






Using biological traits to get insights into the benthic-demersal community sensitivity to trawling in the Celtic Sea

Amaël Dupaix ^{1,2,*}, Laurène Mérillet^{1,3}, Dorothee Kopp ¹, Maud Mouchet³, and Marianne Robert ¹

¹Ifremer, STH—Unité de Sciences et Technologies halieutiques, Laboratoire de Technologie et Biologie Halieutique, Lorient56100, France

²Département de Biologie, ENS de Lyon, 46 allée d'Italie, Lyon 69007, France

³UMR 7204 MNHN-SU-CNRS Centre d'Ecologie et de Sciences de la COnservation, 43 rue Buffon, CP135, Paris 75005, France

*Corresponding author: tel: +33 760086122; e-mail: amael.dupaix@ens-lyon.fr.

Dupaix, A., Mérillet, L., Kopp, D., Mouchet, M., and Robert, M. Using biological traits to get insights into the benthic-demersal community sensitivity to trawling in the Celtic Sea. – ICES Journal of Marine Science, 78: 1063–1073.

Received 30 July 2020; revised 17 December 2020; accepted 19 January 2021; advance access publication 7 February 2021.

Coastal marine ecosystems are under many pressures, including bottom trawling, which is the most widespread human activity that directly affects seabed habitats. Therefore, it is of great importance to characterize the impacts of bottom trawling on benthic-demersal communities, which can be done through the study of indicators sensitive to trawling pressure. Using a functional indicator applied to 54 underwater video transects, we mapped the sensitivity to trawling of epibenthic invertebrates and fish communities in the Celtic Sea. We determined the relative influence of environmental and fishing variables on sensitivity and traits distribution. Our results suggest that community sensitivity to trawling is mainly driven by a spatial gradient of depth and primary productivity that separates the area into two main regions: a shallow, productive area, with low sensitivity and a higher abundance of swimming and crawling organisms, and a deeper, less productive area, with higher sensitivity due to a higher abundance of fixed, filter-feeding organisms. Fishing intensity also drives the sensitivity of communities confirming that they have already been shaped by a long history of mixed fisheries. The methodology used here provides a valuable monitoring tool and could be used to predict communities' response to changes in fishing intensity and climate change.

Keywords: community-weighted mean, ecosystem-based management, fishing and environmental drivers, functional ecology, traits-based indicators, underwater video

Introduction

One of the main goals of applied ecology is to understand the responses of communities to pressures, whether natural or anthropogenic, to inform ecosystem management and conservation mitigation measures (McGill *et al.*, 2006; Harrison and Cornell, 2008). To predict these responses, it is important to assess the vulnerability of ecosystems to human activities, which are known to jeopardize their structure and functioning (Halpern *et al.*, 2008). The vulnerability of marine ecosystems depends on their sensitivity, i.e. the degree to which an ecosystem will respond to a given pressure, as well as on their exposure, i.e. the extent and intensity of the pressure (ICES, 2017). Sensitivity can be broken

down into the direct response of the ecological system to pressure (resistance) and its capacity to recover (resilience), which can both be characterized using biological traits (Tillin *et al.*, 2006; Bolam *et al.*, 2014b; Rijnsdorp *et al.*, 2018).

Assessing the sensitivity to perturbations of ecosystems located on continental margins is of particular interest for their management. Indeed, coastal shelf seas, which only represent 7% of the total ocean area, sustain the landing of 19 million tonnes of fish and invertebrates each year (Amoroso *et al.*, 2018). These ecosystems are subject to several types of pressures of anthropic origin, the most important ones being fisheries (e.g. through direct catch or habitat modification), pollutions (either land or ocean based),

and climate change (which exacerbates the impact of other factors, e.g. through ocean acidification and temperature modification) (Halpern *et al.*, 2008; Diaz *et al.*, 2019). Regarding fishing pressure, bottom trawling is responsible for almost a quarter of global wild marine landings (Amoroso *et al.*, 2018). Bottom trawling also accounts for the highest human physical disturbance on marine ecosystems in continental shelves throughout the world (Watling, 2005; Foden *et al.*, 2011). Trawling footprint shows strong variations between regions, with some regions concentrating most of the trawling activity. For instance, in European waters, nearly 100% of benthic habitats are impacted by bottom trawling in the Kattegat (Pommer *et al.*, 2016) and in the UK waters bottom trawl footprint is estimated to account for up to 99% of the known effect of all human pressure on the seabed (Foden *et al.*, 2011).

Bottom trawling impacts benthic-demersal communities in several ways. First, its impact depends on the exposure, which is the function of fishing gear characteristics and fishing intensity. Bottom trawling impact is then influenced by the resistance of communities, which is determined by the physical (e.g. size, presence/absence of a shell) and behavioural (e.g. position on the substratum, mobility) characteristics of the species (Bolam *et al.*, 2014a; Mérillet *et al.*, 2018b). Finally, the resilience of benthic-demersal communities, mainly determined by the life history of species (e.g. longevity, reproductive mode), plays an important role in determining their response to trawling (Hiddink *et al.*, 2017, 2019). Resilience is also determined by some behavioural traits, such as feeding mode (e.g. scavengers can benefit from dead organisms whereas filter feeders are vulnerable to sediment plume, de Juan *et al.*, 2009).

Several methods have been put forward for assessing species sensitivity (de Juan *et al.*, 2007, 2009; Bolam *et al.*, 2014a; González-Irusta *et al.*, 2018). A particularly well-adapted method to describe the response of epibenthic communities to trawling disturbance consisted in an integrated trait-based indicator based on five biological traits (size, position on the substratum, fragility, mobility, and feeding mode, de Juan *et al.*, 2009). However, these studies mainly focused on benthic organisms without considering fish species, which preclude a global assessment at the ecosystem level. When using traditional scientific fishing gear (otter trawl, beam trawl, dredge, or box-corer), fragile species such as sea pens or hydrozoans may be broken, which hinders the correct counting and identification of individuals (Auster *et al.*, 2011). In addition, when using such sampling methods, the catchability of some elusive, highly mobile species remains unknown. This study aimed at assessing the sensitivity of the whole community living in the benthic-demersal habitat and therefore needed a sampling method free of this sampling bias. The use of underwater video devices circumvents this bias (Mallet and Pelletier, 2014). It also has the advantage of allowing the direct visualization of the seabed over large areas and offers better accuracy for the evaluation of abundance and taxonomic richness (Hewitt *et al.*, 2011; Buhl-Mortensen *et al.*, 2015). However, this non-extractive sampling method depends on water turbidity and does not always enable the identification of taxa at the lowest taxonomic levels (Ninio *et al.*, 2003). A way of by-passing this last issue is to use biological traits, such as position, size, fragility, mobility, or feeding type, that can be determined both at the species level and at a higher taxonomic level (i.e. genus, family, class).

In the context of the implementation of the ecosystem approach to fisheries (Garcia *et al.*, 2003), the global sensitivity of

an ecosystem to fishing has to be quantified. In this study, the sensitivity of both epibenthic invertebrates and demersal species was assessed using underwater video observation, a methodology that makes it possible to properly sample fragile taxa. By analysing together fish species and taxa that had not yet been sampled in traditional surveys, we aimed at unveiling previously unexplored patterns of sensitivity. The main goals were (i) to map the sensitivity of benthic-demersal communities to trawling, (ii) to disentangle the relative influence of the environmental, geographical and fishing variables on the sensitivity of communities, and (iii) to analyse the distribution of each trait determining sensitivity and their spatial covariations in response to environmental and fishing gradients. We used the Celtic Sea as a case study. This area located between France, Ireland, and the United Kingdom is an important fishing ground for European fisheries. It is exploited since the 1950s for the fishing of over 100 species, ranging from algae to top-predator fish (Guénette and Gascuel, 2012; Mateo *et al.*, 2017).

Methods

Sampling design

Sampling was conducted on board the R/V Thalassa in November 2014, 2016, 2018, and 2019 during the EVHOE annual survey (part of the International Bottom Trawl Survey), which primarily aims at providing data for stock assessments purposes. Bottom trawl sampling sites were chosen according to a random stratified design based on depth strata, occurring at fixed sites since 2016. Video sampling sites were chosen among bottom trawl sampling sites to ensure a balanced number of sites across various sediment types. A total of 54 transects were carried out in the Celtic Sea using a camera fixed on a sledge (Supplementary Table 1). The sledge was towed on the seabed at an average speed of ~1.5 knots for 20 min. Due to the low number of transects performed each year and the stability of the demersal communities over this period (Mérillet *et al.*, 2020), the 4 years were considered as a single timeframe to provide a good spatial coverage of the area and allow statistical analysis. On each video, individuals were identified at the lowest taxonomic level possible within the first 15 valid minutes. A minute was considered valid when at least 30 s could be analysed. Individuals that could not be identified at the species level were grouped at higher taxonomic levels (hereafter taxon; e.g. genus, family, and order). Every taxon identifiable on video footage and present in the benthic and demersal zones (i.e. both megabenthic invertebrates living on the sediment and fish species) were considered, to study the whole benthic-demersal community. The density of taxa was calculated for each site, standardizing by the surface of the sampled area. Transect width was calculated using pictures captured every minute. Out of the 15 pictures obtained, ten were sampled randomly. Two lasers placed 0.10 m apart were used to measure the width of the view field on each picture. Transect length was calculated using the GPS of the vessel and measured 475.0 m on average ($SD = 106.3$ m). Transect length and an annual median width value were then used to calculate the surface area of the transects. The use of an annual median width made it possible to account for minor modifications of the parameter of the sledge (camera type and angle for instance) from 1 year to the next. The sampled area per transect was 779.6 m² on average ($SD = 301.5$ m²).

Sensitivity score

We used the trawl disturbance indicator developed by de Juan *et al.* (2009) to characterize the sensitivity of taxa to trawling disturbance. The index combines five biological traits: mobility, size, feeding mode, fragility, and position on the substratum. Since de Juan *et al.* (2009), several studies have highlighted that longevity also plays an important role in the characterization of sensitivity (Rijnsdorp *et al.*, 2018; Hiddink *et al.*, 2019). Longevity was therefore added to the calculation of the sensitivity score (Rijnsdorp *et al.*, 2018; Hiddink *et al.*, 2019). Trait values for each taxon were assigned using online databases (Froese and Pauly, 2000; MarLIN, 2016; Beukhof *et al.*, 2019; Palomares and Pauly, 2019; Foveau *et al.*, 2020) and expert knowledge. For each trait, scores ranging from 0 to 3 were assigned following de Juan and Demestre (2012). Longevity scores were assigned following the classification of Hiddink *et al.* (2019) (i.e. 0: <1 year; 1: 1–3 years; 2: 3–10 years; 3: >10 years) (Supplementary Table 2). Trait scores were then summed to obtain a sensitivity score per taxon. The highest values of this score correspond to the most sensitive taxa (Supplementary Table 3).

The community-weighted mean (CWM) is the weighted average of the distribution of a trait in a community (i.e. the expected value of the trait of an individual chosen randomly in the community) (Diaz *et al.*, 1998; Grime, 1998; Gaüzère *et al.*, 2019). In our study, the CWM was calculated for each transect, using taxon densities and either sensitivity scores (for the first part of the statistical analysis) or the score of each trait separately (for the second part). CWM was calculated as follows, for a community of R taxa:

$$\text{CWM} = \sum_{i=1}^R p_i t_i$$

with p_i is the density of taxon i , and t_i is the value of the trait of taxon i (sensitivity score or individual trait score in our study).

Explanatory variables

We selected anthropogenic and environmental variables known to influence the structure and functioning of ecosystems in North-Eastern Atlantic seas, and more specifically in the Celtic Sea: depth, sediment type, surface chlorophyll a concentration (as a proxy for productivity), bottom temperature, bottom current (BC) velocity, and fishing intensity (Wiedmann *et al.*, 2014; Foveau *et al.*, 2017; Mérillet *et al.*, 2020).

Depth was measured using a Marport device at each transect and ranged from 71 to 216 m (Figure 1a). Sediment type was extracted from EMODnet database (<http://www.emodnet-geology.eu>) when available. Missing values (2 out of the 54 sampling sites) were obtained from the French Service Hydrographique et Océanographique de la Marine (SHOM) world sediment map and adapted to the EMODnet classification (<https://diffusion.shom.fr/loisirs/sedim-mondiale.html>). Five categories were used, according to the Folk classification system: mud to muddy sands, sand, coarse substrate, mixed sediment, and rock and boulders. The Celtic Sea offers a relatively complex habitat with a substratum that is mainly composed of three sediment types (sand, mud, and coarse sediments) (Figure 1b). Chlorophyll a (Chlo) concentrations were obtained from the OceanColour products, based on satellite observations at a 1 km \times 1 km resolution. Values were higher close to the English coast in the North-Eastern part of the

area and decreased towards the end of the continental shelf in the South-West (Figure 1c). Sea bottom temperature (SBT) and BC data were extracted from the Iberian Biscay Irish Ocean Physics data product at a 8 km \times 8 km resolution, which is based on the NEMO v3.6 ocean general circulation model (Madec and the NEMO team, 2016). SBT displayed a latitudinal gradient with warmer waters close to the French coast and colder in the Northern part of the area, close to the Irish coast (Figure 1d). BC was more homogeneous with an increase close to the coasts and close to the continental margin (Figure 1e). These three environmental variables (Chlo, BC, and SBT) were downloaded from Copernicus (<http://marine.copernicus.eu/>). Annual mean values were estimated by averaging the mean monthly values over the year preceding the sampling campaign. Depth, sediment type, Chlo, BC, and SBT will hereafter be referred to as “environmental variables”. The latitude, longitude, and longitude \times latitude interaction were obtained from the vessel GPS for each transect during the survey. These variables will hereafter be referred to as “geographical variables”.

The International Council for the Exploration of the Sea (ICES), as a technical service of the OSPAR Convention (Convention for the Protection of the Marine Environment of the North-East Atlantic), produced spatial data layers of fishing intensity for the *métiers* in contact with the seabed and thus likely to impact it (beam trawl, dredge, demersal seine and otter trawl) (ICES, 2018a). These layers are based on vessel monitoring system (VMS) data and generated at a 0.05° \times 0.05° (\sim 5.5 km \times 5.5 km) resolution. The total surface swept area ratio (SurfSAR), which is the proportion of the estimated swept area of the surface of each grid cell, was used as a proxy of fishing intensity. As these spatial data were only delivered up to 2017, the mean was calculated at every transect location (from 2013 to 2017) and used for 2018 and 2019. This was possible since, on visual inspection, fishing effort seemed stable through space and time (Supplementary Figure 1). The data showed a strong spatial heterogeneity at a small scale and no clear gradient of fishing intensity was observed. However, the highest fishing intensities were observed in the North-Eastern region and lower intensities on the deeper continental shelf, close to the continental slope (Figure 1f).

Statistical analysis

To test the relationship between explanatory variables and the CWM of the sensitivity score, a generalized linear model (GLM) was performed, with a Gaussian link function. All quantitative variables were scaled to enable the comparison of their marginal effect on the sensitivity score, and geographical variables were centred in order to reduce multicollinearity (Legendre and Legendre, 1998). The collinearity among fishing intensity, environmental, and geographic variables was assessed using the variance inflation factor and a release threshold of 10 (Borcard *et al.*, 2011). As autocorrelation was detected in the data (Moran's $I=0.49$, p -val = 0.002) and because it improved the fit of the model (preliminary analysis, not shown), spatial terms were included in the model, i.e. longitude (Long), latitude (Lat), and longitude \times latitude (LongLat).

The best model was selected based on the lowest Akaike information criterion (AIC), which allows to select the model having the best trade-off between the goodness-of-fit and the number of model parameters (Borcard *et al.*, 2011). The goodness-of-fit of the final model was assessed using an adjusted R^2 and a χ^2

statistic. Finally, spatial autocorrelation in the residuals was checked using a permutation test on Moran's I statistic and the Gaussian distribution of the residuals was tested using a Shapiro–Wilk test.

To test covariations between environmental and fishing variables and the distribution of the traits related with sensitivity while partialling out their interaction, a community-weighted mean-redundancy analysis (CWM-RDA) was performed, using the CWMs of each trait (mobility, size, feeding, fragility, position, and longevity) at the transects (Vandewalle et al., 2010; Kleyer et al., 2012). The CWM-RDA combines ordination methods with multi-linear regression to represent the traits as linear functions of the environment. It therefore analyses the relationship between a matrix of scaled trait CWMs and a matrix of scaled explanatory variables (Kleyer et al., 2012). The best CWM-RDA model was then selected based on the lowest AIC value and model, axis, and variable significance were assessed using permutation tests. The goodness-of-fit of the final model was assessed using an adjusted R^2 . Transects were clustered using a K -means clustering algorithm on the RDA scores of the first two axes, and the optimal number of clusters was determined using the Calinski-Harabasz criterion. Explanatory variables and CWMs were then characterized at the transects of the different clusters, by performing Pearson's χ^2 tests between cluster values and overall values. As this characterization consisted in performing a total of 54 tests, a

Bonferroni correction was performed on the p -values, and the tests were considered significant with adjusted p -values inferior to $\alpha = 0.05$.

All analyses were performed using the statistical software R v.3.6.3 (R Core Team, 2020), with the following packages and functions: “FD” v.1.0-12 (Laliberté et al., 2014); “car” v.3.0-7 (Fox and Weisberg, 2019); *stepAIC* function from “MASS” v.7.3-51.5. (Venables and Ripley, 2002); *moran.mc* from “spdep” v.1.1-3 (Bivand and Wong, 2018); and *catdes* function from “FactoMineR” v.2.3 (Lê et al., 2008).

Results

Sensitivity index and CWMs

A total of 23 243 individuals from 55 taxa were identified over the 825 min of observation (Supplementary Table 3). A total of 95% of these individuals belong to 20 taxa and the three most abundant taxa (*Actinauge* spp., Hydrozoa, and Polychaeta) comprised 54% of all the observed individuals. Theoretical sensitivity score can range from 0 (all trait values set to zero) to 18 (all trait values at 3). Sensitivity scores per taxon ranged from 4 (*Munida* spp., which is a small, deep-burrowing, scavenger taxon) to 17 (*Funiculina quadrangularis*, which is a fixed, filter feeding, emergent species with a size of >30 cm), with a median score of 11 (Supplementary Table 3).

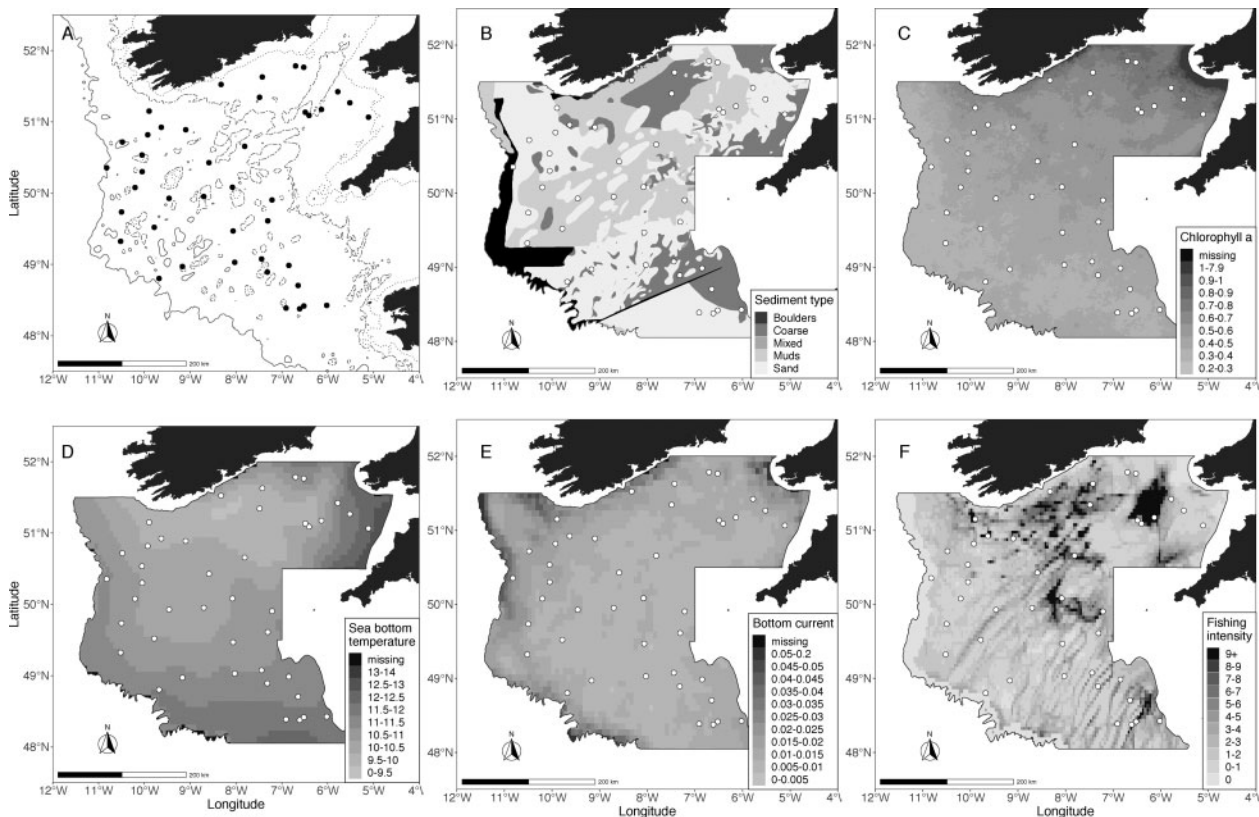


Figure 1. Maps of environmental variables and fishing intensity in the Celtic Sea. (a) Depth: 60-, 100-, and 200-m isobaths (dotted, dashed, and solid black lines, respectively). (b) Sediment type, from EMODNet data, for all stations represented as white dots. The white square represents the transect for which the sediment type was missing in the EMODNet data and therefore adapted from SHOM data (classified as sand). (c) Mean chlorophyll a concentration, expressed in mg m^{-3} . (d) Mean SBT, in $^{\circ}\text{C}$. (e) Mean BC expressed in m s^{-1} . The mean values, represented in maps (c)–(e) were calculated with the four datasets from which the data at transects were extracted (2014, 2016, 2018, and 2019). (f) Mean SurfSAR calculated with OSPAR data from 2013 to 2017. In every map, dots represent transect locations.

Values of CWMs of the sensitivity score ranged from 9.0 to 14.7, with a median of 11.7 ($SD = 1.19$). CWMs displayed a heterogeneous spatial distribution, with increasing values from the North-East to the South-West (Figure 2). Smaller values, which indicate less sensitive communities, were observed in the area between Ireland and the United Kingdom. In the other part of the Celtic Sea, where more sensitive communities were observed, two sub-regions can be distinguished: one with homogeneous values of sensitivity between transects in the South-East and another one with stronger sensitivity variations in the West (Figure 2).

Environmental drivers of sensitivity patterns

The model that elucidated best the spatial pattern of the CWM sensitivity score included depth, chlorophyll *a*, fishing intensity, latitude, longitude, and latitude \times longitude interaction

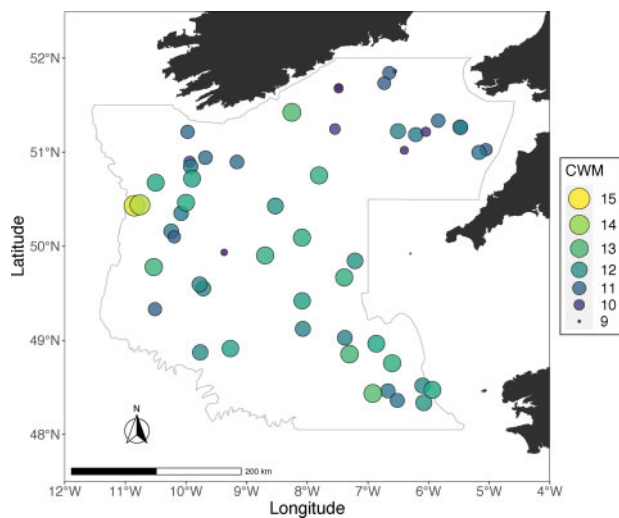


Figure 2. CWMs of the sensitivity score at transects. The transect positions were slightly modified to facilitate visualization. The grey line represents the studied area.

(Table 1). The selected model accounted for ~60% of the observed variance ($R^2_{step} = 0.58$). The permutation test on Moran's *I* statistic showed no significant spatial autocorrelation in the residuals (p -value = 0.60) and residuals' distribution was not significantly different from a Gaussian distribution (Shapiro test: p -value = 0.09).

The GLM on CWM sensitivity score showed that sensitivity to trawling pressure of communities had a positive relationship with latitude (coefficient: 0.67; standard error: 0.25) and longitude (coefficient: 0.73; standard error: 0.21). However, a negative effect of the longitude \times latitude interaction (coefficient: -0.42 ; standard error: 0.18) showed an additional effect of an anisotropic gradient. Depth had the strongest influence on sensitivity scores, as its coefficient had the highest absolute value (3.83; standard error: 0.90). An increase in depth was correlated with an increase in community sensitivity. The two most sensitive communities (sensitivity indices: 14.3 and 14.7) were observed at the deepest transects (206 and 216 m) and the least sensitive (sensitivity index: 9.0) at the shallowest transect (71 m). The robustness of the correlation between depth and sensitivity was tested and showed little influence of these extreme points (results not shown). Both chlorophyll *a* concentration (i.e. productivity) and fishing intensity had a negative impact on the sensitivity of communities (coefficients -1.70 ; standard error: 0.65 and -0.61 ; standard error: 0.18).

Characterization of the different communities

The best CWM-RDA model selected, fitted on the CWM of each trait, is presented in Figure 3. The position of a trait label corresponds to a high score, i.e. close to 3, for the given trait (see Supplementary Table 2 for a detail of the scores for each trait). Angles between variables, either response (trait scores) and/or explanatory (fishing intensity and environment), reflect their correlation (Borcard *et al.*, 2011). The selected model included chlorophyll *a* concentration, depth, longitude, longitude–latitude interaction, and fishing intensity. It accounted for 46.8% of the total observed variance, with an adjusted R^2 of 0.41 (p -value = 0.001). The first two axes of the CWM-RDA were significant

Table 1. GLMs performed on the CWMs of the sensitivity scores at transects.

	Explanatory variable	Estimate	Significance (p -value)
Selected model	LongLat	-0.42	2.23×10^{-2}
	Long	0.73	1.24×10^{-3}
	Lat	0.67	9.22×10^{-3}
	Chlo	-1.70	1.20×10^{-2}
	Depth	3.83	9.49×10^{-5}
	Fishing	-0.61	1.24×10^{-3}
	χ^2 between null and selected model = 47.3, $p = 1.60 \times 10^{-8}$		
Complete model	AICc = 142.5		
	LongLat	-0.35	
	Long	0.76	1.42×10^{-2}
	Lat	0.58	3.50×10^{-2}
	BC	0.30	
	SBT	-0.65	
	Chlo	-1.95	1.35×10^{-2}
	Depth	3.40	1.74×10^{-3}
	Sedim_sand	0.31	
	Sedim_muds	-0.06	
	Fishing	-0.55	1.46×10^{-2}
	χ^2 between null and complete model = 49.1, $p = 3.87 \times 10^{-7}$		
AICc = 153.1			

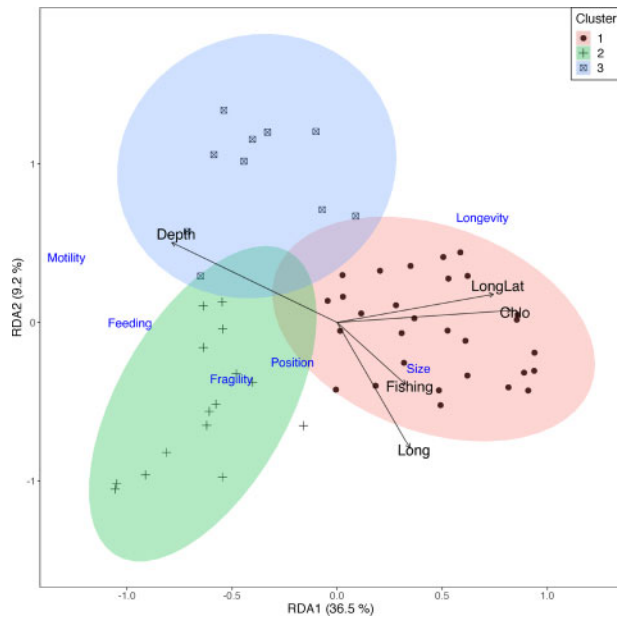


Figure 3. Biplot of the CWM-RDA, performed on trait scores CWMs, constrained by explanatory variables. Percentages on axis are the percentage of the total observed variance explained by the axis. Because traits are coded using increasing numeric numbers, the location of a trait label corresponds to higher scores of the given trait. For example, motility and depth show a correlation, meaning that deeper transects present high motility sensitivity scores (i.e. a high proportion of sessile organisms—score = 3—and a low proportion of mobile organisms—score = 0).

(p -values = 0.001 and p -value = 0.003, respectively) and accounted for 36.5% and 9.2% of the observed variance. The first CWM-RDA axis was strongly correlated with chlorophyll *a* concentration (biplot score = 0.83), depth (−0.79), and longitude–latitude interaction (0.74) and showed lower correlations with longitude (0.35) and fishing intensity (0.33). The first CWM-RDA axis therefore represented a spatial gradient from deep transects with low chlorophyll *a* concentration and little fishing intensity, to shallower transects with high chlorophyll *a* concentration and higher fishing intensity. It also allowed good discrimination of trait responses to explanatory variables. Notably, the correlations between mobility and feeding mode and their higher scores in less productive deep transects highlight the high proportion of sessile and filtering organisms in the deepest area. Fragility and position on the substratum also seemed correlated since they presented higher scores in an intermediate position on the depth–chlorophyll gradient. Finally, the more long-lived taxa appeared to be mostly found in shallow and productive transects. The second CWM-RDA axis was strongly correlated with longitude (biplot score = −0.79) and showed correlation with depth (0.50) and fishing intensity (−0.39). It confirmed a geographical gradient of fishing intensity, visible in the data (Figure 1f), which increased towards shallower waters in the North-East. The discrimination of trait responses to variables by the second axis was much lower than the one by the first axis. The second CWM-RDA axis showed a tendency to higher longevity and lower mobility towards the West as well as a tendency to more fragility, a higher position on the substratum and a larger size towards the East.

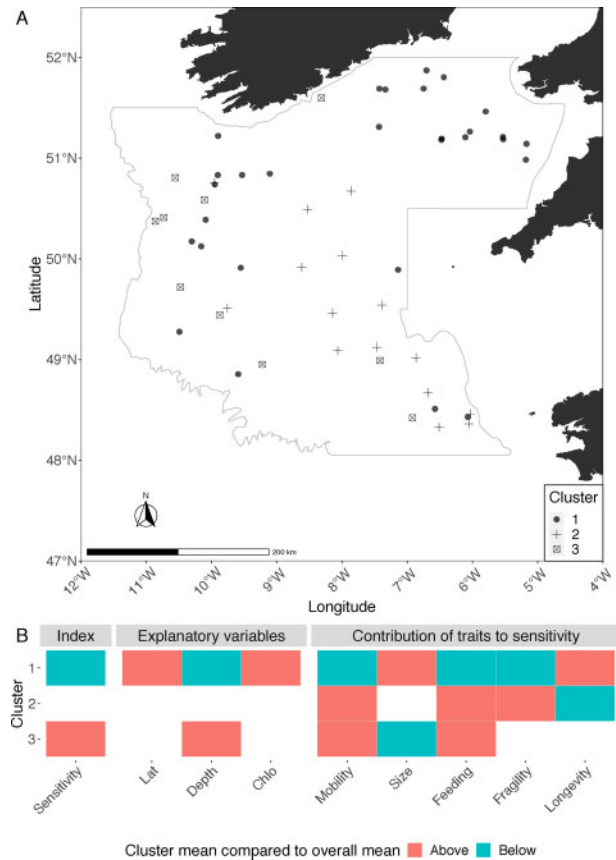


Figure 4. Characterization of the clustering performed on the RDA scores. (a) Map of the transects, point shapes represent the group in which the transect is clustered. (b) Mean values of each cluster compared to overall mean values for sensitivity scores, explanatory variables, and trait scores. Red cells represent higher mean cluster values, blue cells represent lower mean cluster values, and white cells represent no significant difference (corrected p -value of Pearson's χ^2 test >0.05). Only the variables and traits for which a Pearson's χ^2 test was significant for at least one cluster are represented.

The optimal number of clusters was 3 according to the Calinski-Harabasz criterion. The first cluster was separated from the two others on the first CWM-RDA axis, and the second axis discriminated clusters 2 and 3 (Figure 3). The first cluster gathered the highest number of transects (i.e. 29 transects) and was significantly less sensitive to trawling (score = 10.8) than the overall mean (11.7; corrected p -value of the χ^2 test: 3.58×10^{-6}) (Figure 4). It comprised all the communities from transects between Ireland and the United Kingdom, and from other transects, mainly in the North-West (Figure 4a). It was composed of communities present in shallow waters, mainly in the North of the Celtic Sea, in an area with high primary production (significantly higher chlorophyll *a* concentrations) (Figure 4b). As expected from the CWM-RDA biplot, these communities presented lower sensitivity due to their mobility characteristics, suggesting a higher proportion of swimming and crawling organisms and a lower proportion of sessile organisms. It was also characterized by a lower proportion of fragile organisms and filter feeders. However, they were also characterized by high sensitivity due to size, as well as longevity, thus suggesting a higher proportion of

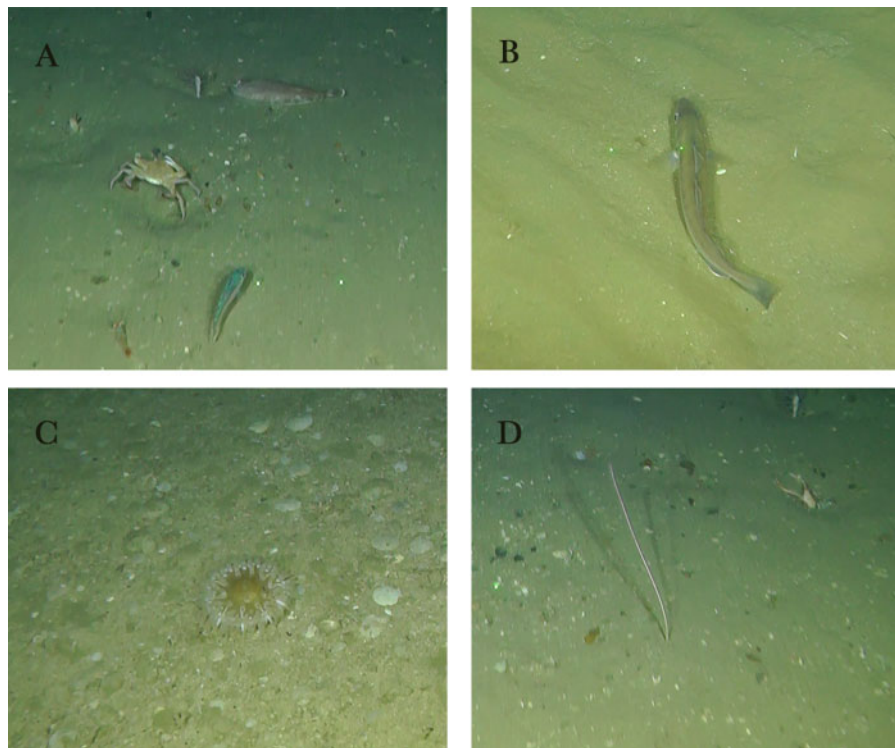


Figure 5. Images of taxa representative of the different clusters. Cluster 1 located mostly in the North-Eastern region, whose sensitivity tends to be lower than average for most traits, with a high proportion of highly mobile (a, *Scomber scombrus*, Pleuronectiforme; b, *Merlangius merlangus*) and deposit-feeding taxa (a, Brachyura). Cluster 2 whose sensitivity tends to be slightly higher than average, with a high proportion of short-lived, sessile and filter-feeding organisms (c, Actiniaria). Cluster 3, whose sensitivity is above average, with a high proportion of emergent, sessile, filter-feeding (d, *F. quadrangularis*), and small-sized taxa (d, *Munida* spp.).

long-lived taxa with a large body size (Figure 5a and b and Supplementary Figure 2).

The second cluster, composed of 15 transects, was slightly more sensitive (score = 12.3) than the overall mean (11.7), but insignificantly (corrected p -value of the χ^2 test: 0.76). It was mainly located in the South-East of the study area (Figure 4a). The communities clustered in this group presented low sensitivity in regard to longevity (more short-lived taxa), but they showed higher sensitivity due to mobility (more sessile taxa), fragility (more fragile taxa), feeding mode (more filter-feeder taxa), and position on the substratum (emergent/demersal taxa) (Figures 4b and 5c and Supplementary Figure 2).

The last cluster comprised ten transects and had the highest mean sensitivity (score = 13.0; corrected p -value of the χ^2 test: 2.23×10^{-3}). It included transects mainly located in the West of the study area, in deep waters (Figure 4). Similarly to the second cluster, it was composed of highly sensitive communities due to mobility (more sessile taxa) and feeding mode (more filter-feeder taxa) (Figures 4b and 5d). Its communities were also characterized by lower sensitivity due to size, hence a higher proportion of small organisms (Supplementary Figure 2).

Discussion

Characterizing the sensitivity of communities to trawling pressure and determining the underlying biological processes of resistance and resilience are of great interests to inform ecosystem-based management. In this study, we integrated longevity to the indicator developed by de Juan *et al.* (2009) and characterized the

sensitivity to trawling of benthic-demersal communities in the Celtic Sea. Using the CWM of this sensitivity indicator and the CWMs of each trait individually, we characterized three community archetypes. Our findings suggest two main regions in the Celtic Sea: a North-Eastern area close to the Irish Sea and an area that stretches along an arch from the Irish coast to French Brittany, closer to the continental slope. The North-Eastern region, between Ireland and the United Kingdom, is dominated by one community archetype whose sensitivity score tends to be lower than average for most traits. Its low sensitivity to trawling is explained by a high proportion of highly mobile, deposit-feeding organisms together with a low proportion of fragile organisms. The second region is more heterogeneous and encompasses the three community archetypes. The two other archetypes are only encountered in this area and both show a higher sensitivity due to a higher proportion of fixed and filter-feeding organisms than in the North-Eastern region. The most sensitive of these two archetypes is essentially located in the deepest waters and characterized by the presence of small-sized organisms. However, the second archetype is marginally more sensitive than the overall mean (but not significantly) and characterized by the presence of fragile but short-lived organisms.

Community sensitivity is mainly determined by a spatial gradient from shallow productive areas in the North-East to deep and less productive areas close to the continental slope sheltering the most sensitive communities. These findings are consistent with a study in the North Sea, where a depth-productivity gradient was an important driver of the distribution of the life-history traits

related to sensitivity of the community (Pecuchet *et al.*, 2018). Deep communities are characterized by higher proportions of fixed, filter-feeding, and small body-sized organisms. Nevertheless, across many ecosystems, deep-water fish communities generally exhibit larger body sizes than inshore communities (Mindel *et al.*, 2016; Pecuchet *et al.*, 2018). This pattern was not observed in our study probably because of the small depth range (from 71 to 216 m) and the wide range of organisms considered. Indeed, the higher abundance of small sized organisms towards the deeper area is driven small size filter feeders such as Hydrozoa and *Caryophyllia* spp. in deep transects, while shallower transects display a higher proportion of large fish species. Sensitivity scores and CWM of traits may hence be driven by dense populations of a few taxa (e.g. crinoids in the Bay of Biscay, Mérillet *et al.*, 2018b). Finally, a lower level of natural disturbance in deeper transects could also explain the presence of these more sensitive communities (Mengual *et al.*, 2016).

Sea surface productivity also influences community sensitivity to trawling: communities present in productive areas are less sensitive, and characterized by highly mobile, deposit-feeding, and long-lived organisms. However, productivity is usually linked with high proportions of filter-feeding and short-lived organisms (Pecuchet *et al.*, 2017, 2018). The patterns observed here could result from the high trawling pressure exerted over the area that hampers the settlement of filter feeding but not of deposit-feeding organisms. To our knowledge, spatio-temporal index of benthic productivity is not available in our study area. However, it is commonly accepted that surface productivity can have an indirect impact on benthic-demersal communities, especially invertebrates, through strong benthic-pelagic coupling over continental shelf. Although not significant in our study, other factors, such as BC, could also influence seabed productivity and food availability for filter-feeding species and hence influence the abundance of these species as well as community sensitivity (van Denderen *et al.*, 2015; Foveau *et al.*, 2017). Moreover, the upwelling close to the shelf break in the Celtic Sea raises nutrients up from deeper waters and could decouple surface productivity and seabed food availability (Pingree and Mardell, 1981; Joint *et al.*, 2001; Sellers *et al.*, 2020).

As expected, community sensitivity was negatively impacted by fishing intensity, although to a lesser extent than by environmental variables. Our results showed that areas subjected to high fishing pressure exhibit communities that are faintly sensitive to fishing. Indeed, the history of fishing disturbance is likely to influence abundance and species richness on a long-term basis (Sciberras *et al.*, 2018), depending on the community recovery time, which could take >20 years for some species (Hiddink *et al.*, 2017; Kaiser *et al.*, 2018). The Celtic Sea has been heavily exploited since the 1950s, with major changes occurring in the 1950s–1970s. It was then followed by a decreasing trend of fishing mortality reported since the mid-1990s, with both fishing and environment acting as the main drivers on these ecosystems from 1985 onward (Guénette and Gascuel, 2012; Mateo *et al.*, 2017; ICES, 2018b; Hervann and Gascuel, 2020). Hence, in accordance with Mérillet *et al.* (2020) and Hily *et al.* (2008), our study strongly suggests that benthic-demersal communities were already shaped by a long history of mixed fisheries. Areas of the Celtic Sea subjected to high fishing pressure since the 1950s are occupied by less sensitive communities and a lower proportion of fixed and filter-feeding organisms. Similar results were also observed in other European seas, such as the Kattegat (Pommer

et al., 2016). However, environmental and fishing variables act in synergy on community's sensitivity. Sensitive taxa could also be naturally abundant in areas where fishing intensity is lower because these areas could be too deep, or too rocky, for example. In the absence of a known reference state, we cannot assess in detail the extent to which fisheries have shaped community composition and its sensitivity. In addition, our predictor variables are averaged values in cells of size 1 km × 1 km to 8 km × 8 km depending on the variable. Hence, the value obtained for each transect might not reflect small-scale environmental conditions. Nevertheless, data at a finer scale were not available.

Most studies that assess the impact of environmental and fishing variables on community sensitivity in coastal waters, focused either on benthic communities (de Juan and Demestre, 2012; van Denderen *et al.*, 2015; Sciberras *et al.*, 2018; Jørgensen *et al.*, 2019) or on benthic and pelagic communities separately (Pecuchet *et al.*, 2018). Considering benthic-demersal communities highlighted different signals than the one observed when focusing only on benthic communities. More precisely, sediment type seems to be an important factor which influences benthic community sensitivity (Hily *et al.*, 2008; Bolam *et al.*, 2014b; Mérillet *et al.*, 2018a). However, when including fish species, less dependent on substrate, we could not find any significant influence of sediments. Assessing fish and epibenthos sensitivity separately would have allowed to focus on specific underlying mechanisms but would have diminished the global view of the ecosystem. By considering both epibenthic invertebrates and fish, our study depicts emergent and more integrated patterns.

Assessing community sensitivity as a whole is a stepping stone towards a more integrated ecosystem assessment of fishing impact. The implementation of an ecosystem approach to fisheries management relies on a more holistic understanding of fishing effects on community structure and ecosystem functioning (Garcia *et al.*, 2003). It refers to several management goals and methods (Morishita, 2008), including multi-species management and the protection of vulnerable habitats (Jennings, 2005; OSPAR Convention, 2018). Here, we implemented a multi-specific indicator, which allowed to determine the most sensitive communities and, by extension, to locate vulnerable habitats. This indicator focuses on only one aspect of vulnerability: the degree to which communities will respond to trawling pressure (i.e. sensitivity) (ICES, 2017). The second component of vulnerability, exposure (i.e. the extent and intensity of the pressure, ICES, 2017), can be assessed by calculating fishing effort, through VMS data, fishing gear characteristics and catch compositions. However, community exposure to fishing pressure was not assessed here due to the lack of spatial precision in the catch (landings and discards) data at international level and biomass estimates for non-commercial taxa. Moreover, accessibility to international fine scale VMS data and information on catch per *métier* for research purposes are still challenging, despite recent advances (Skaar *et al.*, 2011).

The integrative indicator used here enabled to highlight several areas whose sensitivity to fishing was due to different components of the ecosystem (sessile filter feeders and large fishes). As a complementary tool, future research could better characterize the spatial patterns of sensitivity to trawling by considering the different traits separately. The modification of de Juan *et al.*'s indicator could be particularly useful in spatial planning. If applied on a long-term basis, this indicator could provide valuable information on the temporal dynamics of communities' sensitivity in

response to changes in fishing intensity and to climate change. Underwater video surveys should therefore be largely deployed for better spatial and temporal coverage. Moreover, modelling the evolution of this trait-based indicator in response to a decrease in fishing intensity could allow the determination of areas where sensitivity would remain high. It would then be possible to infer where potential fishing area closure would be the most interesting place to promote, for example the conservation or the recovery of the most sensitive communities to fishing.

Supplementary data

[Supplementary material](#) is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

We thank all those who made data sampling possible during the EVHOE surveys, as well as F. Morandeau and J.-J. Rivoalen for their help in video processing.

Data availability

The data underlying this study are available in the article and the [supplementary materials](#). Raw data can be achieved upon request at the Station Ifremer de Lorient.

Author contributions

LM, DK, MM, and MR originally formulated the idea. AD and LM performed statistical analyses. DK, MM, and MR provided advice on data analysis. All authors participated in writing the manuscript.

References

- Amaroso, R. O., Pitcher, C. R., Rijnsdorp, A. D., McConnaughey, R. A., Parma, A. M., Suuronen, P., Eigaard, O. R., *et al.* 2018. Bottom trawl fishing footprints on the world's continental shelves. *Proceedings of the National Academy of Sciences of the United States of America*, 115: E10275–E10282.
- Auster, P. J., Gjerde, K., Heupel, E., Watling, L., Grehan, A., and Rogers, A. D. 2011. Definition and detection of vulnerable marine ecosystems on the high seas: problems with the “move-on” rule. *ICES Journal of Marine Science*, 68: 254–264.
- Beukhof, E., Dencker, T. S., Palomares, M. L. D., and Maureaud, A. 2019. A trait collection of marine fish species from North Atlantic and Northeast Pacific continental shelf seas. *PANGAEA*. <https://doi.org/10.1594/PANGAEA.900866>.
- Bivand, R., and Wong, D. W. S. 2018. Comparing implementations of global and local indicators of spatial association. *TEST*, 27: 716–748.
- Bolam, S. G., Eggleton, J., Garcia, C., Kenny, A., Buhl-mortensen, L., Gonzalez, G., Kooten, T., *et al.* 2014a. Biological traits as functional indicators to assess and predict (using statistical models) the status of different habitats. <https://core.ac.uk/display/33417689> (last accessed 23 March 2020).
- Bolam, S. G., Coggan, R. C., Eggleton, J., Diesing, M., and Stephens, D. 2014b. Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: a biological trait approach. *Journal of Sea Research*, 85: 162–177.
- Borcard, D., Gillet, F., and Legendre, P. 2011. *Numerical Ecology* with R. Springer, New York, NY. <http://link.springer.com/10.1007/978-1-4419-7976-6> (last accessed 31 March 2020).
- Buhl-Mortensen, L., Buhl-Mortensen, P., Dolan, M. J. F., and Gonzalez-Mirelis, G. 2015. Habitat mapping as a tool for conservation and sustainable use of marine resources: some perspectives from the MAREANO Programme, Norway. *Journal of Sea Research*, 100: 46–61.
- de Juan, S., Demestre, M., and Thrush, S. 2009. Defining ecological indicators of trawling disturbance when everywhere that can be fished is fished: a Mediterranean case study. *Marine Policy*, 33: 472–478.
- de Juan, S., and Demestre, M. 2012. A Trawl Disturbance Indicator to quantify large scale fishing impact on benthic ecosystems. *Ecological Indicators*, 18: 183–190.
- de Juan, S., Thrush, S. F., and Demestre, M. 2007. Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). *Marine Ecology Progress Series*, 334: 117–129.
- Diaz, S., Cabido, M., and Casanoves, F. 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science*, 9: 113–122.
- Díaz, S., Settele, J., Brondizio, E., Ngo, H., Guèze, M., Agard, J., Arneth, A., *et al.* 2019. IPBES (2019): Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES, Bonn, Germany. <https://uwe-repository.worktribe.com/output/1493508>.
- Foden, J., Rogers, S., and Jones, A. 2011. Human pressures on UK seabed habitats: a cumulative impact assessment. *Marine Ecology Progress Series*, 428: 33–47.
- Foveau, A., Jac, C., Llapasset, M., Guillerme, C., Desroy, N., and Vaz, S. 2020. Updated biological traits' scoring and protection status to calculate sensitivity to trawling on mega-epibenthic fauna. *SEANOE*.
- Foveau, A., Vaz, S., Desroy, N., and Kostylev, V. E. 2017. Process-driven and biological characterisation and mapping of seabed habitats sensitive to trawling. *PLoS One*, 12: e0184486.
- Fox, J., and Weisberg, S. 2019. *An R Companion to Applied Regression*. Sage, Thousand Oaks, CA. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.
- Froese, R., and Pauly, D. 2000. *FishBase 2000: Concepts, Design and Data Sources*. ICLARM; Lons Baños, Laguna, Philippines.
- García, S. M., Zerbi, A., Aliaume, C., Do Chi, T., and Lasserre, G. 2003. The ecosystem approach to fisheries. Issues, terminology, principles, institutional foundations, implementation and outlook. *FAO Fisheries Technical Paper*. FAO, Rome. 71 pp.
- Gauzère, P., Doucier, G., Devictor, V., and Kéfi, S. 2019. A framework for estimating species-specific contributions to community indicators. *Ecological Indicators*, 99: 74–82.
- González-Irusta, J. M., De la Torre, A., Punzón, A., Blanco, M., and Serrano, A. 2018. Determining and mapping species sensitivity to trawling impacts: the Benthos Sensitivity Index to Trawling Operations (BESITO). *ICES Journal of Marine Science*, 75: 1710–1721.
- Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, 86: 902–910.
- Guénette, S., and Gascuel, D. 2012. Shifting baselines in European fisheries: the case of the Celtic Sea and Bay of Biscay. *Ocean & Coastal Management*, 70: 10–21.
- Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., *et al.* 2008. A global map of human impact on marine ecosystems. *Science*, 319: 948–952.
- Harrison, S., and Cornell, H. 2008. Toward a better understanding of the regional causes of local community richness. *Ecology Letters*, 11: 969–979.
- Hernvann, P.-Y., and Gascuel, D. 2020. Exploring the impacts of fishing and environment on the Celtic Sea ecosystem since 1950. *Fisheries Research*, 225: 105472.
- Hewitt, J. E., Julian, K. A., and Bone, E. 2011. Chatham-Challenger Ocean Survey 20/20 Post-Voyage Analyses: Objective 10, Biotic Habitats and Their Sensitivity to Physical Disturbance. Ministry of Fisheries.
- Hiddink, J. G., Jennings, S., Sciberras, M., Bolam, S. G., Cambiè, G., McConnaughey, R. A., Mazon, T., *et al.* 2019. Assessing bottom

- trawling impacts based on the longevity of benthic invertebrates. *Journal of Applied Ecology*, 56: 1075–1084.
- Hiddink, J. G., Jennings, S., Sciberras, M., Szostek, C. L., Hughes, K. M., Ellis, N., Rijnsdorp, A. D., *et al.* 2017. Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proceedings of the National Academy of Sciences of the United States of America*, 114: 8301–8306.
- Hily, C., Le Loc'h, F., Grall, J., and Glémarec, M. 2008. Soft bottom macrobenthic communities of North Biscay revisited: long-term evolution under fisheries-climate forcing. *Estuarine, Coastal and Shelf Science*, 78: 413–425.
- ICES. 2017. Report of the ICES/PICES Workshop on Regional Climate Change Vulnerability Assessment for the Large Marine Ecosystems of the Northern Hemisphere (WKSICCME-CVA): 69.
- ICES. 2018a. Spatial Data Layers of Fishing Intensity/Pressure per Gear Type for Surface and Subsurface Abrasion, for the Years 2009 to 2017 in the OSPAR Regions II and III (ver. 2, 22 January 2019). ICES data product release.
- ICES. 2018b. Celtic Seas Ecoregion? Fisheries Overview, Including Mixed-Fisheries Considerations. ICES. [http://www.ices.dk/sites/pub/Publication Reports/Forms/DispForm.aspx?ID=35064](http://www.ices.dk/sites/pub/Publication%20Reports/Forms/DispForm.aspx?ID=35064) (last accessed 10 June 2020).
- Jennings, S. 2005. Indicators to support an ecosystem approach to fisheries. *Fish and Fisheries*, 6: 212–232.
- Joint, I., Wollast, R., Chou, L., Batten, S., Elskens, M., Edwards, E., Hirst, A., *et al.* 2001. Pelagic production at the Celtic Sea shelf break. *Deep Sea Research Part II: Topical Studies in Oceanography*, 48: 3049–3081.
- Jørgensen, L., Primicerio, R., Ingvaldsen, R., Fossheim, M., Strelkova, N., Thangstad, T., Manushin, I., *et al.* 2019. Impact of multiple stressors on sea bed fauna in a warming Arctic. *Marine Ecology Progress Series*, 608: 1–12.
- Kaiser, M. J., Hormbrey, S., Booth, J. R., Hinz, H., and Hiddink, J. G. 2018. Recovery linked to life history of sessile epifauna following exclusion of towed mobile fishing gear. *Journal of Applied Ecology*, 55: 1060–1070.
- Kleyer, M., Dray, S., Bello, F., Lepš, J., Pakeman, R. J., Strauss, B., Thuiller, W., *et al.* 2012. Assessing species and community functional responses to environmental gradients: which multivariate methods? *Journal of Vegetation Science*, 23: 805–821.
- Laliberté, E., Legendre, P., and Shipley, B. 2014. FD: Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology.
- Lê, S., Josse, J., and Husson, F. 2008. FactoMineR: a package for multivariate analysis. *Journal of Statistical Software*, 25: 1–18.
- Legendre, P., and Legendre, L. 1998. *Numerical Ecology*. Elsevier Science BV, Amsterdam. 852 pp.
- Madec, G. and the NEMO team 2016. NEMO ocean engine. Note du Pôle de Modélisation, Institut Pierre-Simon Laplace (IPSL), France, No 27. ISSN: 1288–1619.
- Mallet, D., and Pelletier, D. 2014. Underwater video techniques for observing coastal marine biodiversity: a review of sixty years of publications (1952–2012). *Fisheries Research*, 154: 44–62.
- MarLIN. 2016. Marine Life Information Network. Marine Biological Association of the United Kingdom, Plymouth. www.marlin.ac.uk
- Mateo, M., Pawlowski, L., and Robert, M. 2017. Highly mixed fisheries: fine-scale spatial patterns in retained catches of French fisheries in the Celtic Sea. *ICES Journal of Marine Science*, 74: 91–101.
- McGill, B., Enquist, B., Weiher, E., and Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21: 178–185.
- Mengual, B., Cayocca, F., Le Hir, P., Draye, R., Laffargue, P., Vincent, B., and Garlan, T. 2016. Influence of bottom trawling on sediment resuspension in the ‘Grande-Vasière’ area (Bay of Biscay, France). *Ocean Dynamics*, 66: 1181–1207.
- Mérlillet, L., Kopp, D., Robert, M., Mouchet, M., and Pavoine, S. 2020. Environment outweighs the effects of fishing in regulating demersal community structure in an exploited marine ecosystem. *Global Change Biology*, 26: 2106–2119.
- Mérlillet, L., Mouchet, M., Robert, M., Salaün, M., Schuck, L., Vaz, S., and Kopp, D. 2018a. Using underwater video to assess megabenthic community vulnerability to trawling in the Grande Vasière (Bay of Biscay). *Environmental Conservation*, 45: 163–172.
- Mérlillet, L., Robert, M., Salaün, M., Schuck, L., Mouchet, M., and Kopp, D. 2018b. Underwater video offers new insights into community structure in the Grande Vasière (Bay of Biscay). *Journal of Sea Research*, 139: 1–9.
- Mindel, B. L., Webb, T. J., Neat, F. C., and Blanchard, J. L. 2016. A trait-based metric sheds new light on the nature of the body size-depth relationship in the deep sea. *Journal of Animal Ecology*, 85: 427–436.
- Morishita, J. 2008. What is the ecosystem approach for fisheries management? *Marine Policy*, 32: 19–26.
- Ninio, R., Delean, S., Osborne, K., and Sweatman, H. 2003. Estimating cover of benthic organisms from underwater video images: variability associated with multiple observers. *Marine Ecology Progress Series*, 265: 107–116.
- OSPAR Convention. 2018. Work Priorities for OSPAR Secretariat 2018–2020. 1. https://www.ospar.org/site/assets/files/1202/ospar_secretariat_priorities_2018-2020.pdf (last accessed 1 February 2021).
- Palomares, M. L. D., and Pauly, D. 2019. SeaLifeBase. World Wide Web Electronic Publication. <https://sealifebase.se/search.php> (last accessed 1 February 2021).
- Pecuchet, L., Lindegren, M., Hidalgo, M., Delgado, M., Esteban, A., Fock, H. O., Gil de Sola, L., *et al.* 2017. From traits to life-history strategies: deconstructing fish community composition across European seas. *Global Ecology and Biogeography*, 26: 812–822.
- Pecuchet, L., Reygondeau, G., Cheung, W. W. L., Licandro, P., van Denderen, P. D., Payne, M. R., and Lindegren, M. 2018. Spatial distribution of life-history traits and their response to environmental gradients across multiple marine taxa. *Ecosphere*, 9: e02460.
- Pingree, R. D., and Mardell, G. T. 1981. Slope turbulence, internal waves and phytoplankton growth at the Celtic Sea shelf-break. *Philosophical Transactions of the Royal Society of London. Series A, Mathematical and Physical Sciences*, 302: 663–682.
- Pommer, C., Olesen, M., and Hansen, J. 2016. Impact and distribution of bottom trawl fishing on mud-bottom communities in the Kattegat. *Marine Ecology Progress Series*, 548: 47–60.
- R Core Team. 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rijnsdorp, A. D., Bolam, S. G., Garcia, C., Hiddink, J. G., Hintzen, N. T., van Denderen, P. D., and van Kooten, T. 2018. Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. *Ecological Applications*, 28: 1302–1312.
- Sciberras, M., Hiddink, J. G., Jennings, S., Szostek, C. L., Hughes, K. M., Kneafsey, B., Clarke, L. J., *et al.* 2018. Response of benthic fauna to experimental bottom fishing: a global meta-analysis. *Fish and Fisheries*, 19: 698–715.
- Sellers, A. J., Leung, B., and Torchin, M. E. 2020. Global meta-analysis of how marine upwelling affects herbivory. *Global Ecology and Biogeography*, 29: 370–383.
- Skaar, K. L., Jørgensen, T., Ulvestad, B. K. H., and Engås, A. 2011. Accuracy of VMS data from Norwegian demersal stern trawlers for estimating trawled areas in the Barents Sea. *ICES Journal of Marine Science*, 68: 1615–1620.

- Tillin, H., Hiddink, J., Jennings, S., and Kaiser, M. 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Marine Ecology Progress Series*, 318: 31–45.
- van Denderen, P., Bolam, S. G., Hiddink, J., Jennings, S., Kenny, A., Rijnsdorp, A., and van Kooten, T. 2015. Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. *Marine Ecology Progress Series*, 541: 31–43.
- Vandewalle, M., de Bello, F., Berg, M. P., Bolger, T., Dolédec, S., Dubs, F., Feld, C. K., *et al.* 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and Conservation*, 19: 2921–2947.
- Venables, W. N., and Ripley, B. D. 2002. *Modern Applied Statistics with S*. Springer, New York. <http://www.stats.ox.ac.uk/pub/MASS4> (last accessed 1 February 2021).
- Watling, L. 2005. The global destruction of bottom habitats by mobile fishing gear. *In* *Marine Conservation Biology: The Science of Maintaining the Sea's Biodiversity*, pp. 198–210. Ed. by M. E. Soule, A. E. A. Norse and L. B. Crowder. Island Press, Washington, DC.
- Wiedmann, M. A., Primicerio, R., Dolgov, A., Ottesen, C. A. M., and Aschan, M. 2014. Life history variation in Barents Sea fish: implications for sensitivity to fishing in a changing environment. *Ecology and Evolution*, 4: 3596–3611.

Handling editor: Silvana Birchenough