

# Sediment heterogeneity shapes spatial variability of resuspension-induced CO<sub>2</sub> 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 ~~carbon-matter~~ during bottom trawling enhances oxic mineralisation, converting stored organic ~~matter-carbon~~ into aqueous CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> production (RCO<sub>2</sub>P). Using a resuspension assay at 57 sites, we quantified RCO<sub>2</sub>P accompanied by measurements of sediment grain size, organic matter content and quality, and phytopigments. Boosted regression tree analysis revealed that 15 organic matter content has the strongest influence on RCO<sub>2</sub>P variability, followed by coarse grained sand content and water depth. Non-linear relationships with RCO<sub>2</sub>P further indicate context-dependent mechanisms controlling RCO<sub>2</sub>P and allowed for the identification of three clusters with differing levels of vulnerability to resuspension impacts and different environmental ~~conditions-influencesinfluencing this vulnerability~~. Overall, risk of resuspension-induced CO<sub>2</sub> 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 20 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

25 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 30 benthic shellfish. Approximately 21.9 Gt of sediment are resuspended globally ~~each year~~ by this technique ~~each year~~ (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).

35 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 likely removing any redox gradients or physical protections that preserved the organic  
40 matter ~~within the sediment~~ (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  
45 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.

50 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<sub>2</sub> of 1.7 – 493 t CO<sub>2</sub> km<sup>-2</sup> yr<sup>-1</sup> (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),  
55 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 ~~the~~ spatially highly 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 ~~the role of~~ varying  
60 sediment properties for are known to influence undisturbed organic C mineralisation and burial ~~is known~~, the resuspension impact on this process is less clear as experiments often use only one sediment type or compare sand vs. mud to three sediment types (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<sub>2</sub> 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's ~~North Island~~. 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) while 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 ~~characterisation~~-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 ( $\pm 2$  °C), and resuspension assay incubations were conducted within two hours of sampling.

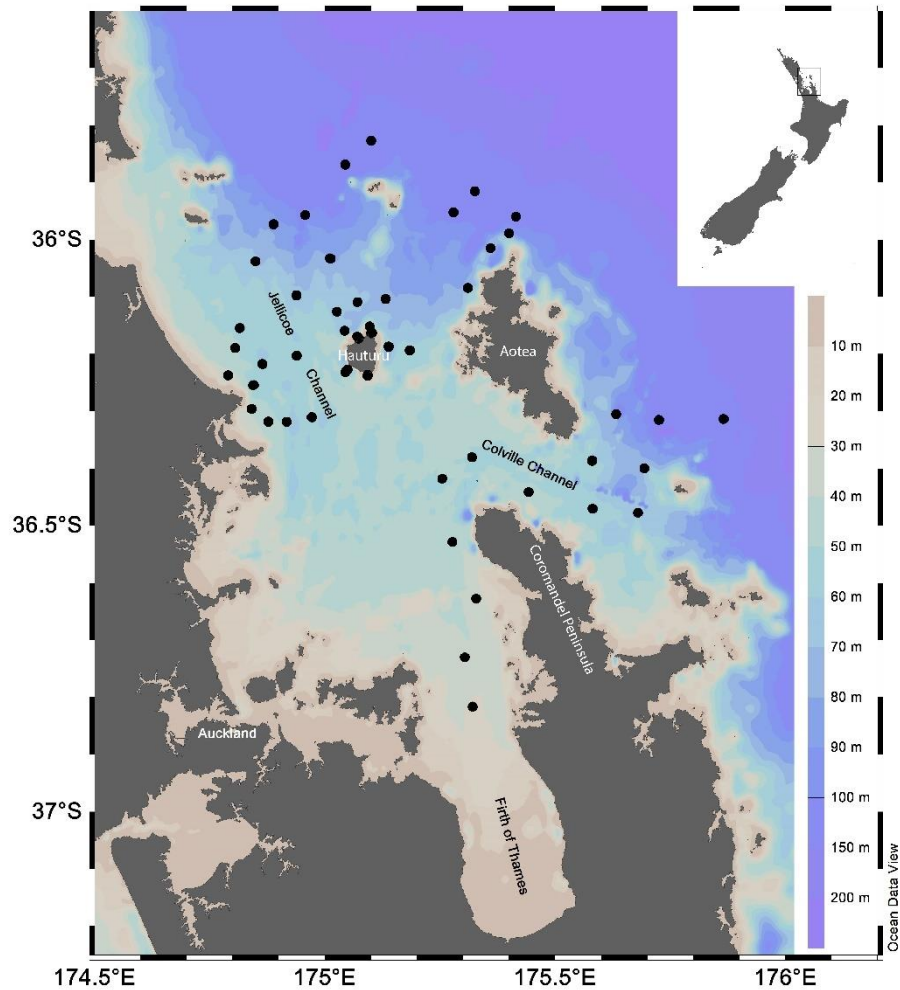


Figure 1: Study sites in the Hauraki Gulf, New Zealand (black dots). Coloured shading represents bathymetry.

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## 2.2 Resuspension assay

To quantify aqueous CO<sub>2</sub> 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

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was resuspended by gentle inversion for 30 s. In both undisturbed cores and resuspension treatments, SOD ( $\text{mmol m}^{-2} \text{h}^{-1}$ ) was calculated from oxygen concentrations measured at the start and end of the 4 – 6 h incubations (OXROB10 probe and FireSting GO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> production (RCO<sub>2</sub>P) was calculated as the difference in CO<sub>2</sub> production between resuspended and undisturbed samples. The factor increase in CO<sub>2</sub> production was obtained by dividing resuspended values by undisturbed values. RCO<sub>2</sub>P serves as a proxy for the vulnerability of sediment organic C to severe resuspension, with higher RCO<sub>2</sub>P indicating greater vulnerability.

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### 2.3 Sediment characteristics

Organic matter content was determined by loss on ignition, burning dried (~~60 °C for 7 d~~) sediments (~~60 °C for 7 d~~) at 450 °C for four hours. For grain size analysis, sediments were digested with 10 % H<sub>2</sub>O<sub>2</sub> 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 ~~used in data analysis 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 ~~in-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 et al. (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

140 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 RCO<sub>2</sub>P, we applied  
supervised machine learning using boosted regression trees (BRTs; (Friedman, 2001). BRTs are ensemble models that  
sequentially build decision trees, with each tree correcting errors from the previous iteration, improving predictive  
145 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).

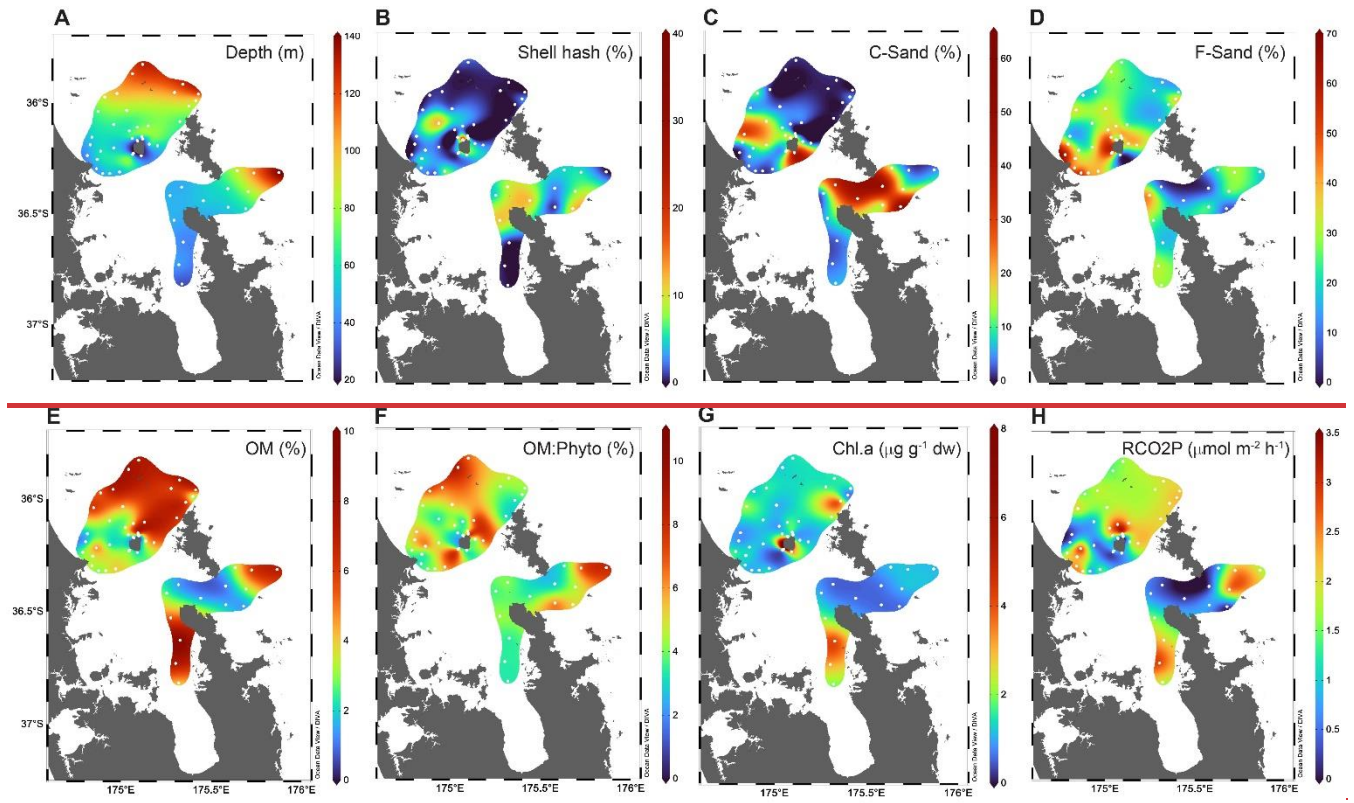
Our dataset included the following variables indicative of sediment heterogeneity: water depth (Depth), shell hash and gravel  
150 content (S/G), coarse sand (C-Sand), medium sand (M-Sand), fine sand (F-Sand), mud (Mud), organic matter content (OM),  
and the organic matter-to-total phytopigment ratio (OM:Phyto). The response variable was resuspension-induced CO<sub>2</sub>  
production (RCO<sub>2</sub>P). 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.  
155 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  
160 RCO<sub>2</sub>P (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 RCO<sub>2</sub>P 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 RCO<sub>2</sub>P. Within each cluster, Pearson correlation analysis was used to determine relationships  
between features and RCO<sub>2</sub>P. All analyses were conducted in Python (v3.12.7) using the packages *scikit-learn* (v1.6.1;  
165 Pedregosa et al., 2011) and *SHAP* (v 0.47.1; Lundberg et al., 2017, 2020).

### 3 Results

#### 3.1 Distribution of sediment characteristics and resuspension-induced CO<sub>2</sub> 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  
170 dominated channels and areas around Hauturu (Figure 2A–C; Figure S3), while finer sands and mud prevailed near the main  
coast and at deeper outer-shelf sites (Figure 2D; Figure S3). OM content ranged from 0.9 – 9.6 %, with highest values at outer-

shelf sites and inner-shelf areas west of Coromandel Peninsula (Figure 2E). OM freshness varied widely irrespective of OM content or water depth (OM:Phyto = 1.2 – 16.1; Figure 2F). Algal biomass, indicated by Chl.a, was mainly concentrated at shallow inner-shelf sites, reaching up to  $8 \mu\text{g g}^{-1} \text{ dw}$ , ~~but (Figure 2G). Notably, Chl.a concentrations~~ of  $2 - 4 \mu\text{g g}^{-1}$  were also detected at several sites deeper than 50 m, suggesting either microphytobenthos presence or substantial sedimentation of algal material (Figure 2G).  $\text{CO}_2$  production rates were 1.4 – 19.5 times higher in resuspended sediments than in undisturbed sediments (Figure S4).  $\text{RCO}_2\text{P}$  ( ~~$0.1 - 3.5 \text{ mmol CO}_2 \text{ m}^{-2} \text{ h}^{-1}$~~ ) showed strong spatial variability ( $0.1 - 3.5 \text{ mmol CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ), with elevated rates observed at multiple shallow and deep sites (Figure 2H).



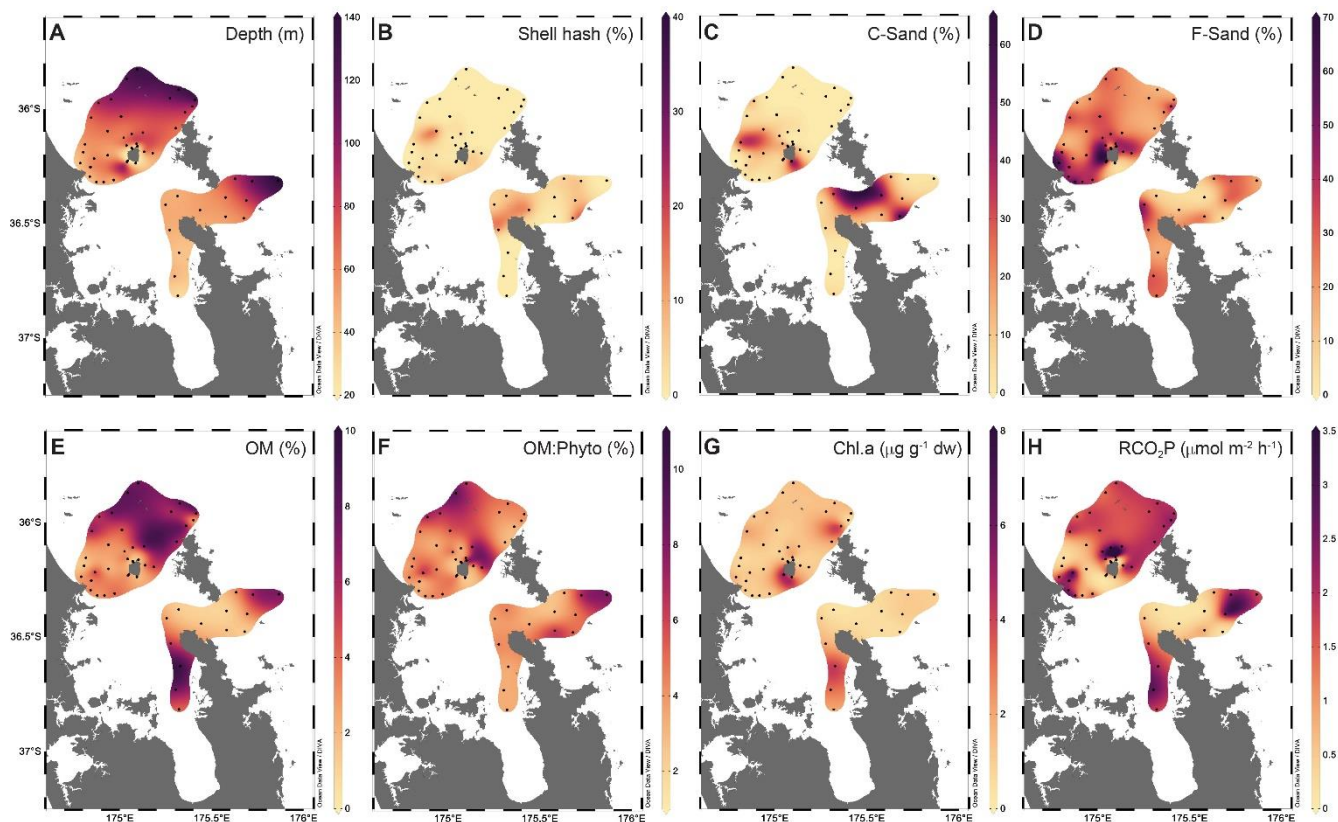


Figure 2: Environmental features water depth (A), shell hash/gravel (B), coarse grained sand (500 – 2000  $\mu\text{m}$ , C), fine grained sand (63 – 250  $\mu\text{m}$ , D), organic matter content (E), ratio of organic matter and phytopigments (F), and Chlorophyll a content (G) as well as resuspension-induced  $\text{CO}_2$  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, 2025).

### 3.2 Most important features and relationships

The 50 BRT model iterations performed well in predicting  $\text{RCO}_2\text{P}$ , with an  $R^2$  of  $0.58 \pm 0.11$  and a root mean squared error of  $0.54 \pm 0.07 \text{ mmol CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ , 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 ( $\sim 0.1$ ), 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,  $\text{RCO}_2\text{P}$  variability was primarily driven by the individual effects of OM, C-Sand, Depth, and F-Sand, with only minor contributions from interactions.

**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 RCO<sub>2</sub>P. 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
<b>OM</b>	0.47 (0.010)	1.0 (0.00)	<b>OM + C-Sand</b>	0.061 (0.005)
<b>C-Sand</b>	0.13 (0.008)	2.5 (0.23)	<b>OM + Depth</b>	0.056 (0.006)
<b>Depth</b>	0.10 (0.008)	3.6 (0.31)	<b>F-Sand + Depth</b>	0.033 (0.003)
<b>F-Sand</b>	0.09 (0.006)	3.7 (0.29)	<b>OM + F-Sand</b>	0.029 (0.003)
<b>OM:Phyto</b>	0.07 (0.006)	4.6 (0.29)	<b>OM + Chl.a</b>	0.025 (0.002)
<b>Chl.a</b>	0.04 (0.003)	6.1 (0.20)	<b>C-Sand + Depth</b>	0.023 (0.002)
<b>S/G</b>	0.04 (0.005)	6.5 (0.26)	<b>Other interaction pairs</b>	<0.023

SHAP dependence plots revealed predominantly non-linear relationships between modelled RCO<sub>2</sub>P and features (Figure 3).  
 205 Across the OM gradient, SHAP values shifted from negative to positive at ~3 % OM, indicating highest RCO<sub>2</sub>P in sediments containing 3–10 % OM (Figure 3A). Similarly, sediments with C-Sand below 8 % and from depths of 56 – 100 m exhibited positive SHAP values, linking these conditions to higher RCO<sub>2</sub>P (Figure 3B, C). Although less influential overall, F-Sand and OM:Phyto showed more linear relationships with RCO<sub>2</sub>P, with highest SHAP values at F-Sand > 27 % and OM:Phyto < 4.7, suggesting that greater CO<sub>2</sub> production corresponds to higher F-Sand content and fresher organic matter (Fig. 3D, E). No clear  
 210 relationships were observed for Chl.a or S/G (Figure 3F, G).

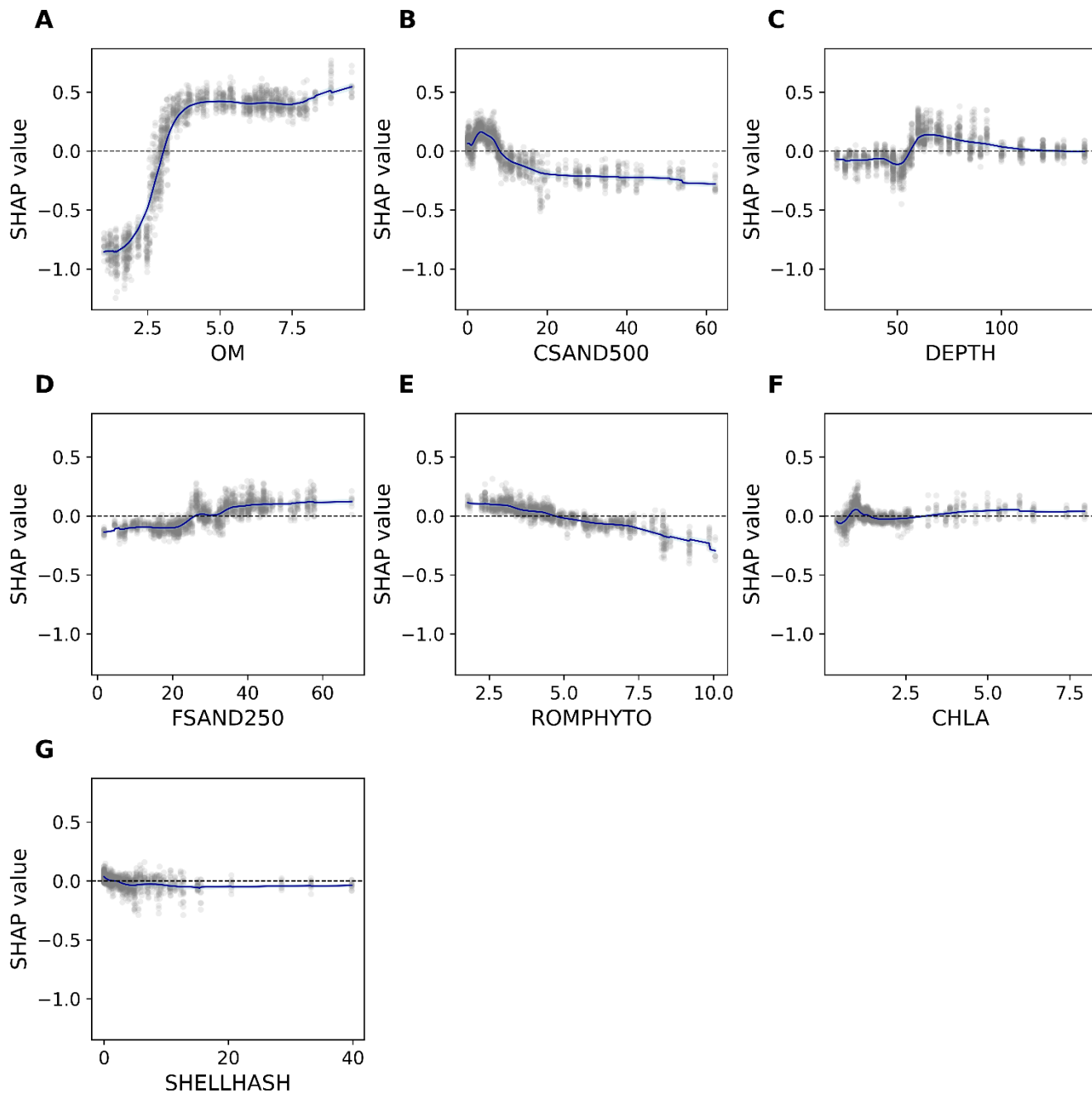


Figure 3: Partial-dependence-plots showing the relationship between SHAP values and features. Positive SHAP values reflect a positive contribution of the feature-value to model output, i.e. to higher RCO<sub>2</sub>P than average, and vice versa. Lowess smooth function was applied for each of the 50 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.

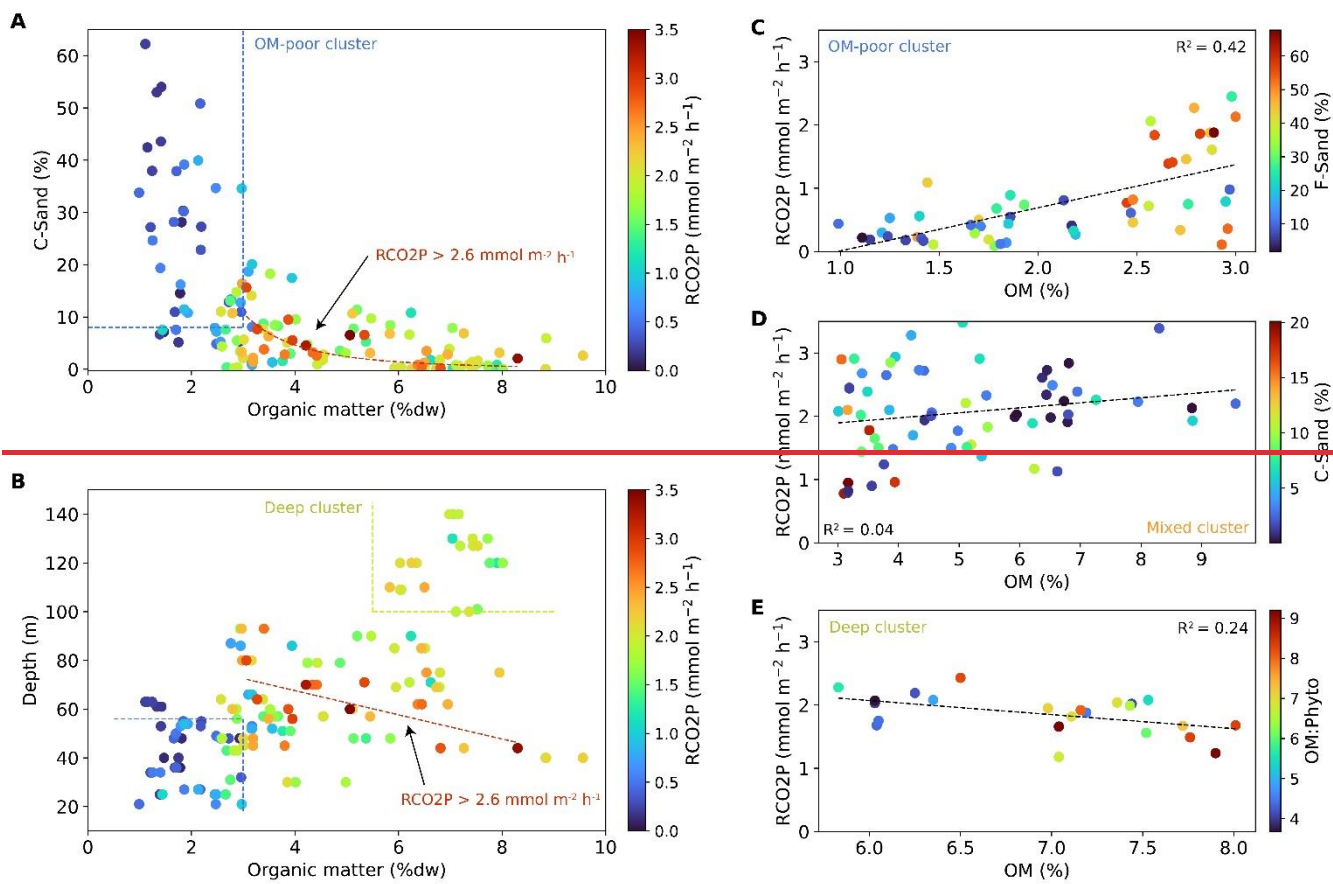
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### 3.3 Clusters with different levels of RCO<sub>2</sub>P and differing relationships

220 To visualise which sediment types are most vulnerable to CO<sub>2</sub> release upon resuspension, we produced scatter heat maps from the original dataset and used BRT results to identify clusters (Figure 4, Table 2). Lowest RCO<sub>2</sub>P rates ( $0.5 \pm 0.3 \text{ mmol m}^{-2} \text{ h}^{-1}$ ) occurred in sandy sediments ( $> 8 \%$  C-Sand,  $> 27 \%$  F-Sand) with low organic matter content ( $< 3 \%$ ) and shallow depths ( $< 56 \text{ m}$ ), forming a distinct OM-poor cluster (Figure 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<sub>2</sub> release (Figure 2H, Table 2). Within this cluster, RCO<sub>2</sub>P 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 (Figure 4C). At depths  $\geq 100 \text{ m}$ , both OM content and RCO<sub>2</sub>P were high and relatively uniform, with RCO<sub>2</sub>P about four times higher than in the OM-poor cluster (Table 2). This Deep-cluster showed a negative correlations between RCO<sub>2</sub>P and OM, and slightly higher rates at lower OM:Phyto ratios, reflecting fresher organic matter (Figure 4E).

230 Mixed sediments ( $> 3 \%$  OM,  $< 8 \%$  C-Sand) from intermediate depths ( $56 - 100 \text{ m}$ ,  $> 3 \%$  OM,  $< 8 \%$  C Sand) formed a Mixed cluster with RCO<sub>2</sub>P ranging from  $0.8 - 3.5 \text{ mmol m}^{-2} \text{ h}^{-1}$ , equivalent to 3 – 19.5 times higher CO<sub>2</sub> release than in undisturbed sediments (Figure 4A, B, Table 2). No clear correlations were found here (Table 2, Figure 4D). Within the Mixed cluster contained the highest 10 % of RCO<sub>2</sub>P values ( $> 2.6 \text{ mmol m}^{-2} \text{ h}^{-1}$ ) which occurred along interactions between

235 OM and C-Sand ( $\text{C-Sand} = 270.08 \times \text{OM}^{-2.93}$ ,  $R^2 = 0.51$ ,  $p = 0.003$ ) and OM and Depth ( $\text{Depth} = -4.97 \times \text{OM} + 87.45$ ,  $R^2 = 0.32$ ,  $p = 0.029$ ; Fig. 4A,B). Together, the Mixed and Deep cluster cover 73 % of the sampled sites and are moderately to very highly vulnerable to releasing CO<sub>2</sub> when disturbed (Table 2, Figure 2 H).



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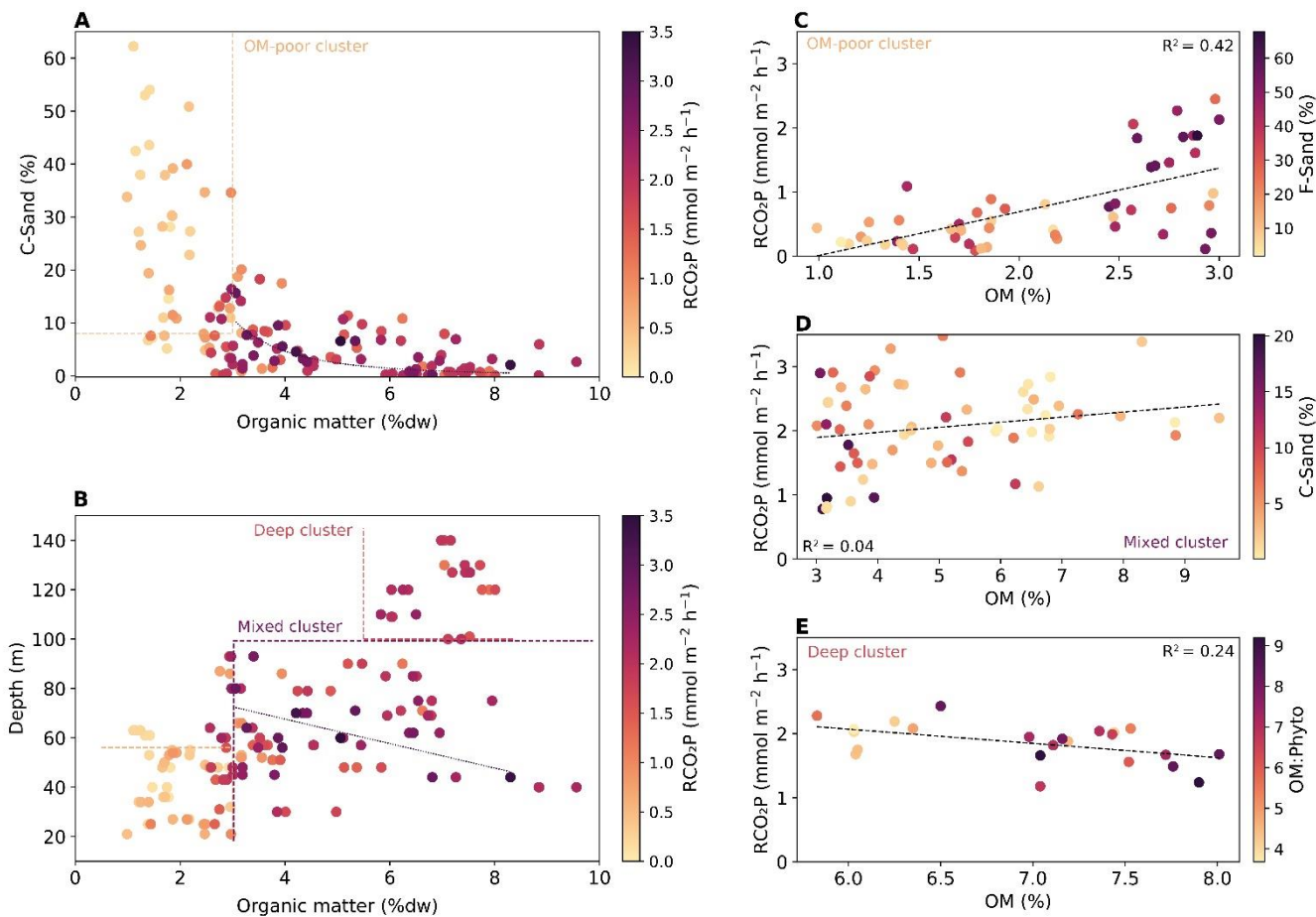


Figure 4: Scatter heatmaps showing the resuspension-induced  $\text{CO}_2$  production ( $\text{RCO}_2\text{P}$ , colour gradient) over organic matter content and C-Sand (A), and over organic matter content and water depth (B). Blue-Light orange dashed lines represent the boundaries of the OM-poor cluster, the green-red dashed line for the represent the deep-Deep cluster, and the red-purple dashed lines for the Mixed cluster. The dotted lines in (A) and (B) shows the fit of the 90<sup>th</sup> quantile of  $\text{RCO}_2\text{P}$  rates ( $> 2.6 \text{ mmol m}^{-2} \text{ h}^{-1}$ ) 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 ( $y = -4.97x + 87.45$ ,  $R^2=0.32$ ,  $p=0.029$ ) along which the 90<sup>th</sup> quantile of  $\text{RCO}_2\text{P}$  rates align. Panels C-E show relationships of environmental variables with  $\text{RCO}_2\text{P}$  in the OM-poor cluster (C), the Mixed cluster (D), and the Deep-cluster (E). Ranges and correlation coefficients are given in Table 2.

Table 2: Average (Avg), standard deviation (Std), and ranges of environmental features and **C storage vulnerability risk of CO<sub>2</sub> release** in the three clusters identified through BRT analysis. Pearson correlation coefficients (R) are provided for relationships of RCO<sub>2</sub>P 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 RCO<sub>2</sub>P rates and the factor increase relative to CO<sub>2</sub> production from undisturbed sediments cores.

Cluster	Features						C storage vulnerability		
	Metric	OM	C-Sand	Depth	F-Sand	OM:Phyto	RCO <sub>2</sub> P	Factor increase	level
OM-poor cluster (n=53)	Avg ± Std	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	<b>0.651</b>	<b>-0.472</b>	0.156	<b>0.516</b>	-0.258			
	p	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.264	<b>&lt;0.001</b>	0.062			
Deep cluster (n=23)	Mean ± Std	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	<b>-0.493</b>	0.153	-0.134	-0.253	<i>-0.393</i>			
	p	<b>0.017</b>	0.486	0.541	0.245	<i>0.064</i>			
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 Discussion

270 Our results show that resuspension of the 3-cm surface sediment strongly enhances organic C mineralisation producing up to 20 times more CO<sub>2</sub> 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<sub>2</sub> production and their non-linear relationships indicate context-dependent controls and allowed us to identify three clusters with different levels of C storage vulnerabilities.

### 275 4.1 Spatial variability of resuspension-induced CO<sub>2</sub> 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 RCO<sub>2</sub>P rates that we measured. While we expected variability of RCO<sub>2</sub>P due to sampling across substantial sediment heterogeneity, the extent of variability and the location of apparent hotspots was surprising. ~~Variability of RCO<sub>2</sub>P was partitioned into~~ We found three clusters of C storage vulnerability in which RCO<sub>2</sub>P 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 RCO<sub>2</sub>P 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, 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 RCO<sub>2</sub>P was ~10 % higher when OM was fresher, suggesting that quality of the resuspended organic matter influences mineralisation when the substrate is abundant.

290 We could not derive mechanistic explanations of RCO<sub>2</sub>P 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 RCO<sub>2</sub>P and may have been underrepresented in our set of features. While ~~the 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<sup>13</sup>C signatures, or n-alkane signatures (Sikes et al., 2009), may help resolve spatial RCO<sub>2</sub>P patterns. RCO<sub>2</sub>P 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, 2010; Lengier et al., 2024; Reader et al., 2019). Lastly, the  
300 composition and activity of the microbial community and their response to being resuspended could influence RCO<sub>2</sub>P  
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 RCO<sub>2</sub>P 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 sediments cluster](#), future targeted  
305 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 ~ 58 % of variability in RCO<sub>2</sub>P forming a strong basis for using BRT models like ours to predict C  
310 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 (~40 %) can perhaps be achieved  
through integrating more nuanced features as discussed above (see section 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  
315 communities (Hale et al., 2017; Pusceddu et al., 2014; Tianio et al., 2022; Zhang et al., 2024). As a result, RCO<sub>2</sub>P 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  
320 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.

#### 325 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<sup>-2</sup> d<sup>-1</sup>) align with our empirical RCO<sub>2</sub>P measurements (2 – 88 mmol C  
330 m<sup>-2</sup> d<sup>-1</sup>). 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 RCO<sub>2</sub>P 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 our 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<sub>2</sub> 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<sub>2</sub> production using respiratory quotients (see section 2.2). This quantification may overestimate CO<sub>2</sub> 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<sub>2</sub>: 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<sup>-1</sup> ww) compared to higher AVS levels in sediments impacted by a mussel farm (2 – 12 µmol g<sup>-1</sup> ww, 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<sub>2</sub> 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 (Bennion et al., 2024), while sediment C storage vulnerability was not considered (Bennion et al., 2024). Trawling remains allowed in areas deeper than 50 m (Hauraki Gulf bottom trawling corridor proposals chucked on ice - Newsroom, 2025), which, based on our results, includes nearly all sediments ~~at-with~~ high to very high ~~C vulnerability~~~~risk-of~~ ~~CO<sub>2</sub>-release-when-disturbed~~. 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  
365 habitats ultimately maintaining the undisturbed functioning of seafloor ecosystems.

## 5 Conclusion

The risk of CO<sub>2</sub> 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<sub>2</sub> release is  
linked to sediment characteristics resulting in local environmental conditions controlling resuspension impacts. Using  
370 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  
375 and sustain natural C sinks that contribute to global climate stabilisation.

## Data and code availability

Sediment characteristics and resuspension-induced CO<sub>2</sub> production rates from the Hauraki Gulf are available at  
<https://doi.org/10.17608/k6.auckland.27948264> (Bartl and Thrush, 2025a)(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)(Bartl and Thrush, 2025b).  
380 ~~Data and software code will be published upon acceptance of the manuscript but are made available to the reviewers of this~~  
~~manuscript.~~

## 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.

## 385 Competing Interests

The authors declare that they have no conflict of interest.

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