Original Articles

Small-scale spatial variations of trawling impact on food web structure

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ARTICLE INFO

ABSTRACT

Bottom trawling is one of the main anthropogenic pressures that impact soft-bottom habitats, directly affecting benthic and demersal communities, as well as their food web structure. To analyse local scale impacts of bottom trawling on food web structure we combined biological (species abundance and diets obtained from scientific bottom trawl surveys) and anthropogenic pressure (fishing effort obtained from Vessel Monitoring Systems, VMS) data. Using generalised additive models we explored the effect of bottom-trawling in nine community and trophic indicators across a gradient of fishing effort. We found an extensive effect of fishing on community indicators: with increasing fishing pressure, the biomass of seven out of fifteen functional groups declined, as well as that of the whole benthic-demersal community. Species richness was also significantly affected by bottom trawling, both at community and trophic level. We also showed a negative relationship between fishing effort and mean Trophic Level (mTL) of benthic and demersal communities at small-scale spatial resolution. Despite the apparent reduction of fishing effort observed in the study area in the last decade, we found a strong local influence of this anthropogenic pressure on the benthic-demersal food webs, demonstrating that small spatial resolution is crucial when investigating the effects of spatially heterogeneous pressures, such as fishing. Thus, we highlight the importance of analysing the effect of fishing on ecological indicators and trophic structure at local scales.

1. Introduction

Marine ecosystem functioning highly depends on ecosystem structure, diversity and integrity and is subject to many environmental and anthropogenic pressures that provoke alterations on ecosystem components at high, intermediate and low trophic levels (Cury et al., 2005; Bundy et al., 2010; Link et al., 2010; Heymans et al., 2014; Coll et al., 2016). Understanding the way marine ecosystems respond to perturbations is a key question still awaiting a precise answer. Among human impacts, fishing is one of the main drivers of food web reorganization, bottom trawling, being one of the most controversial fishing methods due to its negative impact on soft-bottom benthic communities (e.g. Jennings and Reynolds, 2000; Jennings et al., 2002; Kaiser et al., 2003; Sánchez and Olaso, 2004; Hiddink et al., 2006, 2008; Johnson et al., 2015; Collie et al., 2016). However, the impact of bottom trawling on predator–prey interactions, its transmission through the food web and its implications on ecosystem functioning have not been fully addressed to date (Jennings et al, 2002; Johnson et al., 2015; Arroyo et al., 2017).

During the last decades, one of the main challenges for food web

ecologists has been to come up with indicators able to summarise food web complexity while tackling three main criteria: measurability, specificity and sensitivity (Rice and Rochet, 2005; Link et al., 2010; Shin et al., 2010). The focus of food web indicator development has thus relied on a few main food web properties, namely structure, functioning and dynamics, as well as ecological attributes of marine ecosystems such as resource potential, functional biodiversity or resilience (Bundy et al., 2010; Rombouts et al., 2013). However, recent efforts aim at developing integrative food web indicators, placing a special emphasis on their ability to respond to multiple anthropogenic pressures (Rombouts et al., 2013; Piroddi et al., 2015; Torres et al., 2017; Tam et al., 2017). Many studies have explored historical changes in fishing pressure and its potential for driving changes in ecosystem functioning (e.g. Sánchez and Olaso, 2004; Cury et al., 2005; Blanchard et al. 2010; Möllmann and Diekmann, 2012; Gascuel et al., 2016; Pekcan-Hekim et al., 2016; Piroddi et al., 2017; Moullec et al., 2017; Torres et al., 2017), invariably arguing whether a food web indicator should be a state, pressure or surveillance indicator (Tam et al., 2017). Identifying, disentangling and understanding the drivers behind ecosystem change
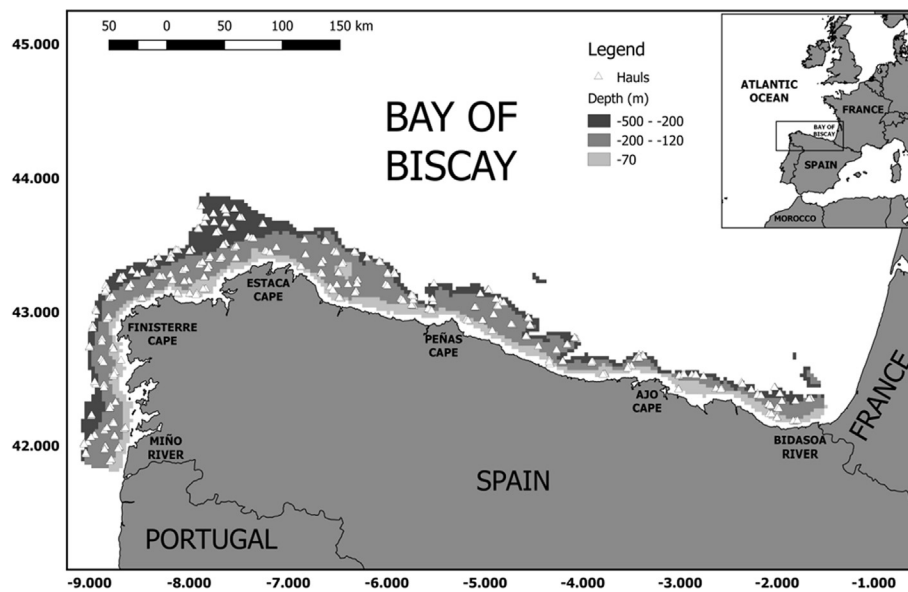

Fig. 1. Map of the study area showing the hauls (white triangles) carried out during the IBT Demersales survey every autumn. Depth ranges are shown in grey scale. Only data from 2007 to 2010 were taken into account in the present study.

Table 1
Summary of ecological indicators calculated. To see the species involved in the calculations of each indicator see Tables II and III of Supplementary Material (SM).

	Indicators	Species involved
Community indicators	Total biomass of the community Species richness Shannon diversity in biomass Shannon diversity in number	208 invertebrate and fish species (SM, Table II)
Trophic indicators	Fullness index Trophic richness Diet diversity in volume Diet diversity in number	35 benthic and demersal fish species (SM, Table III)
mTL	Mean Trophic Level	208 invertebrate and fish species (SM, Table II)

requires indicators that unequivocally link pressure to ecosystem state at the appropriate spatial and temporal resolution for devising effective management plans. In this sense, developing robust strategies based on modelling approaches to inform on the integrative ecosystem dimensions (Piroddi et al., 2015; Lynam et al., 2016; Masi et al., 2017; Shin et al., 2018), while addressing fundamental properties of the ecosystem, such as predator–prey interactions, is of paramount importance.

One of the most widely used food web indicators is the average trophic level of fisheries and/or communities. Pauly and Watson (2003) were the first to propose that the health and sustainability of fisheries could be assessed by monitoring the trends in the average trophic level of landings. The rationale behind their hypothesis was that when trophic level (TL) values begin to drop, it indicates that fisheries are relying on ever smaller fish and that stocks of the larger predatory fish are beginning to collapse. Nowadays, TL-based indicators (using landings, surveys and/or model estimations) are well-established ecological indicators capturing fishing impacts on marine communities at the community level (e.g. Pauly et al., 1998; Pinnegar et al., 2002; Pauly and Palomares, 2005; Freire and Pauly, 2010; Blanchard et al., 2010; Navarro et al., 2011; Shannon et al., 2014; Kleisner et al., 2015; Bourdaud et al, 2016; Reed et al., 2017). However, there are still key questions regarding mean Trophic Level (mTL) data sources and TL cut-offs which are subject to debate (Shannon et al., 2014; Arroyo et al., in press). As a common feature, all these studies prioritized a temporal approach of the effect of fishing on changes in mTL, while the spatial

variability of the indicator has either been obviated or assigned to ecosystem inherent variation in community structure along geographical gradients.

In the present work, we attempt to explore the spatial effect of variable bottom trawling pressure on ecosystem structure at the local level based on aggregated ecological indicators (community and trophic indicators) using the rationale that both types of indicators respond similarly to the pressure. To this aim, it is essential to count on highly spatially-resolved pressure data, such as the accurate location of the fishing fleet activity available after the implementation of the BlueTraker Vessel Monitoring System (VMS) in fishing vessels longer than 15 m. VMS data allow estimating high-resolution fishing effort from the bottom trawling fleet (Mills et al., 2007; Gerritsen and Lordan, 2011) which can be coupled with ecological data obtained from scientific independent surveys. In the study area most of the hauls carried out during these surveys matched those fishing grounds used by the otter trawl fleet, a good opportunity to analyse, at a local scale, the direct impact of fishing vessels on the aggregated ecological indicators.

The main goal of the present work was to use these data sources to explore the direct link between the intensity of bottom trawling, as the main fishery pressure on soft-bottoms, and its impact on the structure of the benthic and demersal communities inhabiting them. We hypothesise that this fishing impact spreads through the benthic-demersal food web, and thus can be detected using trophic indicators. Particularly, we investigate the performance of the mean Trophic Level (mTL) of the

Table 2

Results of the Generalised Additive Models performed for the four community indicators (Total biomass, Species richness, Shannon diversity in biomass, Shannon diversity in number). Degrees of freedom (df), relative importance (Δ Deviance) and statistical significance of the explanatory variables of each GAM model are shown.

	df/edf	Δ Deviance	F	p-value
Total biomass (Deviance explained: 12.2%)				
Year	3	9.08	3.57	< 0.001
VMS	1.9	5.53	7.79	< 0.001
Depth	2.1	1.31	0.99	0.297
Sediment type	3	0.86	0.65	0.565
Species richness (Deviance explained: 15%)				
Year	3	10.08	4.73	< 0.001
VMS	1	1.25	4.15	0.042
Depth	1	1.04	2.75	0.098
Sediment type	3	7.52	1.77	0.076
Shannon diversity in biomass (Deviance explained: 18.2%)				
Year	3	13.80	4.43	< 0.001
Depth	2.67	7.68	10.16	< 0.001
Sediment type	3	3.25	0.63	0.305
VMS	1	0.24	1.01	0.316
Shannon diversity in number (Deviance explained: 6.38%)				
Year	3	9.17	2.96	0.003
Depth	2.07	10.62	4.75	0.009
Sediment type	3	5.52	0.94	0.429
VMS	1.38	0.88	0.28	0.599

benthic-demersal community as a spatially-resolved ecological indicator that responds to fishing pressure. Historical changes in mTL in the Bay of Biscay have been recently explored (Arroyo et al., in press) showing an increasing trend since the 90′s. This pattern was observed both in the French and Spanish continental shelves, and suggests a recovery of the demersal communities during the last decades. As a case study, we explore whether this recovery is homogenously taking place across the study area or on the contrary, there is spatial heterogeneity in ecosystem recovery related to trawling intensity.

2. Material and methods

2.1. Study area and sampling design

The study area is the Cantabrian Sea, set on a narrow continental shelf on the southern Bay of Biscay (North-east Atlantic) (Fig. 1). Biological data were obtained during the International Bottom Trawl (IBT) surveys carried out along the Cantabrian continental shelf (70–500 m depth) every autumn between 2007 and 2010 for demersal ecosystem assessment. Hauls carried out in the scientific survey match those fishing grounds used by the otter trawl fleet. All surveys follow a random stratified sampling design with 5 geographical sectors and 3 depth strata. During these surveys, trawling operations were carried out during daylight at 3 knots for 30 min, using a baka 44/60 otter trawl with a 10 mm mesh-size net at the codend (Sánchez, 1993). In each haul, all fish and invertebrates were separated and identified to species level and weighted.

As part of the biological sampling, the diet of most demersal and benthic fish species was systematically analysed by identifying their stomach contents following the methodology described in Olaso (1990). Broadly, a maximum of ten specimens per predator were randomly selected from each haul and set aside for this analysis. The stomach pellet was removed from the predator's stomach and its volume measured using a set of graduated semi-cylinders ("trophometer" *sensu* Olaso, 1990). Prey were then separated and identified to the lowest taxonomical resolution (species level whenever possible), recording their digestion state, size and relative contribution to the stomach volume. The diets of 35 benthic-demersal fish species were used to

calculate trophic indicators, to establish functional groups and to estimate the trophic levels of the benthic-demersal fish in the community.

2.2. Spatial fishing pressure data

The spatial distribution of the swept area was obtained from the Vessel Monitoring System (VMS), installed in fishing vessels longer than 15 m, and from logbook data (gear information). Both were provided for the period 2007–2010 by the Spanish Ministry of Agriculture, Food and Environment. 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 the swept area, hauls were assigned to individual 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). We used a 20 m width gear for otter trawls (the information about gear type was also obtained from the logbooks, Castro et al., 2007). The mean annual swept area for each cell (km^2) was converted into the number of times it was trawled by dividing the mean annual swept area by the cell area (3×3 km). The final map gives the mean value of the 4 years analysed (2007–2010). Our fishing effort map cover all the trawling effort present in the area since all bottom trawlers are longer than 15 m and thus affected by the VMS legislation (González-Irusta et al., 2018).

VMS continuous data were used to establish discrete Fishing Effort (FE) levels as follows: very low effort (swept area $\leq 0.19\,km^2$), low effort (swept area between $0.20\,km^2$ and $0.96\,km^2$), medium effort (swept area between $0.97\,km^2$ and $1.62\,km^2$), high effort (swept area between $1.63\,km^2$ and $3.82\,km^2$) and very high effort (swept area $\geq 3.83\,km^2$). The five discrete areas covered all depth ranges (Supplementary material, Table I) and were determined in order to assure a similar number of hauls by level: very low (n = 114), low (n = 86), medium (n = 92), high (n = 102), very high (n = 98). These five discrete levels were only used for the analyses of the total biomass of functional groups.

2.3. Ecological indicators

To study the effect of fishing pressure on the community composition, several community and trophic indicators were calculated by haul, i.e. total biomass, total richness and species diversity (Table 1). Species belonging to the pelagic compartment were removed from the analyses to avoid the low catchability of pelagic species. To analyse the effect of bottom trawling on food web structure, we computed four trophic indicators, i.e. fullness index, trophic richness and trophic diversity (in volume and number), based on the analysed fish diets. Trophic indicators were calculated using the diets of 35 benthic and demersal fish species (Supplementary material, Table III). The fullness index (FI) was calculated as the volume of the stomach standardised by individual predator body weight:

$$fullness\ index\ (FI) = \left(\frac{stomach\ volume}{predator\ weight} \right) \times 100 \tag{1}$$

where stomach volume is the volume (in cc) of each individual fish and predator weight is its individual's individual weight (g). Empty stomachs were excluded from the analyses. Fullness index was calculated pooling the stomach volume of the whole fish community in each haul. Trophic richness (prey richness) is the number of different prey taxa in a single stomach. Shannon-Wiener diversity was used to estimate trophic diversity indices using two types of diet data: volume (H'_v) and abundance (H'_n) of each prey taxa in the stomach. In the first case, trophic diversity was calculated computing the total volume occupied by the whole prey in each haul. In the second one (H'_n), the diet matrix was constructed using the total number of prey taxa by haul. The reason behind the use of both trophic diversities was to discern the role of large
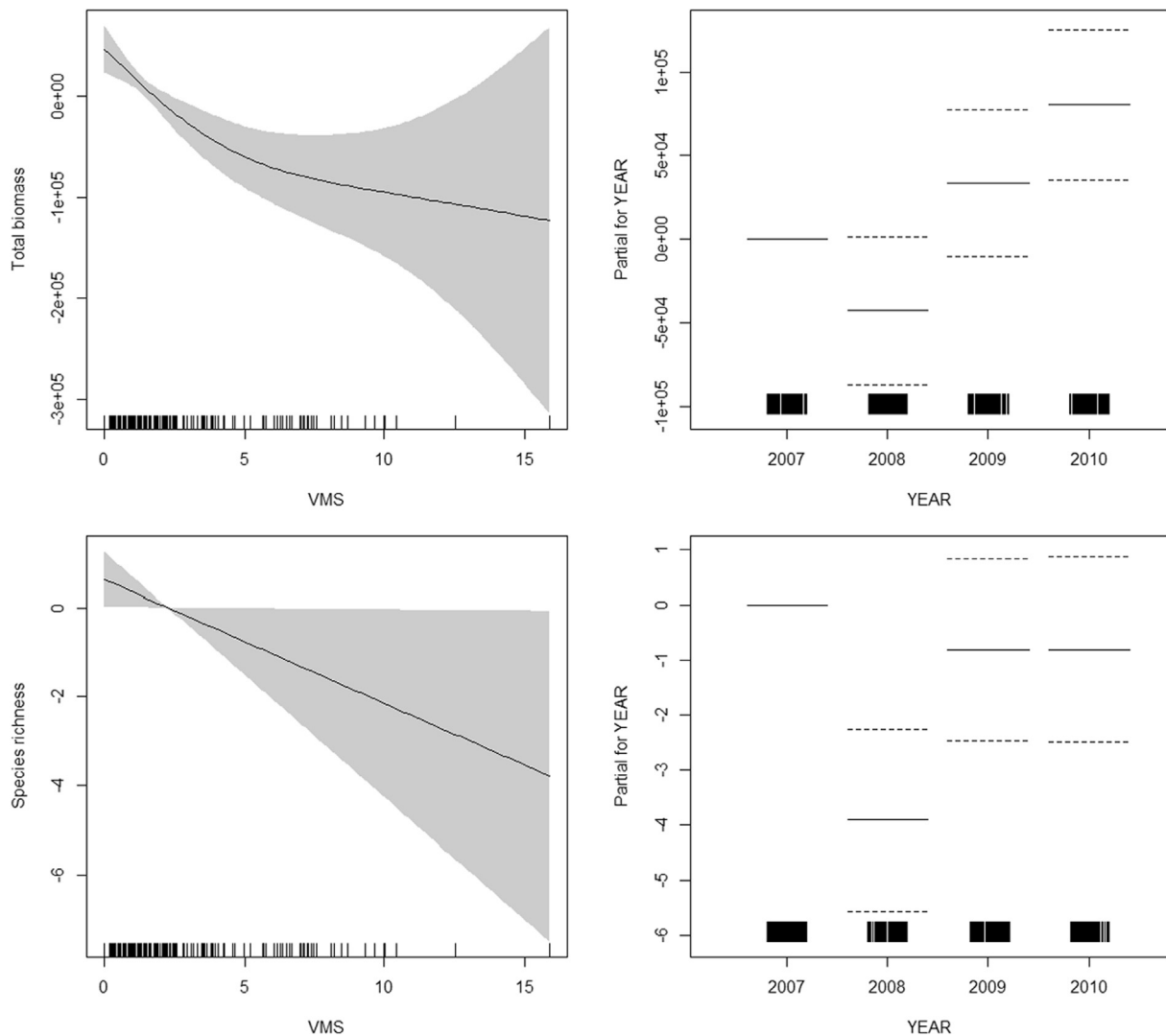
Fig. 2. Results of the GAM performed using VMS, Depth, Sediment type and Year as explanatory variables of changes observed in community indicators: Total biomass and Species richness. Only models where fishing-related variable (VMS) is significant are shown.

prey (with low abundances), versus small prey (with high abundances).

The mTL of the community was calculated as the mean trophic position of species in relation to their relative biomass in the study area. TLs assigned to each species were collated from various sources prioritizing local TL estimates in the study area (Arroyo et al., in press): (1) Local TL estimates from stomach content and stable isotope analyses carried out during the IBT "Demersales" survey, (2) TL estimates from stable isotope analyses in adjacent ecosystems (Chouvelon et al., 2012; Lassalle et al., 2014; Le Loc'h and Hily, 2005; Le Loc'h et al., 2008; Pinnegar et al., 2002), (3) TL values from online global information systems [i.e. Fishbase (http://www.fishbase.org/) and Sealifebase (http://www.sealifebase.org/)]. The mTL was calculated using 208 benthic-demersal species (with a TL ≥ 2 cut-off).

All taxa, fish and invertebrates, were grouped into 15 functional groups (Supplementary material, Table II). Functional group assignation was mainly based on the categorization proposed by Arroyo et al. (2017), complemented with FishBase (www.fishbase.org) biological data of the species and our own observations on the feeding habits of the main species. Unlike Sánchez and Olaso (2004) and Arroyo et al. (2017), we incorporated the main commercial species into their corresponding functional groups (e.g. European hake *Merluccius merluccius* was considered within the Large Demersal Fish, LDF, functional group), since we focused on the impact of fishing on the structure of food webs

independently of the commercial value of particular species.

2.4. Effect of fishing pressure on ecological indicators

The relationship between community and trophic indicators by haul and fishing disturbance (VMS data) was analysed using General Additive Models (GAMs). Depth, Sediment type and Year were also included as explanatory variables in the models as these are key variables defining biological communities in the study area and, therefore, expected to affect ecological indicators (Serrano et al., 2006, 2008; González-Irusta et al., 2012, 2013). Sediment types were derived from EMODNET (2012) and comprised five levels: mud - sandy mud (e.g. < 1% coarser than 2 mm, and at least 20.1% < 63 μm), sand - muddy sand, coarse sand and mixed sediment and rock. Since rocky areas are not sampled in the IBT survey, they were not included in the model. The Depth layer was supplied by the Spanish Institute of Oceanography in a GIS raster with an original resolution of 200 m and resampled to a final resolution of 3000 m using bilinear interpolation.

Before performing the GAM, the correlation between the explanatory variables was checked for colinearity using Spearman rank correlations and Variance Inflation Factors (VIFs) (Zuur et al., 2009). Since the spearman rho values were lower than 0.6 in all cases and VIF was lower than 3, colinearity between variables was discarded and all

Table 3
Results of the Generalised Additive Models performed for the four trophic indicators (Fullness index, Trophic richness, Trophic diversity in volume, Trophic diversity in number). Degrees of freedom (df), relative importance (Δ Deviance) and statistical significance of the explanatory variables of each GAM model are shown.

	df/edf	Δ Deviance	F	p-value
Fullness index (Deviance explained: 10.7%)				
Year	3	18.46	3.36	< 0.001
Depth	2.8	7.69	5.44	0.002
VMS	1	2.68	3.96	0.047
Sediment type	3	0.04	1.34	0.621
Trophic richness (Deviance explained: 34.8%)				
Year	3	19.77	7.14	< 0.001
Depth	2.9	10.82	12.46	< 0.001
VMS	2.7	4.68	5.57	0.002
Sediment type	3	4.89	0.22	0.026
Trophic diversity in volume (Deviance explained: 2.91%)				
Year	3	0.86	1.87	0.061
VMS	1	0.63	1.84	0.176
Sediment type	3	0.92	0.91	0.359
Depth	1	0.73	0.10	0.752
Trophic diversity in number (Deviance explained: 14.7%)				
Depth	2.9	15.18	10.44	< 0.001
Sediment type	3	8.27	2.87	0.004
VMS	2.6	5.51	3.82	0.018
Year	3	3.74	2.18	0.029

variables were included in the model. When data were normally distributed we used a GAM with a Gaussian distribution and a log link function. For non-normal data distribution, we applied log transformation to achieve normality. To avoid overfitting, all the smoothers were constrained to 4 knots. This limitation reduced the potential complexity of the smoothers by limiting the maximum degrees of freedom of the smoothers to 3. The full model for the nine ecological indicators was:

$$B = \beta_1 + s(\text{VMS}) + s(\text{Depth}) + f(\text{Sediment type}) + f(\text{Year}) + \varepsilon \quad (2)$$

where β_1 is the intercept, s is an isotropic smoothing function (thin plate regression splines, one for each variable and model), f indicates the variables which were included as factors in the formula and ε is the error term. Selection of explanatory variables for the final model was carried out using a backwards/forwards stepwise selection process based on the Akaike's Information Criteria (AIC).

Total biomass of each functional group was tested for normality and homocedasticity using Shapiro-Wilk and Levène tests, respectively. To assess differences in biomass as a function of fishing effort (FE) levels Kruskal-Wallis one-way analyses of variance by ranks were performed. Post-hoc Dunn-Bonferroni tests were used to identify the groups responsible for significant differences.

2.5. Spatial effect of fishing pressure on mTL

Spatial prediction was only performed in mTL indicator. Except the variable Year, all the response variables were in a raster format which allows projecting the GAM results in a map and therefore predicting the mTLs in space for a specific year (we used 2007 for the resulting map). The 3 km grid was the final resolution for all environmental layers, including sediment type and fishing effort (VMS).

In addition to this map (based on the real fishing effort values) we produced a no-fishing scenario and the difference between both scenarios (fishing versus non-fishing) was assessed by computing the percentage of change in the mTL produced by fishing at the 3 km grid as follows:

$$\% \text{ Change in mTL} = ((\text{mTL\_noF} - \text{mTL\_F})/\text{mTL\_noF}) * 100 \quad (3)$$

where mTL_F is the result of modelling the mTL in a fishing (real)

scenario and mTL_noF is the result of modelling the mTL in a no-fishing scenario (all values in the VMS layer were substituted by 0). We used the fitted GAM from Eq. (2).

All statistical analyses were performed using R software (R Core Team, 2017), using the package "mgcv" (Wood, 2011) to construct the GAMs.

3. Results

3.1. Effect of fishing pressure on community and trophic indicators

The final GAM for Total biomass, using VMS, Depth, Sediment type and Year as independent variables, explained 12.2% of the variance (Table 2), including all the variables although only VMS and Year had a significant effect (Table 2, Fig. 2). Total biomass strongly decreased with increasing fishing effort, particularly for VMS values smaller than 5 (Fig. 2), notwithstanding the effect of year, which clearly pointed to a higher biomass in 2010 (Fig. 2). The GAM for Species richness explained 15% of the variance, including all variables although, once again, only VMS and Year displayed a significant effect (Table 2, Fig. 2). Species richness decreased linearly with increasing fishing effort while a drop in species richness was apparent in 2008. The GAMs performed on Shannon diversity indicators, H'_b and H'_n, explained 18.2% and 6.38% of the variance respectively (Table 2). These models revealed a strong effect of the variables Year and Depth on diversity, however fishing effort seemed to have a weak effect/no effect on these indicators (Table 2).

The GAM for Fullness index explained 10.7% of the variance (Table 3), with only the variables VMS, Depth and Year having a significant effect (Table 3, Fig. 3). We found a linear and positive effect of VMS on Fullness index (Fig. 3), while its response to Depth was non-linear, with higher values at shallower depths and lowest values at depths ranging between 300 and 350 m (Fig. 3). The model for Trophic richness explained 34.8% of the variance, and all variables showed a significant effect (Table 3, Fig. 3). Trophic richness decreased with increasing fishing effort (Fig. 3), showing also higher values at shallower depths, while lower values in mud sediments (Fig. 3). The GAM performed on Trophic diversity in volume explained 2.91% of variance but no variable seemed to have a significant effect. In contrast, Trophic diversity in number explained 14.7% of the variance (Table 3), and all the variables were significant (Table 3, Fig. 3). Trophic diversity in number showed non-linear response with VMS and Depth, similar to that of trophic richness. A sharp decrease in Trophic diversity with increasing effort was observed for VMS between 0 and 5 units. The relationship of Trophic diversity with Depth showed a drastic decline at intermediate depths (170–180 m) followed by a significant increase at 340–350 m depths.

When analysing Total biomass in each functional group, our analyses detected a significant decrease in Total biomass with increasing fishing effort in seven out of fifteen functional groups. Overall, significantly higher biomasses were detected in FE levels 1 and 2 compared with FE levels 3, 4 and 5. Benthic cephalopods, benthivorous fish, carnivorous and deposit-feeders echinoderms, large demersal fish, rays and squids reproduced this general pattern, showing decreasing biomasses as the FE level increased (Table 4, Fig. 4). Six groups showed no apparent relation between biomass and FE level (Table 4), while the two groups of decapods showed the opposite trend, with increasing biomass trends under higher fishing intensities (Table 4, Fig. 4).

3.2. Spatial effect of fishing pressure on mean trophic level (mTL)

The GAM on mean Trophic Level, using VMS, Depth, Sediment type and Year as independent variables, explained 21.1% of the mTL variance and included all the variables except Depth (Table 5). There was a significant and negative proportional relationship between mTL and VMS, showing a significant decrease in the mTL with increasing fishing
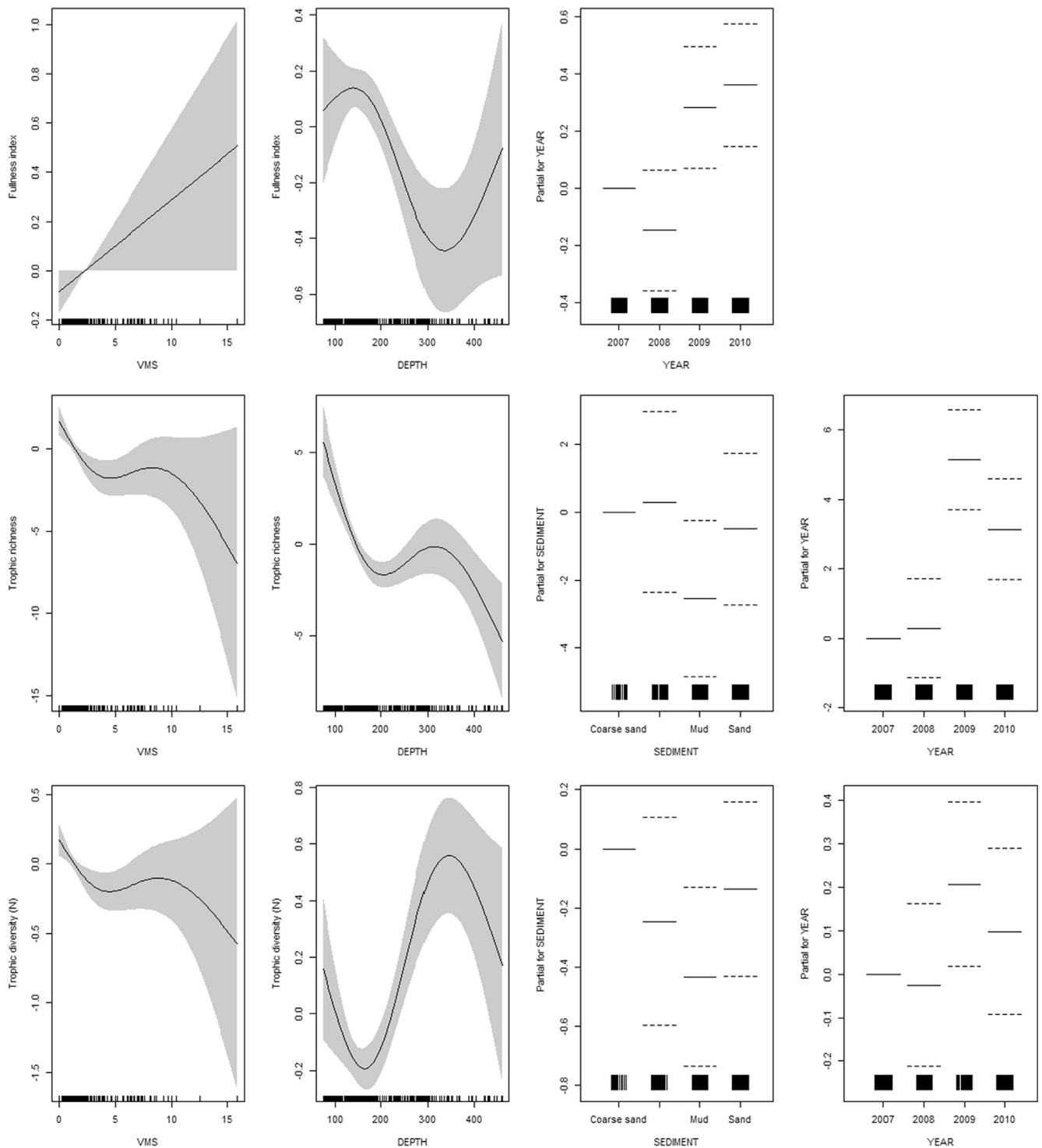
Fig. 3. Results of the GAM performed using VMS, Depth, Sediment type and Year as explanatory variables of changes observed in trophic indicators: Fullness index, Trophic richness and Trophic diversity in number (H'$_n$). Only significant variables are shown.

effort (Fig. 5). The effect of Year on mTL was also detected, with increasing trophic levels in the last two years (Fig. 5) although with the short period examined, no temporal trend can be established. Type of sediment also showed a significant effect, with lowest mTL values in those areas where mixed sediments dominated (Fig. 5).

Differences between GAM predictions of mTL with the actual fishing pressure levels and with a no-fishing scenario are shown in Fig. 6. Taking into account the spatial differences, the range in mTL reduction due to fishing pressure reaches 21% in heavily fished areas such as the

continental slope on the North-west of the study area (Fig. 6).

4. Discussion

4.1. Effect of bottom trawling on ecological indicators

Our results confirm that the impact of bottom trawling spreads through benthic-demersal food webs, the intensity of its effects being directly related to the intensity of fishing in a specific area, even at

Table 4

Variations in biomass of 15 functional groups among FE levels, showing Kruskal-Wallis non-parametric test and post-hoc Dunn test results. Percentage (%) contribution to total biomass is shown. Different letters indicate significant differences. FE levels: 1 = very low, 2 = low, 3 = medium, 4 = high, 5 = very high.

	% contribution	Statistics	Post-hoc tests
Benthic cephalopods	1.4	K-W chi-squared = 31.21***	1ª 2ᵃᵇ 3ᵇᶜ 4ᶜ 5ᶜ
Benthic decapods	0.7	K-W chi-squared = 59.01***	1ª 2ª 3ª 4ª 5ᵇ
Benthivorous fish	14.9	K-W chi-squared = 101.03***	1ª 2ª 3ᵇ 4ᵇ 5ᵇ
Carnivorous echinoderms	1.4	K-W chi-squared = 62.31***	1ª 2ª 3ª 4ᵇ 5ᵇ
Carnivorous polychaetes	0.01	K-W chi-squared = 7.43	1ª 2ª 3ª 4ª 5ª
Deposit-feeders decapods	2.6	K-W chi-squared = 45.75***	1ª 2ª 3ª 4ª 5ᵇ
Deep-demersal fish	0.8	K-W chi-squared = 4.78	1ª 2ª 3ª 4ª 5ª
Deposit-feeders echinoderms	0.7	K-W chi-squared = 40.69***	1ª 2ª 3ª 4ª 5ᵇ
Deep sharks	1.1	K-W chi-squared = 4.93	1ª 2ª 3ª 4ª 5ª
Gastropods	0.1	K-W chi-squared = 4.39	1ª 2ª 3ª 4ª 5ª
Large demersal fish	16.7	K-W chi-squared = 72.35***	1ª 2ª 3ᵇ 4ᵇᶜ 5ᶜ
Nektophagous fish	54.1	K-W chi-squared = 7.17	1ª 2ª 3ª 4ª 5ª
Rays	2.9	K-W chi-squared = 41.60***	1ª 2ᵃᵇ 3ᵇ 4ᵇᶜ 5ᶜ
Suspension feeders	0.2	K-W chi-squared = 8.12	1ª 2ª 3ª 4ª 5ª
Squids	2.3	K-W chi-squared = 31.14***	1ª 2ª 3ᵇ 4ᵇ 5ᵇ

*p < 0.05, ** p < 0.01, ***p < 0.001.

small-scale spatial resolution. We demonstrate these effects using community and trophic indicators at a sub-regional scale. The decrease in community biomass, species richness, trophic richness and trophic diversity with increasing levels of fishing effort, leave little doubt on the negative impact of bottom trawling on benthic-demersal communities. We were also able to reproduce these results for the mean Trophic Level (mTL) at a local scale. This metric has been widely used as an indicator of food web structure, and for the first time, we quantified its direct response to fishing effort at small scales. By identifying this pressure-state relationship with such a detailed resolution, we overcame one of the main challenges in ecosystem management and conservation, i.e. the scale mismatch due to the lack of appropriate fine-resolution data (Guerrero et al., 2015).

The study area comprises a narrow continental shelf characterized by a patchy and overlapping distribution of the benthic communities along the depth gradient (Sánchez and Serrano, 2003; Serrano et al., 2006, Punzón et al., 2010). Accordingly, a strong habitat selectivity of bottom trawling activities exists, trawling effort being patchily distributed and highly selective, targeting mainly circalitoral soft-bottoms, with large fractions of fishing grounds being heavily or moderately fished, while small fractions are lightly fished or un-fished altogether (Punzón et al., 2016). Although inter-correlation between trawling impact and depth-related community structure may complicate the interpretation of some results, the decreasing trend observed in community biomass and other trophic indicators between non-fished and moderately fished areas confirms the impact of bottom trawling on benthic-demersal communities. Decreasing trends in benthic biomass and species richness with increasing fishing effort are consistently found throughout the literature (e.g. Henry et al., 2006; Hiddink et al., 2006; van Denderen et al., 2015; Collie et al., 2016), otter trawls having been estimated to cause the removal of 6% of the biota (Hiddink et al., 2017). In our study un-trawled or slightly trawled areas showed higher values in most ecological indicators, except for the fullness index. Indeed, the amount of prey consumed (stomach fullness) seemed to be benefited by trawling, showing the highest values at high fishing efforts. High fullness values in areas of high fishing effort could be explained by the dominance in consumers' diets of a few abundant and large prey, such as fish and decapod crustaceans, in agreement with the low values of diet diversity. Similar results were obtained by Johnson et al (2015), who demonstrated an overall reduction in abundance and biomass of prey availability for two flatfishes as fishing effort increased, although the flatfish were able to maintain consistent levels of feeding even in highly trawled areas. Whether this is beneficial to predators cannot be assessed with the methods used in this work and would need additional analyses (e.g. condition factor). Hiddink et al (2008) showed a positive effect of trawling on those species feeding on small benthic

invertebrates. Fishing gears disturb soft sediments causing the re-suspension of organic and inorganic matter and the release of nutrients, which may in turn benefit scavengers and detritivorous organisms (Kaiser et al., 2003) and ultimately, benthic fish that feed on these invertebrates (Serrano et al., 2003a; Hiddink et al., 2008; López-López et al., 2011).

Bottom trawling does not only remove fish and benthic invertebrates from the ecosystem, but also alters predator–prey relationships (Arroyo et al., 2017; Hinz et al., 2017). Our study highlights that fishing can effectively shapes the trophic links of the benthic-demersal community. We found a negative effect of bottom fishing on trophic richness, affecting not only communities but also the trophic spectrum of predator's diet, indicating a decline in prey availability with increasing bottom trawling. Although trophic diversity showed a weak response to fishing effort when considering the volume of prey, we did find a significant decreasing trend in the diversity in number with increasing fishing effort. Changes in diet composition and/or variations in size and prey quality under different levels of fishing effort could be involved in the non-linear responses observed. Even though we did not attempt to investigate changes in diet composition of each species, the patterns described by trophic richness and diversity suggest a negative pressure on functional diversity, with potential negative implications for ecosystem resilience and stability (Bundy et al., 2010; Arroyo et al., 2017). The diversity of fish diets, interpreted as a non-dimensional property of trophic interactions, is highly dependent on the species' foraging behaviour and many variables outside the scope of this work might be involved in the results. The interpretation of trophic diversity at the community level (pooling the diets of multiple predators) is certainly challenging.

Non-linear patterns were obtained when analysing the impact of fishing effort on total biomass, trophic richness and trophic diversity, with a clear negative effect at small and moderate fishing which became less evident at higher fishing intensities. While the scarcity of data at high fishing intensities is a hurdle to predict how the indicators are behaving under very high fishing pressures, our results seemed to indicate that small to moderate bottom trawling suffices to strongly modify the structure of bentho-demersal communities.

4.2. Effect of bottom trawling on functional groups

From a food web perspective, several factors are deemed crucial to establish clear pressure-state relations, such as considering the whole community, combining data on fish and invertebrates, or assessing the impact of bottom trawling on both commercial and non-commercial species. The present work is one of the few including a wide range of functional groups involving 208 fish and invertebrate species both of
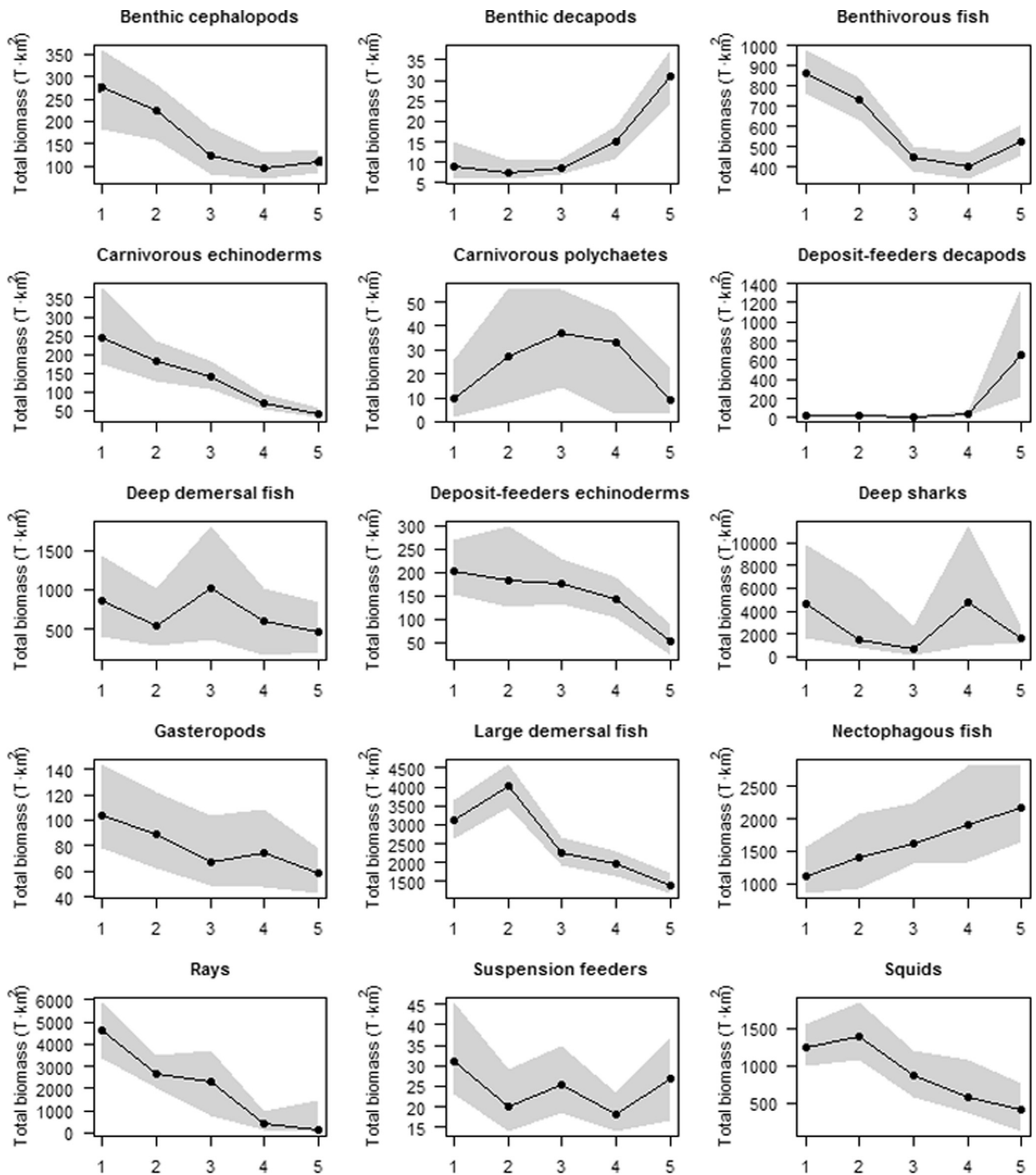
Fig. 4. Total biomass (T km^{-2}) of the 15 functional groups in the five FE levels. Black points = median, grey shaded = 90% confidence intervals. FE levels: 1 = very low (swept area $\leq$ 0.19 km^2), 2 = low (swept area between 0.20 km^2 and 0.96 km^2), 3 = medium (swept area between 0.97 km^2 and 1.62 km^2), 4 = high (swept area between 1.63 km^2 and 3.83 km^2), 5 = very high (swept area > 3.83 km^2).

commercial and non-commercial interest. When these species were combined into functional groups, seven out of fifteen groups were strongly affected by bottom trawling and while the effect was mostly negative, non-commercial functional groups, such as benthic decapods, increased their biomass in the most impacted areas. Sköld et al. (2018) found similar patterns in brittle stars, showing higher abundances with increasing fishing intensity. They attributed the response to a reduction

in their predators' abundance. In the study area, benthic crabs and shrimps represent key prey taxa for most demersal predatory fish (Serrano et al., 2003b; Olaso et al., 2005; Preciado et al., 2006, 2009; López-López et al., 2011), so the removal of large biomasses of these predators could release their predation pressure on benthic decapods, which would increase in abundance.

Deposit-feeding decapods also showed higher biomasses under

Table 5

Results of the Generalised Additive Model of mTL of benthic-demersal communities. Degrees of freedom (df), relative importance (Δ Deviance) and statistical significance of the explanatory variables for the GAM model. Deviance Explained: 21.1%.

	df	Δ Deviance	F	p-value
VMS	1	4.76	95.7	< 0.001
Sediment type	3	1.09	7.29	< 0.001
Year	3	0.52	3.48	0.016

Significant codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 ''
Deviance Explained: 21.1%.

increasing fishing effort. In this case, the positive trend could respond not only to a release of predation pressure but also to an increase in prey availability, in the form of injured prey and carrion supplied by discards (Ramsay et al., 1996; Olaso et al., 2002), since scavengers, such as squat lobsters or pagurid crabs may take advantage of dead and injured animals left by otter trawls (Freire et al., 1992; González-Irusta et al, 2018).

4.3. Spatial effect of bottom trawling on mTL indicator

Our results showed a significant and decreasing trend in mTL with increasing fishing pressure, demonstrating that mTL can be a good indicator to monitor changes in food web structure, with a direct response to a manageable pressure such as fishing. Under European legislation, the new revised Commission Decision EU/2017/848 states that food-web indicators (Descriptor 4) must be used for "surveillance" to monitor changes in the food web, rather than respond tightly to a manageable pressure (ICES, 2014). However, we showed that the mTL can achieve both objectives: it responded to changes in food web structure but also showed a clear and negative relationship with a manageable pressure (bottom trawling effort derived from VMS data). Indeed, our model predicted nearly a 21% decrease in the mTL between

the fishing and non-fishing scenarios, in highly fished areas. While the effect of fishing pressure on the structure of ecosystems has been traditionally treated using a temporal approach (e.g. Pauly et al., 1998; Pinnegar et al., 2002; Sánchez and Olaso, 2004; Blanchard et al., 2010; Shannon et al., 2014; Kleisner et al., 2015; Bourdaud et al, 2016; Reed et al., 2017; Arroyo et al., in press), our study shows, for the first time, its ability to identify subtle pressure effects at smaller spatial scales, magnifying its potential as a monitoring tool in ecosystem based management strategies. The small temporal scale used in our study (2007–2010), most likely explains the lack of a clear interannual variability as identified by the model, where "Year" was a significant factor in eight out of nine models. In any case, the temporal approach was never one of the aims of the study, as longer VMS series are needed to give such a focus to the analyses. Likewise, no clear conclusions can be achieved regarding the low values of mTL obtained in mixed sediments due to the low number of data on these types of sediments.

Spatially, we showed the local impact of bottom trawling and the patchy response of the mTL indicator. Considering the whole of our study area, Arroyo et al (in press) showed an increasing trend of the MTL in the last decades, partially attributing to the apparent recovery of the bentho-demersal ecosystem reported in various studies (Modica et al., 2014; Arroyo et al., 2017). However, when analysing the same indicator in the same area at small spatial scales it seemed that this recovery is only taking place in certain areas. The expansion of demersal fisheries to deeper zones concluded by Arroyo et al (in press) is corroborated by our results, the negative effect of fishing pressure on mTL being more acute in deeper areas. In fact, these trends in depth can also be observed for other trophic indicators in our models which consistently showed non-linear patterns in depth, pointing to a distinct response in the upper continental slope area.

Overall, our results demonstrate that GAMs can be suitable tools to identify impacted areas at high spatial resolution levels, and to quantify the impact of anthropogenic pressures on ecological indicators. These results can be useful to establish management measures, such as
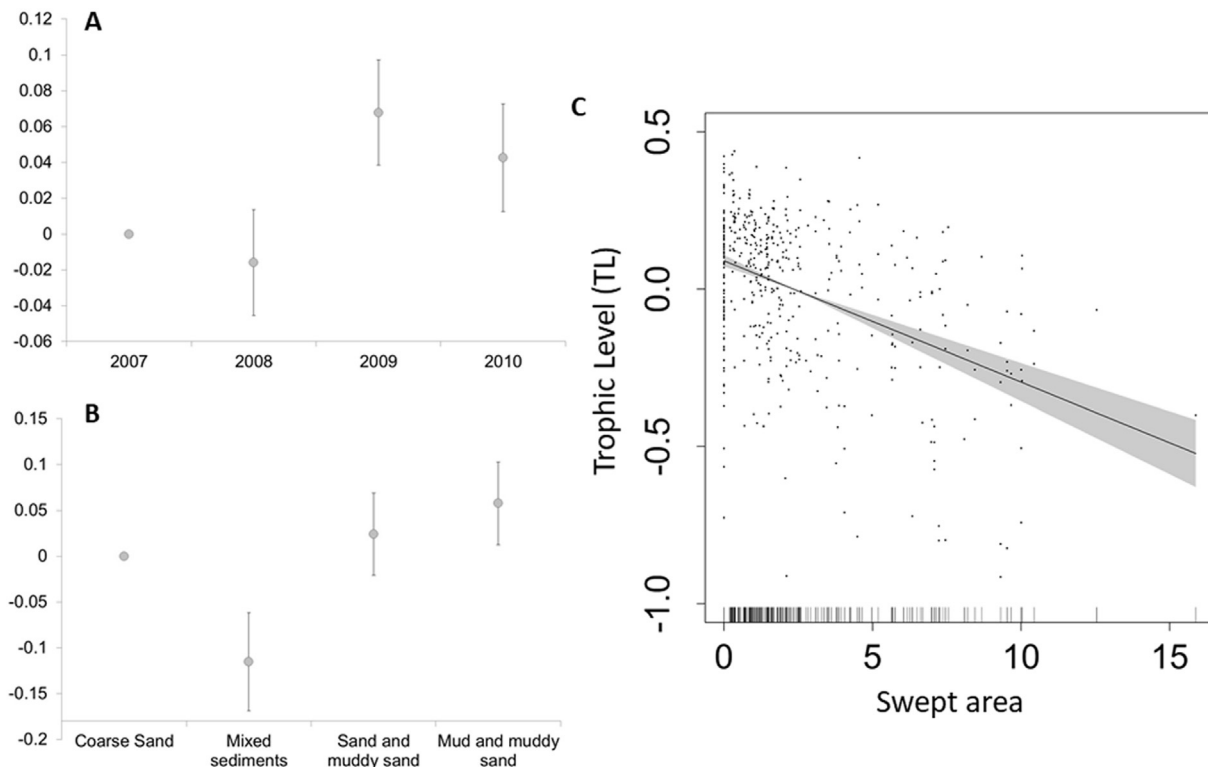

Fig. 5. Results of the GAM performed using VMS, depth, sediment type and year as explanatory variables of changes observed in mTL (TL ≥ 2). Only significant variables are shown.
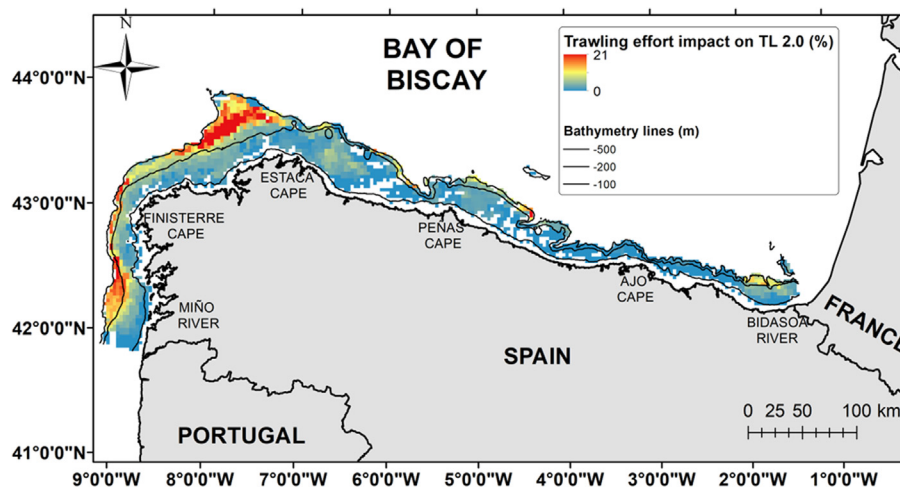
Fig. 6. Map showing the decrease in mTL of the community between fishing and non-fishing scenarios according to the predictions made by the Generalised Additive Model (see Table 5).

restricted areas to fishing. Despite the promising results shown in this study, we believe that the spread of fishing impacts through, up and down the food web deserves further exploration. Spatial effects of fishing pressure have been analysed only for the mTL indicator, and additional research on other ecological indicators will be required in the near future. Integrative studies using food web indicators, benthic habitats indicators and ecosystem models following a spatial approach, would greatly contribute to achieve the much sought after ecosystem-based management of marine ecosystems.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2018.11.024.

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