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A temporal comparison of benthic macrofaunal communities and the impact of bottom trawling, West Greenland continental shelf

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Project declaration

I hereby declare that this thesis:

"A temporal comparison of benthic macrofaunal communities and the impact of bottom
trawling, West Greenland continental shelf"

is entirely my own work. Data collection aboard a vessel in Greenland was done by my supervisors Dr. Kirsty Kemp and Dr. Chris Yesson, and taxa identification on benthic photographs was done, in majority, by me, with the help of my supervisors along with Chris Turner, Jessica Fisher, and Sarah Gougeon. The compilation of a dataset and all subsequent analyses and writing were done by me. I received guidance and suggestions from my supervisors at all stages of my work, including background information on the project, the identification of rare organisms, and editorial comments during writing.

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Abstract   Bottom trawling is an essential source of income for the economy of Greenland, but the practice is damaging to benthic habitats and communities, especially sessile, habitat forming epifauna. This first long-term historical comparison examines differences in diversity and community composition of benthic macrofauna in relation to the spatial and temporal disturbance of a shrimp (*Pandalus borealis*) trawl fishery in West Greenland. Benthic photography was used to compare 28 station pairs between historical (1978-1985) and recent years (2011-2015). Historical stations were significantly more diverse and had a higher proportion of ecologically important epifauna (e.g. Anthozoa and Porifera), while the proportions of motile and scavenger fauna (e.g. Ophiuroidea) were higher in recent stations. Additionally, the sizes of corals and sponges have decreased in the last three decades, while total abundance was higher in recent stations, possibly due to selection pressure by trawl gear and observation bias due to the lower resolution of historical images. This study found no direct negative impacts of increased trawling. Finally, there was a higher proportion of most classes in areas with greater recovery time. Although the decrease in diversity and the proportion and size of important taxa are not directly linked to trawling impact, this study advises caution for future fishing management. Corals and sponges form habitats for small marine fish and invertebrates, and the reduction in size or removal of these epifauna may have implications not only on species communities and the food web, but on the economically vital shrimp stock as well.

Introduction

Fishing is a major food industry that sustains millions of people worldwide; however, fishing practices, especially bottom-contacting fishing gear, often have chronic negative impacts on ocean environments (Collie et al. 2000; Jennings et al. 2002; Hinz et al. 2009). The health of the seafloor environment has a large impact on fish stocks as well as overall biodiversity (Hinz et al. 2009). The improper management of fisheries has led to the collapse of dozens of fish stocks globally (e.g. Newfoundland cod and Peruvian anchovies) due to overfishing and environmental damage (see Walters and Maguire 1996; Myers et al. 1997; Hutchings 2000). As an increasing number of fisheries apply for sustainability certifications (MSC 2014), it is important to review and understand the impact these fisheries have not only on the stock of the target species but on its habitat as well.

This study provides a long-term comparison of data between 1978 and 2015. A four-dimensional assessment of the extent of a fishery's environmental impact is vital in providing guidelines for future management. Small-scale experimental studies (see Collie et al. 2000; Kaiser et al. 2006) do not account for subtle cumulative effects of fishing disturbance, which may only be noticeable over larger temporal and spatial scales. Although this study has limitations due to the lack of precise data from the past, it would like to highlight the importance of historical comparisons for fishery assessments. The comprehensive analysis and methods used in this paper can provide a significant assessment and new ideas for further studies to solve the raised problem in the near future.

Bottom Trawling

Bottom (otter) trawling is used to catch semi-pelagic, demersal, and benthic species including cod, halibut, and shrimp, and affects approximately 75% of the world's continental shelf (Kaiser et al. 2002). The towed trawl net (~30m in width) is held open by two three-tonne metal 'trawl doors' that scrape the seafloor (Watling and Norse 1998; Rice 2006). Both the overall impacts of bottom trawling and the subsequent recovery from this disturbance, which can take from days to centuries, vary based on the features of the seafloor, the species present, the type of gear used, and the history of human activity (Freese 2001; Rice 2006).

The practice of bottom trawling is damaging to both the habitats and the communities found on ocean floors (Watling and Norse 1998; Collie et al. 2000; Jennings et al. 2002; Hinz et al.

2009). Trawling causes 'flattening' by removing major habitat features, thus reducing the complexity of the seafloor (Freese et al 1999; Hiddink et al. 2006; Rice 2006). Boulders, essential three-dimensional features, are often displaced or rolled over by the trawl gear, destroying any attached organisms (Freese et al 1999). The greatest impact is seen on hard, complex bottoms (Rice 2006) and where natural disturbance is low, particularly on the outer continental shelf and slope (Watling and Norse 1998; Hiddink et al. 2006).

Trawling impacts non-target epifauna (organisms living on or above the substrate) as it alters the relative abundance of species by destroying, burying, or exposing them (Jones 1992; Watling and Norse 1998; Freese et al. 1999; Collie et al. 2000). Emergent epifauna (i.e. habitat forming corals and sponges) function as vital ecosystem engineers by creating a complex habitat and substratum for other organisms and influencing the biogeochemistry of the sediment and water column (Coleman and Williams 2002; Buhl-Mortensen et al. 2009; Yesson et al. 2015). Their functions include shelter for fish, shrimp, brittle stars, and polychaete worms, thereby serving as high-diversity aggregation features (Collie et al. 2000; Coleman and Williams 2002; Boutillier et al. 2010). Trawling activities cause the abundance of structurally fragile and long-lived species with low turn-over (e.g. corals and sponges) to decrease, while the abundance of short-lived organisms and scavengers (e.g. worms and starfish) is unaffected or even increases (Freese et al 1999; Jennings et al. 2002; Curtis et al. 2013). Due to the ecological importance of emergent epifauna, the consequences of bottom trawling extend beyond the removal of specific species to affect the entire benthic ecosystem and even the marine food web (Coleman and Williams 2002; Hiddink et al. 2006; Hinz et al. 2009).

West Greenland

The geological and oceanographic conditions of West Greenland are generally well-known. Greenland's continental shelf has been severely impacted by the melting of the ice sheets following the Last Glacial Maximum as depressions and troughs were carved by glacial erosion (Holtedahl 1970), creating an unusual shelf morphology of deep troughs (> 300m) mixed with shallow banks (< 50m). The retreating glaciers (between 8,000 and 12,000 years BP) deposited large amounts of sediment (Hogan et al. 2012), which influences the present substrate of the seafloor and subsequently the type of habitats and communities formed (Gorham 2014; Yesson et al. 2015). The West Greenland Current system is characterised by two major currents: i) the East Greenland Current with cold, low saline water (< 1 C, < 34 PSU) near the surface and coast; and ii) the Irminger Current (a branch of the North Atlantic Current) with warmer, more

saline water (~4.5 C, >34.95 PSU) deeper and further away from the coast (Stein and Buch 1991; Buch 2000).

Greenland has experienced dramatic climatic variability in the last 50 years (Buch 2000), which has had a notable impact on its long history of fishing (Buch et al. 2004). Greenland's economy has always been heavily reliant on marine resources and has been characterised by seal hunting, followed by cod fishing, and finally shrimp trawling (Hamilton et al. 2000; Buch et al. 2004; Ribergaard et al. 2004). Two major cold events, influenced by strong positive phases of the North Atlantic Oscillation (NAO), occurred between 1982-84 and 1989-94 (Stein and Buch 1991; Buch 2000). These cold trends, coupled with overfishing, led to the decline and subsequent collapse of Greenland's cod fishery in the early 1990s (Hamilton et al. 2000; Buch et al. 2004). Conversely, shrimp (and halibut) experienced increased recruitment success with colder temperatures (Buch et al. 2004), and intense shrimp fishing (>50,000 tonnes/year) began in the mid-1970s and replaced cod as the main fishery in the 1990s (Hamilton et al. 2000).

Due to the growth of the shrimp (*Pandalus borealis*) trawling industry, the Greenland Institute of Natural Resources (GINR) conducted shrimp stock assessments. In these studies Kanneworff (1979) used benthic photography to assess the shrimp stock based on shrimp counts of different size classes. The use of benthic photography was beneficial as it was quicker, cheaper, safer and easier to take pictures compared to the traditional experimental trawls used for stock assessments (Carlsson and Kanneworff 1994). Photographs were taken from 1977 to 1985 and the photos were provided for this study. It is important to note that prior to these surveys, intense shrimp trawling had already begun and a record of trawling frequency and length has been kept by GINR. A study by Chemshirova (2014) found no relationship between trawling intensity on community composition between the mid-1970s and mid-1980s, possibly due to the short window of time. A comparison on a larger time-scale to include recent years (2010s) has not yet been undertaken.

The West Greenland Cold Water Prawn Trawl Fishery, henceforth 'the Greenland fishery,' operates on the West Greenland continental shelf, in NAFO subarea 1 (Lassen et al. 2013). Its consumer base is largely in the United Kingdom and recently several UK supermarkets have adopted sustainability causes (GreenPeace 2005). Due to these policy changes, the Greenland fishery has entered into a certification process by the Marine Stewardship Council (MSC), which identifies three principles as performance indicators: i) a healthy stock; ii) limited environmental impact; and iii) effective management systems (GreenPeace 2005; MSC 2010 & 2014). Consequently, products from MSC certified fisheries carry a blue ecolabel on the

packaging and receive a price premium (GreenPeace 2005). The certification was provisionally approved by the MSC in 2013 (Lassen et al. 2013), but until 2017, the Greenland fishery is subject to conditions that must be met and demonstrated in four annual audits. The Institute of Zoology (IoZ) of the Zoological Society of London (ZSL), collaborating with GINR, is tasked with providing independent research on benthic trawling impact as the basis of this assessment process.

Project Aims

As shallower habitats are fished out globally, deeper, offshore waters are becoming increasingly likely to be affected by trawling (Coleman and Williams 2002; Hinz et al. 2009; Levin and Dayton 2009). Additionally, trawling activities in West Greenland have moved northward following a perceived northward shift in the density of shrimp populations (Kemp and Yesson pers. comm.). Therefore, concerns for the environmental impact of the Greenland fishery can be raised. However, as the management of seafloor habitats cannot be generalised, case-specific analysis and planning is required (Rice 2006). Furthermore, as it is the behaviour of fishermen that determines the extent of the impact of fishing activities, a record of the spatial and temporal variation in the frequency and intensity of fishing disturbance is required for assessing fishery-scale impacts (Jennings et al. 2002; Kaiser et al. 2006; Hinz et al. 2009).

In this project, 'historical' (1978-85) and 'recent' (2011-15) photographic images of the benthos of the West Greenland shelf are used and taxa and communities are identified. Coupled with a record of fishing activity in the region since 1975, this project aims to examine the chronic impacts of trawling and recovery time on seafloor communities. This study hypothesizes:

    i)   greater historical diversity;

    ii)   greater historical abundance and/or proportion of sessile, attached epifauna;

    iii) greater recent abundance and/or proportion of motile, scavenger epifauna;

    iv) a decrease in diversity with increased fishing effort; and

    v)   greater abundance and/or proportion of all organisms with increased recovery time.

This project contributes to the independent research that forms the basis of the assessment of the Greenland fishery for the Marine Stewardship Council certification.

Materials and Methods

Image collection

Benthic photography is the primary data of this study. Historical photographs (1978-1985) were taken by Per Kanneworff and the 56 reels of camera film along with location data for the survey stations were provided by GINR. Recent images (2011-2014) were taken by Kirsty Kemp and Chris Yesson aboard the R/V Paamiut, a shrimp trawler operated by GINR. A total of 221 imaging 'stations,' or sampling locations, have been surveyed since 2011, but only 28 could be paired with historical stations surveyed by Kanneworff (Figure 1). In order to conduct a temporal comparison, historical stations were paired with recent ones when they were separated by less than 5km for an increased probability that environmental variables, such as substrate type, depth, and slope were similar between the stations of a pair. Where possible, stations pairs were chosen from 1984 and 2014 (n = 15) to fix the time period between observations.
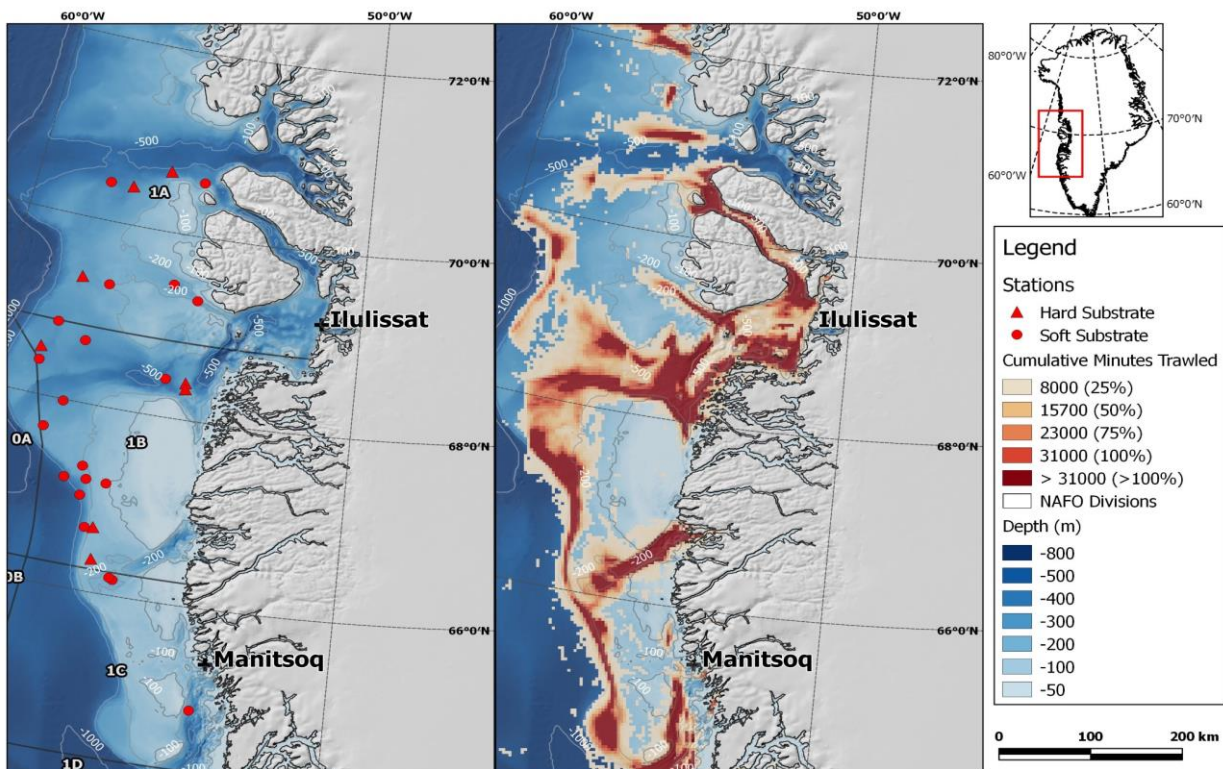

Fig. 1 Map of West Greenland shelf with (left) the location of the 28 station pairs (64º 54′ N to 70º 39 N) situated within the NAFO Divisions (e.g. 1A) and (right) the spatial distribution of trawling activity between 1985 and 2014. Triangles indicate hard substrate and circles indicate soft substrate stations. Light grey lines indicate depth contours (100, 200, and 500m depths)

The sampling methodologies for both the recent and historical surveys were similar. Historical stations were chosen to cover most of the shrimp distribution (Kanneworff 1979) and the 2014 survey targeted these locations. The vessel stopped at a GPS-ed location, and the camera, mounted on a frame with weights, was lowered to the seafloor using a winch. The flash and subsequent photograph were triggered when the trigger weight, suspended slightly below the camera frame, hit the seafloor. The camera and frame were then raised 10-20m for 1 minute, then lowered again to take the next photograph (10 images in the recent surveys and 100-200 in historical surveys). The drift of the vessel with the ocean current was found to be sufficient to move the camera so as to not create overlapping images.

The methodologies differed in the photograph quality and field of view. Recent images were taken using a Nikon digital SLR camera covering $0.32m^2$ of the seafloor (see Appendix 1 for further details). Historical photos were taken using a 35mm camera at a 10º angle, producing images covering a much larger $3.39m^2$ (Kanneworff 1979). For historical stations, the first 10 clear images (i.e. minimal smudging/scratches, well-lit) were selected from the beginning of each station reel with 1-minute intervals between photographs (aided by a watch fixed in the corner of each photograph) to correspond with the sampling intensity in recent surveys. These images were digitised and the centres of the images were then cropped using R 3.1.1 to match the area covered by the camera in the recent surveys (Appendix 1).

Taxon identification

The images were processed using the software Poseidon, developed by computer scientists at University College London specifically for the identification of benthic organisms. Benthic macrofauna (>1cm) were identified to the lowest possible taxonomic level, ranging from phylum to family, and tagged on each image (Appendix 1). Taxa were recognised with the help of identification guides and expert collaborators. Colonial organisms (e.g. encrusting bryozoa and asicidians) were counted as 1 individual for each continuous patch or group (Yesson et al. 2015). A majority of fauna were epifauna, but some infauna, animals living within or under the sediment (e.g. polychaete worms, bivalves (clams), and holothurians (sea cucumbers)), were visible and identifiable.

Two phyla, porifera (sponges) and bryozoa (moss animals), were grouped under morphological classes rather than taxonomic classes due to difficulties with identification, which requires high magnification or genome sequencing (Freese et al 1999). Porifera were subdivided into three classes following Yesson et al. (2015): i) arborescent: those with

branching structure, ii) encrusting: those forming a continuous mat, often on a stone/boulder, and iii) massive: those that are large, unbranched sponges. Similarly, bryozoa were divided into classes: i) encrusting: as encrusting sponges, ii) soft: those with a wispy, seaweed-like structure, and iii) stony: those with a rigid branching or lattice structure.

Analysis

The abundances of each taxa were summed from five of the total available images per station (ranging from 5 to 10 photos), selected at random. Sand and mud substrate was categorised as 'soft', while 'hard' substrate was defined by pebbles, rocks, and boulders covering more than half of the image. Previous studies (Gorham 2014; Yesson et al. 2015) have shown that substrate type determines community composition and thus comparing between substrates would lead to false assumptions. In stations with images of both substrate type (n=8), the substrate present in over half of the photos was chosen and designated for the station. Photographs with the other substrate type were then removed from the dataset prior to the randomised selection of five final images. In total, 521 images were processed, and 280 (5 per 56 stations) were used in further analyses.

In addition to taxon data, the two most ecologically important taxa were examined more closely. From the five random photographs selected per station, taxa porifera (massive and arborescent sponges) and alcyonacea (soft corals) were measured and approximate sizes recorded as one of three size categories: small ($< 1cm^2$), medium (< 3 cm^2), and large (> 3 cm^2).

Fishing effort was quantified as cumulative minutes trawled in a fixed area around each station. These 20km grids of fishing effort were compiled from a dataset of trawling and start locations for each activity between 1975 and 2014 (provided by GINR). The mean trawl distance in West Greenland is roughly 10km (6hrs), averaged from all trawling activities since 1975. Therefore a 20km grid cell is highly likely to contain both the start and end of the trawling activity. Fishing effort was a cumulative sum of total minutes spent trawling each year from the year after the historical survey up to the year before the recent survey (i.e. 1985-2013 for a pair from 1984 and 2014). This provided a measurement of disturbance that occurred in the area between the times the two sets of images were taken.

Environmental data for recent stations was gathered at the location of each station using the TOPAZ4 Arctic Ocean Reanalysis oceanographic model. Historical sea surface temperature

data was obtained from the Hadley Centre Sea Ice and Sea Surface Temperature data set (HadISST). Variables with no temporal variation were depth and slope.

Diversity indices (Shannon's H, Pielou's measure evenness and class richness) were determined on the classes present at each station. Abundances (both total and by class) and non-normal environmental variables were transformed via the Box-Cox method after Shapiro normality tests. This is a function that attempts to create a more normal distribution by first attempting a $\log_{10}$ transformation, and if needed, testing a series of power transformations (power of λ) and selecting the one that gives the most normal output (using R package MASS (Ripley et al. 2015) (Appendix 2). The total number of taxa was estimated with Bootstrap, Chao, and 1st order Jackknife extrapolation methods. Diversity indices between historical and recent stations were tested for correlation with Pearson's product-moment correlation, and differences in between-station diversity and class abundances/proportions were tested for with paired Wilcoxon rank-sum tests. The impact of other variables on diversity indices and class proportions were examined using Generalised Linear Models (GLMs) and simplified using the step( ) function. All analysis was performed using the vegan library (Oksanen et al. 2015) of the R 3.1.1 statistical software program (R code team 2015).

Results

Table 1 Summary of station data for historical and recent stations. Class pool estimates are based on taxon accumulation curves. Diversity indices with minimum and maximum values are based on a station-level

	Historical	**Recent**	**Combined**
Number of Stations	28	28	56
Total Abundance	4050	12674	16724
Abundance (min-max)	3 – 911	7 – 2325	3 – 2325
Total Taxa	50	54	56
Total Classes	26	26	27
Class Richness (min-max)	4 – 16	3 – 18	3 – 18
Shannon Index (min-max)	0.5 – 2.2	0.1 – 2.3	0.1 – 2.3
Class Evenness (min-max)	0.2 – 0.9	0.1 – 0.9	0.1 – 0.9
Class pool estimates			
Bootstrap	28.0 ($\pm$ 2.0)	26.9 ($\pm$ 0.9)	27.6 ($\pm$ 0.6)
Chao	38.1 ($\pm$ 17)	26.1 ($\pm$ 0.4)	27.5 ($\pm$ 1.3)
Jackknife	30.8 ($\pm$ 4.8)	26.9 ($\pm$ 0.9)	28.0 ($\pm$ 1.0)
Environment			
Hard Substrate	9	9	18
Soft Substrate	19	19	28
Depth (m) (min-max)	109 – 565	121 – 488	109 – 565
Median depth difference (m) (min-max)	-	-	7 (0 – 170)
Median distance between Stations (m) (min-max)	-	-	952 (269 – 4906)
Sea Surface Temperature (ºC)	-0.3 – 2.1	0.6 – 4.2	-0.3 – 4.2

A total of 28 station pairs (Figure 1) were analysed, of which 9 were characterised as hard substrate and 19 as soft (Table 1). The depth of these survey stations ranged between 109 and 565 meters with half of the observations in the 238 – 304m depth zone. Seafloor temperature is typically a better indicator for benthic communities, but these data were not available for historical stations. However, there was a strong correlation between recent surface and seafloor temperatures (Appendix 3), and sea surface temperature was therefore used as a proxy. Temperature values in historical stations are colder than recent stations, with smaller minimum and maximum values and a difference of 0.4 ºC in the medians (0.7 to 1.3, respectively).

A total of 56 different taxa were identified and sorted into 27 classes (Appendix 4). Taxon accumulation curves (Appendix 5) and class pool estimates (Table 1) give high confidence that all classes have been found. Classes Cephalopoda and Thaliacea were removed from class-level analysis due to only having a single observation.

Table 2 Results from a SIMPER analysis, showing mean (transformed) abundance, standard deviation, and cumulative percent contribution of the most influential classes in historical and recent stations

Set	Class	Abundance (mean ± s.d.)			Cumulative %
Historical	Polychaeta	3.68	±	1.11	34.38
	Ascidiacea	2.65	±	1.22	55.54
	Maxillopoda	2.21	±	0.99	74.08
	Bryozoa encrusting	1.23	±	1.10	79.32
	Porifera encrusting	1.02	±	0.85	84.13
	Malacostraca	0.68	±	0.55	88.46
Recent	Polychaeta	4.65	±	1.85	38.37
	Ascidiacea	2.48	±	1.62	52.49
	Maxillopoda	2.06	±	1.66	62.05
	Bryozoa soft	1.12	±	0.67	69.50
	Bryozoa encrusting	1.12	±	1.01	74.16
	Ophiuroidea	0.77	±	0.56	78.78
	Bivalvia	0.78	±	0.55	83.23
	Porifera encrusting	1.03	±	0.98	87.14

Table 2 summarises the results of a SIMPER analysis, and although five influential classes are shared between historical and recent stations, the community composition is significantly different between historical and recent stations (ANOSIM, R = 0.19, p < 0.001).

Total hours trawled within each NAFO division between 1975 and 2013 is shown in Figure 2. In addition to 20km grid cells, less coarse 3.5km grids were also attempted for recent stations (as end locations of trawls were available post-1985). However, using 3.5km grids granted no further precision in trawling impact as it was highly correlated with data obtained from 20km grids (Appendix 3).

Diversity

Diversity was compared between 'sets' (historical and recent stations) using Pearson's correlations and between the stations using paired Wilcoxon rank-sum tests (Table 3). Shan-
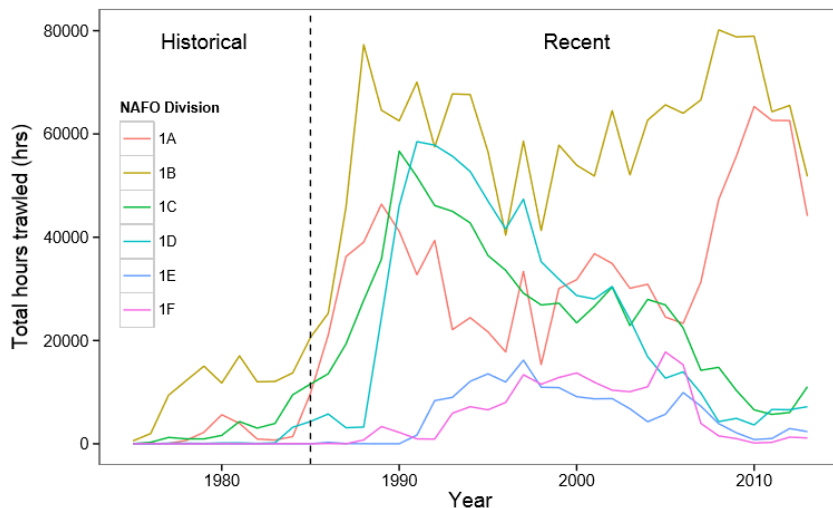
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Fig. 2 Total hours trawled in each NAFO division (North to South, see Fig.1) between 1975 and 2013. Station pairs in this study are located in divisions 1A (n = 8), 1B (n = 17) and 1C (n = 3). Note the decrease in cumulative hours trawled in southern divisions (e.g. 1C-F) since 1990 and the increase in northern divisions (1A)

non's index and class evenness were greater in historical stations; abundance was significantly greater in recent stations; while class richness did not differ significantly by 'set' (Figure 3).

The difference in abundance and proportion of each class within station pairs was examined using paired Wilcoxon rank-sum tests (Table 4). All significantly greater class abundances are in recent stations. To further examine the compositional changes between historical and recent stations, proportions were calculated (class abundance / total station abundance). Classes with significantly greater proportions in recent stations are mainly motile taxa. Classes with significantly greater proportions in historical stations are sessile, habitat forming taxa (Table 4 and Figure 4).

Further examination of two ecologically important taxa, porifera and alcyonacea, was done through size classes. There was a greater number of all size classes of both taxa in historical stations (Figure 5). There has been a large reduction in the number of (especially of large and medium) soft corals in the past three decades. Further analysis could not be conducted as there are too few observations.

Impacts

There was no pattern in diversity indices relative to cumulative minutes trawled. Negative values of change in diversity indices (recent station diversity – historical station diversity)

Table 3 Summary of test statistics for paired differences and correlations between diversity indices of historical and recent stations

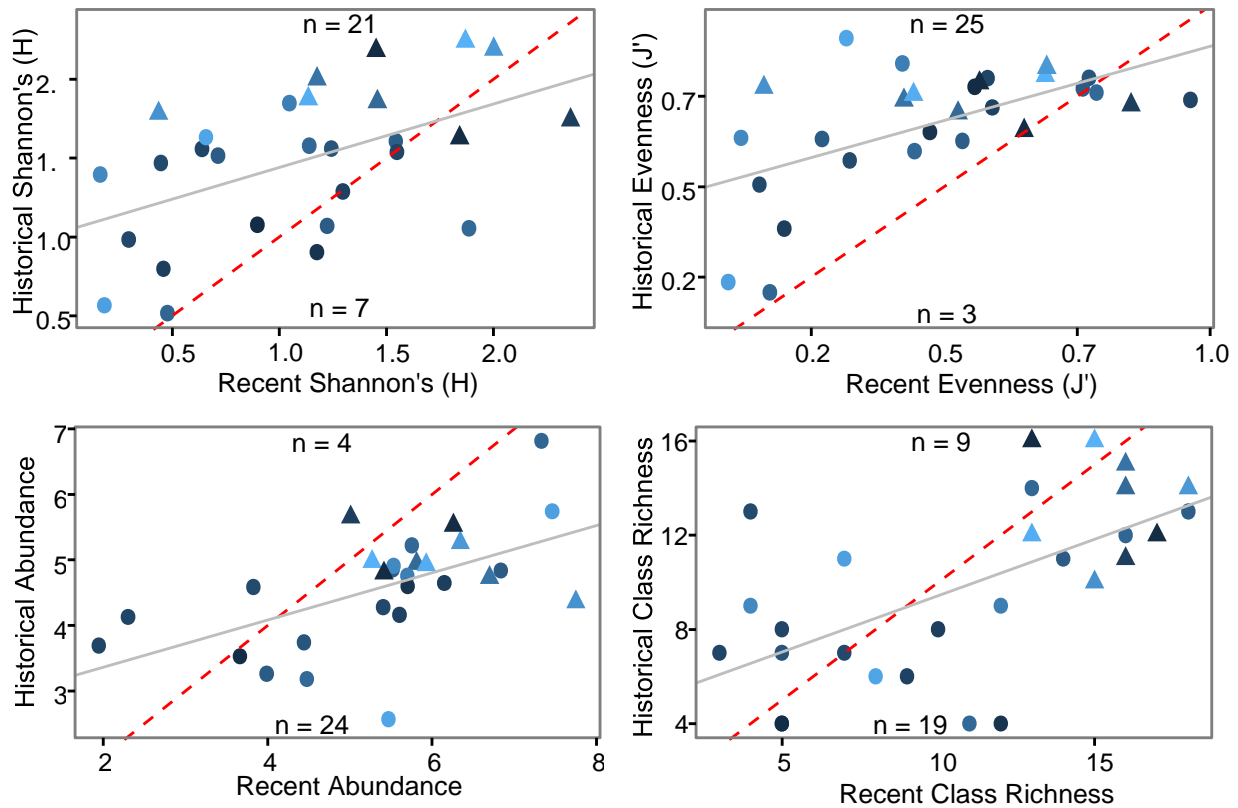| Index	N	V	Conf.int Low	Conf.int High	P - value	r	df	t	P - value
			Paired Wilcoxon rank-sum			Pearson's product - moment correlation			
Shannon	56	342	0.179	0.599	< 0.001*	0.512	26	3.037	< 0.01*
Evenness	56	376	0.113	0.266	< 0.001*	0.581	26	3.644	< 0.001*
Abundance	56	66	-1.212	-0.541	< 0.001*	0.566	26	3.500	< 0.001*
Richness	56	126	-3.000	0.500	0.128	0.613	26	3.960	< 0.001*

Fig. 3 Shannon diversity of historical and recent stations where each point is a station pair. The red dashed line represents the 1-1 line. Points above the line indicate that diversity is greater in the historical station and points below indicate that it is higher in the recent station. The solid grey line is the linear model showing that recent diversity predicts historical diversity (coefficients in Appendix 3)
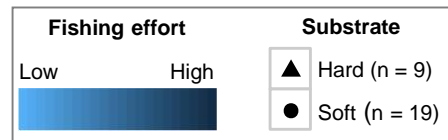
indicate higher diversity in the past, positive values indicate higher diversity in recent years, and values of to 0 indicate no change over the past three decades. The measures of change of Shannon index and class evenness show a positive relationship with fishing effort, indicating a large decrease in diversity in areas of low trawling impact, but smaller differences in diversity in areas of high fishing intensity (Figure 3). Conversely, the difference in abundance is greater in recent stations in areas with low fishing impact and decreases with increased trawling. Class richness showed no relationship.

Other environmental factors were then examined for their influence on the proportion contribution of each class and diversity index using GLMs (Table 5). Increased recovery time had a positive impact on the proportion of most classes except Bryozoa soft and Polychaeta.

Table 4 Results of paired Wilcoxon tests for differences between (transformed) abundances and proportions between historical and recent stations, separated by substrate type. Proportions were calculated as abundance of class / total abundance of station. Letters indicate in which set the difference was significantly greater (R = Recent, H = Historical), while the case of the letter indicates significance level (lower-case $0.01 < p < 0.05$, uppercase $p < 0.01$)

Class	Common Name	Abundances			Proportions		
		All	*Hard*	*Soft*	*All*	*Hard*	*Soft*
Actinopterygii	Ray-finned fishes						
Anthozoa	Corals				h	H	
Ascidiacea	Sea squirts				H	h	h
Asteroidea	Starfish						
Bivalvia	Clams	r	R				
Bryozoa encrusting	Encrusting moss animals					H	
Bryozoa soft	Soft moss animals	R	R	r	R	R	r
Bryozoa stony	Stony moss animals	R	r	r	R		r
Crinoidea	Crinoids						
Cubozoa	Box jellyfish						
Echinoidea	Sea urchins						
Gastropoda	Snails						
Holothuroidea	Sea cucumbers						
Hydrozoa	Hydrozoans						
Malacostraca	Crabs and shrimp						
Maxillopoda	Barnacles				h		H
Nemertea	Ribbon worms						
Ophiuroidea	Brittle stars	r			r		
Polychaeta	Segmented worms	R	R	r			
Polyplacophora	Sea cradles						
Porifera arborescent	Branching sponges						
Porifera encrusting	Encrusting sponges				h		
Porifera massive	Massive sponges						
Rhynchonellata	Lamp shells						
Scaphopoda	Tusk shells						

Trawling, as mentioned above, showed little impact. There was a larger proportion of sessile epifauna (e.g. Anthozoa, Bryozoa and Porifera) on hard substrates and soft-specialist motile epifauna (e.g. Malacostraca, and Polychaeta) on soft substrates. Environmental factors depth, slope, and temperature had a smaller influence on compositions, with a general decrease in proportion contribution with increased depth and slope. Finally, in addition to the Wilcoxon tests on diversity indices between historical and recent stations (Table 3), recovery showed no influence, trawling showed a positive influence on Shannon's index and class evenness, hard substrate had a positive relationship with most indices, and slope and temperature showed varied impacts.
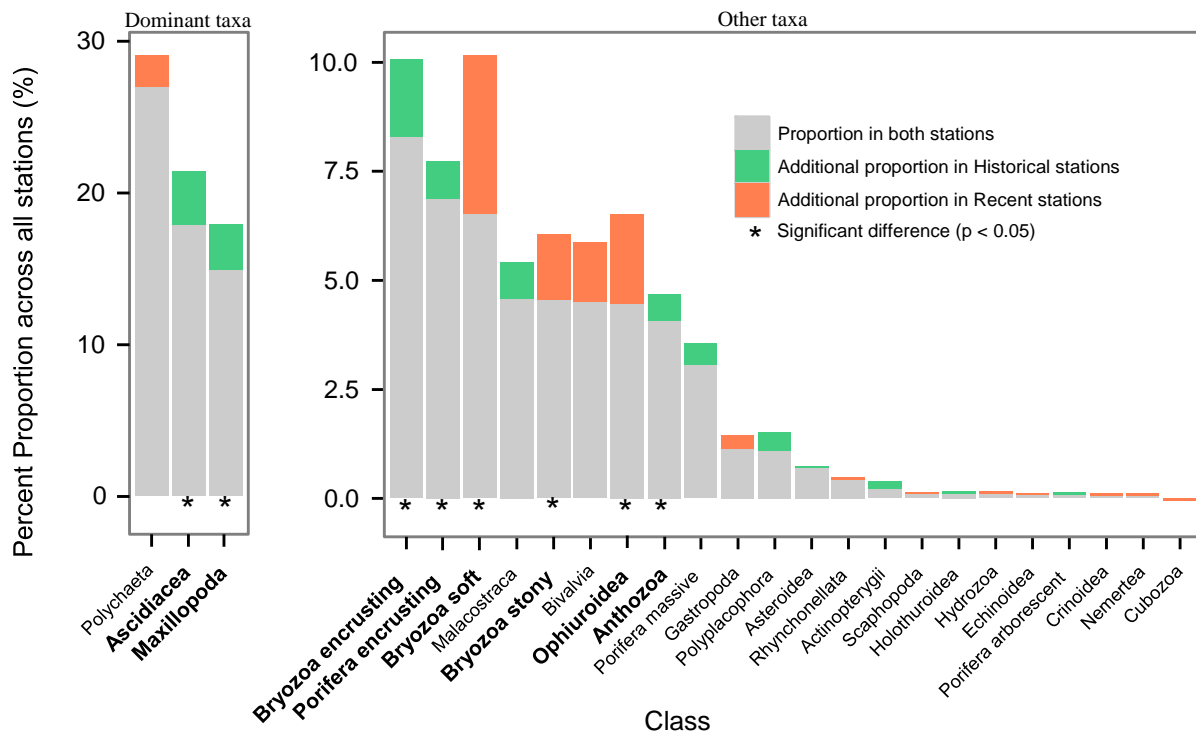
Fig. 4 Percent proportion of transformed abundance of each class. Grey bars represent the proportion found in both historical and recent stations. Green colouring represents the amount by which historical station proportion is greater than recent, while orange colouring represents the amount by which the recent station proportion is greater than historical. Bars with asterisks denote a significant difference (p < 0.05) in pairwise Wilcoxon tests (see Table 4). Note the different scales for dominant and other taxa

Discussion

This study is the first examination of the long-term impacts of shrimp trawling on the West Greenland shelf, using a comparison of the taxon composition of an area in the 1970s – 80s to that observed today. This was combined with the spatial history of fishing activity to provide the first look at the long-term impacts of the fishery. This is essential for understanding and predicting future impacts the fishery may have on benthic habitats, ecosystems, and consequently the marine food web (Hinz et al. 2009).

The diversity of historical stations was higher than of recent stations, while the abundances of taxa were higher in recent stations. Community composition varied between historical and recent sites with larger proportions of Anthozoa, Ascidiacea, and Encrusting Bryozoa and Porifera in the former and larger proportions of Ophiuroidea and Soft and Stony Bryozoa in the latter. Fishing activity, surprisingly, appeared to have little impact on diversity in recent stations. The difference in diversity indices was greater in areas of low trawling impact than in

areas of high disturbance, while the change in abundances showed an inverse relationship with trawling impact. Fishing effort showed a positive relationship with the abundances of many classes as well.
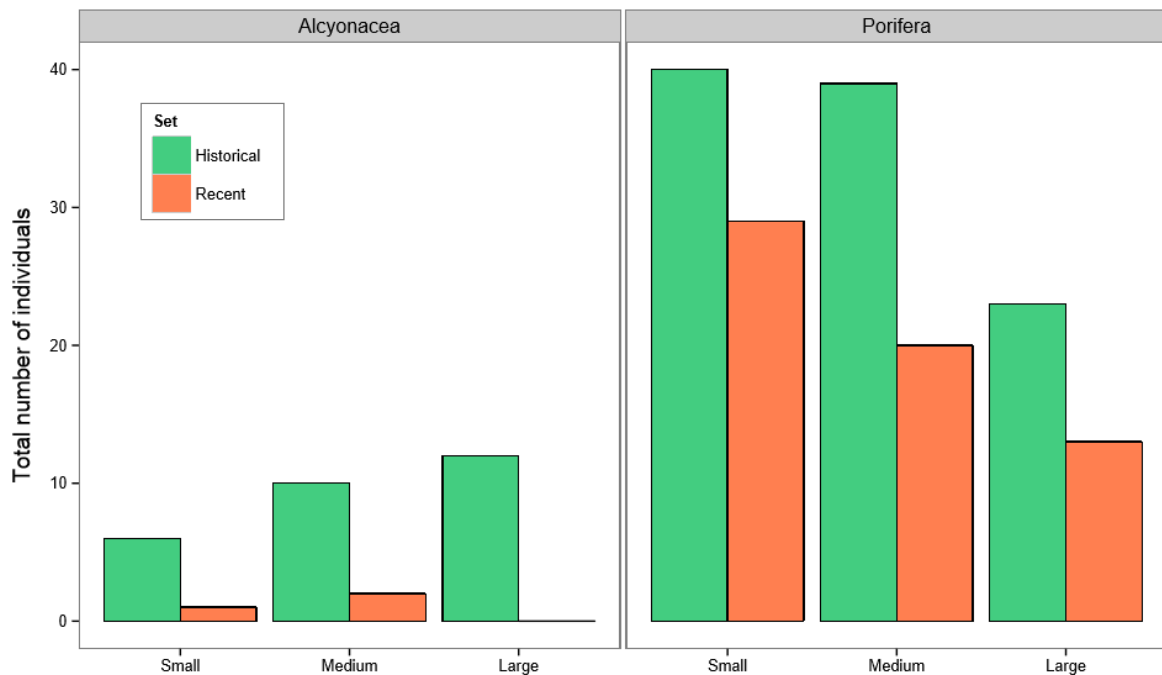
Fig. 5 Total number of individuals of each size class of alcyonacea and porifera found in historical (green) and recent (orange) stations. Small <1cm^2, medium <3cm^2, large >3cm^2

Diversity

Diversity in recent years is notably less than that of 30-35 years ago, despite historical and recent diversity indices being significantly correlated. This is consistent with studies comparing the impacts of bottom trawling between heavily fished and unfished areas (Collie et al. 2000; McConnaughey et al. 2000).

However, the total number of observations in recent images was more than twice that of historical images, and the number of taxa present did not differ significantly. This is contradictory to studies on the benthic impact of trawling (Hiddink et al. 2006; Hinz et al. 2009). Richness in this study was measured as the number of classes as opposed to species, which does not take into account any variance in resilience to trawling between species of the same the order or family. The species present in low and high impacted areas may be different, but this was not demonstrated in class aggregations.

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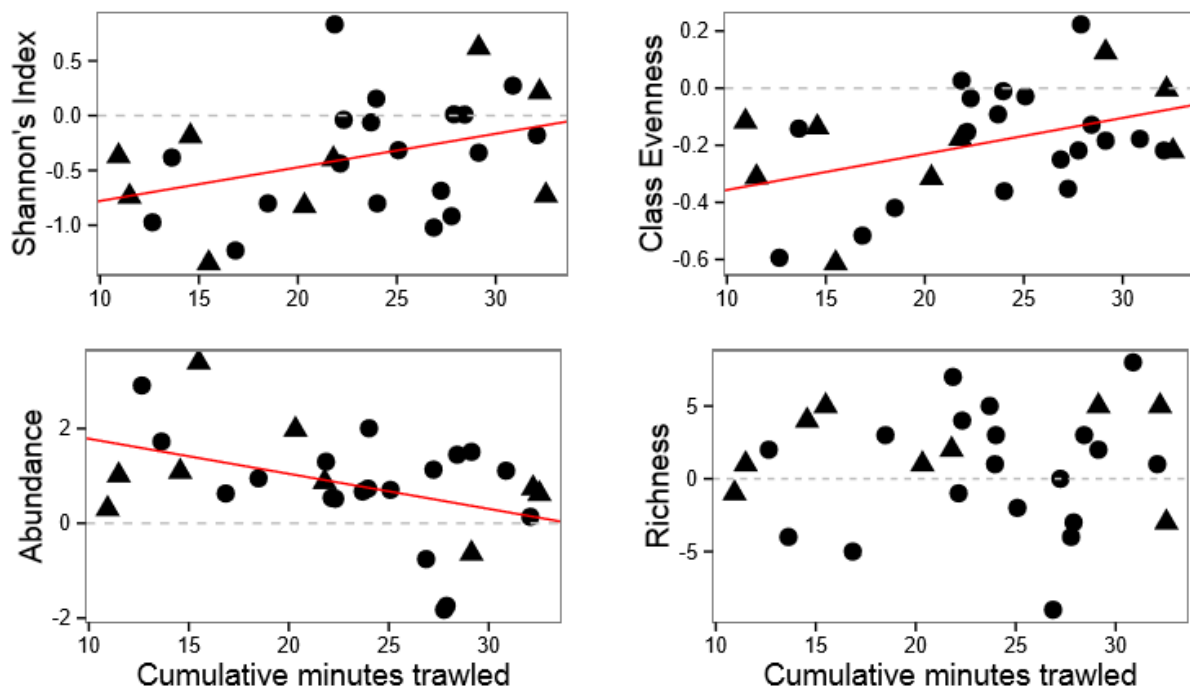**Fig. 6** Change in Shannon's index, class evenness, class richness, and abundance against transformed cumulative minutes trawled. The grey dashed line represents the 1-1 line, where historical and recent values would be equal (recent − historical = 0). Positive values indicate greater diversity index in recent stations (recent − historical > 0) and negative values indicate greater diversity index in historical stations (recent − historical < 0). Solid red lines for graphs represent the linear model showing cumulative minutes trawled predicting the change in diversity (coefficients in Appendix 3). Triangles are hard substrate and circles are soft substrate station pairs

Trawling

This study hypothesized that a decrease in diversity is caused by shrimp trawling; however, cumulative trawling appears to show little impact on diversity. In fact, the proportion of several classes increased with minutes trawled (Table 5). Additionally change in diversity indices increased with minutes trawled, showing that with increased trawling, historical and recent stations present more similar diversities (Figure 6).

This may be due to several factors. The area around each station was a large 20km grid, with the assumption that the end point of each trawl was in the same grid as the start point. This does not account for trawls that are not linear (e.g. circular or curved). It was another assumption that the cumulative fishing impact in the much larger 20km grids was equally distributed across the square, including the much smaller area (~2km in length) that was sampled. This inaccuracy in the fishing data may explain why shrimp trawling appears to

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increase the proportion of many classes. However, there are simply no data available for years prior to 1985 to make the fishing data more accurate for a long-term historical comparison.

Table 5 Summary of the estimate coefficients of minimum adequate generalized linear models with the dependent variables: proportion of classes and diversity indices. The terms are the columns. Models were simplified using the step( ) function in R 3.1.1. Numbers in bold indicate significance (p < 0.05). *Note*: AIC values are displayed in Appendix 3

Variable (Class and Diversity)	Intercept	Recovery (yrs)	Trawling (mins)	Set (1=hist 2=rec)	Substrate (1=hard 2=soft)	Depth (m)	Slope ($\log_{10}$ º)	Tempe-rature (ºC)
Actinopterygii	**0.00**							
Anthozoa	0.02	**0.02**		-0.01	**-0.02**	0.00		
Ascidiacea	**0.07**			**-0.06**	-0.03	**0.00**	-0.01	
Asteroidea	0.00	0.02	0.00			-0.01	-0.01	0.01
Bivalvia	**0.04**							
Bryozoa encrusting	**0.11**				**-0.07**			
Bryozoa soft	**0.06**	**-0.05**		**0.04**			0.01	**-0.04**
Bryozoa stony	**0.05**	**0.01**		**0.01**	**-0.04**			
Crinoidea	**0.00**	**0.00**	**0.00**					
Cubozoa	**0.00**			0.00	**-0.01**		-0.01	0.03
Echinoidea	**0.01**		-0.01	**0.00**	0.00	**-0.01**		
Gastropoda	**0.03**			**0.02**	**0.02**	-0.01		
Holothuroidea	0.01	0.00			0.00	**-0.01**		
Hydrozoa	**0.00**	0.00		0.00	**0.00**			
Malacostraca	0.02				**0.04**			
Maxillopoda	**0.13**			**-0.07**	0.05			
Nemertea	0.00		**0.00**		0.00		0.00	-0.01
Ophiuroidea	**0.13**			**0.04**		**-0.01**		
Polychaeta	**0.21**	**-0.05**		0.04	**0.11**			
Polyplacophora	**0.02**			-0.01	-0.01			
Porifera arborescent	0.00	0.00	0.00	0.00		-0.01		
Porifera encrusting	**0.07**	**0.03**	0.00	**-0.03**	**-0.05**		0.01	
Porifera massive	**0.04**		0.00	**-0.01**	**-0.03**		0.00	**-0.01**
Rhynchonellata	**0.01**		**-0.01**	0.00				
Scaphopoda	0.00	0.00					**0.00**	
Shannon's H'	**1.69**		**0.02**	**-0.57**	**-0.71**			
Evenness J'	**0.76**			**-0.19**	**-0.17**			0.14
Class Richness	**-4.75**		**0.14**				1.18	-2.33
Total Abundance	**4.37**			**0.80**	-0.57	0.00		**-0.71**

Based on the data in this study, the decreased diversity in recent stations is therefore not directly linked to fishing impact. However the significantly greater proportions of sessile epifauna suggests that fishing impact may have an indirect effect by systematically removing large emergent epifauna and thereby decreasing diversity (Buhl-Mortensen et al. 2009). There appears to be variation in the acute and chronic impacts of trawling. The greatest impact on the seafloor is caused by the first few fishing events (Rice 2006), therefore the extent of damage may not vary greatly between areas of 'medium' and 'high' fishing impact. An alternate

method of quantifying fishing effort would be to sum the number of trawls in each fixed area (Hinz et al. 2009) and disregard the duration of the trawls. This would differentiate between few, long trawls (e.g. 2 trawls of 5 hours) compared to several short trawls (e.g. 5 trawls of 2 hours). In the current methodology both scenarios would equate to similar 'cumulative minutes trawled' (10 hours), whereas the five individual trawls would have a larger impact on undisturbed seafloor habitats (Rice 2006).

Other factors

Environmental factors were examined, using GLMs, for their influence on diversity and the proportion of each class. Substrate type was an important factor and coincides with the specialist nature of taxa (Appendix 5), where sessile, attached taxa were more dominant on hard substrates, and soft-specialist, motile taxa on soft substrates (Yesson et al. 2015). Furthermore, diversity indices were greater on hard substrates, suggesting the importance of avoiding trawling on rocky seafloor (Yesson et al. 2015). There was a greater proportion of corals with increased depth, and a greater proportion of echinoderms and molluscs in shallower areas (Mayer and Piepenburg 1996). Temperature had little influence on the community composition, with only the proportions Bryozoa soft and Porifera massive showing a significant increase at lower temperatures.

The greater abundance of nearly all classes in recent stations may be explained by i) selection pressure and/or ii) observation bias. The standard minimum mesh size on shrimp trawls in Greenland is 40mm with a mandatory fish excluding device to reduce non-target bycatch (Lassen et al. 2013). This mesh size is significantly greater than the minimum size of the organisms identified in the benthic photographs (10mm). Through a potential selection pressure, organisms larger than the 4cm mesh size (e.g. shrimp, corals, sponges and large ascidians) are systematically removed from the substrate, selecting for individuals small enough to fit through the gaps of the mesh and gear.

To examine the effects of selection pressure, the size of ecologically important taxa was measured. There was a greater number of both soft corals and sponges in historical stations, consistent with similar studies (Freese et al. 1999; Collie et al. 2000; McConnaughey et al. 2000). The vast contrast in the total amount, and a decrease of larger sizes of porifera and alcyonacea (Figure 5), may also be attributed to the selection pressure of shrimp trawling. Larger organisms may be more likely to suffer breakage due to the fishing gear or get caught in the trawl net and removed entirely from the sediment (Buhl-Mortensen et al. 2009).

Members of the crew operating the R/V Paamiut have presented anecdotal evidence that they no longer find large corals (sometimes >1m in diameter) in their trawl nets, though they did 30 years ago (Kemp and Yesson pers. comm.). However, further empirical evidence is required to conclusively link this difference in the size of alcyonacea and porifera to extensive trawling.

The impact of this decrease in size of ecosystem engineers extends to the ecosystem level (Jones 1992). Smaller corals and sponges provide less habitat complexity and cease to serve as protection for small fish and invertebrates from predators (Buhl-Mortensen et al. 2009). Therefore the decrease in the size of corals and sponges present on the West Greenland shelf may indirectly lead to trophic imbalance which alters the marine food web (Hinz et al. 2009), and has potential impacts on the economically essential *P. borealis* stock.

An additional factor for increased abundances is observation bias. Recent images were high resolution photographs taken with digital cameras. Historical photographs were taken on film and then scanned, producing images of a much lower resolution. This creates observation bias as there are fewer pixels covering the same area in historical images, thus making it more difficult to spot and identify organisms. Colourless or nearly transparent organisms (e.g. Bryozoa soft and Hydrozoa) and rare, difficult-to-identify organisms (e.g. polynoidea (class Polychaeta)) were more easily spotted in recent images due to the higher resolution.

It is also important to note the 10º tilt of the camera in historical photographs, which created photographs that were wider at the top than at the bottom. This tilt, rather than the top-down orientation of photographs from recent stations, may have skewed the results of historical coral size counts due to inaccurate size measurements.

Recovery

In areas of greater recovery time, there was a more even community composition, as the environment naturally regenerates after chronic disturbance (Curtis et al. 2013). The amount of recovery shows a significant positive relationship with the proportion of sessile, attached epifauna such as Anthozoa, Bryozoa stony, Crinoidea, and Porifera encrusting. As trawl gear crushes emergent epifauna and displaces boulders and rocks, these organisms that attach to rocks and other substrate are severely damaged (Freese et al. 1999). Unlike in warm waters, the recovery time of coldwater emergent epifauna exceeds several to dozens of years (Freese 2001, Boutilier et al. 2010). As deep-and-coldwater sponges and corals are subjected to less natural disturbance, the natural sustainable rate of population loss is very low (between 5% and less than 1%) (Watling and Norse 1998; Boutilier et al 2010). Therefore, any further

anthropogenic disturbance to deepwater corals may have severe long-term impacts if populations are not allowed to recover (Jones 1992; Boutilier et al. 2010; Rooper et al. 2011).

As the GLMs examined the impact of variables on the proportion of classes, a smaller proportion of sessile fauna in low-recovery areas must result in a higher proportion of organisms that are more resilient to trawling (Jennings et al. 2002; Curtis et al. 2013). Although Soft bryozoa are sessile organisms, their soft structure may in fact mitigate the crushing impact of trawl gears. Polychaete worms, short-lived, small organisms were abundant in recently disturbed areas, where sessile organisms were destroyed by the fishing gear, thus exhibiting a high proportion.

Limitations and further study

Temporal bias was introduced through solely sampling at night. This was due to the unavailability of the vessel during the day, which may create bias in the abundance (or altogether presence) of taxa that exhibit diurnal migration, such as the exploited shrimp *P. borealis* (Carllson and Kanneworff 1994).

This study can be improved and extended. In future sampling trips, targeting even more areas in close proximity to already present historical stations surveyed by Kanneworff would increase the sample size dramatically. More specifically, targeting stations south of 64°N, where hard substrate is more common (Gougeon 2015; Yesson et al. 2015), would create a more balanced distribution of substrate types and expand the sample size of the alcyonacea and porifera size class counts.

Furthermore, a suggested change to the methodology would include a shift from abundance counts to size counts (Jennings et al. 2002) to investigate further the potential of selection pressure. This would require developing an accurate way to measure the size of the organisms on the two-dimensional photographs while taking into account the angle of the camera in historical images. Finally, incorporating further work on the larger assessment of the Greenland fishery – such as habitat mapping (Gougeon 2015) and the impact of trawling on functional groups (Fisher 2015) – would aid in determining the key drivers of diversity and the influence of shrimp trawling on the West Greenland shelf.

The comparisons in this study highlight the importance of historical data in benthic community assessment. The direct effects of decreased size of important taxa and the change in community composition in the last three decades are already visible today and this study raises a potential concern for the future health of the West Greenland benthos and consequently

of the target shrimp stock. Studies such as this are essential for informing the advocated shift to an ecosystem approach in not only the sustainability certification processes, but in fisheries management as well (Hinz et al. 2009).

Conclusions

This study is the first long-term comparison of the benthic diversity of the West Greenland continental shelf. Only one of the five hypotheses of this study was rejected:

i) historical stations were indeed more diverse and, due to selection pressure and observation bias, ecologically important taxa, such as corals and sponges, have decreased in size while recent stations had greater abundances,

ii) there was indeed a greater proportion of ecologically important sessile epifauna, including Anthozoa, and Porifera in historical stations,

iii) there was indeed a greater proportion of motile scavengers, such as Ophiuroidea in recent stations,

iv) shrimp trawling had no apparent impact on diversity, and the differences in diversity indices and abundance decreases with increased fishing effort, and

v) there was indeed a higher proportion of most classes in areas of longer recovery.

This study advises caution for future trawling effort, particularly on hard substrate areas, the preferred habitat for ecologically important taxa. Further reduction in the abundance, distribution, and size of these emergent epifauna may have implications for benthic habitats, the entire food web, and the health of the target shrimp stock.

References

Boutillier J, Kenchington E, Rice J (2010) A Review of the Biological Characteristics and Ecological Functions Served by Corals, Sponges and Hydrothermal Vents, in the Context of Applying an Ecosystem Approach to Fisheries. DFO Can. Sci. Advis. Sec. Res. Doc. 2010/048. iv + 36p.

Buch E (2000) Air-sea-ice conditions off Southwest Greenland, 1981-97. Journal of Northwest Atlantic Fishery Science 26:123–136

Buch E, Pedersen SA, Ribergaard MH (2004) Ecosystem Variability in West Greenland Waters. Journal of Northwest Atlantic Fishery Science 34:13–28

Buhl-Mortensen L, Vanreusel A, Gooday AJ, Levin LA, Priede IG, Buhl-Mortensen P, Gheerardyn H, King NJ, Raes M (2009) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Marine Ecology 31:21-50

Carlsson DM, Kanneworff P (1994) Problems with bottom photography as a method for estimating biomass of shrimp (*Pandalus borealis*) off West Greenland. NAFO Sci.Coun.Studies 20:93-102

Chemshirova I (2014) Establishing historical baselines of benthic diversity and community composition, Western Greenland. BSc Project, Imperial College London. 54pp.

Coleman FC, Williams SL (2002) Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends in Ecology and Evolution 17(1):40-44

Collie JS, Escanera GA, Valentine PC (2000) Photographic evaluation of the impacts of bottom fishing on benthic epifauna. ICES Journal of Marine Science 57:987-1001

Curtis JMR, Poppe K, Wood CC (2013) Indicators, impacts, and recovery of temperate deepwater marine ecosystems following fishing disturbance. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/125. v + 37pp.

Fisher J (2015) Impacts of otter trawling on macrobenthic functional diversity in western Greenland. Master Thesis, University College London, UK

Freese L, Auster PJ, Heifetz J, Wing BL (1999) Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. Mar.Eco.Prog.Ser, 182:119-126

Freese L (2001) Trawl-induced damage to sponges observed from a research submersible. Marine Fisheries Review, 63(3):7-13

Gorham T (2014) Impacts of shrimp trawling on community composition of the macrobenthic fauna of West Greenland. Masters Thesis, Imperial College London, UK

Gougeon S (2015) Mapping and classifying the seabed of West Greenland. Masters Thesis, Imperial College London, UK

GreenPeace (2005) A recipe for disaster: Supermarket's insatiable appetite for seafood.

Hamilton, L, Lyster P, Otterstad O (2000) Social change, ecology and climate in the 20th-century Greenland. Climatic Change 47:193-211

Hinz H, Prieto V, Kaiser MJ (2009) Trawl disturbance on benthic communities: chronic effects and experimental predictions. Ecological Applications 19(3): 761-773

Holtedahl O (1970) On the morphology of the West Greenland shelf with general remarks on the "marginal channel" problem. Marine Geology 8:155-172

Hogan KA, Dowdeswell JA, Cofaigh CO (2012) Glacimarine sedimentary processes and depositional environments in an embayment fed by West Greenland ice streams. Marine Geology 311:1-16

Hutchings JA (2000) Collapse and recovery of marine fishes. Nature 406:882-885

Jennings S, Nicholson MD, Dinmore TA, Lancaster JE (2002) Effects of chronic trawling disturbances on the production of infaunal communities. Marine Ecology Progress Series, 243:251-260.

Jennings S, Kaiser MJ (1998) The Effects of Fishing on Marine Ecosystems. Advances in Marine Biology 34:201–212

Jones JB (1992) Environmental impact of trawling on the seabed: a review. N.Z.Jour.Mar.Fresh.Res. 26:59-67.

Jørgensen OA, Tendal OS, Arboe NH (2013) Preliminary mapping of the distribution of corals observed off West Greenland as inferred from bottom trawl surveys 2010-2012. NAFO. Nuuk.

Kaiser M, Collie J, Hall S, Jennings S. et al. (2002) Modification of marine habitats by trawling activities: prognosis and solutions. Fish and Fisheries 3(2):114-136

Kaiser M, Clarke KR, Hinz H, Austen MCV, Somerfield PJ, Karakassis I (2006) Global analysis of response and recovery of benthic biota to fishing. Mar.Ecol.Prog.Ser 311:1-14

Kanneworff P (1979) Stock biomass 1979 of shrimp (Pandalus borealis) in NAFO subarea 1 estimated by means of bottom photography. NAFO SCR Doc. 79/XI/9. 6pp.

McConnaughey R, Mier KL, Dew, CB (2000) An examination of chronic trawling effects on soft-bottom benthos of the eastern Bering Sea. ICES Journal of Marine Science 57(5): 1377-1388

Lassen A, Powles H, Bannister C, Knapman P (2013) Marine Stewardship Council (MSC) Final Report and Determination for the West Greenland Cold Water Prawn Trawl Fishery Client. (http://www.msc.org/track-a-fishery/fisheries-in-the-program/cer tified/arctic-ocean/West-Greenland-Coldwater-Prawn/assessmentdownloads-1/20130122_FR_PRA126.pdf)

Levin LA, Dayton PK (2009) Ecological theory and continental margins: where shallow meets deep. Trends in Ecology and Evolution 24(11): 606-617

MSC (2010) The MSC principles and criteria for sustainable fishing. MSC, London, UK. 4pp.

MSC (2014) Marine Stewardship Council: Global Impacts Report 2014. MSC, London, UK. 44pp.

Myers RA, Hutchings JA, Barrowman NJ (1997) Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecological Applications 7:91–106

Oaksanen J, Blanchet F.G, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner, H (2015) vegan: Community Ecology Package. R package version 2.0-10. (http://cran.r-project.org/package=vegan)

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Ribergaar MH, Pedersen SA, Adlandsvik B, Kliem N (2004) Modelling the ocean circulation on the West Greenland shelf with special emphasis on northern shrimp recruitment. Continental Shelf Research 24:1505-1519.

Rice (2006) Impacts of Mobile Bottom Gears on Seafloor Habitats, Species, and Communities: A Review and Synthesis of Selected International Reviews. DFO Can. Sci. Advis. Sec. Res. Doc. 2006/057. iv + 35p.

Ripley B, Venables B, Bates DM, Hornik K, Gebhardt A, Firth D (2015) MASS: Support functions and datasets for Venables and Ripley's MASS. R package version 7.3-43. (http://cran.r-project.org/package=MASS)

Rooper CN, Wilkins ME, Rose CS, Coon C (2011) Modelling the impacts of bottom trawling and the subsequent recovery rates of sponges and corals in the Aleutian Islands, Alaska. Continental Shelf Research 31:1827-1834

Stein E, Buch M (1991) Are subsurface ocean temperatures predictable at Fylla Bank, West Greenland? NAFO Scientific Council Studies 15:25-30

Walters C, Maguire J-J (1996) Lesson for stock assessment from the northern cod collapse. Reviews in Fish Biology and Fisheries 6:125-137

Watling L, Norse EA (1998) Disturbance of the Seabed Forest by Mobile Fishing Gear: Comparison to Clearcutting. Society for Conservation Biology 12(6):1180–1197.

Yesson C, Simon P, Chemishirova I, Gorham T, Turner CJ, Hammeken Arboe N, Blicher ME, Kemp KM (2015) Community composition of epibenthic megafauna on the West Greenland Shelf. Polar Biology 38(8)

Appendix 1 Table of Camera specifications for historical and recent images (top) and example images of a) a 'recent' image, b) a recent image after tagging via Poseidon, c) an original, scanned 'historical' image and d) the same historical image cropped to match the area covered by recent images (below)

	Historical	Recent
Camera	35mm camera	Nikon digital SLR camera
Angle	10º	0º
Film	Kodac Safety Film 5035 (ISO 400)	N/A (digital)
Housing	-	DSC-10000 Digital Ocean Imaging System
Flash Unit	-	200W-S (DOIS, Model 3831)
Scanner	Reflecta i-Scan 3600	N/A
Software	CyberView X	N/A
Area covered	3.39m^2	0.32m^2

Cropping

Historical images were cropped by calculating the percent of the area recent images would cover of the historical images (~11.8%), excluding the watch in the corner (Figure A1c). This was followed by drawing a box covering that same area that was an equal distance from the top and bottom and from the right and left sides, and then the central box was cropped.
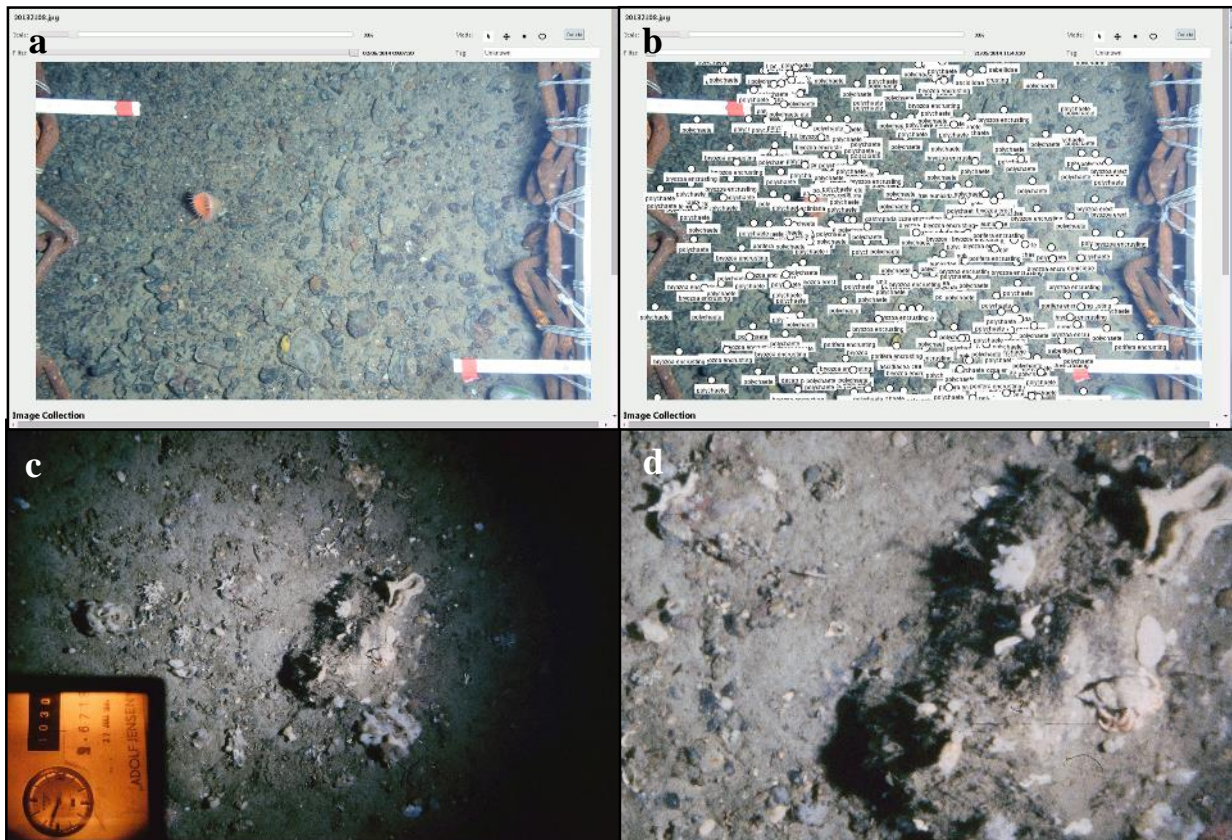
Appendix 2 Power (λ) of Box-Cox transformations for various non-normally distributed variables and class abundances. Also indicated is the constant added (1) to data to avoid negative values during the Box-Cox function. *Note:* A lambda value of 1 is a basic $\log_{10}$ transformation. The code for executing the function quickly is provided after the table

Variable	Constant Added	Lambda (λ)
Slope	-	1
Recovery	1	-0.8
Trawling	1	0.1
Total abundance	-	1
Class		
Actinopterygii	1	-7.6
Anthozoa	1	-0.5
Ascidiacea	1	0.1
Asteroidea	1	-2.4
Bivalvia	1	-0.5
Bryozoa encrusting	1	-0.2
Bryozoa soft	1	-0.4
Bryozoa stony	1	-0.5
Cephalopoda	Cannot transform (too few data)	
Crinoidea	1	-11.4
Cubozoa	1	-14.25
Echinoidea	1	-9.5
Gastropoda	1	-1.9
Holothuroidea	1	-9.9
Hydrozoa	1	-11.4
Malacostraca	1	-0.4
Maxillopoda	1	0
Nemertea	1	-13.3
Ophiuroidea	1	-0.6
Polychaeta	1	0
Polyplacophora	1	-1.95
Porifera arborescent	1	-9
Porifera encrusting	1	-0.2
Porifera massive	1	-0.7
Rhynchonellata	1	-3.8
Scaphopoda	1	-7.6
Thaliacea	Cannot transform (too few data)	

R 3.1.1 code of Box-Cox transformations (written by Dr. Chris Yesson)

```r
require(MASS)

bcx<-function(x, drop1=F) {
# check for negative numbers. If we find, then add a constant to get rid of them

        x.min<-min(x,na.rm=T)
        if(x.min<=0) {
                print(paste("adding constant",x.min+1,"to avoid negatives"))
                x1<-x-x.min+1
        } else {
                x1<-x
        }

# gradually increase lambdas as required
        for(i in 2:20){

# try box cox
                d<-boxcox(x1~1,plotit=F,lambda=seq(-1*i,i,i/20))
                l<-d$x[d$y==max(d$y)]

# check if lamda is at limit
                if(abs(l)!=i){
                        if(l==0) {
                        x.transformed<-log(x1)
                        } else {
                                if(l< -2 && drop1){
                                        x.transformed<-(x1^l)/l
                                } else {
                                        x.transformed<-(x1^l - 1)/l
                                }
                        }
                print(paste("lambda=",l))
                 return(x.transformed)
                }
        }
# if we get here then we can't do anything useful

        print("warning: can't transform this dataset")
        return(x)
}

#Example:
Data$AbunTransformed = bcx(Data$Abundance)
```

Appendix 3 Coefficient tables.
Left: AIC values from GLMs (Table 5)
Top Right: Estimates of linear models for the prediction of 'set' on diversity indices (Figure 3) and the impact of trawling on the change in diversity indices (Figure 6).
Bottom Right: Pearson's product-moment correlation statistics (test statistics, degrees of freedom, low and high 95% confidence intervals, and R and P values). 'Fishing grids' is a correlation of cumulative minutes trawled in 20km grid cells and 3.5km grid cells, while 'Temperature' is a correlation of seafloor and surface temperatures.

Variable	AIC
Actinopterygii	-452.37
Anthozoa	-247.49
Ascidiacea	-134.92
Asteroidea	-272.60
Bivalvia	-187.64
Bryozoa encrusting	-190.99
Bryozoa soft	-175.30
Bryozoa stony	-279.32
Crinoidea	-597.63
Cubozoa	-699.48
Echinoidea	-403.69
Gastropoda	-235.41
Holothuroidea	-401.54
Hydrozoa	-608.14
Malacostraca	-156.04
Maxillopoda	-112.54
Nemertea	-622.55
Ophiuroidea	-101.94
Polychaeta	-85.60
Polyplacophora	-327.79
Porifera arborescent	-563.40
Porifera encrusting	-216.83
Porifera massive	-291.96
Rhynchonellata	-424.43
Scaphopoda	-522.08
Shannon's H'	67.14
Evenness J'	-19.00
Class Richness	289.27
Total Abundance	169.90

Variable	Intercept	Set	R2
Shannon	0.14	**0.65**	0.23
Evenness	-0.07	**0.82**	0.31
Richness	3.19	**0.78**	0.35
Abundance	1.35	**0.89**	0.29
		Trawling	
Change in Shannon	**-1.09**	**0.03**	0.11
Change in Evenness	**-0.48**	**0.01**	0.14
Change in Richness	0.44	0.03	-0.03
Change in Abundance	**2.5**	**-0.07**	0.15

Statistic	Fishing grids	Temperature
t	3.630	9.582
df	54	26
Confidence interval (Low)	0.201	0.760
Confidence interval (High)	0.630	0.945
R	0.440	0.883
P - value	< 0.001***	< 0.001***

Appendix 4 A list of all taxa identified in the photographs with respective taxonomic classifications, common names, broad life-style category, and feeding behaviour.
Notes: P/S/D = Predator / scavenger / deposit feeder; Varied = Predator / filter feeder / parasitic, G = Generalist, H = Hard-specialist, S = Soft-specialist (designation by class-level, see Yesson et al. 2015, supplementary materials).

Phylum	Class	Subclass	Order	Family	Common Name	Life style	Feeding	Spec-ialist
Annelida	Polychaeta				Polychaete worm	Motile	Filter	S
	Polychaeta	Palpata	Canalipalpata	Sabellidae	Fan worm	Sessile	Filter	S
			Enucida	Eunicidae	Eunicid worm	Sessile	Filter	S
		Aciculata	Phyllodocida	Polynoidae	Scale worm	Motile	Deposit	S
Arthropoda	Malacostraca	Eumalacostraca	Amphipoda		Amphipod	Motile	P/S/D	S
			Decapoda	Brachyura	Crab	Motile	P/S/D	S
				Pandalidae	Northern shrimp	Motile	P/S/D	S
			Isopoda		Isopod	Motile	P/S/D	S
	Maxillopoda	Thecostraca	Sessilia		Barnacle	Sessile	Filter	G
	Pycnogonida				Sea spider	Motile	Deposit	G
Branchi-opoda	Rhynchonellata		Terebratulida		Lamp shell	Sessile	Filter	H
Bryozoa	"Encrusting"				Encr. moss animal	Sessile	Filter	H
	"Soft"				Soft moss animal	Sessile	Filter	S
	"Stony"				Stony moss animal	Sessile	Filter	H
Chordata	Actinopterygii	Neopterygii	Perciformes		Perch-like fish	Motile	Predator	-
			Pleuronectiformes		Flatfish	Motile	Predator	-
			Scorpainoformes		Sculpin	Motile	Predator	-
	Ascidiacea				Ascidian	Sessile	Filter	G
	Thaliacea				Salp	Motile	Filter	-
Cnidaria	Anthozoa	Hexacorallia	Actiniaria		Sea anemone	Sessile	Filter	H
			Scleractinia		Stony coral	Sessile	Filter	H
			Zoantharia	Epizoanthidae	Colonial anemone	Sessile	Filter	H
		Octocorallia	Alcyonacea		Soft coral	Sessile	Filter	H
			Pennatulacea		Sea pen	Sessile	Filter	H
	Cubozoa				Box jellyfish	Motile	Predator	-
	Hydrozoa				Hydroid coral	Sessile	Filter	H
Echinodermata	Asteroidea				Sea star	Motile	P/S/D	G
	Asteroidea		Valvatida	Goniasteridae	Sea star	Motile	P/S/D	G
				Solasteridae	Sun star	Motile	P/S/D	G
	Crinoidea				Feather star	Sessile	Filter	G
	Echinoidea				Sea urchin	Motile	Filter	G
	Holothuroidea				Sea cucumber	Motile	Filter	G
	Ophuiroidea				Brittle Star	Motile	P/S/D	G

Phylum	Class	Subclass	Order	Family	Common Name	Life style	Feeding	Spec-ialist
Mollusca	Bivalvia				Bivalve	Motile	Filter	G
	Cephalopoda	Coleodiea	Octopoda		Octopus	Motile	Predator	-
	Gastropoda				Shelled snail	Motile	Predator	G
	Gastropoda		Nudibranchia		Sea slug	Motile	Predator	G
	Polyplacophora				Chiton	Motile	Filter	H
	Scaphopoda				Tusk shell	Motile	P/S/D	G
Nemertea					Ribbon worm	Motile	Varied	-
Porifera	"Arborescent"				Branching sponge	Sessile	Filter	H
	"Encrusting"				Encrusting sponge	Sessile	Filter	H
	"Massive"				Massive sponge	Sessile	Filter	H
	Demospongiae		Hadromerida	Polymastiidae	Massive sponge	Sessile	Filter	H

Appendix 5 Taxon accumulation curves based on all samples (light blue), recent samples only (orange), and historical samples only (green)