Deliverable 1.2

Impact of Bottom Trawling on Sea Bed Integrity

Due date of deliverable: month 48 (September 2016)

Actual submission date: month 50 (November 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

The research leading to these results has received funding from the European Community's Seventh Framework Programme (FP7/2007-2013) under grant agreement n° 312088

Main Contributors:

Adriaan D. Rijnsdorp,

Partner 1, DLO-IMARES, Netherlands

Stefan G. Bolam, Clement Garcia,

The Secretary of State for Environment, Food and Rural Affairs

Partner 3, CEFAS, UK

Niels Hintzen,

Partner 1, DLO-IMARES, Netherlands

P. Daniel van Denderen

Danmarks Tekniske Universitet

Partner 9, DTU-Aqua, Denmark

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
Rijnsdorp	Final draft	1	29-11-2016

SUMMARY

This paper studies the longevity composition of the benthic community as a basis to estimate the impact of bottom trawling and the corresponding status of the seabed on a continuous scale. The rationale is that long-lived species are more sensitive to additional mortality due to their lower pace of life (low growth, late maturation) and more likely comprise of species that change their habitat (bio-engineers). The longevity composition can be expressed as a logistic regression of the cumulative biomass and longevity. The longevity composition differed across EUNIS-3 habitats and was affected by sediment (%gravel), depth, tidal shear stress and trawling intensity. Habitats exposed to high levels of natural disturbance were shown to be less sensitive for bottom trawling. The sensitivity to trawling increased with depth and with an increase in the percent gravel.

Trawling impact is estimated according two approaches. Approach 1 estimates the trawling impact as the cumulative biomass of species which can close their life cycle without being disturbed by a bottom trawl: e.g. those species for which their life span is less than the average time interval between two successive bottom trawling events. Approach 2 builds on the statistical effect of bottom trawling on the longevity composition and estimates the reduction in the biomass of taxa with a longevity of 10 years or more. The effect of trawling on the longevity composition can also be used to estimate the critical trawling intensity at which the biomass of long-lived taxa is reduced to a certain percentage. This will allow managers to set reference values to assess the status of the seabed.

Longevity approach useful method to derive transparent and empirically based indicators of the impact of trawling on seafloor habitats, which directly relates the trawling intensity with the relevant biological trait. The method can be improved when more precise estimates become available on the longevity of the benthic taxa, and when data are included covering a wider range on environmental conditions such as temperature and primary production. The status of the seafloor refers to the equilibrium state. The metric therefore cannot be used to study the dynamics of the benthic community. As the longevity-based indicators are all expressed on a continuous scale, they can be used to monitor the consequences of management measures aimed at reducing the benthic impact. The method avoids the subjectivity of expert judgement to classify habitat sensitivity and trawling intensity.

TABLE OF CONTENTS

INTRODUCTION

The seafloor is affected by a multitude of anthropogenic activities(Eastwood et al., 2007; Foden et al., 2011). While mining, dredging, and sand- and gravel extraction are localised activities, generally limited to coastal regions, bottom trawling (i.e. demersal trawls and dredges) occurs over large parts of the continental shelf (Halpern et al., 2008; Foden et al., 2011). The footprint of bottom trawling on the European continental shelf varies between 53-99% per habitat type of the seafloor down to 200m (Eigaard et al., 2017). Within each management area, bottom trawling shows a heterogeneous distribution in both space and time with some areas being trawled several times per year and other areas being trawled only partly or not at all (Rijnsdorp et al., 1998; Lee et al., 2010; Gerritsen et al., 2013; van Denderen et al., 2015b).

Bottom trawling disturbs the seafloor, damages biogenic structures and kills benthic invertebrates, affecting both structure and functioning of the benthic ecosystem (Dayton et al., 1995; Thrush and Dayton, 2002); (Kaiser, 1998). The impact of trawling differs between fishing gears and is related to the surface and sub-surface footprint of the gear, varying with respect to the weight and speed with which the heavy parts of the gear are towed over the seafloor and the extent and intensity spectrum of bottom trawling (Eigaard et al., 2016; O 'Neill and Ivanović, 2016; Rijnsdorp et al., 2016). The impact is further modulated by the sensitivity of the seafloor habitat, which is related, to some extent, by the degree of natural disturbance (Hall, 1994; Diesing et al., 2013). Biogenic habitats, for example, which are associated with comparatively physically stable conditions, are particularly sensitive to bottom trawling (Collie et al., 2000b; Kaiser et al., 2006).

The EU has developed a policy “Marine Strategy Framework Directive” (MSFD, CEC 2008) to maintain or achieve good environmental status (GES) for a number of ecosystem components such as the seafloor. To support the MSFD, indicators of the status of the seafloor are required as well as criteria to determine GES. To support the MSFD, an assessment methodology is needed which allows to estimate impact of the different bottom trawling gears on the various seafloor habitats of the European shelf. The methodology to assess trawling impact has traditionally used expert judgement to derive sensitivity of different habitats for specific bottom trawl fisheries (Eno et al., 2013; Grabowski et al., 2014). Habitat sensitivity is estimated from the resistance and resilience of a selection of species/biogenic structures that are typical for the habitat. This approach is flexible allowing the incorporation of additional or new information the experts consider to be relevant. The approach is particularly useful to distinguish sensitive habitats in the context of the establishment of marine protected areas. However, the categorical method cannot be quantitatively linked to trawling intensity since class boundaries are arbitrarily defined. In addition, the method lacks transparency as the expert opinion is subjective and the assessment will be difficult to reproduce and compare between different studies or areas. As such, the approach is less appropriate to provide guidance in the regulation of bottom trawling in soft sediment habitats that dominate the seafloor of the European shelf seas and are widely used by bottom trawlers.,.

For application to the more intensively trawled sedimentary habitats that dominate the European continental shelf, an assessment methodology is needed that builds on the pressure-state relationships on a continuous scale. Empirically derived pressure-state relationships can be based on quantitative knowledge on the mortality imposed by a trawling event, the recovery rate of the benthos and the time interval between successive trawling events. If such empirical estimates of these three variables are available, the reduction in biomass due to trawling can be calculated both at the level of the grid cell and aggregated over larger management areas (Ellis et al., 2014; Pitcher et al., 2016). Alternatively, the impact of bottom trawling can be estimated from the intensity spectrum and the community composition with regard to the longevity of the taxa. The trawling impact can be expressed as the proportion of the unimpacted biomass of the community assuming that the taxa with a longevity smaller than the average time interval between successive trawling events will be unimpacted (Rijnsdorp et al., 2016). Since longevity is positively related to other biological traits such as body size and age at maturation, it has specific relevance for ecosystem structure and functioning. Also bio-engineers will be more prominent among the larger and longer lived taxa.

In this paper, we study how the longevity composition of the benthic community varies across benthic habitats and estimate how this is related to different environmental variables (i.e. natural disturbance, depth and habitat sediment). The additional effect of trawling intensity on the longevity composition is estimated per habitat type and used to derive pressure-state relationships. Subsequently, these are used to determine the critical trawling intensity at which the biomass of long-lived taxa will be below a certain level relative to the untrawled community. The analysis is carried out for the total community, as well as for a subset of taxa representing the bio-turbators and the surface depositors. The analysis also allows to estimate the status of the seabed as the percentage of biomass of long-lived taxa relative to the untrawled community. Finally, we provide information relevant to trade-off the reduction in trawling impact with the loss in the fisheries catch. The results are discussed in the light of the implementation of a quantitative framework to assess the status of the seafloor.

MATERIAL AND METHODS

Benthic samples.

The longevity composition of the benthic community was estimated using benthic samples collected in the North Sea and English Channel with 0.1 or 0.078 m2 grabs or box-cores (Figure 1). These sampling gears provide a quantitative estimate of the biomass of the smaller epi- and infaunal part of the benthic community. One data set comprises samples taken in UK waters between 2000-2010 (Bolam et al., 2014). The second data set comprises annual benthic samples taken in the Dutch part of the North Sea together with samples taken along different trawling gradients across the North Sea as compiled by (van Denderen et al., 2015a; van Denderen et al., 2014). A total of 403 stations were sampled at least once (Table 1) with replicates (between 2 and 6) for 97 stations. In total 392 replicate samples were taken. Some sampling stations had replicates while others were sampled annually over multiple (replicate) years. All samples were sieved over a 1 mm mesh sieve and the retained organisms were identified to the lowest taxonomic level possible. In most sampling stations, biomass per taxonomic grouping was estimated in wet weight, while the samples in the Dutch part of the North Sea were estimated in grams ash free dry weight. These differences in methodology will have limited effects on our outcome as the longevity approach only use proportional data to predict the longevity composition of a benthic community at each sampling location.

For each sampling station, the sediment characteristics (%gravel, %sand, %mud) and depth were recorded and also used to determine EUNIS habitat. Table 1 shows the number of stations and benthic samples taken per EUNIS habitat. The average annual primary production of each station was estimated from a GETM-ERSEM model (General Estuarine Transport Model-European Regional Seas Ecosystem Model) (Baretta et al., 1995). For 14 stations in the English Channel, that were outside the spatial coverage of the ERSEM model, primary production was predicted from statistical relationships between primary production and depth and bottom shear stress. The trawling intensity for each station was estimated as the average annual swept area ratio (surface abrasion) of the corresponding 1x1 minute grid cell for all bottom trawl metiers in the period 2010-2012 (Eigaard et al., 2017). The distributional ranges of the sampling stations in terms of the different environmental variables are shown in Figure 2. The percentage sand, percentage silt, depth and primary production were significantly correlated (Table 2).

Longevity composition of the benthic community

The longevity composition of the infaunal community was estimated by assigning longevity (<1, 2-3, 5-10, >10 years) by taxon as compiled by Bolam et al (2014). Separate analysis were carried out for different subsets of the taxa sampled, representing different ecological functional groups (bioturbation, suspension feeders) and taxa with different vertical positions in the sediment (epifauna and taxa living less than 2-cm deep in the sediment).

The longevity composition for the total community and these separate groups is estimated as the cumulative biomass (B) longevity relationship fitted by the following logistic mixed effect model:

B ~ intercept + log(longevity) + habitat + log(longevity)*habitat + log(trawling) + log(trawling)*habitat + error_1 + (random(station intercept/replicates) + error_2)

We used a mixed effect model to take account of the dependency of the cumulative biomass estimates for each station. Error_1 represents a binomial error. Error_2 represents the normally distributed error of the random effect on the intercept and slope by station and the replicates nested within the stations. The habitat parameter represents either the EUNIS habitat class assigned to the stations, or the continuous habitat covariables (%gravel, depth and tidal shear stress). Trawling intensity, depth and tidal shear stress were log-transformed to improve the model fit. A value of 10^{-2} was added to the trawling intensity and shear stress estimates, close to the minimum observed value, to avoid taking the log of zero.

The mixed effect model was estimated using library lme4 in R version 3.02.

Trawling impact

Approach 1

Approach 1 will estimate trawling impact using the longevity composition of the benthic community, while it does not include an estimate of the effect of trawling intensity on the cumulative biomass – longevity relationship (Rijnsdorp et al., 2016). The approach makes the assumption that taxa with a longevity that exceed the average trawling interval will be impacted by bottom trawling. Hence, the trawling impact can be estimated as the proportion of the cumulative biomass represented by the taxa with a longevity that is larger than the reciprocal of the annual trawling intensity. The corresponding metric for the resulting state of the seafloor is given by the cumulative biomass of the taxa with longevities equal or smaller than the reciprocal of the annual trawling intensity. These metrics can be averaged over a habitat or management area to provide a single metric that can be used to assess the changes over time, or to compare the impact or status across management areas or habitats.

Approach 2

The 2nd approach extends approach 1 by including the habitat-specific effect of bottom trawling on the longevity composition estimated from empirical data. The cumulative biomass (B_{lht}) is now a logistic function of $\log_e$ longevity (l) and the habitat characteristics (h) and bottom trawling (t):

$$B_{lht} \sim \beta_0 + \beta_1 \ln(l) + \beta_2 Habitat + \beta_3 \ln(Trawling) + \beta_4 \ln(Trawling) * Habitat + \beta_5 \ln(l) * Habitat$$

the impact of trawling can be expressed as the reduction in biomass of long-lived taxa ($B_{10,h,t}$) relative to the untrawled situation ($B_{10,h,0}$).

With the same model, we can estimate the sensitivity of the seafloor in terms of the critical trawling intensity (*T*) at which the cumulative biomass of long-lived taxa (l=10) is reduced to a certain proportion (in %) of the untrawled biomass.

$$T_d = exp\left[\ \left(\ln(d) - (\beta_0 + \beta_1 \ln(10) + \beta_2 Habitat + \beta_5 \ln(10) * Habitat)\right) / \left((\beta_3 + \beta_4\, Habitat)\right)\right]$$

Functional groups

The analysis above can be performed on the total benthic community or on subsets that represent specific ecological functions or a specific position in the seafloor habitat. Based on the biological trait classification of Bolam et al (2014), we analysed the suspension feeding taxa that play an important role in the benthic-pelagic coupling, and the bio-turbating taxa that are responsible for the aeration, irrigation and mixing of the sediments. Further, we analysed the subset of taxa living on the surface of the seafloor that are exposed to all bottom contacting gears (surface abrasion sensu Eigaard et al., 2016), and the taxa that live down to 5 cm deep in the seabed that are exposed to subsurface abrasion only.

RESULTS

Cumulative biomass – longevity relationships by EUNIS habitat

The most parsimonious mixed effect model showed that the cumulative biomass – longevity relationship differed between habitats and was affected by trawling intensity (Table 3). The effect of bottom trawling did not differ between habitats since the AIC of the model including the interaction between trawling intensity and habitat was almost 7 units higher that the model with the lowest AIC. The proportion of long-lived species was highest in coarse sediment habitat (A5.1) and lowest in muddy sediments (A5.3). Sandy sediments (A5.2) and mixed sediments (A5.4) were intermediate (Figure 3a). Bottom trawling reduced the proportion of long-lived species (Figure 3b).

The analysis for different subsets of the community showed that taxa living on the surface of the seabed are dominated by short-lived taxa in all habitats (Figure 4). The longevity composition of the taxa living on or within the top 5cm of the seabed is close to the composition of the total community. Suspension feeders are more long-lived than bio-turbators. The community of coarse sediments (A5.1) and mixed sediments (A5.4) comprise of a larger proportion of long-lived taxa. The effect of habitat is significant for the surface and the surface + subsurface habitat subsets but not for the two functional groups (Table 4). Trawling intensity reduced the proportion of long-lived taxa although this effect was only significant for bioturbators and the subset of surface taxa.

Effects of environmental variables on the longevity composition

The significant differences in the cumulative biomass – longevity relationships raise the question which of the environmental variables affects the longevity distribution. As the correlation matrix of the environmental variables showed significant correlations between %sand, %silt, depth, tidal shear stress and primary production (Table 2), the co-variables %sand, %silt and primary production were excluded in the analysis. The most parsimonious mixed effect model included $\log_e$ depth, %gravel, $\log_e$ tidal shear stress and $\log_e$ trawling intensity as significant co-variables (Table 5). Log_e trawling intensity showed a significant interaction with $\log_e$ depth and $\log_e$ tidal shear stress. Including the 3^{rd} order interaction between these three co-variables further improved the model. The residuals did not deviate from a normal distribution.

The effect of the significant environmental variables on the longevity composition is illustrated in Figure 5 for two levels of water depth and gravel content, and two levels of natural and trawling disturbance. In the untrawled community, the proportion long lived species in the community increases with an increase in the %gravel and depth (Fig. 5a), while tidal shear stress reduces the proportion long lived species in the community (Fig. 5b). Bottom trawling reduces the proportion of long lived species. The effect of bottom trawling is particularly pronounced if the level of natural disturbance (tidal shear stress) is low and in deeper waters. In high shear stress, or shallow habitats, the longevity composition of a community is not affected by trawling (Fig. 5c and 5d).

The effect of the environmental variables on the proportion of long-lived taxa with in the subset of the community corresponded to the effects found in the analysis of the total community (all taxa), although the number of significant variables was less than in the analysis of the full community (all taxa) (Table 6).

Critical trawling intensity

With the parameter estimates of the trawling effect on the cumulative biomass – longevity relationship (Table 4), the critical trawling intensity at which the proportion of long-lived taxa (10 years and older) is reduced to an arbitrarily chosen reference value of 80% of the untrawled community is estimated for different combinations of habitat characteristics (Figure 7). Tidal shear stress shifts the critical trawling intensity upwards. Already at a low tidal shear stress, the effect of bottom trawling is reduced and long-lived taxa sustain their biomass above 80% in shallow waters (Figure 7a). The depth range where the long-lived taxa remain within 80% of their untrawled biomass increases with increasing tidal shear stress. At a high level of tidal shear stress, habitats down to 50m sustain their biomass above 80%. The isolines are rather flat at higher fishing intensities. Gravel habitats show similar patterns although the isolines are shifted downward, indicating that the long-lived taxa are reduced at lower trawling intensities in gravel habitats and in deeper waters. Figure 8 shows a map of the critical trawling intensities for the North Sea. In the southern North Sea and on the Dogger Bank, the critical trawling intensity is estimated to be well above 1. In the deeper waters of the central and northern North Sea, however, the critical trawling intensity is generally less than 0.5 and 0.1, respectively.

Trawling impact

Approach 1

Figure 9 shows a map with the reduction in the status of the seafloor estimated as the proportion of the biomass of the taxa with a longevity that is larger than the reciprocal of the trawling intensity given the parameter estimates of Table 5. Because the longevity distribution of the benthic community living on the surface differs from the longevity distribution of the total community, the status of the seafloor was estimated using the subsurface abrasion. In large parts of the North Sea, the status of the seafloor is above 0.80. In the southern North Sea and along the Norwegian trench and localised areas in the north-western North Sea, the status is estimated to be less than 0.2.

Approach 2

The status of the seafloor estimated with approach 2 is shown in Figure 10. This approach takes account of the effect of bottom trawling on the cumulative biomass – longevity relationship and expresses the state of the seafloor in terms of the relative biomass of long-lived taxa. According to this approach, the seafloor in the southern North Sea generally has a good status (>0.8), despite trawling intensities of more than once per year. Only in the area of the Oyster Grounds, and in some small localised seabed areas in the German Bight and along the coast of England, are there areas with a lower status. In the deeper waters of the central and northern North Sea, the status of the seabed is low with values less than 0.20 in the intensively trawled areas and values between 0.2 – 0.8 in the areas trawled less intensively.

DISCUSSION

The sensitivity of long-lived taxa for trawling is related to their slower pace of life, determined by their slower growth rate and later onset of sexual maturity. These characteristics result in such taxa possessing a slower rate of recovery after a disturbance event (Charnov, 1993; (Tillin et al., 2006). This makes this trait particularly useful to estimate the trawling impact on the benthic community (Thrush et al., 2005; Rijnsdorp et al., 2016). The trait is not only related to the recovery rate, but is also related to body size and the vulnerability to physical disturbance by trawling. Taxa that build biogenic structures on the seafloor, or build a burrows in the sediment, generally comprise of longer-lived and larger taxa that are more vulnerability for physical disturbance by bottom trawls (Clark et al., 2016). A decrease in the longer lived species will likely result in a decrease in species richness and habitat diversity.

Longevity composition of the benthic community

The grab and box-core samples analysed showed that the longevity composition of the benthos varied spatially in relation to sediment characteristics, depth and bed shear stress. The proportion of long-lived taxa increased with increasing depth and gravel content, and decreased with increasing shear stress. The longevity composition of the benthic community differed between epifauna (i.e. those living on or above the seabed) and infauna (i.e. those living within the sediment) with the epifauna being dominated by shorter-living taxa and the infauna being dominated by longer-lived taxa.

Whether the longevity distribution found in the present study is representative for other sea areas remains to be studied. It is expected that the longevity distribution in tropical or polar regions may differ, as temperature will influence the pace of life and hence the recovery rate after a disturbance event. Also, one would expect that the food availability for the benthos as reflected in the primary production will affect the longevity composition. If more data become available, the model may be extended by including more relevant environmental variables.

Trawling effects on the longevity composition

Bottom trawling reduced the proportion of long-lived taxa, in particular in deeper water. In shallow waters, no effect of trawling was detected. These results are in general agreement with the results reported in the literature (Bolam et al., 2014; Bolam and Eggleton, 2014; van Denderen et al., 2015a; van Denderen et al., 2014). Seafloor habitats that are exposed to a high level of natural disturbance are characterised by a community of shorter lived species compared to those of deeper, more physically benign habitats. The areas where the critical trawling intensity to reduce the biomass of long-lived taxa to 80% in the present study corresponds to areas shown to exhibit high natural disturbance due to tidal currents and waves (Bricheno et al., 2015; Diesing et al., 2013). Habitats where the natural disturbance is relatively low as compared to the trawling disturbance are muddy substrates and deep circalittoral habitats (Diessing et al 2013). In our analysis we could only include the tidal shear stress due to tides. Since in some areas, the shear stress due to waves will be important, the models may be improved in future by including both tidal and wave induced shear stress as explanatory variables (Aldrige et al., 2015).

The increase in trawling impact associated with increased sediment gravel content observed here may relate to the higher proportion of epifaunal taxa that are attached to the hard structures in gravely and mixed sediments; these sessile taxa have been observed to be relatively vulnerable for the disturbance by bottom trawling (Collie et al., 2000a).

Trawling impact

The relative proportion of long-lived taxa can thus be used as an indicator for the sensitivity of the seafloor for bottom trawling. Indeed, this trait forms an important component of the current sensitivity assessment based on expert judgement (Eno et al., 2013 ; Grabowski et al., 2014). By estimating the cumulative biomass – longevity relationship of the untrawled seabed for different habitats based on empirical data as conducted here offers an approach that is both transparent and reproducible and can be applied to all sedimentary benthic habitats.

The continuous relationship can be coupled to the continuous scale at which trawling intensities are estimated to estimate the trawling impact and index of the status of the seabed (Rijnsdorp et al., 2016). Under the assumption that those taxa will be affected by trawling if the interval between two trawling events is less than their life span (approach 1), the critical trawling intensity is given by the reciprocal of the longevity and the trawling impact can be estimated in terms of the cumulative biomass of the unimpacted taxa.

To estimate the trawling impact and the status of the seafloor, we used the subsurface abrasion (Eigaard et al., 2017) as a pressure layer. In addition, the penetration depth of the bottom trawls needs to be taken into account to improve the estimate of impact on the sea bed. The rationale for this choice is that our analyses showed that surface taxa are dominated by short-lived species, and that the longevity distribution of all taxa is close to the distribution of the subset of taxa living on the seabed or in the top 5cm of the seabed. In addition, we expect the younger stages of the taxa that live deep in the sediment as adults to live closer to the surface and may be exposed to bottom trawling.

The above estimate reflects a worst-case scenario as it assumes that a taxon will be fully impacted by one trawling event during its life span. In reality, a single bottom trawling event is unlikely to remove all biomass of these taxa. A more realistic approach could be to use the cumulative biomass – maturation age relationship. Following the same logic, a similar indicator can be estimated based on the distribution of the age at maturation of the benthic community. This indicator will reflect more closely the trawling intensity at which the taxa can at least reproduce once before it is impacted by a trawling event.

Maturation age and adult life spawn are correlated and show typical slopes for different taxonomic group (Charnov, 1993). In fish and Pandalus shrimps for example, the adult life span is about 0.5 time the age at maturation (Charnov and Berrigan, 1990). Although these relationships have not been fully described in marine benthic invertebrates, (Ridgway et al., 2011) found a significant linear relationship between the adult life span and age at maturation in bivalves. Applying the life history invariant value of 0.5, the biomass distribution in relation to the age at maturation was estimated for a typical unfished community. This biomass distribution was used in the present study to estimate the second Sea Bed Integrity indicator. Under the assumption that this relationship can be applied to all benthic invertebrates, the longevity biomass distribution can be converted into a maturation biomass distribution and used to estimate a second indicator.

A more important draw back of the approach-1 is that ignores the effect of the natural disturbance on the vulnerability of the benthos for bottom trawling. Bottom trawling and natural disturbance have a similar influence on the composition of the benthic community, reducing the proportion of long-lived taxa (van Denderen et al., 2015a). Hence, approach-1 will overestimate the impact of bottom trawling in areas that are exposed to a moderate or high level of natural disturbance, such as in the southern North Sea, resulting in underestimations of the status of the seafloor.

The status of the seafloor estimated using approach-2 indeed gave a different result (Figure 10). Approach-2 estimates the status of the seafloor in the southern North Sea to be above 0.8, whereas the status of the seafloor in the relatively moderately trawled western North Sea was estimated to be between 0.2 and 0.6, much lower than suggested by approach-1 (Figure 9).

The results of approach-2 are considered to be more realistic as they are based on a more elaborate statistical model of observations. The cumulative biomass – longevity relationships underpinning approach-2 are based on grab and box-core samples collected in recent years in areas that were trawled at different intensities. However, since intensive bottom trawling has been carried out for more than a century (Engelhard, 2008; Kerby et al., 2013; Kerby et al., 2012), the community composition of the stations that were not trawled during the study period may still be affected by historic trawling activities. Therefore, we cannot exclude that the vulnerable taxa have disappeared in response to the historic trawling, leading to an underestimate of the impact of trawling (Thrush et al. 2008; Kaiser et al., 2000).

Trawling impact and ecosystem functioning

Suspension feeders comprise of a larger proportion of long-lived taxa in comparison with for instance bio-turbating taxa, suggesting that the suspension feeding function is more vulnerable to bottom trawling.

Technical limitations

Due to convergence problems, we were restricted in testing models and could not test all possible models including the all combinations of co-variables, including their 1st and 2nd order interaction terms. We a priori excluded co-variables that were strongly correlated to other co-variables to avoid the collinearity. The variability in the cumulative biomass - longevity relationship subscribed to for instance depth therefore could be partly related to variability in primary production which is correlated to depth.

The longevity trait information collated by Bolam et al (2014) could not be assigned in great detail and was expressed in four classes. Also the longevity of many taxa is unknown, and the longevity was assigned based the higher taxonomic level.

Conclusion

1. Longevity approach useful method to derive transparent and empirically based indicators of the impact of trawling on seafloor habitats, which directly relates the trawling intensity with the relevant biological trait.
2. The method can be improved when more precise estimates become available on the longevity of the benthic taxa, and when data are included covering a wider range on environmental conditions such as temperature and primary production.
3. The status of the seafloor refers to the equilibrium state. The metric therefore cannot be used to study the dynamics of the benthic community.
4. If reference levels are set by the managers, the method can be used to estimate the footprint of bottom trawling relative to the reference level and assess the status of the seafloor.
5. As the longevity-based indicators are all expressed on a continuous scale, they can be used to monitor the consequences of management measures aimed at reducing the benthic impact.
6. The method avoids the subjectivity of expert judgement to classify habitat sensitivity and trawling intensity.

REFERENCES

Baretta, J., Ebenhöh, W., and Ruardij, P. 1995. The European regional seas ecosystem model, a complex marine ecosystem model. Netherlands Journal of Sea Research, 33: 233-246.

Bolam, S. G., Coggan, R. C., Eggleton, J., Diesing, M., and Stephens, D. 2014. Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: A biological trait approach. Journal of Sea Research, 85: 162-177.

Bolam, S. G., and Eggleton, J. D. 2014. Macrofaunal production and biological traits: Spatial relationships along the UK continental shelf. Journal of Sea Research, 88: 47-58.

Bricheno, L. M., Wolf, J., and Aldridge, J. 2015. Distribution of natural disturbance due to wave and tidal bed currents around the UK. Continental Shelf Research, 109: 67-77.

Charnov, E. L. 1993. Life history invariants*,* Oxford University Press, Oxford, U.K. 167 pp.

Charnov, E. L., and Berrigan, D. 1990. Dimensionless numbers and life history evolution: age of maturity versus the adult lifespan. Evolutionary Ecology, 4: 273-275.

Clark, M. R., Althaus, F., Schlacher, T. A., Williams, A., Bowden, D. A., and Rowden, A. A. 2016. The impacts of deep-sea fisheries on benthic communities: a review. ICES Journal of Marine Science: Journal du Conseil, 73: i51-i69.

Collie, J. S., Escanero, G. A., and Valentine, P. C. 2000a. Photographic evaluation of the impacts of bottom fishing on benthic epifauna. Ices Journal of Marine Science, 57: 987-1001.

Collie, J. S., Hall, S. J., Kaiser, M. J., and Poiner, I. R. 2000b. A quantitative analysis of fishing impacts on shelf-sea benthos. Journal of Animal Ecology, 69: 785-798.

Dayton, P. K., Thrush, S. F., Agardy, M. T., and Hofman, R. J. 1995. Environmental-Effects of Marine Fishing. Aquatic Conservation-Marine and Freshwater Ecosystems, 5: 205-232.

Diesing, M., Stephens, D., and Aldridge, J. 2013. A proposed method for assessing the extent of the seabed significantly affected by demersal fishing in the Greater North Sea. ICES Journal of Marine Science: Journal du Conseil, 70: 1085-1096.

Eastwood, P. D., Mills, C. M., Aldridge, J. N., Houghton, C. A., and Rogers, S. I. 2007. Human activities in UK offshore waters: an assessment of direct, physical pressure on the seabed. Ices Journal of Marine Science, 64: 453-463.

Eigaard, O. R., Bastardie, F., Breen, M., Dinesen, G. E., Hintzen, N. T., Laffargue, P., Mortensen, L. O., et al. 2016. Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. ICES Journal of Marine Science: Journal du Conseil, 73: i27-i43.

Eigaard, O. R., Bastardie, F., Hintzen, N. T., Buhl-Mortensen, L., Buhl-Mortensen, P., Catarino, R., Dinesen, G. E., et al. 2017. The footprint of bottom rawling in European waters: distribution, intensity, and seabed integrity. – ICES Journal of Marine Science, doi:10.1093/icesjms/fsw194.

Ellis, N., Pantus, F., and Pitcher, C. R. 2014. Scaling up experimental trawl impact results to fishery management scales — a modelling approach for a “hot time”. Canadian Journal of Fisheries and Aquatic Sciences, 71: 733-746.

Engelhard, G. H. 2008. One hundred and twenty years of change in fishing power of English North Sea trawlers. *In* Advances in Fisheries Science 50 years on from Beverton and Holt, pp. 1-25. Ed. by A. Payne, Cotter, J. and Potter, T. Blackwell Publishing, London.

Eno, N. C., Frid, C. L. J., Hall, K., Ramsay, K., Sharp, R. A. M., Brazier, D. P., Hearn, S., et al. 2013. Assessing the sensitivity of habitats to fishing: from seabed maps to sensitivity mapsa. Journal of Fish Biology: n/a-n/a.

Foden, J., Rogers, S. I., and Jones, A. P. 2011. Human pressures on UK seabed habitats: a cumulative impact assessment. Marine Ecology Progress Series, 428: 33-47.

Gerritsen, H. D., Minto, C., and Lordan, C. 2013. How much of the seabed is impacted by mobile fishing gear? Absolute estimates from Vessel Monitoring System (VMS) point data. Ices Journal of Marine Science, 70: 523-531.

Grabowski, J. H., Bachman, M., Demarest, C., Eayrs, S., Harris, B. P., Malkoski, V., Packer, D., et al. 2014. Assessing the Vulnerability of Marine Benthos to Fishing Gear Impacts. Reviews in Fisheries Science & Aquaculture: 142-155.

Hall, S. J. 1994. Physical Disturbance and Marine Benthic Communities - Life in Unconsolidated Sediments. Oceanography and Marine Biology, 32: 179-239.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., et al. 2008. A global map of human impact on marine ecosystems. Science, 319: 948-952.

Kaiser, M. J. 1998. Significance of bottom-fishing disturbance. Conservation Biology, 12: 1230-1235.

Kaiser, M. J., Clarke, K. R., Hinz, H., Austen, M. C. V., Somerfield, P. J., and Karakassis, I. 2006. Global analysis of response and recovery of benthic biota to fishing. Marine Ecology-Progress Series, 311: 1-14.

Kerby, K., Cheung, W. L., and Engelhard, G. H. 2012. The United Kingdom’s role in North Sea demersal fisheries: a hundred year perspective. Reviews in Fish Biology and Fisheries, 22: 621-634.

Kerby, T. K., Cheung, W. W. L., van Oosterhout, C., and Engelhard, G. H. 2013. Entering uncharted waters: Long-term dynamics of two data limited fish species, turbot and brill, in the North Sea. Journal of Sea Research, 84.

Lee, J., South, A. B., and Jennings, S. 2010. Developing reliable, repeatable, and accessible methods to provide high-resolution estimates of fishing-effort distributions from vessel monitoring system (VMS) data. Ices Journal of Marine Science, 67: 1260-1271.

O 'Neill, F. G., and Ivanović, A. 2016. The physical impact of towed fishing gears on soft sediments. Ices Journal of Marine Science, 73 (suppl 1): i1-i14.

Pitcher, C. R., Ellis, N., Jennings, S., Hiddink, J. G., Mazor, T., Kaiser, M. J., Kangas, M. I., et al. 2016. Estimating the sustainability of towed fishing-gear impacts on seabed habitats: a simple quantitative risk assessment method applicable to data-limited fisheries. Methods in Ecology and Evolution.

Ridgway, I. D., Richardson, C. A., and Austad, S. N. 2011. Maximum Shell Size, Growth Rate, and Maturation Age Correlate With Longevity in Bivalve Molluscs. The Journals of Gerontology Series A: Biological Sciences and Medical Sciences, 66A: 183-190.

Rijnsdorp, A. D., Bastardie, F., Bolam, S. G., Buhl-Mortensen, L., Eigaard, O. R., Hamon, K. G., Hiddink, J. G., et al. 2016. Towards a framework for the quantitative assessment of trawling impact on the seabed and benthic ecosystem. ICES Journal of Marine Science: Journal du Conseil, 73: i127-i138.

Rijnsdorp, A. D., Buys, A. M., Storbeck, F., and Visser, E. G. 1998. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. Ices Journal of Marine Science, 55: 403-419.

Thrush, S. F., and Dayton, P. K. 2002. Disturbance to marine benthic habitats by trawling and dredging: Implications for marine biodiversity. Annual Review of Ecology and Systematics, 33: 449-473.

Thrush, S. F., Lundqust, C. J., and Hewitt, J. E. 2005. Spatial andTemporal Scales of Disturbance to the seafloor: a generalized framework for active habitat management. *In* American Fisheries Society Symposium, pp. 639-649.

Tillin, H. M., Hiddink, J. G., Jennings, S., and Kaiser, M. J. 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Marine Ecology-Progress Series, 318: 31-45.

van Denderen, P. D., Bolam, S. G., Hiddink, J. G., Jennings, S., Kenny, A., Rijnsdorp, A. D., and van Kooten, T. 2015a. Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. . Marine Ecology Progress Series, 541: 31-43.

van Denderen, P. D., Hintzen, N. T., Rijnsdorp, A. D., Ruardij, P., and van Kooten, T. 2014. Habitat-Specific Effects of Fishing Disturbance on Benthic Species Richness in Marine Soft Sediments. Ecosystems, 17: 1216-1226.

van Denderen, P. D., Hintzen, N. T., Van Kooten, T., and Rijnsdorp, A. D. 2015b. Temporal aggregation of bottom trawling and its implication for the impact on the benthic ecosystem. Ices Journal of Marine Science, 72: 952-961.

Table 1. Number of stations and samples by Eunis habitat

Eunis_4	Habitat	Number of stations	Number of samples
A5.13	Infralittoral coarse sediment	9	9
A5.14	Circalittoral coarse sediment	85	149
A5.15	Deep circalittoral coarse sediment	28	51
A5.23	Infralittoral fine sand	66	280
A5.24	Infralittoral muddy sand	1	1
A5.25	Circalittoral fine sand	70	88
A5.26	Circalittoral muddy sand	21	21
A5.27	Deep circalittoral sand	73	91
A5.35	Circalittoral sandy mud	4	4
A5.37	Deep circalittoral mud	23	78
A5.43	Infralittoral mixed sediments	3	3
A5.44	Circalittoral mixed sediments	20	20
Total		403	795

Table 2. Correlation matrix of the environmental variables and trawling intensity

	$\log_e$ Depth	$\log_e$ Stress	$\log_e$ Trawling	%Gravel	%Sand	%Silt	Primary production
$\log_e$Depth	1	-0.194	0.091	-0.072	-0.221	0.344	-0.187
$\log_e$Stress		1	0.170	0.402	-0.086	-0.270	0.710
$\log_e$Trawling			1	-0.220	-0.045	0.263	0.327
%Gravel				1	-0.719	-0.177	0.140
%Sand					1	-0.612	0.004
%Silt						1	-0.258
Primary production							1

Table 3. Parameter estimates of the of the effects $\log_e$ trawling intensity and Eunis-3 habitat class on the cumulative biomass – longevity relationship as given by the selected mixed effect model with the random intercept (station/replicates)

Random effects:

Groups Name	Variance	Std.Dev.	Corr
ID (Intercept)	0.31353	0.5599	
Loge(longevity)	0.01684	0.1298	1.00

Number of obs: 2385, groups: ID, 403

Fixed effects:

	Estimate	Std Error	Z value	Pr(>|z|)	
(Intercept)	-4.47878	0.37264	-12.019	< 2e-16	***
Loge(longevity)	2.85119	0.22092	12.906	< 2e-16	***
as.factor(Eunis)A5.2	-1.22175	0.45169	-2.705	0.006834	**
as.factor(Eunis)A5.3	-0.13806	0.80792	-0.171	0.864311	
as.factor(Eunis)A5.4	0.30105	1.06435	0.283	0.777290	
Loge(trawling intensity)	0.13699	0.03693	3.709	0.000208	***
Loge(longevity):as.factor(Eunis)A5.2	0.91707	0.26663	3.440	0.000583	***
Loge(longevity):as.factor(Eunis)A5.3	1.10317	0.64105	1.721	0.085273	.
Loge(longevity):as.factor(Eunis)A5.4	0.14503	0.64778	0.224	0.822844	

\---

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Table 4. Cumulative biomass – longevity relationships estimated for two functional groups (bioturbators, suspension feeders) and the habitat groups (surface: taxa that live on the surface; surface + subsurface: taxa that live on the surface or in the top 5cm of the seabed).

Subset	Model	
All taxa	$\log_e$(longevity) + Eunis + $\log_e$(trawling) + Eunis: $\log_e$(longevity)	
Bioturbators	$\log_e$(longevity) + $\log_e$(trawling)	
Suspension feeders	$\log_e$(longevity)	
Surface	$\log_e$(longevity) + Eunis + $\log_e$(trawling)	
Surface + subsurface	$\log_e$(longevity) + Eunis + $\log_e$(longevity):Eunis	

Table 5. Parameter estimates of the fixed part of the selected mixed effect model of the cumulative biomass as a function of $\log_e$ longevity (ll), $\log_e$ trawling intensity (lfreq) and the habitat variables gravel% (gravel), $\log_e$ tidal shear stress (lstress) and $\log_e$ depth (ldepth).

```
Random effects:
 Groups       Name        Variance Std.Dev.
 replicate:ID (Intercept) 0.0000   0.0000
 ID           (Intercept) 0.2257   0.4751
Number of obs: 2385, groups:  replicate:ID, 795; ID, 403

Fixed effects:
                      Estimate Std. Error z value Pr(>|z|)
(Intercept)          -8.353657   0.776827 -10.754  < 2e-16 ***
ll                    3.383869   0.157321  21.509  < 2e-16 ***
ldepth                0.851955   0.191578   4.447 8.71e-06 ***
Gravel                0.015738   0.011635   1.353  0.17620
lfreq                -1.022283   0.327461  -3.122  0.00180 **
lstress              -0.064257   0.117461  -0.547  0.58434
ll:Gravel            -0.017131   0.006129  -2.795  0.00519 **
ldepth:lfreq          0.291490   0.092250   3.160  0.00158 **
lfreq:lstress        -0.601718   0.222096  -2.709  0.00674 **
ldepth:lfreq:lstress  0.140358   0.059960   2.341  0.01924 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Table 6. Cumulative biomass – longevity relationships estimated for two functional groups (bioturbators, suspension feeders) and the habitat groups (surface: taxa that live on the surface; subsurface: taxa that live on the surface or in the top 5cm of the seabed).

Subset	Model
ALL	$\log_e$(Longevity) + $\log_e$(Depth) + Gravel + $\log_e$(Trawling) + $\log_e$(Stress) + $\log_e$(Longevity):Gravel + $\log_e$(Trawling): $\log_e$(Depth) + $\log_e$(Trawling): $\log_e$(Stress) + $\log_e$(Trawling):$\log_e$(Stress):$\log_e$(Depth)
Bio-turbators	$\log_e$(Longevity) + $\log_e$(Depth) + Gravel + $\log_e$(Trawling) + $\log_e$(Stress) + $\log_e$(Trawling): $\log_e$(Depth) + +$\log_e$(Trawling): $\log_e$(Stress)
Suspension feeders	$\log_e$(Longevity) + $\log_e$(Depth) + Gravel + $\log_e$(Stress)
Surface	$\log_e$(Longevity) + $\log_e$(Depth) + Gravel + $\log_e$(Trawling)
Subsurface	$\log_e$(Longevity) + $\log_e$(Stress)

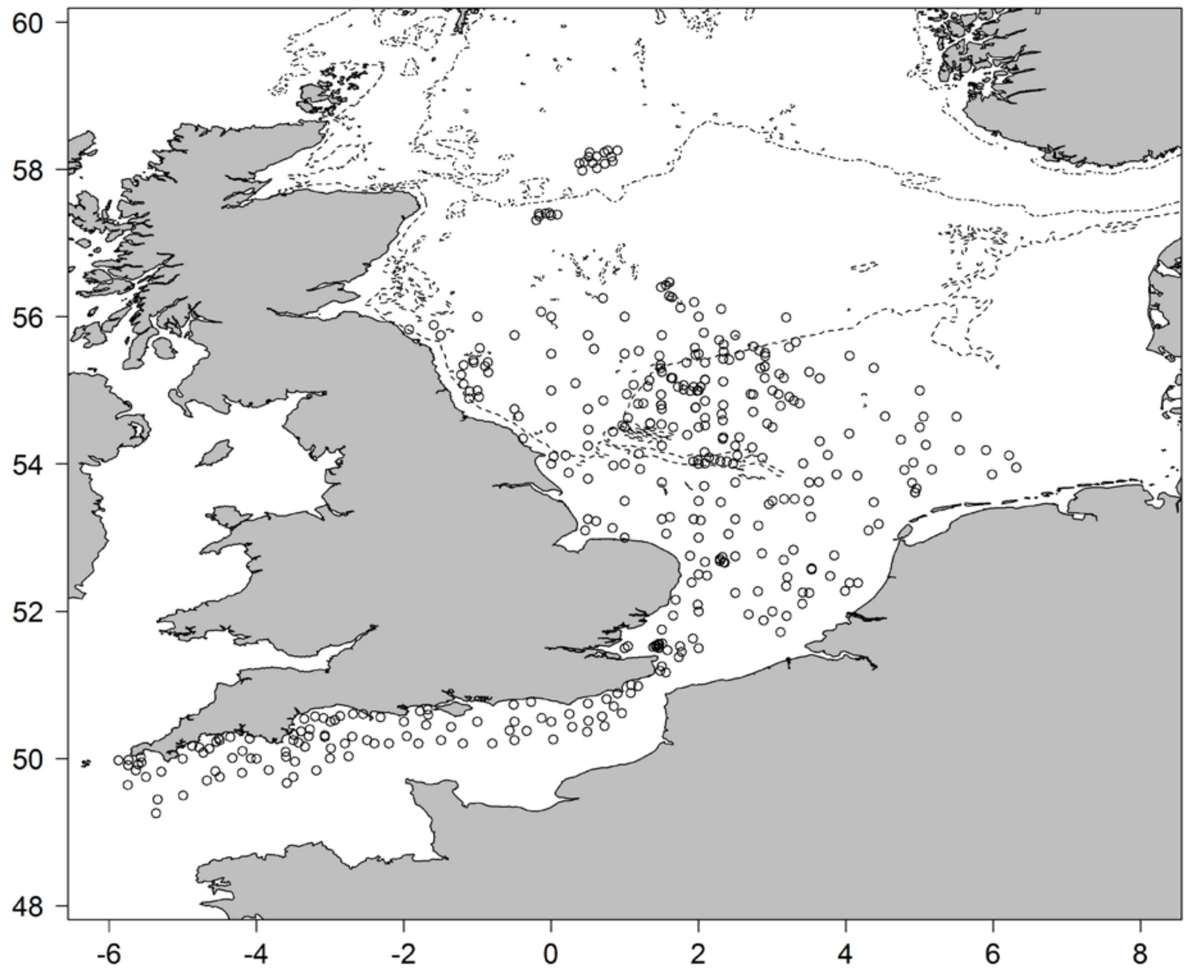

Figure 1. Location of the sampling stations of the infauna

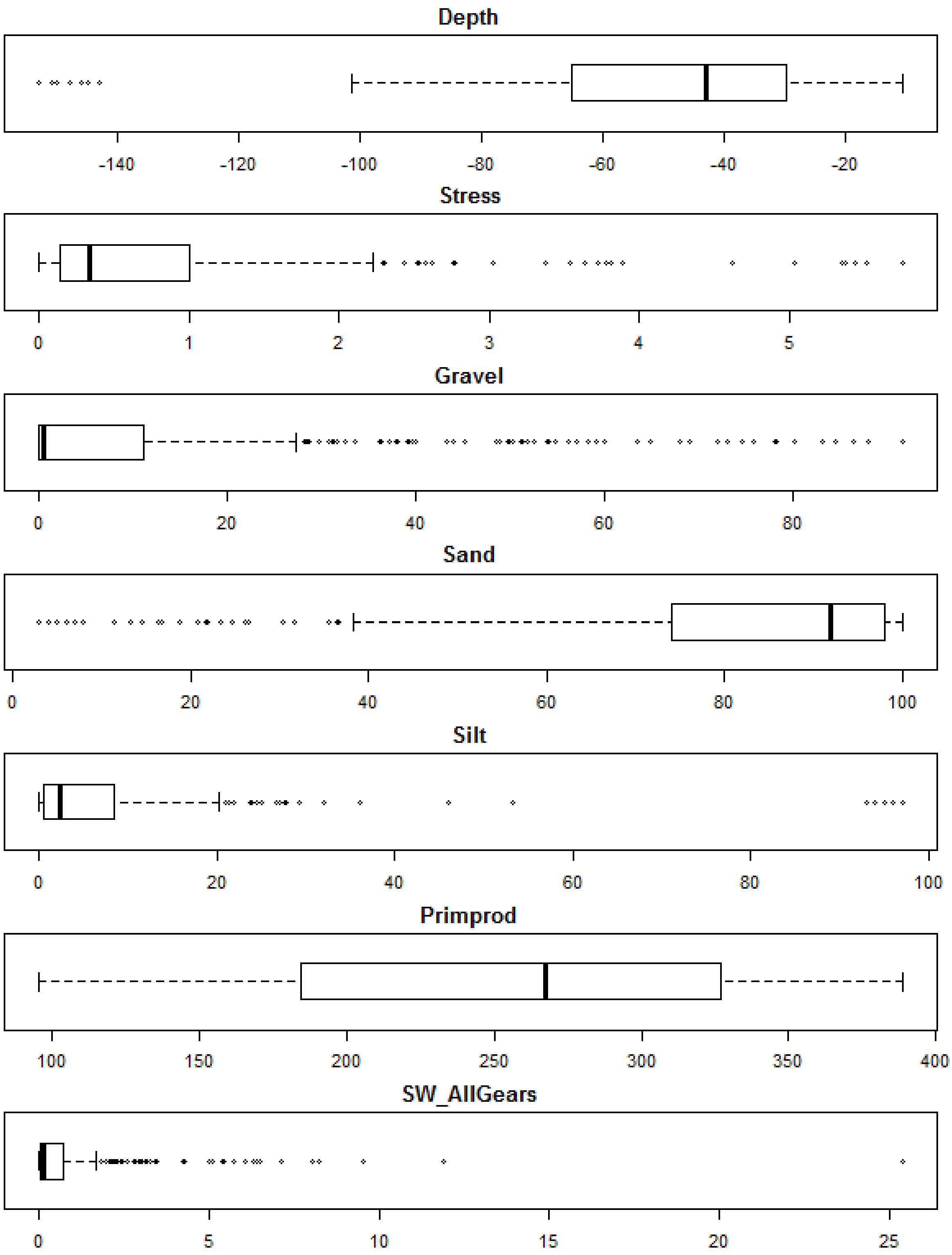

Figure 2. Box plot of the range of environmental conditions of the sampled stations

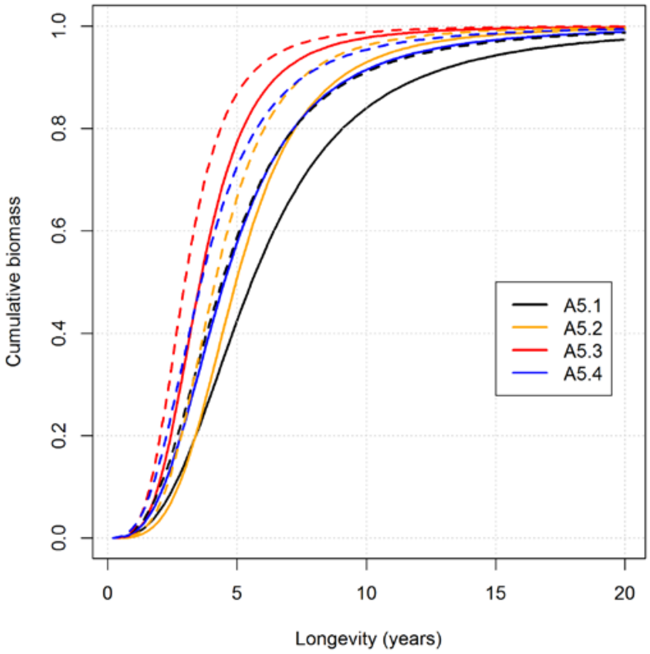

Figure 3. Cumulative biomass (proportion) - longevity (years) relationship as predicted by the generalised additive mixed effect model for four Eunis-3 habitats at an annual trawling intensity of zero (full lines) and one (hatched lines). A5.1 – Coarse sediment, A5.2 – Sand; A5.3 – Mud; A5.4 – Mixed sediment.

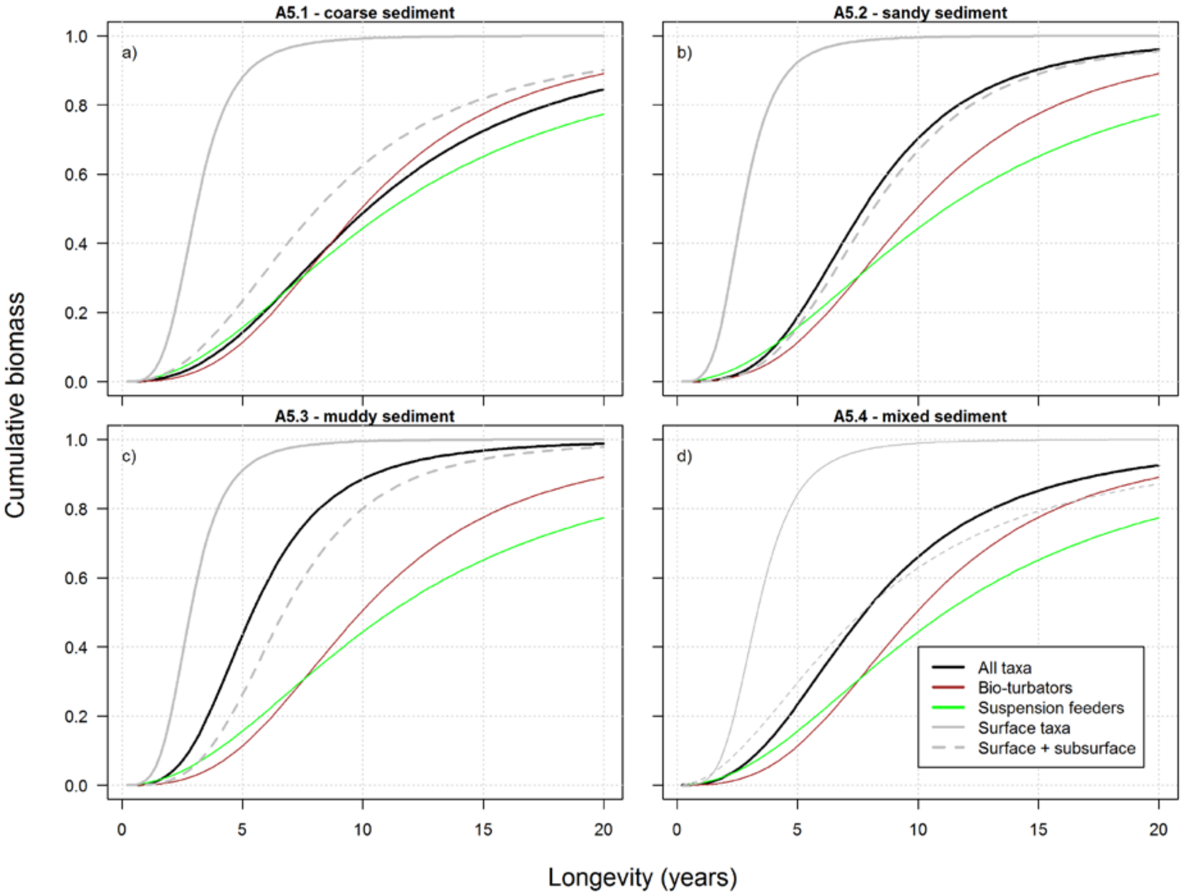

Figure 4. Cumulative biomass (proportion) - longevity (years) relationship for all taxa as well as subsets of two functional groups (bioturbators, suspension feeders) and two habitat groups (surface: taxa that live on the seabed; surface + subsurface: taxa that live on the seabed or in the top 5cm of the seabed) for Eunis-3 habitat: a) A5.1 – coarse sediment; b) A5.2 – Sand; c) A5.3 – Mud; d) A5.4 – Mixed sediment. The relationships were fitted by the selected models of Table 4 assuming %gravel = 0, tidal shear stress = 0.01, trawling intensity = 0.01.

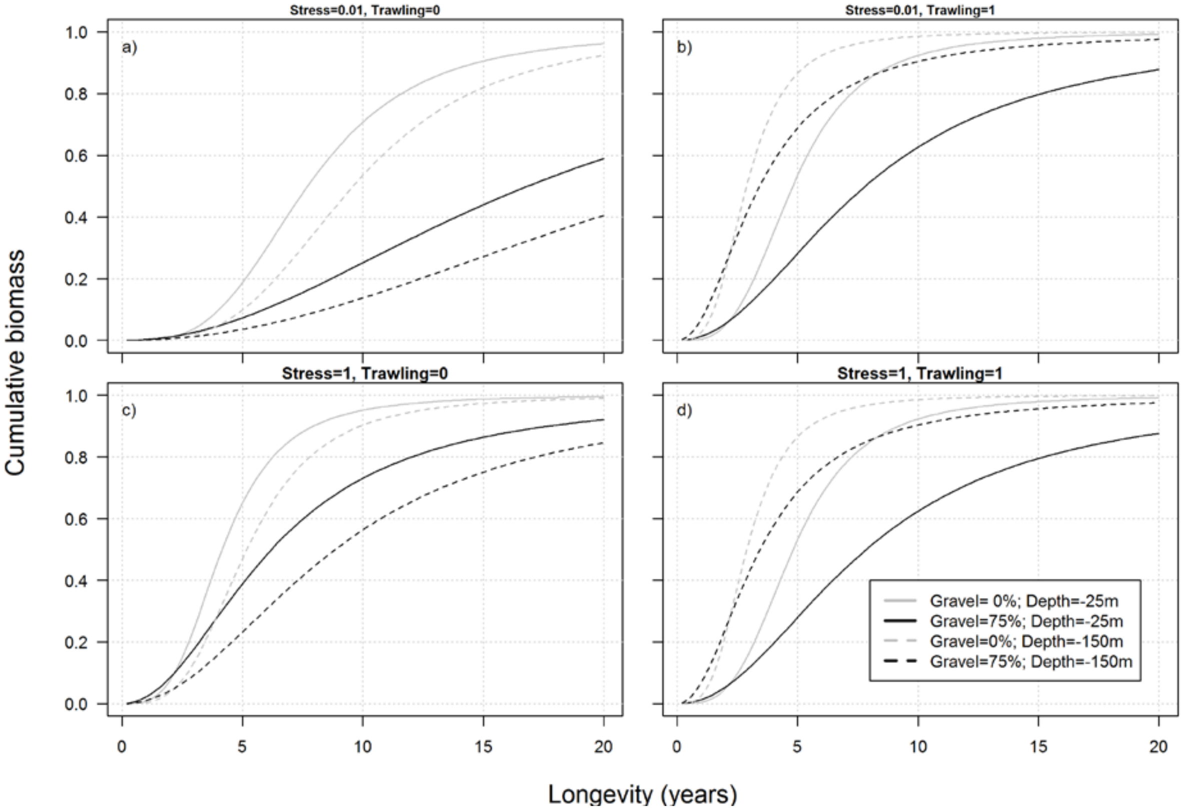

Figure 5. Cumulative biomass - longevity relationships for untrawled habitats (panels a and c) and habitats trawled at an intensity of 1 year^{-1} (panels b and d) for a low (stress=0: panel a and c) and high (stress=1: panel b and d) level of tidal shear stress. The relationships are shown for a habitat with 0% and 75% gravel at a depth of 25m and 150m. Relationships are predicted by the most parsimonious mixed effect model m21b (random intercept of station/replicates).

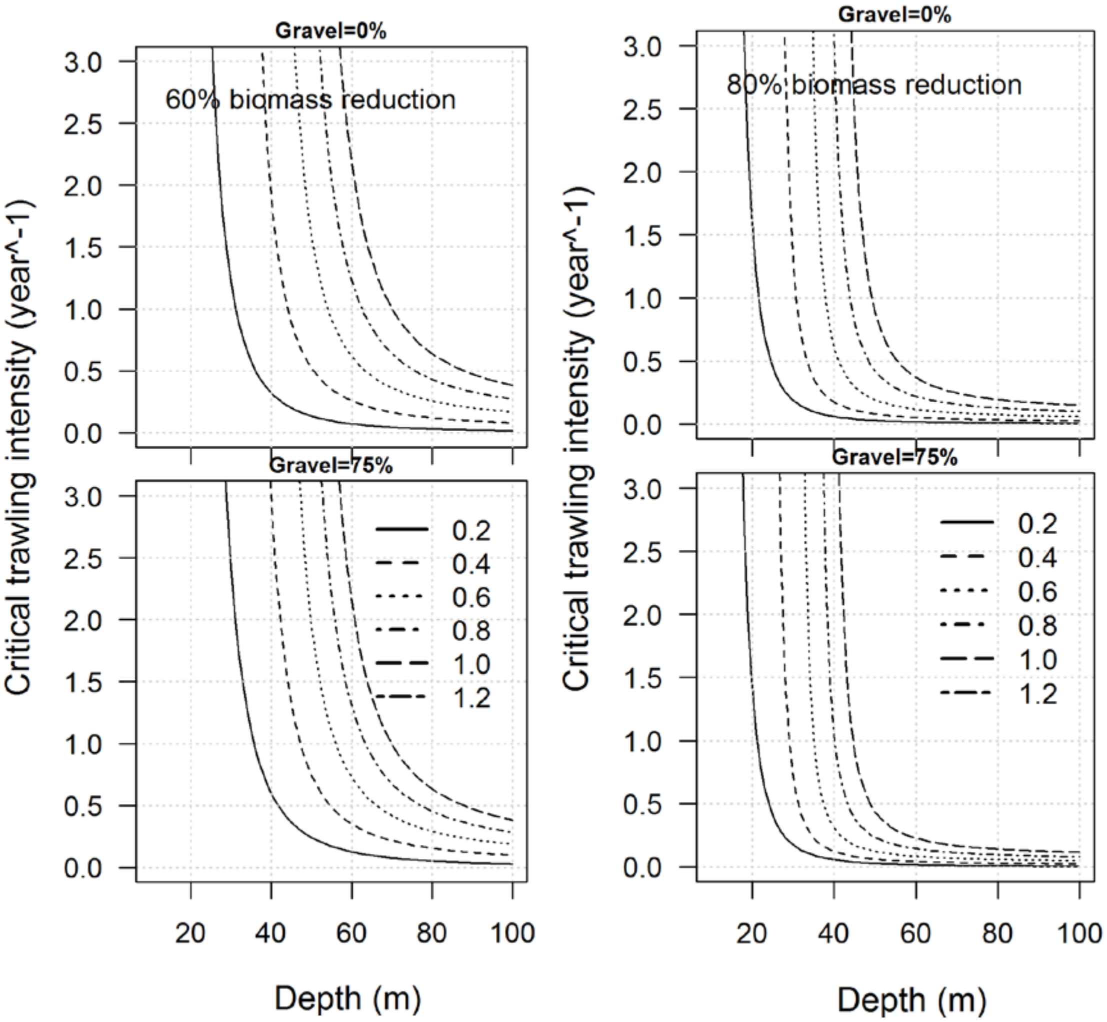

Figure 7. Critical trawling intensity at which the biomass of long-lived taxa (10 years or more) is reduced to 60% (left panels) or 80% (right panels) in relation to depth for a seabed with 0% or 75% gravel and tidal shear stress levels between 0.2 and 1.2 units. Relationships estimated with the parameter estimates of Table 4.

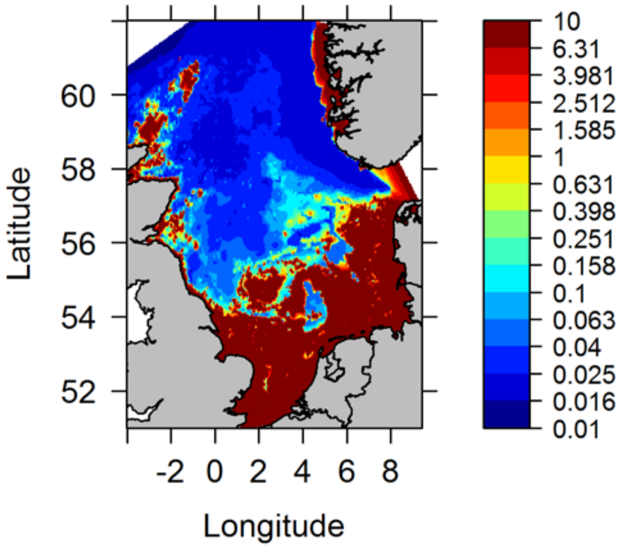

Figure 8. Critical trawling intensity at which the proportion of long lived taxa (life-span of 10 years of more) is reduced to 80% of the untrawled biomass.

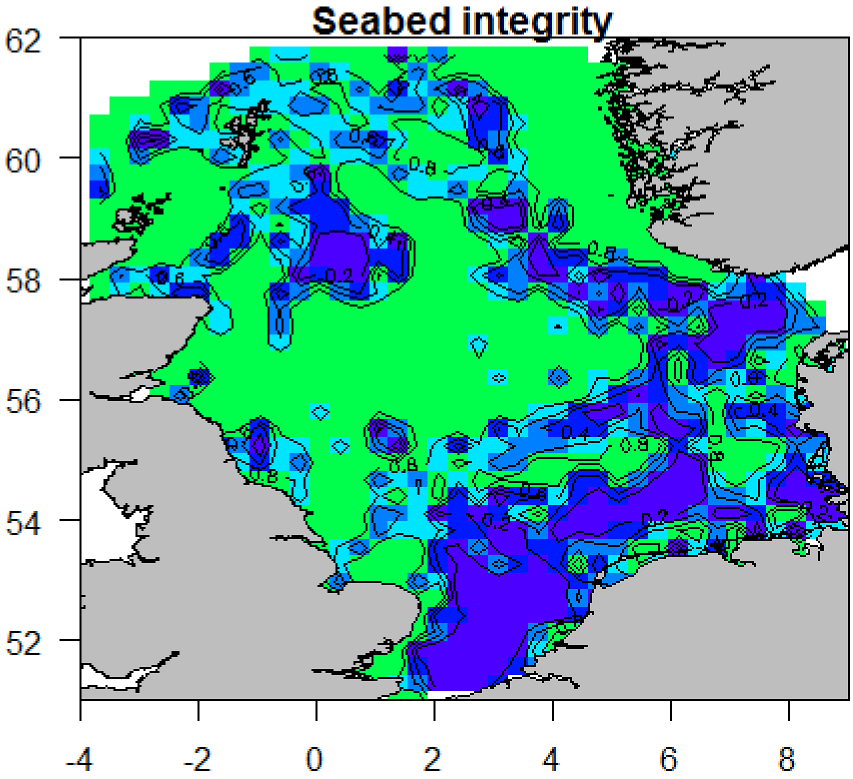

Figure 9. Status of the seafloor estimated by approach 1 assuming that taxa will be adversely affected by bottom trawling if their longevity exceeds the reciprocal trawling intensity. Green colours indicate a seafloor integrity above 0.8.

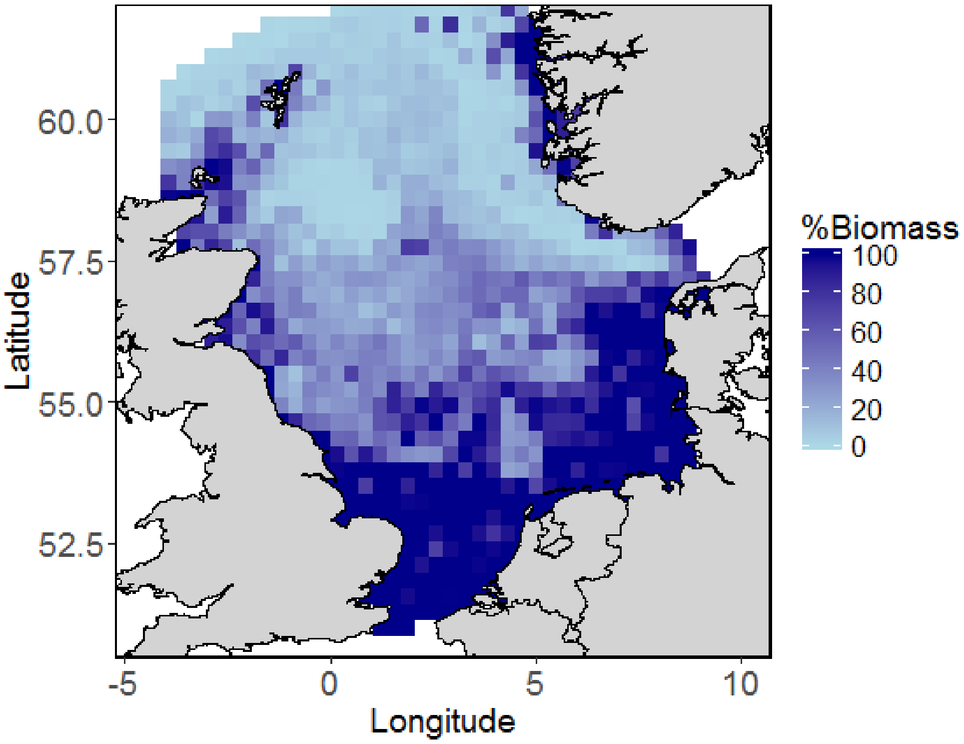

Figure 10. Status of the seabed given the annual trawling intensities per grid cell as observed in the period 2010-2012. A status of 100 represents an unaffected state