and diversity.

Bottom trawling intensity is the most important factor determining the overall abundance of benthic organisms, accounting for 12-16% of variance on hard and soft substrates. Sessile erect organisms, such as corals, show statistically significant negative response to fishing pressure. Environmental conditions, including temperature at the seabed and natural disturbance from iceberg scouring, also show significant associations with the abundance of individual taxonomic classes. Soft sediment communities show more resilience than rocky areas. Overall abundance is lower for recently trawled sites. On soft sediments we can find significantly lower abundance at sites trawled less than five years ago, but for hard/mixed ground the effect is more persistent and reduced abundance is seen on all sites trawled up to a decade ago. Continued monitoring of benthic habitats is an essential part of evaluating ongoing impacts of trawl fisheries.

Keywords

Fishing impact, benthos, epibenthic invertebrates, iceberg concentration, recovery, trawling

Introduction

Seafloor communities are an integral part of marine ecosystems. Benthic habitats in deep and cold water provide a diverse set of ecosystem services including water filtration, nutrient cycling, and carbon storage (Danovaro *et al.,* 2008; Kahn *et al.,* 2015). Epibenthic organisms provide structures where other organisms settle, shelter or breed. Organisms with complex structures such as corals, tube-forming polychaetes, bryozoans and sponges, create biogenic habitats that are crucial for the preservation of biodiversity in the deep sea (Buhl-Mortensen *et al.,* 2010). These potentially vulnerable groups can have narrow environmental affinities related to properties of the sea floor, which makes them effective as indicator groups to assess the health and quality of the environment (McConnaughey *et al.,* 2000).

The effects of trawling

Anthropogenic impacts on the seafloor are widespread, and bottom trawling is, perhaps, the greatest of these, affecting approximately 75% of continental shelf area globally (Kaiser *et al.,* 2002). Benthic habitats subject to intensive trawling have been found to exhibit reduced diversity, degraded sedimentary habitats, and impaired ecosystem functionality (Hiddink *et al.*, 2006; Hinz *et al.*, 2009; Jennings & Kaiser, 1998; Kaiser *et al.,* 2006). Trawling (and other activities such as dredging) can remove emergent sessile epifauna, many of which are habitat forming ecosystem engineers (Clark *et al.,* 2016; Collie *et al.,* 2000; Danovaro *et al.,* 2008; Pusceddu *et al.,* 2014). A review of trawling impacts in Northeast Atlantic deepwater ecosystems showed that corals and sponges incur negative effects, attributed to slow growth rates, sedentary motility, and emergent structures inhibiting post-impact recovery rates (Curtis *et al.,* 2013). Conversely, highly mobile taxa that are able to escape trawls are more dominant in highly disturbed communities (Hixon & Tissot, 2006). High levels of disturbance selects for short life-cycles and fast growth-rates, including mobile species and rapid colonists (Thrush and Dayton 2002). Initially disturbance can bring scavengers that feed on damaged or dead animals (Ramsay *et al.,* 1996). Post disturbance, communities may be dominated by fast-growing motile dispersers such as polychaete worms (Burd *et al.,* 2002; Jones, 1992).

The effects of trawling are not uniformly negative or impactful (Jennings & Kaiser, 1998). In some systems with high levels of natural disturbance changes in macrofaunal community structure are not detectable (Simpson & Watling 2006; McConnaughey *et al.,* 2000; Kenchington *et al.,* 2001). The intermediate disturbance hypothesis suggests that low levels of perturbations increase biodiversity through recolonisation and recruitment (Blanchard *et al.,* 2004). Although the majority of studies show benthic invertebrate community responses to trawling conform to a pattern of large and slow-growing species becoming rarer, with overall species diversity and evenness decreasing (Hall, 1999; Hiddink *et al.*, 2006; Jennings & Kaiser, 1998).

The majority of studies investigating trawling impacts have been focussed on the shallower waters of northern Europe or eastern North America (e.g. Bolam *et al.,* 2014; Collie *et al.,* 2000; Hinz *et al.*, 2009). However, it may be difficult generalising from these studies (predominantly focussed on the relatively shallow, wave disturbed environments of the North Sea) given that the impact of trawling may be dependent on regionally variable factors such as gear types, fishing intensity, spatial scale of the fishery, connectivity of animal populations, productivity and substrate type (Bolam *et al.,* 2014).

The environment of the West Greenland continental shelf

Trawling is one of many factors that can influence benthic diversity and community composition. Environmental conditions including geology and currents impact substrate variability, grain size, and nutrient supply, affecting the composition of certain communities (Buch *et al.,* 2004). Studies indicate substantial differences in community composition of Arctic benthic habitats dependent on environmental conditions including temperature, depth and substrate (Yesson *et al.,* 2015; Sejr *et al.,* 2010; Jørgensen *et al.,* 2015).

The continental shelf of west Greenland extends from the high Arctic (85°N) to subarctic (60°N). Further south there is a relatively narrow and clearly defined shelf breaking at less than 50km from the shore. Here the West Greenland current is relatively strong and runs over a rocky seabed. Moving north the seabed becomes less consolidated, the currents weaker and the shelf is less clearly defined (Myers *et al.,* 2007; Boertmann and Mosbech, 2011; Yesson *et al.,* 2015). South of 70°N the West Greenland shelf consists of a mix of deep troughs that are natural extensions of numerous fjord systems, and several shallow off-shore banks. The community composition of epibenthic fauna varies over a latitudinal gradient. The communities in the south are characterised by a more diverse group of hard-substrate specialist taxa, while further north (extending up to c. 72°N) there are more soft-sediment specialists and more of the commercially exploited shrimp species *Pandalus borealis* (Yesson *et al.,* 2015).

Western Greenland is subject to a natural disturbance regimen through the mechanism of iceberg scouring, which has been observed at depths up to 600m in the region (Gutt 2001). Grounding ice can plough sediments and break, crush or displace seabed fauna (Conlan *et al.,* 1998). Disturbance of iceberg scouring has been likened to that of anthropogenic disturbances (Lenihan & Oliver, 1995). The typical size of observed impact from iceberg scouring (admittedly in NE Atlantic) was shown to be a similar size to the width of an otter trawl (Robert *et al.,* 2014). It is important that any assessment of trawling impact in West Greenland should seek to incorporate the impact of iceberg scouring.

West Greenland shrimp fishery

Trawling on the continental shelf of West Greenland began in the 1950s. The intensity of trawling picked up in the mid 1970s as the shrimp fishery took predominance in the economy of Greenland. The fishery uses otter trawls to target the northern shrimp *Pandalus borealis*, operating from the southern end of the continental shelf to 74°N at depths of 150-600 m, and constitutes the main anthropogenic impact on the seabed of much of western Greenland. Today it constitutes around 50% of Greenland's total exports and 89,000 tonnes of shrimp were caught in 2014, down from a high of c.150,000 in 2005 (Buch *et al.,* 2004; Lassen *et al.,* 2013; Hammeken Arboe, 2015). Regulations require the use of rolling rockhopper ground gear and toggle chains of at least 72 mm to keep trawl netting off the seabed. Additional requirements include a cod-end mesh size of at least 40 mm stretched and 22-mm bar spacing on sorting grids to reduce bycatch (Hammeken Arboe 2014). The fishery was certified as sustainable by the Marine Stewardship Council in 2013, although with conditions for improved performance in fishery management and environmental impacts mitigation (Lassen et al., 2013).

A movement towards Ecosystem-Based Fishery Management requires careful assessment of benthic habitats and an understanding of the relationship between fishing and biodiversity (Hiddink et al 2007; FAO 2003; Sinclair & Valdimarsson 2003). From a management perspective, it is useful for habitat assessments to be done on the scale of the fishery in order to describe the full range of potential impacts on different habitat types (Lambert et al 2011). This is perhaps even more important in under-sampled areas such as Western Greenland.

Aims

This study uses a geographically extensive survey and three decades of fishing effort data to test the hypothesis that bottom trawling has a significant negative impact on the abundance and community composition of benthic macro-invertebrates. The exceptionally long trawl history is used to investigate recovery potential with a focus on vulnerable taxa and functional groups.

Methods

Benthic images were collected aboard the R/V Paamiut during the five summers of 2011-2015. Ten images, each covering approximately 0.3m^2, were taken at each site, with a 1 minute interval between images (average drift 20-50m). Sites were selected to reflect a balance of geography, depth, and fishing impact over the range of the shrimp fishery of West Greenland. A detailed description of survey methods is provided in Yesson *et al.* (2015), although it is noted that the present study incorporates an additional two years of surveys (2014-15).

Taxa were identified in each image to the level of taxonomic class following methods described in Yesson *et al.* (2015). Abundance of each taxon was counted for each site. Colonial organisms were tallied by colony (or distinct patch), and no measure of biomass was attempted. Taxonomic groups were aggregated into functional groups detailed in Supplementary Appendix 1. In brief these are MFS – Mobile Free Swimming taxa, MC – Mobile Crawling, MSM – Mobile Slow Moving, SEF – Sessile Epifauna, demersal or Flat, SEP – Sessile Epifauna, Protruding. Due to variable quality of images (i.e. sediment disturbance or deployment failure), not every station had 10 analysable images. All images with a clear and standard view of the seabed (i.e. camera perpendicular to the seabed) were analysed. A minimum of five images were required for a station to be included in the analysis, and summed taxon counts for five images were used to represent each station. Where more than five images were available for a station, a station 'average' was constructed by calculating taxon totals for all possible combinations of 5 images, with median values used to represent the station. Diversity measures, number of taxonomic classes, simpson diversity, shannon index and taxonomic evenness were calculated on the final station data using the vegan package of R (Oksanen *et al.,* 2013).

Stations were classified as either 'hard' or 'soft' substratum sites by visual inspection of the images (Yesson *et al.,* 2015). Sites were classified as 'hard' where some evidence of rocky surfaces were present (including sites with substantial rocky components located on soft substratum). Hard and mixed substrata can support an abundance of emergent epifauna, while soft substrata are normally characterised by burrowing or motile infauna (Watling and Norse, 1998).

Fishing data

Data on trawling effort for all fisheries has been collected by the Greenland Institute of Natural Resources until 1999, and since then by the Greenland Fishery and License Control. The fleet is required to keep log books of the time, position and depth of seabed at the start and end of every commercial trawl. This requirement was introduced for vessels of more than 50 gross register tonnage in 1986 and applied to all vessels since 1997. Trawls were represented as straight lines and overlaid on a 3.5km x 3.5km grid. Cumulative time trawled was calculated for each grid cell by summing the duration of the trawls overlapping the cell, proportionate with the length of the trawl overlapping that cell (i.e. if a trawl starts in the middle of one 3.5 x 3.5 km cell and finishes in the middle of the adjacent cell then 50% of the trawl duration will be assigned to each cell's total). The 1st

and 99^{th} percentile of trawls were discarded based on duration of trawl in an effort to remove outliers and erroneous data (a small number of trawls were reported to last zero minutes or in excess of one day). Annual grids of cumulative minutes trawled were constructed for the period 1986-2013.

A metric of 'recovery' time was calculated by counting the number of years since a station had been trawled (e.g. recovery of 0 was assigned if the area was trawled in the previous year). Additionally, total cumulative minutes trawled was calculated by summing the annual cumulative trawl minutes at each station for the 10 years prior to sampling.

Environmental data

The TOPAZ4 Arctic Ocean Reanalysis three dimensional oceanographic model (http://marine.copernicus.eu/documents/PUM/CMEMS-ARC-PUM-002-ALL.pdf) was used to estimate environmental conditions for each station. This is a 2.5D grid of with data for depth tiers of 5, 30, 50,100, 200, 400, 700m in our study area, each tier has a resolution of 12.25km x 12.25km. Measures of temperature, salinity, current speed and sea ice coverage were extracted based on the location and depth of each station. A 2 stage interpolation was carried out: first depth tiers above and below the station depth were extracted using the 'extract' tool from the 'raster' library of the statistical software R (Hijmans, 2015) using the bilinear interpolation method. Subsequently a linear interpolation between the depth tiers above and below the reported station depth was used to assign a value to the station.

Other (2 dimensional) environmental variables were selected for analysis. The topographic environment metrics of slope and rugosity were calculated from the IBCAO v4 bathymetry grid using the gdaldem software. Finally, the SAR sea iceberg concentration dataset (http://marine.copernicus.eu/documents/pum/cmems-osi-pum-011-007.pdf) was used as a measure of potential iceberg scouring (referred to in the text as iceberg concentration). These data record the number of icebergs per 10 x 10 km grid cell. Tiles representing sweeps of satellites were stitched together and normalised based on the number of observations and annualised.

Modelling

Linear regression models are a widely used tool for investigating associations between a response variable and independent explanatory variables. Model formulas followed the form: diversity (response) ~ environmental variables + trawling impact (explanatory) and were performed for each diversity measure using the 'lm' function in the statistics package R version 3.1.3 (R Core Team, 2015). Abundance values (counts of number of individuals observed at each station) were log transformed prior to analysis. The environmental variables slope, current speed, iceberg concentration and cumulative minutes trawled were log transformed to normalise their distribution profiles. Correlation between explanatory variables was assessed by an iterative process of variance inflation factor (VIF) calculation and removal of the variable with the highest correlation (VIF score) until all variables showed low correlation (VIF<5) (Heiberger and Holland 2004). VIF calculations were performed using the R library HH (Heiberger 2015). . The variables temperature, current speed, depth, slope, iceberg concentration, cumulative minutes trawled and recovery time were selected for the final model process. These were chosen to represent a set of ecologically meaningful, uncorrelated set of environmental descriptors.. In Greenland we see significant differences in community composition and abundance of organisms on different types of seabed, soft sediment areas are inhabited by more burrowing organisms, and areas with more rocks include more potentially vulnerable, attached, erect organisms (Yesson et al., 2015). Therefore models were run separately for sites on soft/hard seabed to investigate whether response to fishing pressure differed on hard and soft ground.

Linear models based on all variables were subjected to stepwise deletion of insignificant variables (R Core Team, 2015). The calc.relimp function in the package 'relaimpo' (Grömping, 2006) was used to calculate the relative importance of each variable (measured as the proportion of variance explained).

Linear models carry assumptions about the data to be analysed, and violating these assumptions can result in erroneous or misleading results. Checking the validity of model assumptions is a useful way of examining the quality and reliability of models (Peña and Slate, 2012). The 'gvlma' R library was used to test assumptions of skewness, kurtosis, heteroscedascity, validity of link function and a global validity of model assumptions (Peña and Slate, 2014). The 'car' package (Fox and Weisberg, 2011) was used to test constancy of error variance (ncvTest function), and residual autocorrelation (DurbinWatsonTest function). Finally spatial autocorrelation of residuals was checked with the lm.morantest function from the R package 'spdep' (Bivand and Piras, 2015). These tests of model assumptions were measured as failed if $p<0.01$ after Bonferroni correction of p-values (to correct for multiple comparisons).

The study area covers a wide latitudinal gradient (60-72°N), with stations up to 1,400km apart. The environment varies greatly over this area. Factors such as depth and temperature are known to influence diversity patterns, so it is important to disentangle the effect of environmental variation from site comparisons. A direct comparison of diversity and fishing will be confounded by the environmental variation over this area. One approach, to remove potential confounding factors from the analysis, is to compare the target explanatory variable (i.e. fishing effort) with the component of the response variable (i.e. abundance) not explained by environment, by examining the residuals of a linear model of abundance~environment (Fox & Weisburg, 2011).

A measure of abundance corrected for environmental biases was constructed by extracting the residuals of linear models of the form: abundance ~ temperature + current + icebergs + depth + slope. This residual abundance variable was highly correlated with the raw abundance measure but removed the information component of the underlying environmental gradient. This variable was treated as a 'corrected' abundance measure, with high (positive) values signifying greater abundance and low (negative) values indicating low abundance. A direct assessment of trawling impact was made by comparing residual abundance with the presence/absence of trawling in the past 10 years (termed recently trawled / recently untrawled), an analysis of variance was performed to test for significant difference between the recently trawled and recently untrawled groups using R version 3.13 (R Core Team, 2015). Box plots of residual abundance by recently trawled / untrawled groups were examined to visualise the spread of data within these groups.

An investigation of temporal trends was performed by changing the duration of time used to define “recently trawled” and “recently untrawled” groups. Every possible time period was trested, starting with defining the “recently trawled” group as sites fished only in the previous year, and ending with sites classified as “recently trawled” if they had been impacted any time in the past 25 years. Sites were divided into “recently trawled” and “recently untrawled” groups using each possible temporal definition, and abundance and diversity of each group were compared using boxplots and associated statistics. The median and confidence intervals generated by the boxplot.stats function were used to plot temporal trends for the recently trawled / untrawled groups (Chambers *et al.,* 1983).

Results

A total of 201 stations were analysed (Table 1). These incorporated 113 soft sediment sites and 88 on hard substrata. More than 92,000 taxon observations were made at these sites. The most abundant site included 2,951 taxonomic observations, whilst only 6 observations were made at the least abundant site. More than half of taxonomic observations were of class Polychaeta. The next most frequent class was Ophiuroidea representing just over 10% of observations. A full taxonomic profile of these data is presented in Yesson *et al.* (2015). Typically, more diversity and abundance was seen at sites on hard substrata. There is a significant negative correlation of diversity and latitude (Pearson's $r = -0.38$, $p<0.001$), but high-diversity sites are found over the full range of the study area (Figure 1).

The compilation of fishing impact data required the examination of more than 1 million trawls spanning 1986-2013. Average trawl duration was 238 minutes. Trawling is most widespread in the area surrounding Disko Bay (Figure 1). Since 1986 82% of our study area has been subject to some trawling impact (study area as Figure 1, limited to 200-500m depth zone). 174 (87%) of our sampling sites are in areas with some trawling activity. If we consider only the past decade then 121 (60%) stations are in trawl-impacted areas, and 62 of these were trawled in the last year (zero recovery time). Total cumulative trawling times range from negligible (~1 minute) to 3600 hours (more than 100 hours per year). Fishing impact is linked with environmental conditions; more trawling occurs on soft sediment sites (median trawl time of 110 hours, compared to 40 hours on hard sediments), and environmental conditions vary significantly over hard and soft ground (e.g. current speed is faster on hard ground – Supplementary Appendix 2). Furthermore, recently-trawled sites are environmentally distinct on both hard and soft substrates, for example icebergs are more common in fished areas on soft sediment, but less common in fished areas on hard ground (Supplementary Appendix 2).

Diversity and abundance are correlated with many environmental factors (Supplementary Appendix 3). Notably overall abundance is significantly negatively correlated with cumulative trawling time, and positively correlated with recovery time. The study region covers a wide latitudinal and environmental gradient, but the effect of trawling can still be seen in multivariate analysis that incorporates environmental factors (Table 2, Supplementary Appendix 4). Trawling intensity explains 12/16% of variance in overall abundance on hard/soft substrata and is the most important factor. The functional group of sessile flat (SEF) organisms (i.e. encrusting sponges or encrusting bryozoa) are not impacted by measures of trawling effort. In contrast the abundance of sessile protruding taxa (SEP – including cold water corals and large sponges) show significant relationships with trawling intensity. Temperature, depth and iceberg concentration are important factors for predicting taxon abundance.

The complex picture of multiple environmental drivers to diversity and abundance was simplified by examining the influence of trawling pressure on a 'corrected' measure of abundance that removes the influence of environmental biases. This 'residual abundance' measure is highly correlated with abundance (Pearson correlation coefficient 0.92 ($p<0.001$) on hard substrate and 0.89 ($p<0.001$) on soft substrate), but strips out potentially confounding environmental correlates from the analysis. A simplified picture of trawling impact on residual abundance is presented in Figure 2. Overall this corrected (residual) abundance measure is significantly different between recently trawled and untrawled sites (recently trawled means some trawling in the past 10 years). Residual abundance is significantly higher in untrawled areas (this pattern is repeated for raw abundance values), and this is driven by patterns observed for taxonomic classes Anthozoa and Ophiuroidea. These were the only common classes showing significant differences ($p<0.01$).

The 10 year cut-off for classifying sites as trawled or untrawled is a somewhat arbitrary choice. A choice of 5 years rather than 10, creates a more marked difference in abundance levels between “recently trawled” and “recently untrawled” sites (Figure 3 a). Conversely, if we change the definition of “recently untrawled” to no activity for the past 20 years then we cannot distinguish abundance between recently trawled and untrawled groups (Figure 3 a). Investigating the choice of time period to define recently trawled/untrawled sites creates a time series that gives insight into potential recovery (Figure 3). If we separate our sites by hard/mixed and soft substrata (Figure 4), there is a strong signal of longer-lasting impact on hard/mixed ground and a relatively short-term impact on soft sediments, but it is noted that the confidence intervals are wider on these reduced sample sizes.

Discussion

Trawling & environment

Trawling impact is a significant factor determining abundance, diversity and community composition on both muddy and rocky seabeds in West Greenland. Temperature, depth, current speed and substrata are also important factors influencing abundance (notably temperature is the most important factor for many groups in rocky areas). Iceberg concentration (a proxy for iceberg scouring events) is a natural (but temporally irregular) disturbance regime that influences abundance of some groups. Iceberg concentration is focussed towards the coastline of West Greenland (Figure 1) and will primarily impact the Disko area of this study. Many environmental parameters are known to influence the distributions of many benthic taxa (i.e. global cold water coral distributions Yesson *et al.,* 2012) and our findings are in keeping with previous studies in Greenland (Yesson *et al.,* 2015, Piepenburg & Schmid, 1996). Although trawling is found to be the most significant factor, the proportion of variance explained by trawling in the models is relatively low (12-16% for overall abundance). Other studies, using a variety of different approaches, report higher variance explained by trawling, for example Hinz et al. (2009) report r^2 of 0.46 for models of infauna and epifauna abundance based on fishing intensity, but this example followed a strict experimental design to keep environmental variables constant.

Taxonomic & functional groups

Taxonomic groups expected to be vulnerable to the effects of trawling show cumulative impact and recovery time as significant influencing factors. For example Anthozoa, Porifera and other fixed organisms that live erect in the water column (sessile protruding taxa) show a significant response to cumulative trawling time. This is in line with studies showing some arborescent and emergent growth forms as vulnerable to trawling (Asch & Collie, 2008; Buhl-Mortensen *et al.*, 2016; Jørgensen *et al.*, 2016). However, the soft corals observed in the area are predominantly Octocorallia from the family Nephtheidae, and this group were not considered to be sensitive taxa in the benthic impact assessment of the Gulf of St Lawrence shrimp trawl fishery (DFO, 2012), and Nephtheidae show a positive correlation with fishing intensity in the Barents Sea (Buhl-Mortensen *et al.,* 2016). Nephtheidae have been shown to recover quickly from experimental crushing impacts (Henry *et al.,* 2003).

In contrast, the sessile prostrate/encrusting groups (such as encrusting sponges and bryozoa) are not influenced by our measures of trawling intensity. These groups are less likely to be caught by trawl nets and are expected to be more resilient to trawling impact (Jørgensen *et al.*, 2016). Indeed, encrusting bryozoans are one of the few immobile benthic fauna shown to benefit from trawling disturbance due to rapid colonisation speed in post-disturbed habitat (Asch & Collie, 2008), although this study was from the shallows (40-90m) of the temperate (40°N) Georges Bank. No significant impact was found for Bryozoa in the Barents (Buhl-Mortensen *et al.,* 2016). However, we do see a significant negative response in these groups to high iceberg concentration, suggesting a negative effect of natural disturbance on abundance. Despite their fast growth rates, encrusting bryozoans are susceptible to smothering by suspended sediment, which may be evident at sites with prolonged repeat disturbance (Jones, 1992).

Some groups are expected to benefit from trawling, such as scavenging members of the brittle star class Ophiuroidea (Engel & Kvitek, 1998), or at least be low risk from negative impacts (Jørgensen *et al.*, 2016). In contrast, our study shows a significant negative response to trawling for this group. The coarse temporal scale of our dataset (annual/decadal measures of trawling) may not be able to detect the short-term, transient scavenging response to disturbance (Bergmann *et al.,* 2002). Furthermore, brittle stars are also susceptible to physical damage from trawling and have been found to decrease in abundance in highly impacted study sites (Freese *et al.,* 1999), and an insignificant negative response to fishing pressure is reported for Ophiuroids in the Barents (Buhl-Mortensen *et al.,* 2016).

One notable positive response to trawling impact is the abundance of class Maxillopoda (mostly observations of barnacles). These are most abundant in rocky areas that have been recently trawled with abundance peaking for sites with intermediate levels of cumulative trawling. This may be an example of the intermediate disturbance hypothesis (Dial and Roughgarden, 1988).

Time & Recovery

The majority of the western Greenland shelf (below 72°N) has been trawled at some point in the past quarter century, which is in line with global trends (Kaiser *et al.,* 2002). In such circumstances it is difficult to find comparable sets of trawled and untrawled locations, so examining a gradient of fishing impact may be the best alternative (see Kaiser *et al.*, 2006). Many studies of fishing impact focus on cumulative or average trawling area over recent years (e.g. Bolam *et al.,* 2014; Pusceddu *et al.,* 2014). This focus on recent impact may be due to the availability of fishing data, but if the negative impacts are felt most strongly by slow-growing, long-lived (and often habitat-forming) organisms (Clark *et al.,* 2016), then longer-term fishing impacts should be considered. The quarter-century of data available for the Greenlandic shrimp fishing fleet is an unusually detailed and lengthy time series that provides an opportunity to examine longer term patterns (see also Moritz *et al.,* 2016). However, even this extensive dataset does not cover half the duration of the fisheries' operation and decades of trawling activity (pre-1986) are unaccounted for in this study. If the first impact has a significant and potentially long-lasting negative effect on the most vulnerable benthic fauna (i.e. Cook *et al*., 2013) and longer-term impacts have no significant additional influence (Moritz *et al*., 2016) then we may expect a limited signal from our analysis of trawling effort.

This study shows an immediate negative impact of trawling, followed by a period of recovery (at least for total abundance). There appears to be greater resilience in soft sediment communities, which is in line with many previous findings (reviewed in Clark *et al*., 2015). However, these analyses are focussed on recovery in overall abundance levels, but peak abundance of organisms may occur during successional phases of habitat restoration, and climax communities may be characterised by a smaller number of larger organisms. Furthermore, post-disturbance communities of small mobile infaunal species may constitute an alternate stable state with no potential for recovery to the previous complex community (Kaiser *et al.,* 2002).

Methodology

The abundance measure used in these analyses favours a large number of small organisms, which may favour organisms expected to benefit from disturbance (Thrush and Dayton 2002). However, overall biomass is an important measure, particularly for habitat forming and colonial organisms, where climax communities may be represented as a small number of larger individuals/colonies. The relatively small size of our images may not sample larger, more sparsely distributed organisms, which may be more sensitive to disturbance. Conclusions about the impact of trawling on some taxa regarded as most vulnerable to trawling are limited by the fact that these are generally not well represented in this dataset. For example, we have never observed the large (>1m) seapen *Umbellula* in our images although this is seen as regular bycatch in some areas in West Greenland (Jørgensen *et al.,* 2013). Such large seapens can have multi-decadal lifespans and are vulnerable to trawling (de Moura Neves *et al.,* 2015). However, despite the bias away from potentially more vulnerable organisms, there is a signal of negative impact of trawling in our data. The fact that we are able to document a statistically significant negative impacts on groups of less vulnerable organisms, seems to indicate that the composition of the entire community is altered. Increasing sampling by taking more images per site may help to pick up these rarer taxa in future studies. Alternative methods such as physical sampling (e.g. analysis of bycatch as in Buhl-Mortensen *et al.*, 2016 and Jørgensen *et al.*, 2016, or beam trawling surveys), should complement the present study and potentially sample these vulnerable organisms.

Benthic impact assessments are commonly confounded by interference from effects other than trawling, and this problem is exacerbated as spatial scale increases (Jennings *et al.,* 2005). There are strong environmental gradients over the West Greenland shelf, and this has a significant impact on diversity and abundance (Yesson *et al.,* 2015). The present study seeks to account for potentially confounding environmental factors by employing a multivariate linear modelling approach. The variable importance of trawling metrics in our models is relatively small but significant, as found in other studies (Buhl-Mortensen *et al*., 2015). Additional environmental variables may give greater insight (and better fitting models) in future studies, but relatively low importance values should not negate the impacts of anthropogenic disturbance, which may be transformative in some areas.

Conclusions

Bottom trawling is one of the most widespread human impacts on the sea floor, and has the potential to inflict significant damage on benthic habitats and ecosystems, as has been shown in this study along with numerous others (see reviews Clark *et al*., 2016; Kaiser *et al*., 2002). More detailed and comprehensive assessment of benthic habitats is necessary to improve management of anthropogenic impacts of all kinds, especially in deep water (Martin *et al*., 2015). However, a historical baseline and ongoing monitoring data are missing for many parts of the world, placing limitations on the ability of fisheries to fully understand and effectively mitigate their impacts (Jennings et al 2005, Grieve et al 2015).

This study represents a valuable first step in documenting the effects of bottom trawling on the West Greenland shelf, and has shown a significant negative impact on the overall abundance of epibenthic organisms on the West Greenland shelf. The trawl impact signal is strong for some taxa and functional groups, while environmental factors, including natural disturbance from icebergs, are more important than trawling pressure in determining overall taxon composition and abundance for some groups. Soft sediment communities appear to be more resilient, while the effect on hard substrate can be seen in places trawled a decade ago. This study provides an example of how seabed imaging and analysis at higher taxonomic levels and functional groups can be used to assess the impacts of fishing in a hitherto understudied location, and at a scale that is relevant to fisheries management.

Tables

Table 1. Station summary statistics.

	Hard	Soft	Total
Number of stations	88	113	201
Observations	54,435	38,037	92,472
Classes	29	29	29
Station details			
Abundance			
Min	48	6	6
Median	480	104	258
Max	2460	2945	2945
Classes			
Min	3	1	1
Median	4	4	4
Max	5	5	5
Simpson Diversity			
Min	0.022	0.000	0.000
Median	0.564	0.362	0.486
Max	0.712	0.685	0.712
Trawl Minutes			
Min	0	0	0
Median	145	320	195
Max	99,690	128,600	128,600
Recovery Years			
Min	0	0	0
Median	7	3	6
Max	28	28	28
Depth (m)			
Min	61	68	61
Median	218	230	260
Max	484	725	725

Table 2. Results of multivariate generalised linear models for a series of response variables. All response variables (except Simpson diversity and Number of classes) are log-transformed abundance data for the named group. Functional groups defined in Supplementary Appendix 1. The numbers below the explanatory variables are variable importance (proportion of variance explained by this variable), with variable significance of the linear model denoted by * notation (*** p<0.001, ** p<0.01, * p<0.05). Tests column indicate results of checking model assumptions for 8 measures (skewness, kurtosis, heteroscedascity, constancy of error variance, residual autocorrelation, validity of link function, global validity of model assumptions and spatial autocorrelation of residuals).

Hard/Mixed Substrate		**Variable importance and significance**								
Response	**R^2**	**Temp-erature**	**Current Speed**	**Iceberg Concentration**	**Depth**	**Slope**	**Recovery Years**	**Cumulative Fishing**	**Fishing X Icebergs**	**Tests**
Abundance	0.24		0.10**	0.01	0.04**			0.12***		8/8
Number of Classes	0.08					0.07*	0.03*	0.01		8/8
Simpson Diversity	0.33	0.24***		0.06*	0.03*		0.03*			7/8
Abundance of Functional Groups										
SEP	0.45	0.44***		0.01				0.02*		8/8
SEF	0.25	0.09**		0.10**	0.08**					8/8
MC	0.07		0.05*				0.04*			8/8
MSM	0.21		0.03*	0.08**	0.01	0.03*		0.11***		6/8
Abundance of Taxonomic Groups										
Anthozoa	0.25			0.11**		0.11***		0.06*		8/8
Ascidiacea	0.52	0.50***		0.03**						8/8
Bryozoa (encrusting)	0.15			0.07*	0.10**					8/8
Bryozoa (soft)	0.52	0.21**	0.21	0.01**	0.06**		0.02	0.01	0.03*	8/8
Bryozoa (stony)	0.33	0.31***						0.04*		8/8
Hydrozoa	0.54	0.24*	0.30***				0.01*	0.01		8/8
Maxillopoda	0.34	0.17***		0.01	0.06*		0.13***			8/8
Ophiuroidea	0.33	0.22***			0.09**			0.03		8/8
Polychaeta	0.19			0.14***	0.02*			0.05**		8/8
Porifera (encrusting)	0.20	0.12**		0.09**				0.02		8/8
Porifera (massive)	0.30	0.22***		0.01	0.08**			0.02*	0.01	8/8

Soft Substrate		**Variable importance and significance**								
Response	**R^2**	**Temp-erature**	**Current Speed**	**Iceberg Concentration**	**Depth**	**Slope**	**Recovery Years**	**Cumulative Fishing**	**Fishing X Icebergs**	**Tests**
Abundance	0.28			0.00**			0.07	0.16***	0.08***	7/8
Number of Classes	0.08			0.02				0.07**		8/8
Simpson Diversity	0.07			0.02		0.03*		0.00	0.05*	8/8
Abundance of Functional Groups										
SEP	0.33	0.07*	0.02	0.07***	0.06**			0.15**		8/8
SEF	0.07			0.07**	0.01					8/8
MC	0.22			0.13**		0.07*	0.02*	0.02*		8/8
MSM	0.21	0.06		0.00*				0.11***	0.06**	7/8
Abundance of Taxonomic Groups										
Anthozoa	0.21			0.01	0.14***			0.08*		8/8
Ascidiacea	0.36		0.03*	0.08***	0.07***	0.05		0.12***	0.04**	8/8

Bryozoa (encrusting)	0.05									7/8
Bryozoa (soft)	0.36	0.14***		0.03*	0.05*		0.16***			8/8
Bryozoa (stony)	0.18	0.04		0.06***	0.02		0.02*	0.04**	0.03*	8/8
Hydrozoa	0.11		0.02		0.11***					6/8
Maxillopoda	0.27	0.06			0.15***			0.07		8/8
Ophiuroidea	0.12	0.06*			0.04**	0.02*		0.04*		7/8
Polychaeta	0.07			0.00	0.02			0.03*	0.04*	5/8
Porifera (encrusting)	0.05			0.03*	0.03*			0.01	0.02	8/8
Porifera (massive)	0.10			0.03**			0.04**	0.03***	0.03*	8/8

Figures

Figure 1. Map showing stations analysed for this study. Stations on hard substrate are shown as triangles, soft sediment sites are circles. All stations are coloured relative to diversity (White = Simpson diversity of 0, Darkest green = Simpson diversity 0.7). Trawling intensity is based on cumulative hours trawled for all records (1986-2013).

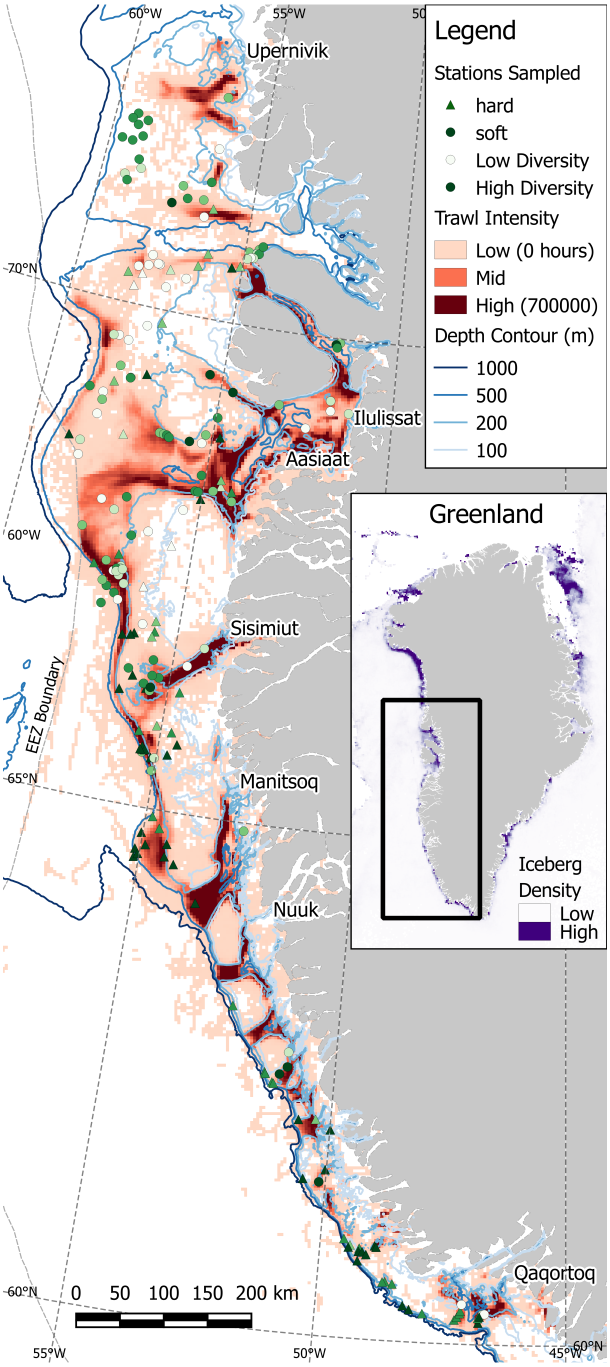


Figure 2. Box plots of residual abundance for recently trawled and recently untrawled sites. Residual abundance is the component of abundance that is not explained by the environment (using residuals of a linear model, diversity~environment (excluding trawling effort), removes the influence of different environments from the comparison of trawled and untrawled sites). Plots show the range of data (lines), with outliers represented as dots, the main box is approximately the first and third quartile, and the black line shows the median, the 'notch' around the black line shows an approximate 95% confidence interval for the median. Recently trawled sites are defined as those areas with any non-zero level of trawling recorded in the 10 years prior to sampling. Star notation indicates significance level of an analysis of variance: *** p<0.001; ** p<0.01.

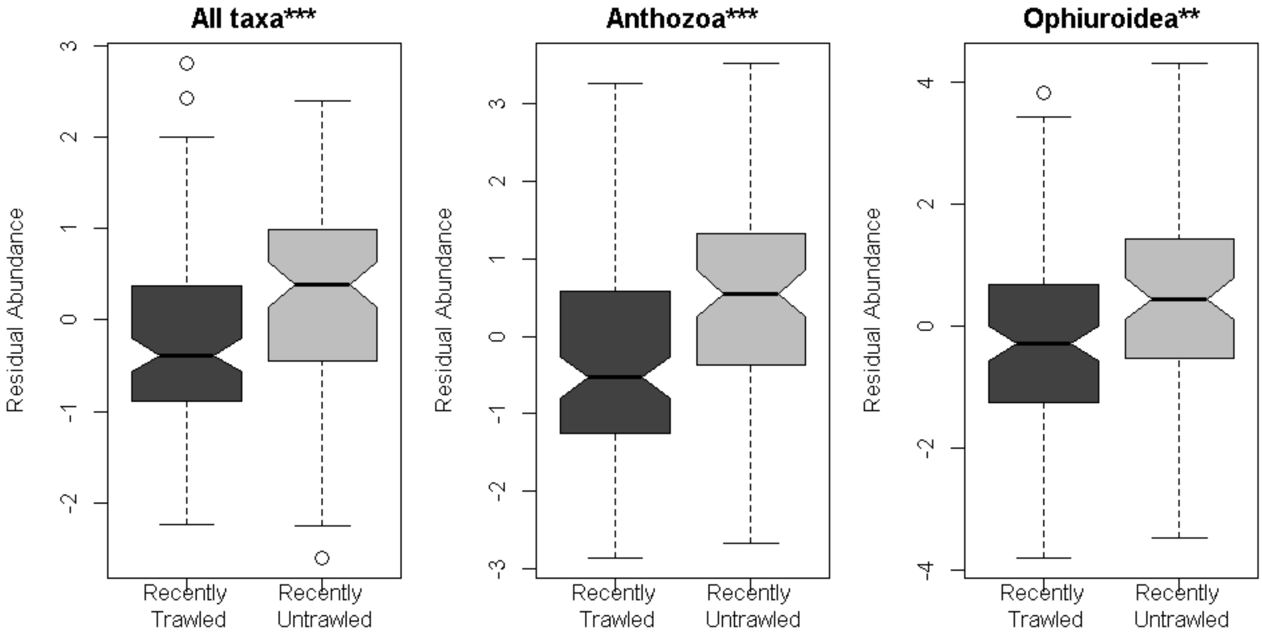


Figure 3. Investigation of the influence of the time period used to define recently trawled / untrawled sites. a) Box plots comparing residual abundance of sites that have been trawled/untrawled in the past 5/10/20 years. Using a 5 year definition, we see a significant difference in abundance levels for trawled and untrawled sites (box notches do not overlap). However, there is no significant difference between trawled/untrawled sites using the 20 year definition (notches overlap). b) Plotting all possible definitions of recently trawled and untrawled sites allows us to generate a time series. c) Focussing on the notches of the box plots shows that the notches overlap at the 20 year period. d) Removing the original boxplots simplifies the figure to highlight group means and confidence intervals.

521

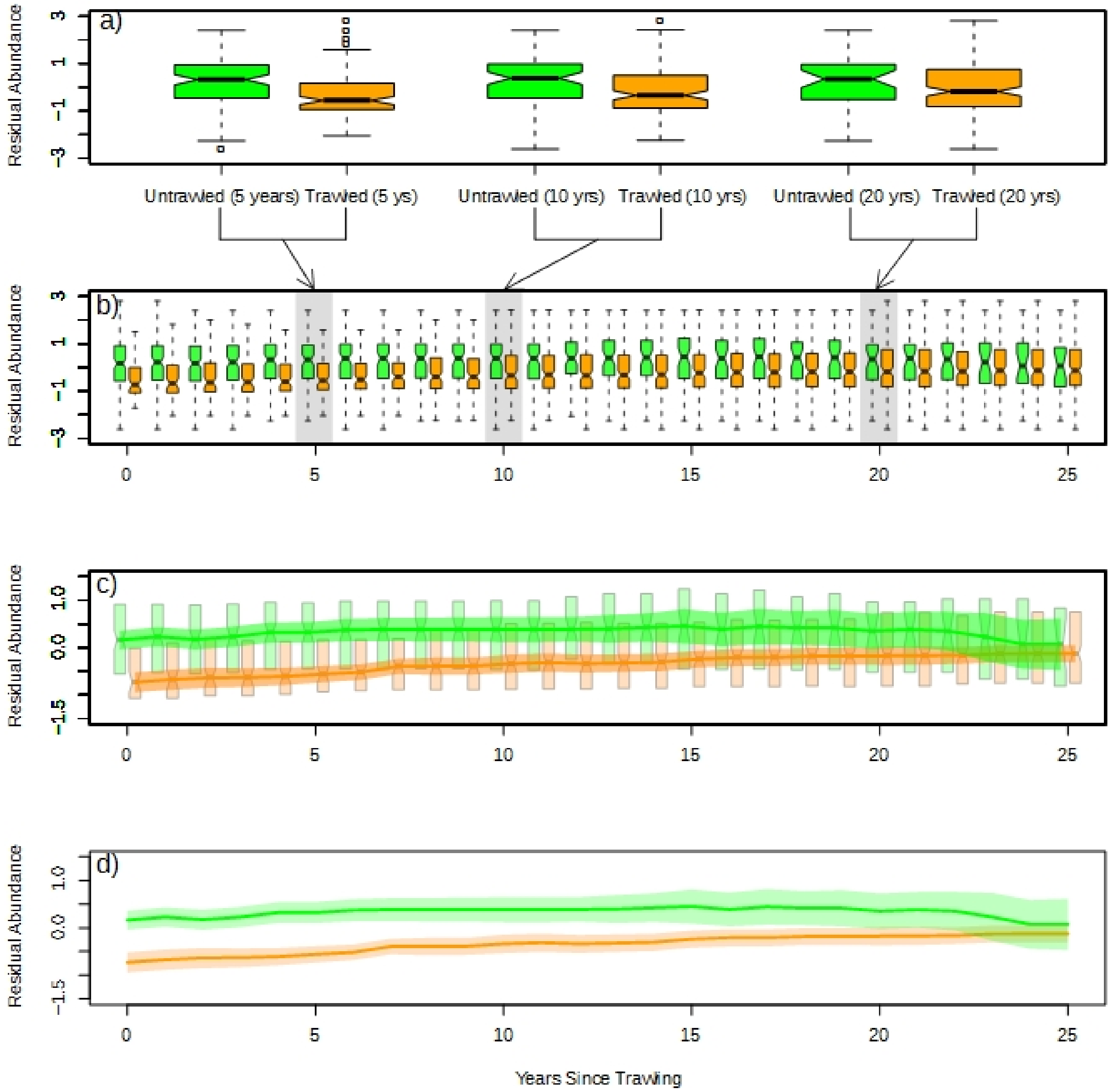
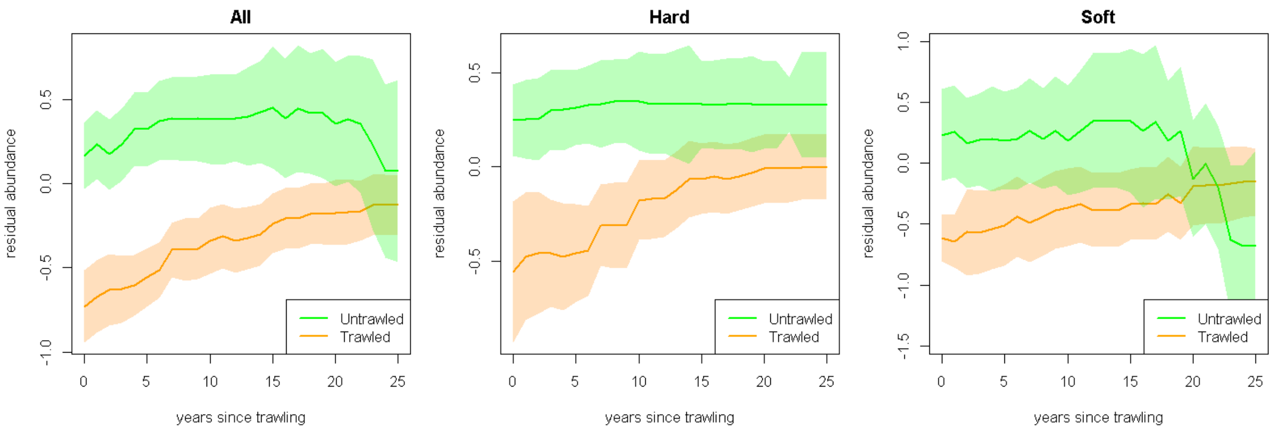

a)
b)
c)
d)
Residual Abundance
Untrawled (5 years) Trawled (5 ys)
Untrawled (10 yrs) Trawled (10 yrs)
Untrawled (20 yrs) Trawled (20 yrs)
Years Since Trawling

Figure 4. Time series showing the difference in abundance between recently trawled and recently untrawled sites. The time series shows the effect of changing the definition of 'recently', where recently trawled sites are any site that has some trawling activity in the past X years and recently untrawled sites are those which have had none in that same time period. Lines show median values and confidence intervals (based on boxplot statistics). All, hard and soft refer to substrate classification of stations. Note there is a very small sample size of soft sediment stations recently untrawled for X=23-25 years.



References

Asch, R. G., and Collie, J. S. 2008. Changes in a benthic megafaunal community due to disturbance from bottom fishing and the establishment of a fishery closure. Fisheries Bulletin, 106: 438–456.

Blanchard, F., LeLoc'h, F., Hily, C., and Boucher, J. 2004. Fishing effects on diversity, size and community structure of the benthic invertebrate and fish megafauna on the Bay of Biscay coast of France. Marine Ecology Progress Series, 280: 249–260.

Boertmann, D., and Mosbech, A. (eds) 2011. Eastern Baffin Bay-A strategic environmental impact assessment of hydrocarbon activities. DCE Danish Centre for Environment and Energy, Aarhus University, Aarhus.

Bolam, S. G., Coggan, R. C., Eggleton, J., Diesing, M., and Stephens, D. 2014. Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: A biological trait approach. Journal of Sea Research, 85: 162–177.

Buch, E., Pedersen, S. A., and Ribergaard, M. H. 2004. Ecosystem Variability in West Greenland Waters. Journal of Northwest Atlantic Fishery Science, 34: 13–28.

Buhl-Mortensen, L., Ellingsen, K. E., Buhl-Mortensen, P., Skaar, K. L., and Gonzalez-Mirelis, G. 2016. Trawling disturbance on megabenthos and sediment in the Barents Sea: chronic effects on density, diversity, and composition. ICES Journal of Marine Science: Journal du Conseil, 73(suppl 1): i98-i114.

Buhl-Mortensen, L., Vanreusel, A., Gooday, A. J., Levin, L. a., Priede, I. G., Buhl-Mortensen, P., and Raes, M. 2010. Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Marine Ecology, 31: 21–50.

Burd, B. J. 2002. Evaluation of mine tailings effects on a benthic marine infaunal community over 29 years. Marine Environmental Research, 53: 481–519.

Chambers, J. M., Cleveland, W. S., Kleiner, B. and Tukey, P. A. 1983. Graphical Methods for Data Analysis._Wadsworth & Brooks/Cole. New Jersey. 395 p.

Clark, M. R., Althaus, F., Schlacher, T. A., Williams, A., Bowden, D. A., and Rowden, A. A. 2016. The impacts of deep-sea fisheries on benthic communities: a review. ICES Journal of Marine Science: Journal du Conseil, 73(suppl 1): i51-i69.

Collie, J. S., Escanero, G. A., and Valentine, P. C. 2000. Photographic evaluation of the impacts of bottom fishing on benthic epifauna. ICES Journal of Marine Science: Journal du Conseil, 57: 987–1001.

Conlan, K. E., Lenihan, H. S., Kvitek, R. G. and Oliver, J. S. 1998. Ice scour disturbance to benthic communities in the Canadian High Arctic. Marine Ecology Progress Series,166: 1-16.

Cook, R., Fariñas-Franco, J. M., Gell, F. R., Holt, R. H., Holt, T., Lindenbaum, C., Porter, J. S., Seed, R., Skates, L.R., Stringell, T.B., and Sanderson, W. G. (2013). The substantial first impact of bottom fishing on rare biodiversity hotspots: a dilemma for evidence-based conservation. PloS one, 8(8): e69904.

Curtis, J. M. R., Poppe, K., and Wood, C. C. 2013. Indicators, impacts and recovery of temperate deepwater marine ecosystems following fishing disturbance. Fisheries and Oceans Canada, Canadian Science Advisory Secretariat. Available from http://publications.gc.ca/collections/collection_2013/mpo-dfo/Fs70-5-2012-125-eng.pdf.

Danovaro, R., Gambi, C., Dell'Anno, A., Corinaldesi, C., Fraschetti, S., Vanreusel, A., Vincx, M., and Gooday, A. J. 2008. Exponential Decline of Deep-Sea Ecosystem Functioning Linked to Benthic Biodiversity Loss. Current Biology, 18: 1–8.

DFO. 2012. Assessment of the Impact of Northern Shrimp Trawling on Benthic Habitats Communities in the Estuary and Northern Gulf of St Laurence. Quebec.

Dial, R., and Roughgarden, J., 1998. Theory of marine communities: the intermediate disturbance hypothesis. Ecology, 79: 1412-1424.

Engel, J., and Kvitek, R. 1998. Effects of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary. Conservation Biology, 12: 1204-1214.

Freese, L., Auster, P. J., Heifetz, J., and Wing, B. L. 1999. Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. Marine Ecology Progress Series, 182:119–126.

Fox, J., and Weisberg, S. 2011. An {R} Companion to Applied Regression, Second Edition. Thousand Oaks CA: Sage.

Grömping, U. 2006. Relative Importance for Linear Regression in R: The Package relaimpo. Journal of Statistical Software, 17: 1–27.

Grieve, C., Brady, D. C., and Polet, H. 2015. Best practices for managing, measuring and mitigating the benthic impacts of fishing. Marine Stewardship Council Science Series, 3: 81–120.

Gutt, J., 2001. On the direct impact of ice on marine benthic communities, a review. Polar Biology, 24: 553-564.

Hall, S.J. 1999. The Effects of Fishing on Marine Ecosystems and Communities. Oxford: Blackwell Science.

Hammeken Arboe, N. 2014. The Fishery for Northern Shrimp (*Pandalus borealis*) off West Greenland, 1970-2014. NAFO SCR Doc. 14/061.

Hammeken Arboe, N. 2015. Catch Table Update for the West Greenland Shrimp Fishery. NAFO SCR 15/049 Seriel No. N6484.

Hijmans, R. J. 2015. raster: Geographic Data Analysis and Modeling. R package version 2.3-33.

Heiberger, R. M. 2015. HH: Statistical Analysis and Data Display: Heiberger and Holland. R package version 3.1-23.

Heiberger, R. M., and Holland, B. 2004. Statistical Analysis and Data Display: An Intermediate Course with Examples in S-Plus, R, and SAS. Springer-Verlag, New York.

Henry, L., Kenchington, E. L. R., and Silvaggio, A. 2003. Effects of mechanical experimental disturbance on aspects of colony responses, reproduction, and regeneration in the cold-water octocoral Gersemia rubiformis. Canadian Journal of Zoology, 81: 1691–1701.

Hiddink, J. G., Jennings, S., Kaiser, M. J. 2007. Assessing and predicting the relative impacts of disturbance on habitats with different sensitivities. Journal of Applied Ecology, 44: 405-413.Hiddink, J. G., Jennings, S., Kaiser, M. J., Queirós, A. M., Duplisea, D. E., and Piet, G. J. 2006. Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. Canadian Journal of Fisheries and Aquatic Sciences, 63: 721-736.

Hinz, H., Prieto, V., and Kaiser, M. J. 2009. Trawl disturbance on benthic communities: chronic effects and experimental predictions. Ecological Applications, 19: 761-773.

Hixon, M. A., and Tissot, B. N. 2007. Comparison of trawled vs untrawled mud seafloor assemblages of fishes and macroinvertebrates at Coquille Bank, Oregon. Journal of Experimental Marine Biology and Ecology, 344: 23–34.

Jennings, S. 2005. Indicators to support an ecosystem approach to fisheries. Fish and Fisheries, 6: 212–232.

Jennings, S., and Kaiser, M. J. 1998. The effects of fishing on marine ecosystems. Advances in Marine Biology, 34: 201-352.

Jones, J. B. 1992. Environmental impact of trawling on the seabed: A review. New Zealand Journal of Marine and Freshwater Research, 26: 59–67.

Jørgensen, L. L., Ljubin, P., and Skjoldal, H. R. 2015 Distribution of benthic megafauna in the Barents Sea: baseline for an ecosystem approach to management. ICES Journal of Marine Science, 72: 595–613.

Jørgensen, L. L., Planque, B., Thangstad, T. H., and Certain, G. 2016. Vulnerability of megabenthic species to trawling in the Barents Sea. ICES Journal of Marine Science: Journal du Conseil, 73 (suppl 1): i84-i97

Jørgensen, O. A., Tendal, O. S., and Hammeken Arboe, N. 2013 Preliminary mapping of the distribution of corals observed off West Greenland as inferred from bottom trawl surveys 2010-2012. NAFO SCR Doc. 13/07.

Jørgensen, O. A., Bastardie, F., and Eigaard, O. R. 2014. Impact of deep-sea fishery for Greenland halibut (*Reinhardtius hippoglossoides*) on non-commercial fish species off West Greenland. ICES Journal of Marine Science: Journal du Conseil, 71.4: 845-852.

Kahn, A. S., Yahel, G., Chu, J. W. F., Tunnicliffe, V., and Leys, S. P. 2015. Benthic grazing and carbon sequestration by deep-water glass sponge reefs. Limnology and Oceanography, 60: 78–88.

Kaiser, M., Collie, J., Hall, S. Jennings, S., and Poiner, I. R. 2002. Modification of marine habitats by trawling activities: prognosis and solutions. Fish and Fisheries, 3: 114–136.

Kaiser, M. J., Clarke, K. R., Hinz, H., Austen, M. C. V., Somerfield, P. J., and Karakassis, I. 2006. Global analysis of response and recovery of benthic biota to fishing. Marine Ecology Progress Series, 311: 1-14.

Kenchington, E. L. R., Prena, J., Gilkinson, K. D., Gordon Jr., D. C., MacIsaac, K., Bourbonnais, C., and Vass, W. P. 2001. Effects of experimental otter trawling on the macrofauna of a sandy bottom ecosystem on the Grand Banks of Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences, 58: 1043–1057.

Lambert, G., I., Jennings, S., Kaiser, M., J., Hinz, H, Hiddink, J., G. 2011 Quantification and prediction of the impact of fishing on epifaunal communities. Marine Ecology Progress Series 430:71-86

Lassen, H., Powles, H., Bannister, C., and Knapman, P. 2013 Marine Stewardship Council (MSC) Final report and determination for the west greenland cold water prawn trawl fishery client. Available from (https://www.msc.org/track-a-fishery/fisheries-in-the-program/certified/arctic-ocean/West-Greenland-Coldwater-Prawn/assessment-downloads-1/20130122_FR_PRA126.pdf)

Lenihan, H. S., and Oliver, J. S., 1995. Anthropogenic and natural disturbances to marine benthic communities in Antarctica. Ecological Applications, 5: 311-326.

Martin, C. S., Tolley, M. J., Farmer, E., Mcowen, C. J., Geffert, J. L., Scharlemann, J. P. W., Thomas, H. L., van Bochove, J. H., Stanwell-Smith, D., Hutton, J. M., and Lascelles, B. 2015. A global map to aid the identification and screening of critical habitat for marine industries. Marine Policy, 53: 45-53.

McConnaughey, R. A., Mier, K. L., and Dew, C.B. 2000. An examination of chronic trawling effects on soft-bottom benthos of the eastern Bering Sea. ICES Journal of Marine Science, 57: 1377–1388.

Moritz, C., Gravel, D., Savard, L., McKindsey, C. W., Brêthes, J. C., and Archambault, P. 2015. No more detectable fishing effect on Northern Gulf of St Lawrence benthic invertebrates. ICES Journal of Marine Science: Journal du Conseil, 72(8): 2457-2466.

de Moura Neves, B., Edinger, E., Layne, G. D., and Wareham, V. E. 2015. Decadal longevity and slow growth rates in the deep-water sea pen *Halipteris finmarchica* (Sars, 1851) (Octocorallia: Pennatulacea): implications for vulnerability and recovery from anthropogenic disturbance. Hydrobiologia, 759(1): 147-170.

Myers, P. G., Kulan, N., and Ribergaard, M.H. 2007. Irminger Water variability in the West Greenland Current. Geophysical Research Letters, 34: L17601.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., and Wagner, H. 2013. vegan: Community Ecology Package. R package version 2.0-10. (http://CRAN.R-project.org/package=vegan)

Pena, E.A, and Elizabeth, H.S. 2014. gvlma: Global Validation of Linear Models Assumptions. R package version 1.0.0.2.

Piepenburg, D., and Schmid, M.K. 1996. Distribution, abundance, biomass, and mineralization potential of the epibenthic megafauna of the Northeast Greenland shelf. Marine Biology, 125: 321–332.

Pusceddu, A., Bianchelli, S., Martin, J., Puig, P., Palanques, A., Masqué, P., and Danovaro, R. 2014. Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. Proceedings of the National Academy of Sciences, 111: 8861–8866.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramsay, K., Kaiser, M., and Hughes, R. 1996. Changes in hermit crab feeding patterns in response to trawling disturbance. Marine Ecology Progress Series, 144: 63-72.

Robert, K., Jones, D., and Huvenne, V. 2014. Megafaunal distribution and biodiversity in a heterogeneous landscape: the iceberg-scoured Rockall Bank, NE Atlantic. Marine Ecology Progress Series, 501: 67–88.

Bivand, R., and Piras, G. 2015. Comparing Implementations of Estimation Methods for Spatial Econometrics. Journal of Statistical Software, 63: 1-36.

Sejr, M. K., Włodarska-Kowalczuk, M., Legeżyńska, J., and Blicher, M.E., 2010. Macrobenthic species composition and diversity in the Godthaabsfjord system, SW Greenland. Polar Biology, 33: 421-431.

Simpson, A. W., and Watling, L. 2006. An investigation of the cumulative impacts of shrimp trawling on mud-bottom fishing grounds in the Gulf of Maine: effects on habitat and macrofaunal community structure. ICES Journal of Marine Science: Journal du Conseil, 63: 1616-1630.

Sinclair, M., and Valdimarsson, G. 2003. Responsible Fisheries in the Marine Ecosystem. CABI Publishing, Cambridge, MA. Thrush, S. F., and Dayton, P. K. 2002. Disturbance to Marine Benthic Habitats by Trawling and Dredging: Implications for Marine Biodiversity. Annual Review of Ecology and Systematics, 33: 449–473.

Watling, L., and Norse, E. A. 1998. Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. Conservation Biology, 12: 1180-1197.

Yesson, C., Simon, P., Chemshirova, I., Gorham, T., Turner, C. J., Hammeken Arboe. N., Blicher,

M. E., and Kemp, K. M. 2015. Community composition of epibenthic megafauna on the West Greenland Shelf. Polar Biology, 38: 2085-2096.

Yesson, C., Taylor, M. L., Tittensor, D. P., Davies, A. J., Guinotte, J., Baco, A., Black, J., Hall-Spencer, J. M., and Rogers, A. D. 2012. Global habitat suitability of cold-water octocorals. Journal of Biogeography, 39: 1278-1292.