Using underwater video to assess megabenthic community vulnerability to trawling in the Grande Vasière (Bay of Biscay)

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Abstract :

Trawling activities are considered to be one of the main sources of disturbance to the seabed worldwide. We aimed to disentangle the dominance of environmental variations and trawling intensity in order to explain the distribution of diversity patterns over 152 sampling sites in the French trawl fishing-ground, the Grande Vasière. Using a towed underwater video device, we identified 39 taxa to the finest taxonomic level possible, which were clustered according to their vulnerability to trawling disturbance based on functional traits. Using generalized linear models, we investigated whether the density distribution of each vulnerability group was sensitive to trawling intensity and habitat characteristics. Our analyses revealed a structuring effect of depth and substratum on community structure. The distribution of the more vulnerable group was a negative function of trawling intensity, while the distributions of the less vulnerable groups were independent of trawling intensity. Video monitoring coupled with trait-based vulnerability assessment of macro-epibenthic communities might be more relevant than the traditional taxonomic approach to identifying the areas that are most vulnerable to fishing activities in conservation planning.

INTRODUCTION

To develop an ecosystem approach to fisheries, precise identification and quantification of fishing impacts is essential as contact fishing has a direct physical impact on benthic communities (Gray *et al.* 2006). In particular, bottom trawling is one of the main sources of seabed disturbance worldwide, impacting the structure and the functioning of benthic communities (Kaiser *et al.* 2006). Through frequent ploughing of the seabed, resuspension and homogenization of sediments, and removal of parts of the habitat and benthic fauna, bottom trawling leads to a decrease in biodiversity, abundance and distribution of species (Thrush & Dayton 2010; Palanques *et al.* 2014; Clark *et al.* 2016). Because of their specific biological traits, species are not equally vulnerable to trawling (Bremner *et al.* 2006*a*, 2006*b*) and can respond differently to disturbances (de Juan & Demestre 2012). Species' biological traits are linked to their functions within the ecosystem (Snelgrove 1998) and changes in observed trait patterns can make it possible to identify functional shifts (Tillin *et al.* 2006). Assessing species and community vulnerability is thus critical to identify and prioritize areas requiring conservation measures in seascape and fisheries planning (Clark *et al.* 2016). The list of Vulnerable Marine Ecosystems (VMEs; UNGA Resolution 61/105 2006), encompasses various ecosystems characterised by high structural complexity and a low recoverability, and recognized as strongly vulnerable to fishing disturbance, *e.g.* seamounts, hydrothermal vents and cold corals. VMEs house rare and/or fragile species of functional significance. However, delineating VMEs remains problematic due to the lack of reliable and consistent methodology to identify indicator species and to quantify adverse fishing impacts (Auster *et al.* 2011). Vulnerable mega-epibenthic species, such as large hydrozoans, seapens, crinoids and anemones, are usually used as indicator species

(ICES 2016*a*). However, they are hardly sampled by traditional and scientific fishing gears (Auster *et al.* 2011) such as trawls, grabs or dredges, due to their over-dispersed distribution on the seabed and low catchability. The recent development of underwater video devices (Mallet & Pelletier 2014) could provide an alternative sampling method.

The vulnerability of mega epibenthic species based on video data can be difficult to assess in the absence of empirical knowledge of species' responses to trawling (Certain *et al.* 2015), compounded by difficulties in identifying fauna to species level. Using traits that can be visually assessed (*e.g.* size or position on the substratum), at both fine (species) and high (often genus) taxonomic levels, can circumvent these limitations.

Several biological and life history traits allow assessment of vulnerability to trawling activities, such as feeding type, mobility and fragility for instance (Tillin *et al.* 2006; Hily *et al.* 2008; Thrush & Dayton 2010), and have been used in different vulnerability assessment frameworks (Bremner *et al.* 2006a; Tyler-Walters *et al.* 2009; de Juan *et al.* 2009; Bolam *et al.* 2014; Costello *et al.* 2015). Traits can be partitioned into response traits, characterising species responses to environmental disturbances or changes in resources availability, and effect traits, defining taxa that affect ecosystem properties (Lavorel & Garnier 2002, Beauchard *et al.* 2017). Among these frameworks, de Juan & Demestre's (2012) focus on traits that can be visually assessed rather than life-history traits, appears to be particularly suited to video surveys in areas with strong knowledge gaps on species biology and demography. The framework assesses a taxon's response to trawling disturbance and clusters them into vulnerability groups, according to: (1) position on the substratum, determining exposure to the gear; (2) feeding type (*e.g.* scavengers can feed on

dead or damaged individuals, or filter feeding may be clogged by resuspended sediments); (3) mobility, characterising the ability of individuals to escape; (4) size, dictating selectivity of a trawl net; and (5) presence of a hard external body structure, preventing the individuals from being damaged (Tillin *et al.* 2006; Hily *et al.* 2008; de Juan *et al.* 2009; Thrush & Dayton 2010) (Table S1).
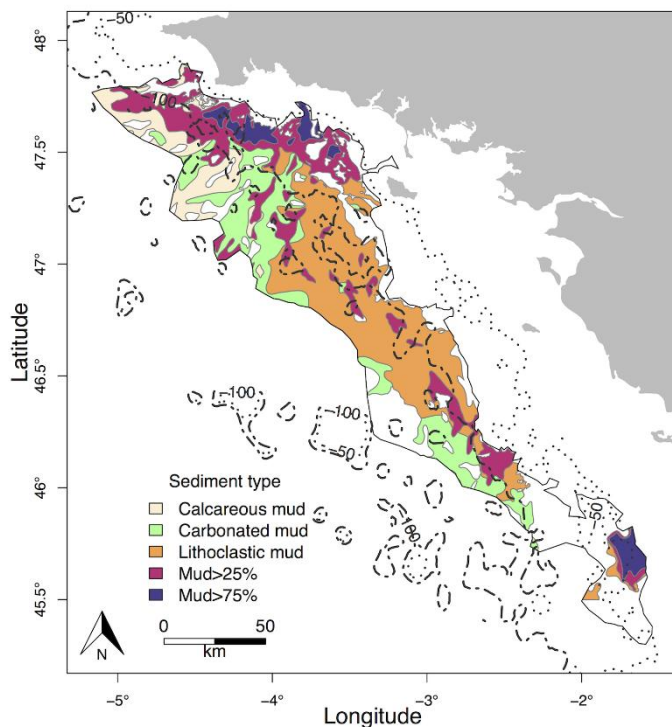
The Grande Vasière in the northern part of the Bay of Biscay is a historical fishing ground and has been exploited for many years. Although negative impacts of trawling have been documented worldwide (Watling & Norse 1998; Kaiser *et al.* 2006; Gray *et al.* 2006; Clark *et al.* 2016), the few studies that investigated biodiversity in this area found no direct and tangible link between the observed biodiversity patterns and the fishing pressure (Blanchard *et al.* 2004; Vergnon & Blanchard 2006). This raises the question of whether the magnitude of environmental variation masks correlations between biodiversity patterns and trawling intensity. The main goal of this study was therefore to (1) map patterns of vulnerability to trawling, based on response traits of organisms encountered on underwater video footage routinely acquired for the *Nephrops* stock assessment, (2) analyse the relative density of vulnerability groups to evaluate whether there are associations among groups or whether some tend to be dominant and (3) disentangle the relative impacts of environment and trawling in explaining vulnerability patterns.

METHODS

Study area

The Grande Vasière is located on the continental shelf, in the Northeastern Bay of Biscay. The area is 225 km long by 40 km wide and stretches from Penmarc'h cape (47°48N) to Rochebonne cape (46°10N), covering around 12000 km^2 (Hily *et al.*

2008). The sampling sites had a depth range from 66 m to 133 m. The substratum is composed of a mosaic of sediments (Bouysse *et al.* 1986): fine sediments containing > 75% fine mud ("mud>75%"), > 25% fine mud ("mud>25%"), carbonate mud ("carbo_mud"), calcareous mud ("calc_mud") and lithoclastic mud (*i.e.* sandy mud, "litho_mud") (Fig. 1). Average temperature, salinity and speed current on the seabed were extracted from the model MARS3D (Lazure *et al.* 2009) for the year 2014.

Data collection

Videos of the seabed were recorded using a camera (Kongberg oe 14-366, 0.48 megapixel) fixed on a sledge dropped onto the seabed and towed behind the Celtic Voyager RV for 10 min in September 2014. The sledge was equipped with CTD and GPS devices, recording depth and geographic position as well as two lasers, spaced 0.75 m apart, that delineated the area covered by the camera (calibrated for a consistent spacing of the area filmed). The locations of 152 sampling sites were chosen along a regular square grid of 4.7x4.7 miles resolution, built from a

first point picked randomly inside the limits of the study area. At each site, a video transect was recorded at an average speed of 0.85 knots. Transects covered a mean length of 183.7 m corresponding to a mean area of 137.7 m^2.

Each individual recorded on the videos was identified to the lowest possible taxonomic level. The first seven complete minutes with sufficient visibility for taxonomic identification were used to count individuals (Lordan *et al.* 2011). A total of 39 taxa were identified (Table S2). When identification at the lowest taxonomic level was not possible, we clustered individuals at a higher taxonomic level ensuring a sufficient consistency in biological traits. For instance, individuals clustered as Actinopterygii are all mobile, swimming in the water column and without a hard external structure. Abundances per min were summed to obtain the total abundance of each taxon per transect. These values were then divided by the distance covered by the sledge over the selected minutes multiplied by 0.75 m, to obtain a standardized density value per m^2. Taxonomic richness was also estimated for each transect.

Vulnerability assessment

The methodology of de Juan & Demestre (2012) was used to assess the vulnerability of benthic communities to trawling disturbance. This framework is based on the use of functional traits from morpho-anatomical and behavioural characteristics (*i.e.* position on the substratum, mobility, size, feeding habits and fragility). Scores from 0 to 3 were attributed to each biological trait and then summed for each taxon to obtain a total vulnerability score per taxon (Table S1 and S2). The taxa that were the least vulnerable to trawling disturbance had the lowest scores, and were classed in group A while the most vulnerable taxa, with the highest scores,

were classed in group D. Assessment of scores may vary across the sources of information (*e.g.* online database, local expert knowledge), and following the plasticity of traits, but is robust to minor changes in scores (Hewitt *et al.* 2011). Consequently, one scoring is likely specific to a dataset and an environmental context.

Densities of the taxa were summed per vulnerability group at each sampling station. In absence of biomass data, all species are thus considered as equivalent regardless of their size. To map the vulnerability patterns, densities of each vulnerability group were interpolated among stations using the Inverse Distance Weighting interpolation method under QGIS versions 2.12.1-Lyon (Fig. 2).

A visual investigation of how vulnerability groups occuring together was then conducted, following Jørgensen *et al.* (2016). Percentages of each group were plotted on pie charts to display how the groups were distributed at each site.

Explaining spatial patterns of vulnerability

We investigated the patterns of density distribution of the vulnerability groups as a function of environmental variables (depth, sediment type, longitude, latitude, and current, salinity and temperature at the seabed level) and trawling intensity. We used fishing effort (hours) as a proxy of trawling intensity. Access to official data was provided by the French Direction of Maritime Fisheries and Aquaculture (DPMA), for fishing vessels > 12m. These data were standardized outputs from the IFREMER SACROIS algorithm (Demaneche *et al.* 2010) that filter VMS data according to vessel speeds (< 4.5 knots) and the distance to the nearest port to select records assumed to correspond to fishing operations. Data can be delivered at a 10'x10', 3'x3' or 1'x1' resolution. We selected the 3'x3' resolution, which was the closest to the

resolution of our biological sampling grid (4.7x4.7 miles). Spatial mismatch between the very local scale of biological data collected at one transect and the larger scale of fishing effort data is not considered as critical here since the mismatch can be reduced by the homogenization of effort occurring over the years inside the same grid cell (Ellis *et al.* 2014) and trawling effort used is representative of the recent period (average landings and exploitation patterns were stable - ICES, 2016*b*).

We considered the period from the beginning of April to the end of September, which corresponds to the *Nephrops* fishing season (the dominant fishing activity in terms of trawling in the area) and sum the monthly fishing hours of trawling in each grid cell.

Collinearity among variables was investigated using variance inflation factor (VIF) coupled with a stepwise selection and a release threshold of VIF>2.5 when both variables were quantitative, and a Kruskal-Wallis test for relationships among quantitative and qualitative variables. Then, a generalized linear model (GLM), fitted with a negative binomial error distribution to handle over dispersion, was used to investigate which environmental and trawling variables influenced the density distribution of each vulnerability group. Commercial and non-commercial taxa have different relationships with trawling that targets commercial species. For this reason, we performed GLM models on commercial and non-commercial taxa separately, in the case of groups A and B, which are the only two groups gathering both fractions (see Table S3 and Fig. S1 in Supplementary material). We expressed the density distribution of each vulnerability group as a function of the explanatory variables and their quadratic terms. We also included interaction terms and the spatial coordinates of the sites (*i.e.* linear and quadratic terms of longitude and latitude) to account for the significant spatial autocorrelation of the density (all groups together) distribution

(Moran's I = 0.58; p = 1.00.e^{-3}). We also included an offset of the log-transformed area sampled to account for bias in the estimation of the density per station.

For each GLM model, the most significant variables were selected using stepwise procedures (*stepAIC* function in R). We compared the results of two stepwise procedures, based on the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC), respectively (Lelièvre *et al.* 2014). The two models selected were then compared with a Taylor diagram (Taylor 2001) to select the best model. Finally, the goodness of fit of the selected models was assessed by performing a χ² test between the null and the selected model. Analyses were performed in R version 3.2.3 (R Development Core Team, 2015) (see supplementary for details on the packages used).
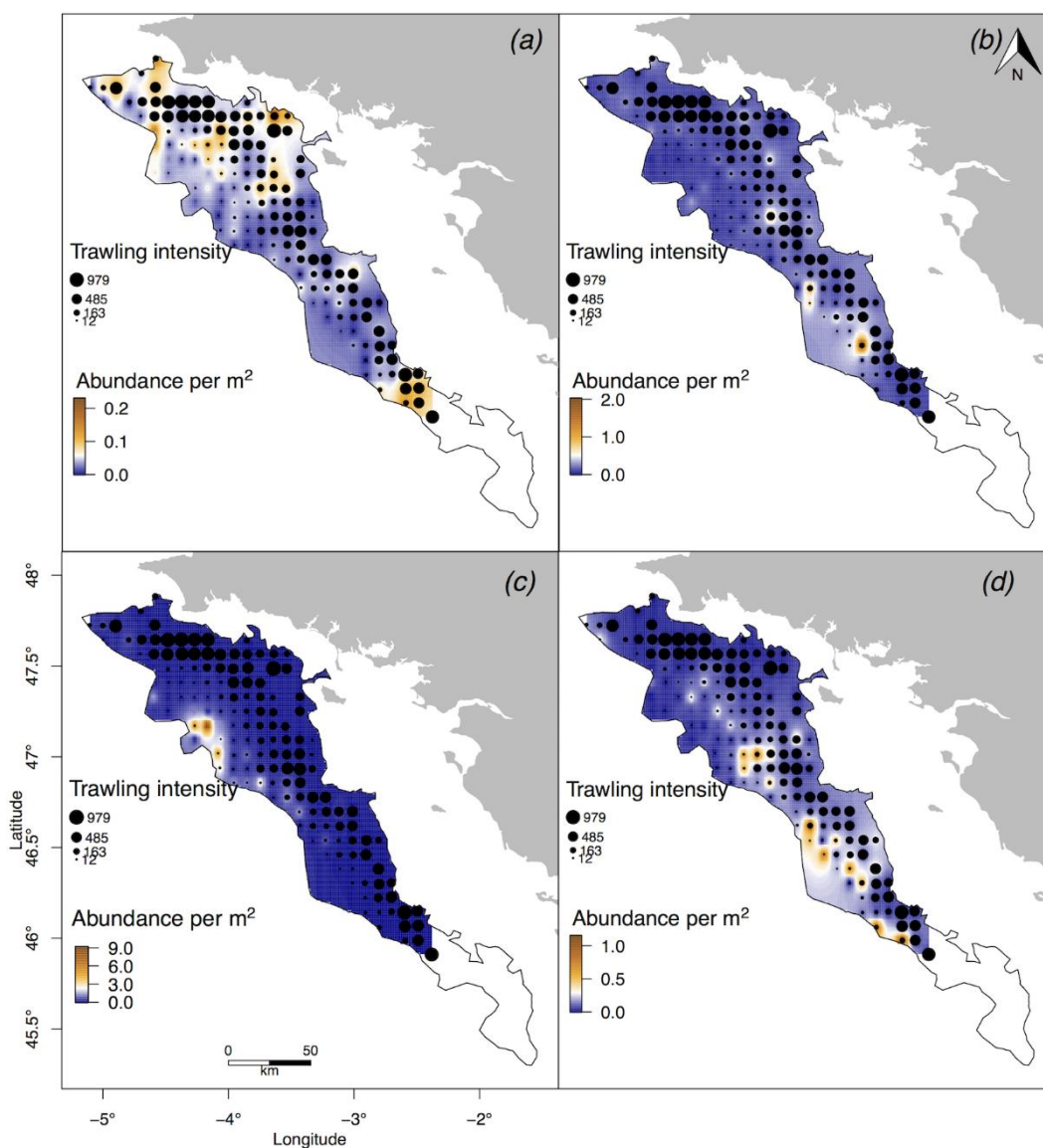
RESULTS

Trawling intensity

From the beginning of April to the end of September 2014, fishing effort ranged from 0.16 to 979.20 fishing hours over the Grande Vasière, with an average per grid cell of 236.30 fishing hours. This corresponds to a swept area ranging from 0.05 km² to 342.70 km² and a trawling frequency ranging from 0.003 to 16.20 trawl.y^{-1} (Eigaard *et al.* 2016, see supplementary). Trawling intensity was not homogeneous over the area with the highest trawling intensity exerted along the coastline (Fig. 2). In contrast, intensity was lower offshore (< 50 fishing hr over the studied period), leading to a relationship between trawling intensity, depth and current.

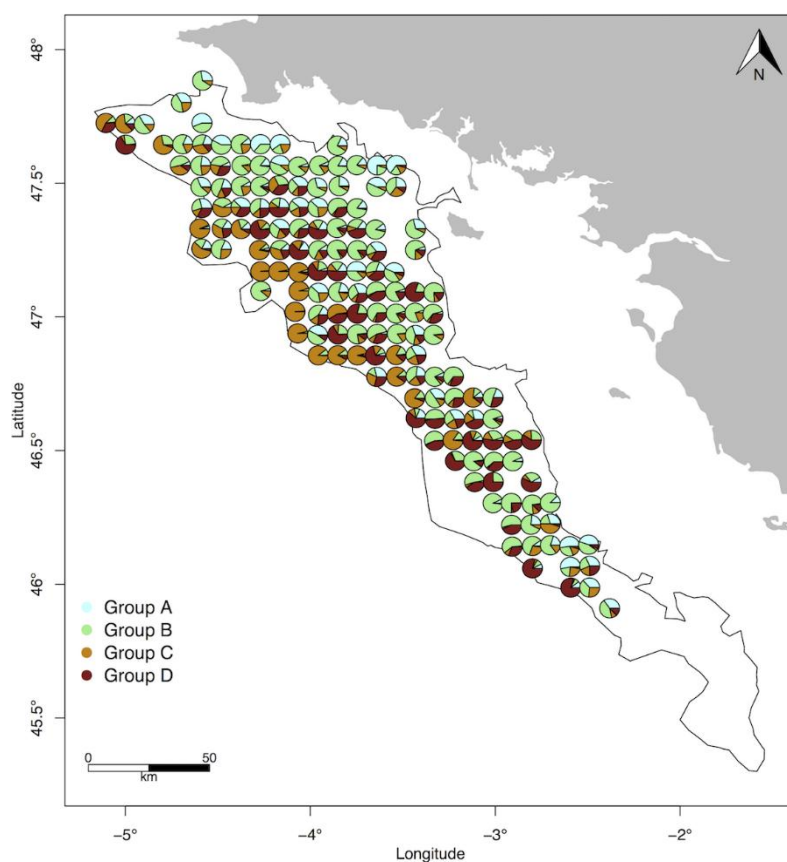### Distribution and co-occurrence of vulnerability groups

Group A, composed of the taxa least vulnerable to trawling disturbance, was mainly present in the North and at southern end of the area, where the trawling

pressure is the strongest (Fig. 2, A); it included *Nephrops*, angular crab and other non-identified crabs and shrimps. Group B was observed in the central and southern areas (Fig. 2, B); it contained slightly more vulnerable taxa, mostly fish (Table S2). Group C was composed of non-mobile taxa, crinoids and Pennatulacea for instance, and was clustered on the external border (Fig. 2, C). Finally, group D consisted of the most vulnerable taxa, *i.e.* hydrozoans and Alcyonacea, which mainly occurred in the central and southern external border (Fig. 2, D).

Group C tended to be dominant at the sites in which it occurred (Fig. 3). Individuals of this group were mostly crinoids (85% of the group total density). In a

similar way, group D was dominated by hydrozoans (98% of total density). Density of group A and B was more balanced between the dominant species: crabs, shrimps and *Nephrops* accounted for 90% of group A total density, while Actinopterygii and squat lobster represented 89% of group B total density. Individuals from group A and B often occurred together at the same site, as did individuals from group B and D. Conversely, individuals from group C and D were rarely found together in high proportions.

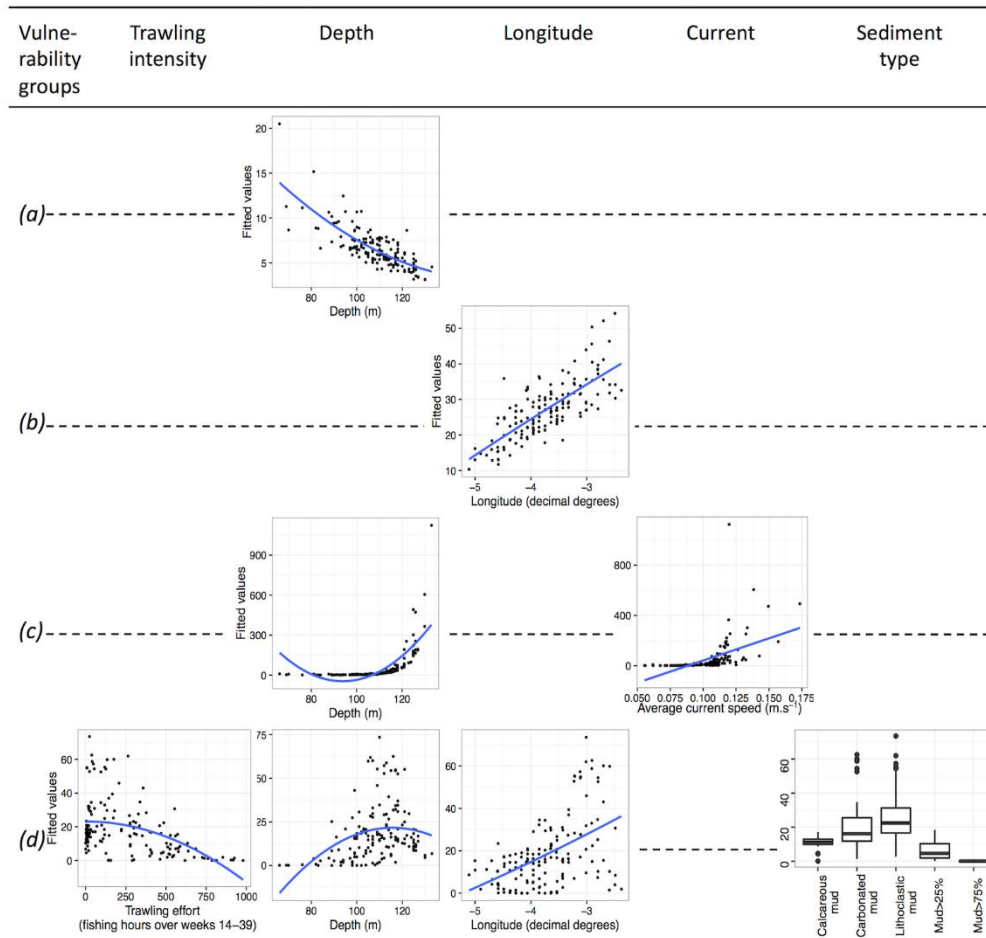**Factors influencing vulnerability patterns**

All final models appeared to be significantly better than null expectations and no interactions were significant regardless of the vulnerability group (Table 1). The stepwise selection procedure retained at least depth or longitude in each GLM model (Table 1). Overall, selected models included quadratic terms, highlighting the

complexity and non-linearity of relationships between the distribution of each group and environmental and fishing variables.

The distribution of the least vulnerable group, group A, was influenced, negatively but non-linearly, by depth (Table 1, Fig. 4). Likewise, distribution of group B density was positively and non-linearly influenced by longitude (Fig. 4). Only groups A and B clustered commercial and non-commercial species. When testing environmental and fishing variables against density patterns of each fraction separately, only patterns of commercial taxa differed from previous results (Table S3 and Fig. S1). In both groups A and B, density patterns of commercial taxa as expected depended on trawling intensity only (Table S3 and Fig. S1). Both depth and its quadratic term and current significantly predicted the density patterns of group C. Finally, the distribution of group D density varied according to all variables, except current, and was the only group significantly influenced by trawling intensity and sediment type (Table 1, Fig. 4).

Table 1 Outcomes of the stepwise selection procedure on the GLM models. The departure of the deviance of the model from deviance of the null model was tested with a χ^2 test. The significance of each variable was then tested with a χ^2 test whose p-value is given in the column "Significance".

	Explanatory variable	Estimate	Deviance	Significance
GROUP A	Depth^2	$-1.07.e^{-4}$	12.61	$3.84.e^{-4}$
	χ^2 between null and selected model = 12.08, p=5.10.e^{-4}			
GROUP B	Lon^2	$-5.35.e^{-2}$	12.30	$4.52.e^{-4}$
	χ^2 between null and selected model = 11.90, p=5.62.e^{-4}			
GROUP C	Depth^2	$2.60.e^{-3}$	154.89	$<2.20.e^{-16}$
	Depth	$-4.66.e^{-1}$	21.55	$3.45.e^{-6}$
	Current	25.81	12.40	$1.03.e^{-2}$
	χ^2 between null and selected model = 129.48, p<2.00.e^{-16}			
GROUP D	Sediments		42.22	$1.51.e^{-8}$
	carbo_mud	$2.22.e^{-1}$		
	litho_mud	$9.12.e^{-1}$		
	mud>25%	$3.20.e^{-1}$		
	mud>75%	$-2.48.e^{1}$		
	Trawl^2	$-4.39.e^{-6}$	11.23	$8.04.e^{-4}$
	Lon	$5.18.e^{0}$	7.38	$6.60.e^{-3}$
	Depth	$5.63.e^{-1}$	6.18	$1.30.e^{-2}$
	Depth^2	$-2.52.e^{-3}$	9.43	$2.14.e^{-3}$
	Lon^2	$6.11.e^{-1}$	3.36	$6.78.e^{-2}$
	χ^2 between null and selected model = 65.38, p=1.21.e^{-10}			

Vulne-rability groups	Trawling intensity	Depth	Longitude	Current	Sediment type
(a)		(Fitted values vs Depth (m))			
(b)			(Fitted values vs Longitude (decimal degrees))		
(c)		(Fitted values vs Depth (m))		(vs Average current speed (m.s⁻¹))	
(d)	(Fitted values vs Trawling effort, fishing hours over weeks 14–39)	(vs Depth (m))	(vs Longitude (decimal degrees))		(boxplot: Calcareous mud, Carbonated mud, Lithoclastic mud, Mud>25%, Mud>75%)

DISCUSSION

The occurrence of taxa at a site results from environmental constraints and competitive interactions (Weiher & Keddy 2001). The vulnerability assessment made here relates to the former, with depth, longitude, current, sediment type and trawling intensity shown to be important constraining environmental conditions in the Grande Vasière.

The distribution of the least vulnerable taxa (group A) seems weakly related to trawling intensity. These small mobile taxa with a hard shell are less vulnerable to trawling disturbance than other taxa and dominated where trawling intensity was the strongest. Many taxa from this group are scavengers such as *Nephrops*, sea stars

and some crustaceans (Thiel & Watling 2015). Trawling damages animals living on the seabed, thus providing a food source for scavengers (Kaiser & Spencer 1996).

The slightly more vulnerable group B is mainly composed of fish taxa, and occured in higher density in the South. This observed longitudinal gradient in the group B pattern most likely originated from complex relationships among unmeasured factors (see discussion below).

Overall density patterns of groups A and B were likely driven by non-commercial taxa, which represented 73% of the individuals encountered in group A and 92% in group B, the latter being dominated by squat lobster and small non-commercial Actinopterygii. Density patterns of the commercial taxa were significantly driven by trawling intensity. We assume that the positive relationship in the case of group A comes from an expected spatial overlap between fishery activities and density patterns of *Nephrops* that happens to be the only commercial species of this group, and one of the most targeted species in this area. Conversely, the negative relationship of commercial taxa of group B with trawling intensity might either originate from the ability of these mobile taxa to avoid heavily trawled areas or may result in a local depletion of their numbers due to their catch by trawlers.

The two most vulnerable groups, group C and D, included non-mobile taxa and large filter feeders. Density of group C tended to increase in areas where the current was the strongest which is typical for the feeding type of this group. This result has to be considered in the light of the correlations between depth, current and trawling intensity that remain strong after the VIF selection. The stepwise selection can be sensitive to collinearity among explanatory variables. Thus, we suspect that the significant negative effect of trawling intensity on group C in the complete model (results not shown) could have been masked by depth and/or current during the

stepwise procedure. Unravelling the pure effect of trawling intensity from the effect of depth and current is difficult in the absence of a reference state, as variables are interrelated (Handley *et al.* 2014). Indeed, the distribution of group C is limited to the external border of the Grande Vasière, where depth reaches 120 m and trawling intensity is very low due to hard substrates hindering trawling activities. Distribution of group D showed marked environmental preference for deeper (100-120m depth) southern and less trawled stations of lithoclastic and carbonated mud. The spatial mismatch between trawling intensity and the level of vulnerability of communities agrees with other studies (Bremner *et al.* 2006*a,* 2006*b*; Tillin *et al.* 2006; de Juan *et al.* 2012; Hinz *et al.* 2009; Jørgensen *et al.* 2016). The negative co-occurrence between group C and D likely results from diverging environmental preferences since taxa forming group C were found on carbonated mud while the highest densities of taxa forming group D were on lithoclastic mud.

Although our results show that environmental factors mainly drive density patterns of all groups, we cannot exclude that the North-South gradient observed for groups B and D partly encapsulates unmeasured environmental parameters like dissolved oxygen, the mobility of sediments or the amount of organic carbon (Bremner *et al.* 2006*b*). Extreme events (*e.g.* storms) can impact seabed (Watling & Norse 1998), but during summer, the more intensive fishing season, resuspension generated by trawling locally exceeds storm impact (Mengual *et al.* 2016).

Trawling activities could alter the physical structure of the habitats. In the Grande Vasière, Hily *et al.* (2008) noted a significant decrease in the mud and coarse fraction, from 19.8% to 9.1% of the total sampled area since the first extensive study of the area by Glémarec (1969). Simultaneously, the sand fraction increased from 50.5% to 68.3%. A homogenisation of the type of substrata occurred and an

'intermediate' sediment, which was neither very muddy nor very coarse, became dominant. Penetrable substrata are the preferred habitat of burrow builders like *Nephrops* or crabs (Bremner *et al.* 2006*b*) that could be disadvantaged by the shift toward an increase in the sandy fraction (Campbell *et al.* 2009). In the same way, the increase in the sandy fraction would be a threat to filter feeders, such as Pennatulacea or sea anemones that are present on muddy/sandy sediments.

Underwater video can offer a valuable complement to dredge and trawl sampling techniques in the evaluation of trawling impacts (Smith *et al.* 2007) and allows assessing changes over larger areas (Hewitt *et al.* 2011). In particular, the direct visualisation of the seabed habitats provides access to unprecedented information, such as unexpected occurrence of species that are either damaged by conventional trawling surveys or able to escape. Using non-extractive methods during scientific surveys should be encouraged especially when fragile species are present. This idea is illustrated by the recording of the sea pen *Pennatula phosphorea*, considered rare, at 76 stations among the 152 sampled in this study. Thirty-nine taxa observed, including 33 from groups A and B, found in trawled areas, indicate that the number of taxa is not affected by trawling disturbance. However, underwater video samples only large (> 5cm) epifauna and often cannot be used to identify taxa to species. The use of morphological traits from individuals identified at different taxonomic levels conserves the community structure and richness patterns and leads to results in community analysis similar to those at higher taxonomic resolution (Brind'Amour *et al.* 2014). The vulnerability of individuals thus appears to depend more on their morpho-anatomical characteristics than on their taxonomic classification. The assessment of vulnerability conducted in this study, based on

biological traits is therefore not penalized by the use of different taxonomic levels and can be compared to the approach by morphospecies of Howell *et al.* (2010).

Our assessment contributes to an integrated assessment of resilience and resistance of this system. The European Marine Strategy Framework Directive for the evaluation of the overall state of marine ecosystems requires describing the dynamics, the resilience and the resistance of communities to trawling disturbance using more biological traits (*e.g.* life-history traits such as longevity or reproduction) and biomass (Kaiser *et al.* 2006; Tillin *et al.* 2006), unavailable for many taxa considered here. The year 2014 can be considered as representative of the recent period (ICES 2016*b*), however fishing intensity based on a single year is likely not representative of mid- or long-term trends in fishing activities. Thus the time scale considered here does not permit inferring processes linking biodiversity patterns, environmental conditions and fishing activities, which was beyond the scope of our study.

An accurate evaluation of the health status of ecosystems would require the definition of a reference state before the intensification of anthropogenic pressures. However, no usable information about historical states is available for this area and any decline in the abundance of vulnerable taxa might have occurred before any modern monitoring (Roberts 2010). Communities of the Grande Vasière might have already been shaped by fishing activities that can be considered as moderate to high compared to adjacent areas (Eigaard *et al.* 2016). Without a documented reference state, it is challenging to state that a species is absent from an area because it disappeared in response to excessive fishing pressure, or if the species was never present due to habitat preferences and ecosystem interactions.

This study is a first step in the direction of an integrated management of fisheries in the Grande Vasière based on knowledge of the distribution of vulnerable species. To our knowledge, this is the first study evaluating biodiversity vulnerability based on recorded videos routinely acquired for stock assessment. Such trait-based approaches to map the vulnerability level of species and communities could easily be generalised to other fishing grounds surveyed for stock assessment using video and should be very relevant to identify priority areas for management intervention.

SUPPLEMENTARY MATERIAL

For supplementary material accompanying this paper, visit

http://www.journals.cambridge.org/ENC

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FIGURE CAPTIONS

Figure 1 Map of the different substrata types over the Grande Vasière.

Figure 2 Spatial patterns of vulnerability and trawling intensity in the Grande Vasière. The distribution of group A (A), group B (B), group C (C) and group D (D) was interpolated for the illustration. Trawling intensity is expressed as the number of fishing hours per 3'x3' cell grid, from the April to September 2014.

Figure 3 Relative density of vulnerability groups, expressed as the number of individuals of a given group over the overall number of individuals occurring at each site.

Figure 4 Relationships between the fitted values of the final GLM and the explanatory variables selected (trawling intensity, depth, longitude, current and sediment type) for each vulnerability group. Linear or order 2 polynomial smoothing was fitted to the data, depending on whether the relationship with the variable was linear or quadratic.

Supplementary material for: **Using underwater video to assess megabenthic community vulnerability to trawling in the Grande Vasière (Bay of Biscay)**

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The following documents give precisions about: (1) the scoring of the vulnerability for the 5 biological traits considered (Tables S1 and S2); (2) the calculation of the swept area and trawling frequency in each grid cell; (3) the packages used to perform analysis and the outcomes of the GLM models for the commercial and non-commercial species separately (Table S3) and the plotted relationship between the GLM models fitted values and the explanatory variables selected in these models (Fig. S1).

(1) Scoring of the vulnerability for the 5 biological traits considered

Table S1 Five categories of biological traits and their respective scoring scheme (from de Juan *et al.* 2009).

Sensitivity scores	Position	Feeding	Motility	Size	Fragility
0	Deep burrowing	Scavengers	Highly mobile (swimming)	Small < 5 cm	Hard shell, burrow, vermiform, regeneration
1	Surface burrowing (first cm)	Deposit feeders/predators	Mobile (crawling)		Flexible
2	Surface		Sedentary	Medium 5-10 cm	No protection
3	Emergent	Filter feeders	Sessile (attached)	Large > 10 cm	Fragile shell/structure

The lowest scores were assigned to the less vulnerable taxa. For a total score value under 8, taxa were assigned to the least vulnerable group, group A. Likewise, taxa were allocated to group B if their total score value fell between 8 and 9, to group C if it was between 10 and 13, or to group D if it was above 13.

Table S2 Vulnerability scoring for each biological traits and their sum per taxa. The higher scores indicate a higher vulnerability to trawling.

Species	Taxonomic level	Position	Feeding	Motility	Size	Other attributes	Total score
Paguroidae	Superfamily	2	0	1	0	1	4
Gobiidae	Family	2	1	0	0	2	5
Crabs unidentified (Brachyura)	Infraorder	2	1	1	2	1	6
Shrimps unidentified (Decapoda)	Order	2	1	1	0	2	6
Nephrops norvegicus	Species	0	1	2	3	1	7
Goneplax rhomboides	Species	2	1	1	2	1	7
Blenniidae	Family	2	1	0	2	2	7

Taxon	Rank						
Sea star unidentified (Asteroidea)	Class	2	1	1	3	0	7
Munida rugosa	Species	2	3	1	0	2	8
Aphrodita aculeata	Species	2	1	1	3	1	8
Jelly fish unidentified (Cnidaria)	Phylum	3	1	0	3	1	8
Callionymus sp.	Genus	2	1	0	3	2	8
Lepidorhombus sp.	Genus	2	1	0	3	2	8
Triglidae	Family	2	1	0	3	2	8
Microstomus kitt	Species	2	1	0	3	2	8
Lophius sp.	Genus	2	1	0	3	2	8
Flat fish unidentified (Pleuronectiformes)	Order	2	1	0	3	2	8
Octopus unidentified	Genus	2	1	0	3	2	8
Rajiformes	Order	2	1	0	3	2	8
Soleidae	Family	2	1	0	3	2	8
Scyliorhinus sp.	Genus	3	0	0	3	2	8
Actinopterygii ni	Class	3	1	0	2	2	8
Capros aper	Species	3	1	0	2	2	8
Cancer pagurus	Species	2	1	1	3	1	8
Ophiuroidea	Class	2	1	1	2	3	9
Anguilliforme unidentified	Order	3	1	0	3	2	9
Cepola sp.	Genus	3	1	0	3	2	9
Trachurus trachurus	Species	3	1	0	3	2	9
Conger conger	Species	3	1	0	3	2	9
Loligo sp.	Genus	3	1	0	3	2	9
Gadiformes	Order	3	1	0	3	2	9
Argentina sphyraena	Species	3	1	0	3	2	9
Sepiidae unidentified	Family	3	1	0	3	2	9
Spirographis sp.	Genus	2	3	2	0	3	10
Cerianthus sp.	Genus	3	3	3	3	2	12
Crinoidea	Class	3	3	1	2	3	12
Pennatulacea	Order	2	3	3	3	2	13
Hydrozoa	Class	3	3	3	3	3	15
Alcyonacea	Order	3	3	3	3	3	15

(2) the calculation of the swept area and trawling frequency in each grid cell

Fishing hours in a 3'x3' grid cell was taken as a proxy of fishing intensity. However, this metric does not give information on the area of the seabed impacted. Following Eigaard *et al.* (2016), the swept area and the trawling frequency were calculated in each grid cell. Fig. 11 gives a value of the hourly swept area (surface impact) for otter trawl targeting *Nephrops* (OT_CRU) of 0.35km^2 for an average vessel. We checked

this value correspond to the fishing practices in our study area. The swept area per hour for OT_CRU is given by

$$A_{\text{swept per hour}} = W * S$$

Where W the average distance between the doors (considering the gear path width impacts 100% of the surface), and S the average fishing speed.

For an average fishing speed of 3 knots, the average width is 63m. These values are in line with the ones of the standard fishing practices of OT_CRU vessels in the Grande Vasière.

Swept area was obtained multiplying fishing hours data by $0.35 \text{km}^2.\text{h}^{-1}$, following:

$$A_{\text{swept}} = A_{\text{swept per hour}} * E, \text{ where E is the trawling effort in fishing hours.}$$

Area of each grid cell was computed under Qgis versions 2.12.1-Lyon according to the variation with latitude. Trawling frequency was calculated as swept area divided by grid cells area.

Supplementary Reference:

Eigaard, O.R., Bastardie, F., Breen, M., Dinesen, G., Hintzen, N.T., Laffargue, P., Mortensen, L.O., Nielsen, J.R., Nilsson, H.C., O'Neill, F.G., Polet, H., Reid, D.G., Sala, A., Sköld, M., Smith, C., Sorensen, T.K., Tully, O., Zengin, M., Rijnsdorpa, A.D., 2016. Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. ICES J. Mar. Sci. 73, 27–43. doi:10.1093/icesjms/fst176

(3) information on the packages used to perform analysis and the outcomes of the GLM models for the commercial and non-commercial species separately and the plotted relationship between the GLM models fitted values and the explanatory variables selected in these models

All analyses were performed using packages car (Fox and Weisberg, 2011), MASS (Venables & Ripley 2002), fmsb (Nakazawa 2007) and plotrix (Lemon 2006)

Supplementary References:

Fox J. & Weisberg S. (2011) An R Companion to Applied Regression, Second Edition, Sage.

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Table S3 Outcomes of the stepwise selection procedure on the GLM models for commercial and non-commercial taxa in sensitivity groups A and B. The departure of the deviance of the model from deviance of the null model was tested with a χ^2 test. The significance of each variable was then tested with a χ^2 test whose p-value is given in the column "Significance".

	Explanatory variable	Estimate	Deviance	Significance
GROUP A commercial	Trawl	$1.19.e^{-3}$	6.32	$1.19.e^{-2}$
	χ^2 between null and selected model = 6.12, p=1.32.e^{-2}			
GROUP A non commercial	Depth^2	$-1.34.e^{-4}$	11.30	$7.77.e^{-4}$
	χ^2 between null and selected model = 14.55, p=0.005			
GROUP B commercial	Trawl	$-9.39.e^{-4}$	9.60	$1.95.e^{-3}$
	χ^2 between null and selected model = 9.24, p=2.37.e^{-3}			
GROUP B non commercial	Lon^2	$-5.94.e^{-2}$	11.80	$5.92.e^{-4}$
	χ^2 between null and selected model = 11.43, p=7.23.e^{-4}			

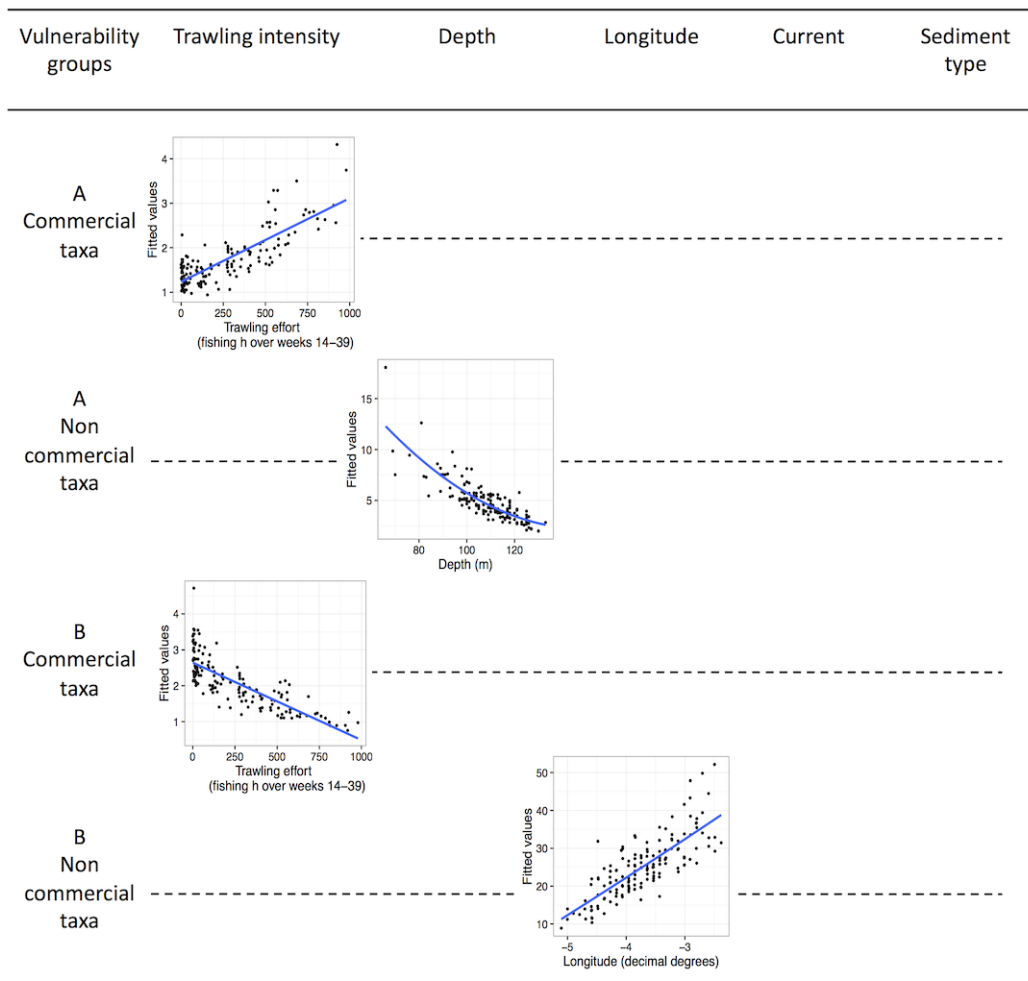| Vulnerability groups	Trawling intensity	Depth	Longitude	Current	Sediment type

Fig S1 Relationships between the fitted values of the final GLM and the explanatory variables selected (trawling intensity, depth, longitude, current and sediment type) for each vulnerability group. Linear or order 2 polynomial smoothing was fitted to the data, depending on whether the relationship with the variable was linear or quadratic.