





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Ecological sensitivity and vulnerability of fishing fleet landings to climate change across regions

Marta Albo-Puigserver^{1,2}, Juan Bueno-Pardo³, Miguel Pinto¹, João N. Monteiro¹, Andreia Ovelheiro¹, Maria A. Teodósio¹ & Francisco Leitão¹

The degree of exposure of fishing communities to environmental changes can be partially determined by the vulnerability of the target species and the landings composition. Hence, identifying the species that ecologically most contribute to the vulnerability of the landings are key steps to evaluate the risk posed by climate change. We analyse the temporal variability in intrinsic sensitivity and the ecological vulnerability of the Portuguese fisheries landings, considering the species proportions derived both from the weights and revenues. To account for the diversification of species of each fleet, we explored the species dependence of the fishery in combination with the vulnerability of them. The analyses were carried out separately for three fleet typologies and three regions. Opposite to what has been observed at a global scale, the ecological sensitivity of the fisheries landings between 1989 and 2015 did not display a decline across areas or fishing fleets. Considering each fleet independently, for trawling, where average vulnerability was lower than in the other fleets, the sensitivity of the landings increased since the 2000s. On the other hand, the high vulnerability found in multi-gear fleets was compensated by diversification of the species caught, while purse-seine fleets targeted low vulnerability species but presented a high fishery dependence on few species. The results highlight the importance of combining information on ecological vulnerability and diversification of fishing resources at a regional scale while providing a measure of the ecological exposure to climate change.

Climate change impacts marine ecosystems at different levels of biological organization, from individuals to populations and ecosystems. Consequently, the goods and services these ecosystems provide to human society are also affected. Among these services, fisheries capture most attention from scientists and managers due to their social and economic relevance^{1,2}. Nevertheless, not all fisheries are expected to be equally impacted by climate change. Among other aspects, the exposure to climate change of fishing communities will depend on the ecological vulnerability of the species catch. Hence, from a management point of view, to increase the resilience of fisher communities, it is important to reduce their dependence not only on single resources but also on highly vulnerable species³⁻⁵.

The vulnerability of species to climate change has been defined as the degree to which the species is susceptible to, or unable to cope with, the adverse effects of climate change. It depends on the level, magnitude and rate of exposure to climate variables (extrinsic factors), its sensitivity to climate change in the sense of the degree to which the population dynamics and life-history traits of a given species are affected by a change in the environment, and its adaptive capacity to respond to climate impacts, whether by adjusting to potential damage or taking advantage of opportunities⁶⁻⁸. At a global scale, it has been observed that ecosystems that are highly exploited present a decreasing trend in the landings of species with high sensitivity values⁹. This is due to the fact that fisheries tend to first remove large, slow-growing, long-lived species that, because of their life-history strategies, tend to be more sensitive¹⁰. To determine the ecological vulnerability of the landings, the sensitivity of species composing the landings should be assessed together with the degree of exposure and the adaptation capacity

¹Centro de Ciências do Mar (CCMAR), Universidade do Algarve, Campus de Gambelas, 8005-139 Faro, Portugal. ²Centro Oceanográfico de Baleares, Instituto Español de Oceanografía (IEO-CSIC), Ecosystem Oceanography Group, Moll de Ponet sn, 07015 Palma, Spain. ³Centro de Investigación Mariña, Universidade de Vigo, Future Oceans Lab, Campus Lagoas-Marcosende, 36310 Vigo, Spain. ✉email: marta.albo.puigserver@gmail.com; fleitao@ualg.pt

of the species, which is driven by aspects related to their biology, ecology, conservation status, or management, among others^{11–13}.

The diversity of the landed species composition (i.e. species portfolio¹⁴) has also been described as an important factor to consider when evaluating the resilience and the vulnerability of a fishery. Previous research suggests that fishery managers and fishers should increase diversification of species landed to reduce the dependence of fishers' activity on single species¹⁵. Hence, to increase the adaptive capacity of the fisheries to current and future environmental change conditions, the diversification of fisheries should ideally be accompanied by the selection of low vulnerability species in the portfolio¹⁶. Considering that economic resources for fisheries adaptation management are usually limited, tools for managers to prioritize efforts are needed. Given the large issues that affect marine fisheries socio-ecological system, different proposals for prioritizing management strategies are available in the literature^{17,18}, with the reduction of the fishery dependence on vulnerable species being a major consensual issue^{5,19}.

In the last decade, different studies have applied climate vulnerability assessments to inform policy-makers at a national level^{20–22}. However, more recent studies have underlined the need to consider the spatial heterogeneity of the socio-ecological system at a regional level in the development of climate vulnerability assessments, in countries that present geographical, environmental and socio-ecological gradients^{23,24}. This is the case of Portugal, which follows a North–South orientation with strong latitudinal environmental gradients^{25–27}, with differentiated oceanographic and geographic characteristics²⁸ that influence fisheries differently across the Portuguese coast^{29–31}.

Total annual landings in Portugal in 2019 were 184 thousand tonnes and composed 3.3% of the fisheries production of the European Union (EU-27; source Eurostat). Despite the low percentage of production, Portugal is ranked fifth among countries in the EU-27 in terms of people employed in the fisheries industry. The fish consumption per capita is the highest in the EU³² and the third highest in the world (about 60.92 kg), being an important source of protein for the Portuguese population^{33,34}. At a local scale, fisheries have a high social and cultural importance and are the economic basis of many communities³⁵. The resources on the Portuguese coast have been highly exploited for some species^{28,36,37}, however not all fisheries are equally exposed to climate change, as their ecological vulnerability depend on the targeted species³⁸. Recently, the ecological vulnerability to climate change and its components (exposure, sensitivity and adaptive capacity) of the main fish and invertebrates with economic interest in Portugal have been defined considering three regions of the Portuguese coast: North, Centre and South³⁹.

Here, we used the case of the Portuguese fisheries to investigate if long-term changes in landing sensitivity have been observed and if the ecological vulnerability of the landing differs between fishing fleets and areas. Specifically, we first evaluated (i) the long-term trends in the sensitivity of the landings estimates based on life history traits of the species. Assuming that these traits are constant through time, we looked at the temporal variability of the sensitivity of the landings considering annual landings composition proportions per fleet and region (both in terms of weight, Kg, and revenues, €). Considering that at a global scale species with low sensitivity have been shown to dominate the catches because of the overexploitation of the most sensitive species⁹, we hypothesize that in the Portuguese fisheries a similar decline in sensitivity would be observed due to the historically high fishing exploitation. Second, (ii) we studied whether the landings of multi-gear, purse-seine and trawling fleets were equally vulnerable to climate change, also in terms of landing weight composition and economic revenue. Finally, (iii) aiming to establish a basis for defining priority action species, we followed the proposed methodology of Johnson and Welch⁷, which combines the vulnerability of the species with their importance for the fishing community. We modified this methodology to propose a decision-support framework that is based on the combination of the vulnerability of the species and the dependence of the fishers on them, by means of landing weights and revenues of the species. Identifying the species that most contribute to the vulnerability of Portuguese fisheries, in terms of landings weight and economic revenue differentiated by area, together with the degree of dependence of each fishery in specific species, will provide the information needed to determine on which species, fishery sector and region of Portugal management should be prioritized, to reduce the ecological exposure of the fishing community to future climate change effects.

The results from the present study provide, hence, a measure of the ecological exposure of fishery communities to climate change, that can be used in future socio-ecological vulnerability assessments and adaptation plans^{5,20}. The use of biological data, with sensitivity and vulnerability indices to climate change in combination with fisheries data is increasingly used to develop climate-informed management frameworks. Accordingly, we argue that the results provided here could be useful for implementing and inform suitable management strategies in the Portuguese fisheries.

Material and methods

Three different fishing fleets (*métiers*) are identified in Portuguese official fishery statistics: i) multi-gear, a fleet mainly composed on artisanal vessels from 5 to 23 m length operating with different licensed gears^{40,41}, such as gillnets, trammel nets, longlines and traps, targeting a high variety of species ii) purse-seine, which targets mainly sardine (*Sardina pilchardus*), Atlantic chub and horse mackerel (*Scomber colias* and *Trachurus trachurus*, respectively), and iii) trawling, which targets species such as Atlantic horse mackerel, European hake (*Merluccius merluccius*), cephalopods and crustaceans^{28,42}. The study area corresponds to the continental Portuguese coast, which was subdivided into three regions considering the oceanographic and fish assemblage's characteristics described in previous studies (North, Centre, South^{42,43}) (Fig. 1).

Two different data sources were used. Species ecological vulnerability values and its dimensions (exposure, sensitivity and adaptive capacity) of 74 commercial marine species were obtained from Bueno-Pardo et al.³⁹, under climate change scenario RCP 4.5 and RCP 8.5. These authors estimated the vulnerability of species to climate change was evaluated following the framework of the 4th Assessment Report of the IPCC and the final

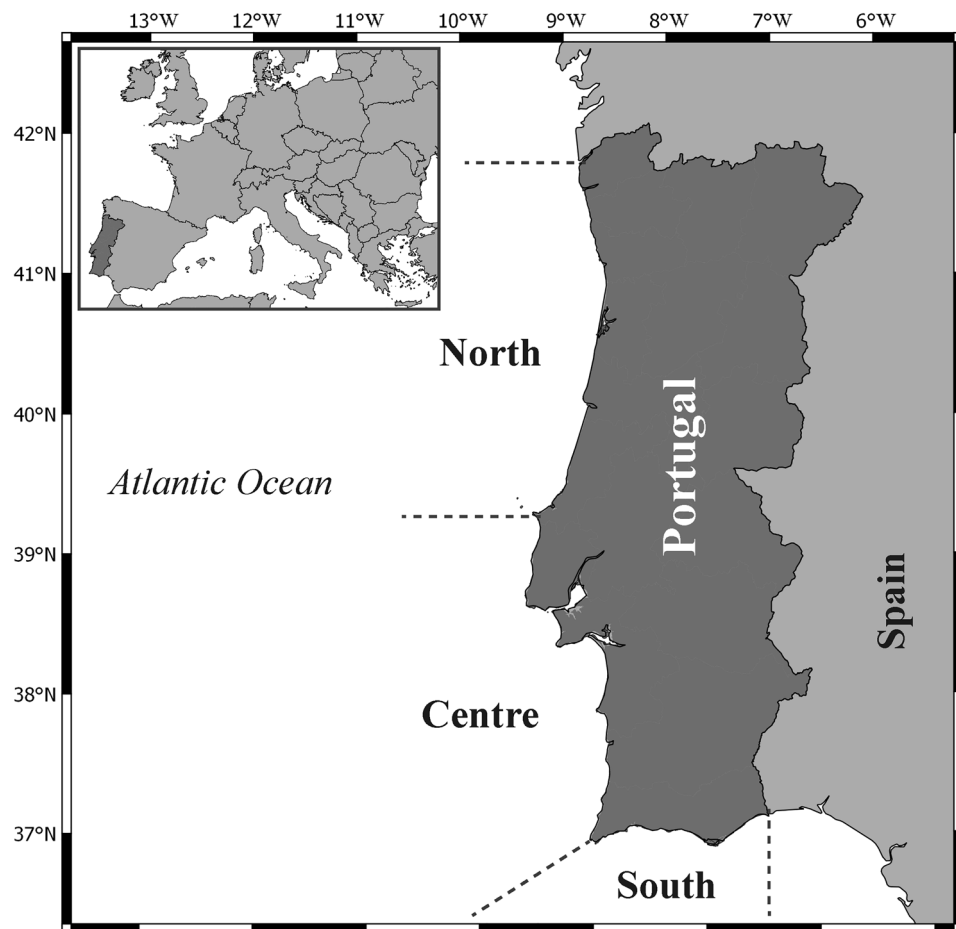


Figure 1. Map of Portugal showing the study area. Horizontal dashed lines delimitate the North, Centre and South area considered in this study. The map was created using QGIS 3.6.3 (<http://qgis.org>).

score of vulnerability for each species was a function of the exposure to the changing environment (RCP 4.5 and RCP 8.5), the sensitivity to the environmental change and the adaptive capacity of the species^{6,39}. Each of these components was evaluated considering different indicators that accounted for aspects related to the environmental variables, biology, ecology and exploitation of the species (see Bueno-Pardo et al.³⁹, for a full description of the indicators). The second data source was the public data on annual official landing weights(kg) and prices (€/kg) for each species, port and fishing fleet obtained for the period 1989–2015 from the Portuguese National Agency Directorate-General for Natural Resources Safety and Maritime Services (DGRM).

Trends in the ecological sensitivity of the landings. Species sensitivity to climate change were retrieved from Bueno-Pardo et al.³⁹. This parameter measures the extent to which the population dynamics or life history traits of a given species will be affected by changes in the environment (i.e. fecundity, growth parameters, age at maturity, planktonic larval duration, among others). Similarly, in previous works, this sensitivity parameter was called “intrinsic vulnerability” and since changes in life history traits occur in the long term, sensitivity is considered to be constant through time and is independent of the climate change scenario⁹. The sensitivity values reported for the main commercial species in combination with annual official landing data were used to explore temporal changes in ecological sensitivity of the landings from 1989 to 2015.

The Ecological Sensitivity of the Landing composition (ESL), in terms of biomass, was calculated and inferred from the average sensitivity of each of the exploited species, weighted by their annual landings, as follows:

$$ESL = \sum_i^n \frac{L_{i, yr} * S_i}{TL_{yr}} \quad (1)$$

where L_i is the landing weight of the species i for the year (yr), S_i is the sensitivity value estimated by Bueno-Pardo et al.³⁹ for the species i , TL_{yr} is the total landings of that year considering all the species and n is the total annual number of landed species. High values of ESL represented a high proportion of very sensitive species in the landings. The yearly ESL was calculated for each area (north, centre and south) and fleet sector (multi-gear, purse-seine, trawling).

To capture general patterns in the temporal trends of changes in sensitivity of the landings for each fishing fleet and area, the ESL was plotted using the “ggplot” package⁴⁴ with a locally weighted regression smoother (*loess* smoother), to reduce the variability and better reflect the underlying long-term trend. The *loess* smoother was fitted using the default span (0.75) of the R software⁴⁵. Additionally, a Dynamic Factor Analysis (DFA) was applied to test if there was a common declining trend in the ESL, within fishing fleets and areas. DFA is a multivariate time series analysis technique used for non-stationary time series analysis which allows us to estimate underlying common trends. A diagonal and unequal error covariance matrix was used for the models, and the corrected Akaike Information Criterion (AICc) was used to compare the models⁴⁶. We used the model given by N time series = linear combination of M common trends + noise. Canonical correlations among time series were used to indicate either a positive or negative relationship. Correlations with an absolute value higher than 0.5 indicate a significant relationship between variables⁴⁷. Response variables were normalized (mean subtracted, divided by standard deviation) prior to the analysis. Data analysis was performed using the software package Brodgar 2.7.5 (www.brodgar.com), considering 5000 iterations for each model. To determine which species contributed the most to the changes in ESL, the sensitivity, weight and landings of the main species contributing more than 3% were plotted (see Supplementary Fig. S1–S3 online).

Ecological vulnerability of the landings. The assessment of the ecological vulnerability of the landings of each fishing fleet and area of Portugal was performed considering the vulnerability of commercial species determined in Bueno-Pardo et al., (2021) for the two scenarios of climate changes (RCP 4.5 and RCP 8.5). The vulnerability values were used in combination with the landing composition of the fishing fleet in terms of landing weight (kg) and economic revenue of the landings (€). Available landing data for the most recent period (2010–2015) was selected as a proxy of the average landing composition, to calculate the actual mean ecological vulnerability of the landings. The ecological vulnerability of the landings was calculated for each year from 2010 to 2015 and then the average of all the years was used as their mean overall ecological vulnerability of the landings.

The Ecological Vulnerability of the Landings, considering weight ($EVL_{(kg)}$), was calculated and inferred from the cumulative contribution of the vulnerability of each of the exploited species for each scenario, weighted by their landings, for each year for the period 2010–2015, as follows:

$$\sum_{2010}^{2015} EVL = \sum_i^n \frac{Li, yr * Vi}{TL_{yr}} \quad (2)$$

In Eq. (2), L_i is the landing weight of the species i for the year (yr), TL_{yr} represents the total landings for the year considering all the species, V_i is the vulnerability estimated by Bueno-Pardo et al.³⁹ for the species i and n is the total number of landed species. The $EVL_{(kg)}$ was calculated yearly for the period 2010–2015 and averaged to obtain the final $EVL_{(kg)}$ value. Higher values of $EVL_{(kg)}$ represented a higher proportion of species with high vulnerability in the landings. The $EVL_{(kg)}$ was estimated separately for each fleet sector (multi-gear, purse-seine and trawling), area (north, centre and south) and climate change scenario (RCP 4.5 and RCP 8.5).

Similarly, to obtain the EVL based on economic revenue, the mean price of each species in nominal value (€/kg) was obtained yearly from the DGRM, and was multiplied by the landings of the species, to obtain the total economic revenue by species. Then, instead of using L_i (in kg) in Eq. (2), the revenue of each species and the total revenue (R_i) of the area and gear type was used to calculate the $EVL_{(€)}$ based on landing revenue. The value of inflation between years was not considered, due to the short period included in the analysis (2010–2015). Revenues are expressed in nominal values (euros).

Since vulnerability of species is the sum of both sensitivity and exposure minus the adaptive capacity³⁹, we explored the analysis of each component of the vulnerability separately. The same procedure was used to calculate the mean exposure, sensitivity and adaptive capacity of the landings for the period 2010–2015, substituting the vulnerability values of each species (V_i in Eq. 2) with the corresponding values of exposure (E_i), sensitivity (S_i) and adaptive capacity (AC_i) by species and area reported in Bueno-Pardo et al.³⁹. Since values of exposure of each species were reported for both scenarios³⁹, the ecological exposure of the landings was calculated for the RCP 4.5 and RCP 8.5. The average and standard deviation of the period 2010–2015 was calculated for each component and scenario.

Differences in EVL between areas, fleets and scenarios were tested by using a two-way analysis of variance (ANOVA test) followed by Tukey’s hsd post-hoc test (aov, base package⁴⁵). The assumptions of ANOVA were checked with a Kolmogorov–Smirnov test for normality and a Levene’s test for homogeneity of variances. In the case ANOVA assumptions were not met the non-parametric test Kruskal–Wallis was used to compare the mean ecological exposure, sensitivity and adaptive capacity of the landings between fishing fleets and areas. The threshold for significance was $\alpha < 0.05$. The proportion contributed by each species to the total EVL was calculated in both landings weight and revenue. Only species contributing more than 3% to the EVL were reported. Additionally, an analysis of similarity percentages (SIMPER) was applied to determine the average dissimilarity in species composition between areas for each fleet sector separately and to identify the main species contributing to the dissimilarity. Bray–Curtis dissimilarity was applied, and SIMPER analysis was done using PRIMER-E 7 software⁴⁸.

Prioritization of species for management. An analysis to identify which species present higher vulnerability and represent an important fraction of landed fish in weight and economic revenue was conducted adapting the methodology proposed in Johnson and Welch⁷. Species’ vulnerability score was classified and obtained from Bueno-Pardo et al.³⁹. The following categories of vulnerability were used: very low (<0.20), low (0.20–0.40),

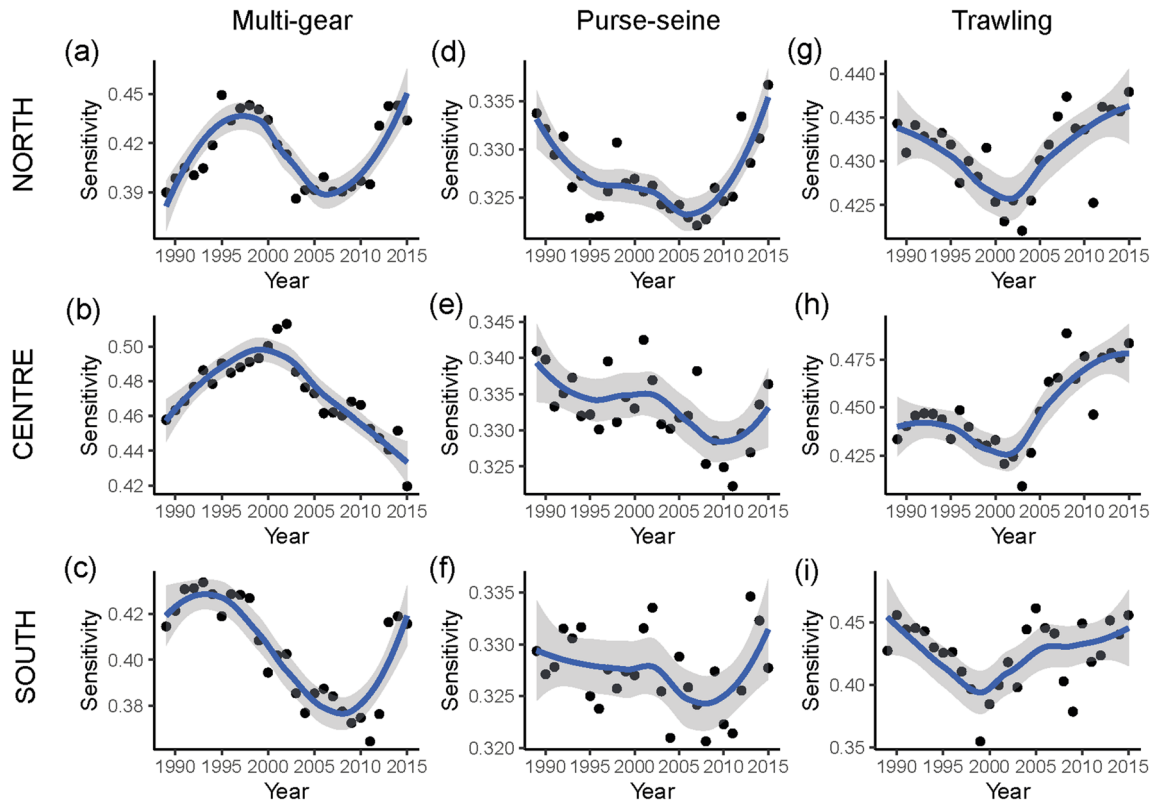


Figure 2. Ecological Sensitivity of the Landing (ESL) time series (dots) and temporal trends from 1989 to 2015 of each fishing fleet and area; Multi-gear (a–North; b–Centre; c–South), purse-seiners (d–North; e–Centre; f–South), and trawlers (g–North; h–Centre; i–South). A local polynomial regression (LOESS) fit is shown in blue, with 95% confidence intervals as a grey shadow.

moderate (0.40–0.60), high (0.60–0.80), and very high (>0.80). The degree of “fisheries dependence” on each target species was defined considering the contribution (%) of each species to the total landings in terms of weight (kg) and revenue (€). Both parameters were averaged to obtain a single index of fisheries dependence for each landed species and was classified in the following categories: very low (<5% contribution), low (5–15%), moderate (15–30%), high (30–50%), and very high (>50%). Only species contributing more than 3% to the total vulnerability and/or to the total landings weight and landing revenue were considered. To provide a visual frame of decision-support for selecting which species to target for priority action, a scatter plot (prioritization plot) with the classification of the vulnerability, and fisheries dependence on species was represented. High levels of dependency are indicative of a low degree of species diversification of the fishing fleet, while low levels of dependence indicate a higher degree of species diversification. The categorization of vulnerability and fisheries dependence aim to facilitate the visualization of the results, but should be interpreted as relative values comparing results of this study.

Results

Trends in sensitivity of the landings. Landings of purse-seine had lower values of sensitivity than multi-gear and trawling between 1989 and 2015 for the three areas. Sensitivity values of purse-seine landings were between 0.321 and 0.342, whereas multi-gear and trawling landings in most years had values above 0.4, with sensitivities between 0.364 and 0.513, and 0.355 and 0.489 for multi-gear and trawling, respectively.

We observed different temporal patterns between areas within each fleet (Fig. 2 and 3). The sensitivity for multi-gear in the north shift across years and the periods with higher sensitivity values corresponded mainly to the decrease in landings of *Sardina pilchardus* (Fig. 2a; Supplementary Fig. S1 online). In the centre area, maximum values of sensitivity in the period 2000–2002 corresponded to the decline in landings of *Lepidopus caudatus* from 1997, and to the increase in species with higher sensitivity, such as *Aphanopus carbo* and *Centroscymnus coelolepis* (Fig. 2b; Supplementary Fig. S1 online). From 2003, the decline of ESL was associated with the increase in landings of species with lower sensitivity, such as *Scomber colias*. In the south area, the decline in ESL in the period 1995–2012 was explained by the combination of a decline in contribution of species with a sensitivity score higher than 0.45, such as *Merluccius merluccius*, *Lepidopus caudatus* and *Conger conger* and the increase in species with a lower sensitivity such as *S. colias* (Fig. 2c; Supplementary Fig. S1 online). The only increase in ESL was recorded between 2013 and 2015 due to the increase in landings of *Octopus vulgaris* and the decline of *S. pilchardus* and *S. colias*.

For purse-seiners the ESL was similar in the three areas and presented low values (sensitivity values lower than 0.35) for the entire period (Fig. 2d,f). The main species that contributed to the ESL were *S. pilchardus*, followed by

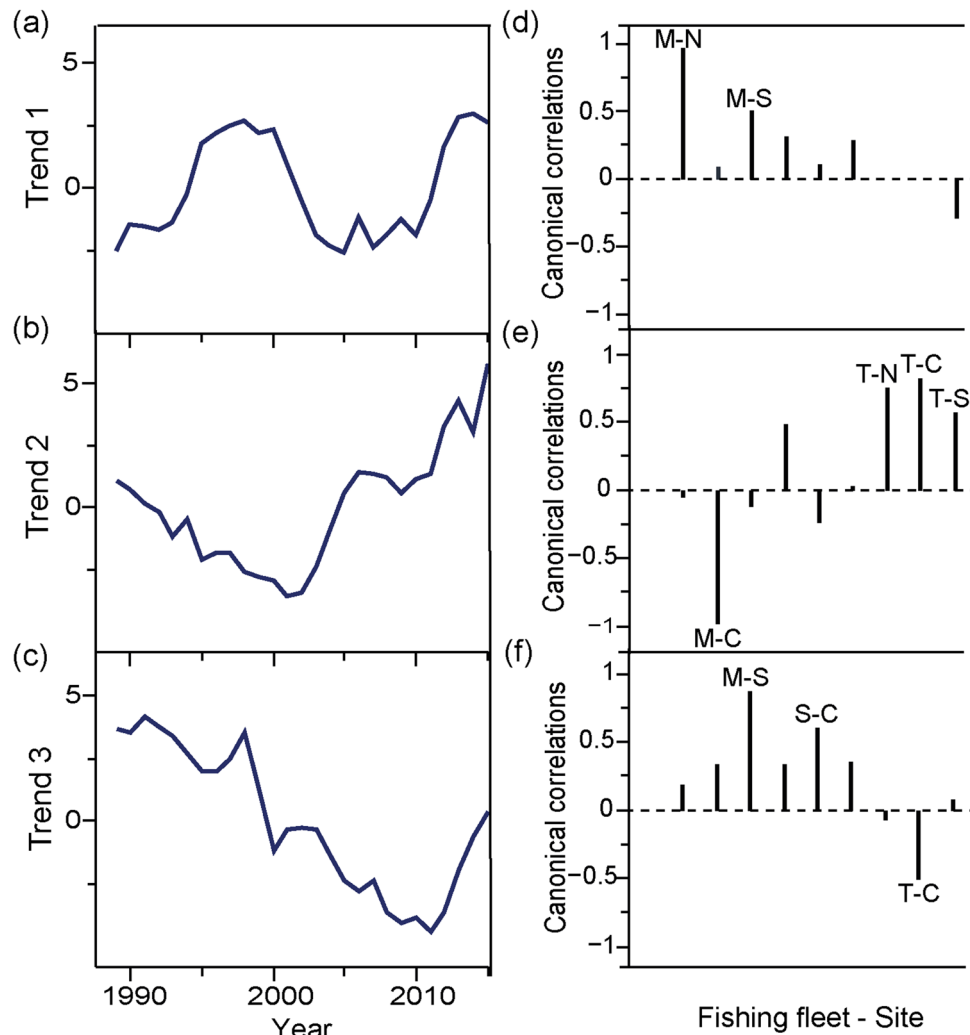


Figure 3. Common trends (left; **a, b, c**) and the corresponding canonical correlations (right; **d, e, f**) for the ecological sensitivity of the landings (ESL) series obtained by the model containing three common trends. Common trends are unitless. Labelled correlations correspond to the significant correlations (>0.5). The first letter of the abbreviation corresponds to the fishing fleet (M = Multi-gear; S = purse-Seine; T = Trawling) and the second letter to the area (N = North; C = Centre; S = South).

S. colias (Fig. 2; Supplementary Fig. S1 online). In the north area, the dominance of *S. pilchardus* was maintained until 2011 when the proportion of sensitivity explained by *S. colias* and *Trachurus trachurus* increased due to the decline in landings of *S. pilchardus* and the increase in *S. colias* (Fig. 2d; Supplementary Fig. S2 online). In the centre and south areas, a decline in the contribution of *S. pilchardus* to the ESL started in 2005, coinciding with the increase in *S. colias* landings (Fig. 2e,f; Supplementary Fig. S2 online).

Trawling ESL increased in the three areas from 2000 or 2003 onwards (Fig. 2). The main species contributing to the sensitivity in the north was *T. trachurus* (Fig. 2g, Supplementary Fig. S3 online), while in the centre and south areas, ESL variability was mainly affected by the decline of *T. trachurus* and the increase of *Micromesistius potassou* from 2003 onwards (Fig. 2h,i), and the increase of *Parapenaeus longirostris*, between 1997 and 2003 in the south area (Fig. 2i, Supplementary Fig. S3 online).

No common trends in ESL were observed across areas or fishing fleets. Results from DFA revealed three different trends (Fig. 3; Supplementary Table S1 online). Trend 1 is oscillatory and better represents multi-gear ESL time series scores in the north and south area (Fig. 3a,d; Supplementary Table S1 online). Trend 2 reveals a decrease in sensitivity until 2001 increasing onwards. This trend was positively correlated with the trawling fleet in the three areas and presented a negative correlation with multi-gear fleets in the centre area (Fig. 3b,e). Trend 3 presented a clear decline in ESL until 2011 and the higher positive correlations with this trend were observed in multi-gear fleets in the south and purse-seine fleets in the centre area (Fig. 3c,f; Supplementary Table S1 online).

Ecological vulnerability of the landings. The ecological vulnerability of the landings was significantly different between areas (kg; $F_{(2,45)} = 47.47$, $p < 0.001$) and fleets (kg; $F_{(2,45)} = 208.09$, $p < 0.001$) in terms of weight and economic revenue (€; $F_{\text{area}(2,45)} = 50.27$, $p < 0.001$; $F_{\text{fleet}(2,45)} = 255.35$, $p < 0.001$). Multi-gear and purse-seine

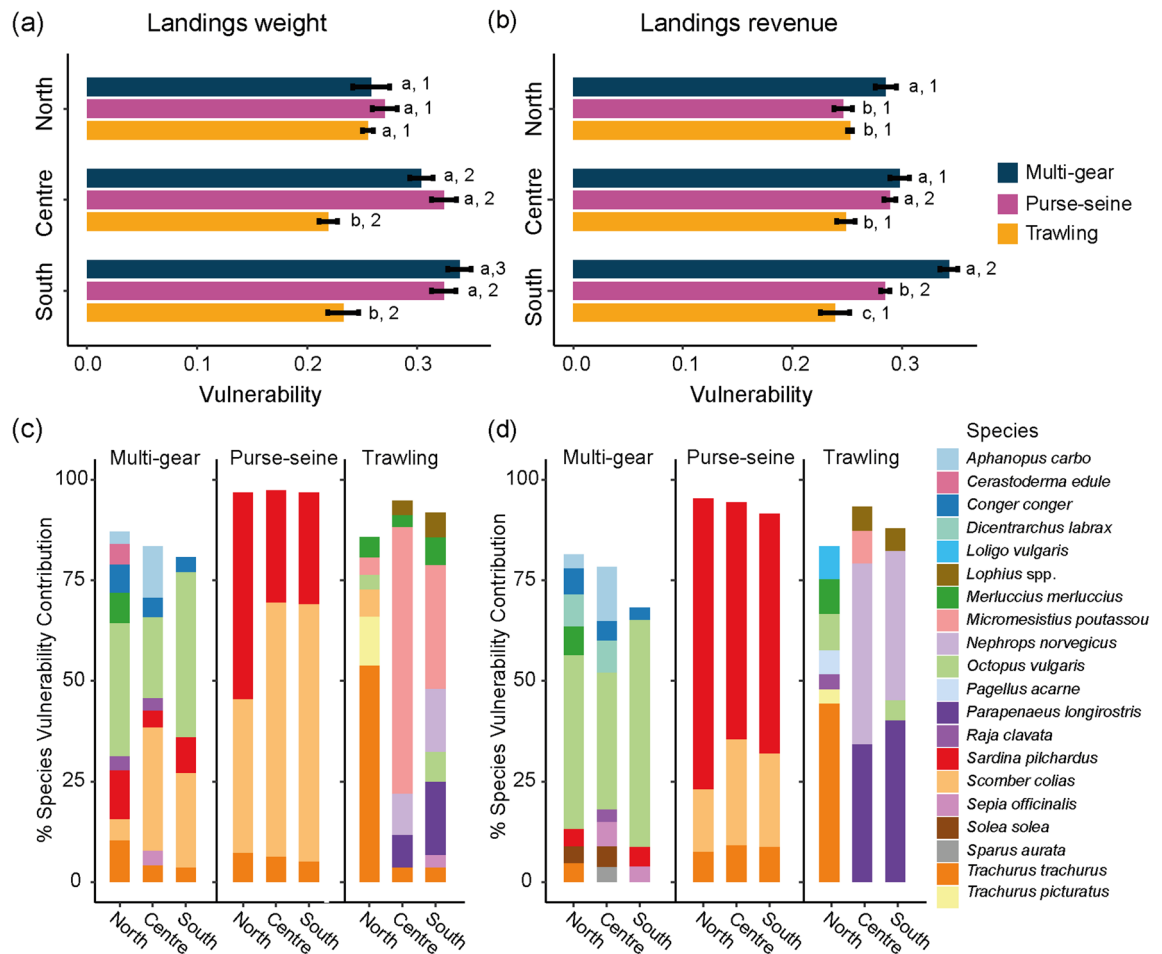


Figure 4. Ecological vulnerability of the landings weight (a) and economic revenue (b) by gear type and area calculated for the average period 2010–2015 and RCP 8.5. Each gear type is represented with a different colour. Tukey's HSD Test for multiple comparisons between fleets within the same area are indicated with letters and comparisons between areas within each fleet sector are indicated with a number. Pairs that were similar are indicated with the same number or letter and pairs that were significantly different ($p < 0.05$) are indicated with a different number or letter. The contribution of each species to the total ecological vulnerability of the fleet in terms of landings weight (c) and landings revenue (d) is represented for each gear type (Multi-gear; Purse-seine; Trawling). Only species contribution with $> 3\%$ to the total vulnerability are represented in the graph.

fleets in the centre and south areas presented the highest EVL in weight (Fig. 4). The highest ecological vulnerability of the landings, according to the revenues, was found for multi-gear fleets in the south. Values of ecological vulnerability and exposure were slightly higher in the climate change scenarios RCP 8.5 (Table 1). Thus, considering the similarity between both scenarios, results based on the RCP 4.5 are reported in the supplementary material.

EVL—landings weight. The $EVL_{(kg)}$ of multi-gear and purse-seine fleets were higher in the south and centre areas, whereas for trawling the vulnerability was higher in the north area (Fig. 4a, Table 1). Tukey's multiple comparison HSD Test revealed that the three fleets had similar $EVL_{(kg)}$ in the north, whereas in the centre and south area trawling had significantly lower $EVL_{(kg)}$ than the other two fleet sectors (Fig. 4a, Supplementary Fig. S4 online).

For each fleet, differences observed between areas were explained by dissimilarities in the species composition that most contributed to the $EVL_{(kg)}$. SIMPER analysis for multi-gear fleets showed higher dissimilarities in species contributing to the vulnerability between the north and the other two areas (Supplementary Table S2 online). *S. colias*, contributed the most to the dissimilarity between the north and the centre and south areas. Also, *Cerastoderma edule* contributed to the lower $EVL_{(kg)}$ values in the north. Dissimilarities between the south and centre areas were mainly explained by the higher contribution of *A. carbo* in the centre area and the higher proportion of *O. vulgaris* in the south area (Fig. 4a,c).

The $EVL_{(kg)}$ of purse-seine fleets was associated with a small number of species and dissimilarities between areas was low (Fig. 4a; Supplementary Table S3 online). SIMPER analysis for purse-seine showed lowest dissimilarity values between the centre and south areas. In the north, the main species contributing to purse-seine vulnerability was *S. pilchardus*, whereas in the centre and south areas the main species was *S. colias* (Fig. 4c).

Fleet		Multi-gear		Purse-seine		Trawling	
Scenario		RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5
Landings weight							
North	V	0.250 ± 0.017	0.258 ± 0.017	0.262 ± 0.011	0.270 ± 0.011	0.247 ± 0.005	0.255 ± 0.005
	E	0.472 ± 0.013	0.480 ± 0.013	0.508 ± 0.001	0.517 ± 0.001	0.459 ± 0.005	0.466 ± 0.005
	S	0.424 ± 0.022		0.330 ± 0.005		0.434 ± 0.016	
	AC	0.645 ± 0.028		0.577 ± 0.010		0.645 ± 0.011	
Centre	V	0.278 ± 0.010	0.304 ± 0.011	0.297 ± 0.011	0.324 ± 0.011	0.195 ± 0.008	0.219 ± 0.008
	E	0.453 ± 0.012	0.479 ± 0.012	0.517 ± 0.002	0.545 ± 0.002	0.404 ± 0.010	0.428 ± 0.010
	S	0.446 ± 0.016		0.329 ± 0.05		0.473 ± 0.013	
	AC	0.622 ± 0.013		0.549 ± 0.010		0.682 ± 0.012	
South	V	0.322 ± 0.010	0.338 ± 0.011	0.308 ± 0.011	0.324 ± 0.011	0.219 ± 0.014	0.233 ± 0.014
	E	0.511 ± 0.005	0.527 ± 0.005	0.529 ± 0.002	0.545 ± 0.002	0.428 ± 0.007	0.441 ± 0.007
	S	0.394 ± 0.025		0.327 ± 0.05		0.440 ± 0.016	
	AC	0.582 ± 0.016		0.547 ± 0.011		0.648 ± 0.008	
Landings revenue							
North	V	0.277 ± 0.010	0.285 ± 0.010	0.238 ± 0.008	0.246 ± 0.008	0.245 ± 0.002	0.253 ± 0.002
	E	0.463 ± 0.006 ^a	0.471 ± 0.006	0.510 ± 0.002	0.519 ± 0.002	0.450 ± 0.002	0.458 ± 0.002
	S	0.477 ± 0.010		0.330 ± 0.002		0.435 ± 0.004	
	AC	0.633 ± 0.013		0.602 ± 0.011		0.640 ± 0.005	
Centre	V	0.271 ± 0.008	0.298 ± 0.009	0.262 ± 0.005	0.289 ± 0.005	0.224 ± 0.008	0.249 ± 0.008
	E	0.451 ± 0.007	0.477 ± 0.008	0.514 ± 0.003	0.541 ± 0.003	0.437 ± 0.005	0.462 ± 0.005
	S	0.478 ± 0.006		0.337 ± 0.004		0.409 ± 0.009	
	AC	0.658 ± 0.007		0.589 ± 0.006		0.623 ± 0.005	
South	V	0.326 ± 0.008	0.343 ± 0.008	0.269 ± 0.004	0.285 ± 0.004	0.225 ± 0.013	0.239 ± 0.013
	E	0.505 ± 0.003	0.522 ± 0.003	0.526 ± 0.003	0.542 ± 0.003	0.449 ± 0.003	0.464 ± 0.003
	S	0.424 ± 0.007		0.339 ± 0.006		0.388 ± 0.013	
	AC	0.603 ± 0.004		0.597 ± 0.005		0.612 ± 0.003	

Table 1. Mean and standard deviation values of ecological vulnerability (V), exposure (E), sensitivity (S) and adaptive capacity (AC) of the landings weight and landings revenues for each area (North, Centre and South), fleet (multi-gear, purse-seine and trawling) and climate change scenario (RCP 4.5 and RCP 8.5).

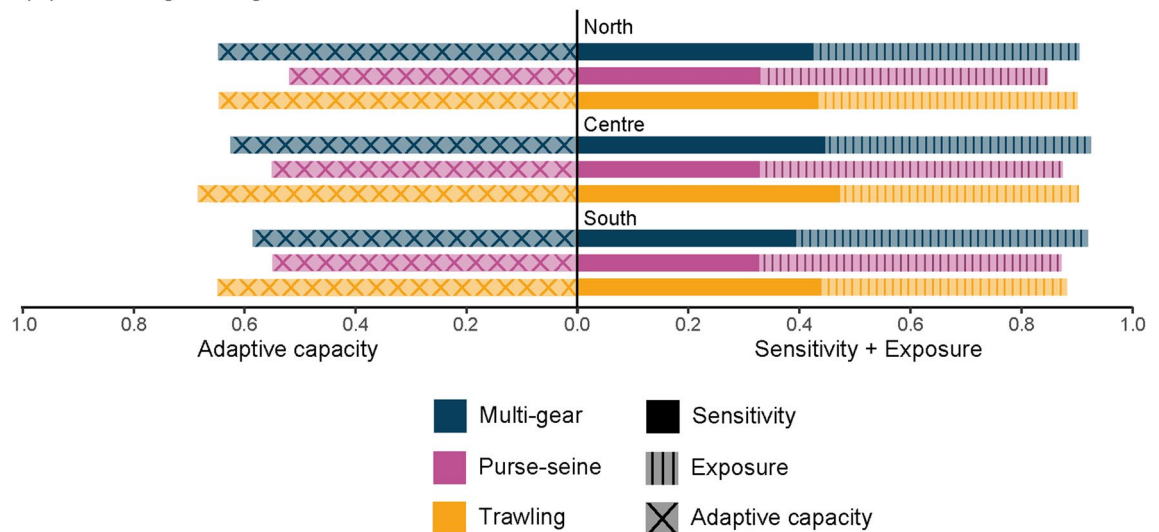
These differences in species contribution to $EVL_{(kg)}$ of purse-seine fleets explained the higher dissimilarity found between north area compared to both centre and south areas (see Supplementary Table S3 online). For trawling, high dissimilarities in the species contributing to vulnerability were observed between north and centre, and north and south areas (Supplementary Table S4 online). The main species that contributed to the dissimilarity between areas for $EVL_{(kg)}$ were *T. trachurus* in the north, *M. poutassou* in the centre and south areas, followed by *P. longirostris* and *N. norvegicus* (Fig. 4c). In the south, *O. vulgaris* was the species most contributed to the dissimilarity with the centre area (Supplementary Table S4 online).

When analysing the components of the $EVL_{(kg)}$ (sensitivity, exposure and adaptive capacity), we found that the fleet with the highest sensitivity was trawling (Supplementary Table S5 online), whereas purse-seine had the lowest sensitivity values, in the three areas (Fig. 5a; Supplementary Table S6 online). For exposure, an inverse pattern was observed when compared to sensitivity. Purse-seine landings had the highest values of exposure in all areas, followed by multi-gear and trawling (Fig. 5a). The ecological adaptive capacity was higher in trawling landings in the centre and south, whereas in the north multi-gear and trawling landings presented similar adaptive capacity. In the three areas, purse-seine landings had the lowest adaptive capacity (Fig. 5a).

EVL—landings revenue. The ecological vulnerability of fisheries in revenue ($EVL_{(€)}$) differed from the $EVL_{(kg)}$. We observed an increase in the importance of high price species, such as *O. vulgaris* in multi-gear, *S. pilchardus* in purse-seine and *P. longirostris* or *Nephrops norvegicus* in trawling (Fig. 4d). The $EVL_{(€)}$ of multi-gear was higher in the south, while the purse-seine showed similar $EVL_{(€)}$ in the central and south areas. Trawling did not present differences between areas (Fig. 4b). In the north and south, multi-gear had the highest $EVL_{(€)}$, while trawling had a significantly lower $EVL_{(€)}$ in the centre and south areas (Fig. 4b, Supplementary Fig. S4 online).

For multi-gear, an increase in the contribution of *O. vulgaris* in terms of economic revenue was observed in comparison to the contribution of landing weights (Fig. 4c,d). This is due to the higher average price of *O. vulgaris* (4.33 €·Kg⁻¹) compared to *S. pilchardus* (1.57 €·Kg⁻¹) and *T. trachurus* (1.60 €·Kg⁻¹). Dissimilarity in $EVL_{(€)}$ was higher between the north and south area (Supplementary Table S3 online). *A. carbo* contributed the most to the dissimilarity between areas followed by *O. vulgaris*, which contributed to the dissimilarity of the south area (Fig. 4d).

(a) Landings weight



(b) Landings revenue

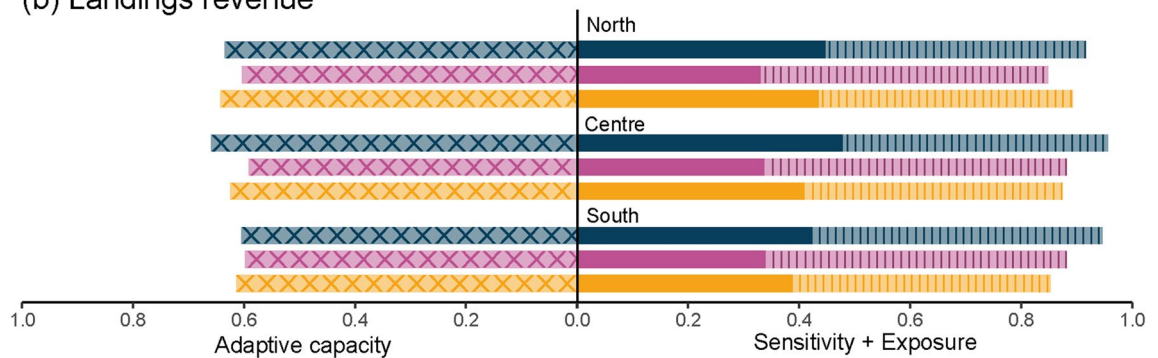


Figure 5. Values of the vulnerability components for the period 2010–2015 (sensitivity + exposure – adaptive capacity). Adaptive capacity is represented in the left of the y axis, while sensitivity and exposure are represented in the right side of the y axis. Each component is represented with a different texture. All components are represented by gear type (colour) and area (north, centre and south). For exposure values correspond to the RCP 8.5. In the top panel the components in terms of landings weight are represented (a) and in the bottom panel the components in terms landings economic revenue are represented (b).

The species that contributed the most to the $EVL_{(e)}$ in the purse-seine fleet was *S. pilchardus*. The proportion of contribution of *S. pilchardus* in $EVL_{(e)}$ increased in comparison to the contribution to landing weights, due to the higher average price of *S. pilchardus* ($1.57 \text{ €}\cdot\text{Kg}^{-1}$) compared to *S. colias* ($0.29 \text{ €}\cdot\text{Kg}^{-1}$). Dissimilarities in $EVL_{(e)}$ of purse-seine fleets were low between areas, and *S. colias* contributed the most (Supplementary Table S4 online). Similar to multi-gear and purse-seine fleets, the trawling fleets $EVL_{(e)}$ presented differences across areas. While in the north, *T. trachurus* was the main species, in the centre and south area, *P. longirostris* and *N. norvegicus* contributed the most to the $EVL_{(e)}$, due to their high average price ($15.66 \text{ €}\cdot\text{Kg}^{-1}$ and $15.33 \text{ €}\cdot\text{Kg}^{-1}$, respectively) (Fig. 4D). *M. poutassou* showed a low contribution in terms of economic revenue due to its low average price ($0.57 \text{ €}\cdot\text{Kg}^{-1}$). High dissimilarity in $EVL_{(e)}$ was observed between the north and the two other areas, whereas the dissimilarity between the centre and south areas was low (Supplementary Table S6 online).

The sensitivity, exposure and adaptive components of the $EVL_{(e)}$ (Fig. 5b) showed patterns different from those calculated in terms of $EVL_{(kg)}$. The sensitivity of multi-gear landings revenue was higher in the centre and south area, whereas in the north, multi-gear and trawling presented similar sensitivity values. Purse-seine landings revenue presented the lower sensitivity values in the three areas. For exposure, purse-seiner landings revenue had the highest values among the three areas. The ecological adaptive capacity of multi-gear and trawling landings revenues were higher than in purse-seine fleets in the three areas, although differences in the south were minimal (Fig. 5b; Supplementary Table S6 online).

Prioritization of species for management. In general, most of the species were in the lower-left of the prioritization plot (Fig. 6). Specifically, multi-gear fleets showed higher numbers of species with moderate vulnerability, but with low dependence on them in the three areas (Fig. 6a, Supplementary Table S7 online). However, for *O. vulgaris* in the north and centre areas the dependence was moderate and in the south the dependence was high, with more than 40% of the landings weights and revenues of multi-gear in the south being obtained from this species. In the centre area, the dependence on *A. carbo* was also classified as moderate.

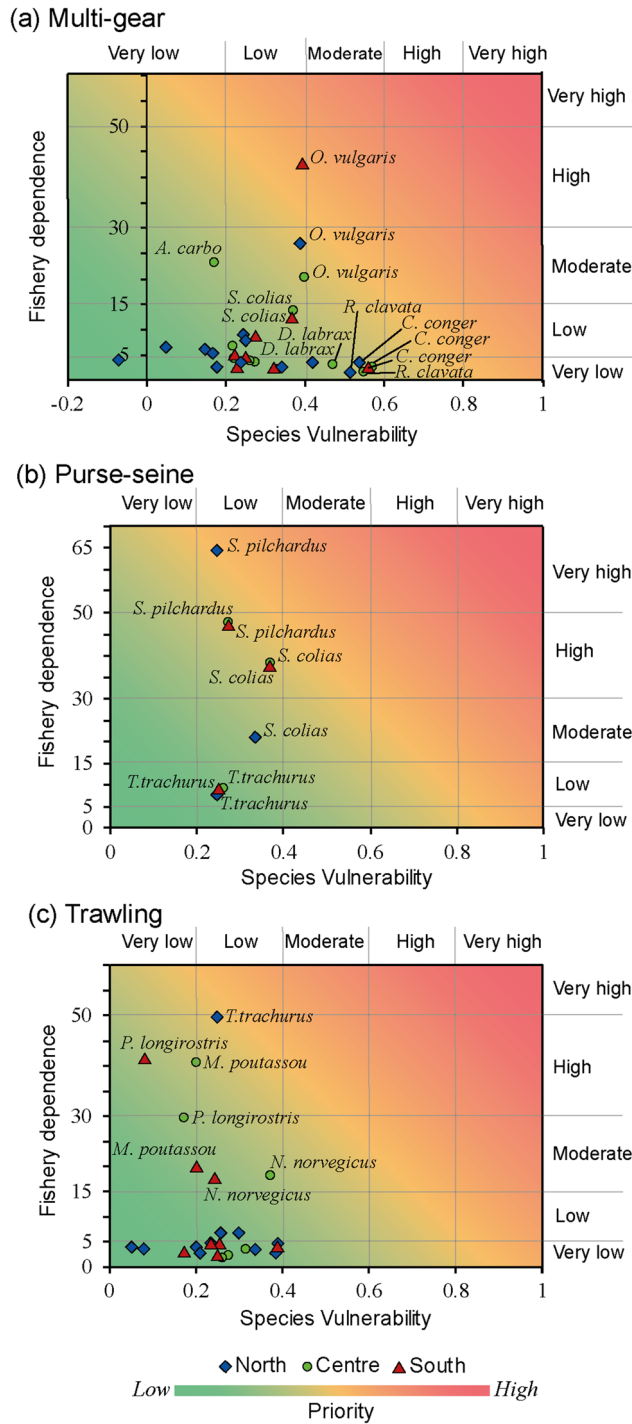


Figure 6. Prioritization plots of species of each fishing fleet (a-Multi-gear; b-Purse-seine; c-Trawling) and area (North-red; Centre-blue; South-green), considering the main species contributing to the total ecological vulnerability for the RCP 8.5 scenario (*x* axis) and considering the fisheries dependence on the species (*y* axis; average contribution of landings weight and landing economic revenue). These type of plots are adapted from⁷. Only species that contributed to the total vulnerability of the fisheries landings or revenues in more than 3% are plotted and only species with higher priority are labelled. See tables of Supporting Information S7, S8 and S9 for a full list of species and classification. Green colour represents low prioritization values and red high prioritization.

In purse-seine fleets, the species targeted were classified as low vulnerability species (Supplementary Table S8 online). However, the number of species landed was low. Consequently, for of *S. pilchardus* the fishery

dependence was high in the centre and south area and very high in the north (Fig. 6b). The dependence on *S. colias* was classified as high in the centre and south and *T. trachurus* was classified as low fishery dependence in the three areas (Fig. 6b).

Trawling fleet target species were mainly classified as very low or low vulnerability. On the other hand, the fishery dependence on some species was moderate or high. Specifically, in the north, the fishery had a high to very high dependence on *T. trachurus* (Fig. 6c). *M. potassou* in the centre area and *P. longirostris* in both the centre and south areas were seen as species with a high dependence from fisheries. The fishery dependence on *N. norvegicus* in the centre and south areas was moderate (Fig. 6c).

Discussion

In many ecosystems, the high exploitation of fishing resources has resulted in the decline of long-lived species, that are usually highly sensitive to environmental changes and anthropogenic pressures^{49–51}. In Portugal, there has been a decline in species that are classified as long-lived and highly sensitive, such as elasmobranchs, related to high fishing pressures^{39,52}. However, no common trends in ESL were observed across areas or fishing fleets and we did not observe a general decline in the ESL between 1989 and 2015, because species with higher sensitivity were not the most landed species. Thus, their contribution to the average sensitivity was low. Also, the group of elasmobranchs composed mainly of long-lived species in many cases are under-reported in the official landings or are not reported at a species level, limiting the inclusion of these groups, such as *Raja sp.*, in the sensitivity analysis^{52,53}. The reconstruction of the landings for mainland Portugal between 1938 to 2009 revealed that landings peaked in the period between 1964 and 1972 followed by a decline⁴². Hence, the years evaluated here (1989–2015) correspond to a period with declining landings and we cannot exclude the possibility that the abundance of more sensitive species were already diminished, shifting the perception of the baseline^{54,55}.

Spatial differences in ESL within each fleet were probably related to the differentiated ecological assemblages off the Portuguese coast⁵⁶, such as *S. colias*, which is more abundant in centre-south Portugal⁵⁷, and showed greater contributions to the ESL of purse-seiners in the central and south areas compared to the north where *S. pilchardus* is the main species. Moreover, spatial differences might be a consequence of cultural and traditional specific fisheries and licensed gears, such as the case of the *A. carbo* for multi-gear fleets in the central area^{58,59}. Trawling was the only fleet that presented similar trends in the ESL between areas and could be related to the lower degree of selectivity in trawling fleets^{60,61}.

As expected, fluctuations in species landings partially explained the temporal changes in ecological sensitivity of the landings. Previous studies described a decline in landings of *L. caudatus* and *C. conger* in the late 1990s and an increase in *S. colias*^{28,62}. The decline in moderately and highly sensitive species, such as *C. coelolepis*, *L. caudatus* and *C. conger*, in combination with the increase in species of low sensitivity, such as *S. colias*, explained ESL decline in the centre and south areas for multi-gear landings. The ESL in purse-seine fleets had low variability because they target pelagic short-life-span and fast-growing small and medium pelagic fishes with low sensitivity^{9,63}. The increase in sensitivity in trawling fleets in the early 2000s coincided in time with significant species compositional community changes in distribution and abundance in Portugal described by Moura et al. (2020) from independent fisheries data. Other factors, such as the exploitation of new or deeper areas³⁷, as well as the recovery of stocks with higher sensitivity due to management measures, may have also contributed to the increase in sensitivity of the landings in trawling fleets. The analysis of temporal changes in sensitivity of the landings allowed us to account for the life history traits of species landed and understand how this could affect the ecological vulnerability of the landings in the long term.

The ecological vulnerability of the landings is partially determined by the sensitivity of the species, but also by their exposure and adaptive capacity²⁰. The EVL was similar between both climate change scenarios (RCP 4.5 and RCP 8.5), with slightly higher values for the RCP 8.5 as expected, since the reported vulnerability values of the species are higher for this scenario³⁹. Differences in vulnerability between climate change scenarios were driven by the level of exposure and when combined with the information on sensitivity, adaptive capacity and landings, the weight of differences in exposure had a lower impact on the overall EVL. At spatial level, between 2010 and 2015, only multi-gear fleets presented a latitudinal gradient with an increasing EVL_(kg) from north to south. This latitudinal gradient was mainly driven by the increase in ecological exposure and decrease in adaptive capacity southwards. A higher exposure to environmental changes and higher vulnerability of fisheries has been described for the south of Portugal in comparison to the centre and north areas^{39,62,64}. Therefore, management plans for adaptation to and mitigation of climate change should consider this regional vulnerability differences. Proposing management measures to decrease the exposure of species to climate change would be difficult, since this depends on large-scale processes³⁹, but management measures to increase the adaptive capacity can be implemented at a regional level. The adaptive capacity of the species in Bueno-Pardo et al.⁵⁹ was mainly calculated on indicators related to the fishing stock status and exploitation. Thus, any measure directed at decreasing overfishing and improving the sustainable management of the fisheries would increase the overall adaptive capacity of the target species and decrease the EVL¹.

Differences in vulnerability of landing weights and revenues between fishing fleets and areas were explained by changes in species contribution to vulnerability and differences in species mean price (€·kg⁻¹), highlighting the importance of considering the economic value of species for a proper understanding of the exposure of fisher communities^{11,65}. Specifically, the higher vulnerability of multi-gear fleets in the south was mainly explained by *O. vulgaris*, where the fishing community highly depends on this resource^{62,66}. The vulnerability of *O. vulgaris* is low to moderate³⁹, but there are still important uncertainties in the direction of the effects of climate change on this species^{62,67,68}. In the case of the purse-seine fleets, the differences between areas were explained by the greater dominance of *S. pilchardus* in the north and *S. colias* in the centre and south areas. Due to the socio-cultural importance of sardines in Portugal^{34,43}, its price is higher than the price of *S. colias* and the contribution of

sardines to the $EVL_{(€)}$ of purse-seine fleets in the central and south areas was higher. Opposite to multi-gear and purse-seine fleets, trawling fleets in the central and south areas presented the lowest $EVL_{(kg)}$, because the main contributor was the blue whiting, which is considered a low vulnerability species with a high adaptive capacity³⁹. Still, in terms of economic revenue, blue whiting has a low value and other species with higher commercial value, such as the crustaceans *P. longirostris* and *N. norvegicus*, contributed the most to $EVL_{(€)}$. Interestingly, *P. longirostris* has increased in abundance in the Mediterranean and has shown northward expansion presenting new fishing opportunities^{69,70}. Climate-related changes have been positively related to the dynamics of the stock⁷¹. Therefore, considering that in Portugal, the landings of this species have increased in the last decades^{28,62}, it may contribute to increasing the resilience of trawling landings, diversifying the species targeted with the inclusion of low vulnerability species.

The vulnerability of the species is only one aspect to account for in the management of marine resources and fisheries. To increase the resilience of the fisheries, it is necessary to have an ecological-based approach for diversification of resources^{37,72}. In different areas of the world, it has been observed that fishing communities that had a higher diversification of target species were able to cope better with fluctuations, not only in the landings, but also in the market prices^{3,4,73}. In Portugal, the purse-seine fishing fleet presented the least species diversity. The main target species of this fishing fleet are pelagic species that tend to have higher exposure to climate change. However, the high exposure of these species is compensated with a low sensitivity which, together with measures to improve the adaptive capacity of the stocks, could lower the vulnerability of the fishery. It should be noted, however, that in the three areas considered, the fishing fleet presented a high to very high fishing dependence on sardines and a collapse of this species could have a large impact on the socio-economy of this sector⁷⁴, as has occurred in the past due to a combination of environmental fluctuations^{75,76}, poor management, and high exploitation rates^{77,78}. For the purse-seine fishery, we suggest a special focus on the management of small pelagic fishes, considering the diversification of species captured, economic processing at auction (fishery valorisation) or gear/license diversification, among other measures, to increase the resilience and adaptive capacity of the purse-seine fleet landings. For example, seines could target other species with marketable interest such as anchovy, which have been increasing in purse-seine fleets recently⁷⁹. Such changes would contribute to increasing the resilience of the seine fishery.

On the other hand, landings of the multi-gear fleet rely on a wider range of species due to the diversity of gears used. Thus, although this was found to have the highest EVL, this vulnerability is compensated with a low fishing dependence on a single species^{35,62}. However, the high dependence of multi-gear fleets on *O. vulgaris* and the limited knowledge about how the population dynamics of this species might be affected by changes in the environment, should be accounted for when managing this fishery⁸⁰. Also, considering trawling, the species portfolio was wide, but three species were classified as high fishing dependence: *T. trachurus*, *P. longirostris* and *M. potassou*. Focusing on the landing weights of *T. trachurus* and *M. potassou*, the fishing dependence was very high, but the mean auction price (€/kg) was very low. Increasing the first sell price of these species could benefit fishers' income and potentially reduce the need for high fishing rates⁸¹. However, a full socio-economic assessment of the value chain of the species should be performed to avoid unintended consequences or maladaptation⁸². For example, high increases in prices for final consumers for species that are important sources of protein could have unintended consequences on communities with low wages, such as may be the case of *T. trachurus* in certain social sectors of Portugal⁸³. The species prioritization plots allowed us to identify in an easy and rapid manner which are the fleets with higher dependence on more vulnerable species. This tool can be used to discuss and advice potential management strategies. But, other aspects such as conservation of key species for the ecosystem can be also combined with the criteria used.

Future fishing adaptation plans should combine information on ecological vulnerability and diversification of resources at a regional scale to ensure a successful assessment and implementation of measures, as it has been recently emphasized in a climate risk assessment at European scale²⁴. The values of EVL calculated in this study express relative vulnerabilities comparing values within Portugal and only allow comparison between the study area⁸⁴. Most estimation regardless fishing fleets rely below 0.5 vulnerability. Thus overall, the expected impact is moderate to low. The vulnerability of a species is not a static value and partially depends on adaptive capacity, which is affected by how well the resources are managed³⁹. High adaptive capacity at present does necessary means that the necessary measures are being implemented to maintain this capacity in the future⁸⁵. Considering that the stock exploitation status could change in the future, a periodic update of the vulnerability of species and ecological vulnerability of landings is required, evaluating the changes in exposure and adaptive capacity. The ecological vulnerability of the species landed, evaluated in the present study, can be considered as a measure of the ecological exposure of the fishery itself, and is a first step toward integrating ecological information within an entire socioeconomic vulnerability assessment of the fisheries.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Author contributions

M.A.P., J.B.P. and F.L. designed the study. M.A.P., J.B.P., M.F. and F.L. performed the analyses and data curation, with support from J.N.M. and A.O. who also contributed to data curation. M.A.P. wrote the original draft and J.B.P., F.L., M.A.T. edited and reviewed the original draft. M.A.T. and F.L. obtained the funding for the study. All authors discussed the analyses, commented on the manuscript and approved the final manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to M.A.-P. or F.L.

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