

Ecosystem impacts of intertidal invertebrate harvesting: from benthic habitats to bird predators

Leo J. Clarke

**This thesis has been submitted in partial fulfilment of the
requirements of the degree of Doctor of Philosophy.**

**Bournemouth University in collaboration with Natural
England and the Southern Inshore Fisheries and
Conservation Authority.**

This copy of the thesis has been supplied on condition that anyone who consults it is understood to recognise that its copyright rests with its author and due acknowledgement must always be made of the use of any material contained in, or derived from, this thesis.

Abstract

Leo J. Clarke

Ecosystem impacts of intertidal invertebrate harvesting: from benthic habitats to bird predators.

Intertidal harvesting of marine invertebrates has significant potential to come into conflict with the interests of nature conservation. This is particularly so for overwintering shorebirds that rely heavily on invertebrate prey to maintain body condition throughout the winter and to fuel migration towards breeding grounds. Harvesting activities in these areas therefore require careful management to achieve sustainability and to maintain healthy ecosystem functioning. This thesis investigates impacts of intertidal harvesting on benthic habitats and invertebrate communities as well as the potential impacts of harvesting on shorebird populations. Implications for management of inshore and intertidal fisheries are discussed.

A meta-analysis investigated the response of key invertebrate prey groups to different gear types used in different intertidal habitats. Hand gathering most severely reduces prey abundance, which is likely to be due to the accuracy of harvesting with these gear types, while recovery trends vary between different combinations of gear and habitat and taxonomic groups. Results suggest that impacts may persist for longer in sandy habitats than in muddy habitats.

In some cases fishermen may develop gears in response to local circumstance and the development of harvestable populations of new and introduced species.

Extensive fieldwork was carried out to assess benthic impacts of ‘pump-scoop’ dredging in Poole Harbour, UK, a designated Special Protection Area under the European Union Birds Directive. The pump-scoop dredge is a novel gear type developed by local fishermen following the introduction of the manila clam *Ruditapes philippinarum* in the 1980s. The use of this gear type elicits significant changes to macrobenthic community structure and a loss of fine sediments, while reductions in abundance of the target species of up to 95% occur in some areas throughout the open season. Although population dynamics of *R. philippinarum* vary across a gradient of fishing pressure, determining cause and effect is prevented by a lack of environmental data that could help isolate fishing impacts more confidently.

Data on fishing effort is often lacking, particularly in inshore fisheries where Vessel Monitoring Systems (VMS) data are not collected. The analysis of aerial imagery collected by an unmanned aerial system (UAS) was used as an alternative measure of fishing effort in intertidal areas. Results indicate that the physical scarring of the sediment (quantified through image classification methods and calculation of a measure of image texture) is a reliable proxy for the distribution and intensity of fishing effort in intertidal areas. Remote sensing techniques offer an alternative source of data, useful to inform management of inshore fisheries, where no log book program or VMS data exists.

A combination of fieldwork and individual-based modelling (IBM) was used to investigate the effect of shellfish dredging on shorebird populations in Poole Harbour. Field surveys showed no significant effect of dredging on shorebird

feeding or intake rates, nor species distribution across the site, although continued monitoring is recommended. IBM results indicate that increased shellfish landings in Poole Harbour elicit a behavioural response in the Eurasian oystercatcher *Haematopus ostralegus* population, characterised by an increase in the time spent feeding and the amount of marine worms consumed. These shifts in behaviour and diet represent compensatory measures in response to a loss of preferred shellfish prey.

The work presented in this thesis can directly contribute to ecosystem-based management of inshore fisheries. Results from the meta-analysis will assist managers in predicting the effects of harvesting on benthic ecosystems and provide useful evidence of recovery patterns, while survey data provide information on the impacts of pump-scoop dredging in Poole Harbour, directly contributing to management. Other work provides demonstration of how tools such as remote sensing and IBMs can be applied to accurately quantify disturbance and predict the responses of shorebird populations to harvesting. The work presented will help ensure sustainable fishing, productive benthic habitats and healthy shorebird populations into the future.

Acknowledgements

Firstly I would like to thank my supervisors Richard Stillman, Roger Herbert and Luciana Esteves for all their time, patience and efforts over the last three years. Without their assistance this project would not have been possible. I have learned a great deal from them on various subjects, not just limited to the research topic but also academia, the research process and publication of research, as well as more informal life/career advice! I have also received help and advice on my project from various other academic staff at Bournemouth University, notably including Duncan Golicher and Rick Stafford whose statistical expertise have helped me greatly.

The project was funded by Natural England and the Southern Inshore Fisheries and Conservation Authority (SIFCA) and I would like to thank all the people I have worked with from those organisations. Notably Patrick Cooper, Sarah Birchenough and Rob Clark at the SIFCA whose knowledge of Poole Harbour and the fisheries that operate in the harbour has been invaluable. I would also like to thank Susan Burton, Andrzej Narosanzki and Richard Morgan at Natural England who have provided advice and assistance on the more applied and policy-based aspects of the project.

The wider PhD community in Bournemouth and a few people in particular have helped make the last three years enjoyable and a time I shall remember fondly, as well as providing valuable advice as to how to handle the PhD process and various aspects of working at the university. I have got to know and enjoyed spending time with many people but in particular Tadhg Carroll, Tea Basic, Alice Hall, Danny Sheath, Alex Lovegrove, Catie Gutmann Roberts, John Atkinson and other students

who I have shared the office with have made the last three years a lot of fun, in various ways.

Lastly I would like to thank all of my family and in particular my girlfriend Jennifer, and my parents, without whom none of this would have been possible. My parents have always encouraged me to do what I enjoy and their support, in many forms, has been greatly appreciated whilst living 250 miles from home. I couldn't have done this without them.

Author's Declaration

I confirm that the work presented in this thesis is my own, with the following exceptions:

Chapter 2 is published in collaboration with Kathryn M. Hughes of Bangor University, Luciana S. Esteves, Roger J. Herbert, and Richard A. Stillman as:

Clarke, L. J., Hughes, K. M., Esteves, L. S., Herbert, R. J. and Stillman, R. A. 2017. Intertidal invertebrate harvesting: a meta-analysis of impacts and recovery in an important waterbird prey resource. *Marine Ecology Progress Series*. 584, 229-244.

Chapter 3 has been published in collaboration with Luciana S. Esteves, Richard A. Stillman and Roger J. Herbert as:

Clarke, L. J., Esteves, L. S., Stillman, R. A. and Herbert, R. J. H. 2018. Impacts of a novel shellfishing gear on macrobenthos in a marine protected area: pump-scoop dredging in Poole Harbour, UK. *Aquatic Living Resources*. 31, DOI 10.1051/alr/2017044.

Table of Contents

Copyright Statement	i
Abstract	ii
Acknowledgements	v
Author’s Declaration	vii
Table of Contents	viii
List of Figures	xii
List of Tables	xix
List of Appendices	xxiv
Abbreviations	xxv
1. Introduction	1
1.1 An Introduction to Intertidal Ecosystems: Conservation Importance and Ecosystem Services.....	1
1.2 Benthic Impacts of Intertidal Bottom-Contact Fishing.....	3
1.3 Impacts of Harvesting on Bird Predators	7
1.4 Ecosystem-Based Management of Human Activities.....	12
1.5 Case Study: The Dutch Wadden Sea	14
1.6 Individual-Based Models	16
1.7 Evidence Gaps	17
1.7.1 Impacts of Intertidal Fishing.....	17
1.7.2 Non-Native Fisheries and Impacts of Novel Gears.....	18
1.7.3 Quantifying Intertidal Fishing Disturbance	18
1.7.4 Response of Shorebird Populations to Fishing Disturbance	19
1.8 Research Aims and Thesis Structure	20
2. Intertidal invertebrate harvesting: a meta-analysis of impacts and recovery in an important shorebird prey resource	22
2.1 Introduction.....	22
2.2 Methods	26
2.2.1 Data Collection	26
2.2.2 Response Variables and Effect Size	27

2.2.3	Combining Effects	28
2.2.4	Initial Impacts.....	29
2.2.5	Moderating Variables.....	30
2.2.6	Analysis Notes	32
2.3	Results.....	33
2.3.1	Studies.....	33
2.3.2	Initial Impacts.....	34
2.3.3	Recovery Patterns	43
2.4	Discussion.....	52
3.	Impacts of a novel shellfishing gear on macrobenthos in a marine protected area: pump-scoop dredging in Poole Harbour, UK.....	59
3.1	Introduction	59
3.2	Materials and Methods.....	62
3.2.1	Study Area	62
3.2.2	Sampling.....	65
3.2.3	Measuring fishing effort.....	66
3.2.4	Sediment Analysis	67
3.2.5	Statistical Analysis.....	67
3.3	Results.....	70
3.3.1	Environmental Factors	71
3.3.2	Biological Assemblage.....	74
3.3.3	Community Descriptors and Habitat Quality	83
3.4	Discussion.....	87
4.	Remote sensing methods as a tool for quantifying the spatial extent and intensity of shellfish dredging in a marine protected area.....	94
4.1	Introduction	94
4.2	Materials and Methods.....	97
4.2.1	Image Classification.....	103
4.2.2	Texture Analysis	105
4.2.3	Comparison between Methods	106
4.3	Results.....	107
4.3.1	Image Classification.....	107
4.3.2	Texture Analysis	112
4.3.3	Comparison between Methods and with Known Fishing Distribution	115

4.4	Discussion	117
5.	Chapter: Population dynamics of the commercially harvested non-native Manila clam <i>Ruditapes philippinarum</i> in Poole Harbour, UK.....	121
5.1	Introduction.....	121
5.2	Methods	123
5.2.1	Study Area	123
5.2.2	Sampling.....	123
5.2.3	Analysis.....	127
5.3	Results	131
5.3.1	Clam Size and Abundance	131
5.3.2	Changes in Abundance during Fishing Season	135
5.3.3	Natural Mortality.....	138
5.3.4	Condition Index and Secondary Productivity	138
5.3.5	Cohort Analysis.....	140
5.3.6	Relationship between Clam Length and Weight.....	142
5.3.7	Growth of <i>R. philippinarum</i>	144
5.4	Discussion	146
6.	Shorebird distribution and feeding rates in relation to shellfish dredging: insights from Poole Harbour, UK.	151
6.1	Introduction.....	151
6.2	Methods	153
6.2.1	Study Area	153
6.2.2	Bird Observations	156
6.2.3	Intake Rates.....	158
6.2.4	Distribution and Intensity of Fishing Effort	160
6.2.5	Statistical Analysis	161
6.2.6	Cautionary Notes.....	162
6.3	Results	163
6.3.1	Species Distribution in Relation to Dredging Disturbance	163
6.3.2	Feeding and Intake Rates	169
6.3.3	Daily Energy Requirements	173
6.4	Discussion	174
7.	Individual-based models help inform fisheries management: applications on a novel shellfishery in Poole Harbour, UK.....	180
7.1	Introduction.....	180

7.2	Methods.....	182
7.2.1	Study Site	182
7.2.2	Poole Harbour Model.....	183
7.2.3	Fishing Simulations	195
7.2.4	Analysis	196
7.3	Results.....	196
7.3.1	Testing the Model	196
7.3.2	Fishing Scenarios.....	197
7.4	Discussion.....	202
8.	Discussion and Conclusions	211
8.1	Introduction and Thesis Overview	211
8.2	Impacts of intertidal harvesting: an overview	212
8.3	A novel, non-native fishery in a marine protected area	213
8.4	Quantifying the extent and intensity of intertidal harvesting	215
8.5	Distribution and intake rates of bird populations in response to fishing disturbance	217
8.6	Modelling overwinter survival of a shorebird population within a commercial shellfishery.....	218
8.7	Implications for Management.....	219
8.8	Limitations and Further Research.....	224
8.9	Final Conclusions.....	226
9.	References.....	228
10.	Appendices.....	276

List of Figures

Figure 1.1. Conceptual diagram of the potential mechanisms by which intertidal fishing disturbance can impact upon coastal bird populations.	11
Figure 2.1. Mean ($\pm 95\%$ confidence intervals) effect of fishing disturbance on abundance of benthic taxa at 0-10 days post-fishing according to (a) fishing	

gear type and (b) Folk habitat group. The horizontal dotted line represents no significant effect. Gear abbreviations: HDg = hand digging; HPu = hand pump; Rk = hand raking; HyD = hydraulic dredge; Mech = mechanical dredge. Habitat abbreviations: (g)mS = gravelly/muddy sand; M = mud; mS = muddy sand; msG = muddy/sandy gravel; S = sand; sM = sandy mud. Adequate test for significant impact is whether the 95% confidence interval overlaps the horizontal zero effect line. The number of observations is indicated in brackets..... 38

Figure 2.2. The mean effect of fishing disturbance on the abundance of target (a) and non-target (b) species across time categories (no. days) since fishing. The dotted horizontal line represents no significant effect. Adequate test for significant impact is whether the 95% confidence interval overlaps the horizontal zero effect line. The number of observations is indicated in brackets. 40

Figure 2.3. Classification tree representing the interaction between fishing gear and taxonomic group with regards to changes in abundance 0-10 days post fishing. Each node presents a partition in the data. For the data at each branch of the tree the mean effect (Hedges' d) is given, along with the mean percentage change in abundance. Other Phyla: Echinodermata, Phoronida, Nemertea. ... 42

Figure 2.4. Response in taxa abundance to fishing disturbance across four time categories following fishing. Data are mean response \pm 95% confidence intervals. Significant deviation from zero effect (i.e. no response) is considered to occur if the error bars do not overlap with the dotted horizontal line. Gaps in the data are present for some gear/habitat combinations. Gear abbreviations: Dg = hand digging; HPu = hand pump; Rk = hand raking; HyD =

hydraulic dredge; Mech = mechanical dredge. The number of observations is indicated in parentheses.....	44
Figure 2.5. Response of (a) molluscs ($F = 16.08$, $R^2 = 0.28$, $p < 0.001$) and (b) pooled taxa (annelids, crustaceans) ($F = 32.86$, $R^2 = 0.37$, $p < 0.001$) abundance to mechanical dredging in intertidal mud. Horizontal dotted line represents no significant effect.....	47
Figure 2.6. Response of benthic taxa to (a) hydraulic dredging in mud ($F = 12.51$, $R^2 = 0.31$, $p < 0.001$), (b) hand raking in sand ($F = 4.20$, $R^2 = 0.18$, $p < 0.01$) and (c) mechanical dredging in sand ($F = 8.83$, $R^2 = 0.27$, $p < 0.01$). Horizontal dotted line represents no significant effect.....	49
Figure 2.7. Mean effect of fishing on benthic diversity (a) and biomass (b) across four time categories following fishing. Data are mean response $\pm 95\%$ confidence intervals. Significant deviation from zero effect (i.e. no response) is considered to occur if the error bars do not overlap with the dotted horizontal line.....	51
Figure 3.1. a) The pump-scoop dredge used in Poole Harbour, UK. b) Aerial imagery of scarring from pump-scoop dredging within Poole Harbour. Modified with permission from Jensen <i>et al.</i> (2005) and Footprint Ecology Ltd. (Fearnley <i>et al.</i> , 2013) respectively. No scale bar was included in original publication, although the circular scars generally range from 5-15m across.....	61
Figure 3.2. The study area in Poole Harbour known as Wytch Lake, indicating the sampling stations visited in June and November 2015. The Wytch Lake Bird Sensitive Area (BSA) is indicated by the hatching. The southern hatching represents the area closed to dredging (control) and the northern hatching	

represents the area open July 1st –October 31st (newly opened, short-term dredging). The most northerly sampling grid outside of the hatching has historically been heavily fished. The southern tip of Round Island is indicated immediately north of the study site. Shellfish dredging is permitted outside of the BSA from 25th May – 24th December. The location within Poole Harbour, the UK south coast and the UK is also indicated..... 63

Figure 3.3. Sediment particle size cumulative volume curves for each site in June and November 2015. a) heavily dredged site; b) newly dredged site; c) control. 73

Figure 3.4. Two-dimensional MDS plot derived from the log (x+1) transformed similarity matrix indicating the similarity between the macrofaunal assemblages at sampling locations in June (black) and November (grey) 2015. Circles = newly dredged site/medium dredging intensity (open July – October), squares = heavily dredged site, triangles = control site..... 77

Figure 3.5. Canonical ordination for the discriminant analysis of log+1 transformed species abundance data. Spearman rank correlations of individual species abundance are overlaid (restricted to those with vector lengths < 0.4). Black symbols = June 2015; grey symbols = November 2015. Circles = newly dredged site (open July – October), squares = heavily dredged site (historically dredged, open all season), triangles = control site. 79

Figure 3.6. Mean (\pm S.E.) densities of common species in June (dark grey bars) and November (light grey bars) 2015 at each site. *H. diversicolor* (Phyllodoceidae), *Tubificoides* spp. (Tubificidae), *A. marioni* (Cirratulidae), *S. shrubsolii* (Spionidae), *P. ulvae* (Hydrobiidae), *A. tenuis* (Semelidae). 82

Figure 3.7. Mean (\pm S.E.) total number of individuals per m² observed in samples from each site in June (dark grey bars) and November (light grey bars) 2015. 85

Figure 4.1. The study site of Wytch Lake within Poole Harbour, UK. Labelled survey sector polygons are overlaid (CH: long-term, chronic dredging; AC: short-term, acute dredging; CN: control, no commercial dredging). The dashed and solid areas indicate areas open to dredging from 1st July – 31st October and closed to dredging respectively..... 101

Figure 4.2. Aerial imagery of the study site obtained at low tide on November 23rd 2015 with survey sectors overlaid (CH: long-term, chronic dredging; AC: short-term, acute dredging; CN: control, no commercial dredging). White areas indicate no data, which were cut from the image before analyses were undertaken..... 102

Figure 4.3. Results of the image classification process. The extent of each raster band in each of the survey sectors is evident. The magnified images on the right correspond to the extent indicators on the main map of the survey site. Round Island is the area immediately to the north of survey sector CH1..... 108

Figure 4.4. Percentage of each survey sector scarred by pump-scoop dredging derived from image classification. Dark grey bars indicate values for whole sites. 112

Figure 4.5. Mean (\pm S.D.) diversity value of pixels in each survey sector derived from the moving window neighbourhood analysis method. 113

Figure 4.6. a) Mean pixel diversity plotted against % scarred sediment; b) no. fishing sightings vs. mean pixel diversity; and c) no. fishing sightings vs. % scarred sediment for each survey sector..... 116

Figure 5.1. Locations sampled by pump-scoop dredge for the clam and cockle stock assessment in June 2015 and revisited in January 2016 (white circles). The northern-most site is Upton Lake (closed site), the westerly site is the area around Seagull Island in Holton Mere (high intensity fishing), and the southerly site is Wytch Lake (intermediate intensity fishing). The small black circles indicate SIFCA fishing sightings during 2015. Sampling locations in Wytch Lake are within the intertidal saltmarsh, not on land as the figure suggests. The locations in the UK and on the UK's south coast are inset. 125

Figure 5.2. The hand-held dredge used to sample smaller clam sizes in each location (Matthew Harris, University of Portsmouth PhD Thesis, 2016)..... 126

Figure 5.3. Size frequency histograms of clams sampled by pump-scoop dredging in June 2015 and January 2016 (three dredges pooled). The dashed black line in each plot indicates the minimum legal landing size of 35mm..... 133

Figure 5.4. Size Frequency histograms of clams sampled using the hand dredge with a 1mm mesh size in each site in January 2016 (six hand dredges pooled). 134

Figure 5.5. Mean (+/- 95% C.I.) proportional change in abundance of legally harvestable (>35mm) clams at each site over the course of the 2015 dredging season..... 136

Figure 5.6. Mean (+/- 95% C.I.) proportional change in clam densities in each 5mm size class during the 2015 dredging season at each site sampled. 137

Figure 5.7. The relationship between length and condition index in clams from each site sampled in January 2016. Seagull Island: $y = 1.38 + 0.07x + 0.69$, $R^2 = 0.37$; Wytch Lake: $y = 3.04 + 0.04x + 0.91$, $R^2 = 0.11$; Upton Lake: $y = 2.94 + 0.03x + 0.94$, $R^2 = 0.08$ 139

Figure 5.8. Mean (\pm 95 % C.I.) AFDM in mg of clams sampled in each site in January 2016.....	140
Figure 5.9. The relationship between length and weight (in mg AFDM) of <i>R. philippinarum</i> in areas of different fishing intensity within Poole Harbour. Black line = Seagull Island (heavy fishing); red line = Wytch Lake (intermediate fishing); grey line = Upton Lake (low fishing).....	143
Figure 5.10. Von Bertalanffy growth curves fitted to length-at-age data of clams from each site in Poole Harbour. a) Seagull Island; b) Wytch Lake; c) Upton Lake.	145
Figure 6.1. Poole Harbour Special Protection Area (hatched area) on the south coast of the UK.	155
Figure 6.2. The study site, Wytch Lake, located within Poole Harbour on the south coast of the UK. The black lines indicate the boundaries of the bird sensitive area (BSA). The solid line indicates the area in which dredging is prohibited. The dashed line indicates the area in which dredging is permitted from 1st July – 31st October. Dredging is permitted outside of the BSA throughout the dredge season from 25th May – 24th December (Table 6.1). The southerly extent of Round Island can be seen to the north of the peninsula on the south east of the map.	156
Figure 6.3. The nine survey patches in which bird counts and observations were conducted throughout winter 2015/16, indicated by the hatched polygons.	157
Figure 6.4. Generalised linear models of species densities against pixel diversities as a proxy for sediment disturbance.	166

Figure 6.5. Mean (+/- S.E.) feeding rate (number of swallows) per 90s in each species during winter 2015/16. BW = black-tailed godwit, CU = curlew, OC = oystercatcher..... 169

Figure 6.6. Intake rates (grams AFDM) per 90 seconds in each species for which feeding data was collected across a range of pixel diversity values as a proxy of fishing intensity. 172

Figure 7.1. Mean response values (+/- 95% C.I.) for the Poole Harbour oystercatcher population under scenarios of increased landings of shellfish removed across all patches open to dredging simultaneously in Poole Harbour, UK. The point at which the response deviates significantly from initial values is indicated with asterisks..... 199

Figure 7.2. The relationship between increased shellfish landings in tonnes of wet weight and time spent feeding (a), the proportion of the population using fields (b), and the amount of marine worms in the diet (c) of oystercatchers within Poole Harbour. 201

List of Tables

Table 2.1. Number of studies (n=38, from 16 publications) included in the analysis with regards to the region, gear type and habitat within each study. Habitat: (g)mS = gravelly/muddy sand; M = mud; mS = muddy sand; msG = muddy/sandy gravel; S = sand; sM = sandy mud.....	34
Table 2.2. Weighted mean summary effect sizes from random-effects models for the main taxonomic groups at 0-10 days following fishing disturbance.....	35
Table 2.3. Weighted mean summary effect sizes from random-effects models for each of the five main species for the period 0-10 days post-fishing. Each of these species are known prey species for waders and other avian predators .	36
Table 2.4. Results of one-way ANOVA of abundance of pooled taxa between grouped time categories for each gear/habitat combination for which sufficient data were available to undertaken the analysis. Data for other gears and habitats were too scarce for this analysis. nd = no data available for that gear/habitat combination. Values highlighted in bold indicate a significant change in the magnitude of the effect across grouped time periods.	46
Table 3.1. Fishing intensity and seasonal openings of each site sampled under the dredge permit by-law, which came in to force on 1 st July 2015.....	64
Table 3.2. Fishing intensity in each area as represented by the number of Southern Inshore Fisheries and Conservation Authority (SIFCA) patrol sightings in each area during the 2015 season and the estimated disturbed area from image classification methods.....	71

Table 3.3. Mean (\pm 95 CI) organic content (mass Loss On Ignition (g)) and % volume sediment $<$ 0.63 μ m across each site in June and November 2015. Significant changes throughout the study period are indicated in bold. 71

Table 3.4. Results of a two-factorial PERMANOVA on community abundance data across sites between June and November 2015 and including environmental covariates. d.f. = degrees of freedom; S.S. = sum of squares; M.S. = mean squared..... 75

Table 3.5. Results of pairwise comparison of macrofaunal assemblage between sites in June and November 2015 following the PERMANOVA analysis..... 76

Table 3.6. ANOVA results for individual species abundance across the study period and between sites. 81

Table 3.7. Standardised mean differences in abundance of each species plus total number of individuals at newly and heavily dredged sites, compared to control conditions across both sampling times..... 83

Table 3.8. Mean (\pm 95% C.I.) diversity and biotic indices (AMBI: AZTI Marine Biotic Index; BO2A: Benthic Opportunistic Annelid Amphipods) for each site in June and November 2015. Significant changes over time are highlighted in bold. Thresholds for each biotic indices are included below..... 86

Table 4.1. Fishing intensity and seasonal openings of each site sampled under the dredge permit byelaw, which came in to force on 1st July 2015. Site codes: CN = control; AC = short-term, acute dredging; CH = long-term, chronic dredging. 98

Table 4.2. Inclusion criteria for each of the three groups into which output classes from the unsupervised classification were included. The scale factor applied to

each group to calculate an estimate of spatial extent of scarring is indicated.	105
Table 4.3. Measures of dredging extent derived from the image classification process described above, including the estimate for each class using the scale factors from Table 2. Sector labels denoted with * indicate areas where data is missing and values are calculated using available data only.	109
Table 4.4. Zonal statistics for each individual survey sector. Each statistic is derived from the pixel diversity values of the output raster from the moving window neighbourhood analysis described in the methods.	114
Table 5.1. Study sites in Poole Harbour, UK in which Manila clams were sampled in June 2015 and January 2016.	124
Table 5.2. Mean length, CPUE and density of clams from each site in June 2015 and January 2016. Values in bold indicate a significant difference between months.	132
Table 5.3. Mean (+/- S.E.) Log+10 transformed natural (non-fishing) clam mortality in each survey site in January 2016.	138
Table 5.4. Clam cohort estimates derived from Bhattacharya’s method within FiSAT II and the mixdist package in R.	141
Table 5.5. Parameter estimates of the Von Bertalanffy growth curves fitted to length-at-age data of clams from each site sampled in January 2016.	144
Table 6.1. Fishing intensity and seasonal openings of each site sampled under the dredge permit byelaw, which came in to force on 1st July 2015.	155

Table 6.2. Outputs from best-fit generalised linear models to assess the effect of predictor variables on species distributions throughout the study site in winter 2015/16. 167

Table 6.3. Effect of image pixel diversity (as a proxy for fishing intensity) on feeding rate and intake rates in each species. Results represent outputs of best-fit quasi-poisson, gamma or negative binomial GLMs. 171

Table 6.4. Estimated daily intake rates of the three study species during winter 2015/16. The ‘lower’ and ‘upper’ columns reflect the minimum and maximum predicted intake values from the model fit across all fishing intensities. Minimum and maximum values are provided based on the highest and lowest published assimilation efficiencies for benthic prey taxa. Oystercatcher consume all prey without the shell and therefore the minimum and maximum values are the same (i.e. assimilation efficiency is unchanged). Daily energetic requirements are also presented as field metabolic rates (FMR) calculated from published equations. 173

Table 7.1. Parameters included in the Poole Harbour shellfishing model. 189

Table 7.3. Characteristics of the patches included in the Poole Harbour shellfish model. 192

Table 7.4. Start of winter numerical density of shellfish prey in each size class included in the Poole Harbour model. 193

Table 7.5. Start of winter flesh content (g AFDM) of shellfish prey in each size class included in the Poole Harbour shellfish model. 194

Table 7.6. Tests of the Poole Harbour oystercatcher model. The sources for observations are given at the foot of the table. 197

Table 7.7. Effect of increasing shellfish landings (tonnes removed per year) on responses in the Poole Harbour oystercatcher across a modelled winter.....	200
Table 8.1. Methods of data collection and monitoring used in this research, the type of data collected and its practical application for management.	222

List of Appendices

Appendix 1. Supplementary material to Chapter 2: Invertebrate diets of common waterbird species and studies included and excluded from analysis.....	273
Appendix 2. Supplementary material to Chapter 3 Impacts of a novel shellfishing gear on macrobenthos in a marine protected area: pump-scoop dredging in Poole Harbour, UK.....	288
Appendix 3. Supplementary material to Chapter 6: Shorebird distribution and feeding rates in relation to shellfish dredging: insights from Poole Harbour, UK....	299

Abbreviations

AFDM	Ash-Free Dry Mass
AMBI	AZTI Marine Biotic Index
ANOVA	Analysis of Variance
BACI	Before-After-Control-Impact
BEQI	Benthic Ecological Quality Index
BO2A	Benthic Opportunist Annelids Amphipods
BSA	Bird Sensitive Area
BTO	British Trust for Ornithology
CAP	Canonical Analysis of Principal Coordinates
CBD	Convention on Biological Diversity
CD	Chart Datum
CPUE	Catch per Unit Effort
D-SLR	Digital Single-Lens Reflex
EBM	Ecosystem-based Management
EC	European Commission
EEC	European Economic Community
EMS	European Marine Site

EU	European Union
FAO	Food and Agriculture Organisation
FiSAT	Fish Stock Assessment Tool
GIS	Geographic Information Systems
GLM	Generalised Linear Model
HD	High Definition
HM Government	Her Majesty's Government
IBM	Individual-based Model
ICES	International Council for the Exploration of the Sea
JNCC	Joint Nature Conservation Conservancy
LCT	Lower Critical Temperature
LiDAR	Light Detection and Ranging
LOI	Loss on Ignition
MBES	Multi-beam Echo Sounder
MCZ	Marine Conservation Zone
MDS	Multi-dimensional Scaling
MEA	Millennium Ecosystem Assessment
MIDAS	Met Office Integrated Data Archive System

MMO	Marine Management Organisation
NE	Natural England
NNR	National Nature Reserve
PERMANOVA	Permutational Analysis of Variance
PRIMER	Plymouth Routines in Multivariate Ecological Research
RPA	Remotely Piloted Aircraft
SAC	Special Area of Conservation
SIFCA	Southern Inshore Fisheries and Conservation Authority
SIMPER	Similarity Percentage
SPA	Special Protection Area
SSSI	Site of Special Scientific Interest
UAS	Unmanned Aerial System
UAV	Unmanned Aerial Vehicle
UK	United Kingdom
VMS	Vessel Monitoring System
WeBS	Wetland Birds Survey

1. Introduction

1.1 An Introduction to Intertidal Ecosystems: Conservation Importance and Ecosystem Services

Intertidal systems form where the marine and terrestrial environments meet, extending from the lowest astronomical tide to the upper limits of the shore. Submerged at high tide and exposed to the air at low tide, intertidal areas are unique habitats and the organisms that occupy these environments must be highly adapted and tolerant of challenging and dynamic environmental conditions including periodic desiccation and large fluctuations in temperature and salinity (Underwood, 1981; Underwood and Jernakoff, 1984; Kaiser *et al.*, 2011). The ease of access to intertidal habitats has resulted in decades of observations and experimental manipulations being conducted in these areas that have greatly contributed to ecological theory (Paine, 1977). Intertidal areas are of significant conservation importance, from both an ecological perspective and with regards to the provision of valuable ecosystem services that humans derive. Ecologically these areas can be highly productive, with primary productivity supporting benthic invertebrate communities that sustain numerous and diverse species assemblages at higher trophic levels, including fish, birds and mammals that are of conservation importance (Kaiser *et al.*, 2011). Many intertidal areas are legally protected to preserve these interests.

These habitats and associated species also provide important ecosystem services such as carbon sequestration (Tang *et al.*, 2011), coastal protection (Scyphers *et al.*,

2011), water quality regulation and nutrient cycling (Nelson *et al.*, 2004), and fish nursery grounds (Harding and Mann, 1999; Scyphers *et al.*, 2011), as well as supporting numerous other economically important activities. Coastal areas are becoming increasingly heavily populated, supporting vital industries such as shipping, transport and significant inshore fisheries and aquaculture of commercially important species. These areas also contribute to local economies by attracting visitors for recreation (Miller and Auyong, 1991) and wildlife watching (Davenport and Davenport, 2006).

The multiple uses of the coastal and intertidal zone must be considered alongside other global pressures on marine and coastal ecosystems that result in complex and varied impacts. In coastal areas pressures can arise from terrestrial or marine sources, and locally within an area or from distant regions (Browman and Stergiou, 2005). Habitat-destruction and fragmentation (Fahrig, 2003), recreational disturbance (Anderson, 1995) the introduction of invasive species (Molnar *et al.*, 2008), climate change and ocean acidification (Hoegh-Guldberg and Bruno, 2010), pollution (Clark *et al.*, 1989), and unsustainable resource use and overexploitation (Kropp *et al.*, 2005) all threaten the conservation of biodiversity, globally and locally. Such varied pressure sources require an integrated management approach and consideration for cumulative effects to ensure sustainability. In particular, intertidal fishing activities have the potential to affect trophic interactions and disrupt intertidal and estuarine food-webs, removing or reducing the abundance of key target and non-target taxa that perform critical functions in the transfer of energy from the benthic environment to higher trophic levels (Raffaelli and Hall,

1996; Gili and Coma, 1998), and support many of the ecosystem services derived by human society.

1.2 Benthic Impacts of Intertidal Bottom-Contact Fishing

Fishing activities represent one of the largest sources of anthropogenic disturbance to marine ecosystems. In intertidal areas, the majority of the fishing industry involves the harvesting of benthic invertebrates and shellfish in particular. These harvesting activities range from small-scale hand collection and bait digging for personal use to the commercial dredging of shellfish using bottom-contact fishing gears. Bottom-contact fishing is the most globally widespread source of human disturbance to the seabed (Sciberras *et al.*, in review), with a quarter of all global seafood landings from 2011 to 2013 being caught by bottom-trawling (FAO, 2016). These gears are used to target benthic or demersal species living on or within the seabed (Jennings and Kaiser, 1998). In order to harvest such species these gears must necessarily physically interact with the seabed through being towed along the substrate, such as trawling, or being dragged through it, as with dredging. As a result the biological impacts of these gears may be severe compared with other pelagic gears, reducing benthic diversity, abundance, biomass, and causing a change in overall benthic community structure (Dayton *et al.*, 1995; Jennings and Kaiser, 1998; Auster and Langton, 1999; Collie *et al.*, 2000; Kaiser *et al.*, 2006).

Gears that penetrate the sediment more deeply have more dramatic impacts on benthos (Hiddink *et al.*, 2017) and larger, slow-growing species are more vulnerable to bottom-contact fishing gears. Benthic communities that have historically been characterised by such species may demonstrate a shift to more fast-growing

opportunistic species, such as amphipods and polychaetes following fishing disturbance (Gilkinson *et al.*, 2005; Sciberras *et al.*, in review). Impacts are not limited to target species, with density and biomass of non-target fauna also demonstrating significant changes (Collie *et al.*, 2000; Hiddink, 2003; Kaiser *et al.*, 2006; Kraan *et al.*, 2007). While numerous meta-analyses of the impacts of bottom-fishing have been carried out (Collie *et al.*, 2000; Kaiser *et al.*, 2006; Hiddink *et al.*, 2017, Sciberras *et al.*, in review), changes in broad-scale ecosystem function under different levels and gradients of fishing effort are difficult to quantify.

Due to the direct interaction with the seabed, bottom-contact fishing also elicits physical impacts. These interactions can be characterised as either geotechnical, as a result of mechanical interaction between seabed and fishing gear, or hydrodynamic, due to the turbulence and mobilisation of sediments into the water column (O'Neill and Ivanovic, 2015). Geotechnical interactions can leave significant scarring up to depths of 30cm through 'ploughing' of the seabed (Dayton *et al.*, 1995; Kraan *et al.*, 2007), while the hydrodynamic interaction can cause a winnowing of finer sediments that are lost following resuspension (Pranovi *et al.*, 1998; Palanques *et al.*, 2014; Martin *et al.*, 2015). Over time, repeated interactions between benthic habitats and fishing gear leads to a coarsening of sediment and a loss of habitat complexity. The magnitude and scale of these physical impacts is determined by the type of fishing (which is itself determined by the species being targeted) and the habitat and local environmental conditions (Kaiser *et al.*, 2001, Spencer *et al.*, 1998; Hall, 1994).

Subsequent recovery of the habitat depends heavily on physical processes such as sediment transport and suspended sediment concentrations and overlying hydrodynamic conditions (Spencer *et al.*, 1998; Hall and Harding, 1997; Kaiser *et al.*, 2001; Dornie *et al.*, 2003). There is therefore considerable variation in recovery rates between habitats. Habitats subject to high levels of natural disturbance with unconsolidated sediments and high sediment loads may recover within days, while in low energy, soft-sediment habitats, impacts can persist for much longer, over months or years (Collie *et al.*, 2000; Kaiser *et al.*, 2006; Hiddink *et al.*, 2017).

Biological recovery is mediated by much the same processes as outlined above, as faunal recolonisation first requires recovery of the habitat (Ferns *et al.*, 2000). Benthic habitats support resident fauna with life-history adaptations suited to prevalent environmental conditions (Kaiser *et al.*, 2001). Infaunal assemblages found in naturally dynamic environments with unconsolidated sediments are likely to be adapted to regular disturbance, and fishing disturbance within the limits of natural variation may not result in significant ecological impacts (Kaiser *et al.*, 1998, Hall, 1994). Recovery of the community to pre-fishing conditions in habitats dominated by numerous fast-growing species may therefore occur over relatively short periods through recolonisation from surrounding areas (Collie *et al.*, 2000, Kaiser *et al.*, 2006). In more stable habitats exposed to fewer disturbance events, fishing may result in more severe initial impacts and a longer recovery period (Jennings and Kaiser, 1998). These communities may be dominated by less mobile, longer-lived sessile or tube-dwelling species for which recolonisation is dependent on larval supply and recruitment of juveniles, which may take many months or even

years (Beukema, 1995; Collie *et al.*, 2000; Kaiser *et al.*, 2006; Hiddink *et al.*, 2017). Fishing-induced physical changes such as the loss of silt and finer sediments may have subsequent implications for larval settlement and hence future stocks (Piersma *et al.*, 2001).

An important concept in both fisheries management and broader environmental management is the idea of 'shifting baselines' (Pauly, 1995), which is receiving increasing recognition when considering sustainable use of marine natural resources. 'Shifting baseline syndrome' is defined as a gradual decline or shift in baseline conditions, often over generations, which leads to an inaccurate assessment of healthy ecosystem condition. Pauly (1995) first identified and defined this concept with regards to fisheries management, specifically assessments of 'baseline', pre-exploitation population sizes. The concept is now also applied in wider marine conservation, particularly in assessments of the management of protected areas, which, as a result of shifting baselines, may designate already degraded and exploited systems for protection in their current state. Managers should therefore be vigilant towards shifting baselines, and environmental legislation often requires management to aim to "maintain *or restore*, at favourable conservation status, natural habitats and species" (European Habitats Directive, 92/43/EEC), to strive to not just maintain sites but to restore them to historical levels of ecological quality and biodiversity. The extent to which this is implemented in reality however may vary as management aims to reconcile the interests of nature conservation with the interests of commercial activities, of which fishing is a significant example.

1.3 Impacts of Harvesting on Bird Predators

Waterbirds (comprised of waders (Order Charadriiformes) and waterfowl (Order Anseriformes)) are important components of intertidal and estuarine ecosystems (Hill *et al.*, 1993; Stroud *et al.*, 2004) and are protected under numerous and extensive national and international legislation such as the European Birds Directive (2009/147/EC). Both migratory and resident bird species rely on the invertebrate communities in these areas as critical prey resources, to fuel annual migrations between wintering and breeding grounds and to maintain body fat reserves during the winter months (Goss-Custard *et al.*, 2004; Durell *et al.*, 2006a). Overwintering birds, especially long distance migratory species, use areas of various food quality during the non-breeding season and migration. Their energetic requirements therefore vary throughout the year, with ecological conditions in non-breeding and staging grounds having potentially significant impacts on migration and future reproductive success (Baker *et al.* 2004). Survival during migration and winter months may be more important for the long-term survival of wader populations than the productivity at breeding grounds (Saether *et al.*, 1996; Piersma and Baker, 2000).

Coastal bird populations utilise the same intertidal areas that are targeted by humans for commercial or personal purposes and often target the same species (Hanekom and Baird 1992; de Boer and Longamane 1996; Norris *et al.*, 1998; Shepherd and Boates 1999). This spatial overlap and potential direct competition for resources means that waterbird populations are particularly vulnerable to the impacts of coastal harvesting activities, with excessive shellfishing causing declines

in the availability of key prey species (Shepherd and Boates, 1999; Ens, 2006, Kraan *et al.*, 2007). Such food shortages reduce habitat quality and create suboptimal feeding conditions, potentially increasing feeding competition and resulting in reduced individual body condition and increased mortality in shorebirds when their energetic requirements cannot be met (Durell *et al.*, 2006b).

Different wader species forage on prey of various taxonomic groups and size classes, with species' diets determined by factors such as bill morphology, digestive capacity and risk of bill damage (Goss-Custard *et al.* 2006; Rutten *et al.*, 2006). Some wader species are more generalist feeders, consuming prey of a variety of groups and size classes, while others are more specific in their feeding habitats. Along with the reductions in the abundance, density and overall biomass of target and non-target species of the fishery as described above, changes to the size frequency distributions of harvested species may occur due to size selective fishing techniques (Humphreys *et al.*, 2007; Wijnhoven *et al.*, 2011), as harvesting generally removes larger and therefore older individuals from a population. Such 'regime shifts' in the abundance or size of invertebrate communities could therefore reduce the available prey suitable for consumption (Cayford, 1993; Bowgen *et al.*, 2015), with subsequent population impacts to shorebirds (Atkinson *et al.*, 2003; Ens *et al.*, 2004; Atkinson *et al.*, 2010). Birds can compensate for reduced feeding conditions by altering the structure, size and function of digestive organs and subsequently their digestive capacity relatively rapidly to adjust to local conditions (Piersma and Drent 2003). Red Knot *Calidris canutus*, for example, can rapidly and reversibly alter their gizzard size up to 50% within a week, eliciting energetic benefits by increasing the

efficiency of shell-crushing (Dekinga *et al.* 2001). Birds may also attempt to feed on prey of different sizes or species than they would under optimal feeding conditions, although given the impacts of harvesting on non-target species (Piersma *et al.*, 2001; Kraan *et al.*, 2007) and the fact that many invertebrates burrow deeper in the sediment during winter months and lose 30-60% of body mass (Zwarts and Wanink, 1993), such compensation may not be sufficient.

A recent modelling study showed the effects of regime shifts in invertebrate prey on waders in Poole Harbour, UK (Bowgen *et al.*, 2015). Curlew and black-tailed godwits, examples of large waders with limited ability to compensate for a loss of prey, were two of the first species affected, resorting to feeding on earthworms in suboptimal terrestrial habitats. Other more omnivorous species, such as oystercatcher, appeared able to tolerate prey reductions by switching feeding mode, surviving multiple scenarios of regime shifts (Bowgen *et al.*, 2015). This modelling study demonstrates the importance of the larger prey items in a wader's diet. The largest reductions in bird numbers supported by the system resulted from the loss of the largest invertebrates, which is often a result of overharvesting (Olive, 1993; Goss-Custard *et al.*, 2004). Bowgen *et al.* (2015) showed that redshank switch from feeding on worms to a more crustacean dominated diet, which resulted in a less dramatic decline in numbers than other species, demonstrating the importance of the ability to compensate in overwinter survival in response to changes in prey availability.

Figure 1.1 presents a summary of the mechanisms and impact pathways by which intertidal fishing impacts benthic communities and subsequently bird predators at both the individual and population level.

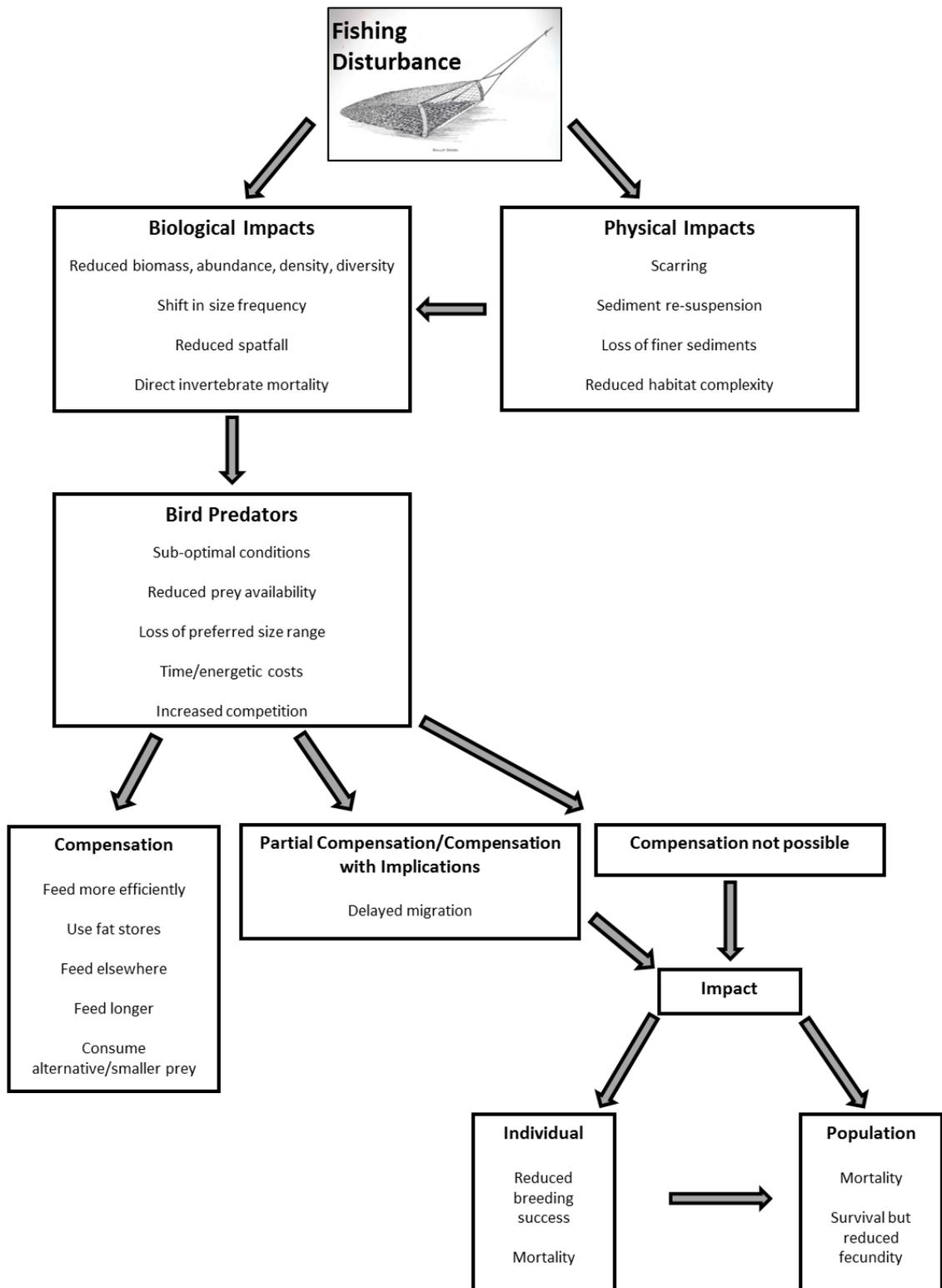


Figure 1.1. Conceptual diagram of the potential mechanisms by which intertidal fishing disturbance can impact upon coastal bird populations.

1.4 Ecosystem-Based Management of Human Activities

As mentioned, fishing is just one of a number of goods and services that human society derives from the marine environment that impact upon marine biodiversity and ecosystems and requires careful management. The ecosystem approach to management or ecosystem-based management (EBM) has been at the forefront of marine planning and management of human activities in recent years. This drive has largely been in response to increasing warnings that current trends in global biodiversity and ecosystem health are leading society to a number of tipping points in ecosystem function, resulting in large-scale reductions in ecosystems' ability to provide essential services that society derives (Long, 2012). Definitions of EBM are numerous and varied, from both scientific and legal perspectives (Long, 2012), although most share the common overarching principles laid out by the Convention on Biological Diversity (CBD). The CBD describes EBM as "a strategy for the integrated management of land, water and living resources that promotes conservation and sustainable use in an equitable way", a strategy that results in the fair sharing of all benefits that arise from the use of natural resources (CBD, 2004; JNCC, 2014). The International Council for Exploration of the Seas (ICES) defines EBM as an integrated management approach to human activities that is based on "the best scientific knowledge about the ecosystem and its dynamics...achieving sustainable use of ecosystem goods and services and maintenance of ecosystem integrity" (Rice *et al.*, 2005). This approach therefore aims to maintain ecosystem function and resilience to allow the natural environment to respond to human-induced changes. In doing so this approach must recognise the multiple interactions between human activities and species and habitats (MEA, 2005; HM Government,

2011). The ecosystem-based approach is becoming increasingly used in fisheries management, aiming to achieve long-term sustainable fishing while maintaining healthy ecosystem functioning (Garcia and Cochrane, 2005).

The nature conservation interests of coastal habitats are often recognised at an international level through the designation of European Natura 2000 sites, including Special Protection Areas (SPAs) and Special Areas of Conservation (SACs), under the European Birds (79/409/EEC) and Habitats (92/43/EEC) Directives respectively. These are often alongside national designations such as Marine Conservation Zones (MCZs), Sites of Special Scientific Interest (SSSIs) and National Nature Reserves (NNRs). European Union Member States are obligated to maintain Natura 2000 sites in 'favourable condition' for the features for which they receive designation, such as internationally important bird populations (and their supporting habitats) under the EU Birds Directive or a habitat of conservation interest under the EU Habitats Directive. In protected sites in particular EBM is therefore key to conserving the protected features of a site and minimising adverse effects of commercially important activities on the ecosystem as a whole.

1.5 Case Study: The Dutch Wadden Sea

Numerous studies have documented the ecosystem impacts of harvesting, although perhaps the most well-known example of over-exploitation of shellfish leading to a population crash in coastal bird populations is the case of the Dutch Wadden Sea cockle and mussel fisheries in the 1980s and 1990s. The Dutch Wadden Sea is a 2400km² area of intertidal sand and mudflats, barrier islands and shallow coastal sea in the south east of the North Sea in northwest Europe and the vast intertidal flats have historically supported significant mussel and cockle fisheries. In the late 1980s however conflict began to arise between conservationists and fishermen following mass mortality of molluscivorous birds in the Wadden Sea, particularly oystercatchers *Haematopus ostralegus* and eider *Somateria mollissima*.

Until the early 1990s each fishery was managed under an open access regime (Steins, 1999), with limitations only applied to when in the year harvesting could take place and what sizes of shellfish could be harvested. By the late 1980s however intertidal mussel beds in the Wadden Sea had almost completely disappeared (Ens *et al.*, 2004) following intense harvesting as a seed fishery for subtidal beds (Smit *et al.*, 1998). Widespread suction dredging for cockles occurred during the same period. This, coupled with severely low spatfall of both species in the early 1990s due to severe winters, a natural feature of wild shellfish populations (Beukema, 1982; Beukema *et al.*, 1993), led to a reduction in available food for molluscivorous bird species. A coarsening of sediments in the area led to further reductions in bivalve recruitment in the 1990s (Piersma *et al.*, 2001), which ultimately contributed to the mass mortality of oystercatcher and eider populations and an

increase in the number of birds that preferentially eat worms in the region (Camphuysen *et al.*, 2002; van Roomen *et al.*, 2005; Weijerman *et al.*, 2005; Piersma, 2007; van Roomen *et al.*, 2012). By 1992/93 eider numbers in the Wadden Sea were around 64,000, 50% lower than mean numbers between 1970 and 1990 (Smit *et al.*, 1998). Oystercatcher numbers declined from around 250,000 to 150,000 over a 15-year period from 1986 (Verhulst *et al.*, 2004).

These dramatic shifts in ecosystem health and function prompted changes to fisheries management within the Wadden Sea, introduced in 1993. These new management measures are centred on three key principles of areas closed to shellfishing, preservation of sufficient food stocks for bird populations and cooperative management (Ens *et al.*, 2004). The permanently closed areas aim to restore key habitats, whilst the policy of preserving sufficient food aims to restore numbers of molluscivorous birds in the region to those observed in the 1980s (Ens *et al.*, 2004). This requires careful management during years of low shellfish stocks. To allow for cooperative management the government partly delegates responsibility for policy implementation to the fisheries sector, allowing self-regulation with regards to policy enforcement and penalties (Ens *et al.*, 2004).

The new management measures are informed by on-going research and monitoring within the Wadden Sea, including reviews of the causes of mortality and food availability. This monitoring has since driven amendments to the management regime including additional closures and reservation of subtidal food stocks following further eider mortality and changes to mussel culture practices (Ens *et al.*,

2004). The case of the Wadden Sea fisheries highlights the need for an integrated, adaptive and cooperative approach to ecosystem management.

1.6 Individual-Based Models

A useful tool when considering the effects of environmental change on wildlife populations is the use of agent-based or individual-based models (IBMs), which allow the prediction of population-level changes through the use of foraging and game theory (Stillman *et al.*, 2001). IBMs work on the principle that individuals within a population are the building blocks of an ecosystem (Grimm and Railsback, 2005), simulating an environment in which individuals interact with the available resources in the modelled system (DeAngelis and Mooij, 2005). Within the modelled system each individual of a given species is modelled on the same principles, while other state-variables and behaviours in the model vary across given statistical distributions (Hogeweg and Hesper, 1990; DeAngelis and Mooij, 2005). Across these statistical distributions, individuals with the same modelled principles will differ in their behaviours while making decisions in order to maximise their perceived fitness in the environment. The behaviours of individuals are then validated using real-world observations (McLane *et al.*, 2011).

IBMs of shorebird populations have been applied to a number of sites around the UK in recent years in relation to disturbance, habitat loss, shellfishing and habitat quality (Stillman *et al.*, 2001; Stillman *et al.*, 2003; Caldow *et al.*, 2004). In these studies, models successfully predicted the effects of environmental change on overwinter survival rates in various bird species. These models allow the prediction of winter mortality rates and can identify whether the conservation objectives of a

site will be met. In recent years studies have also used IBMs to quantify the food requirements of shorebird populations, in order to inform fisheries management (Stillman *et al.*, 2001; Goss-Custard *et al.*, 2004; Durell *et al.*, 2006; Stillman *et al.*, 2010). For example, Stillman *et al.* (2010) concluded that in order for 100% of the oystercatcher population at Burry Inlet, UK to be maintained over a winter, at least three times the amount of food that the birds actually consume would be required, due to the effects of competition and interference. Given the history of conflicts between commercial fishing interests and nature conservation in coastal sites, IBMs are potentially a key tool in implementing the EBM to inshore and intertidal fisheries management.

1.7 Evidence Gaps

Large amounts of research have been carried out on the environmental impacts of fishing, the wider ecosystem impacts and the behavioural ecology and conservation of shorebird populations in relation to environmental disturbance. However, gaps in current understanding remain.

1.7.1 Impacts of Intertidal Fishing

While many individual studies have described the impacts of local harvesting methods on intertidal benthic fauna, the magnitude of impacts and recovery times vary drastically between gear types, habitats and benthic taxa. A number of meta-analyses of global fishing impacts in all habitats exist in the published literature (Collie *et al.*, 2000; Kaiser *et al.*, 2006; Hiddink *et al.*, 2017), although a comprehensive analysis of the impacts of the many gear types used in intertidal habitats specifically, and particularly on key prey groups for coastal bird populations

of international conservation importance, is lacking. Such an analysis would provide valuable information to environmental managers and policy-makers.

1.7.2 Non-Native Fisheries and Impacts of Novel Gears

One of the largest threats to global biodiversity is the introduction of non-native species (Molnar *et al.*, 2008). Introduced species occur in many intertidal systems globally, having been introduced incidentally or intentionally (Garcia-Berthou *et al.*, 2005). In some cases these introductions result in commercially harvestable populations that become important to the local economy and support sustainable fisheries. The introduced razor clam *Ensis directus*, for example, is harvested from the lower intertidal using a hydraulic dredge in the Dutch Wadden Sea (Marine Stewardship Council, 2017). The razor clam is native to the western Atlantic, although was introduced to the North Sea in the 1970s and the fishery has now been certified as sustainable by the Marine Stewardship Council. The types of gear and methods used to harvest intertidal invertebrates vary greatly from place to place, and are often developed by fishermen in response to local factors such as local environmental conditions and the distribution and life-history of the target species. When local fisheries arise from non-native introductions, novel gear types may be developed (Pranovi *et al.*, 2004) and the impacts on the local environment and benthic communities associated with their use must be considered, in addition to the ecological impacts of species introductions.

1.7.3 Quantifying Intertidal Fishing Disturbance

One of the most challenging aspects of assessing impacts of fishing is accurately quantifying the scale and intensity of disturbance. Relating any observed impacts to

fishing effort is necessary to accurately understand the nature of disturbance on marine ecosystems, although estimates of fishing effort are difficult to obtain and may not be accurate. In offshore fisheries, fishing vessels over 12m in length are required to carry a Vessel Monitoring System (VMS) that automatically sends information regarding the vessel's position, course and speed to a monitoring centre. In inshore areas and intertidal fisheries however there is no such requirement and data on fishing effort is often sparse or lacking completely, although trials of inshore-VMS have been conducted for regulating fishing within a marine protected area in Lyme Bay, UK (MMO, 2016). In intertidal areas the affected habitat is exposed at low water, and the physical extent of fishing may be evident in scarring of the sediment. In such cases, new and emerging technologies such as aerial drones, or unmanned aerial systems (UAS), and remote sensing methods may assist in quantifying fishing effort in remote areas of low accessibility.

1.7.4 Response of Shorebird Populations to Fishing Disturbance

A large amount of research has been undertaken on the impacts of environmental change on coastal bird populations, from recreational disturbance (Stillman *et al.*, 2007) to sea level rise (Galbraith *et al.*, 2002) and fishing (Atkinson *et al.*, 2010) that has identified the general relationships between sources of environmental disturbance and conservation of bird populations. Locally, however, the interactions between such disturbances and shorebird populations can vary greatly. A number of published studies have documented the impacts of shellfishing activities on coastal bird populations, and on oystercatchers *Haematopus ostralegus* in particular (Atkinson *et al.*, 2003; Goss-Custard *et al.*, 2004; Atkinson *et al.*, 2010). However,

little work has been done on the survival of oystercatchers that rely on non-native shellfish prey for overwinter survival (Caldow *et al.*, 2007) and whether the impacts of novel gears designed to harvest such shellfish differ from other more widespread methods.

1.8 Research Aims and Thesis Structure

Given the gaps in the current understanding of the mechanisms by which fishing disturbance impacts intertidal habitats and how these impacts may elicit higher-level trophic impacts to the wider ecosystem, the aims of this PhD research are:

1. Assess the impacts and recovery trends of various intertidal harvesting methods on benthic invertebrate communities and key prey groups for bird predators;
2. Investigate the impacts of a novel, non-native fishery on intertidal habitats, target and non-target species within a marine protected area;
3. Assess the efficacy of remote sensing techniques in accurately quantifying the spatial extent and intensity of intertidal fishing disturbance;
4. Utilise field surveys and individual-based models to predict the functional response and overwinter survival of a shorebird population within an operational dredge fishery for a commercially valuable introduced bivalve in a marine protected area.

In order to meet the aims of the research, this thesis follows the following structure:

Chapter 1 – Introduction to the research topic and research aims and objectives.

Chapter 2 – Intertidal invertebrate harvesting: a meta-analysis of impacts and recovery in an important waterbird prey resource.

Chapter 3 – Impacts of a novel shellfishing gear on macrobenthos in a marine protected area: pump-scoop dredging in Poole Harbour, UK.

Chapter 4 - Remote sensing methods as a tool for quantifying the spatial extent and intensity of shellfish dredging in a marine protected area.

Chapter 5 - Shorebird distribution and feeding rates in relation to shellfish dredging: insights from Poole Harbour, UK.

Chapter 6 - Population dynamics of the commercially harvested non-native Manila clam *Ruditapes philippinarum* in Poole Harbour, UK.

Chapter 7 - Modelling overwinter survival of Eurasian oystercatcher *Haematopus ostralegus* in an operational shellfishery: insights from Poole Harbour, UK.

Chapter 8 – Discussion and Conclusions.

2. Intertidal invertebrate harvesting: a meta-analysis of impacts and recovery in an important shorebird prey resource

2.1 Introduction

Commercial harvesting of marine invertebrates in soft sediment intertidal areas often comes into conflict with nature conservation interests, in particular the conservation of nationally and internationally important populations of shorebirds (orders Anseriformes (ducks and geese e.g. common shelduck *Tadorna tadorna*, common eider *Somateria mollissima*) and Charadriiformes (waders e.g. common redshank *Tringa tetanus*, Eurasian oystercatcher *Haematopus ostralegus*)) (Camphuysen *et al.*, 1996; Auster and Langton, 1999; Camphuysen *et al.*, 2002; Atkinson *et al.*, 2003; Ens *et al.*, 2004). Populations of these birds heavily rely on the invertebrate prey resources in these areas during the non-breeding season and may compete with fishermen for the same resource (Ens *et al.*, 2004; Roberts and Jones, 2009).

Shorebirds and waterfowl rely on intertidal prey resources to maintain body condition over winter and fuel annual migrations between wintering, staging and breeding grounds (Goss-Custard *et al.*, 2004; dit Durell *et al.*, 2006). Shortages in suitable intertidal invertebrate prey may create suboptimal feeding conditions, leading to reduced individual body condition and increased mortality in shorebirds when their energetic requirements cannot be met (dit Durell *et al.*, 2006). Different bird species forage on prey of various taxonomic groups and size classes, determined by factors such as bill morphology, digestive capacity and risk of bill damage (Goss-Custard *et al.* 2006; Rutten *et al.*, 2006). Some wader species are

more generalist feeders, consuming prey of a variety of groups and size classes, while others are more specific in their feeding habits. The preferred prey and winter intertidal habitat of common European bird species are listed in Table A1.1 in Appendix 1.

Intertidal harvesting may remove or damage non-target species (Jennings and Kaiser, 1998; Kraan *et al.*, 2007), decrease benthic productivity (Kaiser *et al.*, 2002) and elicit physical changes to seabed characteristics with associated changes to benthic community composition (Dayton *et al.*, 1995; Jennings and Kaiser, 1998; Kaiser *et al.*, 2002). As a consequence, reductions in prey abundance, density, quality and size (Dayton *et al.*, 1995; Collie *et al.*, 2000; Kaiser *et al.*, 2006) are widely reported, with well-documented case studies of mass mortality in shorebird populations as a result of human harvesting activities (Ens *et al.*, 2004; Goss-Custard *et al.*, 2004; Atkinson *et al.*, 2010). More gradual and sub-lethal changes in shorebird assemblages have also been reported on individual sites, with numbers of worm-eating birds increasing following shellfish removal (van Roomen *et al.*, 2005, Atkinson *et al.*, 2010).

While ecosystem-based management (EBM) of fisheries is a well-accepted concept it is more usually considered in the context of large-scale offshore fisheries (Pikitch *et al.*, 2004; Möllman *et al.*, 2014;). Intertidal fishing is widespread in global coastal environments, ranging from small-scale hand collection and bait digging to commercial exploitation through dredging and other mobile harvesting gear (Kaiser *et al.*, 2001). Of an overall annual value of approximately US\$129 billion (£100 billion) from global marine fisheries (FAO, 2014), the value of the global baitworm

industry alone has recently been calculated as almost £6 billion, with calls for management of these resources commensurate to other fisheries (Watson *et al.*, 2017). The ease of access to the resource in such fisheries requires careful management for sustainability. In addition to burrowing fauna, species of commercial importance in intertidal areas may include biogenic reef-building species such as oysters *Crassostrea* spp. (Beck *et al.*, 2011; Scyphers *et al.*, 2011) and mussels *Mytilus* spp. (Buschbaum *et al.*, 2008) that collectively provide important ecosystem services such as carbon sequestration (Tang *et al.*, 2011), coastal protection (Scyphers *et al.*, 2011), water quality regulation and nutrient cycling (Nelson *et al.*, 2004) and fish nursery grounds (Harding and Mann, 1999; Scyphers *et al.*, 2011).

Many intertidal areas that support commercially important stocks of invertebrates are low energy environments with well-consolidated soft sediments. Benthic communities in these habitats may be vulnerable to physical disturbance from mobile fishing gear including sediment re-suspension (Dayton *et al.*, 1995; Stokesbury *et al.*, 2011) and smothering (McLachlan *et al.*, 1996; Norkko *et al.*, 2002) and may experience much longer recovery times than more dynamic sediments and their associated fauna (Wynberg and Branch, 1994; Kaiser *et al.*, 1998; Collie *et al.*, 2000; Dornie *et al.*, 2003). A previous meta-analysis focused on all marine habitats (Kaiser *et al.*, 2006) demonstrated that intertidal habitats are severely affected by fishing activities that remove key ecosystem engineers such as clams and shrimp (Beukema 1987; Pauly, 1995; Handley *et al.*, 2014), inducing

regime shifts from larger, slow growing species of low fecundity towards more opportunistic, fast-growing and smaller biota.

Ecosystem-based management seeks to manage human activities while acknowledging the interactions between all components of an ecosystem, maintaining ecosystem function and the provision of services (Pikitch *et al.*, 2004). To achieve an EBM approach to the management of intertidal ecosystems subjected to harvesting activities, it is therefore necessary to understand the consequences of harvesting on other components of the system. EBM has previously been implemented in this regard following collapses of Eurasian Oystercatcher, *Haematopus ostralegus* and common eider, *Somateria mollissima* populations in the Dutch Wadden Sea (Camphuysen *et al.*, 2002; Verhulst *et al.*, 2004), and tools such as individual-based models can help predict population effects and inform management decisions (Atkinson *et al.*, 2003; Stillman *et al.*, 2003). The recent certification of the Ben Tre hand clam fishery in Vietnam by the Marine Stewardship Council demonstrates an example of sound EBM of an intertidal fishery (Marine Stewardship Council, 2016).

The objective of this study was to undertake a meta-analysis to quantify the effect of intertidal harvesting activities on benthic shorebird prey. Meta-analysis is becoming increasingly popular as a tool for ecologists (Koricheva *et al.*, 2013) to answer questions at a broader scale than is possible in a single study (Collie *et al.*, 2000), and to identify more generally applicable trends and relationships that might inform management decisions in a more statistically powerful way. This study therefore addresses the following research questions: 1) What is the immediate

response in invertebrate prey to intertidal harvesting in the first ten days following fishing? 2) How does the habitat and gear type used affect the magnitude of the response and does this vary between taxa? 3) Does the response differ for target vs. non-target species of the fishery? 4) What are the recovery trends in intertidal communities following harvesting disturbance?

2.2 Methods

2.2.1 Data Collection

Data were extracted from publications that were identified by following a systematic review protocol (Hughes *et al.* 2014). A total of 16 publications, comprising 38 separate studies on intertidal harvesting disturbance, met the inclusion criteria of this meta-analysis (Appendix Table A1.2). Inclusion criteria were: (i) the publication should be a study of the quantitative biological response in invertebrate communities to actual or simulated harvesting disturbance in intertidal habitats, along with information on control or pre-fishing conditions, (ii) information on the gear type and habitat type in which the study took place must be included and (iii) the study should report a mean value of the relevant biological metric, a measure of the variance, and the sample size. A further 18 studies were identified as relevant from the systematic review but excluded from data analysis because they did not meet the inclusion criteria (Appendix Table A1.3).

A “study” was defined as an individual manipulation or observation of the response of benthic communities to intertidal fishing. Factors such as the harvesting gear type, scale and extent of the disturbance, habitat type, geographic region, the taxonomic level (e.g. phylum, species or community) of the reported outcomes or

the sampling gear used are treated as predictor variables. When a publication reported results from, for example, experimental harvesting in two different habitats, these two different habitat treatments were considered as two separate “studies”. Habitats were differentiated according to the Folk sediment classification scheme (Folk, 1954). This was done based on information provided in the publication on the relative proportion of different particle size categories.

2.2.2 Response Variables and Effect Size

Studies reported a range of community metrics including species abundance, biomass, diversity indices, richness, evenness, primary productivity and the abundance of specific feeding traits (e.g. suspension feeders). However these were often not relevant to the research questions and did not occur with sufficient replication among our population of studies. Thus for the purpose of this paper we focus only on taxa abundance, biomass and diversity indices. Benthic invertebrate abundance and biomass are clearly key factors in determining prey availability and thus energetic intake rates in coastal shorebirds. Changes in diversity indices may indicate a shift in invertebrate community composition, with implications for shorebird assemblages that are often comprised of species that preferentially feed on different taxonomic groups. Furthermore, diversity provides an indication of the resilience of benthic ecosystems to environmental change (Folke *et al.*, 2004). The response in the Shannon-Wiener Index, Simpson’s Index and species richness were pooled for this analysis given that the direction of the response to fishing will be consistent across all measures (i.e. a lower value of each measure indicates a reduction in diversity).

The size of the effect for each response was calculated as the standardised mean difference in fished conditions when compared to control conditions, or Hedges' d , using

$$d = \frac{(X_1 - X_2)}{S_{within}}$$

where X_1 and X_2 are the sample means of the two groups (e.g. fished and unfished areas) and S_{within} is a measure of the within study variance:

$$\sqrt{\frac{(n_1 - 1)S_1^2 + (n_2 - 1)S_2^2}{n_1 + n_2 - 2}}$$

where n_1 and n_2 are the group sample sizes and S_1 and S_2 are the standard deviations of the two groups. All analyses were carried out within R Studio (Version 0.98.1062) and the R metafor package (Viechtbauer *et al.*, 2010).

2.2.3 Combining Effects

In most cases a study reported the response of multiple species to fishing disturbance. In order to assess impacts upon the benthic community as a whole, a "study-level" effect was calculated by combining the effect size (Hedges' d) for data from individual species reported within that study. The combined effect size for a study was calculated as the mean of the response across all species.

When calculating the variance of the study-level effect size, it must be considered that the response of each species to fishing disturbance in the study may not be wholly independent of one another. The level of correlation between the outcomes

must therefore be taken into account. The variance of the study-level effect size was calculated using

$$Var = \left(\frac{1}{m}\right)^2 \left(\sum Vi + \sum (r_{ij} \sqrt{Vi} \sqrt{Vj})\right)$$

where m is the number of outcomes reported within the study, Vi is the variance of the i th outcome and r_{ij} is the correlation between the outcomes with variances of Vi and Vj . Study-level variances may be calculated using $r = 1$ (assuming complete correlation) or $r = 0$ (assuming full independence). The former is likely to overestimate the variance and underestimate the precision, while the latter is likely to underestimate the variance and overestimate the precision (Sciberras *et al.*, 2013). In order to avoid the consequences of working with these extreme assumptions, $r = 0.5$ was used when combining effects.

An overall summary effect was then calculated as the mean effect size across all studies using a random-effects model; such that weight is assigned to each study as the inverse of its variance (i.e. 'study' is included as a random-effect and more weight is assigned to studies with less variance) (Borenstein *et al.*, 2009). When results of this model indicated significant heterogeneity between study-effect sizes, the effect of additional moderating variables added to the model (such as habitat, gear type, region etc.) was investigated.

2.2.4 Initial Impacts

In order to investigate the initial impacts of intertidal fishing disturbance, we combined data across 0 to 10 days after fishing. While using this method may mask some of the short-term variation in the effect of fishing during the first few days

after disturbance, it has the benefit of nullifying potential effect of scavengers on the measured responses and makes the dataset more balanced for analysis (Kaiser *et al.*, 2006). Once Hedges' *d* was calculated for all studies, a summary effect size at 0-10 days post-fishing was calculated using the methods described above. This summary effect size was first calculated as the mean across all taxa, before investigating the initial impacts on the main taxonomic groups in the data that represent key prey groups for coastal shorebirds in the intertidal. These included annelid worms, crustaceans and molluscs. Individual species effect sizes were also calculated for the common cockle (*Cerastoderma edule*, Cardiidae), Baltic tellin (*Macoma balthica*, Tellinidae), catworm (*Nephtys* spp., Nephtyidae), mudsnail (*Hydrobia ulvae* now *Peringia ulvae*, Hydrobiidae) and the spionid polychaete *Scoloplos* spp. (Spionidae).

2.2.5 Moderating Variables

Further analyses followed the methods used by Kaiser *et al.* (2006) in a global review of the impacts of bottom-fishing on benthic habitats to investigate in more detail the effect of other predictors on the effect size. This allowed for a more intuitive analysis of the dataset against the research questions, providing more relevant insights into the overall trends in intertidal harvesting impacts for environmental managers and policy-makers.

2.2.5.1 Habitat, Gear and Target vs. Non-target Species

In order to further investigate the response of effect modifiers (e.g. habitat, gear type, target vs. non-target species) a more simplistic ANOVA approach was used to test for differences in the magnitude of the initial effect (0-10 days post

disturbance) between groups. By calculating summary-effect sizes across studies as described above, such factors are lost from the analysis, and this ANOVA approach allows for a more workable and balanced dataset for testing further hypotheses.

2.2.5.2 Gear and Taxa Interactions

In order to generalise the sensitivity of different taxa to different gear types, fishing gears were grouped together and a classification tree was created through recursive partitioning. This was done to assess the immediate post-harvesting effect of different gear types on the abundance of different taxonomic groups.

2.2.5.3 Recovery Trends

An ANOVA approach was also used to investigate recovery patterns for each gear/habitat combination present in the data as it allowed for a comparison of the magnitude of the effect between time points since fishing. Only abundance data was available with sufficient replication for this analysis of recovery in gear/habitat combinations. We grouped data from 0-10 days post-fishing, 11-50 days, 51-500 days and > 500 days. This approach of categorising data, while resulting in the “loss of fine-scale variation in the response time to post-fishing” (Kaiser *et al.*, 2006), allows the differences in the response across these time periods to be identified more effectively. For this recovery analysis, we included data for all taxa present in each gear/habitat combination regardless of the direction of the initial response to harvesting, as to assess recovery only in those taxa that demonstrate a negative initial response would introduce selection bias and allow for artefactual evidence of recovery (Kaiser *et al.*, 2006). For each gear/habitat combination that showed an effect of time, we then re-analysed the data using linear regression with log+1

transformed time since fishing in days as a continuous variable. Analysis of covariance was first carried out for these data, and where no difference in the slope of the response between taxonomic groups was identified the data were pooled. Recovery may not always be linear, and in some cases a curvilinear relationship better fit the available data, in which case a generalised additive model was used to represent the recovery trend. In this analysis recovery was considered to occur at the point at which non-significance of the effect from control conditions is evident, equivalent to a 5% significance level test and rejecting the null hypothesis of no impact. Only a subset of the data reported changes in diversity and biomass and this was therefore integrated across all habitats, gears and taxa present in the data and analysed using the ANOVA approach described above to investigate initial impacts and subsequent recovery.

2.2.6 Analysis Notes

As Kaiser *et al.* (2006) discuss in great detail, from a purely statistical standpoint there are issues in the ANOVA analysis of our meta-database, not least a largely unbalanced dataset and non-independence of individual data points that are often derived from the same study. Strictly speaking, each study should contribute only a single data point to our analysis due to the inherent variation in habitats, gear types and geographic locations. However to introduce 'study' as a random effect into our ANOVA analyses to recognise this variation at the study level, while also appropriately accounting for gear, habitat, time and individual taxa responses would reduce the available degrees of freedom to a level at which no model could be constructed.

Although averaging the response across all taxa in our ANOVA introduces the problem of within-study correlations, it is preferred over reducing the data to a single response for each study. Consistent with Kaiser *et al.* (2006), a reduction in residual degrees of freedom to the magnitude of the number of studies would only occur if taxa were perfectly correlated, and in reality any within-study correlation will simply reduce the *F*-statistics' degrees of freedom to some extent compared to those quoted here.

Given such challenges, rather than constructing an unworkable model we have taken the somewhat optimistic approach of Kaiser *et al.* (2006) and we echo their caveats when interpreting our results and plots; although our methods may be viewed as statistically naïve, they allow for a more intuitive analysis for the reader and for policy-makers. Given these caveats, it is encouraged that emphasis should be placed on the higher-level trends and relative recovery patterns that this study identifies, which are unlikely to be affected by non-independence. With this in mind the number of observations from which mean responses are derived is indicated in each of our plots for context to aid the reader in interpreting results.

2.3 Results

2.3.1 Studies

The majority of studies that met the inclusion criteria were carried out in Northern Europe (Table 2.1), with most undertaken in the UK. Hand gathering comprised the majority (27 of 36) of the harvesting techniques investigated by the studies, with hand digging and hand raking the most commonly studied harvesting types (Table 2.1). This may be due to the fact that the use of hand gathering techniques, and

therefore the ease of studying these techniques, is relatively low cost and requires few resources, in addition to the logistical ease of carrying out these studies. Most studies focused on the use of fishing gears in sandy and muddy habitats. The dominance of these habitats in the dataset likely represents their geographic extent and the association of the target species with a specific habitat.

Table 2.1. Number of studies (n=38, from 16 publications) included in the analysis with regards to the region, gear type and habitat within each study. Habitat: (g)mS = gravelly/muddy sand; M = mud; mS = muddy sand; msG = muddy/sandy gravel; S = sand; sM = sandy mud.

Geographic Region	No. Studies	Harvesting Technique	No. Studies	Habitat	No. Studies
Australia	1	Hand Digging	11	(g)mS	1
North America	8	Hand Pump	3	M	5
Northern Europe	22	Hand Raking	13	mS	12
South Africa	4	Hydraulic Dredge	5	msG	1
Southern Europe	3	Mechanical Dredge	6	S	12
				sM	7

2.3.2 Initial Impacts

2.3.2.1 Taxonomic Response

Fishing activity caused a significant reduction in the average abundance across all taxa (across all habitats and gears) in the first ten days following disturbance, with a weighted mean Hedges' *d* estimate of -0.55 (95% CI: -1.06 to -0.005) ($z = -2.15$, $p < 0.05$). This indicates that abundance is on average 42% lower in harvested plots than in non-harvested plots across all studies (Table 2.2). All three of the main

taxonomic groups for which data were available were reduced in abundance immediately (0–10 days) following fishing disturbance, although only annelids show a significant response (Table 2.2).

Table 2.2. Weighted mean summary effect sizes from random-effects models for the main taxonomic groups at 0-10 days following fishing disturbance.

Taxonomic Group	Hedges' <i>d</i> (95% CI)	% change	z-value	Probability
Mean	-0.55 (-1.06 to -0.05)	- 42.31	-2.15	0.032
Annelida	-0.50 (-0.82 to -0.18)	- 39.17	-3.05	0.002
Crustacea	-0.35 (-0.94 to 0.24)	- 29.61	-1.17	0.243
Mollusca	-0.42 (-0.96 to 0.14)	- 33.76	-1.47	0.143

The results of the random-effects model on all abundance data suggest considerable heterogeneity between the study effect sizes (Test of heterogeneity: $p < 0.001$). Including gear type, habitat, and the minimum extent of the fishing disturbance as moderating variables in a mixed-effects model accounts for only 9% of residual variation in the model, with further unexplained variance remaining between the study outcomes, possibly accounted for by other variables not considered within the model, or introduced through sampling error (Test of heterogeneity: $p < 0.001$). The effects of these additional variables have been explored in further analysis presented below.

2.3.2.2 Species-level Response

Summary effect sizes for individual species are reported in Table 2.3. Only *Scoloplos* spp., the deepest burrowing of the fauna reported, shows a significant reduction in

abundance (Table 2.3), although all species other than *M. balthica* indicate a reduction in abundance following harvesting.

Table 2.3. Weighted mean summary effect sizes from random-effects models for each of the five main species for the period 0-10 days post-fishing. Each of these species are known prey species for waders and other avian predators

Species	Hedges' <i>d</i> (95% CI)	% change	z-value	Probability
<i>C. edule</i>	-0.27 (-0.56 to 0.02)	- 23.58	-1.80	0.071
<i>M. balthica</i>	0.13 (-0.24 to 0.50)	+ 14.09	0.70	0.483
<i>Nephtys</i> spp.	-0.18 (-0.56 to 0.21)	- 16.18	-0.90	0.370
<i>H. ulvae</i>	-0.64 (-2.34 to 1.06)	- 47.25	-0.74	0.461
<i>Scoloplos</i> spp.	-0.67 (-1.08 to -0.26)	- 48.78	-3.19	0.001

2.3.2.3 Effects of Gear Type and Habitat

Initial impacts of each gear type and habitat were first investigated separately (Figure 2.1). Results show significant differences in the magnitude of the effect at 0-10 days post-fishing between gear types ($F_{(4,287)} = 2.93$, $p < 0.05$), when hand digging and the use of a mechanical or hydraulic dredge significantly reduce abundance. A post-hoc Tukey test shows the use of a hand pump most negatively affects initial post-fishing abundance, significantly more-so than mechanical and hydraulic dredging and hand raking. There is considerable variability around the mean effect size for this gear type however.

Harvesting in sand, gravelly and muddy sand, muddy sand and sandy mud habitats cause significant initial reductions in abundance. The magnitude of the reduction between habitats is significant ($F_{(4,287)} = 5.36$, $p < 0.001$) (Figure 2.1b), with a decreasing trend in the severity of impacts from sandy habitats to sandy mud. No significant impact is evident in muddy sands and gravel.

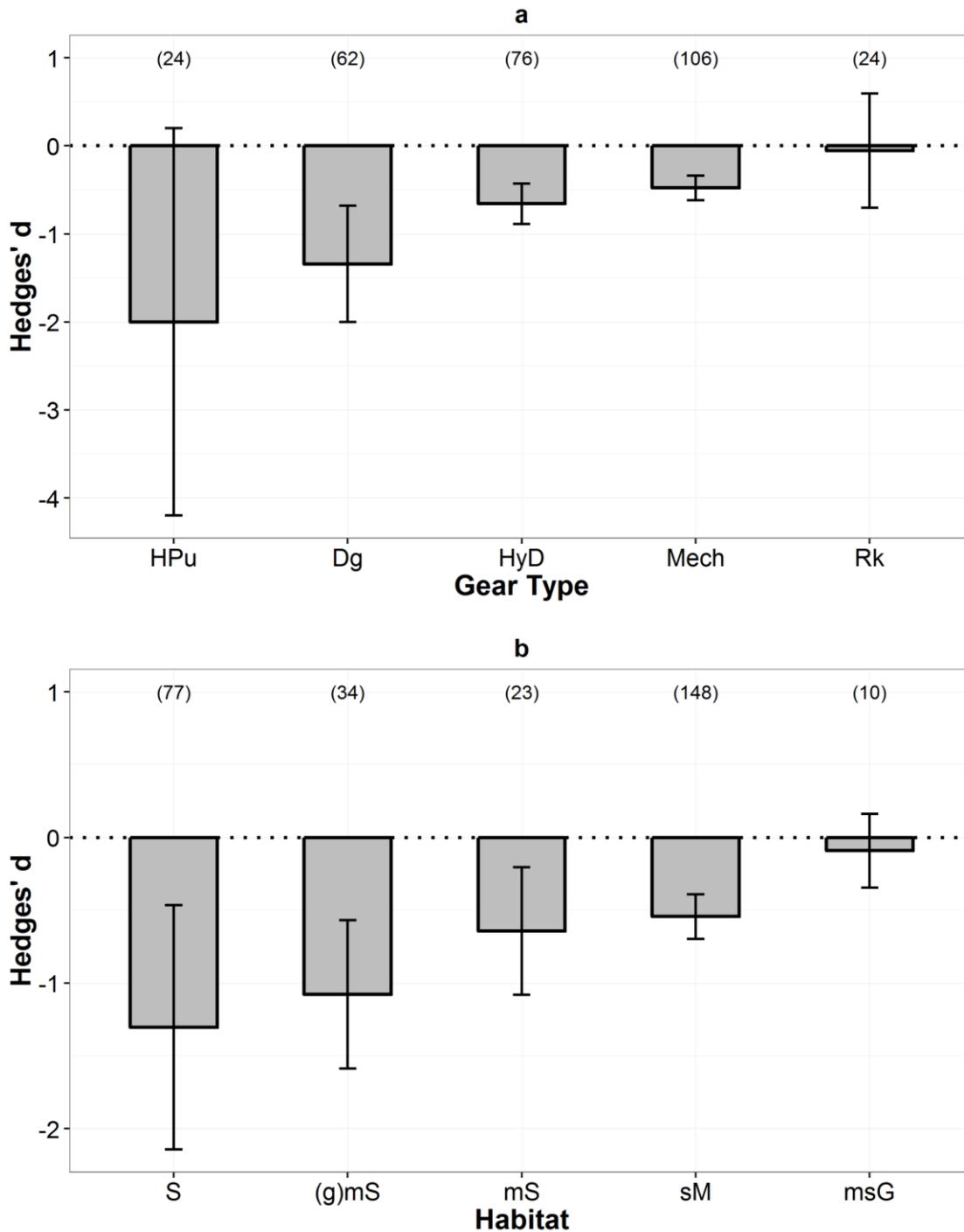


Figure 2.1. Mean ($\pm 95\%$ confidence intervals) effect of fishing disturbance on abundance of benthic taxa at 0-10 days post-fishing according to (a) fishing gear type and (b) Folk habitat group. The horizontal dotted line represents no significant effect. Gear abbreviations: HDg = hand digging; HPu = hand pump; Rk = hand raking; HyD = hydraulic dredge; Mech = mechanical dredge. Habitat abbreviations: (g)mS = gravelly/muddy sand; M = mud; mS = muddy sand; msG = muddy/sandy gravel; S = sand; sM = sandy mud. Adequate test for significant impact is whether the 95% confidence interval overlaps the horizontal zero effect line. The number of observations is indicated in brackets

2.3.2.4 Target vs. Non-target Species

Given that no size data was reported in the meta-database, when the response of a target species was reported it has been assumed that these were of harvestable size where minimum landing sizes may apply. One study did differentiate between juvenile and adults of the target species and data on juveniles was therefore omitted from this analysis. The abundance of target species might be expected to be most severely affected by fishing activities. However, there was no significant difference in the effect size on abundance of target or non-target species 0-10 days post-fishing. Initial impacts actually appear more severe for non-target species than target species, with a mean Hedges' d of -0.45 (95% CI: -0.80 to -0.11) for target species and -0.82 (95% CI: -1.09 to -0.56) for non-target species and a reduction of 37% compared to 56% ($F_{(1,283)} = 2.86, p = 0.09$) (Figure 2.2).

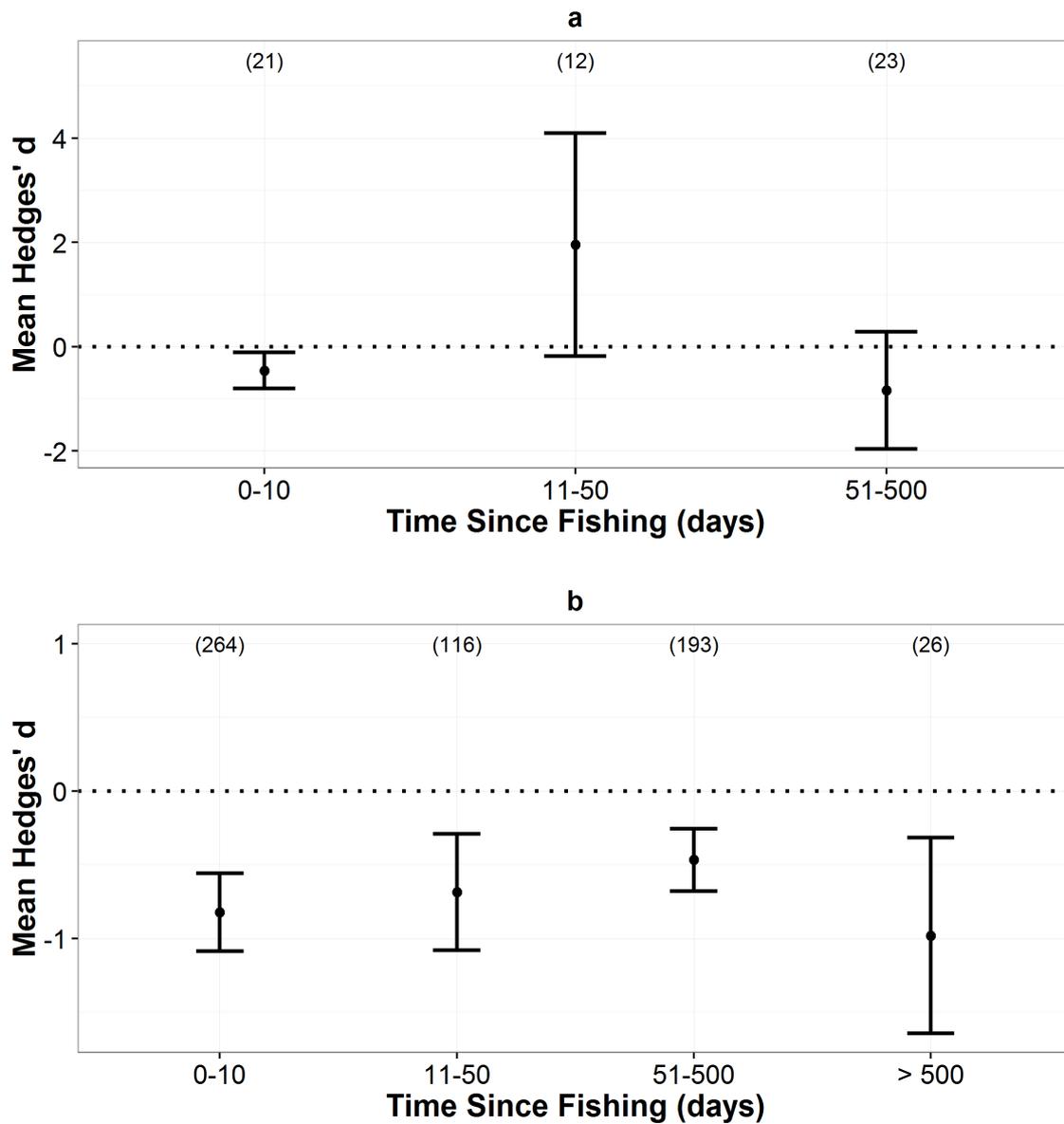


Figure 2.2. The mean effect of fishing disturbance on the abundance of target (a) and non-target (b) species across time categories (no. days) since fishing. The dotted horizontal line represents no significant effect. Adequate test for significant impact is whether the 95% confidence interval overlaps the horizontal zero effect line. The number of observations is indicated in brackets.

2.3.2.5 Gear and Taxa Interactions

Figure 2.3 shows a classification tree of the size of the effect according to gear type on different phyla. For this analysis, hand raking, hand digging and hand pump were grouped into a single “hand gathering” to better generalise the sensitivities of different taxa to harvesting methods. Abundances of crustaceans appear more markedly reduced than other phyla (which are primarily annelids and molluscs) immediately after harvesting. The magnitude of the reduction in these taxa however depends on the harvesting method. Hand gathering results in a more severe reduction in abundance (mean reduction of 93%). For other phyla however there is no significant effect of gear type on the magnitude of the change in abundance (mean reduction of 48% across all gear types).

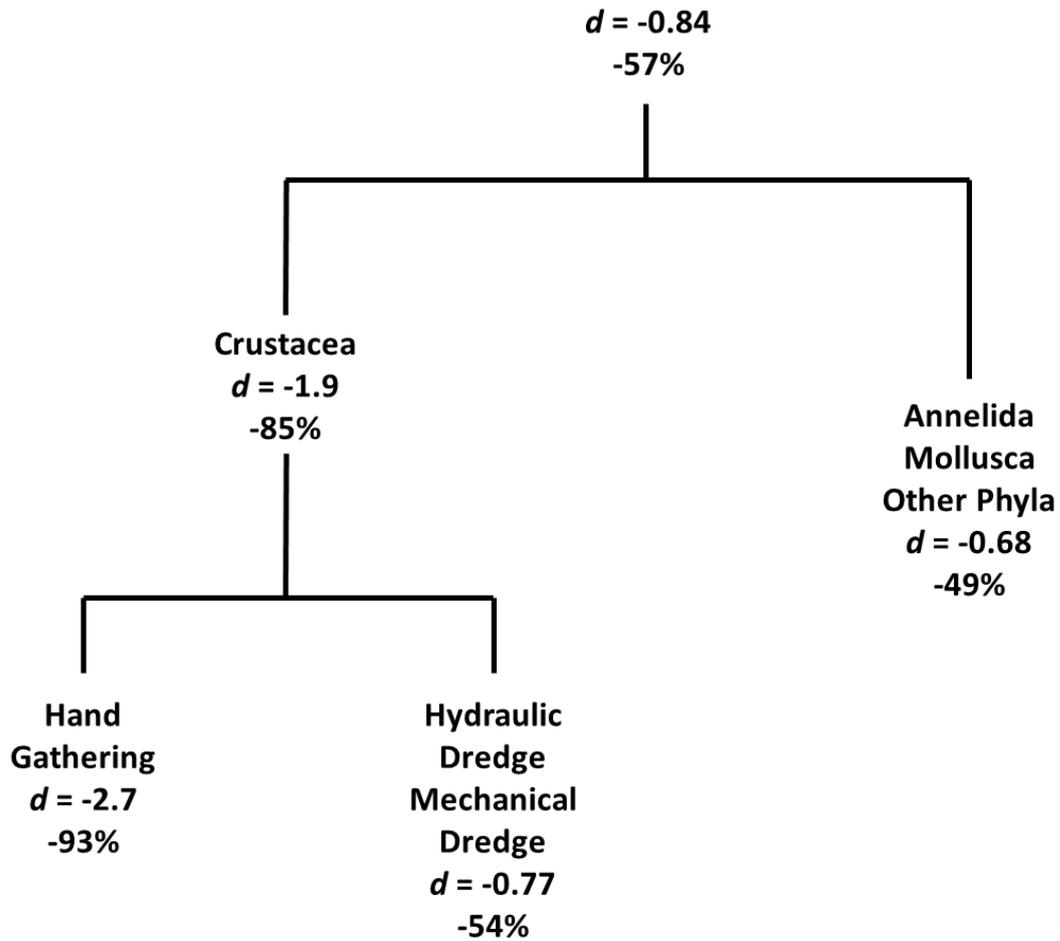


Figure 2.3. Classification tree representing the interaction between fishing gear and taxonomic group with regards to changes in abundance 0-10 days post fishing. Each node presents a partition in the data. For the data at each branch of the tree the mean effect (Hedges' d) is given, along with the mean percentage change in abundance. Other Phyla: Echinodermata, Phoronida, Nemertea.

2.3.3 Recovery Patterns

2.3.3.1 Target vs. Non-target Species

No significant effect of time is evident on the magnitude of the effect size for either target ($F_{(2,53)} = 3.05$, $p = 0.06$) or non-target ($F_{(3,595)} = 1.83$, $p = 0.14$) species. For non-target species recovery (i.e. non-significance of the effect) does not appear > 500 days post-fishing, in fact a further reduction in abundance occurs at this time, potentially suggesting delayed impacts. However, this analysis is integrated across all habitats, and some habitats may demonstrate a trend towards recovery at 51-500 days (Figure 2.2). The effect on target species is somewhat idiosyncratic, likely due to the low power for this group (Figure 2.2a); the majority of the data reports the response in non-target species abundance, resulting in fewer degrees of freedom in the analysis of target species.

2.3.3.2 Gear/Habitat Combinations

Due to a paucity of data for gear types used in each habitat, the Folk habitat classifications used in previous analyses were grouped together into broad “mud” and “sand” categories. Figure 2.4 presents the trends over time for the response in benthic abundance for each gear/habitat combination present in the data. The data indicate that all fishing gear cause a reduction in abundance in each habitat during the first period following fishing, with the exception of hand digging in mud and hand raking in sand, which cause a slight increase in abundance. Recovery trends for most gear and habitat combination appear unstable and highly variable.

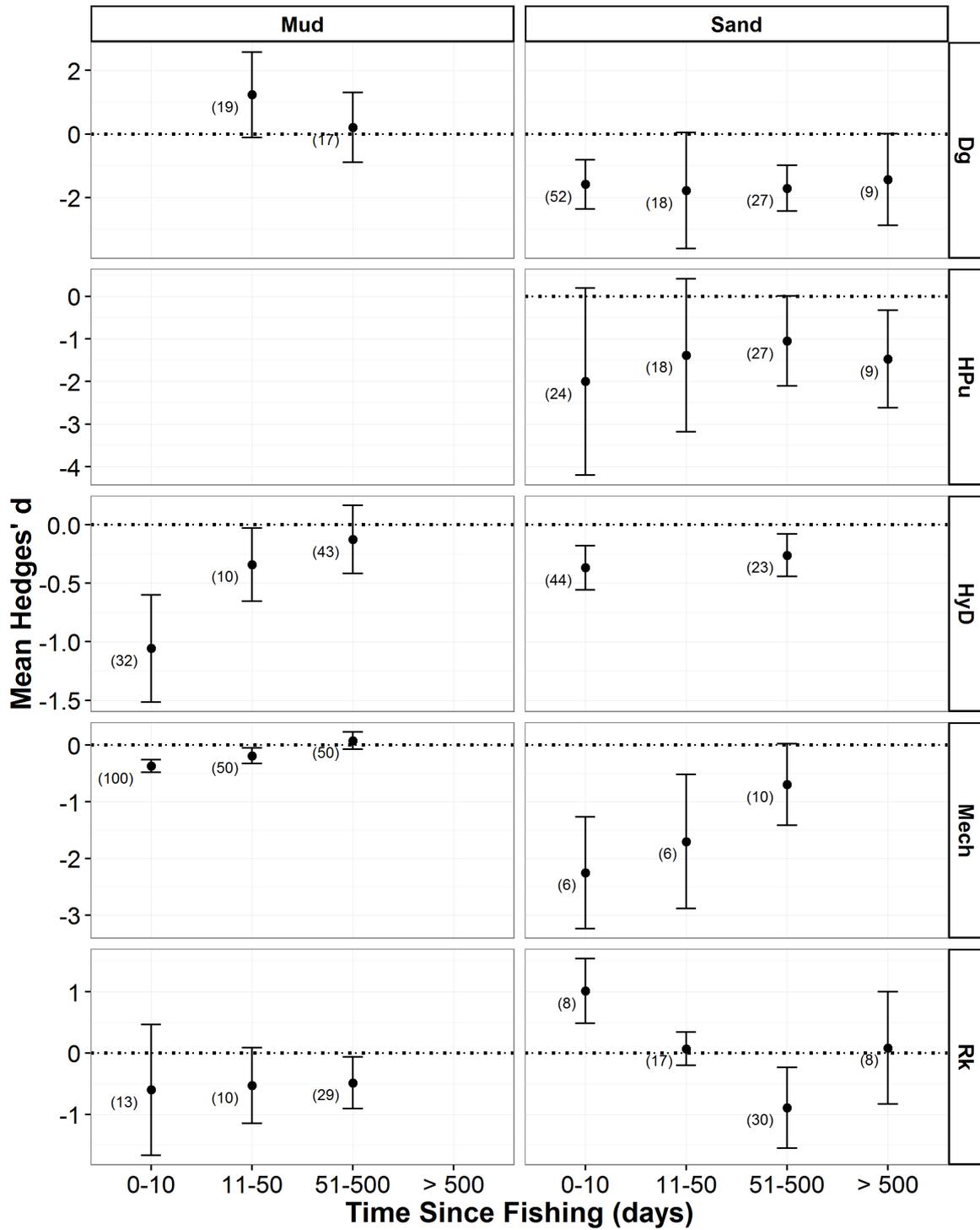


Figure 2.4. Response in taxa abundance to fishing disturbance across four time categories following fishing. Data are mean response \pm 95% confidence intervals. Significant deviation from zero effect (i.e. no response) is considered to occur if the error bars do not overlap with the dotted horizontal line. Gaps in the data are present for some gear/habitat combinations. Gear abbreviations: Dg = hand digging; HPU = hand pump; Rk = hand raking; HyD = hydraulic dredge; Mech = mechanical dredge. The number of observations is indicated in parentheses.

Results indicate significant changes in the magnitude of the effect across time points for hand raking and mechanical dredging in sand and for hydraulic and mechanical dredging in mud (Table 2.4). Figures 2.5 and 2.6 indicate the recovery trends of those gear/habitat combinations that showed an effect of time on taxa abundance. A significant difference from control conditions is taken as when the model confidence intervals do not overlap with zero, and recovery as indicated by the model is taken as the point at which the confidence interval overlaps the horizontal line of no significant effect. A difference between phyla in the recovery slope from mechanical dredging in mud is evident, with a decline in mollusc abundance compared to a positive trend (suggesting recovery) in other phyla ($F_{(1,194)} = 26.50, p < 0.001$) (Figure 2.5). While initial impacts may not be dramatic (and in fact data indicate no immediate decline), molluscs demonstrate no trend of recovery 60 days post-fishing; rather they show a decline in abundance over this period.

Table 2.4. Results of one-way ANOVA of abundance of pooled taxa between grouped time categories for each gear/habitat combination for which sufficient data were available to undertaken the analysis. Data for other gears and habitats were too scarce for this analysis. nd = no data available for that gear/habitat combination. Values highlighted in bold indicate a significant change in the magnitude of the effect across grouped time periods.

Gear Type	Habitat					
	Sand			Mud		
	F	df	p	F	df	p
Hand Pump	0.25	3,74	0.863	n.d	n.d	n.d
Digging	0.06	3,102	0.981	1.52	1,34	0.226
Raking	7.90	3,59	0.000	0.03	2,49	0.975
Hydraulic Dredge	0.67	1,65	0.414	5.98	2,82	0.004
Mechanical Dredge	4.70	2,19	0.022	11.86	2,197	0.000

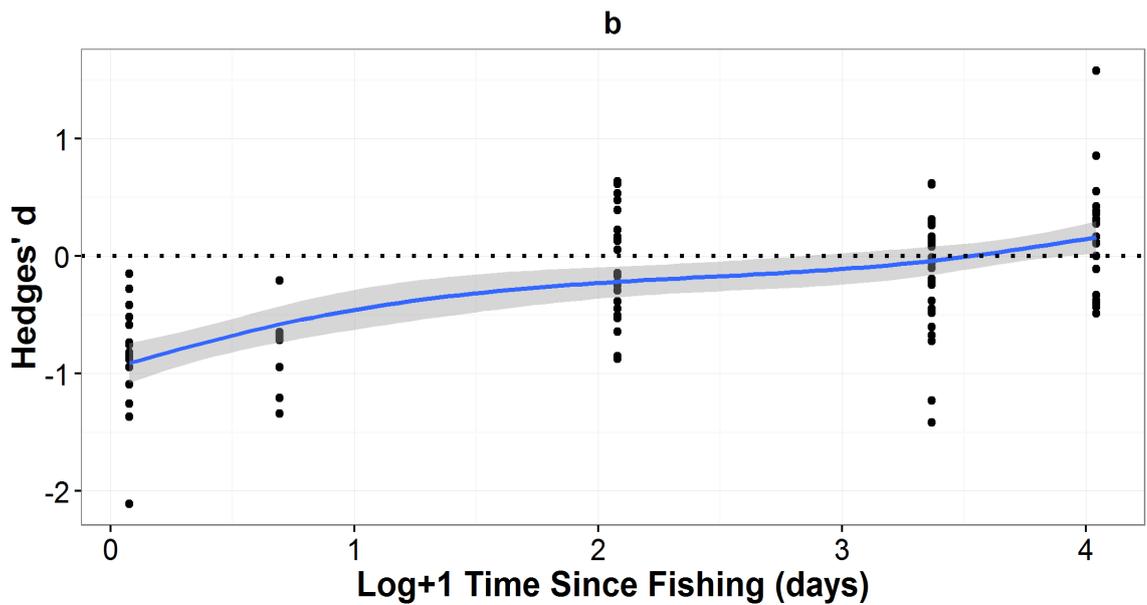
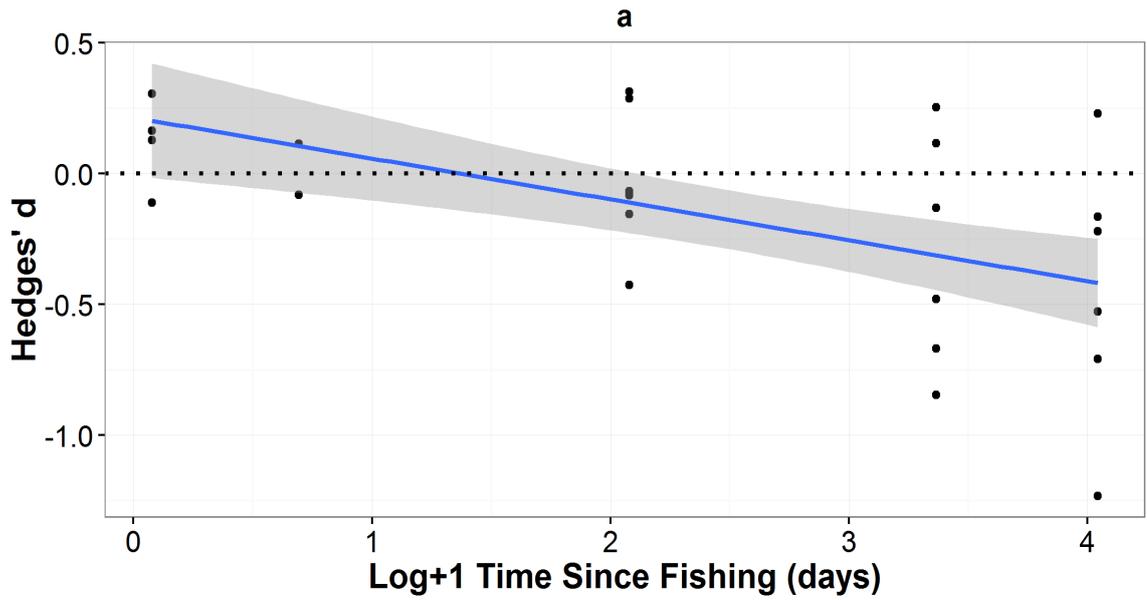


Figure 2.5. Response of (a) molluscs ($F = 16.08$, $R^2 = 0.28$, $p < 0.001$) and (b) pooled taxa (annelids, crustaceans) ($F = 32.86$, $R^2 = 0.37$, $p < 0.001$) abundance to mechanical dredging in intertidal mud. Horizontal dotted line represents no significant effect.

For other gear/habitat combinations, ANCOVA of response data indicates no difference between the recovery slopes of different taxa, so data were pooled. The recovery trend for hydraulic dredging in mud indicates relatively short-term impacts on abundance, with a reduction in the effect size within 10 days post-fishing, and the model remaining close to no significant effect from around 10 days post-fishing for the remainder of the time period covered by the data (Figure 2.6a), although there is some variability. The recovery trend for hand raking in sand appears more unstable, indicated by the low R-squared value and relatively poor fit of the GAM. It appears however that following a small initial increase in abundance, there is a further decline, with a small shift towards control or pre-harvesting conditions only after 400 days (Figure 2.6b). Despite relatively few data points, recovery following mechanical dredging in sand (Figure 2.6c) indicates a positive trend, with the model confidence intervals suggesting at least partial recovery after 400 days.

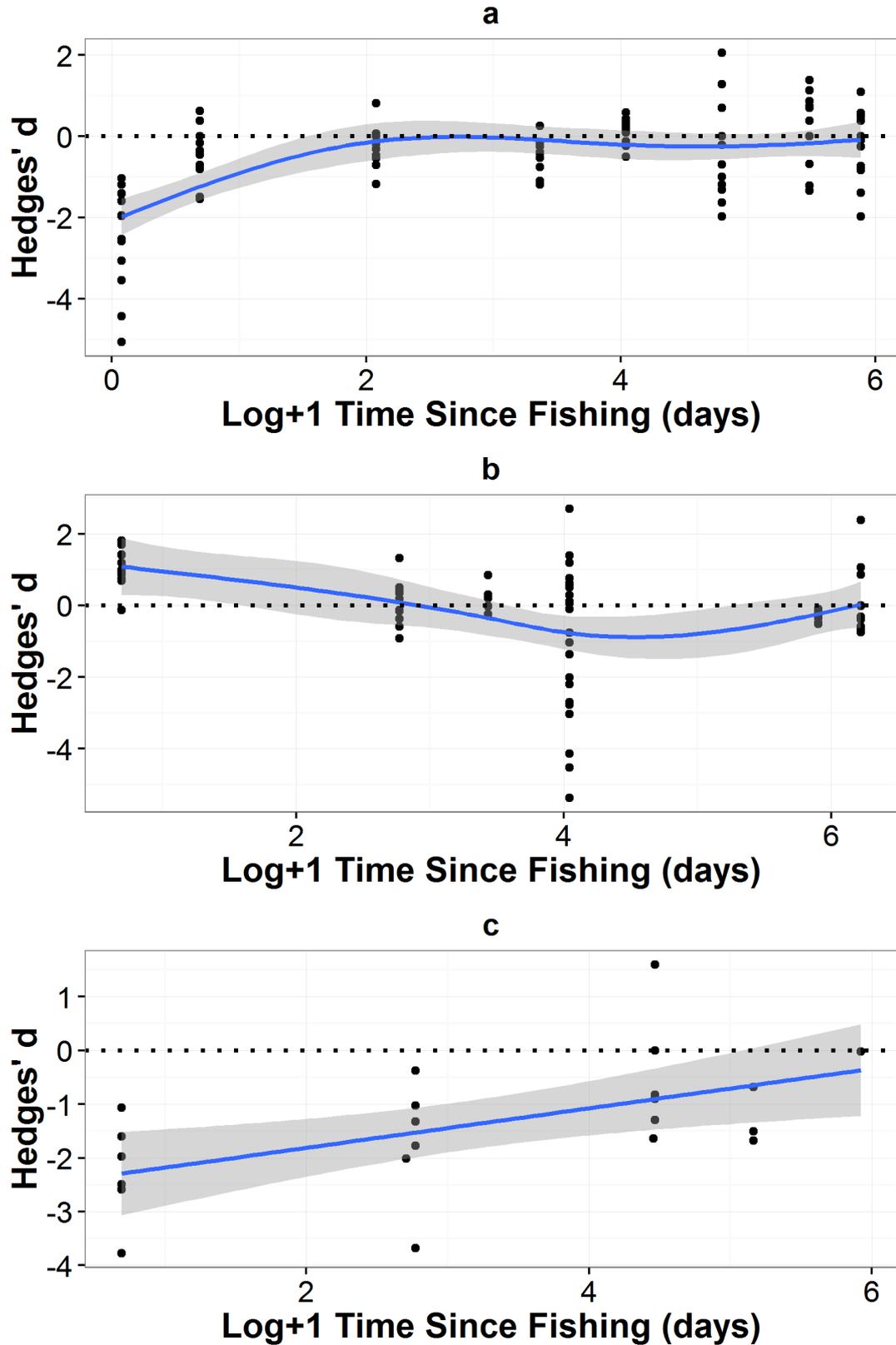


Figure 2.6. Response of benthic taxa to (a) hydraulic dredging in mud ($F = 12.51$, $R^2 = 0.31$, $p < 0.001$), (b) hand raking in sand ($F = 4.20$, $R^2 = 0.18$, $p < 0.01$) and (c) mechanical dredging in sand ($F = 8.83$, $R^2 = 0.27$, $p < 0.01$). Horizontal dotted line represents no significant effect.

2.3.3.3 *Diversity and Biomass*

Diversity data (pooled species richness, Shannon-Wiener Index and Simpson's Index) indicate a mean Hedges' d of 0.33 (95% CI: -2.58 to 3.24) in the first ten days following disturbance, representing a mean increase in diversity indices of 39% (Figure 2.7a) although this is non-significant. The increase in diversity following fishing appears to subsequently decrease, with a significant reduction in diversity occurring 51-500 days post fishing. By > 500 days the effect is non-significant, and no significant effect of time is observed on the magnitude of the response. The available biomass data indicate a significant reduction in benthic biomass compared to control or pre-fishing conditions and this remains across all time periods present in the data and > 500 days post fishing (although based on only four data points). ANOVA of the response over time periods shows a change in the magnitude of the response ($F_{(2,21)} = 7.80, p < 0.01$), with a trend towards recovery by > 500 days (Figure 2.7b).

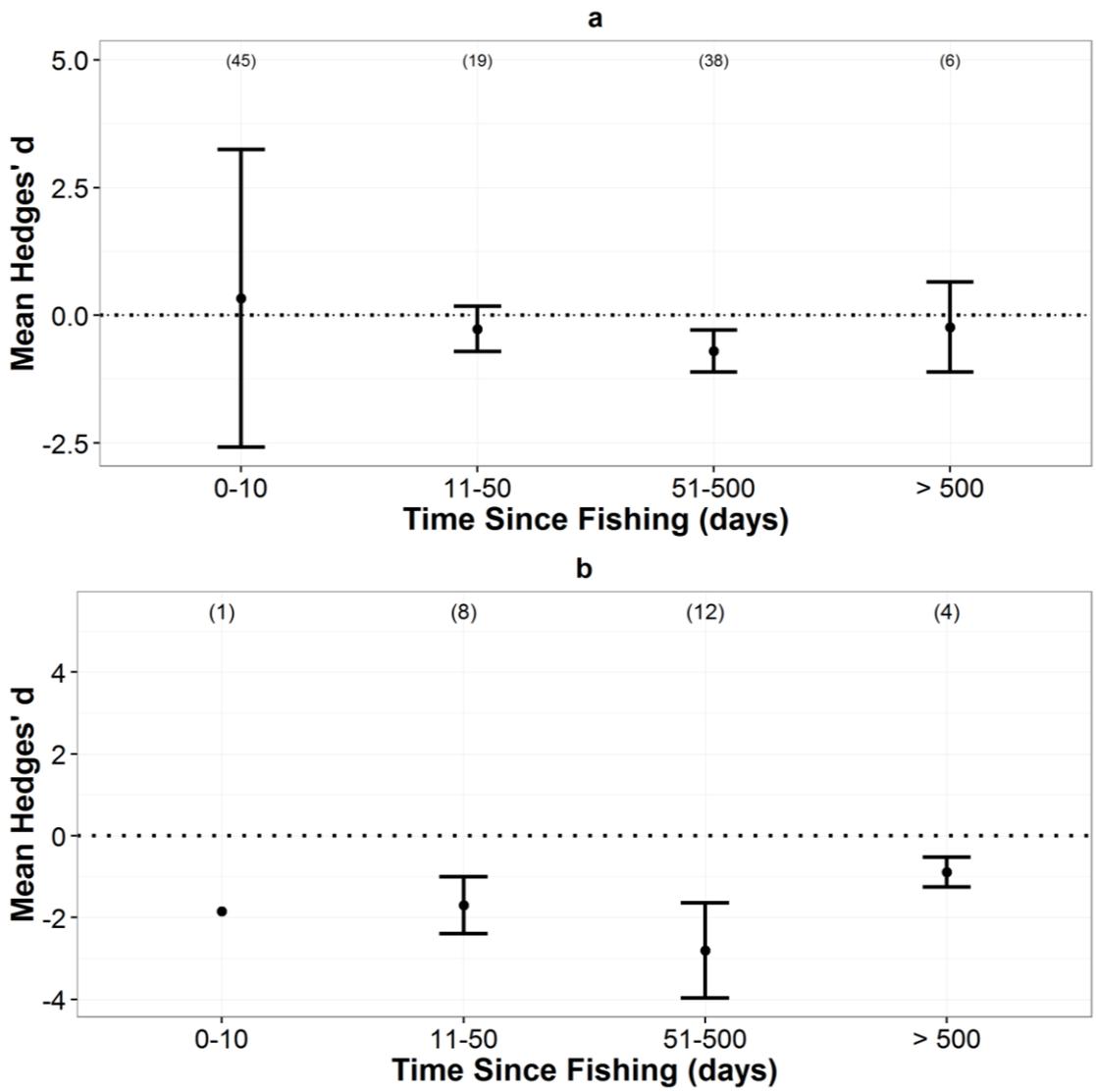


Figure 2.7. Mean effect of fishing on benthic diversity (a) and biomass (b) across four time categories following fishing. Data are mean response \pm 95% confidence intervals. Significant deviation from zero effect (i.e. no response) is considered to occur if the error bars do not overlap with the dotted horizontal line.

2.4 Discussion

Unlike bottom trawling in subtidal habitats, intertidal harvesting is often carried out more systematically given the direct access to the resource at low water. Furthermore, the depth to which intertidal fishing activities penetrate the habitat means that in many cases depletion of the biota is more extreme than for bottom-trawling (Kaiser *et al.*, 2006). As it is possible to place sampling devices more precisely in an intertidal environment, sampling error in experimental studies is likely to be lower than for subtidal studies in which error is introduced due to vessel positioning issues. As a result the data from intertidal studies should provide strong signals of fishing impacts when they occur.

Data from the first ten days following fishing disturbance show overall significant reductions in the abundance of annelids, one of the main bird prey groups, and a significant reduction in the average abundance across all taxa. Annelid worms are often targeted with high accuracy through bait harvesting (Blake, 1979; Watson *et al.*, 2007), with harvesting efficiency of up to 70% reported in a study of digging for lugworm (Blake, 1979). This higher efficiency is reflected in the larger initial reductions following the use of hand-held gears shown in Figure 2.1. Furthermore annelid worms may be sensitive to damage through non-target interactions with harvesting gear (Skilleter *et al.*, 2005; Griffiths *et al.*, 2006; Watson *et al.*, 2007). Baitworm harvesting targets the larger species such as the king ragworm *Alitta virens* and lugworms *Arenicola* spp.; these represent key prey resources for worm-eating bird species such as common Redshank *Tringa totanus*, Black-tailed Godwit *Limosa limosa* and Eurasian Curlew *Numenius arquata*. In many places hand

techniques can be highly localised and small in scale, although in some areas the footprint of such practices combined may be thousands of square metres, as is the case in Poole Harbour in the UK (Fearnley *et al.*, 2013). However this impact is still likely to be relatively limited compared to wide-scale commercial harvesting efforts that may cover hundreds of square kilometres (Piersma *et al.*, 2001).

Annelid worms, along with crustaceans, another important prey group, appear to recover more quickly compared to other phyla, particularly molluscs. Molluscs are a key prey group for species such as Eurasian oystercatcher *Haematopus ostralegus*, common eider *Somateria mollissima* and red knot *Calidris canutus*, and data indicate that abundance can remain suppressed for greater than 60 days following dredging in muddy sediments (Figure 2.5a). While molluscs are relatively sedentary, annelids and crustaceans are more motile, with potential for recolonization of an area through adult migration as well as larval dispersal (Pearson and Rosenberg, 1978; Levin, 1984). Bivalve colonisation relies on pelagic larval settlement, which is largely influenced by hydrographic conditions, or the subsequent migration of juveniles (Armonies and Hellwig-Armonies, 1992). Low spatfall levels that inhibit recovery have been shown to coincide with periods of intensive fishing (Beukema, 1992; Smit *et al.*, 1998). Furthermore the dominance of coarser sediments through the regular resuspension and loss of finer grain sizes, known as “winnowing” (Martin *et al.*, 2015) can result in poor feeding conditions for deposit-feeding bivalves (Taghon, 1982; Kang *et al.*, 1999), resulting in lower prey quality for molluscivorous birds. Recolonization of an area following mechanical shellfishing will generally require migration or settlement to occur over a much larger area than

for recovery from more localised hand techniques and long-term suppression of bivalve prey abundance and subsequent settlement may result (Ens *et al.*, 2004). Such shifts to communities dominated by fast-growing worm species can subsequently lead to declines in populations of molluscivorous shorebird species and a shift towards more worm-eating waders (Atkinson *et al.*, 2010).

Results show persistence of impacts in sandy habitats for longer than in muddy habitats, which is contrary to a prevailing view that physical recovery occurs relatively rapidly in sandier substrates, allowing for earlier recolonisation (Hall, 1994; Jennings and Kaiser, 1998). Similar inconsistencies were identified in a previous, wider meta-analysis on general fishing impacts that found relatively low impacts of harvesting in mud and no obvious ranking of impacts across habitats (Collie *et al.*, 2000). Figure 2.1 indicates that harvesting in sand (all gears pooled) causes the largest initial reduction in abundance across all taxa, with less-dramatic initial impacts in muddier habitats. At low tide intertidal sand is much more safely accessible on foot than softer muddy habitats that remain unreachable, and hand harvesting at low water in sandy habitats may therefore be more intense and widespread. The temporal trends indicated in Figures 2.4 and 2.6 suggest that recovery in sand may be variable, with clear trends towards recovery only evident for hydraulic and mechanical dredging in sandy habitats. Conversely recovery following the use of hand harvesting techniques (digging, hand pump and raking) show less evidence of recovery and potentially delayed impacts. Again, hand harvesting is often very precise and disturbs sediment to a deeper depth than dredges that may only penetrate the sediment to a few centimetres. Furthermore

densities of species in muddy habitats are generally higher than in sandier habitats (Heck *et al.*, 1995; Van Hoey *et al.*, 2004) perhaps providing more potential for recolonization from neighbouring areas.

Hydrodynamic conditions overlying the affected habitat exert a large influence on biological recovery through the mediation of infilling rates of disturbed patches, causing considerable variation in recovery rates in different mud habitats (Dernie *et al.*, 2003). This is an important consideration locally when predicting medium and long-term impacts following cessation of harvesting, particularly in intertidal areas of low energy where the substrate may be dominated by well consolidated finer sediments.

While most intertidal harvesting causes a reduction in invertebrate abundance, hand digging in mud and raking in sand appear to cause an initial increase in all taxa pooled. Such techniques may allow for increased movement of scavengers or opportunistic invertebrate species into the area (Cesar and Frid, 2009) or bring deeper burrowing or infaunal species to the surface, temporarily increasing abundance and species diversity within the raked area. These techniques do not generally remove the sediment; rather it is left in situ, and bird predators are often observed to exploit these disturbed sites immediately after harvesting, before avoiding the area, presumably after prey has been depleted (Ferns *et al.*, 2000). Recovery trends of each of the gear/habitat combinations clearly differ however (Figure 2.4) and a more comprehensive multivariate analysis of the benthic assemblage may allow further insight into this trend and identify such shifts in community composition (Sousa Leitão and Baptista Gaspar, 2007). Given that

studies are undertaken across numerous locations and geographic regions and therefore report the response in often vastly different sets of species, from which a robust dataset for multivariate analysis could not be created, this type of analysis was not possible. Changes in diversity indices may provide some indication of changing dominance patterns in faunal communities however (Figure 2.7).

Non-target species may be significantly more affected than target species by intertidal fishing activities, with recovery patterns indicating prolonged effects. This is consistent with previous studies that show significant reductions of non-target species up to a year after intertidal dredging (Kraan *et al.*, 2007).

The changes to Dutch fisheries policy in the 1990s (Smit *et al.*, 1998) demonstrate the need for adaptive management in intertidal fisheries, with consideration of more mechanised harvesting of species that have limited potential for recovery. The declines in the Wadden Sea Eurasian Oystercatcher and common Eider populations and Eurasian Oystercatchers in The Wash, UK (Atkinson *et al.*, 2003; Atkinson *et al.*, 2010) serve as reminders of the wider ecological implications of fishery mismanagement (Camphuysen *et al.*, 1996; Smit *et al.*, 1998). An important consideration in management of intertidal invertebrate resources is the size of prey which, while not reported in many studies, is an important factor in determining the available food for shorebird populations (Bowgen *et al.*, 2015). Prey size can be an indicator of prey quality in addition to abundance data alone and is a strong determinant of an individual's energy intake and fitness (Bowgen *et al.*, 2015).

Management measures to regulate the harvesting of intertidal organisms are already in place in many locations, largely through spatial and temporal restrictions

on harvesting activity (Halpern and Warner, 2002; Halpern, 2003), rather than limits on effort and allowable catch or harvests. Extensive research has demonstrated the effectiveness of marine reserves or no-take areas in subtidal ecosystems in conserving ecosystem function and productivity (Sciberras *et al.*, 2013); the limited work carried out in intertidal habitats suggests the benefits may be comparable (Byers, 2005; Griffiths *et al.*, 2006).

Our results can contribute to ecosystem-based management and the achievement of sustainable fishing while achieving conservation objectives of international requirements under the European Union Birds Directive (Directive 2009/147/EC) and similar national legislation. The evidence suggesting long term detriment to shorebird prey from intertidal harvesting may have significant management implications. For policy-makers and environmental managers, the ranking of impacts in Figure 2.1 and recovery trends shown in Figures 2.4, 2.5 and 2.6 are likely of most interest. Given the long-term impacts of dredging on mollusc abundance, we urge managers to ensure that shellfish harvesting is limited to ensure sufficient adult stock, both as prey for shorebird populations and as a source of larval supply and for future population viability. In fact, much work has been done on the subject of calculating the amount of bivalve prey required to support shorebird populations overwinter (Goss-Custard *et al.*, 2004; Stillman *et al.*, 2010; Stillman and Wood, 2013; Stillman *et al.*, 2016). Whether this is achieved through spatial and temporal restrictions or assigning allowable catches or effort limitations would likely be driven by local circumstance. Hand fisheries are often difficult to regulate due to the ease of access, although due to the evidence of prolonged impacts in hand fisheries

presented here and their significant global value we agree with Watson *et al.* (2017) that their management should be brought in line with other fisheries to ensure sustainability. The clear trends in recovery in annelids and crustaceans, common taxa targeted by hand, suggest that sustainability of such fisheries is certainly achievable with sufficient closures to allow adequate larval settlement or recolonisation.

3. Impacts of a novel shellfishing gear on macrobenthos in a marine protected area: pump-scoop dredging in Poole Harbour, UK

3.1 Introduction

In the marine environment the use of bottom-fishing gears is one of the largest sources of anthropogenic disturbance on habitats and species (Dayton *et al.*, 1995; Collie *et al.*, 2000; Kaiser *et al.*, 2006; Martin *et al.*, 2015). However the types of gear employed may vary greatly at local and regional scales, depending on the target species and local physical environment. The increasing introduction of non-native marine species is generally seen as a threat to biosecurity and nature conservation interests (Meyerson and Reaser, 2002; Bax *et al.*, 2003; Molnar *et al.*, 2008), yet harvestable populations of significant commercial value can emerge that can lead to development of novel fishing techniques by local fishermen (Pranovi *et al.*, 2004). While the impacts of bottom-fishing overall are well understood (Dayton *et al.*, 1995; Collie *et al.*, 2000; Kaiser *et al.*, 2006), it is important to consider the risks of such new or novel gear types where they arise and whether their impacts differ from more established and common fishing gears.

The Manila clam *Ruditapes philippinarum* (Adams and Reeve, 1850) (genus synonyms: *Venerupis*, *Tapes*) has spread throughout Europe in recent decades and is harvested recreationally and commercially (Pranovi *et al.*, 2004; Beck *et al.*, 2015; Mosbahi *et al.*, 2016). The species was introduced to a number of locations in the United Kingdom in the early 1980s with the intentions of establishing commercial aquaculture including Poole Harbour on the south coast of the UK (Utting and Spencer, 1990; Britton, 1991, Humphreys *et al.*, 2015). It has since become

naturalised in Poole Harbour and has been exploited under a licensed fishery using a 'pump-scoop' dredge (Jensen *et al.* 2005; Humphreys *et al.* 2015) since 1994 (Jensen *et al.*, 2005). The fishery is of significant regional economic importance, with a peak annual value in 2004 of around £1.5 million (Franklin *et al.*, 2012). Pump-scoop dredges are relatively small (46x46x30cm) and penetrate the sediment to a depth of a few centimetres. This method of harvesting is currently unique to this location, and utilises a water pump powered by the vessel's engine to rinse sediment through the rear of the dredge basket as it is towed alongside the vessel (Figure 3.1a). This type of dredge is distinct from hydraulic or suction dredges that fluidise the sediment in front of the dredge, and was developed by local fishermen as an improvement to the previously used hand-held clam 'scoop', which is a physically demanding gear (Jensen *et al.*, 2005). The dredge is worked on shallow drafted vessels less than 10m in length within intertidal and shallow subtidal areas of mud and sandy mud. The common cockle *Cerastoderma edule* is also harvested using the pump-scoop dredge, although landings are only around 5% of manila clam landings. At low tide, extensive dredge scars in a spiral pattern are visible that resemble rounded troughs (Figure 3.1b), indicating the vessel movements (Parker and Pinn, 2005; Fearnley *et al.*, 2013). Previous work on the impact of these gears is limited; however there are concerns that they may affect benthic communities, reducing species richness and abundance (Parker and Pinn, 2005).

In protected areas, fisheries and environmental managers must assess and monitor habitat condition to ensure sustainable development and inform management. This study assessed the impacts of pump-scoop dredging through analysis of the

biological assemblage and physical characteristics within areas subject to different fishing intensities, therefore contributing to the limited evidence of the environmental impacts of this gear type. We achieved this by answering the following research questions: How does short-term pump-scoop dredging affect macrobenthic communities compared to an un-dredged control area? How does pump-scoop dredging affect the physical benthic environment and sediment characteristics compared to an un-dredged control area? If any, what changes in macrobenthic community structure and biotope characterise these impacts?

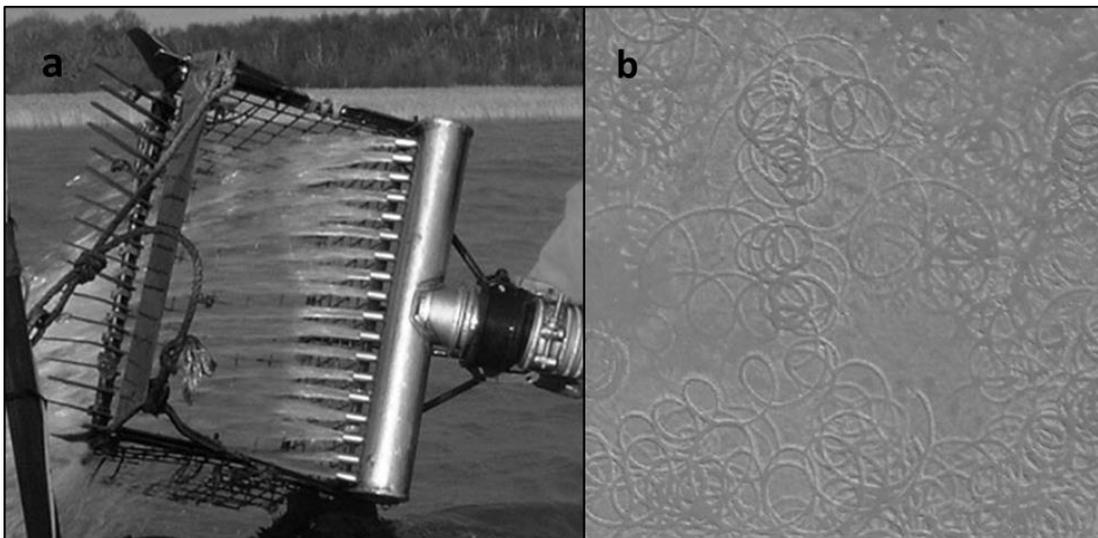


Figure 3.1. a) The pump-scoop dredge used in Poole Harbour, UK. b) Aerial imagery of scarring from pump-scoop dredging within Poole Harbour. Modified with permission from Jensen *et al.* (2005) and Footprint Ecology Ltd. (Fearnley *et al.*, 2013) respectively. No scale bar was included in original publication, although the circular scars generally range from 5-15m across.

3.2 Materials and Methods

3.2.1 Study Area

Poole Harbour is located in Dorset on the south coast of England (Figure 3.2) and comprises extensive areas of mudflats, sandflats and saltmarsh. The harbour covers an area of 36,000km² at high tide, and is micro-tidal, with a range of 1.8m on spring tides and 0.6m on neap tides (Humphreys, 2005). Poole Harbour experiences two high tides a day, with a relatively long slack water period at high tide that results in a water level above that of mean tide level for the majority of the day (Humphreys, 2005). The Harbour is designated for its conservation importance as a European Marine Site (EMS) (European Birds Directive 79/409/EEC) and Ramsar site. From September, large numbers (> 25,000) of migratory waterfowl arrive in the harbour to feed and over-winter.

Due to a historic prevalence of illegal fishing and high risk of disturbance to protected feeding areas for over-wintering birds, a new permit system came into force in the harbour in 2015, replacing the previous management regime under a new by-law. This by-law restricts the use of a dredge to an open season that runs from May to December annually and within spatial restrictions, while attempting to ensure a viable fishery, and since its implementation has achieved high compliance and reduced illegal poaching. Under this new management regime, some areas of the harbour designated as 'bird sensitive areas' (BSA) for overwintering waders and waterfowl that had previously been closed to fishing activity were opened to clam dredging from 1st July to 31st October. The changes in the management measures in the study area under the by-law are summarised in Table 3.1. Other bird sensitive

areas in the harbour now remain closed to dredging all year round. Monitoring of impacts is critical within an adaptive management process, and the opening of these areas provided opportunity for the local fisheries authority to study the effects of pump-scoop dredging on littoral soft-sediment habitats and in relation to the new management measures.

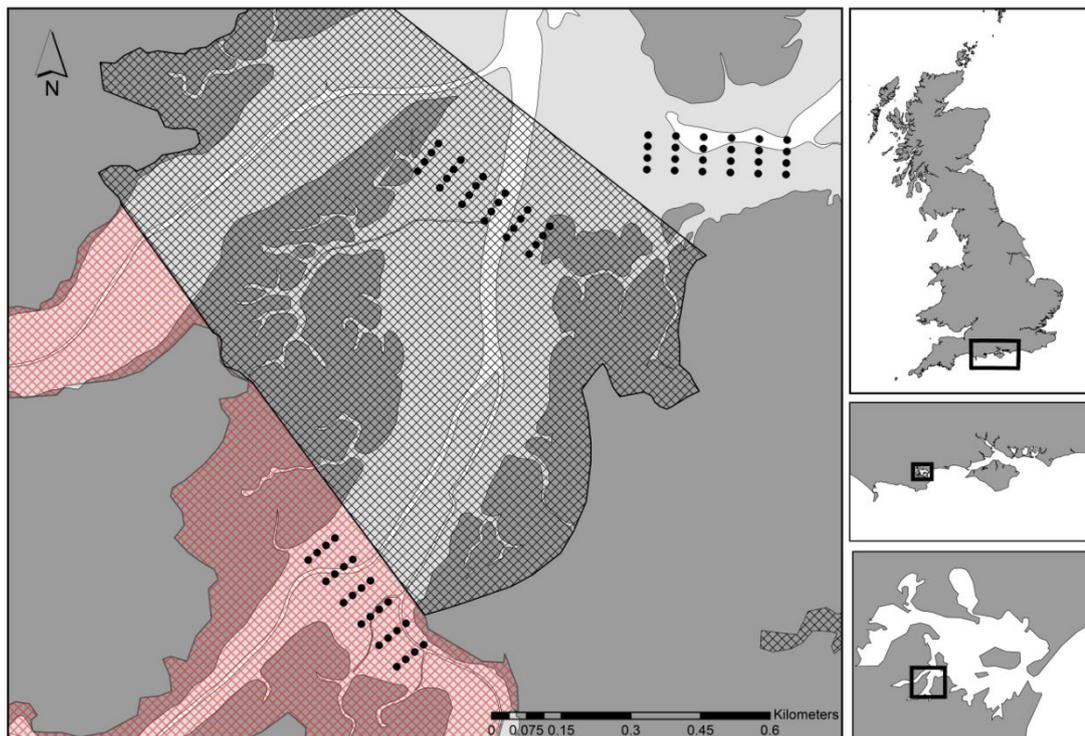


Figure 3.2. The study area in Poole Harbour known as Wytch Lake, indicating the sampling stations visited in June and November 2015. The Wytch Lake Bird Sensitive Area (BSA) is indicated by the hatching. The southern hatching represents the area closed to dredging (control) and the northern hatching represents the area open July 1st –October 31st (newly opened, short-term dredging). The most northerly sampling grid outside of the hatching has historically been heavily fished. The southern tip of Round Island is indicated immediately north of the study site. Shellfish dredging is permitted outside of the BSA from 25th May – 24th December. The location within Poole Harbour, the UK south coast and the UK is also indicated.

The study area (Figure 2) is a relatively sheltered intertidal channel of reduced salinity influenced by the Rivers Corfe and Frome at the uppermost extent of the

channel. Environmental data across the site was extracted from a validated tidal flow model of Poole Harbour that predicts environmental changes throughout the harbour over two spring and neap tide cycles (HR Wallingford, 2004; Herbert *et al.*, 2012). Light Detection and Ranging (LiDAR) data indicate that elevation is within 0-2m above chart datum throughout the study area. Existing bathymetric data used in the tidal flow model (HR Wallingford 2004) indicate a range of 0.48m in mean elevation (metres above chart datum) across the different dredge management areas within the study site. The site is of reduced salinity, with mean median salinity values extracted from the model within 27.3–27.4ppt across all dredge management areas. Mean maximum velocities range from 0.13 to 0.25m/s across the management areas.

Table 3.1. Fishing intensity and seasonal openings of each site sampled under the dredge permit by-law, which came in to force on 1st July 2015.

Site	Pre-by-law	Post-by-law
Control	Closed	Closed
Newly Opened	Closed	Open (1 st July - 31 st October)
Heavy Dredging	Open	Open (25 th May - 24 th December)

The intertidal assemblages in this region of the harbour are largely dominated by the polychaete *Hediste diversicolor* and the bivalve *Macoma balthica* in littoral sandy mud (Herbert *et al.* 2010). The locations of each area are indicated in Figure 3.2. Although dredging occurs throughout the harbour (subject to spatial restrictions) this site was chosen for the study as it provides three areas under

different management regimes in close proximity of one another, easily sampled within the time and budget constraints of the project.

3.2.2 Sampling

Sampling followed a before-after-control-impact (BACI) design, in relation to the four month open season within the BSA, which is widely used in assessing environmental impacts (Underwood, 1993). The design allows for the detection of any changes relative to spatial and temporal variation associated with the opening of the area to dredging. The magnitude of any effect relative to the control area is therefore of greatest interest. While the use of a 'beyond BACI' design, or multiple control sites, would perhaps allow detection of an impact more robustly than a single control site (Underwood, 1992), this design was considered most appropriate given the resources available to the project.

This enabled a comparison of the impact of pump-scoop dredging in an area that had previously been closed (newly opened, short-term dredging) with the control site (low fishing effort) and heavily dredged (long-term, high fishing effort) areas (Table 3.1). A sampling grid was placed across each area that comprised 24 sampling points in a 6x4 rectangular design at 50m intervals. As it is difficult to predict fishing distribution in a newly opened area, a grid design was employed to capture dredging pressure in the BSA. Core samples from each of the three sites (Figure 3.2) were taken at high water from a local fishing vessel in June and November 2015. At each location a single core of 10cm diameter and 30cm depth was taken for faunal analysis using a hand-held suction corer. This is a standard-diameter corer for use in intertidal environments that was designed to sample deeper than the usual 15cm

depth corers in order to better sample larger and deeper burrowing fauna. In the laboratory, samples were sieved through a 0.5mm sieve and all macrofauna retained were preserved in 5% formal buffered saline. Samples were then sorted, measured and identified to species level with the latest nomenclature according to the World Register of Marine Species (WoRMS, 2017: last accessed 7th November 2017).

3.2.3 Measuring fishing effort

Fishing intensity in each area was determined based on historic sightings data provided by the Southern Inshore Fisheries and Conservation Authority (SIFCA). Fishery officer observers recorded the presence of clam dredging and any other activity during the study period during weekly patrols (Table 3.1). At low tide (spring tide, LW 1325, Height 0.5m) on 23rd November 2015, after the closure of the BSA to dredging on the 31st October, and with fishing continuing outside of the BSA boundary a DJI Phantom 3 Pro quad-copter Unmanned Aerial System (UAS) was flown over the study site to acquire vertical stereo aerial photographs (VSAP) of 3.5cm resolution. This imagery was then used to map the level of sediment scarring in each area as a result of dredging. The aerial imagery was loaded into ArcMap 10.1 Geographic Information System (GIS) and image classification was undertaken to estimate the extent of dredge scarring in each management area as a measure of fishing intensity. Pixels were grouped into classes to represent scarred or unscarred sediment and the percentage of scarred sediment in each area was then calculated using the area of each pixel class. A detailed description and discussion of these methods is presented in Chapter 4.

3.2.4 Sediment Analysis

A second core was taken from each sampling point in June and November 2015 for sediment analysis. Each sample was homogenised across all sediment depths before a 10g subsample was taken. Organic content was then measured by Loss on Ignition, placed in a muffle furnace at 450°C for 12h. A Malvern Mastersizer 3000 (Malvern, 2017) laser particle size analyser was then used to quantify sediment particle size from the same subsample, from which cumulative volume curves were produced and the % volume of sand and silt calculated.

3.2.5 Statistical Analysis

Data were analysed using the software PRIMER v6 (Anderson, Clarke and Gorley, 2008) and the vegan package within RStudio version 1.0.136. Univariate analysis of individual responses (i.e. sediment characteristics and species abundances) was carried out using two-factorial ANOVAs including site (i.e. treatment) and sampling time as fixed factors and an interaction term between the two. Any environmental effect of dredging in relation to the BACI sampling design (i.e. an indication of whether the magnitude of the temporal effect between sampling points differs between sites) was identified by significance of the interaction term. Where variances were heterogeneous ANOVA with White's adjustment for heteroscedasticity was used. In order to quantify the size of the effect, the Eta-squared value is reported, an effect size specifically used in ANOVA models that describes the amount of variation in the response variable attributable to a particular level of the predictor (Cohen, 1988). For individual species and overall community abundances, Hedges' *d* was calculated to indicate the size of the effect

(Cohen, 1988). This value is a standardised measure of the difference between groups and is more informative than p-values alone, with a value of zero indicating no significant effect (Borenstein *et al.*, 2009).

Multivariate analysis was undertaken on a Bray-Curtis similarity matrix derived from log+1 transformed species abundance data using PRIMER 6 and the vegan package in RStudio (Clarke and Gorley, 2006). This allows better assessment of changing dominance patterns rather than over-compensate the contribution of rarer species by using other coefficients or a simple presence/absence matrix (Clarke and Gorley, 2006). In order to identify similarities between the macrofaunal assemblages at different sampling points and sites CLUSTER and SIMPER (similarity percentages) analyses were undertaken. A PERMDISP (Clarke and Gorley, 2006) routine within PRIMER v6 was utilised to characterise the amount of dispersion within the multivariate dataset between sampling times and sites, as a potential indicator of environmental stress (i.e. as a result of fishing disturbance). Permutational analysis of variance (PERMANOVA) was then undertaken with site and time included as fixed factors and an interaction term between the two, to identify differences in the overall community structure present between sampling sites and before or after the four month fishing period. By using permutations the PERMANOVA test is unaffected by correlation structures that may exist in the data (any correlation is destroyed through randomly shuffling samples) and is a powerful procedure in assessing changes in community structure in a variable environment (Anderson, 2001; Anderson *et al.*, 2008; Anderson and Walsh, 2013). PERMANOVA was performed on untransformed data once homogeneity of variance had been

identified. Environmental covariates were also included in the PERMANOVA analysis to investigate their influence on the community assemblage.

Canonical Analysis of Principal Coordinates (CAP) was carried out on the Bray-Curtis similarity matrix. CAP is a constrained ordination procedure that identifies axes through a multivariate cloud of data points. A discriminant CAP was used in this study. This method of CAP identifies axes that best discriminate between *a priori* groups, known as canonical discriminant analysis. Discriminant canonical analysis therefore allows the investigation of an *a priori* hypothesis to identify and characterise differences between groups, such as those identified as significant through PERMANOVA which may not be clearly visualised through MDS, and is a useful ordination technique for species abundance data (Anderson and Willis, 2003).

Values for the AMBI (AZTI Marine Biotic Index) (Borja *et al.*, 2000) and BO2A (Benthic Opportunist Annelids Amphipods) (Dauvin and Ruellet, 2009) biotic indices were calculated for each site across the study period. These values provide an indication of overall habitat quality. AMBI was developed to quantify the ecological quality of European coasts, providing a classification of pollution or disturbance levels in a site (Borja *et al.*, 2000). BO2A represents the ratio between opportunistic species and sensitive species in estuarine environments (Dauvin and Ruellet, 2009) as a measure of benthic habitat quality used in ecological assessments. AMBI values were calculated using the BEQI2 package in the R software, and BO2A values were calculated as:

$$BO2A = \log_{10} [(f_{oa} / f_{sa} + 1) + 1]$$

Where f_{oa} is the frequency of opportunistic annelids, Oligochaeta and Hirudinea within a sample, divided by the total abundance within the sample, and f_{sa} is the frequency of amphipods, excluding opportunistic *Jassa* spp., divided by the total abundance in a sample (Dauvin *et al.*, 2016).

3.3 Results

Since no Vessel Monitoring System (VMS) or logbook data from this fishery exists, the fishing intensities at each site during the study period were quantified by fisheries patrol sightings data (provided by SIFCA) and by aerial imagery obtained from the drone survey across the site. Results indicate that the extent of dredging in the newly opened and historically dredged sites is similar, but slightly higher in the new site (Table 3.2). Sightings are notably higher in the heavily dredged site despite similar estimates for both sites, which may be due to the infrequency of SIFCA patrols. The scarring identified in the control site through this method is considered to be due to the 2015 stock assessment that was carried out over a single day in May 2015 by SIFCA in the area which used a local pump-scoop fisherman to sample clams in the area, as no sightings were observed by patrol officers throughout the study period and discussions with local fishermen indicated that this area was not fished commercially during the study period.

Table 3.2. Fishing intensity in each area as represented by the number of Southern Inshore Fisheries and Conservation Authority (SIFCA) patrol sightings in each area during the 2015 season and the estimated disturbed area from image classification methods.

Site	Fishing Intensity	No. Sightings	Estimate Disturbed Sediment (% area)
Control	Low (none during study period)	0	20.11
Newly Opened	Intermediate (short-term)	11	68.03
Heavy Dredging	High (long-term)	38	67.94

3.3.1 Environmental Factors

Particle size distribution curves for each site in June and November are presented in Figure 3.3. Both organic content and volume of fine sediments decreased in all sites throughout the study period, with the largest reduction in each measure observed in the heavily dredged site (Table 3.3).

Table 3.3. Mean (\pm 95 CI) organic content (mass Loss On Ignition (g)) and % volume sediment < 0.63 μ m across each site in June and November 2015. Significant changes throughout the study period are indicated in bold.

Site	Organic Content (g)		% Fine Sediment	
	June	November	June	November
Control	6.39 \pm 1.08	6.25 \pm 0.72	83.25 \pm 3.30	80.71 \pm 1.50
Newly Opened	5.71 \pm 0.66	5.58 \pm 0.56	81.20 \pm 2.30	75.68 \pm 3.03
Heavy Dredging	3.19 \pm 0.39	2.48 \pm .39	64.87 \pm 4.18	54.73 \pm 4.67

Two-factorial ANOVAs show a significant main effect of site ($F(2,138) = 109.01$, $p < 0.001$) and of time ($F(1,138) = 21.19$, $p < 0.001$) on the proportion of fine sediments (% volume $< 0.63\mu\text{m}$). Tukey post-hoc tests indicated that a significant reduction in proportion of fine sediment was only found at the heavily dredged site throughout the study period. In both June and November, fine sediment content at this site was significantly lower than that at both the control site and newly opened site, while no difference was present between the newly opened and control sites. The interaction term is non-significant ($F(2,138) = 2.82$, $p = 0.06$), with an eta-squared value of the interaction of 0.01, indicating a small effect of dredging on the fine sediment content throughout the study period.

A slight reduction in sediment organic content was observed in all sites although this was largest in the heavily dredged site (Table 3.3; Figure 3.3). A two-factorial ANOVA shows no significant effect of time ($F(1,138) = 1.46$, $p = 0.23$) on the organic content of sediment, but a significant main effect of site ($F(2,138) = 63.84$, $p < 0.001$). Tukey post-hoc testing indicates significantly less organic content at the heavily dredged site than both the newly dredged and control sites, which showed no difference. Results show no significant interaction term between the effect of site and time on organic content ($F(2,138) = 0.51$, $p = 0.60$), with an eta-squared value of < 0.01 , indicating only a very slight effect (Cohen, 1988).

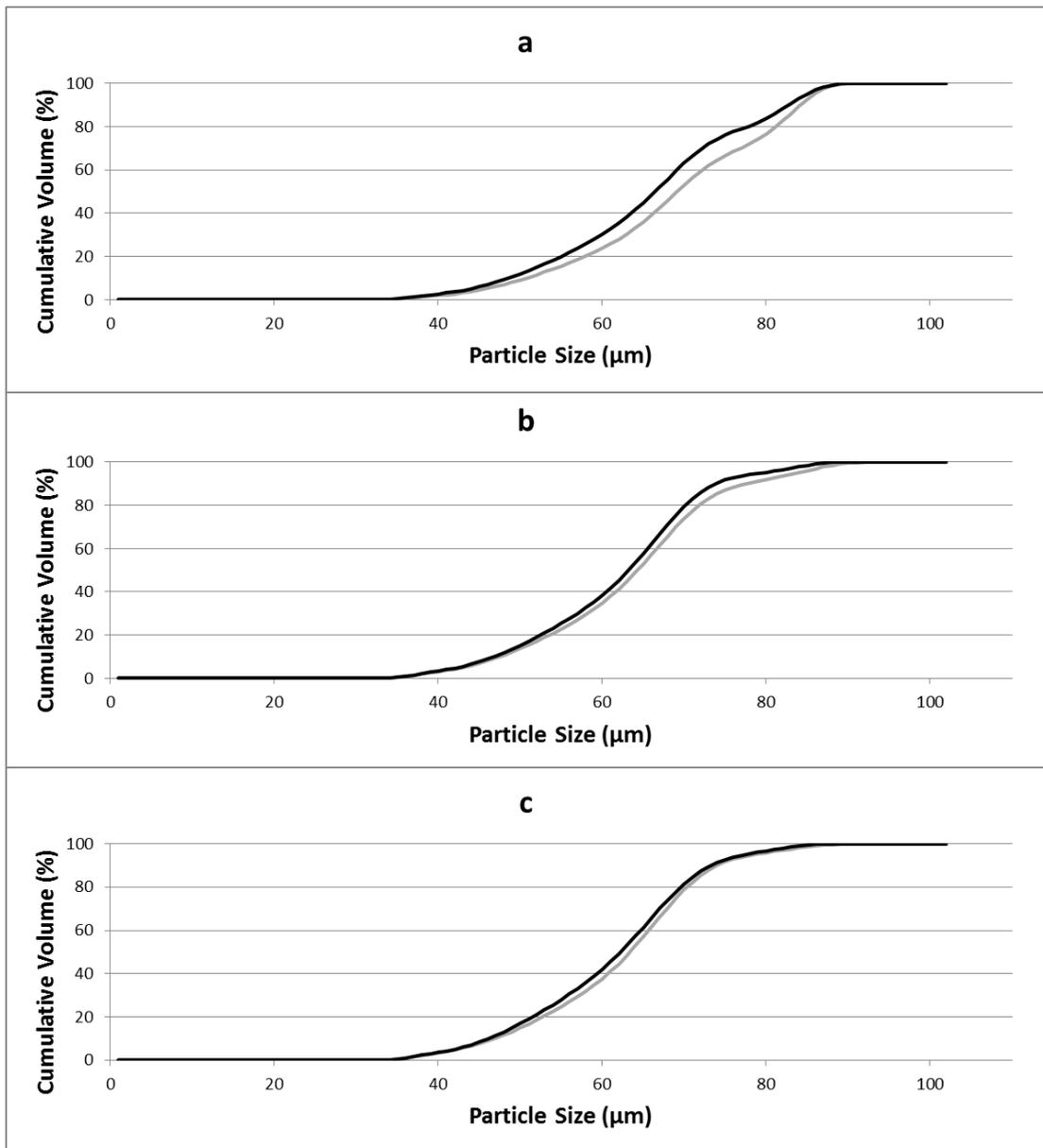


Figure 3.3. Sediment particle size cumulative volume curves for each site in June and November 2015. a) heavily dredged site; b) newly dredged site; c) control.

3.3.2 Biological Assemblage

A total of 49 taxa (Table A2.1, Appendix 2) were identified in samples from June and November and the assemblages in the study area were similar to that found in the area during a previous, unrelated biotope survey across the whole harbour (Herbert *et al.* 2010). SIMPER analysis indicates that *Hediste diversicolor*, *Tubificoides* spp. and the bivalve *Abra tenuis* dominate assemblages at all sites (Tables A2.2 to A2.4 (Appendix 2)). Although *H. diversicolor* is the dominant species, abundance varied between treatments. The contribution of other species also differs between sites, with species within the order Actiniaria and the cirratulid *Aphelochaeta marioni* making the largest contribution to the similarity of samples across the heavily dredged site. Although species assemblages were similar across the newly opened and heavily dredged sites, species occurred in different abundances. Table A2.4 (Appendix 2) indicates comparatively higher abundances of the polychaetes *H. diversicolor* and *A. marioni* at the heavily dredged site. In the nMDS plot derived from the Bray-Curtis similarity matrix clearer grouping of samples between sites taken in November 2015 is apparent than in June (Figure 3.4). Two plots based on June and November data separately are presented in Appendix 2 (Figure A2.2) for clarity.

A test for homogeneity in the multivariate dispersions indicates no difference between groups ($p = 0.90$) and PERMANOVA was therefore considered appropriate and performed on untransformed data. Two-factorial PERMANOVA shows a significant main effect on the macrofaunal assemblage of both site and time (before and after fishing) (Table 3.4). Moreover a significant interaction between site and

time indicates that the magnitude of the change in the overall assemblage throughout the study period varies between sites. The proportion of sandy sediment ($> 0.63\mu\text{m}$) has a significant influence on the community structure, although no significant effect of organic content is evident. Proportion of fine sediments was removed from this analysis due to significant co-linearity with sand content.

Table 3.4. Results of a two-factorial PERMANOVA on community abundance data across sites between June and November 2015 and including environmental covariates. d.f. = degrees of freedom; S.S. = sum of squares; M.S. = mean squared.

Source	d.f.	S.S.	M.S.	Pseudo-F	p-value
Site	2	5.90	2.95	17.48	0.001
Month	1	0.84	0.84	5.01	0.002
Site*Month	2	0.94	0.47	2.80	0.002
% Sand	1	0.41	0.41	2.42	0.027
Organic Content	1	0.27	0.27	1.61	0.112
Residuals	136	22.94	0.17		

Pairwise comparison shows that macrofaunal community structure differed significantly between sites both before and after dredging (Table 3.5). The magnitude of this difference appears to have changed however throughout the fishing period, as demonstrated by the interaction term. The t-statistics, representing the ratio of between- to within-group variability, indicate an increase in this difference between the control site and both the newly and heavily dredged

sites, with a difference in the t-statistic between June and November of 0.82 and 0.97 at the newly and heavily dredged sites respectively. The difference between the two dredged sites decreased however, with a reduction in the t-statistic of 0.23 between June and November, consistent with the clearer grouping in November in Figure 3.4 (and Figure A2.2, Appendix 2).

Table 3.5. Results of pairwise comparison of macrofaunal assemblage between sites in June and November 2015 following the PERMANOVA analysis.

Comparison	Month	t-statistic	p-value
Control Site : Newly Opened	June	2.3895	0.0001
Control Site : Heavy Dredging	June	3.9779	0.0001
Newly Opened: Heavy Dredging	June	2.6697	0.0001
Control Site : Newly Opened	November	3.206	0.0001
Control Site : Heavy Dredging	November	4.9506	0.0001
Newly Opened: Heavy Dredging	November	2.4434	0.0001

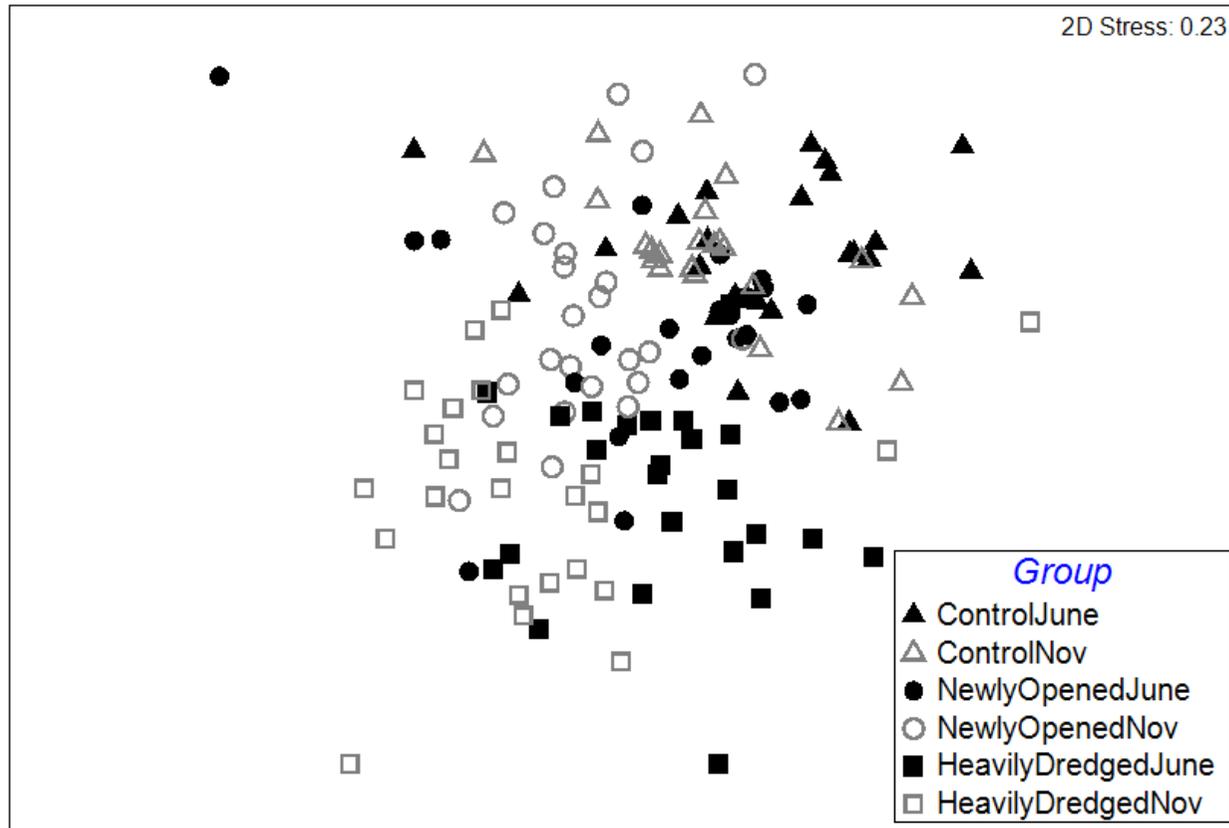


Figure 3.4. Two-dimensional MDS plot derived from the log ($x+1$) transformed similarity matrix indicating the similarity between the macrofaunal assemblages at sampling locations in June (black) and November (grey) 2015. Circles = newly dredged site/medium dredging intensity (open July – October), squares = heavily dredged site, triangles = control site.

CAP was undertaken to characterise the distinctiveness of the differences identified through PERMANOVA more effectively than through MDS ordination, which indicated little notable grouping of samples (Anderson, Gorley and Clarke, 2008). CAP ordination shows clearer grouping between samples from the middle, newly dredged site between June and November (Figure 3.5). Samples from this site from June are predominantly grouped together with control samples, while those from November show more variation. Overlaid species vectors indicate that samples from the heavily dredged site and to some extent the newly opened site obtained in November are characterised by higher abundances of polychaete and oligochaete worms, in particular capitellids, *Hediste diversicolor*, *Tubificoides* spp. and *Aphelochaeta marioni*. Samples from the control site however indicate a dominance of *Peringia ulvae* and *Abra tenuis*.

CAP results indicate that the optimal number of PCO axes required to explain the highest proportion of variance in the data is 4 ($m = 4$). This explains 63.9% of variation within the data, with 59.03% of samples correctly classified (i.e. classified into the correct group based on the data).

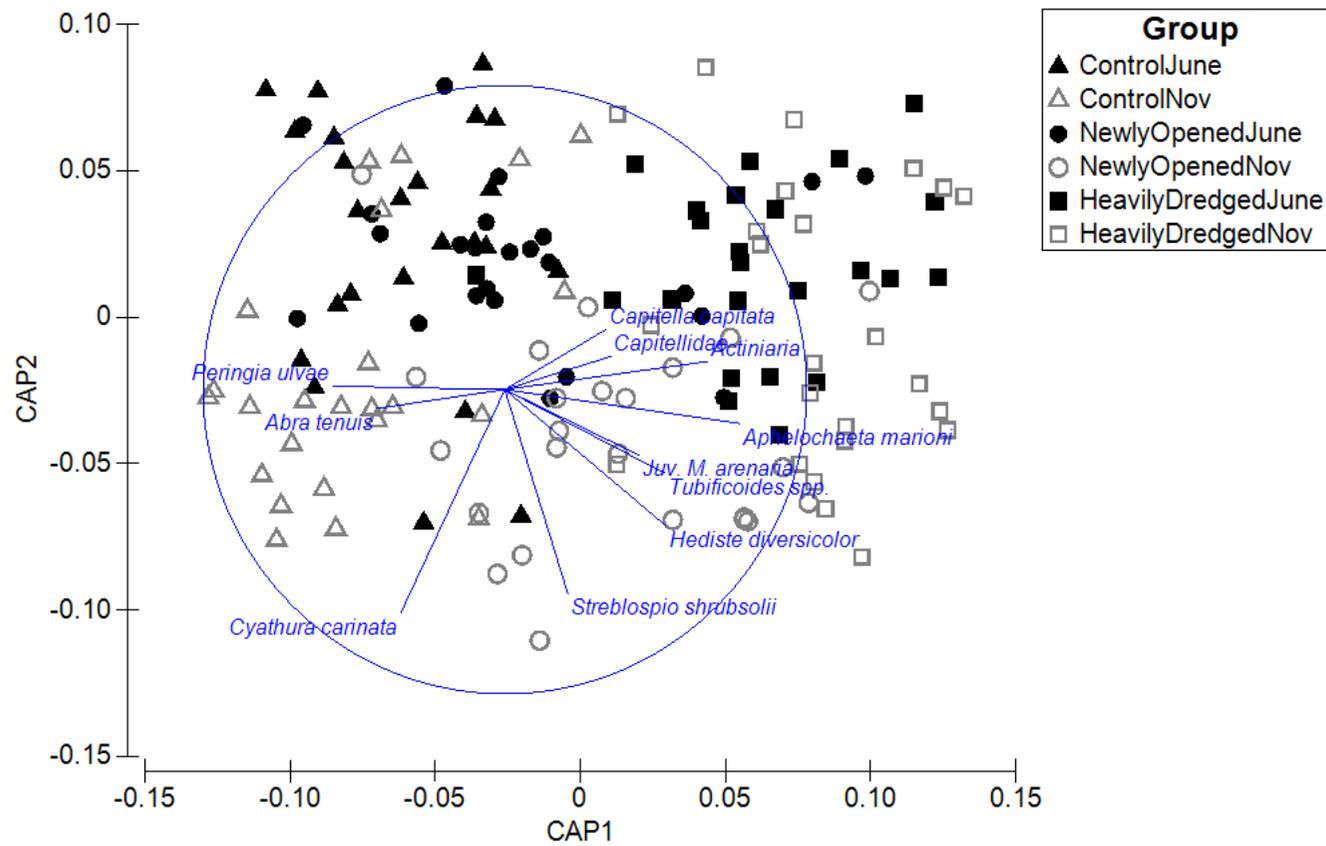


Figure 3.5. Canonical ordination for the discriminant analysis of log+1 transformed species abundance data. Spearman rank correlations of individual species abundance are overlaid (restricted to those with vector lengths < 0.4). Black symbols = June 2015; grey symbols = November 2015. Circles = newly dredged site (open July – October), squares = heavily dredged site (historically dredged, open all season), triangles = control site.

The overall structure of the benthic assemblage at the site newly opened to dredging appears therefore to have shifted further from resembling the control site towards conditions similar to those at the heavily dredged site during the study period. SIMPER analysis identified those species contributing most to the difference at each site between June and November 2015 (Tables A2.5 to A2.7 in Appendix 2). Most species demonstrate an increase in abundance between June and November, regardless of site. At the newly dredged site, notable increases of *H. diversicolor* and *A. marioni* are evident (Figure 3.6), and ANOVA showed significant interaction terms for both these species (Table 3.6). In comparison to the other sites, *A. marioni* was largely absent from the control site and showed a lesser increase at the heavily dredged site, while densities of *H. diversicolor* remained relatively stable at both the control and heavily dredged sites throughout the study period, although more than doubled in the site newly opened. These increases in *H. diversicolor* largely represent increases in smaller (< 10mm) individuals. Throughout the study period the proportion of this size class increased on average from 27% to 55% and from 11% to 58% of all *H. diversicolor* in samples from the newly and heavily dredged sites respectively. No such trend is evident at the control site where the relative proportions of each size group appeared stable (18% and 19% in June and November respectively).

Densities of the spionid *Streblospio shrubsolii* also increased dramatically at the newly dredged site compared to the other sites. In contrast, densities of the molluscs *A. tenuis* and *Peringia ulvae* decreased at both the dredged sites, compared to increases at the control site. The reduction of *A. tenuis* was largest at

the heavily dredged site (Figure 3.6), and a significant ANOVA interaction term was evident found for this species (Table 3.6). Densities of all species are generally much lower at the control site, which appear more stable throughout the study period than at the two dredged sites, at which the magnitude of the change is much larger.

Table 3.6. ANOVA results for individual species abundance across the study period and between sites.

Species	Site		Month		Site*Month	
	F-value	p-value	F-value	p-value	F-value	p-value
<i>H. diversicolor</i>	20.10	< 0.001	1.38	0.241	7.37	< 0.001
<i>Tubificoides</i> spp.	13.59	< 0.001	4.81	< 0.05	0.25	0.78
<i>A. marioni</i>	18.58	< 0.001	0.004	0.95	3.38	< 0.05
<i>S. shrebsolii</i>	1.56	0.21	11.25	< 0.01	1.89	0.16
<i>P. ulvae</i>	5.00	< 0.01	2.98	0.09	1.38	0.25
<i>A. tenuis</i>	11.96	< 0.001	8.09	< 0.01	8.01	< 0.001

The size of the effect (Hedges' *d*) in changes in abundance for each species at both the newly and heavily dredged sites shows a positive effect of fishing on the abundance of all species except *A. tenuis* and *P. ulvae*, with the largest change evident in the increase of *H. diversicolor* at the newly dredged site (Table 3.7).

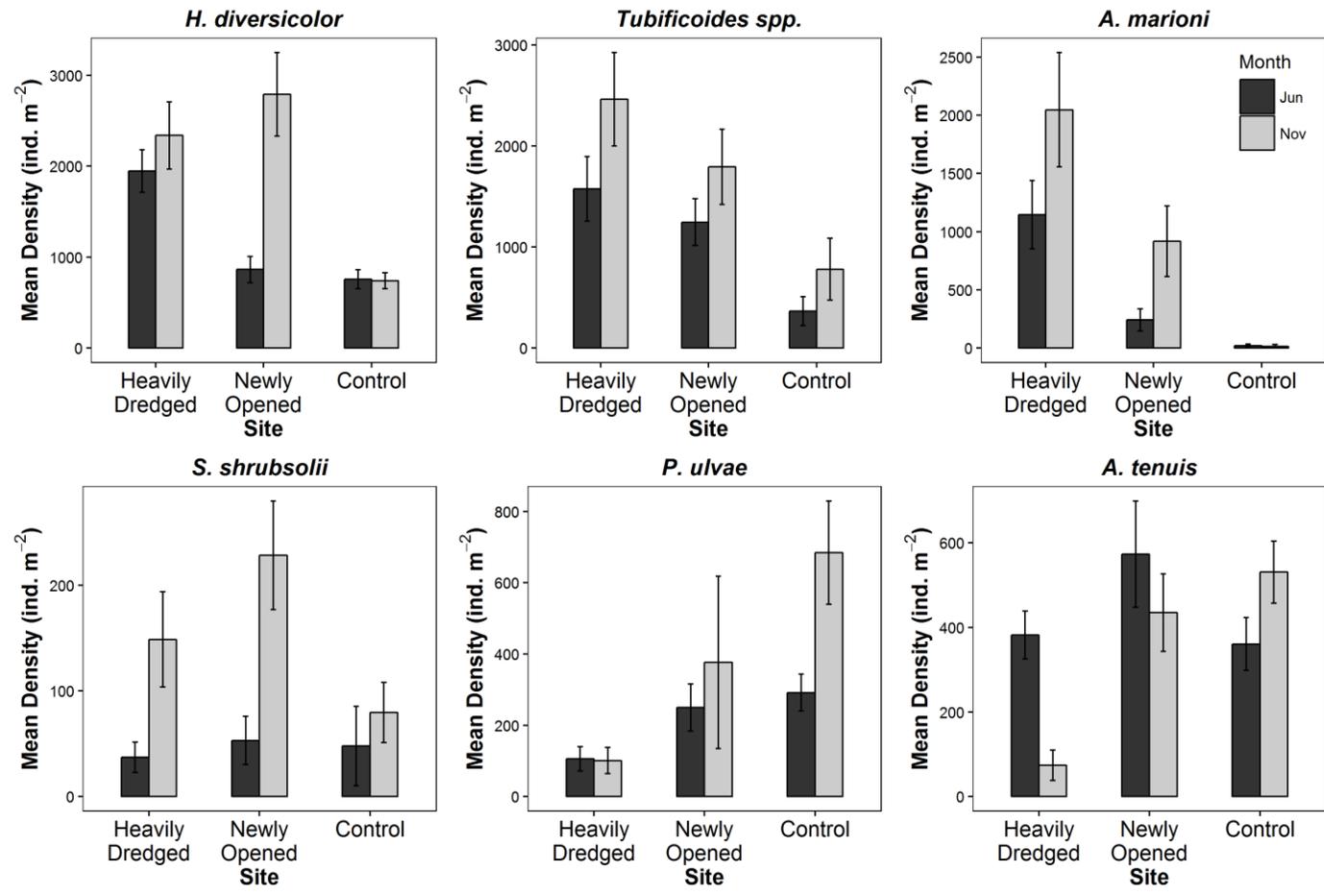


Figure 3.6. Mean (\pm S.E.) densities of common species in June (dark grey bars) and November (light grey bars) 2015 at each site. *H. diversicolor* (Phyllodocidae), *Tubificoides* spp. (Tubificidae), *A. marioni* (Cirratulidae), *S. shrubsolii* (Spionidae), *P. ulvae* (Hydrobiidae), *A. tenuis* (Semelidae).

Table 3.7. Standardised mean differences in abundance of each species plus total number of individuals at newly and heavily dredged sites, compared to control conditions across both sampling times.

Species	Newly Opened vs. Control		Heavy Dredging vs. Control	
	Hedges' <i>d</i>	S.E.	Hedges' <i>d</i>	S.E.
<i>H. diversicolor</i>	1.169	0.426	0.289	0.409
<i>Tubificoides</i> spp.	0.006	0.412	0.100	0.413
<i>A. marioni</i>	0.678	0.413	0.522	0.411
<i>S. shrebsolii</i>	0.691	0.419	0.476	0.415
<i>P. ulvae</i>	-0.581	0.416	-0.755	0.415
<i>A. tenuis</i>	-0.273	0.409	-1.499	0.432
Total Individuals	0.267	0.427	0.175	0.418

3.3.3 Community Descriptors and Habitat Quality

Diversity indices indicate a significant main effect of site ($F(2,138) = 13.161$, $p < 0.001$) on species richness across both months, with a significantly higher number of species occurring in samples from the dredged sites compared to the control site (Table 3.8). A significant main effect of month ($F(1,138) = 14.99$, $p < 0.001$) was also observed, although pairwise comparisons indicate that this increase was only significant in the site newly opened. The interaction term however was non-significant ($F(2,138) = 1.30$, $p = 0.27$).

Simpson indices, which provide a measure of dominance within assemblages, were similar across sites with only a slight but non-significant change apparent over the study period in the heavily dredged site (Table 3.8).

Results show a significant main effect of site ($F(2,138) = 3.19, p < 0.05$) and time ($F(1,138) = 7.30, p < 0.01$) on Shannon-Wiener indices, with an increasing trend apparent from the control site at the upper reaches of the creek to the outer, heavily dredged site (Table 3.8). A post-hoc Tukey test indicates that mean Shannon-Wiener values differ significantly between the site newly open to dredging in November and the control site in June. No significant interaction was observed ($F(2,138) = 1.35, p = 0.26$).

Two-factorial ANOVA shows a significant effect of both site ($F(2,138) = 28.21, p < 0.001$) and time ($F(1,138) = 15.68, p < 0.001$) on the total number of individuals found in samples (Figure 3.7). The interaction term of the model was non-significant ($F(2,138) = 1.90, p = 0.15$). Pairwise comparisons however indicate a significant increase in the total number of individuals at the newly dredged site, while no such difference was observed at the control or heavily dredged sites. Total number of individuals was significantly higher at the heavily dredged site than at the control site across the study period. By November the total abundance had increased at the site newly opened and was now similar to the heavily dredged site and significantly higher than at the control site.

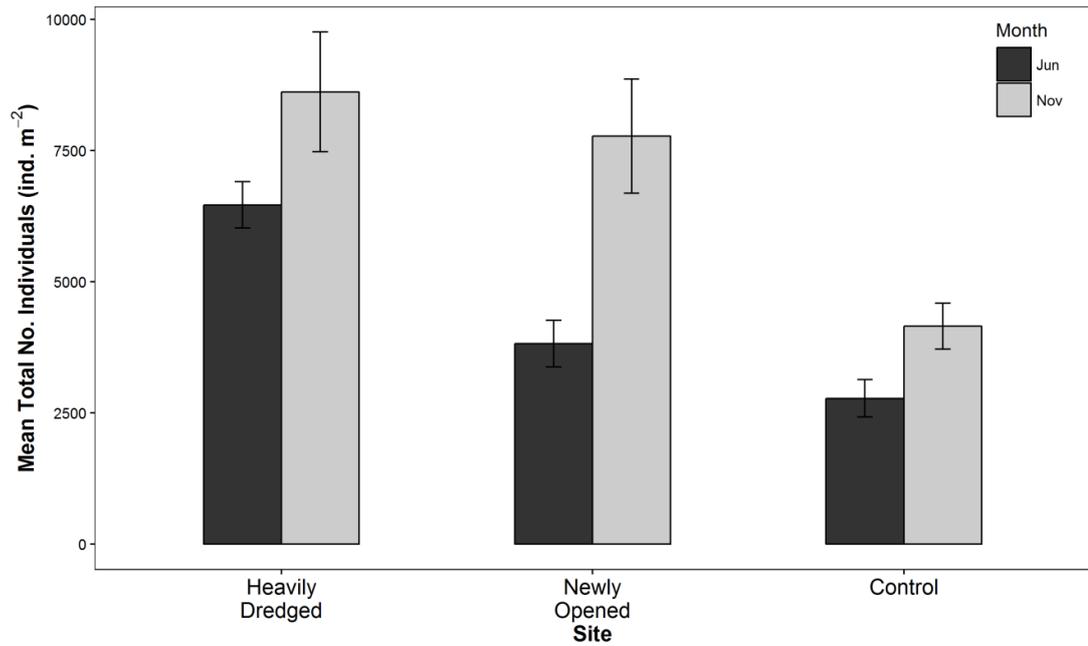


Figure 3.7. Mean (\pm S.E.) total number of individuals per m² observed in samples from each site in June (dark grey bars) and November (light grey bars) 2015.

Biotic indices indicate site differences in both AMBI ($F(2,138) = 11.94, p < 0.001$) and BO2A ($F(2,138) = 29.43, p < 0.001$) values, although no significant effect of month or the interaction term. Despite significant site differences in the AMBI values, all sites are classed as ‘moderately disturbed’ (Borja *et al.*, 2000). BO2A results indicate that at both sampling times the control site and the newly dredged site are of ‘good’ quality, while the heavily dredged site is of ‘moderate’ quality (Dauvin and Ruellet, 2009) (Table 3.8).

Table 3.8. Mean (\pm 95% C.I.) diversity and biotic indices (AMBI: AZTI Marine Biotic Index; BO2A: Benthic Opportunistic Annelid Amphipods) for each site in June and November 2015.

Significant changes over time are highlighted in bold. Thresholds for each biotic indices are included below.

Site	Species Richness		Simpson		Shannon-Wiener		AMBI		BO2A	
	June	Nov	June	Nov	June	Nov	June	Nov	June	Nov
Control	5.33 \pm 0.71	6.29 \pm 0.60	0.87 \pm 0.22	0.88 \pm 0.02	1.56 \pm 0.13	1.73 \pm 0.10	3.36 \pm 0.24	3.52 \pm 0.24	0.05 \pm 0.02	0.06 \pm 0.02
Newly Opened	5.83 \pm 0.79	7.88 \pm 0.88	0.86 \pm 0.02	0.87 \pm 0.02	1.63 \pm 0.12	1.87 \pm 0.12	4.02 \pm 0.25	3.81 \pm 0.24	0.12 \pm 0.06	0.11 \pm 0.04
Heavy Dredging	7.33 \pm 0.75	8.13 \pm 1.29	0.86 \pm 0.03	0.84 \pm 0.08	1.80 \pm 0.12	1.83 \pm 0.21	4.06 \pm 0.27	4.01 \pm 0.27	0.16 \pm 0.06	0.16 \pm 0.06
AMBI Disturbance Thresholds: < 1.2 = undisturbed; 1.2 \leq 3.3 = slightly disturbed; 3.3 \leq 5.0 = moderately disturbed; 5.0 \leq 6.0 = heavily disturbed; 6.0 \leq 7.0 = extremely disturbed.										
BO2A Quality Status: < 0.025 =high; 0.025–0.130 = good; 0.130–0.199=moderate; 0.199–0.255=poor, >0.255=bad.										

3.4 Discussion

This study assessed the impacts of a novel pump-scoop dredge for which data is currently lacking. In the strictest sense, the sampling design used in this study is not fully replicated, although while the BACI design lacks replication of treatments, with inherent issues of pseudoreplication and distinguishing site vs. treatment differences, it was the most appropriate option within an established and operational fishery with limited resources available for the study. A grid design was considered likely to best capture any fishing effort in the newly opened area, which is hard to predict. While other sampling designs may be more effective in reducing uncontrolled variability and distinguishing treatment differences over site differences (Cotter *et al.*, 1997), the BACI design allows for changes due to dredging to be identified while accounting for natural spatial and temporal variability.

PERMANOVA results show site differences in the benthic community structure before the opening of the 2015 dredge season. No gradient in salinity exists across sites, and given the significant effect of sand content on community structure this is likely driven by the gradient in sediment type from the southerly reaches of the creek to the lower dredged areas where conditions are sandier.

Accurate data on fishing intensity of inshore vessels less than 15m is hard to obtain due to a lack of VMS data and a fishermen's logbook program tailored to the fishery. While our data only provides estimates of fishing intensity derived from SIFCA patrols and image analysis, following discussions with fishery officers and fishermen, we are confident that it accurately represents the distribution and relative intensity of fishing in the study area. Results of the aerial imagery analysis

show the newly opened site was subject to heavy dredging comparable to the site that has been historically dredged, and over the course of the first season, the community structure in the newly opened site shifted significantly from conditions that were initially similar to the control site to those comparable to the site under heavy fishing pressure. Results indicate that this change was characterised by an increase in the abundance of marine worms, particularly *H. diversicolor* and *A. marioni*, but a decrease in abundance of the bivalve *A. tenuis*, for which the interaction terms of the ANOVAs were all significant. Despite the significant change in community structure at the newly opened site, no change in the biotope or ecological quality of either of the dredged sites was identified. BO2A values however show the site subject to previous dredging is of poorer quality, indicating relatively higher abundances of opportunistic species within Polychaeta and Oligochaeta, such as those that increased most dramatically throughout the study period at the newly dredged site and demonstrated a significant interaction term.

Such opportunists colonise disturbed areas through rapid dispersal and high reproductive rates (Grassle, 1974, Diaz-Castaneda *et al.*, 1993), and may demonstrate large-scale spatial and temporal fluctuations in response to environmental changes (Fauchald and Jumars, 1979; Grassle, 1974; Pearson and Rosenberg, 1978; Bridges *et al.*, 1994; Rossi and Lardicci, 2002; Dean, 2008). The observed increases in these groups are consistent with past studies following environmental or physical disturbance (Thistle, 1981; Sarda and Martin, 1993; Hall and Harding, 1997; Spencer *et al.*, 1998; Lardicci *et al.*, 1997; Chainho *et al.*, 2006). Cesar (2003) observed similarly large increase in abundances of tubificid

oligochaetes and polychaetes *A. marioni*, *Polydora coliata* and *Phyllodoce malcatula* in the area around Round Island in the proximity of the study area (Figure 3.2) following six weeks of pump-scoop dredging, along with increases in *H. diversicolor* as observed in this study.

Clearly, seasonal changes in species abundances are evident throughout the study period. In many species, spawning and recruitment occurs throughout the summer months and into autumn when peaks in abundance may be observed (George, 1964; Scaps, 2002; Rossi and Lardicci, 2002), and the proportion of small (< 10mm) *H. diversicolor* in samples did increase in November 2015. Many of these recruits may be lost by the following spring however due to natural mortality throughout winter (Buchanan *et al.*, 1978; Gray, 1981). The BACI design allows for assessment of changes relative to such temporal variation however, and overall the biological changes observed were largest in the site newly subjected to dredging disturbance, the only site at which significant increases in species richness and total abundance were observed; not dissimilar to changes observed following the use of other dredge gears (Hall and Harding, 1997). This perhaps indicates preferential settlement of *H. diversicolor* and *A. marioni* in this newly disturbed area following dredging, in the absence of larger individuals and adults that reduces competition for space and food (Caswell and Cohen, 1991). *H. diversicolor* is a scavenger species and may therefore benefit in the short-term from dredging disturbance (Britton and Morton, 1994). It has been suggested that benthic disturbance itself may actually stimulate reproduction in infaunal species (Barry, 1989), allowing species to utilise

newly available patches and resources previously exploited by the dominant species in an area (Thistle, 1981; Pickett and White, 1985).

Physical disturbance is generally considered to reduce habitat heterogeneity and three-dimensional complexity (Auster *et al.*, 1996; Thrush *et al.*, 1998), although results are complicated by the different scales at which impacts occur. Locally, in low-energy, soft sediment environments such as the study area where high amounts of organic content and fine sediment occur, intermediate physical disturbance may increase habitat heterogeneity (Levin and Whitfield, 1994), promoting sediment oxygenation and turnover and perhaps facilitating juvenile settlement and an influx of species. Physiological stress due to a shallow redox layer may inhibit organisms' ability to occupy such sediments, perhaps evident in the lower levels of diversity and species abundances seen towards the more sheltered reaches of the study area in the control site, where higher levels of organic content and anoxic sediment were observed. McIlquham (2003) postulated that this may be the reason for an observed increased diversity in some areas of Poole Harbour subjected to heavy pump-scoop dredging for clams and cockles.

Body size plays an important role in defining and detecting the magnitude of a species' response to disturbance (Sanders *et al.*, 2007), and the observed changes are largely in small-bodied fauna that respond rapidly to environmental fluctuations (Pearson and Rosenberg, 1978; Bridges *et al.*, 1994; Rossi and Lardicci, 2002; Dean, 2008). While core sampling may under-sample larger species that are likely to be most affected by bottom-fishing (Lindeboom and de Groot, 1998; Bergman and van Santbrink, 2000), including the target species of the fishery, it is known that larger

and longer-lived species, particularly worms are currently rare in Poole Harbour (Herbert *et al.*, 2010). Furthermore, the shallow depth at which the pump-scoop dredge penetrates the sediment means that larger and deeper-burrowing species may be less likely to be affected by fishing.

Those species demonstrating a decline throughout the study (*A. tenuis* and *P. ulvae*) are small and relatively fragile molluscs that may suffer mortality from interaction with fishing gear and were the only species to demonstrate a reduction in abundance relative to the control site. A complete absence of epifaunal mollusc species and a significant reduction in the abundance of *A. tenuis* following mechanical dredging have been reported from nearby Langstone Harbour on the south coast of England (Southern Science, 1992). Bivalve molluscs such as *A. tenuis* comprise key prey items for molluscivorous shorebirds (Goss-Custard *et al.*, 2006) and managers must consider implications on the SPA and BSA designations in Poole, although monitoring may be necessary to investigate long-term impacts and recovery.

No impact on the organic content was observed throughout the study period, although fine sediments were significantly reduced at the heavily dredged site. Bottom-towed fishing gear can result in a significant sediment plume (Ferré *et al.*, 2008; O'Neill and Summerbell, 2011; Bradshaw *et al.*, 2012; Martin *et al.*, 2015), which can contribute to the loss of organic content and finer sediment (Mayer *et al.*, 1991; Schwinghamer *et al.*, 1998). Both organic content and the volume of fine sediments were lower in the heavily dredged site, perhaps reflecting the higher intensity of fishing or a more dynamic environment where coarser sediments

dominate. It is uncertain whether dredging caused the observed loss of fine sediments, and past studies have found no significant effect of pump-scoop dredging on sediment composition in Poole (McIlquham, 2003). Long-term or chronic fishing can nonetheless cause permanent shifts in habitat characteristics and community structure (Pauly, 1995; Handley *et al.*, 2014), with implications for settlement and recruitment patterns (Wilson, 1990; Pinedo *et al.*, 2000; Sebesvari *et al.*, 2006). No significant change in sediment composition was evident at the site where settlement appeared the greatest however.

As mentioned, despite the changes identified no large-scale shift in the overall biotope at the study sites has occurred between sampling events (Herbert *et al.* 2010) and there has been no change in habitat quality. Most species present are small-bodied and likely to pass through the dredge unharmed, and demonstrate natural fluctuations in abundance throughout the year (Grassle, 1974; Pearson and Rosenberg, 1978; Bridges *et al.*, 1994; Rossi and Lardicci, 2002; Dean, 2008). Assessments carried out by fisheries and environmental managers often monitor and assess the condition of marine ecosystems and habitats in relation to high-level targets and indicators in response to anthropogenic pressures, and are subsequently more concerned with shifts in habitat or biotope type larger than those observed. Under the European Marine Strategy Framework Directive (MSFD) environmental managers work towards maintaining favourable conservation status and achieving 'Good Environmental Status'. Given that fisheries managers are increasingly attempting ecological risk management processes to fishing activities (Gibbs and Browman, 2015), the observed short-term changes may be of low

concern to regulators and managers. Regular and long-term disturbance of this kind however may cause a permanent regime shift in community structure (Kraberg *et al.*, 2011) and more chronic reduction in abundances of bivalve molluscs (Piersma *et al.*, 2001), of which a number of species are present across the three sites.

It is recognised that recovery trends following fishing disturbance are an important consideration, which can vary according to the scale and intensity of the disturbance (Collie *et al.*, 2000; Kaiser *et al.*, 2006). Sampling following fishing disturbance was only undertaken once and due to the length of the season it is difficult to be certain when the last fishing disturbance took place within the study area. Clearly, changes have occurred in the BSA that coincide with its opening to short-term dredging, although evidence of the longevity and persistence of these changes is lacking, demonstrating the importance of continuous monitoring to inform adaptive management.

The Manila clam is spreading to other estuaries along the south coast of England and throughout Europe (Herbert *et al.* 2012; Humphreys *et al.* 2015; Chiesa *et al.*, 2017) which is likely to tempt fisherman to exploit populations with these or other novel gears. Fisheries managers must be vigilant with regards to the development of novel gears, particularly when incentivised by the introduction of commercially harvestable non-native species. Adaptive management should also evaluate monitoring methods to determine impacts within these environmentally sensitive habitats.

4. Remote sensing methods as a tool for quantifying the spatial extent and intensity of shellfish dredging in a marine protected area

4.1 Introduction

Bottom-contact fishing involves the use of fishing gears that physically interact with the seabed in order to harvest species living on or in the sediment, such as dredging, trawling or digging (Kaiser *et al.*, 2006). Often the most obvious and easily identifiable impact of such fishing activity is scarring of the seabed in areas where bottom-gears have been deployed, and the biological impacts on community abundance, diversity and biomass are well documented (Dayton *et al.*, 1995; Collie *et al.*, 2000; Kaiser *et al.*, 2006). In intertidal areas such impacts have implications for the conservation of shorebird populations that rely on benthic invertebrate prey resources for overwinter survival or to fuel onward migration (Stillman *et al.*, 2001; Atkinson *et al.*, 2003; Goss-Custard *et al.*, 2004). In protected areas in particular, bottom-fishing needs to be carefully managed to minimise such disturbance and accurate information on the distribution and intensity of fishing pressure is critical.

In many cases, understanding and predicting fishing impacts in order to inform management is complicated by difficulties in accurately quantifying the extent and intensity of disturbance. Many areas subject to fishing disturbance are remote, with difficulties relating to ease of access and in the case of subtidal environments, not being visible without the use of advanced seabed mapping techniques. Quantifying fishing effort and distribution in subtidal environments generally requires the use of costly techniques such as side-scan sonar, bathymetric light detection and ranging

(LiDAR) and multi-beam echo sounders (MBES) (Kenny, 2003). This is often coupled with detailed data on vessel movements from vessel monitoring systems (VMS). Inshore and intertidal fisheries however are often exploited by smaller vessels (<15m) on which VMS or logbook data are not compulsory. In these areas scars are often visible in the sediment when exposed at low tide and such areas may be easily accessed and photographed using unmanned aerial systems (UASs) (also known as drones, unmanned aerial vehicles (UAVs) and remotely piloted aircraft (RPA)). Such imagery represents valuable data to which remote sensing techniques are often applied.

The conspicuousness of physical scarring from fishing disturbance and the increased availability and affordability of UAS technology for environmental management and conservation purposes (d'Oleire-Oltmanns *et al.*, 2012; Watts *et al.*, 2012) provides an accessible and low-cost approach for quantifying the extent and intensity of bottom-fishing disturbance in intertidal habitats. Past studies have utilised aerial imagery and remote sensing techniques to map intertidal habitat extents (Thomson *et al.*, 2003), to monitor intertidal morphological changes (Mason *et al.*, 2010) and to quantify propeller scarring in shallow subtidal seagrass beds (Robbins, 1997; Dunton and Schonberg, 2002; Phinn *et al.*, 2008), although their use in assessing impacts of intertidal bottom-contact fishing remains largely untapped.

Two commonly used remote sensing methods in ecological studies are image classification and image texture analysis. Image classification of raster data is an often-used remote sensing technique for characterising land use/land cover (LULC) and habitat extent. Image classification can be broadly grouped into two methods:

unsupervised classification, whereby the classification aims to group together data from a multiband raster according to their relative spectral qualities with no user intervention, or supervised classification, in which data are allocated according to their similarity to pre-defined, user characterised classes (Foody, 2002). Image texture has previously been used in ecological studies as a proxy for vegetation structure and habitat complexity (Wood *et al.*, 2012). Wood *et al.* (2013) built on this application of texture analysis, exploring the efficacy of image texture derived from Landsat TM satellite imagery and infrared air photography as a predictor of high quality habitat and of avian species richness. Results showed image texture measures to strongly account for variation in avian density and species richness, more so than field-measures such as foliage height density, diversity and horizontal vegetation structure. These results demonstrate the potential for predicting the effects of changes in land use or habitat quality or complexity on biodiversity.

In Poole Harbour, UK, the non-native Manila clam *Ruditapes philippinarum* and the common cockle *Cerastoderma edule* are harvested using a 'pump-scoop' dredge. The pump-scoop dredge is a method unique to Poole Harbour, developed by local fishermen for use in intertidal and shallow subtidal areas (Jensen *et al.*, 2005), and is described in detail in Section 3.1. The dredge season runs from 25th May to 25th December each year, with additional seasonal restrictions on dredging within certain areas of designated "Bird Sensitive Areas" (BSAs), which allow dredging from 1st July to 31st October. Spiral scarring from pump-scoop dredging is clearly seen in intertidal areas at low water, ranging from around 5 to 12 metres in diameter. Previous work has sought to quantify the magnitude or extent of such disturbance

(Fearnley *et al.*, 2013), although largely relying on a semi-quantitative assessment of the intensity of the disturbance. The present study assesses the efficacy of the two methods of image classification and image texture in accurately quantifying the spatial extent and intensity of shellfish dredging in intertidal mudflats using aerial imagery of dredge scarring. These methods represent valuable tools for fisheries managers in accurately and effectively assessing fishing disturbance, with potentially profound implications for management. Results of each method are compared with sightings data routinely collected by the Southern Inshore Fisheries and Conservation Authority (SIFCA) to assess their efficacy.

4.2 Materials and Methods

The study was carried out in Wytch Lake, one of the designated BSAs in Poole Harbour. This site is the same study site as in Chapter 3, and represents areas subject to different dredging management measures. This comprised an area that has historically been dredged intensively by fishermen (chronic dredging intensity), an area within the BSA open to short-term (acute) dredging from July to October each year from 2015, and an area in which all dredging activity is prohibited (i.e. control conditions). For this study, each of these areas was labelled according to the dredging intensity (CH: long-term, chronic dredging; AC: short-term, acute dredging; CN: control conditions, no commercial dredging) (Table 4.1). Fishing intensity is derived from Southern Inshore Fisheries and Conservation Authority sightings data and discussions with local fishermen.

Table 4.1. Fishing intensity and seasonal openings of each site sampled under the dredge permit byelaw, which came in to force on 1st July 2015. Site codes: CN = control; AC = short-term, acute dredging; CH = long-term, chronic dredging.

Site	Fishing Intensity	Pre-byelaw	Post-byelaw
Control (CN)	Low (none)	Closed	Closed
Acute (AC)	Intermediate	Closed	Open (1 st July - 31 st October)
Chronic (CH)	High	Open	Open (25 th May - 24 th December)

At low tide (spring tide, LW 13:25, Height 0.5m) on 23rd November 2015 a DJI Phantom 3 Pro quad-copter Unmanned Aerial System (UAS) was flown automatically over the study site (Figure 4.1) using the Drone Deploy application. This was after the closure of the BSA to dredging on the 31st October and with fishing continuing outside of the BSA boundary (in the CH site). The UAS was flown in a conventional aerial survey pattern of parallel flight lines to acquire vertical stereo aerial photographs (VSAP). The orientation, length and spacing of this flight was designed to account for wind direction and strength (to minimise drift and crabbing and abrupt changes in altitude due to gusting of winds aloft) and to ensure sufficient photo overlap. All flights were undertaken with wind speeds less than 15 mph and at the maximum permissible altitude of 400ft. Reported units are in imperial, as is used in aviation law and practice, including the operation of UAS.

A total of 1191 12-megapixel images were acquired in Joint Photographic Experts Group (JPEG) format. These images were then processed using multi-angle, convergent photogrammetry in Agisoft Photoscan Professional. Initial exterior orientation of individual images was estimated using six degrees-of-freedom (DoF)

ephemeris data (eastings, northings, elevation, kappa, phi and omega). This method was also used to determine the relative exterior orientation between images. Unmatched images were rejected, leaving 1049 images. The resulting sparse point cloud of tie points between images was reduced in terms of numbers of cross-correlated VSAP, reprojection error, reprojection uncertainty and projection accuracy per point. Camera calibration, location and orientation were optimised based upon the remaining 145,496 tie points, using a bundle adjustment.

Each image was ortho-rectified and the resulting orthophotographs were mosaicked and reprojected to Ordnance Survey British National Grid (OS BNG) projection, using Airy Spheroid (1936) (Figure 4.2). The resulting 24-bit red, green and blue (RGB) orthophotograph mosaic had a ground sample distance (GSD, i.e. pixel size) of 3.05cm. Due to mud flats dominating the imagery, with associated safety concerns and limited tidal windows, it was not deemed feasible to utilize ground control points (GCP). Therefore it was only possible to perform exterior orientation based on the aforementioned 6 DoF ephemeris. For this reason the theoretical absolute locational uncertainty of each pixel is +/- 3m, although in reality the bundle adjustment is likely to have improved this considerably (but by an unquantifiable level). The relative locational uncertainty is likely to be considerably better still and of the order of a few pixels (i.e. approximately 12cm).

Images were loaded into the ArcMap 10.1 Geographic Information System (GIS) software for analysis. Individual images were first merged together using the software's spatial analyst tools. The merged image was then clipped to the extent of the intertidal habitat within the study site and divided into nine separate survey

polygons. These related to a sister study (Chapter 6) in which monthly bird observations had been carried out during the winter of 2015/2016 (Figures 4.1 and 4.2).

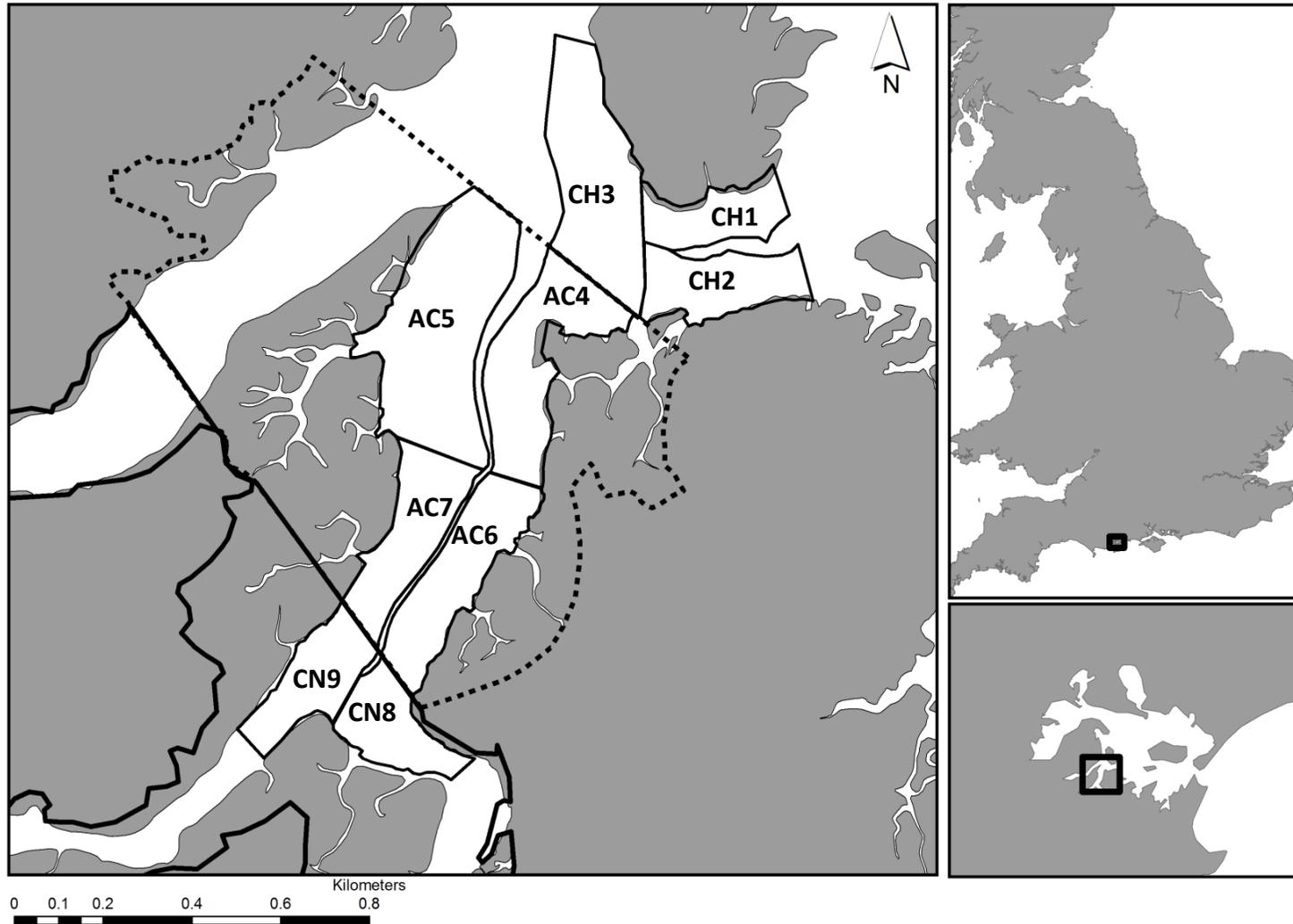


Figure 4.1. The study site of Wytch Lake within Poole Harbour, UK. Labelled survey sector polygons are overlaid (CH: long-term, chronic dredging; AC: short-term, acute dredging; CN: control, no commercial dredging). The dashed and solid areas indicate areas open to dredging from 1st July – 31st October and closed to dredging respectively.

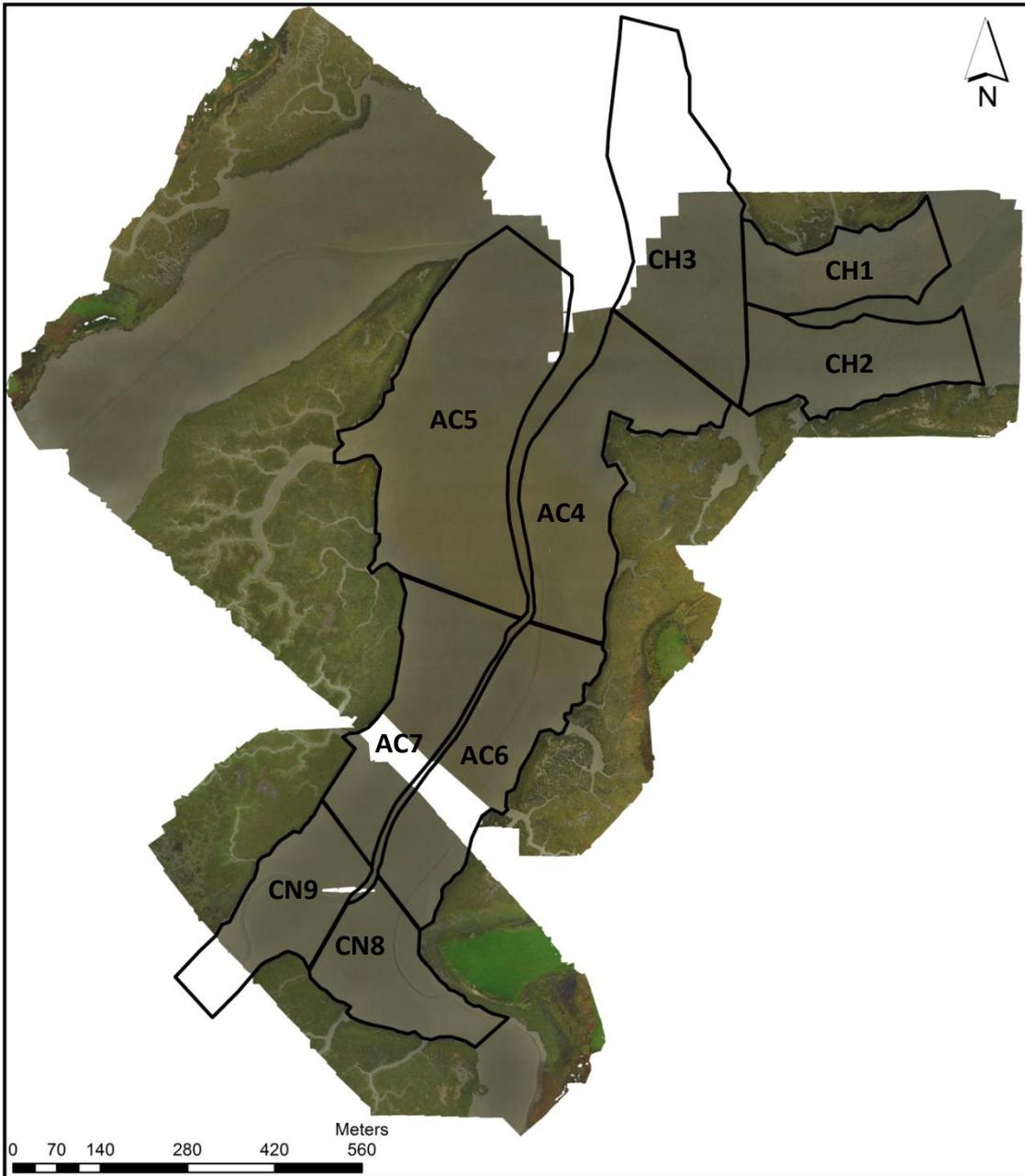


Figure 4.2. Aerial imagery of the study site obtained at low tide on November 23rd 2015 with survey sectors overlaid (CH: long-term, chronic dredging; AC: short-term, acute dredging; CN: control, no commercial dredging). White areas indicate no data, which were cut from the image before analyses were undertaken.

4.2.1 Image Classification

An unsupervised classification was performed using ArcMap 10.1 on the aerial imagery covering the intertidal study area clipped to each survey sector. Areas of no data were removed from the image and were not included in the analysis. The unsupervised classification process groups image pixels according to their individual spectral values. The user defines the maximum number of output classes (or groups) into which pixels are allocated, which is usually approximately 10 times the number of bands in the input raster. A maximum of 30 output classes were specified for the unsupervised classification process, which grouped pixels from the study area into 20-30 classes. This was performed on the aerial imagery clipped to each survey sector separately.

Next, each of the output pixel classes was manually grouped into one of three categories: 1 – scarred sediment; 2 – a combination of scarred and naturally disturbed or undisturbed sediment; 3 – undisturbed sediment. This process was done iteratively using best judgement, by highlighting an individual output class from the image classification process and determining whether pixels within that class represented either: scarred sediment as a result of pump-scoop dredging (i.e. physically disturbed sediment through fishing effort), undisturbed sediment, or a combination of the two. These classes and the criteria for their selection are summarised in Table 4.2. It was decided during initial exploratory analysis that using three classes was the optimal approach, as in some cases a single image class was mixed in its composition, representing spatially separated areas of both disturbed and undisturbed sediment. Areas such as this were allocated separately within the

middle group in order to account for this uncertainty and take a conservative approach. This can result from, for example, geomorphological processes along creeks and channels, natural hydrodynamic processes and gradients in sediment characteristics across shore heights, and partial physical recovery of older scars.

Once image classes had been grouped together, the reclassify tool in ArcMap 10.1 was used to create three new classes based on each of the groups described above. The area of each of these output classes was then calculated using the calculate geometry tool. A scale factor was assigned to each group based on the confidence in the classification in correctly characterising disturbed vs. undisturbed sediment due to dredging activity, and the absolute area of each class was then multiplied by the corresponding scale factor (Table 4.2). This was done in order to account for the uncertainty in the second class, in which some image classes represented a combination of dredged, naturally disturbed and undisturbed sediment. The method therefore takes a conservative approach in applying a scale factor of 0.5 to such pixel classes.

Table 4.2. Inclusion criteria for each of the three groups into which output classes from the unsupervised classification were included. The scale factor applied to each group to calculate an estimate of spatial extent of scarring is indicated.

Group	Class Selection Criteria	Scale Factor
1	Estimated > 80% pixels correctly classified as disturbed or scarred sediment. High confidence in classification.	1
2	Estimated 50% pixels correctly classified. Intermediate confidence in classification.	0.5
3	Estimated > 80% pixels correctly classified as undisturbed sediment. High confidence in classification.	0

4.2.2 Texture Analysis

Image texture analysis was also carried out on the aerial imagery (excluding areas of no data, which had been removed) using the focal statistics tool in ArcMap 10.1. Neighbourhood analysis was utilised, whereby the value of each cell, or pixel, in the output raster is calculated as a function of the original pixel values within a specified 'neighbourhood' surrounding that pixel. In this case a 'pixel diversity', or variety value, was assigned to each image pixel, calculated as the number of unique pixel values in a surrounding grid of a specified size, thus providing a measure of image texture or pixel diversity (Figure 3). This neighbourhood analysis used a moving window of 200 x 200 pixels, or 7 x 7m, thereby covering an area of 49m² which, given the diameter of dredge scarring from the image was generally measured as between 5 and 12 metres, covers sufficient area to capture any variation in sediment spectral characteristics due to dredging activity. Pixel values in the output

raster therefore represent the diversity in the pixel values across the surrounding 49m² of mudflat. The x,y position of the processing pixel in the grid was determined by:

$$X = (\text{width of neighbourhood} + 1) / 2$$

$$Y = (\text{height of neighbourhood} + 1) / 2.$$

Pixel diversity values from the raster output from the neighbourhood analysis were then summarised for each of the survey sectors using the zonal statistics tool. These could then be used to compare relative texture across the study area as a surrogate for dredging effort; a higher mean pixel diversity value was taken as indicative of increased habitat heterogeneity and sediment disturbance.

4.2.3 Comparison between Methods

In order to compare the two analysis methods a Spearman's rank correlation was carried out on the results for each of the nine survey sectors. To assess the strength with which each method relates to the known distribution of dredging effort, the number of SIFCA patrol sightings in each survey sector from 2011 to 2015 was correlated with the results from each method using Kendall's correlation. This method provides an estimate of Kendall's tau-b correlation coefficient, which is more effective when there are ties within the data. This was the case with the sightings data with no sightings observed from 2011 to 2015 in four of the survey sectors.

4.3 Results

4.3.1 Image Classification

Some areas of the survey site were missed during the UAS flight, indicated by areas of white (Figure 4.3). These were cut from the image before the analysis was undertaken. It is evident that dredging effort is mainly concentrated in the outer reaches of the Wytch Lake channel and to the south of Round Island (Figure 4.3), and mainly to the east of the main channel in the site subject to acute fishing pressure within the BSA. Inset on Figure 4.3 are magnified images of areas broadly characterised by each of the three output classes.

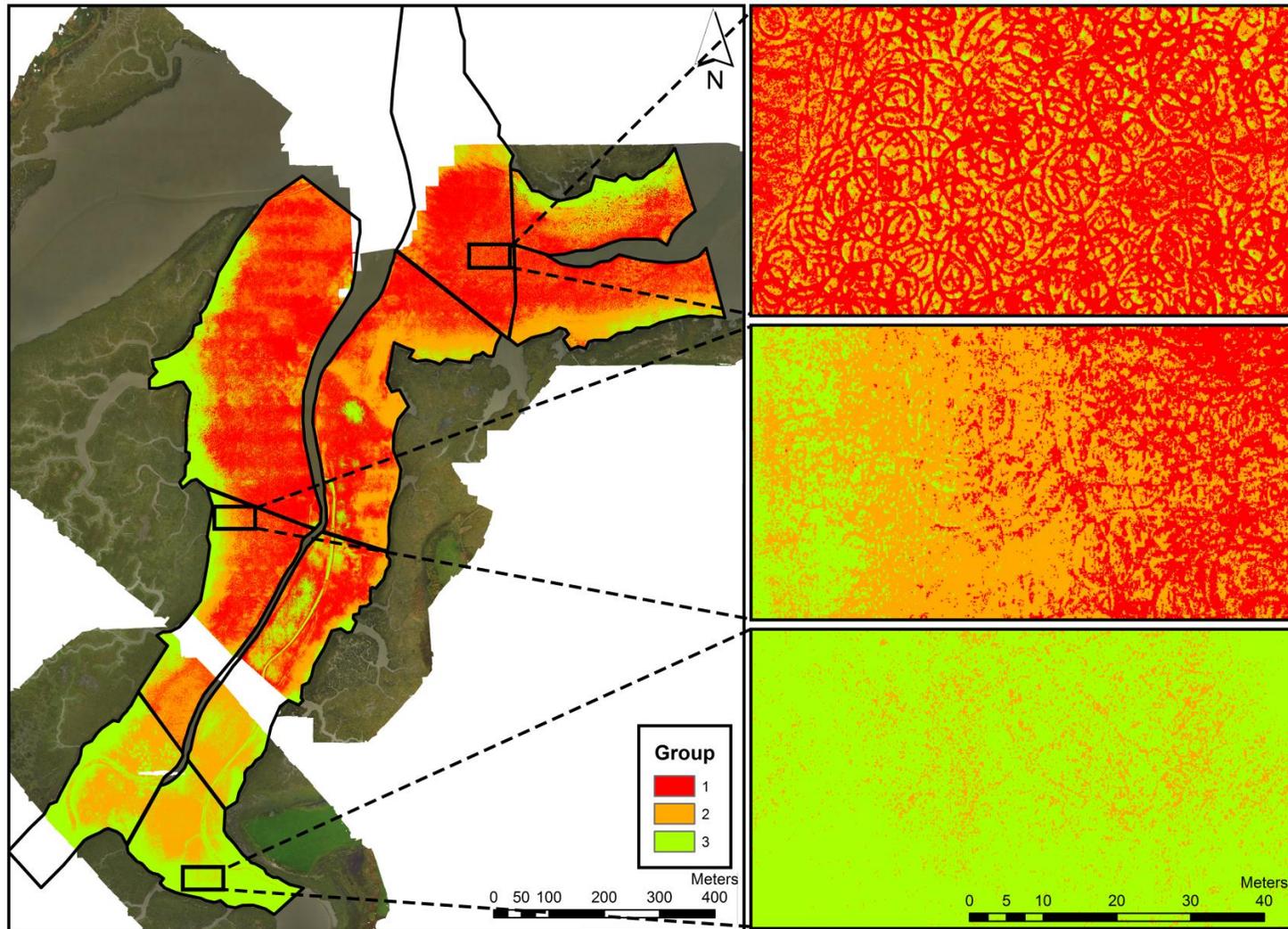


Figure 4.3. Results of the image classification process. The extent of each raster band in each of the survey sectors is evident. The magnified images on the right correspond to the extent indicators on the main map of the survey site. Round Island is the area immediately to the north of survey sector CH1.

Table 4.3. Measures of dredging extent derived from the image classification process described above, including the estimate for each class using the scale factors from Table 2.

Sector labels denoted with * indicate areas where data is missing and values are calculated using available data only.

Site (fishing pressure)	Sector Label	Recoded Image Class	Area (ha)	Cover (%)	Scarring Estimate (ha)	Scarring Estimate (%)	Estimated Total % Scarred
Chronic	CH1	1	1.33	10.03	1.33	10.03	14.82
		2	1.27	9.59	0.63	4.79	
		3	10.63	80.38	0.00	0.00	
	CH2	1	20.83	43.84	20.83	43.84	68.33
		2	23.26	48.97	11.63	24.49	
		3	3.42	7.19	0.00	0.00	
	CH3*	1	31.79	69.15	31.79	69.15	82.82
		2	12.57	27.33	6.28	13.67	
		3	1.62	3.51	0.00	0.00	
Site Total	CH	1	53.94	50.55	53.94	50.55	67.94
		2	37.10	34.77	18.55	17.38	
		3	15.66	14.68	0.00	0.00	

Acute	AC4	1	35.64	47.33	35.64	47.33	70.52
		2	34.91	46.36	17.46	23.18	
		3	4.75	6.30	0.00	0.00	
	AC5*	1	72.64	57.27	72.64	57.27	70.12
		2	32.61	25.71	16.31	12.85	
		3	21.60	17.03	0.00	0.00	
	AC6*	1	27.79	48.63	27.79	48.63	66.71
		2	20.67	36.16	10.33	18.08	
		3	8.70	15.22	0.00	0.00	
	AC7*	1	17.72	36.40	17.72	36.40	60.27
		2	23.25	47.75	11.62	23.87	
		3	7.72	15.86	0.00	0.00	
Site Total	AC	1	153.80	49.94	153.80	49.94	68.03
		2	111.43	36.18	55.72	18.09	
		3	42.76	13.88	0.00	0.00	
Control	CN8	1	0.00	0.00	0.00	0.00	17.42

		2	13.54	34.83	6.77	17.42	
		3	25.34	65.17	0.00	0.00	
	CN9*	1	0.00	0.00	0.00	0.00	23.08
		2	16.27	46.16	8.14	23.08	
		3	18.98	53.84	0.00	0.00	
Site Total	CN	1	0.00	0.00	0.00	0.00	20.11
		2	29.81	40.22	14.91	20.11	
		3	44.32	59.78	0.00	0.00	
Total	All	1	207.74	42.50	207.74	42.50	60.74
		2	178.35	36.48	89.17	18.24	
		3	102.74	21.02	0.00	0.00	

Dredging effort and therefore the area of habitat affected appears to be highest in the heavily dredged site and the area of the BSA opened in 2015 (Figure 4.4; Table 4.3). The extent of scarring in the northerly section of the heavily dredged site (CH1) appears relatively low however, comparable to levels of scarring observed in the control site (Figure 4.4). While no fishing activity was observed by SIFCA in the control site during the study period, the low levels of scarring are evident in the results.

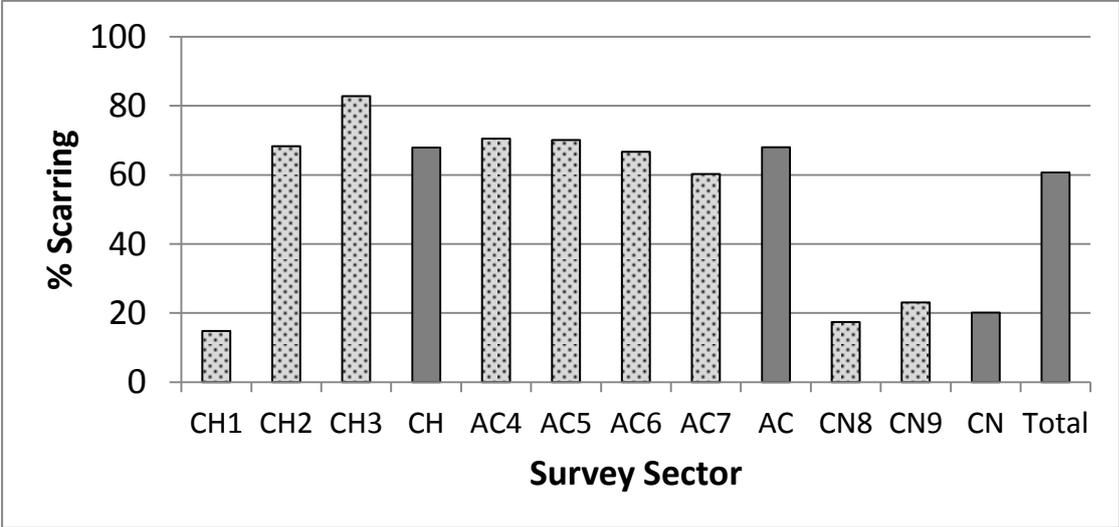


Figure 4.4. Percentage of each survey sector scarred by pump-scoop dredging derived from image classification. Dark grey bars indicate values for whole sites.

4.3.2 Texture Analysis

Results of the neighbourhood analysis follow the same broad trend as results from the image classification methods (Table 4.4; Figure 4.5). Taken as estimates of image texture, higher mean values of variance are attributed to the site subject to chronic fishing pressure and a decreasing trend occurs towards the control site at the upper reaches of the channel, where the lowest mean variance values are observed. This indicates that image texture is greater in areas subject to more

intense fishing. This trend is consistent for most measures presented in Table 4.4. Due to the large sample size deriving from the high resolution imagery, standard error values of pixel values are too small to be visible when plotted (Table 4.4), so standard deviations are presented (Figure 4.6) with one-way ANOVA indicating high significance between pixel diversity values between survey sectors ($F(8, 430109098) = 12046456.95, p < 0.0001$).

The range of pixel diversity values is lowest in the control sectors and highest in sectors in the site dredged most intensely. The largest range is observed in sector CH3, consistent with the largest extent of scarring identified through the image classification process. Conversely however sector CH1 shows the second highest range of pixel values, in contrast to the lowest extent of scarring identified through image classification of all sectors.

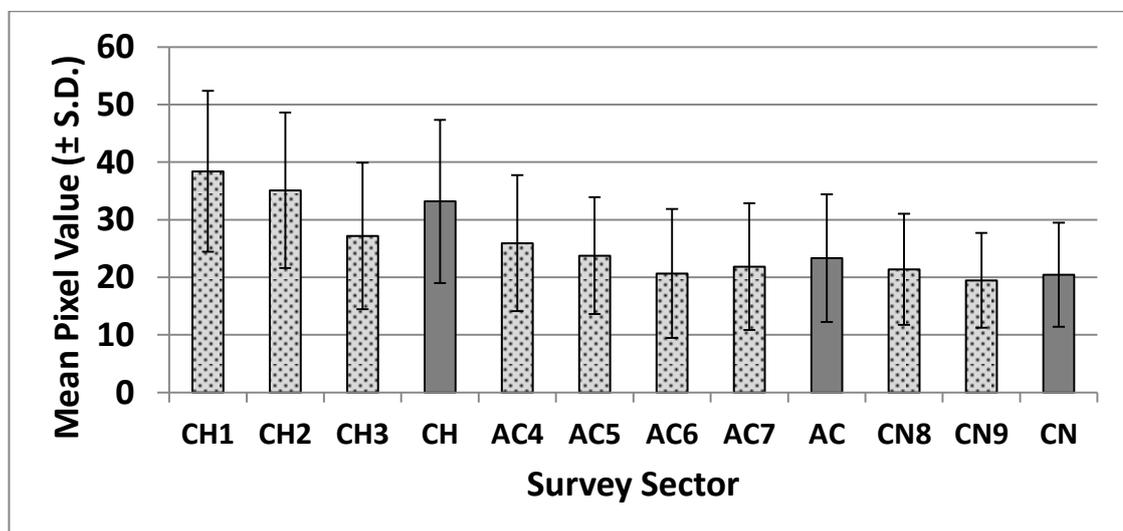


Figure 4.5. Mean (\pm S.D.) diversity value of pixels in each survey sector derived from the moving window neighbourhood analysis method.

Table 4.4. Zonal statistics for each individual survey sector. Each statistic is derived from the pixel diversity values of the output raster from the moving window neighbourhood analysis described in the methods.

Site	Survey Sector	Min	Max	Range	Mean (\pm S.D.)	S.E.	Variety	Majority	Minority	Median
CH	CH1	13	140	127	38.41 \pm 14.00	0.0026	128	25	13	36
	CH2	14	134	120	35.11 \pm 13.52	0.0022	121	28	116	32
	CH3	2	151	149	27.20 \pm 12.73	0.0020	150	17	99	23
	Site	2	151	149	33.18 \pm 14.17	0.0014	150	26	135	30
AC	AC4	10	127	117	25.93 \pm 11.81	0.0015	118	17	124	22
	AC5	2	113	111	23.76 \pm 10.17	0.0001	112	18	101	21
	AC6	2	120	118	20.66 \pm 11.23	0.0016	119	15	117	17
	AC7	2	109	107	21.86 \pm 10.99	0.0016	108	18	108	19
	Site	2	127	125	23.33 \pm 11.09	0.0001	126	17	124	20
CN	CN8	12	82	70	21.39 \pm 9.65	0.0017	71	17	79	18
	CN9	2	88	86	19.47 \pm 8.24	0.0015	87	16	87	17
	Site	2	88	86	20.46 \pm 9.04	0.0012	87	16	87	17

4.3.3 Comparison between Methods and with Known Fishing Distribution

Results show no correlation between the percentage of scarred sediment in each survey sector and the mean pixel diversity (Figure 4.8) ($r_s = 0.21$, $p = 0.58$). However, with CH1 removed from the analysis, the sector in which scarring was lowest and a clear outlier in the scatterplot, a significant correlation between the two is evident ($r_s = 0.74$, $p < 0.05$).

Results indicate a significant positive relationship between the number of sightings of dredge activity in each survey sector and the mean pixel diversity (Figure 4.8b) ($\tau = 0.81$, $p < 0.001$), but a non-significant relationship with the percentage of scarred sediment (Figure 4.8c) ($\tau = 0.09$, $p = 0.75$). With the outlier of CH1 removed the significance of this relationship is unchanged with pixel diversity remaining significant ($\tau = 0.75$, $p < 0.05$) and the correlation with scarring extent still non-significant ($\tau = 0.43$, $p = 0.15$).

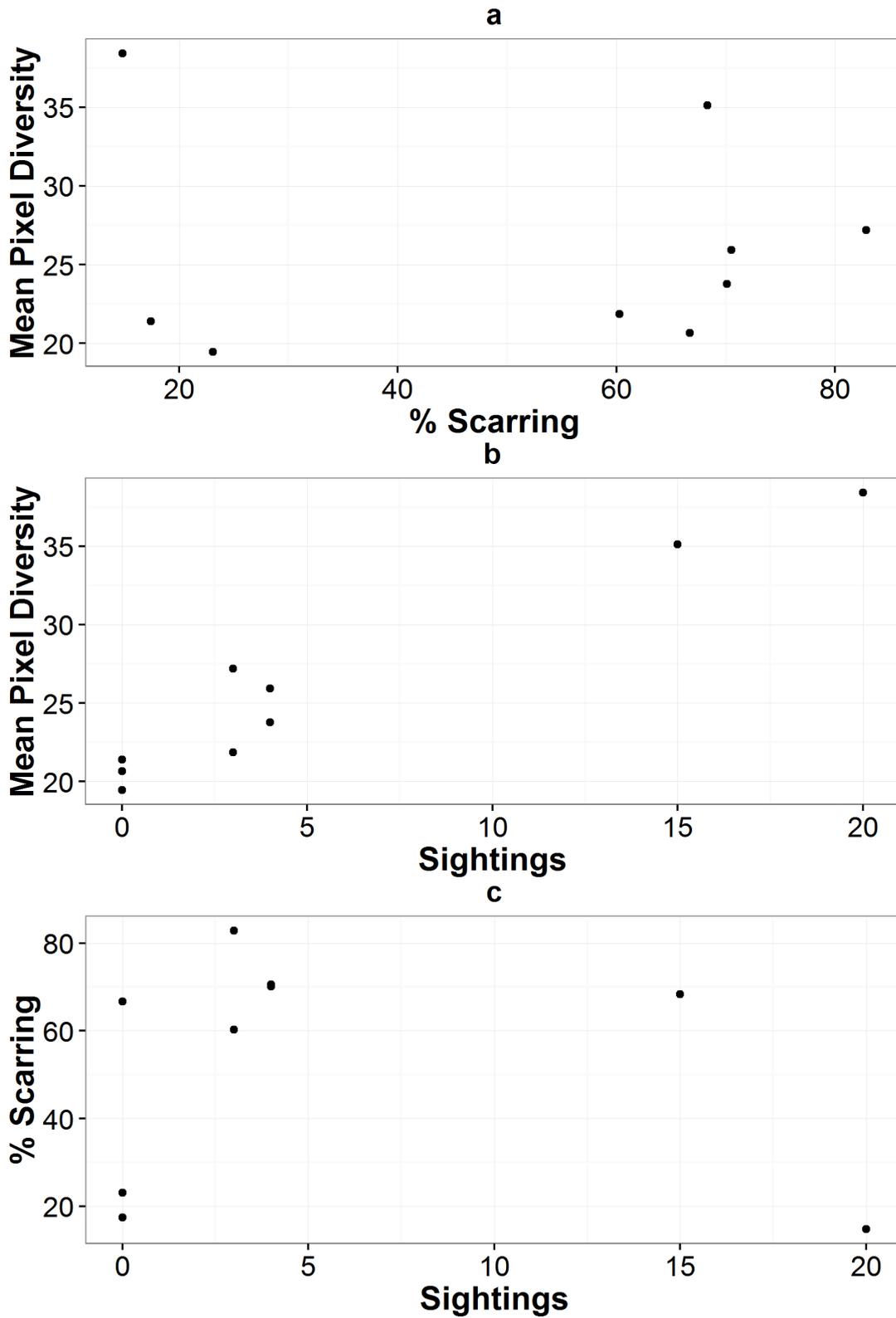


Figure 4.6. a) Mean pixel diversity plotted against % scarred sediment; b) no. fishing sightings vs. mean pixel diversity; and c) no. fishing sightings vs. % scarred sediment for each survey sector.

4.4 Discussion

With the outlier of CH1 removed from the analysis a significant correlation between the two methods was shown, indicating that the results are equivalent. When compared to actual fisheries sightings data results suggest that pixel diversity, and hence habitat heterogeneity, may be a more accurate measure of dredging disturbance than image classification results. Pixel classes were allocated to Group 2 when pixels within a class represented scarred sediment in one place and undisturbed sediment in another. These inconsistencies may arise due to the relative homogeneity of the study site. Remote sensing techniques are generally applied at a much broader scale than that used in this study (Hall *et al.*, 1991; Quattrochi and Goodchild, 1997) to identify different land use or habitat extents over many hectares, which may influence results. Soft sediment intertidal mudflats and sandflats are comparably uniform habitats however, potentially affecting the accuracy with which the classification process can identify spectral differences.

Results from the classification process may be confounded by other sources of disturbance causing similar spectral values to those disturbed by pump-scoop dredging, such as natural hydrodynamic processes. Other confounding factors include the gradient in sediment characteristics at different shore levels and the pooling of water within scars, resulting in similar spectral values to natural channels and small creeks. The method used accounts for such inconsistencies, although the lack of a significant relationship between the extent of scarring calculated through this method and the fisheries sightings data demonstrates the potential inaccuracies. Low levels of sediment disturbance detected through image

classification methods in the control site may indicate sediment disturbance from the processes described above, particularly as this area is close to a main channel and likely to be subject to higher hydrodynamic forces, or perhaps as a result of old scarring from illegal fishing activity that has shown partial recovery.

Broadly speaking, the texture analysis results indicate that pixel diversity measures follow the general trend identified through image classification, with lowest measures of variance in the control site, and values increasing towards the outer extents of the channel towards the heavily dredged site. While this is true of the broad trend, some survey sectors follow a different trend to the image classification procedure, notably sector CH1. The high pixel diversity values in this survey sector (the highest of all sectors) are not reflected in the scarring estimate from the image classification output, which is the lowest. This disparity is likely due to areas of high variance in sediment characteristics (and therefore pixel diversity) being grouped into the middle group during the image classification process, and therefore likely to be under-represented in the estimates of scarring extent. Sector CH1 does indeed have large areas of habitat categorised as Group 2 (Figure 4.3), which may explain the observed disparity, and with this removed from the correlation analysis a significant relationship between scarring and pixel diversity is observed.

It is worth noting that fisheries patrols are not carried out at the same frequency at which fishing occurs. Patrols are carried out irregularly, although approximately weekly, and sightings data are likely to vastly underestimate fishing activity. If scarring extent was correlated with true fishing values in each sector a stronger relationship may be observed. However while VMS data is lacking these sightings

are the best available data and pixel diversity most strongly correlates with this distribution of effort.

It is acknowledged that replication in this study is relatively low due to the number of survey sectors used. The site may have been divided into more sectors, perhaps using a gridded design. An investigation into the effect of scale over different grid sizes, particularly in image texture, may be worthwhile, as scale is an important consideration in remote sensing (Woodcock and Strahler, 1987). The approach taken in this study required *a priori* information on the nature of the disturbance (i.e. the size of the spiral scarring) to decide on an appropriate scale at which to run the analysis.

The application of both image classification and texture analyses as a means of quantifying fishing pressure in intertidal, and indeed subtidal habitats, is currently limited. Such methods may also be applied successfully in subtidal environments to characterise images obtained through Light Detection and Ranging (LiDAR) or side-scan sonar methods. This study shows how routinely collected aerial imagery can complement fisheries patrols, strongly increasing confidence in mapping fishing effort in inshore and intertidal fisheries and providing valuable information for management. By validating the results with official sightings data the image texture analysis yields more accurate results.

To conclude, the aerial imagery obtained shows clear evidence of pump-scoop dredging in the intertidal sediments of the study area. This study was carried out in a remote intertidal channel in Poole Harbour surrounded by privately owned land where access is prohibited. The use of the UAS to obtain imagery from this site

demonstrates their potential in obtaining valuable information from areas where access is difficult. The UAS was deployed from a publicly accessible nature reserve approximately 2km away from the furthest points from which data was collected. Where resources are limited and regular patrols to monitor fishing distribution are unfeasible or impractical, the methods investigated in this study may offer a low-cost solution for monitoring the extent and intensity of bottom-fishing in intertidal areas. The methods used here may help effectively map and quantify fishing effort of bottom-towed fisheries that interact physically with the seabed, and are worthy of further investigation.

5. Chapter: Population dynamics of the commercially harvested non-native Manila clam *Ruditapes philippinarum* in Poole Harbour, UK.

5.1 Introduction

In addition to wider impacts on benthic habitats and the overall benthic community structure (Dayton *et al.*, 1995; Collie *et al.*, 2000; Kaiser *et al.*, 2006), fishing represents non-random selective mortality in target species. This involves preferentially removing certain individuals from a population over others and potentially causing ultimate evolutionary change (Law, 2000; Conover *et al.*, 2005; Hutchings, 2005; Walsh *et al.*, 2006). Much past research has identified phenotypic changes in commercial fish stocks. Increases in weight at age and length at age (de Veen, 1976; Millner and Whiting, 1996), and the earlier onset of sexual maturation (Borisov, 1978; Haug and Tjemsland, 1986; Jorgensen, 1990; Bowering and Brodie, 1991) have been described due to fishing pressure. Evolutionary changes may also occur indirectly as a result of fishing, such as reducing intra-specific competition or due to changes to interactions with non-target species (Law, 2000). While much of the evidence for such changes reports on fish populations, similar changes in size and weight-at maturity have been reported for commercially harvested populations of gastropods (Torroglosa and Giminez, 2010) and crustaceans (Melville-Smith and de Lestang, 2006; Zheng, 2008).

Fishing-induced invertebrate regime shifts can alter the size frequency distribution of target species populations and potentially remove the most profitable food resources for shorebird populations (Bowgen *et al.*, 2015). Prey size is an important factor in determining the amount of available food for different bird species that

feed on prey within specific size ranges (Goss-Custard *et al.*, 2006) due to limitations according to their individual morphology, particularly bill size (dit Durell, 2000). Harvesting may lead to a reduction in settlement of bivalve prey and reduce prey quality, with a lower flesh to shell ratio that ultimately reduces local survival in molluscivorous shorebird species (van Gils *et al.*, 2006).

The Manila clam *Ruditapes philippinarum* was introduced for aquaculture purposes in Poole Harbour, UK in 1988, and despite predictions to the contrary the population naturalised (Jensen *et al.*, 2005). Although a non-native species in the UK, the introduction of the Manila clam has provided an additional food source for molluscivorous bird predators, reducing overwinter mortality in oystercatcher *Haematopus ostralegus* within Poole Harbour (Caldow *et al.*, 2007). Goss-Custard *et al.* (2006) describe the size classes of individual prey items consumed by shorebird species, allowing the impacts of any regime shifts to be predicted (Bowgen *et al.*, 2015). A maximum size of 42mm in Manila clam in the harbour has been demonstrated (Humphreys *et al.*, 2007), in contrast to a maximum size of 60mm elsewhere in Europe (Beninger and Lucas, 1984; Mortensen *et al.*, 2000) and South America (Ponurovskii, 2000). This is considered to be due to the 40mm minimum landing size (MLS) enforced in the harbour until 2007. Such shifts in size frequency may be representative of selective pressure from minimum landing sizes that are commonly enforced as management measures, and past work suggests as much as 75% of legal-size clams may be removed in some areas through fishing efforts (Humphreys *et al.*, 2007).

A sister study to this work (Chapter 3) assessed the impact of pump-scoop clam dredging on overall benthic community composition, with regards to changes in species abundance and habitat quality associated with a four month dredge season. This study will focus on the impacts of the entire dredging season in Poole Harbour (1st July – 25th December) on the main target species of the fishery, *R. philippinarum*. The main objectives of this study are to: assess how the clam and cockle dredge season in three areas of Poole Harbour (high intensity fishing, intermediate intensity, closed) affects clam abundance and size distribution; investigate clam population dynamics (recruitment, length at age, secondary productivity) in areas of different fishing intensity; and quantify mortality rates and overall condition index of clams in the different areas of the harbour.

5.2 Methods

5.2.1 Study Area

The study was carried out in Poole Harbour, in Dorset, UK. The harbour is described in detail in Section 3.1.1.

5.2.2 Sampling

The use of a sediment core is limited in sampling species such as the Manila clam that occur at lower densities than would be captured by a 10cm diameter core. This study therefore used a combination of pump-scoop dredging and a bespoke hand dredge to sample for this species. Consultation with local fishermen and fishing sightings data obtained from the Southern Inshore Fisheries and Conservation Association (SIFCA) allowed the identification of significant shellfish beds throughout the harbour before sampling.

Pump-scoop dredge sampling was undertaken on 19th June 2015 and the 15th January 2016; before and after the dredging season that runs from 1st July to 25th December each year. Sampling was carried out in three areas: one each of high, intermediate and low (i.e. closed) fishing effort, determined from routinely collected SIFCA fisheries sightings and consultation with a local fisherman. Despite the limitations of using a single control site (Underwood, 1992) when detecting impacts of human activities, sites visited during a SIFCA stock assessment in June 2015 were revisited, and this control site was considered the best available for comparison. These areas are detailed in Table 5.1. The locations of these sites and individual sample points which were dredged in June and revisited in January are indicated in Figure 5.1.

Table 5.1. Study sites in Poole Harbour, UK in which Manila clams were sampled in June 2015 and January 2016.

Site	Fishing Intensity
Seagull Island, Holton Mere	High (open 1 st July – December 25 th)
Wytch Lake	Intermediate (open 1 st July – October 31st)
Upton Lake	Low (closed)

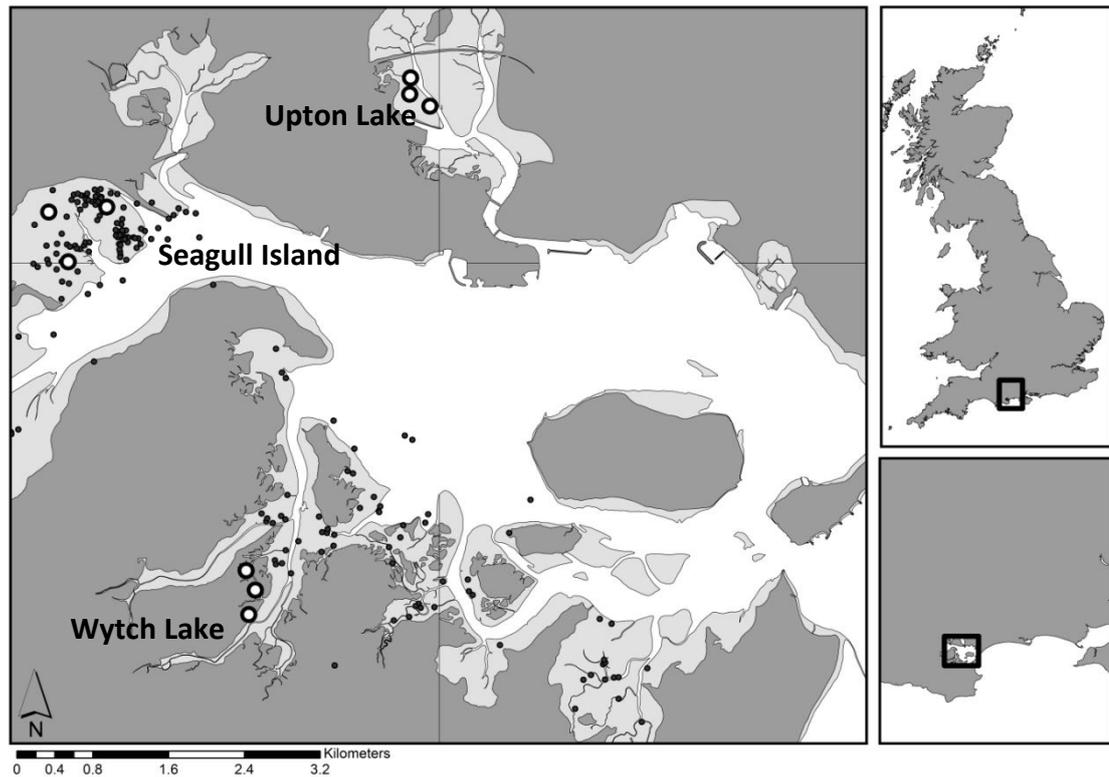


Figure 5.1. Locations sampled by pump-scoop dredge for the clam and cockle stock assessment in June 2015 and revisited in January 2016 (white circles). The northern-most site is Upton Lake (closed site), the westerly site is the area around Seagull Island in Holton Mere (high intensity fishing), and the southerly site is Wytch Lake (intermediate intensity fishing). The small black circles indicate SIFCA fishing sightings during 2015. Sampling locations in Wytch Lake are within the intertidal saltmarsh, not on land as the figure suggests. The locations in the UK and on the UK's south coast are inset.

Three dredges were randomly carried out at each site using a trailed pump-scoop dredge (dimensions 460mm x 460mm x 30mm) with a bar width spacing of 18mm. Each time the dredge was towed along the seabed for two minutes at a speed of 1.8 knots. After two minutes the dredge was lifted aboard the vessel and the contents were emptied onto a sorting deck for analysis. From each dredge all dead shells of *R. philippinarum* were retained and taken back to the laboratory in order to estimate levels of natural or non-fishing mortality. Live individuals were sorted, counted and measured on board the vessel.

Given the relatively large mesh size of 18mm on the pump scoop dredge, undersized and juvenile clams are unlikely to be retained using this method. Therefore, on 10th February 2016, each area was revisited and samples were obtained using a bespoke hand-held naturalist's dredge. Six hand-held dredges were taken randomly across each site. This hand-held dredge is designed specifically for sampling smaller individuals. The dredge has an aluminium frame with a 45° handle used to drag the dredge through the top layer of the sediment for 1m. The dredge mouth is 30cm wide with a 1mm mesh bag attached to retain any fauna (Figure 5.2), covering an area of 0.3m² (Matthew Harris, University of Portsmouth PhD Thesis, 2016). Samples were sieved through a 2mm mesh sieve while on board the vessel before being retained for further analysis in the laboratory.



Figure 5.2. The hand-held dredge used to sample smaller clam sizes in each location (Matthew Harris, University of Portsmouth PhD Thesis, 2016).

Around 100 individuals of *R. philippinarum* were retained from both pump-scoop dredges and hand dredges for ash-free dry mass (AFDM) calculations. It was ensured that these clams were representative of all size classes within the samples.

Clams were stored at -80°C in Bournemouth University laboratories before analysis was undertaken.

5.2.3 Analysis

5.2.3.1 *Abundance and Size Frequency*

Clams sampled using the pump-scoop dredge were sorted, counted and length measurements taken to the nearest mm while on board the vessel (electronic callipers were deemed unsuitable for use on board the vessel). Individual clams from hand dredge samples were sorted in the laboratory and counted before lengths were taken to the nearest 0.01mm. Length measurements were taken by measuring each clam across the longest distance from the anterior end to the posterior end of the shell. Shellfish densities are a much more informative measure than abundance or CPUE when considering shorebird prey, so CPUE was converted to density per square metre by calculating the area covered by the vessel ($1.8 \text{ kn} = 0.514 \text{ m/s} \times 120 \text{ seconds} = 111.12\text{m}$) and the area of the dredge ($0.46\text{m} \times 0.46\text{m} = 0.2116\text{m}^2$). The area dredged during each individual sample was therefore calculated as $111.12 \times 0.2116 = 25.513\text{m}^2$.

5.2.3.2 *Natural Mortality*

Humphreys *et al.* (2007) found some dead clam shells from samples in Poole Harbour to be clean and shiny on the inside, presumed to be recently dead. In contrast, others were more dirty and worn, suggesting a longer time period since death. As dredging removes individuals from the population live in their shell, these dead shells provide an indication of non-fishing or natural mortality. Natural

mortality levels were therefore calculated for each site visited using the following formula, taken from Humphreys *et al.* (2007):

$$\text{Mortality (\%)} = (N_{\text{newdead}} / (N_{\text{newdead}} + N_{\text{alive}})) * 100$$

where the number of newly dead and live clams in each sample are denoted by *Nnewdead* and *Nalive* respectively.

5.2.3.3 Ash-Free Dry Mass and Condition Index

Ash-free dry mass (AFDM) of clams retained and stored in the laboratory was calculated through loss-on-ignition (LOI). Clams were first dried for 24 hours at 105°C before being burned to a constant weight at 560°C for four hours. Dry flesh and shell weights were recorded to five decimal places, and the difference between pre- and post-furnace flesh mass was taken as the AFDM. The relationship between clam length and weight at each site was then modelled using a generalised linear model framework and a gamma error structure.

The following formula was used to calculate condition index (CI) (Sahin *et al.*, 2006):

$$\text{Condition Index} = (\text{Dry Flesh Weight (g)} / \text{Dry Shell Weight(g)}) * 100$$

The relationship between clam length and condition index was then investigated within a linear modelling framework to assess differences in clam condition between sites.

5.2.3.4 Ageing and Cohort Analysis

The number of external concentric growth rings on the shell has been used in past studies to age individuals of marine bivalves (Jones, 1980; Breen *et al.*, 1991;

Ponurosvkii, 2000), although results of this method in *R. philippinarum* have been shown to be inaccurate (Ohba, 1959), and this proved the case with samples from this study. Therefore two different methods of aging were used to derive age estimates from the size frequency histograms.

Firstly, the Fish Stock Assessment Tool (FiSAT: version II) provided by the Food Agriculture Organisation of the United Nations (FAO) was used. Bhattacharya's (1967) method was used within FiSAT to analyse length frequency histograms from each study site. This method uses modal progression analysis to identify individual size cohorts as individual normal distributions within a composite distribution of multiple age groups. This method is frequently used in the assessment of fish populations but has increasingly been applied to shellfish stocks (Pauly and Morgan 1987; Nurul Amin *et al.*, 2008; Schmidt *et al.*, 2008; Wrange *et al.*, 2010). To take a conservative approach and to reduce bias it was ensured that the separation index between modes was > 2 and whenever possible age groups were derived from at least three points consecutively (Gayanilo, 1997; Amin *et al.*, 2008). Size classes of 2mm were used for this analysis as preliminary analyses using 5mm showed that additional modes in the data were lost using the larger size class.

Secondly, length-frequency histograms were analysed using the mixdist package in the R statistical programming language (R Studio version 0.98.1062). This method utilises maximum-likelihood estimation to fit finite mixture distribution models to length frequency histograms as normal distributions. Mixdist results estimate age distributions (π : the number of each age group present as a proportion of the population), mean length at age (μ) and standard deviations of length at age (σ).

The mixdist method first requires the researcher to input initial values for π , μ and σ following visual examination of the length frequency histogram (Hoxmeier and Dieterman, 2011). These priors are then used to produce estimates of μ . Results of this method were again used to establish the number of separate age cohorts present within the population and to validate those identified through Bhattacharya's method.

In both of these methods, age groups were derived from size cohorts based on a "known-age" reference group of age-0 (< 20mm). This is based on the reported average length of 15-20mm reached by spring recruits by the end of their first winter (Ohna, 1959; Matthew Harris, unpublished PhD Thesis, 2016). Given the inclusion of prior information in the mixdist analysis, results of this method were more accurate in identifying cohorts within the data. Therefore, these results were carried forward when ageing individual clams. The mixing proportion of each cohort was then applied to the data to calculate the age of any given individual based on its shell length and the relative probabilities of each size cohort. These ages were then used for calculation of growth parameters as described below.

5.2.3.5 Growth Parameters

Growth parameters for length-at-age in clams from each area of the harbour were estimated using the Von Bertalanffy growth function in the R package FSA. The typical Von Bertalanffy growth curve is represented as:

$$E[L|t] = L_{\infty}(1 - e^{-K(t-t_0)})$$

where $E[L|t]$ is the predicted average length at age (or time t), L_{∞} is the asymptotic average length (i.e. the theoretical largest average length obtained by an individual in the population), K is the unitless growth rate coefficient and t_0 is the theoretical age at which length is zero (Beverton, 1954; Beverton and Holt, 1957). These parameters were then used to plot growth curves in length of clams as a function of age, allowing for comparison of growth in *R. philippinarum* at different sites around the harbour.

5.3 Results

5.3.1 Clam Size and Abundance

No significant effect of sampling month is evident on clam density although results show site differences ($F(2, 12) = 8.37, p < 0.01$) and a significant interaction term ($F(2, 12) = 12.22, p < 0.01$). The magnitude of the change in abundance is greatest around Seagull Island, the heaviest dredged site (Table 5.2; Figure 5.3). As density data was derived from CPUE data this analysis was not carried out for CPUE.

A reduction in the average clam length is evident in all sites throughout the season (Table 5.2). ANOVA results show a significant main effect of site ($F(2, 2007) = 413.28, p < 0.001$) and of sampling month ($F(1, 2007) = 101.26, p < 0.001$) on clam length plus a significant interaction term ($F(2, 2007) = 10.94, p < 0.001$). Cohorts of juvenile (< 20mm) clams are evident at each site (Figure 5.4), indicating recruitment during summer of 2016 occurred at all sites.

Table 5.2. Mean length, CPUE and density of clams from each site in June 2015 and January 2016. Values in bold indicate a significant difference between months.

Length (mm)			
Site	Month	Mean	S.E.
Seagull	June 2015	34.80	0.13
	January 2016	31.05	0.25
Wytch Lake	June 2015	36.89	0.42
	January 2016	35.35	0.26
Upton Lake	June 2015	40.66	0.21
	January 2016	36.70	0.19
CPUE (no. clams per dredge)			
Site	Month	Mean	S.E.
Seagull	June 2015	259.00	17.01
	January 2016	67.33	40.76
Wytch Lake	June 2015	33.00	17.21
	January 2016	81.67	11.70
Upton Lake	June 2015	112.33	21.43
	January 2016	117.67	34.42
Density (no. clams m⁻²)			
Site	Month	Mean	S.E.
Seagull	June 2015	10.15	0.67
	January 2016	2.64	1.60
Wytch Lake	June 2015	1.29	0.67
	January 2016	3.20	0.46
Upton Lake	June 2015	4.40	0.84
	January 2016	4.61	1.35

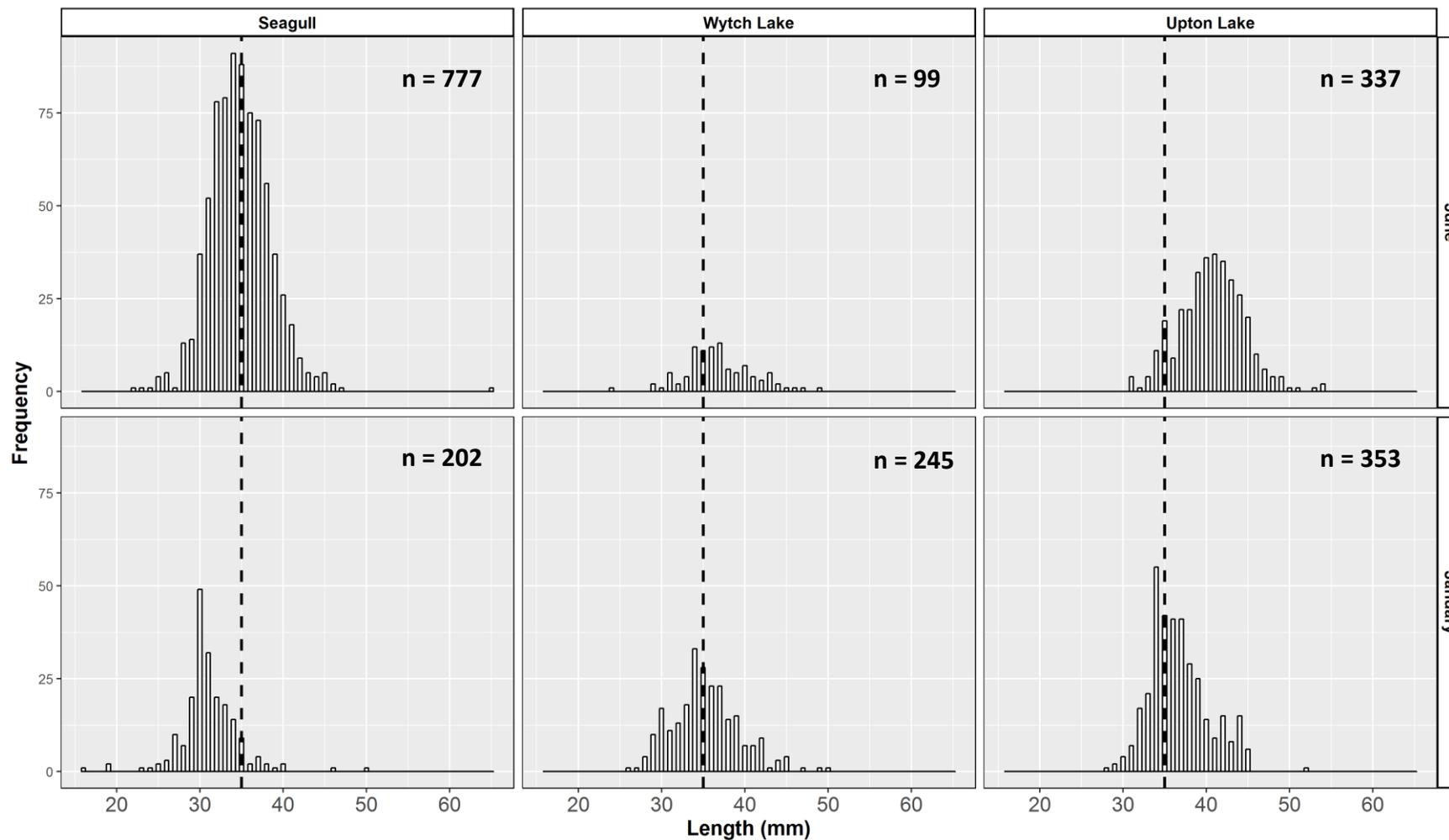


Figure 5.3. Size frequency histograms of clams sampled by pump-scoop dredging in June 2015 and January 2016 (three dredges pooled). The dashed black line in each plot indicates the minimum legal landing size of 35mm.

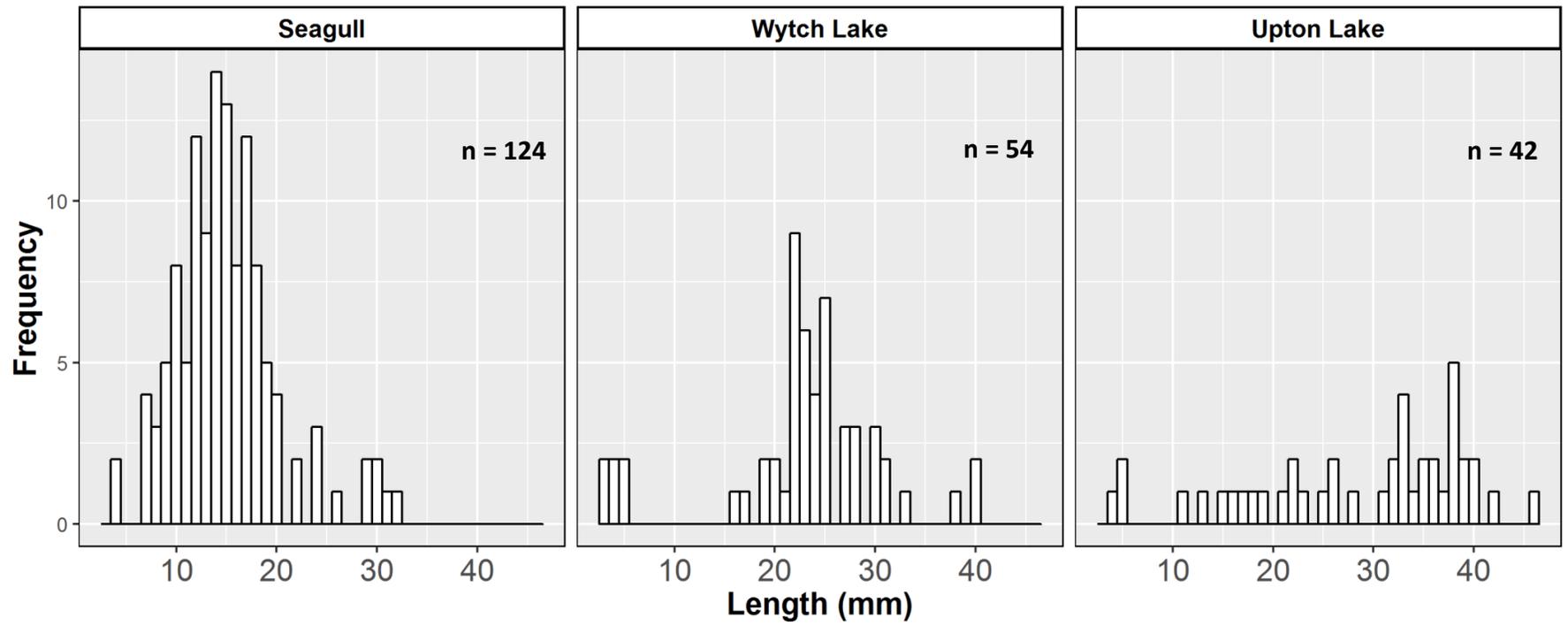


Figure 5.4. Size Frequency histograms of clams sampled using the hand dredge with a 1mm mesh size in each site in January 2016 (six hand dredges pooled).

5.3.2 Changes in Abundance during Fishing Season

The changes in abundance following heavy fishing around Seagull Island are clearly evident (Figures 5.5 and 5.6), with 95% of legally harvestable clams (> 35mm) and a large proportion of those between 30mm and 35mm extracted from this site throughout the 2015 dredging season. The proportional change in abundance of harvestable clams was significantly greater around Seagull Island (ANOVA: $F(2,6) = 32.26$, $p < 0.001$) than the other two sites, between which no difference is evident (Figure 5.5). A smaller loss (20%) of harvestable clams is evident in Upton Lake and at Wytch Lake an increase in the abundance of harvestable clams by 90% is apparent despite this area being open to dredging July – October. Neither of these changes is significant compared to pre-dredging conditions however. All 5mm size classes above 35mm show a significant reduction in density from pre-dredging conditions around Seagull Island (Figure 5.6).

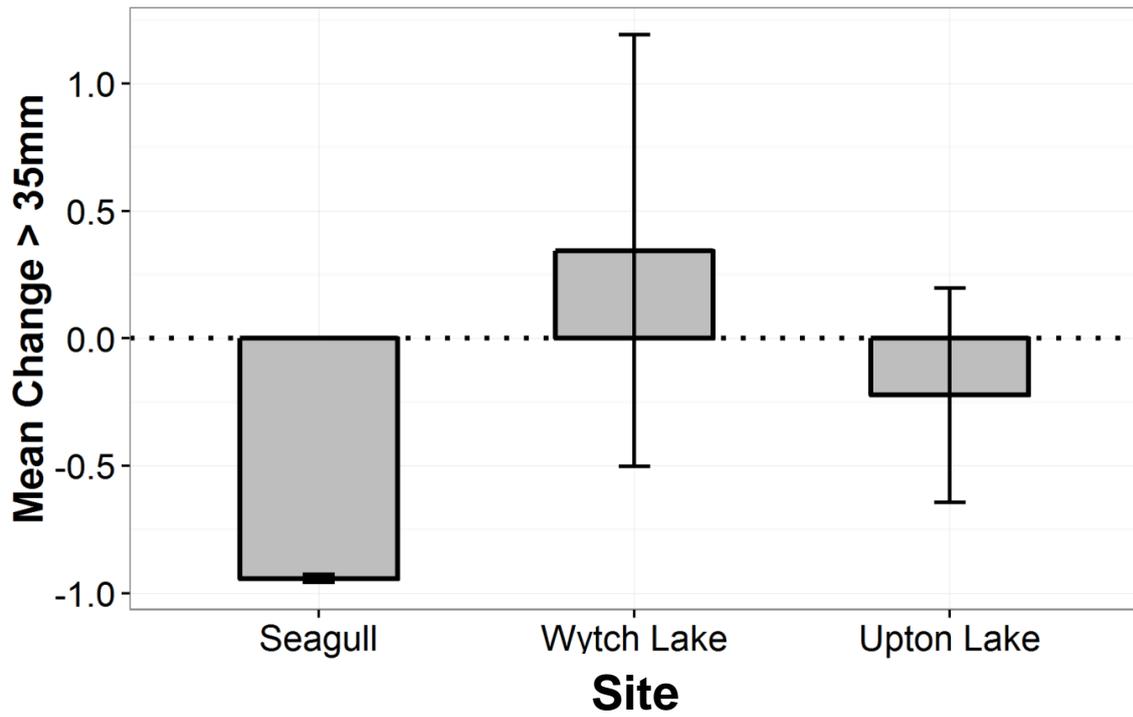


Figure 5.5. Mean (\pm 95% C.I.) proportional change in abundance of legally harvestable (>35mm) clams at each site over the course of the 2015 dredging season.

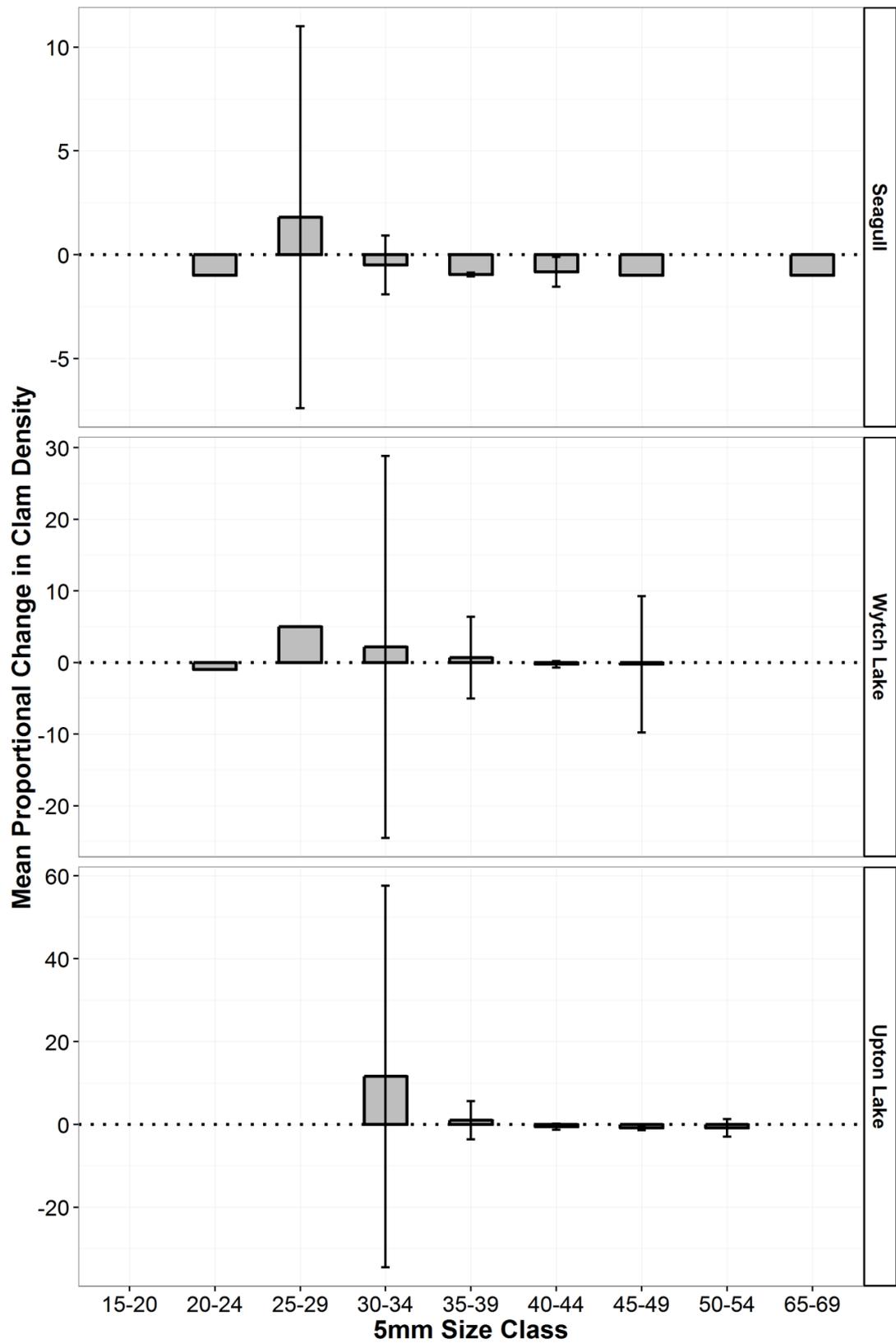


Figure 5.6. Mean (+/- 95% C.I.) proportional change in clam densities in each 5mm size class during the 2015 dredging season at each site sampled.

5.3.3 Natural Mortality

Data on natural or non-fishing mortality was log+10 transformed to achieve normality and was similar across sites (ANOVA with White's adjustment for heteroscedasticity: $F(2,3) = 1.16$, $p = 0.38$) (Table 5.3).

Table 5.3. Mean (+/- S.E.) Log+10 transformed natural (non-fishing) clam mortality in each survey site in January 2016.

Site	Log+10 % Non-Fishing Mortality	S.E.
Seagull Island	1.28	0.13
Wytch Lake	1.09	0.04
Upton Lake	1.04	0.02

5.3.4 Condition Index and Secondary Productivity

Mean condition index of clams was significantly different between sites (ANOVA: $F(2,276) = 30.73$, $p < 0.001$), with clam condition lowest at Seagull Island in Holton Mere and highest in Wytch Lake. Clam length is a significant predictor of clam condition index, although there is significant difference in the slope of this relationship between clams at Seagull Island and Upton Lake ($p < 0.05$). In contrast to the trend in overall mean condition, clam condition increases more for every mm in length around Seagull Island than in Upton Lake, where the increase in condition per mm of length is smaller (Figure 5.7).

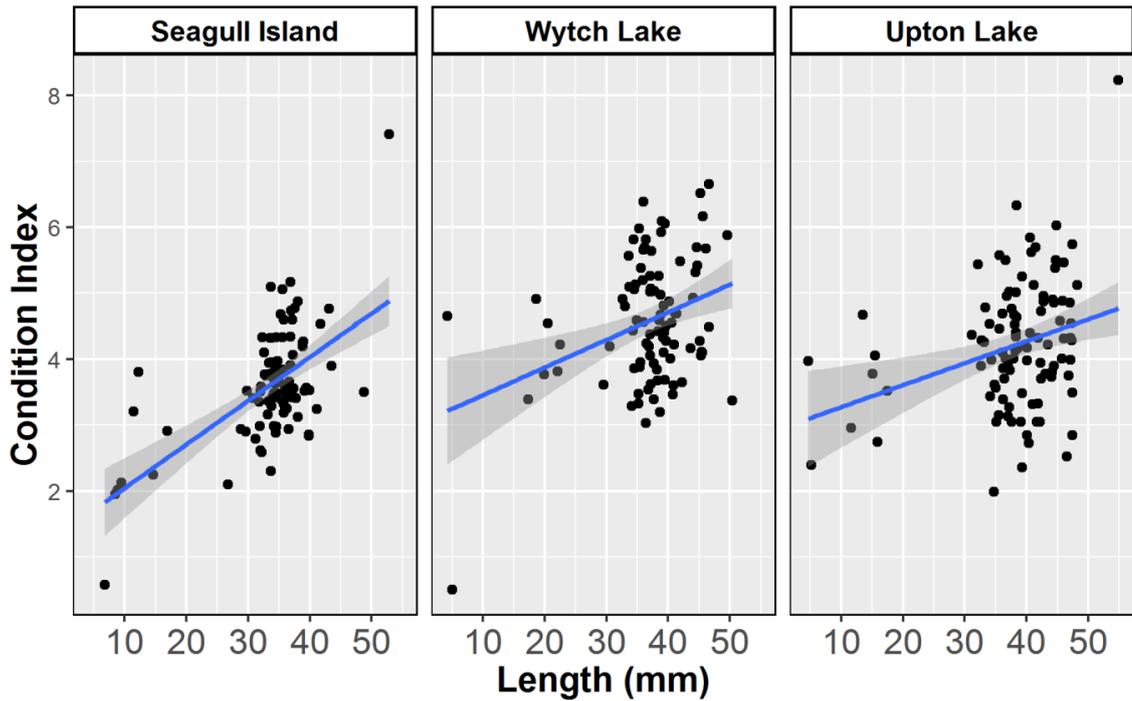


Figure 5.7. The relationship between length and condition index in clams from each site sampled in January 2016. Seagull Island: $y = 1.38 + 0.07x + 0.69$, $R^2 = 0.37$; Wytch Lake: $y = 3.04 + 0.04x + 0.91$, $R^2 = 0.11$; Upton Lake: $y = 2.94 + 0.03x + 0.94$, $R^2 = 0.08$

Mean clam AFDM shows significant differences between sites (ANOVA: $F(2,279) = 16.73$, $p < 0.001$), with secondary productivity (g AFDM per clam) lowest at Seagull Island, significantly lower than at Wytch Lake and Upton Lake, between which there is no difference (Figure 5.8).

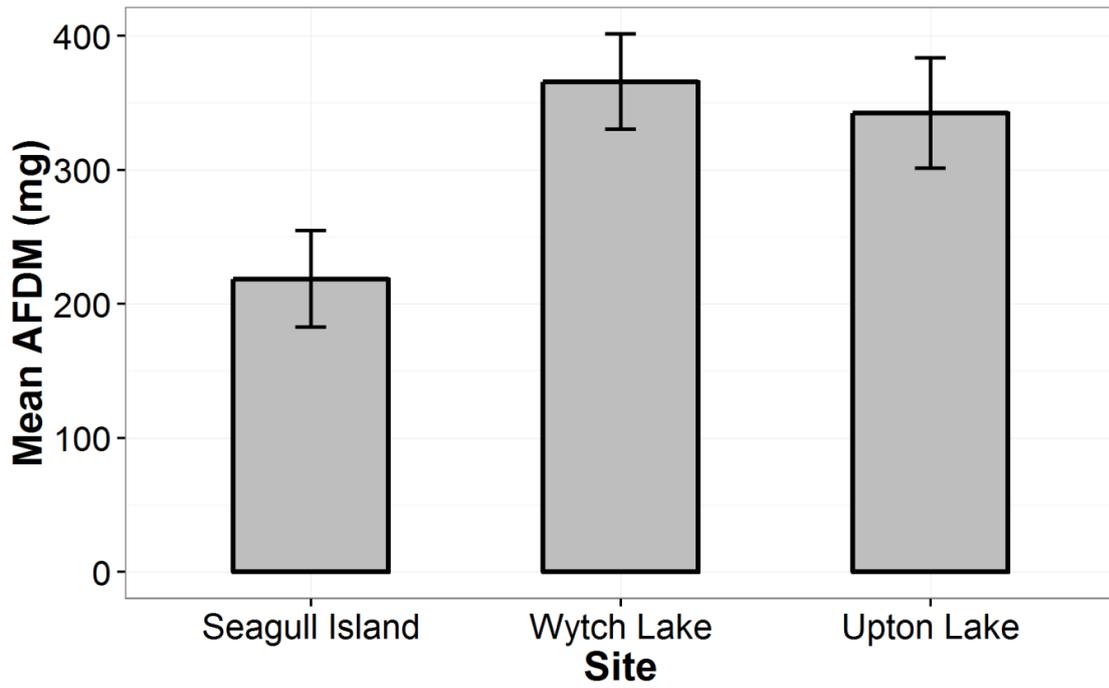


Figure 5.8. Mean (+/- 95 % C.I.) AFDM in mg of clams sampled in each site in January 2016.

5.3.5 Cohort Analysis

Given the changes in clam densities evident through the 2015 dredge season only data from prior to the dredge season was included in the size cohort analysis (Table 5.4).

Table 5.4. Clam cohort estimates derived from Bhattacharya's method within FISAT II and the mixdist package in R.

Site	Mean Cohort Size (mm)		Age Class
	Bhattacharya	mixdist	
Seagull Island, Holton Mere	NA	NA	0
	25.00	24.20	1
	34.79	33.78	2
	NA	37.81	3
Wytch Lake	NA	NA	0
	30.00	31.80	1
	36.96	34.94	2
	42.96	40.65	3
	NA	NA	4
Upton Lake	NA	NA	0
	NA	NA	1
	34.30	34.27	2
	40.87	40.61	3
	54.01	53.13	4

The size cohorts identified through the two methods appear comparable, with a maximum difference of around 2mm in the estimates in the Wytch Lake data. Size cohorts identified from June 2015 data appear similar at Wytch Lake and Upton Lake, although the estimate of the first (1-year) size cohort is lower at Seagull Island than at these sites by approximately 5mm. However the next estimates appear similar, with 2-year clams reaching around 35mm at all sites. As with our previous results it appears however that the larger cohorts in the Seagull Island population are smaller than those identified at the other two sites, where 3-year clams reach around 41mm in length compared to 37mm at Seagull Island.

5.3.6 Relationship between Clam Length and Weight

The relationship between clam length and weight showed differences between sites. Results of a GLM with a gamma error structure show that both the intercept (GLM: $p < 0.001$) and the slope (GLM: $p < 0.001$) of the trend between clam length and weight is significantly different at Seagull Island compared to the other two sites (Figure 5.9). Clams at Seagull Island contain significantly more AFDM per mm of length than those at Wytch Lake or Upton Lake. There is no difference in the slope between Wytch Lake and Upton Lake.

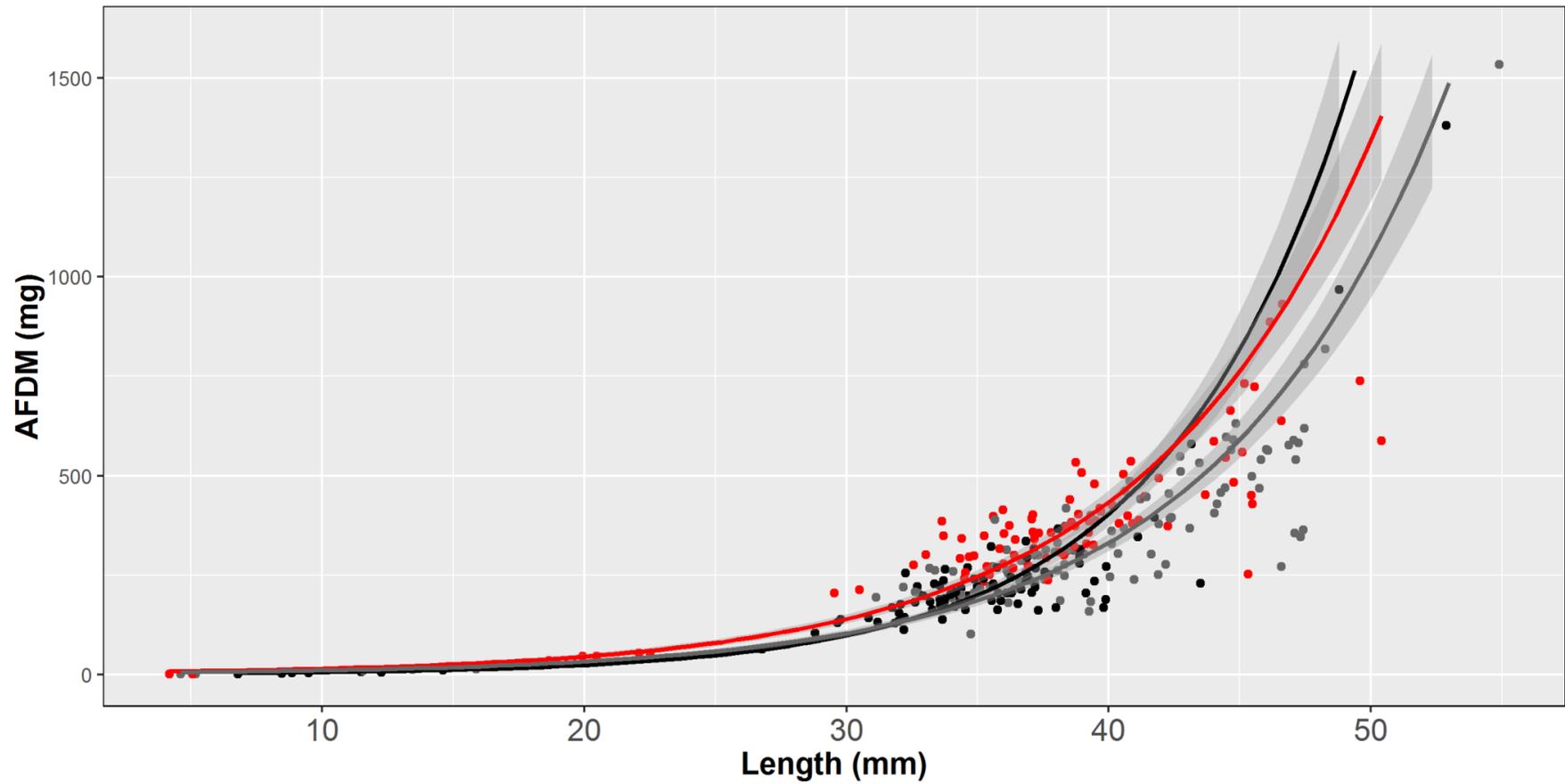


Figure 5.9. The relationship between length and weight (in mg AFDM) of *R. philippinarum* in areas of different fishing intensity within Poole Harbour. Black line = Seagull Island (heavy fishing); red line = Wytch Lake (intermediate fishing); grey line = Upton Lake (low fishing).

5.3.7 Growth of *R. philippinarum*

Von Bertalanffy growth curves fitted to length-at-age data indicate differences in the asymptotic average length of clams in each site. The asymptote of the model fitted to data from clams at Seagull Island shows a model asymptote of 46.02mm, indicating that on average, clams from this site do not grow to larger than 46mm (Table 5.5; Figure 5.10). Clams grow to a larger size at Wytch Lake and Upton Lake, where the fitted growth models show clams to grow to an average maximum size of 57mm and 66mm respectively (Table 5.5; Figure 5.10). The inverse trend is apparent in growth rates of, with the growth coefficient, K , indicating that *R. philippinarum* grow fastest around Seagull Island and slowest in Upton Lake (Table 5.5).

Table 5.5. Parameter estimates of the Von Bertalanffy growth curves fitted to length-at-age data of clams from each site sampled in January 2016.

Site	L_{∞} +/- S.E.	K +/- S.E.	t_0 +/- S.E.
Seagull Island	46.02 +/- 2.47	0.54 +/- 0.08	-0.53 +/- 0.08
Wytch Lake	57.52 +/- 6.10	0.35 +/- 0.08	-0.81 +/- 0.16
Upton Lake	66.29 +/- 9.69	0.27 +/- 0.08	-0.77 +/- 0.15

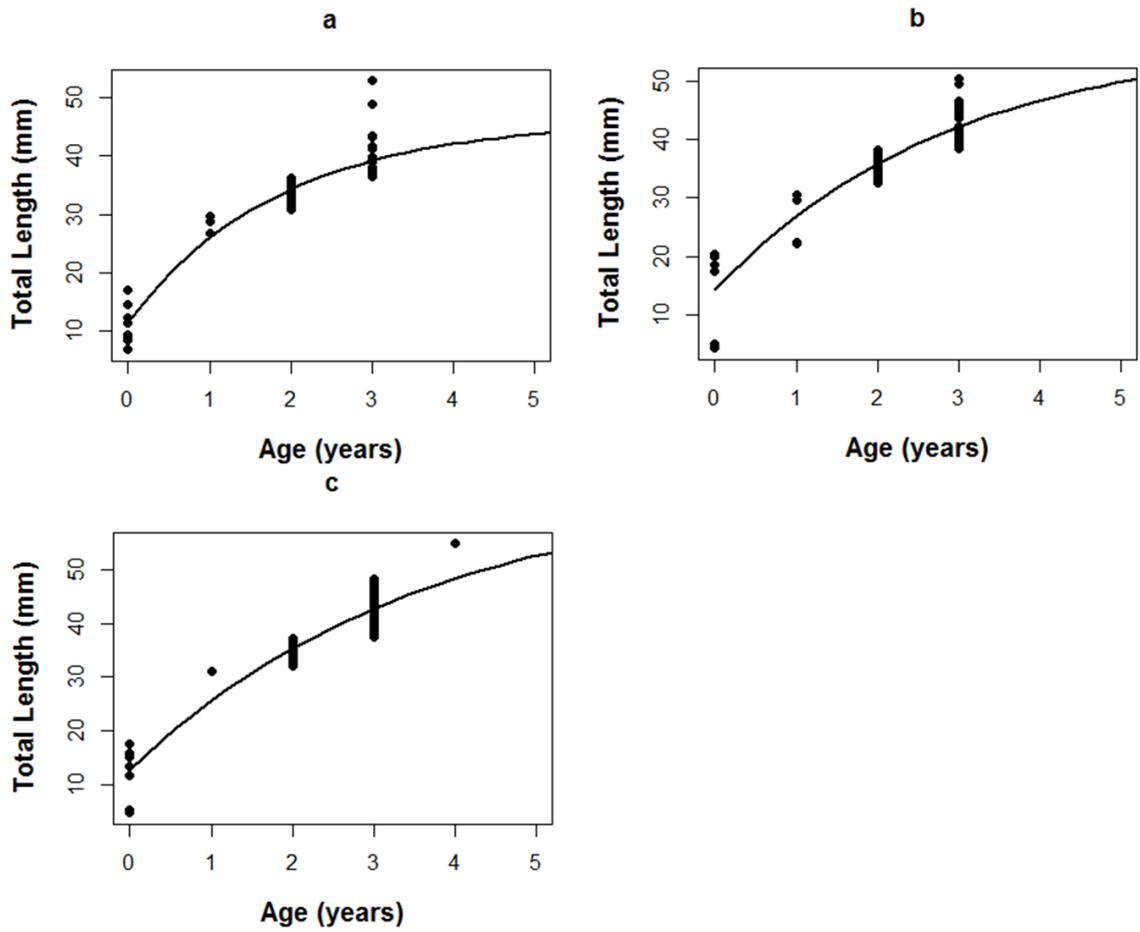


Figure 5.10. Von Bertalanffy growth curves fitted to length-at-age data of clams from each site in Poole Harbour. a) Seagull Island; b) Wytch Lake; c) Upton Lake.

5.4 Discussion

The effects of the 2015 dredge season on *R. philippinarum* populations in Poole Harbour are clearly evident in the dramatic decline of legally harvestable clams in the heavily fished area around Seagull Island. Results suggest that landable clams may be harvested by pump-scoop dredging with up to 95% efficiency (Figure 5.5), which is higher than a previous estimate in the harbour of up to 75% (Matt Harris, unpublished PhD Thesis, 2016). Although Wytch Lake was open from July – October 2015 no significant reduction in harvestable clams occurred, perhaps indicating the intensity with which fishermen focused on Seagull Island during the season and/or the patchy distribution of effort within Wytch Lake.

The changes in each 5mm size class show the same trend and are more informative when considering changes in bird diets that feed on discrete size classes of bivalves (Goss-Custard *et al.*, 2006; Caldow *et al.*, 2007). Notably the changes in abundance of the 30-35mm size class at Seagull Island shows high variability, and inspection of Figure 5.3 suggests that this may be due to removal of some clams under the 35mm minimum landing size from this area. The Holton Mere area of the harbour and particularly around Seagull Island has been heavily fished in past years and the pre-season mean size of clams here of 34.80mm may be indicative of this. This is a decline in mean size from a previous study (Humphreys *et al.*, 2007), perhaps indicating the effects of selective fishing pressure since the minimum landing size was reduced from 40mm to 35mm in the harbour in 2007 (Lambourn and Le Berre, 2007). The mean size in this area further reduced during the course of the season to 31.05mm, which may provide further evidence of undersized harvesting.

The asymptote of the Von Bertalanffy growth model for Seagull Island however is 46mm; higher than the mean size observed both before and after the dredging season (Figure 5.10a; Table 5.5). This suggests that the dramatic short-term impacts of dredging in removing larger individuals are not reflected on the population as a whole; despite higher dredging pressure reducing the mean length, individuals of *R. philippinarum* still achieve lengths markedly higher than the MLS at this site. This clearly is an important consideration for the sustainability of the fishery and stocks of harvestable individuals. However, according to Francis (1988), L_{∞} is only relevant in populations where mortality is at sufficiently low levels that individuals can actually reach the age at which growth completely ceases. Therefore due to heavy fishing at this site the asymptote of the model may not be entirely realistic if clams are harvested before reaching the theoretical age at which increases in length begin to slow down or stop. It appears that at all sites *R. philippinarum* reaches the legally harvestable length of 35mm at between 2 and 3 years of age, and clams older than 3 years of age are only present in the data at Upton Lake, where no fishing occurs.

While fishing-induced changes to clam size and abundance are clear in the data, assigning causality to the trends in growth, condition index and clam body weight is less straightforward and such trends may be down to a number of factors such as flow rates (Hadley and Manzi, 1984), food availability (Norkko *et al.*, 2005) and dissolved oxygen (Ferreira *et al.*, 2007). Condition index data show that clams around Seagull Island are overall in poorer condition than in other areas of the harbour, with a lower flesh/shell ratio. Due to the clear differences in densities between sites this may be due to density-dependent processes or food availability,

a strong driver of changes in condition index (Norkko *et al.*, 2005). At higher densities intraspecific competition can limit individual growth and potentially survivorship, reducing flesh content (Smalley, 1984; Fogarty and Murawski, 1986), shell length (Peterson, 1984; Smalley, 1984; Olafsson, 1986; Weinberg, 1998) and shell width (Cerrato and Keith, 1992). Such space-driven self-thinning (SST) (Frechette and Lefaivre, 1990) has been described in many species of shellfish in response to increased densities. In the Venice Lagoon, Italy, densities of Manila clam reach up to 4000 ind./m² and biomass of over 1kg/m² (Brusa *et al.*, 2013), suggesting that the densities within Poole are relatively low and would not have significant implications for population viability.

It is noteworthy that clams from Seagull Island appear to both increase in condition per mm of length and increase in length for each year of age faster than individuals at other sites. This could be a result of regular fishing disturbance removing significant numbers of individuals from the population. Shellfish may demonstrate increased growth rates when natural densities are lowered, exploiting newly available resources following removal of intraspecific competition due to fishing (Dixon and Day, 2004). *R. philippinarum* grows more slowly and deposits less body flesh at the other sites sampled, perhaps contrary to the generally considered view that at lower densities growth rates are higher due to lower competition (Hadley and Manzi, 1984). Understanding such density-dependent processes is important for fisheries management, especially when such effects can compensate for fishing-induced changes (Rose *et al.*, 2001).

The higher densities around Seagull Island may mean that despite lower AFDM values, overall secondary productivity is similar across sites. As only around 100 clams were retained from each site for AFDM calculations, however, an accurate estimation of secondary productivity per unit area per unit time such as grams per square metre per day ($\text{g m}^{-2} \text{d}^{-1}$) was not possible. To store and analyse all clams retained per dredge to allow such an analysis would have been unfeasible given limits to available laboratory space and the project timeline. These limitations also applied with regards to repeated sampling. Instead, productivity is expressed simply as the mean AFDM of clams in each site (Figure 5.8) and the relative density of clams presented above may be used for context.

Although the higher densities of *R. philippinarum* at Seagull Island may limit shell growth, the further decline in mean length at this site since the lower MLS was introduced does suggest this may be as a result of fishing pressure. Changes in shell length may appear trivial, although if associated with other life-history traits that impact individual fitness such as survivorship, condition index (as our results suggest) or fecundity, they may be critical in determining population dynamics and hence the viability of a local shellfish industry (Weinberg *et al.*, 1986; Weinberg *et al.*, 1997; Weinberg, 1998).

Non-fishing mortality was similar across all sites sampled. Such natural mortality where dead shells are left *in situ* may be indicative of predation rates of clams across the harbour. The heteroscedasticity in the untransformed data may therefore be indicative of the patchy distribution of oystercatcher, the main predator of the Manila clam in the harbour (Caldow *et al.*, 2007). Predation from

shorebirds at or immediately following recruitment has also been suggested as a potential cause in differences in density of adult Manila clam in Japan (Ishii *et al.*, 2001).

Despite the differences evident between sites, hand dredge data indicate that successful recruitment into the population is occurring at all sites, with clams < 10mm present in all samples. It is clear that heavy dredging effort dramatically reduces clam abundance and average length, although data on environmental factors such as flow rates, chlorophyll α and dissolved oxygen would provide further insight into the trends in growth rates and condition index, allowing for isolation of fishing-induced changes from natural processes. Unfortunately the collection of such data was beyond the scope of this study and requires longer-term monitoring than was feasible. It is clear however that fishing effort targets the area of the harbour where clams are more abundant yet of lower body size and in lower relative condition. Given the potential for density-driven changes to body length to act in combination with changes in condition index and fecundity - which is heavily correlated with body size (Yap, 1977; Harding *et al.*, 2007) - to determine long-term population dynamics, it is suggested therefore that regular monitoring of *R. philippinarum* in the harbour, as is carried out as part of the yearly stock assessment by the SIFCA, should continue to help identify any changes in the viability of the species and hence the fishery and oystercatcher prey availability in Poole.

6. Shorebird distribution and feeding rates in relation to shellfish dredging: insights from Poole Harbour, UK.

6.1 Introduction

Inshore shellfishing activities can be highly intensive and often overlap with important overwintering or migratory stopover sites for internationally significant populations of waders (order Charadrii) and waterfowl (order Anseriformes) (Atkinson *et al.*, 2003; van de Kam *et al.*, 2004). Locally, harvesting activities such as dredging may occur within the few intertidal areas that are of sufficient quality to support feeding activities of long-distance migrants (van Gils *et al.*, 2006). Many shorebird species are dependent on a relatively low number of sites throughout their annual life-history cycle (Skagen and Knopf, 1993; Piersma *et al.*, 1994) and are therefore particularly vulnerable to environmental change or degradation at these sites (Piersma and Baker, 2000; Bowgen *et al.*, 2015).

In the non-breeding season, shorebirds require sufficient energy to maintain body temperature and vital metabolic processes, and to fuel critical behaviours such as predator avoidance and searching for prey (Evans, 1976). Migratory species must also maintain sufficient fat reserves to fuel onward migration to summer breeding grounds (Berthold, 1975). Winter survival is therefore determined by the balance between an individual bird's energetic expenditure through these metabolic and thermoregulatory processes, and the amount of energy acquired through feeding (Evans, 1976; Stillman *et al.*, 2001). The amount of energy acquired is determined by the amount of time available to a bird for feeding and its intake rate while doing so (Stillman *et al.*, 2001). Intake rates in turn depend on a number of factors,

including prey quality and density, individual foraging efficiency, disturbance and competition (Goss-Custard, 1984; Stillman *et al.*, 2001).

In addition to direct disturbance through displacement (Goss-Custard and Verboven, 1993), shellfishing and other harvesting practices can disrupt key benthic processes and cause reductions in benthic prey stocks for bird populations, including both target and non-target species (Townshend and O'Connor, 1993; Shepherd and Boates; 1999; review in Goss-Custard *et al.*, 2000; Zharikov and Skilleter, 2004). By removing the largest and most energetically profitable prey (Zwarts *et al.*, 1996) selective harvesting can cause shifts in the size distributions of key prey items and further reduce their availability to bird predators which are known to consume prey within specific size ranges (Goss-Custard *et al.*, 2006; Bowgen *et al.*, 2015).

As well as direct removal of prey species through harvesting, mechanical gears such as dredging can alter habitat sediment characteristics and reduce settlement of bivalve prey, resulting in a long-term decline in feeding conditions (Piersma *et al.*, 2001; van Gils *et al.*, 2006). The potential for mass mortality of shorebird populations as a result of harvesting activities has therefore been recognised (Stillman *et al.*, 2001; Atkinson *et al.*, 2003; Ens, 2006; Atkinson *et al.*, 2010), even with the creation of protected areas in which harvesting is prohibited (Verhulst *et al.*, 2004). Such effects may therefore result in an overall increase in competition as birds are forced to compete in sub-optimal conditions for a resource that is less readily available. In the short term this may result in overwinter mortality events, as has been well-documented in the Dutch Wadden Sea (Smit *et al.*, 1998;

Camphuysen *et al.*, 2002; Swart *et al.*, 2008), causing a long-term reduction in the carrying capacity of a site.

This study assessed impacts of a shellfish dredging season on the distribution and feeding rates of overwintering bird populations within an international nature conservation site on the south coast of the UK, as well as potential impacts of opening a previously closed 'bird sensitive area' for a new four month dredge season. The work addressed the following research questions: 1) how does the spatial distribution and intensity of shellfish dredging influence bird distribution and densities? 2) Is there any relationship between dredging intensity and bird feeding rates? and 3) does any change in feeding rates as a result of dredging intensity affect overall energetic intake rates of shorebirds within the study area?

6.2 Methods

6.2.1 Study Area

Poole Harbour is a natural harbour on the south coast of the UK and a designated European Marine Site under the European Birds Directive (79/409/EEC) and Ramsar site (Figure 6.1), covering an area of 36,000km² at high tide. The majority of the harbour is comprised of extensive mudflats, sandflats and saltmarsh. There is freshwater influence to the west of the harbour from the Rivers Frome, Piddle and Corfe. Tides are micro-tidal, ranging from 1.8m on spring tides to 0.6m on neap tides, with two high tides a day and a relatively long slack water period (Humphreys, 2005). Although highly protected, the harbour supports a unique 'pump-scoop' dredge fishery of local economic significance that runs from May to December every year, harvesting the non-native Manila clam *Ruditapes philippinarum*, and the

cockles *Cerastoderma edule* and *Cerastoderma glaucum*. The fishery is managed by the Southern Inshore Fisheries and Conservation Authority (SIFCA). Recent landings data suggest the fishery is worth in excess of £1 million per year (S. Birchenough, 2017, pers. comm.). These species are harvested from intertidal areas that support significant overwintering bird populations for which the harbour receives its designation.

The study was carried out within the Wytch Lake area of Poole Harbour (Grid Ref: 50.6796, -2.0238). Wytch Lake is a sheltered intertidal channel in the south west of Poole Harbour that falls within the boundary of the Poole Harbour Special Protection Area, with freshwater influence from the Rivers Frome and Corfe (Figure 6.2). The outer area of Wytch Lake around Round Island has historically been intensively dredged by local fishermen and is open for the whole of the dredge season that runs from 25th May to 24th December each year. The channel is a locally designated bird sensitive area (BSA), in which all harvesting activities were prohibited until a change in the management of the pump-scoop dredge fishery in 2015. Under this new management an area of the channel was opened to dredging between 1st July and 31st October each year. The upper area of the channel remains closed to dredging, effectively representing a control site with regards to dredging pressure. These fisheries management measures are summarised in Table 6.1. LiDAR data indicate that elevation is similar throughout the study area, within 0-2m above chart datum, and existing bathymetric data obtained from Poole Harbour Commissioners (HR Wallingford, 2004) indicate a range of 0.48m in mean elevation across the different dredge management areas within the study site.

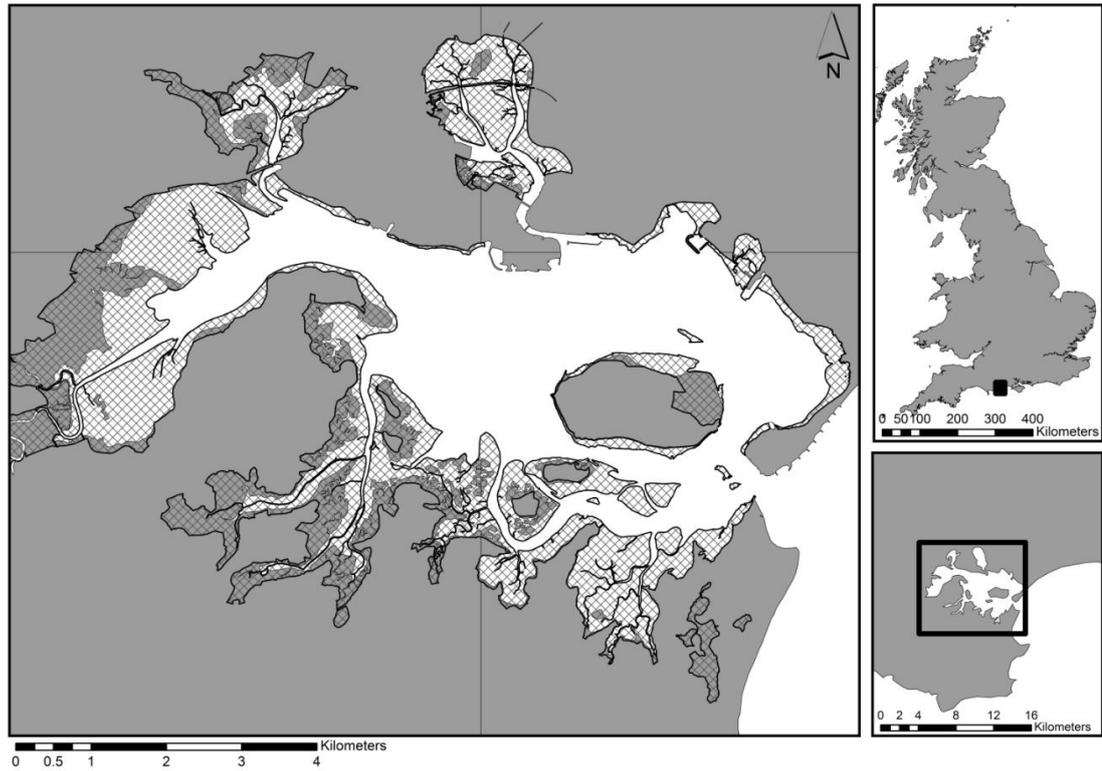


Figure 6.1. Poole Harbour Special Protection Area (hatched area) on the south coast of the UK.

Table 6.1. Fishing intensity and seasonal openings of each site sampled under the dredge permit byelaw, which came in to force on 1st July 2015.

Site	Fishing Intensity	Pre-byelaw	Post-byelaw
Control	Low (none)	Closed	Closed
Short-term dredging	Intermediate	Closed	Open (1 st July - 31 st October)
Long-term historic dredging	High	Open	Open (25 th May - 24 th December)

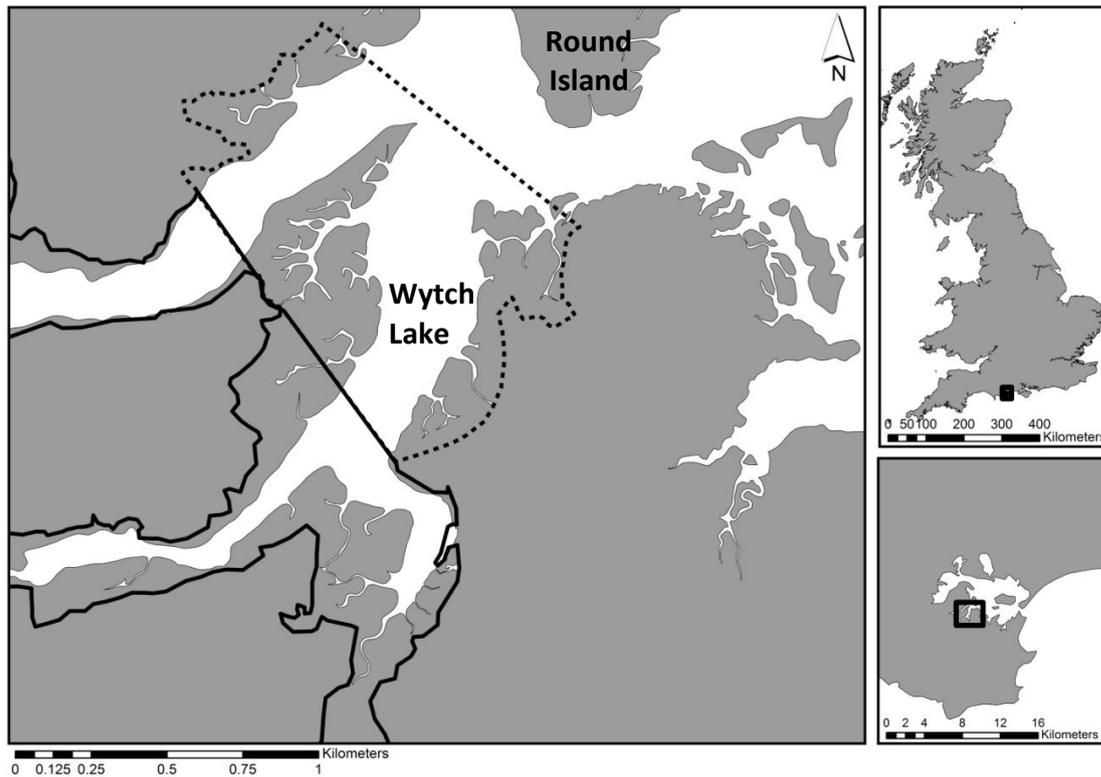


Figure 6.2. The study site, Wytch Lake, located within Poole Harbour on the south coast of the UK. The black lines indicate the boundaries of the bird sensitive area (BSA). The solid line indicates the area in which dredging is prohibited. The dashed line indicates the area in which dredging is permitted from 1st July – 31st October. Dredging is permitted outside of the BSA throughout the dredge season from 25th May – 24th December (Table 6.1). The southerly extent of Round Island can be seen to the north of the peninsula on the south east of the map.

6.2.2 Bird Observations

Bird observations were carried out during the winter from September 2015 to March 2016. The site was visited twice a month on a low spring tide, with the exception of October 2015 when only a single count was conducted. On each visit species counts were made and detailed individual observations were made of the main species present throughout the study area. This was done across each area subject to different levels of dredging effort throughout the 2015/16 winter (Figure 6.2; Table 6.1). For ease of counting each site was subdivided into smaller ‘patches’,

defined by local features such as saltmarsh or channel boundaries. These are indicated in Figure 6.3.

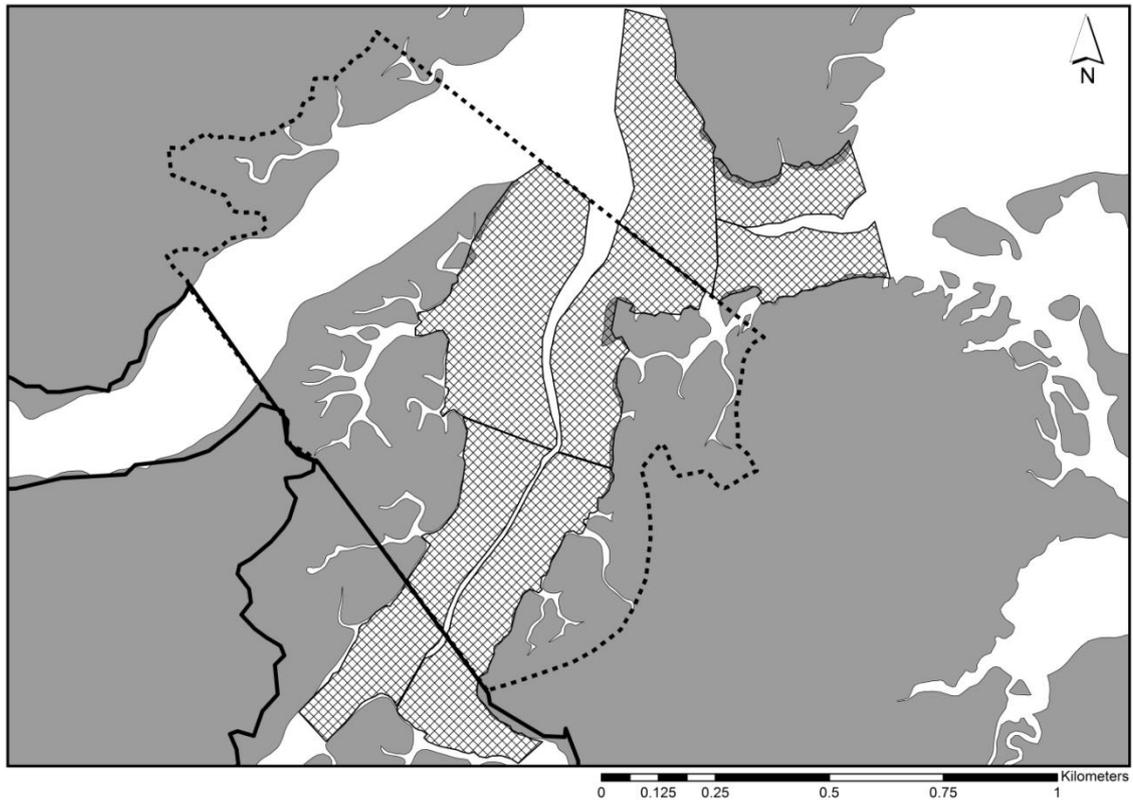


Figure 6.3. The nine survey patches in which bird counts and observations were conducted throughout winter 2015/16, indicated by the hatched polygons.

Each observation was conducted on a low tide of 0.9m or lower and as close to the lowest spring tide as permitted by daylight hours. Observations were conducted using a Swarovski STS 80 HD spotting scope at distances of 50 – 500m (depending on the survey patch). In each study site, bird numbers in each patch were counted every half hour, starting from one hour prior to low tide to one hour after low tide.

In the time between species counts, videos of individual birds were recorded using a Pentax K-30 D-SLR camera and a Swarovski Telephoto Lens System used to fit the camera to the spotting scope. Each individual bird was recorded for a period of 90

seconds and feeding rates (or prey capture rates) were calculated as the number of successful swallows per 90s. These feeding rate observations were carried out for Eurasian oystercatcher *Haematopus ostralegus*, Eurasian curlew *Numenius arquata* and black-tailed godwit *Limosa limosa islandica*, a designated feature of the Poole Harbour SPA; the larger and more abundant species present across the site which were more easily captured using this recording method at distance. Prey capture is easily identifiable in these species due to the characteristic head movement involved in swallowing.

6.2.3 Intake Rates

Initial feeding rates recorded in videos were used to estimate intake rates (grams of AFDM consumed per 90s) using a weighted average based on the relative abundance of prey items within the diets of each of the three species for which feeding observations were taken. Species diets and prey size classes were based on Goss-Custard *et al.* (2006) and prey abundance in each size class was based on core samples taken from each management area in November 2015 (described in detail in Chapter 3). This weighted average AFDM (M) in grams, across all prey size classes that could potentially be consumed by each bird species, was calculated by first using:

$$M = \sum_{i=1}^n p_i m_i$$

Where n = number of size classes, p_i = proportion of size class i (i.e. numerical abundance of size classes divided by the total numerical abundance of all prey size classes that could potentially be consumed), and m_i = published ash-free dry mass

(AFDM) value for size class i . This approach assumes that birds consumed prey size classes in proportion to their abundance. The AFDM values were published values that have been used in a number of previous modelling studies that have used individual-based models (IBMs) to predict the effects of environmental change on wading birds (Stillman *et al.*, 2001; Durell *et al.*, 2006; Bowgen *et al.*, 2015). The weighted average was then used to estimate the intake rates of individuals from each species based on the feeding rate observed through video analysis (i.e. feeding rate multiplied by the weighted average intake). As core sampling of the invertebrate assemblage was conducted in a grid design and did not cover the whole of each management area, this weighted average was extrapolated across all survey patches within each of the dredge management areas (i.e. dredging prohibited, dredging permitted July – October and dredging permitted May – December). With the caveat that these provide only an estimate of intake rates that may vary between locations throughout the study area, intake rates were compared for each species across dredging intensities.

Minimum and maximum daily intake rates were then extrapolated from our model outputs (the highest and lowest predicted values from the model fit) to place results in the context of species daily energy requirements. Intake rates were adjusted using published assimilation efficiencies of invertebrate prey groups for each study species. Many invertebrates have indigestible chitinous body parts that cause the actual assimilation of energy to be less than 100%. For oystercatcher, a species that opens its prey and removes the shell before consumption, this assimilation efficiency is 0.85 (Norton-Griffiths, 1967; Goss-Custard *et al.*, 2006). For

other species that consume prey whole, an efficiency of 0.75 is given for worms and bivalves and 0.85 for crustaceans (Kersten and Piersma, 1987; Goss-Custard *et al.*, 2006). Intake rates were therefore calculated twice for these species (using 0.75 and 0.85), indicating the minimum and maximum potential intake rates.

Daily intake rates were extrapolated from our measures of AFDM per 90 seconds based on an average of 12 hours feeding per day across winter. Daily energy requirements were calculated using published allometric equations of field metabolic rates (FMR) (kJ/day) in birds from Nagy, Girard and Brown (1999) whereby a species' FMR is calculated as:

$$FMR = aM^b$$

where $a = 10.5$ (Nagy, Girard and Brown, 1999; all bird equation), M = body mass of the study species (mean body mass estimates were derived from Johnson (1985) and Schroeder (2010)), and $b = 0.68$ (Nagy, Girard and Brown, 1999; all bird equation). Daily intake rates in grams of AFDM were converted to kJ using a published conversion multiplier of 22kJ g^{-1} , taken from Zwarts and Wanink (1993).

6.2.4 Distribution and Intensity of Fishing Effort

Shellfish dredging was ongoing throughout the early winter months of 2015/16 (Table 6.1) and ceased on 31st October in the outer BSA area and on 25th December outside of the BSA. As local fishermen do not keep logbooks and Vessel Monitoring Systems (VMS) are not currently required on inshore vessels, no quantitative data on fishing effort are available. SIFCA officers carry out approximately weekly enforcement patrols in the harbour during the dredge season to monitor dredging

throughout the harbour however. Aerial imagery was captured from the study site in November 2015 and remote sensing methods were therefore used to quantify fishing intensity throughout the site. These methods and results are discussed in detail in Chapter 4. Following validation of these results, image texture as represented by pixel diversity values were carried forward into the analysis of shorebird data as a proxy for fishing disturbance. A Spearman's rank correlation showed this measure of disturbance to correlate significantly with sightings of fishing activity (Chapter 4). These results were incorporated into the present analyses in order to better quantify dredging disturbance and to provide a robust analysis of the effect of this disturbance on our response variables.

6.2.5 Statistical Analysis

Distribution of waders and waterfowl was variable throughout the study site across the winter of 2015/16, with only a few species consistently present in large numbers. Distribution of the species most numerically abundant in the dataset in relation to fishing disturbance was investigated using measures of sediment disturbance (pixel diversity) derived from Chapter 4 as a proxy for dredging effort. Analysis was undertaken within a generalised linear model (GLM) framework. The appropriate error distribution for each species model was determined based on the over-dispersion parameter (θ) and the distribution of model residuals. The Akaike Information Criterion (AIC) value and diagnostic plots for each model were then taken as indicative of model quality. In this analysis each half-hourly count during each survey was treated as a replicate. The number of days through the winter (from the first survey on 02/09/2015) and/or the height of low water were

also included as covariates to account for residual variation where AIC values indicated a better model fit when included.

Feeding and intake rate data were also analysed within a generalised linear model framework, using the same methods to identify the best-fitting model. Quasi-poisson, gamma or negative binomial error distributions were used where most appropriate to account for over-dispersion, with a log-link function.

6.2.6 Cautionary Notes

Pseudoreplication is evident in the dataset as for each survey patch there is only one measure of pixel diversity (i.e. fishing intensity) and the same value re-occurs each time the patch is analysed, resulting in non-independence. Furthermore, long-lived shorebirds such as the species observed in this study display strong between-year and season-long site fidelity (Ens and Goss-Custard, 1986; Marks and Redmond, 1996; Finn *et al.*, 2001). Therefore, the birds observed in each fortnightly count may be considered to likely be the same individuals and hence also non-independent (Zharikov and Skilleter, 2004). However, introducing random-effects or repeated measures into the model to account for this would reduce the analysis down to impractical degrees of freedom. Using a generalised linear model to specify the appropriate error structure and link function takes into account the over-dispersion and the heterogeneity of variance in the data due to non-independence, and is considered the best option here. The GLM models used in our analyses therefore represent the best-fitting models that deal with these issues while allowing for a biologically reasonable analysis to be undertaken, identifying the

broad trends between species distributions, feeding rates and intakes rates and fishing intensity.

6.3 Results

A total of 27 bird species were observed using the study site during the winter of 2015/2016 (Table A3.1, Appendix 3), of which 24 were wader and waterfowl species.

6.3.1 Species Distribution in Relation to Dredging Disturbance

The species most consistently present during the study period and for which density data were analysed were Eurasian oystercatcher *Haematopus ostralegus*, Eurasian curlew *Numenius arquatus*, black-tailed godwit *Limosa limosa*, redshank *Tringa totanus* and shelduck *Tadorna tadorna*. Numbers of all species were variable over the course of the winter and across the management areas.

6.3.1.1 Oystercatcher *Haematopus ostralegus*

A GLM with a log-link gamma error structure including the number of days through winter and the height of low water on the survey as covariates best fit the oystercatcher data. Results indicate that oystercatcher densities are significantly higher in areas of increased sediment disturbance (Figure 6.4a; Table 6.2) and on higher tides (Table 6.2), both of which are significant predictors. In contrast, there is a small yet significant negative effect of the number of days through winter on oystercatcher densities, indicating that densities of this species fell slightly throughout the study period.

6.3.1.2 Curlew *Numenius arquata*

Curlew densities significantly increase with higher values of sediment disturbance, based on a log-link gamma GLM (Figure 6.4b; Table 6.2). The best-fitting model includes height of low water as a significant covariate, with birds occurring at higher densities at higher tides (Table 6.2). Days since the first survey was excluded from the model as this had no significant effect on curlew densities and reduced the model fit.

6.3.1.3 Black-tailed godwit *Limosa limosa*

A negative binomial GLM with a log-link error function including days throughout winter and height of low water as covariates best fit the black-tailed godwit data (Figure 6.4c; Table 6.2). No significant effect of pixel diversity or days throughout winter is observed on godwit densities, although tidal height has a significant negative effect on godwit densities throughout the study site, indicating that godwit occur at lower densities in the study site during higher tides (Table 6.2).

6.3.1.4 Redshank *Tringa totanus*

A negative binomial GLM with a log-link error function including days throughout winter best fit the redshank density data (Figure 6.4d; Table 6.2). No significant effect of pixel diversity is observed, although a significant effect of days through winter is evident on redshank densities throughout the study site, indicating that redshank densities increased throughout the study period (Table 6.2).

6.3.1.5 Shelduck *Tadorna tadorna*

A gamma distributed GLM with a log-link error function best fit shelduck density data, with no covariates included in the model (Figure 6.4e; Table 6.2). Results

indicate a significant effect of pixel diversity on shelduck densities throughout the study area, showing that shelduck occur at higher densities in areas subject to more dredging pressure (Table 6.2).

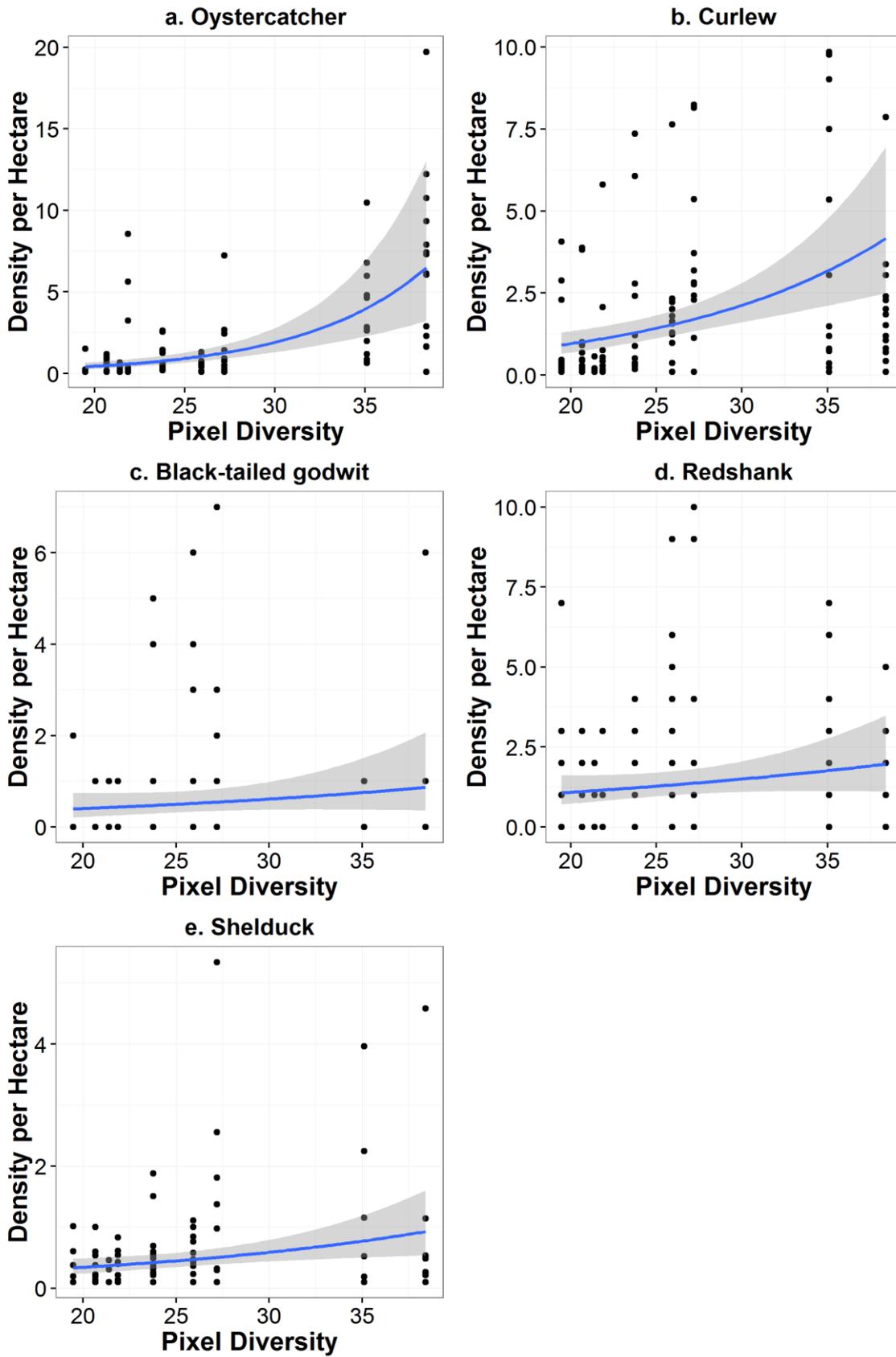


Figure 6.4. Generalised linear models of species densities against pixel diversities as a proxy for sediment disturbance.

Table 6.2. Outputs from best-fit generalised linear models to assess the effect of predictor variables on species distributions throughout the study site in winter 2015/16.

Oystercatcher						
Model	Parameter	Estimate	S.E.	Test Statistic	Probability	Theta
Density ~ Pixel Diversity + Days Through Winter + LW Height	Diversity	0.182	0.216	8.436	< 0.001	1.16
	Days Through Winter	-0.004	0.002	-2.007	< 0.05	
	LW Height	1.718	0.516	3.328	< 0.01	
Curlew						
Model	Parameter	Estimate	S.E.	Test Statistic	Probability	Theta
Density ~ Pixel Diversity + LW Height	Diversity	0.118	0.019	6.262	< 0.001	1.48
	LW Height	0.624	0.453	3.585	< 0.001	
Black-tailed godwit						
Model	Parameter	Estimate	S.E.	Test Statistic	Probability	Theta
Density ~ Pixel Diversity + Days Through Winter + LW Height	Diversity	0.007	0.031	0.219	0.826	0.48
	Days Through Winter	-0.005	0.003	-1.814	0.070	

	Winter					
	LW Height	-3.276	0.818	-4.006	< 0.001	
Redshank						
Model	Parameter	Estimate	S.E.	Test Statistic	Probability	Theta
Density ~ Pixel Diversity + Days Through Winter	Diversity	0.033	0.020	1.683	0.092	0.92
	Days Through Winter	0.011	0.002	4.728	< 0.001	
Shelduck						
Model	Parameter	Estimate	S.E.	Test Statistic	Probability	Theta
Density ~ Pixel Diversity	Diversity	0.054	0.020	2.681	< 0.01	1.29

6.3.2 Feeding and Intake Rates

A total of 355 videos were recorded of oystercatcher (n = 150), black-tailed godwit (n = 73) and curlew (n = 132) throughout the study site. Species feeding rates across all survey patches appear variable throughout the winter of 2015/16 (Figure 6.5), although no clear trend or significant difference between months is apparent for any of the species for which this data was collected (oystercatcher ($F(6,143) = 0.97$, $p = 0.45$); black-tailed godwit ($F(5,67) = 1.01$, $p = 0.42$); curlew ($F(6,125) = 0.86$, $p = 0.52$)). Data across all months were therefore pooled before further analyses were undertaken.

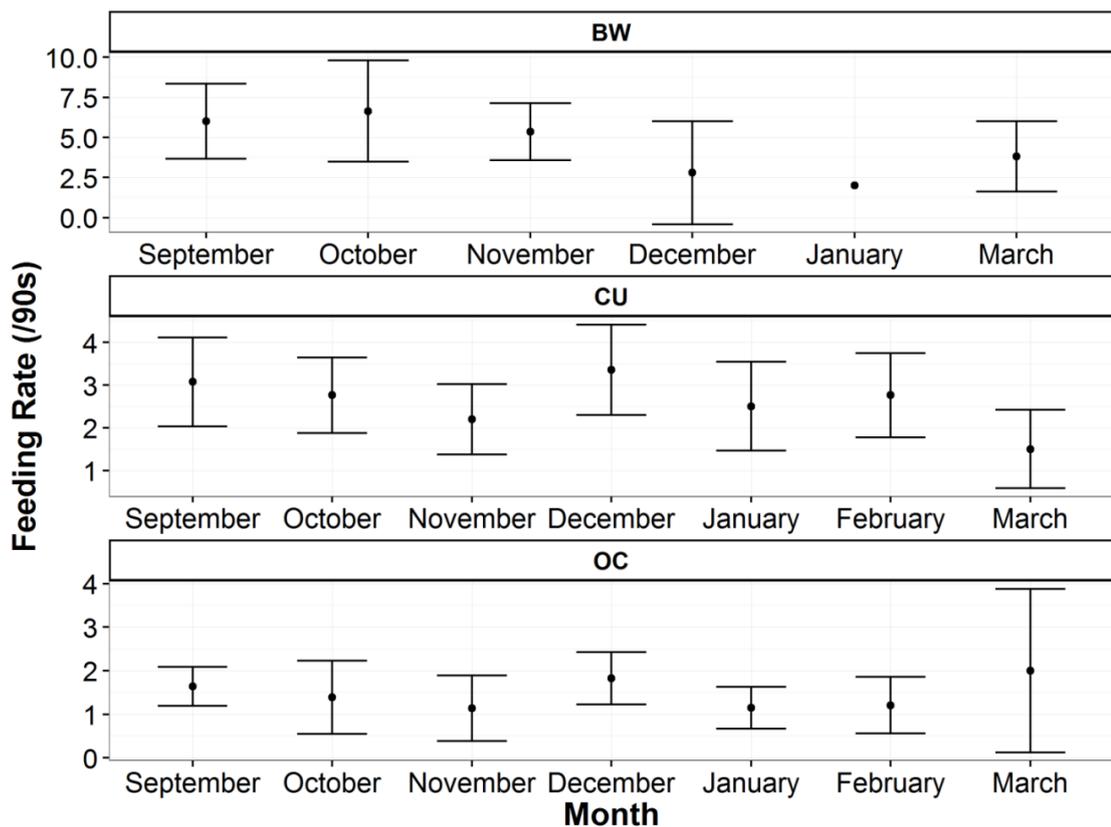


Figure 6.5. Mean (+/- S.E.) feeding rate (number of swallows) per 90s in each species during winter 2015/16.

BW = black-tailed godwit, CU = curlew, OC = oystercatcher.

6.3.2.1 Oystercatcher

No significant effect of sediment pixel diversity is observed on oystercatcher feeding rates, although results show a significant positive effect on intake rates (Table 6.3), indicating that oystercatcher in the study site obtain more energy in areas of higher fishing disturbance during winter 2015/16 (Figure 6.6a).

6.3.2.2 Black-tailed godwit

Feeding rates of black-tailed godwit appear significantly lower in areas of higher sediment disturbance/pixel diversity (Table 6.3). However, the same trend is not evident in intake rates; although the data shows a negative trend there is no significant effect on mean AFDM intake evident throughout the study area (Figure 6.6b).

6.3.2.3 Curlew

Feeding and intake rates of curlew show a similar trend to black-tailed godwit, with significantly lower feeding rates observed in areas of higher sediment disturbance/pixel diversity. Again however this does not result in a reduction in AFDM intake (Table 6.3; Figure 6.6c).

Table 6.3. Effect of image pixel diversity (as a proxy for fishing intensity) on feeding rate and intake rates in each species. Results represent outputs of best-fit quasi-poisson, gamma or negative binomial GLMs.

Species	Response	Estimate	S.E.	Test Statistic	Probability
Oystercatcher	Feeding Rate	0.010	0.013	0.800	0.425
	Intake Rate	0.021	0.007	3.249	< 0.01
Black-tailed godwit	Feeding Rate	-0.032	0.014	-2.242	< 0.05
	Intake Rate	-0.003	0.002	-1.454	0.150
Curlew	Feeding Rate	-0.033	0.012	-2.962	< 0.01
	Intake Rate	0.001	0.004	0.179	0.858

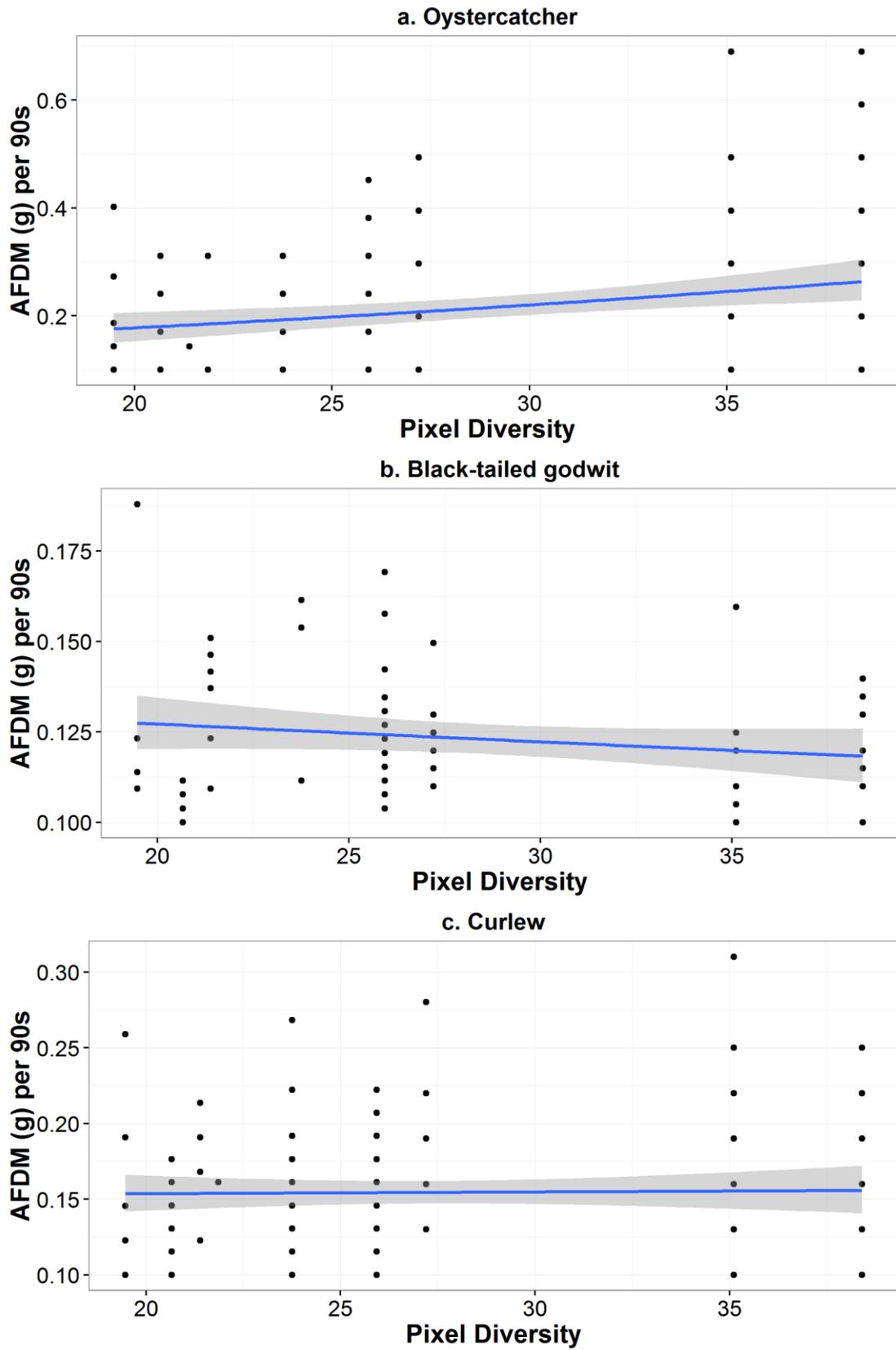


Figure 6.6. Intake rates (grams AFDM) per 90 seconds in each species for which feeding data was collected across a range of pixel diversity values as a proxy of fishing intensity.

6.3.3 Daily Energy Requirements

Using the model predictions of intake rates in AFDM (Figure 6.6), converted to kJ using published energy conversion factors, all species appear to meet their daily energy requirements (FMR in kJ day^{-1}) across the study area, even using the lowest predicted model intake rates and on prey with the lowest assimilation efficiencies (i.e. the minimum values for the lower estimate in the table) (Table 6.4).

Table 6.4. Estimated daily intake rates of the three study species during winter 2015/16. The 'lower' and 'upper' columns reflect the minimum and maximum predicted intake values from the model fit across all fishing intensities. Minimum and maximum values are provided based on the highest and lowest published assimilation efficiencies for benthic prey taxa. Oystercatcher consume all prey without the shell and therefore the minimum and maximum values are the same (i.e. assimilation efficiency is unchanged). Daily energetic requirements are also presented as field metabolic rates (FMR) calculated from published equations.

Species	Mean Body Mass (g)	FMR (kJ day^{-1})	Estimated Daily Intake Rate (kJ day^{-1})			
			Lower		Upper	
			Min	Max	Min	Max
Oystercatcher	503	721.53	1615.68	1615.68	2333.76	2333.76
Curlew	750	946.74	1188.00	1346.40	1267.20	1436.16
Black-tailed godwit	280	484.46	950.40	1077.12	1029.60	1166.88

6.4 Discussion

Previous work on the impacts of pump-scoop dredging on benthic communities in Poole Harbour (Chapter 3) showed a decline in bivalve molluscs and an increase in polychaetes and other opportunistic worms in areas of the study area due to dredging. Sampling of the target species, Manila clam, showed a dramatic reduction in harvestable (> 35mm) clams in areas of heavy dredging pressure due to fishing mortality (Chapter 5). It would therefore be reasonable to assume that those bird species for which bivalve molluscs comprise a key dietary component (e.g. oystercatcher, curlew (Goss-Custard *et al.*, 2006)) would be more susceptible to the impacts of this kind of dredging. However results suggest that there is currently no significant effect of dredging pressure in determining species distribution patterns throughout the site. In fact, for the two species for which molluscs represent a significant prey item, oystercatcher and curlew, there appears a positive trend between dredging intensity and species densities. This preference for areas more disturbed by dredging potentially highlights that these birds depend on the same areas targeted by clam fishermen throughout the winter, in which case both may be competing for the same resource of bivalve prey.

Given that in excess of 100% of a population's winter food requirements needs to be maintained for population survival, due to the effects of competition and interference (Goss-Custard *et al.*, 2004; Stillman and Wood, 2013), this spatial overlap of impact and conservation interests could be of concern should insufficient prey remain after the closure of the fishery in December, in particular the target species of the fishery (clams and cockles) for molluscivorous oystercatcher and

curlew. The fishery is managed through the new permit system and spatial and temporal restrictions; although clearly there remains spatial and temporal overlap with the overwintering period for shorebird populations, and managers should remain vigilant that effort is controlled through the permit system to allow sufficient food to remain.

The height of low water on each survey, when included in the GLMs, has a positive effect on species densities, with the exception of black-tailed godwit. Higher tides likely forces birds to feed higher up the shore and in a relatively smaller area, increasing densities. Black-tailed godwit however, a designated SPA species, appear to occur at lower densities on higher tides, potentially indicating that they leave the study area at higher tides. It may be that at higher tides when more of the study area is inundated, this species needs to leave the site to feed elsewhere to fulfil its daily energy requirements, which cannot be met in the upper reaches of the study area.

Many long-lived shorebird species demonstrate high site-fidelity (Marks and Redmond, 1996; Milsom *et al.*, 2000; Finn *et al.*, 2001). Individuals may not respond immediately to declines in feeding conditions, remaining in unprotected areas, or “ecological traps”, even when adjacent protected areas support higher prey densities where survival rates and individual body condition may be higher (Verhulst *et al.*, 2004). A single winter after a change in shellfishery management is unlikely to provide strong signals of impacts to bird survival or fitness, for which temporal trends across years are much more representative (Cook *et al.*, 2013), with past work showing that over a period of ten years oystercatcher populations

demonstrated no movement out of affected areas despite large-scale mortality (Atkinson *et al.*, 2003). However the trends in feeding and intake rates indicate no significant effect of dredging pressure on energetic intake of the study species over the winter of 2015/16. Despite lower feeding rates in heavily dredged areas for curlew and black-tailed godwit, this reduction does not translate to a significant reduction of AFDM intake; potentially suggesting that prey in these areas is more profitable than in areas of lower dredging pressure where feeding rates are higher. Size of prey is a key determinant in the availability and profitability to bird predators, as birds cannot consume individuals above certain sizes and other prey items may be too small to be profitable (Zwarts and Blomert 1992; Piersma *et al.* 1993; Zwarts and Wanink 1993).

The apparent disparities between feeding rates and intake rates are likely due to the relative abundance or size of prey in each of the dredge management areas. While oystercatchers appear to feed at a relatively stable rate across all management areas, they consume more AFDM of prey in areas subject to higher dredging disturbance. This again is probably due to the fact that much of their diet, mainly comprised of bivalve molluscs and larger worms (Goss-Custard *et al.*, 2006), represent target species of the fishery and co-occurring species and occur in areas targeted by fishermen. Mean AFDM intake rates of neither black-tailed godwit nor curlew appear to be affected by fishing, although a significant decline in feeding rates of both species is associated with dredging intensity, and a negative effect (albeit non-significant) on intake rates. This suggests that there are fewer prey

items available in areas of higher dredging disturbance, although they are larger and more profitable prey than in other areas, meaning birds feed more efficiently.

Comparison of daily energy requirements with the calculated intake rates for the study species may indicate whether birds within the study area are likely to meet their energetic demands, and hence whether they will need to resort to their fat stores and lose body mass throughout the winter. The somewhat crude estimates of daily energetic intake presented suggest that the study species are currently meeting their energetic demands in the study area, with even the lowest estimates indicating that daily intake is in excess of the requirements for all species. Furthermore, even the lowest estimates are likely to underestimate energetic intake due to the assumption in our weighted average that birds feed on prey in proportion to their abundance, rather than selectively feeding on larger and more profitable prey. These estimates are calculated in the absence of any inter- or intra-specific competition or interference however, which may increase when birds occur at higher densities on higher tides. The intake rates actually experienced by birds may therefore be lower (Goss-Custard, 1984; Stillman *et al.*, 2001). However, the low densities of birds observed throughout the study site and the fact that these estimates are in some cases more than double the calculated species FMR would suggest that competition and interference is unlikely to have significant implications. The minimum and maximum daily intake values are based on 'worst and best-case' scenarios with regards to assimilation efficiencies. The minimum values assume birds are feeding solely on crustaceans, prey with lower assimilation efficiency, and are likely to underestimate overall intake rates, while the maximum

values assume a diet comprised only of the most efficiently assimilated prey and likewise will tend to result in overestimates. The excess energy consumed would likely also provide birds in the study area with enough fat stores to cover thermoregulatory costs during the coldest months of winter (Kersten and Piersma, 1987).

The British Trust for Ornithology's (BTO) Wetland Bird Survey (WeBS) Alerts system reports on species trends throughout the UK and issues "alerts" for species that have demonstrated a decline over various time periods (Cook *et al.*, 2013). Alerts in Poole Harbour are issued for a number of the study species reported here: shelduck, curlew and redshank, all of which have demonstrated a decline in numbers in the harbour since its designation as an SPA (Cook *et al.*, 2013). This report lists site issues that may threaten wetland birds within the harbour, which includes the expansion of the Manila clam population following introduction, although does not mention potential impacts of the dredge fishery that the species' introduction has facilitated.

While the results of this study currently show no impact of pump-scoop dredging on bird distribution and intake rates within the SPA, it is important to emphasise that an apparent lack of impacts of the fishery should not be seen as trivial in the context of waterbird conservation, especially given the declines already apparent for some SPA species and the evidence of the importance of the Manila clam population in supporting overwintering birds within the harbour (Caldow *et al.*, 2007). As is pointed out by Gill *et al.* (2001), environmental managers often fail to accurately rank the importance of conservation issues within a site (Caughley, 1994;

Sutherland, 1998a). Furthermore, it is important to understand how local changes in distribution and habitat use have impacts at the population level (Sutherland, 1998b; Goss-Custard *et al.*, 2000). Conservation is much easier to achieve when multiple users and stakeholders are not denied access, with stakeholder involvement in the management process a key tenet of ecosystem-based management (EBM) (Pikitch *et al.*, 2004). Another key principle of EBM is constant monitoring and adaptive management (Pikitch *et al.*, 2004; MMO, 2014). The current Poole Harbour dredge fishery management regime is a successful example of management developed in close consultation with local fishermen and managers should remain vigilant to potential conflicts with shorebird conservation. Given the potential for an “ecological trap” and delayed evidence of impacts, monitoring of bird populations within the harbour, such as those carried out during WeBS counts, should be ongoing.

7. Individual-based models help inform fisheries management: applications on a novel shellfishery in Poole Harbour, UK.

7.1 Introduction

Many intertidal estuarine areas support significant shorebird populations and receive nature conservation designations to reflect their conservation importance, such as Special Protection Areas under the EU Birds Directive (79/409/EEC). In many of these areas, shellfish stocks provide a key prey resource for species such as Eurasian oystercatcher *Haematopus ostralegus*, red knot *Calidris canutus* and common eider *Somateria mollissima* (Goss-Custard *et al.*, 2006; Ens *et al.*, 2004) that depend heavily on bivalve prey such as cockles *Cerastoderma edule* and mussels *Mytilus edulis*. Often however these shellfish stocks are targeted by inshore fishing industries of significant economic value. Intertidal fishing activities can cause reductions in prey density, quality and size (Kaiser *et al.*, 2006; Humphreys *et al.*, 2007), often targeting specific bivalve species within a well-defined size range that represent the most profitable prey items for shorebirds. Numerous incidences of conflicts between the interests of shorebird conservation and local fishing industries have been reported (Smit *et al.*, 1998; Ens *et al.*, 2002; Atkinson *et al.*, 2003). Perhaps the most extreme examples of these conflicts have been the culling of around 10,000 oystercatchers in the 1970s in an attempt to reconcile issues regarding local cockle and mussel fisheries (Andrews, 1974; Prater, 1974), and the mass mortality of oystercatcher and eider in the Dutch Wadden Sea in the 1980s and 1990s following overharvesting of intertidal cockle and mussel beds (Smit *et al.*, 1998; Camphuysen *et al.*, 2002). Issues of shorebird conservation are further

complicated by their life history, often undertaking long-distance, cross-border migrations between overwintering and breeding grounds.

Over the last two decades, individual-based models (IBMs) have increasingly been utilised to make predictions on the effects of environmental change on shorebird populations (Stillman and Goss-Custard, 2009), whether with regard to habitat quality and climate change (Durell *et al.*, 2006), disturbance (West *et al.*, 2002) or shellfishing (Stillman *et al.*, 2003). IBMs offer a useful tool to environmental managers and may contribute to the implementation of ecosystem-based management (EBM), helping inform fisheries managers when determining catch quotas or temporo-spatial restrictions on inshore bivalve fisheries (Goss-Custard *et al.*, 2004) to ensure that activities within protected sites do not compromise site integrity and habitat quality.

A number of IBMs have been developed in recent years to make ecological predictions in various systems (Stillman *et al.*, 2000; West *et al.*, 2002; Atkinson *et al.*, 2003; Dunstan and Johnson, 2005; Durell *et al.*, 2006; Bowgen *et al.*, 2015). In this study, an existing model framework has been utilised to model overwinter survival of oystercatcher within an economically significant clam and cockle dredge fishery in a Special Protection Area in Poole Harbour on the south coast of the UK. Fishermen in Poole use a novel 'pump-scoop' dredge to harvest cockles *Cerastoderma edule* and the non-native manila clam *Ruditapes philippinarum* from June to December each year. The pump-scoop method and the management measures in place in the harbour are described in detail in Chapter 3. The manila clam was introduced into the harbour for aquaculture purposes in the 1980s,

although has since naturalised and is now the main target species of the fishery, also contributing to survival of oystercatcher throughout the winter (Caldow *et al.*, 2007). Following a number of years of high levels of illegal and unregulated dredging, the introduction of a new management regime for the dredge fishery in 2015 has seen an increase in compliance and support from local fishermen (Patrick Cooper, 2017, pers. comm.). The work is therefore timely to help inform on-going adaptive management of the fishery in the Poole Harbour SPA.

The present study aims to demonstrate the potential for applying an IBM framework to a novel, non-native shellfishery to inform fisheries management. The study addresses the following research questions: how does the oystercatcher population in Poole Harbour respond to increases in fishing intensity and removal of clam and cockle stocks? How do oystercatchers in the harbour compensate for reductions in prey densities throughout the winter? Is there a threshold of fishing effort above which oystercatcher mortality begins to increase?

7.2 Methods

7.2.1 Study Site

Poole Harbour is a natural harbour covering 36 km² located on the south coast of the UK. During the non-breeding season, the harbour supports large numbers of coastal birds, waders and waterfowl and is a designated Special Protection Area (SPA), Ramsar site and Site of Special Scientific Interest (SSSI). The SPA features for which Poole receives designation include internationally important numbers of black-tailed godwit (*Limosa limosa islandica*), Pied avocet (*Recurvirostra avosetta*) and common shelduck (*Tadorna tadorna*). Nationally important numbers of dunlin

(*Calidris alpina*), common redshank (*Tringa totanus*) and Eurasian curlew (*Numenius arquata*) are also present in the overwintering period (JNCC, 2006). Although not a feature of the SPA, oystercatchers occur in large numbers in the harbour and are of particular regional importance and the main molluscivorous species in the harbour and therefore vulnerable to interactions with the local shellfishery. Numerous other human activities occur in and around the harbour including commercial shipping and various recreational activities.

7.2.2 Poole Harbour Model

MORPH (Stillman, 2008), an existing IBM, was parameterised to simulate the Poole Harbour study system, including the existing shellfish beds, and to define the behaviour and energetics of individual oystercatchers within the system, including daily energy expenditure, rate of feeding and energy assimilation, and the availability of shellfish prey across the study system.

The model simulated 212 days, running from 1st September to 31st March, representing the overwintering period of oystercatchers in the UK. Throughout the modelled winter, time was divided into 5,088 hour-long 'time steps'. In each time step environmental conditions were assumed to remain constant. The diurnal cycle was incorporated in the model; each time step occurred either during daylight hours or at night, with variation in daylight hours derived from US Naval Observatory data for Poole Harbour from the winter of 2011/2012 (Table 7.1). Hourly mean air temperature was incorporated in the model based on 50-year average values for Poole Harbour from the Met Office Integrated Data Archive System (MIDAS) from 1963 to 2013, as this affects birds' energetic requirements.

The intertidal area of Poole Harbour was divided into 15 ‘patches’ that represent the available habitat for the oystercatcher population (Table 7.2). The mean elevation of each patch based on a pre-existing hydrodynamic model of the harbour (Benson, 2016) was also included, based on methods of a previous published modelling study in Poole Harbour (Bowgen *et al.*, 2015). The exposure of each patch was determined by the tidal height in each timestep, included in the model using TideWizard data (Smartcom Software, 2009) for the harbour from the winter of 2011/2012. Terrestrial fields were also included in the model as a separate patch at the very top of the shore. Fields are important additional habitat for shorebirds (Goss-Custard, 1969; Heppleston, 1971; Townshend, 1981; Navedo *et al.*, 2013; Furnell and Hull, 2014), providing an important supplementary food source during mid-winter when birds cannot meet their energy requirements from a solely marine diet. During this time oystercatcher are known to feed on earthworms, which at times can form up to 77% of a bird’s stomach contents (Heppleston, 1971).

7.2.2.1 Modelling Available Shellfish Prey Biomass

Prey resources in each model patch were incorporated using invertebrate data from a 2009 biotope survey of Poole Harbour, consisting of 80 intertidal sample sites in a grid design across the harbour (Herbert *et al.*, 2010). From this data, oystercatcher prey resources were included in the model as “cockle-clams”, combined data for cockles and clams, representing the main prey resources for oystercatchers and the target species of the dredge fishery. This was done as it is assumed that oystercatchers do not differentiate between cockles and clams when feeding, based on field observations of oystercatcher in Poole Harbour. Pooled densities of clams

and cockles in each patch were therefore used (Table 7.3). As the length-weight relationship differs for cockles and clams, a weighted mean AFDM (M) value for each size class in each patch was calculated, weighted according to the relative proportion of clams and cockles using:

$$M = \sum_{i=1}^n p_i m_i$$

where p_i = proportion of each species in size class i and m_i = published ash-free dry mass (AFDM) value for size class i . The relationship between size and AFDM for each species was based on Thomas *et al.* (2004). This then provided a mean AFDM in each size class based on the pooled densities of clams and cockles and weighted by the relative proportion of each species (Table 7.4).

The flesh content of shellfish declines over winter, and this was included in the model by incorporating a linear decline of 0.39 in AFDM content of prey over the modelled winter (Zwarts, 1991; Zwarts and Wanink, 1993). Natural mortality (i.e. not as a result of oystercatcher depletion) was also incorporated in this way as a 0.3 reduction in available shellfish densities throughout winter (Zwarts and Wanink, 1993). As the model incorporates energy content as kJ of energy, as opposed to AFDM, a conversion multiplier of 22.5kJ g⁻¹ was applied per gram of AFDM (Zwarts and Wanink, 1993).

7.2.2.2 Modelling the Poole Harbour Oystercatcher Population

The initial oystercatcher population size at the beginning of the modelled winter was taken as 850 birds, the latest five-year monthly mean count from Wetland Bird Survey (WeBS) counts from the British Trust for Ornithology (BTO), rounded to the

nearest 50. All birds were present in the system on September 1st, the first day of the modelled winter and remain present until the final day of the model (March 31st, day 212). All model patches and shellfish beds and the upper shore are accessible by birds in relation to their tidal exposure, although fields can only be accessed during daylight.

Individual birds begin the modelled winter with an arrival mass and aim to increase this body mass to a mid-target mass on day 106 (15th December), and a final target mass by the end of the winter (Table 7.1). These masses are converted into kJ of energy using 34.3kJ g⁻¹ of fat reserves (Kersten and Piersma, 1987). Once a bird meets its target energy store, it increases its resting time and reduces the amount of time spent feeding. When an individual does not meet its daily energy requirements, energy is drawn from fat stores, reducing the overall energy store of the bird. A starvation mass (Table 7.1), derived from field observations from starved birds, is incorporated into the model, and if energy stores fall to zero the bird starves and is removed from the system. Starvation is the only form of mortality for oystercatchers included in this model. Given the hard shell of the prey species, less than 100% of energy contained within a prey item can be assimilated by an individual oystercatcher, and modelled birds therefore have a prey assimilation efficiency of 85% (Kersten and Piersma, 1987) (Table 7.1). Oystercatchers leave behind 10% of flesh when consuming shellfish, reducing the total flesh consumed to 90% per prey item, which is also incorporated in the model (Goss-Custard *et al.*, 2004).

Foraging efficiencies vary between individuals; they are governed by the individual foraging efficiency of the bird as well as interference and competition. Oystercatchers in the model are parameterised with a unique foraging efficiency derived from a normal distribution around 1. Interference effects are included based on a dominance constant that is again unique to the individual and taken from a uniform distribution between 0 and 1.

Non-shellfish prey, which for oystercatchers generally only represents marine worms (other than when feeding in terrestrial fields) (Goss-Custard *et al.*, 2006) was incorporated into the model based on methods used in previous behaviour-based models of oystercatcher (Stillman *et al.*, 2000), and extended 10cm higher up the shore than the clam and cockle beds. This was done as in estuarine environments such as Poole Harbour, the upper extents at the top of the intertidal are largely characterised by polychaetes such as *Hediste diversicolor*, *Nephtys hombergii* and oligochaetes (e.g. *Tubificoides* spp.). These species dominate upper estuarine communities where little sediment turnover occurs and few infaunal species are supported (Connor *et al.*, 2004). This marine worm prey did not deplete over winter and intake rates were fixed at 1.00 AFDM second⁻¹ based on the asymptotic intake rate of oystercatchers feeding on *Hediste* spp. from Goss-Custard *et al.* (2006).

Intake rates in fields were also included based on those used by Stillman *et al.* (2000) and fixed at a rate of 0.53 AFDM second⁻¹. Field patches include an additional parameter that prevented birds feeding in fields at temperatures below 6°C, when the ground would be too hard and prohibit feeding. Intake rates are converted into kJ h⁻¹ then divided by the available energy density for each diet on the patch. The

interference free intake rate (*IFIR*) in mg s^{-1} when feeding on shellfish prey is calculated as in Stillman *et al.* (2014) and then affected by interference:

$$IFIR = f \frac{IFIR_{max} B}{B_{50} + B}$$

Where f stands for an individual's foraging efficiency, B is the density of prey biomass prey for size range consumed (mg m^{-2}), $IFIR_{max}$ is the maximum interference free intake rate and B_{50} is the density of prey biomass when at 50% of the maximum intake rate.

The maximum intake rate (*MaxIR*) limits the maximum amount of food that a bird can consume within a time step based on Kirkwood (1983), using the equation:

$$MaxIR = \left(1713 * \left(\frac{550}{1000} \right)^{0.72} \right) / (AssimilationEfficiency * DietEnergyDensity)$$

Basal metabolic rate (BMR) of oystercatchers is calculated by:

$$BMR = 437 * (Mass \text{ in } kg)^{0.729}$$

from Kersten and Piersma (1987), plus a further 10% cost of flight, based on 20 minutes of flight per day (Zwarts *et al.*, 1996). For every degree below the 10°C lower critical temperature (LCT), 31.8kJ is added to a bird's energetic demands (Zwarts *et al.*, 1996).

Individual birds in the model decided whether to forage within the patch which maximised their energy assimilation rate (i.e. energy assimilated during a time step) or returned to the roost. Birds fed if their energy store was less than 95% of its target value (i.e. they had been losing mass), or if any of the available diets yielded

an energy assimilation rate greater than the average achieved over the last 24 hours (i.e. relatively high quality prey were available). If their energy store was greater than 95% of its target value (i.e. they had not been losing mass), and if none of the available diets yielded an energy assimilation rate greater than the average over the last 24 hours (i.e. only relatively low quality prey were available), then birds roosted. This rule meant that birds chose to roost during high water unless they were losing mass, in which case they would supplement their intertidal feeding by feeding in terrestrial fields.

Table 7.1. Parameters included in the Poole Harbour shellfishing model.

Time and environmental conditions		
Parameter		Value
Duration of model		1 st September – 31 st March (212 days), 5,088 hours (Timesteps)
Daylight		Hourly, based on US Naval Observatory website (1/9/2011-31/3/2012)
Tide Heights (m Chart Datum)		Hourly, based on TideWizard values for Poole Harbour (01/09/2011-31/3/2012)
Temperature (°C)		Hourly, based off 50 year average for Poole Harbour (1963 – 2013).
Prey Patches		
Parameter		
Number of patches	Fields/Upshore	1 each
	Cockles/Clams	15
Available	Fields/Upshore	During daylight
	Cockles/Clams	Tide permitting
Energy density of prey flesh	Cockles/Clams	22.5 kJ g ⁻¹
Number of size classes	Field Prey	1
	Upshore Prey	1
	Cockles/Clams	8
Width of size classes (mm)	Field/Upshore	N/A
	Prey	5-10; 10-15; 15-20; 20-25; 25-30; 30-35; 35-40; 40-45
	Cockles/Clams	35; 35-40; 40-45
Density of prey at start of winter (m ⁻²)	Field Prey	100
	Upshore Prey	100

	Cockles/Clams	See Table 3
Expression to update resource density (over-winter non-bird mortality of prey)	Field Prey Upshore Prey Cockles/Clams	100 100 0.30
Ash-Free dry mass (AFDM) at start of winter (g)	Field Prey Upshore Prey Cockles	0.1 0.1 See Table 4
Express to update resource energy (over-winter decline AFDM)	Field /Upshore Prey Cockles/Clams	None 0.39 (39%) decline over winter
Foragers Parameters		
Number of Forager Types	Oystercatcher	850
Arrival Day		1
Energy density of fat reserves		34.3 kJ g ⁻¹
Arrival mass (g)	Oystercatchers	503
Mid Target mass (g) Day 106 for Oystercatchers	Oystercatchers	550
Final Target mass (g)	Oystercatchers	598
Starvation mass (g)	Oystercatchers	350
Foraging Efficiency	Oystercatchers	Normal distribution around 1 (0.125 SD)
Night Efficiency	Oystercatchers	1
Dominance	Oystercatchers	Uniform distribution between 0 and 1
Aggregation Factor	Cockle/Clams	10
Regulated Density (/ha)	Cockle/Clams	53.84
Interference Coefficients <i>a; b; c; d</i> <i>a, b (Rank); c (Day); d (Threshold)</i>	Oystercatchers	-0.5; 0.5; 0.01 (100/ha)
Diet types	Oystercatchers	Fields Diet Upshore Diet Cockle/Clam Diet
Number of resources in each diet and size classes covered	Oystercatchers	Fields: 1 Upshore: 1 Shellfish Beds: 6; 15-45mm
Rate of consumption (mg AFDM/second)	Oystercatchers Fields Upshore	0.53 (for >6°C) 1.00

(kJ/hour)	Cockles/Clams	$((237.7687 * \text{DietEnergyDensity}) / (1.45813 + \text{DietEnergyDensity}))$
Maximum intake rate (kJ per hour)		$(1713 * (550/1000)^{0.72}) / (\text{Assimilation Efficiency} * \text{DietEnergyDensity})$
Energy expenditure – non-thermoregulatory (kJ d ⁻¹)	Oystercatchers	678 (inc. 30 kJ for 20mins flight per day)
Lower Critical Temperature	Oystercatchers	10°C
Energy expenditure – thermoregulatory (kJ °C d ⁻¹)	Oystercatchers	31.8
Prey assimilation efficiency	Oystercatchers	0.85
Left over prey in shells	Oystercatchers	10% (0.9)
Fat storage efficiency	Oystercatchers	0.884
Feeding, resting metabolic rate (kJ/hr)	Oystercatchers	$((648 + 30) + \max(31.8 * (10 - \text{Temperature}, 0))) / 24$

Table 7.2. Characteristics of the patches included in the Poole Harbour shellfish model.

Patch Name	Maximum Exposed Area (m²)	Mean Shoreheight (m CD)
Upshore	50000	1.749
Sandbanks	452401	1.086
LittleSea	220540	1.189
PoolePark	212376	1.029
HolesBay	1856842	1.495
Hamworthy	117259	0.689
RocklyPoint	190251	1.109
Lytchett	823333	1.559
HoltonMereOut	554793	1.176
HoltonMereln	943542	1.509
WarehamIn	2073971	1.471
WarehamArne	665418	1.088
Arne	243558	1.659
WytchMBere	1305410	1.640
OwerNewtonBrand	3804661	1.197
Brownsea	392022	0.896

Table 7.3. Start of winter numerical density of shellfish prey in each size class included in the Poole Harbour model.

Patch Name	Fields Prey	Upshore Prey	Cockles/Clams in mm size classes (per m ²)							
			5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45
Fields	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Upshore	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sandbanks	0.000	0.000	0.000	0.000	0.000	8.488	0.000	0.000	0.000	0.000
LittleSea	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PoolePark	0.000	0.000	25.465	0.000	0.000	0.000	0.000	0.000	16.977	0.000
HolesBay	0.000	0.000	2.829	2.829	8.488	11.318	2.829	8.488	2.829	0.000
Hamworthy	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
RocklyPoint	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lytchett	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
HoltonMereOut	0.000	0.000	0.000	12.733	31.831	31.831	6.366	25.465	12.733	25.465
HoltonMereIn	0.000	0.000	8.488	8.488	8.488	8.488	0.000	8.488	0.000	0.000
WarehamIn	0.000	0.000	0.000	0.000	0.000	0.000	1.959	0.000	0.000	0.000
WarehamArne	0.000	0.000	0.000	0.000	8.488	4.244	4.244	8.488	4.244	0.000
Arne	0.000	0.000	0.000	0.000	0.000	0.000	0.000	25.465	0.000	0.000
WytchMBere	0.000	0.000	10.914	0.000	0.000	7.276	3.638	0.000	0.000	0.000
OwerNewtonBrand	0.000	0.000	3.473	2.315	4.630	5.788	4.630	4.630	1.158	1.158
Brownsea	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table 7.4. Start of winter flesh content (g AFDM) of shellfish prey in each size class included in the Poole Harbour shellfish model.

Patch Name	Fields Prey	Upshore Prey	Cockles/Clams in mm size classes (g AFDM)							
			5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45
Fields	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000
Upshore	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000
Sandbanks	0.00000	0.00000	0.00000	0.00000	0.00000	0.10601	0.00000	0.00000	0.00000	0.00000
LittleSea	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000
PoolePark	0.00000	0.00000	0.00300	0.00000	0.00000	0.00000	0.00000	0.00000	0.57666	0.00000
HolesBay	0.00000	0.00000	0.00311	0.01510	0.04134	0.10013	0.20622	0.32152	0.37838	0.00000
Hamworthy	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000
RocklyPoint	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000
Lytchett	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000
HoltonMereOut	0.00000	0.00000	0.00000	0.01428	0.04465	0.09188	0.20622	0.27490	0.37838	0.65195
HoltonMereIn	0.00000	0.00000	0.00277	0.01428	0.03897	0.10601	0.00000	0.24693	0.00000	0.00000
WarehamIn	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.15003	0.00000	0.00000	0.00000
WarehamArne	0.00000	0.00000	0.00000	0.00000	0.04252	0.08246	0.20622	0.35881	0.57666	0.00000
Arne	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.35881	0.00000	0.00000
WytchMBere	0.00000	0.00000	0.00300	0.00000	0.00000	0.10601	0.20622	0.00000	0.00000	0.00000
OwerNewtonBrand	0.00000	0.00000	0.00277	0.01510	0.04074	0.10601	0.19217	0.30287	0.57666	0.65195
Brownsea	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000
Sandbanks	0.00000	0.00000	0.00000	0.00000	0.00000	0.10601	0.00000	0.00000	0.00000	0.00000
LittleSea	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000
PoolePark	0.00000	0.00000	0.00300	0.00000	0.00000	0.00000	0.00000	0.00000	0.57666	0.00000

7.2.3 Fishing Simulations

In order to simulate different fishing scenarios, multiple runs of the model were performed following re-parameterisation for increasing weights of shellfish landings above that of 2009, when the invertebrate data were collected. These new parameter files were based on manipulations of the pooled densities of oystercatcher's "cockle-clam" diet to represent reductions due to fishing. This was done at the beginning of the modelled winter and was done iteratively for increasing reductions in harvestable bivalves in 10% increments, ranging from no reduction in resources (i.e. no fishing activity) to a 100% reduction of harvestable bivalves (high intensity fishing). These iterative reductions were expressed as the number of tonnes of shellfish landed.

These changes to the resource parameters were only performed for patches in which dredging is permitted under the dredge permit byelaw in Poole Harbour and for legally harvestable size classes. Given that the minimum landing size (MLS) of cockles and clams in Poole differs – 24mm and 35mm respectively – for size classes between these values a weighted reduction in densities based on the relative proportion of cockles to clams was used. Weighted reductions were also used when a model patch falls across different management areas of the harbour, i.e. where dredging is permitted in one area of the model patch and prohibited in another. This was only the case for one patch in the model however, where the upper reaches of the Middlebere and Wytch channels are closed to dredging and the outer reaches are open, all falling within one patch.

7.2.4 Analysis

The model was run five times under each fishing scenario and results averaged. The key output was the mean number of oystercatcher that survived the winter, expressed as percentage survival in the population. Other outputs reported include the proportion of marine worms within a bird's diet, the final body mass of birds in relation to their target weight at the end of the winter and the mean proportion of time spent feeding. These all provide information on the condition of the Poole Harbour oystercatcher population and the functional response to different levels of fishing effort.

The trends in the mean responses were first plotted against each of the discrete fishing scenarios and ANOVA was used to test for differences between each level of harvesting and to identify at what point a significant deviation from the initial values was evident in the response. For those responses where a significant deviation from baseline values was observed, data were re-plotted across a continuous scale of increasing landings and the effect analysed within a linear model framework to better characterise the effect of increased shellfish catch.

7.3 Results

7.3.1 Testing the Model

Before multiple simulations were performed, the model predictions were tested against observed responses that were available in various published literature (Table 7.6). These included the proportion of birds surviving the winter and the proportion of time spent feeding during the winter. Results show that the model performs well when compared against published values for each of these

responses, and was therefore carried forward for predictions of the effects of shellfishing to be made.

Table 7.5. Tests of the Poole Harbour oystercatcher model. The sources for observations are given at the foot of the table.

Value	Predicted	Observed	% Difference
Proportion survived	1	0.99 ¹	1
Proportion of time spent feeding	0.56	0.59 ²	3
1. Atkinson <i>et al.</i> (2003) 2. C. Collop, Unpublished PhD Thesis.			

7.3.2 Fishing Scenarios

Increasing landings of shellfish in Poole Harbour has no significant effect on oystercatcher mortality rates or the final body weight of birds at the end of winter (Figure 7.1). The percentage of the oystercatcher population feeding in areas closed to fishing is variable, with no apparent trend according to landed weights of shellfish (Figure 7.1).

A significant effect of shellfish landings was evident for the proportion of time spent feeding ($F(10,44) = 197.03, p < 0.001$), the proportion of the population using fields ($F(10,44) = 198.32, p < 0.001$) and the proportion of marine worms in the diet ($F(10,44) = 339.29, p < 0.01$). Both the proportion of time spent feeding and the number of oystercatcher feeding in fields increased significantly from the initial model predictions following removal of 20% of harvestable shellfish, or approximately 200 tonnes of wet weight cockles and clams. The proportion of marine worms (e.g. *Hediste/Nereis*) in the diet of oystercatchers increased

significantly from initial model predictions following a 30% reduction in harvestable stock, or approximately 270 tonnes wet weight.

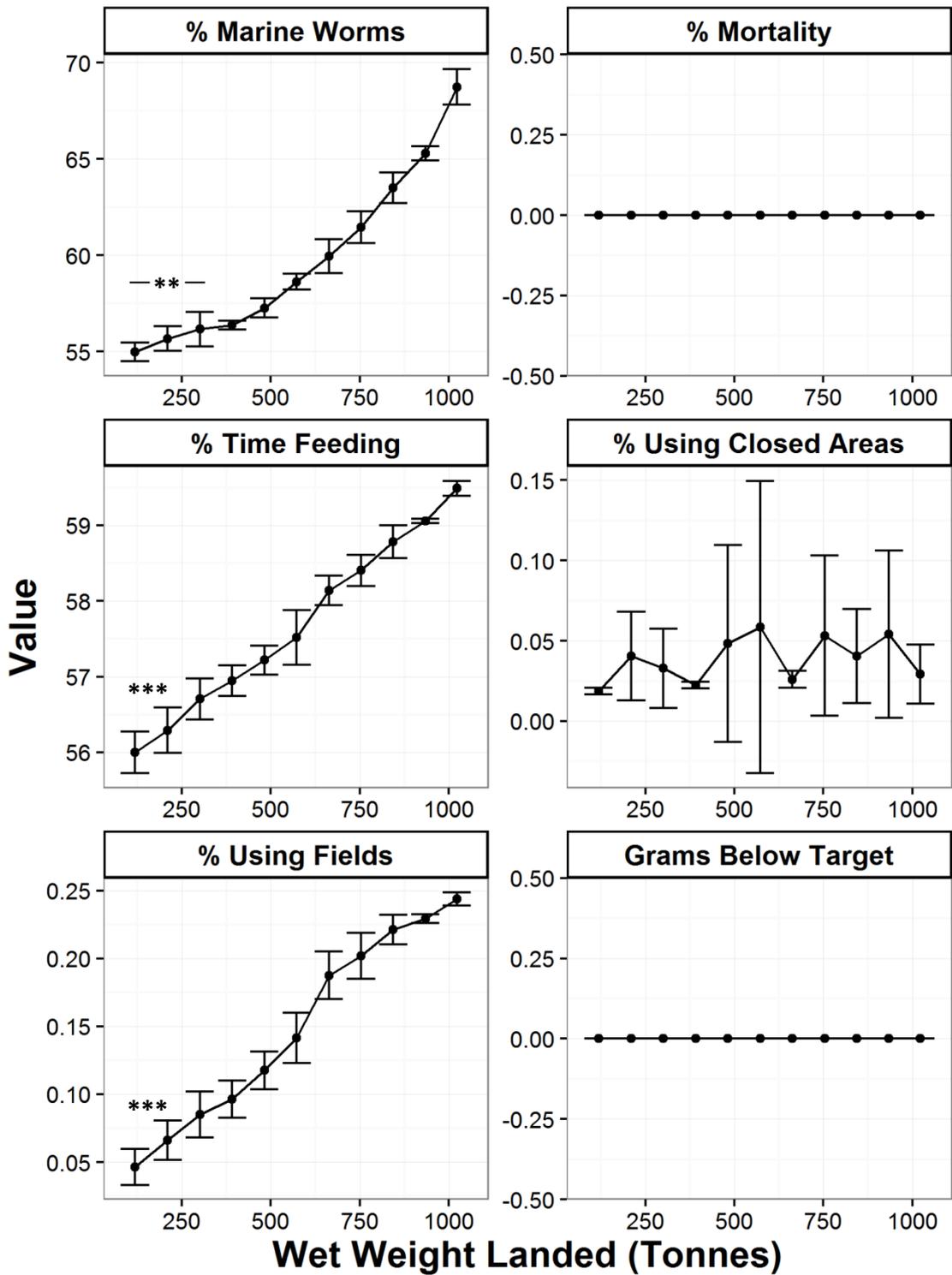


Figure 7.1. Mean response values (+/- 95% C.I.) for the Poole Harbour oystercatcher population under scenarios of increased landings of shellfish removed across all patches open to dredging simultaneously in Poole Harbour, UK. The point at which the response deviates significantly from initial values is indicated with asterisks.

With landings included as a continuous variable, results show that despite the highly significant relationship between landings and the behavioural responses observed, for every tonne of shellfish removed the observed increases in each of the responses is small (Table 7.7). The best-fitting model to describe the increase in worm consumption with increased shellfish landings was a polynomial curve (Figure 7.2c), indicating that the shift to consuming more worms in the diet is initially slow, before increasing in magnitude as shellfish prey becomes more scarce.

Table 7.6. Effect of increasing shellfish landings (tonnes removed per year) on responses in the Poole Harbour oystercatcher across a modelled winter.

Response	Model	Estimate	S.E.	t-value	p-value
% Time Feeding	Regression	0.004	0.0001	43.74	< 0.0001
% Using Fields	Regression	0.0002	0.0001	35.97	< 0.0001
% Marine Worms in diet	Quadratic	0.00002	0.0001	15.12	< 0.0001

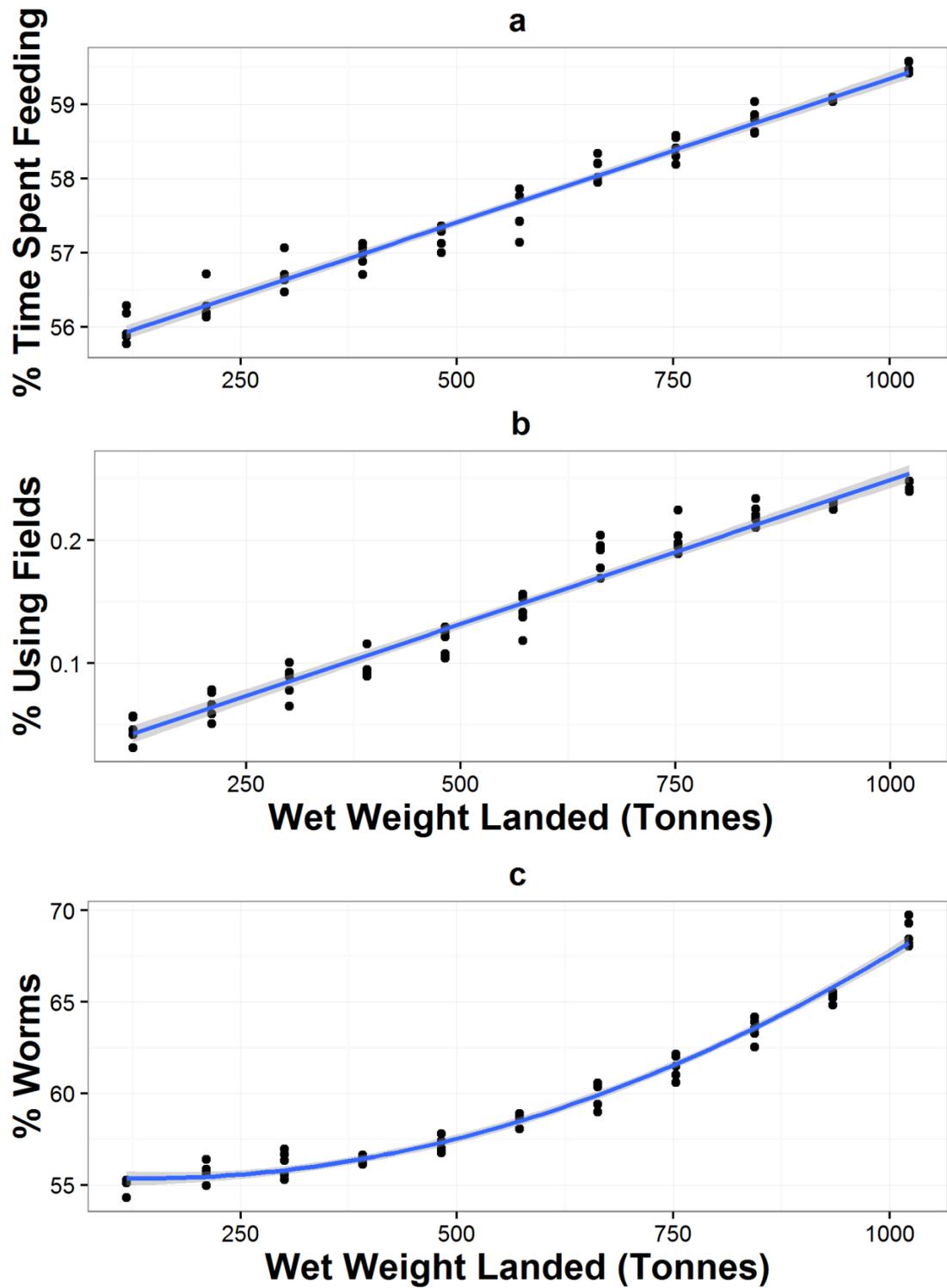


Figure 7.2. The relationship between increased shellfish landings in tonnes of wet weight and time spent feeding (a), the proportion of the population using fields (b), and the amount of marine worms in the diet (c) of oystercatchers within Poole Harbour.

7.4 Discussion

There has been much concern expressed over the conflicts between shellfisheries and shorebirds - in particular oystercatchers – although results show no population response in oystercatchers in Poole Harbour under all scenarios of shellfish dredging, even with all legally harvestable shellfish removed from the system. The present study investigates the effects of a simultaneous reduction in shellfish at the start of the overwintering period, before the model is run. In reality the dredge season in Poole currently opens in June each year and closes in December, with dredging occurring for the first four months of the modelled winter. Incorporating a gradual depletion of shellfish prey into the model throughout the winter consistent with a realistic distribution of fishing effort that may change through time was considered too complex and beyond the scope of the study. However, landings data from the most recent year available indicate a marked decline in landings of cockles and clams within the harbour after September, following a peak in landings during the first months of the season, when approximately 70% of the winter's catch is landed (S. Birchenough, 2017, pers. comm.). It was therefore considered appropriate to incorporate a simultaneous removal of shellfish before the model begins, when the majority of shellfish are harvested from the harbour.

The latest available landings data from 2015 indicate that during the course of the season a total of 324.6 tonnes of cockles and clams were harvested in the harbour. Comparison of this value with the model predictions in Figure 7.1 indicates that recent harvesting levels in Poole Harbour are within sustainable levels. Landings may be sufficient to elicit a significant change in behaviour from baseline levels in

order for oystercatchers to meet their target mass by the end of the winter, but this does not result in a population impact.

Under all scenarios of increased landings, no significant effect on overall mortality in the population is evident, with all birds included in the model reaching their target weight of 598g by the end of the modelled winter. This suggests that oystercatchers have the capacity to adjust to reduced availability of the most profitable bivalve prey, with behavioural responses compensating for the loss of the species' preferred prey items. Even in the absence of oystercatcher mortality the results indicating behavioural shifts in the Poole Harbour oystercatcher population are likely to be of interest to conservation managers. While the observed behavioural changes do not elicit a population response in the present study, an understanding of behavioural responses to anthropogenic impacts is critical in conservation practice (Berger-Tal *et al.*, 2011), and subtle behavioural changes such as those predicted are important when understanding the true impacts of environmental change. Patterns of movement, habitat use and foraging behaviours are key domains of behavioural ecology that can ultimately affect population dynamics, and information on behavioural changes in response to human activities is necessary to inform conservation in practice (Angeloni *et al.*, 2008; Berger-Tal *et al.*, 2011).

Results show that oystercatchers compensate for lost shellfish prey by increasing the time spent feeding throughout the winter, and increasingly switching from an almost equal marine diet of bivalves and annelid worms to one dominated by worms (almost 70% of prey consumed) when approximately 900 tonnes of bivalve prey, or all legally harvestable shellfish, are removed by fishing (Figure 7.1). The

switch to increasing consumption of worms over bivalve prey therefore appears sufficient to meet the energetic demands of the Poole Harbour oystercatcher population, with all birds reaching their target mass at the end of the winter and none falling to their starvation mass. Given that these model predictions are based on non-depleting marine worm prey, such a change in diet may be more problematic in reality and worthy of consideration for managers.

Both the proportion of birds using the surrounding fields and the time spent feeding show significant increases from baseline values following removal of just 20% of legally harvestable shellfish from the harbour. While the significant results in these behavioural responses may be interpreted as indicating that the oystercatcher population is highly sensitive to shellfish removal, the actual magnitude of the increase is small (Table 7.6), with each tonne of shellfish removed resulting in an increase of < 0.01% in the use of fields and the time spent feeding. It does indicate however that with increasing loss of shellfish stocks birds may have difficulty meeting their energetic demands from marine prey alone and must compensate by changing their behaviour. As temperatures decrease in mid-winter, the availability of marine food drops as invertebrates burrow deeper in the sediment (Zwarts and Wanink, 1993) and as a result intake rates drop, with those in December observed to be 57% of those in October (Heppleston, 1971). An increase in the number of birds feeding in fields is therefore an indication that daily energy requirements cannot be met from marine food alone and earthworms are needed to supplement their diet. The change in the use of fields is an order of magnitude less than that observed in worm consumption or time spent feeding however, suggesting that

birds more efficiently meet their energetic demands by feeding for longer and consuming more worms. Feeding in fields can therefore be considered a last resort; a maximum of around 0.25% feeding in fields is observed even with 100% of all harvestable shellfish removed.

Past work on the effects of disturbance has shown similar increases in time spent feeding; suggesting that oystercatchers extend their foraging time in order to meet their daily energy demands rather than increase their rate of feeding (Urfi *et al.*, 1996; Yasuè, 2005). Similar increases in time spent feeding occur in response to increased competition (Yasuè, 2005) and habitat loss (Evans, 1976; Goss-Custard, 1977). Increased feeding time inherently carries greater risks for individuals, with longer exposure to potential disturbance, competition and predation than under benign conditions.

Given that the invertebrate data included in this model includes only the main oystercatcher prey items, in reality it is likely that more food is available to birds than that included in the model, such as other bivalves such as *Macoma balthica* and *Scrobicularia plana* (Goss-Custard *et al.*, 2006), which may also provide further potential to compensate for reductions in densities of the target species of the fishery.

The invertebrate data incorporated into the model is based on a 2009 biotope survey of Poole Harbour (Herbert *et al.*, 2010), which is the most recent data available of sufficient detail (with prey densities and size data included) upon which a model can be based. The cockle and clam fishery was operational in Poole in 2009 although was managed under the Poole Fishery Order 1985, a hybrid

Several/Regulating Order, and a Cockle Fishing Byelaw. The clam fishery was regulated through the annual issue of 25 licences, with fishing permitted in October, November and December, while the cockle fishery was separate to the licenses, with a closed season enforced from 1st February to 30th April each year (S. Birchenough, 2017, pers. comm.). Dredging was therefore ongoing at the time at which data was collected, and consequently our baseline predictions do not represent unfished conditions. Data from 2009 for cockles and clams supplied by SIFCA were used to represent the starting values for landings of wet weight.

Models such as the one used in this study rely on robust datasets and results are only as accurate as the data that inform the model. The invertebrate data included in this study, along with the various parameters incorporated into the model, have been used in previous published studies that have predicted the effects of wider environmental change on shorebirds in Poole Harbour (Durell *et al.*, 2006; Bowgen *et al.*, 2015) and the data is therefore considered to allow accurate predictions of model scenarios. Comparison of model predictions with field observations (Table 7.6) also shows that the model results can be considered accurate, with high similarity between predicted and observed values.

While other shorebird species also overwinter in Poole Harbour in important numbers (JNCC, 2006), the specialised feeding mode of oystercatchers has long been considered to reduce their vulnerability to interspecific competition (Dewar, 1915). It is therefore not unreasonable to assume that the effect of increased shellfish landings would be similar with other overwintering shorebird species included in the model. Oystercatchers are the main predator of shellfish of

harvestable size, despite low levels of predation from herring gulls, *Larus argentatus*, as other shorebird species generally feed on smaller bivalves that minimises the risk of bill damage when feeding (Durell, 2000; Goss-Custard *et al.*, 2006), although they may target damaged clams that remain in the sediment after dredging.

No trend is evident in the number of birds using areas closed to fishing, suggesting that whilst shellfish landings increase, model birds compensate for reduced prey densities by feeding for longer and including more worms in their diet in preference to relocating to areas closed to fishing. A reasonable assumption would be that the main areas targeted by fishermen, and consequently designated open to fishing under the current management measures, are those that support the highest shellfish densities, whilst closed areas support relatively lower prey densities and are not important feeding areas. Other work has shown however that the strong site-fidelity shown by oystercatchers can prevent them from leaving an area to forage elsewhere, even when prey is of such low quality to reduce survival (Verhulst *et al.*, 2004). While that is clearly not the case in the present study (all birds survive the winter under all fishing scenarios) it is an important consideration when using shorebird numbers as indicators of habitat quality in the short-term (Piersma *et al.*, 2004). While the closed areas of Poole Harbour may not support high enough prey densities to be of critical importance as feeding areas, shellfish in these areas are larger than in other areas of the harbour (Chapter 5), and have been shown to represent important sources of larval supply (Herbert *et al.*, 2012). Annual recruitment is critical for sustainability of both the dredge fishery and shorebird

populations within the harbour, and annual stock assessments carried out by the Southern Inshore Fisheries and Conservation Authority can help monitor recruitment levels and inform adaptive management.

Whilst shellfish prey comprises the main component of oystercatchers' diet, differences in diet choice have been widely observed, with some individuals feeding solely on mussels (*Mytilus*), while others feed on a combination of various bivalves and worms (Sutherland *et al.*, 1996). Extensive mussel beds do not exist in Poole Harbour (Herbert *et al.*, 2010) and oystercatchers depend largely on cockles and clams as their primary prey species. These species are much more susceptible to environmental changes and local densities can fluctuate rapidly (Desprez *et al.*, 1992; Rybarczyk *et al.*, 1996; Zwarts *et al.*, 1996). More omnivorous birds may be more adapted to fluctuations in prey availability and are consequently more able to compensate by switching diets. Furthermore, many passerine birds that rely on unpredictable food resources as their main diet keep more fat reserves than those that depend on predictable prey resources (Rogers, 1987; Ekman and Hake, 1990; Ekman and Lilliendahl, 1993; Gosler, 1996). While such variations in baseline fat reserves are not incorporated into the model, in real systems it is worth considering that this may afford further 'flexibility' than that demonstrated in the results in the ability of a population that relies on regularly fluctuating prey resources to adjust to fishing-induced reductions.

Previous work has shown that oystercatchers in Poole Harbour consume clams between 16 and 50mm in length (Caldow *et al.*, 2007), while oystercatchers will consume any cockles larger than 15mm in length that are present (Goss-Custard *et*

al., 2006). The minimum legal landing size of cockles and clams of 24mm and 35mm respectively should therefore allow smaller individuals within the size ranges consumed by oystercatchers to remain available. While it is clear from the model results that sufficient food remains in the system under all fishing scenarios to sustain the Poole oystercatcher population, the survey from which the invertebrate data is derived shows that large, longer-lived species of marine worm (e.g. *Alitta virens*) are relatively uncommon in Poole Harbour (Herbert *et al.*, 2010). Such species would comprise valuable prey items for oystercatchers in the absence of high quality shellfish prey. There is evidence to suggest that some under-sized shellfish are harvested by the dredge fishery in Poole (Chapter 5). While these under-sized landings are not incorporated into the present model, a decrease in the availability of consumable shellfish prey below the minimum landing size due to undersized landings, coupled with a lack of high-quality worm prey could result in impacts to the Poole Harbour oystercatcher population.

Coastal habitats are subject to environmental change from numerous sources globally and locally, including disturbance (Anderson, 1995; West *et al.*, 2002), sea level rise (Galbraith *et al.*, 2002), climate change (Hoegh-Guldberg and Bruno, 2010), habitat loss (Goss-Custard *et al.*, 2006a) and pollution (Clark *et al.*, 1989; Burger *et al.*, 1993). Past work has sought to integrate numerous stressors into a single IBM in order to predict synergistic effects of these pressures on coastal bird populations (Bowgen *et al.*, 2015). While this study focuses solely on shellfish harvesting at high water (where disturbance is not an issue), it adds to the growing number of demonstrations of the potential for IBMs to be applied to inform an

ecosystem-based approach to shellfisheries management, and in particular how they can be used as a rapid and relatively low cost tool to predict the effects of novel and quickly emerging shellfisheries that may be facilitated by non-native species introductions (Humphreys *et al.*, 2015; Chiesa *et al.*, 2016). In the future managers should seek to understand such synergistic effects, particularly when the predicted response may increase vulnerability to other pressures through extended feeding times, and when possible monitor shorebird behavioural responses to annual shellfish landings alongside other potential stressors to ensure sustainable use while maintaining site integrity and conservation of wildlife populations.

8. Discussion and Conclusions

8.1 Introduction and Thesis Overview

In order to achieve sustainability, inshore fisheries managers must understand the environmental impacts and recovery times of various fishing gears in different habitats, which may vary from region to region according to local environmental factors and the species being harvested. Additionally, ecosystem-based management requires consideration of the impacts of fishing on wider ecosystem function, which in intertidal areas includes coastal bird populations of significant conservation importance. Past work has for the most-part involved individual studies on the use of well-established gears, although little work has sought to bring together existing evidence or to study the effects of novel fisheries that arise from non-native introductions.

The aims of this PhD research were to:

1. Assess the impacts and recovery trends of various intertidal harvesting methods on benthic invertebrate communities and key prey groups for bird predators;
2. Investigate the impacts of a novel, non-native fishery on intertidal habitats, target and non-target species within a marine protected area;
3. Assess the efficacy of remote sensing techniques in accurately quantifying the spatial extent and intensity of intertidal fishing disturbance;
4. Utilise field surveys and individual-based models to predict the functional response and overwinter survival of a shorebird population within an

operational dredge fishery for a commercially valuable introduced bivalve in a marine protected area.

This chapter discusses the key findings of this research in the context of existing knowledge and their relevance to the management of intertidal fisheries and wider conservation efforts. Limitations are also considered and suggestions made as to future research.

8.2 Impacts of intertidal harvesting: an overview

Meta-analysis is a useful tool in collating data from numerous studies to identify common effects with increased power (Borenstein *et al.*, 2009). Chapter 2 provides useful insights for managers and policy-makers on the generalities of intertidal fishing impacts, and impacts of various combinations of gear type and habitat. In particular, results suggest that harvesting activities in sand habitats can cause impacts that persist for longer than those in muddy habitats, potentially due to the life-history of the taxa that are targeted in such habitats. Initial impacts following fishing disturbance suggest that hand techniques elicit more dramatic reductions in benthic abundance. This is likely due to the higher accuracy with which hand harvesting can take place, targeting species such as lugworm *Arenicola* spp. and king ragworm *Alitta virens* using evidence of their distribution such as burrows. Past meta-analyses have not focused on intertidal fishing specifically (Collie *et al.*, 2000; Kaiser *et al.*, 2006), and results showed no clear ranking of gear types (Collie *et al.*, 2000), while Chapter 2 indicates a clear trend in the severity of impacts, with impacts of hand harvesting the most severe. The results in Chapter 2 are in agreement with a more recent meta-analysis of fishing impacts that suggests the

depth of penetration in the sediment is highly correlated with the reduction of benthic biota (Hiddink *et al.*, 2017). Hand techniques can penetrate the sediment to a deeper depth than trawling or other towed gears, over which there is little control over the depth to which they can penetrate. The recovery trends in Chapter 2 indicate taxonomic differences in the time taken to recover to pre-fishing abundances, with molluscs taking longest. Given that this group are highly profitable as bird prey (Goss-Custard *et al.*, 2006), consideration should be made for this prolonged recovery when implementing management measures for shellfisheries. The global value of hand harvested fisheries (Watson *et al.*, 2017), together with the severity of their impacts, suggests that appropriate management measures for these fisheries, which often go under-regulated, should be carefully developed.

8.3 A novel, non-native fishery in a marine protected area

Non-native species introductions can lead to the emergence of new commercial fisheries that require the development of appropriate management before significant environmental impacts can occur. The target species of the Poole Harbour dredge fishery, the Manila clam *Ruditapes philippinarum*, was also introduced to the Venice Lagoon in the 1980s, where a similarly novel harvesting method known as the *rusca* was developed by local fishermen and is used for harvesting from intertidal and shallow areas (Pranovi *et al.*, 2004). This system uses a small outboard engine to disturb sediment in front of an iron cage with a net bag attached to harvest clams (Pranovi *et al.*, 2004). As the generalities of fishing disturbance are well-documented, when such gear types are developed it is

important to determine whether their impacts differ from other, more widely used gears. Chapter 3 contributes to knowledge of these novel gear types, including the mechanisms by which they may develop and their impacts. The results presented in Chapter 3 suggest that the pump-scoop method elicits small changes in the relative abundance of macrobenthic species according to their life history, but at the scale at which management measures are implemented and habitat condition assessments are made, this is likely to be of low concern as there is no change in overall biotope as a result. The magnitude of the changes could be considered to be within the limits of natural change, as stated in the Regulation 33 conservation advice provided for the Poole Harbour SPA. Furthermore, none of the species stated in the Regulation 33 advice as key prey items showed a significant decline in the study (English Nature, 2000).

As would perhaps be expected (Law, 2000), there is some evidence of selective fishing pressure on the population of *Ruditapes philippinarum* in Poole Harbour, although with detailed environmental data that is currently lacking higher confidence could be placed in the trends in population demographics and overall conclusions of Chapter 5. Of most relevance to managers and conservationists is perhaps the evidence that harvesting of legal-size clams can be up to 95% efficient in heavily fished areas, which should be considered alongside the recovery period for molluscs evident in Chapter 2. Along with mapping fishing effort using methods such as those used in Chapter 4, this information may allow managers to predict the level of removal of harvestable clams with some accuracy and determine spatial and temporal restrictions needed for stock viability. The overall population of *R.*

philippinarum in Poole appears sustainable as all areas sampled show successful recruitment, regardless of fishing effort. Areas closed to fishing can act as important sources of larval supply and ensure future stock (Byers, 2005; Griffiths *et al.*, 2006), as the closed area of Upton Lake in Holes Bay does in Poole (Herbert *et al.*, 2012) and should be maintained in the future.

In the large extents of the shallow intertidal areas in Poole Harbour, fishermen originally utilised a hand-held scoop to harvest clams, from which the less physically demanding pump-scoop dredge was developed (Jensen *et al.*, 2005). The ever-increasing global spread of non-native species (Katsanevakis *et al.*, 2014) means that other novel fisheries and gears are likely to arise elsewhere and in similar environments both methods of harvesting and impacts may be comparable to the Poole fishery. More locally, fisheries managers are considering introducing the pump-scoop method elsewhere along the south coast, and the results presented in Chapter 3 provide useful insight into the types of changes that may be expected with its introduction. It should be noted however that information on recovery following pump-scoop dredging, a key consideration, is lacking, as is discussed in Chapter 3, due to the limited scope and resources of the study. Future work should seek to address this knowledge gap and investigate recovery trends following pump-scoop dredging.

8.4 Quantifying the extent and intensity of intertidal harvesting

In inshore intertidal fisheries where VMS data is unavailable and fisheries patrols may be infrequent or inaccurate, the methods used in Chapter 4 may provide an accurate assessment of fishing effort. Globally, fisheries have increased and

continue to expand due to increasing human populations and a loss of terrestrial land for farming (Valdimarsson and James, 2001). Effort must be carefully monitored for effective management and to ensure sustainability, as along with the habitat in which fishing takes place, fishing effort is a key determinant of impacts (Bellman *et al.*, 2005). In inshore and smaller-scale fisheries such as Poole, a common approach to obtaining effort data is to interview local fishermen, with data potentially being unreliable (McCluskey and Lewison, 2008). The methods in Chapter 4 may provide a more efficient and more accurate method of measuring effort and together with the results of Chapter 3, allow for effective prediction of impacts and ensure sustainability.

The collection and analysis of aerial imagery has been used for monitoring purposes for decades (e.g. Durako *et al.*, 1992), and Chapter 4 highlights how the increased availability of low-cost technology can assist in environmental monitoring. Unmanned aerial systems (UAS), or drones, can be purchased relatively cheaply from high-street suppliers and results of Chapter 4 show they can prove valuable in monitoring remote areas that are difficult to access.

In a wider context, the remote sensing methods used in this research may be applicable elsewhere. As is discussed in Chapter 4, the same methods may be applied to other types of imagery and other types of gear that leave characteristic scarring or marking. In such situations, for example in subtidal fisheries that harvest via trawling or dredging, image classification of LiDAR or other imagery may help quantify fishing effort.

8.5 Distribution and intake rates of bird populations in response to fishing disturbance

Chapter 6 investigated whether dredging disturbance as quantified in Chapter 4 had an effect on the distribution and feeding and intake rates of bird populations within the study area in Poole Harbour. While no current impacts of the fishery were detected in the study, Chapter 6 highlights the potential for the methods used in Chapter 4 to be applied in predicting changes in biodiversity. Such methods have been used elsewhere (Broughton *et al.*, 2012; Wood *et al.*, 2013) but to the authors' knowledge this is the first time remote sensing methods have been applied to an intertidal fishery and the results used to predict the responses of coastal wildlife to fishing disturbance.

Results suggest that the pump-scoop dredge fishery in Poole is not having an effect on bird distribution or intake rates. Above a given prey density, feeding rates are limited by a species' searching and handling times (Piersma *et al.*, 1995; Goss-Custard *et al.*, 2006). Clearly the densities of prey in the area studied were not reduced by dredging to a level at which a functional response is evident. Other small-scale fisheries have shown a similar lack of impacts on bird predators from local intertidal harvesting (Dias *et al.*, 2008). Despite this, as discussed in Chapter 6, caution should be exercised with regards to the long-term impacts of shellfishing on bird populations as responses may be delayed (Verhulst *et al.*, 2004). Additionally, those species that do not show a behavioural response to environmental disturbance may, conversely, be those most susceptible to its effects (Gill *et al.*, 2001); a lack of response may mean an individual cannot afford to move elsewhere.

Future studies should aim to assess impacts on population demographics such as survival and reproductive success rather than the functional response of individuals within a site (Gill *et al.*, 2001).

8.6 Modelling overwinter survival of a shorebird population within a commercial shellfishery

Individual-based models (IBMs) allow managers and conservationists to predict the effects of environmental change quickly and quantitatively. Chapter 7 predicts a number of responses of the oystercatcher *Haematopus ostralegus* population in Poole Harbour under various scenarios of the dredge fishery. This, to the authors' knowledge, is the first time in which IBMs have been utilised to predict the response of a shorebird population to a non-native fishery. It appears that harvesting of the manila clam in Poole Harbour does not result in mortality of their main predators, oystercatchers, although this is due to behavioural changes and shifts in diet that help compensate for a loss of shellfish prey. Clams occupy a similar ecological niche to native *Cerastoderma* spp. and there is no evidence to suggest that native bivalves have declined in Poole Harbour as a result of their introduction (Langston *et al.*, 2003; Humphreys *et al.*, 2007), although where other populations of non-native species are exploited that outcompete native populations the functional response of shorebird populations may differ. Model predictions suggest that current landings (based on most recent data available) are within sustainable levels and will not result in adverse impacts to bird populations in the harbour, although increasing landings will result in behavioural and dietary shifts

which are likely to be of concern to conservationists, despite not resulting in mortality directly.

8.7 Implications for Management

Much of the PhD research presented in this thesis has strong practical implications for the regulation of intertidal fisheries and will help inform an ecosystem-based management (EBM) of inshore fisheries. The 10 key principles of EBM as defined by a recent study on behalf of the Marine Management Organisation (MMO, 2014) are:

1. Clear long-term ecosystem objectives, targets and indicators against which progress is monitored;
2. Integration of social and economic factors;
3. Establishing a robust dynamic baseline;
4. Considering all forms of information;
5. Engaging with all relevant sectors of society and scientific disciplines;
6. Monitoring, review and adaptive management;
7. Conserving ecosystem structure and function and managing within functional limits;
8. Adopting a coordinated and integrated approach to management of human activities;
9. Using appropriate spatial and temporal scales; and
10. Planning and management should be decentralised to the lowest appropriate level.

The results of this PhD research are therefore directly applicable to a number of these principles. In practice, many of these principles are already applied in marine planning through existing legislation and directives, at the national or international level. Within this legislative framework the work presented in this thesis may contribute to the achievement of sustainable intertidal fisheries, without compromising the integrity of ecosystem function and in particular the coastal bird populations that form key components of estuarine food webs (Moreira, 1997) and are highly protected (EC/2009/147).

Results of meta-analyses such as those presented in Chapter 1 allow accurate understanding of the impacts of intertidal fishing, with information on recovery also allowing managers to assess what spatial and temporal scales of management may be necessary, as is laid out in Principle 9, and therefore allowing conservation of ecosystem function (Principle 7). Meta-analysis and the systematic review process is a useful tool in collating existing evidence and when updated periodically, as has been done over the last few years on the subject of fisheries impacts (Collie *et al.*, 2000; Kaiser *et al.*, 2006; Hiddink *et al.*, 2017; Sciberras *et al.*, in review), can also contribute to adaptive management, a key principles of EBM, when new evidence becomes available.

The study presented in Chapter 2 highlights the importance of social factors in management and inclusion of important stakeholders in the management process, as incorporated in Principles 2, 5 and to some extent Principle 10. The development of the pump-scoop dredge by local fishermen in Poole indicates both the emergence of new gears to exploit introduced species and the importance of

considering social factors and working with key stakeholders in the local industry when developing management measures. The development of the 2015 Poole Harbour Dredge Byelaw involved detailed discussions and feedback with the local industry, and has successfully achieved high levels of compliance in a fishery that previously suffered with issues of illegal harvesting, and other associated societal issues (S. Birchenough, 2017, pers. comm.). In addition, the results presented in Chapter 2 and Chapter 4 on the impacts of this gear type on target and non-target species suggest that this may be a sustainable harvesting method. Chapter 6 supports this view, with no apparent effect on benthic habitat condition, the target species population or the dependent bird populations. The Poole Harbour dredge fishery could provide an example of successful management, involving key stakeholders in the management process and using monitoring as in Chapter 3 and Chapter 4 – SIFCA’s annual stock assessments if not such detailed analyses - to achieve sustainability.

Ecosystem-based management can be greatly aided by the use of various tools that support its delivery (MMO, 2014). Along with other examples of computer software, individual-based models (IBMs) are one such valuable tool for ensuring sustainability of intertidal fisheries. IBMs allow the prediction of overwinter survival in important bird populations and have in the past been used to set sustainable limits on fishing to ensure sufficient food availability (Goss-Custard *et al.*, 2004). The remote sensing methods described in Chapter 4 may also be a useful tool in the monitoring process and assessing any changes in fishing effort.

Monitoring and adaptive management, and using all sources of information to do so, are listed in Principles 4 and 6. Monitoring is a fundamental part of the planning process and is critical for periodic review of the effectiveness of any management plan against the relevant objectives, targets and indicators. These may include indicators of Good Environmental Status under the EU Marine Strategy Framework Directive (MSFD) or conservation objectives as defined by EU Habitats and Birds Directives, as translated into UK law by the Marine and Coastal Access Act 2009.

The work presented in this thesis has utilised numerous data sources and methods of data collection, demonstrating the application and importance of various methods and types of data in contributing to management of inshore fisheries. These are summarised in Table 8.1.

Table 8.1. Methods of data collection and monitoring used in this research, the type of data collected and its practical application for management.

Methods/Data Source	Data Type	Application
Systematic Review and Meta-Analysis	Biological	<ul style="list-style-type: none"> • Review of current knowledge of harvesting impacts on benthic communities
Benthic Sampling/Monitoring	Biological/Physical	<ul style="list-style-type: none"> • Monitoring and assessment of habitat condition • Understand impacts of new gears • Inform computer models
Fisheries Patrols	Spatial	<ul style="list-style-type: none"> • Pressure mapping
Stock Assessment/Population Dynamics	Biological	<ul style="list-style-type: none"> • Population monitoring • Assess stock viability • Identify selective fishing pressure
Anecdotal evidence (e.g. engagement with local fishermen)	Spatial	<ul style="list-style-type: none"> • Pressure mapping

Methods/Data Source	Data Type	Application
Aerial Surveys	Image/Spatial	<ul style="list-style-type: none"> • Pressure mapping
Individual-based modelling	Spatial/Biological	<ul style="list-style-type: none"> • Predict effects of fishing on bird populations • Determine allowable catches
WeBS Monitoring/Field Surveys	Biological	<ul style="list-style-type: none"> • Population monitoring

Principle 8 of the EBM approach refers to the need to adopt a coordinated and integrated approach to management. So far the research presented in this PhD thesis has focused solely on the issue of harvesting activities and their ecosystem impacts, although it is important to note that management efforts are often implemented at a regional or site level, particularly in the case of designated nature conservation sites. Such areas are often subject to multiple uses and varied pressure sources, and management must consider all activities. Inshore areas are often vulnerable to other issues such as pollution, sea level rise, disturbance and habitat loss. Consideration must be given for cumulative effects of such multiple uses, a key aspect of marine planning (Crain *et al.*, 2008; Gilliland *et al.*, 2008; Foley *et al.*, 2010), which may be additive, synergistic, or antagonistic (Crain *et al.*, 2008) between various stressors. Nonetheless the research presented in this thesis should contribute to the evidence base on the impacts of inshore activities and to sustainable development.

It is noteworthy that no recognition of shifting baselines is given in the widely accepted principles of EBM listed above. Shifting baseline syndrome carries significant implications for the management of inshore fisheries and protected

areas, and wherever possible managers should seek to not just ensure conservation of habitats and species at current levels, but that where possible measures are introduced to enhance biodiversity and increase ecological quality to historic levels. Many consider any protected area in which fishing activities occur to be protected in name only (Pomeroy et al., 2005), although managers face a difficult task in reconciling economic and social factors with the needs of conservation and biodiversity. By including measures such as no-take zones (Francini-Filho and Moura, 2008) and simple alterations to some gear designs to reduce associated impacts (Pravin et al., 2013) managers can aim to restore as well as maintain habitat condition, resilience and biodiversity, as is required by current international legislation (European Habitats Directive, 92/43/EEC).

8.8 Limitations and Further Research

Much of the work presented in this thesis has focused on the pump-scoop fishery in Poole Harbour. Therefore, in management terms, many of the conclusions of these studies may only apply locally and results may differ elsewhere. The implications for management will vary between regions, given that environmental, economic and social conditions are critical in determining the type and extent of fishing disturbance and the appropriateness of policy. Despite this, many of the methods used in this PhD research are applicable more widely and their use demonstrates their potential for monitoring and informing management efforts elsewhere. Future work may seek to build upon some of the practical methods demonstrated here, such as the remote sensing techniques, to investigate their efficacy in other locations, and to perhaps assess the accuracy by which the extent of disturbance as

quantified by these methods can be used to predict the impacts of harvesting on benthic communities and habitats. Likewise, the IBM approach used in Chapter 6 could be applied elsewhere and where invertebrate data is available, managers should exploit its potential to help determine sustainable harvest limits.

The work presented in Chapters 3 and 4 is novel in that there has been little work carried out on the impacts of pump-scoop dredging on benthic fauna and the target species itself in the UK. As the manila clam and other non-native species spread around the UK (Humphreys *et al.*, 2015) and new populations that may be commercially harvestable arise, fisheries managers should work closely with local fishermen to ensure sustainability. If novel gears develop, future research should aim to assess the impacts of these techniques compared to more traditional harvesting methods.

As mentioned previously, meta-analyses are generally carried out periodically to capture results of more recent research, and/or to investigate research questions with more advanced statistical methods. It is suggested that this trend continues going forward so as to maintain a robust understanding of the nature of fishing disturbance, and in intertidal studies, impacts upon bird prey species. Critically, in order for future studies on intertidal harvesting activities to be of most use, researchers should seek wherever possible to include size data in their work, essential information when considering food supply of coastal bird populations (Goss-Custard *et al.*, 2006). None of the studies included in Chapter 2 presented such data, although if possible a similar analysis investigating the shifts in prey size classes as a result of various gear types would certainly be beneficial.

The model in Chapter 7 demonstrates the potential for IBMs to be rapidly applied in new systems and new fisheries where data is available, although the model is limited in that it currently only considers impacts of harvesting on one species. More detailed models that were not possible to construct within the scope of this PhD project could include various sources of environmental disturbance, as well as other bird species and other methods of harvesting (for example where more than one fishery operates within a system) in order to make predictions that are more widely applicable.

8.9 Final Conclusions

The work presented in this thesis shows that the nature of impacts resulting from intertidal fishing disturbance may vary dramatically between gear types, habitats and taxonomic groups. Larger and slower growing invertebrate species are more sensitive to the impacts of harvesting, while also representing more profitable prey items for bird predators that may be sensitive to harvesting and shellfishing in particular. Despite this, these impacts may not always elicit an individual response due to the energetic costs associated with a behavioural response or even a population impact, due to their compensatory abilities. These are important considerations when considering monitoring data. Remote sensing and individual-based models can assist in the sustainable management of inshore fisheries and help achieve conservation objectives for coastal bird populations, although such models require accurate and robust empirical data. The collection of such data as part of ongoing monitoring efforts can inform adaptive management as well as such

models, and can contribute greatly to sustainability, ensuring that society continues to derive the benefits that coastal ecosystems provide us for years to come.

9. References

- Anderson M., Gorley, R. N. and Clarke, K. R., 2008. Permanova+ for Primer: Guide to Software and Statistical Methods. *PRIMER-E: Plymouth, UK*.
- Anderson, M. J. and Willis, T. J., 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology*. 84(2), 511-525.
- Anderson, M.J. and Walsh, D. C., 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? *Ecological Monographs*. 83(4), 557-574.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology*. 26(1), 32-46.
- Anderson, S.H., 1995. Recreational disturbance and wildlife populations. Wildlife and recreationists: coexistence through management and research. Island Press, Washington, DC. USA, pp.157-168.
- Andrews, J., 1974. Death on the sands. *Birds*. 5, 32-33.
- Angeloni, L., Schlaepfer, M. A., Lawler, J. J., Crooks, K. R., 2008. A reassessment of the interface between conservation and behavior. *Animal Behaviour*. 75, 731–737.
- Armonies, W. and Hellwig-Armonies, M., 1992. Passive settlement of *Macoma balthica* spat on tidal flats of the Wadden Sea and subsequent migration of juveniles. *Netherlands Journal of Sea Research*. 29 (4), 371-378.
- Atkinson, P. W., Clark, N. A., Bell, M. C., Dare, P. J., Clark, J. A. and Ireland, P. L., 2003. Changes in commercially fished shellfish stocks and shorebird populations in the Wash, England. *Biological Conservation*. 114 (1), 127-141.

- Atkinson, P. W., Maclean, I. M. and Clark, N. A., 2010. Impacts of shellfisheries and nutrient inputs on waterbird communities in the Wash, England. *Journal of Applied Ecology*. 47 (1), 191-199.
- Auster, P. J. and Langton, R. W., 1999. The effects of fishing on fish habitat, *American Fisheries Society Symposium* (Vol. 22).
- Barry, J.P., 1989. Reproductive response of a marine annelid to winter storms: An analog to fire adaptation in plants? *Marine Ecology Progress Series*. 54(1), 99-107.
- Bax, N., Williamson, A., Agüero, M., Gonzalez, E. and Geeves, W., 2003. Marine invasive alien species: a threat to global biodiversity. *Marine Policy*. 27(4), 313-323.
- Beck, F., Pezy, J. P., Baffreau, A. and Dauvin, J. C., 2015. Effects of clam rake harvesting on the intertidal *Ruditapes* habitat of the English Channel. *ICES Journal of Marine Science*. 72(9), 2663-2673.
- Beck, M. W., Brumbaugh, R. D., Airoidi, L., Carranza, A., Coen, L. D., Crawford, C., Defeo, O., Edgar, G. J., Hancock, B. and Kay, M. C., 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. *Bioscience*. 61 (2), 107-116.
- Bellman, M.A., Heppell, S.A. and Goldfinger, C., 2005. Evaluation of a US west coast groundfish habitat conservation regulation via analysis of spatial and temporal patterns of trawl fishing effort. *Canadian Journal of Fisheries and Aquatic Sciences*. 62(12), 2886-2900.
- Beninger, P. G. and Lucas, A., 1984. Seasonal variations in condition, reproductive activity, and gross biochemical composition of two species of adult clam

- reared in a common habitat: *Tapes decussatus* L.(Jeffreys) and *Tapes philippinarum* (Adams and Reeve). *Journal of Experimental Marine Biology and Ecology*. 79 (1), 19-37.
- Benson, T. D., 2016. MERMAID – Matlab Executable Routine for Model Animation and Interrogation of Data, User Guide. Report DDK2275_RT001. Wallingford, UK: HR Wallingford
- Berger-Tal, O., Polak, T., Oron, A., Lubin, Y., Kotler, B.P. and Saltz, D., 2011. Integrating animal behavior and conservation biology: a conceptual framework. *Behavioral Ecology*. 22(2), 236-239.
- Bergman, M. and Van Santbrink, J., 2000. Fishing mortality of populations of megafauna in sandy sediments. *In: Kaiser, M. J. and de Groot, S. J. (eds). (Herausg.): Effects of fishing on non-target species and habitats*. Blackwell Science, Oxford, 49-68.
- Berthold, P., 1975. Migration: control and metabolic physiology. *Avian Biology*. Academic Press, 77-128.
- Beukema, J. J., 1992. Expected changes in the wadden sea benthos in a warmer world: Lessons from periods with mild winters. *Netherlands Journal of Sea Research*. 30 (C), 73-79.
- Beverton, R. J. and Holt, S. J., 1957. On the dynamics of exploited fish populations, Fishery Investigations Series II, Vol. XIX, Ministry of Agriculture. *Fisheries and Food*. 1, 957.
- Beverton, R. J., 1954. *Notes on the use of theoretical models in the study of the dynamics of exploited fish populations*. US Fishery Laboratory.

- Bhattacharya, C., 1967. A simple method of resolution of a distribution into Gaussian components. *Biometrics*. 23 (1), 115-135.
- Blake, R. W., 1979. Exploitation of a Natural Population of *Arenicola marina* (L.) from the North-East Coast of England. *Journal of Applied Ecology*. 16 (3), 663-670.
- Borenstein, M., Hedges, L. V., Higgins, J. P. T., and Rothstein H. R., 2009. Introduction to meta-analysis. John Wiley and Sons, Hoboken, New Jersey.
- Borisov, V., 1978. The selective effect of fishing on the population structure of species with a long life cycle. *Journal of Ichthyology*. 18, 896-904.
- Borja A., Franco, J. and Pérez, V., 2000. A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. *Marine Pollution Bulletin*. 40(12), 1100-1114.
- Bowering, W. and Brodie, W., 1991. Distribution of commercial flatfishes in the Newfoundland-Labrador region of the Canadian Northwest Atlantic and changes in certain biological parameters since exploitation. *Netherlands Journal of Sea Research*. 27 (3-4), 407-422.
- Bowgen, K. M., Stillman, R. A. and Herbert, R. J. H., 2015. Predicting the effect of invertebrate regime shifts on wading birds: Insights from Poole Harbour, UK. *Biological Conservation*. 186, 60-68.
- Bradshaw, C., Tjensvoll, I., Sköld, M., Allan, I. J., Molvaer, J., Magnusson, J., Naes, K. and Nilsson, H. C., 2012. Bottom trawling resuspends sediment and releases bioavailable contaminants in a polluted fjord. *Environmental Pollution*. 170, 232-241.

- Breen, P. A., Gabriel, C. and Tyson, T., 1991. Preliminary estimates of age, mortality, growth, and reproduction in the hiattellid clam *Panopea zelandica* in New Zealand. *New Zealand Journal of Marine and Freshwater Research*. 25 (3), 231-237.
- Bridges, T. S., Levin, L. A., Cabrera, D. and Plaia, G., 1994. Effects of sediment amended with sewage, algae, or hydrocarbons on growth and reproduction in two opportunistic polychaetes. *Journal of Experimental Marine Biology and Ecology*. 177(1), 99-119.
- Britton, W, 1991. Clam Cultivation Manual - No. 8. A special publication of Aquaculture explained in conjunction with Taighde Teo.
- Broughton, R.K., Hill, R.A., Freeman, S.N., Bellamy, P.E. and Hinsley, S.A., 2012. Describing habitat occupation by woodland birds with territory mapping and remotely sensed data: an example using the Marsh Tit (*Poecile palustris*). *The Condor*. 114(4), 812-822.
- Brusà, R. B., Cacciatore, F., Ponis, E., Molin, E. and Delaney, E., 2013. Clam culture in the Venice lagoon: stock assessment of Manila clam (*Venerupis philippinarum*) populations at a nursery site and management proposals to increase clam farming sustainability. *Aquatic Living Resources*. 26 (1), 1-10.
- Brylinsky, M., Gibson, J. and Gordon Jr, D. C., 1994. Impacts of Flounder Trawls on the Intertidal Habitat and Community of the Minas Basin, Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences*. 51 (3), 650-661.
- Buchanan, J. B., Sheader, M. and Kingston, P. F., 1978. Sources of variability in the benthic macrofauna off the south Northumberland coast, 1971–1976.

Journal of the Marine Biological Association of the United Kingdom. 58(1), 191-209.

Burger, J., 1993. Metals in avian feathers: bioindicators of environmental pollution. *Reviews In Environmental Toxicology*. 5, 203-311.

Buschbaum, C., Dittmann, S., Hong, J.-S., Hwang, I.-S., Strasser, M., Thiel, M., Valdivia, N., Yoon, S.-P. and Reise, K., 2008. Mytilid mussels: global habitat engineers in coastal sediments. *Helgoland Marine Research*. 63 (1), 47.

Byers, J. E., 2005. Marine reserves enhance abundance but not competitive impacts of a harvested nonindigenous species. *Ecology*. 86 (2), 487-500.

Caldow, R. W. G., Stillman, R. A., Durell, S. E. A. L. V. D., West, A. D., McGrorty, S., Goss-Custard, J. D., Wood, P. J. and Humphreys, J., 2007. Benefits to shorebirds from invasion of a non-native shellfish. *Proceedings of the Royal Society B-Biological Sciences*. 274 (1616), 1449-1455.

Camphuysen, C. J., Berrevoets, C. M., Cremers, H. J. W. M., Dekinga, A., Dekker, R., Ens, B. J., van der Have, T. M., Kats, R. K. H., Kuiken, T., Leopold, M. F., van der Meer, J. and Piersma, T., 2002. Mass mortality of common eiders (*Somateria mollissima*) in the Dutch Wadden Sea, winter 1999/2000: starvation in a commercially exploited wetland of international importance. *Biological Conservation*. 106 (3), 303-317.

Camphuysen, C., 1997. Ecologisch profiel van de Eidereend *Somateria mollissima* RIKZ-werkdocument 96.146 x. *Nederlands Instituut voor Onderzoek der Zee, Texel*.

Camphuysen, K. C. J., Ens, B. J., Heg, D., Hulscher, J. B., Van Der Meer, J. and Smit, C. J., 1996. Oystercatcher *Haematopus ostralegus* winter mortality in The

- Netherlands: The effect of severe weather and food supply. *Ardea*. 84 (A), 469-492.
- Caswell, H. and Cohen, J. E., 1991. Disturbance, interspecific interaction and diversity in metapopulations. *Biological Journal of the Linnean Society*. 42(1-2), 193-218.
- Caughley, G., 1994. Directions in conservation biology. *Journal of Animal Ecology*. 63 (2), 215-244.
- Cerrato, R. M. and Keith, D. L., 1992. Age structure, growth, and morphometric variations in the Atlantic surf clam, *Spisula solidissima*, from estuarine and inshore waters. *Marine Biology*. 114 (4), 581-593.
- Cesar, C. P. and Frid, C. L. J., 2009. Effects of experimental small-scale cockle (*Cerastoderma edule* L.) fishing on ecosystem function. *Marine Ecology*. 30, 123-137.
- Cesar, C. P., 2003. *The Impact of Clam Fishing Techniques on the Infauna of Poole Harbour*. Dissertation submitted in partial fulfilment of the requirements for the degree of MSc (Oceanography), School of Earth and Ocean Science, University of Southampton.
- Chainho, P., Costa, J. L., Chaves, M. L., Lane, M. F., Dauer, D. M. and Costa, M. J., 2006. Seasonal and spatial patterns of distribution of subtidal benthic invertebrate communities in the Mondego River, Portugal—a poikilohaline estuary. *Hydrobiologia*. 555(1), 59-74.
- Chiesa, S., Lucentini, L., Freitas, R., Marzano, F.N., Breda, S., Figueira, E., Caill-Milly, N., Herbert, R.J., Soares, A.M. and Argese, E., 2017. A history of invasion: COI

- phylogeny of Manila clam *Ruditapes philippinarum* in Europe. *Fisheries Research*. 186, 25-35.
- Clarke, K. R., Gorley, R.N., 2006. *PRIMERv6: User Manual/Tutorial*. PRIMER-E: Plymouth.
- Cohen, J., 1988. *Statistical power analysis for the behavioral sciences* Lawrence Earlbaum Associates. Hillsdale, New Jersey, 20-26.
- Collie, J. S., Hall, S. J., Kaiser, M. J. and Poiner, I. R., 2000. A Quantitative Analysis of Fishing Impacts on Shelf-Sea Benthos. *Journal of Animal Ecology*. 69 (5), 785-798.
- Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. and Reker, J.B., 2004, The Marine Habitat Classification for Britain and Ireland Version 04.05-Sublittoral Sediment Section. Peterborough: Joint Nature Conservation Committee (JNCC).
- Conover, D. O., Arnott, S. A., Walsh, M. R. and Munch, S. B., 2005. Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*). *Canadian Journal of Fisheries and Aquatic Sciences*. 62 (4), 730-737.
- Cook, A.S.C.P., Barimore, C., Holt, C.A., Read, W.J. and Austin, G.E. (2013). Wetland Bird Survey Alerts 2009/2010: Changes in numbers of wintering waterbirds in the Constituent Countries of the United Kingdom, Special Protection Areas (SPAs) and Sites of Special Scientific Interest (SSSIs). BTO Research Report 641. BTO, Thetford. Available from: <http://www.bto.org/volunteer-surveys/webs/publications/webs-annual-report>. [Accessed 5th December 2017].

- Cotter, A., Walker, P., Coates, P., Cook, W. and Dare, P., 1997. Trial of a tractor dredger for cockles in Burry Inlet, South Wales. *ICES Journal of Marine Science: Journal du Conseil*. 54 (1), 72-83.
- Crain, C.M., Kroeker, K. and Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*. 11(12), 1304-1315.
- Dauvin, J. C., Andrade, H., de-la-Ossa-Carretero, J. A., Del-Pilar-Ruso, Y. and Riera, R., 2016. Polychaete/amphipod ratios: An approach to validating simple benthic indicators. *Ecological Indicators*. 63, 89-99.
- Dauvin, J. C., Ruellet, T., 2009. The estuarine quality paradox: is it possible to define an ecological quality status for specific modified and naturally stressed estuarine ecosystems? *Marine Pollution Bulletin*. 59(1), 38-47.
- Dayton, P. K., Thrush, S. F., Agardy, M. T. and Hofman, R. J., 1995. Environmental effects of marine fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems*. 5 (3), 205-232.
- De Veen, J., 1976. On changes in some biological parameters in the North Sea sole (*Solea solea* L.). *ICES Journal of Marine Science*. 37 (1), 60-90.
- Dean, H.K., 2008. The use of polychaetes (Annelida) as indicator species of marine pollution: a review. *Revista de Biologia Tropista*. 56(4), 11-38.
- DeAngelis, D. L. and Mooij, W. M., 2005. Individual-based modeling of ecological and evolutionary processes. *Annual Review of Ecology, Evolution and Systematics*. 36, 147-168.

- Dekinga, A., Dietz, M. W., Koolhaas, A. and Piersma, T., 2001. Time course and reversibility of changes in the gizzards of red knots alternately eating hard and soft food. *Journal of Experimental Biology*. 204 (12), 2167-2173.
- Dernie, K. M., Kaiser, M. J. and Warwick, R. M., 2003. Recovery Rates of Benthic Communities Following Physical Disturbance. *Journal of Animal Ecology*. 72 (6), 1043-1056.
- Desprez, M., Rybarczyk, H., Wilson, J. G., Ducrotoy, J. P., Sueur, F., Olivesi, R. and Elkaim, B., 1992. Biological impact of eutrophication in the bay of Somme and the induction and impact of anoxia. *Netherlands Journal of Sea Research*. 30, 149-159.
- Dewar, J. M. (1915). The relation of the Oystercatcher to its natural environment. *Zoologist*. 19, 281-291.
- Dias, M. P., Peste, F., Granadeiro, J. P. and Palmeirim, J. M., 2008. Does traditional shellfishing affect foraging by waders? The case of the Tagus estuary (Portugal). *Acta Oecologica*. 33(2), 188-196.
- Diaz-Castañeda, V., Frontier, S. and Arenas, V., 1993. Experimental re-establishment of a soft bottom community: utilization of multivariate analyses to characterize different benthic recruitments. *Estuarine, Coastal and Shelf Science*. 37(4), 387-402.
- Dixon, C. D. and Day, R. W., 2004. Growth responses in emergent greenlip abalone to density reductions and translocations. *Journal of Shellfish Research*. 23 (4), 1223.

- d'Oleire-Oltmanns, S., Marzloff, I., Peter, K. D. and Ries, J. B., 2012. Unmanned aerial vehicle (UAV) for monitoring soil erosion in Morocco. *Remote Sensing*. 4 (11), 3390-3416.
- Dunstan, P. K., and Johnson, C. R., 2005. Predicting global dynamics from local interactions: individual-based models predict complex features of marine epibenthic communities. *Ecological Modelling*. 186(2), 221-233.
- Dunton, K. H. and Schonberg, S. V., 2002. Assessment of propeller scarring in seagrass beds of the south Texas coast. *Journal of Coastal Research*. 100-110.
- Durako, M.J., Hall, M.O., Sargent, F. and Peck, S., 1992. Propeller scars in seagrass beds: an assessment and experimental study of recolonization in Weedon Island State Preserve, Florida. *Proceedings of 19th Annual Conference of Wetland Restoration and Creation*. Hillsborough Community College, Tampa, FL, 42-53.
- Durell, S. E. A. L. V. d., Stillman, R. A., Caldow, R. W. G., McGroarty, S., West, A. D. and Humphreys, J., 2006. Modelling the effect of environmental change on shorebirds: A case study on Poole Harbour, UK. *Biological Conservation*. 131 (3), 459-473.
- Durell, S. E. L. V. D., 2000. Individual feeding specialisation in shorebirds: population consequences and conservation implications. *Biological Reviews*. 75 (4), 503-518.
- Ekman, J.B. and Hake, M.K., 1990. Monitoring starvation risk: adjustments of body reserves in greenfinches (*Carduelis chloris* L.) during periods of unpredictable foraging success. *Behavioural Ecology*. 1, 62-67.

- Ekman, J.B. and Lilliendahl, K. 1993. Using priority to food: fattening strategies in dominance structured willow tit *Parus montanus* flocks. *Behavioural Ecology*. 4, 232,238.
- English Nature, 2000. Poole Harbour European marine site English Nature's advice given under Regulation 33(2) of the Conservation (Natural Habitats &c.) Regulations 1994.
- Ens, B. and Goss-Custard, J., 1986. Piping as a display of dominance by wintering Oystercatchers *Haematopus ostralegus*. *Ibis*. 128 (3), 382-391.
- Ens, B. J., Smaal, A. and De Vlas, J., 2004. *The effects of shellfish fishery on the ecosystems of the Dutch Wadden Sea and Oosterschelde*. Rijkswaterstaat, RIKZ.
- Ens, B., 2006. The conflict between shellfisheries and migratory waterbirds in the Dutch Wadden Sea. *GC Boere, CA Galbraith, and DA Stroud (red.), Waterbirds around the world*, 806-811.
- Ens, B.J., 2002. What we know and what we should know about mollusc fisheries and aquacultures in the Wadden Sea. *In: Wolff, W.J., Essink, K., Kellerman, A., van Leeuwe, M.A. (eds.), Proceedings of the 10th International Scientific Wadden Sea Symposium*. Ministerie van LNV, Den Haag.
- Evans, P., 1976. Energy balance and optimal foraging strategies in shorebirds: some implications for their distributions and movements in the non-breeding season. *Ardea*. 64 (1), 117-139.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*. 34 (1), 487-515.

- FAO, F., 2014. The state of world fisheries and aquaculture.
- Fauchald, K., Jumars, P. A., 1979. The diet of worms: a study of polychaete feeding guilds. Aberdeen University Press.
- Fearnley, H., Cruickshanks, K., Lake, S. and Liley, D., 2013. The Effects of Bait Harvesting on Bird Distribution and Foraging Behaviour in Poole Harbour SPA: Footprint Ecology for Natural England.
- Ferns, P. N., Rostron, D. M. and Siman, H. Y., 2000. Effects of mechanical cockle harvesting on intertidal communities. *Journal of Applied Ecology*. 37 (3), 464-474.
- Ferré, B., De Madron, X.D., Estournel, C., Ulses, C. and Le Corre, G., 2008. Impact of natural (waves and currents) and anthropogenic (trawl) resuspension on the export of particulate matter to the open ocean: application to the Gulf of Lion (NW Mediterranean). *Continental Shelf Research*. 28(15), 2071-2091.
- Ferreira, J. G., Hawkins, A. J. S. and Bricker, S. B., 2007. Management of productivity, environmental effects and profitability of shellfish aquaculture – the Farm Aquaculture Resource Management (FARM) model. *Aquaculture*. 264, 160-174.
- Finn, P., Catterall, C. and Driscoll, P., 2001. The low tide distribution of Eastern Curlew on feeding grounds in Moreton Bay, Queensland. *Stilt*. 38, 9-17.
- Fogarty, M. J. and Murawski, S. A., 1986. Population dynamics and assessment of exploited invertebrate stocks, *North Pacific workshop on stock assessment and management of invertebrates. Canadian Special Publication of Fisheries and Aquatic Sciences*. 92, 228-244.

- Foley, M. M., Halpern, B. S., Micheli, F., Armsby, M. H., Caldwell, M. R., Crain, C. M., Prahler, E., Rohr, N., Sivas, D., Beck, M. W. and Carr, M. H., 2010. Guiding ecological principles for marine spatial planning. *Marine Policy*. 34(5), 955-966.
- Folk, R. L., 1954. The distinction between grain size and mineral composition in sedimentary-rock nomenclature. *The Journal of Geology*. 62 (4), 344-359.
- Food and Agricultural Organisation of the United Nations, 2016. The state of world fisheries and aquaculture.
- Foody, G. M., 2002. Status of land cover classification accuracy assessment. *Remote Sensing of Environment*. 80 (1), 185-201.
- Francis, R., 1988. Are growth parameters estimated from tagging and age-length data comparable? *Canadian Journal of Fisheries and Aquatic Sciences*. 45 (6), 936-942.
- Franklin D. J., Humphreys, J., Harris, M., Jensen, A. C., Herbert, R. J. H. and Purdie, D. A., 2012. An investigation into the annual cycle of phytoplankton abundance in Poole Harbour and its relationship with Manila clam nutrition. Report for the Marine Management Organisation.
- Frechette, M. and Lefaivre, D., 1990. Discriminating between food and space limitation in benthic suspension feeders using self-thinning relationships. *Marine Ecology Progress Series*. 65 (1), 15-23.
- Furnell, J. and Hull, S. L., 2014. Cliff top habitats provide important alternative feeding resources for wading birds of conservation importance wintering on non-estuarine coasts. *Estuarine, Coastal and Shelf Science*. 139, 119–126.

- Galbraith, H., Jones, R., Park, R., Clough, J., Herrod-Julius, S., Harrington, B. and Page, G., 2002. Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. *Waterbirds*. 25 (2), 173-183.
- Garcia, S. M. and Cochrane, K. L., 2005. Ecosystem approach to fisheries: a review of implementation guidelines. *ICES Journal of Marine Science*. 62 (3), 311-318.
- García-Berthou, E., Alcaraz, C., Pou-Rovira, Q., Zamora, L., Coenders, G. and Feo, C., 2005. Introduction pathways and establishment rates of invasive aquatic species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences*. 62 (2), 453-463.
- Gayanilo, F., 1997. *Fisat: FAO-ICLARM Stock Assessment Tools, Reference Manuals*. Food and Agriculture Org.
- George, J., 1964. The life history of the cirratulid worm, *Cirriformia tentaculata*, on an intertidal mudflat. *Journal of the Marine Biological Association of the United Kingdom*. 44 (1), 47-65.
- Gibbs, M. T., Browman, H. I., 2015. Risk assessment and risk management: a primer for marine scientists. *ICES Journal of Marine Science: Journal du Conseil*. 72 (3), 992-996.
- Gili, J.-M. and Coma, R., 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. *Trends in Ecology and Evolution*. 13 (8), 316-321.
- Gilkinson, K. D., Gordon, D. C., Maclsaac, K. G., McKeown, D. L., Kenchington, E. L. R., Bourbonnais, C. and Vass, W. P., 2005. Immediate impacts and recovery trajectories of macrofaunal communities following hydraulic clam dredging

- on Banquereau, eastern Canada. *ICES Journal of Marine Science*. 62 (5), 925-947.
- Gill, J. A., Norris, K. and Sutherland, W. J., 2001. Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation*. 97 (2), 265-268.
- Gilliland, P.M. and Laffoley, D., 2008. Key elements and steps in the process of developing ecosystem-based marine spatial planning. *Marine Policy*. 32(5), 787-796.
- Gosler, A.G., 1996. Environmental and social determinants of winter fat storage in the great tit *Parus major*. *Journal of Animal Ecology*. 65, 1-17.
- Goss-Custard, J. and Verboven, N., 1993. Disturbance and feeding shorebirds on the Exe estuary. *Wader Study Group Bulletin*. 68 (Special Issue), 59-66.
- Goss-Custard, J. D., 1969. The winter feeding ecology of the redshank *Tringa totanus*. *Ibis*. 111(3), 338–356.
- Goss-Custard, J. D., 1977. The Ecology of the Wash. III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). *Journal of Applied Ecology*. 14 (3), 721–739.
- Goss-Custard, J. D., Burton, N. H. K., Clark, N. A., Ferns, P. N., McGroarty, S., Reading, C. J., Rehfisch, M. M., Stillman, R. A., Townend, I., West, A. D. and Worrall, D. H., 2006a. Test of a Behaviour-Based Individual-Based Model: Response of Shorebird Mortality to Habitat Loss. *Ecological Applications*. 16 (6), 2215–2222.
- Goss-Custard, J. D., West, A. D., Yates, M. G., Caldow, R. W. G., Stillman, R. A., Bardsley, L., Castilla, J., Castro, M., Dierschke, V., Durell, S. E. A. L. D.,

- Eichhorn, G., Ens, B. J., Exo, K. M., Udayangani-Fernando, P. U., Ferns, P. N., Hockey, P. A. R., Gill, J. A., Johnstone, I., Kalejta-Summers, B., Masero, J. A., Moreira, F., Nagarajan, R. V., Owens, I. P. F., Pacheco, C., Perez-Hurtado, A., Rogers, D., Scheiffarth, G., Sitters, H., Sutherland, W. J., Triplet, P., Worrall, D. H., Zharikov, Y., Zwarts, L. and Pettifor, R. A., 2006. Intake rates and the functional response in shorebirds (Charadriiformes) eating macro-invertebrates. *Biological Reviews*. 81 (4), 501-529.
- Goss-Custard, J., Clarke, R. and Ditt Durell, S. I. V., 1984. Rates of food intake and aggression of oystercatchers *Haematopus ostralegus* on the most and least preferred mussel *Mytilus edulis* beds of the Exe estuary. *Journal of Animal Ecology*. 233-245.
- Goss-Custard, J., Stillman, R., West, A., Caldow, R., Triplet, P., Ditt Durell, S. I. V. and McGrorty, S., 2004. When enough is not enough: shorebirds and shellfishing. *Proceedings of the Royal Society of London. Series B: Biological Sciences*. 271 (1536), 233-237.
- Goss-Custard, J., Stillman, R., West, A., McGrorty, S., Ditt Durell, S. and Caldow, R., 2000. The role of behavioural models in predicting the ecological impact of harvesting. *Conservation Biology Series-Cambridge*. 34, 65-84.
- Grassle, J. F., Sanders, H. L. 1973. Life histories and the role of disturbance. *Deep Sea Research and Oceanographic Abstracts*. 20 (7), 643-659.
- Grassle, J., 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. *Journal of Marine Research*. 32, 253-284.
- Gray, J., 1981. *The Ecology of Marine Sediments: An Introduction to the Structure and Function of Marine Sediments*. Cambridge Studies in Modern Biology 2.

- Grieve, C., Prime, M., Brady, D. C. and Polet, H., 2011. Best Practices for Managing, Measuring and Mitigating the Benthic Impacts of Fishing.
- Griffiths, J., Dethier, M. N., Newsom, A., Byers, J. E., Meyer, J. J., Oyarzun, F. and Lenihan, H., 2006. Invertebrate community responses to recreational clam digging. *Marine Biology*. 149 (6), 1489-1497.
- Grimm, V. and Railsback, S. F., 2005. *Individual-based modeling and ecology*. Vol. 2005. BioOne.
- Gurevitch, J. and Hedges, L. V., 1999. Statistical issues in ecological meta-analyses. *Ecology*. 80 (4), 1142-1149.
- Hall, F. G., Botkin, D. B., Strebel, D. E., Woods, K. D. and Goetz, S. J., 1991. Large-scale patterns of forest succession as determined by remote sensing. *Ecology*. 72 (2), 628-640.
- Hall, S. J. and Harding, M. J. C., 1997. Physical Disturbance and Marine Benthic Communities: The Effects of Mechanical Harvesting of Cockles on Non-Target Benthic Infauna. *Journal of Applied Ecology*. 34 (2), 497-517.
- Hall, S. J., 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanography and Marine Biology: An Annual Review*. 32, 179-239.
- Halpern, B. S. and Warner, R. R., 2002. Marine reserves have rapid and lasting effects. *Ecology Letters*. 5 (3), 361-366.
- Halpern, B. S., 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecological Applications*. 13 (1), S117-S137.
- Handley, S. J., Willis, T. J., Cole, R. G., Bradley, A., Cairney, D. J., Brown, S. N. and Carter, M. E., 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.
- Hanekom, D., 1992. Growth, production and consumption of the thalassinid prawn *Upogebia africana* (Ortmann) in the Swartkops estuary. *African Zoology*. 27 (3), 130-139.
- Hannavy, J., 2013. *Encyclopedia of nineteenth-century photography*. Routledge.
- Harding, J. M. and Mann, R., 1999. Fish species richness in relation to restored oyster reefs, Piankatank River, Virginia. *Bulletin of Marine Science*. 65 (1), 289-299.
- Harding, J. M., Mann, R. and Kilduff, C. W., 2007. The effects of female size on fecundity in a large marine gastropod *Rapana venosa* (Muricidae). *Journal of Shellfish Research*. 26 (1), 33-42.
- Haug, T. and Tjemsland, J., 1986. Changes in size-and age-distributions and age at sexual maturity in Atlantic halibut, *Hippoglossus hippoglossus*, caught in North Norwegian waters. *Fisheries Research*. 4 (2), 145-155.
- Heck, K., Able, K., Roman, C. and Fahay, M., 1995. Composition, abundance, biomass, and production of macrofauna in a New England estuary: comparisons among eelgrass meadows and other nursery habitats. *Estuaries and Coasts*. 18 (2), 379-389.
- Heppleston, P. B., 1971. The Feeding Ecology of Oystercatchers (*Haematopus ostralegus* L.) in Winter in Northern Scotland. *Journal of Animal Ecology*, 40 (3), 651-672.

- Herbert R. J., K. Ross, Hübner, R., Stillman, R. A. S., 2010. Intertidal invertebrates and biotopes of Poole Harbour SSSI and survey of Brownsea Island Lagoon. Bournemouth University Report to Natural England.
- Herbert, R.J., Willis, J., Jones, E., Ross, K., Hübner, R., Humphreys, J., Jensen, A. and Baugh, J., 2012, Invasion in tidal zones on complex coastlines: modelling larvae of the non-native Manila clam, *Ruditapes philippinarum*, in the UK. *Journal of Biogeography*. 39(3), 585-599.
- Hiddink, J. G., 2003. Effects of suction-dredging for cockles on non-target fauna in the Wadden Sea. *Journal of Sea Research*. 50 (4), 315-323.
- Hiddink, J. G., Jennings, S., Sciberras, M., Szostek, C. L., Hughes, K. M., Ellis, N., Rijnsdorp, A. D., McConnaughey, R. A., Mazor, T., Hilborn, R. and Collie, J. S., 2017. Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proceedings of the National Academy of Sciences*. 114(31), 8301-8306.
- Hill, D., Rushton, S. P., Clark, N., Green, P. and Prys-Jones, R., 1993. Shorebird communities on British estuaries: factors affecting community composition. *Journal of Applied Ecology*. 220-234.
- HM Government, 2011. *The Ecosystem Approach*. Post Note No. 377. May 2011. 4p.
- Hoegh-Guldberg, O. and Bruno, J. F., 2010. The impact of climate change on the world's marine ecosystems. *Science*. 328 (5985), 1523-1528.
- Hogeweg, P. and Hesper, B., 1990. Individual-oriented modelling in ecology. *Mathematical and Computer Modelling*. 13 (6), 83-90.

- Hoxmeier, R. and Dieterman, D. J., 2011. *Application of mixture models for estimating age and growth of stream dwelling brook trout*. Study 675. Technical Report F-26-R, Minnesota Department of Natural Resources, Lake City, MN.
- HR Wallingford, 2004. Poole Harbour Approach Channel Deepening: Hydrodynamic and Sedimentation Studies. Technical Report EX 4945, Wallingford, UK.
- Hughes, K. M., Kaiser, M. J., Jennings, S., McConnaughey, R. A., Pitcher, R., Hilborn, R., Amoroso, R. O., Collie, J., Hiddink, J. G. and Parma, A. M., 2014. Investigating the effects of mobile bottom fishing on benthic biota: a systematic review protocol. *Environmental Evidence*. 3 (1), 1-10.
- Humphreys J., 2005. 3. Salinity and tides in Poole Harbour: Estuary or lagoon? *In*: Humphreys, J. and May, V., eds. *The Ecology of Poole Harbour*. Proceedings in Marine Science. 7, 35-47.
- Humphreys, J., Caldow, R. W. G., McGroarty, S., West, A. D. and Jensen, A. C., 2007. Population dynamics of naturalised Manila clams *Ruditapes philippinarum* in British coastal waters. *Marine Biology*. 151 (6), 2255-2270.
- Humphreys, J., Harris, M. R., Herbert, R. J., Farrell, P., Jensen, A. and Cragg, S. M., 2015. Introduction, dispersal and naturalization of the Manila clam *Ruditapes philippinarum* in British estuaries, 1980–2010. *Journal of the Marine Biological Association of the United Kingdom*. 95 (6), 1163-1172.
- Hutchings, J. A., 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*. 62 (4), 824-832.

- Ishii, R., Sekiguchi, H., Nakahara, Y. and Jinnai, Y., 2001. Larval recruitment of the manila clam *Ruditapes philippinarum* in Ariake Sound, southern Japan. *Fisheries Science*. 67 (4), 579-591.
- Jackson, J. B., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J. and Warner, R. R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science*. 293 (5530), 629-637.
- Jennings, S. and Kaiser, M. J., 1998. The effects of fishing on marine ecosystems. *Advances in Marine Biology*. 34, 201-352.
- Jensen, A., Humphreys, J., Caldow, R. and Cesar, C., 2005. 13. The Manila clam in Poole Harbour. In: Humphreys, J. and May, V., eds. *The Ecology of Poole Harbour*. Proceedings in Marine Science. 7, 163-173.
- Johnson, C., 1985. Patterns of seasonal weight variation in waders on the Wash. *Ringing and Migration*. 6(1), 19-32.
- Joint Nature Conservation Committee, 2008. Poole Harbour: Natura 2000 Standard Data Form. Version 1.1, 05/05/06
- Joint Nature Conservation Committee, 2014. The Ecosystem Based Approach. [online]. Available from: <http://jncc.defra.gov.uk/page-2518>. [Accessed 4th December 2017].
- Jones, D. S., 1980. Annual cycle of shell growth increment formation in two continental shelf bivalves and its paleoecologic significance. *Paleobiology*. 6 (3), 331-340.

- Jones, P., 1999. Economic and sociocultural priorities for marine conservation. *Effects of Fishing on Non-Target Species and Habitats: Biological, Conservation and Socio-Economic Issues. Blackwell Science, Oxford*, 354-365.
- Jørgensen, T., 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *ICES Journal of Marine Science*. 46 (3), 235-248.
- Kaiser, M. J., Attrill, M. J., Jennings, S., Thomas, D. N., Barnes, D. K. A., Brierley, A. S., Hiddink, J. G., Kaartokallio, H., Polunin, N. V. C. and Raffaelli, D. G., 2011. *Marine Ecology: Processes, Systems, and Impacts*. Oxford University Press.
- Kaiser, M. J., Broad, G. and Hall, S. J., 2001. Disturbance of intertidal soft-sediment benthic communities by cockle hand raking. *Journal of Sea Research*. 45 (2), 119-130.
- Kaiser, M. J., Clarke, K. R., Hinz, H., Austen, M. C. V., Somerfield, P. J. and Karakassis, I., 2006. Global analysis of response and recovery of benthic biota to fishing. *Marine Ecology Progress Series*. 311, 1-14.
- Kaiser, M. J., Collie, J. S., Hall, S. J., Jennings, S. and Poiner, I. R., 2002. Modification of marine habitats by trawling activities: prognosis and solutions. *Fish and Fisheries*. 3 (2), 114-136.
- Kang, C., Sauriau, P.-G., Richard, P. and Blanchard, G., 1999. Food sources of the infaunal suspension-feeding bivalve *Cerastoderma edule* in a muddy sandflat of Marennes-Oléron Bay, as determined by analyses of carbon and nitrogen stable isotopes. *Marine Ecology Progress Series*. 187, 147-158.
- Katsanevakis, S., Coll, M., Piroddi, C., Steenbeek, J., Ben Rais Lasram, F., Zenetos, A. and Cardoso, A.C., 2014. Invading the Mediterranean Sea: biodiversity patterns shaped by human activities. *Frontiers in Marine Science*. 1, 32.

- Kenny, A., Cato, I., Desprez, M., Fader, G., Schüttenhelm, R. and Side, J., 2003. An overview of seabed-mapping technologies in the context of marine habitat classification. *ICES Journal of Marine Science*. 60 (2), 411-418.
- Kersten, M. and Piersma, T., 1987. High-levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. *Ardea*. 75(2), 175–187.
- Kirkwood, J.K., 1983. A limit to metabolisable energy intake in mammals and birds. *Comparative Biochemistry and Physiology*. 75, 1-3.
- Koricheva, J., Gurevitch, J. and Mengersen, K., 2013. *Handbook of meta-analysis in ecology and evolution*. Princeton University Press.
- Kraan, C., Piersma, T., Dekinga, A., Koolhaas, A. and Van der Meer, J., 2007. Dredging for edible cockles (*Cerastoderma edule*) on intertidal flats: short-term consequences of fisher patch-choice decisions for target and non-target benthic fauna. *ICES Journal of Marine Science: Journal du Conseil*. 64 (9), 1735-1742.
- Kraberg, A.C., Wasmund, N., Vanaverbeke, J., Schiedek, D., Wiltshire, K.H. and Mieszkowska, N., 2011. Regime shifts in the marine environment: the scientific basis and political context. *Marine Pollution Bulletin*. 62 (1), 7-20.
- Kristensen, E., 1983a. Ventilation and oxygen uptake by three species of *Nereis* (Annelida: Polychaeta). I. Effects of hypoxia. *Marine Ecology Progress Series*. 12 (3), 289-297.
- Kristensen, E., 1983b. Ventilation and oxygen uptake by three species of *Nereis*(Annelida: Polychaeta). II. Effects of temperature and salinity changes. *Marine Ecology Progress Series*. 12(3), 299-306.

- Kropp, J., Eisenack, K. and Scheffran, J., 2005. Marine overexploitation: a syndrome of global change. *Multiple Dimensions of Global Environmental Change*. Teri Press, New Delhi: in print.
- Lambourn, S. and Le Berre, A., 2007. Opinion on the reduction of the minimum landing size (MLS) of the Japanese clam. North Western Waters Regional Advisory Council.
- Langston, W. J., Chesman, B. S., Burt, G. R., Hawkins, S. J., Readman, J. W. and Worsfold, P., 2003. Characterisation of the South West European Marine Sites: Poole Harbour SPA. *Occasional Publication of the Marine Biological Association*. 12.
- Lardicci, C., Ceccerelli, G. and Rossi, F., 1997. *Streblospio shrubsolii* (Polychaeta: Spionidae) temporal fluctuations in size and reproductive activity. *Cahiers de Biologie Marine*. 38 (3), 207-214.
- Law, R., 2000. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*. 57 (3), 659-668.
- Levin, L. A., 1984. Life History and Dispersal Patterns in a Dense Infaunal Polychaete Assemblage: Community Structure and Response to Disturbance. *Ecology*. 65 (4), 1185-1200.
- Levin, S. A. and Paine, R. T., 1974. Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences*. 71(7), 2744-2747.
- Levin, S. and Whitfield, M., 1994. Patchiness in marine and terrestrial systems: from individuals to populations [and Discussion]. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*. 343(1303), 99-103.

- Lindeboom, H. and De Groot, S., 1998. IMPACT-II: The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems.
- Long, J. S. and Ervin, L. H., 2000. Using heteroscedasticity consistent standard errors in the linear regression model. *The American Statistician*. 54 (3), 217-224.
- Long, R., 2012. Legal aspects of ecosystem-based marine management in Europe. *Ocean Yearbook*. Hijhoff.
- Malvern, 2017. Available from: <http://www.malvern.com/en/products/product-range/mastersizer-range/mastersizer-3000/>. [Accessed February 2017].
- Manzi, J. J., Hadley, N., Battey, C., Haggerty, R., Hamilton, R. and Carter, M., 1984. Culture of the northern hard clam *Mercenaria mercenaria* (Linné) in a commercial-scale, upflow, nursery system. *Journal of Shellfish Research*. 4 (2), 119-124.
- Marine Management Organisation, 2011. Information and Guidance on the Inshore Vessel Monitoring System. [online]. Available from: <https://www.gov.uk/government/publications/inshore-vessel-monitoring-system-ivms>. [Accessed 4th December 2017].
- Marine Management Organisation, 2014. Practical Framework for Outlining the Integration of the Ecosystem Approach into Marine Planning in England. A report produced for the Marine Management Organisation, 181p. MMO Project No: 1048. ISBN: 978-1-909452-336.
- Marine Stewardship Council, 2016. [online]. Available from: <https://www.msc.org/newsroom/news/vietnams-ben-tre-hand-gathered-clam-fishery-proves-its-sustainable-again> [accessed 13 June 2017]

- Marine Stewardship Council, 2017. DFA Dutch North Sea Ensis. [online]. Available from: <https://fisheries.msc.org/en/fisheries/dfa-dutch-north-sea-ensis/about/>. [Accessed 4th December 2017].
- Marks, J. S. and Redmond, R. L., 1996. Demography of Bristle-thighed Curlews *Numenius tahitiensis* wintering on Laysan Island. *Ibis*. 138 (3), 438-447.
- Martín, J., Puig, P., Palanques, A. and Ribó, M., 2014. Trawling-induced daily sediment resuspension in the flank of a Mediterranean submarine canyon. *Deep Sea Research Part II: Topical Studies in Oceanography*. 104, 174-183.
- Mason, D., Scott, T. and Dance, S., 2010. Remote sensing of intertidal morphological change in Morecambe Bay, UK, between 1991 and 2007. *Estuarine, Coastal and Shelf Science*. 87 (3), 487-496.
- Mayer, L. M., Schick, D. F., Findlay, R. H. and Rice, D. L., 1991. Effects of commercial dragging on sedimentary organic matter. *Marine Environmental Research*. 31(4), 249-261.
- McCluskey, S.M. and Lewison, R.L., 2008. Quantifying fishing effort: a synthesis of current methods and their applications. *Fish and Fisheries*. 9(2), 188-200.
- McIlquham, G. J., 2003. *Assessment of infaunal community recovery following cockle fishing in Poole Harbour*. Dissertation submitted in partial fulfilment of the requirements for the degree of MSc (Oceanography), School of Earth and Ocean Science, University of Southampton.
- McLachlan, A., 1996. Physical factors in benthic ecology: effects of changing sand particle size on beach fauna. *Marine Ecology Progress Series*. 131, 205-217.

- McLane, A. J., Semeniuk, C., McDermid, G. J. and Marceau, D. J., 2011. The role of agent-based models in wildlife ecology and management. *Ecological Modelling*. 222 (8), 1544-1556.
- Melville-Smith, R. and De Lestang, S., 2006. Spatial and temporal variation in the size at maturity of the western rock lobster *Panulirus cygnus* George. *Marine Biology*. 150 (2), 183-195.
- Meyerson, L. A. and Reaser, J. K., 2002. Biosecurity: moving toward a comprehensive approach. *BioScience*. 52(7), 593-600.
- Millennium Ecosystem Assessment, 2005. *Ecosystems and human well-being: synthesis*. Island, Washington, DC.
- Miller, M. L. and Auyong, J., 1991. Coastal zone tourism: A potent force affecting environment and society. *Marine Policy*. 15 (2), 75-99.
- Millner, R. and Whiting, C., 1996. Long-term changes in growth and population abundance of sole in the North Sea from 1940 to the present. *ICES Journal of Marine Science*. 53 (6), 1185-1195.
- Milsom, T., Langton, S., Parkin, W., Peel, S., Bishop, J., Hart, J. and Moore, N., 2000. Habitat models of bird species' distribution: an aid to the management of coastal grazing marshes. *Journal of Applied Ecology*. 37 (5), 706-727.
- Möllmann, C., Lindegren, M., Blenckner, T., Bergström, L., Casini, M., Diekmann, R., Flinkman, J., Müller-Karulis, B., Neuenfeldt, S. and Schmidt, J. O., 2014. Implementing ecosystem-based fisheries management: from single-species to integrated ecosystem assessment and advice for Baltic Sea fish stocks. *ICES Journal of Marine Science: Journal du Conseil*. 71 (5), 1187-1197.

- Molnar, J. L., Gamboa, R. L., Revenga, C. and Spalding, M. D., 2008. Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment*. 6 (9), 485-492.
- Moreira, F. 1997. The importance of shorebirds to energy fluxes in a food web of a south European estuary. *Estuarine, Coastal and Shelf Science*. 44(1), 67-78.
- Mortensen, S. H., Strand, Ø. and Høiscøter, T., 2000. Releases and recaptures of Manila clams (*Ruditapes philippinarum*) introduced to Norway. *Sarsia*. 85 (1), 87-91.
- Mosbahi, N., Pezy, J. P., Dauvin, J. C. and Neifar, L., 2016. Immediate Effect of Clam Harvesting on Intertidal Benthic Communities in the Mudflat Zones of Kneiss Islands (Central Mediterranean Sea). *Journal of Aquaculture Research Development*. 7(454), 2.
- Nagy, K. A., Girard, I. A. and Brown, T. K., 1999. Energetics of free-ranging mammals, reptiles, and birds. *Annual Review of Nutrition*. 19 (1), 247-277.
- Navedo, J. G., Arranz, D., Herrera, A. G., Salmon, P., Juanes, J. A. and Masero, J. A., 2013. Agroecosystems and conservation of migratory waterbirds: importance of coastal pastures and factors influencing their use by wintering shorebirds. *Biodiversity and Conservation*. 22(9), 1895–1907.
- Nelson, K. A., Leonard, L. A., Posey, M. H., Alphin, T. D. and Mallin, M. A., 2004. Using transplanted oyster (*Crassostrea virginica*) beds to improve water quality in small tidal creeks: a pilot study. *Journal of Experimental Marine Biology and Ecology*. 298 (2), 347-368.

- Neuhoff, H., 1979. Influence of temperature and salinity on food conversion and growth of different *Nereis* species (Polychaeta, Annelida). *Marine Ecology Progress Series*. 1, 255-262.
- Newell, R. I., 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. *Journal of Shellfish Research*. 23 (1), 51-62.
- Norkko, A., Rosenberg, R., Thrush, S.F. and Whitlatch, R.B., 2006. Scale-and intensity-dependent disturbance determines the magnitude of opportunistic response. *Journal of Experimental Marine Biology and Ecology*. 330(1), 195-207.
- Norkko, A., Thrush, S. F., Hewitt, J. E., Cummings, V. J., Norkko, J., Ellis, J. I., Funnell, G. A., Schultz, D. and MacDonald, I., 2002. Smothering of estuarine sandflats by terrigenous clay: the role of wind-wave disturbance and bioturbation in site-dependent macrofaunal recovery. *Marine Ecology Progress Series*. 234, 23-42.
- Norkko, J., Pilditch, C., Thrush, S. and Wells, R., 2005. Effects of food availability and hypoxia on bivalves: the value of using multiple parameters to measure bivalve condition in environmental studies. *Marine Ecology Progress Series*. 298, 205-218.
- Norris, K. and Johnstone, I., 1998. The functional response of oystercatchers (*Haematopus ostralegus*) searching for cockles (*Cerastoderma edule*) by touch. *Journal of Animal Ecology*. 67 (3), 329-346.

- Norton-Griffiths, M., 1967. Some ecological aspects of the feeding behaviour of the oystercatcher *Haematopus ostralegus* on the edible mussel *Mytilus edulis*. *Ibis*, 109 (3), 412-424.
- Nurul Amin, S., Zafar, M. and Halim, A., 2008. Age, growth, mortality and population structure of the oyster, *Crassostrea madrasensis*, in the Moheshkhali Channel (southeastern coast of Bangladesh). *Journal of Applied Ichthyology*. 24 (1), 18-25.
- O'Neill F. and Summerbell, K., 2011. The mobilisation of sediment by demersal otter trawls. *Marine Pollution Bulletin*. 62(5), 1088-1097.
- Ohba, S., 1959. Ecological studies in the natural population of a clam, *Tapes japonica*, with special reference to seasonal variations in the size and structure of the population and to individual growth. *Biological Journal of Okayama University*. 5, 13-42.
- Olafsson, E., 1986. Density dependence in suspension-feeding and deposit-feeding populations of the bivalve *Macoma balthica*: a field experiment. *Journal of Animal Ecology*. 55, 517-526.
- Olive, P., 1993. Management of the exploitation of the lugworm *Arenicola marina* and the ragworm *Nereis virens* (Polychaeta) in conservation areas. *Aquatic Conservation: Marine and Freshwater Ecosystems*. 3 (1), 1-24.
- O'Neill, F. and Ivanović, A., 2015. The physical impact of towed demersal fishing gears on soft sediments. *ICES Journal of Marine Science*. 73 (suppl_1), i5-i14.
- Paine, R., 1977. Controlled manipulations in the marine intertidal zone and their contributions to ecological theory. *Proceedings of the Academy of Natural Sciences* (Vol. 12, pp. 245-270).

- Palanques, A., Puig, P., Guillén, J., Demestre, M. and Martín, J., 2014. Effects of bottom trawling on the Ebro continental shelf sedimentary system (NW Mediterranean). *Continental Shelf Research*. 72, 83-98.
- Parker, L., E. Pinn, 2005, 19. Ecological effects of pump-scoop dredging for cockles on the intertidal benthic communities. *In: Humphreys, J. and May, V., eds. The Ecology of Poole Harbour. Proceedings in Marine Science*. 7, 163-173.
- Pauly, D. and Morgan, G., 1987. *Length-based methods in fisheries research*. Vol. 13. WorldFish.
- Pauly, D., 1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution*. 10 (10), 430.
- Pearson, T. and Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology Annual Review*. 16, 229-311.
- Peterson, C. H., Summerson, H. and Duncan, P., 1984. The influence of seagrass cover on population structure and individual growth rate of a suspension-feeding bivalve, *Mercenaria mercenaria*. *Journal of Marine Research*. 42 (1), 123-138.
- Phinn, S., Roelfsema, C., Dekker, A., Brando, V. and Anstee, J., 2008. Mapping seagrass species, cover and biomass in shallow waters: An assessment of satellite multi-spectral and airborne hyper-spectral imaging systems in Moreton Bay (Australia). *Remote Sensing of Environment*. 112 (8), 3413-3425.
- Pickett S.T. and P.S. White, 1985. Patch dynamics. *Unknown Journal*. 371-384.

- Piersma, T. and Baker, A., 2000. Life history characteristics and the conservation of migratory shorebirds. *Conservation Biology Series-Cambridge*. 105-124.
- Piersma, T. and Drent, J., 2003. Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology and Evolution*. 18 (5), 228-233.
- Piersma, T. and Lindström, Å., 2004. Migrating shorebirds as integrative sentinels of global environmental change. *Ibis*. 146(s1), 61-69.
- Piersma, T., 2007. Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *Journal of Ornithology*. 148 (1), 45.
- Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P. and Wiersma, P., 1993a. Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the western Wadden Sea in relation to food, friends and foes. *Netherlands Journal of Sea Research*. 31 (4), 331-357.
- Piersma, T., Koolhaas, A. and Dekinga, A., 1993b. Interactions between stomach structure and diet choice in shorebirds. *The Auk*. 110 (3), 552-564.
- Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J. J., Dekker, R. and Essink, K., 2001. Long-Term Indirect Effects of Mechanical Cockle-Dredging on Intertidal Bivalve Stocks in the Wadden Sea. *Journal of Applied Ecology*. 38 (5), 976-990.
- Piersma, T., Van Gils, J., De Goeij, P. and Van Der Meer, J., 1995. Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. *Journal of Animal Ecology*. 64 (4), 493-504.

- Piersma, T., Verkuil, Y. and Tulp, I., 1994. Resources for long-distance migration of knots *Calidris canutus islandica* and *C. c. canutus*: how broad is the temporal exploitation window of benthic prey in the western and eastern Wadden Sea? *Oikos*. 393-407.
- Pikitch, E., Santora, E., Babcock, A., Bakun, A., Bonfil, R., Conover, D., Dayton, P., Doukakis, P., Fluharty, D. and Heheman, B., 2004. Ecosystem-based fishery management. *Science*. 305 (Weekly), 346-347.
- Pinedo, S., Sardá, R., Rey, C. and Bhaud, M., 2000. Effect of sediment particle size on recruitment of *Owenia fusiformis* in the Bay of Blanes (NW Mediterranean Sea): an experimental approach to explain field distribution. *Marine Ecology Progress Series*. 203, 205-213.
- Pomeroy R.S., Watson L.M., Parks J.E. and Cid G.A., 2005. How is your MPA doing? A methodology for evaluating the management effectiveness of marine protected areas. *Ocean & Coastal Management*, 48(7-8), 485-502.
- Ponurovskii, S., 2000. Size and age structures of the bivalve mollusk *Ruditapes philippinarum* population in the shallow waters of South Primor'e. *OCEANOLOGY C/C OF OKEANOLOGIJA*. 40 (5), 693-699.
- Pranovi, F., Da Ponte, F., Raicevich, S. and Giovanardi, O. 2004. A multidisciplinary study of the immediate effects of mechanical clam harvesting in the Venice Lagoon. *ICES Journal of Marine Science*. 61 (1), 43-52.
- Pranovi, F., Giovanardi, O. and Franceschini, G., 1998. Recolonization dynamics in areas disturbed by bottom fishing gears. *Recruitment, Colonization and Physical-Chemical Forcing in Marine Biological Systems*. Springer, 125-135.
- Prater, A., 1974. Oystercatchers v. Cockles. *BTO News*. 64, 1-2.

- Pravin, P., Gibinkumar, T.R., Sabu, S. and Boopendranath, M.R., 2013. Bycatch reduction devices. In *Ecosystem Approaches to the Management and Conservation of Fisheries and Marine Biodiversity in the Asia Region. Regional Symposium, Extended Abstracts, Cochin* (pp. 117-120).
- Quattrochi, D. A. and Goodchild, M. F., 1997. *Scale in remote sensing and GIS*. CRC press.
- Raffaelli, D. G. and Hall, S. J., 1996. Assessing the relative importance of trophic links in food webs. *Food Webs*. Springer, 185-191.
- Rice, J., Trujillo, V., Jennings, S., Hylland, K., Hagstrom, O., Astudillo, A. and Jensen, J. N., 2005. Guidance on the application of the ecosystem approach to management of human activities in the European marine environment. *Cooperative Research Report - International Council for the Exploration of the Sea*, 273.
- Robbins, B. D., 1997. Quantifying temporal change in seagrass areal coverage: the use of GIS and low resolution aerial photography. *Aquatic Botany*. 58 (3-4), 259-267.
- Roberts, T. and Jones, P. J., 2009. Shellfishing, eider ducks, and nature conservation on the wash: questions raised by a fractured partnership. *Society and Natural Resources*. 22 (6), 538-553.
- Rogers, C.M., 1987. Predation risk and fasting capacity: do winter birds maintain optimal body mass? *Ecology*. 68, 1051-1061.
- Rose, K. A., Cowan, J. H., Winemiller, K. O., Myers, R. A. and Hilborn, R., 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries*. 2 (4), 293-327.

- Rossi F. and Lardicci, C., 2002. Role of the nutritive value of sediment in regulating population dynamics of the deposit-feeding polychaete *Streblospio shrubsolii*. *Marine Biology*. 140(6), 1129-1138.
- Rutten, A. L., Oosterbeek, K., Ens, B. J. and Verhulst, S., 2006. Optimal foraging on perilous prey: risk of bill damage reduces optimal prey size in oystercatchers. *Behavioral Ecology*. 17 (2), 297-302.
- Rybarczyk, H., Elkaim, B., Wilson, J. G. and Loquet, N., 1996. Eutrophication in the Baie de Somme: Consequences and impacts on the benthic population. *Oceanologica Acta*. 19, 131-140.
- Sæther, B.-E., Ringsby, T. H. and Røskaft, E., 1996. Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. *Oikos*. 217-226.
- Sahin, C., Düzgüneş, E. and Okumuş, İ., 2006. Seasonal variations in condition index and gonadal development of the introduced blood cockle *Anadara inaequalvis* (Bruguiere, 1789) in the southeastern Black Sea coast. *Turkish Journal of Fisheries and Aquatic Sciences*. 6 (2), 155-163.
- Sanders, J. L., Kendall, M. A., Hawkins, A. J. and Spicer, J. I., 2007. Can functional groups be used to indicate estuarine ecological status? *Hydrobiologia*. 588(1), 45-58.
- Sardá R., and Martin, D., 1993. Populations of *Streblospio* (Polychaeta: Spionidae) in temperate zones: demography and production. *Journal of the Marine Biological Association of the United Kingdom*. 73 (04), 769-784.

- Scaps P., 2002. A review of the biology, ecology and potential use of the common ragworm *Hediste diversicolor* (OF Müller)(Annelida: Polychaeta). *Hydrobiologia*. 470(1-3), 203-218.
- Schmidt, A., Wehrmann, A. and Dittmann, S., 2008. Population dynamics of the invasive Pacific oyster *Crassostrea gigas* during the early stages of an outbreak in the Wadden Sea (Germany). *Helgoland Marine Research*. 62 (4), 367.
- Schroeder, J., 2010. *Individual fitness correlates in the black-tailed godwit*. University Library Groningen][Host].
- Schwinghamer, P., Gordon, D.C., Rowell, T.W., Prena, J., McKeown, D.L., Sonnichsen, G. and Guigné, J.Y., 1998. Effects of Experimental Otter Trawling on Surficial Sediment Properties of a Sandy-Bottom Ecosystem on the Grand Banks of Newfoundland. *Conservation Biology*. 12(6), 1215-1222.
- Sciberras, M., Hinz, H., Bennell, J. D., Jenkins, S. R., Hawkins, S. J. and Kaiser, M. J., 2013. Benthic community response to a scallop dredging closure within a dynamic seabed habitat. *Marine Ecology Progress Series*. 480, 83-98.
- Scyphers, S. B., Powers, S. P., Heck Jr, K. L. and Byron, D., 2011. Oyster reefs as natural breakwaters mitigate shoreline loss and facilitate fisheries. *PloS one*. 6 (8), e22396.
- Sebesvari, Z., Esser, F. and Harder, T., 2006. Sediment-associated cues for larval settlement of the infaunal spionid polychaetes *Polydora cornuta* and *Streblospio benedicti*. *Journal of Experimental Marine Biology and Ecology*. 337(1), 109-120.

- Secretariat of the Convention on Biological Diversity, 2004. The Ecosystem Approach, (CBD Guidelines) Montreal: Secretariat of the Convention on Biological Diversity, 2004 50p.
- Shepherd, P. C. and Boates, J. S., 1999. Effects of a commercial baitworm harvest on semipalmated sandpipers and their prey in the Bay of Fundy hemispheric shorebird reserve. *Conservation Biology*. 13 (2), 347-356.
- Skagen, S. K. and Knopf, F. L., 1993. Toward conservation of midcontinental shorebird migrations. *Conservation Biology*. 7 (3), 533-541.
- Skilleter, G. A., Zharikov, Y., Cameron, B. and McPhee, D. P., 2005. Effects of harvesting callianassid (ghost) shrimps on subtropical benthic communities. *Journal of Experimental Marine Biology and Ecology*. 320 (2), 133-158.
- Smalley, T., 1984. The possible effects of intraspecific competition upon the population-structure of a solitary vermetid mollusk. *Pacific Science*. 38, 92-93.
- Smartcom Software, 2009. TideWizard UK. Portsmouth, UK: Smartcom Software. Retrieved from <http://www.smartcomsoftware.co.uk/tidewizard.html>
- Smit, C. J., Dankers, N., Ens, B. J. and Meijboom, A., 1998. Birds, mussels, cockles and shellfish fishery in the Dutch Wadden Sea: how to deal with low food stocks for eiders and oystercatchers? *Marine Biodiversity*. 29 (1), 141-153.
- Sousa Leitão, F. M. and Baptista Gaspar, M., 2007. Immediate effect of intertidal non-mechanised cockle harvesting on macrobenthic communities: a comparative study. *Scientia marina*. 71 (4), 723-733.
- Southern Science, 1998. An experimental study on the impact of clam dredging on soft sediment macro invertebrates. Report to English Nature.

- Spencer, B. E., Kaiser, M. J. and Edwards, D. B., 1998. Intertidal clam harvesting: benthic community change and recovery. *Aquaculture Research*. 29 (6), 429-437.
- Steins, N. A., 1999. *All hands on deck: An interactive perspective on complex common-pool resource management based on case studies in the coastal waters of the Isle of Wight (UK), Connemara (Ireland) and the Dutch Wadden Sea*. Wageningen, 228p.
- Stillman, R. A. and Goss-Custard, J. D., 2009. Individual-based ecology of coastal birds. *Biological Reviews*. 85, 413-434.
- Stillman, R. A. and Wood, K. A., 2013. Towards a simplified approach for assessing bird food requirements on shellfisheries. A report to the Welsh Government. Bournemouth University.
- Stillman, R. A., 2008. MORPH - An individual-based model to predict the effect of environmental change on foraging animal populations. *Ecological Modelling*. 216 (3-4), 265-276.
- Stillman, R. A., Goss-custard, J. D. and Wood, K. A., 2014. Predicting the mussel food requirements of oystercatchers in the Exe Estuary. Bournemouth University.
- Stillman, R. A., Goss-Custard, J. D., West, A. D., Durell, S. E. A. L. D., Mcgrorerty, S., Caldow, R. W. G., Norris, K. J., Johnstone, I. G., Ens, B. J., Van der Meer, J. and Triplet, P., 2001. Predicting shorebird mortality and population size under different regimes of shellfishery management. *Journal of Applied Ecology*. 38 (4), 857-868.

- Stillman, R. A., Goss-Custard, J. D., West, A. D., Durell, S. E. A. L. V. D., Caldow, R. W. G., McGrorty, S. and Clarke, R. T., 2000. Predicting mortality in novel environments: Tests and sensitivity of a behaviour-based model. *Journal of Applied Ecology*. 37 (4), 564–588.
- Stillman, R. A., West, A. D., Caldow, R. W. and Durell, S. E. L. V., 2007. Predicting the effect of disturbance on coastal birds. *Ibis*. 149 (s1), 73-81.
- Stillman, R. A., West, A. D., Goss-Custard, J. D., Caldow, R. W., Mcgrorty, S., Durell, S. E. L. V., Yates, M. G., Atkinson, P. W., Clark, N. A. and Bell, M. C., 2003. An individual behaviour-based model can predict shorebird mortality using routinely collected shellfishery data. *Journal of Applied Ecology*. 40 (6), 1090-1101.
- Stillman, R. A., Wood, K. A. and Goss-Custard, J. D., 2016. Deriving simple predictions from complex models to support environmental decision-making. *Ecological Modelling*. 326, 134-141.
- Stillman, R., Moore, J., Woolmer, A., Murphy, M., Walker, P., Vanstaen, K., Palmer, D. and Sanderson, W., 2010. Assessing waterbird conservation objectives: an example for the Burry Inlet, UK. *Biological Conservation*. 143 (11), 2617-2630.
- Stokesbury, K. D., Baker, E. P., Harris, B. P. and Rheault, R. B., 2011. Environmental impacts related to mechanical harvest of cultured shellfish. *Shellfish Aquaculture and the Environment*. 319-338.
- Stroud, D. A., Davidson, N., West, R., Scott, D., Haanstra, L., Thorup, O., Ganter, B. and Delany, S., 2004. *Status of migratory wader populations in Africa and Western Eurasia in the 1990s*. International Wader Study Group.

- Sutherland, W. J., 1998a. The effect of local change in habitat quality on populations of migratory species. *Journal of Applied Ecology*. 35 (3), 418-421.
- Sutherland, W. J., 1998b. The importance of behavioural studies in conservation biology. *Animal Behaviour*. 56 (4), 801-809.
- Sutherland, W. J., Ens, B. J., Goss-Custard, J.D. and Hulscher, J. B., 1996. Specialisation. In: *The Oystercatcher : from Individuals to Populations* (ed.) J. D. Goss-Custard, 56-76.
- Swart, J. and Van Andel, J., 2008. Rethinking the interface between ecology and society. The case of the cockle controversy in the Dutch Wadden Sea. *Journal of Applied Ecology*. 45 (1), 82-90.
- Taghon, G. L., 1982. Optimal foraging by deposit-feeding invertebrates: roles of particle size and organic coating. *Oecologia*. 52 (3), 295-304.
- Tang, Q., Zhang, J. and Fang, J., 2011. Shellfish and seaweed mariculture increase atmospheric CO₂ absorption by coastal ecosystems. *Marine Ecology Progress Series*. 424, 97-104.
- Thistle D., 1981. Natural physical disturbances and communities of marine soft bottoms. *Marine Ecology Progress Series*. 6(2), 223-228.
- Thomas, N. S., Caldow, R. W. G., McGroarty, M., Durell, S. E. A. L. V. D., West, A. D. and Stillman, R. A., 2004. Bird Invertebrate Prey Availability in Poole Harbour. Poole: Poole Harbour Study Group.
- Thomson, A., Fuller, R., Yates, M., Brown, S., Cox, R. and Wadsworth, R., 2003. The use of airborne remote sensing for extensive mapping of intertidal sediments and saltmarshes in eastern England. *International Journal of Remote Sensing*. 24 (13), 2717-2737.

- Thrush, S. F., Hewitt, J. E., Cummings, V. J., Dayton, P. K., Cryer, M., Turner, S. J., Funnell, G. A., Budd, R. G., Milburn, C. J. and Wilkinson, M. R., 1998. Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery. *Ecological Applications*. 8(3), 866-879.
- Torroglosa, E. M. and Giménez, J., 2010. Temporal variation in size at maturity of the snail *Zidona dufresnei* from the southwestern Atlantic Ocean after ten years of fishery exploitation. *Aquatic Biology*. 11 (2), 163-167.
- Townshend, D. and O'Connor, D., 1993. Some effects of disturbance to waterfowl from bait-digging and wildfowling at Lindisfarne National Nature Reserve, north-east England. *Wader Study Group Bulletin*. 68 (47), 52.
- Townshend, D. J., 1981.a The Importance of Field Feeding to the Survival of Wintering Male and Female Curlews *Numenius arquata* on the Tees Estuary. In: Jones, N. V, and Wolff, W. J., eds. Feeding and Survival Strategies of Estuarine Organisms. Springer US, 261–273.
- Underwood A.J., 1981. Structure of a rocky intertidal community in New South Wales: patterns of vertical distribution and seasonal changes. *Journal of Experimental Marine Biology and Ecology*. 51(1), 57-85.
- Underwood A.J. and Jernakoff P., 1984. The effects of tidal height, wave-exposure, seasonality and rock-pools on grazing and the distribution of intertidal macroalgae in New South Wales. *Journal of Experimental Marine Biology and Ecology*, 75(1), 71-96.
- Underwood A., 1993. The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. *Austral Ecology*. 18(1), 99-116.

- Urfi, A.J., Goss-Custard, J.D., Lev, S.E.A. and Durell, D., 1996. The ability of oystercatchers *Haematopus ostralegus* to compensate for lost feeding time: field studies on individually marked birds. *Journal of Applied Ecology*. 33, 873-883.
- Utting S. and Spencer, B., 1991. The hatchery culture of bivalve mollusc larvae and juveniles. Ministry of Agriculture, Fisheries and Food, Directorate of Fisheries Research.
- Valdimarsson, G. and James, D., 2001. World fisheries—utilisation of catches. *Ocean and Coastal Management*. 44(9), 619-633.
- van de Kam, J., 2004. *Shorebirds: an illustrated behavioural ecology*. KNNV.
- van Gils, J. A., Piersma, T., Dekinga, A., Spaans, B. and Kraan, C., 2006. Shellfish dredging pushes a flexible avian top predator out of a marine protected area. *PLoS biology*. 4 (12), e376.
- Van Hoey, G., Degraer, S. and Vincx, M., 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. *Estuarine, Coastal and Shelf Science*. 59 (4), 599-613.
- Van Roomen, M., Van Turnhout, C., Van Winden, E., Koks, B., Goedhart, P., Leopold, M. and Smit, C., 2005. Trends in benthivorous waterbirds in the Dutch Wadden Sea 1975–2002: large differences between shellfish-eaters and worm-eaters. *Limosa*. 78, 21-38.
- Verhulst, S., Oosterbeek, K., Rutten, A. and Ens, B., 2004. Shellfish fishery severely reduces condition and survival of oystercatchers despite creation of large marine protected areas. *Ecology and Society*. 9 (1), 17.

- Viechtbauer, W., 2010. Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*. 36 (3), 1-48.
- Wallingford, H., 2004. Poole Harbour approach channel deepening: hydrodynamic and sedimentation studies. *Report EX*, 4945.
- Walsh, M. R., Munch, S. B., Chiba, S. and Conover, D. O., 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecology Letters*. 9 (2), 142-148.
- Warwick, R.M. and Clarke, K.R., 1993. Increased variability as a symptom of stress in marine communities. *Journal of Experimental Marine Biology and Ecology*. 172(1-2), 215-226.
- Watson, G. J., Farrell, P., Stanton, S. and Skidmore, L. C., 2007. Effects of bait collection on *Nereis virens* populations and macrofaunal communities in the Solent, UK. *Journal of the Marine Biological Association of the United Kingdom*. 87 (3), 703-716.
- Watson, G. J., Murray, J. M., Schaefer, M. and Bonner, A., 2017. Bait worms: a valuable and important fishery with implications for fisheries and conservation management. *Fish and Fisheries*. 18 (2), 374-388.
- Watts, A. C., Ambrosia, V. G. and Hinkley, E. A., 2012. Unmanned aircraft systems in remote sensing and scientific research: Classification and considerations of use. *Remote Sensing*. 4 (6), 1671-1692.
- Weijerman, M., Lindeboom, H. and Zuur, A. F., 2005. Regime shifts in marine ecosystems of the North Sea and Wadden Sea. *Marine Ecology Progress Series*. 298, 21-39.

- Weinberg, J. R., Leavitt, D. F., Lancaster, B. A. and Capuzzo, J. M., 1997. Experimental Field Studies with *Mya arenaria* (Bivalvia) on the Induction and Effect of Hematopoietic Neoplasia. *Journal of Invertebrate Pathology*. 69 (2), 183-194.
- Weinberg, J., 1998. Density-dependent growth in the Atlantic surfclam, *Spisula solidissima*, off the coast of the Delmarva Peninsula, USA. *Marine Biology*. 130 (4), 621-630.
- Weinberg, J., Caswell, H. and Whitlatch, R., 1986. Demographic importance of ecological interactions: how much do statistics tell us? *Marine Biology*. 93 (2), 305-310.
- West, A.D., Goss-Custard, J.D., Stillman, R.A., Caldow, R.W., dit Durell, S.E.L.V. and McGrorty, S., 2002. Predicting the impacts of disturbance on shorebird mortality using a behaviour-based model. *Biological Conservation*. 106(3), 319-328.
- Wheeler, R. S., Stillman, R. A. and Herbert, R. J. H., 2014. *Ecological impacts of clam and cockle harvesting on benthic habitats and waterfowl*. Bournemouth University.
- Wijnhoven, S., Escaravage, V., Herman, P. M. J., Smaal, A. C. and Hummel, H., 2011. Short and mid-long term effects of cockle-dredging on non-target macrobenthic species: a before-after-control-impact experiment on a tidal mudflat in the Oosterschelde (The Netherlands). *Marine Ecology*. 32, 117-129.

- Wolf, W., 1973. The estuary as a habitat. An analysis of data on the soft- bot- tom macrofauna of the estuarine area of the rivers Rhine, Meuse, and Scheldt. *Zoologische Verhandelingen*. 126, pp.1-242.
- Wood, E. M., Pidgeon, A. M., Radeloff, V. C. and Keuler, N. S., 2012. Image texture as a remotely sensed measure of vegetation structure. *Remote Sensing of Environment*. 121, 516-526.
- Wood, E. M., Pidgeon, A. M., Radeloff, V. C. and Keuler, N. S., 2013. Image texture predicts avian density and species richness. *PloS one*. 8 (5), e63211.
- Woodcock, C. E. and Strahler, A. H., 1987. The factor of scale in remote sensing. *Remote sensing of Environment*. 21 (3), 311-332.
- WoRMS, 2017. World Register of Marine Species. Available from: <http://www.marinespecies.org/> [Accessed: 10th November 2017].
- Wrange, A.-L., Valero, J., Harkestad, L. S., Strand, Ø., Lindegarth, S., Christensen, H. T., Dolmer, P., Kristensen, P. S. and Mortensen, S., 2010. Massive settlements of the Pacific oyster, *Crassostrea gigas*, in Scandinavia. *Biological Invasions*. 12 (5), 1145-1152.
- Wynberg, R. P. and Branch, G. M., 1994. Disturbance associated with bait-collection for sandprawns (*Callinassa kraussi*) and mudprawns (*Upogebia africana*): long-term effects on the biota of intertidal sandflats. *Journal of Marine Research*. 52 (3), 523-558.
- Yap, W. G., 1977. Population biology of the Japanese little-neck clam, *Tapes philippinarum*, in Kaneohe Bay, Oahu, Hawaiian Islands.

- Yasué, M., 2005. The effects of human presence, flock size and prey density on shorebird foraging rates. *Journal of Ethology*. 23(2), 199-204.
- Yates, M., Goss-Custard, J., McGroarty, S., Lakhani, K., Durell, S. L. V. D., Clarke, R., Rispin, W., Moy, I., Yates, T. and Plant, R., 1993. Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. *Journal of Applied Ecology*. 30 (4), 599-614.
- Zharikov, Y. and Skilleter, G. A., 2004. Potential interactions between humans and non-breeding shorebirds on a subtropical intertidal flat. *Austral Ecology*. 29 (6), 647-660.
- Zheng, B., Chen, X.-J. and Li, G., 2008. Relationship between the resource and fishing ground of mackerel and environmental factors based on GAM and GLM models in the East China Sea and Yellow Sea [J]. *Journal of Fisheries of China*. 3, 007.
- Zwarts, L. and Blomert, A.-M., 1992. Why knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. *Marine Ecology Progress Series*. 83 (2/3), 113-128.
- Zwarts, L. and Wanink, J. H., 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Netherlands Journal of Sea Research*. 31 (4), 441-476.
- Zwarts, L., 1991. Seasonal variation in body weight of the bivalves *Macoma balthica*, *Scrobicularia plana*, *Mya arenaria* and *Cerastoderma edule* in the Dutch Wadden sea *Netherlands Journal of Sea Research*. 28 (3), 231-245.

Zwarts, L., Ens, B. J., Goss-Custard, J. D., Hulscher, J. B. and Le V. Dit Durell, S., 1996.

Causes of variation in prey profitability and its consequences for the intake rate of the Oystercatcher *Haematopus ostralegus*. *ARDEA-WAGENINGEN*. 84, 229-268.

Zwarts, L., Ens, B. J., Goss-Custard, J. D., Hulscher, J. B. and Kersten, M., 1996. Why oystercatchers *Haematopus Ostralegus* cannot meet their daily energy requirements in a single low water period. *Ardea*. 84 (Part A), 269–290.

10. Appendices

Appendix 1. Supplementary material to Chapter 2 Intertidal invertebrate harvesting: a meta-analysis of impacts and recovery in an important shorebird prey resource.

Table A1.1. Preferred prey and winter habitat of common bird species in the intertidal. Adapted from Goss-Custard *et al.* (2006).

Species	Preferred Prey Genus	Preferred Winter Habitat	References
Bar-tailed Godwit <i>Limosa lapponica</i>	<i>Scrobicularia</i> <i>Macoma</i> <i>Hediste</i> ¹ <i>Arenicola</i>	Tidal sand and muddy-sand flats in intertidal estuaries. Associated with more exposed bays and estuaries.	Johnsgard (1981), del Hoyo <i>et al.</i> (1996), Goss-Custard <i>et al.</i> (2006).
Black-tailed Godwit <i>Limosa limosa</i>	<i>Scrobicularia</i> <i>Macoma</i> <i>Hediste</i> <i>Crangon</i>	Subspecies <i>limosa</i> favours freshwater wintering habitats, while <i>islandica</i> winters on intertidal mudflats in sheltered bays and estuaries. Favours muddier sites than	Johnsgard (1981), del Hoyo <i>et al.</i> (1996), Goss-Custard <i>et al.</i> (2006).

		<i>L. lapponica</i> which winters in sandier areas.	
Eurasian Curlew <i>Numenius arquata</i>	<i>Mya</i> <i>Cerastoderma</i> <i>Scrobicularia</i> <i>Macoma</i> <i>Hediste</i> ¹ <i>Arenicola</i> <i>Carcinus</i>	Sheltered mud and sandflats in coastal areas and estuaries.	Johnsgard (1981), del Hoyo <i>et al.</i> (1996), Goss-Custard <i>et al.</i> (2006).
Eurasian Oystercatcher <i>Haematopus ostralegus</i>	<i>Mytilus</i> <i>Mya</i> <i>Cerastoderma</i> <i>Scrobicularia</i> <i>Macoma</i> <i>Hediste</i> ¹ <i>Arenicola</i> <i>Carcinus</i>	Widespread in coastal areas including rocky and sandy shores, commonly winters on estuarine mud and sandflats and areas of saltmarsh. Favours sandier habitats over finer sediments.	Johnsgard (1981), Goss-Custard <i>et al.</i> (1992), del Hoyo <i>et al.</i> (1996), Goss-Custard <i>et al.</i> (2006).

Common Redshank <i>Tringa totanus</i>	<i>Mya</i> <i>Scrobicularia</i> <i>Macoma</i> <i>Hydrobia</i> <i>Corophium</i> <i>Hediste</i> ¹ <i>Carcinus</i> <i>Crangon</i>	Various coastal habitats although mainly estuaries and coastal lagoons where they are most associated with sheltered tidal mudflats.	Johnsgard (1981), del Hoyo <i>et al.</i> (1996), Goss-Custard <i>et al.</i> (2006).
Dunlin <i>Calidris alpina</i>	<i>Scrobicularia</i> <i>Macoma</i> <i>Hydrobia</i> <i>Corophium</i> <i>Hediste</i> ¹	Estuarine and coastal tidal flats. Prefers muddier sites.	Johnsgard (1981), del Hoyo <i>et al.</i> (1996), Goss-Custard <i>et al.</i> (2006).
Red Knot <i>Calidris canutus</i>	<i>Mytilus</i> <i>Mya</i> <i>Cerastoderma</i>	Sheltered coasts, tidal mud and sandflats. Sheltered sandy beaches.	Johnsgard (1981), del Hoyo <i>et al.</i> (1996), Goss-Custard <i>et al.</i> (2006).

	<i>Scrobicularia</i> <i>Macoma</i> <i>Hydrobia</i> <i>Hediste</i> ¹		
Grey Plover <i>Pluvialis squatarola</i>	<i>Scrobicularia</i> <i>Macoma</i> <i>Hydrobia</i> <i>Hediste</i> ¹ <i>Arenicola</i>	Intertidal mudflats, sandflats and saltmarsh in coastal areas, sheltered bays and estuaries	Johnsgard (1981), del Hoyo <i>et al.</i> (1996), Goss-Custard <i>et al.</i> (2006).
Ringed Plover <i>Charadrius hiaticula</i>	<i>Hydrobia</i> <i>Corophium</i> <i>Hediste</i> ¹	Sandy and gravel shores and tidal mud and sandflats.	Johnsgard (1981), del Hoyo <i>et al.</i> (1996), Goss-Custard <i>et al.</i> (2006).
Sanderling <i>Calidris alba</i>	<i>Crangon</i> <i>Nerine</i> <i>Bathyporeia</i> <i>Eurydice</i>	Sandy beaches on open exposed coastlines.	Johnsgard (1981), Brearey, (1982) del Hoyo <i>et al.</i> (1996), Goss-Custard <i>et al.</i> (2006).

Common Shelduck <i>Tadorna tadorna</i>	<i>Hydrobia</i> <i>Macoma</i> <i>Corophium</i> <i>Nereis</i> ¹	Muddy and sandy coastlines and tidal flats.	Olney, (1965), Johnsgard (1981), del Hoyo <i>et al.</i> (1996), Goss-Custard <i>et al.</i> (2006).
¹ Along with other polychaete worms			

Table A1.1 References

Brearey, D. M., 1982. *The feeding ecology and foraging behaviour of sanderling calidris alba and turnstone arenaria interpres at Teesmouth NE England*. Durham University.

del Hoyo, J., Elliott, A. and Sargatal, J., 1999. Handbook of the birds of the world, vol. 5. *Lynx Edicions, Barcelona*.

Goss-Custard, J. D., West, A. D., Yates, M. G., Caldow, R. W. G., Stillman, R. A., Bardsley, L., Castilla, J., Castro, M., Dierschke, V., Durell, S. E. A. L. D., Eichhorn, G., Ens, B. J., Exo, K. M., Udayangani-Fernando, P. U., Ferns, P. N., Hockey, P. A. R., Gill, J. A., Johnstone, I., Kalejta-Summers, B., Masero, J. A., Moreira, F., Nagarajan, R. V., Owens, I. P. F., Pacheco, C., Perez-Hurtado, A., Rogers, D., Scheiffarth, G., Sitters, H., Sutherland, W. J., Triplet, P., Worrall, D. H., Zharikov, Y., Zwarts, L. and Pettifor, R. A., 2006. Intake rates and the functional response in shorebirds (Charadriiformes) eating macro-invertebrates. *Biological Reviews*, 81 (4), 501-529.

Johnsgard, P. A., 1981. *The plovers, sandpipers, and snipes of the world*. University of Nebraska Press.

Olney, P., 1965. The food and feeding habits of Shelduck *Tadorna tadorna*. *Ibis*, 107 (4), 527-532.

Table A1.2. Publications included in the analysis, indicating the region, gears employed and the year of study

Publication	Region	Habitats	Gears	Year
Brown, B. and Wilson, W. H., 1997. The role of commercial digging of mudflats as an agent for change of infaunal intertidal populations. <i>Journal of Experimental Marine Biology and Ecology</i> . 218 (1), 49-61.	Walpole, Maine, USA	Mudflats	Hand Digging	1993
Carvalho, S., Constantino, R., Cerqueira, M., Pereira, F., Subida, M. D., Drake, P. and Gaspar, M. B., 2013. Short-term impact of bait digging on intertidal macrobenthic assemblages of two south Iberian Atlantic systems. <i>Estuarine, Coastal and Shelf Science</i> . 132, 65-76.	Iberian Peninsula, Southern Spain	Intertidal flats, saltmarsh	Hand Digging	2009
Castaldelli, G., Mantovani, S., Welsh, D. T., Rossi, R., Mistri, M. and Fano, E., 2003. Impact of commercial clam harvesting on water column and sediment physicochemical characteristics and macrobenthic community structure in a lagoon (Sacca di Goro) of the Po River Delta. <i>Chemistry and Ecology</i> . 19 (2-3), 161-171.	Po River Delta, Italy	Sandflat (sandy-silt sediment)	Hand Raking ("Rasca")	2000

Clarke, S. and Tully, O., 2014. BACI monitoring of effects of hydraulic dredging for cockles on intertidal benthic habitats of Dundalk Bay, Ireland. <i>Journal of the Marine Biological Association of the United Kingdom</i> . 94 (07), 1451-1464.	Dundalk Bay, Ireland	Sandflats	Hydraulic Dredge	2009-2010
Cotter, A., Walker, P., Coates, P., Cook, W. and Dare, P., 1997. Trial of a tractor dredger for cockles in Burry Inlet, South Wales. <i>ICES Journal of Marine Science: Journal du Conseil</i> . 54 (1), 72-83.	Burry Inlet, UK	Sandflats	Mechanical Tractor Dredge	1992
Dernie, K. M., Kaiser, M. J. and Warwick, R. M., 2003. Recovery Rates of Benthic Communities Following Physical Disturbance. <i>Journal of Animal Ecology</i> . 72 (6), 1043-1056.	Anglesey, North Wales	Sand and mud flats (clean sand; silty sand; sandy mud; mud)	Hand Digging	2001
Ferns, P. N., Rostron, D. M. and Siman, H. Y., 2000. Effects of mechanical cockle harvesting on intertidal communities. <i>Journal of Applied Ecology</i> . 37 (3), 464-474.	Burry Inlet, UK	Intertidal muddy sand; Intertidal clean sand	Mechanical Tractor Dredge	1992

<p>Hall, S. J. and Harding, M. J. C., 1997. Physical Disturbance and Marine Benthic Communities: The Effects of Mechanical Harvesting of Cockles on Non-Target Benthic Infauna. <i>Journal of Applied Ecology</i>. 34 (2), 497-517.</p>	<p>Solway Firth, UK</p>	<p>Mudflats</p>	<p>Hydraulic Dredge; Mechanical Tractor Dredge</p>	<p>1993</p>
<p>Kaiser, M. J., Edwards, D. B. and Spencer, B. E., 1996. Infaunal community changes as a result of commercial clam cultivation and harvesting. <i>Aquatic Living Resources</i>. 9 (1), 57-63.</p>	<p>Whitstable, UK</p>	<p>Mudflat</p>	<p>Suction Dredge</p>	<p>1994-1995</p>
<p>Kaiser, M. J., Broad, G. and Hall, S. J., 2001. Disturbance of intertidal soft-sediment benthic communities by cockle hand raking. <i>Journal of Sea Research</i>. 45 (2), 119-130.</p>	<p>Dee Estuary, UK</p>	<p>Silty intertidal sandflat</p>	<p>Hand Raking</p>	<p>1996</p>
<p>Lenihan, H. and Micheli, F., 2000. Biological effects of shellfish harvesting on oyster reefs: resolving a fishery conflict by ecological experimentation. <i>Fishery Bulletin</i>. 98 (1), 86-95.</p>	<p>North Carolina, USA</p>	<p>Sandy to muddy intertidal channels</p>	<p>Hand Raking and Tongs</p>	<p>1996</p>

<p>McLusky, D., Anderson, F. and Wolfe-Murphy, S., 1983. Distribution and population recovery of <i>Arenicola marina</i> and other benthic fauna after bait digging. <i>Marine Ecology Progress Series. Oldendorf</i>, 11 (2), 173-179.</p>	<p>Forth Estuary, UK</p>	<p>Intertidal mudflat</p>	<p>Hand Digging</p>	<p>1980; 1981</p>
<p>Skilleter, G. A., Zharikov, Y., Cameron, B. and McPhee, D. P., 2005. Effects of harvesting callinassid (ghost) shrimps on subtropical benthic communities. <i>Journal of Experimental Marine Biology and Ecology</i>. 320 (2), 133-158.</p>	<p>Moreton Bay, Queensland, Australia</p>	<p>Estuarine intertidal sandflat</p>	<p>Hand Pump ("Yabbie")</p>	<p>1996</p>
<p>Spencer, B. E., Kaiser, M. J. and Edwards, D. B., 1998. Intertidal clam harvesting: benthic community change and recovery. <i>Aquaculture Research</i>. 29 (6), 429-437.</p>	<p>River Exe, UK</p>	<p>Intertidal muddy sand</p>	<p>Suction Dredge</p>	<p>1991-1995</p>
<p>Whomersley, P., Huxham, M., Bolam, S., Schratzberger, M., Augley, J. and Ridland, D., 2010. Response of intertidal macrofauna to multiple disturbance types and intensities—an experimental approach. <i>Marine Environmental Research</i>. 69 (5), 297-308.</p>	<p>Forth Estuary, UK; Crouch Estuary, UK</p>	<p>Mudflats</p>	<p>Hand Raking</p>	<p>2003</p>

<p>Wynberg, R. P. and Branch, G. M., 1994. Disturbance associated with bait-collection for sandprawns (<i>Callinassa kraussi</i>) and mudprawns (<i>Upogebia africana</i>): long-term effects on the biota of intertidal sandflats. <i>Journal of Marine Research</i>. 52 (3), 523-558.</p>	<p>Langebaan Lagoon, South Africa</p>	<p>Sandflats</p>	<p>Hand Digging, Hand Pump</p>	<p>1988</p>
---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------	---------------------------------------	------------------	--------------------------------	-------------

Table A1.3. Publications not included in the analysis, indicating rationale for exclusion

Publication	Exclusion Rationale
<p>Brylinsky, M., Gibson, J. and Gordon Jr, D. C., 1994. Impacts of Flounder Trawls on the Intertidal Habitat and Community of the Minas Basin, Bay of Fundy. <i>Canadian Journal of Fisheries and Aquatic Sciences</i>. 51 (3), 650-661.</p>	<p>Gear used (flounder trawl) is unique with regards to intertidal fishing and as far as the authors are aware is limited to the Bay of Fundy. Therefore not a representative intertidal harvesting method.</p>
<p>Dernie, K., Kaiser, M., Richardson, E. and Warwick, R., 2003. Recovery of soft sediment communities and habitats following physical disturbance. <i>Journal of Experimental Marine Biology and Ecology</i>. 285, 415-434.</p>	<p>Significant outlier in analysis. Large bias and therefore excluded.</p>
<p>Stagnol, D., Renaud, M. and Davout, D., 2013. Effects of commercial harvesting of intertidal macroalgae on ecosystem biodiversity and functioning. <i>Estuarine, Coastal and Shelf Science</i>. 130, 99-110.</p>	<p>Harvesting carried out in rocky intertidal habitats. Not representative.</p>
<p>Godcharles, M. F., 1971. A study of the effects of a commercial hydraulic clam dredge on benthic communities in estuarine areas.</p>	<p>Cannot obtain full text</p>
<p>Glude, J. B. and Landers, W. S., 1953. <i>Biological effects on hard clams of hand raking and power dredging</i>. Vol. 110. US Department of the Interior,</p>	<p>No usable data.</p>

Fish and Wildlife Service.	
Boldina, I. and Beninger, P. G., 2014. Fine-scale spatial distribution of the common lugworm <i>Arenicola marina</i> , and effects of intertidal clam fishing. <i>Estuarine, Coastal and Shelf Science</i> . 143, 32-40.	No usable data.
Watson, G. J., Farrell, P., Stanton, S. and Skidmore, L. C., 2007. Effects of bait collection on <i>Nereis virens</i> populations and macrofaunal communities in the Solent, UK. <i>Journal of the Marine Biological Association of the United Kingdom</i> . 87 (3), 703-716.	No usable data. Data reported not traceable to sampling method.
Simenstad, C. A. and Fresh, K. L., 1995. Influence of intertidal aquaculture on benthic communities in Pacific Northwest estuaries: scales of disturbance. <i>Estuaries</i> . 18 (1), 43-70.	Study investigates addition of gravel for aquaculture rather than harvesting. Not relevant to our study aims.
Moreno, C. A., Sutherland, J. P. and Jara, H. F., 1984. Man as a predator in the intertidal zone of southern Chile. <i>Oikos</i> . 155-160.	No usable data.
Fiordelmondo, C., Manini, E., Gambi, C. and Pusceddu, A., 2003. Short-term impact of clam harvesting on sediment chemistry, benthic microbes	No relevant responses reported.

and meiofauna in the Goro lagoon (Italy). <i>Chemistry and Ecology</i> . 19 (2-3), 173-187.	
Cook, W., 1991. Studies on the effects of hydraulic dredging on cockle and other macroinvertebrate populations 1989-1990. <i>LANCASTER UNIV., LANCASTER(UK). 1991.</i>	Cannot obtain full text.
de Boer, W. F., van Schie, A. M., Jocene, D. F., Mabote, A. B. and Guissamulo, A., 2001. The impact of artisanal fishery on a tropical intertidal benthic fish community. <i>Environmental Biology of Fishes</i> . 61 (2), 213-229.	No usable data. Experimental design unclear.
Cryer, M., Whittle, G. N. and Williams, R., 1987. The impact of bait collection by anglers on marine intertidal invertebrates. <i>Biological Conservation</i> . 42 (2), 83-93.	No variance reported.
Pickett, G., 1973. <i>The impact of mechanical harvesting on the Thames Estuary cockle fishery</i> . Ministry of Agriculture, Fisheries and Food [Directorate of Fisheries Research].	No usable data.
van den Heiligenberg, T., 1987. Effects of mechanical and manual harvesting of lugworms <i>Arenicola marina</i> L. on the benthic fauna of tidal flats in the	No variance reported.

Dutch Wadden Sea. <i>Biological Conservation</i> . 39 (3), 165-177.	
Beukema, J., 1995. Long-term effects of mechanical harvesting of lugworms <i>Arenicola marina</i> on the zoobenthic community of a tidal flat in the Wadden Sea. <i>Netherlands Journal of Sea Research</i> . 33 (2), 219-227.	No variance reported.
Park, S. R., Kim, Y. K., Kim, J.-H., Kang, C.-K. and Lee, K.-S., 2011. Rapid recovery of the intertidal seagrass <i>Zostera japonica</i> following intense Manila clam (<i>Ruditapes philippinarum</i>) harvesting activity in Korea. <i>Journal of Experimental Marine Biology and Ecology</i> . 407 (2), 275-283.	Response only reported for <i>Zostera japonica</i> . Not relevant for research question.
Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J. J., Dekker, R. and Essink, K., 2001. Long-Term Indirect Effects of Mechanical Cockle-Dredging on Intertidal Bivalve Stocks in the Wadden Sea. <i>Journal of Applied Ecology</i> . 38 (5), 976-990.	Sample size unclear.

**Appendix 2. Supplementary material to Chapter 3 Impacts of a novel shellfishing gear on macrobenthos
in a marine protected area: pump-scoop dredging in Poole Harbour, UK.**

Table A.2.1. Mean (\pm S.E.) abundances per m² of taxa across each site in June and November 2015. Names are concurrent with those provided by the World Register of Marine Species (WoRMS, 2017).

	Control				Newly Opened				Heavy dredging			
	June		November		June		November		June		November	
Species	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
PHYLUM CNIDARIA												
Actiniaria	0.00	0.00	5.31	5.31	26.53	15.29	37.14	16.22	328.92	72.27	424.41	73.38
PHYLUM ANNELIDA												
Polychaeta												
<i>Alitta virens</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.31	5.31
<i>Ampharetidae</i> spp.	0.00	0.00	0.00	0.00	0.00	0.00	31.83	31.83	53.05	42.61	5.31	5.31
<i>Aphelochaeta marioni</i>	21.22	12.52	15.92	15.92	244.04	94.77	917.79	302.60	1145.91	294.64	2047.79	490.31
<i>Capitella capitata</i>	0.00	0.00	0.00	0.00	10.61	10.61	0.00	0.00	228.12	153.66	90.19	54.99
<i>Capitellidae</i> spp.	0.00	0.00	0.00	0.00	5.31	5.31	0.00	0.00	180.38	113.14	137.93	82.51
<i>Cirratulidae</i> spp.	0.00	0.00	0.00	0.00	0.00	0.00	5.31	5.31	10.61	10.61	0.00	0.00
<i>Cirratulus cirratulus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	21.22	12.52

<i>Desdemona ornata</i>	10.61	7.34	10.61	7.34	15.92	11.65	15.92	11.65	37.14	23.60	58.36	47.85
<i>Eteone longa</i>	37.14	17.94	10.61	7.34	5.31	5.31	10.61	7.34	63.66	27.63	42.44	18.24
<i>Glycera tridactyla</i>	0.00	0.00	0.00	0.00	0.00	0.00	5.31	5.31	0.00	0.00	21.22	12.52
<i>Hediste diversicolor</i>	758.64	105.22	742.72	87.61	864.74	143.78	2790.51	459.39	1946.99	232.65	2339.57	368.97
<i>Heteromastus filiformis</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	21.22	16.56
<i>Marphysa sanguinea</i>	0.00	0.00	0.00	0.00	0.00	0.00	5.31	5.31	5.31	5.31	0.00	0.00
<i>Melinna palmata</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Neanthes fucata</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.31	5.31	0.00	0.00
<i>Nephtys hombergii</i>	0.00	0.00	0.00	0.00	10.61	7.34	0.00	0.00	0.00	0.00	0.00	0.00
Phyllodoctidae spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.31	5.31	0.00	0.00
<i>Polydora</i> spp.	26.53	21.65	10.61	7.34	0.00	0.00	31.83	22.01	31.83	22.01	42.44	23.83
Spionidae spp.	5.31	5.31	15.92	8.78	0.00	0.00	0.00	0.00	0.00	0.00	5.31	5.31
<i>Streblospio shrubsolii</i>	47.75	37.40	79.58	28.48	53.05	22.89	228.12	51.40	37.14	14.30	148.54	45.12
Oligochaeta												
Tubificidae spp.	5.31	5.31	5.31	5.31	0.00	0.00	5.31	5.31	26.53	13.23	10.61	10.61
<i>Tubificoides</i> spp.	366.06	143.65	779.86	305.92	1246.71	231.82	1793.14	373.02	1575.63	318.11	2461.59	462.49
Oligochaeta spp.	0.00	0.00	0.00	0.00	0.00	0.00	5.31	5.31	37.14	37.14	26.53	26.53
Cirripedia												
<i>Austrominius</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.31	5.31	31.83	31.83

<i>modestus</i>													
Isopoda													
<i>Cyathura carinata</i>	90.19	37.14	334.22	63.58	15.92	8.78	249.34	70.02	15.92	11.65	63.66	21.68	
Amphipoda													
<i>Gammarus spp.</i>	5.31	5.31	0.00	0.00	0.00	0.00	0.00	0.00	26.53	26.53	5.31	5.31	
Ostracoda													
<i>Eusarsiella zostericola</i>	0.00	0.00	0.00	0.00	5.31	5.31	21.22	12.52	10.61	10.61	31.83	13.82	
<i>Ostracoda sp.</i>	525.21	120.53	875.35	233.00	318.31	84.65	583.57	96.92	31.83	19.16	74.27	25.32	
Decapoda													
<i>Carcinus maenas</i>	5.31	5.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
PHYLUM MOLLUSCA													
<i>Abra alba</i>	0.00	0.00	0.00	0.00	0.00	0.00	10.61	10.61	0.00	0.00	0.00	0.00	
<i>Abra spp.</i>	5.31	5.31	0.00	0.00	5.31	5.31	0.00	0.00	5.31	5.31	5.31	5.31	
<i>Abra tenuis</i>	360.75	62.11	530.52	72.98	572.96	125.70	435.02	91.62	381.97	56.32	74.27	35.88	
<i>Cerastoderma edule</i>	0.00	0.00	10.61	10.61	15.92	11.65	26.53	15.29	26.53	21.65	58.36	17.10	
<i>Cerastoderma glaucum</i>	0.00	0.00	0.00	0.00	15.92	11.65	10.61	7.34	0.00	0.00	0.00	0.00	
<i>Dosinia lupinis</i>	0.00	0.00	0.00	0.00	0.00	0.00	21.22	16.56	21.22	21.22	5.31	5.31	
<i>Hydrobiidae sp.</i>	169.76	169.76	5.31	5.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Juv. M. arenaria</i>	0.00	0.00	0.00	0.00	31.83	15.80	90.19	37.14	42.44	12.52	212.21	53.47	

<i>Leptochiton asellus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.31	5.31	0.00	0.00
<i>Littorina saxatilis</i>	37.14	23.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Macoma balthica</i>	5.31	5.31	5.31	5.31	5.31	5.31	5.31	5.31	5.31	10.61	7.34	5.31	5.31
<i>Mya arenaria</i>	0.00	0.00	0.00	0.00	21.22	21.22	5.31	5.31	5.31	10.61	10.61	5.31	5.31
<i>Peringia ulvae</i>	291.78	51.68	684.36	144.77	249.34	66.14	376.67	241.81	241.81	106.10	33.99	100.80	36.74
<i>Retusa obtusa</i>	5.31	5.31	0.00	0.00	68.97	48.46	5.31	5.31	5.31	5.31	5.31	5.31	5.31
<i>Ruditapes decussatus</i>	0.00	0.00	0.00	0.00	0.00	0.00	5.31	5.31	5.31	0.00	0.00	0.00	0.00
<i>Ruditapes phillipinarium</i>	0.00	0.00	5.31	5.31	5.31	5.31	31.83	17.56	17.56	37.14	23.60	31.83	15.80
<i>Scrobicularia plana</i>	0.00	0.00	10.61	7.34	5.31	5.31	15.92	8.78	8.78	0.00	0.00	0.00	0.00
PHYLUM INSECTA													
Insecta sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.31	5.31	0.00	0.00
Carabidae	0.00	0.00	10.61	7.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chironomidae	0.00	0.00	0.00	0.00	5.31	5.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total	2779.9	357.23	4153.93	439.45	3825.02	445.33	7777.35	1086.74	1086.74	6466.98	443.12	8620.87	1138.44

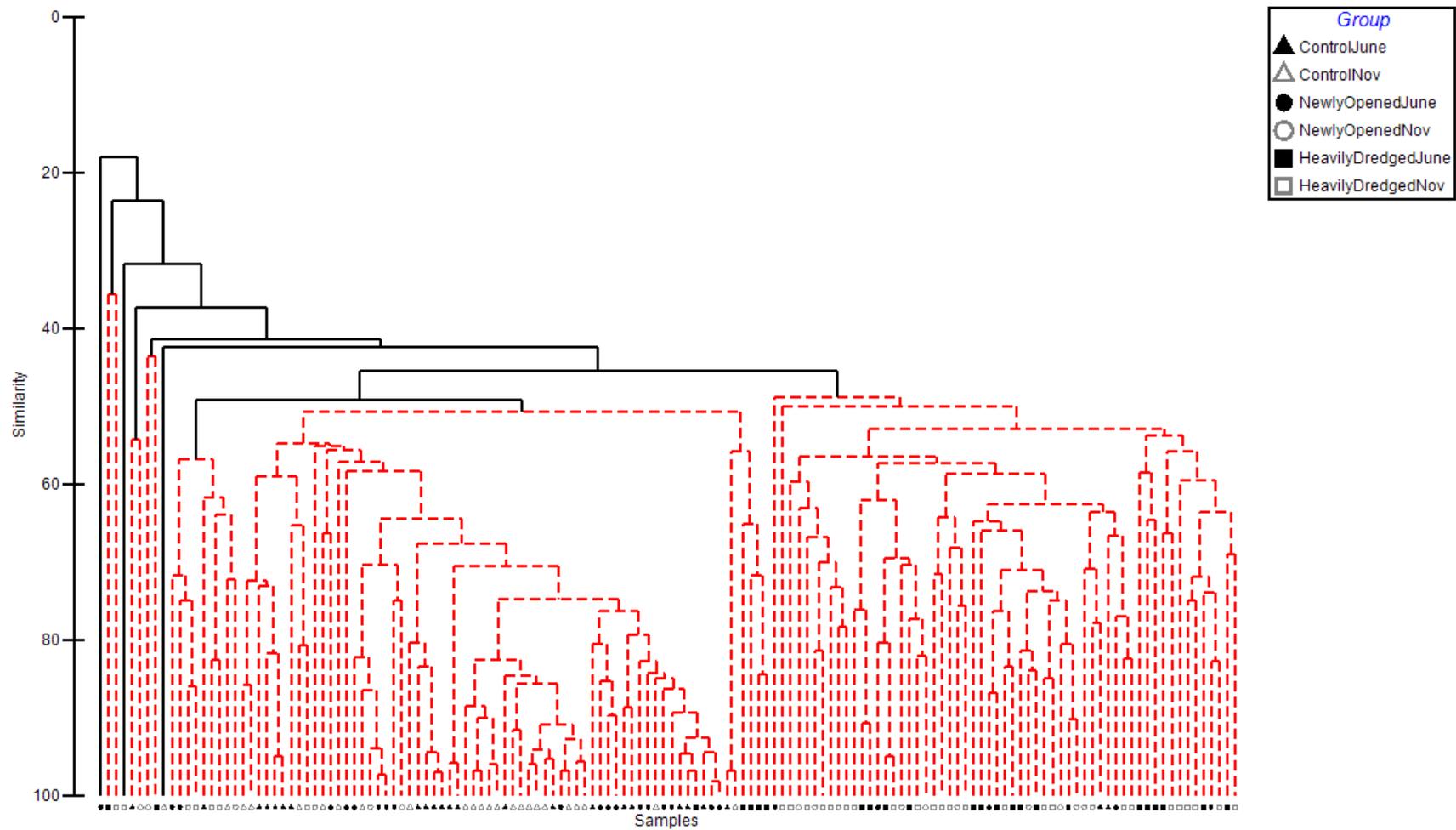


Figure A.2.1. Output of SIMPROF/CLUSTER procedure performed on Bray-Curtis similarity matrix from log-transformed abundance data. Linked black lines indicate significant groups ($p < 0.05$)

Table A2.2. Results of SIMPER analysis on samples taken from the control site across all months. A 90% similarity cut-off has been used.

Species	Mean Abundance (sqrt transformed /m ²)	Mean Similarity	% Contribution	Cumulative %
<i>H. diversicolor</i>	26.11	21.04	38.27	38.27
<i>A. tenuis</i>	18.63	12.75	23.19	61.46
<i>P. ulvae</i>	18.42	10.74	19.53	80.99
<i>Tubificoides</i> <i>spp.</i>	16.24	5.94	10.80	91.78

Table A.2.3. Results of SIMPER analysis on samples taken from the site newly opened to dredging across all months. A 90% similarity cut-off has been used.

Species	Mean Abundance (sqrt transformed /m ²)	Mean Similarity	% Contribution	Cumulative %
<i>H. diversicolor</i>	38.14	18.44	36.75	36.75
<i>Tubificoides</i> <i>spp.</i>	34.30	15.88	31.64	68.39
<i>A. tenuis</i>	18.70	7.67	15.29	83.68
<i>P. ulvae</i>	10.80	2.49	4.96	88.64

<i>A.marioni</i>	14.39	2.19	4.36	93.01
-------------------------	-------	------	------	-------

Table A.2.4. Results of SIMPER analysis on samples taken from the heavily dredged site across all months. A 90% similarity cut-off has been used.

Species	Mean Abundance (sqrt transformed /m²)	Mean Similarity	% Contribution	Cumulative %
<i>H. diversicolor</i>	42.57	17.07	34.97	34.97
<i>Tubificoides</i> <i>spp.</i>	38.26	11.70	23.96	58.94
<i>A.marioni</i>	31.98	8.55	17.52	76.46
Actinaria	16.02	4.84	9.91	86.37
<i>A.tenuis</i>	10.63	2.53	5.17	91.54

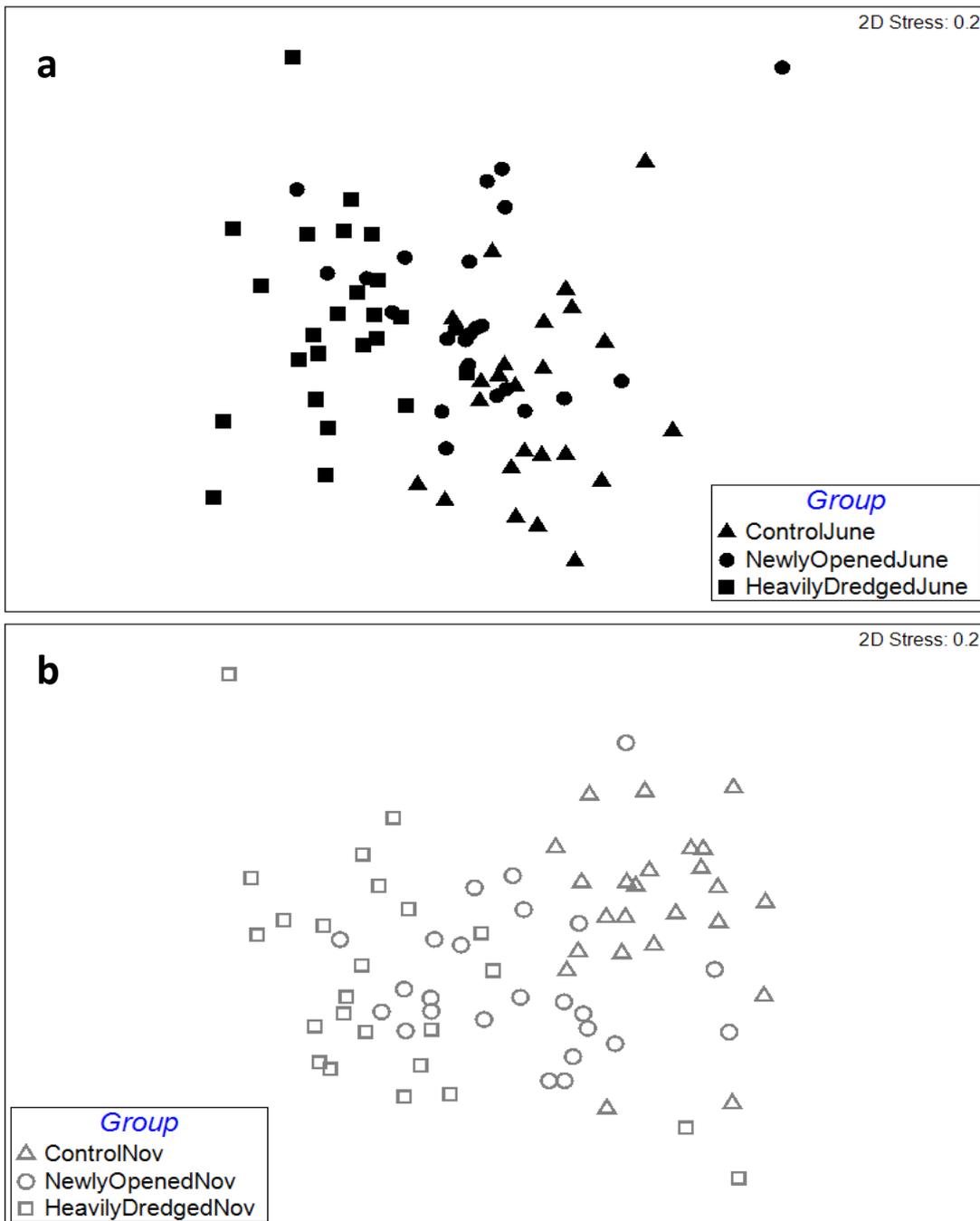


Figure A.2.2. Two-dimensional MDS plot derived from the log (x+1) transformed similarity matrix indicating the similarity between the macrofaunal assemblages at sampling locations in a) June and b) November 2015.

Table A.2.5. SIMPER outputs indicating species dissimilarity for community data at control site in June and November with a 70% cut-off.

Species	Mean abundance (sqrt transformed per m²) Jun 2015	Mean abundance (sqrt transformed per m²) Nov 2015	Mean Dissimilarity	% Contribution	Cumulative %
<i>Tubificoides</i> spp.	12.36	20.12	8.58	18.62	18.62
<i>Peringia</i> <i>ulvae</i>	15.54	22.29	6.90	14.97	33.58
<i>Cyathura</i> <i>carinata</i>	5.12	15.07	6.37	13.82	47.41
<i>Abra tenuis</i>	16.22	21.04	5.67	12.31	59.71
<i>Hediste</i> <i>diversicolor</i>	26.06	26.15	4.75	10.31	70.02

Table A.2.6. SIMPER outputs indicating species dissimilarity for community data at the site newly opened to dredging in June and November with a 70% cut-off.

Species	Mean abundance (sqrt transformed per m ²) Jun 2015	Mean abundance (sqrt transformed per m ²) Nov 2015	Mean Dissimilarity	% Contribution	Cumulative %
<i>Hediste diversicolor</i>	26.98	49.30	8.68	16.67	16.67
<i>Tubificoides spp.</i>	31.57	37.03	7.09	13.61	30.27
<i>Aphelochaeta marioni</i>	8.34	20.43	6.15	11.80	42.07
<i>Abra tenuis</i>	20.14	17.26	5.01	9.62	51.70
<i>Peringia ulvae</i>	11.33	10.27	4.48	8.60	60.30
<i>Streblospio shrubsolei</i>	3.28	11.99	3.84	7.37	67.68
<i>Cyathura carinata</i>	1.41	11.56	3.71	7.12	74.79

Table A2.7. SIMPER outputs indicating species dissimilarity for community data at the heavily dredged site in June and November with a 70% cut-off.

Species	Mean abundance (sqrt transformed per m ²) Jun 2015	Mean abundance (sqrt transformed per m ²) Nov 2015	Mean Dissimilarity	% Contribution	Cumulative %
<i>Tubificoides</i> spp.	33.22	43.29	7.35	14.05	14.05
<i>Aphelochaeta</i> <i>marioni</i>	27.71	36.24	7.17	13.71	27.76
<i>Hediste</i> <i>diversicolor</i>	41.34	43.80	5.58	10.66	38.42
<i>Abra tenuis</i>	17.21	4.04	4.11	7.85	46.27
Actiniaria	14.15	17.90	3.42	6.54	52.81
Juv. M.	3.29	9.96	2.52	4.81	57.61
<i>arenaria</i>					
Capitellidae	5.11	5.14	2.17	4.15	61.77
<i>Peringia</i> <i>ulvae</i>	6.36	5.29	2.15	4.11	65.88
<i>Capitella</i> <i>capitata</i>	4.97	3.91	2.12	4.05	69.93
<i>Streblospio</i> <i>shrubsolii</i>	3.02	7.83	2.02	3.86	73.79

Appendix 3. Supplementary material to Chapter 6: Shorebird distribution and feeding rates in relation to shellfish dredging: insights from Poole Harbour, UK.

Table A.3.1. List of species observed across the study site throughout the winter of 2015/16. Only data from the most numerically abundant species have been included in detailed analyses.

Common Name	Scientific Name
Pied Avocet	<i>Recurvirostra avosetta</i>
Black-tailed Godwit	<i>Limosa limosa</i>
Cormorant	<i>Phalacrocorax carbo</i>
Canadian Goose	<i>Branta canadensis</i>
Eurasian Curlew	<i>Numenius arquata</i>
Dark-bellied Brent Goose	<i>Branta bernicla</i>
Dunlin	<i>Calidris alpina</i>
Wigeon	<i>Anas penelope</i>
Great Black-backed Gull	<i>Larus marinus</i>
Teal	<i>Anas crecca</i>
Great Crested Grebe	<i>Podiceps cristatus</i>
Gadwall	<i>Anas strepera</i>
Greenshank	<i>Tringa nebularia</i>
Grey Plover	<i>Pluvialis squatarola</i>
Grey Heron	<i>Ardea cinerea</i>
Mute Swan	<i>Cygnus olor</i>
Lapwing	<i>Vanellus vanellus</i>
Little Egret	<i>Egretta garzetta</i>

Oystercatcher	<i>Haematopus ostralegus</i>
Redshank	<i>Tringa totanus</i>
Red-breasted Merganser	<i>Mergus serrator</i>
Ringed Plover	<i>Charadrius hiaticula</i>
Spoonbill	<i>Platalea leucorodia</i>
Shelduck	<i>Tadorna tadorna</i>
Marsh Harrier	<i>Circus aeruginosus</i>
Short-eared Owl	<i>Asio flammeus</i>
Kestrel	<i>Falco tinnunculus</i>