

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

Part III – Impact on epifauna





Gwladys Lambert, Lee Murray, Jan Geert Hiddink, Hilmar Hinz, Emily-Kate Moorhead, Harriet Salomonsen & Michel Kaiser

School of Ocean Sciences, College of Natural Sciences, Bangor University

To be cited as follows: Lambert, G. I., Murray, L.G., Hiddink J. G., Hinz H., Salomonsen H, Moorhead E-K. & Kaiser, M.J. (2015). Impact of scallop dredging on benthic communities and habitat features in the Cardigan Bay Special Area of Conservation. Part III – Impact on epifauna. Fisheries & Conservation report No. 61, Bangor University. pp.61

Funded By:



Y Gronfa Pysgodfeydd Ewropeaidd: Buddsoddi mewn Pysgodfeydd Cynaliadwy European Fisheries Fund: Investing in Sustainable Fisheries



Llywodraeth Cymru Welsh Government

Contents

1. INTRODUCTION
2. METHODS
2.1 Experimental design and data collection
2.2 Hypotheses tested
3. DATA ANALYSES AND RESULTS
3.1 Spatial heterogeneity of the experimental area
3.2 Direct impact of fishing on species composition, richness and diversity (H_2)
3.2.1 Drivers of species composition and determination of species indicator of fishing impact (H_{2a})
3.2.2 Fishing impact on species richness and diversity and detection of tolerance thresholds (H _{2b})15
3.2.3 Fishing impact on persistence and colonisation rates and detection of tolerance thresholds (H_{2c}) 20
3.2.4 Detection of species specific extinction thresholds and determination of species of particular interest (H_{2d})
3.3 Direct impact of fishing on species abundance and biomass (H_3) 25
3.3.1 Trends in abundance and biomass responses to the fishing intensity gradient25
3.3.2 Detection of potential thresholds from abundance and biomass data
3.3.3 Further investigation of differences between sand and gravel
3.4 Direct impact of fishing on life history trait composition (H ₄)
3.4.1 Identification of sensitive trait modalities by RLQ and fourthcorner analyses
3.4.2 Fishing impact on sensitive traits41
3.5 Indirect effect of fishing on epifauna and traits via alteration of sediment type (H_5)46
4. DISCUSSION
5. AKNOWLEDGEMENTS
6. REFERENCES
APPENDIX A – Indicator species identified from SIMPER analysis
APPENDIX B – Outputs from GAMMS models on the abundance of the species of interest
APPENDIX C - Outputs from GAMMS models on the abundance of the 24 trait modalities of interest

1. INTRODUCTION

The full background for the study is presented in the first part of the report together with the full executive summary (G. I. Lambert et al., 2015). Briefly, the objective of the work was to determine the effect of scallop dredging on the benthic communities and habitat characteristics in Cardigan Bay SAC and identify sustainable levels of scallop dredging to inform management options. A large scale Before-After Control-Impact (BACI) experiment 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. Here we focus on the impact of fishing on epifauna.

2. METHODS

2.1 Experimental design and data collection

The methods are presented in full extent in the first part of report where a glossary of technical terms can also be found (Lambert et al., 2015). Briefly, the experiment followed a BACI design, where the impact was a gradient of fishing intensities. The objective was to achieve a gradient of 0.25 and 8 times fished. 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, 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 1, Table 1).

Bangor University, Fisheries and Conservation Report No. 61



Figure 1. (A) Experimental design and (B) location of beam trawl samples in March, May and September 2014 (March=blue, May=red and September=green). The gradient of colours in A in a represents the intensity of fishing (see Table 1). The length of the fishing lanes was 1.7kms by 380m wide.

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, Hamon grab, multibeam and side scan sonar. The focus of the present report being on epifauna, only beam trawl sampling will be presented (see parts I and II for reports on infauna and physical seabed). We also used here the sediment data obtained from grab sampling which are presented in the first part of the report (Lambert et al., 2015).

During each scientific survey, three to five 5 minutes beam trawl tows were conducted across the width of each of the 17 sites. The samples were spread out inside the fishing box (Figure 1B). The beam trawl was 2m wide and the mesh size was 4 mm. The fauna was sorted on deck and all individuals identified to the lowest taxonomic level possible and weighed at that level. Non-countable taxa such as hydroids were recorded as present and weighed.

To determine sediment characteristics associated to each beam trawl tow, each tow was associated with the closest grab samples, i.e. samples taken within a buffer zone of 300m around the tow. The distance of 300m was defined so that all beam trawl tows had at least one associated sediment sample. There was an average of 3 grabs associated to each tow. If there was more than one grab sample within 300m, the composition was averaged prior to determining sediment texture using the Gradistat software equivalent in R (package G2Sd, see report part I, Lambert et al. 2015). Tow depth was also averaged from grab associated data.

Box	Target intensity	Achieved intensity	Percentage area fished	Number dredges	Hours fished	Number of beam trawl tows
L01	1	1.09	0.65	6	29	11
L02	3.17	3.05	0.90	8	76	10
L03	4	3.82	0.98	8	98	12
L04	0	0	0	0	0	14
L05	1.59	1.56	0.77	6	41	13
L06	1.26	1.24	0.70	8	31	12
L07	0	0	0	0	0	12
L08	0.5	0.51	0.40	8	12	11
L09	0.71	0	0	0	0	13
L10	0.35	0.23	0.20	14	2	13
L11	6.35	5.33	0.99	14	56	13
L12	2.52	2.29	0.87	14	24	10
L13	0	0	0	0	0	12
L14	5.04	3.87	0.97	14	40	12
L15	0.25	0.29	0.25	14	3	14
L16	8	6.07	0.98	14	58	12
L17	2	1.87	0.84	14	19	12

Table 1. Summary of experimental design and beam trawl sampling.

2.2 Hypotheses tested

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

(H₁) There is no spatial gradient of epifaunal distribution over the all area that could have jeopardised the results of the experiment.

Spatial autocorrelation can pose problem in statistical analyses. If there was a correlation between fishing effort and epifaunal 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 epifaunal 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 H1 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 epifaunal 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 functional groups of epifaunal communities and all functional traits 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) Seabed sediment composition is not linked to epifaunal composition.

The parts I and II of the report have shown that fishing had an impact on sediment. If the sediment composition partly explained the species composition then changing the sediment characteristics by towing dredges on the seabed, i.e. raking features, resuspending fine particles, could have an indirect effect on the benthic communities.

3. DATA ANALYSES AND RESULTS

 Δ Note that the statistical tools used in the present analyses are only listed. For detailed explanations see report part I where methods are explained in the results section and in the glossary (Lambert et al. 2015).

Table 2. Summary of biological data collected during the three scientific surveys around the experiment (mean ± standard error of the mean).

Note that scallops are excluded because they were the target species of the experiment; here we look at impact on associated non-target species. *Abundance and biomass are given excluding brittlestars (*Ophiothrix fragilis*) because the high numbers of *O. fragilis* in brittlestar beds would potentially drive any observed pattern. *O. fragilis* estimates are given separately.

Survey	Number	Species number	*Abundance	*Biomass	Abundance	Biomass
	of tows	(nb/tow)	(nb/100m²)	(kg/100m²)	O. fragilis	O. fragilis
March	62	34.4 (± 1.0)	38.8 (± 2.7)	0.47 (± 0.05)	212 (± 87)	0.25 (± 0.09)
May	74	34.4 (± 0.8)	44.4 (± 2.3)	0.44 (± 0.02)	161 (± 50)	0.22 (± 0.07)
September	70	24.2 (± 0.8)	24.5 (± 1.8)	0.40 (± 0.03)	299 (± 131)	0.40 (± 0.17)

All the following analyses on community composition or total biomass and abundance exclude scallops and brittlestars (*Ophiothrix fragilis*). Scallops were excluded as they were the target of the fishery so their abundance and biomass would obviously decrease with fishing intensity. Brittlestar abundance and biomass changes were analysed separately from all other species due to their high abundance and biomass when forming beds in comparison to any other species. Table 3. Abundance, biomass and occurrence of the most common species caught in beam trawl tows combing all 3 surveys. Species presented were the highest ranking ones in terms of occurrence, abundance and biomass and are ordered based on their occurrence ranking (i.e. percentage presence in tows). Highlighted are the top 5 ranking species of each measured parameter.

Species (common name)	Species (Latin name)	Occurrence (%)	Abundance (nb/100m²)	Biomass (g/100m²)
<mark>A hermit crab</mark>	Pagurus bernhardus	<mark>95</mark>	2.03	25.73
Common dragonet	Callionymus lyra	<mark>92</mark>	1.66	<mark>38.46</mark>
<mark>Green sea urchin</mark>	Psammechinus miliaris	<mark>92</mark>	<mark>4.67</mark>	7.29
<mark>Common brittlestar</mark>	Ophiothrix fragilis	<mark>90</mark>	<mark>223.47</mark>	<mark>292.87</mark>
<mark>Dead man's fingers</mark>	Alcyonium digitatum	<mark>89</mark>	<mark>3.15</mark>	<mark>46.35</mark>
<mark>Common starfish</mark>	Asterias rubens	<mark>88</mark>	<mark>4.19</mark>	<mark>61.31</mark>
A hermit crab	Pagurus prideauxi	88	1.94	9.29
<mark>Serpent's table brittlestar</mark>	Ophiura albida	82	<mark>4.18</mark>	1.70
Poor cod	Trisopterus minutus	76	0.65	6.77
A small crab	Ebalia spp	68	0.59	0.52
Thickback sole	Microchirus variegatus	68	0.40	7.87
Cloak anemone	Adamsia carciniopados	68	1.37	6.44
A small crab	Inachus spp	67	0.93	1.67
A small spider crab	Macropodia spp	67	0.87	0.70
Whelk	Buccinum undatum	58	0.42	33.78
Risso's crab	Xantho pilipes	57	0.35	0.63
Brown shrimp	Crangon crangon	56	0.71	0.75
Norwegian topknot	Phrynorhombus norvegicus	54	0.28	2.13
A brittlestar	Ophiura ophiura	51	0.43	1.08
Flying crab	Liocarcinus holsatus	50	0.42	1.49
Harbour crab	Liocarcinus depurator	49	0.34	1.98
A hydroid	Nemertesia spp	46	-	0.89
Hornwrack	Flustra foliacea	45	-	4.31
A spider crab	Hyas spp	44	0.28	0.38
Oyster drill	Ocenebra erinacea	44	0.18	0.71
Painted top shell	Calliostoma zizyphinum	44	0.20	0.60
A hydroid	Hydrallmania spp	44	-	0.13
A spider crab	Eurynome spp	42	0.23	0.47
Common pelican's foot	Aporrhais pespelecani	39	0.63	4.71
Whiting	Merlangius merlangus	39	0.26	14.19
Long clawed porcelain crab	Pisidia longicornis	37	0.16	0.10
A hydroid	Abietinaria abietina	35	-	0.12
Velvet swimming crab	Necora puber	35	0.16	5.13
Queen scallop	Aequipecten opercularis	34	0.24	5.17
Plumose anemone	Metridium senile	33	0.20	3.25
Dwarf swimming crab	Liocarcinus pusilius	32	0.15	0.14
A snrimp	Panaaius spp	31	0.22	0.26
	Giycymeris giycymeris	30	0.33	13.24
Common spider crab	Maja squinado	28	0.09	53.07
Rea gurnara	Aspitrigia cuculus	28	0.09	5.05
A shrimp	Palaemon spp	20	0.34	0.57
Contrion anider arab		10	0.07	3.81
Brown adible arch	Cancer nagurus	19	0.37	0.91
Small spotted establish	Sculiorhinus canicula	12	0.04	12.20
Sinuii spotted cutsflark	Raia montagui	13	0.03	5 10
Nursehound	Scyliarhinus stallaris	03	0.01	3.10
ivuisenounu	Scynorninus stenuris	02	0.01	4.07

3.1 Spatial heterogeneity of the experimental area

3.1.1.1 Objective

The objective was to analyse spatial aggregation patterns of taxa and the relationship between samples (dis)similarity and fishing intensity in March, i.e. prior to fishing.

3.1.1.2 Methods

Tools: (partial) Mantel's tests and correlograms, Permanova, between group analysis (BGA).

3.1.1.3 Results

Community composition dissimilarity was unrelated to depth (Figures 2c and 2d) but there was a degree of correlation between tows which were less than 2kms apart (Figures 2a and 2b). This meant that there was a spatial gradient of community composition and some degree of spatial autocorrelation between adjacent sites as sites were between about 600 and 900m apart in the northwest south-east direction (but around 2kms apart in the south –west north-east direction).



Figure 2. (Partial) Mantel correlograms for species composition data in March compared to geographic distances (a,b) and depth differences (c,d). The values are the results of the partial Mantel tests (r= coefficient of correlation and p=p-value).

Bangor University, Fisheries and Conservation Report No. 61



Figure 3. Between group analysis (BGA) illustrating differences in species 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. Labels in (a) represent the sites numbers, in (b) the species contributing to differentiating between sites, in (c) the levels of fishing intensity, i.e. control= 0, low= 0-2, medium = 2-4 and high >4 times fished, and in (d) species differentiating between levels of fishing effort.

Overall, community composition in March varied significantly between sites (Permanova, df=16, F=1.512, $R^2=0.35$, p<0.001) but the variation was not linked to the later applied treatment of increasing fishing intensity (Permanova, df=1, F=1.350, R²=0.02, p=0.140). The BGA revealed that site L03 was different from the other sites, especially one of the beam trawl samples which was then subsequently removed from further analyses (i.e. not shown here in Figure 3). 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 3). From the BGA analysis, the difference between sites was mostly driven by sites

on which a high fishing intensity treatment would be applied (rand test for sites, obs = 0.32, p=0.001 - rand test for fishing intensity groups, obs = 0.06, p=0.046 (Figure 3).

3.1.1.4 Conclusions

Prior to fishing, epifaunal composition was not randomly distributed, there was a gradient over the area, although it looked like most of the autocorrelation was driven by similarity among tows that were less than 2kms apart, i.e. within the same sites or directly adjacent ones. The gradient of dissimilarity amongst sites was not related to the gradient in fishing intensity, despite some evidence that sites that would be highly fished were already different prior to fishing. This did not affect the rest of the analyses.

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

3.2.1 Drivers of species composition and determination of species indicator of fishing impact $({\rm H}_{2a})$

3.2.1.1 Objective

The objective was to test if species composition had changed along the fishing gradient between March and May to assess direct impact and between March and September to assess recovery after 4 months. Species of particular interest, i.e. species 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.

3.2.1.2 Methods

Tools: (partial) Mantel's tests and correlograms, nested Permanova, BGA, Simper analysis

3.2.1.3 Results

The Permanova analyses showed that species composition varied with fishing intensity and between surveys (Table 4). The effect of fishing was not different between different sediment types. The

interaction term between survey time (including March, May and September surveys) and fishing intensity was significant. This meant that an effect of fishing on species composition was detected.

Variable	df	F	R^2	p-value
Fishing intensity (FI)	1	3.337	0.017	<0.001***
Survey	2	10.16	0.104	0.001**
Texture	1	2.598	0.013	0.240
Depth	1	3.154	0.016	0.094
FI * Survey	2	2.170	0.023	<0.001***
FI * Texture	1	0.777	0.004	0.777
Survey * Texture	2	1.206	0.012	0.280
FI*Survey*Texture	2	0.871	0.009	0.596

Table 4. Results of the Permanova model on species 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=0.10, p= 0.001) (Figure 4). There appeared to have been a change in community composition between March and May that could visually be linked to fishing intensity, as showed by the results of the Permanova. The samples from September were all different from the two previous surveys and, while low and high intensity sites species composition overlapped, they appeared to remain marginally different from control sites. The species 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 species out of 174 species caught during the three surveys.



Figure 4. Between group analysis (BGA) illustrating differences in species composition between fishing effort levels in March (a - blue), May (b - red) and September (c -green). d represents the species scores on the BGA axes, i.e. species differentiating between groups of fishing effort over all three surveys

3.2.1.4 Conclusions

The analyses of species composition changes over time suggested that fishing had a significant impact. However, figure 4 suggests that this effect might not be linear and mostly due to some changes occurring at medium fishing intensities directly after fishing, i.e. in May. This was explored further using different aspects and characteristics of community composition. 3.2.2 Fishing impact on species richness and diversity and detection of tolerance thresholds (H_{2b})

3.2.2.1 Objective

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

3.2.2.2 Methods

<u>Tools</u>: species accumulation curves, (partial) Mantel's tests and correlogram, Bray Curtis dissimilarities, threshold analysis, linear regression, anova

3.2.2.3 Results

Fishing did not affect species richness (Figures 5 and 6). Species richness was consistently lower in September.



Number of tows

Figure 5. Comparison of species richness pre- to post- fishing impact. The numbers above each panel indicate the fishing effort. The shaded areas represent the 95% confidence intervals.

Figure 6. Comparison of species 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 species composition within sites was homogenised in May and that there was a gradient as dissimilarity in species composition increased with dissimilarity in fishing intensity (Figure 7). However, as suggested in Figure 4, it seemed that the difference was driven by the medium intensity sites as there did not appear to be a significant difference between highly fished sites and control sites (Figure 7 b, e, h). The homogenisation and the effect on medium intensity sites had disappeared by September (see Mantel statistics Figure 7).

Figure 7. Partial Mantel correlograms of species 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 that the difference in species composition between March and May or between March and September was not related to the fishing intensity gradient (Figure 8). The difference in species composition between March and September was higher than the difference between March and May. No threshold was observed.

Figure 8. Bray Curtis estimate of dissimilarity in species composition between surveys along the fishing intensity gradient (top panel) and results of the threshold analysis (bottom panels). The BC dissimilarity coefficient measures the difference in species composition between the first survey (March) and the subsequent surveys (May or September). In red is the dissimilarity in species composition between March and May, in green between March and September.). 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.

3.2.2.4 Conclusions

Fishing did not affect taxa richness nor taxa turnover. There was a higher dissimilarity between March and September communities than between March and May communities which was unrelated to fishing.

3.2.3 Fishing impact on persistence and colonisation rates and detection of tolerance thresholds (H_{2c})

3.2.3.1 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.

3.2.3.2 Methods

Tools: DCA, Bray Curtis dissimilarities, threshold analysis, linear regression, anova

3.2.3.3 Results

There was a low turnover of epifaunal species (DCA axis 1 <3). Persistence was defined as the relative number of species present in March and in subsequent surveys. Colonisation was defined as the relative number of species appearing in subsequent surveys that were not present in March. The number of species persisting between March and May was higher than the number of species common to the March and September surveys, suggesting the disappearance of species over time unrelated to fishing pressure (Figure 9). There were also significantly fewer new taxa in September compared to May, although we previously observed an increase in dissimilarity between the two "after" surveys (Figure 10). This analysis did show a fishing intensity gradient effect on overall persistence rates but not on colonisation rates. Persistence decreased between March and May and mostly so after a threshold situated around 1.8 times fished (Figure 9). By September there was no more significant threshold.

Figure 9. Persistence between March and subsequent surveys along the fishing intensity gradient (top panel) and results of the threshold analysis (bottom panels). In red is the coefficient of persistence between March and May, in green between March and September.

Figure 10. Colonisation between March and subsequent surveys along the fishing intensity gradient (top panel) and results of the threshold analysis (bottom panels). In red is the coefficient of colonisation between March and May, in green between March and September.

3.2.3.4 Conclusions

Persistence rates decreased along the fishing intensity gradient both in May and September, meaning that some species disappeared as a result of an increase in fishing pressure. There appeared to be a threshold at around 1.8 times fished where the persistence rate significantly decreased by about 10% in May but this threshold had disappeared by September. Although we could have expected an increase in the presence of scavengers, the number of new species appearing was not related to

fishing pressure. It has to be noted that this only refers to presence/absence of species and not abundance or biomass which has been analysed separately.

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

3.2.4.1 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.

3.2.4.2 Methods

Tools: binomial linear regression

3.2.4.3 Results

This analysis was based on presence/absence data only. When studying persistence and extinction of specific taxa, 77 taxa were considered as they met the criterion of being present in 5 sites or more in March. Of those 77, 14 taxa appeared to have fishing intensity tolerance/extinction thresholds, varying along the fishing gradient, as they disappeared from higher impact sites in May. However, by September, 12 of those 14 species had reappeared in those fished sites (Figure 11). Only the Ross coral *Pentapora foliacea* and the sand goby *Pomatoschistus minutus* did not reappear at all sites above a certain level of fishing intensity. Twenty three of those 77 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 12). All other taxa showed no disturbance tolerance threshold/overall resilience based on presence/absence data as they were not found again at all sites where they were they were present in March nor could the data be fitted with a significant binomial model.

Figure 11. Sensitive species presence along the fishing gradient. Persistence (blue), extinction between March and May (red), extinction between March and September (green). The black lines represent the extinction threshold as estimated from the binomial models.

Figure 12. Persistent, resilient species presence along the fishing gradient. Note: Those species 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.

3.2.4.4 Conclusions

Two out of 77 taxa showed a tolerance/extinction threshold to fishing, i.e. the Ross coral *P. foliacea* and the sand goby *P. minutus*, as they did not reappear at all sites above respectively 2.3 and 1.2 times fished after 4 months. However, the evidence is weak as these tolerance thresholds only rely on *Pomatoschistus minutus* not having been found at one site in September where it had been in March and no Bonferroni correction (i.e. correction on level of significance due to multiple testing) was applied here. The impact of fishing on those species is investigated further thereafter.

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

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

3.3.1.1 Objective

The objective was to analyse how overall abundance and biomass as well as individual species responded to the gradient of fishing intensity.

3.3.1.2 Methods

Tools: Generalised additive mixed model (GAMM), Linear mixed model (LME)

3.3.1.3 Results

There was no evidence of non-linearity of the response except in sand in September (Figures 13 and 14). Abundance showed a significant response to fishing in both sand and gravel while biomass showed a significant response in sand only. A linear model was run to assess the interaction between fishing intensity and survey time including interactions with sediment texture effect for both abundance and biomass. The summary outputs are given in Table 5 and the direction of the impact is discussed thereafter (Figure 15).

Figure 13. Output of GAMM models testing the effect of fishing on total abundance of epifaunal species. 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 14. Output of GAMM models testing the effect of fishing on total biomass of epifaunal species. 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).

There was a significant decrease in epifaunal abundance along the fishing gradient in May in both sand and gravel, followed by a significant increase in abundance along the fishing gradient in sand only in September (Figure 15c, Table 5). In gravel, although abundance still appeared to decrease in September, the lack of significance of the interaction between fishing intensity and survey time indicates recovery. The biomass data presented similar trends but only the increase in sand in September was significant.

Figure 15. Output of linear mixed effect models testing the effect of fishing on total abundance and biomass of epifaunal species in gravel (top) and sand (bottom). The points are the measured observations (one per beam trawl sample) the lines are the fitted results from the mixed effect linear models (Table 5).

Table 5. Results of the Linear Mixed Effect Models (LMEs) on total abundance and biomass (seeFigure 15). Significant outputs are highlighted.

Response	Variable	ANOVA	F test	Variable category		Sun		
		F value	p-value		Estimate	df	t-value	p-value
Abundance	Fishing intensity (FI)	0.001	0.972		0.05	15	1.055	0.308
	<mark>Survey</mark>	<mark>24.380</mark>	<mark><0.001***</mark>	<mark>May</mark>	<mark>0.60</mark>	<mark>146</mark>	<mark>3.300</mark>	<mark>0.001**</mark>
				September (Sept)	-0.32	146	-1.772	0.078
	Texture	1.281	0.259	Gravelly Sand	0.26	146	1.203	0.231
	FI *Survey	<mark>3.185</mark>	<mark>0.044*</mark>	FI*May	<mark>-0.15</mark>	<mark>146</mark>	<mark>-2.253</mark>	<mark>0.026*</mark>
				FI*September	-0.12	146	-1.491	0.138
	FI * Texture	0.449	0.504	FI*Gravelly Sand	-0.10	146	-1.353	0.178
	Survey * Texture	0.426	0.654	May * Gravelly Sand	-0.35	146	-1.247	0.214
				Sept * Gravelly Sand	-0.35	146	-1.195	0.234
	FI*Survey*Texture	3.041	0.051	FI*May* Gravelly	0.15	146	1.482	0.140
				Sand				
				FI*Sept* Gravelly	<mark>0.28</mark>	<mark>146</mark>	<mark>2.446</mark>	<mark>0.016**</mark>
Piomass	Fishing intensity (FI)	0.049	0.828	Sallu	0.05	15	0.955	0 355
DIOITId35	Survey	0.738	0.480	May	0.43	<u>146</u>	2.160	0.033*
		000		September (Sept)	0.30	146	1.513	0.132
	Texture	0.522	0.471	Gravelly Sand	0.22	146	0.938	0.350
	FI *Survey	1.774	0.173	FI*Mav	-0.14	146	-1.845	0.067
				FI*September	-0.12	146	-1.313	0.191
	Fl * Texture	0.913	0.341	FI*Gravelly Sand	-0.08	146	-0.904	0.367
	Survey * Texture	0.891	0.413	, May * Gravelly Sand	-0.39	146	-1.243	0.216
	,			Sept * Gravelly Sand	<mark>-0.76</mark>	<mark>146</mark>	<mark>-2.336</mark>	0.021*
	FI*Survey*Texture	2.013	0.137	FI*May* Gravelly	0.12	146	1.076	0.284
			-	Sand		-		_
				FI*Sept* Gravelly	<mark>0.26</mark>	<mark>146</mark>	<mark>2.003</mark>	<mark>0.047*</mark>
				<mark>Sand</mark>				

A total of 51 species of particular interest were identified in previous analyses on abundance data (Figures 11 and 12, Appendix A). Of those 51 species, 32 were found in at least 25% of the beam trawl samples. The GAMMs model outputs testing the impact of fishing on those 32 species are presented in Appendix B and the results of the linear mixed effect models (LMEs) for species which showed a linear response in Table 6. Of the species that displayed a linear response, only 3 of them showed a significant interaction between fishing and survey time, i.e. significant effect of fishing after Bonferroni correction. The brown shrimp *Crangon crangon* and velvet crab *Necora puber* both decreased along the fishing intensity gradient in gravel in May but had recovered by September. The dead man's fingers

Alcyonidium digitatum significantly decreased along the fishing gradient in gravel in September (i.e. the slope was significantly different from the slope in March and was negative). The decrease was also observed in May but was only marginally significant after Bonferroni correction

 Table 6. Results of the Linear Mixed Effect Models (LMEs) and threshold analysis on total abundance

 and total biomass and biomass of species of particular interest.

The red signs indicate if fishing impact is positive or negative. df is the 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. Figures illustrating the relationships can be seen in Appendix B (GAMM outputs) and in Figures 16 and 17 for the threshold analysis.

SEDIMENT	SPECIES	LME			THRESHOLD ANALYSIS				
		df	FI*May	FI*Sept	dAIC _{MM}	$dAIC_{MS}$	March-May	March-Sept	
GRAVELLY SAND	TOTAL ABUNDANCE				0.8	1.26	- 0.324 (0.324)	+ 0.43 (0.43)	
	TOTAL BIOMASS				-0.42	-0.13	- 0.162 (0.162)	+ 0.18 (0.18)	
	Alcyonium digitatum	60	- 0.17 (1)	- 0.27 (1)	-2.98	-0.53	- <mark>0.045 (1)</mark>	- 0.144 (1)	
	Crangon crangon	60	- 0.718 (1)	- 0.444 (1)	0.29	-0.13	- 0.24 (1)	- 0.18 (1)	
	Ebalia spp	60	- <mark>0.025 (0.198)</mark>	- 0.093 (0.745)	-4.23	-4.03	- <mark>0.025 (0.862)</mark>	- <mark>0.024 (0.84)</mark>	
	Maja squinado	60	- 0.655 (1)	+ 0.567 (1)	-3.25	-0.79	- <mark>0.039 (1)</mark>	+ 0.125 (1)	
	Necora puber	60	- 0.471 (1)	- 0.433 (1)	-1.32	-0.78	- 0.101 (1)	- 0.125 (1)	
	Ophiothrix fragilis	60	0.999 (1)	+ 0.244 (1)	0.7	-0.9	+ 0.305 (1)	<mark>+</mark> 0.117 (1)	
	Ophiura albida	60	- 0.362 (1)	+ 0.544 (1)	-0.08	-0.19	- 0.194 (1)	+ 0.174 (1)	
	Trisopterus minutus	60	- 0.666 (1)	+ 0.492 (1)	0.41	-0.72	- 0.257 (1)	+ 0.129 (1)	
	Aporrhais pespelecani		non linear		0.39	0.72	- 0.254 (1)	+ 0.299 (1)	
	Asterias rubens		non linear		0.29	-3.85	+ 0.24 (1)	+ <mark>0.026 (0.915)</mark>	
	Glycymeris glycymeris		non linear		-8.43	-7.59	+ <mark>0.004 (0.127)</mark>	+ <mark>0.004 (0.154)</mark>	
	Inachus spp		non linear		-5.23	0.5	- <mark>0.016 (0.543)</mark>	+ 0.26 (1)	
	Liocarcinus depurator		non linear		-1.38	0.38	- 0.098 (1)	+ 0.242 (1)	
	Pagurus bernhardus		non linear		-7.28	-8.94	+ <mark>0.006 (0.213)</mark>	+ <mark>0.002 (0.082)</mark>	
	Pagurus prideauxi		non linear		-2.55	-3.17	+ 0.055 (1)	+ <mark>0.037 (1)</mark>	
	Psammechinus miliaris		non linear		-1.94	-1.66	+ 0.074 (1)	+ 0.079 (1)	
	Archidoris pseudoargus		<25%		0.77	-1.67	+ 0.318 (1)	- 0.078 (1)	
	Cancer pagurus		<25%		-0.01	-0.54	- 0.202 (1)	+ 0.143 (1)	
	Dysidea fragilis		<25%		-5.6	-0.97	<mark>-</mark> 0.013 (0.456)	- 0.113 (1)	
	Gaidropsarus vulgaris		<25%		-1.45	-0.52	+ 0.095 (1)	- 0.145 (1)	
	Inachus dorsettensis		<25%		-7.57	-7.35	- <mark>0.005 (0.187)</mark>	+ <mark>0.005 (0.172)</mark>	

Bangor University, Fisheries and Conservation Report No. 61

	Laevicardium crassum		<25%		-3.2	-0.26	+ <mark>0.04 (1)</mark>	+ 0.167 (1)
	Limanda limanda		<25%		-0.24	<5sites	+ 0.178 (1)	<5 sites
	Pentapora foliacea		<25%		-4.7	-5.8	- <mark>0.02 (0.694)</mark>	- <mark>0.01 (0.359)</mark>
	Polychaete spp		<25%		0.48	<5sites	+ 0.268 (1)	<5 sites
	Sertularia sp		<25%		-2.36	<5sites	- 0.06 (1)	<5 sites
	Tritonia hombergi		<25%		-3.31	<5sites	- 0.038 (1)	<5 sites
SANDY GRAVEL	TOTAL ABUNDANCE				0.22	-3.18	+ 0.223 (0.223)	- <mark>0.037 (0.037*)</mark>
	TOTAL BIOMASS				-0.56	-5.09	- 0.144 (0.144)	- <mark>0.015 (0.015*)</mark>
	Alcyonium digitatum	73	- <mark>0.007 (0.054)</mark>	- 0 (0.004**)	-2.96	-9.07	- <mark>0.042 (1)</mark>	- <mark>0.002 (0.082)</mark>
	Crangon crangon	73	- <mark>0.005</mark> (0.038*)	- 0.22 (1)	-0.91	-3.61	- 0.119 (1)	- <mark>0.03 (1)</mark>
	Ebalia spp	73	- <mark>0.008 (0.061)</mark>	+ 0.893 (1)	-1.33	-3.41	- 0.096 (1)	+ <mark>0.034 (1)</mark>
	Maja squinado	73	- 0.689 (1)	- 0.955 (1)	0.65	-0.33	- 0.288 (1)	- 0.163 (1)
	Necora puber	73	- <mark>0.002</mark> (0.014*)	- 0.696 (1)	-6.28	-7.61	- <mark>0.009 (0.299)</mark>	- <mark>0.005 (0.161)</mark>
	Ophiothrix fragilis	73	- 0.831 (1)	- 0.081 (0.649)	-2.56	-8.84	- 0.051 (1)	- <mark>0.003 (0.091)</mark>
	Ophiura albida	73	+ 0.923 (1)	- 0.176 (1)	1.09	-7.06	+ 0.384 (1)	- <mark>0.006 (0.208)</mark>
	Trisopterus minutus	73	- <mark>0.012 (0.092)</mark>	- <mark>0.038</mark> (0.305)	-9	-11.34	- <mark>0.002 (0.085)</mark>	- <mark>0.001 (0.029*)</mark>
	Aporrhais pespelecani		non linea	r	0.59	0.5	+ 0.278 (1)	- 0.263 (1)
	Asterias rubens		non linea	r	-2.56	0.92	- 0.051 (1)	+ 0.343 (1)
	Glycymeris glycymeris		non linea	r	-0.43	-2.7	+ 0.155 (1)	- <mark>0.048 (1)</mark>
	Inachus spp		non linea	r	0.4	0.02	+ 0.248 (1)	- 0.198 (1)
	Liocarcinus depurator		non linea	r	0.56	0.79	+ 0.273 (1)	+ 0.315 (1)
	Pagurus bernhardus		non linea	r	-3.37	0.41	+ <mark>0.034 (1)</mark>	+ 0.25 (1)
	Pagurus prideauxi		non linea	r	0.02	-1.99	- 0.199 (1)	+ 0.068 (1)
	Psammechinus miliaris		non linea	r	-0.66	0.55	- 0.136 (1)	- 0.272 (1)
	Archidoris pseudoargus		<25%		-2.52	-1.36	- 0.052 (1)	+ 0.094 (1)
	Cancer pagurus		<25%		-3.99	-2.31	- <mark>0.025 (0.887)</mark>	- 0.058 (1)
	Dysidea fragilis		<25%		-5.49	-10.89	<mark>-</mark> 0.012 (0.432)	<mark>-</mark> 0.001 (0.036*)
	Gaidropsarus vulgaris		<25%		-8.28	-8.26	<mark>-</mark> 0.003 (0.118)	<mark>-</mark> 0.003 (0.119)
	Inachus dorsettensis		<25%		-1.63	-0.83	+ 0.082 (1)	+ 0.124 (1)
	Laevicardium crassum		<25%		-3.52	<5sites	+ <mark>0.032 (1)</mark>	< 5 sites
	Limanda limanda		<25%		-2.78	-1.43	+ <mark>0.046 (1)</mark>	- 0.091 (1)
	Mangelia attenuata		<25%		-2.84	0.01	- <mark>0.044 (1)</mark>	+ 0.197 (1)
	Nucula nucleus		<25%		<5sites	-0.63	< 5 sites	- 0.138 (1)
	Palliolum tigerinum		<25%		0.01	1.09	+ 0.198 (1)	+ 0.383 (1)
	Pentapora foliacea		<25%		-1.5	-1.32	+ 0.087 (1)	+ 0.096 (1)
	Polychaete spp		<25%		<5sites	1.84	< 5 sites	+ 0.713 (1)
	Pomatoschistus minutus		<25%		U.53		+ 0.268 (1)	< 5 Sites
	Scyllorninus canicula		<25%		<55ites	-1.15	< 5 siles	- 0.105 (1)
	Sertularia sp		<23%		-4.1	U.SS	+ 0.024 (0.839)	- 0.272 (1)
	Adamsia consistente	105	<23%		1.09	NJSILES	- 0.248 (1)	
ALL SEDIIVIEN I		105	+ 0.243 (1)	+ 0.383 (1)	-1.98	-4.12	+ 0.057 (0.968)	+ 0.018 (0.3)
	Aequipecten opercularis	105	+ 0.25 (1)	+ 0.48 (1)	-0.44	-2.19	+ 0.006 (0.094)	+ 0.05 (0.843)
	Aspitrigia cuculus	192	- 0.525 (1)	- 0.333 (1)	-1.32	-1.30	+ 0.082 (1)	+ 0.078 (1)

Bangor University, Fisheries and Conservation Report No. 61

Buccinum undatum	185	- 0.347 (1)	- 0.449 (1)	0.57	1.25	- 0.254 (1)	- 0.407 (1)
Callionymus lyra	185	- 0.332 (1)	- 0.052 (0.888)	-0.96	-2.73	- 0.1 (1)	- <mark>0.037 (0.629)</mark>
Calliostoma zizyphinum	185	- 0.108 (1)	- 0.261 (1)	-0.81	-1.56	- 0.11 (1)	+ 0.071 (1)
Flustra foliacea	185	- 0.318 (1)	- 0.117 (1)	0.47	0.21	+ 0.237 (1)	- 0.199 (1)
Hyas spp	185	- 0.14 (1)	- 0.421 (1)	0.65	-0.63	+ 0.268 (1)	+ 0.12 (1)
Merlangius merlangus	185	+ 0.208 (1)	+ 0.372 (1)	-0.72	0.08	+ 0.116 (1)	+ 0.184 (1)
Metridium senile	185	- 0.073 (1)	- 0.132 (1)	-5.29	-3.26	- <mark>0.01 (0.169)</mark>	- <mark>0.028 (0.474)</mark>
Microchirus variegatus	185	- 0.06 (1)	- <mark>0.024</mark> (0.401)	-0.95	-1.08	- 0.101 (1)	+ 0.092 (1)
Nemertesia spp	185	+ 0.67 (1)	- 0.5 (1)	-3.33	-3.37	+ <mark>0.028 (0.468)</mark>	+ <mark>0.026 (0.447)</mark>
Ocenebra erinacea	185	- 0.128 (1)	+ 0.848 (1)	-3.07	-2.24	- <mark>0.032 (0.536)</mark>	+ <mark>0.048 (0.822)</mark>
Ophiura ophiura	185	- 0.548 (1)	- <mark>0.021</mark> (0.35)	-5.1	-0.18	- <mark>0.011 (0.187)</mark>	+ 0.157 (1)
Pandalus spp	185	- 0.18 (1)	- 0.803 (1)	-0.72	-2.72	- 0.115 (1)	<mark>-</mark> 0.037 (0.634)
Phrynorhombus norvegicus	185	- 0.528 (1)	+ 0.914 (1)	0.06	1.39	- 0.184 (1)	+ 0.454 (1)
Tapes rhomboides	185	- 0.132 (1)	- 0.717 (1)	-0.76	1.06	- 0.113 (1)	- 0.354 (1)

3.3.1.4 Conclusions

Natural variation was high and of the same magnitude as fishing impact (as seen on the figures where fishing intensity =0). There was an impact of fishing on the total species abundance and biomass. Abundance decreased with fishing intensity in May but by September that trend had disappeared. Data from sand sediment types even showed an increase in abundance and biomass along the fishing intensity gradient 4 months after the impact, i.e. in September. Only a few species individually displayed a significant negative linear response to the fishing intensity gradient and only dead man's fingers *A. digitatum* remained negatively affected along the fishing gradient by September. There was no significant positive linear responses.

3.3.2 Detection of potential thresholds from abundance and biomass data

3.3.2.1 Objective

Although linear models appeared more appropriate than non-linear ones for most species, we investigated the existence of thresholds of fishing intensity after which a major change occurred for all indicator species. This was to determine if there was a level of disturbance that triggered significant changes in the benthic communities, i.e. a cut-off point at which fishing intensity appeared to cause significant changes compared to natural variation.

3.3.2.2 Methods

Tools: threshold analysis on relative difference in biomass

3.3.2.3 Results

Figure 16. Threshold analysis of species that appeared impacted in May (i.e. significant threshold before Bonferroni correction) (see statistics in Table 6). On each plot, the middle line shows the thresholds after which biomass changed most significantly compared to control sites. Top row is for species that were positively impacted, i.e. showed an increase in biomass above a certain threshold; bottom row is for species that were negatively impacted above a certain threshold.

The results of the threshold analysis showed that the most significant change in total abundance and biomass in gravel occurred at a level of around 3.5-4 times fished, as the negative impact of fishing above this threshold was significant 4 months after fishing, in September (Table 6, Figures 16 and 17). There was no threshold detected for either abundance or biomass in May, although most species showed a trend towards a negative impact of fishing in May in all sediments. In September, the patterns were more complex.

Figure 17. Threshold analysis of species that appeared impacted in September (i.e. significant threshold before Bonferroni correction) (see statistics in Table 6). On each plot, the middle line shows the thresholds after which biomass changed most significantly compared to control sites. Top row is for species that were positively impacted, i.e. showed an increase in biomass above a certain threshold; bottom row is for species that were negatively impacted above a certain threshold.

Responses varied at the species level. In sand, the small crab *Ebalia spp.*, the dog cockle *Glycymeris glycymeris*, the Hermit crab *Pagurus bernhardus* and the Ross coral *Pentapora foliacea* showed a consistent response between the two post fishing surveys, i.e. May and September, suggesting an initial impact of fishing which remained visible after 4 months. *G. glycymeris* and *P. bernhardus* showed a positive response to fishing while *Ebalia spp.* and *P. foliacea* showed a negative response. In gravel, the velvet crab *Necora puber*, the poor cod *Trisopterus minutus*, the sponge *Dysidea fragilis* and the three bearded rockling *Gaidropsarus vulgaris* all showed a consistent negative response between the two post fishing surveys. Without sediment distinction, the hydroid *Nemertesia spp.* showed a consistent positive response and the plumose anemone *Metridium senile* a negative one. Note that only the responses of *D. fragilis* and *T. minutus* in gravel in September were significant after Bonferroni correction, although the extinction threshold analysis further suggested that *P. foliacea* had a tolerance level to fishing between 2.5 and 4.5 times fished. The threshold after which *D. fragilis* and *T. minutus* did not appear to have fully recovered in gravel by September was 4.2 times fished.

3.3.2.4 Conclusions

There was no obvious threshold of fishing intensity that could have caused a major immediate change in abundance or biomass of all species in the experimental area. After 4 months, in gravel, overall abundance and biomass were lower in areas that had been fished over 3.5 times.

3.3.3 Further investigation of differences between sand and gravel

3.3.3.1 Objective

The mixed effect modelling and threshold analyses on abundance and biomass revealed that fishing impact was different in sand and gravel habitats. As we had previously observed no overall threshold in community dissimilarities, it was necessary to further investigate this threshold by sediment type.

3.3.3.2 Methods

Tools: Bray Curtis dissimilarities, threshold analysis, linear regression, anova

3.3.3.3 Results

There was no significant difference in BC dissimilarity along the increasing fishing gradient in gravel or in sand (Figure 18). However, in sand, there was evidence of a significant threshold around 0.8 times fished in May but there was no significant threshold in September. In gravel, the non-significant thresholds both in May and September were over 3.5 times fished.

3.3.3.4 Conclusions

Although based on abundance and biomass data there seemed to be different thresholds for different species in September in sand, this did not translate into a unique threshold of significant differences in species composition. Only a short term effect of fishing on species composition was detected in sand around 0.8 times fished while no effect was detected in gravel. When data were not split by sediment type, there was no significant threshold (Figure 8).

Figure 18. Bray Curtis dissimilarity differences between surveys along the fishing intensity gradient in different sediment types (top panels) and results of the threshold analyses (bottom panels).
3.4 Direct impact of fishing on life history trait composition (H₄)

3.4.1 Identification of sensitive trait modalities by RLQ and fourthcorner analyses

3.4.1.1 Objective

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

3.4.1.2 Methods

Tools: RLQ, fourthcorner analysis

3.4.1.2 Results

Figure 19 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 a 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= 0.011, p=0.038). In May and September, there was also a significant correlation between the trait and environmental datasets (obs=0.011, p=0.023 and obs=0.023, p=0.003 respectively). However, the fourthcorner analysis revealed no significant correlations between any traits and any variables after Bonferroni correction of the p-values, for any survey.

Table 7. 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/100m²)
Size range (mm)	<10	S.1	30	0.13
	11-20	S.2	99	5.79
	21-100	S.3	100	173.18
	101-200	S.4	97	26.01
	201-500	S.5	100	177.97
	>500	S.6	97	65.21
Morphology = all done	Soft	M.1	100	131.53
	Tunic	M.2	18	0.77
	Exoskeleton	M.3	100	260.86
	Crustose	M.4	22	0.77
	Cushion	M.5	22	0.60
	Stalked	M.6	98	53.75
Longevity	<1	L.1	28	0.68
	1-2	L.2	99	7.21
	3-10	L.3	100	207.98
	>10	L.4	100	232.42
Larval Development location	Planktotrophic	LD.1	100	365.14
	Lecithotrophic (Pelagic)	LD.2	93	18.92
	Direct (Benthic)	LD.3	94	64.22
Egg development location	Asexual/Budding	ED.1	98	25.98
	Sexual shed eggs (Pelagic)	ED.2	100	230.55
	Sexual shed eggs (Benthic)	ED.3	94	49.30
	Sexual brood eggs	ED.4	100	142.45
Living habit	Tube-dwelling	LH.1	9	0.01
	Burrow-dwelling	LH.2	100	17.80
	Free-living	LH.3	100	354.10
	Crevice/hole/under stone	LH.4	86	11.67
	Epi/endo zoic/phytic	LH.5	96	9.64
	Attached to substratum	LH.6	99	55.05
Sediment position	Surface	SP.1	100	413.60
	Infauna: 0-5cm	SP.2	95	28.16
	Infauna: 6-10cm	SP.3	66	6.43
	Infauna: >10cm	SP.4	24	0.09
Feeding mode	Suspension	FM.1	100	68.08
	Surface Deposit	FIM.2	100	34.06
	Subsurface deposit	FIVI.3	31	0.36
	Scavenger/Opportunist		100	47.07
	Predator	FIVI.5	100	298.09
A A a bility .	Parasite		11	0.01
Μοσιιιτγ	Sessile	MOD 2	100	126.71
	Swilli Crawl/croon/climb	MOD 2	100	120./1
	Burrower		100	251.09
Diaturhatara	Diffusivo mixing	NOB.4	99	13.32
DIOLUIDULOIS	Surface denosition		94	23.15
			100	125./0
	Downwards convoyor	BIO.5	8 11	0.00
	None	BIO.4	100	200.25
	NULL	50.5	100	233.33



Figure 19. Co-inertia between traits and environment for each survey from the RLQ analysis. March=blue; May= red, September= Green

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 20). From this, we selected 33 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 33 modalities, 6 were present in less than 25% of the samples. Most of the other modalities were present in over 80% of the beam trawl samples.



Figure 20. 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).

3.4.1.2 Conclusions

After fishing, both in May and September, the trait composition of the epifaunal 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. Thirty-three 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.

3.4.2 Fishing impact on sensitive traits

3.4.2.1 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.

3.4.2.2 Methods

Tools: GAMM, LME, threshold analysis

3.4.2.3 Results

GAMMs outputs on the log-transformed abundance trait data are presented in Appendix C. Most of the linear trends were not significant after Bonferroni corrections, except for the negative impact of fishing on stalked species (in gravel) (M.6) and on species that live attached to the substratum (in all sediments) (LH.6) which was significant both in May and September as well as the impact of fishing on asexual/budding species (ED.1) which was only significant in September (Table 8). The threshold analysis revealed that the main changed in biomass of ED.1 and LH.6 occurred around 2 times fished. The threshold value for M.6 was similar but not significant after Bonferroni correction. The threshold analyses also showed a threshold for suspension feeders (FM.1) in gravel in September at about 3.5 times fished. On the other hand subsurface deposit feeders (FM.3) increased in biomass in gravel after a fishing intensity of >4.5 times fished in May (the trend had disappeared by September). Cushion shaped species (M.5) had decreased in biomass both in May and September after a fishing effort of about 4 times fished in gravel.

Table 8. Results of the Linear Mixed Effect Models and threshold analysis for total abundance oftrait modalities of particular interest.

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. 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.

			LME	-		-	Threshold analys	is
Sediment	Traits	df	FI*May	FI*Sept	dAIC _{MM}	dAIC _{MS}	March-May	March-Sept
type Gravelly Sand	ED.2	60	+ 0.514 (1)	+ <mark>0.016 (0.114)</mark>	-1.15	-2.19	+ 0.111 (1)	+ 0.06 (1)
	FM.1	60	+ 0.64 (1)	- 0.967 (1)	-0.58	1.44	+ 0.148 (1)	+ 0.493 (1)
	L.1	60	- <mark>0.044 (0.306)</mark>	- <mark>0.01 (0.073)</mark>	-4.81	-5.99	- <mark>0.019 (0.432)</mark>	- 0.009 (0.215)
	L.2	60	- <mark>0.01 (0.067)</mark>	- 0.605 (1)	-4.93	1.48	- <mark>0.018 (0.41)</mark>	+ 0.508 (1)
	M.6	60	- 0.119 (0.832)	- 0.142 (0.995)	-2.75	-0.94	- 0.05 (1)	- 0.115 (1)
	S.4	60	- 0.208 (1)	- 0.832 (1)	-0.02	0.66	- 0.201 (1)	+ 0.288 (1)
	SP.2	60	+ <mark>0.031 (0.22)</mark>	+ <mark>0.022 (0.154)</mark>	-6.32	-4.68	+ <mark>0.009 (0.217)</mark>	+ <mark>0.017 (0.402)</mark>
	BIO.2		non linear		0.27	-1.73	- 0.237 (1)	+ 0.076 (1)
	FM.3		non linear		-5.03	-4.69	+ <mark>0.017 (0.392)</mark>	+ <mark>0.017 (0.401)</mark>
	FM.5		non linear		-0.18	-0.17	- 0.184 (1)	+ 0.176 (1)
	L.3		non linear		0.59	-4.58	- 0.286 (1)	+ <mark>0.018 (0.423)</mark>
	LD.1		non linear		0.38	-0.67	- 0.253 (1)	+ 0.133 (1)
	LH.3		non linear		0.68	-0.74	- 0.302 (1)	+ 0.128 (1)
	M.3		non linear		1	-3.06	- 0.367 (1)	+ <mark>0.039 (0.887)</mark>
	MOB.3		non linear		0.93	-4.34	- 0.353 (1)	+ <mark>0.021 (0.473)</mark>
	S.5		non linear		-0.42	-1.65	- 0.162 (1)	+ 0.079 (1)
	SP.1		non linear		0.14	0.78	- 0.22 (1)	+ 0.31 (1)
	BIO.3		<25%		0.48	0.04	+ 0.268 (1)	- 0.198 (1)
	BIO.4		<25%		0.09	-0.27	- 0.213 (1)	- 0.167 (1)
	M.2		<25%		-0.09	0.13	+ 0.193 (1)	+ 0.208 (1)
	M.4		<25%		-4.99	-6.62	- <mark>0.017 (0.398)</mark>	- <mark>0.007 (0.159)</mark>
	M.5		<25%		-6.77	-1.13	- <mark>0.008 (0.177)</mark>	- 0.104 (1)
Sandy Gravel	SP.4		<25%		0.89	-0.23	- 0.343 (1)	- 0.17 (1)
	ED.2	73	- 0.108 (0.757)	- 0.24 (1)	-1.52	-4.28	- 0.086 (1)	- <mark>0.022 (0.506)</mark>
	FM.1	73	- 0.358 (1)	- <mark>0.01 (0.067)</mark>	0.6	-10.46	+ 0.28 (1)	- <mark>0.001 (0.029*)</mark>
	L.1	73	- 0.665 (1)	+ 0.841 (1)	-1.14	-1.32	+ 0.106 (1)	+ 0.096 (1)
	L.2	73	- 0.567 (1)	- 0.655 (1)	-0.1	0.12	+ 0.186 (1)	- 0.21 (1)
	M.6	73	- <mark>0.004 (0.029*)</mark>	- <mark>0.001 (0.004**)</mark>	-5.21	-7.85	- <mark>0.014 (0.325)</mark>	- <mark>0.004 (0.095)</mark>
	S.4	73	- <mark>0.023 (0.163)</mark>	- 0.131 (0.919)	-0.33	-3.97	- 0.163 (1)	- <mark>0.026 (0.588)</mark>
	SP.2	73	- 0.43 (1)	- <mark>0.02 (0.139)</mark>	1.43	-7.72	+ 0.491 (1)	- <mark>0.004 (0.1)</mark>

	BIO.2		non linear		0.47	-0.33	+ 0.258 (1)	- 0.163 (1)
	FM.3		non linear		-9.58	-0.36	+ <mark>0.002 (0.043*)</mark>	+ 0.16 (1)
	FM.5		non linear		-3.36	-5.8	- <mark>0.034 (0.792)</mark>	- <mark>0.011 (0.245)</mark>
	L.3		non linear		0.21	-1.57	- 0.222 (1)	- 0.084 (1)
	LD.1		non linear		-0.56	-4.57	- 0.144 (1)	- <mark>0.019 (0.44)</mark>
	LH.3		non linear		-0.97	-4.01	- 0.115 (1)	- <mark>0.025 (0.576)</mark>
	M.3		non linear		0.12	-1.02	- 0.21 (1)	- 0.112 (1)
	MOB.3		non linear		-0.84	-1.11	- 0.124 (1)	- 0.107 (1)
	S.5		non linear		-2.97	-6.54	- <mark>0.042 (0.956)</mark>	- <mark>0.008 (0.174)</mark>
	SP.1		non linear		-1.65	-6.63	- 0.081 (1)	- <mark>0.007 (0.166)</mark>
	BIO.3		<25%		1.32	1.75	+ 0.453 (1)	- 0.65 (1)
	BIO.4		<25%		-3.81	-4.01	- <mark>0.028 (0.635)</mark>	- <mark>0.025 (0.576)</mark>
	M.2		<25%		-4.5	-0.76	- <mark>0.02 (0.455)</mark>	- 0.129 (1)
	M.4		<25%		-0.71	-0.7	+ 0.132 (1)	+ 0.133 (1)
	M.5		<25%		-9.66	-14.49	- <mark>0.002 (0.041*)</mark>	- <mark>0 (0.005**)</mark>
	SP.4		<25%		-1.57	-3.66	- 0.084 (1)	- <mark>0.03 (0.682)</mark>
All sediment	ED.1	185	- <mark>0.009 (0.093)</mark>	- <mark>0 (0.002**)</mark>	-10.62	-10.87	- <mark>0.001 (0.01*)</mark>	- <mark>0.001 (0.009**)</mark>
	ED.3	185	- <mark>0.005 (0.052)</mark>	- 0.492 (1)	-6.36	1.12	- <mark>0.008 (0.075)</mark>	- 0.386 (1)
	L.4	185	- 0.155 (1)	- 0.055 (0.555)	-3.14	-3.88	- <mark>0.036 (0.361)</mark>	- <mark>0.025 (0.251)</mark>
	LD.2	185	- 0.169 (1)	- 0.116 (1)	-2.37	-3.11	- 0.053 (0.535)	- <mark>0.037 (0.366)</mark>
	LD.3	185	- <mark>0.014 (0.138)</mark>	- 0.286 (1)	-4.15	-0.24	- <mark>0.022 (0.219)</mark>	- 0.167 (1)
	LH.4	185	- <mark>0.025 (0.247)</mark>	- <mark>0.043 (0.427)</mark>	-1.11	-4.73	- 0.103 (1)	- <mark>0.016 (0.165)</mark>
	LH.6	185	- <mark>0.005 (0.048*)</mark>	- <mark>0 (0.001**)</mark>	-12.58	-13.74	- <mark>0 (0.004**)</mark>	- <mark>0 (0.002**)</mark>
	S.1	185	- 0.675 (1)	+ 0.468 (1)	-2.64	0.8	- <mark>0.047 (0.466)</mark>	+ 0.311 (1)
	S.3	185	- 0.984 (1)	+ 0.449 (1)	0.96	-0.48	+ 0.347 (1)	+ 0.146 (1)
	SP.3	185	+ 0.28 (1)	+ 0.425 (1)	-1.4	0.14	+ 0.088 (0.885)	+ 0.208 (1)



Figure 21. Threshold analysis of trait modalities that appeared positively impacted in May (top row) and negatively impacted (bottom row)



Gravelly Sand

Figure 22. Threshold analysis of trait modalities that appeared positively impacted in September (top row) and negatively impacted (bottom row)

3.4.2.4 Conclusions

Most of the linear trends were not significant except for stalked species, suspension feeders and species living attached to the substratum. Those species were mostly negatively affected when the sites had been fished over 2 times on average. Some other group of species showed some significant thresholds in gravel habitat: subsurface deposit feeders biomass increased in sites over 4.5 times fished in May but the trend had disappeared by September, suspension feeders biomass decreased in gravel in September at about 3.5 times fished and cushion shaped species had decreased in biomass both in May and September after a fishing effort of about 4 times fished.

Table 9. Summary of significant increases and decreases in abundance (numbers/100m²) and biomass (g/100m²) with relation to fishing intensity levels. "Change" corresponds to the percentage difference in average abundance (or biomass) from under to above the fishing intensity threshold or the difference between 0 times fished and 6 times fished from the linear model.

Surveys	Sediment type	Species or species group	Average over all	Linear or	Change
			surveys (/100m²)	threshold analysis	
			(inc. all sediment)		
March-May	Gravel	Crangon crangon	0.80g (±0.13)	Linear (fished x6)	- 17%
		Necora puber	3.14g (±0.60)	Linear (fished x6)	- 51%
		Stalked (M.6)	45.74g (±5.25)	Linear (fished x6)	- 81%
		Subsurface deposit feeders	0.64g (±0.34)	Threshold = 4.6	+ 1450%
		(FM.3)			
		Cushion shaped (M.5)	0.45g (±0.17)	Threshold = 4.6	- 100%
	All sediment	Total abundance	36.30 ind (±2.21)	Linear (fished x6)	- 42%
		Total biomass	457.69g (±25.74)	Linear (fished x6)	- 41%
		Attached (LH.6)	51.59g (±3.96)	Threshold = 2.1	- 78%
		Asexual/budding (ED.1)	24.20g (±1.93)	Threshold = 2.1	- 78%

March-Sept	Sand	Total abundance	40.38 ind (±3.14)	Linear (fished x6)	+ 162%
		Total biomass	446.50g (±41.36)	Linear (fished x6)	+ 127%
	Gravel	Total abundance	36.30 ind (±2.21)	Threshold = 3.4	- 46%
		Total biomass	457.69g (±25.74)	Threshold = 4.2	- 23%
		Total abundance	36.30 ind (±2.21)	Linear (fished x6)	- 52%
		Total biomass	457.69g (±25.74)	Linear (fished x6)	- 57%
		Alcyonium digitatum	39.21g (±4.99)	Linear (fished x6)	- 93%
		Trisopterus minutus	7.05g (±0.77)	Threshold= 4.2	- 96%
		Dysidea fragilis	0.37g (±0.13)	Threshold= 4.2	- 100%
		Stalked (M.6)	45.74g (±5.25)	Linear (fished x6)	- 91%
		Suspension feeders (FM.1)	70.42g (±6.63)	Threshold = 3.4	- 83%
		Cushion shaped (M.5)	0.45g (±0.17)	Threshold = 4.2	- 67%
	All sediment	Attached (LH.6)	51.59g (±3.96)	Threshold = 2.1	- 79%
		Asexual/budding (ED.1)	24.20g (±1.93)	Threshold = 2.1	- 76%
	All sediment	Trisopterus minutusDysidea fragilisStalked (M.6)Suspension feeders (FM.1)Cushion shaped (M.5)Attached (LH.6)Asexual/budding (ED.1)	7.05g (±0.77) 0.37g (±0.13) 45.74g (±5.25) 70.42g (±6.63) 0.45g (±0.17) 51.59g (±3.96) 24.20g (±1.93)	Threshold= 4.2 Threshold= 4.2 Linear (fished x6) Threshold = 3.4 Threshold = 4.2 Threshold = 2.1 Threshold = 2.1	- 96% - 100% - 91% - 83% - 67% - 79% - 76%

3.5 Indirect effect of fishing on epifauna and traits via alteration of sediment type (H₅)

3.5.1 Objective

The objective was to analyse the potential indirect effect fishing on epifaunal communities by studying the relationship between sediment and epifaunal communities' composition, as fishing had shown to have an impact on sediment composition itself.

3.5.2 Methods

Tools: nested Permanova, Simper analysis, Mantel's tests and correlograms

3.5.3 Results

Epifauna abundance, biomass and richness were similar in gravel and sand (see Table 5 for statistics on abundance and biomass – richness: anova - df=1, F<0.001, p=0.977). The non-significant difference in composition between sediment types is illustrated in Figure 23 (see Table 4 for Permanova statistics). The association between fauna and sediment composition was, however, stronger in gravel than in sand (see Mantel's tests results in Figure 24). The trait composition did not vary significantly

between sand and gravel habitats either varied (Figure 25). Mantel's tests showed that trait composition was not associated with sediment composition in either sand or gravel (Table 10).



Figure 23. Difference between gravelly and sandy communities. Orange= Sandy Gravel, Grey = Gravelly Sand



Figure 24. 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.



Figure 25. 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 report part I.

Table 10. Results of the partial Mantel 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	Traits	r (depth)	p (depth)	r (dist)	p (dist)
Sandy Gravel	Size	0.061	0.152	0.057	0.167
	Morphology	0.079	0.095	0.080	0.096
	Life span	0.057	0.164	0.059	0.158
	Larval Development	0.027	0.298	0.028	0.291
	Egg Development	0.072	0.100	0.074	0.092
	Living Habit	0.073	0.107	0.075	0.108
	Sediment position	0.028	0.306	0.028	0.302
	Feeding mode	0.064	0.143	0.066	0.133
	Mobility	0.061	0.152	0.065	0.150
Gravelly Sand	Size	-0.022	0.611	-0.029	0.653
	Morphology	-0.014	0.547	-0.019	0.585
	Life span	-0.053	0.764	-0.053	0.752
	Larval Development	0.001	0.469	-0.003	0.489
	Egg Development	0.003	0.457	-0.002	0.491
	Living Habit	-0.030	0.646	-0.032	0.654
	Sediment position	-0.050	0.765	-0.050	0.756
	Feeding mode	-0.033	0.667	-0.037	0.693
	Mobility	-0.052	0.753	-0.055	0.760

3.5.4 Conclusions

Taxa biomass, abundance, composition and richness were the same in sand and gravel. The association between sediment composition and fauna, in terms of taxa but not traits, was however stronger in gravel than in sand.

4. DISCUSSION

To our knowledge, the present BACI experiment was one of the most substantial scallop dredging impact experiments conducted in the UK and worldwide. It covered an area of over 10km² adding up the 17 fishing and control sites.

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. For epifauna, however, there was no difference between gravel and sand communities.

Infaunal and epifaunal taxonomic richness were not affected by fishing. 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. 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.

Sand and relatively well sorted sediment types generally appear more resilient to fishing but less productive than muddy-gravelly and poorly sorted habitats (Bolam et al., 2014; Collie et al., 2000; Handley et al., 2014; Kaiser et al., 2006). An apparent overall recovery within a few months is in line with the results of previous studies looking at the fishing impact in areas of relatively high energy (Lambert et al., 2014). Studies conducted in the Cardigan Bay SAC had already shown that there was little difference between the open and closed grounds in terms of epifaunal coverage even 50 months

52

after the closure, although some differences in infauna composition was suggested but it was not clear if this was due to a gradient in sediment composition across the SAC (Dutton, 2014; Sciberras et al., 2013). We compare our findings to the published results of a few other studies experimentally testing the impact of scallop dredging or bottom trawling and discuss them in context of their representativeness at the scale of fishing grounds, statistical power and acute vs chronic effects.

A recent work, published by LeBlanc et al. in 2015, showed the results of a very similar experiment conducted in Canada in similar habitat types and depth range. The experiment was conducted over a fishing intensity gradient of 0 to 14 times fished in narrow corridors of 40m by 400m long, i.e. 0.016km² per plot, which was representative of the fishing patterns and exceeded the intensities of their local scallop dredging fishery. In comparison, the fishing plots in the present study were 0.63km², i.e. about 10 times as wide and 3 times as long. However we only tested the effect of fishing an area up to 6 times on average as this was representative of our local fishery and was thought to largely exceed the expected fishing intensity range on scallop fishing grounds (fished up to 3 times a year) (Lambert et al., 2011). Similarly, the size of the plots in the present study was designed based on advice from the local fleet and knowledge of scallop fishing patterns in the Irish Sea, mostly due to our expertise of the scallop fishery of the Isle of Man. The large width of the plots aimed at reducing the chances of rapid recovery via local immigration, a major criticism of small scale BACI experiment studies as this type of recovery could not occur when a large area of the seabed is fished (Collie et al., 2000; Jennings et al., 2001). In the present study the latest sampling event took place 4 months after fishing while LeBlanc et al. (2015) went resampling after a year. The reason for resampling after 4 months was mostly logistical as the start of the experiment was delayed for legal obligations and sampling had to be conducted within the timeframe of the project. However, 4 months also corresponded approximately to the duration of the current closed season (minus less than a month) and therefore made sense in order to study potential management options for the SAC in light of the current management system in place.

Results of the two studies were very similar despite the differences listed above. Both reported a larger effect of natural variation over fishing and very few instances of statistically significant effects along the fishing gradient for species or groups of species, although more were significant when the p-values were not corrected for multiple testing in both studies. While here we did not report the magnitude of natural change at the species level, LeBlanc et al. (2015) estimated it at a similar magnitude to that produced at fairly intensively fished sites. Here the fluctuations in abundance, biomass and composition between sites in March, i.e. pre-fishing, and between control sites over time

suggest similar conclusions. In terms of statistical power, the thorough power analysis conducted by LeBlanc et al. (2015) suggested that their study could reasonably detect elevated effects of fishing mortality. Although they did not report the effect of fishing on overall estimates of abundance and biomass, we found significant evidence of a decrease in both abundance and biomass of epifauna and infauna straight after fishing and more complex patterns after 4 months. The minimum significant impact detected in the study was a negative impact of 17% on the brown shrimp *Crangon crangon* in May and after an intensity of 6 times fished while most detected changes were just over 50%, suggesting that this was the minimum impact level our study could reasonably detect (keeping in mind that most of these significant results came from the threshold analysis which has got its limitations as discussed below). Generally after 4 months the overall impact was not detectable anymore, there was even a suggestion of increasing abundance and biomass in sand.

Our results are comparable to those of many other published studies. Here we only discuss a few relevant ones. Eleftheriou & Robertson (1992) conducted a BACI experiment in a small sandy bay in Scotland, characterised by well sorted sediment, and, although they dredged the corridors (25m²) up to 25 times, they did not find a significant effect on the infaunal communities. Some patterns were observed though. Some species increased in abundance and biomass, notably some bivalves and crustaceans as in the present study, others decreased above certain fishing intensity thresholds. Generally, the most fragile/large epifauna appeared negatively impacted. The study only reported direct impact. In New Zealand, Thrush et al. (1995) conducted an experiment in two distinct areas of 1400m² characterised by coarse sand and small and short-lived species with one area that was on an open fishing ground and the other in a protected area. They not only monitored the direct impact of dredging through an area once but also resampled after 3 months to assess recovery. Similarly to the present study, they found strong temporal changes unrelated to fishing, a generally negative response straight after fishing and more complex responses three months later, with some decreases of different type of species and increases of taxa belonging to crustaceans, polychaetes or bivalve groups, that may have resulted from settlement or colonization from adjacent areas. Currie & Parry (1996) conducted a BACI experiment in a soft sediment area in two plots of 600x600m, i.e. one control one dredged, with a fishing intensity of 2 times fished which represented the medium-high fishing intensity applied by the local scallop fishery in Port Philip Bay, in southern Australia. They found an initial impact of -20 to 30% for most species but the effect of dredging was mostly undetectable when they resampled after 6 months, i.e. after the next recruitment, except for a few species which still appeared affected after 14 months. In comparison, the initial impact for total abundance on all species combined in our study after 6 times fished (i.e. 3 times more intensive than Currie & Parry 1996) was

around -40% for epifauna and -60% for infaunal abundance. Again, in Currie & Parry (1996), some species or species groups seemed to increase and/or decrease as a result of fishing and it was suggested that this could be linked to some functional characteristics such as feeding or depth of occurrence. But although some changes in community composition had remained after 14 months, the changes between seasons and years were greater. Other comparable large scale BACI experiments were conducted to study the impact of bottom trawls and found similar results, i.e. short term impacts and complex patterns after a few months or a year or even full recovery (Kaiser et al., 1998; McConnaughey & Syrjala, 2014; Pitcher et al., 2009; Robinson et al., 2001). This seems to be the case for sandy-gravelly type of fishing grounds but does not include studies of impacts on biogenic habitats where recovery might take years if ever even possible (e.g. Hall-Spencer & Moore, 2000).

In the present study, regardless of fishing intensity or sediment type, there was a high diversity of functional groups both in infauna and epifauna. This is an important result in itself as the diversity in species traits has been highlighted as a key factor in maintaining the adaptive capacity and resilience of communities (Elmqvist et al., 2003). The infauna community was particularly diverse while the biomass of the epifauna community was dominated by free living, mobile species and predators, as well as species with relatively long life spans. The infaunal community constituted the major part of the biomass in the experimental area, despite the generally low densities compared to other sites of potentially similar environmental characteristics (Kaiser & Spencer, 1996; Kaiser et al., 1998). For example, prior to the experiment in March, an average of 720g of epifauna per 100m² was sampled with the 4mm mesh size beam trawl (including brittlestars) while 8.8g of infauna, sieved through 1mm, was sampled per 0.1m², i.e. 8800g per 100m². Fished or disturbed areas are expected to be dominated by infauna (Tillin et al., 2006). This suggests that the area has some degree of resilience. Similarly, areas adapted to natural disturbance are expected to have a relatively high coverage of encrusting species (e.g. Asch & Collie, 2008) but encrusting species were not systematically sampled in the present study and therefore this could not be tested. However, we found that 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 4 months after fishing. Generally, suspension feeders, stalked and asexual/budding species had a lower biomass in September in areas that were fished over 2 to 4 times. The individual body size of organisms was not measured and therefore the impact of fishing on the size of biota was not directly tested. However, abundance appeared to have changed/increased more than biomass overall by September, especially for infauna and in sand for epifauna, suggesting that indeed fishing will have

selected for smaller organisms as has been widely reported elsewhere (Collie et al., 2000; McConnaughey et al., 2005; Tillin et al., 2006).

Expected time to full recovery can seem rather short in experimental studies, especially in comparison to other type of studies on coarser habitats. Blyth et al. (2004) showed that the benthic community of a mixed coarse substratum area impacted by towed gear was approaching the composition of an adjacent non-impacted area 2 years post-fishing. Collie et al. (2005) showed significant increases in abundance and biomass 2.5 years after the closure of a gravel sediment area of the Georges Bank, but increases in numbers and biomass of certain species were still observed up to 5 years after the closure. Recovery from aggregate extraction in similar habitats was also reported to take from 2–4 years to >7 years (Cooper et al., 2007; Desprez, 2000). A criticism of BACI and other in-situ experiments is that they remain small scale compared to the size of fishing ground. Entire fishing grounds will have different recovery dynamics because reproduction and growth may be the main source of observed recovery if immigration from surrounding areas is limited. Here, we have attempted to work around this limitation by fishing over large areas but it remains that a large proportion of the scallop ground around the experimental plots was unfished. If the whole SAC was to be re-opened to fishing this would probably not be the case although the effort would still be expected to be patchily distributed to some extent. Another issue that cannot be accounted for in a BACI experiment is that only the acute impact of fishing on the seabed can be tested while chronic fishing might have a greater effect. Indeed there is a risk that the fished area remains in a permanent altered state and cannot recover (or at least start recovering) when it is closed to fishing (Collie et al., 2000). However, it has been shown that there is potential on heavily scallop dredged grounds of the Irish Sea to start recovering during the first year post-fishing disturbance (Lambert et al., 2014). Also, scallop fishery will tend to disturb the ground in acute pulses, i.e. a ground is intensively fished for a few days before the fleet moves on, potentially returning to the same ground once more before the end of the season (Veale et al., 2000).

Our experiment aimed at defining thresholds of fishing intensity for management. In that sense type II errors are as important to consider as type I error. A type I error is a false positive, i.e. it is the error of rejecting the null hypothesis of no effect when there actually is no effect. A type II error is a false negative, it is the probability of missing a significant impact by accepting the null hypothesis. Considering the high degree of natural variation, it can be expected that our study suffered type II errors, i.e. missed on significant effects. This is why some studies increase the level of significance α to 0.1 (instead of 0.05 here) (Currie & Parry, 1996; McConnaughey & Syrjala, 2014). If we had done so, the number of significant interactions would have increased (even after Bonferroni correction) as fishing appeared marginally significant for a number of species or groups of species. In that sense our

threshold analysis was not as statistically rigorous as our linear approach. Finding the fishing intensity threshold that maximised the difference between "low" and "high" fishing intensity involved multiple testing along the fishing gradient for each species. Although multiple testing between species was corrected with the Bonferroni correction it was not correcting "within species", i.e. to account for the method used to find the most appropriate fishing intensity threshold. Less thresholds would have been identified as significant if this had been corrected for. Therefore, the method we applied was deemed conservative and appropriate for the purpose of the exercise. Ecologically, it is likely that benthic communities will gradually shift in composition along a disturbance gradient, making it difficult to define an ecologically meaningful threshold, but we defined thresholds as the fishing intensity after which the change between pre and post fishing exceeds the change that occurred by natural variation. It resulted in identifying a range of thresholds values for different species or group of species. Overall there was a fairly continuous increase along the fishing gradient in sand, i.e. no threshold, and a decrease in abundance and biomass in gravel over intensities of about 3.5-4 times fished for both infauna and epifauna detectable after 4 months.

Our study, together with the contribution from other published work, shows that fishing has got an impact in the Cardigan Bay SAC but that, if scallop dredging was allowed, there would be potential for recovery under the specific conditions that were tested in the present experiment: the fished ground was closed during summer, part of the SAC remained protected and fishing effort was capped in areas where fishing was allowed. Assuming that the scallop fishing season remains closed from the 1st of May until the 1st of October, as it is now, the results of our experiments suggest that the fished area should not be fished over 3 to 4 times during the open season or else part of the fauna would not have time to fully recover. It is not certain that benthic communities fished below this threshold would fully recover but the area seems to show some degree of resilience. Rotating spatially open and closed areas would insure that communities are given time to fully recover to their present status. From other published work, it seems that 2 to 5 years closures could be recommended. Although this is not always the case, reserves or unfished areas can help replenish fished areas of the seabed with larvae and juveniles across relatively short distances (e.g. Allison, 2004). Therefore, keeping part of the SAC permanently closed, especially where features such as cobble reefs can be identified, would further help to preserve the integrity of the seafloor in the SAC and would help the recovery process of fished grounds as it has been shown that some species can benefit from the proximity of unfished/less fished grounds (e.g. such as large size species, see Lambert et al., 2014). A rule of thumb that has been widely used in other studies and in policy is that 20% of the area should remain unfished (Auster, 2001). This corresponds to a fishing intensity of just under 2 times fished on average if the whole area was

randomly fished, i.e. with an average of 2 times fished overall about 20% of the seabed would remain untouched. However, providing that the fishing ground is large enough, fishing is likely to be patchy, not random, and leave more than 20% of the seabed untouched if fished at an average intensity of 2. In general terms, we conclude that management plans that limit bottom trawls and dredge fisheries to more resilient areas and maintain permanently unfished patches within these areas will minimize the impacts of a given amount of towed bottom-fishing effort on seabed habitats (Lambert et al., 2014).

5. AKNOWLEDGEMENTS

There is a long list of people to thank! We thank all the people, students, ex-students, who participated and particularly volunteered during the three scientific surveys around the experiment and those who conducted the observer work onboard the fishing vessels. Thanks to our colleagues in the Fisheries and Conservation Science research group for being flexible and sharing their RA time during the busy weeks. We thank the owners, skippers and crew of the scallop dredgers participating in the experiment for all the hard work and long hours and who all did an amazing job and were very generous and committed to the project. We thank the captains and crew of the RV Prince Madog for their expertise and hard work. We are grateful to all the staff and research academics of the school of Ocean Sciences who helped with their time at different stages of the project. Thanks to Thomson Ecology who conducted the analysis of infaunal sample in a timely and professional manner. Thanks also to the BENTHIS project for sharing their database of life history traits. This work would not have happened without the collaboration and advice of Natural Resources Wales and members of the Welsh Government, although the results and conclusions only reflect the analyses and views of the authors and in no way those of these two organisations. Finally, none of this would have been possible without the leadership and commitment of the Welsh Fisherman's Association, many thanks to Jim and Carol Evans. This research was funded by the European Fisheries Fund.

6. REFERENCES

- Allison, G. (2004). The influence of species diversity and stress intensity on community resistance and resilience. *Ecological Monographs*, 74(1), 117-134.
- Asch, R. G., & Collie, J. S. (2008). Changes in a benthic megafaunal community due to disturbance from bottom fishing and the establishment of a fishery closure. *Fishery Bulletin, 106*(4), 438-456.
- Auster, P. J. (2001). Defining thresholds for precautionary habitat management actions in a fisheries context. North American Journal of Fisheries Management, 21(1), 1-9.
- Blyth, R. E., Kaiser, M. J., EDWARDS-JONES, G., & Hart, P. J. (2004). Implications of a zoned fishery management system for marine benthic communities. *Journal of Applied Ecology*, *41*(5), 951-961.
- Bolam, S., Coggan, R., Eggleton, J., Diesing, M., & Stephens, D. (2014). Sensitivity of macrobenthic secondary production to trawling in the english sector of the greater north sea: A biological trait approach. *Journal of Sea Research*, *85*, 162-177.
- Collie, J. S., Hall, S. J., Kaiser, M. J., & Poiner, I. R. (2000). A quantitative analysis of fishing impacts on shelf-sea benthos. *Journal of Animal Ecology*, *69*(5), 785-798.
- Collie, J. S., Hermsen, J. M., Valentine, P. C., & Almeida, F. P. (2005). Effects of fishing on gravel habitats: Assessment and recovery of benthic megafauna on georges bank. *American Fisheries Society Symposium, , 41.* pp. 325.
- Cooper, K., Boyd, S., Eggleton, J., Limpenny, D., Rees, H., & Vanstaen, K. (2007). Recovery of the seabed following marine aggregate dredging on the hastings shingle bank off the southeast coast of england. *Estuarine, Coastal and Shelf Science, 75*(4), 547-558.
- 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.
- Desprez, M. (2000). Physical and biological impact of marine aggregate extraction along the french coast of the eastern english channel: Short-and long-term post-dredging restoration. *ICES Journal of Marine Science: Journal Du Conseil, 57*(5), 1428-1438.
- Dutton, T. (2014). The response of benthic communities to closure of a temperate scallop dredging ground: A comparison of open and closed areas within the cardigan bay special area of conservation (M degree thesis, 64pp. Bangor Unviersity:
- Eleftheriou, A., & Robertson, M. (1992). The effects of experimental scallop dredging on the fauna and physical environment of a shallow sandy community. *Netherlands Journal of Sea Research, 30*, 289-299.
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., et al. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, 1(9), 488-494.
- Hall-Spencer, J., & Moore, P. (2000). Scallop dredging has profound, long-term impacts on maerl habitats. *ICES Journal of Marine Science: Journal Du Conseil, 57*(5), 1407-1415.
- Handley, S. J., Willis, T. J., Cole, R. G., Bradley, A., Cairney, D. J., Brown, S. N., et al. (2014). The importance of benchmarking habitat structure and composition for understanding the extent of fishing impacts in soft sediment ecosystems. *Journal of Sea Research*, *86*, 58-68.
- Jennings, S., Dinmore, T. A., Duplisea, D. E., Warr, K. J., & Lancaster, J. E. (2001). Trawling disturbance can modify benthic production processes. *Journal of Animal Ecology*, *70*(3), 459-475.
- 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.
- Kaiser, M., Clarke, K., Hinz, H., Austen, M., Somerfield, P., & Karakassis, I. (2006). Global analysis of response and recovery of benthic biota to fishing. *Marine Ecology Progress Series, 311*, 1-14.
- Kaiser, M., Edwards, D., Armstrong, P., Radford, K., Lough, N., Flatt, R., et al. (1998). Changes in megafaunal benthic communities in different habitats after trawling disturbance. *ICES Journal of Marine Science: Journal Du Conseil, 55*(3), 353-361.

- Lambert, G. I., Murray, L. G., Hiddink, J. G., Hinz, H., Salomonsen, H., & Kaiser, M. J. (2015). *Impact of scallop dredging on benthic communities and habitat features in the cardigan bay special area of conservation. part I impact on infaunal invertebrates.* (Fisheries & Conservation report No. xx). 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.
- McConnaughey, R. A., & Syrjala, S. E. (2014). Short-term effects of bottom trawling and a storm event on soft-bottom benthos in the eastern bering sea. *ICES Journal of Marine Science: Journal Du Conseil, 71*(9), 2469-2483.
- McConnaughey, R. A., Syrjala, S. E., & Dew, C. B. (2005). Effects of chronic bottom effects of chronic bottom trawling on the size structure wling on the size structure of soft-bottom benthic invertebrates. *American Fisheries Society Symposium*, *, 41*. pp. 425-437.
- Pitcher, C., Burridge, C., Wassenberg, T., Hill, B., & Poiner, I. (2009). A large scale BACI experiment to test the effects of prawn trawling on seabed biota in a closed area of the great barrier reef marine park, australia. *Fisheries Research*, *99*(3), 168-183.
- Robinson, S., Bernier, S., & MacIntyre, A. (2001). The impact of scallop drags on sea urchin populations and benthos in the bay of fundy, canada. *Hydrobiologia*, *465*(1-3), 103-114.
- 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.
- Thrush, S., Hewitt, J., Cummings, V., & Dayton, P. (1995). The impact of habitat disturbance by scallop dredging on marine benthic communities: What can be predicted from the results of experiments? *Marine Ecology Progress Series*, *129*(1), 141-150.
- Tillin, H., Hiddink, J., Jennings, S., & Kaiser, M. (2006). Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Marine Ecology Progress Series*, *318*, 31-45.
- Veale, L., Hill, A., Hawkins, S., & Brand, A. (2000). Effects of long-term physical disturbance by commercial scallop fishing on subtidal epifaunal assemblages and habitats. *Marine Biology*, 137(2), 325-337.

APPENDIX A – Indicator species identified from SIMPER analysis.

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

Group A	Group B	Species	cumsum
Medium FI- March	Medium FI- May	Glycymeris.glycymeris	0.06(-)
		Pagurus.bernhardus	0.11(-)
		Alcyonium.digitatum	0.15(+)
		Merlangius.merlangus	0.2(+)
		Asterias.rubens	0.24(-)
		Callionymus.lyra	0.27(-)
		Necora.puber	0.31(+)
		Limanda.limanda	0.33(-)
		Aporrhais.pespelecani	0.36(-)
		Aequipecten.opercularis	0.39(-)
		Buccinum.undatum	0.41(-)
		Flustra.foliacea	0.44(+)
		Scyliorhinus.stellaris	0.46(-)
		Metridium.senile	0.48(+)
		Trisopterus.minutus	0.5(+)
High FI- March	High FI- May	Maja.squinado	0.11(+)
		Glycymeris.glycymeris	0.17(-)
		Buccinum.undatum	0.22(+)
		Alcyonium.digitatum	0.26(+)
		Pagurus.bernhardus	0.3(-)
		Asterias.rubens	0.33(-)
		Microchirus.variegatus	0.36(+)
		Merlangius.merlangus	0.39(+)
		Trisopterus.minutus	0.42(+)
		Laevicardium.crassum	0.44(-)
		Necora.puber	0.46(+)
		Aporrhais.pespelecani	0.49(+)
		Aspitrigla.cuculus	0.51(+)
Control FI- May	High FI- May	Asterias.rubens	0.07(+)
		Buccinum.undatum	0.12(+)
		Glycymeris.glycymeris	0.18(-)
		Alcyonium.digitatum	0.23(+)
		Cancer.pagurus	0.26(+)
		Pagurus.bernhardus	0.29(-)
		Callionymus.lyra	0.32(+)
		Laevicardium.crassum	0.34(-)
		Aporrhais.pespelecani	0.37(+)
		Merlangius.merlangus	0.39(+)
		Microchirus.variegatus	0.41(+)
		Pagurus.prideauxi	0.43(+)
		Aequipecten.opercularis	0.45(+)
		Tapes.rhomboides	0.47(+)

		Aspitrigla.cuculus	0.5(-)
		Adamsia.carciniopados	0.51(+)
Control FI- September	High FI- September	Asterias.rubens	0.09(-)
		Maja.squinado	0.17(-)
		Alcyonium.digitatum	0.23(+)
		Buccinum.undatum	0.28(+)
		Pagurus.bernhardus	0.33(-)
		Scyliorhinus.canicula	0.37(-)
		Callionymus.lyra	0.4(+)
		Psammechinus.miliaris	0.44(-)
		Glycymeris.glycymeris	0.47(-)
		Aspitrigla.cuculus	0.49(-)
		Trisopterus.minutus	0.51(-)
Medium FI- March	Medium FI- September	Asterias.rubens	0.07(-)
		Alcyonium.digitatum	0.12(+)
		Merlangius.merlangus	0.16(+)
		Pagurus.bernhardus	0.2(+)
		Buccinum.undatum	0.24(-)
		Necora.puber	0.28(+)
		Callionymus.lyra	0.31(+)
		Maja.squinado	0.34(-)
		Glycymeris.glycymeris	0.37(+)
		Flustra.foliacea	0.39(+)
		Metridium.senile	0.42(+)
		Trisopterus.minutus	0.44(+)
		Microchirus.variegatus	0.46(+)
		Crangon.crangon	0.48(+)
		Ophiura.ophiura	0.5(-)
High FI- March	High FI- September	Maja.squinado	0.09(+)
		Asterias.rubens	0.15(-)
		Buccinum.undatum	0.2(+)
		Alcyonium.digitatum	0.24(+)
		Pagurus.bernhardus	0.28(-)
		Pagurus.prideauxi	0.31(+)
		Merlangius.merlangus	0.34(+)
		Callionymus.lyra	0.37(+)
		Scyliorhinus.canicula	0.39(-)
		Microchirus.variegatus	0.42(+)
		Psammechinus.miliaris	0.45(-)
		Glycymeris.glycymeris	0.47(-)
		Adamsia.carciniopados	0.49(+)
		Aspitrigla.cuculus	0.52(-)

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

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

- Linear with sediment differences









Linear without sediment difference


















Non-Linear with sediment difference



77







APPENDIX C - Outputs from GAMMS models on the abundance of the 24 trait modalities of interest

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

- Linear with sediment differences















87





- Non linear sediment differences









