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Global meta-analysis of demersal fishing impacts on organic carbon and associated biogeochemistry

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Abstract

The potential threat of fisheries on seabed carbon is a topic of growing concern, yet existing literature presents inconsistencies leaving experts divided on the topic. We conducted a global meta-analysis to synthesize the current knowledge and quantify how demersal fishing impacts various biogeochemical properties. Direct impact studies revealed overall reductions in chlorophyll-a (Chl-a, 17%), phaeopigments (24%), and proteins (32%). Effects on these reactive compounds were more pronounced on surface sediment (0–2 cm), where the impact on total organic carbon (TOC) also became significant, demonstrating the effect of gear penetration, and highlighting that sampling strategies combining sediment layers can mask observed effects. Current velocity and primary productivity significantly influenced the direction and magnitude of fishing impacts. Trawling-induced subsurface reductions of TOC in low-energy habitats may affect carbon sequestration due to the preferential removal of semi-reactive carbon. Intriguingly, fishing intensity gradient studies showed an average increase in TOC in chronically fished areas, possibly reflecting fishing preferences for meso-eutrophic grounds. We estimate a ~300-day recovery period post-fishing for Chl-a, though values for other parameters are less certain. Limited data on seasonality, gear types, and an under-representation of studies in tropical and deep-sea areas pose challenges to quantifying global scale geochemical impacts

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of demersal fisheries. Knowledge gaps persist in understanding the fate of disturbed organic matter including its mineralization, transport, and sequestration. Nonetheless, our insights and estimates provide foundational knowledge that can contribute to science-based approaches for spatial fisheries management while preserving natural carbon dynamics on the seabed.

KEYWORDS

benthic impact, bottom trawling, carbon footprint, gear penetration, geochemistry, sediment

1 | INTRODUCTION

In the face of continuous population growth, fisheries play a vital role in global food provisioning (Costello et al., 2020). However, they may also be the most impactful direct human-induced stressor on the marine environment, given their extensive coverage across the world's oceans (Amoroso et al., 2018; Kroodsma et al., 2018; Watson, 2017). Demersal fisheries, operating along the seafloor, are believed to exert the greatest impact on marine ecosystems. This is attributed to their direct contact with the seafloor, leading to habitat degradation and mortality of benthic species (Boudouresque et al., 2009; Thrush & Dayton, 2002; Watling & Norse, 1998), in addition to their potential to overexploit commercial stocks (Jackson et al., 2001; Lotze et al., 2006). The existing body of knowledge on impacts of demersal fisheries predominantly focuses on their effects on commercial stock species and benthic communities (Hiddink et al., 2017; Sciberras et al., 2018; Thrush & Dayton, 2002). However, there is a notable scarcity of studies assessing the effects of fisheries on sediment biogeochemistry (Paradis et al., 2023).

Recent studies have suggested that their impact on biogeochemical parameters, such as carbon stocks and organic matter, may have far-reaching consequences on global climate change (Atwood et al., 2024; Sala et al., 2021). However, the limited available research on this topic yields contrasting results (Epstein et al., 2022), attributed in part to the diverse interactions between demersal gears and the seafloor.

The scraping action and hydrodynamic drag generated by bottom fishing gears can resuspend large volumes of sediment and organic matter (OM), leading to seafloor erosion (O'Neill & Summerbell, 2011; Puig et al., 2012). Additionally, demersal gears overturn and mix the surface sediment, modifying the natural vertical distribution of OM and altering the oxygenation of the seabed (Hale et al., 2017; Martín, Puig, Masqué, et al., 2014; Tiano et al., 2019). Concurrently, fisheries-induced mortality of benthic organisms and changes to community structure affects the processing of OM (Atkinson et al., 2011; Pusceddu et al., 2014; Ramalho et al., 2018). As a result, certain studies observe a decrease in OM due to sediment erosion (Mayer et al., 1991; Morys et al., 2021), while others report increases in OM attributed to sediment mixing and re-deposition (Palanques et al., 2014; Pusceddu et al., 2005; Sciberras et al., 2016). Both enhanced (Paradis et al., 2019; Polymenakou et al., 2005) and reduced (Pusceddu et al., 2014; Warnken et al., 2003) rates of OM remineralization have been attributed to sediment disturbance by demersal fishing gears, creating uncertainty regarding their ultimate impact on seabed carbon stocks.

These contrasting outcomes and interpretations are also the result of different methodological approaches and spatial variability of these studies. Studies where researchers experimentally disturb a particular site tend to reveal acute and more immediate effects of fishing disturbance (Bhagirathan et al., 2010; Ferguson et al., 2020; Sparks-McConkey & Watling, 2001; Tiano et al., 2021). In contrast, studies that collect samples from commercial fishing grounds often display chronic impacts (Martín, Puig, Palanques, et al., 2014; McLaverty, Eigaard, Dinesen, et al., 2020; Reiss & Kröncke, 2004; Tsikopoulou et al., 2022). Furthermore, different gear types can exert variable degrees of disturbance on the seafloor, resulting in diverse effects on sediment properties and biogeochemistry (Eigaard et al., 2016; Rijnsdorp et al., 2020; Tiano et al., 2019). Environmental conditions could also be an important factor driving the biogeochemical effects of demersal fishing disturbance. For instance, the OM flux to the seafloor decreases and is often found in a more degraded state as water depth increases (Dunne et al., 2007; Martin et al., 1987; Middelburg, 2018; Suess, 1980). The impact on the seafloor varies contingent to the type of substrate due to the different OM contents and remineralization processes inherent in sandy or muddy environments (De Borger et al., 2021; Sciberras et al., 2016).

The conflicting findings in studies examining fishery-induced biogeochemical impacts highlight the complex nature of this topic (Epstein et al., 2022). Furthermore, the influence of context- and site-specific characteristics complicates the extrapolation of these impacts to a global scale and creates uncertainty about our capacity for comprehensive estimates, hampering effective management decisions. The threat of demersal fishing to benthic carbon stocks has been suggested as a potentially significant contributor to global climate change (Sala et al., 2021). However, experts remain divided on the magnitude, uncertainties, and overall significance of this impact (Hiddink et al., 2023). To advance our understanding of this matter, a quantitative synthesis of the available knowledge would offer valuable insights and shed light on diverse perspectives surrounding this controversial subject.

Here, we conduct a meta-analysis of the impacts of demersal fisheries on sedimentological (e.g. grain size) and biogeochemical (e.g. organic carbon, pore-water nutrient concentration) properties. We also investigate how environmental factors such as habitat type season, water depth, bottom current velocity, and surface primary productivity shape the impact of demersal fishing, and we examine the potential recovery following disturbance.

2 | MATERIALS AND METHODS

2.1 | Data extraction and pre-processing

Data for this meta-analysis were extracted from the 'Demersal fishery Impacts on Sedimentary Organic Matter' (DISOM) database, which harmonizes studies assessing the effects of demersal fisheries in marine sediments across different habitat types, continental margins, and seasons (Paradis et al., 2023). Here, we focus on benthic studies where empirical data were collected in situ. Studies primarily based on modelled results, laboratory experiments, and studies addressing water column impacts were excluded from this analysis.

Study designs in this analysis were grouped into three different categories:

1. 'Experimental studies'—samples collected from in situ trawling experiments employing a control–impact (CI), or before–after (BA), or BACI sampling strategy.
2. 'Comparative control–impact studies'—samples collected on fishing grounds and control areas.
3. 'Comparative gradient studies'—samples collected along a fishing intensity gradient.

A more detailed description of the study designs can be found in Text S1. Control areas are defined here as sites that have not been disturbed by bottom fishing gear prior to being sampled in the study. However, we recognize that certain control sites are not 'true controls' since they have been fished in the past and may not represent their baseline conditions (Paradis et al., 2023; Figure S2d).

Studies from DISOM were included in the meta-analysis if they provided data on sedimentological and biogeochemical response properties. Only response variables for which at least three independent studies were available were included in the meta-analysis (Figure S1), leading to only 57 out of the 71 independent studies compiled in DISOM being included in this meta-analysis. Biogeochemical response variables consisted of concentrations of total organic carbon (TOC), total carbon (TC), total nitrogen (TN), chlorophyll-a (Chl-a), phaeopigments and phytopigments, pore-water nitrogen compounds (ammonia NH_x, nitrate NO_x), oxygen (O_2) consumption, and specific molecule classes (lipids, proteins, carbohydrates, and biopolymeric carbon [BPC]). TOC and total organic matter measured through loss on ignition (OM LOI) provide information on organic content and were combined under TOC in this meta-analysis, assuming a similar relative impact of fishing on both parameters. Sedimentological response variables consisted of mean grain size, and different grain size fractions (e.g. clay < 2 μm, mud < 63 μm, silt 2–63 μm, and sand 63–2000 μm).

Mean values, sample size, and a measure of variability (e.g. standard deviation, standard error, variance, 95% confidence interval) were extracted for each response variable and converted into standard deviations to calculate the effect sizes and variance (see Text S1). Where data were provided for individual samples rather than site averages, the mean and standard deviation for each site were calculated. When samples from a study were collected under different (i) environmental conditions (e.g. depth, sediment type, season), (ii) geographical locations, (iii) fishing gear, or (iv) fishing intensity, the means and standard deviations were calculated separately for each of these factors leading to more independent observations for specific response variables than the 57 studies that were included in the meta-analysis (see Text S1).

Metadata of the environmental conditions (e.g. water depth, habitat type, season) and fishing characteristics (e.g. fishing gear and intensity, and time since last fishing disturbance event, hereafter referred to as 'time since disturbance') were extracted from the published papers whenever provided. Additional environmental conditions (e.g. bottom current velocity, surface primary productivity, bottom oxygen concentrations) were extracted from Bio-Oracle (Assis et al., 2018) using the geographic coordinates of the sampling locations.

The sampling techniques varied substantially between studies (Figure S2c). Some studies provided total measurements of homogenized grab samples (~30 cm penetration depth McLaverty, Eigaard, Gislason, et al., 2020) or cores, while others provided measurements for different sediment depth slices. To harmonize sampling strategies, we classified and aggregated data into five different categories based on the biogeochemical processes occurring in them:

- 'Surface', for samples collected between 0 and 2 cm deep (within the lower boundary of oxygen penetration depth where highest degradation rates of organic material occur).
- 'Subsurface', for samples collected between 2 and 5 cm deep (below the most active zone, but with still high bioturbation activity).
- 'Deep', for samples collected between 5 and 10 cm deep (slow mineralization processes and lower boundary of bioturbation activity).
- 'Very deep', for samples collected below 10 cm depth.
- 'Full sample', where a sample was collected after homogenization of sediment within the first 30 cm.

2.2 | Log response ratio for experimental and comparative control–impact studies

The log response ratio (lnRR) was used to quantify the proportional change in sedimentological and biogeochemical parameters due to demersal fishing (Hedges et al., 1999). This metric was used to evaluate the effects of trawling disturbance for both experimental and control–impact studies, which were combined to generalize the broader impact of trawling using the available information. Negative values of lnRR indicate a decrease in the response variable in the fished area relative to the area before disturbance or relative to a control area. Positive values indicate an increase in the response variable in the fished area relative to before the disturbance or relative to a control area. Effect sizes were weighted by the inverse of the within- and between-study variances, calculated from the mean, standard deviation, and sample size values for each study (Borenstein et al., 2009). Observations where both the before and after impact (or control–impact) had a sample size of 1 were removed from the analysis as this prevents the calculation of variances and weights. For studies with sample sizes larger than 1 but where standard deviation values were not reported in papers or not provided by authors after these were contacted, missing standard deviations were imputed following Higgins and Li (2022). If one of either the before or after impact (or control–impact) measured sample size was 1 (i.e. $n=1$), the highest reported standard deviation for that response variable was assigned to the measure. Where the number of missing standard deviations exceeded half of the total reported means within a variable, no imputation was performed and no further analysis besides reporting the response ratio was carried out. Details on the number of removed observations and imputed standard deviations are reported in Tables S1 and S2.

For reporting and ease of interpretation, we quote lnRR values in the results text as % values, calculated as $\left(e^{\ln RR}-1\right)\times 100$. As an illustration, an lnRR of −1 represents a response of −63%, indicating a 63% decrease in response variable in fished area relative to a control, 0 represents no response and +0.7 represents a response of 100% increase.

2.3 | Standardized mean difference for comparative gradient studies

Due to the absence of a true control for most comparative gradient studies (67%), the calculation of lnRR of gradient studies was not possible. For these studies, the correlation coefficient (r) of the effect against fishing intensity gradient was extracted. Correlations were converted to standardized mean differences (SMD) to compare the magnitude of effect sizes across the three different study types (experimental, control–impact, and gradient studies) (Borenstein et al., 2009) (see Text S1). Only studies using quantitative measures of fishing effort (i.e. times fished per year) rather than qualitative (i.e. high, low) were incorporated in the analysis with the assumption that the effect will scale linearly regardless of the unit (Borenstein et al., 2009). While comparing effect size magnitudes between SMD and lnRR is unwarranted, these metrics can still provide a comparable indication of the direction of results.

As with the experimental and control–impact studies, gradient studies within the same study were grouped into different 'observations' based on their distinct environmental conditions such as differing sediment types, geographic location, or temporal circumstances (i.e. seasons).

2.4 | Overall effect of demersal fishing on sediment and biogeochemical parameters

To calculate the overall effect of demersal fishing on biogeochemical (Chl-a, phaeopigments, phytopigments, TOC, TN, TOC/TN, TC, oxygen consumption) and sediment parameters (mean grain size, clay, silt, mud, and/or sand content), multiple response ratios within the same study were first aggregated into a study-level response ratio, using the variance–covariance matrix of the sampling errors to account for dependence of observations coming from the same study. The variance of the study-level estimates was calculated as the sum of covariances of estimates within a study, divided by the number of estimates within a study squared (Viechtbauer, 2010). This step was necessary, as often studies reported (pseudo-) replicates of, for example, surface sediment characteristics, which cannot be treated as independent effect sizes. Subsequently, a random effects model with restricted maximum likelihood estimator (REML) was used to calculate the overall effects (Viechtbauer, 2010).

The analysis for experimental and control–impact studies was separated from that of gradient studies, as different metrics were used to calculate the effect of fishing.

2.5 | Effects of sample depths

The effect of fishing on different sediment depth strata was examined in experimental and comparative control–impact studies for response variables where there were data from at least three different independent studies for a given depth stratum. The mean response ratio per sediment depth stratum was calculated by fitting a weighted mixed effects model, using depth stratum as a factor, lnRR ~1 + depth stratum. Multiple effect sizes per depth stratum, per study, were first averaged as described above. There were insufficient data to examine the effect of fishing with depth stratum for gradient studies.

2.6 | Effects of environmental conditions

To examine the influence of environmental conditions on the physical and biogeochemical response to demersal fishing on different sediment depth layers in experimental and control–impact studies, we fitted linear mixed effects meta-regression models with the following covariables for each depth stratum: bottom current velocity, water depth, surface primary productivity, mean grain size, season, and habitat (e.g. lnRR ~1 + current velocity). It was only possible to examine the influence of fishing intensity and environment on different sediment depth strata when the depth stratum contained at least three different studies ($n=3$). In this analysis, multiple effect sizes within the same study were purposefully kept separate, so to account for between-study variations, we used the study id as a random factor in the mixed effects model (*random* = 1 | *study. ID*) (Viechtbauer, 2010).

2.7 | Recovery following disturbance

To examine the recovery of sedimentological and biogeochemical variables in experimental and control–impact studies following a fishing disturbance event, mixed effects meta-regression models as $\ln(RR) \sim \text{intercept} + \ln(t+1)$ were fitted to the data, where t is time since disturbance (days) and the intercept specifies the initial response to fishing disturbance (i.e. ln(RR) at time = 0). The use of natural logarithms for the days following disturbance was chosen to linearize the data. The slope of this model indicates the change in response variable over time. Not all studies reported time since disturbance, so subsets of the dataset had to be taken to perform this analysis. Time since disturbance was log-transformed since the magnitude of this variable ranged from hours to years.

2.8 | Sensitivity assessment

We explored the influence of studies with imputed study variance on the response to trawling by running a sensitivity analysis using all studies and only those where an associated error (i.e. standard deviation) was provided in the articles. A leave-1-out analysis was carried out. In this analysis, overall effect sizes were calculated as described above, but each time leaving out the data from one study (Viechtbauer, 2010), and subsequently assessing changes to the significance or directionality of the overall effect size. For variables with 10 or more studies, funnel plots were generated based on a trim-and-fill analysis, with the goal of highlighting potential publication bias (Duval & Tweedie, 2000a, 2000b).

All statistical analyses were performed in R (R Core Team, 2022). The metafor package (Viechtbauer, 2010) was used to carry out meta-regression analyses.

3 | RESULTS

3.1 | Dataset characteristics

The 57 studies used in this analysis were clustered mostly in the Northeast Atlantic ($n=19$), the Mediterranean Sea ($n=12$), the Northwest Atlantic ($n=8$), and the Bering Sea ($n=6$) (Figure 1a). Studies were confined to waters shallower than 700 m, with the majority ($n=44$) occurring in depths shallower than 100 m (Figure 1b). Study designs were fairly evenly distributed between the three categories: 'experimental' studies ($n=21$), 'comparative control–impact' studies ($n=19$), and comparative 'gradient' studies ($n=17$) (Figure 1c; see Text S1 for more details). Only 12 of the 57 studies collected samples during multiple seasons, and most samples were collected in summer, followed by spring and autumn (Figure 1d). Due to the under-representation of tropical regions, the dataset exhibited scarce data for both dry and wet seasons. The habitat types consisted of muddy ($n=37$) and sandy ($n=20$) sediments (Figure S2a), although gradient studies were primarily conducted in muddy sedimentary environments (15 out of 17 studies) (Figure S2a). Otter trawling was the most frequently used gear type ($n=31$), followed by towed dredge gear (e.g. scallop dredging, razor shell dredging) ($n=14$), and beam trawling ($n=6$). Hence, there were insufficient independent observations to assess the effect of fishing gear type on the biogeochemical and sedimentological parameters of marine sediments (Figure S2b).

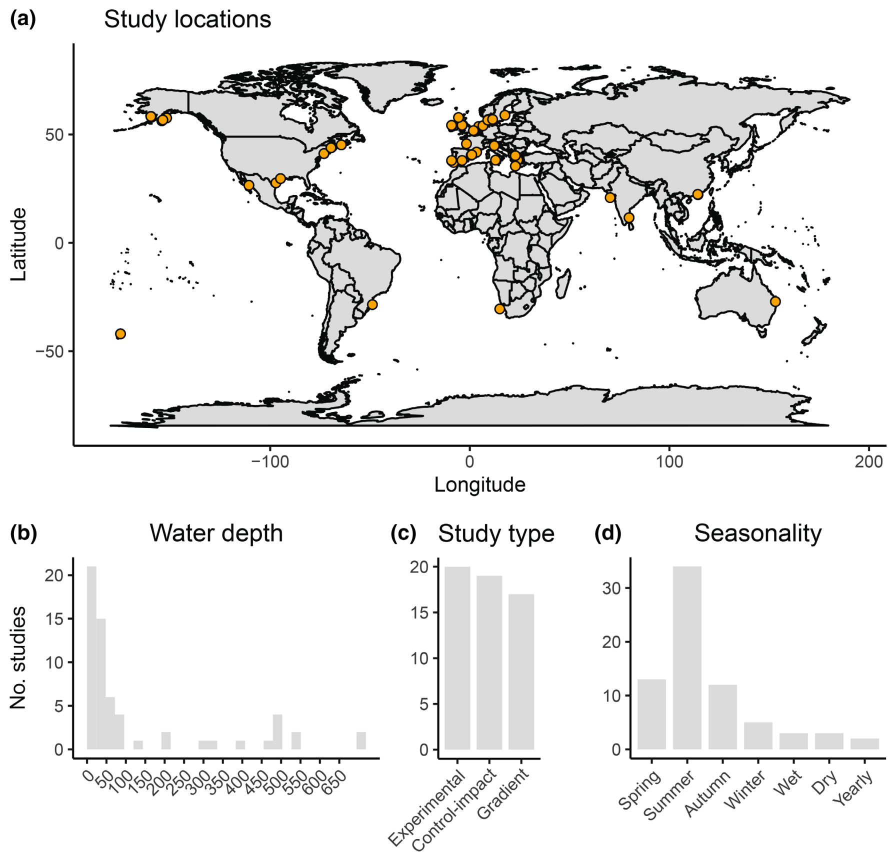

FIGURE 1 Spatial distribution of studies included in the meta-analysis on global continental margins shown as yellow dots (a). Histogram of the depths represented in the studies (b), study types (c), and seasonality (d).

3.2 | Overall effect of demersal fishing on sediment and biogeochemical parameters

In this study, the impact of trawling is statistically significant (i.e. $p<.05$) when the 95% confidence interval ('CI') for a specific parameter does not overlap with zero for either log response ratios (lnRR) or standardized mean differences (SMD). A statistically significant difference indicates that the measured parameter (e.g. concentration of Chl-a) in the trawled area is significantly different from that measured in a non-trawled area (control) or before trawling took place. Similarly, when comparing effect sizes for the same parameters between study designs, non-overlapping confidence intervals indicate a statistical difference (i.e. $p<.05$). While 867 response ratios were extracted from literature for the variables shown in Figure 2a, these were aggregated into 135 study-level responses.

The analysis of experimental and control–impact studies showed that fishing disturbance significantly reduced the concentration of Chl-a and phaeopigments, by 17% [95% CI = 2%–29%] and 24% [9%–37%], respectively (Figure 2a). Effect sizes for total carbon (TC) content significantly increased by 15% [2%–34%] post-fishing. No significant effects on sedimentological properties such as grain size and fractions were observed. Biopolymeric carbon (BPC), carbohydrates, and proteins were significantly reduced by 58% [46%–68%], 62% [19%–82%], and 32% [3%–52%], respectively, after fishing disturbance (Figure 2a). Pore-water concentrations of NO_x were 51% [9%–105%] higher post-fishing, while pore-water NH_x and sediment oxygen consumption rates did not differ significantly (Figure 2a). No other differences between experimental and control–impact studies were statistically significant, although the magnitude of the fishing effect tended to be greater for experimental studies (Figure S3).

Data availability from gradient studies permitted examination of five biogeochemical variables: TOC, TN, Chl-a, mud content, and mean grain size (Figure 2b). Concentrations of TOC (SMD = 0.23 [0.09–0.37]) and TN (SMD = 0.72 [0.01–1.43]) were found to be significantly higher in areas with higher fishing intensities (Figure 2b). The mud content showed a notable increase (SMD = 1.44 [0.76–2.12]) in areas with higher fishing activity, coinciding with statistically significant decreases in mean grain sizes (SMD = −0.68 [−92 to −0.45]) with increasing fishing intensity (Figure 2b).

3.3 | Effect of sample depths

The effects of fishing on sediment properties at different depth strata were assessed for experimental and control–impact studies on Chl-a, phaeopigments, phytopigments, TOC, TN, proteins, mean grain size, silt content, and NH_x concentration (Table S3). Significant reductions in the concentration of Chl-a (18% [95% CI = 7%–29%]), phaeopigments (28% [15%–39%]), TOC (12% [1%–22%]), and

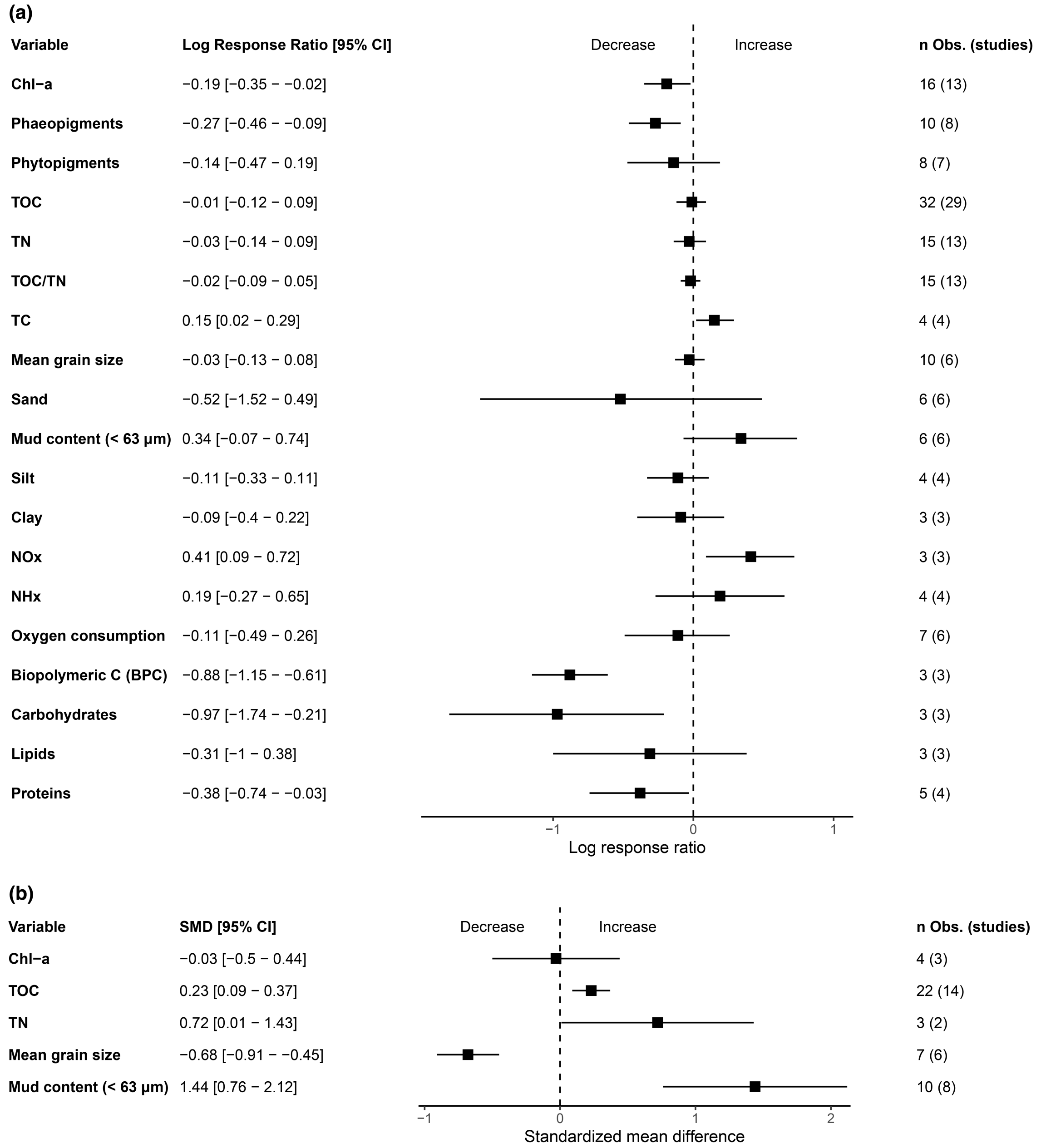

FIGURE 2 Forest plot showing the response of different sedimentological and biogeochemical parameters to bottom fishing disturbance. Response is reported as log response ratios (lnRR) for experimental and comparative control–impact studies (a) and as standardized mean differences (SMD) for studies that collect samples along fishing intensity gradients (b). Squares represent mean lnRR and horizontal lines represent the 95% confidence intervals. The vertical dotted line at lnRR or SMD = 0 indicates no change in the sedimentological or biogeochemical parameter due to fishing disturbance. Values on the right indicate the number of independent observations and in parentheses, the number of independent studies included in the calculation of each response variable. Note that one study can have several independent observations due to sampling during different seasons.

proteins (29% [8%–46%]) due to demersal fishing were detected within the first 2 cm (surface layer) of the sediment but not for deeper sediment layers (Figures 3 and S4).

3.4 | Effect of environmental conditions

The effects of fishing in differing environmental conditions for experimental and control–impact studies could be assessed for Chl-a, phaeopigments, phytopigments, TOC, TN, proteins, mean grain size, silt, and NH_x concentration (Figures 4, S5, and S6). Mean bottom current velocity (ranging from 0.013 to 0.28 $m{\cdot}s^{-1}$ in included studies), water depth (1–550 m), and surface primary productivity (0.002–0.097 $gC{\cdot}m^{-3}{\cdot}d^{-1}$) were found to significantly influence the effect of fishing disturbance (assessed by lnRR) on these sedimentological and biogeochemical parameters, whereas seasonality and habitat type did not exhibit a significant impact (Figures 4, S5, S6; Tables S4–S12).

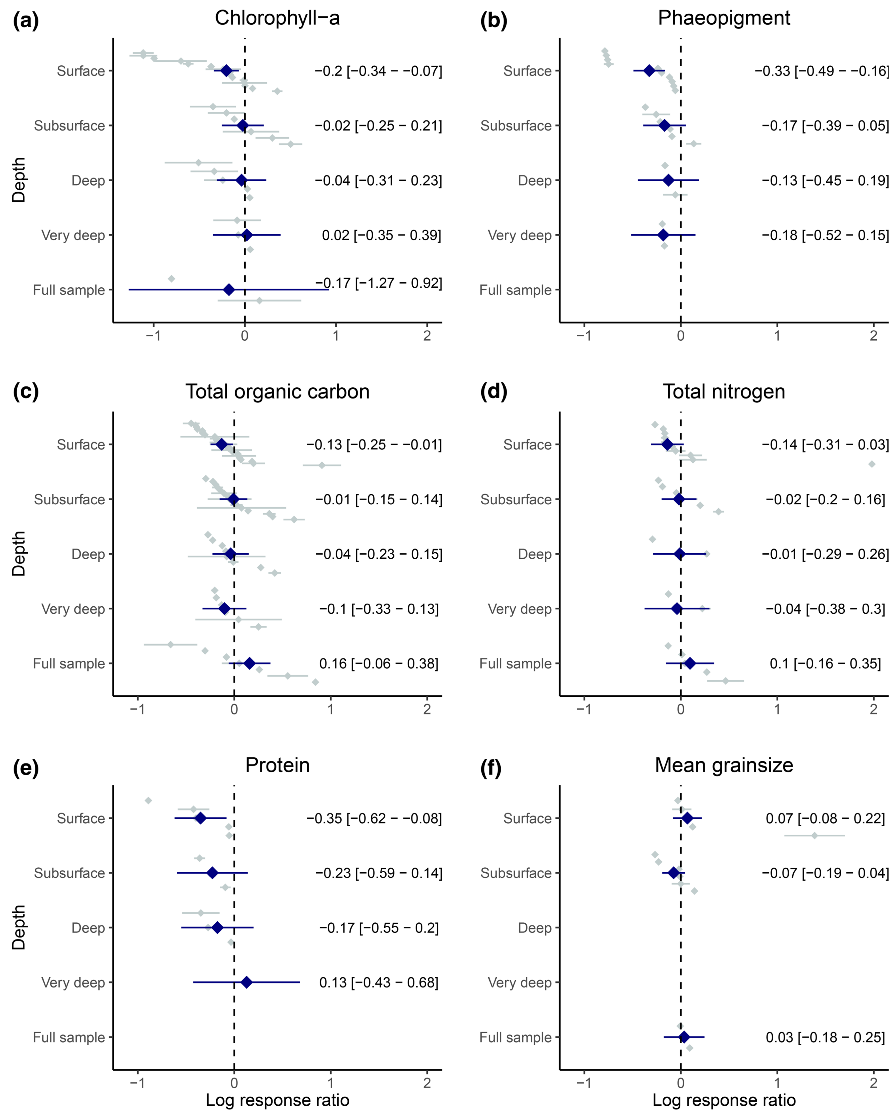

FIGURE 3 Effect of demersal fishing on sedimentological and geochemical properties of marine sediments across different sediment depth strata; (a) Chl-a, (b) phaeopigment, (c) OC, (d) TN, (e) protein, and (f) mean grain size. Dark blue dots and lines indicate the overall mean effect size per depth stratum and 95% confidence interval. Faded grey dots and lines indicate the means and 95% CI for all individual observations (studies, *n*) used to compute the overall mean effect. Significant differences between fished and control areas are present when the 95% CI does not overlap lnRR = 0. Additional forest plots are shown in Figure S4.

The effect of fishing on surface sediment (upper 2 cm) Chl-a was found to increase with bottom current velocity; areas characterized by higher current speeds experienced greatest reductions in surface Chl-a due to fishing activities ($p = .045$), but even in the most quiescent conditions, fishing always caused a decrease in surface Chl-a concentrations (Figures 4d and S6). Conversely, current velocity did not have a significant effect on fishing in surface layers of TOC and TN. Instead, the effect of fishing decreased with current velocity for TOC in subsurface (2–5 cm) layers ($p = .003$) and for the TN in subsurface and deep (5–10 cm) layers ($p < .001$; $p < .001$, respectively) (Figure 4c,e). While subsurface TOC and TN contents were reduced for fishing at current velocities lower than ~0.1 $m \cdot s^{-1}$, effect size values became positive at higher current velocities (Figures 4a and S7).

In surface sediment layers, the effect of fishing on Chl-a ($p = .003$; Figure 4d), phytopigments ($p = .007$), phaeopigments ($p = .012$), and proteins ($p < .001$) increased with surface primary productivity (Figures 4, S5, and S7), with areas characterized by higher surface primary productivity experiencing the greatest reductions of these compounds due to fishing activities. In contrast, the effect of fishing on TN concentrations in subsurface ($p < .001$) and deep ($p < .001$) layers decreased in areas of higher surface primary productivity (Figure 4e). Positive lnRR values were observed when surface primary productivity was >0.006 and 0.002 $g \cdot m^{-3} \cdot d^{-1}$ (Figure 4e and S8).

The effect of fishing on Chl-a in surface layers and full (depth-homogenized) samples of TOC decreased with water depth, with strongest changes due to fishing observed at water depths <20 m (Chl-a, $p < .001$; TOC, $p = .008$; Figures 4c,d and S9). However, the

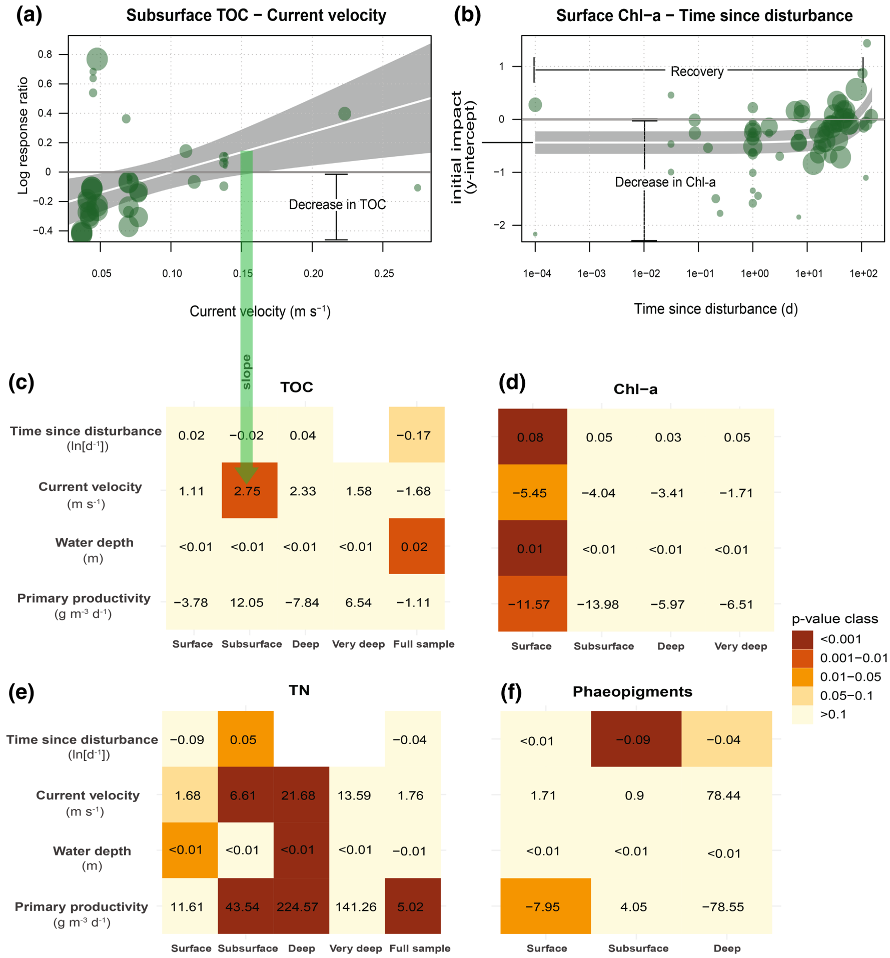

FIGURE 4 Examples of meta-regression bubble plots with the size of the bubbles showing the weight of the observation based on the study's sample size: Subsurface TOC versus current velocity (a) and surface Chl-a versus time since disturbance (*x*-axis on a natural log scale) (b). Additional meta-regression bubble plots are given in Figures S6–S9. An overview of the fitted slopes of the meta-regressions for the individual variables (c–f). Columns show the depth strata, rows show the covariate used in the model. Colours correspond to the significance level of the fitted slopes. For empty cells, the combination of covariate strata could not be fitted due to lack of data. A negative value indicates a negative relationship between lnRR and the covariate, for example, a negative slope for surface Chl-a and current velocity (−5.45) indicates that demersal fishing caused a greater reduction in Chl-a concentration at higher bottom current velocity. A positive slope indicates that reductions of that response variable due to demersal fishing become smaller along the environmental parameter gradient.

effect of fishing on surface TN ($p=.021$), phytopigments in subsurface (2–5 cm) ($p=.014$) and deep sediment (5–10 cm) ($p<.001$) increased with water depth, displaying a more pronounced fishing effect at water depths >20 m for surface TN, and >80 m for deep phytopigments (Figure S9, Tables S4–S12).

3.5 | Recovery trajectory following fishing disturbance

A significant positive slope between lnRR and time since fishing disturbance (log-transformed number of days) was observed for certain parameters indicating that recovery in the concentration of surface Chl-a ($p<.001$; Figure 4d) and subsurface phytopigments ($p=.005$) took place once fishing ceased (Figures 4, S5, and S10). Meta-regressions using data from the available studies estimated that conditions returned to pre-disturbance or control values after approximately 300 days for surface Chl-a and ~40 days for subsurface phytopigments (Figure S10).

There was a significant negative relationship between lnRR and time since fishing disturbance for subsurface phaeopigments ($p<.001$; Figures 4 and S9), showing no recovery in phaeopigments in subsurface sediment (2–5 cm). The remaining response variables analysed (TOC, silt content, mean grain size, and NH_x concentrations) did not present any statistically significant change with time since fishing disturbance (Figure S5).

3.6 | Sensitivity assessment

The leave-1-out analysis showed that results from the overall effect size models were generally robust with no consistent presence of overly dominant studies. However, there were particular instances where influential studies were identified, where effect sizes from the random effects models were shifted away, or towards significance (Figures S11 and S12). For Chl-a, omitting the study by Polymenakou et al. (2005) from the analysis removed the significant negative overall effect size ($p=.054$, Figure S11a). The significant increase in total carbon (TC) was driven by both the studies by Paradis et al. (2021) and Dannheim et al. (2014) (Figure S12a). The study by Rajesh et al. (2019) strongly influenced the positive effect size calculated for NO_x (Figure S12g). The negative effect size measured by van de Velde et al. (2018) shifted the overall effect size for NH_x away from a significant increase (CI: [0.1–0.65], $p=.007$; Figure S12j). Finally, the overall effect size for proteins was significantly negative; however, this result became more pronounced when the study by Mayer et al. (1991) was excluded (Figure S12m).

Assessment of funnel plot asymmetry was conducted for variables with >10 studies (Figure S12), and other funnel plots are reported but not discussed (Figure S13). For Chl-a, phaeopigments, and TN, significant ($p<.05$) funnel plot asymmetry was detected in the trim-and-fill analysis, leading to the imputation of a number of studies to improve asymmetry (Table S13). In this adjusted hypothetical dataset, the significant effect size noted previously for Chl-a and phaeopigments did not hold, whereas for TN an overall significant decrease appeared (previously non-significant).

4 | DISCUSSION

Our quantitative meta-analysis consolidates the published empirical data on the sedimentological and biogeochemical effects arising from fishery-induced disturbances. We identified overall decreases in Chl-a, phaeopigment, and phytopigment content in the sediment alongside other classes of organic compounds (e.g. biopolymeric fraction, proteins, and carbohydrates) resulting from demersal fishing in experimental and comparative control–impact studies. This suggests that fisheries are more likely to impact specific organic matter (OM) fractions, particularly more reactive compounds, while reductions in total organic carbon (TOC) may be less apparent (Figure 2a). The vulnerability of certain types of OM to sediment disturbance is likely due to their proximity to the seabed surface. While the broader spectrum of OM fractions represented in TOC, including less reactive fractions found deeper within the sediment, may dilute the observed impacts (Paradis et al., 2021; Sañé et al., 2013; Sciberras et al., 2016), such effects could lead to a general decline in the nutritional quality of OM available for benthic communities (Pusceddu et al., 2014; Ramalho et al., 2018; Sciberras et al., 2017).

In contrast to organic fractions, an overall increase was found in total carbon (TC) after fishing disturbance, possibly reflecting a relative increase in inorganic carbon, such as $CaCO_3$, as observed in certain studies (Paradis et al., 2019, 2021). This effect has been attributed to the winnowing of fine-grained sediment on fishing grounds and the re-deposition of coarser material, which includes shell fragments rich in $CaCO_3$ (Paradis et al., 2019, 2021). Demersal fisheries cause a general decrease in clay and silt contents (Palanques et al., 2014; Tiano et al., 2019), although our meta-analysis found no significant influence of fishing on the remaining sedimentological parameters, indicating that these effects are context dependent.

Fishing impacts were of the same order of magnitude in experimental studies and in control–impact studies, although they tended to be more pronounced in the former (Figure S3). This discrepancy is likely attributed to the short-term (within hours or a few days) and potentially more precise fishery-induced changes recorded in experimental studies, compared to the longer term (weeks or months) effects measured in control–impact studies, where fished areas may be subject to additional environmental perturbations before sampling.

Gradient studies, on average, reported increases in TOC at highly fished sites (Figure 2b). This apparent discrepancy amidst the commonly attributed decrease in TOC and carbon sequestration due to demersal fishing (De Borger et al., 2021; Jacquemont et al., 2022; Porz et al., 2024; Sala et al., 2021) may prompt questions regarding the specific mechanisms driving increased TOC in trawled areas. However, this outcome may just reflect a preference amongst fishermen for operating in areas that happen to feature higher OM concentrations, which may provide abundant food sources for commercial species (van Denderen et al., 2013). Furthermore, the release of pore-water nutrients into the water column may potentially enhance local primary production, particularly in shallow and/or well-mixed waters, leading to higher OM accumulating in fished areas (Brylinsky et al., 1994; Dounas et al., 2005, 2007; Sciberras et al., 2016).

Our analysis revealed that fishing impacts on sediment biogeochemistry (e.g. TOC, Chl-a, phaeopigments, proteins) were predominant in the surface sediment layer (0–2 cm) (Figure 3). TOC, in particular, was only significantly impacted within surface sediment samples. This localized impact indicates that surface sediments are the most vulnerable to disturbance from bottom-towed gear, due to not only the higher levels of reactive OM present in these upper sections (Hiddink et al., 2023) but also the fact that otter trawl and beam trawl gear examined in the majority of the studies penetrate down to about 2–5 cm within the sediment (Hiddink et al., 2017; Pitcher et al., 2022). These findings indicate that sampling strategies with low sediment depth resolution could mask the assessment of the impact of fishing activity by homogenizing impacted and non-impacted sediment layers. This was evident in studies using grab samplers or composite sediment from the upper 5 to 10 cm, where no significant or positive effects of demersal fishing were detected (Dannheim et al., 2014; Liu et al., 2011; Meseck et al., 2014; Simboura et al., 2008; Van De Velde et al., 2018). In addition to the significant results in surface TOC samples, the magnitude of the effect sizes in the surface layers was greater for Chl-a, phaeopigments, and proteins, which represent the most reactive OM fractions (or their proxies). This provides further evidence that demersal fisheries disproportionately affect more reactive OM (Paradis et al., 2021; Sañé et al., 2013; Sciberras et al., 2016) and that fishing might reduce the reactivity of the total OM pool (Morys et al., 2021; Pusceddu et al., 2014; Tiano et al., 2019), thereby influencing food quality for benthos.

Environmental conditions such as bottom current velocity, water depth, and primary productivity significantly affected the fisheries-induced impact on Chl-a, phaeopigments, and phytopigments in surface sediment. The impacts on these fresh OM fractions were greater in habitats characterized by high surface primary productivity (Figures 4, S5 and S8). This could be due to a greater absolute reduction of OM in areas with elevated OM concentrations, in comparison to situations where OM levels are naturally low due to low surface primary productivity. This phenomenon also accounts for the larger effects in Chl-a concentrations in shallower water depths, where higher Chl-a concentrations and faster current speeds are typically found.

Changes in Chl-a content may be informative for understanding alterations in the more reactive OM fractions. However, as these fractions will eventually be remineralized even in the absence of demersal fishing (Hiddink et al., 2023), assessing the effects on TOC and potentially semi-reactive fractions (such as humic substances, lipids, complex carbohydrates, etc.) might provide a more reliable indicator of longer term impacts from fishing and its effects on the sequestration of organic carbon. Fisheries impacts on TOC and TN in surface layers could not be correlated to any environmental factors, suggesting that organic carbon and nitrogen in these layers are similarly vulnerable in all continental margins. However, the effects of demersal fisheries on TOC and TN increased in *sub*surface layers with decreasing bottom current speed (Figure 4c,e). This deeper impact may be associated with the finer sediment particles found in less energetic environments with weaker bottom current velocities, facilitating the penetration of demersal fishing gears (Pitcher et al., 2022), and causing cumulative impacts in deeper sediment sections (De Borger et al., 2021), highlighting that quiescent environments are more vulnerable to the impacts of fishing disturbance.

Contrary to previous assertions that the impacts of demersal fisheries on TOC increase with water depth due to the lower frequency of natural sediment disturbance processes in deeper environments (Martín, Puig, Masqué, et al., 2014), our results suggest that current speed, rather than water depth, is more important in determining the degree of impact on sedimentary organic matter (Figure 4). The magnitude of bottom currents provides a more accurate representation of the natural physical processes that can resuspend sediment, considering the contrasting hydrodynamic processes occurring at variable water depths across continental margins (Bianchi et al., 2018; Hedges & Keil, 1995).

This analysis revealed that the impact of fishing on Chl-a within the surface sediment (0–2 cm) was significantly reduced with time since fishing disturbance (Figure 4d). Our meta-regressions estimate that it takes around ~300 days (about 10 months) for Chl-a to fully recover to its initial concentrations after fishing disturbance (Figures 4 and S6). However, this may vary greatly depending on environmental characteristics such as seasonality and primary productivity (De Borger et al., 2021). The absence of data replication for region-specific seasons in the dataset (e.g. temperate, sub-tropical, and tropical climates) and the skewed distribution of samples, primarily collected during summer (Figure 1d), prevented the inclusion of seasonality as a factor to assess its significance. Although no consistent recovery of the remaining biogeochemical parameters was observed in the dataset, this lack of evidence may be attributed to the limited sample size (Figure S10) and we cannot draw definitive conclusions about their recovery capacity.

Current challenges for conducting more comprehensive analyses include the limited availability of data on different OM fractions and its remineralization after disturbance (Morys et al., 2021; Paradis et al., 2021; Tiano et al., 2019; Trimmer et al., 2005). Additionally, we found an under-representation of studies assessing the impacts of fishing on benthic sediment and its biogeochemistry from tropical regions and areas deeper than 100 m. Seasonal variation in the amount of fresh OM reaching the seabed is likely to result in seasonal differences in the response to fishing. We attempted to evaluate the influence of season; however, our analysis was hampered by the lack of studies conducted during autumn and winter months, or of studies comparing fishing impacts pre- and post-algal blooms. In addition to excluding the effect of seasonality, sparse information on different used gear hindered our ability to effectively examine the influence of various gear types with deeper penetration on the seafloor such as beam trawls, towed dredges, and hydraulic dredges. This limited information may have contributed to the funnel plot asymmetry detected in our sensitivity runs. As more studies become available, potential heterogeneity and publication bias in the data are likely to decrease in future meta-analyses conducted on this topic. It is thus imperative to expand research efforts to address these knowledge gaps to comprehensively understand and quantify the global biogeochemical footprint of demersal fisheries, and to develop effective management strategies.

Effective fisheries regulation requires: (1) up-to-date stock assessments for setting species-specific regulatory quotas, and (2) consideration of ecosystem effects caused by fishing, which can lead to varying levels of spatial management. Our study informs the latter, emphasizing the sensitivity of OM in the upper sediment to fisheries disturbances with the greatest impact on more reactive OM compounds (i.e. labile organic matter; Pusceddu et al., 2009). Trawl-induced exposure to oxygen speeds up degradation, while resuspended particles can be mobilized away from the trawled area. Such disturbances can reduce the nutritional quality of benthic consumers causing immediate (short-term) ecological consequences. Long-term implications on seabed carbon are less certain as reactive compounds may degrade rapidly even without disturbance. TOC measurements, which include semi-reactive OM fractions (along with reactive and refractory fractions), may be more relevant for assessing impacts on carbon sequestration (Graves et al., 2022) compared to more reactive proxies of organic carbon like chlorophyll-a. We highlight the importance of quantifying changes to surface and subsurface TOC when assessing potential impacts of trawling on long-term carbon dynamics. This is particularly critical in habitats characterized by low bottom current velocity, where fishing gears can penetrate deeper and enhance the degradation of subsurface semi-reactive OM, potentially reducing the sediment carbon sequestration capacity.

In summary, this meta-analysis highlights the vulnerability of OM loads and composition to demersal fishing. The greatest impact is found on reactive OM fractions such as Chl-a, phaeopigments, and proteins in the upper sediment indicating the potential for fisheries to reduce the reactivity of the sediment OM pool at the site of disturbance. This can reduce the quality of food sources for benthos (Pusceddu et al., 2014) and can weaken the sediment's ability to remove nutrients from the water (Rios-Yunes et al., 2023). In areas with low current speeds, the reduction of TOC may indicate a decline in carbon sequestration from those sediments. The overall decline in OM arises from a combination of erosion and subsequent deposition beyond fishing grounds (Paradis et al., 2022), as well as its remineralization into dissolved CO_2 (De Borger et al., 2021; Morys et al., 2021; Tiano et al., 2019).

Despite the expanding body of knowledge on this topic, uncertainties persist regarding the fate of disturbed OM. This, coupled with the need for more research on trawling impacts on carbon sequestration (Hiddink et al., 2023) and water column biogeochemistry (Breimann et al., 2022; Pusceddu et al., 2015), represents key knowledge gaps in understanding how demersal fishing may ultimately influence climate change. We show that fishing effects are context- and site-specific and consideration of sediment sampling depth and environmental factors such as local hydrodynamics and primary productivity are crucial for predicting the effect of fishing on benthic OM pools. Hence, current estimates of fisheries-induced benthic CO_2 emissions that do not consider the influence of environmental factors or localized effects on only the seabed surface might considerably overestimate these impacts (Sala et al., 2021) and should be approached with caution. Despite the limitations in the current data, our synthesis indicates the strong potential of demersal fisheries to disrupt sediment biogeochemistry. Without urgent management strategies, these effects will likely affect the global carbon footprint, ultimately impairing the functioning of marine ecosystems and their ability to provide goods and services to humanity.

AUTHOR CONTRIBUTIONS

J.T., E.D.B., S.P., C.B., A.P., K.S., P.P., P.M., and M.S. conceived the study; J.T., E.D.B., S.P., C.B., C.M., A.P., C.E., and M.S. collected the data; S.P. harmonized the dataset and grouped the data; J.T. and E.D.B. conducted the statistical analysis with input from S.P. and M.S; J.T., E.D.B., and S.P. wrote the manuscript with the contribution of all co-authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data for this meta-analysis was extracted from the "Demersal fishery Impacts on Sedimentary Organic Matter" (DISOM) database (Paradis et al., 2023). The compiled data and R code for this study will be made available at: https://github.com/JCTiano/MetaBioGeoImpact.

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REFERENCES

Amoroso, R. O., Pitcher, C. R., Rijnsdorp, A. D., McConnaughey, R. A., Parma, A. M., Suuronen, P., Eigaard, O. R., Bastardie, F., Hintzen, N. T., Althaus, F., Baird, S. J., Black, J., Buhl-Mortensen, L., Campbell, A. B., Catarino, R., Collie, J., Cowan, J. H., Durholtz, D., Engstrom, N., & Jennings, S. (2018). Bottom trawl fishing footprints on the world's continental shelves. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(43), E10275–E10282. https://doi.org/10.1073/pnas.1802379115

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E. A., De Clerck, O., & Tittensor, D. (2018). Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*, *27*(3), 277–284. https://doi.org/10.1111/geb.12693

Atkinson, L., Field, J., & Hutchings, L. (2011). Effects of demersal trawling along the west coast of southern Africa: Multivariate analysis of benthic assemblages. *Marine Ecology Progress Series*, *430*, 241–255. https://doi.org/10.3354/meps08956

Atwood, T. B., Romanou, A., DeVries, T., Lerner, P. E., Mayorga, J. S., Bradley, D., Cabral, R. B., Schmidt, G. A., & Sala, E. (2024). Atmospheric CO_2 emissions and ocean acidification from bottom-trawling. *Frontiers in Marine Science*, *10*, 1125137. https://doi.org/10.3389/fmars.2023.1125137

Bhagirathan, U., Meenakumari, B., Jayalakshmy, K. V., Panda, S. K., Madhu, V. R., & Vaghela, D. T. (2010). Impact of bottom trawling on sediment characteristics—A study along inshore waters off Veraval coast, India. *Environmental Monitoring and Assessment*, *160*(1–4), 355–369. https://doi.org/10.1007/s10661-008-0700-0

Bianchi, T. S., Cui, X., Blair, N. E., Burdige, D. J., Eglinton, T. I., & Galy, V. (2018). Centers of organic carbon burial and oxidation at the land-ocean interface. *Organic Geochemistry*, *115*, 138–155. https://doi.org/10.1016/j.orggeochem.2017.09.008

Borenstein, M., Cooper, H., & Hedges, L. (2009). Effect sizes for continuous data. In H. Cooper, L. V. Hedges, & J. C. Valentine (Eds.), *The handbook of research synthesis and meta-analysis* (Vol. *2*, 2nd ed., pp. 221–235). Sage.

Boudouresque, C. F., Bernard, G., Pergent, G., Shili, A., & Verlaque, M. (2009). Regression of Mediterranean seagrasses caused by natural processes and anthropogenic disturbances and stress: A critical review. *Botanica Marina*, *52*, 395–418. https://doi.org/10.1515/BOT.2009.057

Breimann, S. A., O'Neill, F. G., Summerbell, K., & Mayor, D. J. (2022). Quantifying the resuspension of nutrients and sediment by demersal trawling. *Continental Shelf Research*, *233*, 104628. https://doi.org/10.1016/j.csr.2021.104628

Brylinsky, M., Gibson, J., & Gordon, D. C., Jr. (1994). Impacts of flounder trawls on the intertidal habitat and community of the Minas Basin, Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences*, *51*(3), 650–661. https://doi.org/10.1139/f94-066

Costello, C., Cao, L., Gelcich, S., Cisneros-Mata, M. Á., Free, C. M., Froehlich, H. E., Golden, C. D., Ishimura, G., Maier, J., Macadam-Somer, I., Mangin, T., Melnychuk, M. C., Miyahara, M., de Moor, C. L., Naylor, R., Nøstbakken, L., Ojea, E., O'Reilly, E., Parma, A. M., & Lubchenco, J. (2020). The future of food from the sea. *Nature*, *588*(7836), 95–100. https://doi.org/10.1038/s41586-020-2616-y

Dannheim, J., Brey, T., Schröder, A., Mintenbeck, K., Knust, R., & Arntz, W. E. (2014). Trophic look at soft-bottom communities—Short-term effects of trawling cessation on benthos. *Journal of Sea Research*, *85*, 18–28. https://doi.org/10.1016/j.seares.2013.09.005

De Borger, E., Tiano, J., Braeckman, U., Rijnsdorp, A. D., & Soetaert, K. (2021). Impact of bottom trawling on sediment biogeochemistry: A modelling approach. *Biogeosciences*, *18*(8), 2539–2557. https://doi.org/10.5194/bg-18-2539-2021

Dounas, C. G., Davies, I. M., Hayes, P. J., Arvanitidis, C. D., & Koulouri, P. T. (2005). The effect of different types of otter trawl ground rope on benthic nutrient releases and sediment biogeochemistry. *Benthic Habitats and the Effects of Fishing*, *41*, 539–544.

Dounas, C., Davies, I., Triantafyllou, G., Koulouri, P., Petihakis, G., Arvanitidis, C., Sourlatzis, G., & Eleftheriou, A. (2007). Large-scale impacts of bottom trawling on shelf primary productivity. *Continental Shelf Research*, *27*(17), 2198–2210. https://doi.org/10.1016/j.csr.2007.05.006

Dunne, J. P., Sarmiento, J. L., & Gnanadesikan, A. (2007). A synthesis of global particle export from the surface ocean and cycling through the ocean interior and on the seafloor. *Global Biogeochemical Cycles*, *21*(4), GB4006. https://doi.org/10.1029/2006GB002907

Duval, S., & Tweedie, R. (2000a). A nonparametric "trim and fill" method of accounting for publication bias in meta-analysis. *Journal of the American Statistical Association*, *95*(449), 89–98. https://doi.org/10.1080/01621459.2000.10473905

Duval, S., & Tweedie, R. (2000b). Trim and fill: A simple funnel-plot–based method of testing and adjusting for publication bias in meta-analysis. *Biometrics*, *56*(2), 455–463. https://doi.org/10.1111/j.0006-341X.2000.00455.x

Eigaard, O. R., Bastardie, F., Breen, M., Dinesen, G. E., Hintzen, N. T., Laffargue, P., Mortensen, L. O., Nielsen, J. R., Nilsson, H. C., O'Neill, F. G., Polet, H., Reid, D. G., Sala, A., Sköld, M., Smith, C., Sørensen, T. K., Tully, O., Zengin, M., & Rijnsdorp, A. D. (2016). Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. *ICES Journal of Marine Science*, *73*, i27–i43.

Epstein, G., Middelburg, J. J., Hawkins, J. P., Norris, C. R., & Roberts, C. M. (2022). The impact of mobile demersal fishing on carbon storage in seabed sediments. *Global Change Biology*, *28*(9), 2875–2894. https://doi.org/10.1111/gcb.16105

Ferguson, A. J. P., Oakes, J., & Eyre, B. D. (2020). Bottom trawling reduces benthic denitrification and has the potential to influence the global nitrogen cycle. *Limnology and Oceanography Letters*, *5*, 237–245. https://doi.org/10.1002/lol2.10150

Graves, C. A., Benson, L., Aldridge, J., Austin, W. E. N., Dal Molin, F., Fonseca, V. G., Hynes, C., Kröger, S., Lamb, P. D., Mason, C., Powell, C., Smeaton, C., Wexler, S. K., Woulds, C., & Parker, R. (2022). Sedimentary carbon on the continental shelf: Emerging capabilities and research priorities for blue carbon. *Frontiers in Marine Science*, *9*, 926215. https://doi.org/10.3389/fmars.2022.926215

Hale, R., Godbold, J. A., Sciberras, M., Dwight, J., Wood, C., Hiddink, J. G., & Solan, M. (2017). Mediation of macronutrients and carbon by post-disturbance shelf sea sediment communities. *Biogeochemistry*, *135*(1–2), 121–133. https://doi.org/10.1007/s10533-017-0350-9

Hedges, J. I., & Keil, R. G. (1995). Sedimentary organic matter preservation: An assessment and speculative synthesis. *Marine Chemistry*, *49*(2–3), 81–115. https://doi.org/10.1016/0304-4203(95)00008-F

Hedges, L. V., Gurevitch, J., & Curtis, P. S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology*, *80*(4), 1150–1156.

Hiddink, J. G., Jennings, S., Sciberras, M., Szostek, C. L., Hughes, K. M., Ellis, N., Rijnsdorp, A. D., McConnaughey, R. A., Mazor, T., Hilborn, R., Collie, J. S., Pitcher, C. R., Amoroso, R. O., Parma, A. M., Suuronen, P., & Kaiser, M. J. (2017). Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(31), 8301–8306. https://doi.org/10.1073/pnas.1618858114

Hiddink, J. G., van de Velde, S. J., McConnaughey, R. A., De Borger, E., Tiano, J., Kaiser, M. J., Sweetman, A. K., & Sciberras, M. (2023). Quantifying the carbon benefits of ending bottom trawling. *Nature*, *617*(7960), E1–E2. https://doi.org/10.1038/s41586-023-06014-7

Higgins, J. P. T., & Li, T. (2022). Exploring heterogeneity. In *Systematic reviews in health research* (pp. 185–203). Wiley. https://doi.org/10.1002/9781119099369.ch10

Jackson, J. B., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J., & Warner, R. R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, *293*(5530), 629–637. https://doi.org/10.1126/science.1059199

Jacquemont, J., Blasiak, R., Le Cam, C., Le Gouellec, M., & Claudet, J. (2022). Ocean conservation boosts climate change mitigation and adaptation. *One Earth*, *5*(10), 1126–1138. https://doi.org/10.1016/j.oneear.2022.09.002

Kroodsma, D. A., Mayorga, J., Hochberg, T., Miller, N. A., Boerder, K., Ferretti, F., Wilson, A., Bergman, B., White, T. D., Block, B. A., Woods, P., Sullivan, B., Costello, C., & Worm, B. (2018). Tracking the global footprint of fisheries. *Science*, *359*(6378), 904–908. https://doi.org/10.1126/science.aao5646

Liu, X.-S., Xu, W.-Z., Cheung, S. G., & Shin, P. K. S. (2011). Response of meiofaunal community with special reference to nematodes upon deployment of artificial reefs and cessation of bottom trawling in subtropical waters, Hong Kong. *Marine Pollution Bulletin*, *63*(5–12), 376–384. https://doi.org/10.1016/j.marpolbul.2010.11.019

Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., Kidwell, S. M., Kirby, M. X., Peterson, C. H., & Jackson, J. B. C. (2006). Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science*, *312*(5781), 1806–1809. https://doi.org/10.1126/science.1128035

Martin, J. H., Knauer, G. A., Karl, D. M., & Broenkow, W. W. (1987). VERTEX: Carbon cycling in the northeast Pacific. *Deep Sea Research Part A. Oceanographic Research Papers*, *34*(2), 267–285. https://doi.org/10.1016/0198-0149(87)90086-0

Martín, J., Puig, P., Masqué, P., Palanques, A., & Sánchez-Gómez, A. (2014). Impact of bottom trawling on deep-sea sediment properties along the flanks of a submarine canyon. *PLoS ONE*, *9*(8), e104536. https://doi.org/10.1371/journal.pone.0104536

Martín, J., Puig, P., Palanques, A., & Giamportone, A. (2014). Commercial bottom trawling as a driver of sediment dynamics and deep seascape evolution in the Anthropocene. *Anthropocene*, *7*, 1–15. https://doi.org/10.1016/j.ancene.2015.01.002

Mayer, L. M., Schick, D. F., Findlay, R. H., & Rice, D. L. (1991). Effects of commercial dragging on sedimentary organic matter. *Marine Environmental Research*, *31*(4), 249–261. https://doi.org/10.1016/0141-1136(91)90015-Z

McLaverty, C., Eigaard, O. R., Gislason, H., Bastardie, F., Brooks, M. E., Jonsson, P., Lehmann, A., & Dinesen, G. E. (2020). Using large benthic macrofauna to refine and improve ecological indicators of bottom trawling disturbance. *Ecological Indicators*, *110*, 105811. https://doi.org/10.1016/j.ecolind.2019.105811

McLaverty, C., Eigaard, O., Dinesen, G., Gislason, H., Kokkalis, A., Erichsen, A., & Petersen, J. (2020). High-resolution fisheries data reveal effects of bivalve dredging on benthic communities in stressed coastal systems. *Marine Ecology Progress Series*, *642*, 21–38. https://doi.org/10.3354/meps13330

Meseck, S. L., Mercaldo-Allen, R., Rose, J. M., Clark, P., Kuropat, C., Pereira, J. J., & Goldberg, R. (2014). Effects of hydraulic dredging for *Mercenaria mercenaria*, northern quahog, on sediment biogeochemistry. *Journal of the World Aquaculture Society*, *45*(3), 301–311. https://doi.org/10.1111/jwas.12114

Middelburg, J. J. (2018). Reviews and syntheses: To the bottom of carbon processing at the seafloor. *Biogeosciences*, *15*(2), 413–427. https://doi.org/10.5194/bg-15-413-2018

Morys, C., Brüchert, V., & Bradshaw, C. (2021). Impacts of bottom trawling on benthic biogeochemistry in muddy sediments: Removal of surface sediment using an experimental field study. *Marine Environmental Research*, *169*, 105384. https://doi.org/10.1016/j.marenvres.2021.105384

O'Neill, F. G., & Summerbell, K. (2011). The mobilisation of sediment by demersal otter trawls. *Marine Pollution Bulletin*, *62*(5), 1088–1097. https://doi.org/10.1016/j.marpolbul.2011.01.038

Palanques, A., Puig, P., Guillén, J., Demestre, M., & Martín, J. (2014). Effects of bottom trawling on the Ebro continental shelf sedimentary system (NW Mediterranean). *Continental Shelf Research*, *72*, 83–98. https://doi.org/10.1016/j.csr.2013.10.008

Paradis, S., Arjona-Camas, M., Goñi, M., Palanques, A., Masqué, P., & Puig, P. (2022). Contrasting particle fluxes and composition in a submarine canyon affected by natural sediment transport events and bottom trawling. *Frontiers in Marine Science*, *9*, 1017052. https://doi.org/10.3389/fmars.2022.1017052

Paradis, S., Goñi, M., Masqué, P., Durán, R., Arjona-Camas, M., Palanques, A., & Puig, P. (2021). Persistence of biogeochemical alterations of deep-sea sediments by bottom trawling. *Geophysical Research Letters*, *48*(2), e2020GL091279. https://doi.org/10.1029/2020GL091279

Paradis, S., Pusceddu, A., Masqué, P., Puig, P., Moccia, D., Russo, T., Iacono, C. L., & Lo Iacono, C. (2019). Organic matter contents and degradation in a highly trawled area during fresh particle inputs (Gulf of Castellammare, southwestern Mediterranean). *Biogeosciences*, *16*(21), 4307–4320. https://doi.org/10.5194/bg-16-4307-2019

Paradis, S., Tiano, J., De Borger, E., Pusceddu, A., Bradshaw, C., Ennas, C., Morys, C., & Sciberras, M. (2023). Demersal fishery impacts on sedimentary organic matter (DISOM): A global harmonized database of studies assessing the impacts of demersal fisheries on sediment biogeochemistry. *Earth System Science Data Discussions*, *2023*, 1–25. https://doi.org/10.5194/essd-2023-412

Pitcher, C. R., Hiddink, J. G., Jennings, S., Collie, J., Parma, A. M., Amoroso, R., Mazor, T., Sciberras, M., McConnaughey, R. A., Rijnsdorp, A. D., Kaiser, M. J., Suuronen, P., & Hilborn, R. (2022). Trawl impacts on the relative status of biotic communities of seabed sedimentary habitats in 24 regions worldwide. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(2), e2109449119. https://doi.org/10.1073/pnas.2109449119

Polymenakou, P. N., Pusceddu, A., Tselepides, A., Polychronaki, T., Giannakourou, A., Fiordelmondo, C., Hatziyanni, E., & Danovaro, R. (2005). Benthic microbial abundance and activities in an intensively trawled ecosystem (Thermaikos gulf, Aegean Sea). *Continental Shelf Research*, *25*(19–20), 2570–2584. https://doi.org/10.1016/J.CSR.2005.08.018

Porz, L., Zhang, W., Christiansen, N. G., Kossack, J., Daewel, U., & Schrum, C. (2024). Quantification and mitigation of bottom trawling impacts on sedimentary organic carbon stocks in the North Sea. *Biogeosciences*, *21*, 2547–2570. https://doi.org/10.5194/bg-21-2547-2024

Puig, P., Canals, M., Company, J. B., Martín, J., Amblas, D., Lastras, G., Palanques, A., & Calafat, A. M. (2012). Ploughing the deep sea floor. *Nature*, *489*(7415), 286–289. https://doi.org/10.1038/nature11410

Pusceddu, A., Bianchelli, S., & Danovaro, R. (2015). Quantity and biochemical composition of particulate organic matter in a highly trawled area (Thermaikos Gulf, Eastern Mediterranean Sea). *Advances in Oceanography and Limnology*, *6*(1/2), 5448. https://doi.org/10.4081/aiol.2015.5448

Pusceddu, A., Bianchelli, S., Martin, J., Puig, P., Palanques, A., Masque, P., & Danovaro, R. (2014). Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(24), 8861–8866. https://doi.org/10.1073/pnas.1405454111

Pusceddu, A., Dell'Anno, A., Fabiano, M., & Danovaro, R. (2009). Quantity and bioavailability of sediment organic matter as signatures of benthic trophic status. *Marine Ecology Progress Series*, *375*, 41–52. https://doi.org/10.3354/meps07735

Pusceddu, A., Fiordelmondo, C., Polymenakou, P., Polychronaki, T., Tselepides, A., & Danovaro, R. (2005). Effects of bottom trawling on the quantity and biochemical composition of organic matter in coastal marine sediments (Thermaikos Gulf, Northwestern Aegean Sea). *Continental Shelf Research*, *25*(19–20), 2491–2505. https://doi.org/10.1016/j.csr.2005.08.013

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rajesh, N., Muthuvelu, S., Mahadevan, G., & Murugesan, P. (2019). Impact of bottom trawling on water and sediment characteristics of Cuddalore and Parangipettai coastal waters. *Indian Journal Of Geo Marine Sciences*, *48*(05), 639–646.

Ramalho, S. P., Almeida, M., Esquete, P., Génio, L., Ravara, A., Rodrigues, C. F., Lampadariou, N., Vanreusel, A., & Cunha, M. R. (2018). Bottom-trawling fisheries influence on standing stocks, composition, diversity and trophic redundancy of macrofaunal assemblages from the west Iberian margin. *Deep Sea Research Part I: Oceanographic Research Papers*, *138*, 131–145. https://doi.org/10.1016/j.dsr.2018.06.004

Reiss, H., & Kröncke, I. (2004). Seasonal variability of epibenthic communities in different areas of the southern North Sea. *ICES Journal of Marine Science*, *61*(6), 882–905. https://doi.org/10.1016/j.icesjms.2004.06.020

Rijnsdorp, A. D., Hiddink, J. G., van Denderen, P. D., Hintzen, N. T., Eigaard, O. R., Valanko, S., Bastardie, F., Bolam, S. G., Boulcott, P., Egekvist, J., Garcia, C., van Hoey, G., Jonsson, P., Laffargue, P., Nielsen, J. R., Piet, G. J., Sköld, M., & van Kooten, T. (2020). Different bottom trawl fisheries have a differential impact on the status of the North Sea seafloor habitats. *ICES Journal of Marine Science*, *77*(5), 1772–1786. https://doi.org/10.1093/icesjms/fsaa050

Rios-Yunes, D., Tiano, J. C., van Rijswijk, P., De Borger, E., van Oevelen, D., & Soetaert, K. (2023). Long-term changes in ecosystem functioning of a coastal bay expected from a shifting balance between intertidal and subtidal habitats. *Continental Shelf Research*, *254*, 104904. https://doi.org/10.1016/j.csr.2022.104904

Sala, E., Mayorga, J., Bradley, D., Cabral, R. B., Atwood, T. B., Auber, A., Cheung, W., Costello, C., Ferretti, F., Friedlander, A. M., Gaines, S. D., Garilao, C., Goodell, W., Halpern, B. S., Hinson, A., Kaschner, K., Kesner-Reyes, K., Leprieur, F., McGowan, J., … Lubchenco, J. (2021). Protecting the global ocean for biodiversity, food and climate. *Nature*, *592*(7854), 397–402. https://doi.org/10.1038/s41586-021-03371-z

Sañé, E., Martín, J., Puig, P., & Palanques, A. (2013). Organic biomarkers in deep-sea regions affected by bottom trawling: Pigments, fatty acids, amino acids and carbohydrates in surface sediments from the La Fonera (Palamós) canyon NW Mediterranean Sea. *Biogeosciences*, *10*(12), 8093–8108. https://doi.org/10.5194/bg-10-8093-2013

Sciberras, M., Hiddink, J. G., Jennings, S., Szostek, C. L., Hughes, K. M., Kneafsey, B., Clarke, L. J., Ellis, N., Rijnsdorp, A. D., McConnaughey, R. A., Hilborn, R., Collie, J. S., Pitcher, C. R., Amoroso, R. O., Parma, A. M., Suuronen, P., & Kaiser, M. J. (2018). Response of benthic fauna to experimental bottom fishing: A global meta-analysis. *Fish and Fisheries*, *19*(4), 698–715. https://doi.org/10.1111/faf.12283

Sciberras, M., Parker, R., Powell, C., Robertson, C., Kröger, S., Bolam, S., & Geert Hiddink, J. (2016). Impacts of bottom fishing on the sediment infaunal community and biogeochemistry of cohesive and non-cohesive sediments. *Limnology and Oceanography*, *61*(6), 2076–2089. https://doi.org/10.1002/lno.10354

Sciberras, M., Tait, K., Brochain, G., Hiddink, J. G., Hale, R., Godbold, J. A., & Solan, M. (2017). Mediation of nitrogen by post-disturbance shelf communities experiencing organic matter enrichment. *Biogeochemistry*, *135*(1–2), 135–153. https://doi.org/10.1007/s10533-017-0370-5

Simboura, N., Zenetos, A., Pancucci-Papadopoulou, M.-A., Thessalou-Legaki, M., & Papaspyrou, S. (2008). A baseline study on benthic species distribution in two neighbouring gulfs, with and without access to bottom trawling. *Marine Ecology*, *19*(4), 293–309. https://doi.org/10.1111/j.1439-0485.1998.tb00469.x

Sparks-McConkey, P. J., & Watling, L. (2001). Effects on the ecological integrity of a soft-bottom habitat from a trawling disturbance. *Hydrobiologia*, *456*(1), 73–85. https://doi.org/10.1023/A:1013071629591

Suess, E. (1980). Particulate organic carbon flux in the oceans—Surface productivity and oxygen utilization. *Nature*, *288*(5788), 260–263. https://doi.org/10.1038/288260a0

Thrush, S. F., & Dayton, P. K. (2002). Disturbance to marine benthic habitats by trawling and dredging: Implications for marine biodiversity. *Annual Review of Ecology and Systematics*, *33*, 449–473. https://doi.org/10.2307/3069270

Tiano, J. C., De Borger, E., O'Flynn, S., Cheng, C. H., van Oevelen, D., & Soetaert, K. (2021). Physical and electrical disturbance experiments uncover potential bottom fishing impacts on benthic ecosystem functioning. *Journal of Experimental Marine Biology and Ecology*, *545*, 151628. https://doi.org/10.1016/j.jembe.2021.151628

Tiano, J. C., Witbaard, R., Bergman, M. J. N., van Rijswijk, P., Tramper, A., van Oevelen, D., & Soetaert, K. (2019). Acute impacts of bottom trawl gears on benthic metabolism and nutrient cycling. *ICES Journal of Marine Science*, *76*, 1917–1930. https://doi.org/10.1093/icesjms/fsz060

Trimmer, M., Petersen, J., Sivyer, D., Mills, C., Young, E., & Parker, E. (2005). Impact of long-term benthic trawl disturbance on sediment sorting and biogeochemistry in the southern North Sea. *Marine Ecology Progress Series*, *298*, 79–94. https://doi.org/10.3354/meps298079

Tsikopoulou, I., Smith, C. J., Papadopoulou, K. N., & Austen, M. C. (2022). Linking species functional traits to specific biogeochemical processes under trawling pressure. *Biology*, *11*(10), 1378. https://doi.org/10.3390/biology11101378

van de Velde, S., Van Lancker, V., Hidalgo-Martinez, S., Berelson, W. M., & Meysman, F. J. R. (2018). Anthropogenic disturbance keeps the coastal seafloor biogeochemistry in a transient state. *Scientific Reports*, *8*(1), 5582. https://doi.org/10.1038/s41598-018-23925-y

van Denderen, P. D., van Kooten, T., & Rijnsdorp, A. D. (2013). When does fishing lead to more fish? Community consequences of bottom trawl fisheries in demersal food webs. *Proceedings. Biological Sciences/the Royal Society*, *280*(1769), 20131883. https://doi.org/10.1098/rspb.2013.1883

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, *36*(3), 1–48. https://doi.org/10.18637/jss.v036.i03

Warnken, K. W., Gill, G. A., Dellapenna, T. M., Lehman, R. D., Harper, D. E., & Allison, M. A. (2003). The effects of shrimp trawling on sediment oxygen consumption and the fluxes of trace metals and nutrients from estuarine sediments. *Estuarine, Coastal and Shelf Science*, *57*(1–2), 25–42. https://doi.org/10.1016/S0272-7714(02)00316-5

Watling, L., & Norse, E. A. (1998). Disturbance of the seabed by mobile fishing gear: A comparison to forest clearcutting. *Conservation Biology*, *12*(6), 1180–1197. https://doi.org/10.1046/j.1523-1739.1998.0120061180.x

Watson, R. A. (2017). A database of global marine commercial, small-scale, illegal and unreported fisheries catch 1950–2014. *Scientific Data*, *4*(1), 170039. https://doi.org/10.1038/sdata.2017.39

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