Structural and functional trends indicate fishing pressure on marine fish assemblages

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Summary

1. Conservation science increasingly focuses on how ecosystem functioning is affected by anthropogenic pressures, which implies an understanding of the structural and functional changes in biological assemblages and requires indicators to detect such changes within a suitable time frame.

2. A novel approach that combines the spatial analysis of fishing gradients (based on vessel monitoring system records) with distance-based linear models was used to assess the response of several functional and structural metrics of fish assemblages to gradients of trawling, within four distinct habitat types. In addition, critical thresholds of trawling intensity were identified for the most sensitive metrics through piecewise regression models.

3. Overall, total biomass and dominance (i.e. number of species that make up 90% of the total biomass) metrics as well as metrics representing vulnerable features (such as chondrichthyes, species with very low resilience and sedentary species) were shown to be sensitive to fishing. Our results suggest that decreasing trends in these indicators are likely to be associated with direct and indirect fishing effects acting synergistically on specific features of fish assemblages leading to its homogenization, with likely impacts on ecosystems resilience.

4. Critical thresholds at high, medium and low fishing intensity levels were identified depending on the metric used to assess fishing impacts, suggesting that it is difficult to define a single global target for fishing management as it ultimately will depend on management and conservation objectives (e.g. maintenance of biomass vs. maintenance of structure and function).

5. Synthesis and applications. A key goal of the applied approach was to provide short-term indicators that are sensitive to gradients of trawling intensity and can be extrapolated to a broader geographical region. The identification of thresholds of fishing pressure that fish assemblages can withstand before ecosystem functioning is altered is key for the development of indicators as warning mechanisms, as well as to assess performance measures for management. Understanding responses to other pressure sources (e.g. pollution, dredging) requires further research, and combining an integrative functional traits approach with a wider range of pressures may help make this achievable.

Key-words: critical thresholds, ecosystem function, fish assemblages, fishing pressure, guild approach, response models, soft-substrate marine habitats, structural and functional metrics

Introduction

In recent years, structural and functional indicators of anthropogenic disturbances on marine assemblages have become an important issue in applied ecology (Bremner 2008; Auster & Link 2009; Mouillot et al. 2012). It is widely recognized that structural and functional approaches, through the analysis of metrics (i.e. measures that describe ecological features), have several advantages in the detection of changes in assemblage functioning, compared with strictly taxonomic-based methods, as they represent the species adaptations to the environment and
their response to stress (Elliott et al. 2007; Juan, Thrush & Demestre 2007; Bremner 2008; Rochet et al. 2010; Mouillot et al. 2012).

Since species have distinct sensitivities, differences in abundance distributions are expected under stress, namely with some species that share the same features decreasing in abundance while others remain stable or even increase (Bremner 2008; Mouillot et al. 2012). On the other hand, some disturbances can lead to changes in species abundances without shifts within functional guilds (i.e. functional redundancy), thus not affecting the assemblage’s function (see Bremner 2008; and Rochet et al. 2010 for details about compensation mechanisms). Biogeographical dissimilarities in species distributions lead to regional variation in assemblages that provides little opportunity for generalization and comparison of anthropogenic effects, a problem that may be overcome by using structural and functional metrics as indicators (Elliott et al. 2007; Bremner 2008).

Together, these findings suggest that structural- and functional-based metrics can be powerful as indicators of changing assemblage in addition to making such changes easier to interpret, compare and predict in a functional perspective (Rochet & Trenkel 2003; Fulton, Smith & Punt 2005; Bremner 2008; Mouillot et al. 2012), as demonstrated for benthic invertebrate assemblages (e.g. Tillin et al. 2006; Juan, Thrush & Demestre 2007). However, while fish population-based metrics are well developed to detect fishing disturbance, considerable less attention has been given to assemblage-based metrics and, in the latter case, the use of trait-based indicators is still in its infancy (see Rochet & Trenkel 2003 for a critical review). Despite the suggestions that some structural and trophic-related metrics are good indicators of exploitation (e.g. Rochet & Trenkel 2003; Cristina et al. 2006; Methratta & Link 2006; Auster & Link 2009; Rochet et al. 2010; Dimech et al. 2012), information concerning a wide range of structural measures and functional guilds (i.e. diversity, abundance, trophic structure, mobility, resilience) is still lacking or dispersed, which implies a poor understanding of fishing effects on assemblage functioning. Additionally, most previous short-term assessments focused on sites with distinct levels of fishing disturbance (e.g. heavily fished vs. un-fished sites). Consequently, there is an urgent need to find short-term indicators that are sensitive to gradients of fishing pressure in order to better understand the patterns of change and follow environmental impact gradients, which constitutes an essential property of a good indicator (i.e. to be capable of detecting changes along gradients of pressure; Greenstreet & Rogers 2006).

By modifying seabed habitats, disrupting food web processes and removing species (e.g. target, large-bodied, vulnerable, bycatch), bottom trawling activities can have dramatic consequences on marine ecosystems (Gristina et al. 2006; Tillin et al. 2006; Juan, Thrush & Demestre 2007; Dimech et al. 2012). This study relies on both structural and functional metrics of soft-substrate fish assemblages to assess patterns of change under gradients of trawling intensity. The applied approach compared the response models of those metrics estimated from 5 years of scientific sampling surveys along the Portuguese coast. The consistency in the metrics response among four habitat types allowed the selection of a set of measures sensitive to increasing levels of fishing intensity and, respectively, threshold points. These results support discussion about the usefulness of fish-based metrics as indicators of changes in assemblage function, with likely effects on marine ecosystems functioning.

Materials and methods

STUDY AREA AND HABITAT TYPES

The study area extends from 36°N to 42°N, covering all the Portuguese continental coast with a depth range between 20 m and 460 m (Fig. 1). Since the distribution of marine fish species is affected by habitat features, depending on their ecological needs and physiological tolerances (Rice 2005), the study area was divided into four habitat types based on previous studies on the distribution patterns of fish assemblages, topographical features, oceanographic conditions (Fiúza, Macedo & Guerreiro 2005). The consistent in the metrics response among four habitat types allowed the selection of a set of measures sensitive to increasing levels of fishing intensity and, respectively, threshold points. These results support discussion about the usefulness of fish-based metrics as indicators of changes in assemblage function, with likely effects on marine ecosystems functioning.
1982; Gomes, Serrao & Borges 2001; Sousa, Azevedo & Gomes 2005; Figueiredo et al. 2007) and sediment charts from Hydrographic Institute of Portugal (Charts 1: 150 000): (1) north habitat type, continental shelf (<200 m deep) located from Minho River to Cape Raso (38°42’0°N), which is relatively wide and flat with a predominance of coarse sand and gravel substrates as well as several rocky areas; (2) centre habitat type, located between Cape Raso and Cape São Vicente (37°13’30″N), also corresponds to a continental shelf section (<200 m deep) but narrower and steeper with predominance of coarse sand substrates and some rocky patches; (3) south habitat type, steeper section of the continental shelf (<200 m deep) from Cape São Vicente to Vila Real de Santo António, characterized by fine and medium sand sediments poorly calibrated; (4) deep habitat type, continental slope throughout the coast (>200 m deep) mainly composed of fine sands and mud sediments.

**STRUCTURAL AND FUNCTIONAL METRICS OF FISH ASSEMBLAGES**

The fish assemblage database was compiled from a 5-year time series (2006–2010) of scientific sampling surveys carried out by the Portuguese Institute of Sea and Atmosphere (IPMA), with the RV ‘Noruega’, during September–October. Each survey followed a mixed sampling scheme comprising 97 sampling stations (66 stations distributed over a fixed grid with 5 per 5 miles and 30 random stations) spread throughout the study area, where 30-min trawls were performed at a constant speed (3.5 knots) during the daylight using a bottom trawl (14 m headline; ground rope with rollers; 20 mm cod-end mesh size).

In order to analyse structural and functional changes in soft-substrate fish assemblages due to trawling impacts, a set of functional features was assigned to every species, according to the previous classification of Henriques et al. (2008) updated with available literature and FishBase online database (Froese & Pauly 2012), namely: trophic level, length at first maturity, life span, mobility, trophic guild, abundance, commercial value, resilience (see Appendix S1). Afterwards, 24 metrics representing a range of fish assemblage attributes, including measures of species composition and diversity, abundance, trophic structure, resilience and mobility, were estimated per sample (haul) after standardization per unit of effort (Table 1). Individuals were quantified in biomass (kg h⁻¹), as it is expected to be the most sensitive measure to fishing-induced changes (Houle et al. 2012). Metrics were selected based on the ecological features of marine soft-substrate fish assemblages and their response to anthropogenic pressures, including fishing (Rochet & Trenkel 2003; Fulton, Smith & Punt 2005; Labropoulou & Paparistomou 2005; Greenstreet & Rogers 2006; Henriques et al. 2008; Blanchard et al. 2010; Rochet et al. 2010; Shin et al. 2010; Dimech et al. 2012). As pelagic species are strongly affected by climatic and environmental factors (Coll et al. 2008), are not entirely dependent on the substrate and their abundance is underestimated in bottom trawl samples (Labropoulou & Papaconstantinou 2005), they were excluded from the analyses (see Appendix S2).

**MAPPING TRAWLING INTENSITY**

Trawling intensity was analysed using vessel monitoring system (VMS) data, obtained from an automated satellite-based onboard system that records time, speed and position of vessels at sea (Witt & Godley 2007; Fock 2008). Since 2005, this system is mandatory in Europe for fishing vessels larger than 15 m (Witt & Godley 2007; Fock 2008), providing a robust way to spatially measure fishing intensity (e.g. Mills et al. 2007; Witt & Godley 2007; Fock 2008). Using VMS data from 2006 to 2007 with records at every 2 h, fishing intensity of trawlers (129 vessels) operating in the Portuguese continental coast was estimated applying GIS techniques in ArcGIS 10.1 software. As VMS is unable to discriminate between different types of activity (e.g. steaming, fishing, in port, navigation), data were filtered by typical trawling speed (2–5 knots) in order to keep only points that likely correspond to fishing operations (Fock 2008; Alemany, Irizarbe & Acha 2012). Route lines per day and vessel were then created by joining successive position points, and a mask of 6 nautical miles from the coast was applied to eliminate the positions where vessels were leaving or nearing ports (Witt & Godley 2007), since trawling activity is forbidden within this area (Portaria no. 1102-E/2000). In addition, a fishing intensity raster was created per year based on the density of route lines per grid cell (pixel area of 1 nm²), and the two annual rasters were then combined, cell by cell, by assigning their mean value into a final raster output (ArcGIS multiple raster operation tools). Each sample was then classified according to raster mean values (fishing intensity). Finally, 5 classes of fishing intensity were defined (1 – none or very low, 2 – low, 3 – moderate, 4 – high and 5 – very high) using Jenks natural break classification for visualization and interpretation purposes only. This classification method outlines the best arrangement among classes by seeking to reduce the variance within classes while maximizing the variance between classes (Alemany, Irizarbe & Acha 2012).

**STATISTICAL ANALYSES**

Mapping of VMS data highlighted considerable heterogeneity in the fishing intensity distribution, with the south coast being the most intensively trawled (Fig. 1). Therefore, the data were analysed according to a gradient of fishing pressure (raster intensity values) per habitat type.

Before identifying sensitive metrics, preliminary analyses were done in order to accomplish the assumptions of the linear modelling analyses (Anderson, Gorley & Clarke 2008). For each habitat type, Draftsman plots were drawn to visually assess when the metric distribution was notably skewed and to detect cases of multicollinearity (Clarke & Gorley 2006; Anderson, Gorley & Clarke 2008). Fish-based metrics were square-root-transformed, and only one of the metrics from redundant pairs (|r| ≥ 0.90) was retained as a proxy for the other (Clarke & Gorley 2006; Anderson, Gorley & Clarke 2008). Extreme multivariate outliers were also identified and removed through the observation of principal coordinates analysis (PCO) plots based on Euclidean distances among all pairs of samples with all metrics previously normalized to place them on a comparable measurement scale (Anderson, Gorley & Clarke 2008). The resultant data sets for the groups of replicate samples (north, centre, south and deep habitat types) comprised non-redundant and non-skewed metrics, samples without extreme outliers and representative metrics.

For each habitat type, distance-based linear models (DISTLM; Anderson, Gorley & Clarke 2008) were used to identify the relationship between fish-based metrics (explanatory variables) and
the gradients of trawling intensity (coded into model matrices based on Euclidean distance among the raster values defined above, inspired in the study of Hallett, Valesini and Clarke 2012). The philosophy behind DISTLM is quite similar to the PERMANOVA routine but for quantitative and continuous variables, and attempts to find which combination of fish-based metrics (data cloud of explanatory variables) best fits the variation observed in fishing gradient (data cloud of response variable), by partitioning the total variation according to regression models (see Anderson, Gorley & Clarke 2008). Fish-based metrics were subject to a forward selection procedure and the best models selected based on the corrected Akaike information criterion (AICc), which was developed for cases where the number of samples (n) relative to explanatory variables (q) is small (Anderson, Gorley & Clarke 2008 and references therein). The final set of metrics that best responded to changes in trawling intensity gradients were selected if they were part of the best solution model in at least half of the types and if they had a predictable steering response (i.e. increase or decrease trend).

All the above-mentioned statistical analyses were performed using PRIMER 6 package with PERMANOVA+ (Clarke & Gorley 2006; Anderson, Gorley & Clarke 2008), and 4999 permutations were used to calculate significance (α = 0.05).

Following the approach of McClanahan et al. (2011) and Samhouri, Levin and Ainsworth (2010), several models (i.e. intercept, linear and piecewise) were used to analyse the global relationships between each selected sensitive metric and the fishing gradient (all data sets pooled together), in order to identify critical thresholds (i.e. values of fishing intensity above which significant changes are detected) to support ecosystem-based management targets. Estimated thresholds correspond to the intersection between two regression functions with different slopes observed for piecewise models (Samhouri, Levin & Ainsworth 2010). The analyses were conducted using the 'segmented' package in R software (R Development Core Team 2008), and the robustness of models and predicted thresholds was assessed through AIC scores, delta AIC across the lower-valued AIC models, significance (α = 0.05) and uncertainty intervals (95%).
Results

The DISTLM results showed that several fish-based metrics responded to increasing levels of fishing intensity (Table 2). The goodness-of-fit of the models was generally high, with the highest percentage of explained variation corresponding to the centre habitat type (64.7%) followed by the south and deep types (45.7% and 41%, respectively) and the lowest value in the north habitat type (29.6%). Although the number of metrics selected in each model varied among types, some metrics were consistently selected (i.e. at least by half of the models; Table 2). These include total biomass, dominance, sedentary individuals, chondrichthyes and individuals with very low resilience, all of which decreased as fishing intensity increased, which in the case of dominance means that the assemblage is progressively dominated by fewer species with the increase in fishing intensity. Among these five metrics, total biomass and dominance stand out since they were selected in at least three of the four models and accounted for a great proportion of explained variation (see Table 2 for details), except in the deep habitat type where the highest variation was explained by the proportion of sedentary individuals.

Although the metrics proportion of chondrichthyes and proportion of individuals with very low resilience were selected in at least half of the models, they explained lower variation in the best solution models (Table 2). These results suggest that the metrics most sensitive to the fishing gradients were total biomass and dominance, followed by the proportion of sedentary individuals and proportion of individuals with very low resilience and finally by the proportion of chondrichthyes.

Some metrics were only chosen by one of the models and were therefore not selected to the final set of sensitive metrics, as they probably represent specific features of a particular habitat type (e.g. total number of species, individuals with high commercial value; Table 2).

Overall, piecewise models had a better fit than intercept and linear models, with the exception of proportion of chondrichthyes where a linear model was selected (gradual decreasing change), and dominance where no significant model was observed (Table 3). Consequently, no significant critical thresholds were identified for these two metrics (Table 3). Piecewise model results evidenced three main critical thresholds of fishing intensity, depending on the type of metric assessed (Fig. 2; Table 3). The first at low levels of trawling intensity for the metric total biomass (1358 route lines nm$^{-2}$; Fig. 2; Table 3), while the second was identified for the metric proportion of sedentary fish at medium levels of fishing intensity (4018 density of route lines nm$^{-2}$). Finally, a break point of 7165 density of trawling route lines nm$^{-2}$ (high fishing intensity class) was observed for the functional metric proportion of biomass of species with very low resilience but with higher uncertainty interval range (Fig. 2; Table 3). Despite some variance identified within data sets, a general decreasing trend as fishing effort increased was observed for these metrics, more marked before break points (see Fig. 2 for details).

Discussion

Several fish-based metrics were identified as sensitive to differences in trawling intensity, indicating that trawling caused changes on both structural and functional aspects of soft-substrate fish assemblages. The consistent changes in a selected set of metrics in most habitat types analysed suggest that trawling pressure was the main factor responsible for these changes, rather than other environmental...
Table 3. Models fitted to selected metrics of fish assemblage along the gradient of fishing intensity in the Portuguese coast: intercept only, linear model and piecewise linear model. Akaike information criterion (AIC) is presented for all models (significant values in bold) as well as the delta AIC value between the two lowest AIC values. The estimated break points (and uncertainty intervals – 95% UI) are shown whenever significant results were obtained for each piecewise model.

<table>
<thead>
<tr>
<th>Metrics</th>
<th>Interception</th>
<th>Linear</th>
<th>Piecewise</th>
<th>Δ AIC</th>
<th>Break point</th>
<th>95% UI</th>
<th>Model selected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total biomass</td>
<td>2210</td>
<td>2198</td>
<td>2185</td>
<td>13</td>
<td>1358</td>
<td>909–1087</td>
<td>Piecewise</td>
</tr>
<tr>
<td>Dominance</td>
<td>396</td>
<td>398</td>
<td>395</td>
<td>1</td>
<td>4018</td>
<td>3064–4972</td>
<td>None</td>
</tr>
<tr>
<td>% chondrichthyes</td>
<td>1212</td>
<td>1210</td>
<td>1213</td>
<td>2</td>
<td>7165</td>
<td>5206–9125</td>
<td>Linear</td>
</tr>
<tr>
<td>% sedentary</td>
<td>1381</td>
<td>1367</td>
<td>1347</td>
<td>20</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% very low resilience</td>
<td>1448</td>
<td>1450</td>
<td>1426</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

constraints, such as habitat and interannual variability (among the 5 years in this study).

Trawling fisheries are characterized by low selectivity with low bycatch survival and a remarkable level of physical damage to habitat, often resulting in heavily exploited areas dominated by few opportunistic or tolerant fish species, as observed in other biological groups like benthic invertebrates (e.g. Tillin et al. 2006; Juan, Thrush & Demestre 2007; Kaiser & Hiddink 2007; Dimech et al. 2012). Such fishing methods can have both direct and indirect effects that ultimately change ecosystem structure and function through dynamic processes of bottom-up, wasp-waist and top-down control (Caddy & Garibaldi 2000; Cury, Shannon & Shin 2001). Present results support these predictions as they indicate trawling-driven gradual declines in total fish biomass, along with an increase in dominance by few species, with particular changes in the most sedentary and very low resilient species as well as in chondrichthyes.

Although total biomass was selected for all models and was very sensitive to fishing (critical threshold point observed at low levels of fishing intensity), its changes can be difficult to predict due to the indirect effects along food webs (e.g. depletion of top predators and eutrophication) and environmental variability (e.g. in upwelling systems). These effects can lead to fluctuations in the abundance of small-sized pelagic and demersal fish species with gregarious behaviour (e.g. Farina, Freire & Gonzalez-Gurriaran 1997; Rogers & Ellis 2000; Coll et al. 2008; Barausse et al. 2011), which in turn can drive to inconsistent responses of total biomass along different levels of fishing effort, as observed by Piet and Jennings (2005). Therefore, here the predictable trend in total biomass was probably detectable due to the exclusion of pelagic species, suggesting that it can be a useful indicator when used with caution and together with other measures (e.g. biomass and/or proportion of functional groups; see Caddy & Garibaldi 2000; Rochet & Trenkel 2003). Total biomass showed a steep slope at low levels of fishing effort that became gradual from the medium effort level up (see Fig. 2), which is in agreement with theoretical principles of strong mortality rates during the first stages of exploitation followed by gradual changes (Piet & Jennings 2005). Still, the use of this earliest point of change for management purposes (i.e. as a critical threshold) should be further investigated, as initial changes may have already occurred in many habitats around the world (Piet & Jennings 2005). These predictions are also supported by Houle et al. (2012) who assessed total biomass as poorly specific to fishing but very sensitive to low effort levels, emphasizing the cautions needed in its use as an indicator.

However, not all fish biomass was similarly affected, suggesting that structural changes are likely to occur with exploitation (Dimech et al. 2012). The observed decreasing trend observed in the proportion of fish with very low resilience and of sedentary species can be linked to their weak capacity to recover (e.g. Gristina et al. 2006), associated with their limited movement beyond home ranges (e.g. Dimech et al. 2012). Such changes can increase the assemblage’s vulnerability and ultimately affect its functioning at least on intensively trawled areas, since the most persistent species and those usually less resilient are negatively affected by this impact. However, further research should focus on the relationships between functional and structural groups and their links within ecosystems processes in order to better understand the consequences of these changes (see Allen & Clarke 2007). Moreover, critical thresholds of these metrics were found at medium and high levels of fishing intensity, contrasting with the threshold observed for total biomass (strong decrease at low levels). This mismatch might be related with differences in the type of measure used between metrics, catch-sampling variability or result from the occurrence of structural changes only at higher levels of effort. Break points of the models measured in proportion (i.e. sedentary and very low resilient species biomass) occurred at higher levels of fishing intensity, which can be due to the fact that they do not reflect the different magnitudes of abundance and/or biomass among fishing intensity levels (which are more difficult to detect), and in contrast, they better reflect shifts in the assemblage function than measures of biomass. Conversely, the high catch-sampling variability characteristic of trawling gears, also influenced by soft-substrate fish assemblage heterogeneity, can have implications in the models’ capacity to detect thresholds
due to the high occurrence of zeros (absence of some species naturally less abundant). In this context, future attempts to find critical thresholds should include similar number of samples at each fishing intensity level. Present results provide insight into how difficult it can be to define a single global target for fishing management since it ultimately will depend on its purposes (e.g. maintenance of biomass vs. maintenance of structure and function) and strengthen the importance of accounting for variability in fisheries management (under the precautionary principle).

As expected, due to their specific life-history strategy characterized by slow growth, late maturity, long life spans and low fecundity ($K$-strategy; Stevens et al. 2000; Gristina et al. 2006), chondrichthyes showed a decreasing linear trend with increasing of trawling intensity. In fact, the greatest proportions of chondrichthyes were detected between none or very low and medium fishing effort (see Fig. 2), but the high number of zeros characteristic of trawl surveys for uncommon species hid a stronger response, leading to a gradual decrease trend without any significant critical threshold identified. Since chondrichthyes are usually top predators, the effects of its stocks depletion can spread through the food chain (top-down control), resulting in large-scale changes on ecosystem functioning (e.g. reduction of lower trophic levels production; Caddy & Garibaldi 2000). Consequently, although no threshold has been identified, a baseline at medium level could perhaps be considered.

All these results pointed to a pattern of ecosystem degradation due to trawling activities, leading to their homogenization and consequent dominance by fewer species. As the stability of structural and functional groups depends on the diversity of life-history strategies, through density-dependent compensation by resilient members (functional redundancy; Tillin et al. 2006; Bremner 2008; Rochet et al. 2010), the homogeneity of fish assemblages can have a profound impact on the ecosystem resilience, making it more vulnerable (Elmqvist et al. 2003). Although the approach presented does not directly measure ecosystem functioning, which is determined by a complex interaction of all physical, chemical and biological components (Bremner 2008), it offers clear insights into how ecosystems are changing, since it focuses on the structural and functional trends of assemblages instead of species alone (Mouillot et al. 2012). Nonetheless, to better address the effects of trawling on ecosystem functioning, surveys must include other biological groups (e.g. mammals, invertebrates, micro-organisms) and abiotic factors along the fishing gradients in order to identify and quantify their interactions and connectivity. Ultimately, this should allow to understanding the underlying dynamic mechanisms responsible for the ecosystem functioning and in turn assess and predict the consequences of human actions, enhancing the sustainable management of marine ecosystems.

Finally, it’s noteworthy that although the mean trophic level, mean life span, proportion of predatory fish (corresponding to macrocarnivores in the present study), average fish weight have been pointed out as a promising indicators of fishing impacts (Rochet & Trenkel 2003; Blanchard et al. 2010; Shin et al. 2010), they were neither selected for the best models of the analysed habitat types

![Fig. 2. Critical threshold points of selected metrics of fish assemblage along the gradient of fishing intensity in the Portuguese coast. Full black lines represent the fitted piecewise or linear model, and dotted black lines represent the estimated break point. Fish assemblage metrics were fitted and represented with square root transformation ($n = 382$).](image-url)
nor showed a predictable response. Two main reasons may account for these results: (1) differences between fish assemblages, and (2) temporal scale and fishing intensity differences. (1) It is expected that fish assemblages under exploitation become gradually shifted to faster and small-sized species (Rochet & Trenkel 2003), but many of the pelagic species removed from the analyses have a gregarious behaviour (high abundance), low trophic levels, short life span and are small sized. Thus, it is possible that the differences of demersal species (usually not gregarious) that share those features are not enough to allow detecting a strong trend in the above metrics. (2) It is possible that long-term changes (along decades) in fish assemblages lead to a general decrease in those metrics, for instance in mean trophic level (e.g. Jennings et al. 2002; Coll et al. 2008), but this might not be detectable at the temporal and spatial scale addressed in the present study. In accordance, Nicholson and Jennings (2004) provide evidence that some of these metrics had low power in the detection of trends when using trawl data at short-term scales (<10 years). Furthermore, differences of fishing intensity along the gradients assessed might not be sufficient to strongly benefit the faster and smaller-sized fish species in the assemblages. Further research should include size-based indicators as they proved to be very sensitive to fishing effort (Piet & Jennings 2005; Houle et al. 2012).

A key goal in the proposed approach was to provide short-term indicators that are sensitive to gradients of trawling intensity and can be extrapolated to a broader geographical region. This represents an important step towards ecosystem-based management, as it provides tools compatible with management time-scales. The identification of short-term sensitive indicators and the establishment of threshold levels of fishing pressure that fish assemblages can withstand before ecosystem functioning is altered can contribute to the development of efficient tools (i.e. indices and ecological quality objectives) to assess the quality status of fish assemblages, as required by the European Marine Strategy Framework Directive (Directive 2008/56/CE). Combining other pressure sources (e.g. organic and inorganic pollution) with a functional traits framework may provide the next steps for more integrative indicators and thresholds to help support the development and use of indicators in marine environmental and fisheries management.

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References


Response of fish-based metrics to fishing pressure


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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Ecological features used to calculate fish-based metrics.

Appendix S2. List of pelagic species excluded from the analyses.