Deliverable 3.5
Functional links between sea-bed habitats and demersal fish stocks

(A generic model of benthic productivity, diversity and natural disturbance, and a dynamic food web model of benthic ecosystem function)

Due date of deliverable: September, 2015
Actual submission date: September, 2015
Revised submission date: March, 2016

Grant Agreement number:	312088
Project acronym:	BENTHIS
Project title:	Benthic Ecosystem Fisheries Impact Study
Funding Scheme:	Collaborative project
Project coordination:	IMARES, IJmuiden, the Netherlands
Project website:	www.benthis.eu

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SEVENTH FRAMEWORK PROGRAMME

The research leading to these results has received funding from the European Community's Seventh Framework Programme (FP7/2007-2013) under grant agreement n° 226661

DOCUMENT CHANGE RECORD

Authors	Modification	Issue	Date
Eggleton, J. Bolam, S.	Draft report	7	14/7/2015
Kenny, A.	Formatted and edited	8	28/9/2015
Rijnsdorp, A.D.	Explanation of deviation added	9	15/3/2016

SUMMARY

An important consideration in assessing the impacts of fishing on seabed habitats is to understand the functional links (as trophic interactions) between populations of demersal fish species and potential benthic invertebrate prey (food) which live on or in the seabed. The type of sea-bed fauna has been shown to respond to both natural variation in habitat conditions and in response to different levels of fishing pressure. The extent to which different commercial fish species will depend on specific combinations of habitat type and fishing disturbance to feed will likely be species specific. It has been suggested that positive changes in growth rates of different demersal fish species are not only related to density-dependent processes, but may also be dependent on increased bottom-trawl disturbance and eutrophication (Millner and Whiting 1996, Rijnsdorp and van Leeuwen 1996, Shephard et al., 2010). However, different trawling and habitat specific responses in relation to fish feeding in different size classes of fish has not been investigated before. The aim[1] of this study is therefore to examine such relationships using biological traits analysis (BTA) through a selected quantification of demersal fish stomach contents and habitat fauna using grab and epi-benthic trawl data previously analysed as part of BENTHIS deliverable D3.4.

The present study addresses two important questions, namely; **i.** what type of sea-bed habitats serve as important feeding areas for different species of demersal fish, and **ii.** what, if any, differences do we observe in habitat preference and diet associated with different size classes of demersal fish, both within and between different fish species. Central to answering these two questions is the need to ensure that the sea-bed habitat characteristics are assessed and described at a scale appropriate to the operation of the fisheries and the assessment of demersal fish stocks.

The study found strong associations between community trait composition and prey consumed by plaice of all sizes under fished conditions for a shallow sand – muddy sand habitat located in the eastern North Sea and Dogger Bank. This result suggests that there is some positive association between fishing and the presence of plaice. By contrast, Long rough dab, haddock, cod and whiting did not appear to target fauna that was abundant in the environment within any one of the habitat clusters under either fished or unfished conditions. These species may therefore be less affected by changes in fishing pressure on a wide range of habitats than those species (such as sole and plaice) which favour living in closer association with the benthic environment.

Secondary production was found to be highest within shallow sand – muddy sand habitat although not significantly so. Bolam et al., 2010 and 2014 indicated that production is indeed affected by bottom disturbance, but as that affects substrate type it is not possible to know whether this is a direct or indirect relationship with fishing pressure.

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[1] The aim of Task 3.2 in WP3 was to statistically model the relationship between macrobenthic functions and seabed disturbance. E.g. productivity being one of those functions along with fishing pressure as a proxy for disturbance. The present report has achieved this using biological traits as proxies of functions (including productivity). The present report therefore deviates only in terms of the specific methods used and not in the aim or expected outcome. A change in method was required because of quantity and quality of data available for analysis precluded the use of the intended method, the method finally adopted was that of generating a series of 'heat' plots to statistically reveal the multivariate relationships between habitat type, disturbance and fish feeding. The original title of D3.5 in the DOW has been changed to more accurately reflect the overall aim of Task 3.2.

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1 FUNCTIONAL LINKS BETWEEN DEMERSAL FISH AND HABITATS

1.1 Introduction

One of the most important and yet fundamental questions fisheries scientists are confronted with "is to what extent do commercial fish target their prey and, subsequent to this, whether the impacts of bottom trawling on the assemblages which form an important role in supporting commercial fish stocks actually contribute to sustaining these populations".

Over the last few decades, an appreciable amount of research has been conducted to target both the acute and chronic impacts of fishing on benthic assemblages (Jennings and Kaiser, 1998; Kaiser et al., 2000, 2002; Collie et al., 2000; Kaiser et al., 2006; Hiddink et al., 2007). Together, these studies have demonstrated large changes on the structure and functioning of benthic assemblages, with varying types and magnitudes of impacts being observed in differing habitats and from different trawl gear types (Kaiser and de Groot, 2000; Tillin et al., 2006). Meanwhile, attempts to improve our understanding of the trophic relationships between the stocks of commercial fish with their prey have been undertaken, primarily based on the assessment of the contents of their stomachs (e.g. Steven, 1930; Braber and De Groot, 1973; Wyche & Shackley, 1986; Molinero and Flos, 1991; Pinnegar, 2014). Such studies have demonstrated that reliance on benthic prey varies between fish species and as the fish age. Prey availability is thought to be one of the most important factors influencing fish distributions (Hinz et al., 2003), however, few studies have attempted to link the prey consumed by the predator to those available in the environment (Hinz et al., 2005; Johnson et al., 2015) and none, to our knowledge, have made these links using a biological trait approach.

In this study, we undertake some analysis which helps bring together these various scientific approaches to further our understanding of the impacts of fishing at a functional level. We make use of the invaluable data regarding the variability in biological traits composition across the different seabed habitats that has been developed under BENTHIS deliverable D3.4. This approach allows us to describe changes in prey availability with respect to their inherent biological traits as opposed to their taxonomic identity that has otherwise to date been undertaken. This trait-based approach is more appropriate for large scale studies of commercial fish diet analysis as it removes geographical taxonomic biases in benthic invertebrates. To directly relate fish predation with prey availability, the changes in fish diets are described in terms of their trait composition, a novel approach in the assessment of the diets of commercial fish. Using these approaches, we aim to address the following;

1. Do commercial fish species target different benthic prey traits, and is this size-specific for fish?
2. Do commercial fish species target benthic prey traits differently in different habitats?
3. Do commercial fish species target benthic prey traits that are resistant or favoured by fishing activity?

Answers to these question will be important in determining the functional value of sea-bed habitats in terms of their importance as providing essential fish habitat and therefore contribute to a better understanding of what constitutes an appropriate assessment of 'sea-bed integrity' under the EU MSFD.

1.2 Methods

1.2.1 Stomach databases

1.2.1.1 ICES Year of the Stomach

The ICES Year of the Stomach dataset[2] collected in 1991 contains the most spatially extensive data covering the North Sea, Skagerrak and Kattegat. This formed the basis of the geographical extent for additional datasets. The database includes stomach information on 35 fish species, although detailed information is only available for nine fish species. The majority of stomachs were collected during the quarterly International Bottom Trawl Surveys of the North Sea (IBTS), which involved nine research vessels belonging to seven nations, with additional samples collected during other research surveys and by commercial vessels (ICES, 1991, ICES, 1997). Samples were collected from ICES statistical rectangles, measuring approximately 30 x 30 nautical miles (one degree longitude x 0.5 degree latitude), using a Grande Ouverture Verticale (GOV) trawl. The database contains information on, for example, date sampled, ICES rectangle, predator size (category), number of stomachs collected, digestion state of the stomach contents (pristine, affected by digestion, skeletal remains), prey abundance and biomass. As the main aim of the 1991 project was to gather information for Multispecies Virtual Population Analysis (MSVPA), effort was focussed on identifying, enumerating and weighing commercially important prey to species level. The remaining invertebrate prey items were identified to species level if time allowed but at the discretion of the co-ordinators. Therefore many invertebrate prey items were only identified to major taxonomic group.

1.2.1.2 DAPSTOM

Further data was sourced from Cefas' in-house database, DAPSTOM - an integrated database and portal for fish stomach records version 4.9 (Pinnegar, 2014a). DAPSTOM includes 226,407 records derived from 449 distinct research cruises, spanning the period 1837-2012. The database contains information from 254,202 individual predator stomachs and 188 predator species. As such, this represents one of the largest and most diverse compilations of marine food-web data anywhere in the world. DAPSTOM was recently re-engineered to make the database more compatible with the ICES year of the Stomach database (see Pinnegar, 2014b) and to include information on prey weights. For example, the many different formats of 'digestion stage' cited in the original sources were re-categorised according to the ICES nomenclature. Where prey weights were absent from the original data source, values have either been calculated using data already contained in the DAPSTOM database or obtained from the literature (see Pinnegar 2014b for further detail).

1.2.1.3 BENTHIS partners data

Stomach data were also provided by BENTHIS partners, Institute of Marine Resources and Ecosystem Studies (IMARES) Wageningen UR and Institute for Agricultural and Fisheries Research (ILVO). The IMARES data was collected in April, June and August-September 1996 using 8 m and 12 m beam trawls (see Rijnsdorp and Vingerhoed, 2001 for detailed methodology) across various parts of the North Sea. The ILVO data was collected using 4m beam trawls from within one ICES rectangle in 2013.

1.2.2 Selection of predator species

Demersal fish species with a diet comprising benthic invertebrates at some stage of their life history, and that were represented by a sufficient number of stomachs containing food, were selected for inclusion in the data analysis. From the ICES Year of the Stomach database 4 fish species were identified: haddock (*Melanogrammus aeglefinnus*), Atlantic cod (*Gadus morhua*), whiting (*Merlangius merlangus*), and long rough dab (*Hippoglossoides platessoides*). No information was available for other flat fish species within this database due to the nature of the survey. From the DAPSTOM database prey information was

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[2] http://ecosystemdata.ices.dk/stomachdata

extracted for haddock, cod, whiting, long rough dab, European plaice (*Pleuronectes platessa*), sole (*Solea solea*) and dab (*Limanda limanda*) over a 20 year period (1990-2010). The data from ILVO contained prey information from stomachs of European plaice, sole and dab, whilst the IMARES dataset comprised prey information from stomachs of sole and plaice. In total the stomach contents of 7 commercial fish species have been analysed in relation to their traits composition.

1.2.3 Stomach data manipulation

For the purposes of the BENTHIS project, only data from 1990 onwards were used so as to temporally align with both the ICES Year of the Stomach data and the infauna and epifaunal datasets used in BENTHIS deliverable D3.4. Stomach records identified as 'Pristine' were selected for analysis for cod, haddock and whiting as 'fresh' prey suggests the species were feeding within the area from which they were captured. This also increases the likelihood of prey identification to genus or even species level, although some of the smaller soft species are still likely to be quickly digested. However, all stomachs, regardless of digestion stage, were selected for analysis for the flatfish species (dab, plaice, long rough dab and sole) due to the paucity of stomach content data classified into the pristine category.

The number of stomachs containing food for each predator were summed according to predator size category (following the size categories used for the ICES year of the stomach project) and used to identify which size classes were in sufficient numbers for use in the traits analysis. Based on this information, three size categories were selected for each predator to represent small, medium and large examples of the species in question.

Prey items were classified into six groups: benthos, fish, cephalopods, pelagic invertebrates, meiofauna and other (fish parasites and foraminifera). The proportions of each prey group, according to abundance and biomass, were calculated to determine the importance of each group to the diet of the predators. All further analyses were conducted on the benthic prey.

The number of stomachs containing food and abundances of benthic prey within these stomachs were calculated and mapped according to ICES rectangle and predator (see Appendix C). This gives an indication on the spatial distribution and variability in numbers of stomachs collected for each predator, and highlights the differences in benthic prey items consumed compared to stomachs collected. It was not possible to calculate the numbers of stomachs containing benthic prey only as many of the samples were pooled.

1.2.4 Biological traits

The biological trait database, developed within BENTHIS deliverable D3.4, was utilised to assign trait scores, for each of the ten trait categories (Table 1), to the benthic prey species identified from the fish stomachs. Further research was undertaken to acquire traits of a few taxa absent from the database. See methods in D3.4.

Table 1: *Traits and trait categories used during BTA. The abbreviation for each trait category as used for presentation within the results section is given in brackets.*

Trait	Categories (infauna and epifauna)	Trait Definition and functional significance

Size range (mm)	≤ 10 (s10) 11 – 20 (s11-20) 21 – 100 (s21-100) 101 – 200 (s101-200) 200-500 (s200-500) >500 (s500)	Maximum recorded size of adult (as individuals or colonies). Implications for the movement of organic matter within the benthic system as large organisms hold organic matter (low turnover) within the system relative to small-bodied species (high turnover) (Pearson and Rosenberg, 1978).
Morphology	Soft (mSoft) Tunic (mTunic) Exoskeleton (mExo) Crustose (mCrus) Cushion (mCush) Stalked (mStal)	External characteristics of the taxon: mSoft are represented mainly by annelid worms, mTunic by tunicates, mExo represents chitinous (lower crustaceans) and calcareous-shelled (e.g. bivalve and gastropod molluscs, echinoderms, higher crustaceans). Crustose, cushion and stalked traits are shown by various sponges, hydroids and bryozoans.
Longevity (years)	<1 (l1) 1 – 2 (l1to2) 3 – 10 (l3to10) >10 (l10)	Maximum reported life span of the adult stage. Indicates the relative investment of energy in somatic rather than reproductive growth and the relative age of sexual maturity, i.e. a proxy for relative r- and k- strategy (Pearson and Rosenberg, 1978). Short-lived taxa (l1) include ostracods and small amphipods, while the molluscs *Buccinum* and *Arctica* represent some of the long-lived taxa.
Larval development strategy	Planktotrophic (ldPk) Lecithotrophic (ldLc) Direct (ldD)	Indicates the potential for dispersal of the larval stage prior to settlement from direct (no larval stage, e.g. cumaceans, tanaids), lecithotrophic (larvae with yolk sac, pelagic for short periods, e.g. terebellid worms) to planktotrophic (larvae feed and grow in water column, generally pelagic for several weeks, e.g. sponges, cnidarians). Affects ability to recover from disturbance with planktonic recruitment affording potentially faster recolonisation than lecithotrophic and direct development (Thrush and Whitlatch, 2001).
Egg development location	Asexual/fragmentation (edAsex) Eggs – pelagic (edSex_pel) Eggs – benthic (edSex_ben) Eggs – brooded (edSex_br)	Indicates dispersal via the egg stage and the potential susceptibility of eggs to damage from fishing. Benthic eggs (e.g., some eunicid worms) are generally more concentrated over smaller areas than eggs released into the pelagia (e.g., hesionid worms). Asexual reproduction allows the potential to increase numbers rapidly, particularly following disturbance. Brooding is widespread within the lower crustaceans (e.g., amphipods).

Living habit	Tube-dwelling (lhTube) Burrow-dwelling (lhBurrow) Free living (lhFree) Crevice/under stone (lhCrev) Epi/endo zoic/phytic (lhEpi) Attached to bed (lhAtt)	Indicates potential for the adult stage to evade, or to be exposed to, physical disturbance.). Various lhTube (e.g., serpulid worms), lhBurrow (some bivalve molluscs), lhCrevice (such as piddocks), lhFree (e.g. eumalacostracan crustaceans), lhEpi (e.g., bryozoans) and lhAtt (e.g., ascidians, bryozoans) taxa will vary in their acute reponses to trawling depending on this trait (in combination with those of other traits such as mobility and sediment position).
Sediment position	Surface (spSurf) 0 – 5 cm (spInf_0to5) 5 – 10 cm (spInf_6to10) >10 cm (spInf_10)	Typical living position in sediment profile. Organisms occupying surficial (e.g. mytilid molluscs, sponges) or shallow positions in the sediment (some bivalves) are more likely to contact trawl gear than those living deeper (e.g. some worms). Sediment position also has implications for the effect of the organism to affect sediment-water nutrient and/or oxygen exchange.
Feeding mode	Suspension (fSusp) Surface deposit (fSurf) Subsurface deposit (fSub) Scavenger (fScav) Predator (fPred)	Feeding mode has important implications for the potential for transfer of carbon between the sediment and water and within the sediment matrix. Feeding mode also has important repercussions for many biogeochemical processes (Rosenberg, 1995).
Mobility	Sessile (mobSess) Swim (mobSwim) Burrow (mobBur) Crawl (mobCrawl)	Adults of faster moving species are more likely to evade capture by trawl gear than slow-moving or sessile individuals. Mobility also affects the ability for adult recolonisation of disturbed areas.
Bioturbation	Diffusive mixer (bDiff) Surface deposition (bSurf) Upward conveyor (bUpward) Downw. conv.(bDownward) None (bNone)	Describes the ability of the organism to rework the sediments. Can either be upward (e.g. maldanid worms), downward (e.g. oweniid worms), onto the sediment (many suspension-feeders) or mixing of the sedimentary matrix (e.g. glyceriid worms). Bioturbation mode has important implications for sediment-water exchange and sediment biogeochemical properties.

1.2.5 Habitat composition and clustering

The habitat composition of each ICES rectangle sampled during the ICES Year of the Stomach 1991 project was determine using EUSeaMap 2012 modelled habitat map[3] (Figure 1). Twenty five main habitats classified to EUNIS level 3 or 4 are mapped in using ARC GIS 10.1 (ESRI). Seventeen further EUNIS habitats (currently unclassified within a EUNIS level) are not shown due to their low representation across the area.

For each ICES rectangle, information relative to the 42 EUNIS habitat-related parameters were used to reduce the number of habitat-related groups (henceforth called "habitat-cluster") into a more

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[3] http://jncc.defra.gov.uk/euseamap

manageable comprehensive number at a scale relevant to fisheries. To do so, the K-means partitioning techniques was used. This method is said divisive and non-hierarchical and is based on least-squares methods. It defines the partition of the ICES rectangle into k groups or cluster such that the ICES rectangle within each cluster are more similar to one another than to the other in the other clusters with respect to the 42 habitat-related parameters. This method was preferred since it is ideal when a “simple” reduction of information to a few groups is sought without any specific reference to gradients or hierarchy in the data. This method, however, requires the number of k groups to be defined *a priori* and tests for which number k the best fit is. Milligan & Cooper (1985) recommend maximising the Calinski-Harabasz criterion (classic F-statistic comparing the among-group to the within-group sum of squares of the partition). Here we tested from 2 to 10 partitions and a “best” compromise of 6 clusters was yielded by the analysis the characteristic of which can be found in Appendix D.

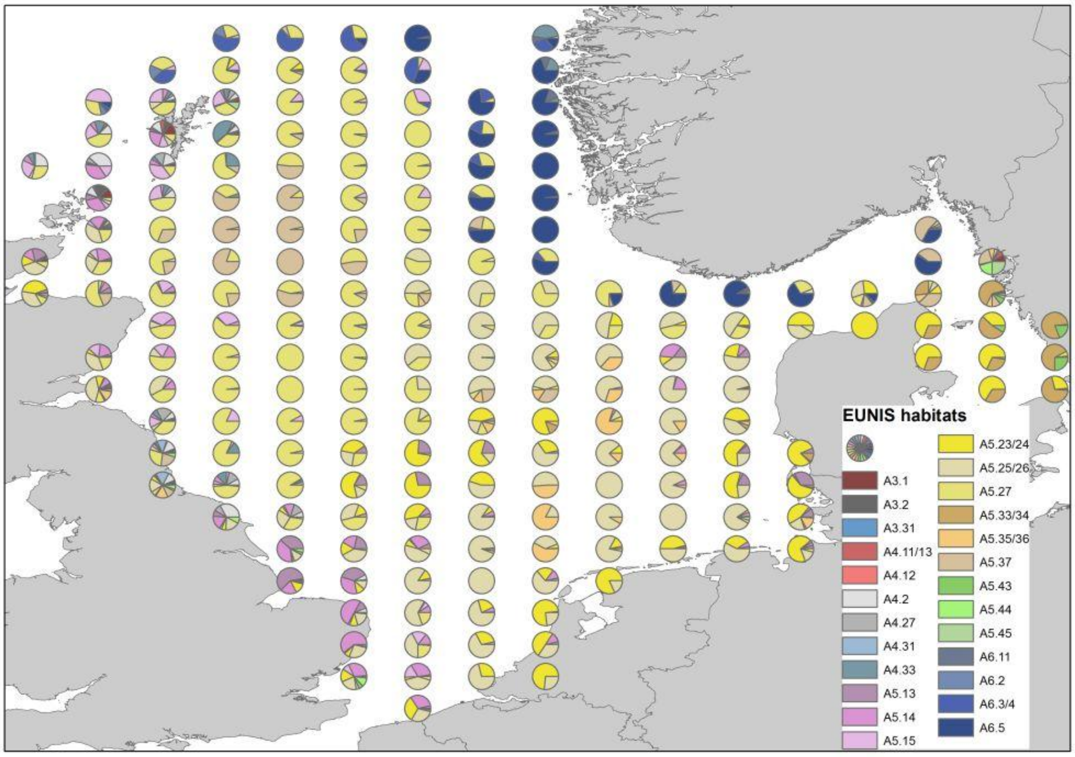


Figure 1. *Habitat composition for each ICES rectangle sampled as part of the ICES Year of the Stomach 1991 project. Habitat descriptions for corresponding main EUNIS habitat codes can be found in Appendix*

A description of each habitat cluster is provided in Table 2 below (full analysis is provided in Appendix D) and the spatial location of each cluster is shown in Figure 2.

Table 2. *Description of each of the six fishery relevant habitat clusters located in the North Sea, Skagerrak and Kattegat*

Habitat cluster	Habitat characteristics and location
1	Mainly comprises infralittoral fine and muddy sand (A5.23/A5.24), with smaller areas of circalittoral fine and muddy sands (A5.25/A5.26), infralittoral coarse sediment (A5.13) and infralittoral fine and sandy muds (A5.33/A5.34). Located across the Dogger Bank, coastal areas of the eastern North Sea and Skagerrak and in the Kattegat
2	Heterogeneous habitat cluster comprising circalittoral and deep sands A5.25/A5.26 and A5.27, along with areas of circalittoral and deep coarse sediments (A5.14 and A5.15). Patches of rock (A4.2) and fine/muddy sands are also present. Located in the coastal waters of the western North Sea, Orkney and Shetland, in isolated areas of the North Sea and in the Skagerrak and Kattegat.

3	Mainly comprises circalittoral fine and muddy sands (A2.25/A5.26) with smaller areas of infralittoral fine and muddy sands (A5.23/A5.24), mud (A5.35/A5.36) and coarse sediment (A5.14). Located across the southern North Sea, Central North Sea and German Bight
4	Deep sea muds (A6.5) and sands (A6.3/A6.4 and A5.27). Located in the Norwegian trench off the southern coast of Norway
5	Dominated by deep sandy sediments (A2.27). Located north of the Dogger bank in the western North Sea
6	Mainly comprises deep muds (A5.37) and to a lesser extent deep sands (A5.27). Located in the Fladen Ground of the northern North Sea and two ICES rectangles in the deeper waters of the Skagerrak.

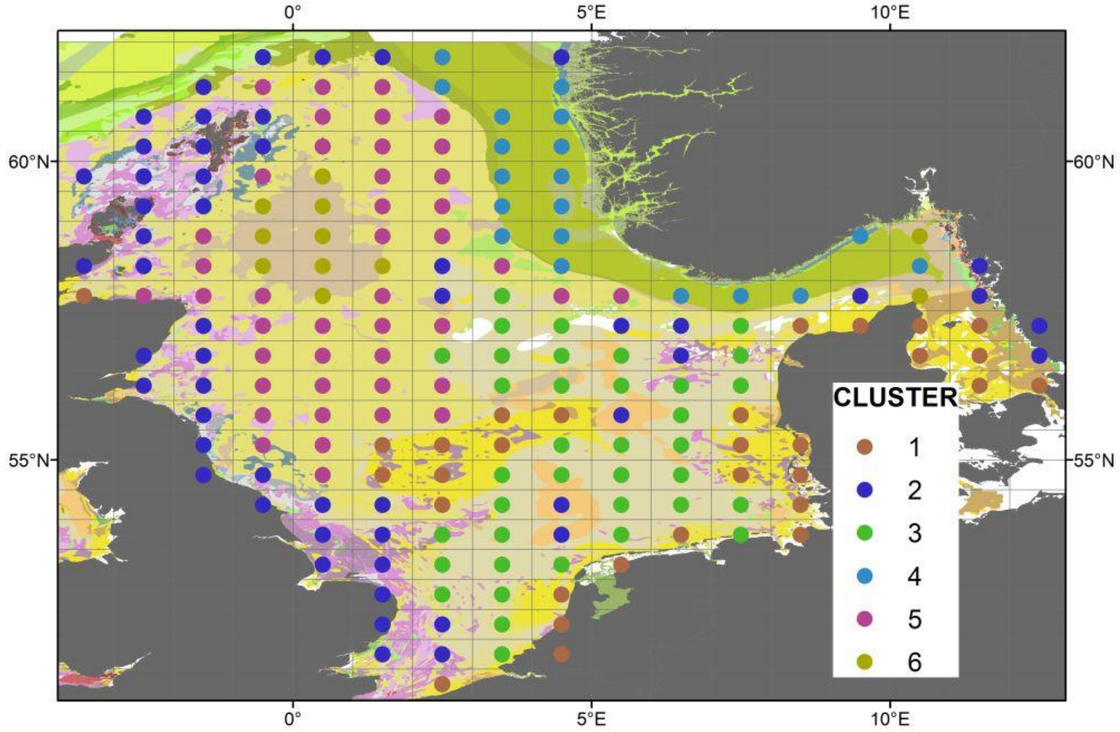


Figure 2. *Spatial location of the six (fishery habitat) clusters overlaid on EUSeaMap EUNIS habitat map for the North Sea.*

1.2.6 Defining trait composition of 'fished' and non-fished' prey assemblages

The outputs of work undertaken for BENTHIS deliverable D3.4 were used during the present study to determine the trait composition of the benthic assemblages that were deemed to represent an unfished (UF) situation and those that reflect some impact of fishing (F), e.g. fished situation. The benthic invertebrate data that were used as part of that assessment were analysed at the EUNIS level 4, and following their categorisation to UF or F, their locations were subsequently mapped and classed according to the relevant habitat clusters (see above) for the stomach content analyses.

To summarise the UF *vs* F categorisation procedure, the functional diversity metric FD (Petchey and Gaston, 2002) was first calculated for each sampled infaunal and epifaunal assemblage. The FD calculation was adapted from the initial community functional diversity calculation from Petchey & Gaston (2002), thus, in our analyses, stations are considered akin to species. We are, therefore, comparing FD values of "stations' traits composition" and not the FD that could be calculated using species/trait matrix in combination with station/species matrix as further developed in Petchey & Gaston (2006). One of the advantages of using this method in the present study is that this index is not influenced by species richness; which means here that the number of stations *per se* will not strongly influence the FD values.

The total fishing pressure of each station for which benthic trait data were available was estimated. Total fishing pressure ('FP' hereafter) was estimated using the methodology developed under BENTHIS WP2 (Eigaard et al., in press). Then, we calculated the FD value of the two stations with the lowest fishing pressure (FP) within each of the EUNIS habitats; this is considered as a first point of reference against which to compare the FD values calculated with the addition of the third station with the next lowest FP (i.e., FD calculated with three stations against FD calculated with two stations). This new value then became the second point of reference against which the FD value with the fourth station with the lowest FP could be compared. This procedure was repeated until all the stations from each EUNIS habitat were integrated.

Once all stations of the EUNIS habitat were included in this process, the differences between each successive point (each point being considered as a reference for the one immediately following) were calculated. This allowed us to characterise the extent of jumps in the FD values following the addition of each new station along a gradient of increasing fishing pressure. Each station was related to its respective fishing pressure (FP) and FD was plotted against an increasing FP gradient. Each point was then compared to the one immediately before, and, where the increase in FD was small, the trait composition of the newly added station was similar to those with lower FP. That is, the additional station was not functionally different from that of preceding stations. On the other hand, if the FD of the additional station was significantly higher compared to those of the preceding stations, it inferred that its trait composition was significantly different and therefore provided an indication of a change in benthic function with respect to a given fishing pressure for a specific habitat type.

The differences in FD values generally followed a normal distribution. The critical limits between small and high values (i.e. when does a difference in FD value result in a significant difference in function) were consequently established using the accepted higher threshold of outliers in such a distribution (Quantile 3 + 1.5 x IQR (Inter Quantile Range)). Following an increasing FP gradient, any point (station) above this threshold could therefore be considered as an abrupt and important deviation from the previous trait composition, namely the threshold at which there is a discernible impact on habitat function resulting from FP.

Once the critical FD difference value was defined (y-axis threshold), the final step was to determine which of these critical values can be considered to be due to fishing pressure (x-axis threshold). Indeed, other factors may change the trait composition, and therefore the FD difference values, irrespective of any fishing effects. To partially account for this, the thresholds at 0 FP were ignored, assuming that these functional changes were due to "natural or other anthropogenic" effects. This allowed us to define a UF *vs* F threshold for the EUNIS habitats. As mentioned above, these stations were then subsequently classed according to their locations with respect to the six habitat groups adopted for the present fish stomach content analyses.

The calculation of the functional diversity was done using the code written by Petchey O., freely available here http://www.thetrophiclink.org/resources/calculating-fd/ using the Xtree function written by Schumacher J.

1.2.7 Data analysis

All analyses were preformed using R (R Core Team, 2014). The primary analytical approach applied is a two-way presentation of cluster analysis results in the form of a heatmap. Heatmaps display a pair-wise visualisation of two dendrograms one for the rows and one for the columns, it then assigns colours to each point that reflect the strength of the link between the initial raw data (rows and columns) ranging from white (weak link) to red (strong link). For both side of the heatmap, the dissimilarity matrix has been computed using Euclidian distance and the clustering was performed following the Ward methods which is known to produce meaningful results from distances that are Euclidean or not (Borcard et al. 2011).

The following R packages were used within this report:
ade4 (v 1.7-2)
dplyr (v 0.4.3)
tidyr (v 0.3.1)
ggplot2 (v 1.0.1)
gplots (2.17.0)
vegan (v 2.3-1)

1.2.8 Production and diversity of prey assemblages

Data pertaining to the infaunal abundance, diversity and secondary production for the study area was restricted to the English region of the North Sea only. These stations corresponded to four of the six habitat clusters; no data were available, therefore, for habitat clusters 4 and 6. The infaunal data were acquired and compiled for a previous project (Defra-funded ME5301), but were used for the current fish stomach content analyses study to provide some context regarding how such infaunal metrics vary within and between habitat cluster groups.

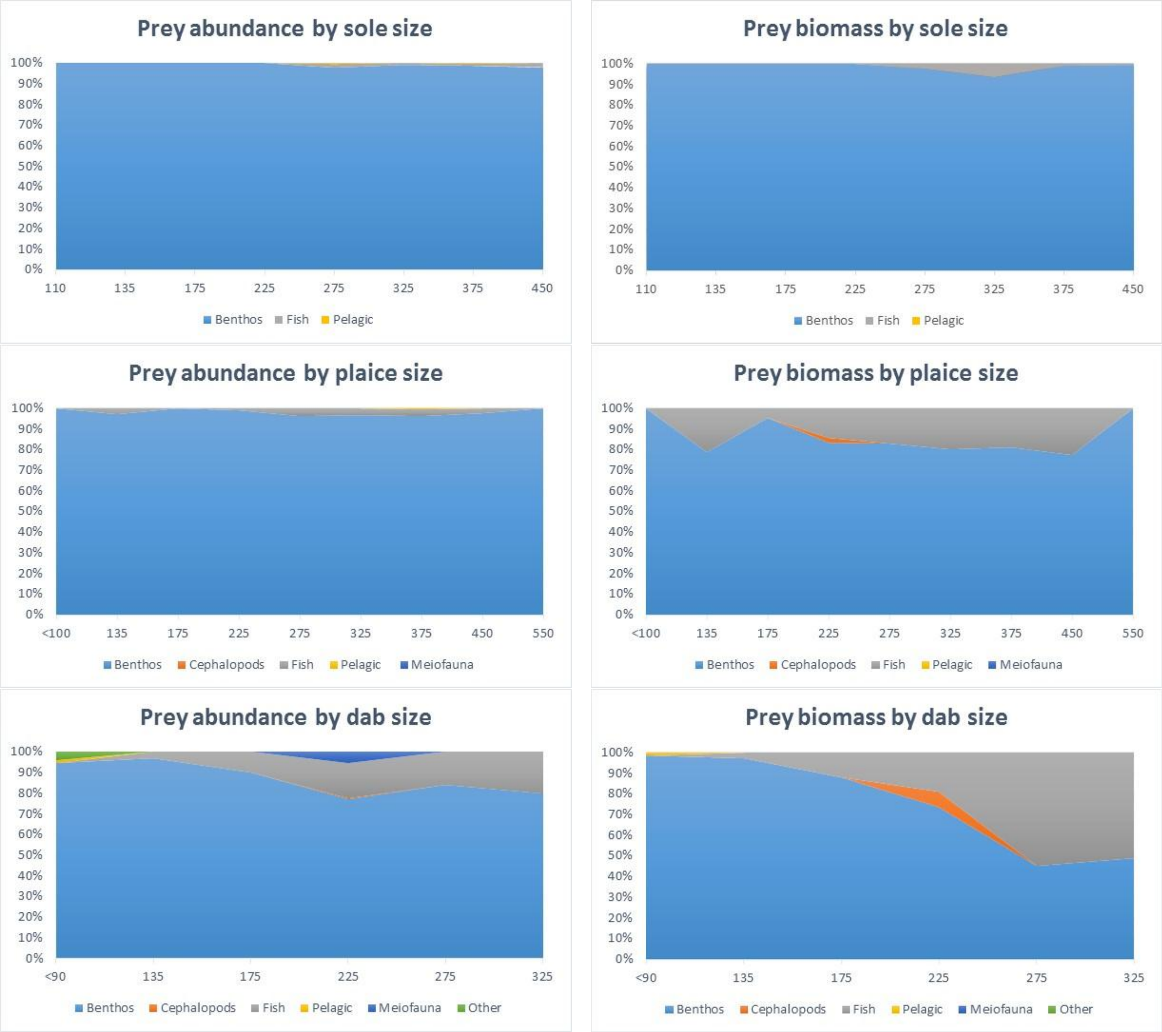
Infaunal abundance and biomass data from which diversity and secondary production were estimated were obtained for 189 stations located in the English part of the North Sea. Samples were collected between 2000 and 2010 using a 0.1m^2 Hamon or Day grab, and all processed using a 1 mm mesh sieve (see Bolam et al., 2014, for further details on methods). Following processing, the abundance data were aggregated to genus level. This reduced problems due to misidentification at the species level and helped standardise the taxonomic resolution across the various surveys which comprised the final dataset. Abundance and Shannon-Weiner diversity (H’) were calculated for each sample and later averaged for each habitat cluster. Variability in these metrics for each of the habitat clusters was determined by calculating the 95% confidence interval.

Total secondary production estimates (kJ m^2 y^1) were derived in a stepwise approach from the abundance and biomass data following the methods described by Bolam et al. (2010; 2011). In summary, the standardised biomass data were initially converted to energy values using published conversion factors. For taxa with shells, biomass data were initially converted to shell-free weights to derive estimates for the metabolically active tissue of such taxa. Data were aggregated to the Family level of taxonomic resolution; it is generally at this level that sufficient numbers of published conversions are available for most taxon, i.e., taking an average conversion factor from a larger number of studies resulted in increased confidence in the conversions ultimately applied (T. Brey; pers. comm.). Energy values were then converted to production values using a spreadsheet freely available on the Internet http://www.thomas-brey.de/science/virtualhandbook/navlog/index.html (Brey, 2001). This method unifies all previous habitat-specific approaches into a multiple regression model estimating annual production of macrobenthos. The Brey model was found to be one of the most reliable and robust models available during a critical appraisal of such methods (Cusson and Bourget, 2005; Dolbeth et al., 2005).

1.3 Results

1.3.1 Diet composition of predators

The importance of benthic fauna in the diet preferences of the seven fish species studied varied considerably, both between predators and according to size class within a predator species (Figure 3). Sole and plaice exhibited closest links to the seabed, feeding almost exclusively on benthic prey throughout their lives. Conversely, cod and whiting’s reliance on the benthos quickly changes to a piscivorous diet as the animals grow. Perhaps surprisingly, the benthic diet of Long Rough Dab comprises less than 70%, which reduces further with increasing size of predator. Over half the prey biomass consumed by Long Rough Dab are fish. Equally benthic biomass consumed by dab appears to decrease and proportion of fish prey increase within increasing size of predator. Haddock also becomes less dependent on benthic prey items with increasing age, although benthic biomass does not reduce beyond 30% of the total diet.



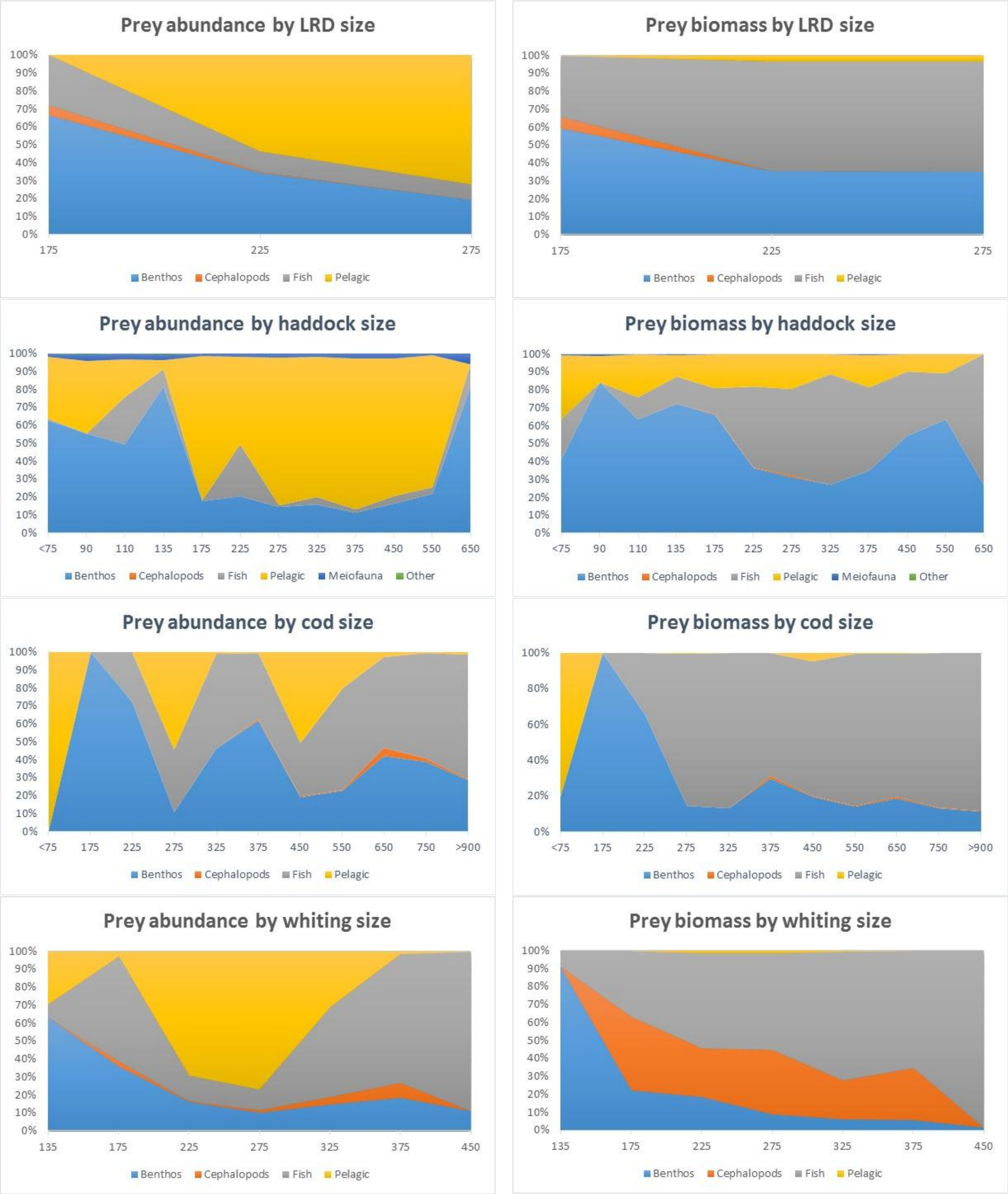


Figure 3. *Diet composition of the seven fish predators by size class analysed in this study according to abundance and biomass of prey item types.*

1.3.2 Trait composition of benthic prey consumed according to predator and size class

Clustering of all prey traits (weighted by abundance) by predator size resulted in three distinctive groups (Figure 4a). All sizes of long rough dab and cod, medium and large sole and medium whiting showed similar prey preferences, targeting small-medium, surface living organisms with a lifespan of 3 - 10 years and which brood their eggs and produce planktotrophic larvae. Within this group, medium and large long rough dab showed stronger preferences for suspension feeders, crawling prey and those that produce pelagic eggs compared to small long rough dab and the other predators. All plaice, regardless of size, showed preferences for prey that were non-mobile, suspension feeding, small – medium size, living in the top layers of the sediment and which produced planktonic eggs and larvae. Within the final group prey selection was less targeted with haddock expressing no clear prey preferences.

Prey traits weighted by biomass clustered into four distinctive groups (Figure 4b). Sole and plaice clustered together due to dominance in their diet of non-mobile, small-medium subsurface feeding prey, living within the surface layers of the sediment. Prey biomass was also dominated by species which produce planktonic eggs and larvae. Prey biomass of whiting, cod and small long rough dab was dominated by small–medium sized predatory prey species which brood their eggs, produce planktotrophic larvae and live for 3 - 10 years. Prey biomass from haddock stomachs was again not dominated by any particular trait modality, whilst benthic prey biomass in the stomachs dab and medium and large long rough dab was dominated by surface crawlers, prey that live 3 - 10 years and have planktotrophic larvae.

1.3.3 Variability in trait composition of prey according to habitat type

To determine whether the patterns in prey trait preference were similar across the different habitat types, where the fish where presumed to be feeding, the prey trait composition from the stomachs of each fish (weighted by abundance and biomass) was determined for each habitat cluster (Figure 5). Whilst some fish species (cod, haddock, whiting and long rough dab) were sampled across the majority of ICES rectangles in the North Sea, the stomach data collected from flatfish species (sole plaice and dab) were mainly collected from the southern part of the North Sea. This may in part reflect the distribution of these species, although the data sources may bias sampling effort and distribution to some extent. Subsequently the benthic prey from flatfish stomachs are restricted to fewer habitat clusters (see Appendix C). Abundance of benthic prey items representing the clusters for each species are also shown in Appendix C and highlight significant variability both within a species and across habitats. This is taken into consideration when interpreting the following results.

Prey selected by cod, haddock, whiting and long rough dab express similar traits and the results are fairly consistent in terms of the dominant prey they consume across the different habitat types: free-living, surface dwellers, which produce planktotrophic larvae and live for 3 - 10 years. Exceptions to this are for haddock, which appear to be less specific (i.e. target a wide range of prey items) in the prey they consume in habitat cluster 6 and whiting which target additional prey traits in habitat cluster 5.

Prey selection by plaice, sole and dab show some trait differences according to habitat cluster and whether the traits are weighted by abundance or biomass. Abundance of prey items consumed by sole in habitat cluster 3 are dominated by free-living, surface dwellers, prey capable of swimming, have an exoskeleton, live for 3 – 10 years and produce planktotrophic larvae. However biomass consumed by sole within this habitat cluster are distributed across a wider range of traits suggesting the most abundant prey are relatively small. Conversely, the relative abundance of prey items consumed by sole in habitat clusters 1 and 2 are spread across a wide range of traits whilst prey biomass is dominated by non- mobile, small-medium, tube-dwellers, prey that live 6 - 10 cm in the sediment and rework sediment using an upwards conveyor-belt movement.

Plaice feeding in habitat clusters 1 and 3 (eastern North Sea) consume higher proportions of infaunal prey which live up to 10 centimetres in the sediment than in clusters 2 and 5 (western North Sea). Plaice from habitat cluster 1 also consume higher relative abundances of surface deposit feeding prey, prey that burrow and bioturbate the sediment by diffusive mixing and consume lower proportions of surface living prey and prey with exoskeletons compared to the other habitats. Prey traits (according to biomass) targeted by plaice in habitat cluster 1 are the same as that for sole.

Prey items from dab stomachs were only in high enough abundances within habitat clusters 1-3 to be representative of prey traits targeted. Similar traits were targeted in these three habitats when weighted by abundance. However, prey biomass from habitat cluster 3 comprised higher proportions of medium sized prey living 0-5 cm in the sediment and prey that release eggs into the water column in comparison to the other habitats. This may be an artefact of reduced spatial coverage within this habitat as it was only represented by stomachs from one ICES rectangle.

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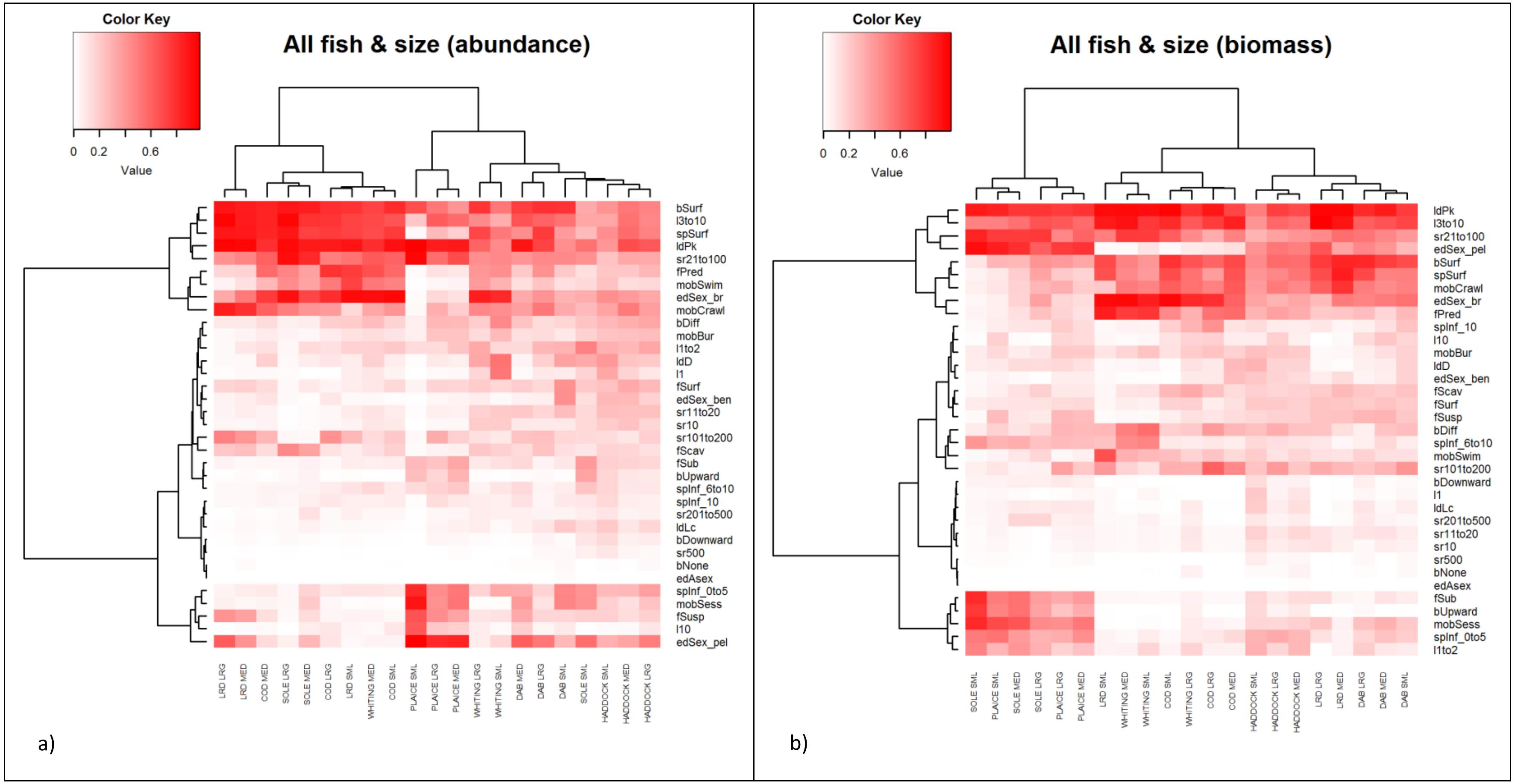
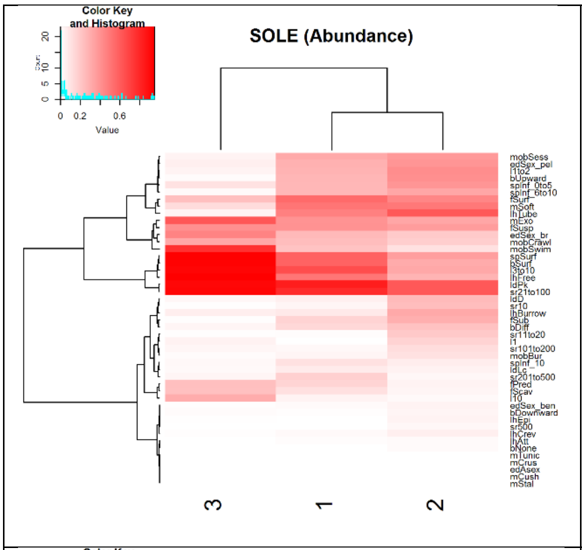


Figure 4. *Trait composition of benthic prey items consumed according to size of predator: weighted by a) abundance and b) biomass*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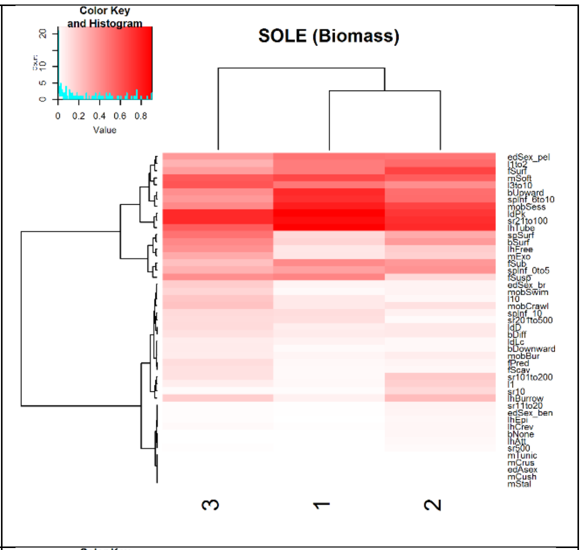
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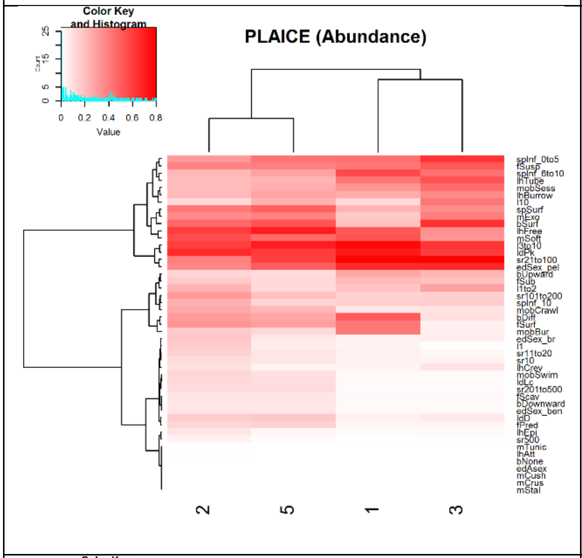
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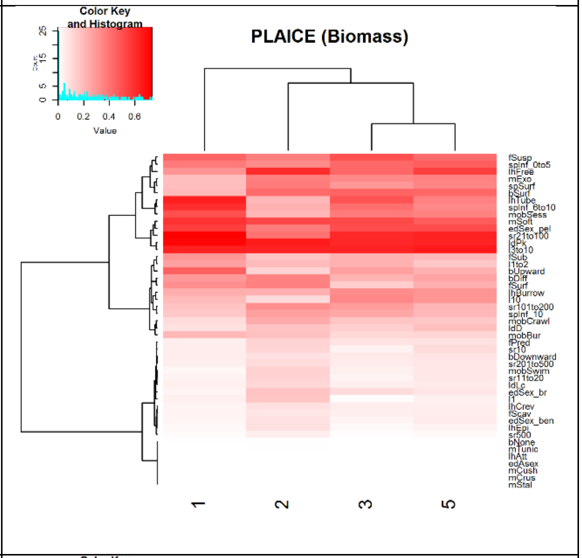
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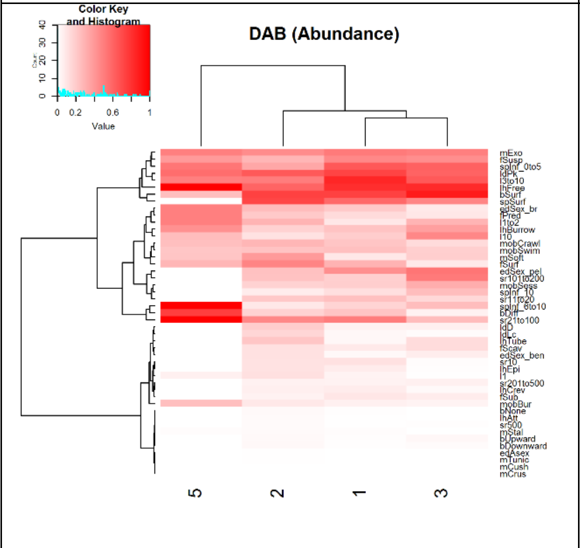
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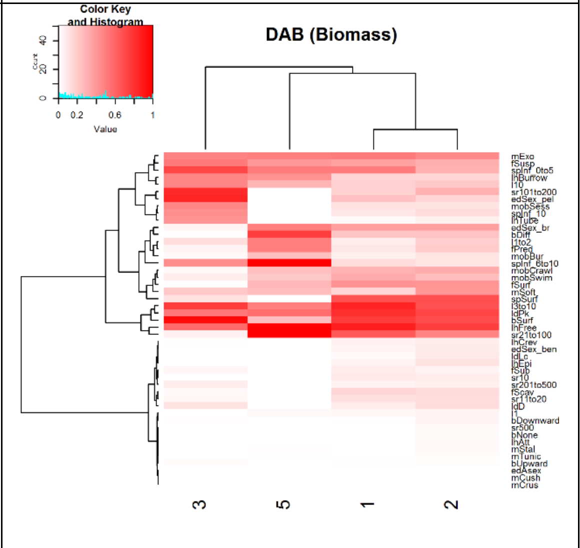
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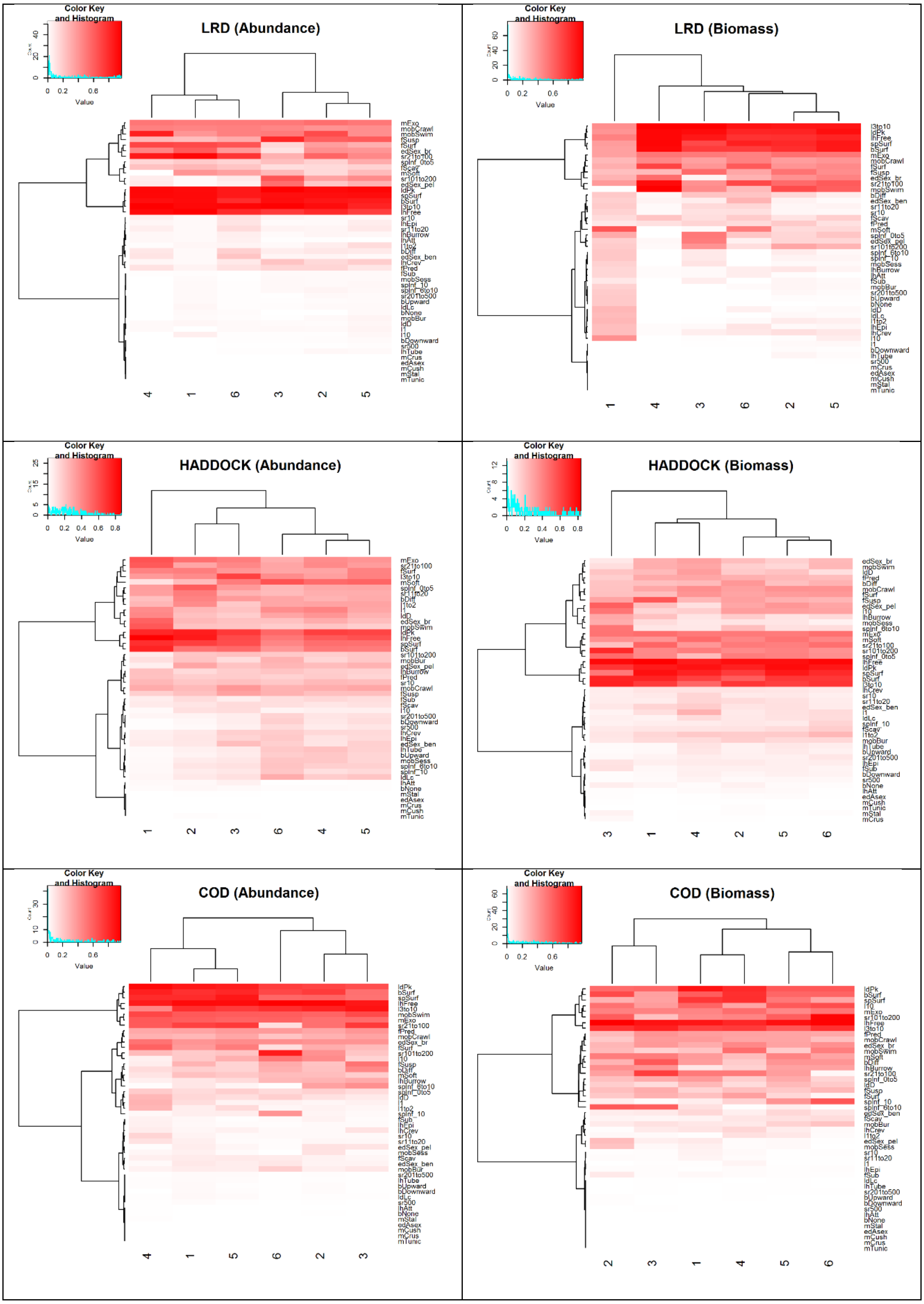
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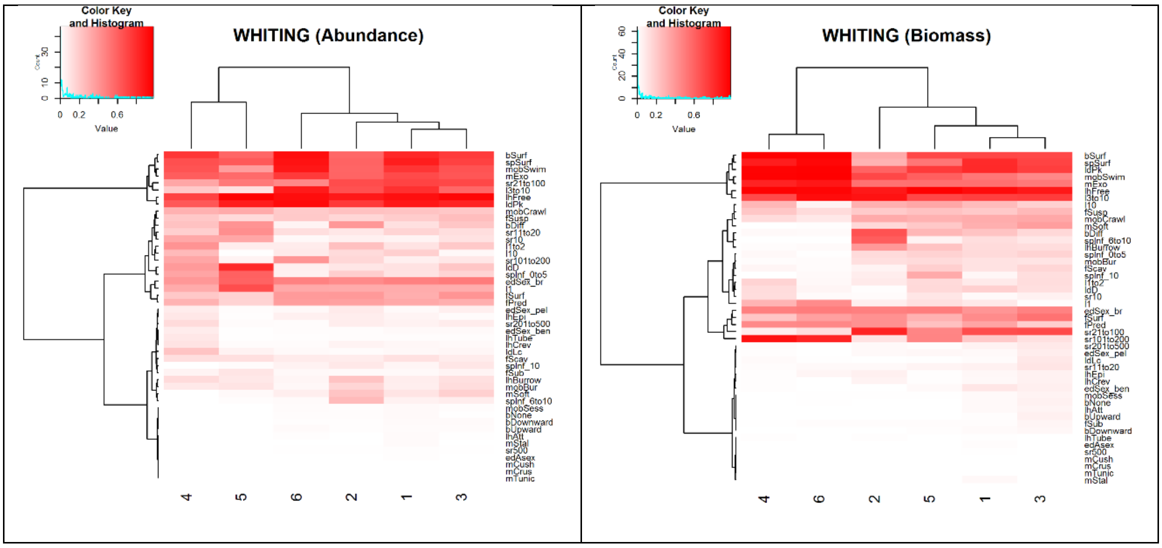

Figure 5. *Trait composition (weighted by (left) abundance and (right) biomass) of benthic prey items consumed according to predator and habitat cluster*

1.3.4 Comparison of prey availability in the environment versus prey selection by fish predators

The relative composition of benthic infaunal and epifaunal traits available in the environment under fished and unfished conditions were compared with benthic prey traits identified from the fish stomachs. Benthic prey from all predators were combined for this analysis and grouped according to their corresponding habitat cluster. Benthic infaunal and epifaunal samples were also grouped according to habitat cluster and identified as representing a fished or unfished state (only fished communities were represented in habitat clusters 4 and 6 for both the infauna and epifauna). The number of trait categories were reduced to eight to allow direct comparison between patterns seen in the infauna versus those seen in the epifauna.

Trait composition of prey targeted versus infauna available in the environment show similar patterns for 2 habitats. Prey consumed within habitat cluster 1 express a similar overall trait composition to the infaunal communities under fished conditions in this habitat cluster. Conversely prey consumed within habitat cluster 3 display similar trait characteristics to the unfished communities present within habitat cluster 3 (Figure 6).

Analysis of epifaunal data (Figure 7), it is evident that prey consumed from habitat clusters 2, 4, 5 and 6 do not exhibit dominance in any trait, suggesting nonselective feeding on the benthos occurring in these habitats. Although clustering separately from the other habitats, prey taken from habitat clusters 1 and 3 share more similarities in trait composition with prey taken from the other habitats than to epifauna available in the environment.

The associations between prey available in habitat clusters 1 and 3 and the prey consumed by fish predators feeding in those habitats are explored in further detail in Figures 8 and 9. Figure 8 shows that all sizes of plaice feed on similar traits that are abundant in habitat cluster 1 under fished conditions, and that medium sole feed on prey freely available in unfished conditions. All other predators feeding within habitat cluster 1 appear to feed on prey that are less abundant in the environment e.g. organisms which live on the sediment surface, which brood their eggs, are predators themselves and are capable of swimming or crawling.

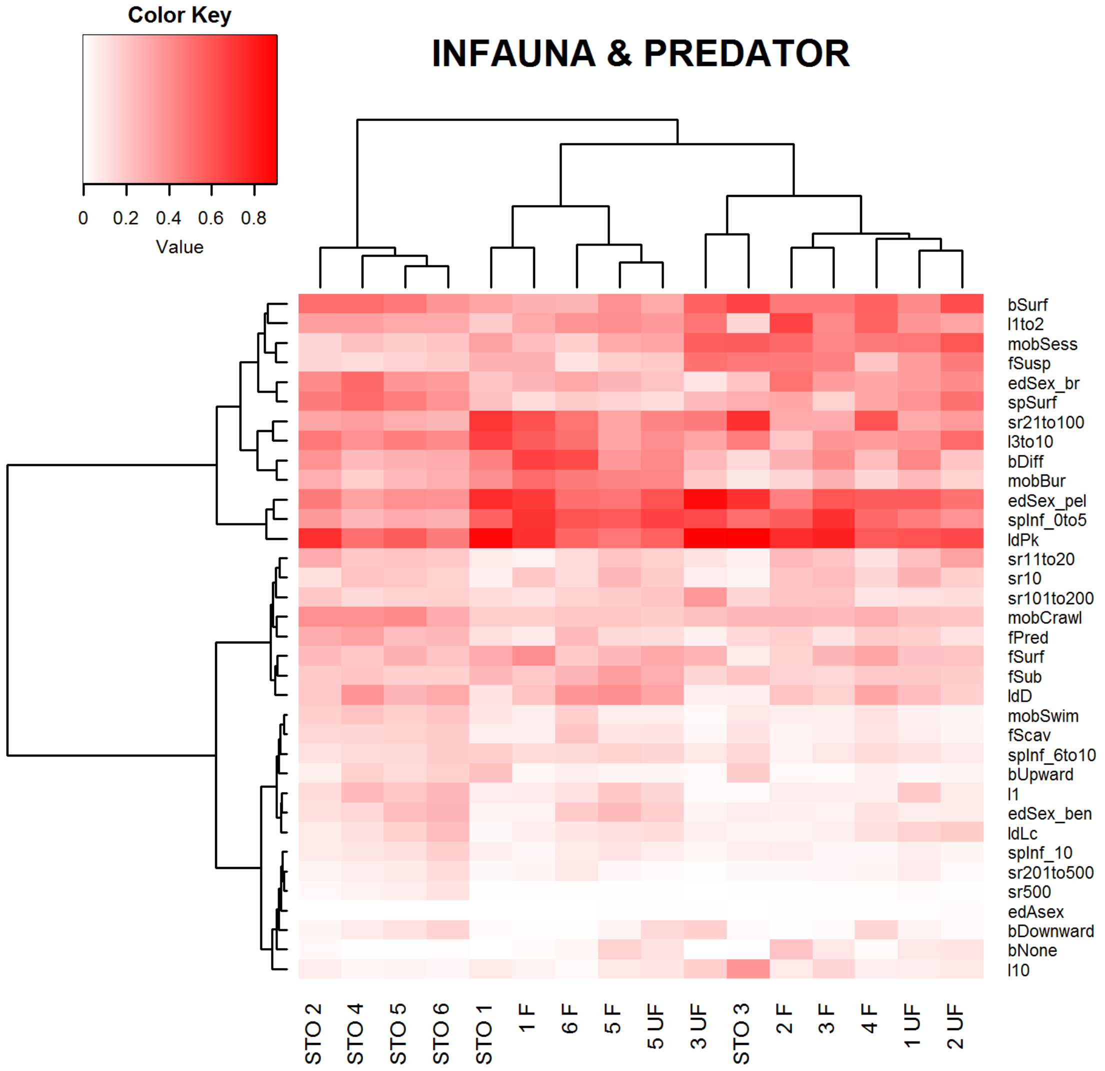

Figure 6. *Trait composition (weighted by abundance) of benthic prey items from stomachs (STO) of all predators combined for each habitat cluster (1-6) and trait composition of available infaunal prey in each habitat cluster under fished (F) and unfished (UF) conditions*

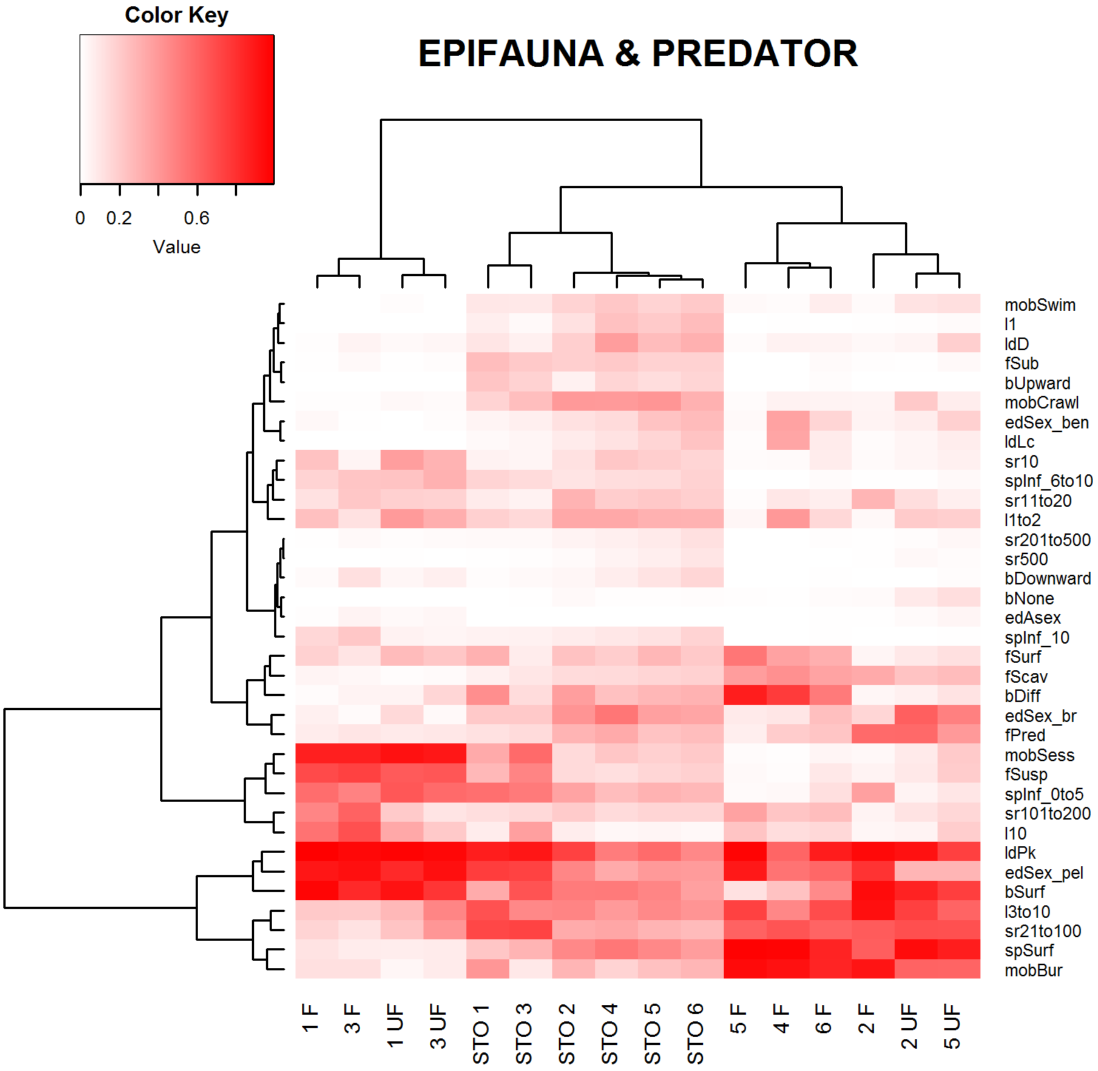

Figure 7. *Trait composition (weighted by abundance) of benthic prey items from stomachs (STO) of all predators combined for each habitat cluster (1-6) and trait composition of available epifaunal prey in each habitat cluster under fished (F) and unfished (UF) conditions.*

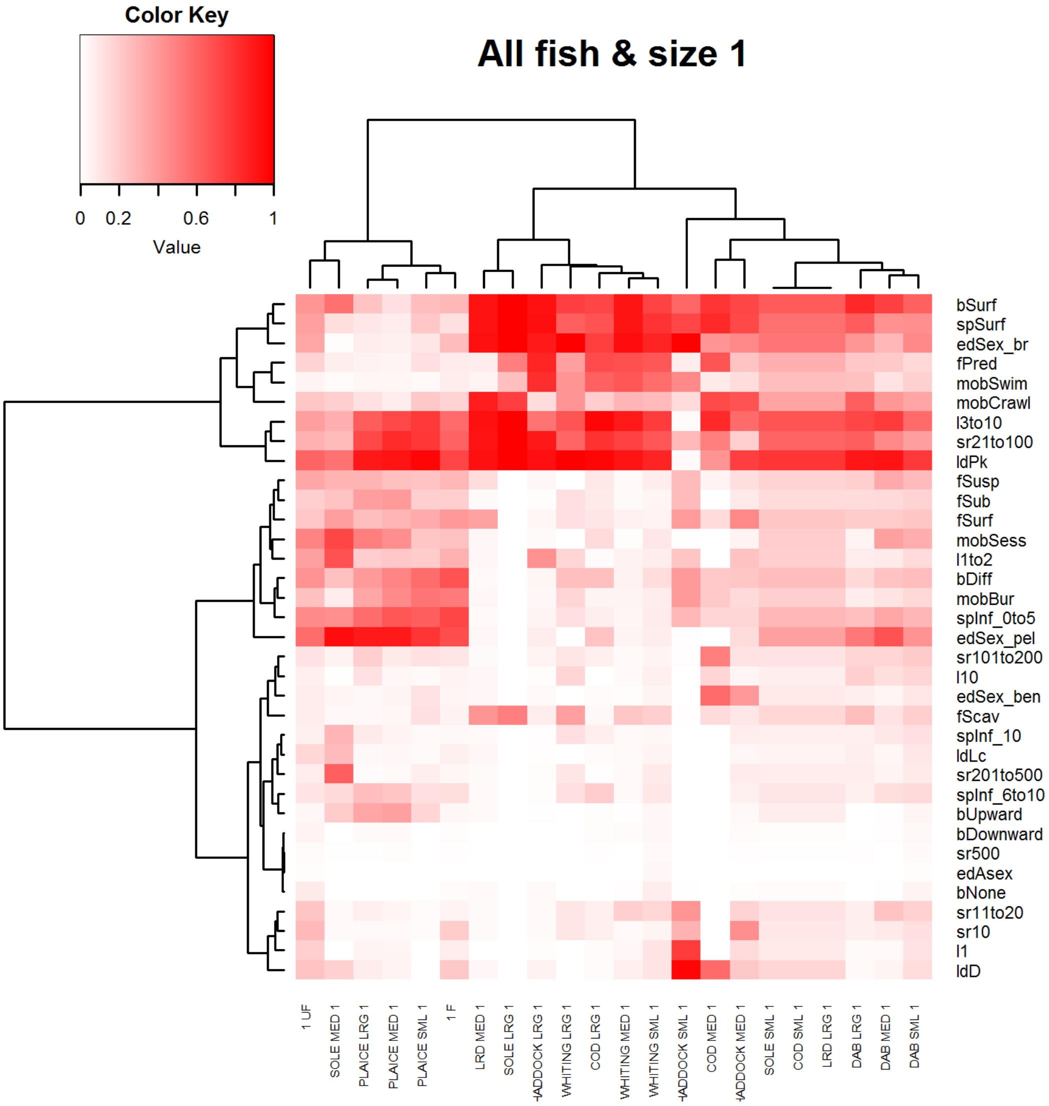

Figure 8. *Heatmap of the trait composition of all fish predators (by size) and prey available in the environment (under fished and unfished conditions) for habitat cluster 1*

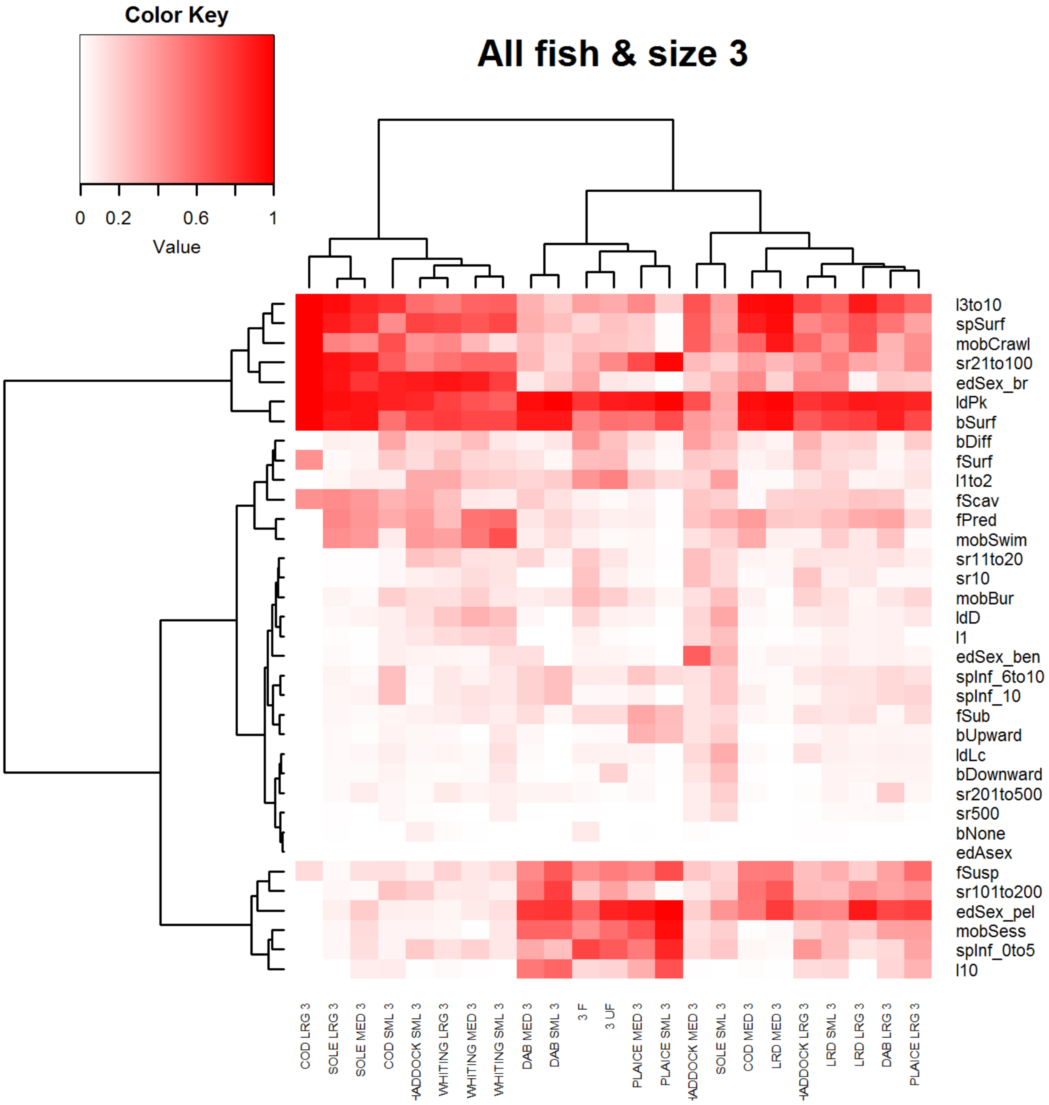

Figure 9. *Heatmap of the trait composition of all fish predators (by size) and prey available in the environment (under fished and unfished conditions) for habitat cluster 3*

In habitat cluster 3 (Figure 9) small and medium dab and plaice feed on prey which are abundant under both fished and unfished conditions. All other predators again appear to feed more selectively on less abundant organisms present within this habitat.

1.3.5 Production and diversity of prey assemblages

The historic benthic infaunal data collated from the English region of the North Sea (summarised in Table 3) indicated that there are some differences in the mean values of benthic infaunal community metrics between the four habitat cluster groups, together with differences in their secondary production estimates. Specifically, the infaunal assemblages of habitat cluster 3 are less densely populated while the diversity of those in cluster 5 is significantly higher. Although the mean values of secondary production vary between the habitat clusters, with those in cluster 1 being higher, such estimates displayed high variability within clusters resulting in low power to detect significant differences. Annelids contributed the greatest to secondary production in all habitats, with the remaining production being governed more-or-less equally by molluscs, echinoderms and crustaceans for each habitat cluster.

Table 3: Summary of total abundance and diversity, together with secondary production estimated of the historical infaunal data for the English region of the North Sea. Data are averaged (with 95% confident intervals) according to their locations across the habitat clusters. Numbers in brackets in the first column depict the numbers of infaunal stations for each habitat cluster

Habitat cluster	Total abundance	Diversity (H')	Total secondary production kJ m-2 y-1	% Total production by major phyla				
				Annelids	Molluscs	Echinoderms	Crustaceans	Miscell.
1 (61)	960.8 ± 225.1	2.3 ± 0.1	71.1 ± 23.9	46.9 ± 6.1	18.5 ± 5.3	13.8 ± 5.3	13.2 ± 4.8	7.7 ± 4.4
2 (70)	1140.8 ± 261.0	2.3 ± 0.2	57.9 ± 15.7	60.7 ± 5.6	13.4 ± 4.0	9.8 ± 4.2	10.7 ± 3.1	5.4 ± 2.9
3 (20)	436.1 ± 30.8	1.8 ± 1.1	49.9 ± 15.1	51.1 ± 7.9	14.2 ± 7.4	23.0 ± 11.4	10.1 ± 6.0	1.6 ± 7.7
5 (38)	1342.4 ± 285.1	2.6 ± 0.1	53.8 ± 14.4	61.8 ± 6.9	14.6 ± 5.7	10.8 ± 3.8	6.1 ± 3.1	6.6 ± 3.3

1.4 Discussion

Trawling activity is thought to influence the prey available to demersal fish in two ways; through the mortality of larger fragile benthos which is then consumed opportunistically and by reducing biomass, size and species richness of the benthic community resulting in increases in secondary productivity (Shephard et al, 2014). We analysed the benthic diet, via analysis of stomach content, of seven demersal and benthivorous fish predators using a biological trait approach to gain insight into their feeding preferences compared with benthic prey availability in the environment under fished and unfished conditions. The fish species ranged from those that feed almost exclusively on the benthos (e.g. benthivorous fish; sole, plaice and dab) to those which have a more varied diet composed of both benthic and hyperbenthic prey (e.g. demersal fish, long rough dab, haddock, cod, whiting). We found strong associations between community trait composition and prey consumed by plaice under fished conditions for a shallow sand – muddy sand habitat located in the eastern North Sea and Dogger Bank (habitat cluster 1). Plaice fed on a higher proportion small-medium sized infaunal burrowers and also deeper dwelling (living 6-10cm in the sediment) infaunal species in this habitat in comparison to other habitats. In terms of biomass, plaice (and sole) ingested a greater proportion of organisms living 6 - 10 centimetres in the sediment in this habitat compared to those ingested from the surface layers. Previous research (Hiddink et al., 2011; Johnson et al., 2015) found that plaice condition was negatively affected by fishing in the Irish Sea. They found that plaice were feeding on larger, but less energy-rich bivalves that live deeper in the sediment and as a consequence increased energy expenditure in foraging for this prey, resulting in poorer fish condition. Although the location of this habitat in the eastern North Sea corresponds to an area closed to demersal trawling, known as the 'plaice box', no infaunal data was available from this area to confirm whether it was representative of a fished or unfished assemblage type.

Long rough dab, haddock, cod and whiting did not appear to target fauna that was abundant in the environment within any of the habitat clusters under fished or unfished conditions. These species may therefore be less affected by fishing pressure than species living in closer association with the benthic environment.

Secondary productivity was found to be highest within habitat cluster 1 although not significantly so. Bolam et al., 2010 and 2014 indicated that production is indeed affected by bottom disturbance, but as that affects substrate type it is not possible to know whether this is a direct or indirect relationship with fishing pressure.

2 BENTHIC ECOSYSTEM FUNCTIONAL FOOD WEB MODEL

2.1 Introduction

It has long been acknowledged that bottom trawl gears have side-effects on non-target organisms, including benthic invertebrates (de Groot 1984). In fact, the effects of trawling have been compared to clearcutting a forest in some ecosystems (Watling and Norse 1998). Bottom trawls can cause the resuspension of nutrients and organic material into the water column (Riemann and Hoffmann 1991, Grant et al. 1997, Pilskaln et al. 1998), modify seabed habitats (Dayton et al. 1995, Watling and Norse 1998, Kaiser et al. 2002, Puig et al. 2012), and impose mortality on benthic invertebrate organisms that are not retained by the net (Collie et al. 2000, Kaiser et al. 2006). Bottom trawls can cause a decline in the number and biomass of large, sessile and low productive benthic organisms, as these are often most vulnerable to the direct passing of trawl gears and have slowest recovery rates. Short-lived, opportunistic benthic species, typically scavengers/predators, are less vulnerable or able to recover more rapidly, and therefore such species usually dominate areas that are trawled frequently (Kaiser et al. 2006). Intensively trawled areas are generally less species rich (e.g. Collie et al. (2000), Hiddink et al. (2006), Hinz et al. (2009), Thrush et al. (1998)) and are altered in their functional composition (Tillin et al. 2006, de Juan et al. 2007, Kenchington et al. 2007). The fact that frequent trawling may lead to trawl-induced shifts in the benthic community and influence the food availability for benthivorous fish can result in changes to the benthivorous fish diet compared with untrawled sites (Smith et al. 2013, Johnson et al. 2014, Rijnsdorp and Vingerhoed 2001). Such changes could potentially affect both growth rates and body condition of benthivorous fish compared with fish that feed in areas where benthic species have not been disturbed by trawling.

Changes in growth rates due to trawl impact were first suggested by Rijnsdorp and Van Beek (1991) who observed growth rate increases in different age-classes of plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the North Sea from the 1960s. The changes in growth rates were only partly explained through density-dependent processes and coincided with increased bottom-trawl disturbance and eutrophication (Millner and Whiting 1996, Rijnsdorp and van Leeuwen 1996). A positive relationship between growth rates of plaice and trawling intensity was also observed in the Celtic Sea in sandy habitat (Shephard et al. 2010). This study also showed a negative effect of trawling on fish growth rates in gravelly habitat, potentially reflecting dietary differences between habitats and/or habitat-specific impacts of bottom trawls. Furthermore, changes in fish body condition in relation to trawl impact were first suggested by Choi et al., (2004) who observed a reduction in groundfish condition at the eastern Scotian Shelf off Novia Scotia from the 1970s onwards. This was thought to be caused by the large depletions of groundfish prey through removals of fish and benthos biomass by fisheries. A negative relationship between fish body condition and trawling intensity was more systematically shown by Hiddink et al. (2011) in the Irish Sea. In this study, it was found that adult plaice body condition was reduced at increased trawling intensity, while effects of trawling on dab and whiting (*Merlangius merlangus*) condition were not detected. The decline in plaice condition was explained through a shift towards energy-poor prey and a potential decline in plaice foraging efficiency due to lower prey densities at the trawled sites (Johnson et al. 2014).

Despite these indications of trawling-induced shifts within the benthic food, and trawling-mediated effects on fish food availability, few studies have investigated the effects of trawling on benthic food webs. In a recent study, van Denderen et al. (2013) showed how the combination of primary effects of trawling (removal of fish), the side-effects of trawling (removal of benthos), the predation of fish on benthos and the competitive interactions between different benthos types interact to shape the net response of benthos to trawling. Their model however assumes only two types of benthos, which differ only in their trawling sensitivity and availability as prey items for fish. Here, we derive and analyse a similar system, but with more functional differentiation in the benthic food web in the form of 3 groups of consumers: scavenger/predators, filter feeders and deposit feeders. These are general guilds that are present in most, if not all, benthic ecosystems. This functional benthic food web is preyed on by two fish groups, small and large fish.

The three groups of benthic invertebrates interact through competition and predation (Figure 10). Filter feeders feed on plankton suspended in the water column, which also precipitates onto the seabed at a fixed rate where it becomes available to the deposit feeders. When this rate is low, deposit feeders get little of the resource which stays mostly available for the filter feeders. In contrast, when this rate is high, the planktonic resource is transferred quickly to resource which the deposit feeders can utilise, which creates indirect competition between the two groups. In addition, food may become available for deposit feeders through faecal pellets produced by the filter feeders. Through this pathway filter feeders may support deposit feeder secondary production. Scavengers feed on the juveniles of both filter and deposit feeders, and small fish feed on small individuals of all benthic invertebrate groups, while large fish feed on all benthic invertebrates.

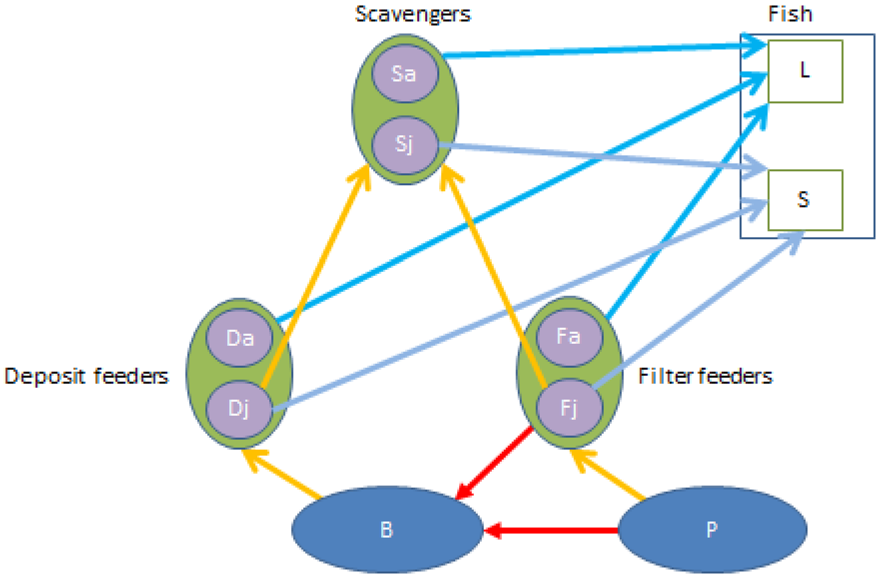

Figure 10. *Schematic representation of the benthic ecosystem food web model. Orange arrows indicate foraging by the benthic groups. Red arrows indicate the degradation and resuspension of the resource. Blue arrows indicate foraging by fish. Da (adult deposit feeders), Fj (juvenile filter feeders), P(plankton or pelagic carbon resource), B(benthic or sea-bed carbon resource), L (large fish), S (small fish).*

Benthic food webs consist of many species, spanning a wide range of forms and functions. Not only does each local or regional benthic ecosystem consist of many species, there is also large difference in species composition between locations and in areas with varying abiotic conditions.

This diversity of life forms is an important aspect of the benthic ecosystem, and is the focus of many scientific publications. However, a focus on complexity can implicitly lead to observing differences between individual species, systems, locations, rather than on finding the underlying causal processes. As a result, a focus on complexity can prevent the development of a fundamental understanding of the essential processes driving benthic ecosystems. In this work, we explicitly look for the underlying processes, which can be used to generate testable hypotheses about the impact of eutrophication, climate change, fisheries and other anthropogenic disturbances.

The food web model is based on the major modes of resource acquisition employed by benthic invertebrate taxa. We choose this criterion because it leads to a system (food web) describing the major flows of mass and energy through the ecosystem, which are the common currency of many ecosystem goods and services. In appendix A, we explore the variation in traits within each feeding group in the data, in order to assess to what extent the data supports our assumption of homogeneity within each feeding group.

Here we study the basic dynamics of this model at increasing primary productivity and discuss how it relates to general principles of food web theory.

2.2 Methods

We use the stage-structured biomass model framework (De Roos et al. 2008) to model the benthic food web. The model consists of 3 groups of benthos, filter feeders (*F*), deposit feeders (*D*) and scavenger/predators (*S*). Each of these functional groups is modelled as 2 separate life stages (juveniles *j* and adults *a*), because these engage in different ecological interactions (Figure 10).

2.2.1 Resource dynamics

The model contains a phytoplankton resource (*P*), used by the filter feeders. This resource also precipitates onto the seafloor, where it is added to the benthic resource (*B*) and becomes available for the deposit feeders.

Phytoplankton (*P*) follows semi-chemostat dynamics and has a loss term based on deposition on the seabed (Figure 10). The phytoplankton resource is hence described by

$$\frac{dP}{dt} = r(P_m - P) - pP - C_P$$

Where r is the resource renewal rate and P_m is the maximum resource abundance in absence of consumption and precipitation. We use semi-chemostat resource dynamics rather than the more common logistic growth, because we consider that only the near-bottom fraction of the water mass is available for phytoplankton consumption by filter feeders, whereas the bulk of phytoplankton production occurs in the upper water layers and reaches the *P* compartment by water mixing and particles sinking. Hence, phytoplankton production is positive even when $P=0$. Phytoplankton precipitates to the seabed at constant rate p, and consumption by filter feeders is given by C_p.

Benthic resource *B* increases by deposition of phytoplankton *P* and production of pseudofaeces by filter feeders (f), and decreases by deposit feeder consumption (C_B), microbial respiration (at rate l) and loss to biologically inactive deep sediments (at rate q):

$$\frac{dB}{dt} = pP + f - qB - lB - C_B$$

2.2.2 Consumer and predator dynamics

The key aspects of the structured biomass community framework are the equations for biomass accumulation governing growth and reproduction, and the equation for maturation. The biomass accumulation is based on the net biomass from feeding

$$\nu_i = \sigma I_i - T_i$$

(where *i* ∈ {D_j, D_a, F_j, F_a, S_j, S_a}). Here I_i is the mass-specific intake rate and T_i is the mass-specific maintenance rate, and σ is the conversion efficiency of resource to consumer biomass. Transfer is juvenile to adult biomass through maturation (*γ*) is governed by

$$\gamma_k = \frac{\nu_{k_j} - \mu_{k_j}}{\left(1 - z_k^{\,1-\frac{\mu_{k_j}}{\nu_{k_j}}}\right)}$$

(where *k* ∈ {*D, F, S*}). This function is derived in such a way that it corresponds exactly to a model with continuous size structure under equilibrium dynamics, and approximates it otherwise (De Roos et al. 2008). Maturation is a function of *v*, the net biomass production rate, the mortality rate *μ*, and *z*, which is the ratio between the size at birth and the size at maturation.

The equation for *v* and *γ* above are the basis of the dynamics of filter feeders (F_j and F_a), deposit feeders (D_j and D_a) and scavenger/predators (S_j and S_a), where the index indicates the juvenile (*j*) or adult (*a*) stage:

$$\frac{dD_j}{dt} = \nu^+_{D_a}(I_{D_a})D_a + \nu_{D_s}(I_{D_s})D_s - \gamma^+_{D_s}(I_{D_s})D_s - \mu_{D_j}D_j$$

$$\frac{dD_a}{dt} = \gamma^+_{D_s}(I_{D_s})D_s + \nu_{D_a}(I_{D_a})D_a - \nu^+_{D_a}(I_{D_a})D_a - \mu_{D_a}D_a$$

$$\frac{dF_j}{dt} = \nu^+_{F_a}(I_{F_a})F_a + \nu_{F_s}(I_{F_s})F_s - \gamma^+_{F_s}(I_{F_s})F_s - \mu_{F_j}F_j$$

$$\frac{dF_a}{dt} = \gamma^+_{F_s}(I_{F_s})F_s + \nu_{F_a}(I_{F_a})F_a - \nu^+_{F_a}(I_{F_a})F_a - \mu_{F_a}F_a$$

$$\frac{dS_j}{dt} = \nu^+_{S_a}(I_{S_a})S_a + \nu_{S_s}(I_{S_s})S_s - \gamma^+_{S_s}(I_{S_s})S_s - \mu_{S_j}S_j$$

$$\frac{dS_a}{dt} = \gamma^+_{S_s}(I_{S_s})S_s + \nu_{S_a}(I_{S_a})S_a - \nu^+_{S_a}(I_{S_a})S_a - \mu_{S_a}S_a$$

In these equations, the terms superscripted by '+' indicate the value lies within the interval [0,∞], e.g. $\nu^+_{S_a} = \max(0, \nu_{S_a})$. This is necessary to ensure that biomass flow from juveniles to adults by maturation and from adults to juveniles by reproduction does not reverse under adverse food conditions. Rather than resorb juveniles by unrealistic 'inverted reproduction', the adult stages lose biomass under starvation. Finally, dynamics are determined by the mortality rates *μ*. Under sufficient food, adults are assumed to convert all biomass gains into offspring, and do not grow.

2.2.3 Ingestion, consumption, mortality and facilitation

The feeding relationships between the groups in the model are summarized in Figure 10. All consumption (except that by fish) follows a type II functional response, with full complementarity of resources (*sensu* Tilman and Sterner (1984)). Intake rates for each consumer group in the model are limited by their biomass specific maximum intake rate *M* and half-saturation constant *H*. Filter feeders and deposit feeders feed only on a single resource compartment, and hence their intake is given by:

$$I_{D_j} = M_{D_j}\frac{B}{H+B},\ \ I_{D_a} = M_{D_a}\frac{B}{H+B},\ \ I_{F_j} = M_{F_j}\frac{P}{H+P} \text{ and } I_{F_a} = M_{F_a}\frac{P}{H+P}.$$

Consequently, the grazing of resources *P* and *B* is given by:

$$C_P = I_{F_j}F_j + I_{F_a}F_a \text{ and } C_B = I_{D_j}D_j + I_{D_a}D_a$$

respectively. Scavengers feed on juvenile filter feeders and deposit feeders, and hence their intake is given by:

$$I_{S_j} = M_{S_j}\frac{F_j+D_j}{H+F_j+D_j} \text{ and } I_{S_a} = M_{S_a}\frac{F_j+D_j}{H+F_j+D_j}$$

for juveniles and adults, respectively.

Mortality of filter feeders, deposit feeders and scavengers consists of a constant stage-specific background mortality, and predation mortality from fish. Furthermore, juvenile filter feeders and deposit feeders also suffer mortality from predation by scavengers.

We model fish as a generalist predator that forages elsewhere when the modelled prey abundance is low (with a type III functional response), and whose maximum abundance (N_s^m and N_l^m) is constant.

Small fish N_s feed on the juvenile stages S_j, D_j *and* F_j, while large fish N_l feed on both the adult and juvenile stages. Consumption of filter feeders, deposit feeders and scavengers by fish hence follows:

$$C_m = N_s M_{N_s}\frac{m}{H+(F_j+D_j+S_j)^2} + N_l M_{N_l}\frac{m}{H+(F_j+D_j+S_j+F_a+D_a+S_a)^2}$$

with $m \in \{D_j, F_j, S_j\}$, for the juvenile filter feeders, deposit feeders and scavengers. Fish maximum intake rate is M and half-saturation density is H. Adults are only prey for large fish, so that the consumption equation simplifies to:

$$C_n = N_l M_{N_l}\frac{n}{H+(F_j+D_j+S_j+F_a+D_a+S_a)^2}$$

with $n \in \{D_a, F_a, S_a\}$.

We can now derive total mortality. For the juvenile filter feeders and deposit feeders this equals:

$$\mu_{D_j} = \eta_{D_j} + M_{S_j}\frac{S_j}{H+F_j+D_j} + M_{S_a}\frac{S_a}{H+F_j+D_j} - C_{D_j}$$

and

$$\mu_{F_j} = \eta_{F_j} + M_{S_j}\frac{S_j}{H+F_j+D_j} + M_{S_a}\frac{S_a}{H+F_j+D_j} - C_{F_j}$$

where η is a stage-specific constant background mortality rate, Q is the stage-specific relative vulnerability to fishing of which E denotes the intensity. The next 2 terms are the predation mortality imposed by juvenile and adult scavengers, and finally the consumption by fish. For the other consumer groups, mortality is simpler and equals:

$$\mu_u = \eta_u + C_u$$

(where $u \in \{D_a, F_a, S_j, S_a\}$).

We further assume a facilitative effect f of filter feeders on benthic resource B, through the production of (pseudo-) faeces. The rate at which this process occurs depends on the consumption rate of the phytoplankton resource and is given by:

$$f = \varepsilon(1-\sigma)C_P.$$

It is hence modelled as a constant fraction ε of the unassimilated consumption ($1-\sigma$) of the phytoplankton resource P (C_p) by filter feeders.

Parameter values are presented in Table 4. Because we model biomass in each model compartment, rather than number of individuals, all rate parameters (those with units t^{-1}) are mass-specific. The functional groups in our model should be interpreted as 'typical members' of the group they represent. This has important consequences for the parameterization. Rather than referring to species-specific values, we use averages for a large number of species, and allometric scaling laws to derive representative parameter values.

Per unit biomass values for maximum intake *M* and maintenance rate *T* are assumed inversely proportional to the quarter power of adult body mass (for which we use body mass at maturation), and we assume further that mass-specific maintenance is generally in the order of 10% of the mass-specific maximum intake rate (Peters and Wassenberg 1983, Yodzis and Innes 1992, Gillooly et al. 2001) Hence, we assume that:

$$M = W_{mat}^{-0.25} \text{ and } T = 0.1\, W_{mat}^{-0.25}.$$

We use an extensive data set of benthic invertebrates from the Dutch Continental Shelf area in the North Sea to derive the average weight (*W*) of individuals in each benthic functional group (*F, D and S).* By combining these samples with a biological trait database (Bolam et al. 2014), in particular with the trait 'maximum size', we can estimate the average size for each of the benthos functional groups in the model (Appendix B). Similarly, we use trait information on longevity to calculate group-specific values for the background mortality (η). Values are listed in Table 4.

Table 4. *Parameters and their values.*

parameter	Default value	Units	Explanation
E	varied	/day	Fishing intensity
P_m	Varied	g/V	Maximum phytoplankton biomass density
R	0.1	/day	Turn-over rate P
N_s^m, N_l^m	0.1	g	Fish maximum abundance
W_d	8	g	Individual body-mass at maturation deposit feeders
W_f	6	g	Individual body-mass at maturation filter feeders
W_s	37	g	Individual body-mass at maturation scavengers
p	0.5	/day	Deposition of P to B
q	0.5	/day	Loss from B to deep sediment
l	0.1	-	Loss from B through Bacterial respiration
η_{D_j}, η_{D_a}	3.70E-03	/day	Background mortality deposit feeders
η_{F_j}, η_{F_a}	3.2E-03	/day	Background mortality filter feeders
η_{S_j}, η_{S_a}	4.2E-03	/day	Background mortality scavengers
ε	0.5	-	Fraction non-assimilated filter feeding transported to B
z	0.01	-	mass at birth: mass at maturation

2.3 Results

2.3.1 Filter feeders and deposit feeders only

Studying the food web with only filter feeders and deposit feeders shows they can coexist. Only at low values of the carrying capacity P_m one or the other goes extinct (Figure 11). Which of the two goes extinct depends on the rates of deposition from phytoplankton to detritus and the faecal deposition rate (Figure 11). When there is sufficient resource for both filter feeders and deposit feeders they coexist. Which species can sustain the lowest P_m values depends on the deposition rate of phytoplankton to detritus (Figure 11, top row). The negative effect of filter feeders on the resource availability for deposit feeders is shown by a decrease in the slope of deposit feeder equilibrium biomass with increasing P_m (Figure 11, left column). Without faecal deposition by filter feeders, deposit feeders cannot enter a system with a low deposition rate (*p*) from phytoplankton to detritus (Figure 11, lower right panel). In this case filter feeders exclude the deposit feeders by reducing the phytoplankton to low levels and thereby minimizing the available energy in the benthic carbon resource.

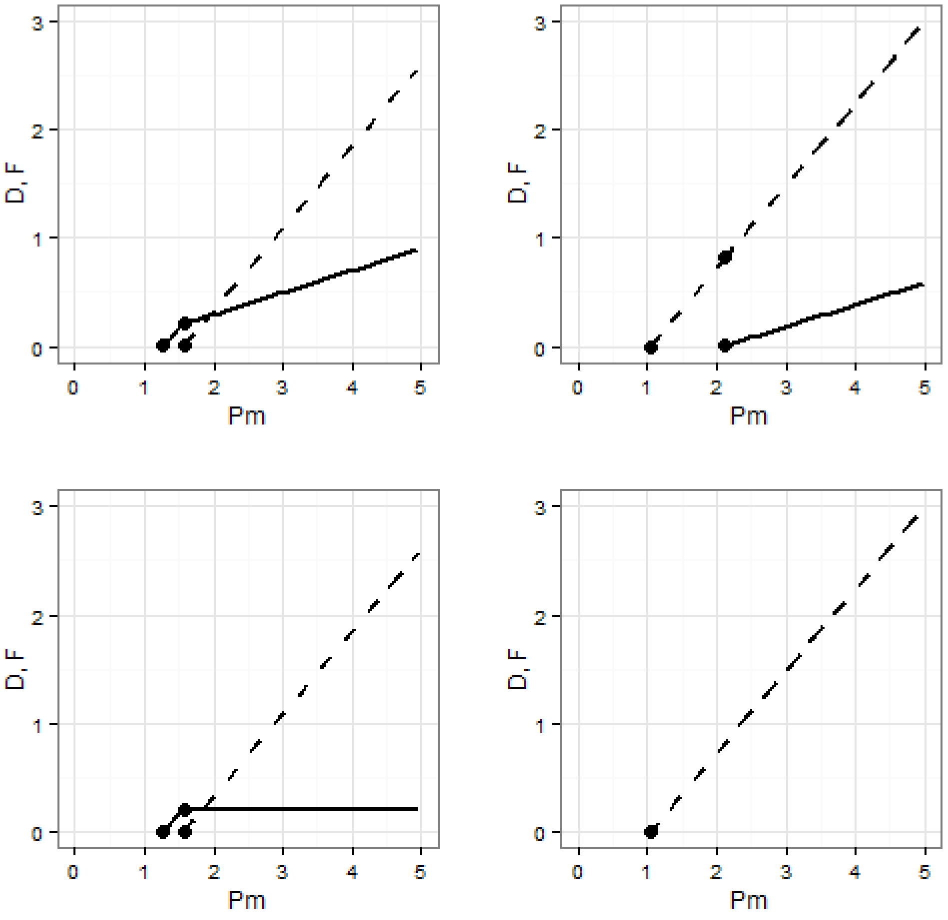

***Figure 11**. Equilibrium population biomass of deposit feeders (solid) and filter feeders (dashed) for different values of p, the infiltration from resource P (eaten by filter feeders) to resource B (eaten by deposit feeders), first row ε =0.5 and second row ε =0; left column p=0.5 and right column p = 0.3. A dot denotes the point of one of the populations entering the system with increasing P_m. Note that scavengers are not present in this system.*

2.3.2 Scavengers, filter feeders and deposit feeders

Scavengers can enter the food web for higher values of P_m when prey abundance is high, following the theory of a linear food chain (Oksanen et al. 1981) (Figure 12). A further increase of P_m results in an increase of scavengers and filter feeders, but a decrease in deposit feeders. This decrease in deposit feeders is due to the fact that they are second in line when it comes to resources and therefore depend on what is not eaten by the filter feeders. The filter feeders are the first to have access to the increasing productivity, and are able to graze down the phytoplankton to a constant minimum level. The increased maximum carrying capacity of the resource results in an increase in filter feeder biomass and not in an increase in detritus. The increase in filter feeder biomass enhances biomass of the scavengers feeding on them. The increase in scavengers increases the predation rate, which for the deposit feeders is not compensated for by a higher food availability. As a result, deposit feeders decrease and eventually are excluded from the system with increasing productivity (Figure 12). After the exclusion of deposit feeders and with further increased values of P_m the equilibrium with scavengers and filter feeders is essentially a linear food chain.

The scope for coexistence of all three groups increases at higher values of p, the rate of deposition of phytoplankton on the seabed, as that promotes the persistence of deposit feeders at high values of P_m (not shown). When the inflow to the detritus resource is too low and deposit feeders cannot enter a system with filter feeders (Figure 11, bottom right), the presence of scavengers does not facilitate persistence, because lack of persistence is the result of insufficient primary productivity (not shown).

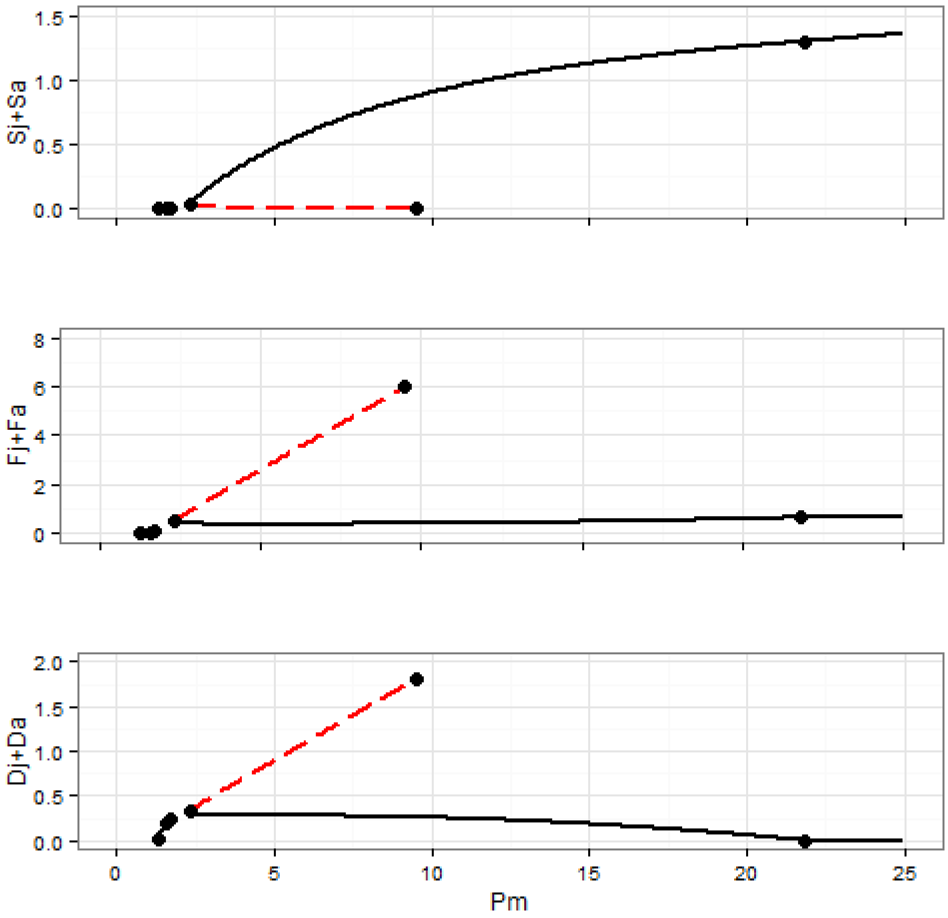

***Figure 12**. Equilibrium total population biomass of scavengers, filter feeders and deposit feeders as function of P_m with pseudo-faeces production (ε = 0.5). The red lines denote the unstable equilibrium for which all three groups coexist. The black lines denote stable equilibria. The dots denote the points at which one or more populations go extinct.*

2.3.3 The role of faecal pellets

When filter feeders produce faecal pellets it is assumed that these add to the resource available to deposit feeders. The production of pseudo-faeces by filter feeders increases the scope for coexistence, and without it deposit feeders are lost already at lower productivity P_m (compare Figure 12 and Figure 13). The scope for coexistence of all three groups is larger at higher faecal deposition and reduced at lower faecal deposition, which can be described in a parameter graph where the extinction point at the opposite sides of the stable equilibrium are plotted (Figure 14). The dashed line represents the point where deposit feeders are excluded from the food web at high values of P_m, and the parameter area of coexistence increases with increasing pseudo faeces availability (ε). The point where the equilibrium collapses at low values of P_m is marginally influenced by the faecal production availability for deposit feeders (Figure 14, solid line).

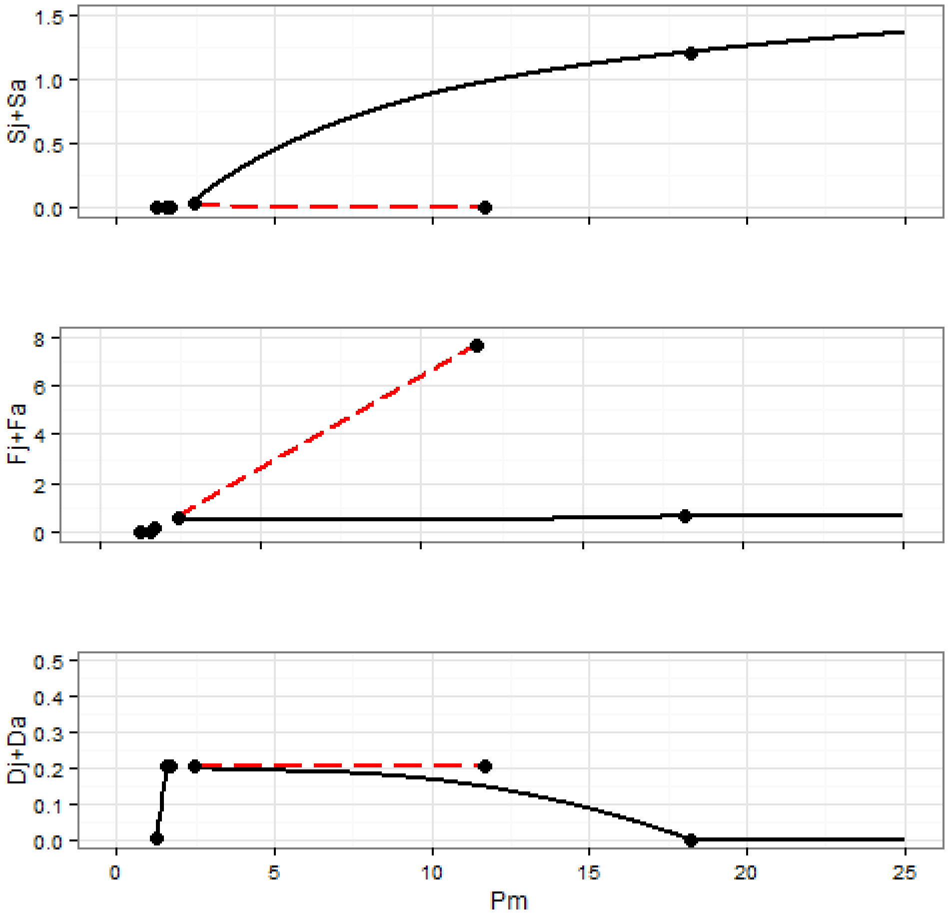

Figure 13. *Equilibrium total population biomass of scavengers, filter feeders and deposit feeders as function of* P_m *when there is no pseudo-faeces production (ε = 0.0). The red lines denote the unstable equilibrium for which all three groups coexist. The black lines denotes stable equilibria. The dots denote the points at which one or more populations go extinct.*

2.3.4 With fish

When fish are added to the system they impose mortality on all stages of the three groups of benthos. The fish are not dynamically modelled, but are considered a constant predation factor. This implies that an increased abundance of a competitor does not promote fish biomass and thereby predation. On the contrary, given the assumption that fish feed on each prey in proportion to their abundance, and they have a limited feeding capacity, the presence of more competitors implies a decrease in fish predation. Including fish into the system therefore promotes persistence of all three groups (Figure 15). The mechanism of apparent competition where an increase in P_m results in more scavenger predation on deposit feeders through the increase of filter feeder biomass (Figure 12) is no longer dominating the dynamics. With fish the deposit feeders are not excluded by enhanced scavenger predation with increased productivity.

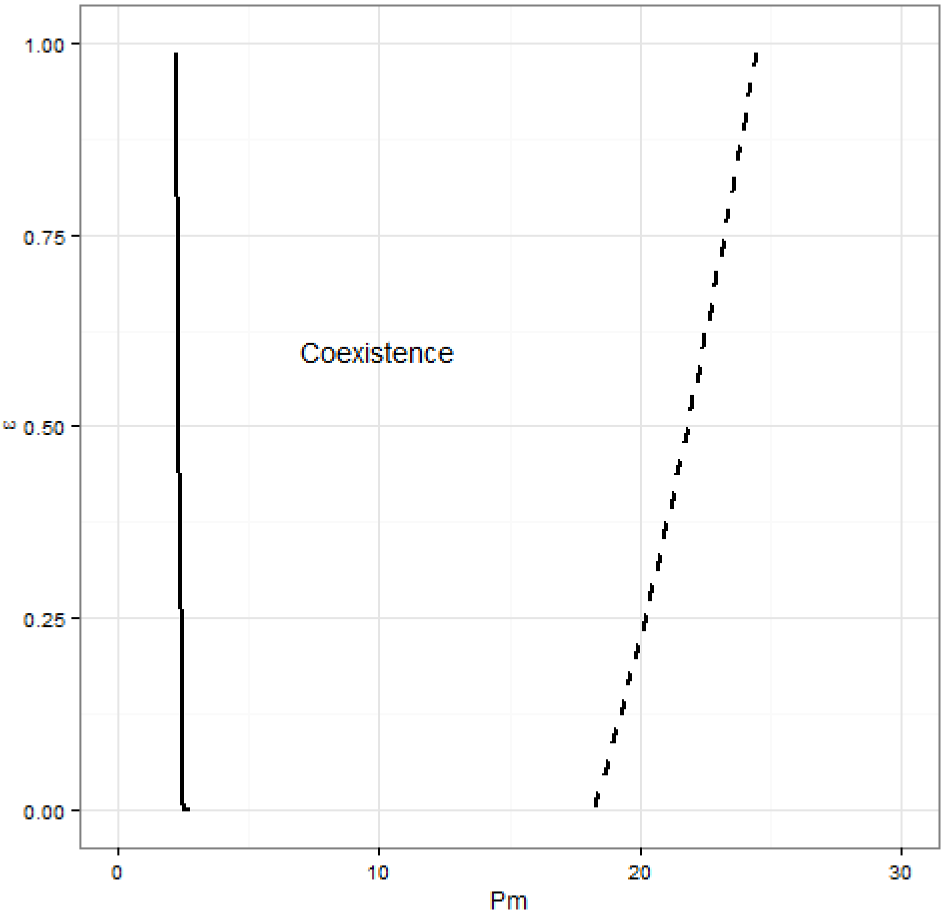

***Figure 14**. The scope for coexistence of scavengers, filter feeders and deposit feeders limited by the point of extinction at low P_m values (solid line) and the deposit feeders extinction point at high P_m values (dashed line), as a function of P_m (maximum biomass of the plankton resource) and ε (fraction of filter feeder faecal deposits available to deposit feeders). Coexistence is possible between the dashed and solid line.*

2.4 Discussion

The benthic food web in the North Sea was classified into three different groups based on common species traits found during sampling. The three groups defined are scavengers, filter feeders and deposit feeders. Filter feeders may compete with deposit feeders for food because they have access to the planktonic organisms and organic material before it is deposited on the seabed. However, there is also potential for a fraction of the plankton resource consumed, but not assimilated by filter feeders, to be deposited in or onto the sediment through the generation of pseudofaeces. Fish are also included in the food web model such that different habitat specific combinations of primary production (P) can be explored in relation to the three groups of benthic organisms.

At low values of phytoplankton production, and without fish, either deposit feeders or filter feeders can invade first. This is determined by the parameter values determining which group can survive at the lowest minimum resource abundance. When filter feeders are the first to invade, the effect on their resource can prevent the invasion of deposit feeders, leading to competitive exclusion (Holt et al. 1994). This mechanism does not work in the opposite direction, as there is only a one-way energy flow from the phytoplankton resource to the benthic resource, and not vice versa. This asymmetry prevents the occurrence of strong competitive exclusion, so that coexistence of filter feeders and deposit feeders occurs at higher productivity. The production of faecal pellets greatly enhances the scope for this coexistence, especially at intermediate productivity, as it further softens the competition between the two groups.

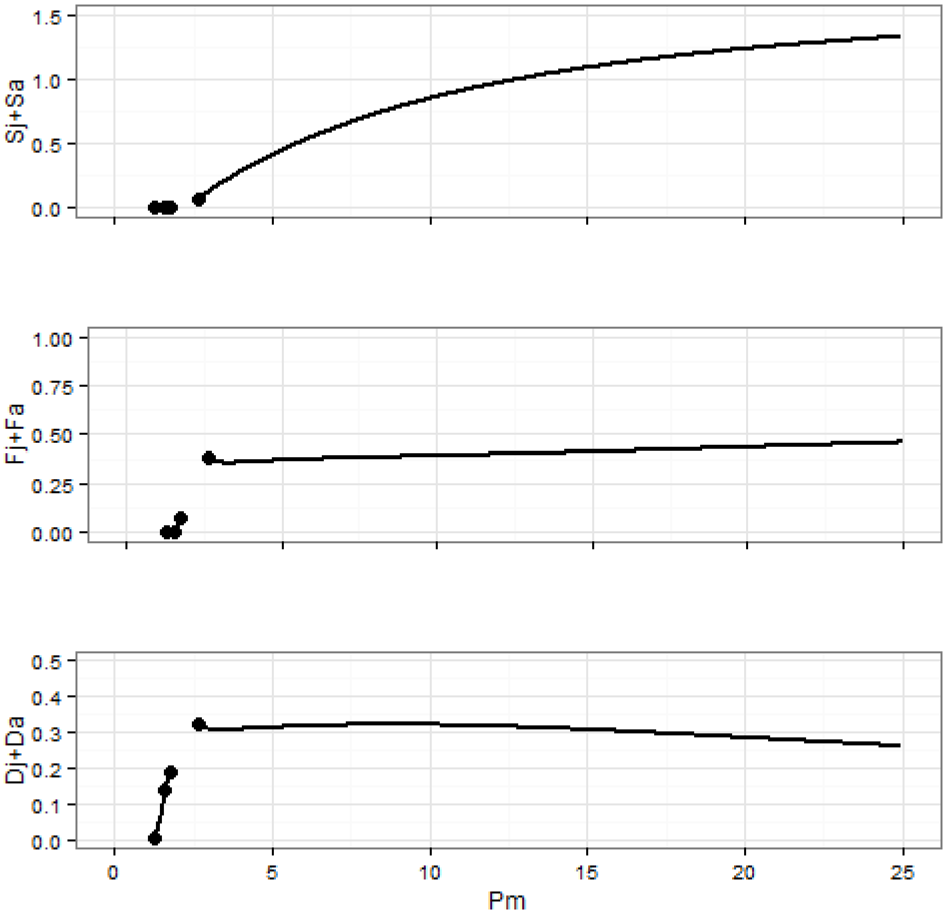

Figure 15. *Equilibrium population dynamics as function of Pm when including fish. ε = 0.5.*

When including scavengers the food web resembles a so-called ‘diamond-shaped food web’ (Holt et al. 1994), that results in apparent competition, where the presence of a predator (here the scavengers) can facilitate coexistence by reducing the competitive superiority of one of the consumers. When the ‘scavenger-mediated apparent competition’ favours one of the consumers, while the ‘real’ competition (via the resource) favours the other, apparent competition can potentially facilitate coexistence. In the present model, predator presence results in exclusion of the deposit feeders at higher resource levels due to increased predation mortality, supported by increased filter feeder biomass. Therefore, ‘apparent competition’ does not increase the scope for competition. Nonetheless, stable coexistence of filter feeders, deposit feeders and scavengers occurs for a wide range of productivity levels. A deviation from the more classical diamond shaped apparent competition system may promote the scope of coexistence, as is the case here. Wollrab et al. (2013) showed that when a predator undergoes an ontogenetic niche shift this also promotes the coexistence of the two resource competitors compared to a more simple system. Deviations of the simplest diamond shaped system results in a decrease in interaction strengths and weakened links thereby promoting persistence (McCann et al. 1998).

The addition of fish adds mortality to all groups in the food web. This further reduces the strength of competition (both resource competition, and scavenger-mediated apparent competition, and hence further increases the scope for competition.

The benthic food web model developed here provides a framework that can easily be parameterized for different regions. The average size and background mortality need to be specified for a regional system based on the characteristics of the species represented in a group and if necessary also the impact of fishing on the different groups. The grouping itself into scavengers, filter feeders and deposit feeders holds for all regions studied within the Benthis project, including the north-east Atlantic region and the Mediterranean (Benthis D4.3).

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APPENDIX A: FUNCTIONAL TRAIT VARIATION OF TAXA WITHIN FEEDING GROUPS

The starting point of this analysis is a dataset of the benthic invertebrate ecosystem on the Dutch Continental Shelf. This dataset of species abundance information, which has been collected annually for the period 1991-2010 has been coupled to a benthic functional trait database (Bolam et al. Benthis Deliverable D3.4), leading to a time series of the abundance of each of the major modes of resource acquisition. This allows us to study the distribution of other traits within each feeding group.

The data compilation and manipulation procedure, from which we use the results, is described in detail elsewhere (van Denderen et. al., in prep) and is described only briefly here.

The basic data consists of samples taken annually using a Reineck Boxcore at specific locations distributed on the Dutch Continental Shelf (Verduin et al. 2012) Figure A1. The majority of benthic macrofauna biomass in these samples has been identified to genus level. A small fraction of the data (<<1%) is identified to higher taxonomic level. This 'biomass by sample' data is then multiplied by a (normalized) fuzzy-coded benthic functional trait matrix, in which each genus present is described in terms of its morphological and ecological functions (Bolam et al, Benthis Deliverable D3.4). The resulting data is split according to the trait 'feeding type', which consists of the modalities predator, scavenger/opportunist, subsurface deposit feeder, surface deposit feeder and suspension feeder.

To explore the homogeneity of these groups in terms of their other traits, we have plotted time series of the relative distribution of all modalities within each trait, for each of the feeding mode groups.

Because of the fuzzy coding of the biological traits database, it is possible that genera are assigned multiple modalities of each trait, either because different species within a genus have different feeding modes, because different life stages within species have different ways of collecting food, or because individuals of species within the genus are capable of multiple feeding modes. To study the degree of overlap between feeding types, we checked the distribution of feeding modes within each individual feeding mode (**Error! Reference source not found.** A1). There is clearly a high degree f overlap between surface and subsurface deposit feeders, and between scavenger/opportunist and predator, in the sense that a large fraction of predators are also scavenger/opportunists (and vice versa), and a large fraction of surface deposit feeders are also subsurface deposit feeders (and vice versa). Further analysis (not shown) also indicates that these groups are similar in most other traits. Because of this overlap, we have combined these groups (indicated as scavenger/predator and deposit feeder) in the rest of the analysis. This results in 3 groups which differ in feeding mode (see Figures A3 – A5) for the trait composition of these groups).

Suspension feeders

For almost all traits, the biomass is strongly concentrated (>50%) in a single modality (**Error! eference source not found.**). The exception is the trait 'sediment position', where no single modality is dominant. The other dominant characteristics are summarized in Table A1.

Deposit feeders

For all but one traits, the biomass is strongly concentrated (>50%) in a single modality (**Error! eference source not found.**). The exception is the trait 'longevity', where no single modality is dominant. The other dominant characteristics are summarized in Table A1.

Scavenger/predators

This group is somewhat more heterogeneous in trait composition than the other two (Figure A5). Scavenger/predators are generally free-living, have a maximum lifespan of 3-10 years, and have a planktonic larval stage. Their morphology is divided between ‘soft’ and ‘exoskeleton’. The vast majority is mobile (‘swimming, ‘crawl’, or ‘burrow’). They generally live on or very near the sediment surface and engage in diffusive bioturbation and/or surface deposition of organic material. Their maximum size varies but is in most cases between 2 and 20 cm. Most have a pelagic egg stage, but benthic eggs and egg brooding also occur (Table A1).

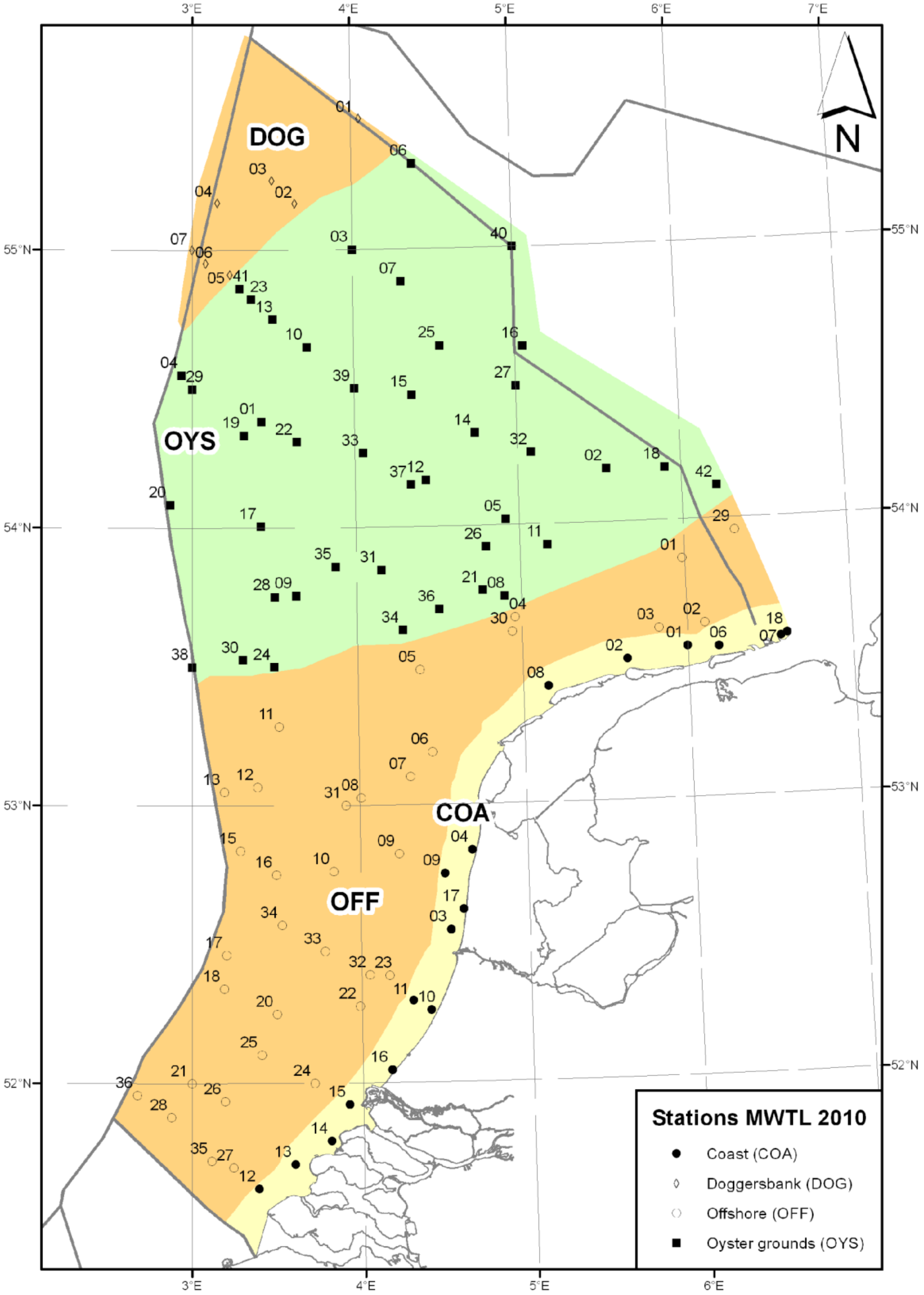
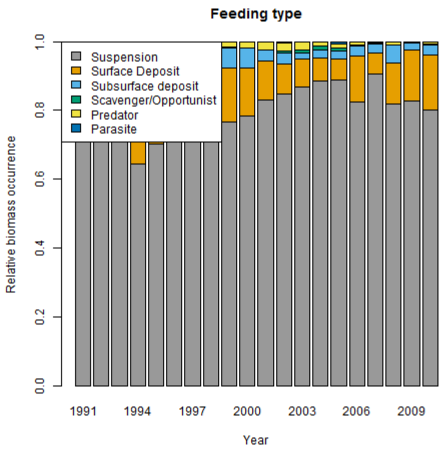


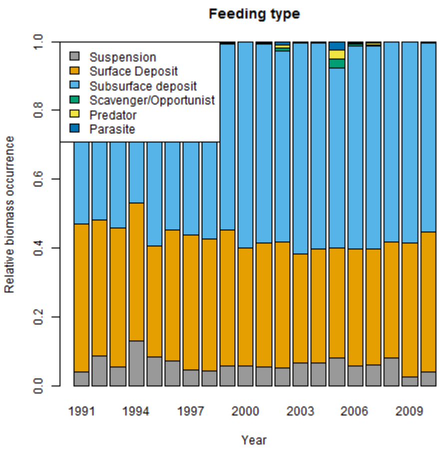
Figure A1. *Sampling locations of boxcore samples used in the analysis. Figure from Verduin et al. (2012).*

Table A1. *General trait composition of the 3 feeding groups*

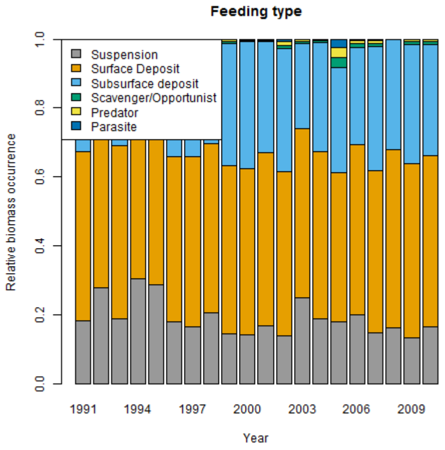
Suspension feeders	**Deposit feeders**	***Scavenger/predator***
Sexual reproduction, pelagic eggs	Sexual reproduction, pelagic eggs	Sexual reproduction, pelagic eggs, some benthic or brood eggs
Planktotrophic larvae	Planktotrophic larvae	Planktotrophic larvae
Burrow-dwelling	Free-living, some burrow dwelling	Free-living and burrow dwelling
Surface depositing	Diffusive mixing	Diffusive mixing and surface deposition
Sessile	Burrowers (some crawlers and sessile)	Mobile (swimers, crawlers, burrowers)
Hard-shelled	Hard shelled	Soft and hard shelled
Maximum age >10y	Longevity variable but >1 year.	Maximum age 3-10y
Max size (10-20cm)	Max size 2-10cm	Max size 2-20cm
Infauna (in top 10 cm)	Infauna, in top 5cm	Epifauna or shallow infauna (<5cm)



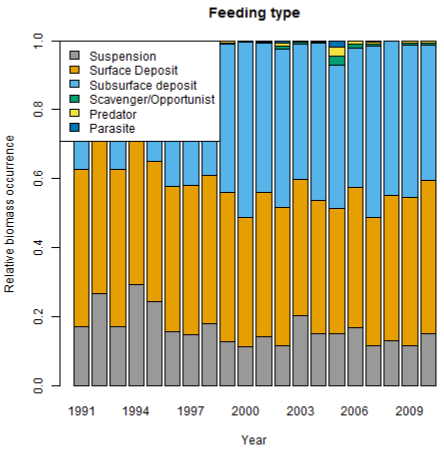
Suspension feeders



Subsurface deposit feeders

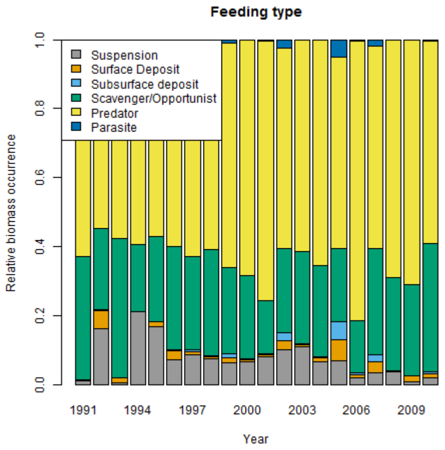


Surface deposit feeders

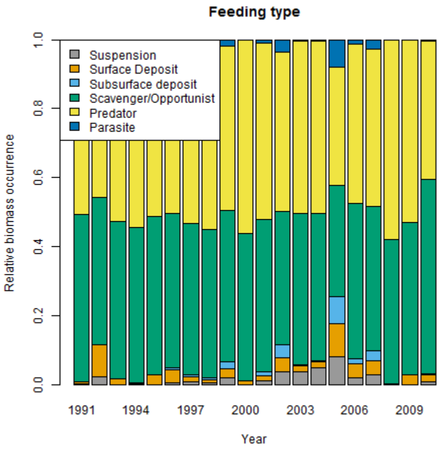


Surface and subsurface deposit feeders combined

Predators



Scavenger/opportunist



Predators and scavenger/opportunist combined

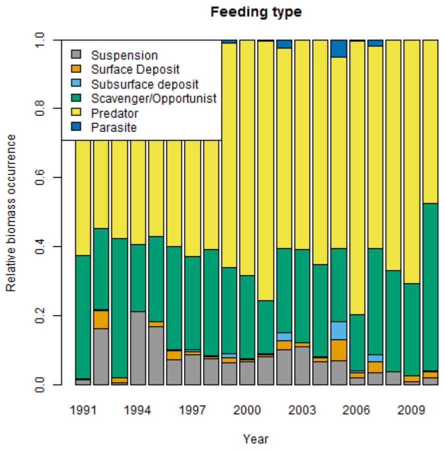
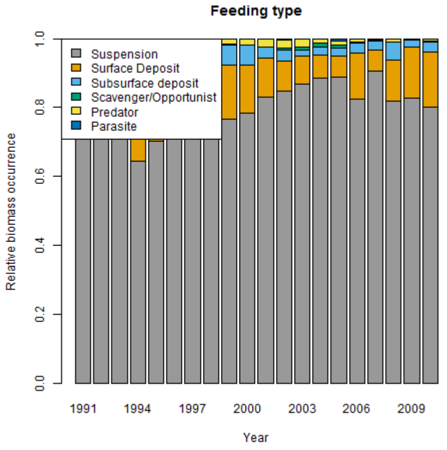
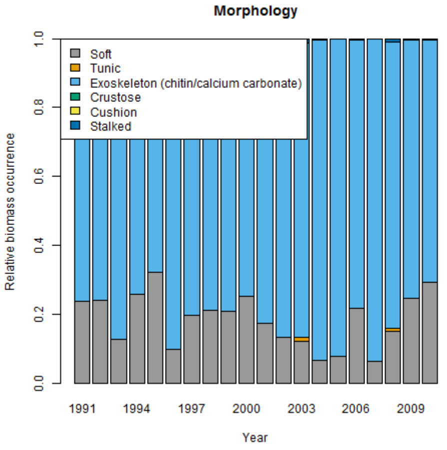
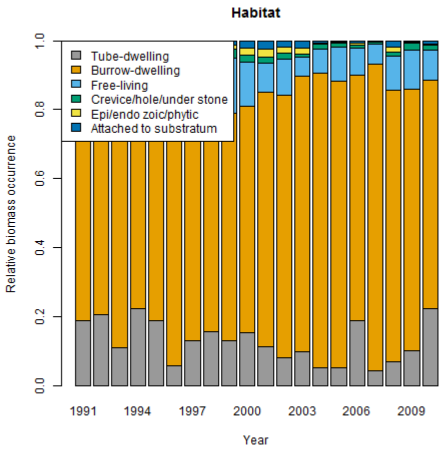
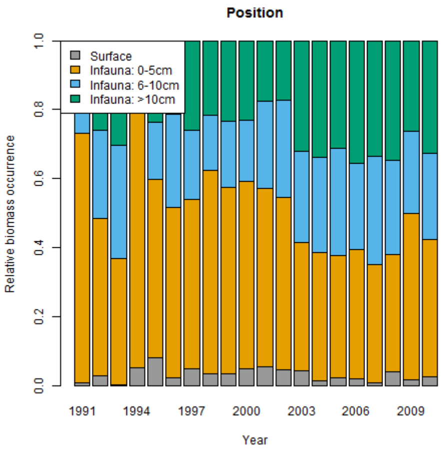


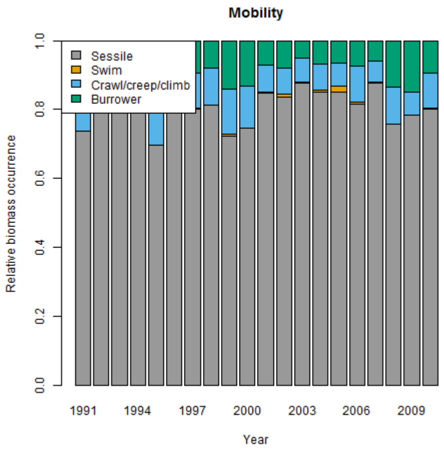
***Figure A2**. Distribution of feeding types within feeding type groups and combinations of feeding groups*

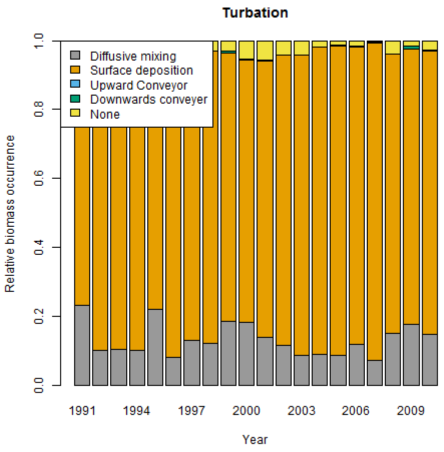


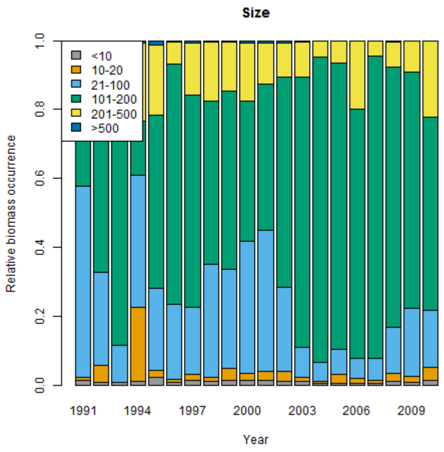


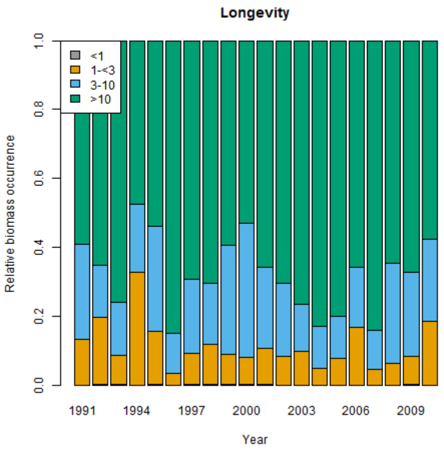

Habitat
Tube-dwelling
Burrow-dwelling
Free-living
Crevice/hole/under stone
Epi/endo zoic/phytic
Attached to substratum
Relative biomass occurrence
0.0
0.2
0.4
0.6
0.8
1.0
1991
1994
1997
2000
2003
2006
2009
Year


Position
Surface
Infauna: 0-5cm
Infauna: 6-10cm
Infauna: >10cm
Relative biomass occurrence
0.0
0.2
0.4
0.6
0.8
1.0
1991
1994
1997
2000
2003
2006
2009
Year


Mobility
Sessile
Swim
Crawl/creep/climb
Burrower
Relative biomass occurrence
0.0
0.2
0.4
0.6
0.8
1.0
1991
1994
1997
2000
2003
2006
2009
Year


Turbation
Diffusive mixing
Surface deposition
Upward Conveyor
Downwards conveyer
None
Relative biomass occurrence
0.0
0.2
0.4
0.6
0.8
1.0
1991
1994
1997
2000
2003
2006
2009
Year


Size
<10
10-20
21-100
101-200
201-500
>500
Relative biomass occurrence
0.0
0.2
0.4
0.6
0.8
1.0
1991
1994
1997
2000
2003
2006
2009
Year


Longevity
<1
1-<3
3-10
>10
Relative biomass occurrence
0.0
0.2
0.4
0.6
0.8
1.0
1991
1994
1997
2000
2003
2006
2009
Year

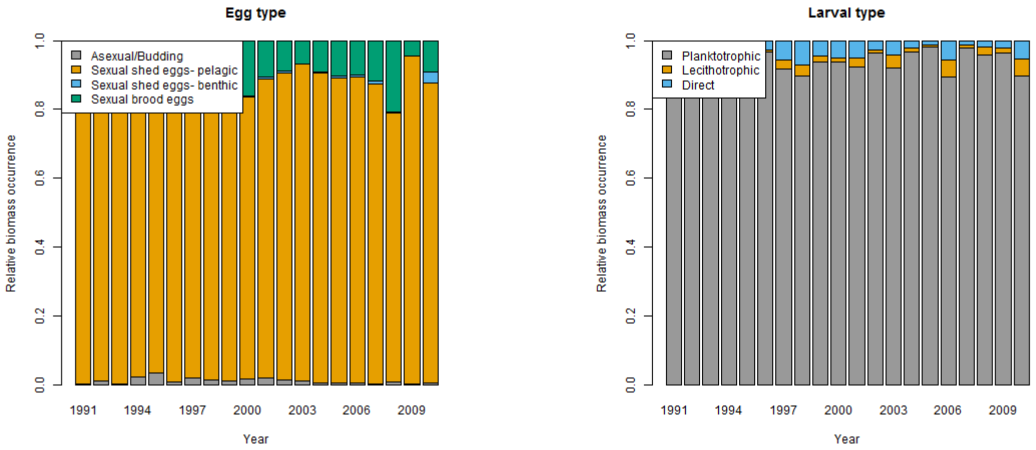
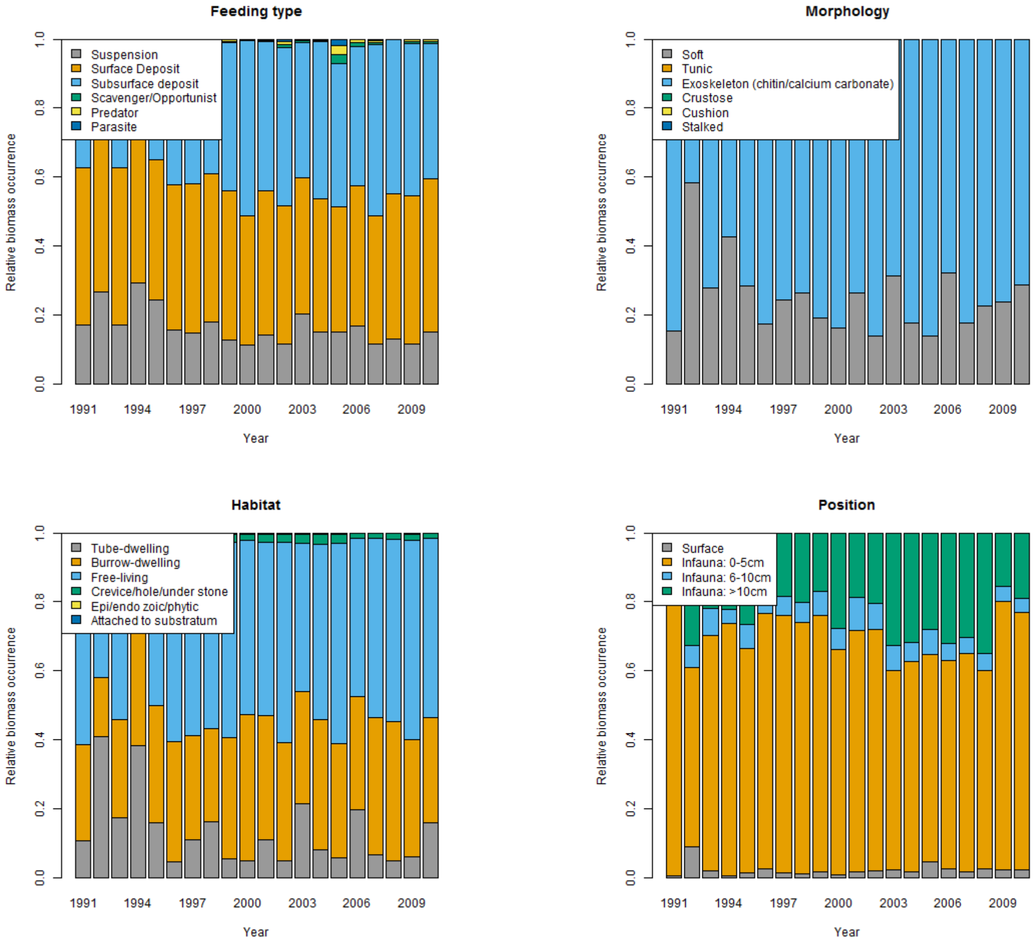


Figure A3. *Trait composition within the feeding type modality 'suspension feeders'*



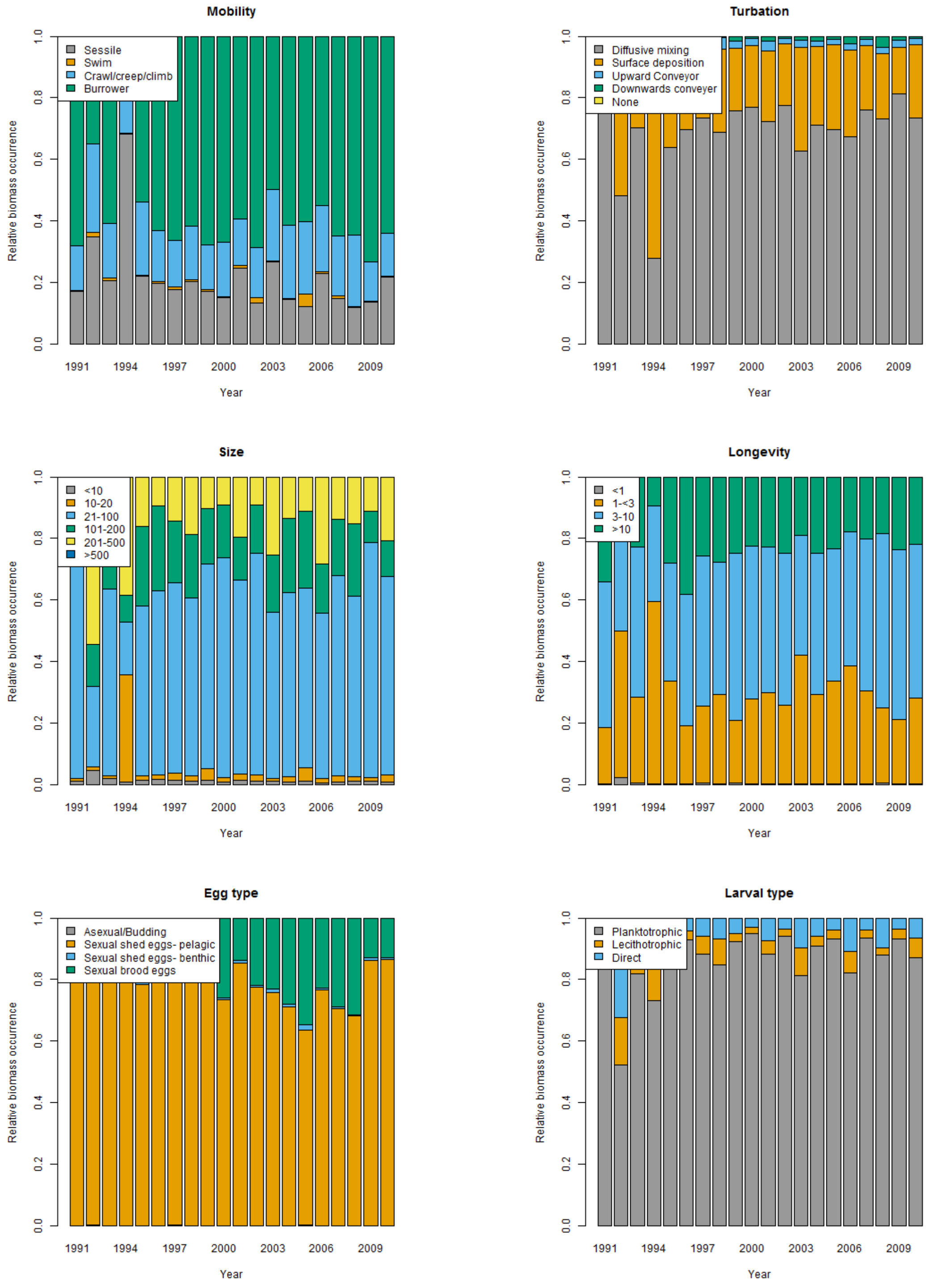


Figure A4. *Trait composition within the feeding type modality 'deposit feeders'*

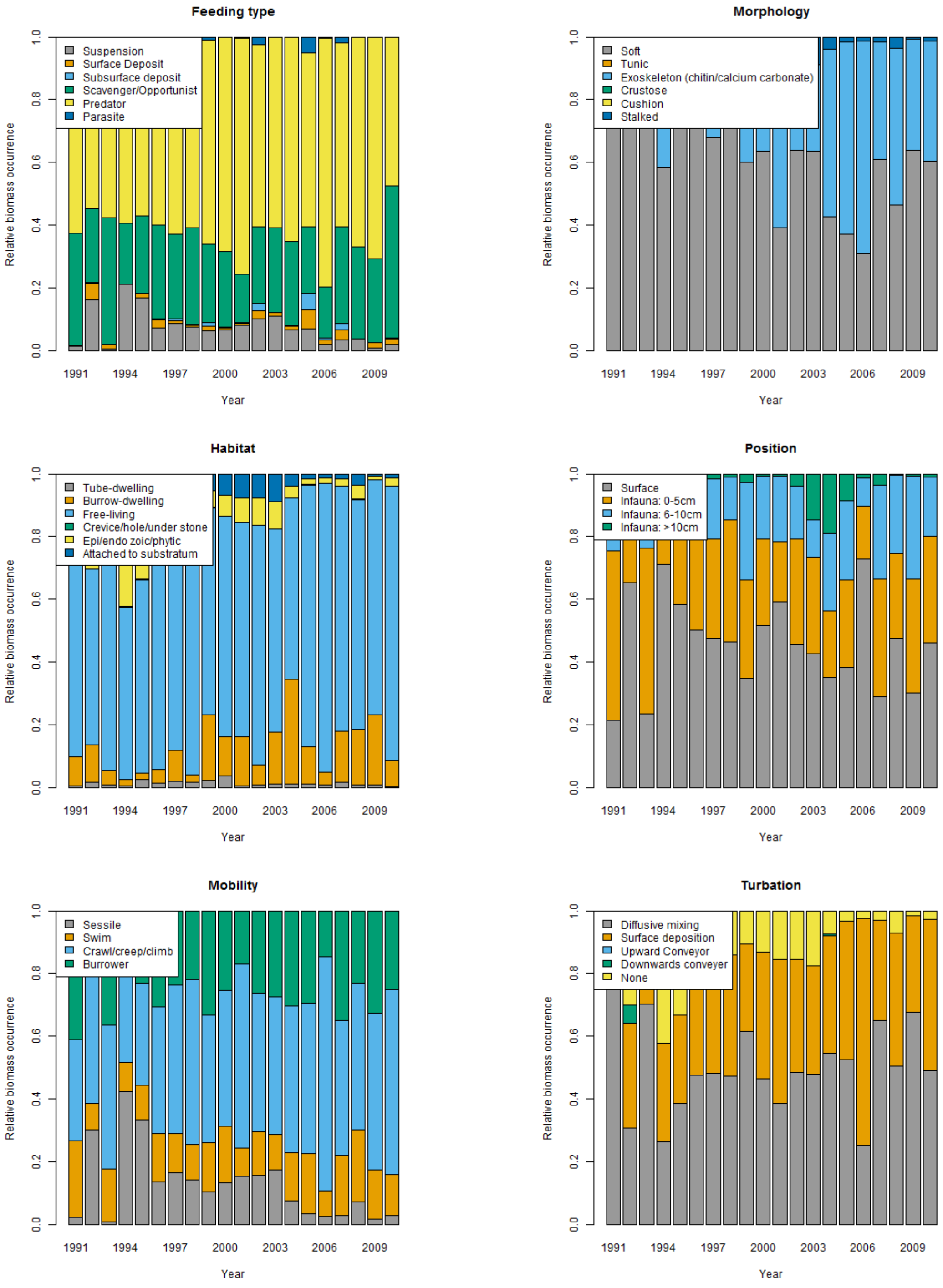

Feeding type
Suspension
Surface Deposit
Subsurface deposit
Scavenger/Opportunist
Predator
Parasite
Morphology
Soft
Tunic
Exoskeleton (chitin/calcium carbonate)
Crustose
Cushion
Stalked
Habitat
Tube-dwelling
Burrow-dwelling
Free-living
Crevice/hole/under stone
Epi/endo zoic/phytic
Attached to substratum
Position
Surface
Infauna: 0-5cm
Infauna: 6-10cm
Infauna: >10cm
Mobility
Sessile
Swim
Crawl/creep/climb
Burrower
Turbation
Diffusive mixing
Surface deposition
Upward Conveyor
Downwards conveyer
None
Relative biomass occurrence
0.0
0.2
0.4
0.6
0.8
1.0
1991
1994
1997
2000
2003
2006
2009
Year

Figure A5. *Trait composition within the feeding type modality 'scavenger/predator'*

APPENDIX B: TRAIT-BASED CALCULATION OF BODY SIZE AND MORTALITY

Background mortality

Background mortality was calculated using the biological traits and data presented in Appendix A. For each longevity category, a midpoint was determined. These were 0.5, 2.0, 6.5 and 20 years. We then calculated an average for all taxa in the data, weighted by their average biomass in the most recent 10 years of data. This yielded an average longevity of 5.1 years for deposit feeders, 6 years for filter feeders and 4.5 years for scavengers.

The longevity trait is defined as the maximum recorded age for each genus. Using these values directly would greatly underestimate background mortality, as the majority of individuals will not survive to the maximum recorded age. We have assumed that 1 in every 1000 individuals reaches the maximum age, so that the mortality rate is given by:

$$-\ln(0.001)/L$$

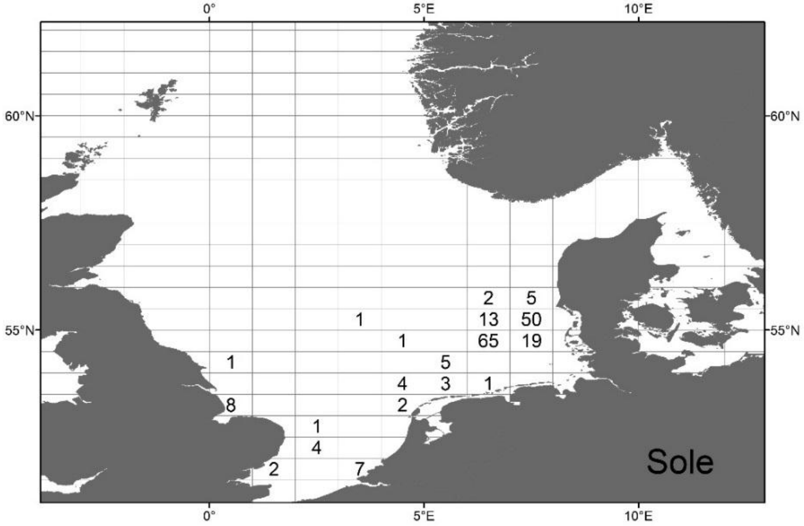
Were L is the calculated longevity. This calculation yields values of $0.0037d^{-1}$ for deposit feeders, $0.0031d^{-1}$ for filter feeders and $0.0042d^{-1}$ for scavenger/predators.

Size at maturation

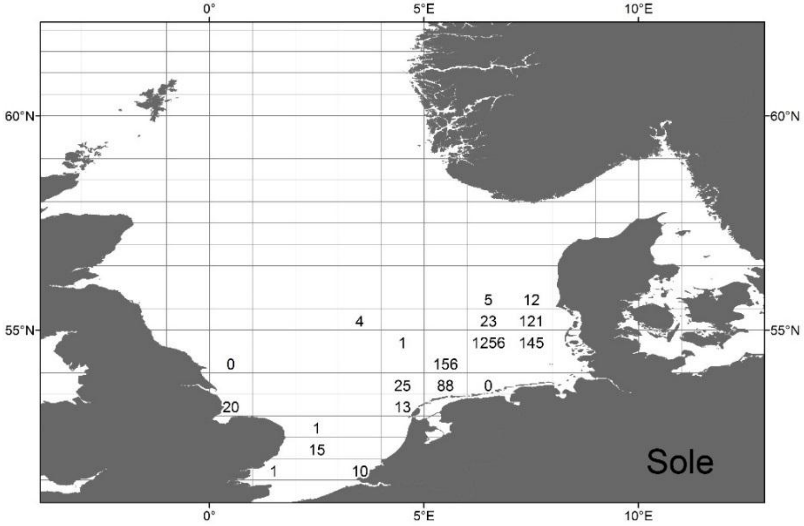
We use size at maturation to calculate the mass-specific maximum intake rate and maintenance rate. Body mass at maturation was calculated using the biological traits and data presented in Appendix A (the maximum size trait). The trait value assigned to each genus reflects the maximum known size. The model on the other hand, assumes that adults do not grow, and instead use all their energy for reproduction. We used the 25th percentile of the width of each size category as an estimate of length at maturation within that category, except for the largest, where we use the category minimum (2.5, 12.5, 40.75, 125.75, 275.75 and 500 mm). We then calculated an average maturation length for all taxa in the data, weighted by the average biomass in the most recent 10 years of data. The resulting average length at maturation was cubed to obtain a (relative) estimate of body mass at maturation. This yielded 8 g for deposit feeders, 6 g for filter feeders and 37 g for scavenger

APPENDIX C: SAMPLE LOCATION, NUMBER OF STOMACHS CONTAINING PREY AND ABUNDANCE OF PREY

Numbers of stomachs with food

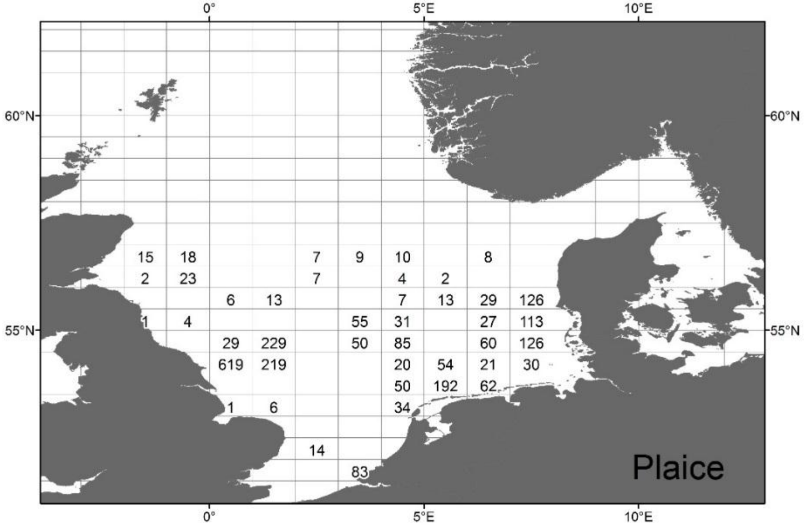


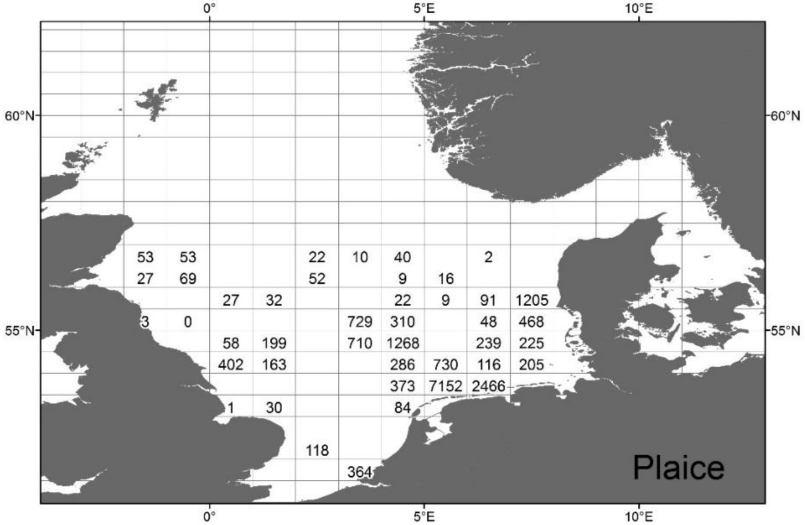
Abundance of benthic prey

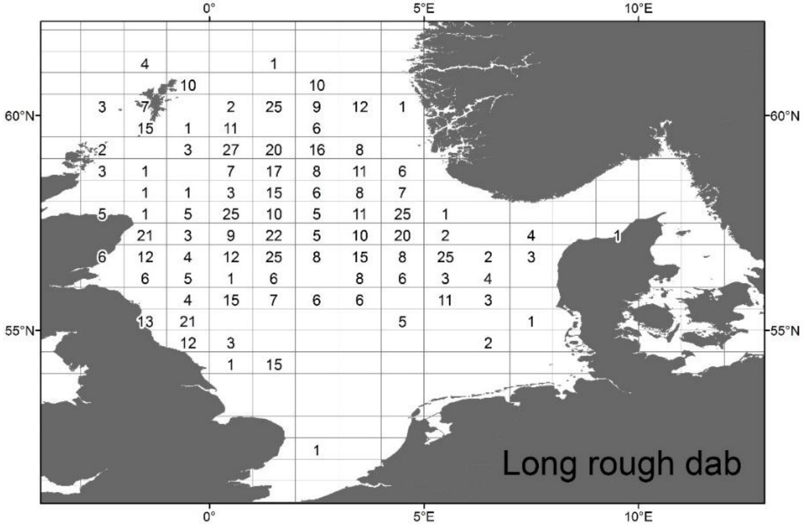


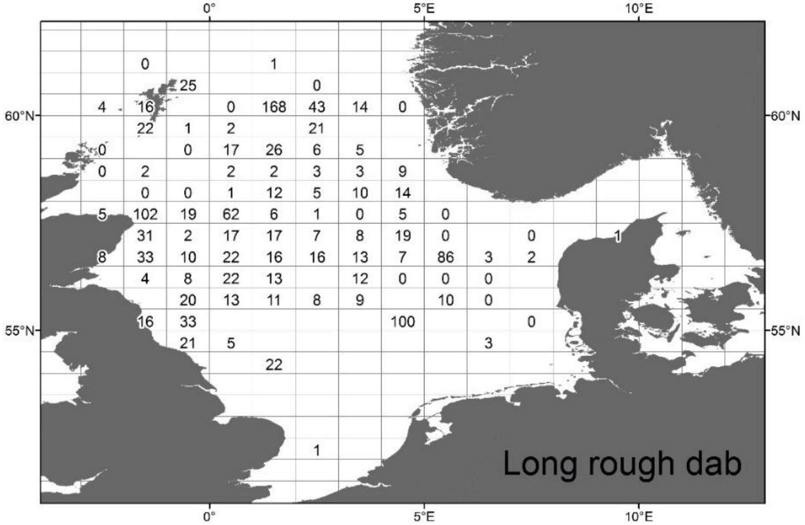
Numbers of stomachs with food

Abundance of benthic prey

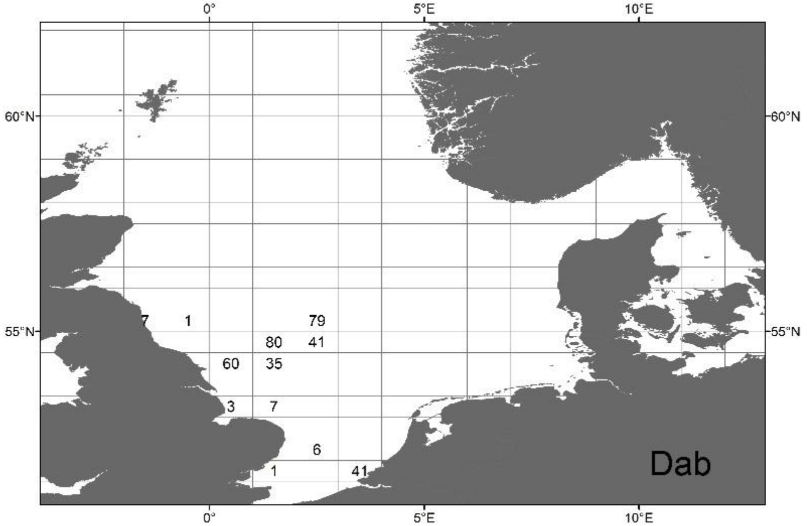


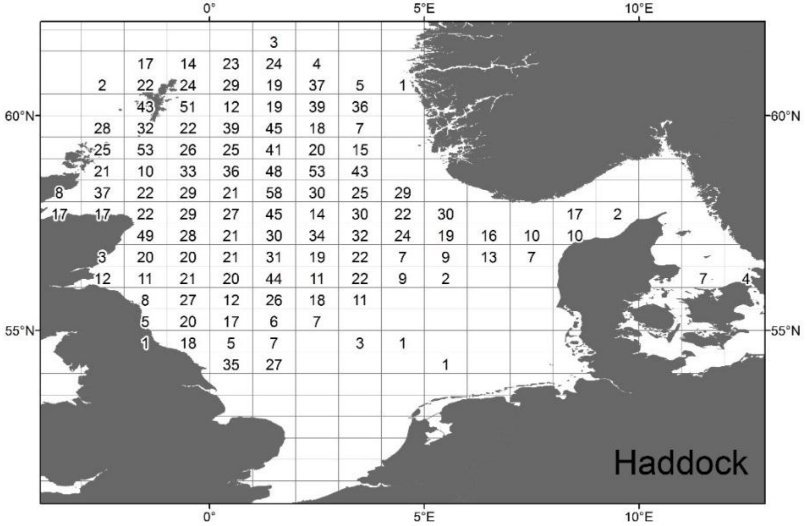




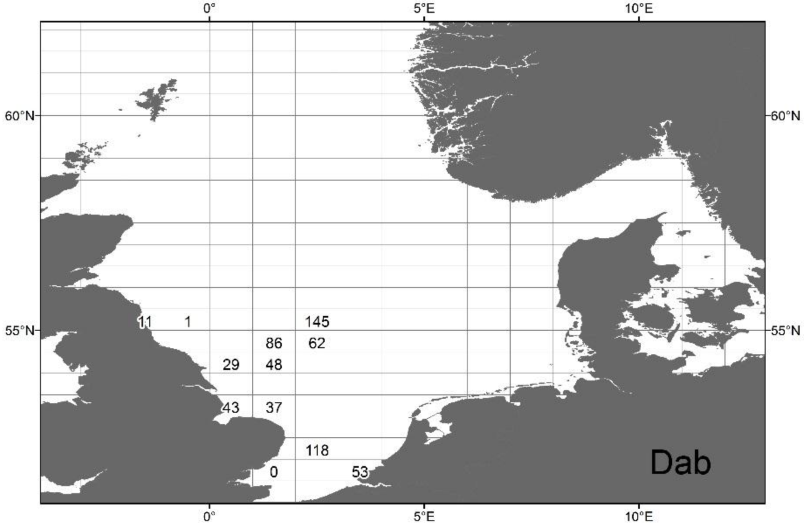


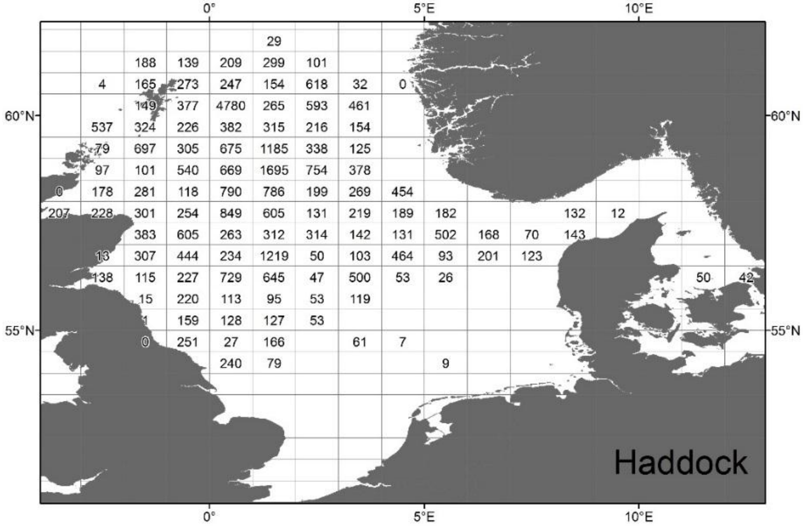
Numbers of stomachs with food





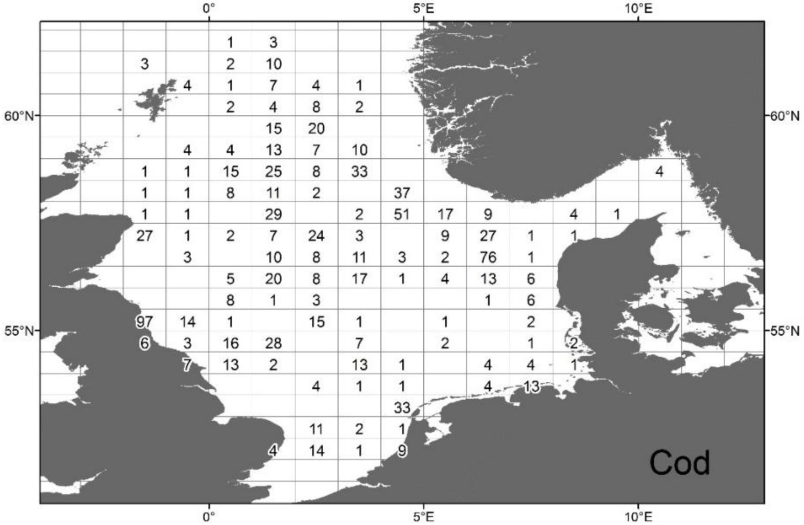
Abundance of benthic prey

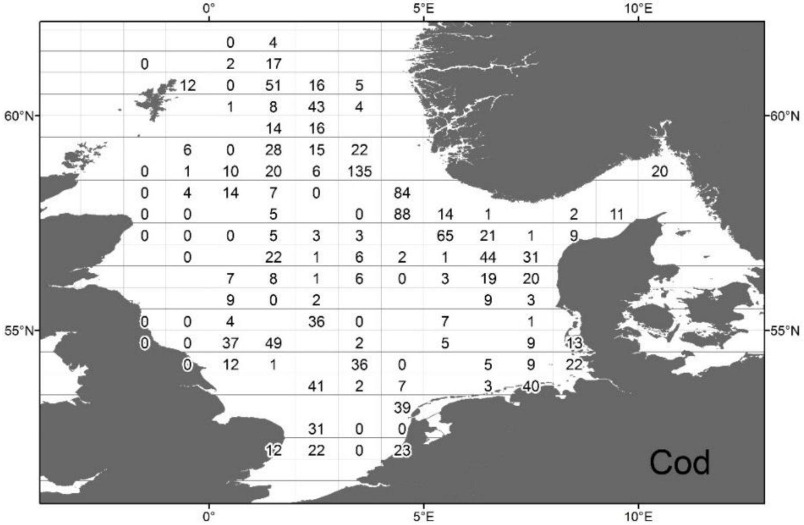


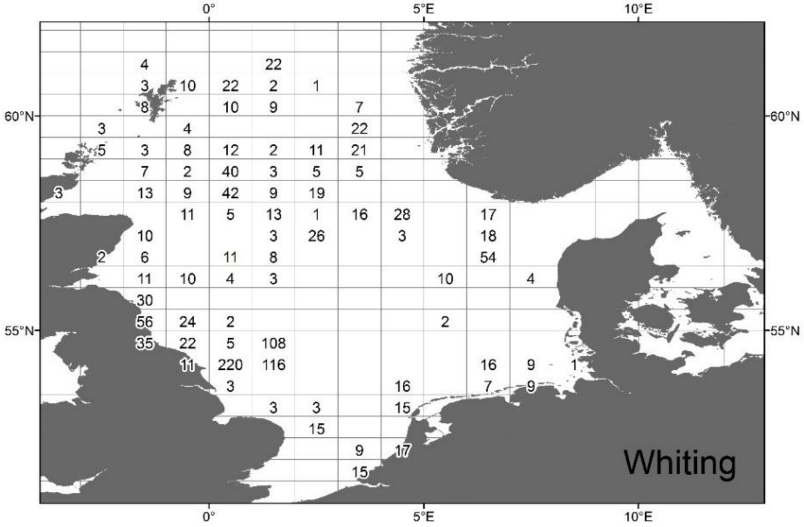


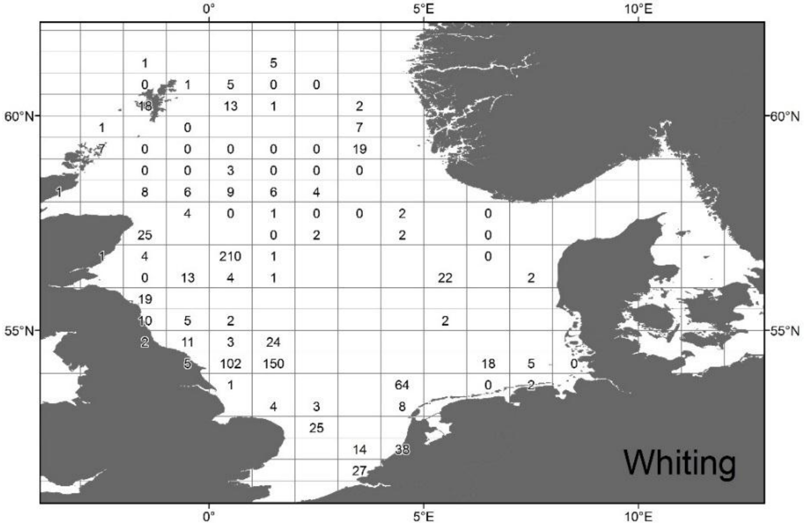
Numbers of stomachs with food

Abundance of benthic prey

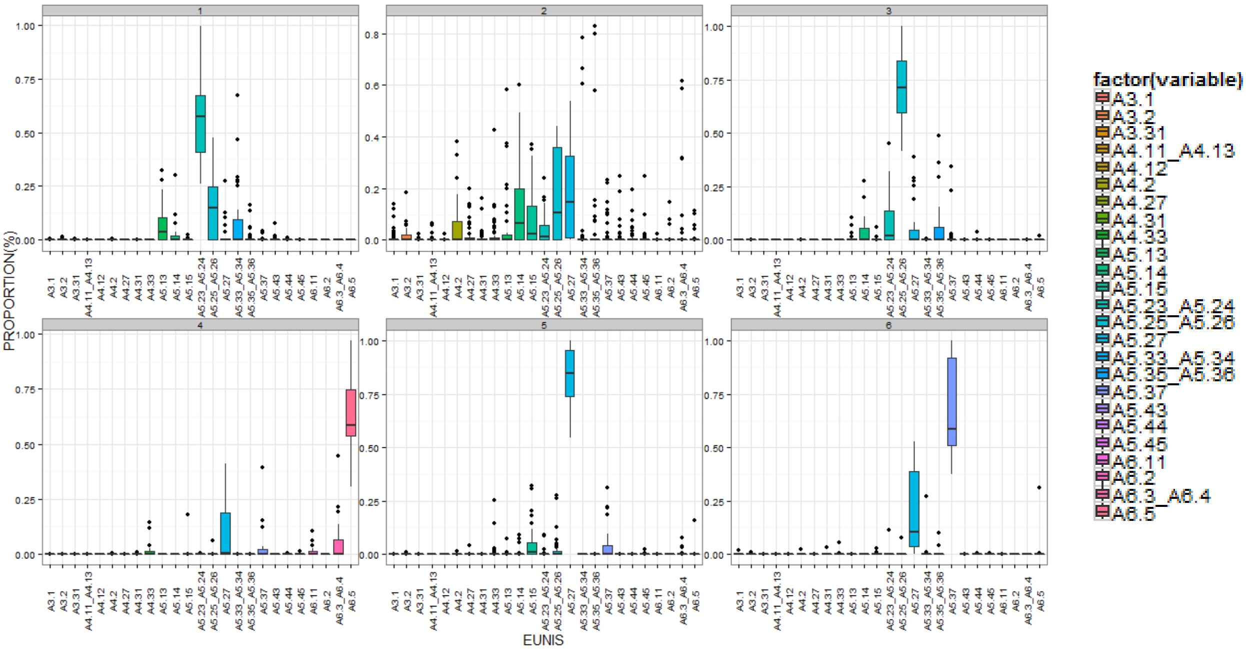


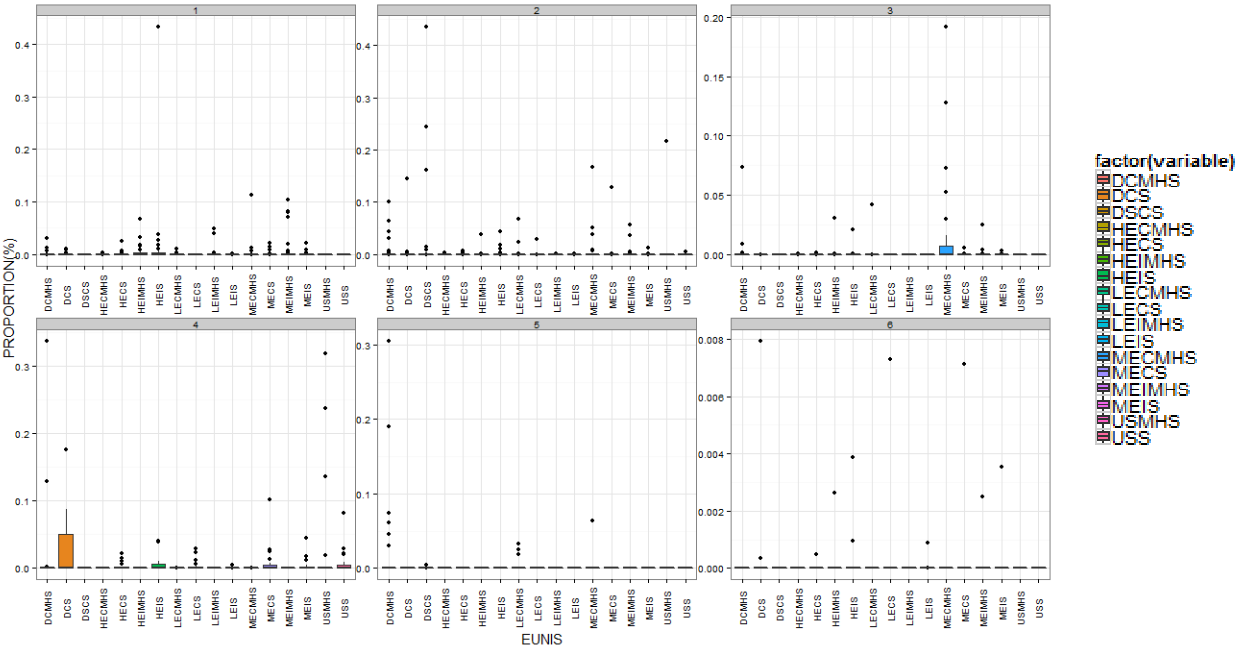






APPENDIX D: HABITAT CLUSTERING





EUNIS habitat codes used in the habitat cluster analysis

Level2	Level2 description	Level3	Level3 description	Level4	Level4 description
A3	Infralittoral rock and other hard substrata	A3.1	A3.1: Atlantic and Mediterranean high energy infralittoral rock		
		A3.2	A3.2: Atlantic and Mediterranean moderate energy infralittoral rock		
		A3.3	A3.3: Atlantic and Mediterranean low energy infralittoral rock	A3.31	A3.31: Silted kelp on low energy infralittoral rock with full salinity

Level2	Level2 description	Level3	Level3 description	Level4	Level4 description
A4	Circalittoral rock and other hard substrata	A4.1	A4.1: Atlantic and Mediterranean high energy circalittoral rock	A4.11 or A4.13	A4.11: Very tide-swept faunal communities on circalittoral rock or A4.13: Mixed faunal turf communities on circalittoral rock
				A4.12	A4.12: Sponge communities on deep circalittoral rock
		A4.2	A4.2: Atlantic and Mediterranean moderate energy circalittoral rock		
			A4.2: Atlantic and Mediterranean moderate energy circalittoral rock	A4.27	A4.27: Faunal communities on deep moderate energy circalittoral rock
		A4.3	A4.3: Atlantic and Mediterranean low energy circalittoral rock	A4.31	A4.31: Brachiopod and ascidian communities on circalittoral rock
				A4.33	A4.33: Faunal communities on deep low energy circalittoral rock
A5	Sublittoral sediment	A5.1	A5.1: Sublittoral coarse sediment	A5.13	A5.13: Infralittoral coarse sediment
				A5.14	A5.14: Circalittoral coarse sediment
				A5.15	A5.15: Deep circalittoral coarse sediment
		A5.2	A5.2: Sublittoral sand	A5.23 or A5.24	A5.23: Infralittoral fine sand or A5.24: Infralittoral muddy sand
				A5.25 or A5.26	A5.25: Circalittoral fine sand or A5.26: Circalittoral muddy sand
				A5.27	A5.27: Deep circalittoral sand
		A5.3	A5.3: Sublittoral mud	A5.33 or A5.34	A5.33: Infralittoral sandy mud or A5.34: Infralittoral fine mud
				A5.35 or A5.36	A5.35: Circalittoral sandy mud or A5.36: Circalittoral fine mud
				A5.37	A5.37: Deep circalittoral mud
		A5.4	A5.4: Sublittoral mixed sediments	A5.43	A5.43: Infralittoral mixed sediments
				A5.44	A5.44: Circalittoral mixed sediments
				A5.45	A5.45: Deep circalittoral mixed sediments
A6	Deep-sea bed	A6.1	A6.1: Deep-sea rock and artificial hard substrata	A6.11	A6.11: Deep-sea bedrock
		A6.2	A6.2: Deep-sea mixed substrata		
		A6.3 or	A6.3: Deep-sea sand or A6.4: Deep-		

Level2	Level2 description	Level3	Level3 description	Level4	Level4 description
		A6.4	sea muddy sand		
		A6.5	A6.5: Deep-sea mud		

Additional codes

CODE	**Habitat description**
DCMHS	Deep circalittoral mixed hard sediments
DCS	Deep circalittoral seabed
DSCS	Deep sea coarse sediment
HECMHS	High energy circalittoral mixed hard sediments
HECS	High energy circalittoral seabed
HEIMHS	High energy infralittoral mixed hard sediments
HEIS	High energy infralittoral seabed
LECMHS	Low energy circalittoral mixed hard sediments
LECS	Low energy circalittoral seabed
LEIMHS	Low energy infralittoral mixed hard sediments
LEIS	Low energy infralittoral seabed
MECMHS	Moderate energy circalittoral mixed hard sediments
MECS	Moderate energy circalittoral seabed
MEIMHS	Moderate energy infralittoral mixed hard sediments
MEIS	Moderate energy infralittoral seabed
USMHS	Upper slope mixed hard sediments
USS	Upper slope seabed