Biomass of slow life history species increases as local bottom trawl effort decreases in the Celtic sea

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To cite this version:

Laurène Mérillet, Sandrine Pavoine, Dorothée Kopp, Marianne Robert, Maud Mouchet. Biomass of slow life history species increases as local bottom trawl effort decreases in the Celtic sea. Journal of Environmental Management, 2021, 290, pp.112634. 10.1016/j.jenvman.2021.112634 . hal-03212489

Abstract

Due to its selective removal, fishing pressure has long influenced the dynamics of species based on their life history traits. Sensitivity to fishing increases along a “fast-to-slow” gradient of life history strategies, and the “slow” species (large, long-lived, late-maturing, giving birth to few large offspring) require the most time to recover from fishing. In the North East Atlantic, after having reached extreme levels, fishing pressure has decreased since the 1980’s due to management measures such as total allowable catch (TAC) or area closure. An effect on the distribution of species as well as a potential recovery could be expected. However, temporal patterns of life history strategies are rarely linked to management measures. In addition, a larger emphasis is often put on exploited or emblematic sensitive species but rarely on assembly processes at the ecosystem scale (both commercial and non-commercial species). Based on a 17-year time series of 101 taxa (fishes, elasmobranchs, bivalves, cephalopods and crustaceans), we observed a negative relationship between the biomass of taxa sensitive to fishing and bottom trawling pressure, as well as an increase in their total biomass in the Celtic Sea. Over the whole area, stochasticity appeared as the dominant assembly process. Deterministic assembly processes were at play in the centre of the area where significant overdispersion (caused by the presence of both slow and fast taxa) were observed. The absence of sensitive taxa from the rest of the Celtic Sea appeared to be caused mainly by an historical effect of environmental filtering when fishing was high. At the local scale, we related the decrease in fishing pressure to the increase in biomass of five of the most sensitive taxa. This local decrease in fishing pressure, resulting from the implementation of an area closure, highlights the positive effect of such management measures in less than two decades.

Keywords

Community weighted mean; Assembly processes; Biological traits; Elasmobranchs; Area closure

1. Introduction

Marine ecosystems experience multiple pressures, the most severe of which include climate change and fishing (Halpern et al., 2015). Climate change already affects the structure, functioning and adaptive capacity of ecosystems by modifying pH, temperature, oxygen concentration and food availability (Henson et al., 2017), which notably results in displacement of species toward higher latitudes and deeper waters (Cheung et al., 2013; Jorda et al., 2020). Its effects occur along with those of fishing (Rogers et al., 2019), which has caused a decrease in biomass and even local extinctions of species worldwide (Worm et al., 2006). It is widely acknowledged that a population’s ability to recover from disturbance depends on its demographic dynamics, which are related to life history strategies (Le Quesne and Jennings, 2012; Wiedmann et al., 2014).

Historically, life history strategies were characterised by their position along the continuum of r strategies (energy allocated to producing many offspring) vs. K strategies (energy allocated to producing a few extremely fit offspring) (Pianka, 1970). More recently, life history strategies of fish were described as a triangle: (i) an opportunistic strategy for small, short-lived and rapidly maturing fish; (ii) a periodic strategy for large, long-lived and highly fecund fish and (iii) an equilibrium strategy for intermediate-sized fish that produce a few large offspring for which they provide parental care (Pecuchet et al., 2018; Winemiller and Rose, 1992). These life history strategies can be summarised along a fast-slow continuum (Beukhof et al., 2019b; Juan-Jorda et al., 2013; Promislow and Harvey, 1990; Rochet et al., 2000) that balances percentage of mortality and optimal size. Large and long-lived species that mature late and give birth to large offspring lie at the “slow” end of the continuum (Wiedmann et al., 2014). These species escape predation and have low natural mortality rate, while the fast end is characterised by the opposite properties. Species with a slow life history strategy are thus particularly sensitive to additional mortality, such as that caused by anthropogenic pressures (e.g. fishing) (Brown et al., 2004; Juan-Jorda et al., 2015; Kozlowski, 2006; Promislow and Harvey, 1990). Understanding the spatio-temporal distribution of these slow life history species is thus particularly useful for ecosystem management (Le Quesne and Jennings, 2012).

Identifying and explaining how species are distributed has long been a core challenge in ecology. Evolutionary history, environmental variables and species interactions drive the spatio-temporal distribution of species (Mouchet et al., 2013; Webb et al., 2002). However, the distribution of the taxa could also arise from random processes and the question of the relative importance of deterministic *versus* stochastic assembly rules remains central (Vellend et al., 2014). Three major non-exclusive assembly rules explain biodiversity patterns (Kraft et al., 2007): stochasticity (Hubbell, 2001) and deterministic processes, namely environmental filtering (Keddy, 1992; Zobel, 1997) and competitive exclusion (Hardin, 1960). Environmental filtering implies strong abiotic control, which results in the survival of species that have a narrow range of traits that enable them to endure environmental pressures. The principle of competitive exclusion assumes that species can coexist if they have different niche-related biological traits (Hardin, 1960). Thus, traits of species in an assemblage may be similar if they are selected via environmental filtering or different if they are selected via competitive exclusion. A careful interpretation is essential and should be based on the biological understanding of the processes at play. Indeed, competition (and more generally biotic interactions) can lead to the same patterns as those driven by environmental filtering (Cadotte and Tucker, 2017; Kraft et al., 2015) and community patterns result in both processes interacting dynamically (Callaway et al., 2002; Kraft et al., 2015). Conversely to these two deterministic assembly rules, neutral theory hypothesises that species coexist regardless of their biological traits due to individual demographic stochastic events of dispersal, birth and death (Hubbell, 2001; Vellend et al., 2014). The relative dominance of stochastic and deterministic processes can be disentangled notably by the comparison of the observed pattern with a null model (Vellend et al., 2014). The prevalence of one assembly rule over the others could depends on the scale considered. At the local scale, stochastic, biotic and abiotic parameters can act on species simultaneously, and determining their relative importance remains challenging (Mouillot et al., 2007). At larger scale, environmental filtering was considered as having a larger effect than the other processes (Freschet et al., 2011).

Assembly processes in exploited marine ecosystems have attracted attention only recently (Dencker et al., 2017; Ford and Roberts, 2020; Pecuchet et al., 2016), as studies have historically focussed on freshwater and estuarine communities (Mouillot et al., 2007; Peres-Neto, 2004; Schmera et al., 2013). Nevertheless the understanding of the processes responsible for the structuration of exploited marine communities can provide valuable inputs for their sustainable management (Dencker et al., 2017). The North East Atlantic fishing grounds have shown signs of over-exploitation since the 1970s (Gascuel et al., 2016), which caused species distribution to be driven by fishing in addition to environmental and habitat characteristics, such as temperature, depth and sediment (Foveau et al., 2017). We hypothesise that gradual enforcement of European Union (EU) fishing policies over the past 40 years that has decreased fishing pressure in the North East Atlantic (Fernandes and Cook, 2013) may have helped the biomass of species with slow life history strategies to increase, reducing the strength of the environmental filter imposed by fishing on taxa. However, temporal patterns of life history strategies of commercial and non-commercial taxa are rarely studied as a function of environmental or anthropogenic variables, and should be taken into account in management measures more frequently (Fromentin and Fonteneau, 2001; Matson and Gertseva, 2020).

The Celtic Sea has been extensively fished for decades with a peak of the number of species significantly exploited in the 1990’s (Gascuel et al., 2016; Guénette and Gascuel, 2012). Fishing thus likely imposed a major filtering on the distribution of the taxa. Fishing mortality has then decreased at the ecosystem scale since 2010 (Moullec et al., 2017) with the implementation of more restrictive TAC and the creation of a closure area in the North of the Celtic Sea (ICES, 2007). Environmental variables in the Celtic Sea were relatively stable over the recent period (2000-2016). Since a clear impact of climate change, such as an increase in bottom temperature, is not visible yet (Mérillet et al., 2020), the decrease in fishing effort most likely had the largest influence on the recent distribution of life history strategies in the Celtic Sea. Based on a 17-year time series, we explore the influence of fishing on the spatio-temporal distribution of life history strategies in the bentho-demersal community by considering 101 commercial and non-commercial taxa. We assessed (i) which assembly processes and (ii) which environmental and anthropogenic variables drive the spatio-temporal distribution of sensitivity to fishing.

Finally, (iii) we focussed on the trend of the biomass of sensitive taxa and bottom trawl fishing at the local scale.

2. Material and methods

2.1. Taxa biomass and life history traits

For the 2000-2016 period, data on species biomass were extracted from the EVHOE (*Evaluation des ressources Halieutiques de l'Ouest de l'Europe*) surveys, an International Bottom Trawl Survey (ICES, 2015) performed every November in the Celtic Sea. These surveys provide reliable and consistent data for evaluating the impact of fishing as they are independent from fishing effort and follow the same standardised protocol each year. EVHOE surveys use a 36/47 GOV (*Grande Ouverture Verticale*) net fitted with a 20 mm cod end mesh, with a horizontal opening of ca. 20 m and a vertical opening of 4 m. Sampling hauls are performed at 4 knots for 30 min and follow a random stratified design based on sediment-depth strata within a bank of possible hauls. They are not at the same location from one year to another, but due to random sampling a same haul can be visited several times across the time series. From 2000-2016, the surveys performed 53-84 valid hauls per year, for a total of 1175 hauls. Due to variations in the accuracy of species identification, some species were grouped into higher taxonomic levels (hereafter, ‘taxon’; genus, for species of *Alloteuthis*, *Argentina*, *Arnoglossus*, *Gaidrosparus*, *Loligo*, *Munida*, *Mustelus*, *Octopus*, *Pomatoschistus* and *Sepiola*; family, for Ammodytidae and Gobiidae). To identify temporal changes in taxa biomass, only those taxa that occurred at more than 5% of the sampling sites in at least one EVHOE depth strata over the time series were kept for analysis and considered correctly sampled. This process identified a total of 101 taxa from six classes

(Actinopterygii, Bivalvia, Cephalopoda, Elasmobranchii, Holocephali and Malacostraca). Biomass was standardised by the area sampled during each haul and then log-transformed to reduce variability. Sampling sites were located at depths of 57-340 m (Fig. 1), mainly on sand, mud, mixed sediments, coarse sediments and boulders (Fig S1).

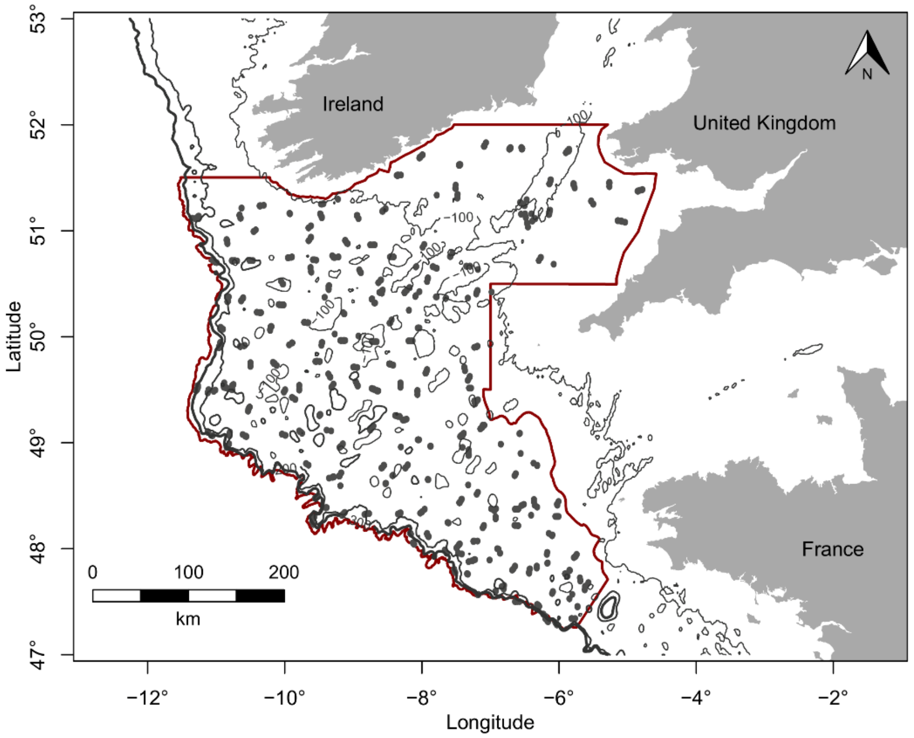

Figure 1. Map of sampling sites (grey dots) in the study area in the Celtic Sea. The red line delineates the limits of the study area, as defined in the EVHOE surveys.

We selected the following biological traits for their known response to fishing pressure: maximum length, longevity, age at maturity, offspring size, reproductive guild and fecundity (Barlow, 1981; Brown et al., 2004; Jennings and Kaiser, 1998; Jeschke and Kokko, 2009; Le Quesne and Jennings, 2012; Pecuchet et al., 2016; Shephard et al., 2012; Tillin et al., 2006; Tyler-Walters et al., 2009; Wiedmann et al.,

2014) (Table 1). Values of these traits were extracted from the literature and the PANGAEA data library (Beukhof et al., 2019a) (see Table S1 for more details).

Table 1: Life history traits used and their relevance, when used all together, to characterise life history strategy and sensitivity to fishing.

Traits	**Description**	**Relevance**
Maximum length	in cm	Relates to many characteristics of an organism (Brown et al., 2004). Fishing is known to have led to the decrease in abundance of large body size taxa (Shephard et al., 2012)
Longevity	in year (maximum reported age)	Fishing is known to have led to the decrease in abundance of long-lived taxa (Shephard et al., 2012; Tillin et al., 2006)
Offspring size	in mm; Diameter of the released eggs, length of the egg case or length of the young for the bearer taxa	Informs on the parental investment and the energy needed for the production of one offspring (Winkler and Wallin, 1987). Perturbations, and thus fishing, select for taxa with small offspring (Jeschke and Kokko, 2009; Wiedmann et al., 2014). Linked to the resilience of the taxa after fishing event.
Age at maturity	in year	Informs on generation time (Pecuchet et al., 2016; Tillin et al., 2006). Fishing favors early maturing taxa (Claireaux et al., 2018; Shephard et al., 2012). Linked to the resilience of the taxa after fishing event.
Reproductive guild	Bearer - giving birth to a free living progeny. Guarder - eggs protected (carried under the abdomen for crustaceans) or guarded. Non guarder - pelagic eggs.	Informs on the parental investment and the energy needed for the production of one offspring (Barlow, 1981; Tillin et al., 2006). Linked to the resilience of the taxa after fishing event.
Fecundity	Segment of offspring number per female 1-1000: low 1000-100,000: medium 100,000-1,000,000: high >1,000,000: very high	Capacity of the population to recover; productivity of the taxa (Pecuchet et al., 2016). Fishing depleted low fecundity taxa (Shephard et al., 2012). Linked to the resilience of the taxa after fishing event.

We used Hill-Smith analysis (Hill and Smith, 1976), which is a principal component analysis that considers both quantitative and qualitative variables, to assess the sensitivity of each taxon based on the six life history traits selected. The first axis of the Hill-Smith analysis explained the most variability in the distribution of life history traits across taxa. It was used as a sensitivity score (the more positive the score, the more sensitive the taxa are) and also reflects the life history strategy of the taxon.

2.2. Community assembly processes

To identify community assembly processes related to life history traits over the 2000-2016 period, we calculated the community-weighted variance (CWV) according to Gaüzère et al., (2019) for the sensitivity score (and each of the six life history traits, see Fig. S2). Assembly rules were assessed using a standard effect size (SES) by comparing the CWV to a null model based on random community assembly (i.e. 1000 random permutations of trait values among taxa) (Gotelli and McCabe, 2002). The null model consists in shuffling the traits of occurring taxa at each site so that taxa richness remains constant at each site. If the observed CWV was not significantly different from the random CWV, stochasticity was at play. Significant deviation of the CWV from the random mean CWV and negative SES values indicated underdispersion, meaning that the observed trait variability was lower than expected by chance. Conversely, significant deviation and positive SES values indicated overdispersion and an observed trait variability higher than expected by chance.

The SES was calculated for each sampling site over the 2000-2016 period as (1).

$$SES_i = \frac{x_{obs,i} - x_{th,i}}{SD_{th,i}} \qquad (1)$$

with $x_{obs,i}$ the observed CWV at site i, $x_{th,i}$the mean of the theoretical values simulated by the null models at site *i* (hereafter referred as “mean random CWV”) and

$SD_{th,i}$ the standard deviation of these theoretical values simulated by the null models at site *i*.

The significance of the deviation of the observed CWV from the random mean CWV was calculated with a permutation test, performed with the *krandtest* function of the “ade4” R package (Thioulouse et al., 2018). P-values of these tests were adjusted for multiple testing (Benjamini and Yekutieli, 2001). Inverse-distance-weighting interpolation was used only for graphical representation.

2.3. Life history trait distribution as a function of environmental and fishing variables

To relate the spatio-temporal distribution of the sensitivity score and the life history traits to environmental and fishing variables over 2000-2016 at the scale of the Celtic Sea, community-weighted means (CWM) were calculated using the “FD” package (Laliberté et al., 2014) for a community of R taxa as followed.

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

with p_i the log(x+1) transformed biomass of taxon *i*, and t_i the value of the sensitivity score of taxon *i* (or each life history trait, see Fig. S3). The CWM of the sensitivity score was modelled with a Gaussian distribution, so it was first transformed to make it positive before applying the log function, ie the CWM of the sensitivity score was log(x+c+1)-transformed, with c=-min(x) to get a positive or null variable. Like for CWV, inverse-distance-weighting interpolation was used only for graphical representation.

We selected environmental and fishing variables known to influence Celtic Sea ecosystems, and more generally North Atlantic shelf ecosystems (Foveau et al., 2017; Mérillet et al., 2020). Depth was recorded at each sampling site. Sediment data according to Folk’s 5-level classification system came from the EMODnet Geology Portal (https://www.emodnet-geology.eu). Data for the few (95) sampling sites that were not included in the EMODnet dataset were extrapolated from the SHOM database (https://diffusion.shom.fr/loisirs/sedim-mondiale.html). As our community data were based on annual sampling, and the 101 taxa studied display a wide variety of life cycles, we assumed that annual means would be the most relevant values for the covariables. Bottom temperature data were downloaded from Copernicus (http://marine.copernicus.eu), from the Atlantic-Iberian Biscay Irish-Ocean Physics Reanalysis data product at 8 km × 8 km resolution, while chlorophyll a data were extracted from satellite observations at 1 km × 1 km resolution. Fishing effort data were derived from the New Fisheries Dependent Information from the EU's Scientific, Technical and Economic Committee for Fisheries (https://stecf.jrc.ec.europa.eu), which provided data on fishing effort for all EU countries in hours fished per statistical rectangle (111.12 km × 55.56 km). Bottom and pelagic trawl were the two dominant *métiers* over the Celtic Sea (Mérillet et al., 2020).

We studied the distribution of sensitivity score CWM as a function of environmental variables (depth, sediment, chlorophyll a and temperature), fishing variables (bottom trawl, pelagic trawl) and time (year). In a preliminary step, a permutation test for Moran’s I statistic (Moran, 1950) indicated that spatial autocorrelation was significant for sensitivity score (Moran’I= 0.29; p-value = 0.001). Collinearity between variables was assessed with a variance inflation factor (VIF) and a threshold of five.

The log(x+c+1)-transformed CWM of the sensitivity score followed a Gaussian distribution and were modelled using simultaneous autoregressive (SAR) models (after testing their advantage compared to GLM models with spatial terms, table S2, and looking at their relationship with environmental variables Fig. S5). This family of models assumes that the response at each location is a function of the explanatory variables but also of neighbouring locations (Kissling and Carl, 2008). The spatial-error model, which is the most reliable SAR model, captures spatial autocorrelation that is not completely explained by the explanatory variables or that is an inherent property of the response variable. To implement this model, we used the *errorsarlm* function in the “SpatialReg” package (Bivand and Piras, 2015). A full model was built with all the environmental, fishing and time variables, as well as spatial variables (latitude, longitude, latitude^2, longitude^2 and latitude x longitude). The model with the lowest AIC was selected using the *dredge* function (“MuMIn” R package). Temporal autocorrelation in the residuals of the model was tested with a Durbin-Watson test (Durbin and Watson, 1971).

2.4. Local temporal trends in the biomass of the taxa most sensitive to fishing

Based on a histogram, the sensitivity score distribution was examined. To inform a global trend over the Celtic Sea between sensitivity and dynamics of the biomass, temporal trends of the *log(x+1)*-transformed biomass of each taxa in the whole Celtic Sea was modelled (biomasses were elevated to the whole Celtic Sea following (Mahe and Poulard, 2005)), as a function of the year with a linear model using a Gaussian distribution (Fig 4, Fig. S4, Table S4). Then a Spearman correlation was computed between the significant slopes of the regressions of the biomass over the time and the sensitivity scores (Fig. 4). Based on a histogram of the sensitivity scores (Fig 4), the most sensitive taxa, which clustered apart from the other taxa (i.e. before the stall in sensitivity score) were examined at a local scale to investigate more precisely the link between temporal evolution of the biomass and fishing effort. In that purpose, the temporal trend over 2000-2016 of the biomass of the most sensitive taxa was investigated in each International Council for the Exploration of the Seas (ICES) statistical rectangle.

Since the number of sampling sites is not homogeneously distributed across rectangles, Y_i the elevated biomass of a taxa *i* was calculated in each rectangle r with the following formula (Mahe and Poulard, 2005):

$$Y_i = \frac{1}{A} * \sum_r A_r * Y_{ri}$$

With Y_r the mean biomass per haul in a rectangle r, for taxa *i*, A_r the area of a given statistical rectangle (all similar in the Celtic Sea), A the sum of the areas of all the rectangles that are included or partially included within the limits of the Celtic Sea considered here. The *log(x+1)*-transformed elevated biomass of each taxa was modelled, in each statistical rectangle, as a function of the year with a linear model using a Gaussian distribution. P-values associated with the coefficient of the year variable were adjusted for multiple tests (Benjamini and Yekutieli, 2001). For each taxon, the coefficient of the year variable was extracted when significant ($p<0.05$). We graphically examined the spatial covariation of biomass and trends in fishing effort over 2000-2016 to assess whether the sampling sites that had an increased biomass of the most sensitive taxa also showed a decrease in bottom trawl effort.

All analysis were conducted R 4.2.1 software (R Core Team, 2020).

3. Results

3.1. Assembly rules based on sensitivity score

Hill-Smith analysis of the selected life history traits enabled us to characterise the extent to which each taxon’s combination of life history traits made it sensitive to fishing. The first axis (used as the sensitivity score) explained 34.3% of the total variability, while the second axis explained 15.2%. The most sensitive taxa (i.e. large, long-lived taxa that mature late, bear their offspring and have low fecundity) had the highest sensitivity scores.

To distinguish the dominant assembly process between environmental filtering, competition and stochasticity at each site, the CWV of the sensitivity score was compared to a random CWV over the 2000-2016 period. At the majority of the sampling sites (1142 over the 1175 sampling sites), the difference between the observed CWV and the mean random CWV of the sensitivity score was not significant, meaning that stochasticity was the dominant assembly process at these sites. No sampling sites had significant negative SES values, indicating that variability in sensitivity score was not significantly lower than that expected by chance (i.e. underdispersed traits). Few significant positive SES values (i.e. wider range of traits values than that expected by chance), i.e. 33 out of 1175, were visible at sampling sites in the centre of the Celtic Sea and indicated overdispersion (Fig. 2).

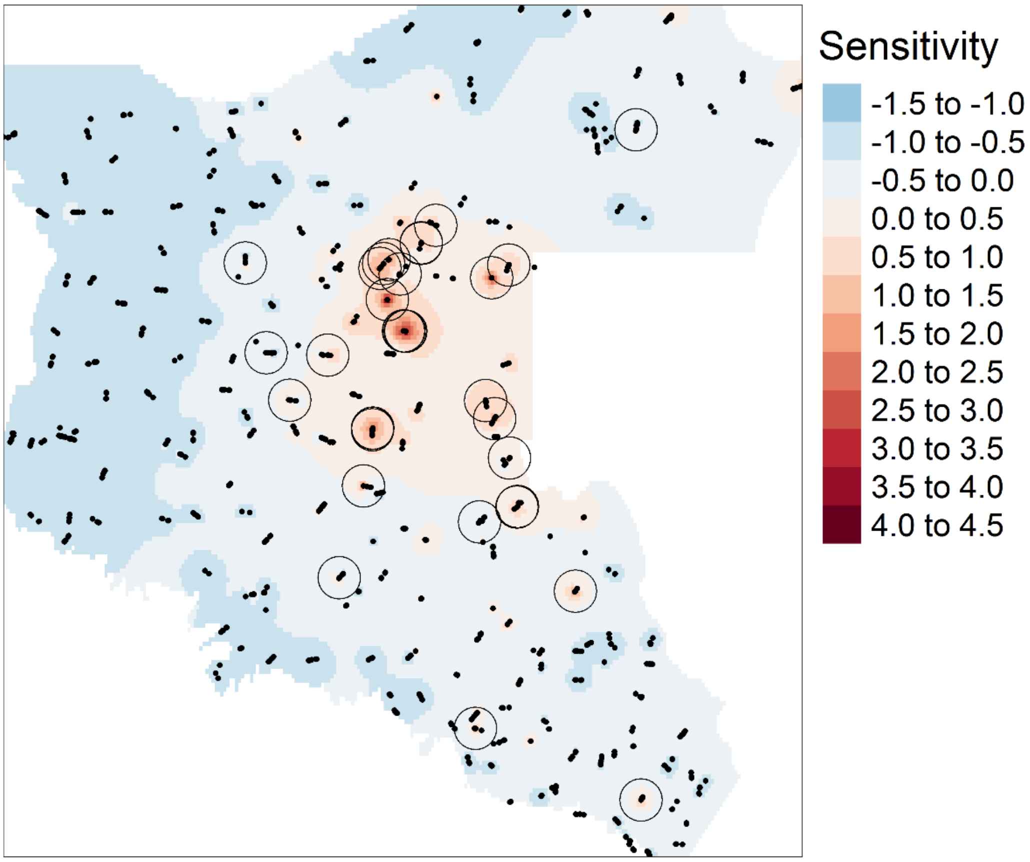

Figure 2. Maps of standard effect size of the community-weighted variance (CWV) of the sensitivity to fishing computed from six life history traits of 101 taxa in the Celtic Sea. Sampling sites surrounded by circles show significant departure from the stochastic assembly process. Positive values (in red) indicate overdispersion in the traits and negative values (in blue) indicate underdispersion.

3.2. Environmental drivers of the distribution of sensitivity score and traits

Overall, most of the Celtic Sea showed low values of sensitivity to fishing, which was indicated by the negative values of CWM of the sensitivity score (Fig. 3). The biomass of sensitive taxa to fishing was highest in the centre-east of the Celtic Sea (Fig. 3). This area also had the widest range of trait values expressed (i.e. overdispersion), indicated by the significant positive SES values of sensitivity score (Fig. 2), and the significant positive SES values associated with maximum length, age at maturity and offspring size (Fig. S2). Thus, sensitive taxa, with large maximum length, age at maturity and offspring size were also present in the centre-east in addition of the low sensitivity taxa present in all the Celtic Sea. Having a closer look at each trait separately, we showed that only longevity showed a slightly different pattern, with the narrowest range of trait values in the north and the widest in the south (Fig. S2). For reproductive guild, two of the three levels (i.e. bearer and guarder) had their highest proportions of biomass in the centre and extreme north-east of the Celtic Sea and were nearly absent elsewhere. Thus, all three reproductive guilds occurred in these two areas (Fig. S2), which agreed with the overdispersion observed there (Fig. S2). Similarly, three levels of the four fecundity levels (i.e. low, medium and very high) had some of their highest proportions of biomass in the centre and were nearly absent elsewhere, which led to overdispersion of the fecundity trait in the centre (Fig. S2).

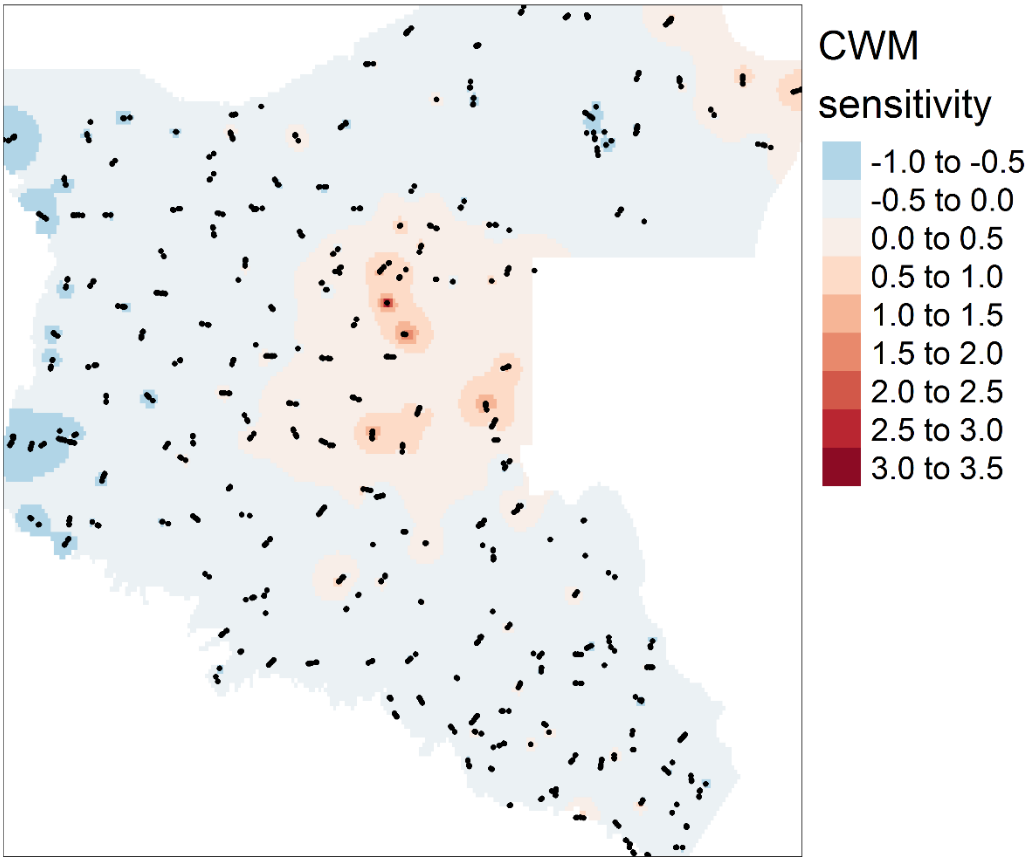

Figure 3. Maps of community-weighted means (CWMs) of the sensitivity to fishing computed from six life history traits of 101 taxa in the Celtic Sea.

The VIF of the model with environmental, fishing and time variable was below 5, so all variables were kept for the full model. Spatial variables were also kept to account for spatial autocorrelation. Moreover, Moran's I indicated no residual autocorrelation (p >0.05) in the selected SAR model of the CWM of the sensitivity score, which was not the case for the GLM (Table S2). In addition, no temporal autocorrelation could be found in the residuals of the selected SAR model for sensitivity score (Durbin-Watson statistic = 1.40, p-value= $1.96.10^{-1}$), neither in the residuals of each traits modelled separately (Fig. S2).

Table 2. Estimates of explanatory variables in spatial autoregressive model of the sensitivity score (log(x+c+1)-transformed). Only significant estimates are shown (p<0.01).

Trait	Depth	Sediment		Chlorophyll a	Bottom temp..	Bottom trawl	Pelagic trawl	Year	Lat.	Long.	Lat.^{2}	Long.^{2}	Lat. × Long.
Sensitivity score		Coarse	-7.08×10^{-3}			-4.05×10^{-6}		5.69×10-3	4.20 ×10-2	1.36 ×10-1	-7.53 ×10-2	-4.96 ×10-2	7.52 ×10-3
		Mix	-7.50×10^{-2}										
		Mud	7.54×10^{-2}										
		Sand	6.56×10^{-2}										

The spatial variables (latitude, longitude, their quadratic effects and interaction) as well as bottom trawl effort, sediment and year were significant drivers of the CWM of the sensitivity score (Table 2). Traits taken separately brought more details on which trait forming the sensitivity score responded to which variables. The models of the sensitivity score and each of the life history traits highlights the importance of the habitat, described by sediments and depth. The biomass of sensitive taxa tends to be higher on mud and sand sediments than on mix and coarse (boulders taken as a reference) (Table 2).

Depth was not a significant driver of the CWM of the sensitivity score, but was a significant structuring variable of some of the CWMs made on the traits taken separately: the relative biomass of taxa with large maximum length and high age at maturity increased in shallower areas (Table S3). Conversely, the relative biomass of taxa that are long-lived, bear their offspring (i.e. bearer) and have low fecundity, as well as that of non-guarder taxa and high fecundity taxa, tended to increase in deeper areas (Table S3).

All CWMs of the sensitivity score and each trait taken separately covaried negatively with bottom trawl effort (Table 2 and Table S3). Areas with little bottom trawl effort tended to have the highest relative biomass of large, long-lived taxa that have low fecundity, mature late and give birth to large offspring. The relative biomass of taxa with very high fecundity also decreased as bottom trawl effort increased. Conversely, areas with large bottom trawl effort had the highest relative biomass of egg-guarding taxa and high fecundity taxa. In comparison, the spatial covariation of CWMs with pelagic trawl effort was significant only for the longevity trait and the non-guarder level. Pelagic trawl effort had a negative influence on the relative biomass of long-lived taxa but a positive influence on that of non-guarder taxa (Table S3).

Regarding temporal trends in CWMs in the Celtic Sea, the relative biomass of sensitive taxa increased over 2000-2016 (Table 2). More precisely, the relative biomass of large taxa that mature late, have low fecundity and large offspring increased from 2000-2016. Conversely, the relative biomass of taxa that guard their eggs and have medium or high fecundity decreased from 2000-2016 (Table S3). As bottom temperature increased, the relative biomass of long-lived taxa increased, while that of non-guarder taxa and taxa with very high fecundity decreased. Taxa with very high and medium fecundity tended to have lower relative biomass at sites with higher chlorophyll a concentrations (Table S3).

3.3. Local variation in the biomass of the most sensitive taxa in relation to local fishing patterns and closure area

Among all taxa, the temporal trend in biomass significantly increased for 19 taxa, significantly decreased for 10 taxa and had no significant trend for 72 taxa (Table S4). At the scale of the Celtic Sea, biomass appeared to increase for the most sensitive slow life history taxa (Fig. 4). This is confirmed by the positive correlation between significant slope of the regression ($p<0.05$) of the biomass of each taxa over time and sensitivity scores (Spearman's $\rho = 0.52$; $p = 0.004$) (Fig S6).

Seven taxa had a distinctly higher sensitivity score than the other taxa (Fig. 4), namely spurdog *Squalus acanthias*, school shark *Galeorhinus galeus*, blue skate *Dipturus batis*, smooth-hound *Mustelus sp.*, velvet belly *Etmopetrus spinax*, rabbit fish *Chimaera monstrosa* and nursehound *Scyliorhinus stellaris* (i.e. sharks, rays and chimaeras).

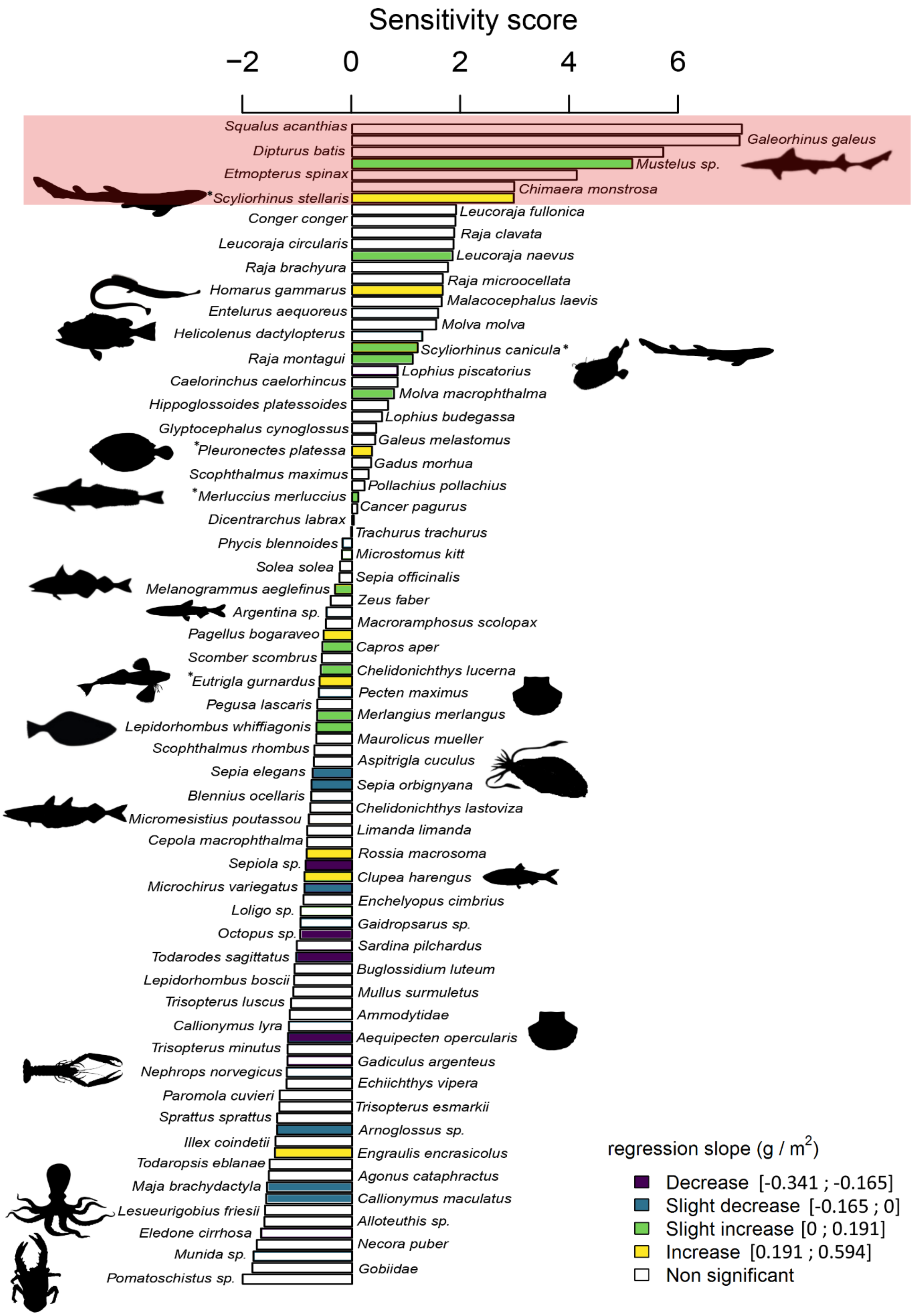
Sensitivity score
−2
0
2
4
6
Squalus acanthias
Galeorhinus galeus
Dipturus batis
Mustelus sp.
Etmopterus spinax
Chimaera monstrosa
*Scyliorhinus stellaris
Leucoraja fullonica
Conger conger
Raja clavata
Leucoraja circularis
Leucoraja naevus
Raja brachyura
Raja microocellata
Homarus gammarus
Malacocephalus laevis
Entelurus aequoreus
Molva molva
Helicolenus dactylopterus
Scyliorhinus canicula*
Raja montagui
Lophius piscatorius
Caelorinchus caelorhincus
Molva macrophthalma
Hippoglossoides platessoides
Lophius budegassa
Glyptocephalus cynoglossus
Galeus melastomus
*Pleuronectes platessa
Gadus morhua
Scophthalmus maximus
Pollachius pollachius
*Merluccius merluccius
Cancer pagurus
Dicentrarchus labrax
Trachurus trachurus
Phycis blennoides
Microstomus kitt
Solea solea
Sepia officinalis
Melanogrammus aeglefinus
Zeus faber
Argentina sp.
Macroramphosus scolopax
Pagellus bogaraveo
Capros aper
Scomber scombrus
Chelidonichthys lucerna
*Eutrigla gurnardus
Pecten maximus
Pegusa lascaris
Merlangius merlangus
Lepidorhombus whiffiagonis
Maurolicus mueller
Scophthalmus rhombus
Aspitrigla cuculus
Sepia elegans
Sepia orbignyana
Blennius ocellaris
Chelidonichthys lastoviza
Micromesistius poutassou
Limanda limanda
Cepola macrophthalma
Rossia macrosoma
Sepiola sp.
Clupea harengus
Microchirus variegatus
Enchelyopus cimbrius
Loligo sp.
Gaidropsarus sp.
Octopus sp.
Sardina pilchardus
Todarodes sagittatus
Buglossidium luteum
Lepidorhombus boscii
Mullus surmuletus
Trisopterus luscus
Ammodytidae
Callionymus lyra
Aequipecten opercularis
Trisopterus minutus
Gadiculus argenteus
Nephrops norvegicus
Echiichthys vipera
Paromola cuvieri
Trisopterus esmarkii
Sprattus sprattus
Arnoglossus sp.
Illex coindetii
Engraulis encrasicolus
Todaropsis eblanae
Agonus cataphractus
Maja brachydactyla
Callionymus maculatus
Lesueurigobius friesii
Alloteuthis sp.
Eledone cirrhosa
Necora puber
Munida sp.
Gobiidae
Pomatoschistus sp.
regression slope (g / m²)
■ Decrease [-0.341 ; -0.165]
■ Slight decrease [-0.165 ; 0]
■ Slight increase [0 ; 0.191]
■ Increase [0.191 ; 0.594]
☐ Non significant

Figure 4. Sensitivity scores from Hill-Smith analysis of the six life history traits of 101 taxa in the Celtic Sea, ranked from most to least sensitive to fishing. Sensitivity scores of individual taxa coloured according to the quartile of the slope of the regression of biomass (g.m^{-2}) from 2000-2016. Non-significant slopes (p >0.05) are coloured in white. The most sensitive taxa before the stall in sensitivity values are framed in red. An asterisk indicates significant slope after adjusting p-values for multiple testing.

Biomass of *Mustelus* sp., *S. stellaris* and, to a lesser extent *S. acanthias* and *D. batis* significantly increased in the north-east of the Celtic Sea (Fig. 5 A. C. D. E.). Areas where the increase happened correspond to the ones that experienced a significant decrease in bottom trawling effort: the seasonal area closure Trevose box and its adjacent area. Nevertheless, the relationship was difficult to assess for *S. stellaris* because of its small range in the Celtic Sea (Fig. 5 E.). Along the southern border of the Celtic Sea, biomass of *Mustelus* sp. and to a lesser extent *G. galeus* increased significantly in statistical rectangles with no significant trends in bottom trawling (Fig. 5 B. and D.). In addition, biomass of *G. galeus* significantly decreased in a statistical rectangle where bottom trawl effort significantly increased, in the centre of the Celtic Sea.

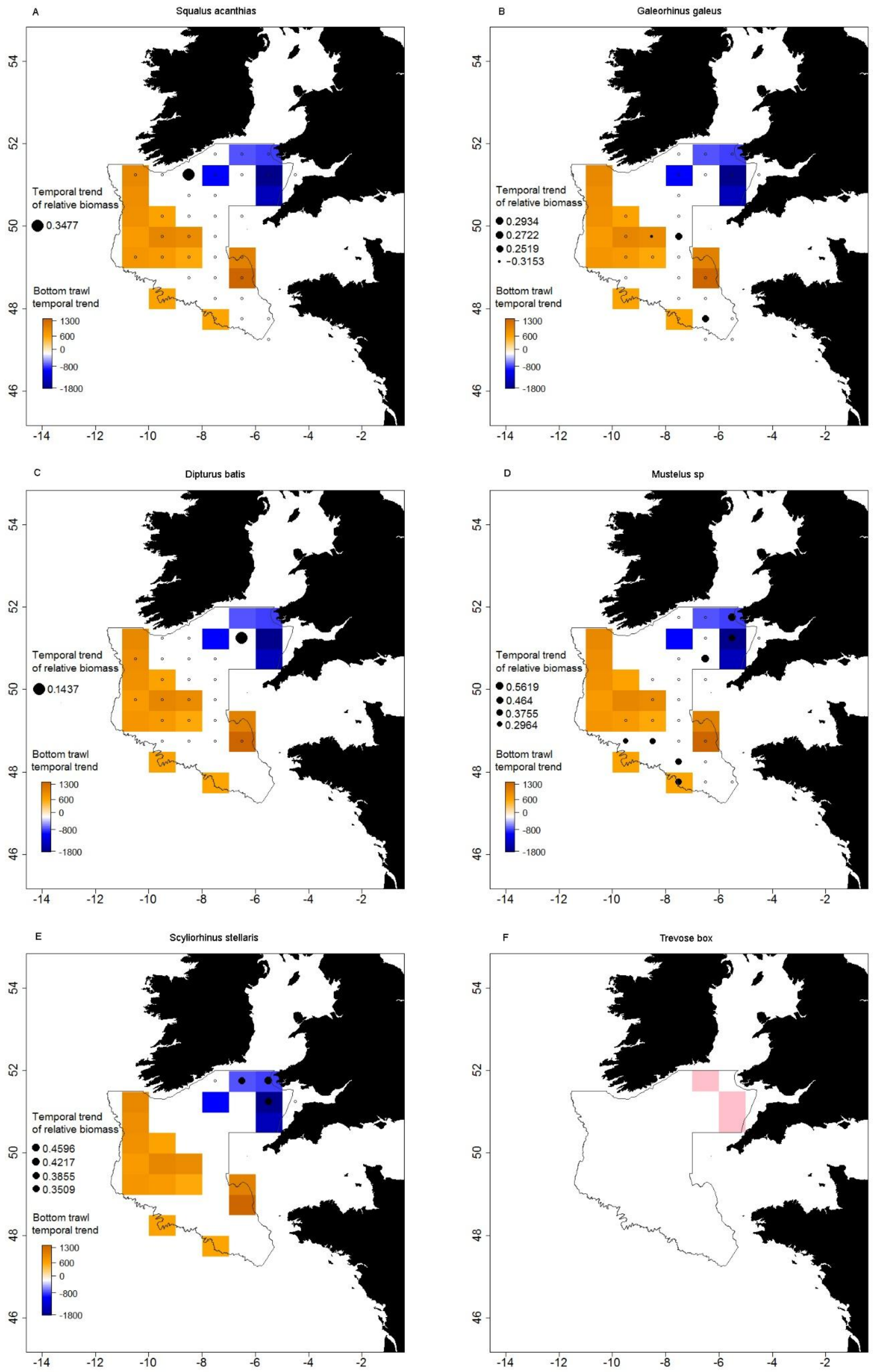
A
Squalus acanthias
Temporal trend of relative biomass
0.3477
Bottom trawl temporal trend
1300
600
0
-800
-1800
B
Galeorhinus galeus
Temporal trend of relative biomass
0.2934
0.2722
0.2519
-0.3153
Bottom trawl temporal trend
1300
600
0
-800
-1800
C
Dipturus batis
Temporal trend of relative biomass
0.1437
Bottom trawl temporal trend
1300
600
0
-800
-1800
D
Mustelus sp
Temporal trend of relative biomass
0.5619
0.464
0.3755
0.2964
Bottom trawl temporal trend
1300
600
0
-800
-1800
E
Scyliorhinus stellaris
Temporal trend of relative biomass
0.4596
0.4217
0.3855
0.3509
Bottom trawl temporal trend
1300
600
0
-800
-1800
F
Trevose box
54
52
50
48
46
-14
-12
-10
-8
-6
-4
-2

Figure 5.(A to E) Map of the slope of the regression of biomass (g/m^2, black circles) in each statistical rectangle (111.12 km × 55.56 km) of the Celtic Sea from 2000-2016. This figure focussed on the taxa the most sensitive to fishing that have a significant variation of their biomass in at least one statistical rectangle. Small open circles represent the distribution of the taxa and filled circle the significant ($p<0.05$) slope of the regression of the biomass over time. Statistical rectangles are coloured according the sign of temporal trend of bottom trawl effort (hours per year within the rectangle) on time (only slopes with $p <0.05$ are coloured). (F) Map of the seasonal area closure Trevose Box.

4. Discussion

To evaluate impacts of fishing on community structure, the distribution of life history traits that are sensitive to fishing was studied to identify assembly rules, as well as their environmental and anthropogenic drivers. At the scale of the Celtic Sea, sensitivity to fishing was mostly distributed according to stochastic assembly process.

Significant overdispersion was mainly detected in the centre-east of the Celtic Sea. Values of life history traits are more diverse than expected by chance there, which suggests more diversified life history strategies. This overdispersion in traits is driven by the co-occurrence of taxa with a slow life history strategy, such as the common skate *Dipturus batis,* and a fast life history strategy, such as the Atlantic horse mackerel *Trachurus trachurus*. Three non-exclusive deterministic processes could explain the distribution of life history traits in the centre-east of the Celtic Sea:

(i) *Competition among coexisting taxa fosters trait overdispersion.* Competition might lead to either competitive exclusion or to spatial and/or temporal avoidance among co-occurring taxa (Cahill et al., 2008; Mayfield and Levine, 2010). However, in the centre of the Celtic Sea were overdispersion occurs, competition between fast and slow life history taxa does not appear as a reasonable explanation of the large range of sensitivity score expressed, as for instance skate and Atlantic horse mackerels do not compete for food.

(ii) *Small-scale seascape heterogeneity provides a greater diversity of niches*, in agreement with the *habitat heterogeneity hypothesis* (Tews et al., 2004). We observed that sediments, which are generally homogenous throughout the Celtic Sea (mud and sand), tend to be patchier where overdispersion occurs (i.e. centre-east). Life history traits define one of at least five dimensions of the species ecological niche (i.e. habitat, life history, trophic, defence and metabolic) Winemiller, Fitzgerald, Bower, & Pianka (2015)). The area where overdispersion was observed could thus provide more available niches than the rest of the Celtic Sea and allow more life history strategies to coexist in accordance with the limiting similarity process (Macarthur and Levins, 1967).

(iii) *Decrease in fishing pressure alleviated the filtering imposed on sensitive taxa*. Overdispersion might occur when new taxa with different trait values arrive or due to changes in taxa biomass among trait values. For the Celtic Sea, we observed stability in the taxonomic structure (no large changes in biomasses of taxa) of these communities despite spatio-temporal changes in anthropogenic pressures (Mérillet et al., 2020). Focusing on traits, we highlight that the biomass of slow life history taxa increased over time in the centre-east and extreme north-east, thereby increasing the frequency of these original trait values in the community and flattening the distribution of trait values. In the extreme north-east, the biomass of sensitive taxa could have increased due to the decrease in fishing pressure. It is likely that when fishing was still high, it acted as a major filter on biodiversity as demonstrated in Guénette and Gascuel (2012). Sensitive taxa may have been filtered from the areas with intensive fishing, whereas the decrease in fishing allowed more diverse taxa to coexist again.

Stochasticity was the dominant assembly process over the majority of the Celtic Sea. Assembly processes thus appeared to be dominated by demographic processes (birth, death, immigration, emigration) occurring at random with respect to the taxon’s identity (Vellend et al., 2014). This seems in line with the high number of mobile fish in the taxa studied and dominance of dispersion of egg as reproductive strategy. However, this might also result from the failure to detect deterministic processes (Vellend et al., 2014) which can be due to the large number of taxa in this study interacting together and reacting to abiotic variables in many different ways.

Underdispersion (even if non-significant) observed in the most of the Celtic Sea could be due to environmental filtering that selects taxa that can endure specific environmental conditions. Depth, sediments, year and bottom trawl effort are the variables that significantly drive the largest number of traits and have thus a particularly structuring effect on their distribution. The dependence of the CWMs on variables that do not vary over time at a given site (i.e. depth and sediments) illustrates the strong structuring effects of habitat. For variable that vary over time and space, bottom trawl effort thus appears to be a severe condition that restricts the distribution of life history traits in the Celtic Sea, with a globally negative relationship with the biomass of slow life history strategy taxa demonstrated in all CWMs models.

We observed temporal variation in the biomass of slow life history strategy taxa that increased from 2000-2016 at the regional scale. At the scale of the Celtic Sea, bottom trawling was stable over the period studied (Mérillet et al., 2020), but this stability masks local differences that are visible at the scale of the statistical rectangle, as showed here. Almost all significant increases in the biomass of the most sensitive taxa occurred in statistical rectangles in which bottom trawling decreased or showed no significant trend. This is particularly clear for *Mustelus* sp., *S. stellaris*, *D. Batis* and *S. acanthia*s, whose populations increase in areas where fishing pressure decreased. The biomass of taxa with a slow life history, especially elasmobranchs, is higher in the centre-east of the Celtic Sea, and the highest part of the increase in biomass of the five elasmobranchs occurred in adjacent areas: the extreme north-east and south-west. This pattern could be due to a local increase in abundance after a decrease in fishing pressure (in the north-east), but also to a replenishment from the larger number of individuals present in the centre-east of the Celtic Sea (Green et al., 2014). As an open sea with relatively homogenous sediment, the Celtic Sea appears to be a seascape that large-bodied and mobile taxa can cross easily. We hypothesize that the centre of the Celtic Sea could have functioned as a refuge and then a source for recolonization of the north-east when fishing pressure began to decrease. A similar recovery of a depleted population from adjacent areas in a fishing ground was observed for predatory fish on the north-west Atlantic shelf (Shackell et al., 2012).

The observed increase in sensitive slow life history taxa could be related to a local decrease in fishing pressure due to management practices. In 2009, the EU began to enforce its Common Fisheries Policy, which decreased overall fishing effort in EU seas (Walter, 2010). In this context, fishing effort was displaced from the north-east to the west and south-west of the Celtic Sea and decreased bottom trawl effort in certain statistical rectangles. It may also have benefited the prey of slow life history taxa, as demonstrated in Georges Bank, a formerly overexploited ecosystem east of

Massachusetts, USA (Mayo et al., 2014), although we did not observe an overall increase in biomass of small pelagic fish. This lack of evidence may have been due to incomplete sampling of pelagic communities. Moreover, the seasonal fishing closures of the Trevose Box (1st February until 31 March each year) prohibits fishing activity in three statistical rectangles in the north-east Celtic Sea (30E4, 31E4 and 32E3). This seasonally closed area created in 2005 (European Commission, 2013; ICES, 2007) has most likely prompted the recovery observed in slow life history taxa, which confirms the hypothesis of the benefits of this closure (Horwood et al., 1998). Indeed, we observed the largest significant decrease in bottom trawl effort and increase in biomass for four of the five aforementioned elasmobranch taxa in this area. This area is also a known spawning ground and nursery for many species, including elasmobranchs (Potter et al., 1997), and could, in addition to serving as a refuge for adults from fishing pressure, favour the replenishment of the population by increasing reproductive success. The increase in biomass of slow life history taxa observed in the Celtic Sea is in line with the increase in equilibrium strategy taxa (e.g. elasmobranchs) observed in the North Sea (Pecuchet et al., 2017) following a decrease in fishing effort and an increase in temperature.

A negative relationship was observed between bottom temperature and the biomass of short lifespan taxa as well as very high fecundity taxa (characteristic of the fast life history strategy). In addition, we also showed that taxa with a significant decrease in biomass tended to be least sensitive to fishing and had fast life history traits (i.e. small maximum length, short-lived, early-maturing, small offspring, non-guarder and high or very high fecundity). This decrease in the biomass of fast life history taxa could thus arise from the significant increase in bottom temperature that occurred in the north of the Celtic Sea over 2000-2016 (Mérillet et al., 2020). This decrease in fast life history taxa was also observed in the English Channel after a warm phase of the Atlantic Multidecadal Oscillation (McLean et al., 2018). Fast life history taxa are highly responsive to an increase in temperature due to their short generation time (McLean et al., 2018). In the North Sea, mixed trends were observed since the biomass of periodic strategy taxa have decreased over the past 30 years, but opportunistic taxa (at the fasted end of the continuum of life history strategy) have increased (Pecuchet et al., 2017). Overall, as in adjacent area, the observed life history patterns in the Celtic Sea most likely result from an interplay between temperature and fishing.

5. Conclusion

Analysis at various spatial and temporal scales enabled us to draw some conclusions about the recent evolutions of sensitivity patterns to fishing in the Celtic Sea. Assembly processes are mostly explained by stochasticity in the demographic events. Nevertheless, environmental filtering applied by fishing pressure on the taxa also appeared to have had an importance. In this historical fishing ground, fishing probably acted as a filter in the north-east and centre-east of the area before the beginning of the time series studied here. This filter got slowly removed allowing significant limiting similarity to be revealed (in a heterogeneous habitat or from the competition between taxa).

We showed the negative relationship between fishing effort and the biomass of taxa exhibiting sensitive traits, but also the increase in biomass of the most sensitive taxa from 2000-2016, in link with the creation of the Trevose box area closure. Rapid changes in the functional structure of the communities are expected in the future as climate change effects become more tangible and superimpose to fishing ones. Management measures leading to short-term improvement of the biomass of sensitive taxa to fishing are thus urgently needed (O'Leary et al., 2017). This study highlights potential positive dynamics for a group of sensitive species due to a local decrease in fishing pressure. Within two decades, mitigation measures, such as area closures that restrict fishing effort spatially or temporally on essential habitats such as spawning and nursery grounds could significantly increase the biomass of the most sensitive taxa, which can then act as a source for recolonization. This positive response to recent EU policies could be a useful feedback for managers. However, a continual caution during ecosystem management of fishing grounds is required, as commercially fished small pelagic taxa could experience a decrease in biomass in the future due to climate change and could eventually be replaced by warm water pelagic taxa.

Acknowledgement

We thank all those who made data sampling possible during the EVHOE surveys. This work is part of a PhD thesis jointly funded by the French Institute for the Exploitation of the Sea (IFREMER) and the National Museum of Natural History (MNHN).

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