The effect of sediment mud content on primary production in seagrass and unvegetated intertidal flats

Georgina J L Flowers

gjlf1@students.waikato.ac.nz

UoW: The University of Waikato https://orcid.org/0000-0001-6298-8091

Hazel R Needham

UoW: The University of Waikato

Richard H Bulmer

NIWA: National Institute of Water and Atmospheric Research

Andrew M Lohrer

NIWA: National Institute of Water and Atmospheric Research

Conrad A Pilditch

UoW: The University of Waikato

Research Article

Keywords: primary production, seagrass, microphytobenthos, estuaries, intertidal, mud gradient

Posted Date: September 18th, 2023

DOI: https://doi.org/10.21203/rs.3.rs-3315615/v1

Version of Record: A version of this preprint was published at Estuaries and Coasts on July 20th, 2024.
See the published version at https://doi.org/10.1007/s12237-024-01403-1.

Abstract

As a consequence of anthropogenic activities and climate change, accelerated terrestrial sediment runoff is causing the gradual mudification of soft sediment estuarine habitats worldwide. Increased sediment mud content (< 63 μm) has been recognised to alter seagrass morphology and cause declines in primary production in unvegetated habitats. However, the effect of increased mud content on primary production in seagrass meadows remains largely unknown. To address this, primary production in intertidal seagrass meadows (*Zostera muelleri*) and adjacent unvegetated habitats was measured *in situ* using benthic incubation chambers across an existing sedimentary gradient (nine sites spanning 5–33% mud content). An additional two unvegetated mudflat sites (39–49% mud content) were also sampled to expand the gradient. Seagrass net (NPP) and gross primary production (GPP) was greater than in the adjacent unvegetated habitat and did not vary with mud content, even after standardising GPP by photosynthesising biomass (i.e., photosynthetic efficiency). In contrast, in the adjacent unvegetated habitat, photosynthetic efficiency declined with increasing mud content. Inclusion of the additional mudflat sites negatively impacted NPP, GPP and photosynthetic efficiency in the unvegetated habitat. Thus, while primary production in seagrass meadows may have some resilience to future increases in mud content (up to 33%), further degradation and loss of seagrass habitat will result in the expansion of unvegetated habitats and ultimately lead to production losses; seen most acutely in areas with high mud content (≥ 39%).

Introduction

Worldwide intertidal seagrass meadows are renowned as a highly productive coastal vegetation type that supports a broad array of ecosystem services (Duarte et al. 2010; Nordlund et al. 2016). Yet, in many areas, unvegetated tidal flats dominated by microphytobenthos (i.e., benthic microalgae), although generally less productive than seagrass meadows on a per area basis (Clavier et al. 2014; Drylie et al. 2018; Gustafsson and Norkko 2016), may make even greater contributions to coastal benthic primary production due to their wider extent. Due to multiple anthropogenic stressors, seagrass meadows are declining worldwide by ~ 7% yr^{-1} (Waycott et al., 2009). As seagrass decline generally results in a subsequent shift to unvegetated sediment habitats, microphytobenthos are likely taking on an increasingly important role in supporting estuarine and coastal production. It is therefore important that we understand the relative contributions of both seagrass and unvegetated habitats to estuarine primary production and how they will respond to future environmental stressors.

Human activities are estimated to have increased riverine transport of terrestrial sediment worldwide by 2.3 ± 0.6 billion metric tons per year (Syvitski et al. 2005); a consequence of rapid population growth, intensive changes in land-use and more recently climate change (Seneviratne et al. 2012; Thrush et al. 2004). While natural levels of terrestrial runoff provide coastal environments with an important source of sediment, organic matter and nutrients, the accelerated rate at which terrestrial sediments are entering coastal waterways is threatening estuarine ecosystems (Thrush et al. 2004). Terrestrial sediment inputs can contain a high proportion of fine silts and clays (< 63 μm), which can be continuously deposited and

resuspended by currents and wind generated waves (Green and Coco 2014), causing an increase in water-column turbidity and a reduction in seafloor light availability (Anthony et al. 2004; Kirk 1985). In areas of low water flow, these fine sediments settle to the seafloor and can accumulate over time, leading to an increased sediment mud content (hereafter 'mud content') stressing benthic communities (Thrush et al. 2004).

Suspended sediments are a major controller of water-column light attenuation (i.e., turbidity; Anthony et al. 2004), and are therefore recognised as an important driver of benthic primary production in coastal environments (Lee et al. 2007; MacIntyre et al. 1996). The distribution of temperate seagrass and microphytobenthos are constrained by their minimum light requirements (e.g., ~ 57 μmol photons m^{-2} s^{-1} for *Zostera muelleri* in New Zealand (Bulmer et al. 2016) and > 37 μmol photons m^{-2} s^{-1} for intertidal microphytobenthos (Migné et al. 2002)), although highest rates of productivity generally occur above light saturation (e.g., > ~200 μmol photons m^{-2} s^{-1} (calculated from whole-plant review by Lee et al. 2007; Mangan et al. 2020a)). Within these limits, benthic primary producers can respond to changing light regimes through a combination of morphological, physiological and/or behavioural adaptations (Consalvey et al. 2004; Kohlmeier et al. 2014; Park et al. 2016). While the effects of changes in light climate on benthic primary production have received some attention, by comparison changes in the sedimentary environment, that often accompanies elevated suspended sediments generated from terrestrial inputs, are much less understood.

When fine terrestrially derived sediments are deposited on predominantly sandy estuarine sediments, they alter the sediment physiochemical properties and benthic macrofaunal community composition. With increases in mud content, sediment permeability is reduced, and substrate surface area is increased (Huettel et al. 2014). This can affect the penetration of light into the sediment (Billerbeck et al. 2007), sediment redox potentials (Glud 2008), phytotoxin concentrations (e.g., hydrogen sulphide (Terrados et al. 1999)), and the transport and exchange of solutes across the sediment-water interface (Huettel et al. 2014; Huettel et al. 2003). Additionally, changes in macrofaunal community composition with increasing mud content include; altering key species size and abundance (e.g., the clam *Austrovenus stutchburyi* (Pratt et al. 2014a)), reducing macrofaunal diversity (e.g., Anderson 2008; Thrush et al. 2003), and modifying organism behaviour (e.g., feeding rates (McCartain et al. 2017) and larval recruitment (Thrush et al. 1996)). To understand how mud content may affect benthic primary production it is therefore important to also consider the indirect effects generated by interactions with other ecosystem components (Thrush et al. 2021; Thrush et al. 2014). For example, changes in macrofaunal biodiversity (which occurs with changing mud content) alters nutrient availability indirectly affecting primary production (e.g., Lohrer et al. 2004; Pratt et al. 2014a; Rodil et al. 2011). Thus, *in situ* studies incorporating these real-world interactions are needed.

For seagrass, changes in mud content have been recognised to alter their morphology and distribution. As mud content increases, the depth limits at which seagrass is found becomes shallower (Ferguson et al. 2016; Krause-Jensen et al. 2011). Moreover, mud content has been correlated with changes in biomass, increases in the ratio of above- to below-ground biomass, and increases in leaf length and area

index (Ferguson et al. 2016; Halun et al. 2002; Terrados et al. 1998; Zabarte-Maeztu et al. 2021). Changes in seagrass growth with changing sediment physio-chemistry also appears to be species-specific (e.g., Livingston et al. 1998; Terrados et al. 1999). For the *Zostera* genus, higher mud content has been shown in *Z. muelleri* to reduce rhizome growth in laboratory mesocosms (Zabarte-Maeztu et al. 2021), and field manipulations have demonstrated that prolonged sediment anoxia (known to accompany increased mud content) can reduce *Z. marina* leaf growth (Terrados et al. 1999). However, the effect of mud content and changes in morphology on seagrass meadow production is unknown.

In unvegetated habitats dominated by microphytobenthos, increases in mud content are recognised to cause a decline in primary production (Billerbeck et al. 2007; Douglas et al. 2018; Pratt et al. 2014a). Reductions in photosynthetic efficiency (i.e., gross primary production (GPP) standardised by chlorophyll α content) with increasing mud content were also observed in a study that spanned nine estuaries (Pratt et al. 2014a). However, most field studies examining the effect of mud content on microphytobenthic production have been restricted in terms of number of sites or treatments (e.g., Billerbeck et al. 2007; Haro et al. 2020; Kristensen et al. 1997). This small-scale approach limits the ability to determine rates of change as mud content increases. Additionally, previous studies have not incorporated multiple habitat types. As the sensitivity to anthropogenic stressors is likely to vary between primary producers, research investigating how different habitats may respond to accelerated terrestrial sediment inputs will be vital in informing future estuarine management decisions.

This study aims to investigate how changes in mud content can affect submerged primary production in intertidal seagrass meadows and adjacent unvegetated habitats. As changes in mud content generally occur over long timescales (i.e., years to decades), we used a space for time approach (Pickett 1989) by using an existing spatial gradient in mud content within a single large estuary. We measured whole-community primary production *in situ* using largescale benthic incubation chambers, incorporating the real-world complexities of estuarine ecosystems. In response to changing sediment physiochemical conditions, based on the literature we predict that increases in mud content will drive changes in seagrass morphology including decreased biomass and increased leaf size which may help maintain rates of primary production. We also predict, consistent with previous studies, that increasing mud content will cause declines in unvegetated primary production. By working across a gradient in mud content, our study will enable us to identify threshold responses in benthic primary production to mud content.

Methods

Study site

Tauranga Harbour, located within the Bay of Plenty region of New Zealand, is a large (200 km^2) barrier enclosed estuary that is predominantly intertidal (66% (de Lange and Healy 1990)). The estuary has a mean water depth of 2.1 m and experiences semi-diurnal tides with a spring-neap range of 1.24–1.62 m (Healy et al. 1996). Within the intertidal regions of the estuary, two dominant habitat types include

seagrass meadows (*Z. muelleri* - New Zealand's sole seagrass species) and unvegetated habitats (i.e., sand-/mud-flats). Across New Zealand, seagrass meadows are mainly restricted to intertidal areas (Turner and Schwarz 2006), and in Tauranga Harbour are not found in sediments with > 35% mud content (Crawshaw 2020). From 1959 to 2019, seagrass distribution in Tauranga Harbour has declined by 73% (Ha et al. 2021; Park 2016). Long-term monitoring has additionally reported an increase in sedimentation in Tauranga Harbour at 59% of monitored sites (n = 65; Lawton and Conroy 2019), consistent with increases in mud content measured across multiple New Zealand North Island estuaries (Mills and Allen 2021).

In Tauranga Harbour, nine intertidal sites with continuous seagrass meadows (> 200 m^2) and nearby adjacent unvegetated flats were selected (Fig. 1). At these sites a study area of approximately 50 m^2 was established > 0.5 m either side of the seagrass fringe. Because the seagrass distribution was restricted to sites with < 35% mud content, a further two sites were added to expand the unvegetated sand-mud gradient (Fig. 1). Within these sites, two study areas > 25 m apart (referred to as Plot 1 & 2) with visually different sediment properties were chosen. All sites were located in the mid-intertidal with emersion periods of ~ 4–6 h.

Field sampling

Field sampling was undertaken from January to mid-March 2019 (austral summer), during midday high tides to ensure high levels of natural irradiance. Site habitats/plots were sampled on the same day, with the exception of TUA, where habitats were sampled on consecutive days due to equipment restrictions. Sampling was undertaken in generally sunny conditions with minimal cloud cover.

Within each habitat/plot, five pairs of light and dark benthic incubation chambers (0.25 m^2; 34–40 L) were positioned parallel to the seagrass fringe and/or the nearest channel. Chambers were deployed at low tide in undisturbed areas with a similar high seagrass percentage cover. Light and dark chambers were separated by ~ 0.5 m, with > 1 m between chamber pairs. Chamber bases (L:W:D = 0.5×0.5×0.15 m) were pushed 5 cm into the sediment and contained a PME miniDOT dissolved oxygen logger (1 min sampling frequency), a HOBO pendant light (Lux) and temperature logger (5 min sampling frequency) and a Seabird CTD pump (on for 5 s every 45 s; to provide consistent intermittent non-directional stirring of chamber water). Perspex transparent dome chamber lids were clamped onto the bases at ~ 0.3 m water depth, following complete air removal of the chamber. Each lid had a nylon tubing sampling port (2 m length; 3.2 mm diameter), with an open inlet on the opposing side to ensure the chamber volume remained constant upon sampling. For dark chambers, shade cloth clamped over the lid ensured full darkness. To account for water-column fluxes, three pairs of light and dark bottles (1 L) were also filled with seawater and positioned near the seabed. For initial sampling, following flushing of sampling hoses, a 60 mL sample was extracted from each chamber using Leur-lock syringes. Three 60 mL ambient water-column samples were also collected from the surrounding area. After a ~ 4–5 h incubation period, another 60 mL sample was extracted from each chamber, alongside a sample collected from each light

and dark bottle. The salinity and dissolved oxygen concentrations (mg/L) of the samples were measured immediately onshore using a YSI ProSolo ODO/CT probe.

Site characteristics

To provide an indication of water-column light attenuation during incubations, light measurements (specifically photosynthetically active radiation (PAR)) were collected above the high tide mark and at the seafloor (referred to as PAR-Site and PAR-Seafloor, respectively) using calibrated Odyssey PAR loggers (integrated 5 min sampling frequency). A HOBO pendant light (Lux) and temperature logger (5 min sampling frequency) was additionally positioned on the seafloor and on shore.

On the day of chamber sampling, five sediment cores (2.6 cm diameter, 2 cm depth) were collected around each chamber, amalgamated into a single replicate per chamber, frozen and stored in the dark until further analysis. To assess macrofauna community composition, a large core (13 cm diameter, 15 cm depth) was taken within 0.5 m of each chamber. The contents of each core were sieved on site over a 500 µm mesh with all material preserved in 70% isopropyl alcohol. Following chamber incubations, two replicates of an additional four sediment cores (2.6 cm diameter, 2 cm depth) were collected around each chamber pair to measure porewater dissolved inorganic nutrient concentrations. For an estimation of seagrass percentage cover, a plan view photograph of each seagrass chamber was taken. To analyse seagrass biomass and leaf characteristics, a large core (13 cm diameter, 15 cm depth) was also collected from within each chamber with the contents sieved over a 1 mm mesh. All seagrass material was stored flat in tin foil and frozen.

Laboratory analysis

For the analysis of sediment properties (median grain size, and mud, organic, water, chlorophyll *a* and phaeophytin content), sediment samples were thawed, homogenised and divided into three subsamples. Median grain size and mud content (% < 63 µm) were measured using a Malvern Mastersizer 2000 (particle size range 0.05–2000 µm) following digestion of organic matter using 10% hydrogen peroxide. Water content was measured from samples dried to a constant weight at 60°C, with organic content subsequently measured by weight loss on ignition from samples held at 550°C for 4 h (Heiri et al. 2001). For chlorophyll *a* and phaeophytin content, freeze dried sediment was steeped in 90% buffered acetone prior to fluorometric measurement (Turner 10-AU fluorometer) before and after acidification by hydrochloric acid (Arar and Collins 1997). Median grain size, and mud, water and organic content were measured from dark chamber samples only (n = 5 per habitat/plot).

To process sediment porewater for nutrients, 4 mL of de-ionised water was added to each porewater sediment sample. Samples were then vortexed and centrifuged, with the supernatant porewater filtered (0.45 µm Whatman GF/C glass fibre filter) and stored at -20°C. Sediment samples were dried at 60°C for determination of porosity. Dissolved inorganic nutrient concentrations (NH_4^+-N, NO_3^--N, NO_2^--N and PO_4^{3-}-P) of sediment porewater were measured using flow injection analysis (Lachat QuickChem 8000

series FIA+ (Zellweger Analytics Inc.)). As NO_3^- & NO_2^- concentrations were close to detection limits, NO_x concentrations were used for statistical analyses.

The abundance and size (maximum shell length; mm) of two key bivalve species (> 10 mm), *Austrovenus stutchburyi* and *Macomona liliana* (Sandwell et al. 2009; Thrush et al. 2006; Woodin et al. 2016), were recorded from each macrofauna core. To provide a general plot assessment of macrofaunal community composition, three dark chamber macrofauna cores (first, third and fifth chamber pairs) from each plot were stained with Rose of Bengal, sorted and identified to the lowest taxonomic level practicable (usually species).

Seagrass percent cover was analysed using 100 point random count analysis (CPCe v4.1) using the classifications of live blades, dead blades and unvegetated (with undefinable points removed; Kohler and Gill 2006). To assess seagrass morphological characteristics, thawed seagrass samples were separated into above- (leaves) and below-ground (sheath, rhizomes, roots) material. All seagrass leaves with visible sheath attachment were counted and the length and width (mm) of 10 leaves selected at random (unbroken where possible) were measured. Above- and below-ground biomass was measured from samples dried at 60°C to a constant weight. Seagrass carbon and nitrogen content (C:N ratio) was measured on an Elementar Vario EL cube CHN analyser using a subsample of the dried above- and below-ground biomass.

Additional environmental data

To understand the spatial drivers of seagrass morphology, we investigated a suite of environmental variables including integrated measures of summer light availability and windwave exposure. In February 2020 (one year after chamber sampling), as part of another study (J. Green, unpublished data), an Odyssey PAR logger (integrated 10 min sampling frequency) was positioned at each of the seagrass sites for five weeks to provide a relative measure of integrated light availability. Median seafloor light intensity during submergence and emergence was calculated using data two hours either side of high and low tide during daylight hours; providing a measure of the ‘normal’ availability of light each seagrass meadow was exposed to. Due to equipment malfunction, an integrated measure of seafloor light data from the ATH site was not acquired, so for statistical analyses the average of the median high and low tide light value from the remaining seagrass sites was used. This approach is consistent with the fact that the light level measured at this site during chamber sampling was similar to the median of all the other sites (Table 1). To determine if wind-wave exposure influenced seagrass morphology, a dimensionless wave exposure variable was calculated for each site (Eq. 1) using mean wind speed, wind direction percentage frequency, and fetch (i.e., distance from each site to nearest land) (Keddy 1982; Turner et al. 1999):

$$Exposure = \sum_{i=0}^{12} meanwindvelocity \times percentfrequency \times fetch$$

1

Wind speed records (2007 to 2017; 10 min sampling interval) were provided by the Bay of Plenty Regional Council from an environmental monitoring station in Mount Maunganui (sourced from: https://envdata.boprc.govt.nz/) and separated into 30° compass wind direction bins.

Data analysis

Macrofauna community composition was analysed using a number of univariate descriptors including number of organisms, number of species, Shannon Weiner diversity index (H') and the abundances of adult *A. stutchburyi* and *M. liliana.* Shannon Weiner index was selected as a measure of species diversity as it accounts for both the abundance and evenness of taxa (Heip and Engels 1974).

Chamber fluxes of dissolved oxygen (μmol O_2 m^{-2} h^{-1}) were calculated from a 10 min average of dissolved oxygen readings from the PME miniDOT logger at the start and end of the incubation period. Water-column fluxes were generally < 5% of the chamber fluxes, so were ignored. Dark chambers provided a measure of sediment community respiration, with light chambers providing a measure of net primary production (NPP). For each chamber pair, a measure of gross primary production (GPP) was calculated by correcting NPP for the sediment community respiration measured in the adjacent dark chamber. If a dark chamber failed (e.g., due to shade cloth lifting; n = 22/110) – indicated by a positive dissolved oxygen flux or detectable chamber light reading – an average of the remaining plot dark chambers was used to the calculate GPP. Photosynthetic efficiency was estimated by standardising GPP by per unit of photosynthesising biomass (seagrass above-ground biomass or sediment chlorophyll α content; Drylie et al. 2018; Pratt et al. 2014a).

Statistical analysis

Principal Coordinate Analysis (PCO) of seagrass traits (leaf count, length, width and surface area, percentage cover, and above-, below-ground and total biomass) was used to evaluate differences in seagrass morphological condition as a function of site. Vectors of seagrass morphological traits and site environmental variables (Pearson's correlation coefficient ≥ 0.3) were overlain to illustrate which variables were correlated with the multivariate distribution of the sites.

To determine if measures of NPP, GPP and sediment community respiration across the mud content gradient differed between adjacent habitats (seagrass and unvegetated), a one-way fixed factor PERMANCOVA was performed (9999 permutations; covariate = mud content). Where mud × habitat interactions were not significant, reduced models (i.e., without the interaction term) were run.

Distance-based Linear Models (DistLM) were used to identify environmental drivers of NPP, GPP and photosynthetic efficiency for the seagrass and unvegetated habitats (which in this analysis included the additional mudflat sites). Environmental predictor variables (light, temperature, sediment properties, porewater nutrients, macrofauna properties, seagrass above- and below-ground C:N ratios, and multivariate measures of seagrass morphology (derived from PCO axes 1 and 2)) were included in the model runs, except for where high co-linearity (r > 0.8) between variables occurred (Dormann et al. 2013). This resulted in the removal of the predictor that explained the least variability in the model. Lux

measurements from the site and individual light chambers, rather than PAR-Site and PAR-Seafloor, were chosen as predictor variables in the DistLM analyses so that between chamber variability in light intensity could be accounted for. Marginal tests were performed to identify significant environmental predictors ($p \leq 0.1$; 9999 permutations). Stepwise procedures (using corrected Akaike information criterion (AICc); Burnham and Anderson 2002) with mud content forced to be included first (regardless of significance in marginal tests) were then used to identify the best combination of predictor variables for the most parsimonious model fit. PCO, PERMANCOVA and DistLM analyses were performed using the PERMANOVA + package on Primer v7 using normalized data and Euclidian distance-based matrices.

Results

Environmental variables

Across all study sites, a sediment mud gradient of 5.6–32.8% in seagrass (n = 9) and 5.0–49. % in unvegetated flats (n = 13) was achieved (Table 1). At most sites (the exception being TUA & BRW), the seagrass habitat was on average 6. % higher in mud content than the adjacent unvegetated habitat (n = 9). Median grain sizes (MGS) ranged from very fine to medium sand (113–251 μm) in the seagrass and from very fine to fine sand (65–248 μm) in the unvegetated habitat. In both habitat types, increasing mud content was correlated with decreasing median grain size ($r \geq -0.64$, $p < 0.001$) and increasing organic and water content ($r \geq 0.68$, $p < 0.001$; see Supplementary Table S2). For the porewater nutrient concentrations, only NH_4^+ in the unvegetated habitat was correlated with increasing mud content ($r = 0.91$, $p < 0.001$; see Supplementary Table S3).

Site light conditions (daily and those integrated over a five-week period) were variable due to short term changes in weather conditions and surrounding site geography (Table 1). Sampling day and integrated high tide seafloor light availability varied between sites (from 136 to 563 μmol photons m^{-2} s^{-1}, respectively), and showed moderate (but not significant ($p > 0.05$)) negative correlations with increasing mud content in the seagrass ($r = -0.63$ & -0.55, respectively) and unvegetated habitat ($r = -0.35$ & -0.61, respectively; see Supplementary Table S3). During chamber incubations, the water-column attenuated between 60–93% of ambient light (Site vs. Seafloor PAR). In the seagrass habitat, water-column light attenuation was positively correlated with mud content ($r = 0.69$, $p < 0.05$), but this relationship was not significant in the unvegetated habitat ($r = 0.54$; see Supplementary Table S3).

Table 1 Site variability in light (integrated (five weeks) and sampling day), sediment characteristics (n = 5), and indicators of primary producer biomass (n = 10) in the seagrass, adjacent unvegetated (Unveg.) and mudflat (Mud) habitats (mean ± 1 SD; excluding long-term light (median)). Symbols indicative of site location presented in Fig. 1

Symbol	Site	Habitat	Integrated light		Sampling day (HT) light		Sediment		Microphytobenthos		Seagrass		
			PAR – LT	PAR – HT	PAR – Site	PAR - SF	Mud content	MGS	Chl *a*	Phaeo	AGB	BGB	AGB:BGB
			(µmol photon m^{-2} s^{-1})		(µmol photon m^{-2} s^{-1})		(% < 63 µm)	(µm)	(µg g^{-1} DW)	(µg g^{-1} DW)	(g DW m^{-2})	(g DW m^{-2})	
▲	ATH	Seagrass	*450	*225	1191 ± 458	481 ± 144	17.6 ± 1.8	217 ± 12	16.1 ± 1.2	8.6 ± 1.1	68 ± 23	122 ± 32	0.6 ± 0.2
		Unveg.					13.8 ± 2.2	209 ± 19	13.0 ± 1.6	6.3 ± 0.8			
×	BRW	Seagrass	473	228	1564 ± 675	516 ± 218	9.5 ± 0.8	251 ± 8	15.2 ± 0.7	6.9 ± 0.5	31 ± 4	67 ± 13	0.5 ± 0.1
		Unveg.					12.2 ± 3.7	208 ± 17	13.9 ± 3.1	6.0 ± 0.8			
■	MAT	Seagrass	503	284	1240 ± 405	257 ± 116	19.4 ± 1.5	172 ± 7	12.1 ± 1.4	8.4 ± 1.7	41 ± 11	98 ± 24	0.5 ± 0.2
		Unveg.					8.8 ± 2.9	211 ± 11	8.0 ± 0.8	3.7 ± 0.5			
○	OMK	Seagrass	373	191	1350 ± 853	399 ± 231	22.3 ± 2.2	122 ± 5	16.1 ± 1.5	10.4 ± 1.4	26 ± 9	60 ± 23	0.4 ± 0.1
		Unveg.					19.7 ± 1.1	126 ± 5	14.7 ± 0.5	8.7 ± 0.6			
●	ONG	Seagrass	409	148	1285 ± 470	256 ± 198	23.7 ± 1.7	135 ± 10	17.5 ± 1.5	11.4 ± 2.0	90 ± 29	148 ± 39	0.6 ± 0.1
		Unveg.					15.8 ± 1.6	169 ± 7	10.9 ± 0.9	6.3 ± 1.0			
▽	OTU	Seagrass	598	275	2070 ± 171	754 ± 17	9.6 ± 1.6	198 ± 14	21.5 ± 3.3	10.2 ± 1.1	85 ± 18	192 ± 62	0.5 ± 0.1
		Unveg.					5.0 ± 0.8	216 ± 10	12.6 ± 1.8	5.5 ± 0.8			
△	TPU	Seagrass	427	236	2089 ± 477	535 ± 141	32.8 ± 1.2	113 ± 6	22.0 ± 1.8	15.8 ± 2.7	56 ± 23	63 ± 23	1.0 ± 0.7
		Unveg.					26.2 ± 2.1	131 ± 7	27.9 ± 1.2	13.6 ± 2.3			
□	TUA	Seagrass	502	274	1621 ± 566	656 ± 226	5.6 ± 0.8	179 ± 6	13.0 ± 1.7	6.2 ± 1.0	65 ± 22	140 ± 23	0.5 ± 0.2
		Unveg.			1678 ± 540	702 ± 208	5.8 ± 1.2	180 ± 6	10.7 ± 1.2	5.7 ± 0.8			
⊗	URE-Mud	Plot 1			1838 ± 177	443 ± 85	41.7 ± 1.6	82 ± 4	18.2 ± 0.8	10.1 ± 0.8			
		Plot 2					39.0 ± 0.6	91 ± 2	16.3 ± 0.9	9.7 ± 0.8			
⊞	WMA-Mud	Plot 1			1994 ± 437	255 ± 64	49.0 ± 2.7	65 ± 6	17.4 ± 1.5	10.3 ± 1.3			
		Plot 2					45.8 ± 4.6	72 ± 10	16.9 ± 2.0	13.3 ± 2.7			
◆	WPA	Seagrass	318	161	1990 ± 194	139 ± 186	26.9 ± 7.0	204 ± 42	32.7 ± 6.6	19.6 ± 4.7	62 ± 23	94 ± 41	0.8 ± 0.5
		Unveg.					18.9 ± 1.5	248 ± 38	21.8 ± 1.5	8.5 ± 0.3			

PAR - photosynthetically active radiation, LT – low tide, HT – high tide, SF – Seafloor, MGS – median grain size, Chl *a* – sediment chlorophyll α concentration, Phaeo – sediment phaeophytin concentration, AGB – above-ground biomass, BGB – below-ground biomass. *Site data NA – Average median value of other seagrass sites

Primary producer biomass & seagrass morphology

Sediment chlorophyll *a* (i.e., an estimate of microphytobenthos biomass) and phaeophytin contents were higher in the seagrass compared to the adjacent unvegetated habitat (by 8–41%), except at TPU where the reverse was true (by 27%; Table 1). Both chlorophyll *a* and phaeophytin pigment content increased with mud content in both the seagrass ($r = 0.49$ & 0.75, respectively, $p < 0.001$) and unvegetated habitats ($r = 0.50$ & 0.71, respectively, $p < 0.001$; see Supplementary Table S2). Only minor variations in chlorophyll α content (< 2 µg g^{-1} DW) were evident between the two plots within the mudflat sites.

Variations in seagrass biomass were evident across the sites with a range of 26–90 and 60–192 g DW m^{-2} for above- and below-ground biomass, respectively (Table 1). Seagrass belowground biomass decreased with increasing mud content ($r = -0.35$, $p < 0.05$), but aboveground and total biomass were not correlated with mud content ($r = 0.20$ & -0.11, respectively, $p > 0.05$; see Supplementary Table S2). The ratio of above- to below-ground seagrass biomass ranged from 0.45–1.01 and increased with mud content ($r = 0.58$, $p < 0.001$).

The principal coordinates analysis (PCO) of multivariate seagrass morphology illustrates overlap across multiple sites (Fig. 2). The first PCO axis explained 42.5% of the variability in seagrass morphology, with biomass metrics (above-, below-ground and total) and seagrass cover being the main variables correlated with this axis (Fig. 2a). Comparatively, seagrass leaf dimension parameters (surface area,

width and length) and the ratio of above- to below-ground biomass appear to be correlated with the second PCO axis which explained 33.9% of the variability. When environmental variables were overlaid on the PCO, the first axis was most correlated to the median low tide light (r = 0.42; Fig. 2b). Conversely, sedimentary variables (mud, organic and phaeopigment content) and exposure were correlated with the second axis. Notably, mud content was the environmental variable most strongly correlated to the second PCO axis (r = 0.47) and appears positively correlated with leaf width and the ratio of above- to below-ground biomass. Since together the first two axes of the seagrass morphology PCO explained 76.4% of the total variability, the first and second PCO axis scores were used as metrics for seagrass morphological condition (referred to as SG cond. 1 and 2) in the DistLM analyses.

Variations in primary production

NPP and GPP in both the seagrass and adjacent unvegetated habitats varied across the nine sites, but there was no significant interaction between mud content and habitat type (p-perm ≥ 0.66; Fig. 3a & b; Table 2). These variables also had no significant relationship with mud content (p-perm ≥ 0.59). Overall, NPP and GPP was higher in the seagrass compared to the adjacent unvegetated habitat (p-perm = 0.0001). Specifically, on average GPP was two times higher in the seagrass compared to the adjacent unvegetated habitat (6482 vs. 3209 μmol O_2 m^{-2} h^{-1}). For the unvegetated habitat, with the inclusion of mudflat sites/plots (extending the sedimentary gradient past the point where seagrass can thrive), NPP and GPP both decreased with increasing mud content (r = -0.71 & -0.70, respectively, p = 0.007; Fig. 3a & b). On average, during chamber incubations, all seagrass sites exhibited net autotrophy (i.e., net production of O_2 in light chambers), while two of the adjacent unvegetated sites (BRW & ONG) and three mudflat plots (URE-plot 1 & WMA-plot 1 & 2) exhibited net heterotrophy (i.e., net consumption of O_2 in light chambers; Fig. 3a).

In the seagrass habitat, site averages of photosynthetic efficiency (i.e., GPP standardised for seagrass above-ground biomass) did not significantly vary with mud content (p = 0.68; Fig. 3c). Conversely, in the unvegetated habitat, photosynthetic efficiency (i.e., GPP standardised for chlorophyll *a* content) decreased with increasing mud content for both the adjacent and extended (i.e., mudflat plots included) unvegetated habitat datasets (r = -0.81, p = 0.0009 & 0.008, respectively).

Table 2
Results of a one-way PERMANCOVA (9999 permutations; Euclidian distance-based matrices) comparing net primary production (NPP) and gross primary production (GPP) between adjacent habitats (fixed factor; 2 levels: seagrass and unvegetated sediment) with sediment mud content as a covariate. See Supplementary Table S4 for sediment community respiration

	Term	df	SS	MS	Pseudo-F	p-perm	Habitat effect
NPP	Mud x Habitat	1	0.13	0.13	0.20	0.6579	
	Mud	1	0.19	0.19	0.29	0.5855	
	Habitat	1	32.22	32.22	49.53	0.0001	Seagrass > Unvegetated
GPP	Mud x Habitat	1	0.066	0.066	0.10	0.7518	
	Mud	1	0.04	0.04	0.06	0.8057	
	Habitat	1	33.85	33.85	53.44	0.0001	Seagrass > Unvegetated

Environmental predictors of primary production

Aside from mud content in the unvegetated habitat, in marginal tests, several environmental variables were independently correlated with NPP, GPP and photosynthetic efficiency both in the seagrass (n = 9) and unvegetated habitats (n = 13; see Supplementary Table S5). Marginal tests indicated that chamber light (Lux) was a strong predictor of NPP and GPP for both seagrass and unvegetated habitats, as well as for photosynthetic efficiency in the unvegetated habitat (explaining 37–54% of the variance; $p = 0.0001$). For the seagrass habitat, the first seagrass morphology PCO axis (Fig. 2), was also reasonably well correlated with NPP and GPP (explaining 21 & 29%, respectively; $p \leq 0.001$). Meanwhile, the first and second seagrass morphology PCO axes each explained ~ 8% ($p \leq 0.07$) of the variability in photosynthetic efficiency in the seagrass habitat.

In stepwise models, 53–77% of the variability in primary production (NPP, GPP and photosynthetic efficiency) in the seagrass and unvegetated habitats was explained by environmental predictors (Table 3). The most influential predictor of each primary production response variable differed between habitat types. In the unvegetated habitat, mud content was the environmental variable explaining the greatest amount of variability for NPP, GPP and photosynthetic efficiency (36–53%). In contrast, porewater phosphate concentration was the single greatest contributor to the total explained variance in the seagrass habitat NPP (44%), whereas, for GPP, chamber light was the greatest contributor (42%; chamber light also contributed 20% to the unvegetated habitat). Temperature contributed an additional 12% to the variability in seagrass GPP. In comparison, four environmental variables contributed similarly (11–17%) to the variability in photosynthetic efficiency in the seagrass habitat; temperature, *M. liliana* count, seagrass morphology PCO axis 2 (Fig. 2), and porewater ammonium concentration.

Table 3

Distance-based Linear Model (DistLM) stepwise results for net primary production (NPP), gross primary production (GPP) and photosynthetic efficiency in seagrass (n = 9) and unvegetated (including 'mud' only sites; n = 13) habitats. Predictor variables are grouped for convenience into physiochemical, sediment, macrofauna, seagrass and porewater nutrients. Results indicate the proportion each environmental predictor adds to the full model, with the force inclusion of sediment mud content (% < 63 μm; regardless of significance). Significance levels of marginal tests of individual predictors: *p ≤ 0.1, **p ≤ 0.05, p ≤ 0.01***. See Supplementary Table S5 for full marginal test results

	Predictor group	Predictor	Seagrass	All unvegetated
NPP	*Physiochemical*	Chamber light		0.09***
		Temperature		0.13*
	Sediment	Mud	0.03	0.36***
	Macrofauna	H'	0.06	0.02**
	Porewater nutrients	PO_4^{3-}	0.44***	0.05***
		Total	0.53	0.64
		AICc	-26.64	-54.80
GPP	*Physiochemical*	Chamber light	0.42***	0.20***
		Temperature	0.12***	
	Sediment	Mud	0.03	0.36***
		Chl α		0.03
	Porewater nutrients	PO_4^{3-}		0.06***
		Total	0.57	0.65
		AICc	-30.27	-57.74
Photosynthetic efficiency	*Physiochemical*	Chamber light		0.02***
		Temperature	0.15*	
	Sediment	Mud	0.01	0.53***
	Macrofauna	Mac. Count	0.17***	0.03***
		N		0.04***
	Seagrass	SG Cond2	0.13**	

Chamber light - Lux, Mud – sediment mud content, H' – Shannon Weiner diversity, Porewater – porewater nutrient concentration, Chl α – sediment chlorophyll a concentration, Mac. – *M. liliana*, count = number per core, N – number of organisms, SG Cond2 – seagrass morphology PCO2 axis (see Fig. 2). Photosynthetic efficiency: Seagrass - above-ground biomass standardised GPP, Unvegetated - chlorophyll α biomass standardised GPP

	Predictor group	Predictor	Seagrass	All unvegetated
	Porewater nutrients	PO_4^{3-}		0.15***
		NH_4^+	0.11*	
		Total	0.56	0.77
		AICc	-24.05	-84.55

Chamber light - Lux, Mud – sediment mud content, H' – Shannon Weiner diversity, Porewater – porewater nutrient concentration, Chl α – sediment chlorophyll a concentration, Mac. – *M. liliana*, count = number per core, N – number of organisms, SG Cond2 – seagrass morphology PCO2 axis (see Fig. 2). Photosynthetic efficiency: Seagrass - above-ground biomass standardised GPP, Unvegetated - chlorophyll α biomass standardised GPP

Discussion

Anthropogenic activities and climate change are accelerating the input of terrestrial sediment into coastal waterways, causing estuarine soft sediment habitats to become muddier (Seneviratne et al. 2012; Syvitski et al. 2005; Thrush et al. 2004). While this process occurs gradually over years to decades, by using a space-for-time substitution (Pickett 1989) this study provides a comparable *in situ* assessment of how primary production in two key soft sediment habitats (seagrass meadows and unvegetated sediments) may alter with future increases in sedimentation. Overall, we found that seagrass meadows were more productive than the adjacent unvegetated habitats (likely owing to a greater photosynthesising biomass); consistent with the findings of previous studies (Clavier et al. 2014; Drylie et al. 2018; Gustafsson and Norkko 2016). However, if seagrass meadow degradation and losses continue at their current rates (Waycott et al. 2009), the shift to unvegetated habitats will ultimately result in a loss of intertidal primary production. Furthermore, the significant reduction in unvegetated primary production as mud content increased indicates that this loss may be exacerbated in muddier conditions.

Unlike seagrass, which had higher rates of primary production and thereby remained autotrophic during incubations, five of the unvegetated plots were heterotrophic. In order to evaluate net trophic states over a daily period (assuming 12 h of light/darkness and constant submersion), we calculated photosynthesis to respiration ratios in the two habitats (Eyre and Ferguson 2002). More than half (5/9) of our seagrass sites exhibited net autotrophy (i.e., photosynthesis to respiration ratio > 1), while all unvegetated sites exhibited net heterotrophy (i.e., photosynthesis to respiration ratio < 1; see Supplementary Fig. S2). While this calculation overestimates GPP (as it does not account for production during emergence (Drylie et al. 2018; Flowers et al. 2023; Migné et al. 2018; Ouisse et al. 2011) or potential reduced light levels at different times of the day), these photosynthesis to respiration ratios highlight the potential shift to a more heterotrophic system if the areal extent of seagrass meadows in Tauranga Harbour continue to decline. As a system shifts from autotrophic to heterotrophic, rather than remineralised inorganic

nutrients being assimilated by primary producers at the sediment water interface, they are released into the overlying water-column (Eyre and Ferguson 2002). This shift in pelagic nutrient availability with increased seafloor heterotrophy is likely to have cascading consequences for coastal ecosystems through increasing water-column algae concentrations (Vitousek et al. 1997), ultimately heightening the risk of an estuary shifting to a more eutrophic state (e.g., Cooper and Brush 1993; Munkes 2005).

Our measurements of submerged primary production and differences between intertidal seagrass and unvegetated sediments are within the range previously measured in New Zealand (e.g., Drylie et al. 2018; Lohrer et al. 2016; Mangan et al. 2020b; Pratt et al. 2014a). Although less productive on a per area basis, when scaled across the intertidal regions of Tauranga Harbour, unvegetated habitats are almost five times more extensive in area than seagrass meadows (6609 vs. 1361 ha, respectively (Shao et al. *in review*)). When scaling production rates (using an average GPP across all sites), based on the area occupied by each habitat within Tauranga Harbour, the importance of unvegetated production rates becomes clear: these unvegetated intertidal flats contribute two times more GPP per hour during submergence than seagrass meadows (~ 178,400 vs. 88,200 mol O_2 h^{-1}, respectively). Although these calculations do not account for temporal variability in intertidal productivity (e.g., Flowers et al. 2023), by taking productivity measurements from ≥ 9 sites across a single estuary, they incorporate variability in production across a wide spatial scale. While unvegetated habitats clearly play a significant role in estuarine productivity, as seagrass are more productive per unit area, these simple estimations highlight the importance of future management and restoration of seagrass meadows. Restoration actions will also increase the additional ecosystem services provided by seagrass meadows including; sediment stability (Heiss et al. 2000), nutrient regeneration (Eyre and Ferguson 2002), and high rates of carbon sequestration (Duarte et al. 2005b; Mcleod et al. 2011).

In the seagrass habitats, NPP, GPP and photosynthetic efficiency (i.e., above-ground biomass standardised GPP) were not affected by changes in mud content. However, variability in *Z. muelleri* morphology was evident across the seagrass sites. Additionally, seagrass morphological condition (based on PCO2 axis coordinates, Fig. 2) was identified as a contributor to seagrass photosynthetic efficiency in the stepwise DistLM model. Consistent with the findings of Ferguson et al. (2016), with increasing mud content, the ratio of above- to below-ground seagrass biomass increased. This was driven by a reduction in below-ground biomass which has high respiratory demands. When light availability is not limiting production rates, to optimise sediment oxygen concentrations (which are reduced with increasing mud content (Glud 2008; Huettel et al. 2014)), seagrass can divert some of their oxygen production to be released from their roots (Enríquez et al. 2001; Sand-Jensen et al. 1982). This subsurface oxygenation may improve the availability of nutrients and reduce the accumulation of phytotoxins (Brodersen et al. 2015; reviewed by Duarte et al. 2005a); factors that could otherwise limit primary production.

Sediment anoxia, and phytotoxins such as hydrogen sulphide, are known to increase with mud content, and have been shown to stunt seagrass growth (Glud 2008; Kilminster et al. 2008; Terrados et al. 1999). In Tauranga Harbour, *Z. muelleri* distribution (and thereby meadow productivity) is limited to areas below

35% mud content (Crawshaw 2020). This is consistent with previous reports (e.g., Moksnes et al. 2018; Short 1987; Wendländer et al. 2020; Zabarte-Maeztu et al. 2020), with only a few exceptions (e.g., up to 72% (Edgar and Shaw 1995)). The trade-off for *Z. muelleri* to prioritise maintaining above-ground biomass, may have enabled sustained rates of productivity in sub-optimal conditions. However, by losing below-ground biomass, this my come at the cost of reducing the aerobic sediment microbiome, in areas where mud content is high. Thus, in sediments > 35% mud content the ability for sub-surface oxygenation may be limited and could be potentially contributing to the restriction of seagrass distribution.

In the unvegetated habitat, the inclusion of mudflat sites (≥ 39% mud content) drove significant declines in NPP and GPP with increasing mud content. This differed to the findings of Pratt et al. (2014a) and Douglas et al. (2018) who found significant decreases in GPP with increasing mud in gradients ≤ 30% mud content. This disparity could be due to differences in the spatial scales of these previous studies; Douglas et al. (2018) sampled 12 locations at a single site, while Pratt et al. (2014a) incorporated data from 18 sites across nine estuaries. Additionally, the sites of these studies may differ in other environmental and/or ecological characteristics (e.g., macrofauna community composition (Lohrer et al. 2016; Sandwell et al. 2009) and water-column turbidity (Drylie et al. 2018; Mangan et al. 2020b; Pratt et al. 2014b)), which could contribute to changes in productivity rates. In this study, sediment chlorophyll *a* content increased with increasing mud content. Previously, microphytobenthos have also been shown to adapt to increased mud content by shifting from a predominantly sedentary to vertically migrating diatom species (Consalvey et al. 2004). This shift in community composition and increase in photosynthetic biomass could have enabled rates of primary production to be maintained in sediments with up to 35% mud content (i.e., adjacent unvegetated sites). Although, consistent with previous studies (Douglas et al. 2018; Pratt et al. 2014a; Thomas et al. 2022), photosynthetic efficiency (i.e., GPP standardised by sediment chlorophyll *a* content) declined with increasing mud across the adjacent unvegetated sites both with and without the inclusion of mudflat sites. This relationship may also have contributed to the significant decline observed in NPP and GPP with the inclusion of mudflat sites.

Light availability was identified as a strong driver of primary production in both of the soft sediment habitats examined. Notably, in the seagrass habitat, chamber light was the greatest contributor to the total variance in GPP in the stepwise models, and contributed to stepwise models of NPP, GPP and photosynthetic efficiency in the unvegetated habitat. Seafloor light availability during chamber incubations for each site was however generally above, or approximately equal to, the submerged photosynthetic saturating irradiance estimated for seagrass and unvegetated habitats at the TUA site (192 and 258 µmol photons m^{-2} s^{-1}, respectively (Flowers et al. 2023)). Only the WPA site light availability was below (by > 50 µmol photons m^{-2} s^{-1}) the saturating irradiance in both habitats but remained above the minimum light requirements for both New Zealand *Z. muelleri* and temperate intertidal microphytobenthos (~ 57 (Bulmer et al. 2016) and > 37 µmol photons m^{-2} s^{-1} (Migné et al. 2002), respectively). However, the median daytime incident light levels collected over a five-week period was below saturating irradiance for two of the seagrass and five of the adjacent unvegetated habitat

sites (by 31–44 and 22–110 µmol photons m^{-2} s^{-1}, respectively). This indicates that some of our sites may regularly experience light limitations which could impact rates of productivity. Although, as benthic primary producers can undertake adaptations to optimise light harvesting (e.g., changes in seagrass pigments (Kohlmeier et al. 2014) and/or microphytobenthos community composition (Consalvey et al. 2004)), these light requirements are site specific (Lee et al. 2007). Nevertheless, this strong influence of light supports previous findings highlighting that increased water-column turbidity, namely through increased terrestrial sediment inputs (Kirk 1985; Thrush et al. 2004), will negatively affect benthic primary production of soft sediment habitats (Drylie et al. 2018; Mangan et al. 2020b; Pratt et al. 2014b).

Water-column light attenuation (i.e., Site vs. Seafloor PAR) decreased with increasing mud content in the seagrass habitat, although this was not statistically significant in the unvegetated habitat. Similarly, while not significant, moderate negative correlations were also found between seafloor light (sampling day- and integrated long-term) and mud content in both habitats. These correlations indicate that we are unable to completely separate the effects of mud content and light availability in this study. Additionally, the coupled effect of mud content and light availability appears to alter seagrass morphology and distribution. With increasing mud content, we found an increase in seagrass leaf width. A similar response was identified in *Z. muelleri* by Ferguson et al. (2016) and *Cymodocea rotundata* (a tropical seagrass species) by Halun et al. (2002), whereby greater leaf lengths were associated with sediments with higher mud content. As increases in leaf size has also been correlated with reduced light availability (Ralph et al. 2007), this morphological adaptation is suggested to increase the light-harvesting area for photosynthesis. Additionally, in muddier sediments Ferguson et al. (2016) and Krause-Jensen et al. (2011) identified reductions in the depth limits of *Z. marina* and *Z. muelleri*, suggesting that higher mud content increases the minimum light required for seagrass. As sea-level is predicted to rise by 1.4 m by 2100 (Rahmstorf 2007), future increases in sedimentation could therefore have substantial effects on the distribution of coastal seagrass meadows.

Rising sea-level and an increase in the frequency of severe weather events predicted with climate change will further increase terrestrial runoff and sediment resuspension (Seneviratne et al. 2012; Thrush et al. 2004). In addition to sediment, terrestrial runoff can also increase estuarine inputs of heavy metals and nutrients (driving estuarine eutrophication), which have been recognised to influence benthic macrofaunal community composition (e.g., Sánchez-Moyano et al. 2010; Schmidt et al. 2017) and/or reduce benthic primary production (e.g., via. increased pelagic production (Krause-Jensen et al. 2012; Stutes et al. 2006)). As this suggests, environmental stressors often occur simultaneously, and the interaction of multiple stressors may have antagonistic, additive or synergistic effects on coastal primary production. In this study, we were able to incorporate a gradient in mud content across two soft sediment habitats, but this was not coupled with a gradient in eutrophication. Across a mud content gradient in an unvegetated habitat, sediment nutrient enrichment was identified by Douglas et al. (2018) to counteract the negative effect of mud content on GPP. Additionally, the biomass of seagrass has been found to influence their resilience to the effects of nutrient enrichment (Gladstone-Gallagher et al. 2018). These examples highlight the complex ways in which anthropogenic stressors may influence soft sediment ecosystems and warrants future research.

Increases in the mud content of estuarine soft sediment habitats have been reported worldwide (Thrush et al. 2004) and without changes in land-use practices to reduce coastal inputs of terrestrial sediments, this trend is likely to continue. In order to ensure effective management of anthropogenic stressors, future research investigating how changes in mud content can influence the mechanisms and processes that drive soft sediment ecosystem functions will be crucial. Our *in situ* study highlights the potential resilience of primary production in seagrass meadows and unvegetated habitats within 0–35% mud content. However, in Tauranga Harbour, intertidal flats with mud contents exceeding 35% are uninhabited by *Z. muelleri*, and in the unvegetated habitat declines in primary production were driven by sites with ≥ 39% mud content. Thus, this study demonstrates that, if anthropogenic stressors continue to drive seagrass decline, the loss of production due to habitat shifts will be exacerbated in areas with high mud content. Regional management of terrestrial sediment runoff is therefore going to be vital to reduce future declines of estuarine production via. habitat degradation and/or loss, especially in the face of global climate change.

Declarations

Acknowledgements

We thank J Green for her assistance with the seagrass C:N analysis and S Mangan for helping process the long-term light data. Thank you to R Gladstone-Gallagher, S Hailes and B Greenfield for their assistance with macrofauna identifications. We also thank the numerous people that assisted with field work and provided guidance with laboratory analysis from the University of Waikato, NIWA as well as friends/family members. Funding was provided by the Bay of Plenty Regional Council, Sustainable Seas National Science Challenge (Project no. C01X1901) and the University of Waikato School of Science Trust. GF also thanks the Waikato Graduate Women Educational Trust Award and the Bay Trust Bruce Cronin Scholarship. The authors declare no conflicts of interest.

Author Contributions

CP conceived the study and secured funding. All authors contributed to the experimental design. All authors assisted with field and laboratory work led by GF. GF, CP & HN conducted the statistical analysis. GF wrote the first draft of the manuscript and all authors contributing to editing and finalising the paper.

References

1. Anderson, M. J. (2008). Animal-sediment relationships re-visited: characterising species' distributions along an environmental gradient using canonical analysis and quantile regression splines. *Journal of Experimental Marine Biology and Ecology* 366: 16-27. doi:10.1016/j.jembe.2008.07.006
2. Anthony, K. R. N., P. V. Ridd, A. R. Orpin, P. Larcombe, and J. Lough. (2004). Temporal variation of light availability in coastal benthic habitats: effects of clouds, turbidity, and tides. *Limnology and*

Oceanography 49: 2201-2211. doi:10.4319/lo.2004.49.6.2201

3. Arar, E. J., and G. B. Collins. (1997). *Method 445.0: In Vitro Determination of Chlorophyll a and Pheophytin a in Marine and Freshwater Algae by Fluorescence.* U.S. Environmental Protection Agency. Cincinnati, OH.
4. Billerbeck, M., H. Røy, K. Bosselmann, and M. Huettel. (2007). Benthic photosynthesis in submerged Wadden Sea intertidal flats. *Estuarine, Coastal and Shelf Science* 71: 704-716. doi:10.1016/j.ecss.2006.09.019
5. Brodersen, K. E., D. A. Nielsen, P. J. Ralph, and M. Kühl. (2015). Oxic microshield and local pH enhancement protects *Zostera muelleri* from sediment derived hydrogen sulphide. *New Phytologist* 205: 1264-1276. doi:10.1111/nph.13124
6. Bulmer, R. H., S. Kelly, and A. G. Jeffs. (2016). Light requirements of the seagrass, *Zostera muelleri*, determined by observations at the maximum depth limit in a temperate estuary, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 50: 183-194. doi:10.1080/00288330.2015.1120759
7. Burnham, K. P., and D. R. Anderson. (2002). *A Practical Information-Theoretic Approach*. New York: Springer.
8. Clavier, J., L. Chauvaud, E. Amice, P. Lazure, M. van der Geest, P. Labrosse, A. Diagne, A. Carlier, and S. Chauvaud. (2014). Benthic metabolism in shallow coastal ecosystems of the Banc d'Arguin, Mauritania. *Marine Ecology Progress Series* 501: 11-23. doi:10.3354/meps10683
9. Consalvey, M., D. M. Paterson, and G. J. C. Underwood. (2004). The ups and downs of life in a benthic biofilm: migration of benthic diatoms. *Diatom Research* 19: 181-202. doi:10.1080/0269249X.2004.9705870
10. Cooper, S. R., and G. S. Brush. (1993). A 2,500-year history of anoxia and eutrophication in Chesapeake Bay. *Estuaries* 16: 617-626. doi:10.2307/1352799
11. Crawshaw, J. A. (2020). *Seagrass Health Monitoring in Tauranga Harbour.* Bay of Plenty Regional Council Environmental Publication 2020/08. Tauranga, New Zealand.
12. de Lange, W., and T. Healy. (1990). Wave spectra for a shallow meso-tidal estuarine lagoon: Bay of Plenty, New Zealand. *Journal of Coastal Research* 6: 189-199.
13. Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. García Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36: 27-46. doi:10.1111/j.1600-0587.2012.07348.x
14. Douglas, E. J., C. A. Pilditch, A. M. Lohrer, C. Savage, L. A. Schipper, and S. F. Thrush. (2018). Sedimentary environment influences ecosystem response to nutrient enrichment. *Estuaries and Coasts* 41: 1994-2008. doi:10.1007/s12237-018-0416-5
15. Drylie, T. P., A. M. Lohrer, H. R. Needham, R. H. Bulmer, and C. A. Pilditch. (2018). Benthic primary production in emerged intertidal habitats provides resilience to high water column turbidity. *Journal*

of Sea Research 142: 101-112. doi:10.1016/j.seares.2018.09.015

16. Duarte, C. M., M. Holmer, and N. Marbà. (2005a). Plant–microbe interactions in seagrass meadows. In *Interactions Between Macro- and Microorganisms in Marine Sediments* Eds. E. Kristensen, R. R. Haese and J. E. Kostka, 31-60. Washington DC: American Geophysical Union. doi:10.1029/CE060p0031
17. Duarte, C. M., N. Marbà, E. Gacia, J. W. Fourqurean, J. Beggins, C. Barrón, and E. T. Apostolaki. (2010). Seagrass community metabolism: assessing the carbon sink capacity of seagrass meadows. *Global biogeochemical cycles* 24: GB4032. doi:10.1029/2010GB003793
18. Duarte, C. M., J. J. Middelburg, and N. Caraco. (2005b). Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* 2: 1-8.
19. Edgar, G. J., and C. Shaw. (1995). The production and trophic ecology of shallow-water fish assemblages in southern Australia III. General relationships between sediments, seagrasses, invertebrates and fishes. *Journal of Experimental Marine Biology and Ecology* 194: 107-131. doi:10.1016/0022-0981(95)00085-2
20. Enríquez, S., N. Marbà, C. M. Duarte, B. I. van Tussenbroek, and G. Reyes-Zavala. (2001). Effects of seagrass *Thalassia testudinum* on sediment redox. *Marine Ecology Progress Series* 219: 149-158. doi:10.3354/meps219149
21. Eyre, B. D., and A. J. P. Ferguson. (2002). Comparison of carbon production and decomposition, benthic nutrient fluxes and denitrification in seagrass, phytoplankton, benthic microalgae- and macroalgae-dominated warm-temperate Australian lagoons. *Marine Ecology Progress Series* 229: 43-59. doi:10.3354/meps229043
22. Ferguson, A. J. P., R. K. Gruber, M. Orr, and P. Scanes. (2016). Morphological plasticity in *Zostera muelleri* across light, sediment, and nutrient gradients in Australian temperate coastal lakes. *Marine Ecology Progress Series* 556: 91-104. doi:10.3354/meps11830
23. Flowers, G. J. L., H. R. Needham, R. H. Bulmer, A. M. Lohrer, and C. A. Pilditch. (2023). Going under: the implications of sea-level rise and reduced light availability on intertidal primary production. *Limnology and Oceanography* 68: 1301-1315. doi:10.1002/lno.12347
24. Gladstone-Gallagher, R. V., R. W. Hughes, E. J. Douglas, and C. A. Pilditch. (2018). Biomass-dependent seagrass resilience to sediment eutrophication. *Journal of Experimental Marine Biology and Ecology* 501: 54-64. doi:10.1016/j.jembe.2018.01.002
25. Glud, R. N. (2008). Oxygen dynamics of marine sediments. *Marine Biology Research* 4: 243-289. doi:10.1080/17451000801888726
26. Green, M. O., and G. Coco. (2014). Review of wave-driven sediment resuspension and transport in estuaries. *Reviews of Geophysics* 52: 77-117. doi:10.1002/2013RG000437
27. Gustafsson, C., and A. Norkko. (2016). Not all plants are the same: exploring metabolism and nitrogen fluxes in a benthic community composed of different aquatic plant species. *Limnology and Oceanography* 61: 1787-1799. doi:10.1002/lno.10334

28. Ha, N.-T., M. Manley-Harris, T.-D. Pham, and I. Hawes. (2021). Detecting multi-decadal changes in seagrass cover in Tauranga Harbour, New Zealand, using Landsat imagery and boosting ensemble classification techniques. *ISPRS International Journal of Geo-Information* 10: 371. doi:10.3390/ijgi10060371
29. Halun, Z., J. Terrados, J. Borum, L. Kamp-Nielsen, C. M. Duarte, and M. D. Fortes. (2002). Experimental evaluation of the effects of siltation-derived changes in sediment conditions on the Philippine seagrass *Cymodocea rotundata*. *Journal of Experimental Marine Biology and Ecology* 279: 73-87. doi:10.1016/S0022-0981(02)00366-0
30. Haro, S., M. Lara, I. Laiz, C. J. González, J. Bohórquez, E. Garcia-Robledo, A. Corzo, and S. Papaspyrou. (2020). Microbenthic net metabolism along intertidal gradients (Cadiz Bay, SW Spain): spatio-temporal patterns and environmental factors. *Frontiers in Marine Science* 7: 1-22. doi:10.3389/fmars.2020.00039
31. Healy, T. R., R. Cole, and W. de Lange. (1996). Geomorphology and ecology of New Zealand shallow estuaries and shorelines. In *Estuarine Shores: Evolution, Environments and Human Alterations* Eds. K. F. Nordstrom and C. T. Roman, 115-154. London: Wiley & Sons.
32. Heip, C., and P. Engels. (1974). Comparing species diversity and evenness indices. *Journal of the Marine Biological Association of the United Kingdom* 54: 559-563. doi:10.1017/S0025315400022748
33. Heiri, O., A. F. Lotter, and G. Lemcke. (2001). Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology* 25: 101-110. doi:10.1023/A:1008119611481
34. Heiss, W. M., A. M. Smith, and P. K. Probert. (2000). Influence of the small intertidal seagrass *Zostera novazelandica* on linear water flow and sediment texture. *New Zealand Journal of Marine and Freshwater Research* 34: 689-694. doi:10.1080/00288330.2000.9516970
35. Huettel, M., P. Berg, and J. E. Kostka. (2014). Benthic exchange and biogeochemical cycling in permeable sediments. *Annual Review of Marine Science* 6: 23-51. doi:10.1146/annurev-marine-051413-012706
36. Huettel, M., H. Røy, E. Precht, and S. Ehrenhauss. (2003). Hydrodynamical impact on biogeochemical processes in aquatic sediments. In *The Interactions between Sediments and Water. Developments in Hydrobiology* Ed., B. Kronvang, 169: 231-236. Dordrecht: Springer. doi:10.1007/978-94-017-3366-3_31
37. Keddy, P. A. (1982). Quantifying within-lake gradients of wave energy: interrelationships of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. *Aquatic Botany* 14: 41-58. doi:10.1016/0304-3770(82)90085-7
38. Kilminster, K. L., D. I. Walker, P. A. Thompson, and J. A. Raven. (2008). Changes in growth, internode distance and nutrient concentrations of the seagrass *Halophila ovalis* with exposure to sediment sulphide. *Marine Ecology Progress Series* 361: 83-91. doi:10.3354/meps07479

39. Kirk, J. T. O. (1985). Effects of suspensoids (turbidity) on penetration of solar radiation in aquatic ecosystems. *Hydrobiologia* 125: 195-208. doi:10.1007/BF00045935
40. Kohler, K. E., and S. M. Gill. (2006). Coral Point Count with Excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. *Computers & Geosciences* 32: 1259-1269. doi:10.1016/j.cageo.2005.11.009
41. Kohlmeier, D., C. A. Pilditch, J. F. Bornman, and K. Bischof. (2014). Site specific differences in morphometry and photophysiology in intertidal *Zostera muelleri* meadows. *Aquatic Botany* 116: 104-109. doi:10.1016/j.aquabot.2014.02.011
42. Krause-Jensen, D., J. Carstensen, S. L. Nielsen, T. Dalsgaard, P. B. Christensen, H. Fossing, and M. B. Rasmussen. (2011). Sea bottom characteristics affect depth limits of eelgrass *Zostera marina*. *Marine Ecology Progress Series* 425: 91-102. doi:10.3354/meps09026
43. Krause-Jensen, D., S. Markager, and T. Dalsgaard. (2012). Benthic and pelagic primary production in different nutrient regimes. *Estuaries and Coasts* 35: 527-545. doi:10.1007/s12237-011-9443-1
44. Kristensen, E., M. H. Jensen, and K. M. Jensen. (1997). Temporal variations in microbenthic metabolism and inorganic nitrogen fluxes in sandy and muddy sediments of a tidally dominated bay in the northern Wadden Sea. *Helgoländer Meeresuntersuchungen* 51: 295-320. doi:10.1007/BF02908717
45. Lawton, R., and E. Conroy. (2019). *Tauranga Moana State of the Environment Report 2019.* Bay of Plenty Reigional Council Environmental Publication 2019/04. Bay of Plenty Regional Council, Tauranga, New Zealand.
46. Lee, K.-S., S. R. Park, and Y. K. Kim. (2007). Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses: a review. *Journal of Experimental Marine Biology and Ecology* 350: 144-175. doi:10.1016/j.jembe.2007.06.016
47. Livingston, R. J., S. E. McGlynn, and X. Niu. (1998). Factors controlling seagrass growth in a gulf coastal system: water and sediment quality and light. *Aquatic Botany* 60: 135-159. doi:10.1016/S0304-3770(97)00079-X
48. Lohrer, A. M., S. F. Thrush, and M. M. Gibbs. (2004). Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* 431: 1092-1095. doi:10.1038/nature03042
49. Lohrer, A. M., M. Townsend, S. F. Hailes, I. F. Rodil, K. Cartner, D. R. Pratt, and J. E. Hewitt. (2016). Influence of New Zealand cockles (*Austrovenus stutchburyi*) on primary productivity in sandflat-seagrass (*Zostera muelleri*) ecotones. *Estuarine, Coastal and Shelf Science* 181: 238-248. doi:10.1016/j.ecss.2016.08.045
50. MacIntyre, H. L., R. J. Geider, and D. C. Miller. (1996). Microphytobenthos: the ecological role of the “secret garden” of unvegetated, shallow-water marine habitats. I. Distribution, abundance and primary production. *Estuaries* 19: 186-201. doi:10.2307/1352224
51. Mangan, S., K. R. Bryan, S. F. Thrush, R. V. Gladstone-Gallagher, A. M. Lohrer, and C. A. Pilditch. (2020a). Shady business: the darkening of estuaries constrains benthic ecosystem function. *Marine Ecology Progress Series* 647: 33-48. doi:10.3354/meps13410

52. Mangan, S., A. M. Lohrer, S. F. Thrush, and C. A. Pilditch. (2020b). Water column turbidity not sediment nutrient enrichment moderates microphytobenthic primary production. *Journal of Marine Science and Engineering* 8: 732. doi:10.3390/jmse8100732

53. McCartain, L. D., M. Townsend, S. F. Thrush, D. S. Wethey, S. A. Woodin, N. Volkenborn, and C. A. Pilditch. (2017). The effects of thin mud deposits on the behaviour of a deposit-feeding tellinid bivalve: implications for ecosystem functioning. *Marine and Freshwater Behaviour and Physiology* 50: 239-255. doi:10.1080/10236244.2017.1364123

54. Mcleod, E., G. L. Chmura, S. Bouillon, R. Salm, M. Björk, C. M. Duarte, C. E. Lovelock, W. H. Schlesinger, and B. R. Silliman. (2011). A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. *Frontiers in Ecology and the Environment* 9: 552-560. doi:10.1890/110004

55. Migné, A., D. Davoult, N. Spilmont, D. Menu, G. Boucher, J.-P. Gattuso, and H. Rybarczyk. (2002). A closed-chamber CO2-flux method for estimating intertidal primary production and respiration under emersed conditions. *Marine Biology* 140: 865-869. doi:10.1007/s00227-001-0741-1

56. Migné, A., R. J. Trigui, D. Davoult, and N. Desroy. (2018). Benthic metabolism over the emersion-immersion alternation in sands colonized by the invasive Manila clam *Ruditapes philippinarum*. *Estuarine, Coastal and Shelf Science* 200: 371-379. doi:10.1016/j.ecss.2017.11.030

57. Mills, G. N., and H. Allen. (2021). *Marine Sediment Contaminant State and Trends in Tāmaki Makaurau / Auckland 2004-2019.* State of the environment reporting. Auckland Council technical report TR2021/10. Auckland, New Zealand.

58. Moksnes, P.-O., L. Eriander, E. Infantes, and M. Holmer. (2018). Local regime shifts prevent natural recovery and restoration of lost eelgrass beds along the Swedish west coast. *Estuaries and Coasts* 41: 1712-1731. doi:10.1007/s12237-018-0382-y

59. Munkes, B. (2005). Eutrophication, phase shift, the delay and the potential return in the Greifswalder Bodden, Baltic Sea. *Aquatic Sciences* 67: 372-381. doi:10.1007/s00027-005-0761-x

60. Nordlund, L. M., E. W. Koch, E. B. Barbier, and J. C. Creed. (2016). Seagrass ecosystem services and their variability across genera and geographical regions. *PLoS One* 11: e0163091. doi:10.1371/journal.pone.0163091

61. Ouisse, V., A. Migné, and D. Davoult. (2011). Community-level carbon flux variability over a tidal cycle in *Zostera marina* and *Z. noltii* beds. *Marine Ecology Progress Series* 437: 79-87. doi:10.3354/meps09274

62. Park, S. G. (2016). *Extent of Seagrass in the Bay of Plenty in 2011.* Bay of Plenty Regional Council Environmental Publication 2016/03. Whakatāne, New Zealand.

63. Park, S. R., S. Kim, Y. K. Kim, C.-K. Kang, and K.-S. Lee. (2016). Photoacclimatory responses of *Zostera marina* in the intertidal and subtidal zones. *PLoS One* 11: e0156214. doi:10.1371/journal.pone.0156214

64. Pickett, S. T. A. (1989). Space-for-time substitution as an alternative to long-term studies. In *Long-Term Studies in Ecology* Ed., G. E. Likens, 110-135. New York, NY: Springer. doi:10.1007/978-1-4615-

7358-6_5

65. Pratt, D. R., A. M. Lohrer, C. A. Pilditch, and S. F. Thrush. (2014a). Changes in ecosystem function across sedimentary gradients in estuaries. *Ecosystems* 17: 182-194. doi:10.1007/s10021-013-9716-6
66. Pratt, D. R., C. A. Pilditch, A. M. Lohrer, and S. F. Thrush. (2014b). The effects of short-term increases in turbidity on sandflat microphytobenthic productivity and nutrient fluxes. *Journal of Sea Research* 92: 170-177. doi:10.1016/j.seares.2013.07.009
67. Rahmstorf, S. (2007). A semi-empirical approach to projecting future sea-level rise. *Science* 315: 368-370. doi:10.1126/science.1135456
68. Ralph, P. J., M. J. Durako, S. Enríquez, C. J. Collier, and M. A. Doblin. (2007). Impact of light limitation on seagrasses. *Journal of Experimental Marine Biology and Ecology* 350: 176-193. doi:10.1016/j.jembe.2007.06.017
69. Rodil, I. F., A. M. Lohrer, L. D. Chiaroni, J. E. Hewitt, and S. F. Thrush. (2011). Disturbance of sandflats by thin terrigenous sediment deposits: consequences for primary production and nutrient cycling. *Ecological Applications* 21: 416-426. doi:10.1890/09-1845.1
70. Sánchez-Moyano, J. E., I. García-Asencio, and J. C. García-Gómez. (2010). Spatial and temporal variation of the benthic macrofauna in a grossly polluted estuary from southwestern Spain. *Helgoland Marine Research* 64: 155-168. doi:10.1007/s10152-009-0175-6
71. Sand-Jensen, K., C. Prahl, and H. Stokholm. (1982). Oxygen release from roots of submerged aquatic macrophytes. *Oikos* 38: 349-354. doi:10.2307/3544675
72. Sandwell, D. R., C. A. Pilditch, and A. M. Lohrer. (2009). Density dependent effects of an infaunal suspension-feeding bivalve (*Austrovenus stutchburyi*) on sandflat nutrient fluxes and microphytobenthic productivity. *Journal of Experimental Marine Biology and Ecology* 373: 16-25. doi:10.1016/j.jembe.2009.02.015
73. Schmidt, A. L., M. Coll, and H. K. Lotze. (2017). Regional-scale differences in eutrophication effects on eelgrass-associated (*Zostera marina*) macrofauna. *Estuaries and Coasts* 40: 1096-1112. doi:10.1007/s12237-016-0204-z
74. Seneviratne, S. I., N. Nicholls, D. Easterling, C. M. Goodess, S. Kanae, J. Kossin, Y. Luo, J. Marengo, K. McInnes, M. Rahimi, M. Reichstein, A. Sorteberg, C. Vera, and X. Zhang. (2012). Changes in climate extremes and their impacts on the natural physical environment. In *Managing the Risks and Extreme Events and Disasters to Advance Climate Change Adaptation* Eds. C. B. Field, V. Barros, T. F. Stocker, D. Qin, D. J. Dokken, K. L. Ebi, M. D. Mastrandrea, K. J. Mach, G.-K. Plattner, S. K. Allen, M. Tignor and P. M. Midgley, Chapter 3, 109-230. Cambridge, UK: Cambridge University Press.
75. Shao, Z., K. R. Bryan, G. J. L. Flowers, M. K. Lehmann, and C. A. Pilditch. (*in review*). Assessing present future benthic primary productivity in a large intertidal estuary using remote sensing and machine learning.
76. Short, F. T. (1987). Effects of sediment nutrients on seagrasses: literature review and mesocosm experiment. *Aquatic Botany* 27: 41-57. doi:10.1016/0304-3770(87)90085-4

77. Stutes, A. L., J. Cebrian, and A. A. Corcoran. (2006). Effects of nutrient enrichment and shading on sediment primary production and metabolism in eutrophic estuaries. *Marine Ecology Progress Series* 312: 29-43. doi:10.3354/meps312029

78. Syvitski, J. P. M., C. J. Vörösmarty, A. J. Kettner, and P. Green. (2005). Impact of humans on the flux of terrestrial sediment to the global coastal ocean. *Science* 308: 376-380. doi:10.1126/science.1109454

79. Terrados, J., C. M. Duarte, M. D. Fortes, J. Borum, N. S. R. Agawin, S. Bach, U. Thampanya, L. Kamp-Nielsen, W. J. Kenworthy, O. Geertz-Hansen, and J. Vermaat. (1998). Changes in community structure and biomass of seagrass communities along gradients of siltation in SE Asia. *Estuarine, Coastal and Shelf Science* 46: 757-768. doi:10.1006/ecss.1997.0304

80. Terrados, J., C. M. Duarte, L. Kamp-Nielsen, N. S. R. Agawin, E. Gacia, D. Lacap, M. D. Fortes, J. Borum, M. Lubanski, and T. Greve. (1999). Are seagrass growth and survival constrained by the reducing conditions of the sediment? *Aquatic Botany* 65: 175-197. doi:10.1016/S0304-3770(99)00039-X

81. Thomas, S., C. A. Pilditch, S. F. Thrush, and C. Savage. (2022). Ecosystem function responses to nutrient enrichment mediated by mud content in soft sediment habitats. *New Zealand Journal of Marine and Freshwater Research* 56: 491-508. doi:10.1080/00288330.2022.2102043

82. Thrush, S. F., J. E. Hewitt, V. J. Cummings, J. I. Ellis, C. Hatton, A. Lohrer, and A. Norkko. (2004). Muddy waters: elevating sediment input to coastal and estuarine habitats. *Frontiers in Ecology and the Environment* 2: 299-306. doi:10.1890/1540-9295(2004)002[0299:MWESIT]2.0.CO;2

83. Thrush, S. F., J. E. Hewitt, M. Gibbs, C. Lundquist, and A. Norkko. (2006). Functional role of large organisms in intertidal communities: community effects and ecosystem function. *Ecosystems* 9: 1029-1040. doi:10.1007/s10021-005-0068-8

84. Thrush, S. F., J. E. Hewitt, R. V. Gladstone-Gallagher, C. Savage, C. Lundquist, T. O'Meara, A. Vieillard, J. R. Hillman, S. Mangan, E. J. Douglas, D. E. Clark, A. M. Lohrer, and C. Pilditch. (2021). Cumulative stressors reduce the self-regulating capacity of coastal ecosystems. *Ecological Applications* 31: e02223. doi:10.1002/eap.2223

85. Thrush, S. F., J. E. Hewitt, A. Norkko, P. E. Nicholls, G. A. Funnell, and J. I. Ellis. (2003). Habitat change in estuaries: predicting broad-scale responses of intertidal macrofauna to sediment mud content. *Marine Ecology Progress Series* 263: 101-112. doi:10.3354/meps263101

86. Thrush, S. F., J. E. Hewitt, S. Parkes, A. M. Lohrer, C. Pilditch, S. A. Woodin, D. S. Wethey, M. Chiantore, V. Asnaghi, S. De Juan, C. Kraan, I. Rodil, C. Savage, and C. Van Colen. (2014). Experimenting with ecosystem interaction networks in search of threshold potentials in real-world marine ecosystems. *Ecology* 95: 1451-1457. doi:10.1890/13-1879.1

87. Thrush, S. F., J. E. Hewitt, R. D. Pridmore, and V. J. Cummings. (1996). Adult/juvenile interactions of infaunal bivalves: contrasting outcomes in different habitats. *Marine Ecology Progress Series* 132: 83-92. doi:10.3354/meps132083

88. Turner, S., and A.-M. Schwarz. (2006). *Management and Conservation of Seagrass in New Zealand: an Introduction*. Science for Conservation. Wellington, New Zealand: New Zealand Department of Conservation.
89. Turner, S. J., J. E. Hewitt, M. R. Wilkinson, D. J. Morrisey, S. F. Thrush, V. J. Cummings, and G. Funnell. (1999). Seagrass patches and landscapes: the influence of wind-wave dynamics and hierarchical arrangements of spatial structure on macrofaunal seagrass communities. *Estuaries* 22: 1016-1032. doi:10.2307/1353080
90. Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman. (1997). Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7: 737-750. doi:10.1890/1051-0761(1997)007[0737:HAOTGN]2.0.CO;2
91. Waycott, M., C. M. Duarte, T. J. B. Carruthers, R. J. Orth, W. C. Dennison, S. Olyarnik, A. Calladine, J. W. Fourqurean, K. L. Heck, A. R. Hughes, G. A. Kendrick, W. J. Kenworthy, F. T. Short, and S. L. Williams. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences* 106: 12377-12381. doi:10.1073/pnas.0905620106
92. Wendländer, N. S., T. Lange, R. M. Connolly, E. Kristensen, R. M. Pearson, T. Valdemarsen, and M. R. Flindt. (2020). Assessing methods for restoring seagrass (*Zostera muelleri*) in Australia's subtropical waters. *Marine and Freshwater Research* 71: 996-1005. doi:10.1071/MF19237
93. Woodin, S. A., N. Volkenborn, C. A. Pilditch, A. M. Lohrer, D. S. Wethey, J. E. Hewitt, and S. F. Thrush. (2016). Same pattern, different mechanism: locking onto the role of key species in seafloor ecosystem process. *Scientific Reports* 6: 26678. doi:10.1038/srep26678
94. Zabarte-Maeztu, I., F. E. Matheson, M. Manley-Harris, R. J. Davies-Colley, and I. Hawes. (2021). Interaction of substrate muddiness and low irradiance on seagrass: a mesocosm study of *Zostera muelleri*. *Aquatic Botany* 175: 103435. doi:10.1016/j.aquabot.2021.103435
95. Zabarte-Maeztu, I., F. E. Matheson, M. Manley-Harris, R. J. Davies-Colley, M. Oliver, and I. Hawes. (2020). Effects of fine sediment on seagrass meadows: a case study of *Zostera muelleri* in Pāuatahanui Inlet, New Zealand. *Journal of Marine Science and Engineering* 8: 645. doi:10.3390/jmse8090645

Figures

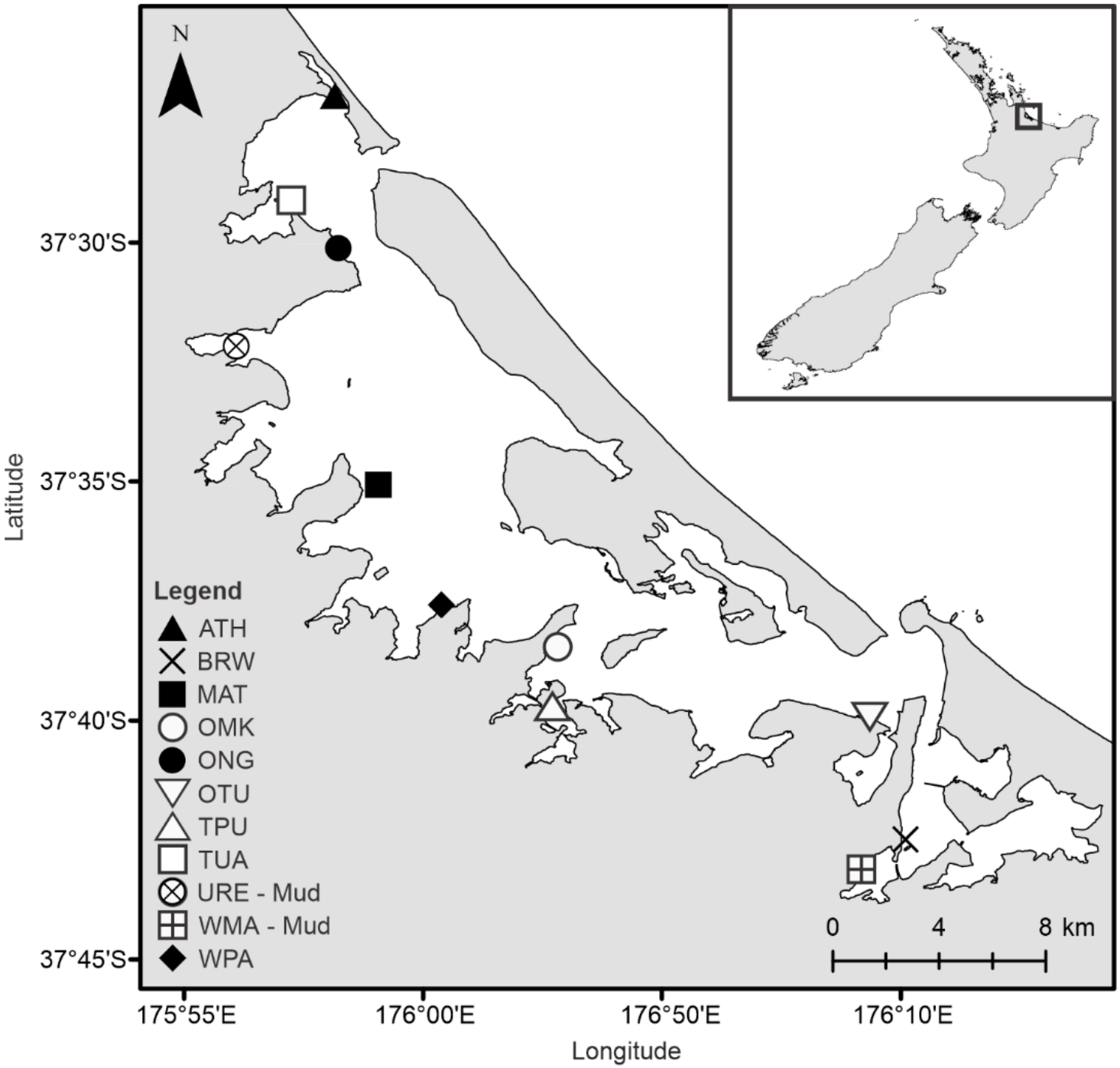

Figure 1

Location of Tauranga Harbour, New Zealand (insert), and the 11 intertidal sites. At nine sites, seagrass and adjacent unvegetated habitats were sampled, whereas URE and WMA ('Mud' sites) had no seagrass, so two unvegetated habitat plots (~25 m apart) were sampled. See Supplementary Table S1 for site-specific GPS coordinates

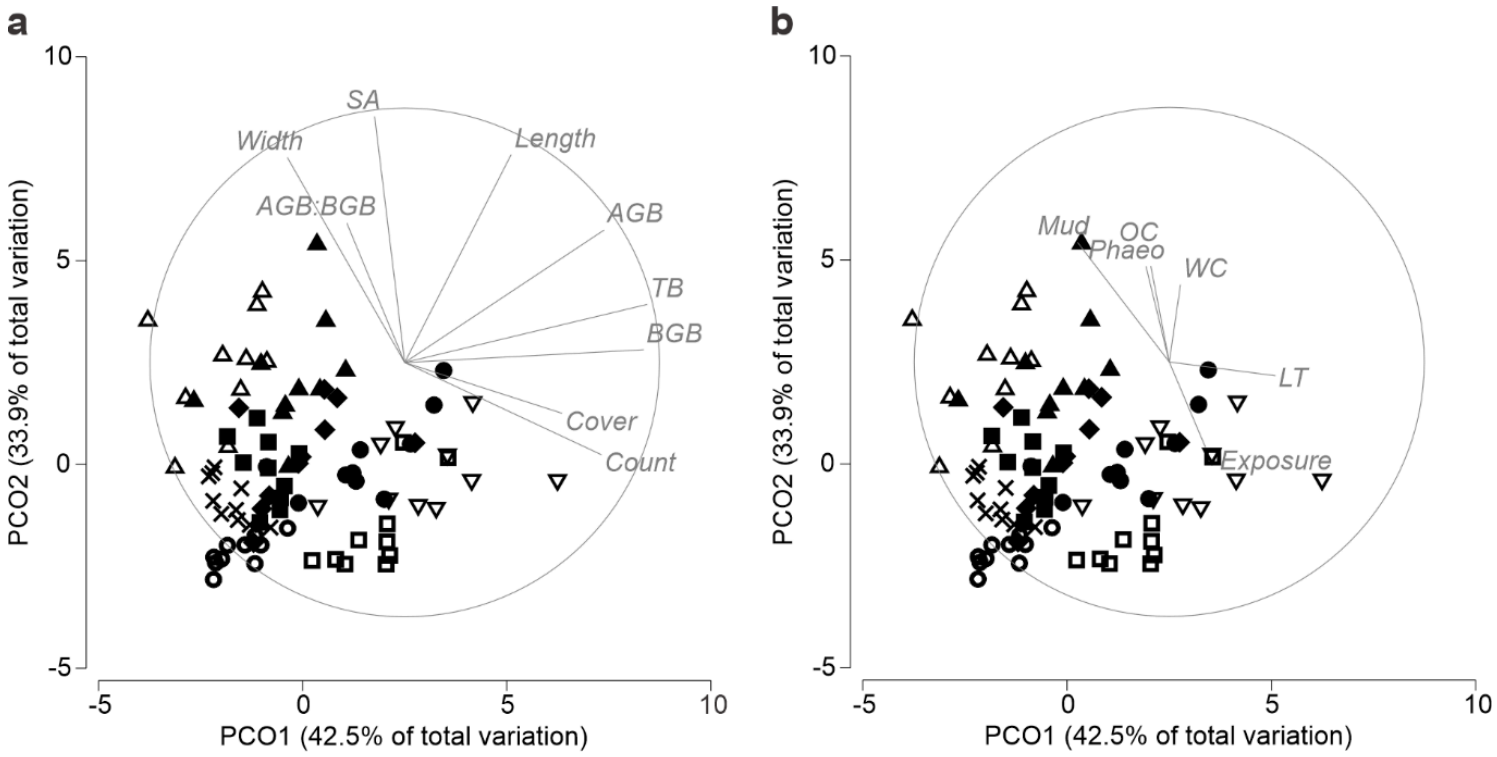

Figure 2

Principal coordinate analysis (PCO; Euclidean distance) of multivariate seagrass morphology as a function of site (n = 10 per site). Symbols indicative of site locations presented in Fig. 1. Vector overlay presents (a) seagrass morphological traits and (b) environmental variables (n = 1-10 per site; only variables with Pearson's correlation (r) ≥ 0.3 with either axis presented (circle limits r = 1)). Vector abbreviations are: AGB – seagrass above-ground biomass (g DW m^{-2}), BGB – seagrass below-ground biomass (g DW m^{-2}), TB – seagrass total biomass (g DW m^{-2}), Cover – seagrass percentage cover (%), Count – blade count (# $core^{-1}$), Width – blade width (mm), SA – blade surface area (mm^2), Length – blade length (mm), Mud – sediment mud content (% < 63 μm), Phaeo – sediment phaeopigment content (μg g^{-1} DW), OC – sediment organic content (%), WC – sediment water content (%), LT – median low tide PAR integrated over a five week period (μmol photons m^{-2} s^{-1}), Exposure – mean wind-wave exposure

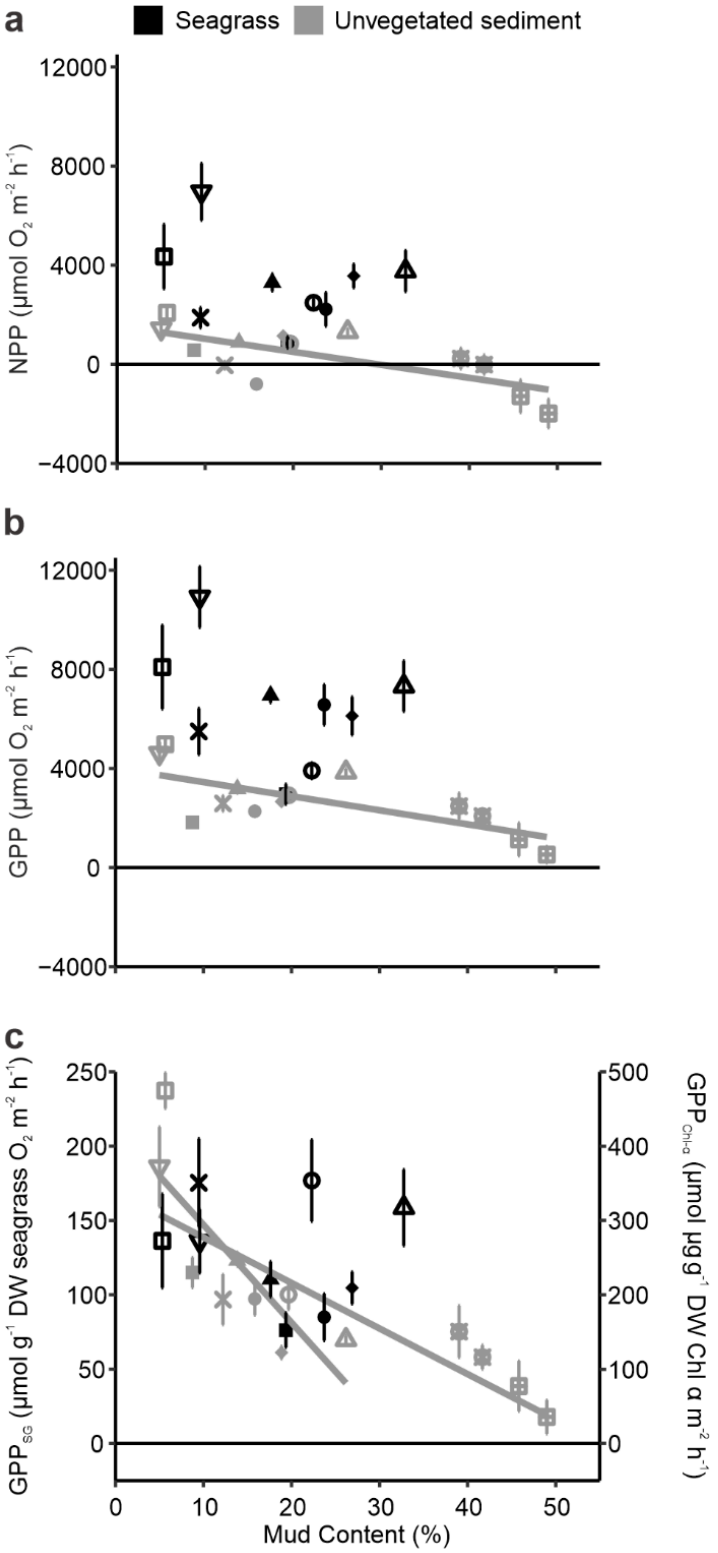

Figure 3

Variation in sediment mud content (% < 0.63 µm) and measures of primary production in seagrass (black) and unvegetated sediment (grey) habitats: a) net primary production (NPP); b) gross primary production (GPP; and c) photosynthetic efficiency (GPP_{SG} = above-ground biomass standardised GPP (seagrass habitat), $GPP_{Chl\text{-}a}$ = chlorophyll a biomass standardised GPP (unvegetated habitat)). Data represent the site average (n = 5) ± 1 SE and symbols are indicative of site locations presented in Fig. 1.

Trendlines fitted represent significant linear correlations (Pearson's r = -0.71- -0.81, p = 0.006-0.0009). There were no significant relationships in the seagrass habitat nor in the unvegetated habitat when the 'mud' only sites were excluded, except for chlorophyll α biomass standardised productivity (c). See Supplementary Fig. S1 for sediment community respiration

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- GFlowersEstuariesandCoastsElectronicSupplementaryMaterial.docx