

Impact of scallop dredging on benthic communities and habitat features in the Cardigan Bay Special Area of Conservation

Part I – Impact on infaunal invertebrates





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EXECUTIVE SUMMARY (for Reports Part I, II and III)

Abstract

Experimental scallop fishing in a closed area of Cardigan Bay SAC was undertaken in spring 2014. The experiment was designed to examine the response of the geology of the seabed, and the response of animal communities living in and on the seabed, to a gradient of scallop fishing activity. The immediate effects of scallop fishing were quantified and then monitored again in September 2014 with a further geological survey undertaken in March 2015.

A total of 17 experimental boxes were set up within the closed area. Four of these boxes acted as controls where no fishing occurred and were used for comparative purposes throughout the study. The remaining boxes were fished at different intensities by commercial scallop dredgers up to a maximum intensity of 6.2 times (i.e. the seabed was swept on average 6.2 times by scallop dredges). A pre-experiment survey demonstrated that the animal communities within each of the boxes differed depending upon the composition of sand and gravel in the sediment. This variation was accounted for in the subsequent analyses.

Two weeks after the boxes had been fished by commercial scallop dredgers, the samples collected revealed small but distinguishable changes in the animal community on the seabed such that the abundance and biomass of organisms decreased relative to the control areas. The strength of this decrease was related to fishing intensity such that the effect was greatest at the highest intensity of fishing. The scour marks created by the scallop dredging were clearly distinguishable using acoustic survey techniques, although the propensity for the seabed to show these scour marks varied depending upon the seabed topography. At the highest intensity of fishing sand wave features on the seabed were flattened.

Between March and May, the initial impact of fishing decreased the abundance and biomass of species by 40 to 60%. By September the biomass and abundance of animals living in and on the seabed was mostly indistinguishable from those living in the control areas, although there were subtle differences in these responses that were related to the composition of sand and gravel in the seabed. Generally, settlement, migration and growth of animals living in the seabed (infauna) resulted in an increase in abundance and biomass (+30% increase in abundance at the highest fishing intensity level, i.e. 6 times fished). This increase was mostly due to an increase in sand as there was still a negative impact in gravel areas when they were fished at the higher intensities (i.e. > 4 times). Similarly, the abundance of organisms living on the seabed (epifauna) had increased by over 100% (relative to control areas) in response to fishing within most of the sandy areas. Epifauna decreased in gravel areas by about 50%, particularly in areas fished more than 3.5 to 4 times. Natural variation was of similar magnitude to fishing impact. Overall, by September, despite some remaining evidence of changes in abundance and biomass, the differences in species composition between control and fished plots were no longer detectable.

By September, the physical marks made by the scallop fishing on the geological features of the seabed remained visible, but had been restored by natural processes to varying extents in different boxes. Hence most boxes were resurveyed in March 2015. At this point in time the marks had mostly disappeared but did remain slightly detectable in a couple of boxes (mostly in one inshore box fished 3.8 times on average).

Conclusions:

The instantaneous effects of scallop fishing on animal communities were detectable at higher scallop dredging intensities (seabed swept more than 2 times completely).

Seabed animal communities living in Cardigan Bay mostly recovered within 4 months of the fishing disturbance, particularly in areas fished less than 4 times. This recovery period coincided with summer recruitment and growth of seabed animals. The current management practice of a seasonal closure over the summer would appear to facilitate recovery of the biological components on the seabed.

The seabed in deeper water offshore seems to be partly reconstructed by natural processes within 4 months of fishing disturbance and certainly 10 months later and would appear to be able to withstand fishing intensities up to 6.2 times complete coverage by scallop dredging. Some areas closer inshore would appear to take longer for the seabed to be reformed by natural processes and may require a full year for this to occur (with fishing intensities of 3.8 times swept per year).

A potential future management system could account for the recoverability of both the seabed biota and the geological features of the seabed. A conservative estimate would indicate that the seabed could tolerate a fishing intensity of less than 3.5 times swept per year in inshore waters (3-6 nm) and in gravel and less than 6.2 times swept per year in offshore waters (6-12 nm) and in sand.

Detailed summary

• The majority of the Cardigan Bay Special Area of Conservation (SAC) has been closed to scallop dredging since 2009. The SAC supports high densities of scallops in areas currently closed to fishing and therefore remains an inaccessible but potentially valuable resource for the scallop industry. The question remains whether scallop dredging can be undertaken in a manner that it compatible with the conservation objectives of the SAC.

• We conducted a large scale Before-After-Control-Impact (BACI) experiment to assess the impact of scallop dredging on the benthic organisms in the closed area of the SAC and to provide managers and stakeholders with quantitative evidence that could inform the development of a fishery management regime that would take account of the conservation objectives of the SAC.

• The study was designed to address the following questions: 1) that the seabed within the SAC is exposed to high levels of natural disturbance, 2) the intensity of fishing disturbance that would not exceed the natural capacity biological and geological features of the system to recover within one fishing season.

• The study was designed to identify the thresholds at which lasting changes occur in species composition, functional composition, species richness, abundance and biomass as well as sediment composition. These thresholds would be used to advise on the limit of fishing intensity that could be supported within the SAC without having detrimental effects on the conservation features of the SAC.

• We fished 17 sites along a fishing intensity gradient in April 2014. We conducted 3 scientific surveys, one prior to fishing in March 2014 and two after fishing, one in May and one in September 2014. During each survey, grab, beam trawl and video samples were taken at each site, as well as side-scan sonar and multibeam images. These samples provided data on infauna, epifauna and sediment that could be compared before and after fishing and along the fishing intensity gradient (from control sites, i.e. 0 times fished, to >6 times fished).

• The seabed in the area of the Cardigan Bay SAC where the experiment was conducted was a mosaic of patches composed of an equal proportion of (gravelly) sand and (sandy) gravel habitats. The initial pre-fishing low density and diversity of infaunal and epifaunal species suggested that the seabed was an unstable, mobile substratum subject to period natural disturbance events.

• There was a high spatial and temporal turnover (= change in species composition) of infaunal invertebrates in the area and a lower turnover of epifauna. The difference in species composition between surveys was higher for infauna than epifauna, and was particularly high between March and September due to the arrival of new infaunal taxa and the decrease in epifaunal species.

• The infaunal communities were different in sand and gravel. Abundance, biomass and richness were higher in gravel than in sand (i.e. 52 individuals and 16g/ grab in gravel vs 35 individuals and 8g/grab in sand, -3.5 species/grab in sand compared to gravel). For epifauna, however, there was no difference between gravel and sand communities.

• In sand, there was a strong association between sediment composition and the taxonomic and traits composition of the infaunal community. Epifaunal community composition did not show any relationship to sediment composition in sand, which is probably related to the lack of potential attachment points for epifauna in sand sediment. The opposite trends were observed in gravel.

• The substrate in the experimental area of Cardigan Bay SAC was highly variable and patchy. Most lanes contained a mixture of fine and coarse sediment. Scallop dredging was found to leave troughs in most areas where it occurred, on a range of sediments from sand through to gravel and cobble. Fishing increased sediment coarseness in sand but sediment composition had mostly recovered by September. Most dredging marks were no longer visible 10 months after fishing.

• Infaunal and epifaunal taxonomic richness did not change along the fishing gradient. There were, however, some changes in species composition due to fishing. Differences in infaunal taxa composition increased with fishing intensity between March and May, and to a lesser extent between March and September. The main difference was found in areas fished over 0.3 to 1.2 times, mostly due to the response of communities living in sand. Similarly some changes in epifaunal composition occurred around 0.8 times fished in sand in May, but these differences had disappeared by September. Taxon persistence and colonisation rates were studied in more detail but any changes observed along the fishing gradient had disappeared by September.

• Overall, both infaunal and epifaunal abundance and biomass displayed similar responses with varying degrees of confidence and high levels of natural variability, comparable to the detected effect of fishing. There was a decrease with fishing intensity in May, i.e. within 2 weeks after fishing.

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However, in September, i.e. 4 months after the impact, patterns were more complex. Abundance and biomass tended to increase in sand and decrease in gravel. The decrease in gravel was, however, not significant, which indicated recovery with exception of the gravel areas fished over 4 times on average, which remained negatively affected.

• In May, the overall trend was for a decrease in abundance and biomass along the fishing gradient which was mostly the result of the impact of fishing on a few functional groups, e.g. asexual/budding and species living attached to the sediment showed a decrease in areas fished over 2 times.

• Four months after fishing (September) there was a continuous increase along the fishing gradient in the abundance and biomass of species living on the seabed in the sand habitats: +162% in abundance and +127% in biomass in heavily fished areas (i.e. 6 times fished) compared to control sites. Infaunal abundance increased in sand in all fished areas but was not related to fishing intensity (i.e. average increase of 84% across all areas above a threshold of 0.2 times fished).

• In gravel, abundance and biomass had decreased in areas fished over 3.5 to 4 times compared to control sites. For infauna, the average difference was -56%. For epifauna, the average difference was - 46% in abundance and - 23% in biomass.

• Those significant changes in September, i.e. increases in sand and decreases in gravel, could partly be explained by some specific taxa and functional groups. For instance, an increase in abundance and biomass of crustaceans and bivalves in areas fished more than 2 times partly explained the increases observed in sand habitats. Their increase could be the result of immigration from adjacent areas and successful settlement. In fact the changes were driven by a very high abundance of the small shrimp *Mysidacea* in the grab samples of some highly fished sites as well as a higher abundance in the bivalve *Glycymeris spp.* and the polychaete *Pectinariidae*. Mysids might not be a good indicator of fishing pressure due to their ephemeral and free swimming nature but trends were similar when they were excluded from the analyses. Generally, there was an increasing trend along the fishing gradient for most functional groups in sand habitat, particularly for very small organisms (<1cm) living inside the sediment as they appeared to have increased in most fished areas. On the other hand, the decrease in biomass in gravel in September was partly explained by the continuous decrease in dead man's fingers *Alcyonium digitatum* biomass along the fishing gradient and the decrease in poor cod *Trisopterus minutus* and sponge *Dysidea fragilis* biomass over a threshold of 4.2

times fished. Again fish might not be a direct indicator of localised scallop dredging. However, generally, suspension feeders, stalked and asexual/budding species had a lower biomass in September in areas that were fished over 2 to 4 times.

1. INTRODUCTION

The Ecosystem Approach to Fisheries (FAO, 2003) requires managers to consider the environmental impacts of fishing in management plans. In Europe, advisory processes supporting the implementation of the Marine Strategy Framework Directive (MSFD; EC, 2008) seek to define targets for 'Good Environmental Status' (GES) for ecosystem components and attributes such as the seabed (EC, 2010). Beyond establishing targets consistent with sustainable impacts, parts of the MSFD imply that targets for GES should be consistent with lower levels of pressure and impact than those needed to achieve sustainable use. Information on the resilience of seabed habitats will help to inform debate about those targets, but it will be the role of society to define them. In contrast to the MSFD, the European Common Fisheries Policy (CFP; EC, 2002) has not sought to define explicit targets for fishing impacts on the environment, but makes general commitments to minimize impacts. One practical interpretation of a commitment to 'minimize' is that managers should seek to reduce the impacts of fishing per unit catch weight or value as well as fulfilling any objectives to manage catch rates or fishing effort. Information on seabed recovery times can be used to define spatial management plans that minimize seabed impacts. Management plans that reduce the relative impacts of fishing, if effective, may also help to strengthen a case for fisheries certification or move a fishery towards 'best practice' in terms of minimizing impacts on the seabed.

The Cardigan Bay Special Area of Conservation (SAC) (960 km²), Wales, UK, was established in 2004. It aimed at protecting bottlenose dolphin, grey seal and lamprey (Sciberras et al., 2013). The location of the SAC coincided with the main scallop fishing ground in Cardigan Bay and in Wales. The activity was not managed any differently to the rest of Wales at first. However, since 2009, the scallop fishing pressure and the potential resulting damage to some habitat features of conservation interest, i.e. cobble reefs. Since then a number of studies have shown that the area is characterized by moderate energy hydrodynamic conditions and is mostly composed of unconsolidated sediments, i.e. sand, gravel and pebble (Hinz, Sciberras, Murray, Benell, & Kaiser, 2010; G. I. Lambert, Murray, Benell, & Kaiser, 2013; Sciberras et al., 2013).

There are two management regimes in the SAC. One area is seasonally open to scallop dredging and the rest of the SAC, corresponding to approximately 75% of the SAC, is permanently closed (Figure 1). The fishing industry would like this management regime to be revised as they see the quality of their catches decrease in the open area with numerous vessels having to concentrate their effort over a

small area. They are also concerned about the wastage of large numbers of large size scallops in the closed area. They argue that the seabed can sustain some degree of fishing in view of the fishing history of the area, the dynamics of the environment and limited variety of associated benthic communities (pers. comm.).



Figure 1. Map of the Cardigan Bay SAC and the experimental area.

The objective of this study was to determine the effect of scallop dredging on the benthic communities and habitat characteristics in the SAC and identify sustainable levels of scallop dredging to inform management options. A large scale <u>Before-After Control-Impact (BACI) experiment</u> was therefore conducted in the western part of the permanently closed area, i.e. closed since 2009, by experimentally dredging areas at different intensities. The benthic fauna was then compared between areas that were fished at different intensities, and recovery from fishing monitored after 4 months.

Please not that due to the complex technicalities of the statistical analyses, a glossary (with help to interpret the figures) for all underline vocabulary is provided at the end of the document.

2. THE EXPERIMENT

2.1 Experimental design

The full extent of the experimental area is 110km² (approximately 8km by 13.5km). It lies between 3 and 12nm offshore, avoiding any potential adverse effects between dolphin prey/dolphin habitat and scallop gear interactions that may occur within 3nm of the coastline as advised by Natural Resources Wales (NRW). Evidence was gathered before the experiment to show that that stony reefs were absent in the area (Lambert et al., 2013). From video analysis, the habitat in the experimental area was mostly mixed with various proportions of pebble, gravel, fine sediment and shells.

The experiment followed a BACI design, where the impact was a gradient of fishing intensities. Fishing intensity is defined as the number of times an area is entirely fished. This is estimated by dividing the total area covered by the towed fishing gear by the size of the fishing ground. For instance, if a vessel has been towing its gear for 20 hours with 7 dredges a side at 3knots, it will have covered a total of approximately 1.2km² of seabed. If its effort was concentrated in an area of 0.5 by 0.5 km, i.e. 0.25km², it will have fished the area on average 1.2/0.25= 4.8 times. The objective was to achieve a gradient of 0.25 and 8 times fished. This was thought to represent and exceed the gradient that can be found on real scallop fishing grounds in the Irish Sea (based on data from the Isle of Man scallop fleet (Lambert, Jennings, Kaiser, Hinz, & Hiddink, 2011). Because it is expected that the first dredge passes have a stronger effect on the benthos than later dredge passes (because there is going to be less fauna around to remove), the target fishing intensities were defined at equal intervals on a log_2 scale. We planned to sample 17 sites, including 3 control sites where no fishing occurred and 14 impact sites to be fished by commercial scallop dredgers, using standard fishing gear (described later), at predefined fishing intensities. The experiment was conducted over one month, between the 1st and 30th of April 2014, and by the end of the month a gradient with a maximum intensity of 6 times fished was achieved and 4 sites were left unfished (Figure 2, Table 1).



Figure 2. (A) Experimental design and (B) location of grab samples in March, May and September 2014. The gradient of colours in a represents the intensity of fishing (see Table 1).

Вох	Target intensity	Achieved intensity	Percentage area fished	Number dredges	Hours fished	Number of grabs taken	Number of PSA	Faunal samples analysed
L01	1	1.09	0.65	6	29	15	11	0
L02	3.17	3.05	0.90	8	76	27	25	21
L03	4	3.82	0.98	8	98	16	13	15
L04	0	0	0	0	0	26	20	24
L05	1.59	1.56	0.77	6	41	16	13	0
L06	1.26	1.24	0.70	8	31	26	20	15
L07	0	0	0	0	0	27	21	0
L08	0.5	0.51	0.40	8	12	15	15	0
L09	0.71	0	0	0	0	22	20	19
L10	0.35	0.23	0.20	14	2	26	22	0
L11	6.35	5.33	0.99	14	56	16	15	16
L12	2.52	2.29	0.87	14	24	16	8	15
L13	0	0	0	0	0	27	23	21
L14	5.04	3.87	0.97	14	40	16	16	15
L15	0.25	0.29	0.25	14	3	17	15	15
L16	8	6.07	0.98	14	58	26	21	24
L17	2	1.87	0.84	14	19	24	14	0

Table 1. Summary of experimental design and grab sampling.

The 17 sites were located on a grid within the experimental area and the distribution of the fishing intensities, including control sites, was randomised. Each site was sampled prior to the fishing experiment, directly after (leaving at least 72h for the impacted organisms to die and for the predators and scavengers to feed on them (Ramsay, Kaiser, Moore, & Hughes, 1997), because once preserved it is not possible to distinguish already dead from still-living animals) and again by the end of summer 4 months later to assess both impact and recovery (see "data collection"). The latest survey was conducted at the end of summer as it may be expected that recovery would be the fastest over the most productive months of the year. No further survey was planned at this stage although if an impact was detected and communities had not fully recovered by September further surveys would be recommended. Each impact site comprised three zones: one fishing box of ca. 1700m long by 370m wide that was positioned in the direction of the main current for the vessels to be able to fish it lengthwise, and two zones at either end in which the vessels could manoeuvre (haul, shoot and turn) (Figure 2). Those 2 zones were therefore partly fished but not studied or sampled. The control sites were the same size as the fishing boxes.

The experimental fishing was carried out by five selected commercial scallop dredgers (Table 2). This was necessary because of the vast area that needed to be fished, which was larger than could be covered by a research vessel, and it was desirable because it realistically replicates the actual fishing activities that we are trying to assess here. Each site was fished by one vessel only and each vessel was attributed between 2 and 4 sites. It was necessary that there was only one vessel per site as the areas were too small to have two vessels working side by side and it was logistically easier as vessels did not work at the same speed and in the same weather conditions. Two vessels towing 7 dredges a side operated within the 6-12nm zone while two vessels towing 4 dredges a side and one vessel towing 3 dredges a side operated within the 3-6nm zone. This was to comply with the Welsh waters scallop dredging legislation on number of dredges, which also imposes restrictions on dredge weight (\leq 150kgs), number and length of teeth (number \leq 8 and length \leq 110mm) as well as tow bar characteristics amongst other restrictions. The scallop dredges were all Newhaven dredges which are 0.76cm wide so 7 dredges corresponds to a width of 5.32m, 4 dredges is 3.02m and 3 dredges is 2.28m. The vessels were given specific instructions to tow a certain number of times across each site based on the width of their gear and the target fishing intensity of the sites they were attributed (see summary information in Table 1). The gear was towed across the whole length of the fishing box and the captain could choose to haul and/or turn with the gear still down in the designated areas at either end of the box. The aim was to homogeneously spread the tows across the width of the box. This was monitored from land with live data from GPS tracking devices and continuous communication

between scientists and fishers. This was thought to result into a more homogeneous pattern that would occur on real fishing ground, depending on individual fisher's behaviour. The scallops that were caught and were over the legal minimum landing size (\geq 110mm) were landed and sold to pay the participants of the experiment and partly funded the subsequent data processing (see Table 2 for logistics summary of the experiment). This was authorised by the Welsh Government as the experiment took place during the scallop fishery open season.

2.2 Data collection and processing

Three scientific surveys were conducted on board the RV Prince Madog. The "before" survey took place between the 15th and 31st of March 2014, fishing took place between the 1st and 30th of April, the "after" survey took place between the 1st and 17th of May 2014 and the "recovery" survey between the 7th and 16th of September 2014. During each survey biological and physical data were collected using video camera, beam trawl, <u>Hamon grab</u>, <u>multibeam</u> and <u>side scan sonar</u>. The focus of the present report being on infaunal invertebrates, only grab sampling will be presented (see parts II and III for reports on epifaunal invertebrates and physical seabed).

The Hamon grab had a bucket area of 0.1m² and sampled down to 10cm deep in the sediment. Five to nine grab samples were taken at each site. The samples were spread out inside the fishing box and positioned away from the edges as much as possible (Figure 2B) so it would capture the impact from fishing and recovery away from unfished areas of the seabed which can bias results because of local immigration of fauna. A sediment subsample (a handful – about 40 grams) was taken from each sample and frozen for particle size analysis in the lab. The fauna was then separated from the sediment of the main sample using the following steps: (1) the grab sample was emptied from a fish box into a large bucket; (2) the bucket was filled up with seawater; (3) it was mechanically swirled for a minute; (4) the seawater was then poured through a round hand-held 1mm sieve; (5) the animals that floated off the sediment sample were picked out of the sieve and put into a pot; (6) the steps 2 to 5 were repeated at least 5 times or until no more animals came out; (7) the residue of sediment was then emptied on a large square 1mm sieve table and searched through for remaining animals which were then put into the same sample pot as in 5; (8) the sediment residue was discarded if it was judged that there was no fauna left. If there was less than 2.5L of sediment and some fauna was likely to remain (e.g. small bivalves in coarse sand samples) then all the sediment was kept. If there was more than 2.5L of sediment left (i.e. more than one sample pot) then only a subsample of sediment was kept. As a result some samples included sub-samples and this was accounted for in the faunal data processing and analyses (i.e. number of animals scaled up based on weight of sediment kept versus weight of discarded sediment). Small stones with encrusting worm tubes were kept in the samples brought back to the lab. Subsampling was necessary as it was not possible to store and sort through this much sediment. Generally about one quarter to one half of the sediment was brought back when the grab had to be subsampled.

Part of the particle size analysis (PSA) of the sediment samples and the laboratory processing of the infaunal samples was funded by the sale of the scallops caught by the scallop dredgers during the experiment (see Table 2 for logistics summary of the experiment). Due to the limited fund available not all of the samples were analysed, a subsample was chosen to cover the fishing intensity range. Table 1 summarises the number of samples processed and used in the present study. The PSA was done on ca. 25 grams of sediment by first using an aqueous deflocullant to separate the fine particles of <63µm and then mechanically dry sieving through a stacked set of Wentworth grade sieves ranging from 63µm to 75mm. Based on the Wentworth scale (Wentworth, 1922), the data from the 42 sieves were aggregated into the following categories: pebble (4-64mm), gravel (2-4mm), coarse sand (0.5-2mm), medium sand (0.25-0.5mm), fine sand (0.125-0.25mm), very fine sand (0.063-0.125mm), silt/clay (<0.063 mm) and were expressed as percentages. In later analyses, this was referred to as the sediment composition dataset. A general description was also obtain of each sediment sample, thereafter called sediment texture or sediment type using the Gradistat software equivalent package in R, G2Sd (Gallon & Fournier, 2013). The categories are defined from the PSA percentages after (Folk, 1954). The infaunal samples were analysed in compliance with the NMBAQC guidelines (Worsfold, Hall, & O'Reilly, 2010) by an environmental consultancy selected after tender. They were sieved again over 1mm sieves and all animals removed from the samples were identified at the family level, where practical, and counted. Non-countable taxa such as colonial organisms were recorded as present and counted as 1 in abundance data analyses. All animals were then gathered into 20 predefined taxonomic groups prior to being weighed and an estimate of biomass per group was produced.

APRIL 2014	
Number of fishing vessels participating	5
Number of dredges used in total	50
Number of hours fished	1118 (~ 19 x 12h days/vessel)
Number of dredge hours fished	12 030 hours
Number of bags landed	7 800
Yield of scallop meat (+gonad)	29.6 tonnes
Revenue generated:	£304 085
Fees for fishing:	£246 018
Funds generated for science:	£58 067
Number of ports landed to	4
Number of onboard observers	9
Number of days at sea/observer	5 to 10
MARCH/MAY/SEPTEMBER 2014	
Number of research vessel days	34
Number of sampling hours	500
Number of volunteers	~20
Number of beam trawl tows	207
Number of grabs	559 (of which 353 successful)
Number of video tows	46

Table 2. Summary of costs and logistics of the experiment

2.3 Hypotheses tested

Our analyses aimed to prove or disprove the following null hypotheses:

(H₁) There is no spatial gradient of sediment or <u>infaunal invertebrates</u>' distribution over the all area that could have jeopardised the results of the experiment.

<u>Spatial autocorrelation</u> can pose problem in statistical analyses. If there was a <u>correlation</u> between fishing effort and sediment or infaunal composition prior to fishing, then this should be accounted for in the subsequent analyses aiming at assessing the effect of fishing on the benthos.

(H₂) Fishing does not impact the composition of infaunal communities and all species are resilient to fishing activities of any intensity.

If the experimental area is mostly composed of unconsolidated sediment and species living there are resilient to a certain level of natural disturbance, it can be expected that the area can sustain some dredging without showing any significant impact or that it can recover quickly. If the effect of fishing is different to the effect of natural disturbance, at least over a certain intensity, then some species would be expected to respond to fishing disturbance and overall communities would be expected to change.

Under H₂ the following hypotheses were tested:

 (H_{2a}) Fishing the sites at different intensities did not cause significant differences in overall species composition

(H_{2b}) Fishing the sites at different intensities did not affect species richness

(H_{2c}) Fishing the sites at different intensities did not affect persistence and colonisation rates

(H_{2d}) Fishing the sites at different intensities did not lead to the extinction of any species

(H₃) Fishing does not impact the biomass and abundance of infaunal communities and all species are resilient to fishing activities of any intensity.

If the effect of fishing is different to the effect of natural disturbance, at least over a certain intensity, then some species would be expected to respond to fishing disturbance and overall or individual biomass and abundance would be expected to change.

(H₄) Fishing does not impact the <u>functional groups</u> of infaunal communities and all <u>functional traits</u> are resilient to fishing activities of any intensity.

If the effect of fishing is different to the effect of natural disturbance, at least over a certain intensity, then some functional traits would be expected to respond to fishing disturbance and biomass and abundance of some groups of species with specific traits would be expected to change.

(H₅) Fishing does not impact the sediment composition of the seabed and seabed sediment composition is not linked to infaunal invertebrates' composition.

If the sediment composition partly explained the species composition then changing the sediment characteristics by towing dredges on the seabed, i.e. raking features, re-suspending fine particles, could have an indirect effect on the benthic communities.

3. DATA ANALYSES AND RESULTS

3.1 Overall description of the experimental area

There were two main sediment textures/types in the experimental area: gravelly sand and sandy gravel in which respectively 37% and 45% of the samples belonged. The rest of the samples were variations of those two textures. Gravel and muddy sandy gravel samples were therefore grouped into the "sandy gravel" category while slightly gravelly (muddy) sand and gravelly (muddy) sand were called "gravelly sand". This is illustrated in figure 3 where each point represents a grab sample and their position reflects the composition of sample in percentage of pebble, coarse sand, fine sand etc. To avoid confusion, "gravelly sand" is thereafter referred to as "sand" and "sandy gravel" as "gravel".





The average abundance, biomass and number of taxa collected during the 3 surveys are presented in table 3. The numbers of the March survey are compared to data collected in 1993 and presented in (Kaiser & Spencer, 1996). Under the hypothesis that data from this earlier study are representative of different habitat types in Welsh waters, the comparison suggests that the experimental area presents

a low density and diversity of species and that the numbers match up with numbers from an unstable, mobile substratum type area.

Table 3. Summary of biological data collected during the three scientific surveys conducted before and after the experiment (mean ± standard error of the mean). Data are given per grab sample. Data from 1993 are extracted from Kaiser & Spencer (1996), collected with a day grab of 0.1m² off the northern coast of North Wales. Species richness for the present study is given as number of families multiplied by 2 as infauna samples were only analysed at the family level here and a pilot study from October 2012 suggested that there was an average of <2 species per family in Cardigan Bay SAC (*unpublished data*).

Survey	Grab number	Species number (nb/grab)	Abundance (nb/grab)	Biomass (g/grab)
March 2014	65	21.4 (± 1.4)	35.5 (± 6.5)	8.8 (± 2.5)
April 1993 - Mobile area		28.5 (± 5.3)	58.5 (± 11.1)	-
April 1993 - Stable area		66.8 (± 2.6)	334.8 (± 18.2)	-
May 2014	68	19.8 (± 1)	25.3 (± 24)	17.0 (± 8.3)
September 2014	67	40.6 (± 2.6)	73.0 (± 10.8)	10.8 (± 2.8)

Table 4 summarises the occurrence, abundance and biomass of the most important species caught in the grab samples. Note that mysids were caught in relatively large quantity and were included in the analyses despite their potentially more pelagic and ephemeral nature. This is because the species were not analysed at the species level so it could not be ruled out that they were actual benthic species. Also mysids may scavenge and feed on detritus therefore they could be treated as most fish (see report part III on epifauna), i.e. fishing may have had an indirect impact on them via its impact on its food.

Table 4. Abundance, biomass and occurrence of the most common species caught in grabs combing all 3 surveys. Species presented were the highest ranking ones in terms of occurrence (i.e. percentage presence in tows) and abundance. They are ordered by groups in which they were weighed. Highlighted are the top 5 ranking species of each measured parameters.

Group	Species (Latin name)	Occurrence	Abundance	Biomass
		(%)	(nb/0.1m²)	(mg/0.1m²)
Bivalvia	Veneridae	34	0.76	10 216
	Glycymerididae	25	0.53	
	Nuculidae	23	0.47	
	Mactridae	19	0.33	
	Cardiidae	12	0.21	
Crustacea	Upogebiidae	30	1.13	479
	Cirolanidae	28	0.89	
	MYSIDACEA	26	<mark>4.63</mark>	
	Ampeliscidae	18	0.25	
	Dexaminidae	13	0.43	
	Gnathiidae	8	0.24	
Echinodermata	Ophiuridae	18	0.33	768
	Amphiuridae	14	0.29	
	Synaptidae	11	0.17	
	Ophiotrichidae	6	0.53	
Nematoda	NEMATODA	14	0.39	-
Nemertea	NEMERTEA	<mark>53</mark>	1.20	34
Polychaete	<mark>Capitellidae</mark>	<mark>76</mark>	<mark>7.47</mark>	489
	<mark>Lumbrineridae</mark>	<mark>70</mark>	<mark>3.16</mark>	
	<mark>Glyceridae</mark>	<mark>56</mark>	1.27	
	<mark>Spionidae</mark>	<mark>53</mark>	<mark>2.43</mark>	
	<mark>Terebellidae</mark>	50	<mark>1.77</mark>	
	Phyllodocidae	36	1.45	
	Nephtyidae	34	0.49	
	Syllidae	32	0.99	
	Cirratulidae	27	0.57	
	Polynoidae	23	0.47	
	Serpulidae	19	1.18	
	Maldanidae	18	0.31	
	Nereididae	17	0.27	
	Scalibregmatidae	17	0.20	
	Goniadidae	16	0.29	
	Pholoidae	15	0.28	
	Eunicidae	15	0.22	
	Poecilochaetidae	14	0.33	
	Dorvilleidae	13	0.22	
	Pectinariidae	12	0.81	
	Sigalionidae	12	0.13	
	Opheliidae	11	0.17	
	Pisionidae	8	0.36	
Polyplacophora	Leptochitonidae	10	0.19	3
Sipuncula	Golfingiidae	24	0.60	148
Cnidaria				226

3.2 Spatial heterogeneity of the experimental area (H₁)

3.2.1 Spatial autocorrelation in sediment and species composition

3.2.1.1 Objective

The objective was to find whether there was a scale at which taxa or sediment composition appeared to aggregate. If this was the case, it needed to be accounted for in subsequent analyses.

3.2.1.2 Methods

We investigated the existence of a gradient in taxa and sediment composition at different scales within the experimental area and the potential effects of the depth gradient. To do so, we used <u>(partial)</u> <u>Mantel's tests</u> and produced <u>Mantel correlograms</u> to test and illustrate the influence of geographic distance and depth differences on <u>samples (dis)similarity</u>, both in terms of fauna and sediment composition.

Mantel's tests examine the correlation between data matrices and partial Mantel's tests allow to control for the effects of a third data matrix (Legendre & Legendre, 2012). Those tests measure the average correlation between all samples of two datasets, i.e. they can be used to test if the difference in composition between samples increases along gradients of environmental differences. Since Mantel's tests only gave an estimate of overall correlation, Mantel correlograms were also used to assess changes in autocorrelation at different distance or depth lags, i.e. to investigate the scale at which data were autocorrelated. Autocorrelation can pose problems when analysing spatial data.

A matrix of geographic distances and a matrix of depth differences between samples were therefore produced and Mantel statistics used to assess the correlation between these matrices and the dissimilarity matrices of faunal and sediment composition. The <u>dissimilarity matrix</u> of faunal data was estimated from square root abundance data using the <u>Bray Curtis index</u> (Bray & Curtis, 1957). Analyses on taxa composition were all performed on the abundance dataset as it was the most accurate, biomass having been estimated for aggregated groups of taxa only (see "2.2 data collection and processing"). Categorised sediment data were expressed as percentages and arcsine square root transformed prior to estimating their Euclidean distance, i.e. their dissimilarity matrix. The significance of the correlation coefficients was established by <u>permutation tests</u>, i.e. randomly permuting the rows and columns of one of the matrices 10000 times.

3.2.1.3 Results

From the samples collected in March 2014, there was a depth gradient from 32 to 44m over the experimental area (Mantel's test of depth vs geographic distance, r=0.3, p<0.001). Figure 4c illustrates this correlation in terms of geographic distance lags. However, sediment composition appeared spatially heterogeneous and unrelated to depth (Figures 4a and 4d).

Community composition dissimilarity was also unrelated to geographic distance (Figure 4b) but presented a clear trend with depth as composition similarity decreased when depth differences increased (Figures 4e and 4f). Communities within a 2m depth range were positively autocorrelated while only communities within 5-8m were negatively autocorrelated. There was no more autocorrelation above 8m depth difference.

3.2.1.4 Conclusions

There is a depth gradient over the experimental area. However, neither infauna nor sediment composition showed any spatial autocorrelation, i.e. their distribution was spatially heterogeneous. Despite some evidence that there was more similarity between infaunal communities living at similar depths (±2m), the gradient was not consistent over the whole depth range. Therefore spatial autocorrelation was not considered an issue here.



Figure 4. (Partial) Mantel correlograms for sediment and taxa composition data in March compared to geographic distances (a,b) and depth differences (d,e,f). c shows the correlation between depth and geographic distance. Open symbols are none significant correlations, filled symbols are significant after Bonferroni correction. The values are the results of the overall (partial) Mantel's tests (r= coefficient of correlation and p=p-value). On the y-axis, the term in brackets corresponds to the fixed matrix in partial tests.

3.2.2 Similarity in sediment and species composition within and between sites

3.2.2.1 Objective

The objective was to assess the similarity of samples taken at different sites in terms of both taxa and sediment composition and to assess the relationship between samples (dis)similarity and fishing intensity prior to fishing. There should not be a link prior to fishing as fishing intensity has been allocated randomly.

3.2.2.2 Methods

We used a <u>Permanova</u> analysis to assess statistically whether the between-site variance was larger than the within-site variance, i.e. whether the fauna and sediment composition significantly differed between the 17 sites prior to the experiment and if the variation between sites was correlated to the fishing intensity gradient (Anderson, 2001; Anderson & Walsh, 2013). This should not have been the case since fishing intensity was allocated randomly. A <u>between group analysis (BGA)</u> was then used to visually assess how sites differed from each other (Culhane, Perriere, Considine, Cotter, & Higgins, 2002). To do so we employed an ordination method which aims at maximizing the variance between groups, by using the "bca" function of the package ade4 in R (Dray & Dufour, 2007). This function is a particular case of <u>Principal Component Analysis with Instrumental Variables (PCAIV)</u> or <u>Redundancy Analysis (RDA)</u>. For the BGA, fishing was categorised into four groups: control (no fishing), low fishing intensity (up to 2 times fished), medium fishing intensity (2 to 4 times fished) and high fishing intensity (>4 times fished).

3.2.2.3 Results

Permanova analysis showed that there was no significant difference in sediment composition between sites (df=16, F=1.338, R²=0.21, p=0.078) nor along the later applied fishing intensity gradient (df=1, F=1.277, R²=0.01, p=0.262). This was further confirmed by the BGA analysis which showed no relationship between sediment composition and sites (rand test, obs = 0.19, p=0.250) nor between sediment composition and sites of different fishing intensity levels (obs= 0.07, p=0.200) (Figure 5).Therefore it could be concluded that each site was a mix of sand and gravel prior to fishing.



Figure 5. Between group analysis (BGA) illustrating differences in sediment composition between sample sites (a-b) and fishing effort levels (c-d) in March, i.e. prior to the experiment. Note: no fishing treatment had yet been applied. See figure 3 for sediment abbreviations.

Overall, taxa community composition in March varied significantly between sites (Permanova, df=10, F=1.274, R²=0.21, p=0.012) but the variation was not linked to the later treatment of continuous fishing intensity gradient (Permanova, df=1, F=0.620, R²=0.01, p=0.923). The BGA revealed that one grab sample from site L03 was an outlier. This sample was removed from subsequent analyses (i.e. not shown here in Figure 6). Despite the lack of relationship between fishing intensity gradient and community composition (before fishing), when fishing intensity was defined as groups (i.e. control, low, medium, high), significant discrepancies appeared (Figure 6). From the BGA analysis, the difference between sites was mostly driven by sites on which a medium fishing intensity treatment would later be applied (rand test for sites, obs = 0.22, p=0.001 - rand test for fishing intensity groups, obs = 0.070, p=0.004) (Figure 6).



Figure 6. Between group analysis (BGA) illustrating differences in taxa composition between sample sites (a-b) and between fishing effort levels (c-d) in March, i.e. prior to the experiment. Note: no fishing treatment had yet been applied.

3.2.2.4 Conclusions

Prior to fishing, sediment composition was heterogeneous and did not create significant differences among sites while infaunal composition was more varied, indicating some spatial turnover, i.e. changes in taxa composition over relatively small geographical distances. There was no clear relationship between these taxa differences and the later applied fishing gradient, except that sites that would be fished at a medium range of fishing intensities appeared different from the other sites but this would not affect the later analyses.

3.3 Direct impact of fishing on species composition, richness and diversity (H₂)

3.3.1 Drivers of species composition and determination of species indicator of fishing impact (H_{2a})

3.3.1.1 Objective

The objective was to test if taxa composition had changed along the fishing gradient between March and May and between March and September. Taxa of particular interest, i.e. taxa which seemed to be most abundant before or after fishing or which seemed most abundant in low or high fishing intensity sites, were also identified for further study.

3.3.1.2 Methods

The joint effect on infauna composition of survey time, fishing intensity, sediment texture, depth and all first and second order interactions excluding depth was tested by Permanova, with permutations restricted within sites, to account for the mixed effect nature of the design. Depth was excluded from the interactions as it was not the main variable of interest and it complicated the model. The effect of interest is the interaction between fishing intensity and survey time. We included the second order interaction, i.e. survey time*fishing intensity*sediment type, in order to test if the effect of fishing was different within sediment type. A BGA analysis was then conducted to visualise the interaction between survey time and fishing intensity level. This analysis was followed up by a <u>Simper analysis</u> (Clarke, 1993) to identify the taxa that were significantly distinguishing between groups of interest, i.e. medium-March vs medium-May, high-March vs high-May, control-May vs high-May, control-September vs high-September, medium-March vs medium-March vs medium-March vs high-March vs high-May, bigh-March vs high-May, bigh-March vs high-May, bigh-March vs high-March vs high-M

3.3.1.3 Results

The Permanova analyses showed that taxa composition varied with fishing intensity, between surveys and sediment texture (Table 5). The effect of fishing was not different within different sediment types. The interaction term between survey time (including March, May and September surveys) and fishing intensity was only marginally significant. This meant that no effect of fishing on taxa composition was detected.

Variable	df	F	R^2	p-value
Fishing intensity (FI)	1	1.431	0.01	<0.001***
Survey	2	4.907	0.06	<0.001***
Texture	1	4.608	0.03	<0.001***
Depth	1	1.541	0.01	0.125
FI * Survey	2	1.290	0.02	0.074 ·
FI * Texture	1	0.822	0.00	0.794
Survey * Texture	2	1.092	0.01	0.376
FI*Survey*Texture	2	1.021	0.01	0.453

Table 5. Results of the Permanova model on taxa composition

The interaction between fishing intensity and survey time was visualised by BGA with groups defined by a combination of survey time and fishing intensity level (rand test, obs=0.09, p <0.001) (Figure 7). The analysis identified one outlier, a grab sample from site L15 surveyed in September, which was removed from the analyses. There appeared to have been a change in community composition between March and May that could visually be linked to fishing intensity, although the Permanova showed no significant effect of fishing on taxa composition (i.e. no effect of the fishing intensity*survey time integration). The samples from September were all different from the 2 previous surveys and, while control and high intensity sites taxa composition overlapped, high intensity sites appeared to remain the most different sites, as observed in May. The taxa that contributed to up to 50% of the difference between groups of interest are listed in Appendix A. This analysis identified a total number of 27 indicator taxa out of a total of 152 taxa (identified at the family level).



Figure 7. Between group analysis (BGA) illustrating differences in taxa composition between fishing effort levels in March (a), May (b) and September (c). d represents the taxa scores on the BGA axes.

3.3.1.4 Conclusions

The analyses on taxa composition did not show a significant effect of fishing along the fishing intensity gradient. However, this was explored further using different aspects and characteristics of community composition as there was some marginal evidence of impact.

3.3.2 Fishing impact on species richness and diversity and detection of tolerance thresholds (H_{2b})

3.3.2.1 Objective

The objective was to test the effect of fishing on taxa richness and diversity as well as to test the hypothesis that fishing may homogenise infaunal communities.

3.3.2.2 Methods

Differences in taxa richness between surveys and along the fishing gradient were visually assessed with <u>species accumulation curves</u>. Species accumulation curves were drawn for each site during each survey using a randomisation procedure of grab samples. They were compared between surveys to show whether taxa numbers had increased or decreased over time at each site.

To show whether taxa were homogenised by fishing, the effect of gradual differences in fishing intensity on faunal composition was explored using partial Mantel's tests and correlograms, controlling for sediment dissimilarities, depth and geographic distances, separately for each survey. This involved creating a Euclidean distance matrix of fishing intensities. We further investigated fishing impact on taxa turnover or <u>β-diversity</u> within sites, regardless of sediment texture, by estimating the Bray Curtis (BC) dissimilarities between March and May and between March and September (Currie & Parry, 1996; LeBlanc, Benoît, & Hunt, 2015). We then tested if the BC dissimilarity estimates changed along the fishing gradient, i.e. if communities became increasingly different as fishing intensity increased, and if there was a significant effect of the interaction between survey time and fishing intensity, i.e. sign of potential impact and/or recovery (using linear regression and <u>anova</u>).

BC dissimilarities were then used in a <u>threshold analysis</u>. The threshold analysis aimed at detecting the existence of a shifting point due to effect of dredging that could be used as a reference point for the management of the fishery. The idea is that there potentially is a continuous change in infaunal communities along the fishing intensity gradient but, passed a certain intensity level, the change might increase significantly, making the communities that were fished over that threshold significantly different from the communities at the control sites. This fishing intensity level would be defined as the fishing intensity threshold over which the effect of fishing is significantly greater than natural variation.

Threshold estimation was conducted using a method developed for the purpose of the exercise. The objective of the method is to define optimized cut-off points to split explanatory variables into 2 categories, low and high. The cut-off points are optimized so that the categories low vs. high (fishing intensity here) explain a significant part of the response variable, i.e. the residual variance is minimum. If the minimum residual variance was found to correspond to a threshold at either extreme of the fishing gradient, then the threshold was redefined at the level of fishing corresponding to the largest sudden change in residual variance. This method always defines a cut-off point, i.e. a threshold of fishing intensity, but this threshold has to be statistically tested to see if the response variable

significantly differ between the "low" and "high" fishing intensity categories. The "low fishing intensity" category always included the control sites, this means that the threshold defined the cutoff point at which the response changes the most compared to natural variation. It was then tested by anova. The possible thresholds were defined by the fishing intensity applied during the experiment i.e. possible thresholds for infauna were between 0 and 0.3, 0.3 and 1.2, 1.2 and 2.3, 2.3 and 3.1, 3.8 and 3.9, 3.9 and 5.3.

3.3.2.3 Results

Fishing did not affect taxa richness (Figures 8 and 9). Taxa richness was consistently higher in September.



Figure 8. Comparison of taxa richness pre- to post- fishing impact. The numbers above each panel indicate the fishing effort. The shaded areas represent the 95% confidence intervals.



Figure 9. Comparison of taxa richness pre- impact to 4 months after impact. The numbers above each panel indicate the fishing effort. The shaded areas represent the 95% confidence intervals.

The Mantel correlograms showed that taxa composition within site was homogenised in May and that there was a gradient as dissimilarity in taxa composition increased with dissimilarity in fishing intensity (Figure 10). This homogenisation had disappeared by September (see Mantel statistics Figure 10).



Figure 10. Partial Mantel correlograms of taxa community differences as a function of differences in fishing intensity for March (blue), May (red) and September (green) surveys. Full squares indicate significant correlations after Bonferroni correction. The variables in bracket are the parameters controlled for in the partial test.

Comparison of BC dissimilarity estimates between surveys showed a significant difference in taxa composition, with dissimilarities increasing along the fishing gradient between March and May. There was also a significant threshold between 0.3 and 1.2 times fished and another one visible (not tested) from the residual variance between 2.3 and 3.1 times fished (Figure 11). The difference in taxa composition between March and September remained high and there was still a significant increase of BC dissimilarity estimates along the fishing gradient. Although the slope was not significantly

different from the slope of the dissimilarity between March and May, it indicated partial recovery. The only visible and significant threshold that remained was between 0.3 and 1.2 times fished.



Figure 11. Bray Curtis dissimilarity differences between surveys along the fishing intensity gradient (top panel) and results of the threshold analysis (bottom panels). The three figures in the bottom panels show (1) the definition of the cut-off point based on the minimum residual variance method and (2-3) the difference in BC dissimilarity between the low and high categories of fishing intensity in May (red) and September (green). The F and p-values give the results of the anova test.

3.3.2.4 Conclusions

Fishing did not affect taxa richness but it affected taxa turnover. The effect was more pronounced directly after fishing impact, in May, and less so in September, although there was still a significant

gradient and a threshold for any site fished over 0.3 to 1.2 times showing that an increase in fishing intensity increased dissimilarities between before to after fishing.

3.3.3 Fishing impact on persistence and colonisation rates and detection of tolerance thresholds $\left(H_{2c}\right)$

3.3.3.1 Objective

The objective was to explore and understand the mechanisms behind the changes in community composition observed above by analysing the taxa persistence and colonisation rates between March and subsequent surveys.

3.3.3.2 Methods

Analyses of species diversity and richness revealed a high turnover of taxa, even though taxa had been identified at the family level. A <u>detrended correspondence analysis</u> (DCA) of all data confirmed the high turnover (axis length of first component >4) (Hill & Gauch Jr, 1980). We therefore further investigated persistence and colonisation rates along the fishing gradient both at the family and at the class level. There were 25 classes comprising 153 taxa. A persistent taxa was defined as a taxa that was present at a site both in March and in the subsequent surveys. A new taxa, or colonising taxa, was defined as a taxa that was not present at a site in March but appeared in the subsequent surveys. The rates were expressed as percentages, i.e. number of persistent (or new) taxa compared to the number of taxa present in March. They were analysed similarly to the BC dissimilarities, i.e. by linear and threshold analysis.

3.3.3.3 Results

The number of taxa (either families or classes) persisting between March and May was lower than the number of taxa common to the March and September surveys. However, there was also significantly more new taxa in September compared to May, contributing to the previously observed increase in dissimilarity between the two "after" surveys (Figure 12). This analysis did not show a fishing intensity gradient effect on overall persistence and colonisation rates but there were significant thresholds.



Figure 12. Persistence and colonisation between March and subsequent surveys at the family and class levels. Red= rates for March to May, green= rates for March to September. The values are the results of the anova.

Persistence decreased between March and May after a threshold situated between 2.3 and 3.1 times fished (Figure 13). Class data also showed a threshold between 3.8 and 3.9 times fished with colonisation rate increasing with fishing intensity above that threshold between March and May. By September there was no more significant threshold of either persistence or colonisation.


Figure 13. Threshold analysis of persistence and colonisation between March and subsequent surveys at the family and class levels. The three figures on each row show (1) the definition of the cut-off point based on the minimum residual variance method and (2-3) the difference in BC dissimilarity between the low and high categories of fishing intensity in May (red) and September (green). The F and p-values give the results of the anova test.

3.3.3.4 Conclusions

Persistence and colonisation rates did not change linearly along the fishing intensity gradient but there was evidence that about 10% of taxa disappeared above a threshold of 2.3-3.1 times fished between March and May while over 40% of new taxa appeared in sites fished over 3.8 times during that same period. By September there was no more detectable change.

3.3.4 Detection of species specific extinction thresholds and determination of species of particular interest (H_{2d})

3.3.4.1 Objective

The objective was to analyse if fishing activity at any level induced the disappearance of some specific taxa and to identify those sensitive taxa.

3.3.4.2 Methods

An analysis was performed to identify resilient and sensitive taxa and their fishing intensity thresholds of extinction. Presence/absence data were used to identify those taxa of particular interest, i.e. taxa for which response along the fishing gradient will be further explored (in addition to the taxa of interest already identified from the Simper analysis). This analysis was conducted on taxa at the family and class level. Taxa that were present in 5 sites or more in March (excluding the control sites) were pre-selected to allow enough points along the fishing gradient to fit a model. For each taxa, the datasets of the May and September surveys were then restricted to those sites where the organisms had been observed in March. We then fitted a binomial model with fishing intensity as a response variable for those selected taxa on the presence/absence data of the May and September surveys. Where the model fitted and was significant, the fishing intensity corresponding to a chance of 50% of losing the taxa was defined as the extinction threshold.

3.3.4.3 Results

When studying persistence and extinction of specific taxa, 33 taxa were considered as they met the criterion of being present in 5 sites or more in March. Of those 33, 7 taxa appeared to have different fishing intensity tolerance/extinction thresholds, varying along the fishing gradient, as they disappeared from higher impact sites in May but by September 5 of those 7 taxa had reappeared in

those impacted sites (Figure 14). Only Sabellariidae and Poecilochaetidae did not reappear at all sites above their tolerance threshold. Nine of those 33 taxa appeared resilient to fishing disturbance, i.e. they were found again at all sites where they were initially observed both in May and September (Figure 15).



Figure 14. Sensitive taxa presence/absence along the fishing gradient. In blue = Persistence, i.e. sites where the taxa were found both in March and in subsequent surveys. In red= Extinction between March and May, i.e. sites where the taxa were found in March but not in May. In green= Extinction between March and September, i.e. sites where the taxa were found in March but not in September. The black lines represent the extinction threshold as estimated from the binomial models (i.e. value of fishing intensity at which there is a 50% chance of the species having disappeared)



Figure 15. Persistent/resilient taxa presence along the fishing gradient. Note: Those taxa were present across the whole intensity gradient at each survey, i.e. they had not disappeared from any site at which they were initially found.

All other taxa showed no disturbance tolerance threshold/overall resilience based on presence/absence data. When grouped at the class level, 8 groups were present at 5 sites or more in March 2014, i.e. Anthozoa, Bivalvia, Holothuroidea, Malacostraca, Ophiuroidae, Polychaeta, Polyplacophora and Sipunculidea. Of those 8 groups, only Polyplacophora showed a tolerance threshold from the May data (at a fishing intensity of 0.65) but that threshold had disappeared by September. Three groups showed resilience across the whole fishing gradient, i.e. Bivalvia, Malacostraca and Polychaeta.

3.3.4.4 Conclusions

Two out of 33 taxa showed a tolerance threshold of fishing intensity, i.e. Poecilochaetidae and Sabellariidae, as they did not reappear at all sites above respectively 0.8 and 2.3 times fished after 4 months. However, the evidence was weak as these tolerance thresholds only relied on Sabellariidae not having been found at one site in September where it had been in March, while for Poecilochaetidae, it relies on the taxa having been found in only one site in May and September.

3.4 Direct impact of fishing on species abundance and biomass (H₃)

3.4.1 Trends in abundance and biomass responses to the fishing intensity gradient

3.4.1.1 Objective

The objective was to analyse how abundance and biomass of taxa responded to the gradient of fishing intensity.

3.4.1.2 Methods

Generalised additive mixed models (GAMMs) were used for univariate analyses of total faunal abundance, total biomass and abundance of taxa of particular interest (as defined above, i.e. taxa identified from the Simper analysis and from the tolerance/extinction analysis), with site within survey as a random factor (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Biomass of the 4 groups (out of 20) with the highest biomass, i.e. bivalves, echinoderms, polychaetes and crustaceans, was also analysed. Bivalves constituted over 80% of the total biomass across all 3 surveys while the 3 other groups shared 70% of the rest of the biomass. The mixed modelling approach was used to deal with the problem of pseudo-replication of the samples, i.e. several grab samples within each site, while additive modelling

rather than linear modelling was chosen to identify non-linear trends and potential thresholds along the fishing intensity gradient.

Total biomass and total abundance data were log(x*100+1) transformed prior to the analyses and a Gaussian distribution was used. Some of the indicator taxa were rare (i.e. present in <25% of the grab samples) and therefore were not used in the present analysis. The cut-off of 25% was based on a rule of thumb which is used to determine when zero-inflated models might be needed (Zuur et al., 2009). The remaining indicator taxa were still zero-inflated and therefore were modelled using a negative binomial family on untransformed abundance data. Since GAMMs do not allow for direct testing of interaction terms, a different model was run for each survey and the results were used to inform the shape of the response to fishing intensity. The independent variables included in the models were fishing intensity, sediment texture and depth.

(eq 1a) Univariate response ~ s(Fishing intensity, by= Texture) + s(Depth), random=~1|Site

(eq 1b) Univariate response ~ s(Fishing intensity) + Texture + s(Depth), random=~1|Site

Fishing intensity was expressed as a smoother function with texture as a covariate (eq 1a) or independent of sediment texture (eq 1b). The Akaike Information Criterion (AIC) and significance of the parameters was used to select the best model. The two continuous variables, fishing intensity and depth, were not correlated (Pearson correlation coefficient 0.04, p=0.542).

If the response to fishing was linear then a generalised linear mixed model was run to assess the interaction between survey time and fishing intensity. Sediment texture was only included if model 1a was selected over model 1b, i.e. if the response to fishing intensity differed between sediment types.

(eq 2) Univariate response ~ Fishing intensity*Survey time (*Texture), random=~1|Site

We applied a Bonferroni correction factor to the p-values of the results of equation 2 to account for multiple testing on the same dataset (Holm, 1979; Rice, 1989).

3.4.1.3 Results

The results of the GAMMs assessing the effect of fishing on total abundance and biomass are presented in figures 16 and 17.



Figure 16. Output of GAMM models testing the effect of fishing on total abundance of infaunal species. The bottom row of plots show the effect of depth on fauna in sandy gravel (gravelly sand not presented as interaction not tested so it would be similar response shape). Each plot represent a smoother output. dAIC is the difference between the AIC of model from equation 1a (outputs presented here) and model from equation 1b (outputs not presented).



Figure 17. Output of GAMM models testing the effect of fishing on total biomass of infaunal species. Each plot represent a smoother output. The bottom row of plots show the effect of depth on fauna in sandy gravel (gravelly sand not presented as interaction not tested so it would be similar response shape). dAIC is the difference between the AIC of model from equation 1a (outputs presented here) and model from equation 1b (outputs not presented).

There was no evidence of non-linearity of the response. Abundance showed a significant response in sand but not in gravel while biomass showed no significant response. Therefore a linear model was run to assess the interaction between fishing intensity and survey time including interactions with sediment texture effect for abundance. For biomass, texture was included in the model but without interaction. The anova of the model on abundance revealed that the interactions with texture were not significant therefore the model was re-run without and the summary outputs are given in Table 6

(Figure 18). There was a significant decrease of infaunal abundance along the fishing gradient in May. By September the total species abundance appeared to have recovered. The biomass data presented similar trends but the interaction was not significant. Abundance and biomass were significantly higher in gravel than in sand.

Response	Variable	ANOVA	F test			Su	mmary	
		F value	p-value	Parameter	Estimate	df	t-value	p-value
Abundance	Fishing intensity (FI)	0.316	0.588	FI	0.003	9	0.193	0.958
	Survey	18.454	<mark><0.001**</mark>	May	0.174	150	-1.604	0.510
				September	0.612	150	2.475	0.053
	Texture	17.579	<mark><0.001**</mark>	Gravelly Sand	-0.651	150	-4.080	<mark><0.001**</mark>
	FI *Survey	5.141	<mark>0.007**</mark>	FI*May	-0.139	150	-2.749	0.086
				FI*September	0.162	150	-0.168	0.096
Biomass	Fishing intensity (FI)	0.356	0.565	FI	0.062	9	0.513	0.620
	Survey	0.870	0.421	May	0.541	150	1.054	0.293
				September	-0.113	150	-0.186	0.853
	Texture	4.218	<mark>0.042*</mark>	Gravelly Sand	-0.632	150	-2.030	<mark>0.044*</mark>
	FI *Survey	2.528	0.083	FI*May	-0.159	150	-1.012	0.313
				FI*September	0.245	150	1.318	0.189

Table 6. Results of the Linear Mixed Effect Models on total abundance and biomass (se	see Figure 18).
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Fishing intensity

Figure 18. Results of the linear mixed model (statistics are given in Table 6). Note: The interaction between sediment textures being not significant we only plotted results for sandy gravel in both the abundance and biomass plots here. Also, there does not appear to be any data points for the highest intensity in September because all the grabs were gravelly sand.

There was a total of 37 taxa of particular interest identified in previous analyses on abundance data (Figures 14 and 15, Appendix A). Of those 37 taxa, only 17 were found in at least 25% of the grab samples. The GAMMs model outputs testing the impact of fishing on those 17 taxa (including 14 families and 3 class levels) plus those of the impact of fishing on the biomass of 3 group of taxa are presented in appendix and the results of the LMEs for species which showed a linear response in Table 7. For taxa that displayed a linear response, none of them, except for the class *Malacostraca* in sand, showed a significant interaction between surveys and intensity after Bonferroni correction, i.e. there was no significant effect of the fishing intensity gradient.

3.4.1.4 Conclusions

There was an impact of fishing on the total species abundance. Abundance decreased with fishing intensity in May but by September that trend had disappeared. Data from sandy sediment types, and to a lesser extent from gravel samples, even suggested an increase in abundance along the fishing intensity gradient 4 months after the impact. There was a high natural variability in both abundance and biomass (as seen on the plots from the variability at control sites, i.e. fishing intensity 0) and no significant effect of fishing on biomass. Only one taxa individually displayed a significant linear response to the fishing intensity gradient. Abundance and biomass were both higher in gravel than in sand.

Table 7. Results of the Linear Mixed Effect Models and threshold analysis on abundance and biomassof taxa of particular interest.

The red signs indicate if fishing impact is positive or negative. df is the number of degrees of freedom. FI*May and FI*Sept are the p-values of the interaction terms between fishing intensity and surveys. They indicate if the slope along the fishing gradient in May/September is significantly different from the slope in March, i.e. if fishing has had a detectable effect on the species. March-May and March-Sept are the p-values of the fishing threshold for relative differences between those surveys. dAIC is the AIC difference between threshold model and null model with MM for March-May and MS for March-September. The values in brackets are the p-values after Bonferroni correction. Highlighted are the significant results (before Bonferroni correction). Figures illustrating the relationships can be seen in Appendix B (GAMM outputs) and in Figures 19 and 20 for the threshold analysis.

		LME (negative binomial)				Three	shold analysis	results
Sediment	Species	df	FI*May	FI*Sept	dAIC _{MM}	$dAIC_{MS}$	March-May	March-Sept
type								
Gravelly	TOTAL ABUNDANCE				0.44	-4.83	+ 0.278 (na)	+ <mark>0.021*(na)</mark>
Sand	Lumbrineridae	67	- 0.511 (1)	+ 0.512 (1)	0.59	-2.65	- 0.303 (1)	+ 0.058 (1)
	MYSIDACEA	67	+ 0.641 (1)	+ 0.235 (1)	-0.41	-7.78	+ 0.178 (1)	+ <mark>0.006**(0.175)</mark>
	NEMERTEA	67	+ 0.744 (1)	- 0.538 (1)	-4.88	0.5	+ <mark>0.023*(0.68)</mark>	+ 0.281 (1)
	Nephtyidae	67	+ 0.324 (1)	+ 0.523 (1)	-2.84	-5.15	+ 0.056 (1)	+ <mark>0.018*(0.555)</mark>
	Phyllodocidae	67	- 0.194 (1)	- 0.111 (0.999)	-0.2	1.24	- 0.198 (1)	- 0.444 (1)
	Spionidae	67	+ 0.125 (1)	+ 0.144 (1)	-2.22	-2.71	+ 0.075 (1)	+ 0.056 (1)
	Terebellidae	67	- 0.348 (1)	- 0.551 (1)	0.47	-2.14	- 0.283 (1)	+ 0.073 (1)
	Upogebiidae	67	- 0.297 (1)	+ 0.821 (1)	-4.04	-9.72	- <mark>0.033*(0.983)</mark>	+ <mark>0.003**(0.076)</mark>
	Veneridae	67	+ 0.322 (1)	+ 0.356 (1)	-0.25	-3.47	+ 0.194 (1)	+ 0.039 (1)
	Malacostraca (class)	67	+ 0.254 (na)	+ <mark>0.001**(na)</mark>	-1.87	-8.16	+ 0.088 (0.264)	+ <mark>0.005**(0.015*)</mark>
	Bivalvia (biomass)	66	+ 0.292 (0.584)	+ 0.179 (0.358)	-1.04	-0.61	+ 0.13 (0.26)	+ 0.155 (0.309)
	Crustacea (biomass)	66	+ 0.615 (1)	+ 0.222 (0.444)	-0.32	-2.88	+ 0.187 (0.373)	+ 0.052 (0.104)
	Cirolanidae		non line	ear	-1.63	-8.06	+ 0.098 (1)	+ <mark>0.005**(0.155)</mark>
	Cirratulidae		non line	ear	-6.52	-10.02	+ <mark>0.011*(0.336)</mark>	+ <mark>0.002**(0.067)</mark>
	Bivalvia (class)		non line	ear	-1.14	-5.79	+ 0.124 (0.373)	+ <mark>0.014*(0.042*)</mark>
	Polychaeta (class)		non line	ear	0.56	-4.59	+ 0.298 (0.895)	+ <mark>0.024*(0.071)</mark>
	Ampeliscidae		present in <25% g	rab samples	0.91	-0.38	<mark>+</mark> 0.365 (1)	+ 0.175 (1)
	Cardiidae		present in <25% g	rab samples	-6.41	-2.69	+ <mark>0.012*(0.352)</mark>	+ 0.057 (1)
	Cerianthidae		present in <25% g	rab samples	0.97	-	- 0.378 (1)	-
	Dexaminidae		present in <25% g	rab samples	-1	0.9	- 0.133 (1)	- 0.356 (1)
	Eunicidae		present in <25% g	rab samples	0.81	1.5	+ 0.344 (1)	+ 0.534 (1)
	Glycymerididae		present in <25% g	rab samples	-1.31	-4.67	+ 0.114 (1)	+ <mark>0.023*(0.688)</mark>
	Golfingiidae		present in <25% g	rab samples	0.79	-2.66	- 0.34 (1)	+ 0.057 (1)
	Goniadidae		present in <25% g	rab samples	0.33	-2.16	+ 0.262 (1)	- 0.073 (1)

		l	LME (negative	e binomial)	Threshold analysis results		results	
	Leptochitonidae		present in <25% g	rab samples	1.88	0.89	- 0.761 (1)	- 0.355 (1)
	Mactridae		present in <25% g	rab samples	-0.76	-0.66	+ 0.15 (1)	+ 0.151 (1)
	Nuculidae		present in <25% g	rab samples	0.73	-0.58	+ 0.328 (1)	+ 0.157 (1)
	Ophiotrichidae		present in <25% g	rab samples	-2.6	-0.45	- 0.063 (1)	- 0.168 (1)
	Ophiuridae		present in <25% g	rab samples	-0.45	0.72	- 0.175 (1)	+ 0.32 (1)
	Oweniidae		present in <25% g	rab samples	-2.54	1.13	- 0.064 (1)	- 0.413 (1)
	Pectinariidae		present in <25% g	rab samples	-1	-3.58	+ 0.133 (1)	+ <mark>0.037* (1)</mark>
	Poecilochaetidae		present in <25% g	rab samples	0.08	0.72	- 0.229 (1)	- 0.319 (1)
	Polynoidae		present in <25% g	rab samples	-5.68	-1.74	- <mark>0.016*(0.482)</mark>	- 0.089 (1)
	Sabellariidae		present in <25% g	rab samples	0.87	-0.47	- 0.358 (1)	+ 0.166 (1)
	Serpulidae		present in <25% g	rab samples	0.62	-2.45	+ 0.308 (1)	+ 0.063 (1)
Sandy	TOTAL ABUNDANCE	-	-	-	-1.78	-3.27	- 0.092 (na)	- <mark>0.043*(na)</mark>
Gravel	Lumbrineridae	69	- 0.243 (1)	- 0.49 (1)	-2.62	-7.57	- 0.062 (1)	- <mark>0.006**(0.191)</mark>
	MYSIDACEA	69	-	-	-	1.62	-	+ 0.586 (1)
	NEMERTEA	69	+ <mark>0.035*(0.315)</mark>	+ 0.167 (1)	-0.7	0.45	+ 0.154 (1)	- 0.274 (1)
	Nephtyidae	69	+ 0.873 (1)	- 0.488 (1)	-2.19	-2.49	- 0.076 (1)	- 0.062 (1)
	Phyllodocidae	69	- 0.262 (1)	- 0.341 (1)	-0.51	-3.65	- 0.169 (1)	- <mark>0.036*(1)</mark>
	Spionidae	69	- <mark>0.016*(0.144)</mark>	+ 0.644 (1)	-0.95	0.85	- 0.136 (1)	- 0.346 (1)
	Terebellidae	69	+ 0.719 (1)	+ 0.689 (1)	-0.21	-0.18	- 0.197 (1)	+ 0.194 (1)
	Upogebiidae	69	+ 0.574 (1)	+ 0.288 (1)	0.66	-0.63	- 0.315 (1)	+ 0.153 (1)
	Veneridae	69	- 0.436 (1)	+ 0.997 (1)	0.32	-1.17	- 0.26 (1)	- 0.117 (1)
	Malacostraca (class)	69	+ 0.253 (na)	+ 0.482 (na)	-2.82	-1	- 0.057 (0.17)	- 0.127 (0.382)
	Bivalvia (biomass)	65	- 0.237 (0.474)	+ 0.478 (0.956)	-1.6	-2.06	- 0.1 (0.199)	+ 0.076 (0.152)
	Crustacea (biomass)	65	- 0.645 (1)	+ 0.163 (0.326)	-3.68	-5.52	- <mark>0.038*(0.077)</mark>	+ <mark>0.016*(0.031*)</mark>
	Cirolanidae		non line	ear	-0.94	-1.9	- 0.137 (1)	- 0.082 (1)
	Cirratulidae		non line	ear	0.4	0.95	- 0.273 (1)	- 0.368 (1)
	Bivalvia (class)		non line	ear	0.62	-1.29	+ 0.307 (0.922)	+ 0.11 (0.331)
	Polychaeta (class)		non line	ear	-3.83	-3.78	- <mark>0.036*(0.108)</mark>	- <mark>0.034*(0.103)</mark>
	Ampeliscidae		present in <25% g	rab samples	-8.86	0.52	- 0.004**(0.125)	- 0.285 (1)
	Cardiidae		present in <25% g	rab samples	1.28	-0.34	+ 0.461 (1)	+ 0.178 (1)
	Cerianthidae		present in <25% g	rab samples	-1.16	1.44	+ 0.123 (1)	+ 0.51 (1)
	Dexaminidae		present in <25% g	rab samples	-	1.48	-	- 0.526 (1)
	Eunicidae		present in <25% g	rab samples	-1.01	0.48	+ 0.132 (1)	- 0.277 (1)
	Glycymerididae		present in <25% g	rab samples	1.47	-2.84	+ 0.527 (1)	+ 0.053 (1)
	Golfingiidae		present in <25% g	rab samples	-0.18	-0.78	+ 0.201 (1)	+ 0.142 (1)
	Goniadidae		present in <25% g	rab samples	-3.13	-0.98	- 0.049*(1)	- 0.129 (1)
	Leptochitonidae		present in <25% g	rab samples	0.07	-1.75	+ 0.228 (1)	+ 0.088 (1)
	Mactridae		present in <25% g	rab samples	-3.88	-4.09	+ 0.035*(1)	+ 0.03*(0.89)
	Nuculidae		present in <25% g	rab samples	-14.43	-5.97	- <mark>0***(0.013*)</mark>	- 0.013*(0.386)
	Ophiotrichidae		present in <25% g	rab samples	-0.82	1.66	- 0.145 (1)	+ 0.61 (1)
	Ophiuridae		present in <25% g	rab samples	0.29	-2.08	- 0.256 (1)	+ 0.075 (1)
	Oweniidae		present in <25% g	rab samples	1.99	-2.37	- 0.939 (1)	- 0.066 (1)
	Pectinariidae		present in <25% g	rab samples	0.82	1.13	- 0.347 (1)	+ 0.411 (1)

		L	.ME (negative	e binomial)	Threshold analysis results			results
	Poecilochaetidae		present in <25% و	grab samples	0.52	-1.19	- 0.292 (1)	- 0.116 (1)
	Polynoidae		present in <25% ខ្	grab samples	1.08	-3.9	+ 0.406 (1)	+ <mark>0.032*(0.972)</mark>
	Sabellariidae		present in <25% و	grab samples	-0.83	-0.06	- 0.144 (1)	- 0.206 (1)
	Serpulidae		present in <25% ខ្	grab samples	-2.48	0.71	+ 0.066 (1)	- 0.318 (1)
All	TOTAL BIOMASS	-	-	-	-2.86	-1.36	<mark>-</mark> 0.052 (na)	<mark>-</mark> 0.107 (na)
Sediment	Capitellidae	183	- 0.12 (0.36)	- 0.521 (1)	1.48	-1.79	- 0.5 (1)	+ 0.067 (0.2)
	Glyceridae	183	- 0.255 (0.765)	+ 0.985 (1)	0.12	-0.61	- 0.2 (0.6)	+ 0.128 (0.385)
	Syllidae	183	- 0.881 (1)	- 0.868 (1)	-1	0.13	- 0.105 (0.315)	<mark>-</mark> 0.198 (0.595)
	Polychaeta (biomass)	178	- 0.192 (na)	+ 0.979 (na)	1.33	-1.88	- 0.442 (na)	+ 0.064 (na)

3.4.2 Detection of potential thresholds from abundance and biomass data

3.4.2.1 Objective

Although linear models appeared more appropriate than non-linear ones for most taxa, we investigated the existence of thresholds of fishing intensity for all indicator taxa. This was to determine if there was a level of disturbance that triggered significant changes in the benthic communities (i.e. knife-edge effect).

3.4.2.2 Methods

We estimated the relative difference in abundance and biomass between March and May and between March and September for all the indicator taxa (including the "rare" ones, i.e. present in less than 25% of the grab samples, and the ones showing linear and non-linear responses to fishing pressure). Relative differences (r) for each site (k) and each taxa (l) were calculated as:

(eq 3) $r_{ijkl} = log (N_{t,i,k,l} / N_{t+1,j,k,l})$

with N the abundance (or biomass) (+0.1 to account for 0 values) at time t= March and t+1= May or September, i is the grab number in March and j the grab number in May or September. This equation was used because of its proportional link to fishing intensity (LeBlanc et al., 2015). Relative differences were then averaged per site (k) and species (I) and tested against fishing intensity using the threshold detection method explained earlier (see section 3.3.2.2).

3.4.2.3 Results

Most significant responses to fishing were observed in sand and in September. The results of the threshold analysis on total abundance showed that, in sand, regardless of fishing intensity, all sites fished presented an increase in relative abundance compared to control sites in September (Table 7, Figures 19 and 20). Most taxa followed this pattern, showing an increase in relative abundance above varying fishing intensity thresholds, although very few taxa presented a significant threshold in their response to fishing pressure after Bonferroni correction. Of those few taxa, bivalves and crustaceans were amongst those which showed a significant increase in abundance and/or biomass between March and September in sites fished over a threshold of 1.2 to 2.3 times (both in sand and gravel for crustaceans). In gravel, less thresholds were detected and total relative abundance decreased in areas fished over 4 times.



Figure 19. Threshold analysis of relative abundance (or biomass) for taxa that appeared positively impacted by fishing in May (top row) and negatively impacted (bottom row). Only taxa and thresholds that were significant before Bonferroni corrections are presented for trends (see statistics in Table 7).



Figure 20. Threshold analysis of relative abundance (or biomass) for taxa that appeared positively impacted by fishing in September (top row) and negatively impacted (bottom row). Only taxa and thresholds that were significant before Bonferroni corrections are presented for trends (see statistics in Table 7).

3.4.2.4 Conclusions

There was no obvious threshold of fishing intensity in May after which responses significantly differed from control sites. In sand, there was an increase in relative abundance above varying levels of fishing effort for different taxa but overall total abundance had increased in all fished areas of sand habitats by September. Bivalves and crustaceans appeared positively affected by fishing over a threshold of 1.2 to 2.3 times. In gravel, total relative abundance decreased in areas fished over 4 times.

3.4.3 Further investigation of differences between sand and gravel

3.4.3.1 Objective

The threshold analysis on abundance and biomass revealed that fishing impact was different in sand and gravel habitats. As we had previously observed an overall threshold in community dissimilarities, it was necessary to further investigate this threshold by sediment type.

3.4.3.2 Methods

We estimated the BC dissimilarities of taxa community composition separately for each sediment type and applied the threshold analysis as described in section <u>3.3.2.2</u>.

3.4.3.3 Results

There was no significant difference in BC dissimilarity along the fishing gradient in gravel or in sand (Figure 21). However, in sand, there was a significant threshold between 2.3 and 3.1 in May but no significant threshold in September. In gravel, the non-significant thresholds both in May and September were found between 0.3 and 1.2. These matched up with the previous results on overall composition where the threshold of 0.3-1.2 was significant both in May and September (Figure 11)



Figure 21. Bray Curtis taxa composition dissimilarity differences between surveys along the fishing intensity gradient in different sediment types (top panels) and results of the threshold analyses (bottom panels). The three figures in the bottom panels show (1) the definition of the cut-off point based on the minimum residual variance method and (2-3) the difference in BC dissimilarity between the low and high categories of fishing intensity in May (red) and September (green). The F and p-values give the results of the anova test.

3.4.3.4 Conclusions

Although based on abundance and biomass data there seemed to be different thresholds for different taxa in September in sandy areas, this did not translate into a unique threshold of significant differences in taxa composition. Only a short term effect of fishing on taxa composition was detected in sand while no effect was detected in gravel. However, when data were not split by sediment type, there was a significant threshold both in May and September at a level of 0.3-1.2 times fished.

3.5 Direct impact of fishing on life history trait composition (H₄)

3.5.1 Identification of sensitive trait modalities by RLQ and fourthcorner analyses

3.5.1.1 Objective

The objective was to identify if there was any functional characteristics of the infaunal invertebrates that appeared to be affected by fishing.

3.5.1.2 Methods

We then investigated the ecological drivers by analysing the relationships between taxa functional trait composition of the communities and environmental variables. To do so, we used the RLQ-ordination method described in (Dolédec, Chessel, Ter Braak, & Champely, 1996). The main objective of this technique is to investigate the relationship between a trait dataset (traits per species matrix; Q-table) and some environmental characteristics (environmental variables per station matrix; R-table) by linking them via a third table (species per station matrix; L-table). The R, L, and Q-tables are transformed by ordination prior to running the RLQ analysis. A correspondence analysis (CA) was therefore applied on the L-table, the species per site table. A principal component analysis (PCA) on the Q-table, the trait dataset. FCA is a method that is used to ordinate fuzzy coded data and maximizes the distance between samples (or taxa here) along independent axes. We used the fuzzy coded trait dataset from the BENTHIS project and completed it for missing taxa (Table 8). Each modality was expressed as a percentage of the trait it belonged to prior to analysis. For both the R-table and the Q-table, the weights from the CA-ordination of the L-table were used. The RLQ-analysis combines the three separate ordinations to maximise the co-variance between environmental factors and trait data

by the use of co-inertia analysis (Bernhardt-Römermann et al., 2008). Permutation tests are used to assess the significance of the co-inertia.

While RLQ consists of a multivariate ordination of taxa abundance constrained by traits and environmental data, another method, the fourth-corner analysis (Legendre, Galzin, & Harmelin-Vivien, 1997) can be used to quantify and test the correlation between the variables in Q and R, i.e. traits and environment (Lacourse, 2009). We therefore used here both RLQ and fourth-corner analyses to study the relationships between traits and environment. The environmental dataset consisted of the first 2 axes of a PCA on sediment composition data, depth and fishing intensity. We ran the analyses on the 3 surveys separately and compared the outputs, i.e. the correlation between fishing intensity and trait modalities, to identify trait modalities of interest.

3.5.1.3 Results

Figure 22 shows the correlations between traits and environment and the amount of co-inertia explained by axes 1 and 2 of the RLQ. The permutation test on the results of the RLQ for March data showed no significant co-inertia between the environmental dataset (i.e. PCA axes 1 and 2 for sediment, depth and fishing intensity) and the trait dataset (Monte Carlo test, obs= 0.183, p=0.197). In May and September however, there was a significant correlation between the trait and environmental datasets (obs=0.020, p=0.032 and obs=0.02, p=0.003 respectively).

Table 8. List of traits and modalities used in the study (from the BENTHIS project) and average biomass and presence in the samples over all 3 surveys.

Trait	Modality	Abbreviation	Occurrence (%)	Biomass (g/0.1m²)
Size range (mm)	<10	S.1	92	5.59
	11-20	S.2	98	8.57
	21-100	S.3	99	14.39
	101-200	S.4	99	9.64
	201-500	S.5	97	5.42
	>500	S.6	76	0.67
Morphology = all done	Soft	M.1	99	30.00
	Tunic	M.2	18	0.19
	Exoskeleton	M.3	94	13.92
	Crustose	M.4	17	0.09
	Cushion	M.5	10	0.02
	Stalked	M.6	25	0.21
Longevity	<1	L.1	62	3.49
	1-2	L.2	97	25.79
	3-10	L.3	99	12.65
	>10	L.4	78	2.47
Larval Development location	Planktotrophic	LD.1	99	20.19
	Lecithotrophic (Pelagic)	LD.2	96	6.66
	Direct (Benthic)	LD.3	97	17.46
Egg development location	Asexual/Budding	ED.1	83	1.14
	Sexual shed eggs (Pelagic)	ED.2	99	16.84
	Sexual shed eggs (Benthic)	ED.3	97	5.28
	Sexual brood eggs	ED.4	98	21.12
Living habit	Tube-dwelling	LH.1	96	9.36
	Burrow-dwelling	LH.2	97	9.75
	Free-living	LH.3	99	19.12
	Crevice/hole/under stone	LH.4	94	2.43
	Epi/endo zoic/phytic	LH.5	94	3.18
	Attached to substratum	LH.6	47	0.69
Sediment position	Surface	SP.1	96	15.96
	Infauna: 0-5cm	SP.2	99	19.97
	Infauna: 6-10cm	SP.3	97	4.72
	Infauna: >10cm	SP.4	92	3.32
Feeding mode	Suspension	FM.1	97	10.04
	Surface Deposit	FM.2	96	9.56
	Subsurface deposit	FM.3	96	12.50
	Scavenger/Opportunist	FM.4	96	3.88
	Predator	FM.5	99	8.00
	Parasite	FM.6	37	0.39
Mobility	Sessile	MOB.1	96	20.36
	Swim	MOB.2	/2	4.59
	Crawl/creep/climb	MOB.3	98	11.06
	Burrower	MOB.4	96	8.41
Bioturbators	Diffusive mixing	BIO.1	97	9.87
	Surface deposition	BIO.2	99	21.75
	Upward Conveyor	BIO.3	84	9.18
	Downwards conveyer	BIO.4	80	2.03
	None	BIO.5	49	1.20



Figure 22. Co-inertia between traits and environment for each survey from the RLQ analysis. March=blue; May= red, September= Green

The fourthcorner analysis revealed no significant correlations between any traits and any variables after Bonferroni correction of the p-values, for any survey.

We extracted the value of the correlation between fishing intensity and trait modalities for each survey and plotted them against each other to identify potential interactions between fishing intensity and survey time and to study further those traits of particular interest (Figure 23). We selected 20 modalities (out of 48) based on their significant correlation with fishing intensity prior to Bonferroni corrections and the apparent changes between the 3 surveys. Of those 20 modalities, 4 were present in less than 25% of the samples (all part of the morphology trait, i.e. M.2, M.4, M.5 and M.6). The

other modalities were present in over 65% of the grab samples except for the parasite modality of the feeding trait, FM.6 (37%).



Figure 23. Correlations between traits and fishing intensity from the RLQ and fourthcorner analyses. The circled points are the significant correlations (of which none are significant after Bonferroni correction). Points on the right of the 0 line suggest a positive correlation with fishing intensity, points on the left suggest a negative correlation. Of interest are the trait modalities for which the correlation seems to vary between the 3 surveys and those that were significant before Bonferroni correction.

3.5.1.4 Conclusions

After fishing, both in May and September, the trait composition of the infaunal communities was partly explained by the environmental dataset (which included fishing intensity). However, there were no significant correlations between any traits and any variables after Bonferroni correction. Twenty trait modalities were selected to be further investigated based on their significant correlation with fishing intensity prior to Bonferroni corrections and the apparent changes between the 3 surveys.

3.5.2 Fishing impact on sensitive traits

3.5.2.1 Objective

Some functional characteristics, or trait modalities, were identified as potentially responding to fishing disturbance. This was therefore investigated further in order to identify the existence of trends and fishing intensity thresholds.

3.5.2.2 Methods

Trait abundance was then calculated for the identified traits of interest by multiplying the taxa abundance by site matrix by the trait by taxa matrix, where traits were expressed as percentages within each modality. Trait abundance was analysed by GAMMs, LMEs and threshold analysis using the same statistical analyses as for taxa abundance. As for taxa, trait modalities that were present in less than 25% of the grabs were excluded from the GAMMs and LMEs analyses but included in the threshold analysis.

3.5.2.3 Results

GAMMs outputs on the log-transformed abundance trait data are presented in Appendix C. None of the linear trends were significant after Bonferroni corrections (Table 9). However, the threshold analysis showed some interesting patterns (Figures 24 and 25). Overall, very small organisms (<1cm) increased above a threshold of 0.3-1.2 times fished in September. In sand, none of the thresholds were significant after Bonferroni correction except for parasite feeding organisms (FM.6), but they showed a consistent response. In September, in sand, most indicator trait modalities presented a positive response to fishing at thresholds of 0.3-1.2 or 1.2-2.3 times fished while there was no overall

threshold response in May. There was no such pattern in gravel, although the data suggested a trend towards negative response to fishing for some traits in May and in September (none significant after Bonferroni correction) at high fishing intensity (around 3.8 times fished).

trait modalities of particular interest (see details in Table 7 caption and abbreviations in Table 8)									
			LME (Gaus	sian)		Thres	hold analysis r	esults	
Sediment type	Trait modality	df	FI*May	FI*Sept	$dAIC_MM$	$dAIC_{MS}$	March-May	March-Sept	
Gravelly Sand	S.4	64	- 0.138 (1)	+ 0.239 (1)	1.51	-3.09	+ 0.543 (1)	+ <mark>0.047*(0.89)</mark>	
	S.6	64	- 0.351 (1)	- 0.62 (1)	0.86	1.16	+ 0.355 (1)	- 0.42 (1)	
	L.1	64	+ 0.913 (1)	+ 0.641 (1)	-0.87	-3.67	+ 0.141 (1)	+ <mark>0.036*(0.684)</mark>	
	FM.1	64	- 0.188 (1)	+ 0.152 (1)	1.06	-6.5	+ 0.4 (1)	+ <mark>0.01*(0.193)</mark>	
	MOB.2	64	+ 0.346 (1)	+ 0.153 (1)	-2.03	-3.32	+ 0.081 (1)	+ <mark>0.042*(0.802)</mark>	
	LH.3	64	- 0.346 (1)	+ 0.122 (1)	0.19	-7.11	+ 0.243 (1)	+ <mark>0.008**(0.148)</mark>	
	LH.4	64	- 0.077 (1)	+ 0.494 (1)	-0.87	-2.57	- 0.141 (1)	+ 0.06 (1)	
	M.1	64	- 0.123 (1)	+ 0.4 (1)	0.33	-5.22	+ 0.263 (1)	+ <mark>0.018*(0.34)</mark>	
	M.3	64	- 0.945 (1)	+ 0.075 (0.975)	0.39	-8.46	+ 0.272 (1)	+ 0.004**(0.083)	
	ED.3	64	- 0.499 (1)	+ 0.367 (1)	0.48	-5.07	+ 0.285 (1)	+ <mark>0.019*(0.364)</mark>	
	LD.2	64	- 0.145 (1)	+ 0.955 (1)	-0.5	-3.8	+ 0.17 (1)	+ <mark>0.034*(0.643)</mark>	
	BIO.2	64	- 0.202 (1)	+ 0.109 (1)	0.7	-5.89	+ 0.322 (1)	+ <mark>0.013*(0.253)</mark>	
	BIO.4	64	- 0.753 (1)	+ 0.275 (1)	-0.77	-2.62	+ 0.148 (1)	+ 0.058 (1)	
	L.4		non linea	ır	-0.37	-6.06	+ 0.181 (1)	+ <mark>0.012*(0.234)</mark>	
	FM.6		present in >25% grab samples		-5.31	-10.31	+ <mark>0.019*(0.358)</mark>	+ <mark>0.002**(0.037*)</mark>	
	M.2		present in >25% gr	ab samples	-2.16	1.28	+ 0.077 (1)	+ 0.455 (1)	
	M.4		present in >25% gr	ab samples	0.39	-2.74	- 0.271 (1)	- 0.055 (1)	
	M.5		present in >25% gr	ab samples	0.45	-3.59	+ 0.281 (1)	- <mark>0.037*(0.709)</mark>	
	M.6		present in >25% gr	ab samples	-0.66	0.74	- 0.157 (1)	- 0.323 (1)	
Sandy Gravel	S.4	62	- 0.157 (1)	+ 0.656 (1)	-6.3	-1.89	- <mark>0.012*(0.234)</mark>	- 0.082 (1)	
	S.6	62	+ 0.176 (1)	+ 0.817 (1)	1.03	-4.15	+ 0.394 (1)	- <mark>0.029*(0.549)</mark>	
	L.1	62	- 0.269 (1)	+ 0.843 (1)	-1.8	0.54	+ 0.091 (1)	+ 0.288 (1)	
	FM.1	62	- 0.553 (1)	+ 0.35 (1)	-1.59	0.33	+ 0.1 (1)	+ 0.256 (1)	
	MOB.2	62	- 0.064 (0.832)	+ 0.967 (1)	-2.86	0.51	- 0.056 (1)	- 0.282 (1)	
	LH.3	62	- 0.231 (1)	+ 0.794 (1)	-3.79	-1.79	- <mark>0.037*(0.698)</mark>	- 0.087 (1)	
	LH.4	62	- 0.906 (1)	- 0.853 (1)	-2.99	-3.99	- 0.053 (0.999)	- <mark>0.031*(0.591)</mark>	
	M.1	62	- 0.113 (1)	+ 0.735 (1)	-5.18	-1.96	- <mark>0.02*(0.378)</mark>	- 0.08 (1)	
	M.3	62	- <mark>0.025*(0.325)</mark>	- 0.922 (1)	-2.21	1.99	- 0.075 (1)	+ 0.941 (1)	
	ED.3	62	- 0.292 (1)	- 0.85 (1)	-5.63	-2.08	- <mark>0.016*(0.311)</mark>	- 0.075 (1)	
	LD.2	62	- 0.943 (1)	+ 0.846 (1)	-3.67	-2.5	- <mark>0.039*(0.735)</mark>	- 0.062 (1)	
	BIO.2	62	- 0.311 (1)	+ 0.608 (1)	-1.25	-0.86	- 0.118 (1)	- 0.137 (1)	

+ 0.843 (1)

non linear

0.55

0.84

-0.66

-2.28

- 0.296 (1)

- 0.351 (1)

BIO.4

L.4

62 + 0.19 (1)

Table 9. Results of the Linear Mixed Effect Models and threshold analysis for total abundance of trait modalities of particular interest (see details in Table 7 caption and abbreviations in Table 8)

- 0.151 (1)

+ 0.068 (1)

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	FM.6		present in >25% gra	ab samples	1.6	1.01	+ 0.584 (1)	+ 0.381 (1)
	M.2		present in >25% gra	ab samples	0.4	-1.05	- 0.272 (1)	- 0.124 (1)
	M.4		present in >25% gra	ab samples	1.45	0.91	- 0.519 (1)	- 0.357 (1)
	M.5		present in >25% gra	ab samples	0.2	0.87	+ 0.244 (1)	- 0.35 (1)
	M.6		present in >25% gra	ab samples	0.89	0.28	- 0.361 (1)	- 0.248 (1)
All sediments	S.1	141	- 0.104 (na)	+ 0.364 (na)	-0.66	-5.89	+ 0.151 (na)	+ <mark>0.013*(na)</mark>



Figure 24. Threshold analysis of relative abundance of trait modalities that appeared impacted by fishing in May. Only traits and thresholds that were significant before Bonferroni corrections are presented for trends (see statistics in Table 9). None were significant after Bonferroni correction.



Figure 25. Threshold analysis of relative abundance of trait modalities that appeared positively impacted by fishing in September (top row) and negatively impacted (bottom row). Only traits and thresholds that were significant before Bonferroni corrections are presented for trends (see statistics in Table 9).

3.5.2.4 Conclusions

None of the linear trends were significant and there was a high natural variation (see plots in Appendix C). However there were some patterns when looking at thresholds of fishing intensity. Very small organisms (<1cm) increased above a threshold of 0.3-1.2 times fished. In sand, most indicator trait modalities presented a positive response to fishing at thresholds of 0.3-1.2 or 1.2-2.3 times fished 4 months after being fished. There was no such pattern in gravel.

Table 10. Summary of significant increases and decreases in abundance (ind) and biomass (g) in relation to fishing intensity levels. "Change above the threshold" corresponds to the difference in average per grab of abundance (or biomass) from under to above the fishing intensity threshold. * Abundance change given without sample L16G18 where very high density of small shrimp

Mysidacea was found, i.e. over 600 individual estimated in one grab sample

Surveys	Sediment type	Species or species group	Average over	Linear or	Change
			all surveys	threshold analysis	above the
			(/grab of 0.1m ²)		threshold
March-May	Gravel	Nuculidae	0.59 ind (±0.20)	Threshold = 3.8	- 57%
	All	**Total abundance	51.63 ind (±5.88)	Linear (fishedx6)	- 63%
March-Sept	Sand	Total abundance	35.17 ind (±8.32)	Threshold = 0.2	+ 220 %
					(* + 84%)
		Malacostraca spp.	12.18 ind (±7.90)	Threshold = 1.8	+ 5462%
					(* + 1228%)
		Bivalvia spp.	2.44 ind (±0.34)	Threshold = 1.8	+ 237%
		Parasite feeders (FM.6)	0.23 ind (0.06)	Threshold = 0.8	+ 9253 %
	Gravel	Total abundance	51.63 ind (±5.88)	Threshold = 4.1	- 56%
		Crustacea (biomass)	0.38 g (±0.09)	Threshold = 1.8	+ 1273%
	All	Very small organisms	5.59 ind (±1.42)	Threshold = 0.8	+ 468%
		(<1cm) (S.1)			
		**Total abundance	51.63 ind (±5.88)	Linear (fished x6)	+ 30%

** Note: For these groups the anova was significant at α =0.05, but the t-test was only significant at α =0.1, results are presented anyway for discussion

3.5.3 Fishing impact on functional groups

3.5.3.1 Objective

The objective was to define functional groups based on the trait analysis and investigate how they responded to the fishing intensity gradient.

3.5.3.2 Methods

An advantage of the RLQ analysis is that one can use the species scores on the RLQ axes to define functional groups. Therefore, a cluster analysis was used to define functional groups based on the output of the RLQ for both May and September. We used a clustering method that defined the optimal number of species cluster. We then estimated the total abundance per cluster, i.e. functional group, and analysed the results by GAMMs, LMEs and threshold analysis.

3.5.3.3 Results and conclusions

There were 10 and 11 functional groups defined from the cluster analysis of the species scores on the RLQ axes in May and September respectively. Those groups were made of various combinations of trait modalities and the resulting outcomes of the GAMMs, LMEs and threshold analyses mirrored the results from the single trait analysis. The results are therefore not presented here.

3.6 Indirect effect of fishing on infauna and traits via alteration of sediment type (H₅)

3.6.1 Objective

The objective was to analyse the potential indirect effect fishing on infaunal communities by studying the relationship between sediment composition and infaunal communities and assessing the effect of fishing on sediment composition itself.

3.6.2 Methods

The correlation between sediment type and composition and infaunal (or trait) composition was assessed using Permanova and Simper analysis for sediment type and Mantel's tests and correlograms for sediment composition data. The directional influence of fishing intensity on sediment composition was then tested and visualised using the *envfit* procedure of the vegan package in R on ordinated data

(Oksanen et al., 2007). Sediment data (arcsine square root transformed percentages) were ordinated by principal component analysis (PCA).

3.6.3 Results

Earlier results showed that composition and abundance was significantly different between sediment types (Tables 5 and 6). There are less individuals and species richness is overall lower in sand (anova - df=1, F=9.725, p=0.002, estimated difference = -3.4 species per grab in sand). The significant difference in composition between sediment types is illustrated in Figure 26. It also shows that the difference remained consistent during all surveys and at all levels of fishing effort. The Simper analysis showed that, even though most taxa were found in both sediment types, some taxa were more abundant in gravel (e.g. Capitellidae, Lumbrineridae, Terebellidae, Spionidae, Nemertea, Glyceridae, Phyllodocidae, Serpulidae) while fewer taxa were more abundant in sand (e.g. Syllidae, Mysidacea, Nepthyidae, Nematoda). The association between fauna and sediment composition was however stronger in sand than in gravel (see Mantel's tests results in Figure 27). Similarly, the trait composition varied significantly between sand and gravel, with sand habitats showing a higher variability (Figure 28). Mantel's tests showed that trait composition was strongly associated with sediment composition in sand but not in gravel (Table 11).



Figure 26. Difference between gravelly and sandy communities in March (A), May (B) and September (C). The 4 panels a-b at each survey show the different fishing effort levels. Orange= Sandy Gravel, Grey = Gravelly Sand



Figure 27. Partial Mantel correlograms illustrating difference in species composition along sediment difference gradient for all 3 surveys combined for a-b sandy gravel samples and c-d gravelly sand samples. (a-c) partial correlograms controlling for geographic distances (b-d) partial correlograms controlling for depth differences. Full squares indicate significant correlations after Bonferroni correction.

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Figure 28. Difference in trait composition between gravelly and sandy communities over all 3 surveys from correspondence analysis. The values are the results of the Permanova tests of differences between sediment types. See modalities abbreviation in Table 8.

 Table 11. Results of the partial Mantel's tests between traits and sediment composition within each

 sediment type.

In brackets are the parameters which are controlled for in the partial test. r is the Mantel correlation coefficient, p is the p-value of significance.

Sediment type	Traits	r (depth)	p (depth)	r (dist)	p (dist)
Sand Gravel	Size	-0.02	0.615	-0.02	0.625
	Morphology	-0.01	0.541	-0.01	0.547
	Life span	-0.01	0.534	-0.01	0.55
	Larval Development	-0.01	0.548	-0.01	0.566
	Egg Development	-0.01	0.514	-0.01	0.533
	Living Habit	0.01	0.398	<0.01	0.406
	Sediment position	<0.01	0.405	< 0.01	0.432
	Feeding Mode	-0.03	0.77	-0.03	0.697
	Mobility	-0.01	0.579	-0.01	0.585
	Bioturbation	<0.01	0.455	<-0.01	0.496
Gravelly Sand	Size	0.21	< 0.001	0.21	< 0.001
	Morphology	0.18	0.002	0.18	0.001
	Life span	0.19	0.001	0.19	< 0.001
	Larval Development	0.21	<0.001	0.21	<0.001
	Egg Development	0.18	0.001	0.18	0.001
	Living Habit	0.24	<0.001	0.24	<0.001
	Sediment position	0.2	0.001	0.2	< 0.001
	Feeding Mode	0.22	<0.001	0.22	<0.001
	Mobility	0.19	0.001	0.19	0.001
	Bioturbation	0.18	0.002	0.18	< 0.001

Sediment type was not related to fishing intensity prior to the experiment but there was a strong association in May and less significant one in September. Fishing increased the coarseness of the sediment in sand but not in gravel and sediment composition appears to have mostly recovered by September (Figure 29). This is consistent with earlier observations of significant and possibly longer lasting impact of fishing in sand compared to gravel. However, when analysing sediment composition changes along the fishing gradient in terms of Euclidean distance, the trend was consistent but not significant and no threshold could be identified (Figure 30). This analysis was also conducted for each sediment type separately but did not show any different results.



Figure 29. Influence of fishing intensity on sediment composition overall (a-b), within gravelly sand (c-d) and within sandy gravel (e-f) from May and September data. The significance (estimated from the *envfit* analysis) is given above each panel.



Figure 30. Sediment composition Euclidean distance between surveys along the fishing intensity gradient (top panel) and results of the threshold analysis (bottom panels). The three figures in the bottom panels show (1) the definition of the cut-off point based on the minimum residual variance method and (2-3) the difference in Euclidean distance between the low and high categories of fishing intensity in May (red) and September (green). The F and p-values give the results of the anova

3.6.4 Conclusions

Taxa were less abundant and richness was lower in sand than in gravel. The association between fauna, in terms of both taxa and traits, and sediment composition was however stronger in sand than in gravel. Fishing slightly increased the coarseness of the sediment in sand but not in gravel but sediment composition appears to have mostly recovered by September.

6. GLOSSARY

Folk's triangle:

<u>Autocorrelation</u>: Similarity between observations as a function of the time or distance lag between them

<u>Anova</u>: Analysis of Variance which aims at statistically analysing the differences between group means <u>BACI design</u> (Before-After-Control-Impact): Experimental design which involves collecting information prior to applying a treatment and after applying a treatment as well as where no treatment was applied. Its aim is to single out the effect of the treatment from any other external effect that could not be controlled for.

BGA (Between group analysis): Analysis used to discriminate samples between groups

<u>Beta diversity</u> (β -diversity): The extent of species replacement or biotic change along environmental gradients (Whittaker 1972). It measure the turnover of species. For instance, compositional dissimilarity can be thought of as a measure of β -diversity.

Bray Curtis index: Index of dissimilarity between two different sites, based on counts at each site.

<u>Colonisation rate:</u> Percentage of new species appearing at one point in time where they did not previously occur.

<u>Colonial organism</u>: An organism composed of multiple constituent organisms. Those components can be recognized as individual organisms in their own right by comparison with evolutionarily related free-living species.

<u>DCA</u> (Detrended Correspondance Analysis): Multivariate statistical technique used to find main factors or gradients in ecological community data.

Dissimilarity matrix: Matrix containing measures of pairwise distances of a set of samples

<u>Fishing intensity</u>: Defined as the number of times an area is entirely fished. This is estimated by dividing the total area covered by the towed fishing gear by the size of the fishing ground. For instance, if a vessel has been towing its gear for 20 hours with 7 dredges a side at 3knots, it will have covered a total of approximately 1.2km² of seabed. If its effort was concentrated in an area of 0.5 by 0.5 km, i.e. 0.25km², it will have fished the area on average 1.2/0.25= 4.8 times.



<u>Functional traits (groups)</u>: Functional traits are those that define species in terms of their ecological roles, how they interact with the environment and with other species (Diaz and Cabido, 2001)

<u>GAMM</u> (Generalised Additive Mixed Model): This is an extension of GAMs (Generalised Additive Models) which are themselves an extension of GLMs (Generalized Linear Models) in which the linear predictor depends linearly on unknown smooth functions of some predictor variables. GAMMs account the mixed effect nature of a given dataset. Mixed effect implies that there are some fixed and random terms in the model. It is particularly useful when they are repeated measures in a study over the same statistical units (this is traditionally dealt with with repeated measures anova).

Hamon grab: bucket used to collect benthic samples, deployed from a vessel.

Infaunal invertebrates: Benthic organisms living within the bottom substratum of a body of water.

<u>LME (Linear Mixed Model)</u>: Mixed effect implies that there are some fixed and random terms in the linear model. It is particularly useful when they are repeated measures in a study over the same statistical units (this is traditionally dealt with with repeated measures anova).

<u>Mantel correlogram</u>: Analogous to an autocorrelation function but performed on a distance (or dissimilarity) matrix. See example below for interpretation:



<u>Mantel's test:</u> Regression in which the variables are themselves distance or dissimilarity matrices summarizing pairwise similarities among sample locations. The test of spatial dependence is averaged over all distances in the simple Mantel's test, and so this test cannot discover changes in the pattern of correlation at different distances. See Mantel correlogram.

<u>Multibeam:</u> A multibeam echosounder is a type of sonar that is used to determine water depth and map the water bottom

<u>NMBAQC</u> (National Marine Biological Analytical Quality Control Scheme): Scheme that provides a source of external Quality Assurance for laboratories engaged in the production of marine biological data.

<u>Permanova</u>: Analyses univariate or multivariate data in response to factors, groups or treatments in an experimental design. Whereas (multivariate) anova assumes normal distributions and, implicitly, Euclidean distance, Permanova works with any distance measure that is appropriate to the data, and uses permutations to make it distribution free.

<u>Permutation tests</u> (also called a randomization test, re-randomization test, or an exact test): Type of statistical significance test in which the distribution of the test statistic under the null hypothesis is obtained by calculating all possible values of the test statistic under rearrangements of the labels on the observed data points.

<u>Persistence rate</u>: Percentage number of species remaining at one point in time where they did previously occur.

<u>PCA (Principal Component Analysis):</u> statistical procedure that uses an orthogonal transformation to convert a set of observations of possibly correlated variables into a set of values of linearly uncorrelated variables called principal components.

<u>PCAIV/RDA</u> (Principal Component Analysis with respect to Instrumental Variables or Redundancy Analysis): Direct gradient analysis technique which summarises linear relationships between components of response variables that are "redundant" with (i.e. "explained" by) a set of explanatory variables

<u>PSA (Particle Size Analysis)</u>: Collective name of the technical procedures, or laboratory techniques, which determines the size range, and/or the average, or mean size of the particles in a powder or liquid sample.

<u>Side scan sonar</u>: Category of sonar system that is used to efficiently create an image of large areas of the sea floor.

<u>Simper analysis</u>: Analysis that breaks down the contribution of each species (or other variable) to the observed similarity (or dissimilarity) between samples

<u>Species accumulation curves:</u> Graph recording the cumulative number of species of living things recorded in a particular environment as a function of the cumulative effort expended searching for them.
<u>Threshold analysis</u>: Analysis which aims at finding the cut-off point along the gradient of a predictor value at which the response variable appears to undergo a significant change. This means that we look for the value of fishing intensity at which the response significantly changes compared to control sites. See examples below for help with interpretation:



Other way to present the significant results:



<u>Wentworth scale</u>: Scale that relates sediment particle size to sediment categories (i.e. >256mm = boulder)

Zero-inflated model: Model with a distribution that allows for frequent zero-valued observations

7. REFERENCES

- Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26(1), 32-46.
- Anderson, M. J., & Walsh, D. C. (2013). PERMANOVA, ANOSIM, and the mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs*, 83(4), 557-574.
- Bernhardt-Römermann, M., Römermann, C., Nuske, R., Parth, A., Klotz, S., Schmidt, W., et al. (2008). On the identification of the most suitable traits for plant functional trait analyses. *Oikos*, *117*(10), 1533-1541.
- Bray, J. R., & Curtis, J. T. (1957). An ordination of the upland forest communities of southern wisconsin. *Ecological Monographs*, *27*(4), 325-349.
- Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*(1), 117-143.
- Culhane, A. C., Perriere, G., Considine, E. C., Cotter, T. G., & Higgins, D. G. (2002). Between-group analysis of microarray data. *Bioinformatics (Oxford, England), 18*(12), 1600-1608.
- Currie, D., & Parry, G. (1996). Effects of scallop dredging on a soft sediment community: A large-scale experimental study. *Marine Ecology Progress Series.Oldendorf, 134*(1), 131-150.
- Dolédec, S., Chessel, D., Ter Braak, C., & Champely, S. (1996). Matching species traits to environmental variables: A new three-table ordination method. *Environmental and Ecological Statistics, 3*(2), 143-166.
- Dray, S., & Dufour, A. (2007). The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software, 22*(4), 1-20.
- EC. (2002). Council regulation (EC) no 2371/2002 of 20 december 2002 on the conservation and sustainable exploitation of fisheries resources under the common fisheries policy. *Official Journal of the European Union, L358,* 59-80.
- EC. (2008). Directive 2008/56/EC of the european parliament and of the council of 17 june 2008 establishing a framework for community action in the field of marine environmental policy (marine strategy framework directive). *Official Journal of the European Union, L164,* 19-40.
- EC. (2010). Commission decision of 1 september 2010 on criteria and methodological standards on good environmental status of marine waters. *Official Journal of the European Union, L232*, 14-24.
- FAO. (2003). The ecosystem approach to fisheries. issues, terminology, principles, institutional foundations, implementation and outlook (FAO Fisheries and Aquaculture Technical Papers No. 443)
- Folk, R. L. (1954). The distinction between grain size and mineral composition in sedimentary-rock nomenclature. *The Journal of Geology,* , 344-359.
- Gallon, R. K., & Fournier, J. (2013). G2Sd: Grain-Size Statistics and Description of Sediment, R Package Version 2.1,
- Hill, M. O., & Gauch Jr, H. G. (1980). Detrended correspondence analysis: An improved ordination technique. *Vegetatio*, 42(1-3), 47-58.
- Hinz, H., Sciberras, M., Murray, L. G., Benell, J. D., & Kaiser, M. J. (2010). Assessment of offshore habitats in the cardigan bay SAC (june 2010 survey) (Fisheries & Conservation report No. 14). Bangor University:
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, , 65-70.
- Kaiser, M. J., & Spencer, B. E. (1996). The effects of beam-trawl disturbance on infaunal communities in different habitats. *Journal of Animal Ecology*, , 348-358.
- Lacourse, T. (2009). Environmental change controls postglacial forest dynamics through interspecific differences in life-history traits. *Ecology*, *90*(8), 2149-2160.

- Lambert, G. I., Murray, L. G., Benell, J. D., & Kaiser, M. J. (2013). *Habitat assessment of the area of the cardigan bay SAC proposed for a fishing intensity experiment.* (Fisheries & Conservation report No. 23). Bangor University:
- Lambert, G., Jennings, S., Kaiser, M., Hinz, H., & Hiddink, J. (2011). Quantification and prediction of the impact of fishing on epifaunal communities. *Marine Ecology Progress Series*, 430, 71-86.
- Lambert, G. I., Jennings, S., Kaiser, M. J., Davies, T. W., & Hiddink, J. G. (2014). Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing. *Journal of Applied Ecology*, *51*(5), 1326-1336.
- LeBlanc, S. N., Benoît, H. P., & Hunt, H. L. (2015). Broad-scale abundance changes are more prevalent than acute fishing impacts in an experimental study of scallop dredging intensity. *Fisheries Research*, *161*, 8-20.
- Legendre, P., Galzin, R., & Harmelin-Vivien, M. L. (1997). Relating behavior to habitat: Solutions to thefourth-corner problem. *Ecology*, *78*(2), 547-562.
- Legendre, P., & Legendre, L. F. (2012). Numerical ecology Elsevier.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., et al. (2007). The vegan package. *Community Ecology Package*,
- Ramsay, K., Kaiser, M. J., Moore, P. G., & Hughes, R. N. (1997). Consumption of fisheries discards by benthic scavengers: Utilization of energy subsidies in different marine habitats. *Journal of Animal Ecology*, , 884-896.
- Rice, W. R. (1989). Analyzing tables of statistical tests. Evolution, , 223-225.
- Sciberras, M., Hinz, H., Bennell, J. D., Jenkins, S. R., Hawkins, S. J., & Kaiser, M. J. (2013). Benthic community response to a scallop dredging closure within a dynamic seabed habitat. *Marine Ecology Progress Series, 480*, 83-98.
- Wentworth, C. K. (1922). A scale of grade and class terms for clastic sediments. *The Journal of Geology,* , 377-392.
- Worsfold, T. M., Hall, D. J., & O'Reilly, M. (2010). *Guidelines for processing marine macrobenthic invertebrate samples: A processing requirements protocol: Version 1.0, june 2010. report to the NMBAQC committee.* (Unicomarine report NMBAQCMbPRP
- Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R* Springer Science & Business Media.

APPENDIX A – Indicator species identified from SIMPER analysis.

The highlighted species are the species which increased in abundance from group A to group B.

Group A	Group B	Species	Cumulative contribution
Medium FI - March	Medium FI - May	Capitellidae	0.08 (+)
		Lumbrineridae	0.13(-)
		NEMERTEA	0.17(-)
		Terebellidae	0.20(-)
		<mark>Syllidae</mark>	0.24(+)
		Glyceridae	0.27(-)
		Spionidae	0.30(-)
		<mark>Veneridae</mark>	0.34(+)
		Oweniidae	0.37(-)
		Phyllodocidae	0.40(+)
		<mark>Ophiuridae</mark>	0.42(+)
		Nuculidae	0.45(+)
		Nephtyidae	0.48(-)
		Eunicidae	0.50(-)
High FI - March	High FI - May	Capitellidae	0.10(-)
		Lumbrineridae	0.17(-)
		Phyllodocidae	0.22(-)
		Glyceridae	0.26(-)
		NEMERTEA	0.30(+)
		Terebellidae	0.33(-)
		<mark>Glycymerididae</mark>	0.37(+)
		<mark>Syllidae</mark>	0.40(+)
		Ophiotrichidae	0.43(-)
		<mark>Serpulidae</mark>	0.46(+)
		Spionidae	0.49(-)
		Goniadidae	0.52(-)
Control FI - May	High FI - May	Capitellidae	0.10(-)
		Lumbrineridae	0.16(-)
		<mark>Serpulidae</mark>	0.20(+)
		NEMERTEA	0.24(+)
		Glyceridae	0.28(-)
		Terebellidae	0.32(-)
		<mark>Syllidae</mark>	0.35(+)
		<mark>Glycymerididae</mark>	0.38(+)
		Spionidae	0.42(-)
		Phyllodocidae	0.45(-)
		Veneridae	0.47(-)
		Nephtyidae	0.50(+)
Control FI - September	High FI - September	MYSIDACEA	0.10(+)
		Capitellidae	0.15(-)
		Spionidae	0.19(-)

		Upogebiidae	0.23(-)
		Terebellidae	0.26(-)
		Lumbrineridae	0.30(-)
		<mark>Cirolanidae</mark>	0.33(+)
		<mark>Glyceridae</mark>	0.36(+)
		Syllidae	0.39(-)
		Dexaminidae	0.41(-)
		NEMERTEA	0.44(-)
		Cirratulidae	0.46(-)
		<mark>Glycymerididae</mark>	0.48(+)
		Nephtyidae	0.50(-)
Medium FI - March	Medium FI - September	<mark>Spionidae</mark>	0.05(+)
		Capitellidae	0.10(+)
		MYSIDACEA	0.14(+)
		<mark>Lumbrineridae</mark>	0.18(+)
		<mark>Terebellidae</mark>	0.21(+)
		<mark>Syllidae</mark>	0.24(+)
		<mark>Pectinariidae</mark>	0.27(+)
		Upogebiidae	0.30(+)
		<mark>Golfingiidae</mark>	0.32(+)
		<mark>Glyceridae</mark>	0.35(+)
		NEMERTEA	0.37(+)
		<mark>Veneridae</mark>	0.40(+)
		<mark>Cirolanidae</mark>	0.42(+)
		Phyllodocidae	0.44(+)
		<mark>Cirratulidae</mark>	0.46(+)
		Oweniidae	0.48(-)
		<mark>Nuculidae</mark>	0.50(+)
		<mark>Nephtyidae</mark>	0.51(+)
High FI - March	High FI - September	MYSIDACEA	0.11(+)
		Capitellidae	0.18(-)
		<mark>Spionidae</mark>	0.23(+)
		Lumbrineridae	0.28(-)
		Phyllodocidae	0.31(-)
		<mark>Glyceridae</mark>	0.35(+)
		<mark>Cirolanidae</mark>	0.38(+)
		<mark>Syllidae</mark>	0.41(+)
		<mark>Terebellidae</mark>	0.44(+)
		Glycymerididae	0.46(+)
		Upogebiidae	0.49(+)
		NEMERTEA	0.51(+)

APPENDIX B – Outputs from GAMMS models on the abundance of the 34 species of interest

Note that some of the models failed to converge leading to missing graphs and NA AIC.



76







79



- Linear responses with no sediment differences





- Non- Linear responses



83

Abundance response at the class level





Biomass responses





APPENDIX C - Outputs from GAMMS models on the abundance of the trait modalities of interest

Note that some of the models failed to converge leading to missing graphs.

- Linear with sediment differences

















