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Sediment heterogeneity shapes spatial variability of resuspension-induced CO_2 production

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Abstract. Demersal fishing is a major anthropogenic disturbance to marine sediments, with global implications for benthic carbon cycling and greenhouse gas emissions. Resuspension of sediment organic matter during bottom trawling enhances oxic mineralisation, converting stored organic carbon into aqueous CO_2 and reducing the long-term carbon storage potential of the seafloor. Sediment heterogeneity likely plays a role in the vulnerability of sedimentary organic carbon to resuspension, but spatial estimates CO_2 release from resuspended sediment rarely accounts for this heterogeneity. We conducted a large-scale survey in the Hauraki Gulf, New Zealand, to assess how sediment characteristics affect resuspension-induced CO_2 production (RCO_2P). Using a resuspension assay at 57 sites, we quantified RCO_2P accompanied by measurements of sediment grain size, organic matter content and quality, and phytopigments. Boosted regression tree analysis revealed that organic matter content has the strongest influence on RCO_2P variability, followed by coarse grained sand content and water depth. Non-linear relationships with RCO_2P further indicate context-dependent mechanisms controlling RCO_2P and allowed for the identification of three clusters with differing levels of vulnerability to resuspension impacts and different environmental influences. Overall, risk of resuspension-induced CO_2 release was moderate to very high in sediments with $> 3\,\%$ organic matter, $< 8\,\%$ coarse grained sand, and at depths > 56 m, comprising 73 % of our sampling sites. Multiple "hotspot" locations were found in the Hauraki Gulf, likely driven by an interplay of organic matter bioavailability and hydrodynamic conditions. Our results demonstrate that accounting for sediment heterogeneity in resuspension impact assessments will create more realistic and ecologically relevant estimates of C vulnerability over regional scales to inform spatial fisheries management.

1 Introduction

With the climate crisis progressing, humanity is in urgent need for undisturbed natural ecosystems to help stabilize the Earth's climate. Coastal and shelf seas hereby play a pivotal role by functioning as carbon (C) sinks as these highly productive systems build up large organic C stocks and high C burial rates in their sediments (Bianchi et al., 2018; Najjar et al., 2018). However, marine anthropogenic activities are a major disruption to the seafloor and its C sink functioning. The most prominent disturbance is demersal fishing whereby weighted gear is dragged over marine sediment to catch bottom-dwelling fish and benthic shellfish. Approximately 21.9 Gt of sediment are resuspended globally each year by this technique (Oberle et al., 2016), destroying benthic habitats and altering benthic C cycling processes (Bradshaw et al., 2021; Polymenakou et al., 2005; Pusceddu et al., 2005a; Thrush and Dayton, 2003).

Benthic C cycling is controlled by complex interactions of physical, chemical and biological processes. For example, the interplay of hydrodynamics, light availability, temperature, oxygen exposure, pH, grain size, permeability, redox state and benthic community structure and activity (fauna, algae, microbes) all affect organic matter reactivity which eventually determines how much of the organic C is naturally mineralised or buried (Arndt et al., 2013; Burdige, 2007; Middelburg, 2018; Snelgrove et al., 2018). Sediment resuspension influences this interplay by mixing organic matter from a certain sediment layer into the water column, thereby

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likely removing any redox gradients or physical protections that preserved the organic matter (Burdige, 2007; Kleber et al., 2021; Mayer, 1994). As a result, the resuspended organic matter is a mixture of dissolved and particulate organic C of different concentrations, bioavailability, composition, and structure altering its overall reactivity (Arndt et al., 2013). Resuspension further changes the abiotic conditions, most prominently oxygen exposure which can alter degradation rates of refractory and labile organic matter (Hulthe et al., 1998). Also the response of microbial community structure and activity to resuspension and priming can alter organic C mineralisation (van Nugteren et al., 2009; Pusceddu et al., 2005b). As a result, sediment resuspension experiments often report higher mineralisation rates in resuspended than in undisturbed sediments (Almroth-Rosell et al., 2012a; Bartl et al., 2025; Polymenakou et al., 2005; Ståhlberg et al., 2006), suggesting that the resuspension impact on physical, chemical and biological drivers stimulates organic C mineralisation thus reducing the fraction of organic C that can be buried long-term.

Based on the concept of resuspension stimulating organic C mineralisation, modelling studies estimated that bottom trawling causes a release of stored organic C as aqueous CO_2 of 1.7–493 t CO_2 km^{-2} yr^{-1} (Luisetti et al., 2019; Muñoz et al., 2023; Porz et al., 2024; Sala et al., 2021). Such estimates differ by up to two orders of magnitude as they rely on different first-order degradation rate constants and different assumptions about organic C lability. Different rate constants are applied across oceanic regions (Muñoz et al., 2023; Sala et al., 2021) or to C pools of varying lability (Porz et al., 2024; Zhang et al., 2019), along with assumptions that either all organic C (Luisetti et al., 2019) or only the labile fraction (Atwood et al., 2024, Sala et al., 2021) is mineralised once resuspended. The used degradation constants and model assumptions have been critically debated around their applicability for spatially variable marine sediments (Atwood et al., 2023; Epstein et al., 2022; Hiddink et al., 2023). Marine sediments display large spatial diversity of sediment properties formed by physical, chemical and biological processes as well as their interactions (Holland and Elmore, 2008; Snelgrove et al., 2018). While varying sediment properties are known to influence undisturbed organic C mineralisation and burial, the resuspension impact on this process is less clear as experiments often use only one sediment type or compare sand vs. mud (Almroth et al., 2009; Almroth-Rosell et al., 2012b; Lønborg et al., 2024; Ståhlberg et al., 2006). Measuring resuspension effects across wider ranges of sediment properties, i.e. across sediment heterogeneity, will provide new and spatially detailed insights on potential impacts on the C storage function.

To empirically quantify variability of resuspension impacts across sediment heterogeneity, we have recently developed a measure of C storage vulnerability through a resuspension assay (Bartl et al., 2025). The assay quantifies potential rates of resuspension-induced organic C mineralisation, and its simple design allows for high sampling resolution within one region. In this study, we conducted a survey in the Hauraki Gulf (New Zealand), a heterogeneous shelf system impacted by dredging and bottom trawling, where we applied the resuspension assay across 57 sites spanning wide ranges of sediment characteristics and water depths. Surface sediment grain size fractions, organic matter content and freshness, and phytopigments were used as indicators of sediment heterogeneity, and we analysed their influence on resuspension-induced CO_2 production using boosted regression tree modelling. Our results provide detailed insights into the relationships between sediment heterogeneity and sediment resuspension impacts on C storage, contributing to discussions around sustainable spatial management of demersal fisheries in shelf sea regions.

2 Methods

2.1 Study site and sampling

The Hauraki Gulf is a semi-enclosed, oligotrophic shelf sea up to 150 m deep, located in the northeast of New Zealand. Its seafloor comprises diverse volcanic and alluvial sediments ranging from coarse calcareous sand and gravel to fine sands and silts rich in clay (Manighetti and Carter, 1999). Water circulation and sediment transport are dominated by the south-eastward flowing East Auckland Current and strong tidal currents (Manighetti and Carter, 1999; Sharples, 1997; Zeldis et al., 2004). Terrestrial organic C input is limited and mainly confined to the Firth of Thames, while in the inner and outer Gulf, sediment organic matter derives from both terrestrial and marine sources (Sikes et al., 2009). Anthropogenic impacts have affected the Gulf for decades, including bottom trawling, dredging, and sand mining (Hauraki Gulf Forum, 2020, 2023). Bottom trawling generally occurs at depths > 50 m (Fig. S1) wile commercial scallop dredging took place in shallower areas (< 50 m) but has been banned since 2022 (Hauraki Gulf Forum, 2020, 2023).

In February and March 2024, 57 sites were sampled aboard the R/V *Te Kaihōpara* (Fig. 1). Sediments were collected using a HAPS corer (KC Denmark, 14 cm diameter), with three replicate cores taken per site. Subsamples from the surface sediment (0–3 cm) were collected for characterisation using acid-cleaned (10 % HCl) polypropylene syringes with cut-off tips, while paired small sediment cores were taken for the resuspension assay using acid-cleaned acrylic core liners (inner diameter = 3.4 cm, height = 14 cm). Sediment samples for characterisation were immediately transferred to acid-cleaned polypropylene containers, kept on ice, and frozen at −20 °C at the end of each sampling day. The small intact cores were stored with open tops in dark seawater tanks at ambient bottom-water temperature (± 2 °C), and resuspension assay incubations were conducted within two hours of sampling.

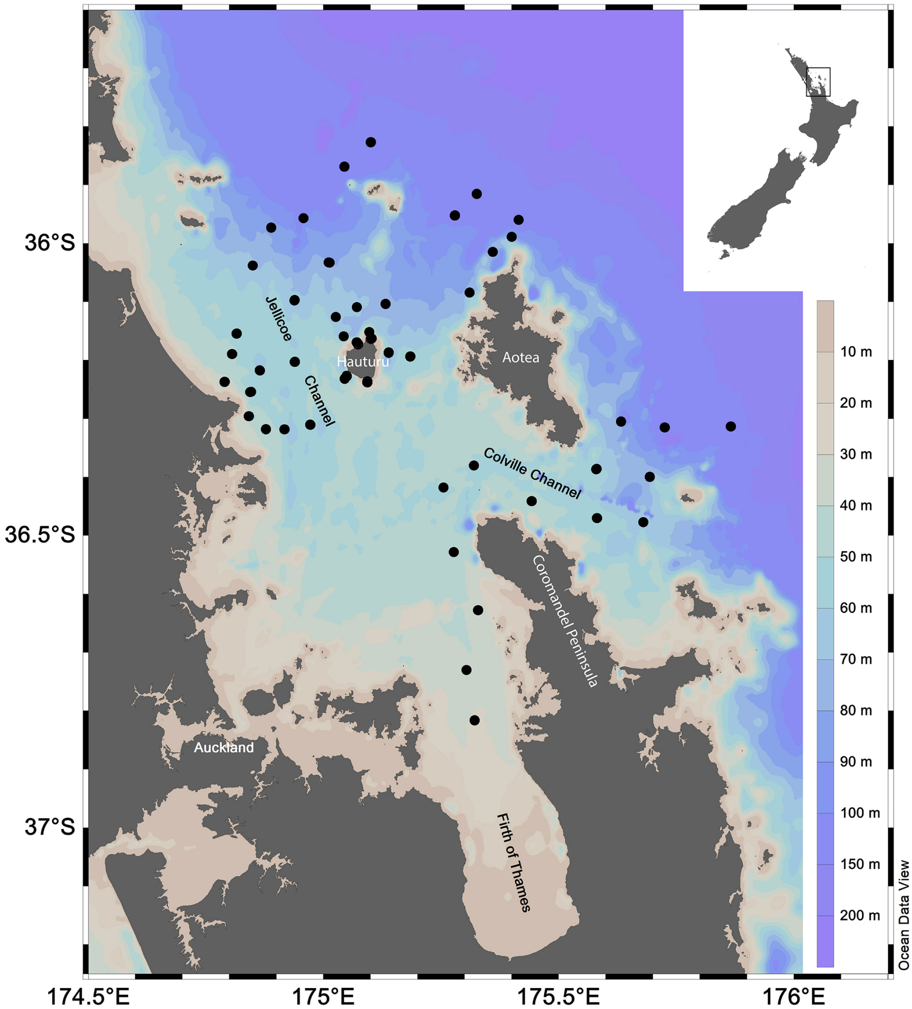

Figure 1. Study sites in the Hauraki Gulf, New Zealand (black dots). Coloured shading represents bathymetry. Map produced using Ocean Data View (Schlitzer, Reiner, Ocean Data View, https://odv.awi.de, last access: 19 November 2025, 2025).

2.2 Resuspension assay

To quantify aqueous CO_2 production in resuspended sediments, we conducted resuspension assays following Bartl et al. (2025). The assay incubates undisturbed sediments in small cores and resuspended sediments in glass bottles, measuring temporal changes in oxygen concentration to determine sediment oxygen demand (SOD). For both treatments, the upper 3 cm of sediment – typically disturbed by trawling and dredging (Hiddink et al., 2017) – were incubated. Optimal sediment-to-water ratios to maintain oxic conditions were 1 : 8 for sandy sediments (250 mL bottles) and 1 : 17 for muddy sediments (500 mL bottles). For the resuspension treatment, sediment was added to glass bottles pre-filled with filtered seawater and the sediment was resuspended by gentle inversion for 30 s. In both undisturbed cores and resuspension treatments, SOD (mmol m^{-2} h^{-1}) was calculated from oxygen concentrations measured at the start and end of the 4–6 h incubations (OXROB10 probe and FireSting GO2 meter, Pyroscience, Germany). Values were normalised to incubation time and sediment surface area. Linear decline in oxygen, a requirement for this calculation, was validated through preliminary tests (Bartl et al., 2025). At each site, three pairs of control cores and resuspension treatments were incubated in the dark at ambient bottom-water temperature, conditions were monitored with loggers (Hobo Pendants, USA). Incubations showing $> 30\,\%$ oxygen decrease between initial and final measurements, or before and after shaking, were discarded (Bartl et al., 2025). Organic C mineralisation to CO_2 was estimated from SOD using a respiratory quotient (RQ) of 0.9 for inner-shelf sites (< 50 m depth) and 0.85 for outer-shelf sites (50–200 m; Jørgensen et al., 2022). Resuspension-induced CO_2 production (RCO2P) was calculated as the difference in CO_2 production between resuspended and undisturbed samples. The factor increase in CO_2 production was obtained by dividing resuspended values by undisturbed values. RCO2P serves as a proxy for the vulnerability of sediment organic C to severe resuspension, with higher RCO2P indicating greater vulnerability.

2.3 Sediment characteristics

Organic matter content was determined by loss on ignition, burning dried (60 °C for 7 d) sediments at 450 °C for four hours. For grain size analysis, sediments were digested with 10 % H2O2 for six weeks to remove organic matter, washed with deionised water, and dispersed in 5 % sodium hexametaphosphate before laser diffraction analysis using a Malvern Mastersizer-3000 (Malvern, UK). Four grain size classes were derived: coarse sand (500–2000 µm), medium sand (250–500 µm), fine sand (63–250 µm), and mud (< 63 µm). This grouping reflects the bimodal grain size distributions observed in most samples while keeping the number of grain size factors for data analysis manageable. Shell hash and gravel were quantified by wet sieving and weighing two dried fractions: > 2 mm (shell hash and gravel) and < 2 mm (remaining sediment). Phytopigments (chlorophyll *a* and phaeophytin) were extracted from 1 g of homogenised, freeze-dried sediment using 3 mL of 90 % aqueous acetone over 24 h (Buffan-Dubau and Carman, 2000; Sun et al., 1991). Pigment absorbances were measured before and after acidification with a spectrophotometer (Duetta, Horiba Scientific), and concentrations were calculated following Lorenzen (1967). Chlorophyll a concentration was used as an indicator of algal biomass, while the ratio of organic matter content to total phytopigment concentration (Chl a + phaeophytin) served to characterise short-term organic matter freshness (Miatta and Snelgrove, 2021). Total phytopigment concentration was used rather than Chl *a* because both photosynthetic Chl *a* and its degradation product represents labile organic matter components (Pusceddu et al., 2010). Lower ratios indicate fresher, less degraded material.

2.4 Data analysis

A total of 171 samples were analysed for each sediment characteristic alongside 171 resuspension assays. After quality assessment of the assay data (lost cores, > 30 % oxygen decline, or large macrofauna), two sites (6 data points) and 21 additional data points were removed. Two Chl *a* values were interpolated as the mean of the remaining site replicates, resulting in a complete dataset of 144 samples. To identify relationships between sediment heterogeneity and RCO2P, we applied supervised machine learning using boosted regression trees (BRT; (Friedman, 2001). BRTs are ensemble models that sequentially build decision trees, with each tree correcting errors from the previous iteration, improving predictive performance. They capture non-linear relationships and interactions, making them suitable for analysing complex ecological datasets while maintaining strong predictive power (Lucas, 2020; Rubbens et al., 2023). BRTs have been widely applied for predicting species distributions, fishing effort, ecosystem services (Cimino et al., 2020; Lohrer et al., 2020; Soykan et al., 2014) and linking biogeochemical variables to environmental factors (Panaïotis et al., 2025; Rijkenberg et al., 2011).

Our dataset included the following variables indicative of sediment heterogeneity: water depth (Depth), shell hash and gravel content (S/G), coarse sand (C-Sand), medium sand (M-Sand), fine sand (F-Sand), mud (Mud), organic matter content (OM), and the organic matter-to-total phytopigment ratio (OM : Phyto). The response variable was resuspension-induced CO_2 production (RCO2P). Mud, M-Sand, and OM were highly collinear ($r > |0.8|$; Fig. S2). While multicollinearity does not affect BRT predictions, it complicates interpretation of feature importance and interactions (Boulesteix et al., 2012; Dormann et al., 2013; Lucas, 2020). We therefore excluded Mud and M-Sand, retaining OM as it is the substrate for C mineralisation. Replacement tests using Mud and M-Sand instead of OM produced similar BRT results (Table S1). To perform BRT the data set was split into a training set (75 % of the samples) and a testing set (25 % of the samples). Hyperparameters were tuned via grid search and 4-fold cross-validation: number of trees = 1000, maximum depth = 3, minimum samples per leaf = 3, learning rate = 0.005, and subsampling = 0.8. To ensure robustness, 50 BRT iterations were run. Model interpretation employed SHAP (SHapley Additive exPlanations) values to assess feature importance, interactions, and feature relationships to modelled RCO2P (Li, 2022; Lundberg et al., 2018; Lundberg and Lee, 2017). Mean absolute SHAP values were used to derive overall feature and interaction importance. SHAP dependence plots visualised how modelled RCO2P increased (positive SHAP values) or decreased (negative SHAP values) across feature values. Feature importance rankings and dependence plots were then used to identify clusters with differing RCO2P. Within each cluster, Pearson correlation analysis was used to determine relationships between features and RCO2P. All analyses were conducted in Python (v3.12.7) using the packages *scikit-learn* (v1.6.1; Pedregosa et al., 2011) and *SHAP* (v 0.47.1; Lundberg et al., 2020).

3 Results

3.1 Distribution of sediment characteristics and resuspension-induced CO_2 production

The sampled sites covered a wide range of sediment types and depths, with S/G, C-Sand, M-Sand, F-Sand, and Mud contents ranging from 0 %–40 %, 0 %–62 %, 1 %–54 %, 2 %–68 %, and 1 %–84 %, respectively. Grain size was spatially variable: coarser sediments dominated channels and areas around Hauturu (Fig. 2a–c; Fig. S3), while finer sands and mud prevailed near the main coast and at deeper outer-shelf sites (Figs. 2d, S3). OM content ranged from 0.9 %–

9.6 %, with highest values at outer-shelf sites and inner-shelf areas west of Coromandel Peninsula (Fig. 2e). OM freshness varied widely irrespective of OM content or water depth (OM : Phyto = 1.2–16.1; Fig. 2f). Algal biomass, indicated by Chl *a*, was mainly concentrated at shallow inner-shelf sites, reaching up to 8 $\mu g\,g^{-1}$ dw, but Chl *a* concentrations of 2–4 $\mu g\,g^{-1}$ were also detected at several sites deeper than 50 m, suggesting either microphytobenthos presence or substantial sedimentation of algal material (Fig. 2g). CO_2 production rates were 1.4–19.5 times higher in resuspended sediments than in undisturbed sediments (Fig. S4). RCO2P showed strong spatial variability (0.1–3.5 mmol $CO_2\,m^{-2}\,h^{-1}$), with elevated rates observed at multiple shallow and deep sites (Fig. 2h).

3.2 Most important features and relationships

The 50 BRT model iterations performed well in predicting RCO2P, with an R^2 of 0.58 ± 0.11 and a root mean squared error of 0.54 ± 0.07 mmol $CO_2\,m^{-2}\,h^{-1}$, indicating good performance for highly variable environmental data. OM was the most important feature, showing the highest mean absolute SHAP value and ranking first across all 50 model runs (Table 1). C-Sand was the second most important feature, with a mean absolute SHAP value 3.6 times lower than that of OM. Depth and F-Sand had similar SHAP importances (~ 0.1), consistently ranking third and fourth, while Chl *a* and S/G were least influential (Table 1). The most significant feature interactions were OM – C-Sand and OM – Depth, which had higher SHAP values than Chl *a* and S/G but remained lower than the top four individual features. Overall, RCO2P variability was primarily driven by the individual effects of OM, C-Sand, Depth, and F-Sand, with only minor contributions from interactions.

SHAP dependence plots revealed predominantly nonlinear relationships between modelled RCO2P and features (Fig. 3). Across the OM gradient, SHAP values shifted from negative to positive at ~ 3 % OM, indicating highest RCO2P in sediments containing 3 %–10 % OM (Fig. 3a). Similarly, sediments with C-Sand below 8 % and from depths of 56–100 m exhibited positive SHAP values, linking these conditions to higher RCO2P (Fig. 3b, c). Although less influential overall, F-Sand and OM : Phyto showed more linear relationships with RCO2P, with highest SHAP values at F-Sand > 27 % and OM : Phyto < 4.7, suggesting that greater CO_2 production corresponds to higher F-Sand content and fresher organic matter (Fig. 3d, e). No clear relationships were observed for Chl *a* or S/G (Fig. 3f, g).

3.3 Clusters with different levels of RCO2P and differing relationships

To visualise which sediment types are most vulnerable to CO_2 release upon resuspension, we produced scatter heat maps from the original dataset and used BRT results to identify clusters (Fig. 4, Table 2). Lowest RCO2P rates (0.5 ± 0.3 mmol $m^{-2}\,h^{-1}$) occurred in sandier sediments (> 8 % C-Sand, > 27 % F-Sand) with low organic matter content (< 3 %) and shallow depths (< 56 m), forming a distinct OM-poor cluster (Fig. 4a, b). Sediments in this cluster are from the Colville and Jellicoe Channels and around Hauturu and show a low to moderate risk of CO_2 release (Fig. 2H, Table 2). RCO2P in the OM-poor cluster correlated positively with OM and F-Sand but negatively with C-Sand, indicating stronger resuspension-driven mineralisation where OM and finer fractions are higher (Fig. 4c). At depths ≥ 100 m, both OM and RCO2P were high and relatively uniform, with RCO2P about four times higher than in the OM-poor cluster (Table 2). This Deep-cluster showed a negative correlation between RCO2P and OM, and slightly higher rates at lower OM : Phyto ratios, reflecting fresher organic matter (Fig. 4e).

Mixed sediments (> 3 % OM, < 8 % C-Sand) from intermediate depths (56–100 m,) formed a Mixed cluster with RCO2P ranging from 0.8–3.5 mmol $m^{-2}\,h^{-1}$, equivalent to 3–19.5 times higher CO_2 release than in undisturbed sediments (Fig. 4b, Table 2). No clear correlations were found here (Table 2, Fig. 4d). Within the Mixed cluster the highest 10 % of RCO2P values (> 2.6 mmol $m^{-2}\,h^{-1}$) occurred along interactions between OM and C-Sand (C-Sand $= 270.08 \times OM^{-2.93}$, $R^2 = 0.51$, $p = 0.003$) and OM and Depth (Depth $= -4.97 \times$ OM $+ 87.45$, $R^2 = 0.32$, $p = 0.029$; Fig. 4a, b). Together, the Mixed and Deep cluster cover 73 % or the sampled sites and are moderately to very highly vulnerable to releasing CO_2 when disturbed (Table 2, Fig. 2h).

4 Discussion

Our results show that resuspension of the 3-cm surface sediment strongly enhances organic C mineralisation producing up to 20 times more CO_2 compared to undisturbed surface sediments in the Hauraki Gulf. Sediment heterogeneity, based on organic matter content, sand content and water depth played an important role explaining the variability of resuspension-induced CO_2 production and their nonlinear relationships indicate context-dependent controls and allowed us to identify three clusters with different levels of C storage vulnerabilities.

4.1 Spatial variability of resuspension-induced CO_2 production driven local environmental settings

The stimulation of organic C mineralisation through sediment resuspension can involve multiple physical, chemical and biological mechanisms (Hulthe et al., 1998; Kleber et al., 2021; van Nugteren et al., 2009; Pusceddu et al., 2005b) which in sum contribute to the RCO2P rates that we measured. While we expected variability of RCO2P due to sam-

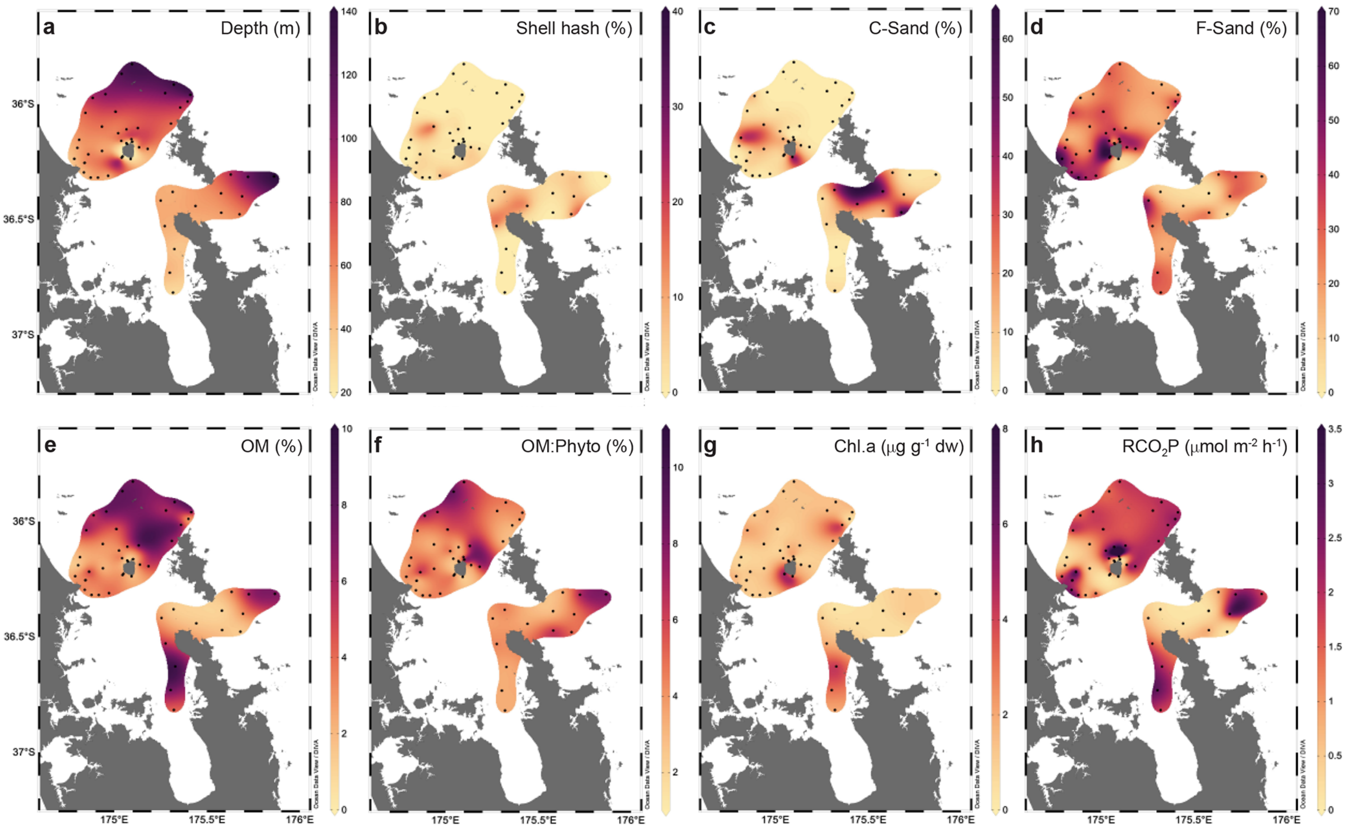

Figure 2. Environmental features water depth **(a)**, shell hash/gravel **(b)**, coarse grained sand (500–2000 µm, **c**), fine grained sand (63–250 µm, **d**), organic matter content **(e)**, ratio of organic matter and phytopigments **(f)**, and Chlorophyll a content **(g)** as well as resuspension-induced CO_2 production rates **(h)** in the Hauraki Gulf, New Zealand. For better visualisation, data were spatially interpolated from the sampling sites (white dots) using DIVA in Ocean Data View (Schlitzer, Reiner, Ocean Data View, https://odv.awi.de, last access: 19 November 2025, 2025).

Table 1. Feature importance of individual features and interacting features based on mean absolute SHAP values. Higher values indicate higher influence of feature on modelled RCO2P. Values in brackets are the 95 % confidence intervals from the 50 model iterations.

individual feature	mean |SHAP| feature importance	Rank stability	interacting features	mean |SHAP| interaction importance
OM	0.47 (0.010)	1.0 (0.00)	OM + C-Sand	0.061 (0.005)
C-Sand	0.13 (0.008)	2.5 (0.23)	OM + Depth	0.056 (0.006)
Depth	0.10 (0.008)	3.6 (0.31)	F-Sand + Depth	0.033 (0.003)
F-Sand	0.09 (0.006)	3.7 (0.29)	OM + F-Sand	0.029 (0.003)
OM : Phyto	0.07 (0.006)	4.6 (0.29)	OM + Chl *a*	0.025 (0.002)
Chl *a*	0.04 (0.003)	6.1 (0.20)	C-Sand + Depth	0.023 (0.002)
S/G	0.04 (0.005)	6.5 (0.26)	Other interaction pairs	< 0.023

pling across substantial sediment heterogeneity, the extent of variability and the location of apparent hotspots was surprising. We found three clusters of C storage vulnerability in which RCO2P appears to be regulated by differing environmental conditions. Firstly, low to moderate vulnerability in the shallow, coarse-grained sediments around Hauturu and in the channels is likely linked to strong tidal and residual currents that winnow fine organic particles and/or naturally enhance organic matter turnover resulting in a smaller resuspension impact (Boudreau et al., 2001; Manighetti and Carter, 1999). The positive relationship of RCO2P with organic matter quantity and finer grained sand content suggests that substrate availability and strong (less F-Sand) vs. calm (more F-Sand) hydrodynamic conditions were controlling the magnitude of the resuspension impact in the OM-poor cluster. At the other end of the spectrum, deep, muddy,

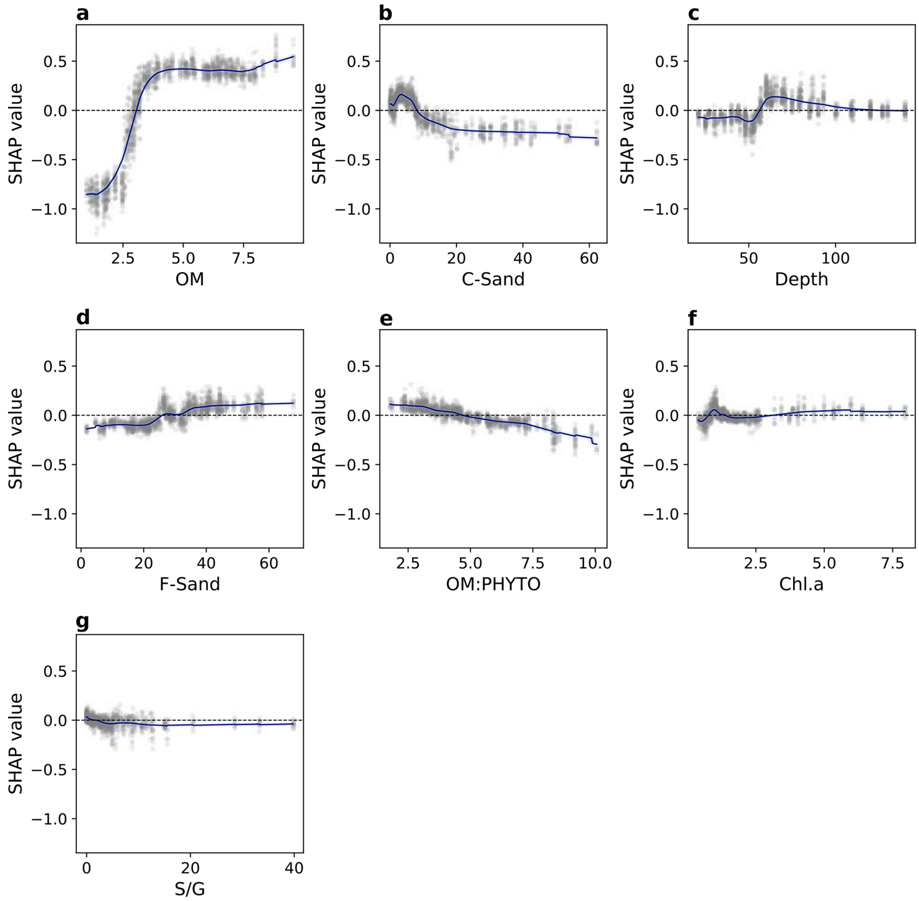

Figure 3. Partial-dependence-plots showing the relationship between SHAP values and features organic matter **(a)**, coarser grained sand **(b)**, water depth **(c)**, finer grained sand **(d)**, organic matter freshness **(e)**, Chlorophyll *a* **(f)**, and shell hash/gravel **(g)**. Positive SHAP values reflect a positive contribution of the feature-value to model output, i.e. to higher RCO2P than average, and vice versa. Lowess smooth function was applied for each of the 50 model iterations and its mean and 95 % confidence interval are shown as dark blue solid line and light blue shading, respectively. The shape of the scatter shows non-linear relationships between SHAP values and features, with strong shifts (across SHAP = 0) at OM = 3 %, C-Sand = 8 %, and Depth = 56 m.

OM-rich sediments showed high to very high C storage vulnerability likely due to the consistently high pool of OM that accumulates in the deep outer shelf area of the Hauraki Gulf. Interestingly, here RCO2P was ∼ 10 % higher when OM was fresher, suggesting that quality of the resuspended organic matter influences mineralisation when the substrate is abundant.

We could not derive mechanistic explanations of RCO2P variability in the mixed sediment cluster based on our sediment data. This suggest that there may be other environmental variables that could explain the spatial variability of resuspension impacts in these sediments. Measures of organic matter quality or bioavailability are likely to influence RCO2P and may have been underrepresented in our set of features. While our use of simple and cost-effective proxies (e.g. loss-on-ignition OM and OM:Phytopigment ratio) enables broad applicability (Bartl et al., 2025) it may overlook important compositional nuances of OM. Incorporating additional measures, such as C : N ratios, δ^{13}C signatures, or n-alkane signatures (Sikes et al. 2009), may help resolve spatial RCO2P patterns. RCO2P variability could also be linked to the concentration and quality of dissolved organic matter that is resuspended with the sediment and can contain a considerable fraction of readily degradable compounds that could enhance microbial mineralisation (Kujawinski, 2011; Lengier et al., 2024; Reader et al., 2019). Lastly, the composition and activity of the microbial community and their response to being resuspended could influence RCO2P irrespective of the amount, composition or biochemical quality of organic matter (DesRosiers et al., 2022). On a broader scale, spatially variable OM supply from benthic or pelagic primary production or lateral transport by cross-shore bottom currents could also drive the spatial pattern of RCO2P in the Hauraki Gulf (Chang et al., 2003; Zeldis et al., 2004). Since we can only speculate about potential underlying mechanisms of resuspension impacts in the Mixed cluster, future

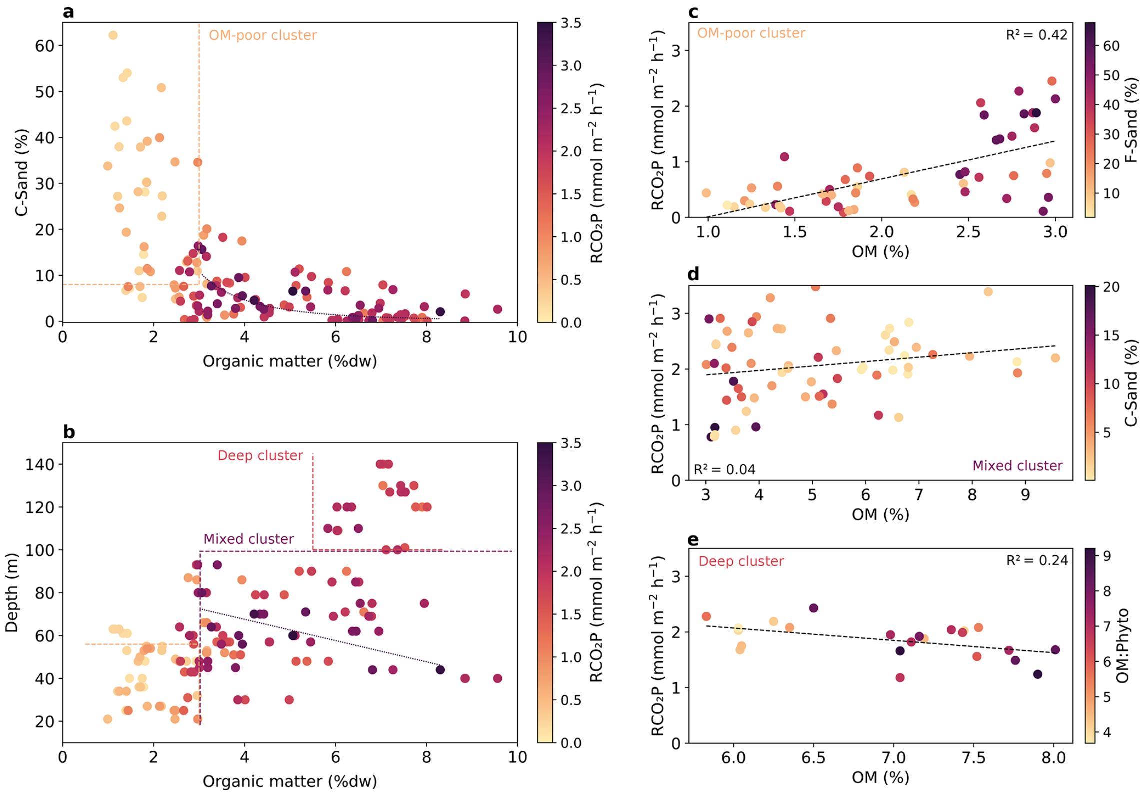

Figure 4. Scatter heatmaps showing the resuspension-induced CO_2 production (RCO2P, colour gradient) over organic matter content and C-Sand **(a)**, and over organic matter content and water depth **(b)**. Light orange dashed lines represent the boundaries of the OM-poor cluster, the red dashed line for the Deep cluster, and the puple dashed lines for the Mixed cluster. The dotted lines in **(a)** and **(b)** show the fit of the 90th quantile of RCO2P rates ($> 2.6\,\mathrm{mmol\,m^{-2}\,h^{-1}}$) along interactions of organic matter and C-Sand ($y = 270.08x^{-2.93}$, $R^2 = 0.51$, $p = 0.003$) and organic matter and water depth ($y = -4.97x + 87.45$, $R^2 = 0.32$, $p = 0.029$). Panels C-E show relationships of environmental variables with RCO2P in the OM-poor cluster **(c)**, the Mixed cluster **(d)**, and the Deep cluster **(e)**. Ranges and correlation coefficients are given in Table 2.

targeted experiments on the role of organic matter bioavailability and the microbial response to resuspension in mixed sediment types will shed more light on underlying mechanisms of resuspension-induced organic C mineralisation.

4.2 Sediment heterogeneity as predictor of sediment C vulnerability?

Our BRT model explained $\sim 58\,\%$ of variability in RCO2P forming a strong basis for using BRT models like ours to predict C storage vulnerability from spatial patterns of sediment characteristics. Sediment grain size and organic matter data often have high spatial resolution and thus represent useful surrogates to quantify large-scale sediment C vulnerability. Improving the performance of our BRT model to capture more of the currently unexplained variability ($\sim 40\,\%$) can perhaps be achieved through integrating more nuanced features as discussed above (see Sect. 4.1). Additionally, history or intensity of trawling can influence both the long-term concentration and reactivity of OM as well as how it is mediated through benthic faunal communities (Hale et al., 2017; Pusceddu et al., 2014; Tiano et al., 2022; Zhang et al., 2024). As a result, RCO2P could be partly driven by the sampling site's trawling disturbance history. However, incorporating a measure of historical disturbance frequency may only improve assessments if the data on trawling activity is collected at the resolution necessary to link it to local sampling coordinates. Compared to first-order model estimations that rely on assumptions of degradation constants and organic C lability (Atwood et al., 2024; Luisetti et al., 2019; Muñoz et al., 2023; Sala et al., 2021), predictions from a BRT model approach are based on empirical measurements of sediment characteristics, resuspension-induced organic C mineralisation rates and the relationships and interactions that they form. This makes it a powerful tool that integrates environmental variability making predictions more realistic and detailed at the regional scale offering opportunities for meaningful regulatory actions for trawling.

Table 2. Average (Avg), standard deviation (SD), ranges of environmental features and C storage vulnerability in the three clusters identified through BRT analysis. Pearson correlation coefficients (R) are provided for relationships of RCO2P and individual features in each cluster. Correlations ($R \geq 0.4$) in bold are significant at $p < 0.05$, and in italic at $p < 0.1$. C storage vulnerability levels are based on RCO2P rates and the factor increase relative to CO_2 production from undisturbed sediments cores.

Cluster	Features						C storage vulnerability		
	Metric	OM	C-Sand	Depth	F-Sand	OM : Phyto	RCO2P	Factor increase	level
OM-poor cluster ($n = 53$)	Avg ± SD	2.1 ± 0.6	20.1 ± 16.0	45.7 ± 16.1	30.0 ± 18.5	4.4 ± 1.9	0.7 ± 0.7	3.9 ± 2.5	low – moderate
	Range	1.0–3.0	0.2–62.2	21.0–87.0	1.8–67.7	1.8–9.9	0.1–2.5	1.4–12.5	
	R	**0.651**	**−0.472**	0.156	**0.516**	−0.258			
	p	< **0.001**	< **0.001**	0.264	< **0.001**	0.062			
Deep cluster ($n = 23$)	Mean ± SD	7.0 ± 0.7	1.3 ± 2.1	120 ± 12.4	22.2 ± 5.4	6.3 ± 1.8	1.9 ± 0.3	9.6 ± 2.3	High to very high
	Range	5.8–8.0	0.0–7.9	100–140	14.3–32	3.7–9.2	1.2–2.4	5.0–13.6	
	R	**−0.493**	0.153	−0.134	−0.253	*−0.393*			
	p	**0.017**	0.486	0.541	0.245	*0.064*			
Mixed cluster ($n = 53$)	Mean ± Std	5.0 ± 1.7	5.3 ± 5.0	62.6 ± 15.5	31.5 ± 9.2	4.6 ± 1.6	2.1 ± 0.7	8.2 ± 3.9	moderate to very high
	Range	3.0–9.6	0.1 ± 20.1	30.0–93.0	16.4–55.9	2.3–10.1	0.8–3.5	3.0–19.5	
	R	0.203	−0.239	−0.042	0.101	−0.087			
	p	0.110	0.059	0.741	0.431	0.496			

4.3 Methodological considerations of resuspension assay quantifications

The resuspension assay provides a simple measure of oxic organic C mineralisation in the top 3 cm of sediment, offering insight into the vulnerability of seafloor C storage. Porz et al. (2024) used a similar approach in their model, defining sediment organic C vulnerability in the top 10 cm as the maximum potential oxic organic C remineralization rate. Their modelled oxic organic C remineralization rates (0.1–100 mmol C m^{-2} d^{-1}) align with our empirical RCO2P measurements (2–88 mmol C m^{-2} d^{-1}). Other experiments investigating the immediate impact of sediment resuspension reported mineralisation rates to be 1.1–4.7 times higher in resuspension treatments compared to controls (Almroth-Rosell et al., 2012a; Niemistö et al., 2018; Ståhlberg et al., 2006). This is comparable but at the lower end of the range of our measurements where RCO2P was 1.4–19.5 times higher in resuspended sediments. The difference may be attributable to a thicker sediment layer being resuspended in our assay (3 cm) compared to the other experiments (0.3 µm to 1 cm) and the different methodological approaches (e.g. in situ chamber vs. bottle incubations). Overall, the comparability of out measurements to both model and experimental studies supports the assay's relevance for resuspension impact assessments.

Two methodological aspects of the assay need to be considered when linking the assay to trawling impacts and organic C mineralisation. Firstly, the assay determines potential CO_2 production after severe resuspension through shaking up sediment in a bottle and therefore may not reflect the true mechanical impact of individual trawling gear and trawling technique (O'Neill and Ivanović, 2016; Rijnsdorp et al., 2021). However, the high sampling frequency that is possible with the assay enhances our spatial understanding of sediment C vulnerability and thus where trawling would be most impactful. Secondly, the assay converts sediment oxygen demand to CO_2 production using respiratory quotients (see Sect. 2.2). This quantification may overestimate CO_2 production if reduced species are oxidised alongside organic C. We incubated the surface sediments from an oligotrophic system where oxygen and nitrate penetration depths (O_2: 3–6 mm, nitrate: 12 mm) and total-to-diffusive oxygen uptake ratios (TOU / DOU = 2.4) indicate strong macrofaunal influence on redox conditions and minimal accumulation of reduced species in both sandy and muddy sediments (30–128 m depth; Cheung et al., 2024). This aligns with findings of low acid volatile sulfide concentrations (AVS) in non-impacted Hauraki Gulf sediments (0–1 µmol g^{-1} w/w) compared to higher AVS levels in sediments impacted by a mussel farm (2–12 µmol g^{-1} w/w, Wilson and Vopel, 2015). Future use of the resuspension assay, particularly in more reduced or eutrophic sediments, should include a validation of the SOD approach by measuring changes dissolved CO_2 or DIC during the incubations.

4.4 Seafloor protection based on C vulnerability

As our understanding of sediment C storage vulnerability grows, its integration into spatial management of demersal fisheries becomes inevitable. In the Hauraki Gulf, recent discussions on confining trawling pressures focused on protecting reef-forming species and habitats, while sediment C storage vulnerability was not considered (Bennion et al., 2024). Trawling remains allowed in areas deeper than 50 m (Bevin, 2025) which, based on our results, includes nearly all sediments with high to very high C vulnerability. This leaves Hauraki Gulf sediments at risk to lose their climate-stabilizing C storage function and will contribute to the green-house gas emission of the NZ fisheries industry. By integrating sediment heterogeneity and the resulting spatial variability of resuspension impacts, highly vulnerable areas can be identified and protected. In a recent modelling study, Porz et al. (2024) compared different seafloor protection scenarios in the North Sea and found that protection based on C vulnerability was most efficient for preserving organic carbon and maintaining benthic macrofauna biomass. This highlights that seafloor carbon protection generates benefits not only for organic C storage, but also for benthic species and habitats ultimately maintaining the undisturbed functioning of seafloor ecosystems.

5 Conclusions

The risk of CO_2 release from the sediment as a consequence of resuspension is not something we can ignore as we seek to limit emissions and meet climate obligations. Our findings show that the variability of resuspension-induced CO_2 release is linked to sediment characteristics resulting in local environmental conditions controlling resuspension impacts. Using measures of sediment heterogeneity and the resuspension assay offers localised insight into where carbon storage is most vulnerable to disturbance, and where management efforts could be focused. Our results support the inclusion of seafloor carbon protection in regional planning, particularly in areas like the Hauraki Gulf where sediment heterogeneity and fishing pressure intersect. Moving forward, combining our empirical assessment with more nuanced data on organic matter quality, physical and biological organic matter inputs, and disturbance history will enhance our ability to estimate human impacts on the seafloor and sustain natural C sinks that contribute to global climate stabilisation.

Code and data availability. Sediment characteristics and resuspension-induced CO_2 production rates from the Hauraki Gulf are available at https://doi.org/10.17608/k6.auckland.27948264 (Bartl and Thrush, 2025a). The code for the BRT model is available at https://doi.org/10.17608/k6.auckland.29442407 (Bartl and Thrush, 2025b).

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Author contributions. SF and IB developed the resuspension assay and planned the campaign; IB conducted the sampling campaign. performed the measurements and analysed the data; IB wrote the manuscript draft; SF reviewed and edited the manuscript.

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