DTU Library

Biological traits of benthic macrofauna show sizebased differences in response to bottom trawling intensity

McLaverty, Ciaran; Dinesen, Grete E.; Gislason, Henrik; Brooks, Mollie E.; Eigaard, Ole R.

1 **Biological traits of benthic macrofauna show size-based differences in response to bottom**

2 **trawling intensity**

3 Ciarán McLaverty[*], Grete E. Dinesen, Henrik Gislason, Mollie E. Brooks, Ole R. Eigaard

4 DTU Aqua, National Institute of Aquatic Resources, Technical University of Denmark, Kemitorvet, 2800 Kgs.

5 Lyngby, Denmark

6 *Corresponding author: cimc@aqua.dtu.dk. Technical University of Denmark, National Institute of Aquatic

7 Resources, Kemitorvet, Building 202, 2800 Kgs. Lyngby, Denmark.

8 **Keywords**

9 Biological trait analysis (BTA); Benthic communities; Seabed function; Community-weighted mean; Fisheries;

10 Trawling impacts; Benthic indicators.

11 **Running page head:** Size-based effects of fishing on benthic traits

12 **Abstract**

13 Bottom trawling results in widespread impacts to the structure and composition of benthic communities.

14 Although an ecosystem approach to fisheries management aims to conserve marine biodiversity and

15 ecosystem function, there remains a lack of empirical evidence regarding the effects of trawling on benthic

16 functional properties. Here, we examine the sensitivity of benthic macrofauna communities to trawling using

17 their biological traits, and compare trait responses across size-categories and survey types. 84 benthic soft-

18 sediment samples were collected by Van Veen grab ($0.1m^2$) in the Kattegat in 2016, and complemented with

19 827 Haps cores ($0.0143m^2$) gathered over a long-term monitoring programme between 2006 and 2013. By

20 analysing trait response in three size categories (small: 1-4 mm fraction, large: ≥4 mm fraction, and full

21 community: all individuals combined), we demonstrate a size-dependent effect of trawling on benthic trait

22 composition, where the traits of large-bodied fauna (≥4mm) were more sensitive. Specifically, larger sessile,

23 deep-living, suspension-feeding, tube-dwelling, subsurface deposit feeding, burrow-dwelling, and long-lived

24 (≥10 years) individuals were among the most affected. Our results based on large fauna were largely in

25 agreement with trait responses observed in the multi-year monitoring data. This would suggest that trait

26 data gathered from a targeted one-off sampling event can convey information on both acute (short-term)

27 and chronic (long-term) trawling impacts. Given that most trawling impact assessment do not consider size-

28 based effects, we outline how size-separating the community can be used to improve the detectability of

29 trawling impacts, and provide new insights into the functional impacts of fishing on the seabed.

30

31

1. Introduction

Commercial bottom trawling (hereafter 'trawling') accounts for roughly one quarter of landings from wild capture fisheries (FAO, 2016), and has been described as the most widespread anthropogenic disturbance to global seabed environments (Halpern et al. 2008). As a result, understanding the wider impacts of trawling on biodiversity and ecosystem function now represent central facets of an ecosystem approach to fisheries management (FAO, 2003; Pikitch et al. 2004). During trawling activities, nets and other collection devices are dragged over the seabed to capture fish and shellfish species. This results in the penetration and re-suspension of sediments (Eigaard et al. 2017; O'Neill and Ivanović 2016), damage to biogenic habitats (Cook et al. 2013), disturbance to demersal food webs (Hiddink et al. 2011), and direct and indirect mortality of benthic fauna (Kaiser et al. 2006, Hiddink et al. 2017, Sciberras et al. 2018). As benthic organisms play a key role in ecosystem processes such as bioturbation, nutrient cycling, and benthic-pelagic coupling (Snelgrove 1998, Lohrer et al. 2004, Queirós et al. 2013, Griffiths et al. 2017), trawling also has considerable potential to impact the functioning of seabed ecosystems (Dayton et al. 1995, Jennings & Kaiser 1998).

Research of the ecological effects of trawling has to date mainly focused on the response of taxonomic (or species-based) characteristics of the benthos, such as diversity and species composition (Kaiser et al. 2006, Hiddink et al. 2017, Sciberras et al. 2018). While taxonomic approaches are important to understand changes to biodiversity, and describe the evolutionary affiliations of species, they also face several limitations. Estimates of species diversity can be highly sensitive to sampling effort (Fleishman et al. 2006), are limited in their ability to describe ecological function or mechanisms of sensitivity (Bremner et al. 2006), and may often be uncorrelated with key ecosystem processes (J. Reiss et al. 2009). Ecologists are therefore increasingly using biological traits as a way to characterise community composition, to interpret ecological state, and better understand how individuals and species respond to biotic and abiotic variation (McGill et al. 2006, Gallagher et al. 2013). Traits essentially describe the phenotypic (i.e. morphological, physiological, behavioural) characteristics of an organism (Violle et al. 2014), and are therefore common to communities across habitats and geographic boundaries. Generally, traits are divided into two broad categories: effect traits, which determine how species affect ecosystem functions, and response traits, that show how species respond to their environment (Lavorel & Garnier, 2002). In combination, these response and effect traits can be used to interpret functionality, and predict the vulnerability of systems to disturbance (Mouillot et al. 2013, Beauchard et al. 2017). Indeed, rapidly developing methods such as joint species distribution modelling combine information on species occurrences, traits, taxonomic relationships, and environmental covariates (Warton et al. 2015, Abrego et al. 2017, Murillo et al. 2020), to simultaneously explore interactions between taxa and the response of communities to their environment. While such approaches are likely to become

1　standard in the near future, there remains a lack of empirical evidence of how trawling impacts benthic trait

2　composition across different seabed habitats and fisheries (Bolam et al. 2017), and studies which examine

3　the response of specific traits (and associated combinations) to trawling (Hinz et al. 2021).

4　The vulnerability of benthic communities to disturbance is mainly governed by their tolerance to disturbance

5　(rate of mortality), and ability to recover (rate of post-disturbance recolonisation) (Hiscock & Tyler-Walters

6　2006). Some of the key species traits which govern benthic sensitivity to trawling have been determined by

7　investigations of trawling impacts to community trait composition (Bremner et al. 2003, Tillin et al. 2006,

8　Bolam et al. 2014, 2017, Van Denderen et al. 2015). Those highlighted include trait categories (and

9　modalities) such as sediment position (e.g. surface vs. deep), living habit (free-living vs. tube-dwelling),

10　feeding strategy (scavenger vs. suspension-feeder), and egg development (parental brooding vs. broadcast

11　spawning), as well as more general traits such as body-size, longevity, and morphology. Regardless of these

12　findings at the community level, relatively few studies have examined the response of specific traits or

13　modalities to trawling. Notable exceptions to this include a trawling disturbance indicator that describes

14　vulnerabilty based on groups of trawling sensitive traits (De Juan and Demestre 2012), and using the longevity

15　characteristics of individuals to describe community sensitivity (Rijnsdorp et al. 2018, Hiddink et al. 2019).

16　The relevance of these studies is that single value metrics or indicators are a favoured approach of the main

17　marine policy directives in Europe, such as the European Union Water Framework Directive (WFD) (Anon.

18　2000) and the Marine Strategy Framework Directive (MSFD) (Anon. 2008). Under these Directives, metrics

19　are used to track and measure progress towards environmental targets. This has led to a proliferation of

20　indicators designed to describe seafloor integrity in recent years (e.g. see Rice et al. 2012, Beauchard et al.

21　2017), and frameworks and criteria to objectively select the most suitable targets and indicators (Rice &

22　Rochet 2005, Rossberg et al. 2017). Despite their increasing use, it remains that while a single value metric

23　can easily convey quantitative information on complex objects of environmental management (Jørgensen et

24　al. 2013), the inherent simplicity of this approach can necessitate careful interpretation. For example, a

25　number of recent trawling impact studies have in fact shown that many commonly used benthic indicators

26　are insensitive to trawling (Hiddink et al. 2020, McLaverty et al. 2020a), and may be more responsive to other

27　environmental gradients (Gislason et al. 2017).

28　Such discrepancies in the outcome of trawling impact studies can occur for a variety of reasons (Gray et al.

29　2006). These may be due to the varying sensitivity of seabed habitats (Collie et al. 2000), differences in the

30　penetration depths of trawling gears between fisheries (Hiddink et al. 2017), and the similar effects of natural

31　stressors on the benthos (van Denderen et al. 2015). In addition, trawling will often exert an uneven rate of

32　mortality across benthic species (Sciberras et al. 2018). For example, large-bodied shallow burrowing infauna

are more prone to damage than smaller body-sized fauna (Queirós et al. 2006), which may be pushed away by the pressure wave that is generated in front of a moving trawl. In addition, , larger macrofauna are typically slower to grow and sexually mature, have lower mortality and population growth rates (Charnov 1993, Savage et al. 2004), and are therefore relatively vulnerable to trawling induced mortality (Duplisea et al. 2002). When communities are dominated by relatively insensitive small-bodied fauna, such as in coastal fishing grounds (Duplisea et al. 2002), losses of trawling sensitive species may therefore be undetectable at the community level, particularly in the presence of strong environmental drivers (Atkinson et al. 2011, Kaiser et al. 1998, McLaverty et al. 2020b). A potential solution to this is to apply a simple body-size threshold in the community. This is done by separating fauna into small and large size fractions (via sieving) during sampling. By separating out the numerically dominant and relatively insensitive small fauna, and focussing on the response of the large-bodied fauna separately, this method has been shown to significantly improve the detectability of trawling impacts, and also reduce variation attributable to other environmental drivers (see McLaverty et al. 2020a). Compared to approaches based on longevity (e.g. Rijnsdorp et al. 2018), which can be difficult to measure and is often uncertain/lacking for many species, size-based methods such as this can be easily applied regardless of community type, composition, and location. Scope therefore exists to combine this method, and the relative advantages of biological trait analysis, to enhance our ability to detect trawling impacts and our understanding of the functional impacts of these activities.

The main aims of this study were to (i) identify which benthic species traits are most sensitive to trawling, (ii) compare sensitivity across body-size categories, and (iii) discuss the implications of our findings in terms of benthic ecosystem function and sustainable fisheries management. To do this, benthic samples were collected along a wide gradient of trawling intensity (including unfished sites) in soft-sediment areas of the Kattegat, a shallow transitional sea located between the Baltic and North Sea. During sampling, sieves were used to separate the benthic community into small (1-4mm) and large (≥4mm) size categories. Firstly, a number of sensitive traits are identified using multivariate ordinations of trait composition. Subsequently, we model the response of these sensitive traits to trawling intensity and other environmental drivers. Furthermore, we compare our observations with data from an independent benthic monitoring dataset gathered in the same area, to examine if our results are representative of long-term trends. The findings of this study provides new evidence of a size-dependent effect of trawling on benthic trait composition, and insights into the functional impacts of fishing on the seabed.

1 **2. Materials and methods**

2 **2.1. Study area**

3 The Kattegat is a shallow transitional sea characterised by an inflow of deep saline water from the North Sea,

4 and an outflow of surface brackish water from the Baltic Sea. Due to increasing nutrient inputs, mainly

5 nitrogen and phosphorus, areas of the Kattegat experience long-standing eutrophication (Pearson et al.

6 1985). The Kattegat also represents an important fishing ground for Danish and Swedish vessels targeting

7 Norway lobster *Nephrops norvegicus* (Linnaeus, 1758) (Figure 1 a-c). The seabed here is composed of shallow

8 sandy sediments to the west, and deep muddy canyons and moraines of mixed sediments in the north and

9 eastern areas. *Nephrops* habitats, and the associated fishery, generally occurs in muddy sediments below

10 20m depth. Fishing is undertaken using single or twin *Nephrops* trawls, with average penetration depths of

11 the gear provided by Eigaard et al. (2016). Approximately 3% of the total gear footprint is comprised by the

12 doors and clumps (10 – 35 cm penetration), 29% by the groundgear (2-10 cm penetration), and 68% by the

13 sweeps and bridles (>0-2 cm penetration). The fishery is also characterised by relatively low catchability and

14 thus comparatively high trawling intensity (Eigaard et al. 2017). Based on trawling effort between 2013 and

15 2016, high trawling intensities (SAR) of up to 12.6 yr^{-1} were observed in the northern Kattegat, in the vicinity

16 of the Vinga trench system (running north to south), and sporadic areas in the south (Figure 1c).

17 **2.2. Data sources – KS16 (2016) and NOVANA (2005 – 2013)**

18 Soft-sediment benthic community data were gathered from two independent surveys undertaken in the

19 Danish Exclusive Economic Zone (EEZ) of the Kattegat between 2005 and 2016. The Kattegat 2016 (KS16)

20 survey represents a single (snapshot) survey undertaken in September 2016 at 21 sampling sites. The survey

21 was designed to gather community data across a wide range of trawling intensity in the Kattegat, and is

22 described in detail in McLaverty et al. (2020a). At each site, 4 faunal samples were collected using a 0.1m^2

23 Van Veen grab. The samples were sieved consecutively over 4 mm and 1 mm mesh sizes to separate the

24 community into large (≥4mm) and small (1-4mm) size fractions. A 1mm mesh size is widely used as benthic

25 macrofauna are generally defined as metazoans retained by a 1 mm sieve, and a 4 mm threshold is used to

26 distinguish larger macrofauna and benthic megafauna. Additionally, a 4 mm threshold has been effectively

27 used to determine the effects of trawling on macrobenthic production (H. Reiss et al, 2009). In the laboratory,

28 all animal material was identified to the lowest taxonomic level possible, and biomass estimates were

29 determined for each taxa as ash-free dry weight. The size-separation of the KS16 data provided 3 separate

30 datasets for analysis; the 'small fraction', the 'large fraction', and the two fractions combined, hereafter

31 referred to as the 'full community'. The second dataset was extracted from the Danish National Monitoring

programme (NOVANA), and included benthic macrofauna data from 22 fixed sites collected between April and May, in the years 2005, 2006, 2007, 2008, 2010, 2011 and 2013. At each site, 4 or 5 replicate sediment samples were collected using a 0.0143m^2 Haps corer, and processed using a single 1 mm sieve (and thus analogous to the KS16 'full community'). All macrofauna were sorted and identified to the lowest taxonomic level possible. Biomass estimates per species were determined as wet weight. An additional sample was collected at each sampling site in both surveys for the determination of sediment grain size (see Section 2.4 for details). The NOVANA programme was designed to monitor the effects of nutrient enrichment in Danish waters (Svendsen et al. 2005), and the dataset is described in further detail in Gislason et al. (2017). As a result, the relative effects of trawling on the benthos may be expected to differ between the NOVANA and KS16 datasets, given the respective aims of the survey designs. The locations of all sampling sites are provided in Figure 1 b-c. Penetration depths of sampling gears are assumed to be consistent between surveys, due to the soft sediments throughout the study area, and the roughly similar penetration depths of the two gears (Van Veen: 33 cm, Haps: 31.5 cm). To compare the representativeness of trait data from the respective surveys, we used trait accumulation curves to determine how well the gears sampled communities across our sampling stations (Supplement – Figure S1). The curves approached asymptotes for the majority of sites in both surveys, indicating a similarly effective sampling of trait composition. Although two surveys generally sampled different areas, sampling sites did overlap at 5 locations (Figure 1 b). In total, 4 datasets were analysed; 3 from the KS16 survey, and 1 representing multiple years captured by the NOVANA surveys. The full species list for the KS16 dataset is provided in Table S1 of the Supplement.
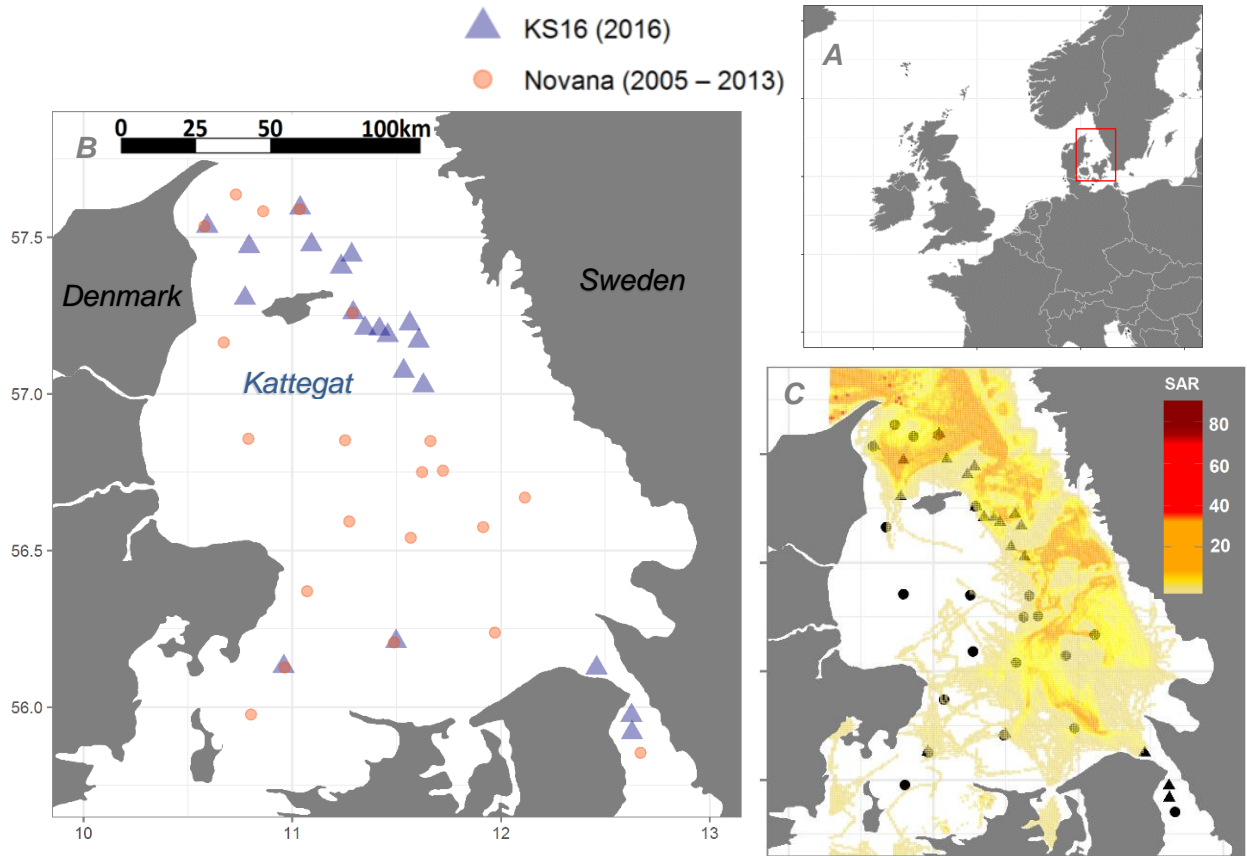
Figure 1. (a) Location of the study area (b) KS16 and NOVANA survey sampling sites in Danish waters (c) cumulative bottom trawling effort between 2013 and 2016 in relation to sampling sites. SAR = swept area ratio, a metric of trawling intensity.

2.3. Estimating trawling intensity

Trawling intensity was estimated as swept area ratios (SAR). The ratio was calculated by aggregating all trawling effort within an 'impact area' of 2 km radius around each sampling site. Effort was then divided by the area of the circle to estimate the number of times the seabed was trawled within a given time period. A 2 km radius was selected as a 2 x 2 km resolution has been shown to provide a relatively consistent compromise between over- and under-estimation of trawling intensity (Lambert et al. 2012) Trawling effort was estimated by combining Vessel Monitoring System (VMS) data with fishing vessel and gear information provided by EU logbooks. VMS receivers are used to collect and send data regarding the vessel location, heading, and speed at an hourly polling frequency (Danish and Swedish vessels). The raw VMS data were processed to preserve data considered to be trawling activity, defined as sailing speeds between 2 and 4 knots, and with a minimum distance of 3 km from port. The raw data points were interpolated using a cubic Hermite spline method (Hintzen et al. 2012) to reconstruct trawling tracks. These tracks were then combined with logbook data on vessel size and gear dimensions (Eigaard et al. 2016; Eigaard et al. 2017), which were

1   used to estimate and calculate the area of seabed 'swept' during each logbook trip. All processing of VMS

2   data and estimation of SAR were conducted using the VMStools package in R (Hintzen et al. 2012). In order

3   to ensure comparability between the KS16 and NOVANA data, only data for fishing vessels ≥15m were used

4   in the study. While VMS has been mandatory for all vessels ≥12m operating in European waters since 2012,

5   VMS was only mandatory on vessels ≥15m between 2005 and 2012, meaning that data are not available for

6   vessel between 12-15m for much of the period covering the NOVANA samples. SARs were calculated based

7   on 12 months of trawling effort prior to the date the individual samples were collected.

8   **2.4. Environmental drivers**

9   In addition to trawling intensity, data for 5 environmental drivers were included as predictor variables in the

10 analysis. These included mud content (%), depth (m), bottom current speed (cm^{-s}), bottom water salinity,

11 and bottom temperature (°C). Depth data were collected in the field, while mud content was determined

12 from particle size analysis (PSA) of sediment samples. PSA was undertaken via mass loss following wet sieving

13 (Danish Standard (DS) 405.9), and resulted in the estimation of mud % (<63μm), sand % (0.063–2mm), and

14 gravel % (≥2mm). Modelled hydrodynamic data for bottom current speed, bottom salinity, and bottom

15 temperature were extracted from the high-resolution Baltic Sea Ice-Ocean Model (BSIOM) (Lehmann et al.

16 2014). These data were back-calculated at a monthly scale, averaged over the 12 months prior to sampling,

17 and based on 2 x 2 km grid cells. Due to the comparatively coarser resolution of the environmental data, a

18 single value was applied to each replicate within a site.

19 **2.5. Biological trait composition**

20 Trait composition was described using 10 categories and 48 descriptive modalities (Table 1). The trait

21 information was provided by a database developed by the EU-funded BENTHIS project (http://www.

22 benthis.eu/en/benthis.htm), and outlined in Bolam et al. (2017). The database was developed for studies of

23 fishing impacts on benthic ecosystems (Bolam 2014), and traits were included to reflect their functional

24 importance to macrofaunal assemblages, and their vulnerability and sensitivity to trawling. In the cases

25 where trait information was not included in the database (for ~10 species), information was supplemented

26 by available literature, and the BIOTIC database (www.marlin.ac.uk/biotic). A 'fuzzy coding' approach

27 (Chevenet et al. 1994) was used to describe trait information across each species. This approach was

28 preferred as species can often exhibit multiple modalities within a trait category, and as it indicates the

29 relative importance of the modalities. A score of 3 was assigned where species demonstrated full affinity to

30 a modalities (e.g. maximum body size). Conversely, if taxa exhibited multiple modalities per trait category, a

31 score was assigned relative to its importance (e.g. the brittlestar *Amphiura filiformis* is a deposit feeder and

1   a facultative suspension feeder, thus scored as suspension = 2 and surface deposit = 2). The fuzzy coding

2   approach also facilitates the description of uncertainty in trait information. While some trait information (e.g.

3   morphology) is widely available, other traits (e.g. longevity) are not documented for large numbers of taxa.

4   In such cases, scores could be assigned to more than 1 modality, and were assigned based on the most closely

5   related taxa following a best professional judgement approach (Bolam 2014). After coding, trait scores were

6   standardised to 1 within each trait category. A trait-by-site matrix was calculated by averaging the trait scores

7   across each species and then multiplying by the relative biomass of that species. This resulted in a value for

8   each modality per sample, also known as a community-weighted mean (CWM). Biomass was selected (rather

9   than density) as it is considered a more appropriate determinant of an organism's role in ecosystem

10   functioning than abundance (Bolam & Eggleton 2014). Absolute CWM trait values were preferred (as oppose

11   to relative values) to preserve spatial and temporal contrasts in trait biomass across the study area

12   (Beauchard et al. 2017).

13   **Table 1. Biological trait categories and modalities used in the study.**

Trait category	Trait modality	Code	Hypothesized relationship
Feeding mode	Parasite Predator Scavenger/Opportunist Subsurface deposit Surface Deposit Suspension	F_para F_pred F_scav F_subs F_surf F_susp	Describes energy transfer (flow of carbon between sediment/water), vulnerability to disturbance, and has implications for number of biogeochemical processes (Rosenberg, 1995), while relative proportions can indicate community structure, and top down and bottom up dynamics of food web (Murillo et al. 2020). We would expect scavengers/predators to be more prevalent in trawled areas, with suspension feeders reduced due to physical damage from trawls or interference with feeding appendages from suspended sediments (De Juan et al. 2007, Tillin et al. 2006)
Larval Development	Direct Lecithotrophic Planktotrophic	LD_dire LD_leci LD_plank	Indicates potential of dispersal of larvae prior to settlement and associated ability to recover from disturbance. Planktonic (larvae feed and grow in water column) recruitment expected to provide potentially faster recruitment than lecithotrophic larvae (larvae use yolk sac), while direct developers have weakest ability to recolonise areas (Thrush & Whitlash, 2001).
Egg development	Asexual/Budding Sexual: benthic eggs Sexual: brood eggs Sexual: pelagic eggs	ED_asex ED_benth ED_brood ED_pele	Indicates dispersal potential of egg stage and potential vulnerability to physical damage. Eggs dispersed in the benthic zone or parental brooders are more susceptible to trawling impacts than pelagic eggs. Asexual reproduction can represent adaptation to disturbed conditions (Wangensteen et al, 2016) and may be more common in regularly fished areas.
Mobility	Burrower Crawl/creep/climb Sessile Swim	M_burr M_crawl M_sess M_swim	Increased mobility is likely to reduce likelihood of damage or capture by trawls, while also being indicative of ability to migrate into disturbed areas. Conversely, slow moving sessile and crawling species will be more vulnerable to

			changes in their environment and therefore trawling (Kenchington et al 2007)
Size range	<10 mm 11-20 mm 21-100 mm 101-200 mm 201-500 mm ≥500 mm	S_<10 S_11-20 S_21-100 S_101-200 S_201-500 S_>500	Indicative of a wide range of biological and ecological dynamics, inducing trophic positon, productivity, trophic position, metabolic rate, and generation time. Key function relates to the movement of organic matter in the benthic system, with larger organisms holding more (low turnover) compared to small-bodies species (high turnover) (Pearson & Rosenberg, 1978). Expected that trawling will reduce biomass of large fauna, while small bodied fauna will be relatively prevalent (Bremner 2008)
Longevity	<1 year 1-3 years 3-10 years ≥10 years	L_1 L_1-3 L_3-10 L_>10	Indicates relative age of sexual maturity, a proxy of relative r- and k-strategy (Pearson & Rosenberg, 1978), and investment of energy in somatic growth. Long-lived species are associated with relatively slow growth and turnover rates, and lower production. Such individuals are more common in unfished or infrequently disturbed areas (Rijnsdorp et al. 2018)
Morphology	Crustose Cushion Exoskeleton Soft Stalked Tunic	MO_crust MO_cush MO_exo MO_soft MO_stalk MO_tunic	Indicates the external characterises of an organism and vulnerability to physical damage. Soft e.g. are represented mainly by annelid species, exoskeleton by chitinous and calcareous shelled organisms, and crustose and stalked by sponges, hydroids and bryozoans. Individuals not covered by exoskeleton may be more easily damaged by trawl gear (e.g. Pham et al 2019)
Living habit	Attached Burrow-dwelling Crevice-dwelling Epi/endozoic/phytic Free-living Tube-dwelling	LH_attach LH_burr LH_crev LH_epi LH_free LH_tube	Indicates differing exposures to physical disturbance or ability to evade damage. May have implications for the topographic structure of seabed habitats. Chronic fishing can reduce species which form physical structures, or inhabit burrows and crevices, while the relative dominance of free-living fauna may increase (Kaiser et al 2000).
Sediment position	Surface 0-5cm deep 6-10cm deep ≥10cm deep	SP_surf SP_0-5 SP_6-10 SP_>10	Position of organisms within the sediment, and indicates role in biogeochemical regulation via sediment/water nutrient and oxygen exchange. Organisms present in surface sediments will be relatively susceptible to damage from trawling, compared to those that occur in deeper sediments (Hiddink et al 2017). However, deeper-living fauna may also be vulnerable to heavy fishing gears.
Bioturbation	Diffusive-mixing Downwards conveyer Non-bioturbator Surface deposition Upward Conveyor	B_diff B_down B_none B_surf B_up	Sediment reworking dynamics of organisms, and indicates potential for fauna-mediated biogeochemical properties and processes such as sediment-water exchange (Sandnes et al, 2000). Expected that trawling may impact bioturbating fauna, with those that diffuse surface sediments or form burrows at the surface potentially vulnerable (Olsgard et al 2008).

2.6. Statistical approach

Analysing trait composition & determining sensitive traits

Analyses of trait composition were carried out using multivariate distance-based linear models (DistLMs), which fit a relationship between community composition data and environmental variables (predictors). The

routine follows a distance-based redundancy analysis (dbRDA) approach (Legendre & Andersson 1999), where constrained ordinations are undertaken using non-Euclidean distance measures. Trait values were log transformed (log(x+1)), and resemblance matrices were calculated using Bray-Curtis similarity. The selection of predictors in the DistLM final model was achieved using an automated step-wise sequential test and small-sample size corrected Akaike information criterion (AICc) (Anderson et al. 2008). DbRDA plots were used to visualise the models, which include vector overlays that indicate the strength and direction of the included predictors. Multiple partial correlations (Pearson's R) were calculated based on the vector overlays, and coefficients used to determine the relative importance of the predictors in each of the datasets. Using a similar approach, the most 'sensitive' trait modalities in each dataset were identified by examining the strength of correlation between each modality and the axis of the redundancy plot that correlated with trawling. The larger the correlation coefficient, the greater contribution of that modality to the dbRDA ordination. While the approach cannot quantify the effect of individual predictors, it is suitable to generate exploratory hypotheses from multivariate data (Anderson et al. 2008). We therefore used the correlation coefficients to rank the sensitivity of each individual modality, and highlighted 10 modalities from each dataset with the largest coefficients. These were combined to provide a composite list of sensitive traits (Table 3b). Analyses were carried out using PRIMER v.7 (Clarke & Gorley 2015) with PERMANOVA+ (Anderson et al. 2008).

Analysis of trait sensitivity to trawling disturbance

Based on the composite list of sensitive traits, we then selected those which exhibited a significant response to dbRDA1 in more than one of the fractions/datasets. The remaining 16 trait modalities were analysed using generalised linear mixed effects models (GLMMs), an approach considered suitable for the quantification of potential correlations in repeated measure designs (Bolker et al. 2009). As the trait values were non-negative, continuous, right skewed, and contained zeros, we applied a Tweedie distribution in the GLMMs (Foster & Bravington 2013). The GLMMs were fitted with a log-link using the glmmTMB package (Brooks et al. 2017). Model selection was undertaken using backwards elimination of model terms based on likelihood ratio tests. Model diagnostics were checked using the DHARMa package (Hartig, 2016). Although collinearity is not necessarily a problem in multiple regression (Morrissey and Ruxton, 2018), all predictors (including trawling) were checked for multicollinearity prior to formal statistical analysis. Pair-wise plots were used to calculate correlation coefficients. All correlations were ≤0.7 (Table S2), meaning that all predictors could be included in the analysis (Dormann et al. 2013) . Additionally, variance inflation factor (VIF) values were checked for models containing all predictors for each dataset. While some level of correlation was present, the VIFs were all below the acceptable threshold of 5 (Kutner et al. 2004). The marginal effects of trawling on each trait

modality were visualised using the 'sjPlot' package (Lüdecke 2016). Plots were based on predicted values from the GLMMs, and are conditional of the effects of the other predictors (environmental variables) included in the final model. All analyses were conducted using R version 3.5.0 (R Development Core Team, 2019).

Other analyses

We examined differences in environmental variables between the KS16 and NOVANA surveys using non-parametric Kruskal–Wallis tests (Kruskal and Wallis, 1952). A comparison of the inter-annual variability of trait data and the underlying species data was undertaken to investigate which data type was more temporally stable. To do this, we used an ANOSIM (Analysis of Similarity) routine (Clarke & Gorley 2015) on all years of the NOVANA data. The routine provides scaled measures (R values) of the effect size of a given factor (in our case 'year'), allowing for the trait and species matrices to be compared directly.

1 **3. Results**

2 **3.1. Comparison of data sources**

3 Due to the respective sizes of the 0.1 m^2 Van Veen grab sampler (KS16) and 0.0143m^2 Haps corer (NOVANA),

4 the area of seabed examined between the two surveys was relatively similar, despite the differences in

5 sampling effort (Table 2). The total number of taxa sampled in the KS16 full community (285) was, however,

6 lower than the NOVANA data (368). Size fractionation of the KS16 data resulted in fewer species recorded in

7 the large (144) than the small fraction (259), although the large fraction accounted for ~90% of biomass. All

8 48 trait modalities were recorded in the KS16 and NOVANA surveys. Comparisons of trait modalities observed

9 between surveys (Figure 2) revealed the commonality of modes such as '0-5cm deep' (sediment position

10 category), 'exoskeleton' (morphology), 'pelagic eggs' (egg development), and 'planktotrophic' (larval

11 development) across species. The proportional representation of modalities within categories were largely

12 comparable between surveys, with only minor differences observed in a small number of modalities e.g.

13 'sessile', 'surface deposit feeder' and 'benthic eggs'. Inter-annual variability of trait data was found to be less

14 than that of species data. This was revealed by the statistically significant and greater effect of 'year' on

15 species composition (R = 0.11. p = 0.001) than on trait composition (R = 0.04. p = 0.05), which was of

16 borderline significance.

17 **Table 2. Summary of sampling effort, benthic community parameters, bottom trawling intensity, and**

18 **environmental variables associated with the KS16 (2016) and NOVANA surveys (2005-2013).**

	KS16 (2016)			NOVANA (2005 – 2013)
	Large fraction	**Small fraction**	**Full community**	**Full community**
Size fraction	≥4 mm	1 – 4 mm	≥1 mm	≥1 mm
Number of samples	84			827
Number of surveys	1			7
Area sampled	8.4 m^2			11.8 m^2
CWM trait modalities represented	46	48	48	48
Total biomass (g)	199.04*	21.46*	220.50*	4,814.13[†]
Total number of taxa	144	259	285	368
Trawling intensity range (mean)	0 - 12.6 (3.8 yr^{-1})			0 - 14.8 (3.4 yr^{-1})
Current speed range (mean)	0.4 - 4.1 (1.6 cm/s)			0.7 – 7.0 (2.5 cm/s)
Depth range (mean)	16.3 - 81 (38 m)			13 – 55 (24 m)
Mud content range (mean)	3.6 - 97 (41 %)			1.1 - 94.7 (26 %)
Min salinity range (mean)	21.6 - 34.5 (32 PSU)			14.4 - 34.5 (29 PSU)
Temperature range (mean)	6.2 - 8.9 (7.6 °C)			5.2 - 9.3 (7.6 °C)
* Ash free dry weight biomass [†] Wet weight (blotted) biomass				

1   Average trawling intensity (KS16: 3.8 yr^{-1}, NOVANA 3.4 yr^{-1}) and range (KS16: 0 - 12.6 yr^{-1}, NOVANA 0 - 14.8

2   yr^{-1}) were similar between surveys (Kruskal-Wallis, p = 0.58), indicating that the trawling gradient sampled in

3   2016 was representative of longer term trawling activities. On the other hand, environmental conditions

4   were less comparable (Table 2). Current speed was generally higher at the NOVANA sites (Kruskal-Wallis, p =

5   <0.001), while depth, mud content, and salinity were all lower (all Kruskal-Wallis, p = <0.001). Temperature

6   was, however, similar between the surveys (Kruskal-Wallis, p = <0.437). Correlations between trawling and

7   other environmental variables were found to be strongest between trawling and mud (R = 0.58) in the KS16

8   data, and between trawling and depth (R = 0.6) in the NOVANA data (Table S2). All relationships were within

9   acceptable thresholds (Kutner et al. 2004; Dormann et al. 2013), meaning that their respective effects can

10   be interpreted independently. A summary of all trawling and environmental values per site is provided in

11   Table S3 of the Supplement.

1
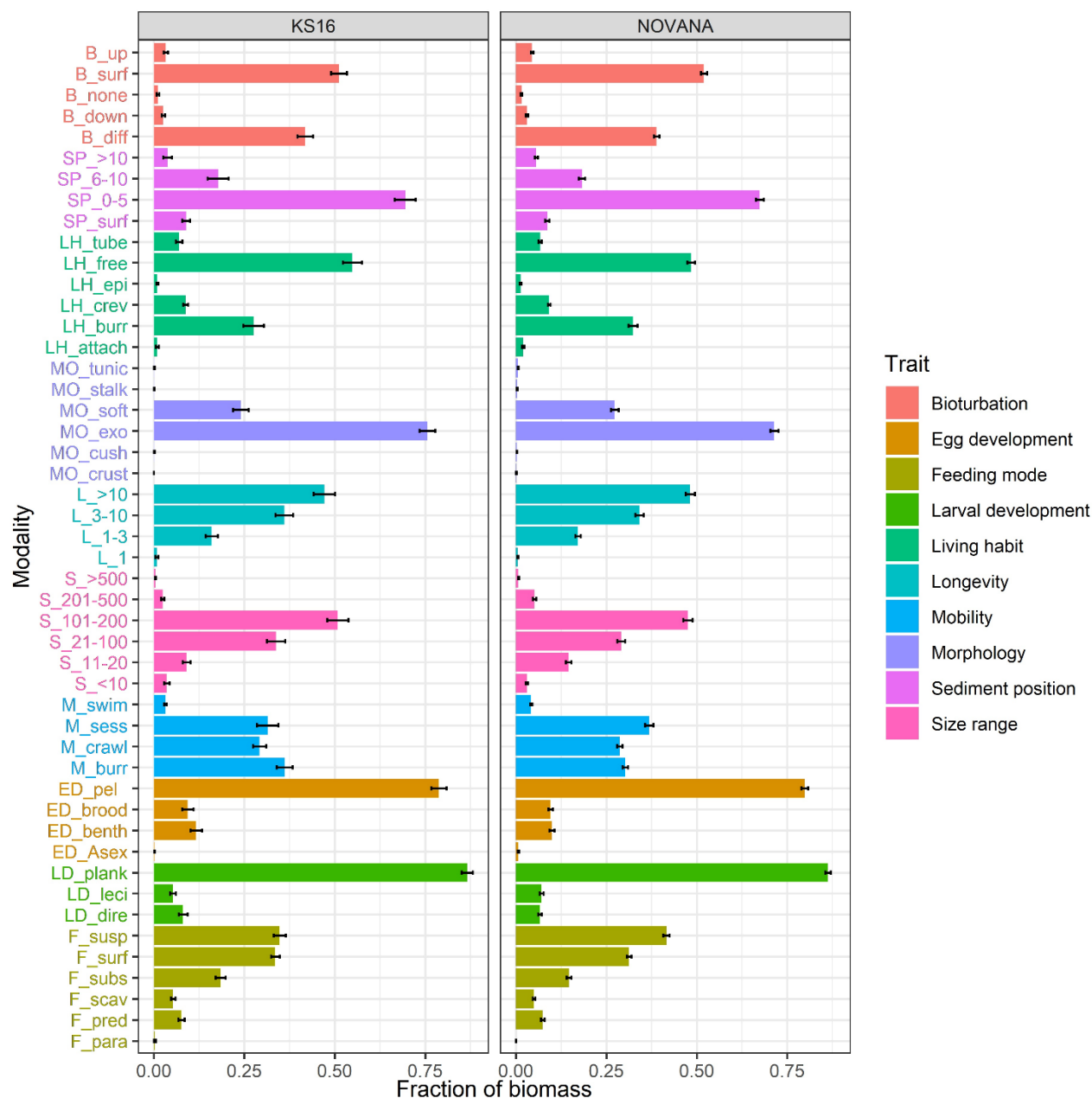
Figure 2: Proportion of CWM trait modalities observed in the KS16 (2016) and NOVANA (2005 − 2013) datasets. Error bars: SE. Trait codes are defined in Table 1.

3.2. Determining sensitive traits

Redundancy analysis ordinations showed that the primary axis (dbRDA1) explained the majority of trait variance. Furthermore, multiple partial correlations revealed that dbRDA1 was significantly correlated with trawling, temperature, and, in particular, depth in each dataset (Table 3a & Supplement – Figure S2). Salinity and mud content were also correlated with trait composition in the KS16 small fraction and NOVANA data.

1 This also revealed that the conditional effect of trawling on trait composition was relatively greater for the

2 KS16 large fraction (R = 0.45). The variance in trait data explained by predictors was low in the NOVANA data

3 (3.3% explained by dbRDA1), compared to that of the KS16 full community (18.2% by dbRDA1). This was

4 further highlighted by the differences in site ordinations in Figure S2 a-d. In these plots, the positions of sites

5 are constrained by the predictors included in the model, thereby indicating relatively different environmental

6 conditions at KS16 and NOVANA sampling sites. The low degree of trait variance explained in the NOVANA

7 data indicates a poor match with the environmental variables, and the possible influence of other non-

8 measured variables at these locations.

9 Correlations between modalities and dbRDA1 were estimated in each dataset, and a composite list of the

10 ten most sensitive traits (strongest correlations) from each is outlined in Table 3b. Most of these 22 trait

11 modalities exhibited negative correlations in both KS16 and NOVANA surveys. The exceptions to this were

12 'diffuse mixing', 'predator', 'lecithotrophic' and 'soft', which were only identified in the KS16 dataset. A

13 negative correlation indicated a decline in trait biomass with increasing trawling intensity, depth,

14 temperature, mud content, and salinity. On the other hand, 'crevice dwelling' and 'free-living' modalities

15 exhibited positive relationships with dbRDA1, indicating an increase in trait biomass with increasing trawling

16 intensity and environmental parameters. Positive correlations were also observed for short-lived fauna ('<1

17 year'), however, these relationship were comparatively weaker and outside the ten most sensitive traits in

18 each fraction. For the next step of the analysis, we selected the modalities which exhibited a significant

19 response to dbRDA1 in more than one of the fractions/datasets. This resulted in the omission of 'non-

20 biotubator', 'diffuse-mixing', 'predator', 'free-living', '1-3years', and '21-100 mm' from further analysis.

21 **Table 3. (a) Multiple partial correlation coefficients (Pearson's R) between environmental variables**
22 **associated with the KS16 (2016) and NOVANA (2005–2013) surveys and main axis of redundancy plots**
23 **(dbRDA1), (b) correlation coefficients between trait modalities and dbRDA1. The 10 strongest correlations**
24 **are highlighted in bold for each dataset. In both (a) and (b), + or − indicates a positive or negative**
25 **relationship, respectively, and blank entries corresponds to a non-significant relationship**

	KS16 (2016)			NOVANA (2005 – 2013)
	Large faction	Small fraction	Full community	Full community
(a)				
Environmental variable	Pearson's R			
Current speed				
Depth	0.75	0.82	0.83	0.37
Mud				0.81
Salinity			0.35	-0.29

Temperature		0.49	0.34	0.30	0.13
Trawling		0.45	0.30	0.41	0.13
dbRDA1 explained variance		12.4%	19.9%	18.2%	3.3%

(b)

Trait	Modality	Pearson's R			
Bioturbation	Surface deposition	**-0.49**	-0.36	**-0.51**	-0.13
	Non-bioturbator	-0.33			**-0.21**
	Diffusive mixing		**-0.43**		
Egg development	Pelagic eggs	**-0.48**	**-0.52**	**-0.5**	-0.16
Feeding mode	Predator		**-0.45**		
	Subsurface deposit	-0.36	**-0.43**	-0.4	-0.15
	Suspension	**-0.52**	-0.32	**-0.55**	**-0.20**
Larval development	Lecithotrophic	-0.23	**-0.46**	-0.4	
	Planktotrophic	**-0.48**	-0.41	**-0.5**	-0.15
Living habit	Crevice-dwelling	-0.35	-0.26	-0.34	**+0.42**
	Free-living		-0.41		**+0.21**
	Tube-dwelling	**-0.47**		-0.47	-0.13
	Burrow-dwelling	-0.43	**-0.41**	**-0.48**	**-0.26**
Longevity	1-3 years			-0.38	**-0.20**
	≥10 years	**-0.50**	-0.29	**-0.51**	-0.16
Mobility	Sessile	**-0.47**	**-0.45**	**-0.51**	**-0.24**
Morphology	Exoskeleton	**-0.47**	-0.34	**-0.49**	-0.15
	Soft	-0.37	**-0.51**	**-0.54**	
Sediment position	0-5cm deep	-0.33	**-0.47**	-0.38	**-0.23**
	6-10cm deep	**-0.45**	**-0.53**	-0.47	**-0.23**
Size range	21-100mm		-0.28		**-0.22**
	101-200mm	**-0.49**	-0.31	**-0.49**	-0.11
Pearson correlation critical values: KS16 = 0.21 & NOVANA = 0.07					

1

3.3. Trait sensitivity to trawling disturbance

Of the remaining 16 trait modalities, GLMMs revealed that 10 were negatively impacted by trawling intensity in the KS16 large fraction. These included 'suspension', 'planktotrophic', 'sessile', 'surface deposition', '≥10 years', '6-10cm deep', 'tube-dwelling', 'subsurface deposit', 'soft', and 'burrow-dwelling'. By comparison, 7 of these 10 modalities were impacted by trawling in the KS16 full community (exceptions being '≥10 years', 'soft' and '6-10cm deep') and similarly, 7 of the 10 were impacted by trawling in the NOVANA full community (exceptions being 'suspension', 'burrow-dwelling', and 'soft') (Table 4, Figure 3 & 4). Accordingly, traits impacted by trawling in the KS16 full community and NOVANA data were both a subset of those identified in the large fraction, potentially indicating the importance of these in driving sensitivity at the community level. Responses observed in the NOVANA data were also most comparable with the results from the large fraction. The traits of 'burrow-dwelling', 'sessile', and 'subsurface deposit' feeders were the only modalities impacted across all KS16 datasets (large, small and full community). In the case of 'sessile' and 'subsurface deposit', these modalities responded across the KS16 and NOVANA datasets, potentially indicating highly sensitive traits. Summary model outputs for all GLMMs are provided in Table S4 of the Supplement.

Table 4. Summarised results of GLMMs for CWM trait modalities associated with the KS16 (2016) and NOVANA (2005−2013) surveys. Significant relationships with trawling are shown with an 'x'. Significant relationships with environmental variables are shown in the 'other' column, where C = bottom current speed, D = depth, M = mud content, T = bottom temperature, S = bottom salinity. Direction of the relationship is shown as positive (+) or negative (-). Model coefficients of determination (R^2) provided as conditional R^2 values (both marginal and random effects combined).

| Trait	Modality	KS16 (2016)									NOVANA (2005 – 2013)		
		Large fraction			Small fraction			Full community			Full community		
		Trawling	Other	R^2	Trawling	Other	R^2	Trawling	Other	R^2	Trawling	Other	R^2
Bioturbation	Surface deposition	x-	D-, T-	0.67		S-, T+	0.44	x-	D-	0.69	x-	C+, M-, S+	0.43
Egg development	Pelagic eggs		D-, T-	0.58		S-, T+	0.40		C+, D-, T-	0.62		S+, T+	0.42
Feeding mode	Subsurface deposit	x-	T-	0.64	x-		0.52	x-	T-	0.62	x-	C+, M-, S+	0.13
	Suspension	x-	D-	0.69		S-, T+	0.48	x-	D-	0.72		C+, M-	0.43
Larval development	Lecithotrophic		S-	0.27		M-, S-	0.51		S-	0.24		D-,M-,T-	0.17
	Planktotrophic	x-	D-	0.58		S-, T+	0.42	x-	D-	0.61	x-	C+, S+	0.41
Living habit	Crevice-dwelling		D-	0.64			0.47		D-	0.69		C+, D+, S-, T+	0.21
	Tube-dwelling	x-	T-	0.80		M-, T-	0.81	x-	T-	0.87	x-	C+, M-, T-	0.82
	Burrow-dwelling	x-		0.77	x-	C-, D-	0.64	x-	M-,T-,	0.79		D-, M-	0.49
Longevity	≥10 years	x-	D-	0.70		D-	0.67		D-, T-	0.69	x-	C+, D+, T+	0.41
Mobility	Sessile	x-	D-	0.83	x-	C-	0.74	x-	D-	0.82	x-	C+, M+, S+, T-	0.90
Morphology	Exoskeleton		C+, D-, T-	0.57		T+	0.52		D-, T-	0.61		C+, S+	0.29
	Soft	x-	T-	0.63		M-, S-	0.58		M-,T-,S-	0.58		C+, D-, S+, T-	0.57
Sediment position	0-5cm deep		D-	0.44		D-	0.39		S-	0.53		C+, M+, S+	0.18
	6-10cm deep	x-	D-, T-	0.83		M-, S-	0.67		D-, T-	0.81	x-	C+, D-, M-, S+	0.67
Size range	101-200mm		D-, T-	0.68		S-, T+	0.48		D-, T-	0.70		C+, M+	0.52

1
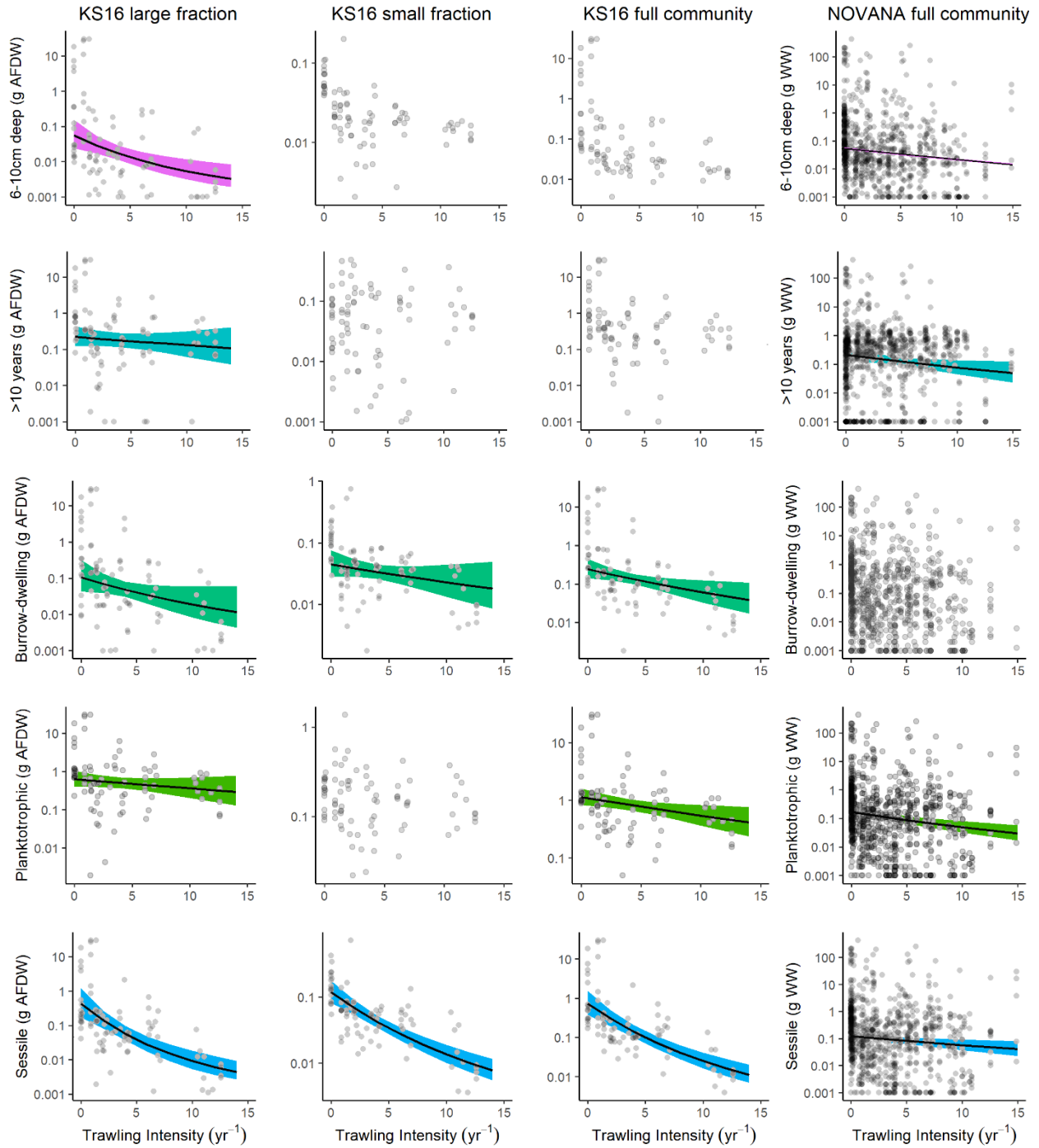
Figure 3. Relationships between trawling intensity and the trait modalities '6-10cm deep', '≥10 years', 'burrow-dwelling', 'planktotrophic', and 'sessile'. Regression lines denote a significant relationship, based on the predicted values from GLMMs presented in Table 4. The raw observations are overlaid as data points. Coloured areas represent 95% confidence intervals, and colours represent trait categories shown in Figure 2. To aid visual interpretation, trait biomass are presented on a log scale. AFDW: ash-free dry weight. WW: wet weight.
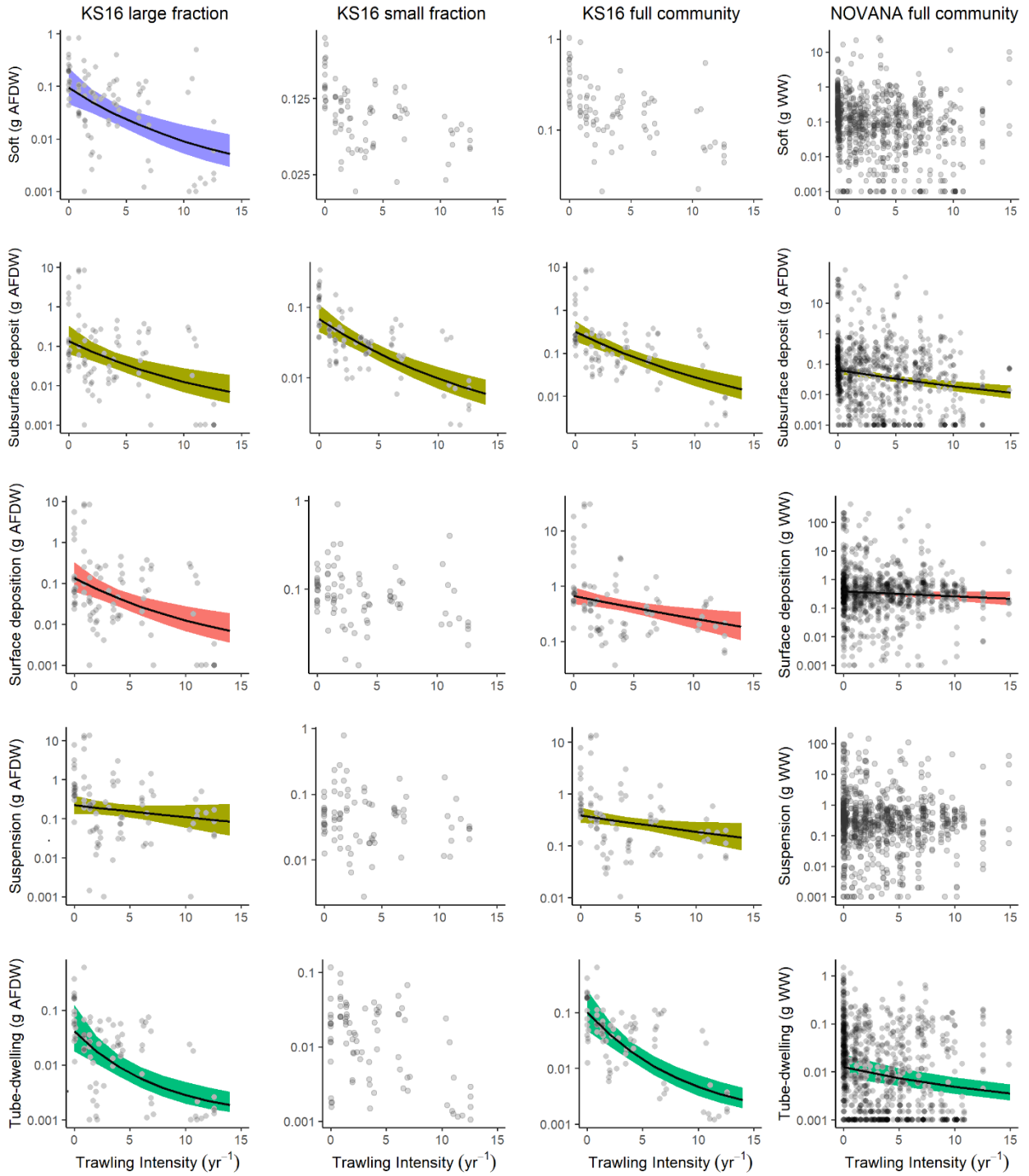
Figure 4. Relationships between trawling intensity and the trait modalities 'soft' 'subsurface deposit', 'surface deposition' 'suspension', and 'tube-dwelling'. Other details as in Fig. 3.

4. Discussion

Monitoring and assessing trawling impacts to the seabed require metrics that accurately describe ecological condition, and acutely respond to changes that occur as a result of fishing. This dual capability is important as seabed communities will vary naturally across fishing grounds, and in relation to gradients in e.g. salinity, sediment type, and depth (Rice et al. 2012, Gislason et al. 2017, Hiddink et al. 2020). Our results highlight a number of benthic species traits that were able to distinguish trawling impacts from the effects of other environmental drivers, while also reflecting key functional and ecological community characteristics. Furthermore, the observed relative sensitivity of large benthos and their traits would indicate a size-dependent effect of trawling on the functional properties of the community. In the following sections we elaborate on these results, discuss their underlying causes, and highlight the implications of our findings from an ecological and management standpoint.

Of the 48 life history modes examined, 10 exhibited by large-bodied fauna were significantly impacted by trawling, with 7 of these impacted at the community level. While the relative sensitivity of larger individuals to trawling disturbance is well documented (Kaiser et al. 2000, McLaverty et al. 2020a, Pitcher 2000, Queirós et al. 2006), we highlight specific traits which may be denuded or lost due to trawling, and those which may be potentially overlooked in assessments based on the full community ('≥10 years', '6-10cm deep', and 'soft' were only impacted in the large fraction). For example, the biomass of large bodied burrow-dwellers, subsurface deposit feeders ('subsurface deposit'), and surface-depositing bioturbators ('surface deposition') were significantly affected by trawling in our study. Large bodied fauna which share these traits are responsible for a significant proportion of sediment bioturbation and reworking (Sandnes et al. 2000), improving nutrient fluxes and benthic production (Lohrer et al. 2004), and provide substantial sources of labile carbon available for higher trophic levels (Ellingsen et al. 2007, Hiddink et al. 2016). Given the dominant functional role of large individuals in processes such as oxygen and nutrient fluxes and nutrient regeneration (Thrush et al. 2006, Norkko et al. 2013), the loss of large individuals and their traits is likely to have strong negative implications for seabed ecosystem functionality.

The range of trait responses observed in our results illustrates how trawling can potentially impact several seabed functions, while providing insights into the potential mechanism of sensitivity. Modalities such as '6-10 deep', '≥10 year', and 'surface deposition' were all highly sensitive to trawling, and also chiefly accounted for by large bivalve taxa (e.g. *Arctica islandica*, *Thracia* spp.), the common heart urchin (*Echinocardium cordatum*), and the slender sea pen (*Virgularia mirabilis*). Marine bivalves are often a key component of macrofauna-mediated benthic processes (Dame 2016), but experience high mortality rates from trawling (Rumohr & Krost 1991, Bergman & van Santbrink 2000). Species such as *Arctica islandica* are periodically

deep-living in the sediment, and exhibit a remarkable lifespan that can exceed 400 years (Abele et al. 2008; Morton 2011). Their large size can contribute up to half of total benthic community production (Brey et al. 1990), and large bivalves are important bioturbators of deeper sediment layers (Morys et al. 2017). Similarly, the activity of species such as *E. cordatum* facilitates the exchange of water and oxygen in surface sediments (Forster & Zettler 2004), while *V. mirabilis* play a key role in deep sediment irrigation (Osinga et al. 1995). These species are, however, relatively vulnerable to physical damage due to their brittle test (*E. cordatum*) and soft feeding appendages (*V. mirabilis*), and trawling-induced declines have been observed in the Kattegat and North Sea (Bergman & van Santbrink 2000, Sköld et al. 2018). As the physical impact of trawling affects these same sedimentary and biogeochemical processes (Sciberras et al. 2016, Tiano et al. 2019), reductions in biologically-mediated functions such as bioturbation may exacerbate impacts to soft sediment environments.

Similarly trawling sensitive traits included those of filter-feeding ('suspension'), non-mobile ('sessile'), and tube-dwelling benthos. Large-bodied filter feeders attached or lodged in the sediment are considered to be characteristic of undisturbed seabed environments (Bremner et al. 2005), and given their prominent position, are easily impacted by demersal gears (Kaiser et al. 1998, 2000, Sciberras et al. 2018). This is as suspension feeders typically possess fragile feeding appendages, which are vulnerable to physical damage and clogging from sediment resuspension (Jennings & Kaiser 1998). From a functional perspective, filter feeders play an important role in benthic-pelagic coupling (Griffiths et al. 2017), nutrient cycling, and the transfer of organic material into the sediment matrix (Rosenberg 2001, Lohrer et al. 2004). Although mobile fishing gears are known to negatively impact populations of tube-dwelling benthos (Collie et al. 1997, Kenchington et al. 2006, Hinz et al. 2009), few trait-based studies have highlighted tube-dwelling as a sensitive trait at the community level. In our study, unfished sites were characterised by a high biomass of maldanid (e.g. *Rhodine gracilior and Maldane sarsi*) and terebellid annelids (e.g. *Anobothrus gracilis*), as well as taxonomically distinct phoronid worms (*Phoronis* spp.). Tube-building fauna typically live at the sediment surface-water interface and are generally slow to recolonise disturbed areas (Bolam & Fernandes 2002). Given that most gradient studies lack unfished sites or true reference conditions (Hiddink et al. 2017), this may mean that densities of tube-builders may remain low even at historically impacted sites, or at relatively low trawling intensity. A potentially important implication of losing these traits from fishing grounds would be that tube-builders are ecosystem engineers, actively modifying their surrounding habitats. Tube-building fauna support increased benthic diversity (Bolam, 1999; Tendal and Dinesen, 2005), improve sediment stability (Noji & Noji 1991, Friedrichs et al. 2000) and conditions for larval settlement (Bolam & Fernandes 2003), and increase food supply for other benthic species (Holte 2001).

Size-separating the KS16 data also provided new insights into how the traits of small-bodied macrofauna respond trawling. While many traits differed in their response to trawling between size fractions, burrow-dwelling, non-mobile ('sessile'), and subsurface deposit feeding ('subsurface deposit') fauna were impacted in both the large and small fractions, as well the KS16 full community. This would suggest that the effects of trawling were equivalent, and not size-dependent, for these traits. While trawling is known to impact size classes <1 mm (Hinz et al. 2008), detecting impacts in communities dominate by small-fauna is often highly challenging (Jennings et al. 2002). The identification of traits which are sensitive to trawling regardless of size may therefore be useful in this regard, and furthermore, may be of relevance to less productive or disturbed systems which support fewer large-bodied fauna. While size-separating the community using a 4 mm mesh size improved the detection of trawling effects in sand dominated areas of the southern North Sea (H. Reiss et al, 2009), and in studies where abundance is used as oppose to biomass (McLaverty et al 2020a), our approach requires further validation and testing across different habitat types and regions.

Given the clear size-based effects observed in this study, our results may have practical implications for the management and monitoring fishing impacts on the seabed. Aside from the classic approach of distinguishing benthos as infauna and epifauna (somewhat a proxy of size), body-size thresholds are not commonly applied in benthic impact assessments. By comparison, the use of thresholds are well established for monitoring the effects of fishing on fish populations (Shin et al. 2005). A well-known example of a body-size threshold is the 'Large Fish Indicator' (LFI). The LFI was first applied in the North Sea to indicate the state of fish stocks, by estimating the proportion of the fish community over a given length threshold (40cm in the North Sea) (Greenstreet et al. 2011). As well as being sensitive to fishing, using a proportion of the community larger than a specific value has the advantage of being easy to communicate and calculate, providing that sampling gear and methodology is consistent (Rice et al. 2012). Accordingly, such approaches have the potential to be particularly useful for benthic community studies, where a single sample may contain thousands of individuals and >100 species. It should be noted, however, that the use of body-size thresholds should be tailored to specific scientific hypothesis, or the goal of a given monitoring program, as information on the whole community may be required for certain studies, such as biodiversity based assessments. Compared to a full community approach, a large amount of ecological information can be potentially lost by size-segregating the community. This is as relatively fewer species are represented by large individuals, and comparatively less information regarding community composition and biodiversity can be conveyed by only the large fauna (Pinto et al. 2009).

The similarity of results between a one-time snapshot survey (KS16 large fraction) and a multi-year monitoring dataset (NOVANA programme) suggests that spatial patterns in large fauna traits are reflective

of long-term or chronic trawling impacts. Due to limitations of resources, practicality, and the relatively short cycles associated with research funding, relationships between ecological units and their environment are most often investigated using snapshot surveys (Fisher et al. 2010). Despite this, ecological communities vary from year-to-year, particularly in dynamic systems, meaning that these surveys can be limited in their ability to overcome this variation. On the other hand, datasets based on larger or longer-lived individuals are potentially less affected by 'noise' caused by inter-annual variations in recruitment (Greenstreet et al. 2011). The biomass-weighted traits of large benthic fauna may represent a feature of benthic communities which are particularly sensitive to trawling impacts, and may be useful as a metric to track and monitor trawling impacts between locations and over time. Furthermore, large fauna represent a relatively small subset of the total community (<25% of the total number of individuals in the KS16 data), and therefore require significantly less laboratory processing times.

5. Perspectives

Trait-based approaches have the advantage of being able to describe the functional and ecological characteristics of benthic communities, and interpret how trawling can alter their structure and composition. Trait information can consequently be used to track and monitor benthic functionality, as well as seabed ecosystem services such as productivity, nutrient cycling, and biodiversity maintenance. In this study, we have demonstrated a size-based sensitivity of several species traits to trawling disturbance, and outlined some of the mechanisms which may underpin their sensitivity. Given the importance of many of these traits in benthic processes, it is likely that the decline or loss of these traits can have considerable implications for the functioning of seabed ecosystems across fishing grounds. In addition, marine ecosystems are currently experiencing considerable changes in local and regional species pools due to e.g. increased human activity and climate change. These aspects together have the potential to alter the functional resilience of seabed ecosystems (Oliver et al. 2015). In light of our results, and as body-size is widely regarded as an ecological driver of ecosystem function (Woodward et al. 2005, J. Reiss et al. 2009), we suggest that greater attention should be paid to size-based methods to meet the requirements of benthic habitat assessments under a fully integrated Ecosystem Approach to Fisheries Management (EAFM). Monitoring ecological systems is often constrained by high ecosystem complexity, and it is therefore crucial to identify and develop methods which effectively distil complex information into metrics of ecological impact and state, which are easy to use, interpret, and communicate. It is hoped that the results of this study can inform future assessments of the ecosystem effects of fishing, using functionally relevant traits that are common across habitat types and geographic areas.

Acknowledgements

Supplementary information

See Supplement below.

References

Abele, D., Strahl, J., Brey, T., Philipp, E.E.R., 2008. Imperceptible senescence: Ageing in the ocean quahog Arctica islandica. Free Radic. Res. 42, 474–480. https://doi.org/10.1080/10715760802108849

Abrego, N., Norberg, A., Ovaskainen, O., 2017. Measuring and predicting the influence of traits on the assembly processes of wood-inhabiting fungi. J. Ecol. 105, 1070–1081. https://doi.org/10.1111/1365-2745.12722

Anderson, M.J., Gorleyt, R.N., Clarket, K.R., 2008. PERMANOVA + for PRIMER : t. Guid. to Softw. Stat. Methods 1, 186. https://doi.org/10.1016/j.isatra.2014.07.008

Anon (2000) Directive 2000/60/EC of the European Parliament and of the Council establishing a framework for the Community action in the field of water policy (Water Framework Directive).

Anon (2008) Directive 2008/56/EC of the European Parliament and of the Council establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive).

Atkinson, L., Field, J., Hutchings, L., 2011. Effects of demersal trawling along the west coast of southern Africa: multivariate analysis of benthic assemblages. Mar. Ecol. Prog. Ser. 430, 241–255. https://doi.org/10.3354/meps08956

Beauchard, O., Veríssimo, H., Queirós, A.M., Herman, P.M.J., 2017. The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. Ecol. Indic. 76, 81–96. https://doi.org/10.1016/j.ecolind.2017.01.011

Bergman, M.J.N., Van Santbrink, J.W., 2000. Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994, in: ICES Journal of Marine Science. pp. 1321–1331. https://doi.org/10.1006/jmsc.2000.0917

Bolam, S.G., 1999. An investigation into the processes responsible for the generation of the spatial pattern of the spionid polychaete Pygospio elegans Claparede. PhD thesis, Napier University of Edinburgh.

Bolam SG. 2014 Predicting the effect of trawling based on biological traits of organisms and functional correlates of these traits to predict which functions may be disproportionally affected. BENTHIS Deliverable 4.3

Bolam, S.G., Coggan, R.C., Eggleton, J., Diesing, M., Stephens, D., 2014. Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: A biological trait approach. J. Sea Res. 85, 162–177. https://doi.org/10.1016/j.seares.2013.05.003

Bolam, S.G., Eggleton, J.D., 2014. Macrofaunal production and biological traits: Spatial relationships along the UK continental shelf. J. Sea Res. 88, 47–58. https://doi.org/10.1016/j.seares.2014.01.001

Bolam, S.G., Fernandes, T.F., 2002. Dense aggregations of tube-building polychaetes: response to small-scale disturbances. J. Exp. Mar. Bio. Ecol. 269, 197–222. https://doi.org/10.1016/S0022-0981(02)00003-5

Bolam, S.G., Fernandes, T 2003. Dense aggregations of Pygospio elegans (Claparede): effect on macrofaunal community structure and sediments. Journal of Sea Research 49.3 (2003): 171-185.

Bolam, S.G., Garcia, C., Eggleton, J., Kenny, A.J., Buhl-Mortensen, L., Gonzalez-Mirelis, G., van Kooten, T., Dinesen, G., Hansen, J., Hiddink, J.G., Sciberras, M., Smith, C., Papadopoulou, N., Gumus, A., Van Hoey, G., Eigaard, O.R., Bastardie, F., Rijnsdorp, A.D., 2017. Differences in biological traits composition of benthic assemblages between unimpacted habitats. Mar. Environ. Res. 126, 1–13. https://doi.org/10.1016/j.marenvres.2017.01.004

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. 24, 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Bremner, J., Frid, C.L.J., Rogers, S.I., 2003. Assessing Marine Ecosystem Health: The Long-Term Effects of Fishing on Functional Biodiversity in North Sea Benthos. Aquat. Ecosyst. Health Manag. 6, 131–137. https://doi.org/10.1080/14634980301470

Bremner, J., Frid, C.L.J., Rogers, S.I., 2005. Biological traits of the North Sea benthos: does fishing affect benthic ecosystem function? in: American Fisheries Society Symposium. 41: 477–489.

Bremner, J., Rogers, S., Frid, C., 2006. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecol. Indic. 6, 609–622. https://doi.org/10.1016/j.ecolind.2005.08.026

Brey, T., Arntz, W.E., Pauly, D., Rumohr, H., 1990. Arctica (Cyprina) islandica in Kiel Bay (Western Baltic): growth, production and ecological significance. J. Exp. Mar. Bio. Ecol. 136, 217–235. https://doi.org/10.1016/0022-0981(90)90162-6

Bremner, J., 2008. Species' traits and ecological functioning in marine conservation and management. J. Exp. Mar. Bio. Ecol. 366, 37–47. https://doi.org/10.1016/j.jembe.2008.07.007

Brooks, Mollie, E., Kristensen, K., Benthem, Koen, J., V., Magnusson, A., Berg, Casper, W., Nielsen, A., Skaug, Hans, J., Mächler, M., Bolker, Benjamin, M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. R J. 9, 378. https://doi.org/10.32614/RJ-2017-066

Chevenet, F., Doleadec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of long-term ecological data. Freshw. Biol. 31, 295–309. https://doi.org/10.1111/j.1365-2427.1994.tb01742.x

Charnov, E. L. 1993. Life history invariants. Oxford University Press, Oxford, UK.

Clarke KR, Gorley RN (2015) Primer v7: user manual/tutorial. PRIMER-E, Plymouth

Collie, J., Escanero, G., Valentine, P., 1997. Effects of bottom fishing on the benthic megafauna of Georges Bank. Mar. Ecol. Prog. Ser. 155, 159–172. https://doi.org/10.3354/meps155159

Collie, J.S., Hall, S.J., Kaiser, M.J., Poiner, I.R., 2000. A quantitative analysis of fishing impacts shelf-sea benthos. J. Anim. Ecol. 69, 785–798. https://doi.org/10.1046/j.1365-2656.2000.00434.x

Cook, R., Fariñas-Franco, J.M., Gell, F.R., Holt, R.H.F., Holt, T., Lindenbaum, C., Porter, J.S., Seed, R., Skates, L.R., Stringell, T.B., Sanderson, W.G., 2013. The Substantial First Impact of Bottom Fishing on Rare Biodiversity Hotspots: A Dilemma for Evidence-Based Conservation. PLoS One 8, e69904. https://doi.org/10.1371/journal.pone.0069904

Dame, R.F., 2016. Ecology of Marine Bivalves, Ecology of Marine Bivalves. CRC Press. https://doi.org/10.1201/b11220

Dayton, P.K., Thrush, S.F., Agardy, M.T., Hofman, R.J., 1995. Environmental effects of marine fishing. Aquat. Conserv. Mar. Freshw. Ecosyst. 5, 205–232. https://doi.org/10.1002/aqc.3270050305

de Juan, D., Thrush, S., Demestre, M., 2007. Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). Mar. Ecol. Prog. Ser. 334, 117–129. https://doi.org/10.3354/meps334117

De Juan, S., Demestre, M., 2012. A Trawl Disturbance Indicator to quantify large scale fishing impact on benthic ecosystems. Ecol. Indic. 18, 183–190. https://doi.org/10.1016/j.ecolind.2011.11.020

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography (Cop.). 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Duplisea, D.E., Jennings, S., Warr, K.J., Dinmore, T.A., 2002. A size-based model of the impacts of bottom trawling on benthic community structure. Can. J. Fish. Aquat. Sci. 59, 1785–1795. https://doi.org/10.1139/f02-148

Eigaard, O.R., Bastardie, F., Breen, M., Dinesen, G.E., Hintzen, N.T., Laffargue, P., Mortensen, L.O., Nielsen, J.R., Nilsson, H.C., O'Neill, F.G., Polet, H., Reid, D.G., Sala, A., Sköld, M., Smith, C., Sørensen, T.K., Tully, O., Zengin, M., Rijnsdorp, A.D., 2016. Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. ICES J. Mar. Sci. 73, i27–i43. https://doi.org/10.1093/icesjms/fsv099

Eigaard, O.R., Bastardie, F., Hintzen, N.T., Buhl-Mortensen, L., Buhl-Mortensen, P., Catarino, R., Dinesen, G.E., Egekvist, J., Fock, H.O., Geitner, K., Gerritsen, H.D., González, M.M., Jonsson, P., Kavadas, S., Laffargue, P., Lundy, M., Gonzalez-Mirelis, G., Nielsen, J.R., Papadopoulou, N., Posen, P.E., Pulcinella, J., Russo, T., Sala, A., Silva, C., Smith, C.J., Vanelslander, B., Rijnsdorp, A.D., 2017. The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. ICES J. Mar. Sci. 74, 847–865. https://doi.org/10.1093/icesjms/fsw194

Ellingsen, K.E., Hewitt, J.E., Thrush, S.F., 2007. Rare species, habitat diversity and functional redundancy in marine benthos. J. Sea Res. 58, 291–301. https://doi.org/10.1016/j.seares.2007.10.001

Food and Agriculture Organization of the United Nations (FAO), 2003. Fisheries management 2: The ecosystem approach to fisheries. FAO Technical Guidelines for Responsible Fisheries (FAO, Rome), 4(Suppl 2):112.

Food and Agriculture Organization of the United Nations (FAO). 2016. The state of the World fisheries and aquaculture: contributing to food security and nutrition for all. FOA, Rome, Italy.

Fisher, J.A.D., Frank, K.T., Leggett, W.C., 2010. Dynamic macroecology on ecological time-scales. Glob. Ecol. Biogeogr. 19:1-15. https://doi.org/10.1111/j.1466-8238.2009.00482.x

Fleishman, E., Noss, R.F., Noon, B.R., 2006. Utility and limitations of species richness metrics for conservation planning. Ecol. Indic. 6, 543–553. https://doi.org/10.1016/j.ecolind.2005.07.005

Forster, S., Zettler, M.L., 2004. The capacity of the filter-feeding bivalve Mya arenaria L. to affect water transport in sandy beds. Mar. Biol. https://doi.org/10.1007/s00227-003-1278-2

Foster, S.D., Bravington, M. V., 2013. A Poisson–Gamma model for analysis of ecological non-negative continuous data. Environ. Ecol. Stat. 20, 533–552. https://doi.org/10.1007/s10651-012-0233-0

Friedrichs, M., Graf, G., Springer, B., 2000. Skimming flow induced over a simulated polychaete tube lawn at low population densities. Mar. Ecol. Prog. Ser. 192, 219–228. https://doi.org/10.3354/meps192219

Gallagher, R. V., Hughes, L., Leishman, M.R., 2013. Species loss and gain in communities under future climate change: Consequences for functional diversity. Ecography (Cop.). 36:531–540. https://doi.org/10.1111/j.1600-0587.2012.07514.x

Gislason, H., Bastardie, F., Dinesen, G.E., Egekvist, J., Eigaard, O.R., 2017. Lost in translation? Multi-metric macrobenthos indicators and bottom trawling. Ecol. Indic. 82, 260–270. https://doi.org/10.1016/j.ecolind.2017.07.004

Gray, J.S., Dayton, P., Thrush, S., Kaiser, M.J., 2006. On effects of trawling, benthos and sampling design. Mar. Pollut. Bull. 52, 840–843. https://doi.org/10.1016/j.marpolbul.2006.07.003

Greenstreet, S.P.R.R., Rogers, S.I., Rice, J.C., Piet, G.J., Guirey, E.J., Fraser, H.M., Fryer, R.J., 2011. Development of the EcoQO for the North Sea fish community. ICES J. Mar. Sci. 68, 1–11. https://doi.org/10.1093/icesjms/fsq156

Griffiths, J.R., Kadin, M., Nascimento, F.J.A., Tamelander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E., Brüchert, V., Gårdmark, A., Järnström, M., Kotta, J., Lindegren, M., Nordström, M.C., Norkko, A., Olsson, J., Weigel, B., Žydelis, R., Blenckner, T., Niiranen, S., Winder, M., 2017. The importance of benthic–pelagic coupling for marine ecosystem functioning in a changing world. Glob. Chang. Biol. 23: 2179–2196. https://doi.org/10.1111/gcb.13642

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. Science (80-.). 319, 948–952. https://doi.org/10.1126/science.1149345

Hartig, F., 2018. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R Packag. version 0.2.0.

Hiddink, J.G., Johnson, A.F., Kingham, R., Hinz, H., 2011. Could our fisheries be more productive? Indirect negative effects of bottom trawl fisheries on fish condition. J. Appl. Ecol. 48, 1441–1449. https://doi.org/10.1111/j.1365-2664.2011.02036.x

Hiddink, J.G., Moranta, J., Balestrini, S., Sciberras, M., Cendrier, M., Bowyer, R., Kaiser, M.J., Sköld, M., Jonsson, P., Bastardie, F., Hinz, H., 2016. Bottom trawling affects fish condition through changes in the ratio of prey availability to density of competitors. J. Appl. Ecol. 53, 1500–1510. https://doi.org/10.1111/1365-2664.12697

Hiddink, J.G., Jennings, S., Sciberras, M., Bolam, S.G., Cambiè, G., McConnaughey, R.A., Mazor, T., Hilborn, R., Collie, J.S., Pitcher, C.R., Parma, A.M., Suuronen, P., Kaiser, M.J., Rijnsdorp, A.D., 2019. Assessing bottom trawling impacts based on the longevity of benthic invertebrates. J. Appl. Ecol. 56, 1075–1084. https://doi.org/10.1111/1365-2664.13278

Hiddink, J.G., Jennings, S., Sciberras, M., Szostek, C.L., Hughes, K.M., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Mazor, T., Hilborn, R., Collie, J.S., Pitcher, C.R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2017. Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. Proc. Natl. Acad. Sci. 114, 8301–8306. https://doi.org/10.1073/pnas.1618858114

Hiddink, J.G., Kaiser, M.J., Sciberras, M., McConnaughey, R.A., Mazor, T., Hilborn, R., Collie, J.S., Pitcher, R., Parma, A.M., Suuronen, P., Rijnsdorp, A.D., Jennings, S., 2020. Selection of indicators for assessing and managing the impacts of bottom trawling on seabed habitats. J. Appl. Ecol. 57: 1199–1209. https://doi.org/10.1111/1365-2664.13617

Hintzen, N.T., Bastardie, F., Beare, D., Piet, G.J., Ulrich, C., Deporte, N., Egekvist, J., Degel, H., 2012. VMStools: Open-source software for the processing, analysis and visualisation of fisheries logbook and VMS data. Fish. Res. 115–116, 31–43. https://doi.org/10.1016/j.fishres.2011.11.007

Hinz, H., Hiddink, J.G., Forde, J., Kaiser, M.J., 2008. Large-scale responses of nematode communities to chronic otter-trawl disturbance. Can. J. Fish. Aquat. Sci. 65, 723–732.

Hinz, H., Prieto, V., Kaiser, M.J., 2009. Trawl disturbance on benthic communities: chronic effects and experimental predictions. Ecol. Appl. 19, 761–773. https://doi.org/10.1890/08-0351.1

Hinz, H., Törnroos, A., de Juan, S., 2021. Trait-based indices to assess benthic vulnerability to trawling and model loss of ecosystem functions. Ecol. Indic. 126, 107692. https://doi.org/10.1016/j.ecolind.2021.107692

Hiscock, K., Tyler-Walters, H., 2006. Assessing the Sensitivity of Seabed Species and Biotopes – The Marine Life Information Network (MarLIN). Hydrobiologia 555, 309–320. https://doi.org/10.1007/s10750-005-1127-z

Holte, B., 2001. Possible ecological effects from maldanid (annelida, polychaeta) "super-dominance" in a small North Norwegian sill system. Ophelia 55, 69–75. https://doi.org/10.1080/00785236.2001.10409474

Jennings, S., Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. Adv. Mar. Biol. 34:201–212. https://doi.org/10.1016/s0065-2881(08)60212-6

Jennings, S., Nicholson, M.D., Dinmore, T.A., Lancaster, J.E., 2002. Effects of chronic trawling disturbance on the production of infaunal communities. Mar. Ecol. Prog. Ser. 243, 251–260. https://doi.org/10.3354/meps243251

Jorgensen, S.E., Burkhard, B., Müller, F., 2013. Twenty volumes of ecological indicators-An accounting short review. Ecol. Indic. 28, 4–9. https://doi.org/10.1016/j.ecolind.2012.12.018

Kaiser, M., Clarke, K., Hinz, H., Austen, M., Somerfield, P., Karakassis, I., 2006. Global analysis of response and recovery of benthic biota to fishing. Mar. Ecol. Prog. Ser. 311, 1–14. https://doi.org/10.3354/meps311001

Kaiser, M.J., Edwards, D.B., Armstrong, P.J., Radford, K., Lough, N.E.L., Flatt, R.P., Jones, H.D., 1998. Changes in megafaunal benthic communities in different habitats after trawling disturbance. ICES J. Mar. Sci. 55, 353–361. https://doi.org/10.1006/jmsc.1997.0322

Kaiser, M.J., Spence, F.E., Hart, P.J.B., 2000. Fishing-Gear Restrictions and Conservation of Benthic Habitat Complexity. Conserv. Biol. 14, 1512–1525. https://doi.org/10.1046/j.1523-1739.2000.99264.x

Kruskal, W.H., Wallis, W.A., 1952. Use of ranks in one-criterion variance analysis. J. Am. Stat. Assoc. 47, 583–621

Kenchington, E.L.R., Gilkinson, K.D., MacIsaac, K.G., Bourbonnais-Boyce, C., Kenchington, T.J., Smith, S.J., Gordon, D.C., 2006. Effects of experimental otter trawling on benthic assemblages on Western Bank, northwest Atlantic Ocean. J. Sea Res. 56, 249–270. https://doi.org/10.1016/j.seares.2006.03.010

Kenchington, E. L. R., Kenchington, T. J., Henry, L., Fuller, S., & Gonzalez, P. (2007). Multi-decadal changes in the megabenthos of the Bay of Fundy: the effects of fishing. Journal of Sea Research, 58, 220–240.

Kutner MH, Nachtscheim CJ, Neter J, Li W (2004) Applied linear statistical models. McGraw-Hill/Irwin, New York, NY

Lambert, G.I., Jennings, S., Hiddink, J.G., Hintzen, N.T., Hinz, H., Kaiser, M.J., Murray, L.G., 2012. Implications of using alternative methods of vessel monitoring system (VMS) data analysis to describe fishing activities and impacts. ICES J. Mar. Sci. 69, 682–693. https://doi.org/10.1093/icesjms/fss018

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct. Ecol. 16, 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Legendre, P., Andersson, M.J., 1999. Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. Ecol. Monogr. 69, 1–24. https://doi.org/10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2

Lehmann, A., Hinrichsen, H.-H., Getzlaff, K., Myrberg, K., 2014. Quantifying the heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified coupled hydrodynamic-oxygen consumption model approach. J. Mar. Syst. 134, 20–28. https://doi.org/10.1016/j.jmarsys.2014.02.012

Lohrer, A.M., Thrush, S.F., Gibbs, M.M., 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. Nature 431, 1092–1095. https://doi.org/10.1038/nature03042

Lüdecke D (2016) sjPlot: data visualization for statistics in social science. http: //cran.r-project.org/package=sjPlot

McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178–185. https://doi.org/10.1016/j.tree.2006.02.002

McLaverty, C., Eigaard, O.R., Gislason, H., Bastardie, F., Brooks, M.E., Jonsson, P., Lehmann, A., Dinesen, G.E., 2020a. Using large benthic macrofauna to refine and improve ecological indicators of bottom trawling disturbance. Ecol. Indic. 110, 105811. https://doi.org/10.1016/j.ecolind.2019.105811

McLaverty, C., Eigaard, O.R., Dinesen, G.E., Gislason, H., Kokkalis, A., Erichsen, A.C., Petersen, J.K., 2020b. High-resolution fisheries data reveal effects of bivalve dredging on benthic communities in stressed coastal systems. Mar. Ecol. Prog. Ser. 642, 21–38. https://doi.org/10.3354/meps13330

Morrissey, M.B. and Ruxton, G.D., 2018. Multiple regression is not multiple regressions: the meaning of multiple regression and the non-problem of collinearity. Philos. Theory Practice Biol., 10 (2018), p. 3, https://doi.org/10.3998/ptpbio.16039257.0010.003

Morton, B., 2011. The biology and functional morphology of Arctica islandica (Bivalvia: Arcticidae) – A gerontophilic living fossil. Marine Biology Research 7(6), 540-553. https://doi.org/10.1080/17451000.2010.535833

Morys, C., Powilleit, M., Forster, S., 2017. Bioturbation in relation to the depth distribution of macrozoobenthos in the southwestern Baltic Sea. Mar. Ecol. Prog. Ser. 579, 19–36. https://doi.org/10.3354/meps12236

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. Trends Ecol. Evol. 28, 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Murillo, F.J., Weigel, B., Bouchard Marmen, M., Kenchington, E., 2020. Marine epibenthic functional diversity on Flemish Cap (north-west Atlantic)—Identifying trait responses to the environment and mapping ecosystem functions. Divers. Distrib. 26, 460–478. https://doi.org/10.1111/ddi.13026

Noji, C.I.-M., Noji, T.T., 1991. Tube lawns of spionid polychaetes and their significance for recolonization of disturbed benthic substrates. Meeresforsch. 33, 235–246.

Norkko, A., Villnäs, A., Norkko, J., Valanko, S., Pilditch, C., 2013. Size matters: Implications of the loss of large individuals for ecosystem function. Sci. Rep. 3, 2646. https://doi.org/10.1038/srep02646

Oliver, T.H., Heard, M.S., Isaac, N.J.B., Roy, D.B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C.D.L., Petchey, O.L., Proença, V., Raffaelli, D., Suttle, K.B., Mace, G.M., Martín-López, B., Woodcock, B.A., Bullock, J.M., 2015. Biodiversity and Resilience of Ecosystem Functions. Trends Ecol. Evol. 30, 673–684. https://doi.org/10.1016/j.tree.2015.08.009

Olsgard, F., Schaanning, M.T., Widdicombe, S., Kendall, M.A., Austen, M.C., 2008. Effects of bottom trawling on ecosystem functioning. J. Exp. Mar. Bio. Ecol. 366, 123–133. https://doi.org/10.1016/j.jembe.2008.07.036

O'Neill, F.G., Ivanović, A., 2016. The physical impact of towed demersal fishing gears on soft sediments. ICES J. Mar. Sci. 73, i5–i14. https://doi.org/10.1093/icesjms/fsv125

Osinga, R., Lewis, W.E., Wopereis, J.L.M., Vriezen, C., van Duyl, F.C., 1995. Effects of the sea urchin Echinocardium cordatum on oxygen uptake and sulfate reduction in experimental benthic systems under increasing organic loading. Ophelia 41: 221–236. https://doi.org/10.1080/00785236.1995.10422045

Pearson, T.H., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. An Annu. Rev. 16, 229–311.

Pearson, T.H., Josefson, A.B., Rosenberg, R., 1985. Petersen's benthic stations revisited. I. Is the Kattegatt becoming eutrophic? J. Exp. Mar. Bio. Ecol. 92, 157–206. https://doi.org/10.1016/0022-0981(85)90094-2

Pham, C.K., Murillo, F.J., Lirette, C., Maldonado, M., Colaço, A., Ottaviani, D., Kenchington, E., 2019. Removal of deep-sea sponges by bottom trawling in the Flemish Cap area: conservation, ecology and economic assessment. Sci. Rep. 9: 15843. https://doi.org/10.1038/s41598-019-52250-1

Pitcher, C., 2000. Implications of the effects of trawling on sessile megazoobenthos on a tropical shelf in northeastern Australia. ICES J. Mar. Sci. 57, 1359–1368. https://doi.org/10.1006/jmsc.2000.0911

Pikitch, E., Santora, C., Babcock, E., Bakun, A., Bonfil, R., Conover, D.,Dayton, P., Doukakis, P., Fluharty, D.,Heneman, B., Houde, E., Link, J.,Livingston, P., Mangel, M., McAllister, M., Pope, J. & Sainsbury, K. (2004) Ecosystem-based fishery management. Science, 305, 346 –347.

Pinto, R., Patrício, J., Baeta, A., Fath, B.D., Neto, J.M., Marques, J.C., 2009. Review and evaluation of estuarine biotic indices to assess benthic condition. Ecol. Indic. 9: 1–25. https://doi.org/10.1016/j.ecolind.2008.01.005

Queirós, A.M., Birchenough, S.N.R., Bremner, J., Godbold, J.A., Parker, R.E., Romero-Ramirez, A., Reiss, H., Solan, M., Somerfield, P.J., Van Colen, C., Van Hoey, G., Widdicombe, S., 2013. A bioturbation classification of European marine infaunal invertebrates. Ecol. Evol. 3, 3958–3985. https://doi.org/10.1002/ece3.769

Queirós, A.M., Hiddink, J.G., Kaiser, M.J., Hinz, H., 2006. Effects of chronic bottom trawling disturbance on benthic biomass, production and size spectra in different habitats. J. Exp. Mar. Bio. Ecol. 335, 91–103. https://doi.org/10.1016/j.jembe.2006.03.001

Reiss, H., Greenstreet, S., Sieben, K., Ehrich, S., Piet, G., Quirijns, F., Robinson, L., Wolff, W., Kröncke, I., 2009. Effects of fishing disturbance on benthic communities and secondary production within an intensively fished area. Mar. Ecol. Prog. Ser. 394, 201–213. https://doi.org/10.3354/meps08243

Reiss, J., Bridle, J.R., Montoya, J.M., Woodward, G., 2009. Emerging horizons in biodiversity and ecosystem functioning research. Trends Ecol. Evol. 24, 505–514. https://doi.org/10.1016/j.tree.2009.03.018

Rice, J.C., Rochet, M.J., 2005. A framework for selecting a suite of indicators for fisheries management, in: ICES Journal of Marine Science 62: 516–527. https://doi.org/10.1016/j.icesjms.2005.01.003

Rice, J., Arvanitidis, C., Borja, A., Frid, C., Hiddink, J.G., Krause, J., Lorance, P., Ragnarsson, S.Á., Sköld, M., Trabucco, B., Enserink, L., Norkko, A., 2012. Indicators for Sea-floor Integrity under the European Marine Strategy Framework Directive. Ecol. Indic. 12, 174–184. https://doi.org/10.1016/j.ecolind.2011.03.021

Rijnsdorp, A.D., Bolam, S.G., Garcia, C., Hiddink, J.G., Hintzen, N.T., van Denderen, P.D., van Kooten, T., 2018. Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. Ecol. Appl. 28, 1302–1312. https://doi.org/10.1002/eap.1731

Rosenberg R (1995) Benthic marine fauna structured by hydrodynamic processes and food availability. Neth J Sea Res 34: 303–317

Rosenberg, R., 2001. Marine benthic faunal successional stages and related sedimentary activity. Sci. Mar. 65, 107–119. https://doi.org/10.3989/scimar.2001.65s2107

Rossberg, A.G., Uusitalo, L., Berg, T., Zaiko, A., Chenuil, A., Uyarra, M.C., Borja, A., Lynam, C.P., 2017. Quantitative criteria for choosing targets and indicators for sustainable use of ecosystems. Ecol. Indic. 72: 215–224. https://doi.org/10.1016/j.ecolind.2016.08.005

Rumohr, H., Krost, P., 1991. Experimental evidence of damage to benthos by bottom trawling with special reference to Arctica islandica . Meeresforschung/Rep. Mar. Res. 33, 340–345.

Sandnes, J., Forbes, T., Hansen, R., Sandnes, B., Rygg, B., 2000. Bioturbation and irrigation in natural sediments, described by animal-community parameters. Mar. Ecol. Prog. Ser. 197, 169–179. https://doi.org/10.3354/meps197169

Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B., Charnov, E.L., 2004. Effects of Body Size and Temperature on Population Growth. Am. Nat. 163, 429–441. https://doi.org/10.1086/381872

Sciberras, M., Hiddink, J.G., Jennings, S., Szostek, C.L., Hughes, K.M., Kneafsey, B., Clarke, L.J., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Hilborn, R., Collie, J.S., Pitcher, C.R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2018. Response of benthic fauna to experimental bottom fishing: A global meta-analysis. Fish Fish. 19, 698–715. https://doi.org/10.1111/faf.12283

Sciberras, M., Parker, R., Powell, C., Robertson, C., Kröger, S., Bolam, S., Geert Hiddink, J., 2016. Impacts of bottom fishing on the sediment infaunal community and biogeochemistry of cohesive and non-cohesive sediments. Limnol. Oceanogr. 61, 2076–2089. https://doi.org/10.1002/lno.10354

Shin, Y.-J., Rochet, M.-J., Jennings, S., Field, J.G., Gislason, H., 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. ICES J. Mar. Sci. 62, 384–396. https://doi.org/10.1016/j.icesjms.2005.01.004

Sköld, M., Göransson, P., Jonsson, P., Bastardie, F., Blomqvist, M., Agrenius, S., Hiddink, J., Nilsson, H., Bartolino, V., 2018. Effects of chronic bottom trawling on soft-seafloor macrofauna in the Kattegat. Mar. Ecol. Prog. Ser. 586, 41–55. https://doi.org/10.3354/meps12434

Snelgrove, P.V.R., 1998. The biodiversity of macrofaunal organisms in marine sediments. Biodivers. Conserv. 7, 1123–1132. https://doi.org/10.1023/A:1008867313340

Solan, M., 2004. Extinction and Ecosystem Function in the Marine Benthos. Science (80-.). 306, 1177–1180. https://doi.org/10.1126/science.1103960

Svendsen, L.M. & Norup, B. (eds.) 2005: NOVANA. Nationwide Monitoring and Assessment Programme for the Aquatic and Terrestrial Environments. Programme Description – Part 1. National Environmental Research Institute, Denmark. 53 pp. – NERI Technical Report No. 532

Tendal, O.S., Dinesen, G.E., 2005. Biogenic sediments, substrates and habitats of the Faroese shelf and slope. BIOFAR Proceedings 2005 - Annales Societas Scientarium Færoenses Supplementum 41, 224-242.

Thrush, S.F., Whitlatch, R.B., 2001. Recovery dynamics in benthic communities: balancing detail with simplification. In: Reise, K., (Ed.) Ecological comparisons of sedimentary shores. Berlin, Springer-Verlag pp. 297–316.

Thrush, S.F., Hewitt, J.E., Gibbs, M., Lundquist, C., Norkko, A., 2006. Functional role of large organisms in intertidal communities: Community effects and ecosystem function. Ecosystems 9, 1029–1040. https://doi.org/10.1007/s10021-005-0068-8

Tiano, J.C., Witbaard, R., Bergman, M.J.N., Van Rijswijk, P., Tramper, A., Van Oevelen, D., Soetaert, K., Degraer, S., 2019. Acute impacts of bottom trawl gears on benthic metabolism and nutrient cycling. ICES J. Mar. Sci. 76, 1917–1930. https://doi.org/10.1093/icesjms/fsz060

Tillin, H., Hiddink, J., Jennings, S., Kaiser, M., 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Mar. Ecol. Prog. Ser. 318, 31–45. https://doi.org/10.3354/meps318031

van Denderen, P., Bolam, S., Hiddink, J., Jennings, S., Kenny, A., Rijnsdorp, A., van Kooten, T., 2015. Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. Mar. Ecol. Prog. Ser. 541, 31–43. https://doi.org/10.3354/meps11550

Violle, C., Reich, P.B., Pacala, S.W., Enquist, B.J., Kattge, J., 2014. The emergence and promise of functional biogeography. Proc. Natl. Acad. Sci. 111, 13690–13696. https://doi.org/10.1073/pnas.1415442111

Wangensteen, O. S., Palacin, C., & Turon, X. (2016). Reproductive strategies in marine invertebrates and the structuring of marine animal forests. In S. Rossi, L. Bramanti, A. Gori, & C. Orejas Saco del Valle (Eds.), Marine animal forests. The ecology of benthic biodiversity hotspots (pp. 1–24). Cham, Switzerland: Springer International Publishing.

Warton, D.I., Blanchet, F.G., O'Hara, R.B., Ovaskainen, O., Taskinen, S., Walker, S.C., Hui, F.K.C., 2015. So Many Variables: Joint Modeling in Community Ecology. Trends Ecol. Evol. 30, 766–779. https://doi.org/10.1016/j.tree.2015.09.007

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A., Warren, P.H., 2005. Body size in ecological networks. Trends Ecol. Evol. 20:402–409. https://doi.org/10.1016/j.tree.2005.04.005