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Original Article

Determining and mapping species sensitivity to trawling impacts: the BEnthos Sensitivity Index to Trawling Operations (BESITO)

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Applying an ecosystem approach requires a deep and holistic understanding of interactions between human activities and ecosystems. Bottom trawling is the most widespread physical human disturbance in the seabed and produces a wide range of direct and indirect impacts on benthic ecosystems. In this work, we develop a new index, the BEnthos Sensitivity Index to Trawling Operations (BESITO), using biological traits to classify species according to their sensitivity to bottom trawling. Seventy-nine different benthic taxa were classified according to their BESITO scores in three groups. The effect of trawling on the relative abundance of each group (measured as biomass proportion) was analysed using General Additive Models (GAMs) in a distribution model framework. The distribution of the relative biomass of each group was mapped and the impact of trawling was computed. Species with the lowest BESITO score (group I) showed a positive response to trawling disturbance (opportunistic response) whereas species with values higher than 2 (group III) showed a negative response (sensitive response). Species with a BESITO score of 2 did not show a significant response to the pressure (tolerant response). Trawling disturbance reduced relative biomass of sensitive species by 31% across the study area. This value increased to 46% when shelf-break was considered in isolation and reached values of 59.6% in the most impacted habitat (deep-sea muddy sands). The new index classified successfully the analysed species according to their sensitivity to trawling allowing modeling the impact of trawling disturbance on sensitive species, without the masking effect of opposed responses.

Keywords: BESITO index, biological traits, distribution models, GAMs, trawling

Introduction

Bottom trawling is probably one of the most significant human impacts on marine ecosystems. This method of fishing occurs on practically every continental shelf around the world (Watling, 2005) and currently produces the highest global seafood landings by value of all the existent fishing methods (FAO, 2016). In these continental shelves, bottom trawling not only affects target species but the benthic community as a whole, damaging seabed habitats and benthic invertebrates in the path of the gear (Kaiser et al., 2002). Moreover, trawling produces a wide range of indirect effects on the benthic ecosystem such as energy subsidies (discards and injured animals that would otherwise not be available for predation), resuspension of sediment and trophic alterations (Collie et al., 2017). Trawling disturbance is so widespread that pristine areas in soft bottoms are challenging to find in European seas (Bolam et al., 2017; Eigaard et al., 2017). However, different habitats and benthic species are not equally affected by trawling (Collie et al., 2000). Some species are more sensitive than others because of their different biological and functional traits. This variability in response can be used to investigate the

effects of disturbance (Bremner *et al.*, 2006) as well as for developing new biotic indicators (de Juan and Demestre, 2012).

Management of the marine environment under the framework of the ecosystem approach demands a better understanding of all resident species and habitats and their interactions with human pressures (Christensen *et al.*, 1996; Long *et al.*, 2015). In recent years, in the context of the gradual implementation of an ecosystem approach into assessment legislation, such as the Marine Strategy Framework Directive (MSFD) or the Habitats Directive (HD), several studies have analysed the effect of bottom trawling on benthic communities using Biological Traits Analysis (BTAs) (e.g. Tillin *et al.*, 2006; de Juan *et al.*, 2007; de Juan and Demestre, 2012; van Denderen *et al.*, 2015). In the present work, these techniques have been used to develop and test (in a large area, the northern coast of Spain) a sensitivity index that classifies benthic species according to their trawling sensitivity: the BEnthos Sensitivity Index to Trawling Operations (BESITO). Species trawling sensitivity plays a key role to the development of biotic indicators. Although some important efforts to classify species according to their sensitivity to trawling have been made (de Juan *et al.*, 2009; de Juan and Demestre, 2012), there is currently no list of ecological groups in relation to trawling disturbance similar to the groups available for other pressures such as organic matter enrichment (Hily, 1984; Glemarec 1986; Grall and Glemarec, 1997). This lack of information is a bottleneck for current indexes, which require these ecological groups, for example: the Azti Marine Biotic Index (AMBI) (Borja *et al.*, 2000), the Benthic Assessment Tool (BAT) (Teixeira *et al.*, 2009), and the Norwegian Quality Index (NQI) (Josefson *et al.*, 2009) as well as for the development of new indicators to assess trawling impacts.

Moreover, classifying species by their sensitivity to trawling also allows us to quantify and map, for each sensitivity group, the impact of trawling using Distribution Models (DMs) avoiding the masking effect of opposite responses (opportunistic response vs. sensitive response). DMs statistically relate the spatial distribution of species to environmental variables (Elith and Leathwick, 2009) and have been used to analyse the distribution of marine species (e.g. Bryan, and Metaxas, 2007; Reiss *et al.*, 2011), functional habitats (Colloca *et al.*, 2009; Lelièvre *et al.*, 2014; González-Irusta and Wright, 2017), biological habitats (Moritz *et al.*, 2013; Serrano *et al.*, 2017), and even functional groups (Drexler and Ainsworth, 2013). However, to the best of our knowledge, this is the first time that DMs have been applied in combination with Vessel Monitoring System (VMS) effort data to map and quantify the impact of bottom trawling on sensitive species.

In this study, we used BTAs to test the BESITO index by classifying benthic species according to their sensitivity to trawling across a trawling disturbance gradient (swept area). The relative biomass of different sensitivity groups in the study area was modelled using GAM-based DMs and the effect of trawling disturbance on the relative biomass of each group was analysed, quantified and mapped with a double objective: (i) to test the accuracy of the BESITO index classifying species according to their sensitivity to trawl fishing pressure and (ii) to determine and map the impact of bottom trawling on benthic habitats and species.

Material and methods
Biological data
Every autumn (September–November) since 1983, with the exception of 1987, the Instituto Español de Oceanografía (IEO) has carried out a bottom trawling survey on the Northern Spanish

Shelf named DEMERSALES (Figure 1). The DEMERSALES survey aims to provide data for the assessment of commercial fish species and benthic ecosystems on the Galician and Cantabrian shelf (ICES, 2010). This survey is part of an international effort to monitor marine ecosystems and is coordinated by the International Bottom Trawling Surveys (IBTS) working group of the International Council for the Exploration of the Sea (ICES). The DEMERSALES survey is based on random stratified (by depth and geographic strata) sampling according to the standard IBTS methodology for western and southern areas, and consists of 30 min hauls towed at a speed of 3.0 knots using Baca 44/60 otter trawl gear (ICES, 2010). Three depth strata (71–120, 121–200, and 201–500) are defined and the number of hauls per stratum is proportional to the surface area available for trawling. Furthermore, additional hauls shallower than 70 m and deeper than 500 m are performed every year if possible. In each haul, all species caught are identified, counted, and weighed.

In order to assure consistency between the available VMS data (2007–2010) and biological data only hauls for the period 2007–2010 were analysed. Furthermore, any hauls at depths shallower than 70 m or deeper than 700 m were removed from the analysis to assure sampling continuity. 459 hauls were used in the final data set. Pelagic, bentho-pelagic, high mobility (including all fishes), and epibionthic species were removed from the analysis to maximize the link between the biological communities and seabed with the exception of some cephalopod and decapod species that have a strong connection with seabed habitats (Boletzky, 1996; Guerra, 2006; Serrano *et al.*, 2006). Rare species (caught <5 times in the studied period) were also removed from the final list. Finally, 79 different taxa were selected to compute the BESITO Index (Supplementary Table S1). The biomass of the selected species sums a mean of 9% ($\pm$12%) of the total biomass cached by haul during the period 2007–2010.

The BESITO index
In order to classify species in relation to their sensitivity to trawling, an index based on BTAs has been developed, namely the BESITO index. The final aim of this index is to improve our capacity to detect long-term changes in benthic communities as consequence of trawling disturbance combining the BESITO index with current multimetric indexes as well as using it for the development of new ones. The eight biological traits used were: size (BT_1), longevity (BT_2), motility (BT_3), attachment (BT_4), benthic position (BT_5), flexibility (BT_6), fragility (BT_7), and feeding habitat (BT_8). The selection of the traits was based on the general knowledge of trawling impacts on epibenthic communities (e.g. trawling gears have more probabilities of damage epibenthos than endobenthos or species with fragile shells than species with hard shells), previous works using BTAs to determine trawling impacts (de Juan *et al.*, 2009; de Juan and Demestre, 2012; Bolam *et al.*, 2014, 2017; Rijnsdorp *et al.*, 2016) and existent information about the trait for the analysed species. Some traits used in previous works such as larval and egg development location (Bolam *et al.*, 2014, 2017) were not included because of the lack of information for some of the species. However, all the traits included in this work have been successfully applied (in the same or similar way) to define trawling sensitivity in previous works. The only exception was attachment (BT_4), which was included for a better separation of filter organisms. Each trait was scored from 1 to 4 based on vulnerability to trawling in the same way as
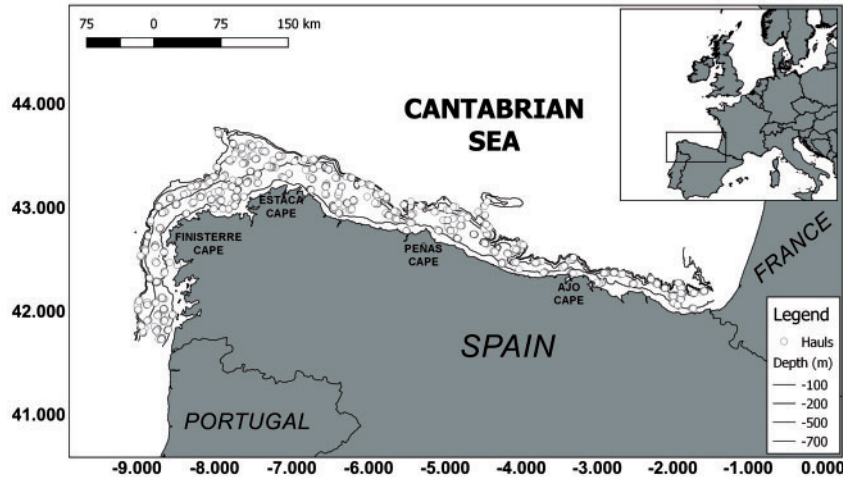
Figure 1. Map of the study area with the selected hauls distribution and the main capes location.

previous works (e.g. de Juan et al., 2009; Bolam et al., 2014; Kenny et al., 2017). A further explanation of these biological traits and the criteria followed to assign the score is given in Table 1. Information about each biological trait was extracted from different sources such as specific websites (http://www.marlin.ac.uk/biotic/ and http://www.marinespecies.org), scientific and grey literature and expert judgement (when no other relevant information source was available or counterpoised assignations were found). The scores of the eight biological traits were combined according to the following equation:

$$BESITO = round\left(\frac{\begin{array}{c}2xBT_1 + 3xBT_2 + BT_3 + BT_4 + BT_5 \\ + BT_6 + 2xBT_7 + 2xBT_8\end{array}}{6.6} - 2\right) \quad (1)$$

In order to assign the weight of the traits in the BESITO formula, the variation in the relative biomass of each trait's level was analyzed (see Supplementary Figure S2). The traits were then weighted according to its sensitivity to trawling from 3 (clear trend with trawling effort) to 1 (no trend). The equation was defined with the only purpose of divided the species in five groups, using species with a well-documented sensitivity to trawling (high or low) as indicators to define the thresholds between groups. BESITO values ranged from 0.7 to 4.7 and were rounded to values between 1 and 5. As such, the formula combines all the BTs in a new metric, the BESITO index with 5 possible outcomes, 1 being the lowest possible value (non-sensitive species) and 5 the maximum (highly sensitive species). The value assigned to each trait for each species as well as the BESITO index value can be found in Supplementary Table S1.

Trawling effort and environmental layers
In order to test how accurately the BESITO index classified species according to their response to trawling disturbance, we used fishing effort data from VMS locations and environmental variables (Supplementary Figure S1); bathymetry (m), sediment type and primary productivity (g Cm^{-3}/day). The spatial distribution of the swept area (by trawlers) was obtained from Vessel Monitoring Systems (VMS), which provides vessel GPS location

every 2 h, and logbook data (gear information). Both were provided by the Spanish Ministry of Agriculture, Food and Environment for the period 2007–2010. Gear and GPS location data were linked using ship code and trip date fields. VMS pings not related to fishing activity were removed using speed and other criteria (Punzón et al., 2016). To obtain the spatial distribution of swept area, hauls were assigned to individuals fishing trips and VMS pings were interpolated to obtain the fishing track of each haul using the cubic-hermite spline interpolation (Hintzen et al., 2010). To compute the swept area the two kinds of trawl gears used by the fishing fleet in the study area (otter trawl and twin trawl) were taken into account. According to Castro et al. (2007) we used a 20 m width gear for otter trawls and 65 m for twin trawls (the information about gear type was also obtained from the logbooks). The mean annual swept area for each cell (km^2) was converted into the number of times each cell was trawled by dividing the mean annual swept area by the cell area (we used for all the environmental layers a 3 km × 3 km cell). The final map gives the mean value of the 4 years provided (2007–2010). It is important to highlight that in Spanish waters the fishing effort maps cover practically all the trawling effort present in the area since all the trawlers are longer than 15 m and therefore all of them are affected by the VMS legislation.

The bathymetry extracted from the IEO database is based on multibeam data with an original resolution of 280 × 280 m, resampled to 3 × 3 km using the implementation resample in the R package raster (Hijmans 2016). The five sediment classes; mud-sandy mud, sand-muddy sand, coarse sand, mixed sediment, and rock were derived from Populus et al., (2017). Since DEMERSALES survey only samples sedimentary bottoms, rocky substrates were not included in the models. Primary production data were obtained from the ocean biogeochemistry non assimilative hindcast product "IBI_REANALYSIS_BIO_005_003", generated and provided by the CMEMS IBI-MFC (Sotillo et al., 2015) and downloaded from www.myocean.eu. In each cell, the mean value of primary production for the first 50 m was computed. Then, the maximum value during the study period for each cell was recorded in the final layer. Finally, the distribution of the main EUropean Nature Information System (EUNIS) level 3 habitats (Connor et al., 2004) present in the northern coast of Spain were downloaded from http://www.emodnet.eu (Populus et al., 2017)

Table 1. Explanation of the biological traits and the scores assigned.

		Score 1	Score 2	Score 3	Score 4
Size	Big organisms are more easily affected by trawling than the smaller ones, which can escape through the net having less probabilities of being affected	Small (<2 cm)	Medium (2–10 cm)	Medium large (10–50 cm)	Large (>50 cm)
Longevity	Long-life organisms have a lower recovery capacity and usually need more time to reach sexual maturity	<5 years	5–10 years	10–50 years	>50 years
Motility	Mobile species are more able to escape from trawling and can colonize trawling grounds by migration	Swimmer	Crawl	Burrow/Crevice/ Occasional crawl	Sessile
Attachment	Species with a permanent attachment cannot survive if they are decoupled, whereas species with a temporal attachment have a chance	No sessile	–	Temporary	Permanent
Benthic position	Exposition to trawling disturbance is highly influenced by benthic position. Burrowing species are less exposed than emergent ones	Burrowing	–	Surface	Emergent (>20 cm)
Flexibility	Sessile species with a high flexibility are less sensitive to trawling than species with low flexibility.	High (>45°) or no sessile	–	Low (10–45°)	None (<10°)
Fragility	Species with a very strong shell (e.g. some mollusca species) are less sensitive to physical impacts than species with a very fragile shell (e.g. *Echinus melo*), which can suffer mortal damage with a higher probability	Hardshell, vermiform	Strong	No protection	Fragile shell
Feeding habit	Scavengers or opportunistic scavenger can prey on dead and injured individuals after trawling, whereas filter animals usually are negative affected by trawling (siltation)	Scavenger	Predators, Omnivores	Deposit-feeders	Filter-feeders

and used to compute the mean reduction in sensitivity species by habitat.

Data analysis

In order to visualize the accuracy of the BESITO index, we divided the 79 taxa into five groups based on their BESITO score and computed the relative biomass (in percentage) and the total biomass (kg/km^2) of each group by haul. The mean relative biomass by haul was then calculated for five levels of trawling effort: very low effort (swept area < 0.2), low effort (swept area > 0.2 and ≤ 0.96), medium effort (swept area > 0.96 and ≤ 1.62), high effort (swept area > 1.62 and ≤ 3.83) and very high effort (swept area > 3.83). These ranges were selected to ensure a similar number of hauls per level and were used only for plotting trawling effect on biomass (relative and total). All the statistical analysis were made using VMS as a continuous variable using swept area rate (number of trawling episodes by cell and year) as measure of fishing effort and only for relative biomass.

The effect of trawling on the relative abundance (%), computed from species biomass (gkm^{-1}) of each group, was statistically analysed using General Additive Models (GAMs) and the R package "mgcv" (Wood 2011). As species with BESITO scores of 4 and 5 were not abundant enough to be modelled separately (too many zeros caused problems with overdispersion) they were merged with species that scored 3 in order to model the relative biomass (in %) of "sensitive species". Therefore, the relative biomass of the species with a BESITO score of 1 (group I), species with a BESITO score of 2 (group II) and species with BESITO score >2 (group III) were modelled. Since the response data was a proportion from 0 to 1, it was analysed using a binomial GAM with Logit as link function (Zuur *et al.*, 2009). Before starting the analysis, correlations between the explanatory variables were

checked for collinearity using Spearman rank correlations and Variance Inflation Factors (VIFs, Zuur *et al.*, 2009). Collinearity in the explanatory variables was discarded, as all variables had Spearman rank correlation values lower than 0.5 and VIF values lower than 3. The smoothers were constrained to 4 knots to avoid overfitting. In order to consider other potential spatial effects produced by unmeasured drivers that could cause spatial autocorrelation in the residuals, the location of each trawl (longitude and latitude) was included in the model. The full binomial model for the three groups was:

$$B = \beta_1 + s(\text{fishing effort}) + s(\text{depth}) + s(\text{Primary Productivity}) + f(\text{sediment type}) + f(\text{year}) + s(\text{Longitude, Latitude}) + \varepsilon_1(3) \quad (2)$$

where B is the relative biomass (proportion) of each sensitivity group, β is the intercept, s is an isotropic smoothing function (thin plate regression splines), f indicates the variables, which were included as factors in the formula and ε is the error term. Explanatory variables were selected for each model using a backwards/forwards stepwise selection process based on Akaike's Information Criteria (AIC). The relative importance of each variable was tested by removing the targeted variable from the final model and computing the deviance variation. The spatial autocorrelation of residuals was analysed for each year and modelled separately using the variogram implementation in the gstat R package (Pebesma, 2004). The semi-variance of the residuals did not show any trend with distance in any year for any of the three models, and therefore, the spatial autocorrelation in the residuals was considered nil.

The statistical models were applied to the GIS layers to generate a geographical prediction of relative biomass distribution (%) for each sensitivity group. For the models of group II and III

(which included year as a factor), the prediction were made for 2008 since this year show intermediate values. Furthermore, in order to show the impact of trawling on the distribution of sensitive species, the percentage reduction of sensitive species as a consequence of trawling was mapped using the following equation:

$$RSS = ((B_{SS\_NT} - B_{SS\_RS})/B_{SS\_NT})) * 100 \qquad (3)$$

Where RSS is percentage Reduction of Sensitive Species, B_{SS_RS} is the result of modelling the relative Biomass of Sensitive Species (SS) in the Real Scenario (RS) and B_{SS_NT} is the result of modelling the relative Biomass of Sensitive Species (SS) in a No Trawling (NT) scenario (all the VMS layer's values are set to 0). In both cases we use the fitted GAM from Equation (2).

The accuracy of the models was tested using cross-validation. Data for each area were randomly divided into a training subsample (with 67% of the total points) and a test subsample (with the other 33%). Models were built using the training subsample and then were used to predict the relative biomass (proportion) of the test subsample. The correlation of the observed and predicted relative biomass was calculated using the Spearman coefficient. This process was repeated 10 times for each model, based on different random selections of training and test subsamples. Mean and standard deviation statistics were computed for each model using the 10 Spearman coefficient values obtained from each repetition.

Results

The BESITO index divided the species into five groups according to their sensitivity to trawling, from 1 (not sensitive) to 5 (highly sensitive). Of the 79 taxa analysed, only two species (*Phakellia ventilabrum* and *Alcyonium palmatum*) had a score of 5 (Supplementary Table S1). Five species received a score of 4, all of which were filter-feeders organisms (three sea pen species and two bivalve species). The group with a BESITO score of 3 was made up of 20 species, most of them echinoderms, including six sea urchin species, three large size sea stars species, two holothurians of the genus *Parastichopus*, one Crinoidea and one Ophiuroidea. Furthermore, filter-feeders organisms with short life cycles such as hydrozoans or Anthozoa were also present in this group. Twenty-five species received a BESITO score of 2. Echinoderms in this group were of smaller sizes than in the previous group. In this group, there were two species of ophiuroids, two medium size sea stars, two small sea urchins and one holothurian. Furthermore, there were several species of Mollusca such as octopus and large gastropods, some polychaeta species and some decapod crustacean. The lowest score was assigned to 27 species, mainly crustaceans such as: *Munida* spp., small crabs, hermit crabs (*Pagurus* spp.), and other small decapods. Small cephalopods and gastropods were also abundant in this group.

The relative biomass (%) and the total biomass (kg/km^2) of each BESITO group across the five levels of trawling effort are shown in Figure 2. The proportion and the weight of species with BESITO score of 1 increased across the trawling gradient with a noticeable increase in areas of very high effort (especially for total biomass). Because of this positive trend in relative and total biomass these species were considered opportunistic species. On the other hand, species with BESITO scores of 3 and 4 showed a decrease with disturbance in both measures. These species were considered to be sensitive to trawling disturbance. Species with a BESITO score of 5 had such low biomass that it was not possible
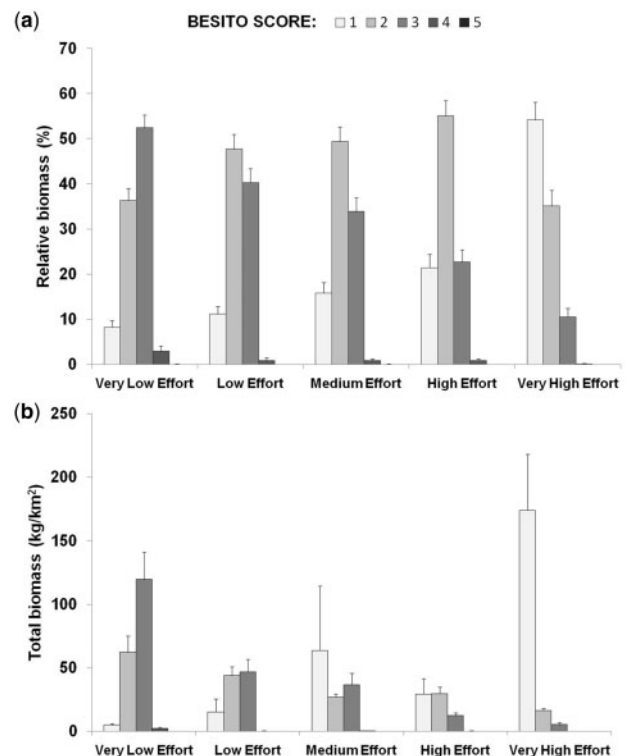

Figure 2. (a) Relative biomass (%) of the benthic species pooled by BESITO score for five levels of trawling effort. (b) Total biomass (kg/km^2) of the benthic species pooled by BESITO score for five levels of trawling effort. The levels of trawling effort are (trawling episodes by cell and year): Very low effort (swept area < 0.2), low effort (swept area > 0.2 and ≤ 0.96), medium effort (>0.96 and ≤ 1.62), high effort (>1.62 and ≤ 3.83) and very high effort (>3.82).

Table 2. Deviance explained and mean spearman coefficient (± SD) value for each GAM.

	Deviance explained (%)	Spearman
GAM opportunistic species	43.9	0.55 ± 0.04
GAM tolerant species	29	0.52 ± 0.07
GAM sensitive species	39.2	0.62 ± 0.07

to appreciate the trend in Figure 2 although raw data values showed a negative trend with trawling effort for both (total and relative biomass). Finally, the Species with a BESITO score of 2 showed a negative trend in total biomass across the trawling gradient (although less clear than the species with a BESITO score of 1) and not trend in relative biomass. These species were considered to be neutral or tolerant to trawling disturbance. A summary of the GAM results for group I (BESITO score of 1), group II (BESITO score of 2) and group III (BESITO score > 2) is shown in Table 2. The GAMs explained 43.9% (group I), 29% (group II), and 39.2% (group III) of the total deviance. The three models showed good performance with Spearman rank correlations ranging from 0.55 ±0.04 (GAM group II) to 0.62 ± 0.07 (GAM group III). Trawling effort was selected as an explanatory variable in all the GAMs although its effect on the relative biomass of species from group II was not statistically significant (Table 3). The spatial effect (longitude and latitude of the hauls) was also included

Table 3. Relative importance (Δ deviance), degrees of freedom (df) or estimated degrees of freedom (edf) and statistical significance of the explanatory variables for the binomial and the negative binomial models.

	Δ Deviance	df/edf	Chi-square	*p* Value
GAM opportunistic species				
Spatial effect	15.92	2	12.06	0.002
Depth	8.67	2.3	10.43	0.012
Primary production	7.98	2.1	6.02	0.077
VMS	5.93	1.5	8.32	0.014
GAM group II				
Spatial effect	32.42	2.9	26.06	<0.001
Primary production	6.36	2.7	9.48	0.018
Depth	5.12	1.8	3.63	0.17
VMS	4.36	2.1	4.19	0.25
Year	3.24	3	2.91	0.41
Sediment type	3.20	3	3.19	0.36
GAM of sensitive species				
VMS	23.98	1.94	27.21	<0.001
Spatial effect	25.25	6.57	20.19	0.017
Sediment type	7.86	3	5.33	0.149
Year	5.94	3	5.31	0.151

in all the models. Sediment type and year were included in the GAMs for group II and III although its effect was not significant in any of them. Finally, depth and primary production were included in the GAMs for group I and II.

The effect of trawling on the biomass of species from group I was positive, with a linear trend for values ranging from 0 to 4 although this was less clear at higher levels of effort (Figure 3). Depth had a positive effect on the proportion of these species, with peak values around 400 m and a negative effect at greater depths. The effect of primary production on the proportion of species from group I was not statistically significant. The spatial effect showed a negative gradient from the north-west of Estaca to the south and to the east. The lowest values were located south of Finisterre Cape (on the border with Portugal) and in the Basque waters (on the border with France).

Trawling had no significant effect on the proportion of species from group II confirming the tolerant response to trawling of these species already observed in Figure 2 for relative biomasss (Table 3). Depth, year, and sediment type did not have a statistically significant effect, although they were included in the model together with trawling since doing so reduce the AIC values. Primary production had a positive effect on the proportion of species from group II, with peak values around 0.11 g Cm^{-3}/day (Figure 4). The spatial effect on the proportion of species from group II was the opposite that observed in species from group I, with a positive gradient from the north-west of Estaca cape to the south and to the east. Finally, trawling had a negative effect on the proportion of species from group III. The trend in the relative biomass was clearly negative for values ranging from 0 to 6 and no trend for values higher than 6 (Figure 5). The spatial effect on the proportion of sensitive species was slightly more complex than for the other models. There was a positive gradient in the proportion of sensitive species south–north from the border with Portugal to Estaca cape and a similar trend east–west from the Basque waters (in the border with France) to Ajo cape. The central Cantabrian Sea (from 2900000 to 3200000 LAEA eastness) had the highest positive effect on the proportion of sensitive

species whereas the lowest was located south of Finisterre Cape, in the border with Portugal.

Distribution and trawling impact

Species from group I showed maximum relative biomass at the shelf break in depths of 200–500 m and especially in the highly disturbed grounds north-west of Estaca cape (Figure 6). Species from group II had high relative biomass values across the whole study area, with maximum values in some areas south of Finisterre (near the border with Portugal) and in the Basque waters (on the border with France). The lowest values were located around Estaca cape and in some areas around Ajo cape, where primary production values were especially low. Finally, group III species showed a distribution inverse of that shown by group I species, with the highest values in areas east of Peñas cape and the lowest in the areas with higher trawling effort, such as north-west of Estaca cape or on the border with France. The standard error was high in areas where explanatory variables had extreme values, such as north-west of Estaca cape (swept area values > 10 trawling episodes by cell and year) or in coastal areas south of Finisterre Cape (on the border with Portugal) where primary production values were very high.

Trawling disturbance reduced the relative biomass of sensitive species (group III) to a maximum of 87% in relation to an undisturbed scenario according to the GAM prediction (Figure 7). The impact is especially apparent on the shelf break where large areas of sea bed showed reductions around this value in the relative biomass of sensitive species. On the other hand, the lack of trawlable grounds around Ajo cape kept these areas relatively unaffected. The mean reduction of sensitive species across the study area was 32%, being higher in the shelf break (46%) than in the continental shelf (23%, Table 4). These values agree with the distribution of trawling effort in the area, which is higher in the slope (3.45 trawling episodes by cell and year) than in the continental shelf (0.84 trawling episodes by year). Deep-sea muddy sands (EUNIS code A6.4) were the most affected EUNIS 3 habitat, with 60% mean reductions in the percentage of sensitive species and also was the most intensely trawled habitat (4.8 trawling episodes by cell and year). Deep-sea sands (A6.3) and Deep circalittoral muds (A5.37) were also impacted with mean reductions of 38% in both cases. On the other hand, Deep circalittoral coarse sediments (A5.15) were the less affected among the main EUNIS 3 habitats present in the study area (only 9% mean reductions). Although in general the most impacted habitats were also the most heavily trawled there were some exceptions. For instance, the Deep circalittoral mixed sediments (A5.45) was less trawled than the Deep circalittoral sand (1.37 and 1.51, respectively) but it showed higher values in the mean reduction of sensitive species (31.69 and 29.17, respectively).

Discussion

The BESITO index encompasses pressure responses at species level using the functionality, biology, and ecology of species, and successfully separates them according to their sensitivity to trawling. This agrees with previous works, which also used BTAs to compute species sensitive to trawling (de Juan *et al.*, 2009; de Juan and Demestre, 2012). Models showed a good performance, explaining percentages of total deviance and having Spearman coefficients similar to or higher than other works,
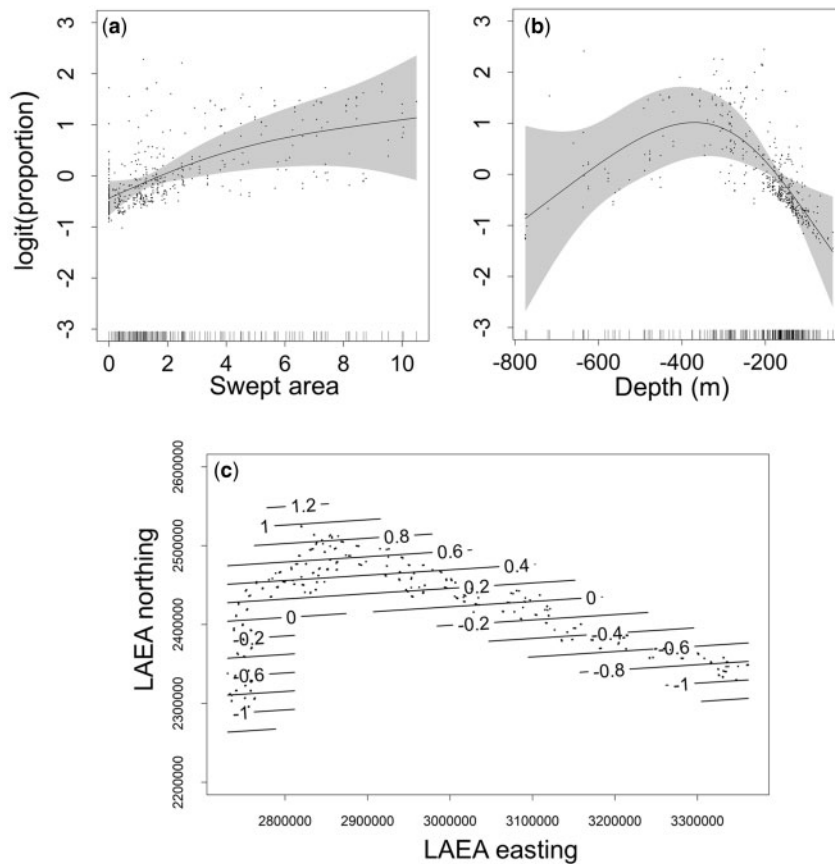
Figure 3. Effect on the relative biomass (%) of opportunistic species (BESITO score of 1) of the explanatory variables. (a) trawling effort (measures as number of trawling episodes by cell and year), (b) depth (m) and (c) spatial effect (longitude and latitude effect). In (a) and (b), the shaded area represents the nominal confidence intervals (95%) and the points are the residuals. Only explanatory variables with a significant effect on relative biomass are showed.
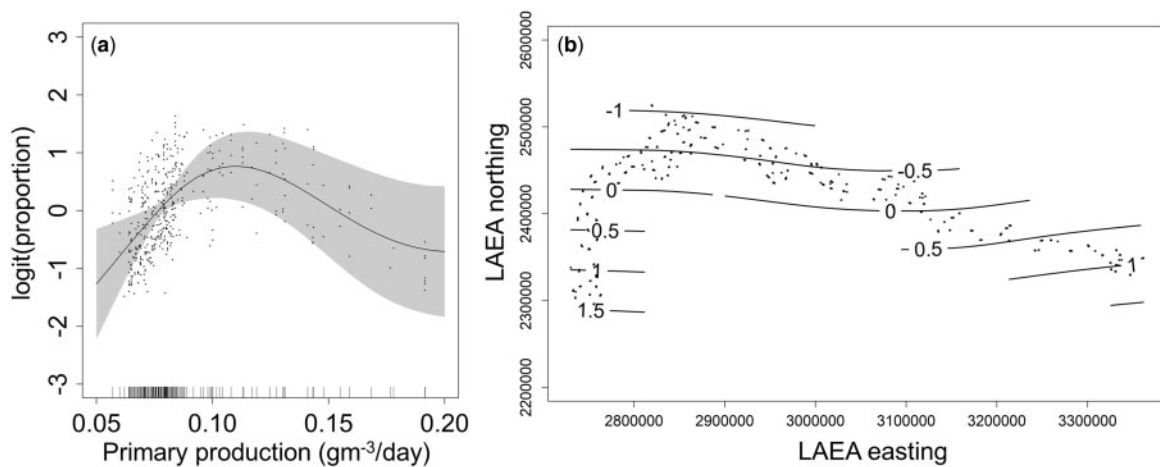

Figure 4. Effect on the relative biomass (%) of tolerant species (BESITO score of 2) of the explanatory variables. (a) Primary production (g Cm^{-3}/day) and (b) spatial effect (longitude and latitude effect). In (a), the shaded area represents the nominal confidence intervals (95%) and the points are the residuals. Only explanatory variables with a significant effect on relative biomass are showed.

which modelled species abundance using GAMs (e.g. Drexler and Ainsworth 2013; Lelièvre *et al.*, 2014; González-Irusta and Wright 2017). However, it is important to highlight that the formula has been developed for a specific set of benthic species (Supplementary Table S1). Caution is necessary in order to use the formula for different species sets and calibration exercises are highly recommended before generalize the BESITO index formula in areas with a very different species composition.
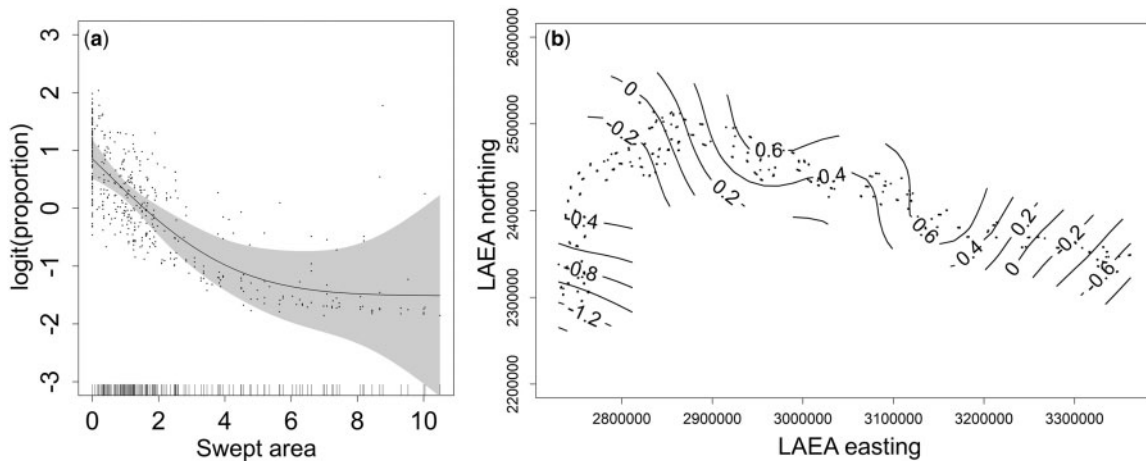
Figure 5. Effect on the relative biomass (%) of sensitive species (BESITO score >2) of the explanatory variables. (a) Trawling effort (measures as number of trawling episodes by cell and year) and (b) spatial effect (longitude and latitude effect). In figure 4a, the shaded area represents the nominal confidence intervals (95%) and the points are the residuals. Only variables with a significant effect are showed.
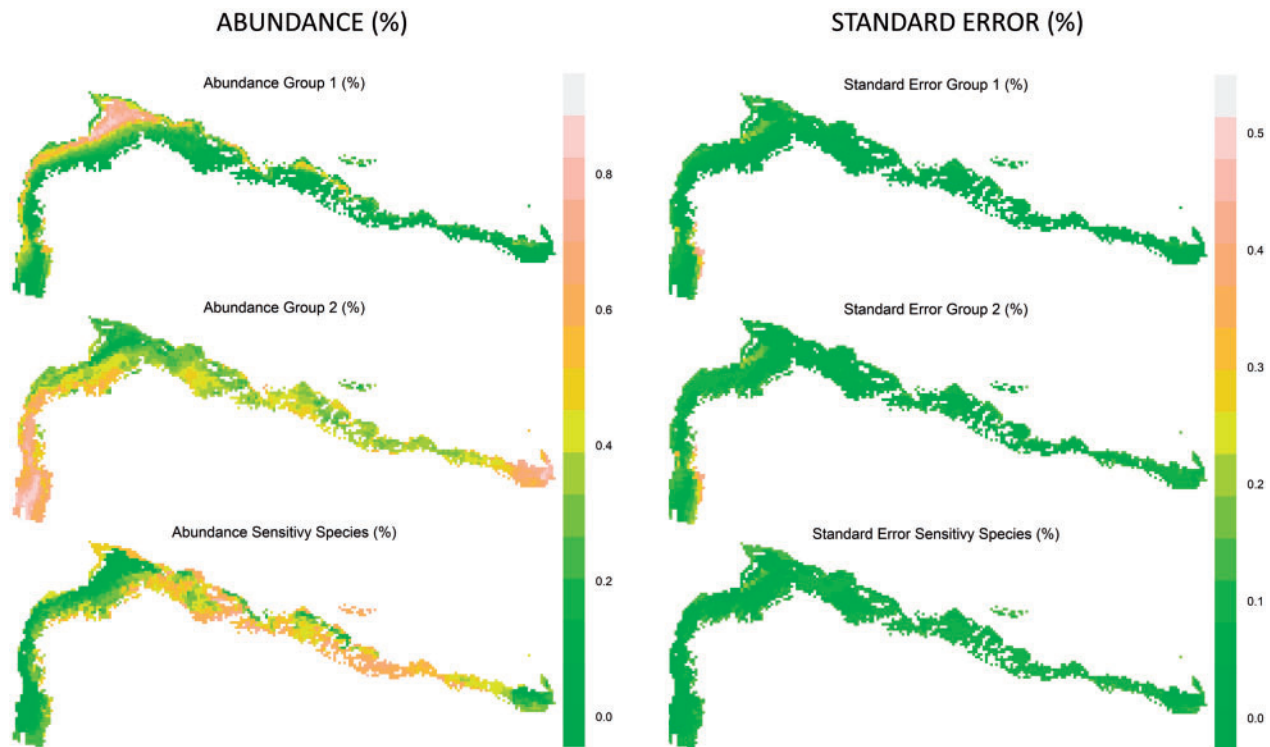

Figure 6. Distribution maps of the relative abundance (%, left column) and its associated standard error (%, right column) for each abundance group; opportunistic species (BESITO score of 1, first row), tolerant species (BESITO score of 2, second row) and sensitive species (BESITO score >2, third row).

Opportunistic species (group I) were more abundant (in terms of relative and total biomass) in areas exposed to trawling. This group was mainly composed of scavengers, generally small-sized and short life cycle, as well as others traits, which provide them with a competitive advantage for resisting physical disturbance (e.g. high mobility, burrowing habits and/or strong shells). Scavenger species such as those found in this study (i.e. *Astropecten irregularis* or hermit crabs) are generally described as opportunistic species in other works (Ramsay *et al.*,1996;

Rumohr and Kujawski 2000; de Juan *et al.*, 2007) or cited as abundant in areas exposed to high levels of trawling disturbance (e.g. *Munida* spp., *Liocarcinus depurator*, Freire *et al.*, 1992, Bergmann and Moore, 2001). Predator reduction (Thurstan and Roberts, 2010; Brown and Trebilco, 2014) and the supply of injured preys and carrion caused by trawling (Ramsay *et al.*, 1996; Olaso *et al.*, 2002) may have a positive effect on species able to resist direct impacts, and therefore, enhance the relative biomass of these species in heavily trawled areas.
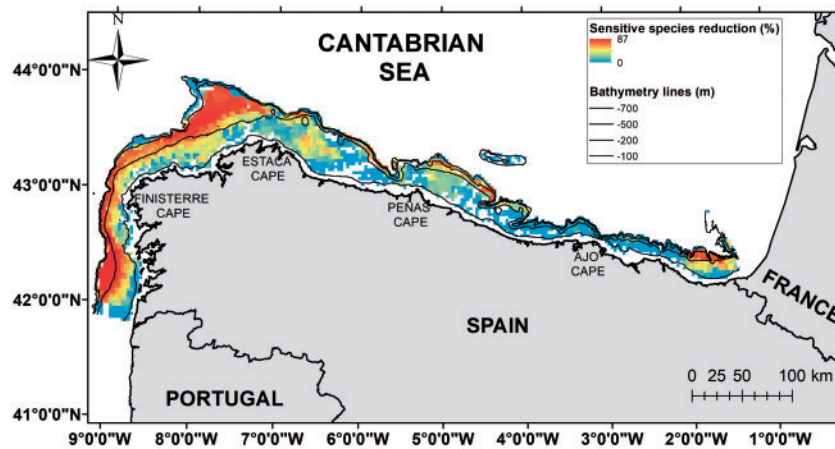
Figure 7. Distribution of the sensitive species (BESITO score > 2) reduction (%) across the study area. The reduction value was computed applying Equation (3).

Table 4. Mean reduction (%) of sensitive species, standard deviation, modelled area (km^2) and mean swept area (trawling episodes by cell and year) for the whole studied area, the continental shelf (70–200 m of depth), the continental slope (201–700 m) and the main Eunis 3 habitats.

	Mean reduction (%)	SD (%)	Modelled area (km^2)	Mean swept area
All the area	32.14	30.13	23 256	2.05
Continental shelf	22.85	23.18	13 905	0.84
Continental slope	45.94	33.79	9351	3.45
Eunis habitats				
A6.4: Deep-sea muddy sand	59.62	30.47	1161	4.8
A6.3: Deep-sea sand	38.19	33.75	4725	1.74
A5.37: Deep circalittoral mud	38.42	23.11	2628	1.77
A5.45: Deep circalittoral mixed sediments	31.69	21.31	621	1.37
A5.27: Deep circalittoral sand	29.17	27.71	11 043	1.51
A6.5: Deep-sea mud	27.79	33.86	1539	0.71
A5.15: Deep circalittoral coarse sediment	9.02	11.75	1341	0.38

Only habitats with a modelled area >400 km^2 were included in the table.

Group II (neutral or tolerant) species were generally resistant to physical disturbance and their relative biomass was not significantly related to trawling. These species mirror some of the traits of opportunistic species (e.g. highly mobile, short life cycles, and strong shells) whilst exhibiting others that make them less resistant to trawling (e.g. they are neither small or scavengers). According to this result, it seems as if this combination of biological traits allows such species to tolerate trawling but not take advantage of it.

Finally, group III was formed by species sensitive to trawling. Indeed, trawling was the most important explanatory variable in the relative biomass model. The GAM showed that these species had a negative trend in their relative biomass when trawling effort ranged from 0 to 6 trawling episodes per cell with no trend after that, probably because after this threshold all the sensitive species in the area had already been removed. These results agree with previous works that studied trawling effects on benthic fauna (Pitcher *et al.*, 2000, Lambert *et al.*, 2017). Sensitive species with the lowest BESITO score (3) were mainly echinoderms, with relatively long life cycles, large sizes and in some cases fragile test (e.g. *Echinus melo*). The negative effect of trawling on longer-life animals has been shown previously (Jones 1992; Rumohr and Kujawski 2000; de Juan *et al.*, 2007) as well as the sensitivity of

some of these species to trawling, for example: *Gracilechinus acutus* (González-Irusta *et al.*, 2012), *Brissopsis lyrifera* (Pommer *et al.*, 2016) or *Marthasterias glaciaris* (Capasso *et al.*, 2010). Other species with a BESITO score of 3 were filter-feeders with short life cycles and small sizes (e.g. *Nemertesia ramosa* and *Lytocarpia myriophyllum*). All species with BESITO scores higher than 3 were filter-feeders, a group considered highly sensitive to trawling (Fossa *et al.*, 2002; de Juan *et al.*, 2007; de Juan and Demestre, 2012; Maynou and Cartes, 2012; van Denderen *et al.*, 2015). These species were rarely found on the trawled grounds of northern Spain, even in areas exposed to very low fishing effort, seemingly confirming their high sensitivity to trawling. However, whether this low biomass in the studied area was a consequence of the natural unsuitability, the result of decades of anthropogenic disturbance, or a combination of both, is something that cannot be disentangled in this work.

Our results show that aside from trawling, environmental variables also had a significant effect on the relative abundance of each group. The effect of environmental variables on biological traits has been previously reported (Bremner *et al.*, 2006, van Denderen *et al.*, 2015). The present work showed opportunistic species peaked in relative biomass around a depth of 400 m. This agrees with previous studies on epibenthic communities of the

Galician and Cantabrian shelf that described some of the most abundant species from group I (e.g. *Astropecten irregularis*, *Munida* sp. or *Pagurus* sp.) as typical of the outer shelf (Serrano *et al.*, 2006, 2008). Primary production had a significant and positive effect on the relative biomass of tolerant species. Some of these species such as octopus (*Octopus vulgaris* and *Eledone cirrhosa*) have recruitment and abundance trends highly influenced by primary production (Otero *et al.*, 2008; Regueira *et al.*, 2014). Furthermore, primary production can enhance organic matter content on sediments (Müller and Suess 1979), which may benefit other abundant tolerant species such as *Ophiura ophiura*, *Nephrops norvegicus* or *Phormosoma placenta*. Although not an environmental variable, the spatial effect may encompass other environmental effects, which have not been included in the model, but which could determine the distribution of benthic species (e.g. salinity, near bottom temperature and seafloor topography). Two areas showed clear environmental differences from the central part of the Cantabrian Sea. The Rias Baixas zone is characterized by enhanced production due to seasonal coastal upwelling (Lavín *et al.*, 2005) and the outwelling of large estuaries (López-Jamar *et al.*, 1992) whereas the Basque shelf (at the eastern most part of the Cantabrian Sea) is characterized by important organic inputs from French rivers and a meridionalization of its communities (Lavín *et al.*, 2005). All of these oceanographic processes may affect the benthic communities producing variation on its composition, which were not cached by any of the environmental variables included in the models.

The relative biomass of sensitive and opportunistic species varied inversely on the northern coast of Spain. The higher relative abundance of opportunistic species was found in areas with large trawlable grounds (e.g. Estaca cape, north east of Peñas cape), parts of which can be trawled up to a mean of 10 times per year. On the other hand, areas with high abundances of sensitive species (and hence lower abundance of opportunistic species) were located in the centre of the study area, around Ajo cape. These areas have a very narrow shelf break with a higher proportion of rocky outcrops, and therefore, they are unsuitable for trawling. Tolerant species were less affected by trawling disturbance, although their relative abundance was also low in areas with very high trawling effort (e.g. to the north-west of Estaca cape). The relative abundance of these species was mainly driven by primary production, being especially high on the continental shelf south of Finisterre cape and in the inner part of the Bay of Biscay, close to French rivers outflows.

According to our model, the relative biomass of sensitive species has declined as a consequence of trawling impacts in most of the soft bottoms of the northern Spanish Shelf, from 100 m (below which trawling is forbidden) to 700 m, with a mean value of a 32% reduction in the relative biomass of sensitive species. This result agrees with Jones (1992) who found that the reduction in k strategist (long-life species) and the consequent increase in r strategist (fast growing) species was one of the main ecological impacts of bottom trawling. This was especially significant on the shelf break where the mean reduction in sensitive species was 46% (with large areas on the north-west showing values around 87%), and in habitats such as deep sea muddy sand, deep sea sand or deep circalittoral sand. Of course, these reduction values may be even higher for the most sensitive species or for those restricted to these types of habitats. The consequent loss of biogenic habitats caused by the reduction in habitat forming species produces ecosystems impacts, which need to be assessed, e.g. the

reduction in habitat complexity and available shelter for small fish and invertebrates (Jones 1992; Kaiser *et al.*, 1999, 2002). On the other hand, less affected habitats such as deep circalittoral coarse sands or rocky areas (unsuitable for trawling) could play an important role as a natural reserve, by sustaining healthy populations of sensitive invertebrates that maintain their presence in the most disturbed areas due to the spillover effect (e.g. Stobart *et al.*, 2009; Albouy *et al.*, 2010). This could also explain why even in the most heavily trawled areas the decrease in the relative biomass of sensitive species did not reach 100% in any case. The present work demonstrates the suitability of BTAs to classify benthic species according to their sensitivity to trawling, a necessary step in the application of current multimetric indexes and in the development of new ones. The BESITO index has been successfully tested in a broad and complex area and we believe this will help develop a list of species classified according to their sensitivity to trawling. Such a list will be of high relevance for national and international legislation (MSFD, HD). Furthermore, pooling species according to their sensitivity to trawling has allowed us to quantify and map the impact of trawling in sensitive species across most of the continental shelf of the northern Spanish coast, and in doing so, determine which habitats (at EUNIS 3 level) are the most affected by this pressure.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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