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The effects of terrestrial sediment inputs on ecosystem functions in seagrass meadows and unvegetated sediments

A thesis

submitted in fulfilment

of the requirements for the degree

of

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at

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by

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Abstract

Ecological functions in estuarine seagrass and unvegetated soft sediment habitats underpin many valuable ecosystem services. However, changing land-use and climate are accelerating inputs of fine terrestrial sediments, threatening these habitats. The prolonged suspension of fine sediments can reduce seafloor light availability and long-term accumulations increase sediment mud content (particles < 63 μm), both of which could have significant consequences on ecosystem functioning. Understanding how ecosystem functioning may respond to environmental change is vital to estuary management. In this thesis, I investigated the short- and long-term effects of elevated terrestrial sediment inputs on benthic primary production and nutrient cycling in intertidal seagrass meadows (*Zostera muelleri*) and microphytobenthos-dominated unvegetated habitats.

To investigate the effects of reduced seafloor light availability and prolonged submergence periods resulting from global heating induced sea-level rise, I conducted a two-year seasonal *in situ* assessment of photosynthesis-irradiance relationships during submerged and emerged conditions in an adjacent seagrass meadow and unvegetated sandflat. Submerged gross primary production (GPP) in both habitats and emerged GPP in the seagrass habitat were strongly controlled by light availability. Higher rates of light-saturated GPP were found during submerged periods compared to emerged periods in both habitats, but this difference was most pronounced in the unvegetated habitat. If the water-column remains clear, sea-level rise could therefore increase daily GPP in soft sediment habitats. However, declines in submerged GPP with increased water-column turbidity will be exacerbated with sea-level rise.

Across a natural mud content gradient, I measured primary production in seagrass and unvegetated habitats to address the long-term implications of elevated sediment inputs. In sediments with ≤ 35 % mud content, net primary production (NPP) and GPP was independent

of mud content in both habitats. However, extending the mud gradient in unvegetated habitats to 49 % (seagrass habitats restricted to ≤ 35 % mud content) resulted in NPP and GPP declining with increasing mud content. These results highlight that loss of seagrass meadows resulting in expansion of unvegetated habitats could lead to reductions in intertidal production; seen most acutely in areas with high mud content (≥ 39 %).

I also investigated the spatial and temporal variability in nutrient cycling in seagrass and unvegetated habitats to examine how environmental gradients affected sediment nutrient fluxes and denitrification rates. Ammonium effluxes were lower in the seagrass compared to the unvegetated habitats and were lower in both habitats during light compared to dark conditions. Denitrification rates were similar in both habitats but were found to decrease with increasing mud content. Overall, denitrification efficiency was highest in the seagrass habitat. These results indicate that future seagrass decline and/or increased mud content in soft sediment habitats will reduce resilience to eutrophication.

This thesis demonstrates that future seagrass decline and elevated terrestrial sediment inputs are likely to have serious implications on the high rates of primary production and nutrient cycling of intertidal seagrass meadows and unvegetated habitats. Furthermore, it highlights the value of measuring ecosystem functions in different soft sediment habitat types across multiple spatial and temporal scales to inform future management against anthropogenic stressors.

Preface

This thesis comprises three research chapters (Chapters 2-4) that have been prepared as independent research papers. As a consequence, there is some repetition with respect to study site descriptions and methodology. Chapter 2 has been published in a peer-reviewed journal, Chapter 3 is currently under review and Chapter 4 is in preparation for submission. I was responsible for the field work, laboratory and data analyses, and writing of this thesis. The ideas in this thesis are my own, unless otherwise referenced. The work of this thesis was produced under the supervision of Professor Conrad Pilditch (University of Waikato), Dr Hazel Needham (University of Waikato), Dr Richard Bulmer (National Institute of Water and Atmospheric Research Ltd. (NIWA) & Tidal Research) and Dr Andrew Lohrer (NIWA).

Chapter 2 has been published in the journal *Limnology and Oceanography* Volume 68: 1301-1315 (2023), under the title "Going under: the implications of sea-level rise and reduced light availability on intertidal primary production" by G.J.L. Flowers, H.R. Needham, R.H. Bulmer, A.M. Lohrer and C.A. Pilditch. doi: 10.1002/lno.12347.

Chapter 3 is under review in the journal *Estuaries and Coasts* under the title "The effect of sediment mud content on primary production in seagrass and unvegetated intertidal flats" by G.J.L. Flowers, H.R. Needham, R.H Bulmer, A.M. Lohrer and C.A. Pilditch. doi: 10.21203/rs.3.rs-3315615/v1.

I also contributed to a publication that accompanies Chapter 2 but not included in this thesis:

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Chapter 1: General introduction

1.1 Background

Estuaries are among the world's most ecologically, economically and culturally important environments (Costanza *et al.*, 2014; Thrush *et al.*, 2013). Estuarine ecosystems provide a multitude of services that support millions of people worldwide, including erosion protection, food provision, water filtration, and climate regulation among others (Snelgrove *et al.*, 2014). These ecosystem services are underpinned by a complex network of ecosystem functions and processes (Snelgrove *et al.*, 2014), many of which are undertaken by benthic primary producers (Hope *et al.*, 2020b; Nordlund *et al.*, 2016). Two common estuarine benthic primary producers are seagrasses and microphytobenthos (MPB). Seagrass is the sole marine angiosperm and can form expansive meadows (e.g., > 180 km^2 (Edgeloe *et al.*, 2022)). MPB are unicellular benthic microalgae that reside within the estuarine surface sediments and are the dominant benthic primary producer of the seemingly 'unvegetated' sediments including sand- and mud-flats (MacIntyre *et al.*, 1996).

Where light availability reaches the seafloor, benthic primary producers including seagrass and MPB are often the dominant contributors to coastal productivity (Cahoon, 1999; Gattuso *et al.*, 2006; Kaldy *et al.*, 2002; Underwood & Krompkamp, 1999). Alongside high rates of primary production, seagrass and MPB help to maintain healthy ecosystem function by regulating nutrient cycling across the sediment-water interface (Eyre & Ferguson, 2002), supporting coastal food webs (Christianen *et al.*, 2017; Duarte & Cebrián, 1996; Jones *et al.*, 2017), trapping and stabilising sediments to the seabed (Decho, 2000; Heiss *et al.*, 2000), and sequestering carbon (Duarte et al. 2005b; Mcleod et al. 2011). The functions undertaken by benthic primary producers also help to sustain ecosystems in adjacent coastal areas, and on a larger scale, across continents facilitated by bird migrations (e.g., via trophic transfers within

coastal foodwebs and organic matter exports) (Christianen *et al.*, 2017; Duarte & Cebrián, 1996; Murray *et al.*, 2015; Savage *et al.*, 2012; Xia *et al.*, 2017). However, the functions undertaken by benthic primary producers, and the services they support, are currently under threat from anthropogenic pressures.

1.1.1 Anthropogenic pressures

In many areas worldwide, seagrass habitats are declining at unprecedented rates (Dunic *et al.*, 2021; Orth *et al.*, 2006; Waycott *et al.*, 2009). A global assessment of seagrass areal extent has revealed that, across the surveyed areas, there has been a 19 % net loss of seagrass cover since 1880 (Dunic *et al.*, 2021). Additionally, as often indicated by changes in seagrass morphology, density and/or biomass, many seagrass meadows are now considered to be in a degraded state (Airoldi & Beck, 2007; Manent *et al.*, 2020; Roca *et al.*, 2016). This decline is predominantly driven by anthropogenic activities resulting from rising global populations and subsequent intensification in land use (i.e., deforestation, farming, agriculture) that are impacting coastal environments more than ever before (Halpern *et al.*, 2008). Alongside seagrass decline, estuarine habitats are being lost through land reclamation as coastal settlements continue to develop (Airoldi & Beck, 2007). Estuaries are particularly vulnerable to the effects of anthropogenic pressures as they form the critical interface between the land and the sea. One of the main ways in which anthropogenic activities are impacting soft sediment habitats is through increasing the inputs of contaminants (e.g., sediment, nutrients etc.) into estuaries (Galloway *et al.*, 2004; Thrush *et al.*, 2004; Vitousek *et al.*, 1997).

Sedimentation is considered one of the greatest threats to estuarine ecosystems (Thrush *et al.*, 2004). While sedimentation occurs naturally, since human colonisation, the input of terrestrial sediments into rivers and coastal waterways has substantially increased worldwide (Hicks *et al.*, 2019; Syvitski *et al.*, 2005). In New Zealand alone, around 180 million tonnes of terrestrial sediment per year is estimated to be transported to the ocean (Hicks *et al.*, 2019). Unlike marine

sediments, the terrestrial sediment entering estuaries contains a high proportion of fine silts and clays (particles < 63 µm; hereafter referred to as mud). As these fine sediments enter estuaries, they can be held in suspension for prolonged periods and can be more easily resuspended from the seafloor than marine sediment. This leads to an overall increase in suspended sediment concentrations (Green & Coco, 2014; Thrush *et al.*, 2004). Over time, the fine terrestrial sediment suspensoids will settle and accumulate on the seafloor. Upon settling, this fine sediment can smother and bury benthic organisms (Lohrer *et al.*, 2004b; Rodil *et al.*, 2011; Zabarte-Maeztu *et al.*, 2020). Over longer time scales (i.e., years to decades), terrestrial sediment depositions can gradually cause an increase in the proportion of mud within sandy soft sediment habitats. As a result, terrestrial sediment inputs can have a multitude of short- and long-term effects on different environmental variables in soft sediment habitats, which through a series of interactions and feedbacks can influence ecosystem functions (Thrush *et al.*, 2004).

1.1.2 Benthic primary production

In intertidal and shallow subtidal estuarine areas, soft sediment habitats are exposed to high availability of light and nutrients, have comparatively warm temperatures, and can therefore maintain higher rates of benthic primary production compared to deeper (> 5 m depth) subtidal habitats (Douglas *et al.*, 2022). In seagrass habitats, benthic primary production is undertaken by seagrass, sediment-dwelling MPB and in some cases epiphytes (Moncreiff *et al.*, 1992). Likely due to a larger photosynthetic biomass, seagrass habitats are often found to have higher rates of primary production per unit area compared to unvegetated habitats (e.g., maximum gross primary production 47.7 vs. 8.4 mmol C m^{-2} h^{-1}, respectively, based on published literature that incorporate both seagrass and unvegetated habitats using whole-community sampling techniques (i.e., benthic chamber or core incubations; see Appendix Table A.1)). However, within estuaries, unvegetated habitats typically have a greater areal extent than

seagrass, and therefore MPB can be large contributors to estuarine production (e.g., up to 50 % (Underwood & Krompkamp, 1999)).

Light availability, specifically photosynthetically active radiation (400-700 nm wavelengths), is a crucial parameter determining the photosynthetic ability of benthic primary producers (Lee *et al.*, 2007; MacIntyre *et al.*, 1996). As such, the distribution of benthic primary producers will be dependent on where there is sufficient light available to offset respiration. In the intertidal, incident light availability is a function of the surrounding geography and/or season, especially in temperate zones. Meanwhile, the underwater seafloor light availability can be influenced by water-depth and suspended material including sediments and phytoplankton (Kirk, 1985, 1994). In low nutrient systems, suspended sediment concentrations have been found to account for up to 80 % of water-column light attenuation (Anthony *et al.*, 2004). As such, increases in water-column turbidity that are driven by elevated terrestrial sediment inputs can cause declines in benthic primary production (e.g., Drylie *et al.*, 2018; Mangan *et al.*, 2020b). Water-column turbidity can also vary across temporal scales resulting from changes in wave-driven resuspension and rainfall (Green & Coco, 2014; Seers & Shears, 2015). Additionally, alongside light, temperature is recognised to be a key driver of benthic processes including primary production (Hubas *et al.*, 2007; Lee *et al.*, 2007; Rasmussen *et al.*, 1983). However, current research quantifying the relationship between benthic primary production and light are often temporally restricted.

In intertidal areas, exposure to water-column turbidity is limited to the tidal submergence period. As benthic primary producers are directly exposed to sunlight during emergence, the emerged period has been suggested to provide resilience for benthic primary producers, especially as water-column turbidity increases (Drylie *et al.*, 2018). In areas with high water-column turbidity, benthic primary production can be restricted to the emerged period (e.g., Guarini *et al.*, 2002; Lin *et al.*, 2020; Migné *et al.*, 2004). However, exposure to high

levels of light can cause photoinhibition (Ralph & Burchett, 1995; Serôdio *et al.*, 2008). Additionally, during emergence, exposure to desiccation, temperature fluctuations, reduced nutrient availability and self-shading of seagrass blades may reduce primary production (Boese *et al.*, 2005; Clavier *et al.*, 2011; Coelho *et al.*, 2009; Miles & Sundbäck, 2000). Although, the severity of these conditions is likely to vary depending on site specific environmental conditions. For example, in muddier sediments with high water content, the effects of desiccation on primary production are likely to be reduced (Lin *et al.*, 2021a). Despite the potential for benthic primary production to occur during submerged and emerged periods, very few studies assess intertidal benthic primary production *in situ* during both tidal states (e.g., Clavier *et al.*, 2014; Denis *et al.*, 2012; Walpersdorf *et al.*, 2017).

Compared to sandier habitats, sediment with higher mud content has lower permeability and sediment particles have a larger surface area, which can subsequently alter the physicochemical properties of the sediment (Billerbeck *et al.*, 2007; Glud, 2008; Huettel *et al.*, 2014). This includes reducing sediment light penetration (e.g., ≥ 7 mm in sandy sediment vs. ≤ 3 mm in muddy sediment (Billerbeck *et al.*, 2007)) and oxic layer depth (Glud, 2008). Additionally, muddy sediments generally have higher organic content which when remineralised can reduce the sediment oxygen supply and increase sediment porewater nutrient concentrations (Blackburn & Blackburn, 1993; Blackburn & Henriksen, 1983; Huettel *et al.*, 2014). Moreover, increasing mud content can drive changes in macrofaunal community composition including declines in diversity and abundances of key species (Pratt *et al.*, 2014a; Rodil *et al.*, 2011; Thrush *et al.*, 2003), and alter their functional roles (Needham *et al.*, 2011). These changes can influence rates of benthic primary production (e.g., Drylie *et al.*, 2020; Lohrer *et al.*, 2010; Lohrer *et al.*, 2016; Sandwell *et al.*, 2009). Consequently, the modifications in environmental condition imposed by increasing mud content can have significant implications on primary production (Billerbeck *et al.*, 2007; Douglas *et al.*, 2018; Pratt *et al.*, 2014a). However, the

influence of increased sediment mud content on benthic primary production has primarily been assessed on unvegetated tidal flats, with little consideration given to seagrass meadows.

To combat changes in environmental conditions, benthic primary producers are recognised to alter their physiology, morphology and/or community structure. In response to a reduction in the availability of light penetrating into the sediment, the community composition of MPB is recognised to shift to favour vertically-migrating diatoms (Consalvey *et al.*, 2004). This allows MPB to optimise the amount of light they are exposed to and reduces the potential for MPB to be resuspended with surface sediment which is more common for finer sediments (Green & Coco, 2014). Large, dense seagrass meadows can increase water clarity by reducing water flow velocities which can increase the settlement of suspended sediments and reduce sediment resuspension (reviewed by Adams *et al.*, 2016 & de Boer, 2007). Additionally, seagrass root and rhizome matrices can enhance sediment stabilisation (reviewed by Adams *et al.*, 2016 & de Boer, 2007). Seagrasses are also recognised to alter their pigment content and change their morphology (e.g., biomass, leaf size) in response to changing light availability and/or sediment mud contents (Andrews *et al.*, 2023; Ferguson *et al.*, 2016; Kohlmeier *et al.*, 2014; Ralph *et al.*, 2007). However, while these adaptations may help to ensure rates of primary production are sufficient to offset respiration costs, the effects of increased water-column turbidity and increased sediment mud content may still reduce the photosynthetic capacity of soft sediment habitats.

1.1.3 Nutrient cycling

Estuaries play a crucial role in the uptake, transformation and removal of the nutrients that can accompany sediments with terrestrial runoff (Costanza *et al.*, 1997). While inorganic nutrients are critical for primary production, in excess they can cause a shift from benthic to pelagic dominated primary production which can ultimately result in estuaries undergoing eutrophication (e.g., Cooper & Brush, 1993; Munkes, 2005). In shallow water environments,

under sub-oxic and anoxic conditions in the sediment, denitrification transforms nitrate (NO_3^-) to di-nitrogen (N_2) gas (Seitzinger *et al.*, 2006)(Figure 1.1). Denitrification has been found to remove up to 80 % of the terrestrially derived bioavailable nitrogen loaded into coastal areas (Nixon *et al.*, 1996; Seitzinger, 1988) and thereby provides resilience to estuaries against eutrophication. While anammox (transformation of NH_4^+ and NO_2^- to N_2 gas (Figure 1.1)) can also result in the removal of nitrogen, in shallow water environments denitrification is considered the major pathway in which nitrogen is removed from the system (Dalsgaard *et al.*, 2005; Hou *et al.*, 2015). Globally, studies measuring net denitrification rates (i.e., N_2 release via denitrification and/or anammox pathways) in both seagrass and unvegetated habitats that incorporate whole-communities have shown that, alongside benthic primary production, higher rates of net denitrification can occur in seagrass habitats (maximum rates 445 vs. 314 µmol N_2-N m^{-2} h^{-1}, respectively; see Appendix Table A.2).

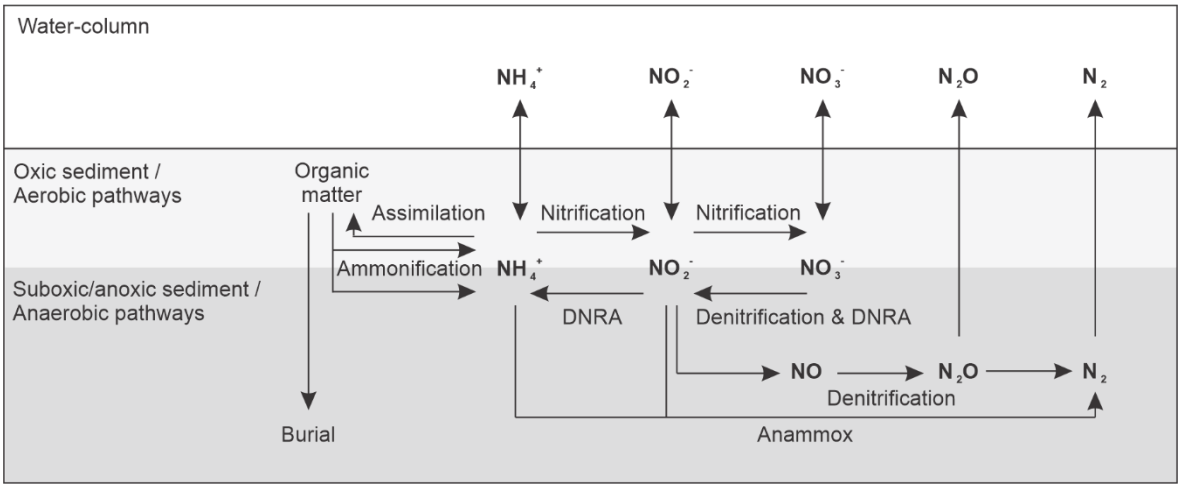


Figure 1.1 Simplified nitrogen cycling pathways between the water-column and the oxic and anoxic sediment within estuaries (DNRA – dissimilatory nitrate reduction to ammonium). Adapted from Stief (2013).

Denitrification generally occurs via two dominant pathways; direct and coupled with nitrification (Seitzinger *et al.*, 2006)(Figure 1.1). Where nitrification and denitrification are coupled, NO_3^- is sourced from the aerobic process of nitrification which transforms ammonium (NH_4^+) to nitrite (NO_2^-) or NO_3^- in the oxic sediment layer. In systems with low water-column

nutrients, removal of excess bioavailable nitrogen is regulated primarily by coupled nitrification-denitrification (Deek *et al.*, 2013; Gongol & Savage, 2016; Hoffman *et al.*, 2019; Seitzinger *et al.*, 2006). However, past research on nutrient cycling in soft sediment habitats is dominated by studies on degraded systems (often in the Northern Hemisphere), that have high water-column NO_3^- concentrations which can directly fuel denitrification (Bartoli *et al.*, 2008; Deek *et al.*, 2013; Vieillard *et al.*, 2020). In contrast, low-nutrient systems, which includes many estuaries in New Zealand (Douglas *et al.*, 2016; Plew *et al.*, 2020), are far less represented in the literature (Vieillard *et al.*, 2020).

Coupled nitrification-denitrification processes can be stimulated by benthic primary producers and macrofaunal communities (e.g., Crawshaw *et al.*, 2019; McGlathery *et al.*, 2004; Vieillard *et al.*, 2021). When seagrass and MPB photosynthesise they oxygenate the surface sediment which increases the availability of oxygen for nitrification (Caffrey & Kemp, 1990; Lin *et al.*, 2021b). Macrofauna can influence coupled nitrification-denitrification (and other pathways of nutrient processing) through their excretion products including organic rich biodeposits which can be an important source of nutrients into the sediment (Welsh, 2003). Additionally, bioturbation, bioirrigation and burrowing activities can regulate the transport of nutrients within the sediment and increase the area of the oxic-anoxic interface, and thereby the area for which coupled nitrification-denitrification can occur (Aller, 1988; Lohrer *et al.*, 2004a; Stief, 2013; Volkenborn *et al.*, 2012). In New Zealand estuaries, two large bivalve species, *Austrovenus stutchburyi* and *Macomona liliana*, make up a large proportion of the macrofaunal community biomass and are recognised to have an important influence on benthic nutrient cycling and primary production (Lohrer *et al.*, 2004a; Sandwell *et al.*, 2009; Thrush *et al.*, 2006). For example, the suspension feeding bivalve, *A. stutchburyi*, plays an important bioturbating role by reworking the surface sediment (Thrush *et al.*, 2006). Furthermore, bioirrigation (via hydraulic pumping) by deposit feeders such as *M. liliana* create porewater

pressure gradients and influence the transport of solutes (Volkenborn *et al.*, 2012; Woodin *et al.*, 2010). However, the feedbacks and interactions between mud content, sediment physicochemical properties and macrofaunal community structure, and consequently benthic primary production, can alter the transport and availability of nutrients and oxygen in the sediment (Glud, 2008; Huettel *et al.*, 2014; Pratt *et al.*, 2014a; Welsh, 2003). Changes in mud content can therefore have a significant influence on biogeochemical nutrient cycling in soft sediment habitats (Douglas *et al.*, 2018; Mangan *et al.*, 2022; Pratt *et al.*, 2014a; Vieillard & Thrush, 2021).

Benthic primary producers utilise dissolved inorganic nutrients (e.g., NH_4^+, phosphate (PO_4^{3-})) to fuel photosynthesis and in doing so play a role in regulating the exchange of dissolved inorganic nutrients between the sediment and the overlying water-column (McGlathery *et al.*, 2004). In systems where photosynthetic rates exceed respiration demands (i.e., autotrophic systems), there is generally a net uptake of dissolved inorganic nutrients (Eyre & Ferguson, 2002). In contrast, in systems with reduced photosynthetic rates that do not exceed respiration demands (e.g., systems with high water-column turbidity or sediment mud content), there can be a greater release of dissolved inorganic nutrients from the sediments (Eyre & Ferguson, 2002; Pratt *et al.*, 2014a; Pratt *et al.*, 2014b). As such, reductions in rates of primary production have resulted in an increased release of ammonium into the water-column (Longphuirt *et al.*, 2009; Pratt *et al.*, 2014b). By regulating the release of nutrients into the water-column, benthic primary producers control the availability of nutrients to fuel pelagic production. Alongside sediments, increased water-column algal concentrations can contribute to water-column light attenuation (Nielsen *et al.*, 2002). Shifts in habitat type and changes to environmental conditions that negatively influence photosynthetic rates could thereby reduce the capacity for soft sediment habitats to uptake nutrients and remove them from the system. Understanding the environmental controls of benthic primary production and nutrient cycling is therefore

critical to ensuring environmental alterations driven by anthropogenic activities, do not push ecosystems towards a degraded state.

1.1.4 Climate change

Alongside the regional effects of elevated terrestrial sediment and nutrient inputs, estuaries globally are being impacted by the increasing intensity of climate change which will impose additional pressures on soft sediment ecosystems (e.g., sea-level rise (Rahmstorf, 2007), more frequent severe weather events (IPCC, 2021), heatwaves (Frölicher *et al.*, 2018) and ocean acidification (Feely *et al.*, 2009)). The increased precipitation with more frequent severe weather events could escalate the quantities of sediment, nutrients and other contaminants into coastal waterways (Seneviratne *et al.*, 2012). Additionally, sea-level rise will alter the period of time current intertidal habitats are submerged and thereby the time benthic primary producers may be exposed to water-column turbidity. In an attempt to combat sea-level rise, more engineered structures are being constructed to protect coastal areas from flooding and erosion (e.g., seawalls). However, this is impeding the natural migration of intertidal habitats landwards, which will ultimately cause a decline in intertidal habitats as they become submerged (Pontee, 2013). Consequently, it is critical we understand the vulnerability of benthic ecosystem functions, in particular primary production and nutrient cycling, to anthropogenic and climate induced stress. Only then can effective management actions be undertaken to ensure that the valuable services provided by estuaries are sustained.

1.2 Rationale

As the impacts of anthropogenic land-use changes and climate change are intensifying, estuarine soft sediment habitats are becoming increasingly under threat from anthropogenic pressure. Soft sediment habitats are extremely complex and the ecosystem functions that occur within them are dependent on a multitude of interconnected environmental factors that may

vary over spatial and temporal scales (Lohrer *et al.*, 2004a; Thrush *et al.*, 2004; Thrush *et al.*, 2012). *In situ* field measurements that include whole-communities are invaluable to understanding how ecosystem functions may vary with environmental change. *In situ* measurements can incorporate behaviours and feedbacks that occur between benthic primary producers and other environmental variables (e.g., MPB vertical migration (Consalvey *et al.*, 2004), macrofauna bioturbation (Lohrer *et al.*, 2016)), that are difficult to replicate with laboratory-based studies. However, the number of studies measuring rates of whole-community primary production and nutrient cycling *in situ* is limited. For example, the review by Mangan *et al.* (2020a) shows that only 11 studies have assessed photosynthesis-irradiance curves in unvegetated habitats *in situ*. Additionally, only 3/12 studies I found that assessed net denitrification in seagrass meadow and unvegetated habitats that incorporate whole-communities included measurements undertaken *in situ* (see Appendix Table A.2). The research undertaken in this thesis is therefore a valuable addition to current literature, as it assesses the response of benthic primary production and nutrient cycling to environmental changes related to elevated terrestrial sediment inputs *in situ*.

Primary production and nutrient cycling in soft sediment habitats are highly variable in space and time. However, the vast majority of *in situ* studies investigating differences in primary production or nutrient cycling in soft sediment habitats are spatially and/or temporally limited. For example, numerous studies focusing on the effects of mud content on ecosystem function only compare a single low-mud/sandy to a high-mud/muddy environment (e.g., Haro *et al.*, 2020; Holmer *et al.*, 2006). More valuable, are studies working across environmental gradients (e.g., Mangan *et al.*, 2020b; Pratt *et al.*, 2014a), so that trends and potential threshold points can be identified (Hewitt & Norkko, 2007). While a few studies have assessed changes in benthic primary production and nutrient cycling in unvegetated sediments across gradients in mud content (Douglas *et al.*, 2018; Pratt *et al.*, 2014a; Vieillard & Thrush, 2021), a

comprehensive assessment of the effect of mud content on these ecosystem functions in seagrass meadows has not yet been undertaken. Assessing differences in the rates of primary production and nutrient cycling across habitats is vital to understanding the potential consequences of future shifts in the proportion of seagrass meadows and unvegetated sediment habitats. Additionally, incorporating the natural heterogeneity of ecosystem functions and soft sediment habitats is vital to scaling up small-scale field studies so that they can be incorporated into management decisions (Thrush & Lohrer, 2012).

The aim of my thesis was to increase the understanding of benthic primary production and nutrient cycling across spatial and temporal scales, and to determine the impact elevated terrestrial sediment inputs may have on these functions in two key estuarine habitats. Reports of net and gross primary production reported in my thesis represent whole-community measurements of primary production.

1.3 Thesis overview

The main body of this thesis is comprised of three field studies aimed to investigate the effects of elevated terrestrial sediment inputs on benthic primary production and nutrient processing in seagrass meadows (*Zostera muelleri* subsp. *novazelandica* (Setch.) S.W.L. Jacobs) and unvegetated sediment (sand-/mud-flat) habitats. The chapters of this thesis specifically investigate how light availability influences benthic primary production seasonally and over a tidal cycle (Chapter 2), and how changes in sediment mud content influences benthic primary production (Chapter 3) and nutrient cycling (Chapter 4) during submergence (Figure 1.2). Work for these chapters was undertaken in Tauranga Harbour in the Bay of Plenty region of New Zealand. The specific aims and objectives of each chapter are described below.

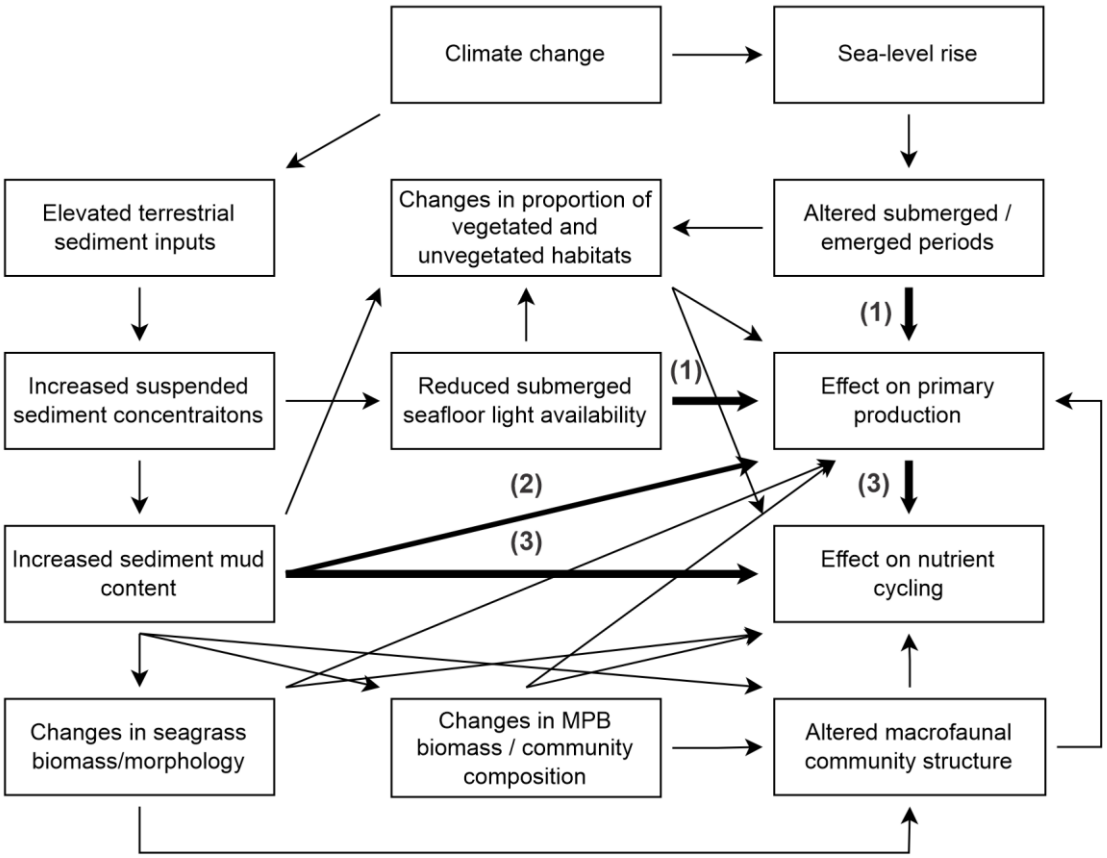


Figure 1.2 Diagram illustrating the progression of my thesis chapters to address how elevated terrestrial sediment inputs affect primary production and nutrient cycling in intertidal seagrass and unvegetated habitats, along with the interactions with additional environmental variables addressed in this thesis (simplified from Thrush *et al.* (2004)). Thick arrows with numbers indicate the chapters where each major pathway is being addressed.

1.3.1 Chapter 2

In this chapter, I conducted a manipulative field experiment that aimed to investigate the effect of light availability on submerged and emerged benthic primary production in a seagrass meadow and an adjacent unvegetated sandflat. For this experiment, I constructed a light manipulation gradient including eight shading treatments. Primary production was measured under the different shading conditions during submerged and emerged periods in the two habitats seasonally over two years to encompass the temporal variability in productivity-light relationships. Seasonally combined photosynthesis-irradiance curves for each tidal state were

then incorporated into a conceptual model to illustrate the potential coupled effects of reduced light availability and increased submergence time as a consequence of future sea-level rise.

Objectives:

1. To evaluate differences in photosynthesis-light relationships across submerged and emerged periods in a seagrass meadow and an unvegetated sandflat habitat.
2. To estimate the combined effects of reduced light availability and altered submerged-emerged periods on daily rates of gross primary production and trophic state in each habitat.

1.3.2 Chapter 3

In this chapter, I aimed to investigate the effects of increased sediment mud content on benthic primary production in soft sediment habitats. I measured primary production during submerged periods at nine sites with adjacent seagrass and unvegetated habitats encompassing a natural gradient in sediment mud content, with an additional two high mud content unvegetated habitat sites (outside the *Z. muelleri* distribution in Tauranga Harbour) also measured. In addition, a suite of environmental variables (climate, physicochemical water-column, sedimentary, macrofaunal and seagrass characteristics) were sampled to identify the environmental variables that were strongly influencing rates of primary production.

Objectives:

1. To quantify the response of benthic primary production to increases in sediment mud content in seagrass meadow and unvegetated habitats.
2. To determine underlying environmental variables contributing to the response of benthic primary production with increasing mud content.

1.3.3 Chapter 4

In this chapter, I aimed to examine how nutrient cycling in seagrass and unvegetated habitats varied across spatial and temporal scales. Data collection for Chapter 4 was undertaken in conjunction with Chapters 2 & 3. During submerged primary production sampling, additional samples of dissolved inorganic nutrients and di-nitrogen gas (i.e., for denitrification estimations) were extracted from the benthic incubation chambers. This enabled me to compare nitrogen and phosphate cycling in seagrass and unvegetated habitats across a spatial gradient in mud content, and across seasons. Additionally, utilising measurements collected for Chapters 2 & 3, I investigated the relationships between nutrient cycling, oxygen fluxes and environmental variables in the soft sediment habitats.

Objectives:

1. To assess the spatial and seasonal variability in nutrient cycling within and between seagrass and unvegetated habitats.
2. To determine the relative importance of primary production and other environmental variables (including mud content) in contributing to the variation in nutrient processing across habitats.

Chapter 2: Going under: the implications of sea-level rise and reduced light availability on intertidal primary production [1]

2.1 Introduction

Estuarine intertidal soft sediment habitats are among the most productive ecosystems in the world (Duarte & Chiscano, 1999; MacIntyre *et al.*, 1996). This productivity is supported by benthic primary producers fuelled by abundant nutrients (sourced from land and stored in sediments) and high seafloor light availability. By oxygenating surface sediment and assimilating nutrients, benthic primary producers alter sediment biogeochemistry, influencing important ecosystem processes such as nutrient regeneration and denitrification, sediment stability, and carbon sequestration (Eyre & Ferguson, 2002; Hejnowicz *et al.*, 2015; Hope *et al.*, 2020b). Through trophic transfers and export of organic matter, intertidal primary production also helps sustain adjacent coastal ecosystems (Christianen *et al.*, 2017). Changes to the environmental factors that regulate intertidal primary production can therefore have cascading effects on coastal environments. Indeed, a loss of seafloor primary production is already cited as a contributing factor to estuarine regime shifts around the world (e.g., Cooper & Brush, 1993; Munkes, 2005).

With over 20 % of the world's population living within 100 km from the coast (Small & Nicholls, 2003), direct and indirect effects of human activities (e.g., dredging, coastal development) are threatening intertidal habitats (Halpern *et al.*, 2007). Globally, anthropogenic stressors are impacting benthic primary production by reducing the extent of intertidal area (e.g., land-reclamation (Airoldi & Beck, 2007)) and simultaneously degrading seafloor light

[1] This chapter has been published in the journal *Limnology and Oceanography* Volume 68: 1301-1315 (2023), under the title "Going under: the implications of sea-level rise and reduced light availability on intertidal primary production" by G.J.L. Flowers, H.R. Needham, R.H Bulmer, A.M. Lohrer and C.A. Pilditch. doi: 10.1002/lno.12347.

intensities. Increased inputs of fine suspended sediments from terrestrial runoff (Thrush *et al.*, 2004) and excess nutrients that drive eutrophication (Duarte, 1995) are primarily responsible for seafloor light reductions. However, emersion periods on intertidal flats may offer primary producers some resilience to increased water-column turbidity, as it provides a window of high light intensity (Drylie *et al.*, 2018; Mangan *et al.*, 2020b).

Climate change may further magnify the impacts of current intertidal stressors. For example, the inputs of terrestrial sediments and nutrients to the coastal zone will be accelerated due to the predicted increase of severe weather events and associated runoff (Seneviratne *et al.*, 2012). Critically, because intertidal areas are situated at the land-sea boundary, small increases in sea-level rise will alter their extent. This impact may be exacerbated where artificial coastal structures exist, generating coastal squeeze (Pontee, 2013). Even in areas of managed retreat, the re-establishment of intertidal habitat in an ecologically relevant time scale is not assured due to the mismatch between predicted sea-level rise and slower evolving morphological responses (Elmilady *et al.*, 2022). Currently, estimates indicate that tidal flats globally are decreasing at a rate of 0.18 % per year (Murray *et al.*, 2019) but, with sea-level rise predictions of 1.4 m by 2100 (Rahmstorf, 2007), this is expected to accelerate. For example, in New Zealand estuaries, a 1.4 m rise in sea-level could result in an estimated 27-94 % loss of estuary intertidal areas (Mangan *et al.*, 2020a). Despite sea-level rise and terrestrial runoff being recognised globally as stressors to coastal environments (Halpern *et al.*, 2007; Thrush *et al.*, 2004), there is little understanding of how varying periods of submergence alongside altered light climates will impact intertidal primary production (Manassa *et al.*, 2017).

In temperate intertidal soft sediment environments, two key habitats are seagrass meadows and unvegetated flats that are dominated by benthic microalgae (microphytobenthos (MPB)). Although MPB contain less photosynthetic biomass than seagrass per unit area, they can contribute up to 50 % of whole-estuary primary production (Underwood & Kromkamp, 1999).

MPB are also a high-quality labile food source (Hope *et al.*, 2020b), compared to seagrass (Duarte & Cebrián, 1996), and can support a large proportion of coastal benthic consumers (e.g., 74 % in the Wadden Sea (Christianen *et al.*, 2017)). Despite the recognised importance of these primary producers, only a few *in situ* studies compare rates of primary production between these key habitats (e.g., Lee *et al.*, 2011; Mishra *et al.*, 2018) and there is a lack of studies addressing how production across habitats may respond to climate related stressors.

Seagrass and MPB production are strongly influenced by light availability (specifically photosynthetically active radiation (PAR)). In intertidal environments, high rates of primary production have been measured during emerged conditions (Lee *et al.*, 2011; Migné *et al.*, 2018) and where water-clarity is sufficient, during submerged conditions (Drylie *et al.*, 2018; Mangan *et al.*, 2020b). During emergence, light availability is controlled by weather and season, but primary production may also be affected by desiccation and nutrient limitation among other variables (Boese *et al.*, 2005; Coelho *et al.*, 2009; Miles & Sundbäck, 2000). In highly turbid estuaries, where benthic primary production is restricted to emerged periods (e.g., Lin *et al.*, 2020; Migné *et al.*, 2004), sea-level rise may reduce this productivity window further. In estuaries with low turbidity, small increases in water depth are likely to have minor effects on seafloor light levels. However, turbidity increases are expected to occur simultaneously with sea-level rise in many places, raising the possibility of synergistic effects on primary production.

Photosynthesis-irradiance (P-I) curves provide a way to assess how primary production varies as a function of light; a proxy for how intertidal systems may be affected by increasing water depth and/or elevated turbidity. Numerous P-I curves have been produced for intertidal primary producers, but many lack a real-world context, using isolated samples (i.e., resuspended MPB (e.g., Guarini *et al.*, 2002) or individual seagrass blades (e.g., Zimmerman *et al.*, 1991; Thom *et al.*, 2008)) and often conducted *ex situ*. Measurements on intact whole-communities are

important as they incorporate feedbacks between primary producers and other components of the ecosystem (e.g., macrofaunal bioturbation enhancing benthic production (Lohrer *et al.*, 2016)). Furthermore, by considering ecosystem metabolism and production simultaneously, it allows an assessment of trophic state (Eyre & Ferguson, 2002). Despite the clear significance of light as a regulator of primary production, I found only five (Clavier *et al.*, 2014; Clavier *et al.*, 2011; Denis *et al.*, 2012; Migné *et al.*, 2018; Walpersdorf *et al.*, 2017) *in situ* comparisons of intertidal P-I curves across tidal states (submergence/emergence), with only one (Clavier *et al.*, 2014) providing a comparison between seagrass and MPB dominated habitats. These data are critical to understanding how potential changes in water-column turbidity and/or sea-level rise will impact intertidal primary production.

To understand how primary production in two key intertidal habitats is likely to respond to climate related reductions in seafloor light intensity and altered submergence/emergence periods, I measured *in situ* P-I curves seasonally for two years in a seagrass meadow (*Zostera muelleri*) and adjacent unvegetated sandflat. Unlike many previous studies, I used large-scale benthic incubation chambers (0.25 m^2) to understand how whole-community production/metabolism varied with changing light availability and tidal state. Using long-term seasonal measurements, I assessed primary production under a wide range of environmental conditions typical of temperate estuaries to determine which environmental drivers influenced primary production in these habitats. The P-I curves generated were used to parametrise a simple model to explore how changes in submergence period and light availability may alter gross primary production and the trophic state of each habitat.

2.2 Materials and methods

2.2.1 Study site

The study was conducted at Tuapiro Point (37°29'5.64"S, 175°57'13.08"E; Figure 2.1), Tauranga Harbour, New Zealand. Tauranga Harbour is a large (201 km^2), barrier enclosed lagoon representative of a globally common estuary type (Stutz & Pilkey, 2001). This meso-tidal estuary has a mean water depth of 2.1 m with semi-diurnal tides and a spring-neap tidal range of 1.24-1.62 m (Heath, 1975). The intertidal regions (66 % of estuary area (de Lange & Healy, 1990)) consist of two main habitat types; seagrass (*Z. muelleri*) meadows and bare-unvegetated sandflats. The seagrass genus *Zostera* is common in temperate intertidal environments and are distributed throughout five of the six bioregions of the world (Short *et al.*, 2007). *Z. muelleri* is New Zealand's sole species of seagrass and is predominantly restricted to intertidal zones (Turner & Schwarz, 2006). In Tauranga Harbour, surveys in 2021 estimated seagrass habitat to cover 9 % of the intertidal area (Ha *et al.*, 2021).

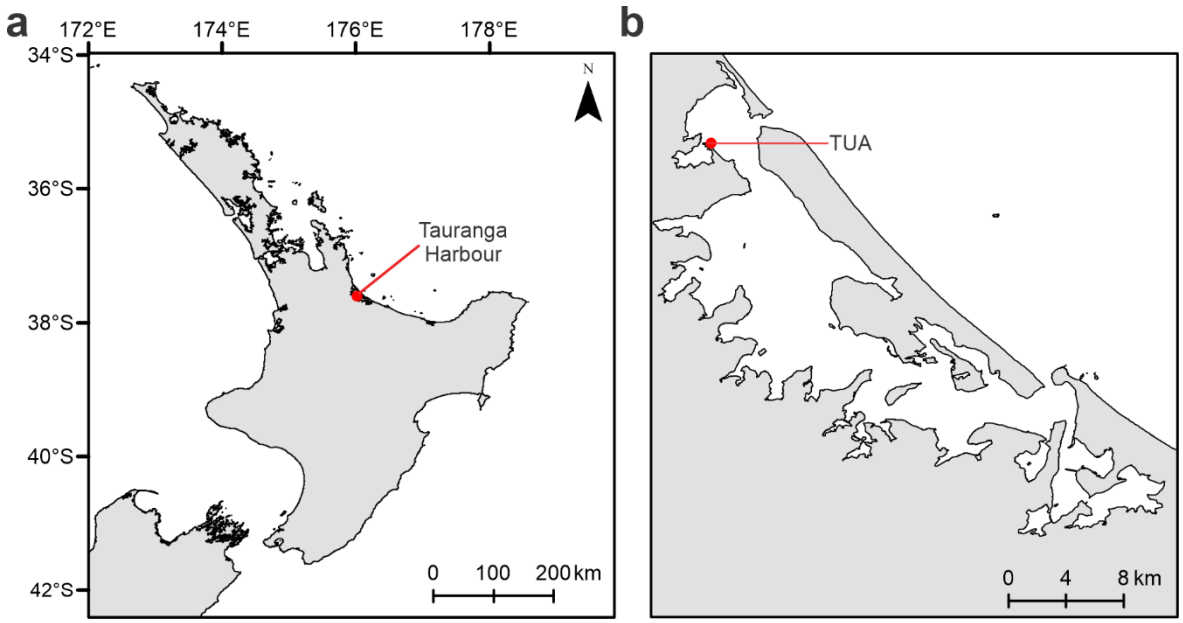


Figure 2.1 Location of Tauranga Harbour within the North Island of New Zealand (a), and the sampling site at Tuapiro Point (TUA; b).

The study site was located in the mid-intertidal with emersion periods of 4-5 h. Within the site, a plot area of 100 m^2 was marked in the seagrass meadow and adjacent sandflat (> 2 m away from the seagrass fringe). Adjacent plots were used for each seasonal period moving along the seagrass fringe (four plots total); allowing a year gap between sampling within the same plot. The close proximity of the habitats and adjacent plots minimised differences in environmental conditions (i.e., temperature, nutrient availability).

2.2.2 Field sampling

Sampling was undertaken seasonally (every three months), for two years between October 2018 (austral spring) and August 2020 (austral winter). Due to Covid-19 restrictions, April 2020 was not sampled. To capture the period of highest natural irradiance, each tidal state was sampled around midday high (submerged) or low (emerged) tides across a two-week period. During two instances, poor weather extended this sampling window to four-weeks (October 2019 & July 2020). Submerged and emerged sampling was conducted over two consecutive days (one per habitat), with the exception of July 2020 due to poor weather.

Within each habitat, 18-22 benthic incubation chambers (0.25 m^2) were deployed in two shore-parallel lines (> 1 m apart; see Appendix Figure B.1). Chamber bases (L:W:D = 0.5×0.5×0.15 m) were inserted approximately 5 cm into the sediment; care was taken to avoid disturbed areas (e.g., ray feeding pits) and to ensure similarities in seagrass cover. The chambers were sealed with Perspex transparent dome lids encapsulating volumes of 34-41 L. Chambers were randomly assigned to one of eight light treatments (0, 8, 15, 30, 45, 60, 85 and 100 % incident light); the 0 and 100 % treatments were replicated three times and the remainder in duplicate. Light treatments were achieved by using shade cloth of varying mesh sizes. Within each sampling period, chamber locations and treatments remained the same for both tidal states (unless disturbed).

2.2.3 Gas flux measurements

2.2.3.1 Submerged

Chamber bases, deployed at low tide, were fitted with a PME miniDOT dissolved oxygen logger (1 min sampling interval), a HOBO pendant light and temperature logger (5 min sampling interval) and a Sea-bird Electronics pump (on for 5 s every 45 s; to provide intermittent non-directional stirring of the chamber water) (see Appendix Figure B.1). While chambers do not incorporate any potential effects of the benthic boundary layer or water movement (via waves/currents) on benthic communities and porewater solute exchange (reviewed by Glud, 2008), pumps ensured homogenous mixing of water under consistent flow conditions. An Odyssey photosynthetically active radiation (PAR) sensor (integrated 5 min samples) was also assigned to one replicate of each light treatment (excluding 0 % light). Nylon tubing sampling ports (2 m length, 3.2 mm diameter) in each chamber lid enabled seawater extraction. A small inlet on the opposing side ensured the chamber volume remained constant. On the incoming tide, at approximately 0.3 m water depth, chamber lids and shade cloth were clamped onto each base, ensuring no air pockets were present. Three pairs of light and dark 1.5 L bottles were also filled, sealed and secured at the seafloor to account for water-column production. Once sealed, sampling hoses were flushed before an initial 60 mL seawater sample was extracted from each chamber using a Leur-lock syringe. Three 60 mL ambient seawater samples were also collected. Following an incubation period of approximately 4 h, another 60 mL sample was taken from each chamber. Each light and dark water bottle was similarly sampled. Once collected, dissolved oxygen concentrations were measured immediately using an optical sensor (YSI ProSolo ODO/CT) to provide a means of comparing chamber and water-column fluxes.

2.2.3.2 Emerged

Chamber bases were deployed approximately 2.5 h before low tide, once seawater had drained from the site. Prior to incubations, chamber bases were covered with the shade cloth for 30 min to allow the microphytobenthos (MPB) and seagrass sufficient acclimation to the light treatment (Drylie *et al.*, 2018). Closed-circuit incubations were conducted using a single modified chamber lid fitted with a battery-powered fan, temperature sensor, pressure vent, and an air-in and -out port connected to a calibrated LI-COR 8100A Automated Soil CO_2 Flux System (following approaches of Streever *et al.* (1998), Migné *et al.* (2002) & Drylie *et al.* (2018); see Appendix Figure B.1). The lid was sequentially clamped to each base with incubations lasting 3.5 min; the initial 30 s was treated as a dead-band period for CO_2 flux stabilisation (removed prior to analysis). This incubation period was determined following preliminary tests that demonstrated a stable linear change in CO_2 concentration with minimal variation in humidity/temperature (average variation < 7 %). During the incubation, a stream of air was circulated from the chamber to the LI-COR 8100A from which CO_2 (ppm) and moisture content (% humidity) was measured (1 Hz frequency). Once all chambers had been sampled, they were resampled sequentially (2-3 times) until tidal inundation was imminent. In addition to light treatment acclimation, both the duration of submerged incubations and sequential resampling of emerged chambers would have likely captured any potential changes in primary production resulting from vertical migration by MPB and/or tidal stage (Pinckney & Zingmark, 1991).

2.2.4 Site characteristics

Alongside chamber light and temperature measurements, air temperature, humidity and sediment temperature (to 5 cm depth during emerged incubations) was also recorded. Light measurements (Odyssey PAR sensor) were taken at the seafloor during submerged and emerged conditions (referred to as ‘seafloor PAR’). An additional Odyssey PAR sensor was

placed on shore during submerged measures (referred to as 'site PAR'), for the determination of water-column light attenuation. To evaluate sediment properties, each day five sediment cores (2.6 cm diameter, 2 cm depth) were collected around each chamber. These were pooled, frozen and stored in the dark for later analysis. After each seasonal sampling event, a 13 cm diameter core was taken to a depth of 15 cm beside each chamber for macrofaunal analysis. This was sieved *in situ* over a 500 µm mesh and preserved in 70 % isopropyl alcohol. For the seagrass habitat, a photograph of each chamber was taken to estimate seagrass percentage cover. To estimate seagrass biomass, a 13 cm diameter core was collected from the centre of the chamber, sieved *in situ* over a 1 mm mesh and frozen within 4 h.

2.2.5 Laboratory analyses

Sediment samples were thawed, homogenised and divided for the analysis of sediment properties. Grain size samples were measured using a Malvern Mastersizer 3000 (particle size range 0.05-2000 µm), following removal of organic matter (10 % hydrogen peroxide digestion). Water content was determined from percentage weight loss of samples dried at 60 °C, with organic content determined from percentage weight loss on ignition (Heiri *et al.*, 2001). Chlorophyll *a* (a proxy for microphytobenthos biomass) and phaeopigment content (µg g dw^{-1}) were determined fluorometrically (Turner 10-AU fluorometer), before and after acidification by hydrochloric acid using freeze-dried samples steeped in 90 % buffered acetone (Arar & Collins, 1997).

As adult bivalves (> 10 mm) have been shown to contribute disproportionally to community metabolism and stimulate primary production (Lohrer *et al.*, 2016; Sandwell *et al.*, 2009), the abundance and size of *Austrovenus stutchburyi* and *Macomona liliana* was measured for each sampling event. Seagrass percentage cover was estimated using a 100 random point count analysis (CPCe v4.1) manually categorised as live blades, dead blades or unvegetated sediment (Kohler & Gill, 2006). Chamber seagrass samples were thawed and separated into

above- (leaves) and below-ground (sheath, rhizomes, roots) biomass and dried at 60 °C until a constant weight.

2.2.6 Estimating primary production

Chamber fluxes of carbon (µmol C m^{-2} h^{-1}) were calculated from the submerged dissolved oxygen and emerged CO_2 measurements. For submerged sampling, dissolved oxygen fluxes were calculated using a 10 min average of oxygen concentrations at the start and end of the incubation period. Water-column processes accounted for < 5 % of the benthic dissolved oxygen fluxes and so were ignored. Dissolved oxygen fluxes were converted into carbon using a photosynthetic quotient of 1.2; a commonly used value for natural communities of both MPB and seagrass (Ryther, 1956). For emerged sampling, fluxes were calculated from the slope of the linear regression of the CO_2 concentration with time (SoilFluxPro v4.0.1). For chambers with multiple measurements during a sampling event, CO_2 fluxes and PAR measurements were averaged.

Dark chambers with 0 % light availability provided measurements of sediment community respiration (SCR) with remaining light treatment chambers (8-100 %) providing measures of net primary production (NPP; representing a whole-community measure of primary production). Estimates of gross primary production (GPP) were calculated by adding the average SCR to the NPP measured in each light chamber.

P-I curves were created using measures of GPP and PAR. For submerged incubations, the average PAR (µmol photons m^{-2} s^{-1}) during the incubation period was calculated from the Odyssey logger within each light treatment chamber. Due to the short duration of emerged incubations, the seafloor Odyssey logger was corrected by the previously determined reductions in light intensity caused by each shade-cloth treatment. Photosynthesis-irradiance (P-I) curves were created using Eq. (1) (Webb *et al.*, 1974):

$$GPP = Pmax * \left(1 - exp\left(-\alpha * \frac{I}{Pmax}\right)\right) \quad (1)$$

Where *Pmax* is the maximum rate of GPP (plateau of the curve), *I* is irradiance in PAR (µmol photons m^{-2} s^{-1}) and alpha (α) is the initial slope of the curve; a measure of the photosynthetic efficiency at low light intensity (µmol C m^{-2} h^{-1} (µmol photons s^{-1})$^{-1}$). This equation was selected as no evidence of photoinhibition was found. *Pmax* and α were estimated using user-specified least squares regression (Statistica v13.0). Consistent with previous literature, R^2 values are presented to describe the strength of the model fit for each P-I curve. The irradiance at which light begins saturating photosynthesis (*Ik*; µmol photons m^{-2} s^{-1}) was calculated from Eq. (2):

$$Ik = Pmax/\alpha \quad (2)$$

For each sampling date, values of GPP obtained at light levels greater than *Ik* (i.e., above light saturation) were extracted for comparative analysis (referred to as 'GPP_{sat}'). As no GPP values above *Ik* were recorded for the submerged sandflat in July 2020 and the emerged seagrass in April 2019 due to cloud cover, values from only the 100 % light treatment chambers were used.

2.2.7 Statistical analyses

To determine if measures of GPP_{sat} varied temporally (season), between tidal states (emerged and submerged) and/or habitats (seagrass and sandflat), a three-way fixed factor PERMANOVA was performed (999 permutations). Where significant interactions (p_{perm} < 0.05) occurred, post-hoc pairwise tests were used to identify which levels differed within each factor.

Distance-based Linear Models were run to identify environmental drivers (e.g., seafloor light intensity, temperature, primary producer biomass, and adult bivalve abundance and size) of GPP_{sat}. Data from all sampling dates, within a habitat/tidal state were aggregated for this

analysis. Where high collinearity (Pearson's $r > 0.9$) between environmental predictors occurred, the predictor explaining the least variability was removed. All variables were normalised prior to analysis and marginal tests were performed to identify significant individual predictors. Stepwise procedures (using AICc (Burnham & Anderson, 2002)), then further identified the best combination of predictor variables to create the most parsimonious model. Statistical analyses were completed using PRIMER v7 software with the PERMANOVA+ package on Euclidean distance-based matrices.

2.3 Results

2.3.1 Environmental variables

Seasonally, and between habitat types, only minor differences in sediment properties and adult bivalve characteristics were evident (Table 2.1). Sediment in seagrass and sandflat habitats was fine sand with similar median grain size (~175 μm) and mud (< 63 μm; ~7 %), water (~26 %) and organic matter (~2.7 %) content. In both habitats, *A. stutchburyi* occurred in greater abundances than *M. liliana* (~20 vs. 3 core^{-1}, respectively). For each species, the mean abundance and size was similar in both habitats.

Table 2.1 Seasonally averaged site characteristics in the seagrass and sandflat intertidal habitats (± 1 SD; n = 7). The observed range between sampling dates is presented in parentheses. See Appendix Table B.1 for individual sampling date data.

	Seagrass		**Sandflat**	
Sediment properties				
Mud content (% < 63 μm)	6.4 ± 0.9	(5.3-7.8)	7.4 ± 1.5	(5.4-9.4)
Median grain size (μm)	175 ± 3	(170-178)	175 ± 4	(170-181)
Water content (%)	26.9 ± 1.4	(25.0-29.3)	26.6 ± 1.2	(24.9-28.2)
Organic content (%)	2.8 ± 0.3	(2.4-3.3)	2.7 ± 0.2	(2.4-3.1)
Adult bivalve abundance (# core^{-1})				
A. stutchburyi	20.0 ± 4.6	(15.5 – 29.9)	19.0 ± 2.0	(15.4 – 21.3)
M. liliana	1.8 ± 0.5	(1.3 – 2.6)	2.9 ± 0.7	(2.2 – 4.1)
Adult bivalve size (mm)				
A. stutchburyi	16.9 ± 0.8	(16.3-18.3)	18.7 ± 0.8	(17.6-20.0)
M. liliana	22.8 ± 0.7	(21.9-23.8)	22.6 ± 0.7	(21.3-23.4)

As a result of weather conditions, temperature and light intensity (PAR) was variable but seasonal patterns were apparent (Table 2.2). Higher temperatures and light levels were generally seen during spring/summer, compared to the autumn/winter. Average temperature and seasonal ranges were higher during emerged conditions (by ~5 and 10 °C, respectively) in both habitats. On average, submergence reduced site light availability at the seafloor by 60 % (site PAR vs. seafloor PAR). No substantial differences in temperature and light regime were detected between habitat types.

Table 2.2 Seasonal variations in temperature, light and indicators of primary producer biomass in the seagrass and sandflat habitats (mean ± 1 SD). Data is arranged by austral season for ease of interpretation.

			Chamber Temperature		**Light Regime**			**Seagrass**			**Microphytobenthos**	
			(°C)	(°C)	PAR - Site (µmol m^{-2} s^{-1})	PAR – Seafloor (µmol m^{-2} s^{-1})		Percent cover (%)	AG biomass (DW g m^{-2})	Total biomass (DW g m^{-2})	Chl *a* (µg g^{-1} DW)	Chl *a* (µg g^{-1} DW)
Season	Date	Habitat	SUB	EMG	SUB	SUB	EMG				SUB	EMG
Spring	Oct-18	Seagrass	17.5 ± 0.6	24.8 ± 1.2	1925 ± 89	711 ± 86	2014 ± 59	64 ± 11	59 ± 12	170 ± 43	16.1 ± 2.1	15.4 ± 3.0
		Sandflat	17.8 ± 0.6	26.1 ± 1.9	1823 ± 363	785 ± 145	1608 ± 610				12.9 ± 1.8	12.9 ± 1.8
	Oct-19	Seagrass	14.2 ± 0.5	16.2 ± 1.5	1463 ± 501	548 ± 167	622 ± 406	38 ± 7	32 ± 7	112 ± 27	13.7 ± 2.2	13.3 ± 2.0
		Sandflat	14.8 ± 0.5	24.2 ± 1.6	1689 ± 498	601 ± 188	2167 ± 156				15.3 ± 1.6	11.4 ± 1.6
Summer	Jan-19	Seagrass	22.7 ± 0.6	28.6 ± 1.8	1641 ± 585	666 ± 236	1381 ± 591	55 ± 10	62 ± 16	207 ± 32	13.0 ± 1.4	14.2 ± 1.8
		Sandflat	22.9 ± 0.5	32.0 ± 1.9	1671 ± 538	698 ± 208	2162 ± 291				11.0 ± 1.5	13.5 ± 1.4
	Jan-20	Seagrass	20.7 ± 0.6	28.4 ± 1.2	2232 ± 146	905 ± 103	2183 ± 403	38 ± 8	33 ± 9	113 ± 25	12.2 ± 1.3	13.4 ± 1.5
		Sandflat	20.8 ± 0.5	30.7 ± 1.1	2202 ± 170	846 ± 86	2294 ± 57				10.6 ± 1.0	14.0 ± 2.3
Autumn	Apr-19	Seagrass	19.9 ± 0.2	20.0 ± 0.5	567 ± 403	250 ± 159	271 ± 89	64 ± 7	45 ± 11	130 ± 32	13.7 ± 1.6	10.3 ± 1.0
		Sandflat	19.5 ± 0.4	26.2 ± 2.3	1000 ± 362	421 ± 145	1678 ± 70				14.5 ± 2.1	13.0 ± 1.6
Winter	Jul-19	Seagrass	14.1 ± 0.3	17.2 ± 2.0	652 ± 371	244 ± 125	991 ± 306	52 ± 7	42 ± 7	103 ± 18	13.9 ± 1.4	12.6 ± 1.0
		Sandflat	14.2 ± 0.3	14.0 ± 0.7	771 ± 314	256 ± 98	330 ± 195				13.9 ± 2.9	10.9 ± 0.8
	Jul-20	Seagrass	14.7 ± 0.5	17.5 ± 1.5	1295 ± 149	454 ± 58	840 ± 344	46 ± 9	36 ± 14	106 ± 27	15.5 ± 1.9	16.1 ± 1.7
		Sandflat	13.7 ± 0.1	20.1 ± 1.4	262 ± 92	150 ± 61	1120 ± 225				11.0 ± 1.2	11.6 ± 0.7

PAR – photosynthetically-active radiation, SUB – submerged, EMG – emerged, Percent cover – live seagrass percent cover, AG – above-ground, DW – dry weight, Chl *a* – sediment chlorophyll *a* content.

2.3.2 Primary producer biomass

Sediment chlorophyll *a* content (a proxy for microphytobenthos biomass) remained relatively consistent across sampling dates in both habitats and did not differ between tidal states (Table 2.2). For seagrass, seasonal patterns in live percentage cover and biomass were observed in the first year of sampling (spring 2018 to winter 2019), with above-ground and total biomass being highest in summer, before decreasing in autumn and again in winter. During the second year of sampling, seagrass above-ground and total biomass did not vary seasonally and remained relatively low (~34 & 110 DW g m^{-2}, respectively). Live seagrass percentage cover was more variable, however consistent with seagrass biomass, a reduction in percentage cover occurred from the first to second year of sampling (by 6-26 %). On average, above-ground biomass accounted for 29-41 % of total seagrass biomass.

2.3.3 Photosynthesis-irradiance curves

To summarise the relationship between light availability and primary production, data from each seasonal sampling event were pooled and integrated photosynthesis-irradiance (P-I) curves for the seagrass and sandflat habitats under submerged and emerged conditions were generated (Figure 2.2; Table 2.3; see Appendix Table B.2 for individual P-I curve parameters and Figure B.2 & Table B.3 for biomass-standardised seagrass curves). P-I curves showed that gross primary production (GPP) during submergence in seagrass and sandflat habitats was strongly driven by light availability (R^2 = 0.75 & 0.69, respectively). However, during emergence, the strength of the modelled relationship remained relatively high in the seagrass (R^2 = 0.45), but this relationship was considerably weaker in the sandflat habitat (R^2 = 0.15). *Pmax* was always higher in seagrass compared to the sandflat habitat, and this difference was more pronounced during emerged compared to submerged conditions (3.8 vs. 1.8 times, respectively). For both the seagrass and sandflat habitats, higher *Pmax* was estimated during submerged compared to emerged conditions (by 1.4 and 2.9 times, respectively). In the

seagrass habitat, the saturation irradiance (*Ik*) was similar during both tidal states (differing by only 8 µmol photons m^{-2} s^{-1}), but in the sandflat habitat *Ik* was 1.7 times lower during emergence when compared to submergence. Community photosynthetic efficiency (α) was also higher (by ~2.6 times) in the seagrass compared to the sandflat habitat, and was reduced in both habitats (by ~1.6 times) during emergence when compared to submergence. This demonstrates that seagrass habitat responded more quickly to increases in PAR and in both habitats, emergence slowed this response.

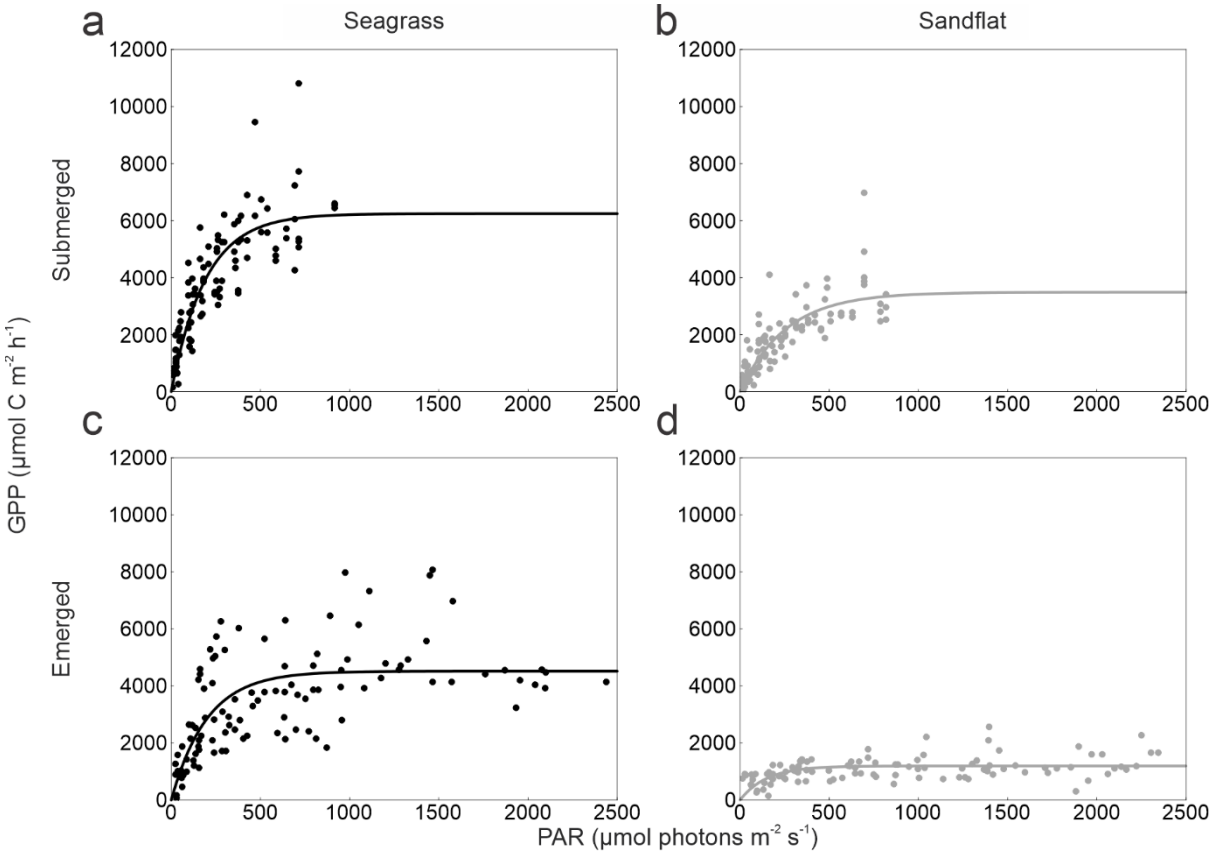


Figure 2.2 Seasonally averaged photosynthesis-irradiance (P-I) curves for intertidal seagrass (black; a & c) and sandflat (grey; b & d) habitats under submerged (a & b) and emerged (c & d) conditions (GPP – gross primary production, PAR – photosynthetically active radiation; see Table 2.3 for parameter estimates). Curves were constructed from seven seasonal sampling events (austral spring (October) 2018 – winter (July/August) 2020).

Table 2.3 Seasonally averaged photosynthesis-irradiance curve parameters (± 95% CI) for seagrass and sandflat habitats under submerged and emerged conditions. Parameter ranges from individual sampling events are presented in parentheses. See Appendix Table B.2 for individual sampling date data.

	Seagrass				**Sandflat**			
	Submerged		**Emerged**		**Submerged**		**Emerged**	
Pmax	6240 ± 540	(4349-7236)	4519 ± 418	(2311-11167)	3485 ± 484	(2524-4330)	1194 ± 98	(729-1920)
α	32.4 ± 5.1	(24.1-58.9)	22.5 ± 6.2	(14.7-29.1)	13.5 ± 2.7	(8.1-27.1)	8.0 ± 3.0	(4.6-99.4)
Ik	192	(86-274)	200	(136-384)	258	(147-455)	148	(9-261)
R^2	0.75	(0.51-0.92)	0.45	(0.63-0.90)	0.69	(0.52-0.95)	0.16	(0.04-0.78)
n	107	(15-17)	105	(15)	106	(14-17)	103	(13-15)

Pmax – photosynthetic maximum (µmol C m^{-2} h^{-1}), *α* – photosynthetic efficiency (µmol C m^{-2} h^{-1} (µmol photons m^{-2} s^{-1})$^{-1}$), *Ik* – saturation irradiance (µmol photons m^{-2} s^{-1}).

2.3.4 Seasonal variations in primary production

Consistent with *Pmax*, light-saturated gross primary production (GPP_{sat}) was always higher in seagrass compared to the sandflat habitat (Figure 2.3; see Appendix Table B.4 for statistical analyses). On average, seagrass GPP_{sat} was 2.1 times higher than the sandflat during submergence (5,093 vs. 2,477 µmol C m^{-2} h^{-1}), a difference that increased to 4.1 times during emergence (4,183 vs. 1,080 µmol C m^{-2} h^{-1}). Submerged seagrass GPP_{sat} was on average 1.3 times higher than the emerged state, but in the sandflat habitat this difference was much more pronounced (2.4 times). Seasonal trends in GPP_{sat} were also observed. During summer, submerged seagrass GPP_{sat} was greater than in any other season, whilst emerged seagrass GPP_{sat} was higher in summer and autumn than in either spring or winter (Figure 2.3a). Highest rates of submerged and emerged GPP_{sat} also occurred in summer for the sandflat, with lowest rates occurring in winter during submergence (Figure 2.3b). Light-saturated net primary production was always positive in each habitat type and tidal state (i.e., more carbon fixation than community respiration; see Appendix Figure B.3 & Table B.4).

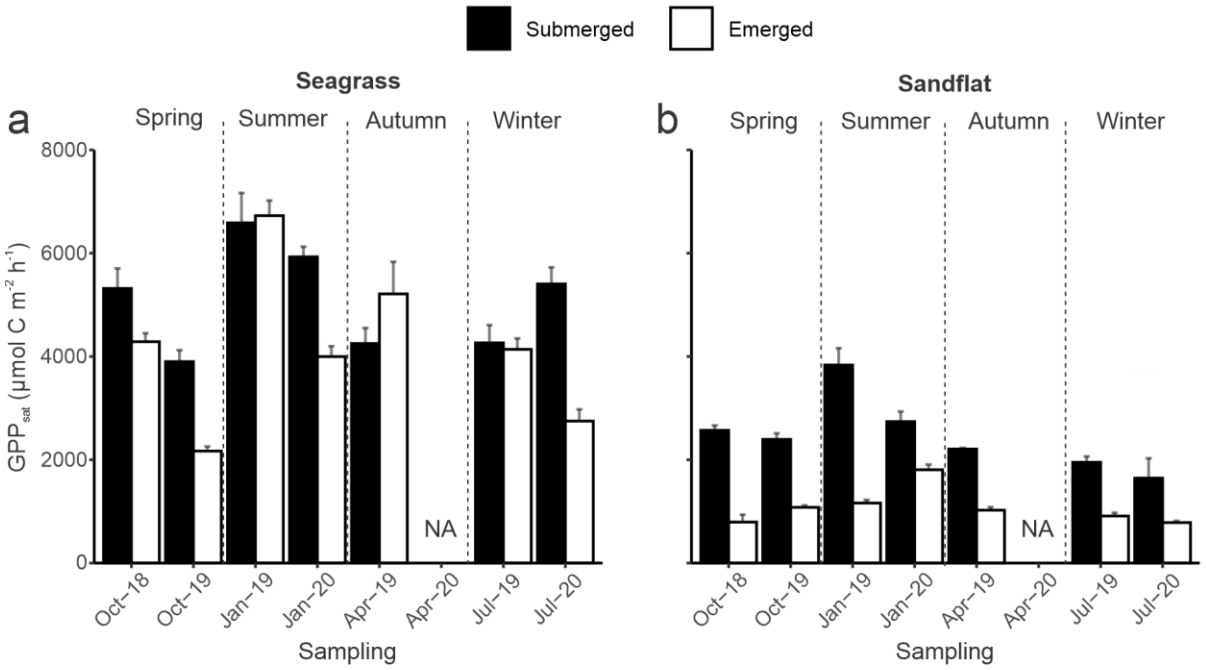


Figure 2.3 Seasonal variations in light-saturated gross primary production (GPP_{sat}) as a function of habitat (a - seagrass, b – sandflat) during submerged (black bars) and emerged (white bars) conditions. Bars (mean + 1 SE; n = 3-15) arranged by austral season. See Appendix Figure B.3 for light-saturated net primary production (NPP_{sat}) and sediment community respiration data.

2.3.5 Environmental predictors of production

Several environmental predictor variables were correlated with measures of GPP_{sat} in marginal tests (see Appendix Table B.5), but few contributed significantly to the stepwise models (Table 2.4). Environmental predictors explained between 44 (submerged) to 63 % (emerged) of the variation in GPP_{sat} for seagrass habitat. In submerged conditions, PAR was the single greatest contributor (35 %) to the variance in seagrass $GPP_{sat,}$ whereas during emergence, temperature was a more important predictor (48 %). Above-ground seagrass biomass contributed a further 15 % of the total explained variance in emerged conditions. In the sandflat habitat, environmental predictors explained between 19 (emerged) and 48 % (submerged) of the variation in GPP_{sat}, with temperature the most significant predictor in both tidal states. (See Appendix Table B.5 & B.6 for marginal tests and stepwise model results for light-saturated net primary production and sediment community respiration).

Table 2.4 Distance-based Linear Model stepwise results for all light-saturated fluxes of GPP (GPP_{sat}) as a function of habitat and tidal state. Significance levels of marginal tests of individual predictors: *p ≤ 0.1, **p ≤ 0.05, p ≤ 0.01***. See Appendix Table B.5 for full marginal test results and Appendix Table B.6 for light-saturated net primary production (NPP_{sat}) and sediment community respiration stepwise results.

		Seagrass		Sandflat	
	Predictor	**Submerged**	**Emerged**	**Submerged**	**Emerged**
GPP_{sat}	PAR	0.35***		0.05***	
	Temperature		0.48***	0.43***	0.19***
	SG %	0.09*			
	SG AGB		0.15***		
	Total	0.44	0.63	0.48	0.19
	AICc	-25.72	-56.83	-26.82	-16.22

PAR – photosynthetically-active radiation, SG % - live seagrass percentage cover, SG AGB - seagrass above-ground biomass.

2.4 Discussion

Seafloor light availability is currently threatened by anthropogenic activities that are driving increasing inputs of terrestrial sediment into coastal waterways (Thrush *et al.*, 2004). To investigate the consequences of reduced seafloor light availability on intertidal primary production, this study obtained *in situ* seasonal measurements of photosynthesis-irradiance (P-I) curves over two years during submerged and emerged conditions in a seagrass meadow and an adjacent unvegetated sandflat. Owing to a substantially greater photosynthesising biomass, the seagrass meadow consistently maintained higher rates of light-saturated gross primary production (GPP_{sat}) compared to the sandflat (as demonstrated by Drylie *et al.*, 2018; Lin *et al.*, 2020). Additionally, primary production was reduced in both habitats during emergence, as environmental factors such as desiccation (Boese *et al.*, 2005; Coelho *et al.*, 2009), nutrient availability (Miles & Sundbäck, 2000) and seagrass self-shading (Clavier *et al.*, 2011) likely limited production.

By undertaking comparable measurements during submergence and emergence, using the seasonally averaged P-I curves I can estimate daily rates of GPP for my intertidal habitats that account for tidal state. Assuming a constant annual average incident PAR of 750 μmol photons m^{-2} s^{-1} (measured previously at the site (Mangan *et al.*, 2020a)), a 60 % reduction in incident

light availability during submergence (Table 2.2), and a 50 % submergence period for a 12 h daily photoperiod, daily GPP was estimated to be 56 & 21 mmol C m^{-2} d^{-1} for the seagrass and sandflat habitats, respectively. Of the daily GPP, the contribution of submerged and emerged production in the seagrass habitat was approximately equal (53 vs. 47 %, respectively), while in the sandflat habitat, the contribution by submerged production was double that compared to the emerged production (67 vs. 33 %, respectively).

My daily GPP estimates were identical to the seasonally averaged integrated GPP_{sat} measurements (Figure 2.3) and consistent with the literature. For example, my sandflat daily GPP estimate was similar to that observed by Migné *et al.* (2004) (25 mmol C m^{-2} d^{-1}) and the mean value reported by Cahoon (1999) based on a review of intertidal microphytobenthos (MPB) production (26 mmol C m^{-2} d^{-1}). Using P-I curves corrected for seagrass biomass (see Appendix Figure B.2 & Table B.3), my daily GPP estimate for the seagrass habitat (1.3 mmol C g^{-1} DW seagrass m^{-2} d^{-1}) was also within the range reported by Duarte *et al.* (2010) that reviewed 13 seagrass species (0.2-10.7 mmol C g^{-1} DW seagrass m^{-2} d^{-1}). Similarly, there is some empirical evidence that my P-I curve parametrisations are broadly applicable. Primarily, the saturation irradiance (*Ik*) values of the P-I curves are consistent with those previously reported in published literature. For the submerged sandflat, *Ik* was identical to the median value (258 µmol photons m^{-2} s^{-1}) reported by Mangan *et al.* (2020a) that reviewed 42 P-I curves from whole-community intertidal unvegetated flats. Similarly, the seagrass *Ik* during both tidal states (192-200 µmol photons m^{-2} s^{-1}) is comparable to the mean *Ik* (194 µmol photons m^{-2} s^{-1}) of nine seagrass populations (seven species) reported by Vermaat *et al.* (1997).

In a global context, my study site would be considered oligotrophic and in a healthy state with abundant shellfish, extensive seagrass meadows and clear water that supports high rates of submerged primary production (Vieillard *et al.*, 2020). My seasonally averaged P-I curves demonstrate that GPP in seagrass meadows and unvegetated sandflats are strongly related to

seafloor light availability during submergence. However, this relationship weakened (i.e., lower R^2 values) during emergence, especially in the sandflat. Oligotrophic systems are underrepresented in intertidal whole-community P-I curve studies, which have focussed on muddy (and turbid) unvegetated flats where production is limited to emerged conditions (Lin *et al.*, 2020; Migné *et al.*, 2004). Unlike mudflats, oligotrophic sandflats do not retain high sediment water content and therefore rarely develop MPB biofilms. This, in turn, can reduce emerged primary production in sand dominated systems as MPB are more likely to be limited by factors such as desiccation and/or nutrient availability (Coelho *et al.*, 2009; Lin *et al.*, 2021a; Miles & Sundbäck, 2000). Integration of data from sandy, oligotrophic systems, and under different tidal states, will therefore have important implications for global intertidal carbon budgets (e.g., those estimated by Lin *et al.*, 2020).

While P-I curves illustrate the potential effects of changing light climate on benthic primary production, my short-term flux measurements do not capture the potential for adaptation to changing light conditions (i.e., changes in pigment/MPB community composition (Du *et al.*, 2009; Kohlmeier *et al.*, 2014)). Across sites of increasing water-column turbidity, Drylie *et al.* (2018) found that seagrass (*Z. muelleri*) meadows were able to up-regulate production during emergence to compensate for decreased submerged production, indicating I may have underestimated the degree to which seagrass ecosystems can compensate for long-term reductions in submerged light availability. However, Drylie *et al.* (2018) observed no such upregulation of emerged GPP with increasing turbidity in MPB dominated sandflats. The sensitivity of sandflat MPB to reduced light climate during submergence, and a lack of capacity to compensate during emergence, may have considerable implications for coastal foodwebs if sea-level rise is accompanied with increased turbidity.

My seasonally averaged submerged sandflat P-I curve indicates that, at ~300-400 µmol photons m^{-2} s^{-1}, further decreases in PAR strongly affect GPP (Figure 2.2), indicating a threshold

correlated with observed shifts in the structure and functioning of intertidal sandflats (Gammal *et al.*, 2022; Thrush *et al.*, 2021). A recent New Zealand wide and globally unique experiment conducted on unvegetated sandflats (24 sites across 15 estuaries, spanning 12 degrees of latitude), demonstrated that benthic ecological interaction networks in turbid systems (daily averaged submerged PAR < 350 µmol photons m^{-2} s^{-1}) were relatively simple, had fewer connections and no feedbacks when compared to sites with clearer water (PAR > 420 µmol photons m^{-2} s^{-1}; Thrush *et al.*, 2021). Furthermore, from the same experiment, Gammal *et al.* (2022) demonstrated shifts in biodiversity-ecosystem functioning relationships when daily submerged PAR was < 420 µmol photons m^{-2} s^{-1}. At lower light levels, macrofaunal biodiversity loss reduced ecosystem multi-functionality; a relationship not seen in clear estuaries. Although, it is recognised that elevated turbidity may impact other ecosystem components (e.g., suspension-feeders (Hewitt & Norkko, 2007)), the correlation between light limitation of MPB and broader changes in the ecosystem emphasises the need to improve coastal light climates.

Alongside changes in light availability, additional environmental variables were identified as important drivers of benthic primary production above light saturation. Notably, temperature was identified as an important predictor of GPP_{sat} in both habitats, illustrating the positive effect it has on metabolic rates. Under future climate scenarios, air and water temperatures are expected to increase (IPCC, 2021; Ruela *et al.*, 2020). However, there are limits to the optimal temperature range for production; 16-35 °C in seagrass (reviewed by Lee *et al.*, 2007) and 20-36 °C in sandflats (Migné *et al.*, 2004; Rasmussen *et al.*, 1983). Proportionally, temperature can have a greater impact on sediment community respiration (SCR) than primary production (Hubas *et al.*, 2006; Lee *et al.*, 2011). Consequently, this can result in an ecosystem becoming more heterotrophic (i.e., community respiration exceeds GPP), but mixed results have been observed (Alsterberg *et al.*, 2011; Burkholz *et al.*, 2019).

Despite both sea-level rise and elevated inputs of terrestrial sediment being described as major threats to coastal ecosystems worldwide (Halpern *et al.*, 2007; Thrush *et al.*, 2004), little is known about the combined impacts on the productivity of intertidal flats. In order to evaluate how the current daily integrated GPP may be affected by simultaneous changes in submergence periods (caused by rising seas) and seafloor light availability (a proxy for turbidity and/or sea-level rise), I devised a simple conceptual model integrating the seasonally averaged P-I data (Figure 2.2; Table 2.3). The model suggests that, provided the water-column remains clear, current integrated GPP should increase with moderate sea-level rise in both habitats (Figure 2.4a & b). This is because exposure to environmental factors that limit production during emergence is reduced. As seafloor light climate during submergence declines, the emerged period contributes a greater proportion of the integrated GPP. However, sea-level rise reduces this productivity window, further accelerating the decline in GPP. There are also important differences between habitats both in terms of absolute rates of integrated GPP and their sensitivity to sea-level rise and reducing light climate. Importantly, seagrass meadows are less sensitive to increasing water-column turbidity because they can maintain higher rates of production during emergence than sandflat MPB (e.g., Drylie *et al.*, 2018; Lin *et al.*, 2020). Integrated GPP in unvegetated habitats is therefore expected to decline more rapidly in response to reduced light levels during submergence, compared to seagrass meadows (Figure 2.4a & b).

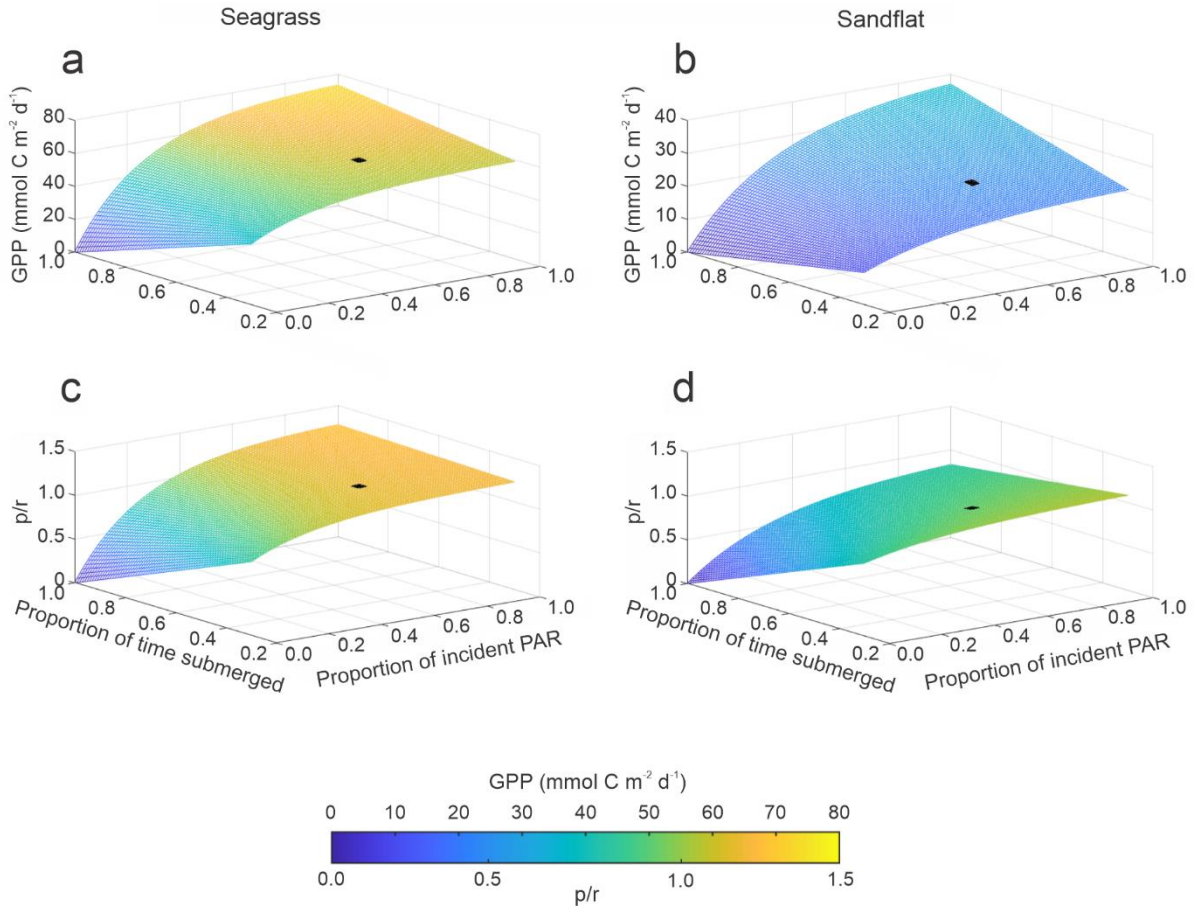


Figure 2.4 Variation in daily integrated gross primary production (GPP; a & b) and production to respiration ratios (p/r; c & d) for intertidal seagrass (a & c) and sandflat (b & d) habitats. Response surfaces are plotted as a function of submergence time (to represent sea-level rise (1 = permanently submerged)) and the proportion of incident PAR (750 µmol photons m^{-2} s^{-1}) reaching the seafloor during submergence (a proxy for turbidity and/or sea-level rise). p/r ratios > 1 indicate the habitat is net autotrophic whereas values < 1 are heterotrophic. Plots were created using seasonally averaged P-I curves and sediment community respiration values derived under submerged and emerged conditions (see text for details). Black squares indicate an estimate of the current seasonal average daily GPP and p/r. Note the difference in GPP Y-axis scales between habitats.

Photosynthesis to respiration ratios (Eyre & Ferguson, 2002) provide an estimate of an ecosystems trophic state; values > 1 indicate systems that are net autotropic (i.e., GPP exceeds community respiration) and those < 1 heterotrophic. Using the seasonally averaged P-I curves and SCR rates (see Appendix Figure B.3) with the assumption of a 12 h light and dark period, I estimated how trophic status varied with light and submergence period (Figure 2.4c & d). The seagrass habitat maintains an autotrophic state over a greater range of light and tidal state conditions than the unvegetated sandflat; a function of the higher rates of GPP and ability to

maintain production during emergence. Conversely, the sandflat habitat was net heterotrophic under most conditions (especially as the light climate worsened), and became less heterotrophic (i.e., higher p/r ratios) as emergence period increased. This somewhat counterintuitive result (sandflat GPP is much lower during emergence), arises because emerged SCR is substantially lower, likely due to reduced macrofaunal activity (see Appendix Figure B.3 & Table B.4). Although seagrass habitats may remain net autotrophic over a greater range of conditions, this does not necessarily translate to a greater resilience for intertidal foodwebs. In temperate coastal foodwebs, few macrofauna feed directly on seagrass blades due to its low food quality and digestibility; seagrass primarily enters the detrital foodweb (Duarte & Cebrián, 1996; Vizzini *et al.*, 2002), whereas MPB are highly labile and often directly consumed (Hope *et al.*, 2020b). This indicates that temperate coastal foodwebs may be more sensitive to changes in MPB production/biomass than seagrass.

My conceptual model (Figure 2.4) contextualises some of the potential changes in benthic primary production as seafloor light intensity and submergence times change. However, climate change and anthropogenic activities could drive interactions with other simultaneously changing environmental variables and further impact benthic primary production. For example, differences in macrofaunal community structure have strong feedbacks to primary production and ecosystem function (Lohrer *et al.*, 2016; Pratt *et al.*, 2014a; Sandwell *et al.*, 2009). Similarly, long-term inputs of terrestrial sediment not only elevates water-column turbidity but also increases sediment mud content (Thrush *et al.*, 2004). This can alter macrofaunal communities (e.g., reduction in diversity (Pratt *et al.*, 2014a)) and negatively influence primary production (Pratt *et al.*, 2014a; Thrush *et al.*, 2003). These examples serve to highlight the complexities of system-level interactions in a rapidly changing world.

Globally, intertidal regions have been or will be affected by changes in water-column turbidity and sea-level rise to some degree (Murray *et al.*, 2019; Thrush *et al.*, 2004). Future research

identifying how soft sediment ecosystems respond to changes in light availability will therefore be invaluable for the management of these threats. My results emphasised that emerged production may not offer much resilience to increasing water-column turbidity, particularly for MPB dominated sandflats. For high turbidity intertidal habitats already reliant on emerged primary production (e.g., Lin *et al.*, 2020; Migné *et al.*, 2004), sea-level rise represents a significant threat. However, my results demonstrate that in more oligotrophic systems, benthic productivity can remain high when the water-column remains clear (Clavier *et al.*, 2011; Mangan *et al.*, 2020b). This highlights that, although a global problem, localised management of coastal water-quality will play a crucial role in providing resilience to benthic primary producers as sea levels rise.

Chapter 3: The effect of sediment mud content on primary production in seagrass and unvegetated intertidal flats [2]

3.1 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 (MPB; i.e., benthic microalgae), although generally less productive than seagrass meadows on a per area basis (Bahlmann *et al.*, 2015; Drylie *et al.*, 2018; Gustafsson & 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 (Dunic *et al.*, 2021; Waycott *et al.*, 2009). As seagrass decline generally results in a subsequent shift to unvegetated sediment habitats, MPB 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). Although, the construction of dams and reservoirs can reduce the amount of terrestrial sediment reaching the coast (Li *et al.*, 2020; Walling, 2006), sediment loading in many coastal areas globally has increased (Thrush *et al.*,

[2] This chapter is under review in the journal *Estuaries and Coasts* under the title "The effect of sediment mud content on primary production in seagrass and unvegetated intertidal flats" by G.J.L. Flowers, H.R. Needham, R.H Bulmer, A.M. Lohrer and C.A. Pilditch. DOI: 10.21203/rs.3.rs-3315615/v1.

2004). For example, since the initiation of land clearance activities in Chesapeake Bay, sedimentation rates have increased by an order of magnitude (Cooper & Brush, 1993). 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; hereafter mud), which can be continuously deposited and resuspended by currents and wind generated waves (Green & 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') influencing 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 highest rates of productivity generally occur above light saturation levels (e.g., > ~200 µmol photons m^{-2} s^{-1} for temperate seagrass (calculated from whole-plant review by Lee *et al.*, 2007) and MPB (reviewed by Mangan *et al.*, 2020a)) and 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 physicochemical 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 community composition (which occurs with changing mud content) alters nutrient availability indirectly affecting primary production (e.g., Lohrer *et al.*, 2004a; 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.*, 2021b). Changes in seagrass growth with changing sediment physico-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 to reduce *Z. muelleri* rhizome growth in laboratory mesocosms (Zabarte-Maeztu *et al.*, 2021b), 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 MPB, increases in mud content are recognised to cause a decline in benthic primary production (Billerbeck *et al.*, 2007; Douglas *et al.*, 2018; Pratt *et al.*, 2014a). Reductions in gross primary production standardised by chlorophyll *a* 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 MPB 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 time-scales (i.e., years to decades), I used a space for time approach (Pickett, 1989) by using an existing spatial gradient in mud content within a single large estuary. I measured whole-community primary production *in situ* using large-scale benthic incubation chambers, incorporating the real-world complexities of estuarine ecosystems. In response to changing sediment physicochemical conditions, based on the literature I hypothesise 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. I 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, my study will enable us to identify threshold responses in benthic primary production to mud content.

3.2 Materials and methods

3.2.1 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 & 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 (Heath, 1975). 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 & Schwarz, 2006), and in Tauranga Harbour have not been reported 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 & Conroy, 2019), consistent with increases in mud content measured across multiple New Zealand North Island estuaries (Mills & Allen, 2021).

In Tauranga Harbour, nine intertidal sites with continuous seagrass meadows (> 200 m^2) and nearby adjacent unvegetated flats were selected (Figure 3.1). 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 (Figure 3.1). 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 and mean high tide water depths of 0.8-1.3 m (see Appendix Table C.1).

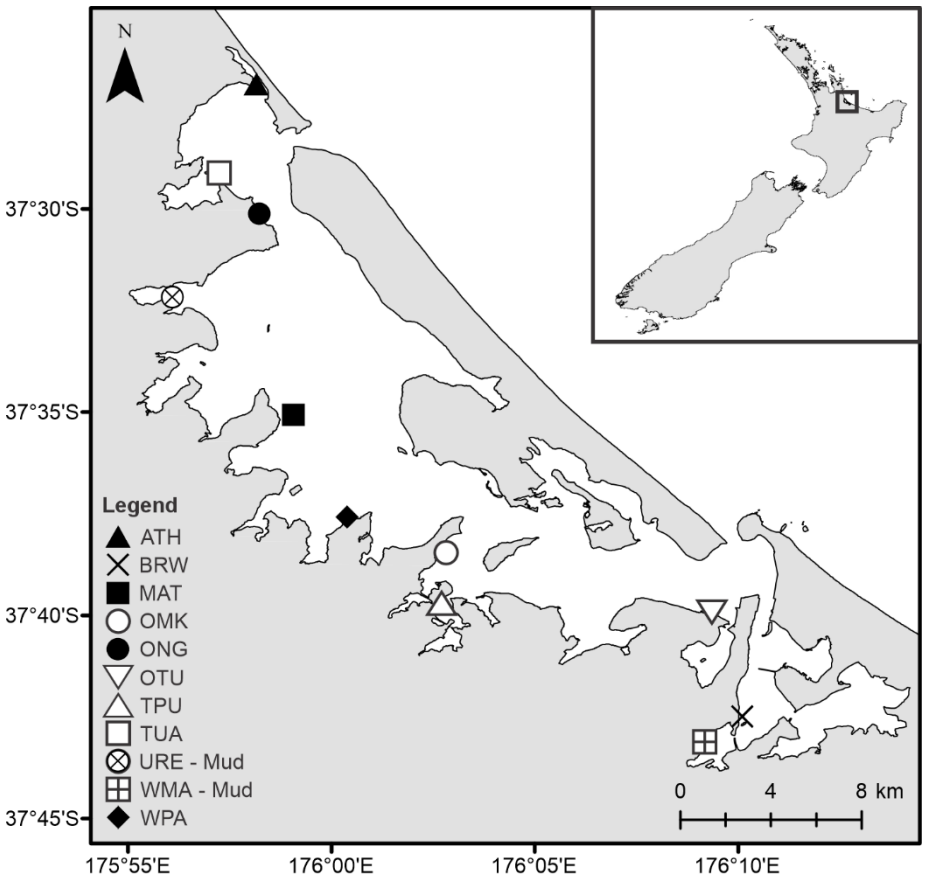


Figure 3.1 Location of Tauranga Harbour, New Zealand (insert), and the 11 intertidal sites. At nine sites, seagrass and adjacent unvegetated habitats were sampled, whereas URE and WMA ('Mud' sites) had no seagrass, so two unvegetated habitat plots (> 25 m apart) were sampled. See Appendix Table C.1 for site-specific GPS coordinates.

3.2.2 Field sampling

Field sampling was undertaken from January to mid-March 2019 (austral summer; see Appendix Table C.1), during mid-day 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; ~37 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 Sea-Bird Electronics 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 (~1.5 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.

3.2.3 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.

3.2.4 Laboratory analysis

For the analysis of sediment properties (median grain size, and mud, organic, water, chlorophyll *a* and phaeopigment 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 3000 (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* (measured as a proxy for microphytobenthos biomass) and phaeopigment 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 & Collins, 1997). Median grain size, and mud, water and organic content were measured from dark chamber samples only (n = 5 per 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 (ammonium (NH_4^+), nitrate (NO_3^-), nitrite (NO_2^-) and phosphate (PO_4^{3-})) of sediment porewater were measured using flow injection analysis (Lachat QuickChem 8000 series FIA+ (Zellweger Analytics Inc.)). As porewater NO_3^- & NO_2^- concentrations were close to detection limits, NO_x concentrations (ug L^{-1}) 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 & 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 from the dark chambers (n = 5 per plot).

3.2.5 Additional environmental data

To understand the spatial drivers of seagrass morphology, I investigated a suite of environmental variables including integrated measures of summer light availability and wind-wave 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 (see Results). 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; see Appendix Table C.1) (Keddy, 1982; Turner *et al.*, 1999):

$$Exposure = \sum_{i=0}^{12} mean\ wind\ velocity\ \times percent\ frequency\ \times fetch \qquad (1)$$

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.

3.2.6 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 & 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 (SCR), 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 SCR 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. Due to the use of benthic chambers, NPP and GPP represent a whole-community measure of primary production. Biomass-standardised GPP was estimated by standardising GPP by per unit of seagrass above-ground biomass or sediment chlorophyll *a* content (Drylie *et al.*, 2018; Pratt *et al.*, 2014a).

3.2.7 Statistical analysis

Principal Coordinate Analysis (PCO) of seagrass traits (leaf count, length, width and surface area, total 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 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 SCR 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). Distance-based Linear Models (DistLM) were used to identify environmental drivers of NPP, GPP and biomass-standardised GPP for the seagrass and unvegetated habitats (which in this analysis included the additional mudflat sites). Environmental predictor variables (light, temperature, porewater nutrients, sediment properties, 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 (Pearson's $r > 0.8$) 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 & 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 normalised data and Euclidean distance-based matrices.

3.3 Results

3.3.1 Environmental variables

Across all study sites, a sediment mud gradient of 5.3-33 % in seagrass (n = 9) and 5.0-49 % in unvegetated flats (n = 13) was achieved (Table 3.1). At most sites (the exception being BRW & TUA), the seagrass habitat was on average 6.3 % higher in mud content than the adjacent unvegetated habitat (n = 7). 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 the seagrass and unvegetated habitats, increasing mud content was correlated with decreasing median grain size ($r = -0.62$ & -0.88, $p < 0.0001$, $n = 45$ & 65, respectively) and increasing organic and water content ($r = 0.68 – 0.90$, $p < 0.0001$, $n = 45$ & 65 for seagrass and unvegetated habitats, respectively; see Appendix Table C.2 & C.3). For the porewater nutrient concentrations, only NH_4^+ in the unvegetated habitat was correlated with increasing mud content ($r = 0.91$, $p < 0.0001$, $n = 13$; see Appendix Table C.4).

At each site, all macrofaunal variables (adult bivalve (*A. stutchburyi* and *M. liliana*) counts, number of species, number of organisms and Shannon diversity index) were generally similar between adjacent seagrass and unvegetated habitats (see Appendix Table C.1 & C.5). The number of species and number of organisms were however higher (by ≥ 1.6 times) in the adjacent unvegetated habitat sites compared to the mudflat sites. In the seagrass habitat, increasing mud content was correlated with decreasing *A. stutchburyi* count and Shannon diversity ($r = -0.38$ & -0.49, $p = 0.01$, $n = 45$ & 27, respectively), and increasing *M. liliana* count ($r = 0.36$, $p = 0.01$, $n = 45$; see Appendix Table C.2 & C.3). Meanwhile, all macrofaunal variables showed negative correlations with increasing mud content in the unvegetated habitats ($r = -0.53 – -0.76$; $p < 0.0001$, $n = 39$-65).

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 3.1). Sampling day and integrated high tide seafloor light availability varied between sites (by 563 and 136 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 ($r = -0.61$ & -0.55, $p = 0.08$ & 0.12, respectively, $n = 9$) and unvegetated habitat ($r = -0.35$ & -0.61, $p = 0.24$ & 0.08, $n = 13$ & 9, respectively; see Appendix Table C.4). During chamber incubations, the water-column attenuated between 58-93 % of ambient light (Site vs. Seafloor PAR). In the seagrass habitat, water-column light attenuation was positively correlated with mud content ($r = 0.69$, $p = 0.04$, $n = 9$), but this relationship was not significant in the unvegetated habitat ($r = 0.51$, $p = 0.07$, $n = 13$; see Appendix Table C.4). In both the seagrass and unvegetated habitats, water-column light attenuation was not significantly correlated with mean high tide water depth ($r = 0.27$ & 0.20, $p = 0.48$ & 0.51, $n = 9$ & 13, respectively).

Table 3.1 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 Figure 3.1. See Appendix Table C.1 for sampling date, water depth, wind-wave exposure and macrofaunal community composition.

			Integrated light		**Sampling day (HT) light**		**Sediment**		**Microphytobenthos**		**Seagrass**		
Symbol	Site	Habitat	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	5.3 ± 0.7	176 ± 4	13.0 ± 1.7	6.2 ± 1.0	65 ± 22	140 ± 23	0.5 ± 0.2
		Unveg.			1678 ± 540	702 ± 208	5.7 ± 1.4	183 ± 8	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 *a* concentration, Phaeo – sediment phaeopigment concentration, AGB – above-ground biomass, BGB – below-ground biomass. *Site data NA – Average median value of other seagrass sites.

3.3.2 Primary producer biomass & seagrass morphology

Sediment chlorophyll *a* (i.e., an estimate of microphytobenthos biomass) and phaeopigments 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 3.1). Both chlorophyll *a* and phaeopigment pigment content increased with mud content in both the seagrass ($r = 0.49$ & 0.75, $p = 0.0006$ & < 0.0001, respectively, $n = 45$) and unvegetated habitats ($r = 0.50$ & 0.71, respectively, $p < 0.0001$ $n = 65$; see Appendix Table C.2 & C.3). Only minor variations in chlorophyll *a* 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 3.1). Seagrass below-ground biomass decreased with increasing mud content ($r = -0.35$, $p = 0.02$, $n = 45$), but above-ground and total biomass were not correlated with mud content ($p = 0.48$ & 0.20, respectively, $n = 45$; see Appendix Table C.2 & C.3). The ratio of above- to below-ground seagrass biomass ranged from 0.4-1.0 (Table 3.1) and increased with mud content ($r = 0.58$, $p < 0.0001$, $n = 45$) as did all metrics of leaf size (width, length and surface area; $r = 0.34$-0.53, $p = 0.0002$-0.02, $n = 45$).

The principal coordinates analysis (PCO) of multivariate seagrass morphology illustrates overlap across multiple sites (Figure 3.2). The first PCO axis explained 46.6 % of the variability in seagrass morphology, with biomass metrics (above-, below-ground and total) and total seagrass cover being the main variables correlated with this axis (Figure 3.2a). 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 ($r = 0.41$; Figure 3.2b). Conversely,

sedimentary variables (mud, organic and phaeopigment content) and exposure were more correlated with the second axis. Notably, mud content was the environmental variable most strongly correlated to the second PCO axis (r = -0.45, n = 45) 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 80.5 % 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.

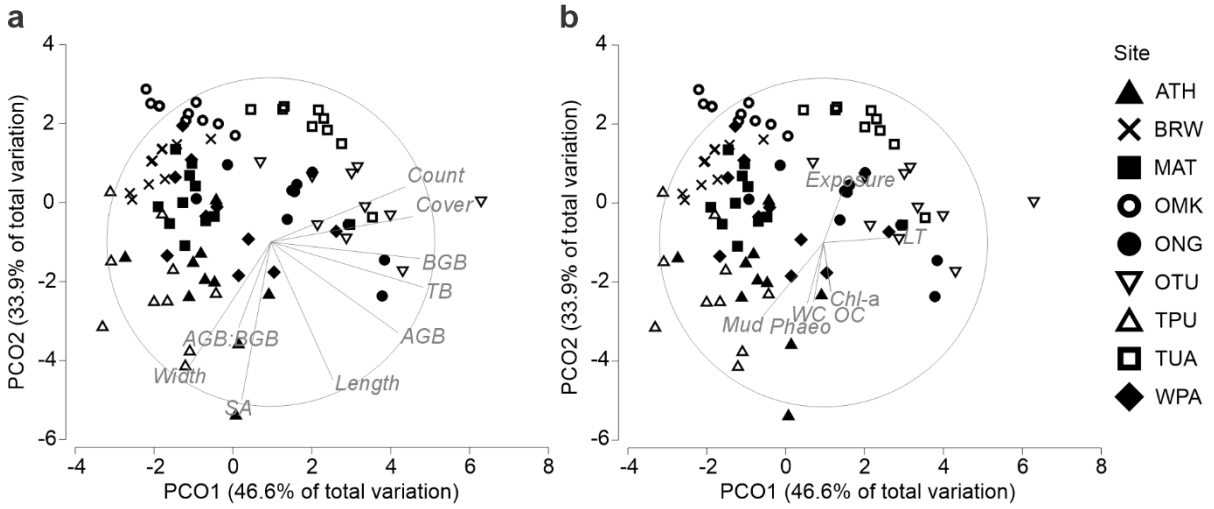


Figure 3.2 Principal coordinate analysis (PCO; Euclidean distance) of multivariate seagrass morphology as a function of site (n = 10 per site). Symbols indicative of site locations presented in Figure 3.1. Vector overlay presents (a) seagrass morphological traits and (b) environmental variables (n = 1-10 per site; only variables with Pearson 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 – total seagrass percentage cover (%), Count – blade count (# $core^{-1}$), Width – blade width (mm), Length – blade length (mm), SA – blade surface area (mm^2), Mud – sediment mud content (% < 63 µm), WC – sediment water content (%), OC – sediment organic content (%), Chl-*a* – sediment chlorophyll *a* content (µg g-1 DW), Phaeo – sediment phaeopigment content (µg g^{-1} DW), LT – median low tide PAR integrated over a five week period (µmol photons m^{-2} s^{-1}), Exposure – mean wind-wave exposure.

3.3.3 Variations in primary production

Net (NPP) and gross primary production (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, n = 45; Figure 3.3a & b; Table 3.2). These variables

also had no significant relationship with mud content (p-perm ≥ 0.59, n = 45). Overall, NPP and GPP was higher in the seagrass compared to the adjacent unvegetated habitat (p-perm = 0.0001, n = 45). Specifically, on average GPP was two times higher in the seagrass compared to the adjacent unvegetated habitat (6,482 vs. 3,209 μmol O_2 m^{-2} h^{-1}, respectively). 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, n = 13; Figure 3.3a & b). On average, during chamber incubations, all seagrass sites exhibited positive NPP (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 negative NPP (i.e., net consumption of O_2 in light chambers; Figure 3.3a).

In the seagrass habitat, site averages of GPP standardised for seagrass above-ground biomass did not significantly vary with mud content (p = 0.34, n = 9; Figure 3.3c). Conversely, in the unvegetated habitat, 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 = -0.83, p = 0.006 & 0.0005, n = 9 & 13, respectively).

Table 3.2 Results of a one-way PERMANCOVA (9999 permutations; Euclidean 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. Significant effects (p < 0.05) are given in bold. See Appendix Table C.6 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	0.07	0.07	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

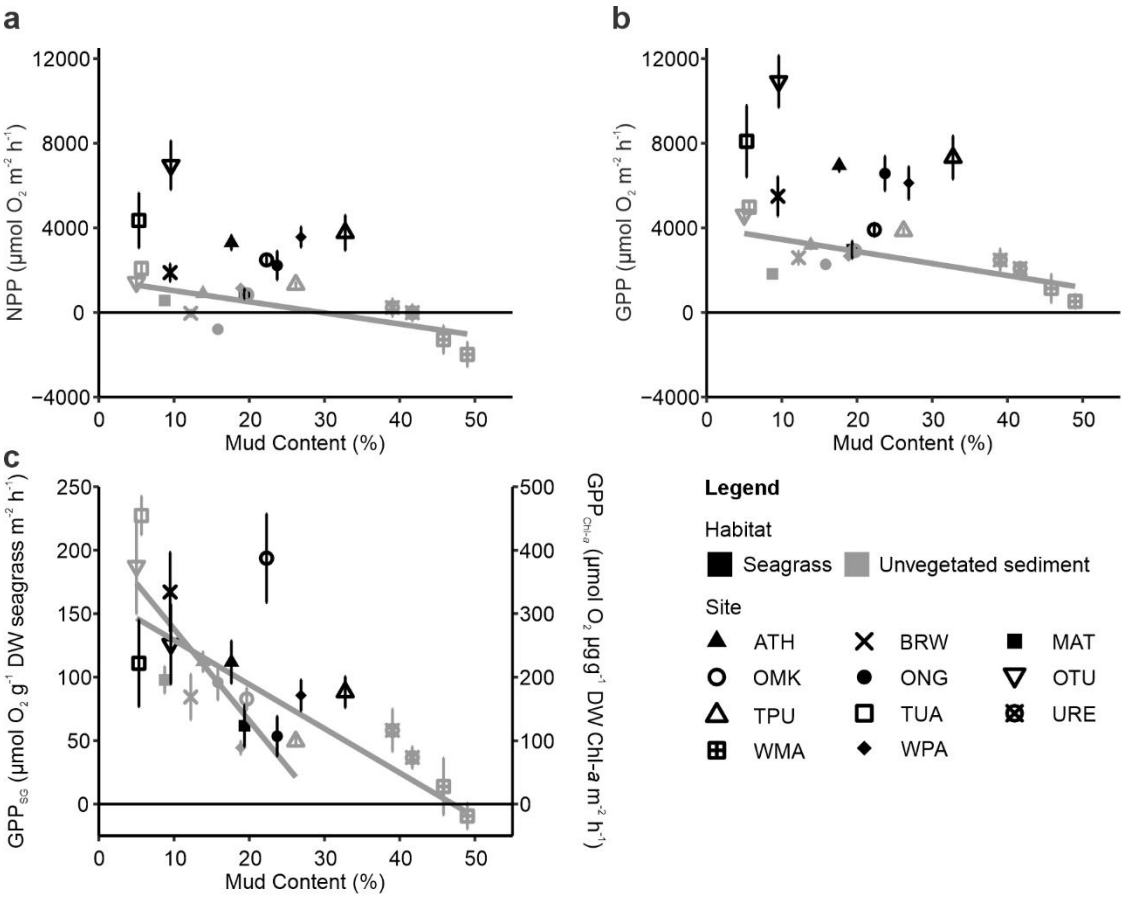


Figure 3.3 Variation in sediment mud content (% < 0.63 µm) and measures of primary production in seagrass (black) and unvegetated sediment (grey) habitats: a) net primary production (NPP); b) gross primary production (GPP); and c) biomass-standardised GPP (GPP_{SG} = seagrass above-ground biomass-standardised 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 Figure 3.1. Trendlines fitted represent significant linear correlations (Pearson's r = -0.70– -0.83, p = 0.007-0.0005). There were no significant relationships in the seagrass habitat nor in the unvegetated habitat when the 'mud' only sites were excluded (p = 0.34-0.65, n = 9), except for chlorophyll *a* biomass-standardised productivity (c). See Appendix Figure C.1 for sediment community respiration.

3.3.4 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 biomass-standardised GPP both in the seagrass (n = 9) and unvegetated habitats (n = 13; see Appendix Table C.7). 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 biomass-standardised GPP in the unvegetated

habitat (explaining 37-61 % of the variance; p = 0.0001, n = 45-65). For the seagrass habitat, the first seagrass morphology PCO axis (Figure 3.2), explained 22 & 30 % (p = 0.001 & 0.0001, n = 45) of the variability in NPP and GPP, respectively. Meanwhile, the first and second seagrass morphology PCO axes each explained 8 & 26 % (p = 0.06 & 0.0006, n = 45), respectively, of the variability in biomass-standardised GPP in the seagrass habitat.

In stepwise models, 54-80 % of the variability in primary production (NPP, GPP and biomass-standardised GPP) in the seagrass and unvegetated habitats was explained by environmental predictors (Table 3.3). 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 the variability in NPP, GPP and biomass-standardised GPP (36-54 %). 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 25 % to the unvegetated habitat). Temperature contributed an additional 12 % to the variability in seagrass GPP. In comparison, seagrass morphology PCO axis 2 (Figure 3.2) explained 21 % of the variability in biomass-standardised GPP in the seagrass habitat with *M. liliana* count contributing a further 18 %.

Table 3.3 Distance-based Linear Model (DistLM) stepwise results for net primary production (NPP), gross primary production (GPP) and biomass-standardised GPP in seagrass (n = 9) and unvegetated (including 'mud' only sites; n = 13) habitats. Variables have been organised into physicochemical, sediment, macrofauna and seagrass. 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 Appendix Table C.7 for full marginal test results.

		Predictor	Seagrass	All unvegetated
NPP	*Physicochemical*	Chamber light		0.11***
		Temperature		0.19*
		PW PO_4^{3-}	0.44***	
	Sediment	Mud	0.03	0.36***
	Macrofauna	Aus. count		0.02***
		H'	0.07	0.03**
		Total	0.54	0.70
		AICc	-26.59	-65.18
GPP	*Physicochemical*	Chamber light	0.42***	0.25***
		Temperature	0.12***	0.02
		PW PO_4^{3-}		0.03***
	Sediment	Mud	0.03	0.36***
		Total	0.57	0.67
		AICc	-30.27	-61.74
Biomass-standardised GPP	*Physicochemical*	Chamber light		0.06***
		Temperature	0.07	0.01
		PW PO_4^{3-}		0.14***
	Sediment	Mud	0.05	0.54***
		Chl *a*		0.04***
	Macrofauna	Aus. count	0.06*	
		Mac. count	0.18***	
	Seagrass	SG Cond1	0.08*	
		SG Cond2	0.21***	
		C:N AGB	0.04	
		Total	0.68	0.80
		AICc	-32.66	-92.07

Biomass-standardised GPP: Seagrass – seagrass above-ground biomass standardised GPP, Unvegetated - chlorophyll *a* biomass standardised GPP. Chamber light - Lux, PW – porewater nutrient concentrations*, Mud – sediment mud content, Aus. – *A. stutchburyi*, count = number per core, H' – Shannon Weiner diversity index*, Chl *a* – sediment chlorophyll *a* content, Mac. – *M. liliana*, SG Cond1 - seagrass morphology PCO1 axis (see Fig. 2), SG Cond2 – seagrass morphology PCO2 axis (see Fig. 2), C:N AGB – carbon to nitrogen content ratio of seagrass above-ground biomass. *Average value per plot used in analyses.

3.4 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; 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, I found that seagrass meadows per unit area were more productive than the adjacent unvegetated habitats (likely owing to a greater photosynthesising biomass); consistent with the findings of previous studies (Bahlmann *et al.*, 2015; Drylie *et al.*, 2018; Gustafsson & Norkko, 2016). However, if seagrass meadow degradation and losses continue to occur (Dunic *et al.*, 2021; Waycott *et al.*, 2009), the shift to unvegetated habitats could 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 net primary production (NPP) remained positive during incubations, five of the unvegetated plots had negative NPP. In order to evaluate net trophic states over a daily period (assuming 12 h of light/darkness and constant submersion), I calculated photosynthesis to respiration ratios in the two habitats (Eyre & Ferguson, 2002). More than half (5/9) of my 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 Appendix Figure C.2). While this calculation overestimates gross primary production (GPP; as it does not account for production during emergence (Chapter 2, Flowers *et al.*, 2023; Drylie *et al.*, 2018; 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 can be released in greater amounts into the overlying water-column (Eyre & Ferguson, 2002). A 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 & 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 (6,609 vs. 1,361 ha, respectively (Shao *et al.*, 2024)). 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., Chapter 2, 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 *et al.*, 2011), and high rates of carbon sequestration (Duarte *et al.*, 2005b; Mcleod *et al.*, 2011).

In the seagrass habitats, NPP, GPP and 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, Figure 3.2) was identified as the main contributor to seagrass biomass-standardised GPP 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 sub-surface 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, reports of *Z. muelleri* distribution (and thereby meadow productivity) are limited to areas ≤ 35 % mud content (Crawshaw, 2020). This is consistent with previous reports of *Zostera* distributions (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 & 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 may 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 Douglas *et al.* (2018) and Pratt *et al.* (2014a) 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 (MPB) have also been shown to adapt to increased mud content by shifting from a predominantly sedentary (episammic) to vertically migrating (epipelic) 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), GPP standardised by sediment chlorophyll *a* content declined with increasing mud content 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 biomass-standardised GPP 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 (Chapter 2, Flowers *et al.*, 2023)). Only the WPA site light availability was below (by > 50 µmol photons m^{-2} s^{-1}) the TUA saturating irradiance in both habitats but the site still had a net production of oxygen in the light chambers (i.e., positive NPP). 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 my 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 MPB 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) increased 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 I am 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, I found an increase in seagrass leaf size (length, width and surface area). 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. Furthermore, for *Z. muelleri* largest leaf areas were found in the muddy (~35 % mud content) site compared to the primarily sand-based sites by Andrews *et al.,* (2023). 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 (Folt *et*

al., 1999). In this study, I was 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. My *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 % appear uninhabited by *Z. muelleri*, and in the unvegetated habitat declines in primary production were driven by sites with ≥ 39 % mud content. Thus, the results of this study indicate that, if anthropogenic stressors continue to drive seagrass decline, the loss of production due to habitat shifts are likely to 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.

Chapter 4: Nutrient cycling variability in seagrass meadows and unvegetated tidal flats

4.1 Introduction

Globally, nutrient loading into estuaries is increasing, particularly due to the intensification of land-based agricultural activities (Galloway *et al.*, 2004; Vitousek *et al.*, 1997). Excess nutrients can cause a shift from benthic to pelagic dominated primary production which can reduce light availability to the seafloor and increase the release of nutrients from the sediment (Duarte, 1995; Pratt *et al.*, 2014b). This can result in a negative feedback loop whereby decomposing algal blooms leads to hypoxic or anoxic conditions that further exacerbate nutrient release from sediments, continuing the eutrophication spiral (Cloern, 2001; Vahtera *et al.*, 2007). Processes that reduce the release of inorganic nutrients into the water-column and promote nutrient removal are therefore crucial for providing resilience against eutrophication.

Shallow coastal soft sediment environments are well recognised for their value in nutrient cycling; contributing to the transformation, supply and removal of bioavailable nitrogen (Costanza *et al.*, 1997). Of particular importance for the removal of excess bioavailable nitrogen, is the anaerobic process of denitrification which transforms nitrate (NO_3^-) into N_2 gas (Nixon *et al.*, 1996; Seitzinger, 1988). Denitrification occurs via two dominant pathways (Seitzinger *et al.*, 2006). Firstly, denitrification can be directly fuelled by the diffusion of NO_3^- across the sediment-water interface. This pathway is generally more common in systems with high water-column NO_3^- concentrations (Bartoli *et al.*, 2008; Dong *et al.*, 2000). Secondly, denitrification is coupled with the aerobic process of nitrification which transforms ammonium (NH_4^+) into NO_3^-. Coupled nitrification-denitrification is the major denitrification pathway in oligotrophic systems where water-column NO_3^- concentrations are low (Gongol & Savage, 2016; Seitzinger *et al.*, 2006). As the coupled nitrification-denitrification process requires both

aerobic and anaerobic conditions, it occurs across the sediment oxic-anoxic interface. While the environmental controls of nutrient cycling in eutrophic systems are well studied (reviewed by Burgin & Hamilton, 2007), these controls may differ in oligotrophic systems (Vieillard *et al.*, 2020). Oligotrophic systems can act as potential 'benchmarks for recovery' of eutrophic estuaries as they can demonstrate the functionality that has been lost as a consequence of high nutrient inputs. Therefore, it is important to understand how nutrient cycling is regulated under 'healthier' conditions so a baseline for the recovery of eutrophic systems can be determined (Vieillard *et al.*, 2020).

In shallow oligotrophic systems where light penetrates to the seafloor, biogeochemical nutrient cycling is tightly coupled with benthic primary production. In temperate estuaries, two key primary producers are seagrasses, which can form extensive meadows, and sediment-dwelling microphytobenthos (benthic microalgae), which dominate unvegetated habitats (MacIntyre *et al.*, 1996). These benthic primary producers assimilate nutrients (e.g., NH_4^+ and phosphate (PO_4^{3-})) for photosynthesis (McGlathery *et al.*, 2004). While these nutrients can be sourced from the water-column, in systems with low water-column nutrient concentrations, nutrients are predominantly sourced from the sediment (Touchette & Burkholder, 2000; Zimmerman *et al.*, 1987). Sediment nutrient cycling therefore plays a crucial role in regulating the availability of nutrients to support benthic primary production (Anderson *et al.*, 2003; Romero *et al.*, 2006).

Benthic primary producers can influence the exchange of nutrients across the sediment-water interface (McGlathery *et al.*, 2004). Sediment nutrient uptake for benthic production, likely reduces the diffusion of inorganic nutrients into the water-column (Eyre & Ferguson, 2002; Sundbäck *et al.*, 2000). Additionally, the subsequent photosynthetic release of oxygen into the surface sediment can stimulate the coupled nitrification-denitrification process (An & Joye, 2001; Caffrey & Kemp, 1990). Accordingly, rates of benthic primary production have previously been reported to be correlated to NH_4^+ effluxes and enhanced denitrification rates

(e.g., Eyre *et al.*, 2011; O'Meara *et al.*, 2020; Rysgaard *et al.*, 1995). Compared to unvegetated sediments, lower NH_4^+ effluxes and higher denitrification rates have also been found in seagrass meadows (Eyre *et al.*, 2011; Eyre *et al.*, 2013; Smyth *et al.*, 2013), which are often found to have higher rates of productivity (Clavier *et al.*, 2014; Drylie *et al.*, 2018; Gustafsson & Norkko, 2016). Consequently, variables that affect primary production, such as light availability (Clavier *et al.*, 2014; MacIntyre *et al.*, 1996), temperature (Lee *et al.*, 2007; Migné *et al.*, 2004) and macrofaunal community composition (Lohrer *et al.*, 2016; Pratt *et al.*, 2014a), will also affect nutrient cycling.

Globally, seagrass habitats are declining at unprecedented rates due to increasing anthropogenic stressors including excess nutrients and eutrophication (Burkholder *et al.*, 2007; Orth *et al.*, 2006; Waycott *et al.*, 2009). As seagrass beds are lost, they are generally replaced by unvegetated habitats. This shift in habitat type is likely to result in changes to the nutrient processing capacity of estuaries. To provide an indication of the generality of nutrient cycling measurements in soft sediment habitats it is important to incorporate measurements over spatial and temporal scales. However, most studies investigating nutrient cycling in estuaries undertake single habitat comparisons and/or involve *ex situ* sampling techniques (e.g., Eyre *et al.*, 2011; Piehler & Smyth, 2011; Smyth *et al.*, 2013). Additionally, the variability of nutrient cycling across temporal scales has been largely overlooked. This is despite a number of factors known to influence nutrient cycling being temporally variable (e.g., temperature (Boynton *et al.*, 2018; Crawshaw *et al.*, 2019), freshwater discharge (Anderson *et al.*, 2014)). Furthermore, measurements across environmental gradients can demonstrate how ecosystem functions might be affected by future environmental change including reductions in seagrass area (Pickett, 1989).

Alongside nutrient loading, anthropogenic land-use changes are elevating the rate of terrestrial sediment inputs into estuaries (Thrush *et al.*, 2004). Because these sediment inputs have a large

proportion of fine particles (< 63 µm), they can cause estuarine habitats to gradually become muddier (Thrush *et al.*, 2004). Although, the deposition of fine sediments within an estuary is often not uniform (e.g., sediment mud contents ranging from < 0.1 to 76 % in Tauranga Harbour, New Zealand (Ellis *et al.*, 2013)). Increased mud content alters the physicochemical properties of the sediment, for example reducing light penetration (Billerbeck *et al.*, 2007) and redox potentials (Glud, 2008). As increased mud content reduces sediment permeability, the advective transport of solutes is reduced and is more dependent on diffusion (Huettel *et al.*, 2014; Huettel *et al.*, 2003). This can influence the exchange of solutes across the sediment-water interface and the availability of nutrients to benthic organisms including nitrifying and denitrifying bacteria (Huettel *et al.*, 2014; Huettel *et al.*, 2003). These changing environmental conditions can subsequently alter other soft sediment habitat characteristics (e.g., macrofaunal community structure and their functional roles (Anderson, 2008; Needham *et al.*, 2011)), influence the remineralisation of organic matter (Blackburn & Blackburn, 1993), and reduce rates of primary production (Billerbeck *et al.*, 2007; Douglas *et al.*, 2018). As a result, nutrient fluxes in soft sediment habitats can vary considerably across sites with differing mud content (e.g., Bartoli *et al.*, 2021; Holmer *et al.*, 2006; Pratt *et al.*, 2014a; Vieillard & Thrush, 2021).

Working across different sites with a range of sedimentary conditions, this study aims to compare rates of nutrient cycling in intertidal seagrass meadows (*Zostera muelleri*) and unvegetated sediments within Tauranga Harbour. Like many other New Zealand estuaries, Tauranga Harbour has low water-column and porewater nutrient concentrations (Douglas *et al.*, 2016; Plew *et al.*, 2020), indicating it is in a relatively oligotrophic state. This research will assess the variability of nutrient cycling in seagrass meadows and unvegetated habitats across both spatial and temporal scales. I hypothesise that primary production will lower the release of nutrients from the sediment as nutrients are taken up by benthic primary producers to fuel photosynthesis. Secondly, owing to higher rates of primary production, I hypothesise that

sediment nutrient release will be reduced and there will be higher rates of nutrient removal via denitrification in the seagrass meadows compared to the unvegetated habitats. Additionally, based on the effects of increased mud content on the transport and availability of solutes, I predicted that increasing mud content will cause a decline in denitrification rates in both habitats.

4.2 Materials and methods

4.2.1 Study site and design

This study was carried out in seagrass meadow (*Z. muelleri*) and unvegetated sediment habitats that dominate the intertidal regions of Tauranga Harbour. *Z. muelleri* is a common seagrass species in temperate estuaries and is the sole species in New Zealand (Short *et al.*, 2007; Turner & Schwarz, 2006). Data collection was undertaken in conjunction with the two previous thesis chapters which investigated spatial (Chapter 3, Flowers *et al., in review*), and temporal (Chapter 2, Flowers *et al.*, 2023) variations in primary production. All sites experienced emersion periods of ~4-6 h and were sampled during generally sunny conditions with mid-day high tides.

For the spatial component of this study, nine intertidal sites (Figure 4.1) with adjacent seagrass meadow and unvegetated sediment habitats were selected. These sites spanned a gradient in sediment mud content (see Results). At each site, a plot area of ~50 m^2 was established in both the seagrass meadow and the unvegetated habitat (> 0.5 m from the seagrass fringe). As reports of seagrass meadows in Tauranga Harbour are limited to areas with ≤ 35 % mud content (Crawshaw, 2020), two additional unvegetated sites were selected to extend the mud gradient for the unvegetated habitat (up to 49 % mud content). Within each of the two high (≥ 35 %) mud sites, two plot areas were chosen (> 25 m apart), that visually appeared to have differences in sediment mud content (referred to as 'mudflats'). Within each plot, in a line running parallel

to the seagrass fringe and/or nearest channel, five pairs of light and dark benthic incubation chambers were deployed (> 1 m apart). Sampling was undertaken during austral summer from January to March 2019 with all habitats/plots sampled on the same day, with the exception of TUA (see below).

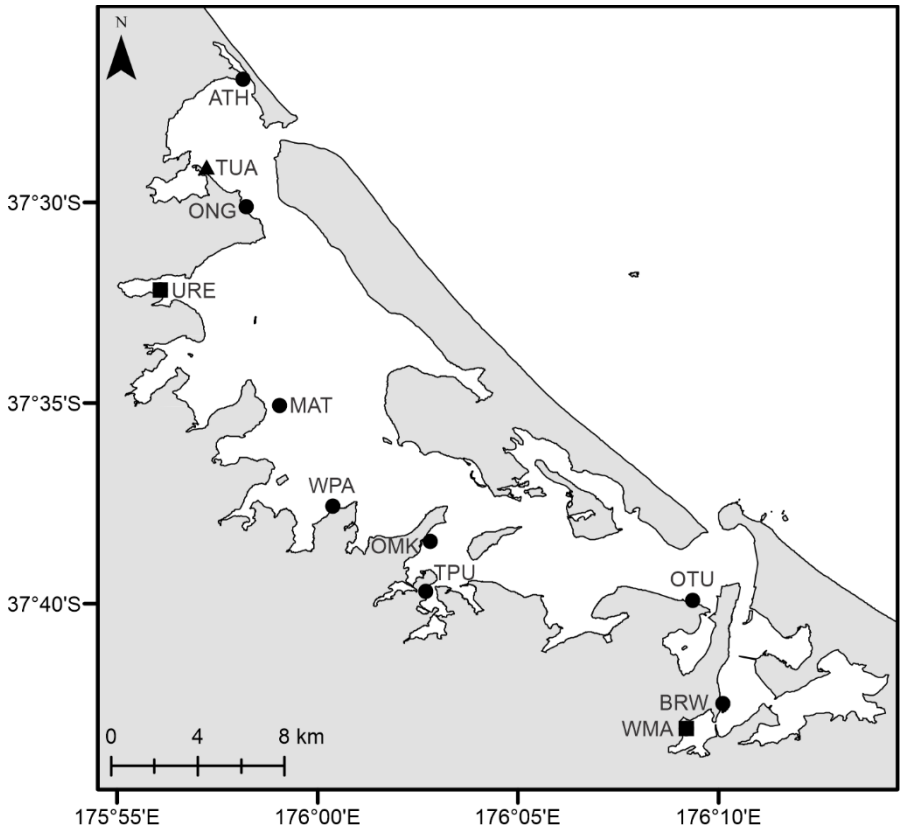


Figure 4.1 Site locations within Tauranga Harbour, New Zealand. Nine sites included adjacent seagrass and unvegetated habitats and were sampled during austral summer 2019 (circles & triangle), with TUA sampled seasonally from spring 2018, to winter 2020 (triangle). URE and WMA (squares) had no seagrass present but included two separated (by > 25 m) 'mudflat' unvegetated plots. See Table D.1 for site-specific GPS coordinates.

Sampling was undertaken seasonally at TUA (Figure 4.1) every three months from austral spring 2018 (October) to winter 2020 (August), with habitats sampled (as described above) over two consecutive days. In austral summer 2019, five light and dark benthic chambers were deployed in each habitat, whereas for the remaining sampling events three light and dark chambers were deployed in each habitat (see Chapter 2, Flowers *et al.*, 2023).

4.2.2 Chamber sampling

During low tide, chamber bases (0.25 m^2) were inserted 5 cm into the sediment. Each base contained a PME miniDOT dissolved oxygen and temperature logger (1 min sampling frequency), HOBO light (Lux) and temperature logger (5 min sampling frequency), and a Sea-Bird Electronics pump (on for 5 s every 45 s). On the incoming tide (~0.3 m water depth), following complete air removal, chambers were clamped closed with a Perspex transparent dome lid (encapsulating 34-37 L). For the dark chambers, shade cloth covered each lid. Samples were collected after chambers were sealed and again after an incubation period of ~4-5 h. A 60 mL sample was collected from each chamber using syringes for dissolved inorganic nutrient measurements. During sampling in austral summer 2019, each dark chamber was also sampled using two air-tight 60 mL syringes for di-nitrogen (N_2) gas concentrations at the start and end of the incubation. Alongside the chambers, three pairs of light and dark bottles (~1.5 L) were also filled with seawater, incubated and sampled to account for any water-column processes. Nutrient samples were filtered immediately on shore (0.45 µm Whatman GF/C glass fibre filter) and frozen at -20 °C. N_2 samples were transferred into airtight exetainers (Labco, UK), spiked with zinc chloride for gas preservation and kept at 4 °C until analysis. Salinity was measured from seawater samples using a YSI-ProSolo ODO/CT.

4.2.3 Site characteristics

Light availability at the seafloor and above the high tide mark was measured during sampling using Odyssey PAR (photosynthetically active radiation) loggers (integrated 5 min samples; referred to as PAR-Seafloor and PAR-Site, respectively) and HOBO loggers (5 min sampling interval; Lux). For the determination of sediment properties, five sediment samples (2.6 cm diameter, 2 cm depth) were collected from around each chamber (within 0.5 m). Samples were combined into a single replicate per chamber, frozen and stored in the dark. For the analysis of porewater dissolved inorganic nutrient concentrations, two replicates consisting of an

additional four sediment cores (2.6 cm diameter, 2 cm depth) were collected from five separate locations (> 2 m apart) within each plot. To assess macrofaunal community composition, a large core (13 cm diameter, 15 cm depth) was collected near each chamber (within 0.5 m), sieved (500 µm mesh) and preserved in 70 % isopropyl alcohol. For the analysis of seagrass biomass, a large core (13 cm diameter, 15 cm depth) was collected from within each chamber and sieved (1 mm mesh). All seagrass material was stored flat in tin foil and frozen.

4.2.4 Laboratory analysis

Sediment samples were thawed, homogenised and divided into three subsamples for the determination of chlorophyll *a* (as a proxy for microphytobenthos biomass) and phaeopigment content (fluorometrically using freeze-dried sediment (Turner 10-AU fluorometer; Arar & Collins, 1997)), mud content (< 63 µm) and median grain size (following digestion of organic matter using 10 % hydrogen peroxide (Malvern Mastersizer 3000; 0.05-2000 µm)), and water and organic content (by weight loss on drying (60 °C), and on ignition (550 °C), respectively (Heiri *et al.*, 2001)).

To extract porewater from the sediment for nutrient analysis, within 24 h of collection, 4 mL of de-ionised water was added to each sample which was then vortexed and centrifuged. Porewater samples were extracted from the sediment, filtered (0.45 µm Whatman GF/C glass fibre filter) and stored at -20 °C. The sediment was subsequently dried (60 °C) to determine porosity. Nutrient concentrations (ammonium (NH_4^+), nitrate (NO_3^-), nitrite (NO_2^-) and phosphate (PO_4^{3-})) from chamber and porewater samples were analysed using flow injection analysis on a Lachat QuickChem 8000 series FIA+ (Zellweger Analytics Inc.). N_2 gas concentrations from chamber incubations were analysed using Membrane Inlet Mass Spectrometry (MIMS; Kana *et al.*, 1994; O'Meara *et al.*, 2020). *In situ* temperature and salinity measurements were used to calculate N_2 concentrations using the N_2:Ar method (Hamme & Emerson, 2004; Kana *et al.*, 1994).

From each macrofauna core, the abundance of adult (≥ 10 mm) *Austrovenus stutchburyi* and *Macomona liliana* were recorded as these large bivalve species are known to influence nitrogen fluxes in soft sediment habitats (e.g., Hillman *et al.*, 2021; Sandwell *et al.*, 2009; Thrush *et al.*, 2006). For sampling in summer 2019, three dark chamber macrofauna cores (first, third and fifth chamber pairs per plot) were stained (Rose of Bengal), sorted and macrofauna were identified to the lowest practicable taxonomic level (usually species). Seagrass above- (leaves) and below-ground (sheath, rhizomes and roots) material were separated and dried (60 °C) before weighing for biomass.

4.2.5 Data analysis

Macrofaunal community composition was assessed through a series of univariate measures; adult *A. stutchburyi* & *M. liliana* abundance, number of species, number of organisms (excluding adult *A. stutchburyi* & *M. liliana*) and Shannon Weiner diversity index (H'; Heip & Engels, 1974). Fluxes of inorganic nutrients and N_2 gas were calculated from the difference between the initial and final chamber measurements which was standardised by chamber volume, sediment surface area and incubation time (μmol m^{-2} h^{-1}). Negative nutrient fluxes are indicative of nutrient influx/sediment uptake, while positive fluxes are indicative of nutrient efflux/export from the sediment. Dark chambers with positive dissolved oxygen fluxes, or those that had light readings (e.g., due to shade cloth lifting), were removed from the analyses due to the likely occurrence of photosynthesis (18 % of samples). Positive N_2 fluxes are indicative of the net loss of N_2 gas from sediments via denitrification and/or anammox pathways (i.e., net denitrification; Burgin & Hamilton, 2007; Seitzinger *et al.*, 2006). While both denitrification and anammox produce N_2 gas, denitrification has been shown to be the major source of N_2 gas in shallow soft sediment habitats (Dalsgaard *et al.*, 2005; Hou *et al.*, 2015). Negative N_2 fluxes were removed from analyses based on the likelihood of oxygen contamination within the chambers or exetainers (< 10 % of remaining samples (Eyre *et al.*,

2002)). Where possible, duplicate uncontaminated measures of N_2 at the start and end of the incubation were averaged for flux calculations (77 % of samples). On average, NH_4^+ comprised 90 % of the total dissolved inorganic nitrogen (DIN) flux. As NO_3^- and nitrite NO_2^- concentrations in chamber samples were below or close to detection limits (0.07 μM), they were not individually statistically analysed. Alongside NH_4^+ and N_2 fluxes, denitrification efficiency (DE) was also calculated (percent of total dissolved inorganic nitrogen released as N_2 (Eyre & Ferguson, 2002)) as an assessment of soft sediment nitrogen cycling.

4.2.6 Statistical analysis

To determine if NH_4^+ and PO_4^{3-} fluxes differed by habitat (2 levels; adjacent seagrass and unvegetated), treatment (2 levels; light and dark) and/or site (9 levels) or season (4 levels), three-way fixed factor PERMANOVA analyses were performed. Two-way fixed factor PERMANOVA analyses were performed to determine if N_2 effluxes and DE significantly varied with habitat (2 levels) and/or site (9 levels) or season (4 levels). As inorganic nutrients in the surface sediment can diffuse into the water-column or be transformed (e.g., via nitrification (Seitzinger *et al.*, 2006)), two-way fixed factor PERMANOVA analyses were performed to determine if porewater NH_4^+ and PO_4^{3-} concentrations varied with habitat (2 levels) and/or site (9 levels) or season (4 levels). To determine if there were any differences in nutrient fluxes (light and dark where applicable), DE or porewater nutrient concentrations between the spatial seagrass-adjacent unvegetated habitats and mudflat plots, one-way PERMANOVA analyses were undertaken. For all two- and three-way PERMANOVAs where significant interactions ($P_{perm} \leq 0.05$) occurred, post-hoc pairwise tests were undertaken to identify the levels that differed within each factor, with main effects (and two-way interactions in the presence of a significant three-way interaction) ignored. Statistical analyses were performed on normalised data using the PERMANOVA+ package on Primer v7 with Euclidean distance-based matrices.

Net primary production (NPP) and sediment community respiration (SCR) measurements calculated in Chapters 2 (Flowers *et al.*, 2023) and 3 (Flowers *et al., in review*) were also used in this study. NPP was measured from the light chambers and therefore represent a whole-community measure of primary production, and SCR was measured from the dark chambers (see Sections 2.2.6 & 3.2.6). The incorporation of this data was important as primary production is fuelled by the uptake of nutrients and surface-sediment oxygenation can influence nutrient cycling (An & Joye, 2001; Caffrey & Kemp, 1990; Eyre & Ferguson, 2002). Additionally, SCR is a measurement of community metabolism and the breakdown of organic matter that regenerates nutrients. Pearson correlations, combining spatial and temporal data (with the exception of N_2 and DE (spatial dataset only)), were undertaken to reveal the relationships between nutrient and oxygen fluxes, and other environmental variables.

4.3 Results

4.3.1 Environmental variables

Across sites sampled during summer 2019, sediment mud content (hereafter 'mud content') ranged from 5.6-33 % in the seagrass and from 5.0-26 % in the adjacent unvegetated sediments, respectively (Table 4.1). Mud content, median grain size (predominantly fine sands), organic and chlorophyll *a* content, and univariate macrofauna community variables were similar between adjacent habitats. An exception to this was the number of macrofauna organisms which was higher (by ~50 individuals per core) in the seagrass, compared to the adjacent unvegetated habitat. Across adjacent habitat sites, seagrass above- and below-ground biomass differed by 64 & 132 g DW m^{-2} respectively, with the ratio of above- to below-ground biomass varying by 0.6. Seafloor light availability varied by 615 µmol photons m^{-2} s^{-1} across sites, with the water-column attenuating (PAR-Site vs. PAR-Seafloor) 58-93 % of ambient light. Between sites, chamber temperature varied by ~5 °C and salinity by ~3.7 psu.

Table 4.1 Overall spatial (adjacent seagrass and unvegetated – n = 9, mudflat - n = 4) and seasonal (TUA; n = 7) averages (with range in parentheses) in light availability, physicochemical water-column properties, sediment characteristics, indicators of primary producer biomass (microphytobenthos & seagrass) and macrofauna community composition in the seagrass, adjacent unvegetated sediment and mudflat habitats. See Table D.1 & D.2 for individual site data and Table D.3 for individual season data.

		Spatial			**Seasonal - TUA**	
		Seagrass	Unvegetated	Mudflat	Seagrass	Unvegetated
Light availability	PAR - Site (µmol m^{-2} s^{-1})	1600 (1191-2089)	1606 (1191-2089)	1916 (1838-1994)	1396 (567-2232)	1345 (262-2202)
	PAR - SF (µmol m^{-2} s^{-1})	444 (139-754)	431 (139-754)	349 (255-443)	540 (244-905)	537 (150-846)
Physicochemical	Chamber temperature (°C)	22.1 (19.2-24.2)	21.9 (19.2-24)	22.9 (22-23.9)	17.8 (14.2-22.7)	17.8 (13.8-23.0)
	Salinity (psu)	33.1 (29.4-34.5)	33.1 (29.4-34.5)	30.8 (30.3-31.2)	34.4 (32.3-36.1)	34.4 (32.2-35.9)
Sediment	Mud content (% < 63 µm)	18.6 (5.6-32.8)	19.2 (5.0-26.2)	43.9 (39.0-49.0)	6.4 (5.4-8.1)	7.5 (5.2-9.9)
	Median grain size (µm)	176 (113-251)	173 (126-248)	78 (65-91)	176 (171-181)	175 (169-182)
	Organic content (%)	3.6 (2.3-5.1)	3.1 (1.7-4.6)	5.3 (4.6-6.2)	2.8 (2.4-3.1)	2.7 (2.3-3.4)
Microphytobenthos	Chlorophyll *a* (µg g^{-1} DW)	18.5 (12.1-32.7)	15.7 (8.0-27.9)	17.2 (16.3-18.2)	14.1 (12.4-15.5)	12.4 (10.4-15.5)
	Phaeopigment (µg g^{-1} DW)	10.8 (6.2-19.6)	8.2 (3.7-13.6)	10.8 (9.7-13.3)	8.0 (6.2-9.1)	7.6 (5.7-9.1)
Seagrass	AGB (g DW m^{-2})	58 (26-90)			46 (34-65)	
	BGB (g DW m^{-2})	109 (60-192)			88 (59-140)	
	AGB:BGB	0.6 (0.4-1.0)			0.6 (0.4-1.1)	
Macrofauna community	*A. stutchburyi* count (# $core^{-1}$)	9 (0-26)	8 (0-24)	0 (0-0)	19 (12-27)	20 (15-24)
	M. liliana count (# $core^{-1}$)	2 (1-4)	3 (2-6)	1 (0-1)	2 (1-2)	3 (2-5)
	Number of species (# $core^{-1}$)	19 (16-23)	15 (11-20)	6 (5-7)		
	Number of organisms (# $core^{-1}$)	207 (94-375)	157 (89-278)	27 (9-57)		

PAR – photosynthetically active radiation, SF – seafloor, AGB – above-ground biomass, BGB – below-ground biomass.

In the additional unvegetated mudflat plots, mud content ranged from 39-49 % (Table 4.1). Compared to the seagrass-adjacent unvegetated habitats, the mudflat plots had lower median grain size (very fine sands) and higher organic content (by up to 2.6 %). Mean chlorophyll *a* content, temperature and salinity were similar across the mudflat and adjacent unvegetated plots. All univariate measures of macrofauna community composition were lower in the mudflat plots, with no adult *A. stutchburyi* found in any of the samples (Table 4.1, see Appendix Table D.1 & D.2). Seafloor light availability at the mudflat plots were in the lower-range of the adjacent unvegetated sites and in the upper-range for water-column light attenuation (~82 %; Table 4.1).

Compared to the other sites, the seasonal sampling at TUA was at the low end of the mud and chlorophyll *a* range, upper-range for *A. stutchburyi* and *M. liliana* counts but were mid-range for median grain size and organic content (Table 4.1). Sediment properties and chlorophyll *a* content showed only minor seasonal variability. TUA seagrass above- and below-ground biomass varied by 31 & 81 g DW m^{-2}, respectively across seasons which was lower than the between site variability (see above). The variability in the ratio of above- to below-ground biomass was similar across sites and seasons (~0.6). Seafloor light availability across seasons had a slightly larger range than across sites (~680 µmol photons m^{-2} s^{-1}). The range of seasonal seafloor light availability extended above the highest light availability measured across sites. Seasonal water-column light attenuation was less variable than across sites (24 vs. 35 %, respectively) and was generally at the low end of the range observed across sites. Across seasons, temperature varied by ~9 °C, with site sampling during summer 2019 at the upper end of this seasonal range. Seasonal variation in salinity was similar to that measured across sites (~3.8 psu). Across both the spatial and seasonal datasets, in both the seagrass and unvegetated habitats (including mudflats), mud content was strongly correlated with other sedimentary variables, notably organic content ($r = 0.74$-0.87, $p < 0.001$; see Appendix Table D.4 & D.5).

4.3.2 Porewater nutrient concentrations

For the spatial dataset, there was a significant interaction between site and habitat on porewater NH_4^+ concentrations (p-perm = 0.01; Figure 4.2a; see Appendix Table D.6). However, only at WPA, porewater NH_4^+ concentrations differed between habitats; ~3.1 times higher in seagrass than the unvegetated habitat (see Appendix Table D.1 & D.6). By contrast, porewater NH_4^+ concentrations were on average 5.9 times higher in the mudflat plots than the adjacent unvegetated sediment (71 vs. 12 μmol NH_4^+ L^{-1}; p-perm = 0.003; Figure 4.2a; see Appendix Table D.7). Across seasons at TUA, there was no habitat effect on porewater NH_4^+ concentrations (p-perm = 0.17; Figure 4.2a; see Appendix Table D.8). However, winter porewater NH_4^+ concentrations were higher than all other seasons (see Appendix Table D.3), resulting in a significant seasonal effect (p-perm = 0.0006; see Appendix Table D.8). Average porewater NH_4^+ concentrations were 1.5 times higher across sites than across seasons in the seagrass habitats (21 vs. 14 μmol NH_4^+ L^{-1}; Figure 4.2a). By contrast, average porewater NH_4^+ concentrations were 1.6 times higher across seasons than across sites in the unvegetated habitats (19 vs. 12 μmol NH_4^+ L^{-1}).

Across sites and seasons, porewater PO_4^{3-} concentrations did not differ between habitats (p-perm = $\geq$ 0.40; Figure 4.2b; see Appendix Table D.6 & D.8) and nor were they different between adjacent unvegetated and mudflat plots (~2 % difference, Figure 4.2b). However, at sites with adjacent habitats, site specific differences in porewater PO_4^{3-} concentrations were observed (p-perm = 0.0001; see Appendix Table D.6). TUA porewater PO_4^{3-} concentrations differed with season (p-perm = 0.006; see Appendix Table D.8) driven by significantly lower porewater PO_4^{3-} concentrations in winter than all other seasons (that did not differ significantly from each other; see Appendix Table D.3 & D.8). Overall, average porewater PO_4^{3-} concentrations were ~2 times higher across seasons than across sites in both the seagrass and

unvegetated habitats (by 2.0 times in the seagrass, and 2.1 times in the unvegetated habitats (Figure 4.2b)).

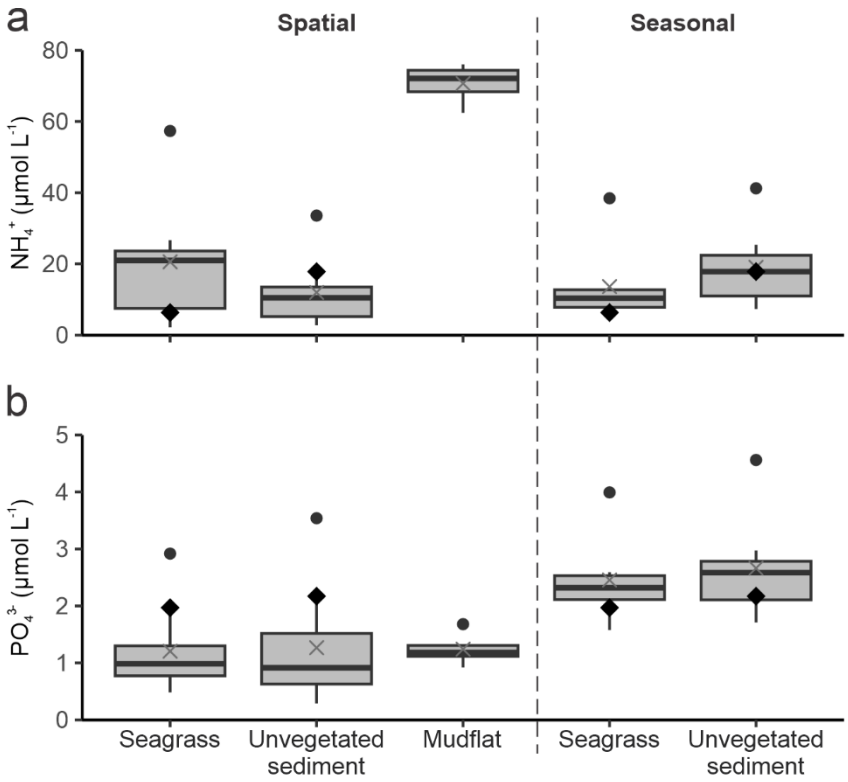


Figure 4.2 Spatial (n = 9 seagrass & unvegetated sediment, n = 4 mudflat) and seasonal (n =7) variability in porewater (a) NH_4^+ and (b) PO_4^{3-} concentrations (µmol L^{-1}) as a function of habitat type. Crosses indicate mean values with black diamonds indicating TUA summer 2019 sampling. Note the difference in Y-axis scale between plots. See Appendix Table D.1 & D.3 for variability of porewater NH_4^+ and PO_4^{3-} concentration at individual sites and seasons, respectively.

Across both the spatial and seasonal datasets, porewater NH_4^+ and PO_4^{3-} concentrations were found to be correlated with sediment mud and organic content in both the seagrass and unvegetated habitats (NH_4^+ r = 0.44-0.85, respectively, $p < 0.001$; PO_4^{3-} fluxes r = -0.17– -0.61, respectively, $p = < 0.05 – < 0.001$; see Appendix Table D.4 & D.5). Additionally, in the seagrass habitat, porewater NH_4^+ and PO_4^{3-} concentrations were correlated with seagrass below-ground biomass (r = 0.25 & 0.19, $p < 0.01$ & < 0.05, respectively; see Appendix Table D.4).

4.3.3 Nutrient cycling

4.3.3.1 DIN fluxes

Across sites and seasons, sediments in both habitats (seagrass and unvegetated sediments) were sources of NH_4^+ during dark incubations, and with the exception of 1-2 sites/seasons, this pattern remained under light conditions (Figure 4.3a, see Appendix Figure D.1 & D.2). Irrespective of habitat, NH_4^+ fluxes across all sites were significantly higher (by 1.9 times on average) during dark conditions compared to light (72 vs. 38 μmol NH_4^+ m^{-2} h^{-1}; p-perm = 0.0001; Figure 4.3a; see Appendix Table D.6). There was a significant interaction between site and habitat on NH_4^+ flux (p-perm = 0.003; see Appendix Table D.6) where effluxes were ~1.7 times higher in the unvegetated sediment than in the seagrass habitat across both light and dark conditions (70 vs. 41 μmol NH_4^+ m^{-2} h^{-1}; Figure 4.3a). However, at sites BRW, MAT and TPU, the difference between habitats was not significant (see Appendix Figure D.1 & Table D.6). During both dark and light conditions, NH_4^+ effluxes between the adjacent unvegetated habitats and the additional mudflat plots did not significantly differ (p-perm = ≥ 0.08; Figure 4.3a; see Appendix Table D.7). In the mudflat habitat, NH_4^+ effluxes were 2.4 times higher in dark compared to light conditions (134 vs. 57 μmol NH_4^+ m^{-2} h^{-1}).

Consistent with the spatial sampling, significant differences between NH_4^+ fluxes during light and dark conditions were observed across seasons at TUA (p-perm = 0.002; Figure 4.3a; see Appendix Table D.8). Specifically, across both habitats, NH_4^+ fluxes were on average 1.7 times higher in dark conditions compared with light (71 vs. 41 μmol NH_4^+ m^{-2} h^{-1}). Irrespective of treatment, a significant habitat effect (p-perm = 0.0005) was also observed, with average NH_4^+ fluxes 2.1 times higher in the unvegetated habitat compared to the seagrass (75 vs. 36 μmol NH_4^+ m^{-2} h^{-1}). There was no significant effect of season on NH_4^+ fluxes (p-perm = 0.34; see Appendix Table D.8). Overall, average NH_4^+ fluxes were similar across sites and seasons in both habitats (~1.0-1.3 times difference; Figure 4.3a).

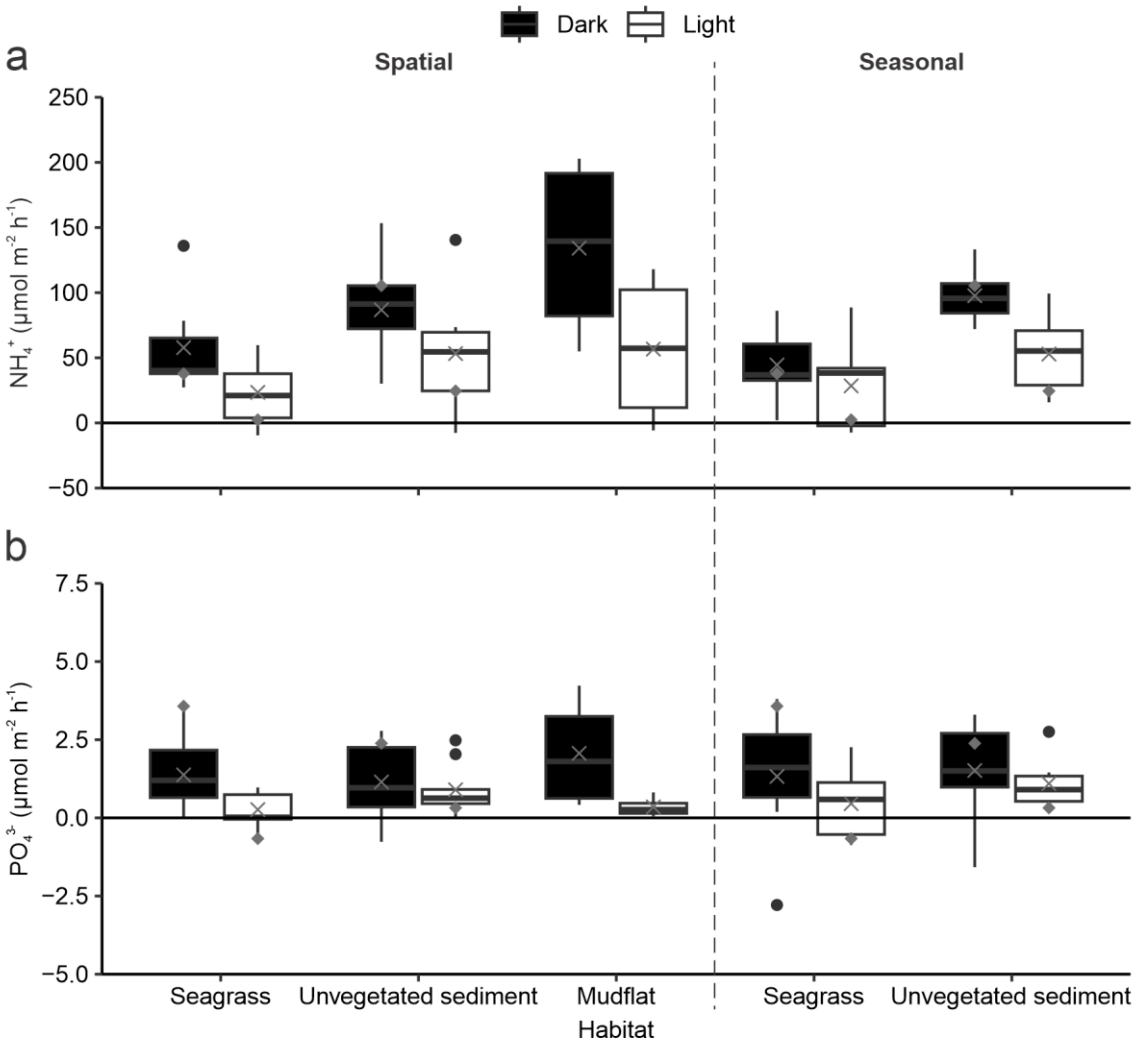


Figure 4.3 Spatial (n = 9 seagrass & unvegetated sediment, n = 4 mudflat) and seasonal (n =7) variability in (a) NH_4^+ and (b) PO_4^{3-} fluxes under dark (black boxes) and light (white boxes) conditions as a function of habitat type. Crosses indicate mean values with grey diamonds indicating TUA summer 2019 sampling. Negative values indicate nutrient uptake, positive values indicate nutrient export. Note the difference in Y-axis scale between NH_4^+ and PO_4^{3-} plots. See Appendix Figure D.1 & D.2 for variability of NH_4^+ and PO_4^{3-} fluxes at individual sites and seasons, respectively.

Across all adjacent habitat sites, there was a significant interaction between treatment and habitat on PO_4^{3-} flux (p-perm = 0.01; see Appendix Table D.6). During light conditions, PO_4^{3-} fluxes were ~3.4 times higher in the unvegetated habitat compared to the seagrass (0.26 vs. 0.90 µmol PO_4^{3-} m^{-2} h^{-1}; Figure 4.3b; see Appendix Table D.6). However, the difference between habitats was not significant during dark conditions. Additionally, unlike the unvegetated habitat, there was a significant difference between treatments in the seagrass

habitat, with PO_4^{3-} fluxes on average 5.2 times higher in dark conditions compared to light (1.4 vs. 0.3 µmol PO_4^{3-} m^{-2} h^{-1}). For PO_4^{3-} fluxes, there was also a significant interaction between treatment and site (p-perm = 0.0002; see Appendix Figure D.6). However, a significant difference between treatments only occurred at two sites (OTU and TUA), with PO_4^{3-} fluxes higher in dark compared to light conditions (see Appendix Figure D.1 & Table D.6). Consistent with NH_4^+ fluxes, adjacent unvegetated habitats and mudflat plots did not show any differences in PO_4^{3-} fluxes in either light or dark conditions (p-perm ≥ 0.12; Figure 4.3b; see Appendix Table D.7).

At TUA, no significant individual or interactive effect of habitat on PO_4^{3-} fluxes was found (p-perm ≥ 0.38; Figure 4.3b, see Appendix Table D.8). There was a significant interaction between treatment and season on PO_4^{3-} flux at TUA (p-perm = 0.05; see Appendix Table D.8). In summer, average PO_4^{3-} fluxes were 2.8 times higher in dark compared to light conditions, but there was no effect of treatment on PO_4^{3-} fluxes in any other season (see Appendix Figure D.2 & Table D.8). During light conditions, PO_4^{3-} fluxes were higher in summer compared to all other seasons (that did not significantly differ). Meanwhile, during dark conditions, there was no effect of season on PO_4^{3-} fluxes. Overall, PO_4^{3-} fluxes were similar between spatial and seasonal datasets in the unvegetated habitats, and during dark conditions in the seagrass (~1.0-1.3 times difference; Figure 4.3b). By contrast, during light conditions in the seagrass habitat, PO_4^{3-} fluxes were on average 1.7 times higher across seasons than across sites.

4.3.3.2 Denitrification

In dark chambers, net denitrification (i.e., N_2 efflux) was evident in all habitats during summer 2019 (Figure 4.4a) and a significant interaction between site and habitat on net denitrification was observed (p-perm = 0.01; Figure 4.4a; see Appendix Table D.6). However, a significant difference between habitats only occurred at two sites, ATH and OTU, with net denitrification 2.9 & 1.9 times higher in the seagrass than the unvegetated habitat, respectively (see Appendix

Figure D.3 & Table D.6). Denitrification efficiency (DE) was significantly different between habitats (p-perm = 0.01; see Appendix Table D.6). On average, DE was 1.3 times higher in the seagrass habitat compared to the unvegetated sediment (61 vs. 47 %; Figure 4.4b). For DE, there was no significant interaction between site and habitat, nor a significant effect of site (p-perm > 0.09; see Appendix Table D.6). Net denitrification and DE in the mudflat plots did not significantly differ to the adjacent unvegetated habitats (p-perm ≥ 0.08; Figure 4.4a & b; see Appendix Table D.7).

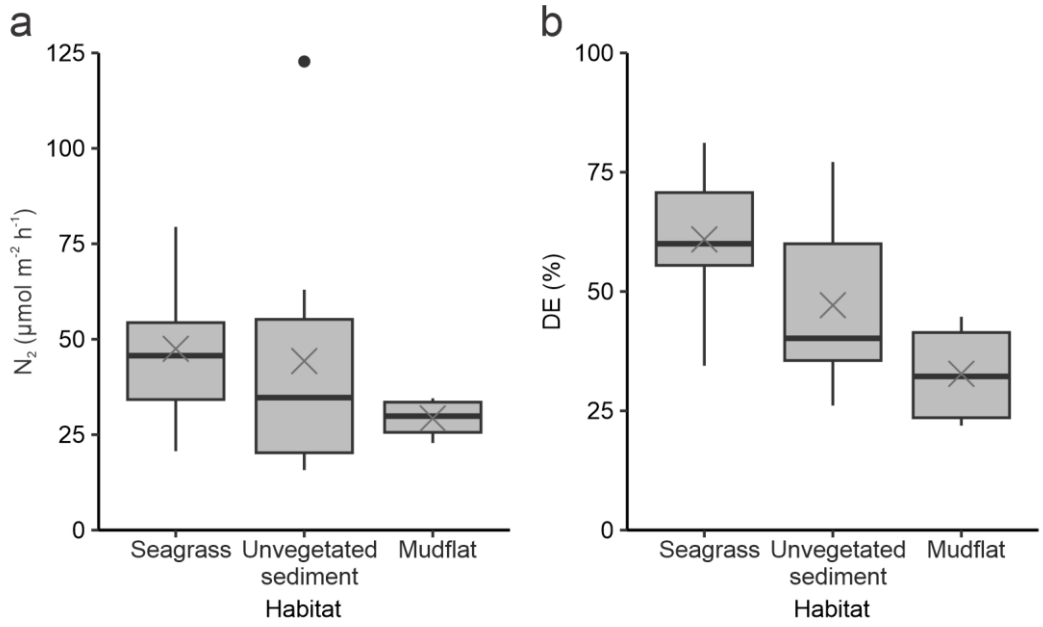


Figure 4.4 Site variability in (a) N_2 effluxes (net denitrification) and (b) denitrification efficiency (DE) in seagrass, adjacent unvegetated sediment and mudflat (n = 9, 9 & 4, respectively). Crosses indicate mean values. See Appendix Figure D.3 for individual site variability in N_2 fluxes and DE.

4.3.4 Correlations between nutrient cycling, primary production and environmental variables

Across both the spatial and seasonal datasets, NH_4^+ fluxes decreased with increasing net primary production (NPP) in the unvegetated habitat (including mudflats) during light conditions ($r = -0.46$, $p < 0.0001$), but this relationship was not significant in the seagrass habitat ($p = 0.82$; Figure 4.5a; see Appendix Table D.4 & D.5). NPP was not correlated with

PO_4^{3-} fluxes in either habitat under light conditions (p = 0.46-0.84; Figure 4.5b; see Appendix Table D.4 & D.5). During dark conditions, sediment community respiration (SCR) was positively correlated with NH_4^+ fluxes in both the seagrass and unvegetated habitats (r = 0.46 & 0.50, p = 0.0006 & < 0.0001, respectively), and with PO_4^{3-} fluxes in the unvegetated habitat (r = 0.26, p = 0.035, respectively; Figure 4.5c & d; see Appendix Table D.4 & D.5). However, in the seagrass habitat, the relationship between SCR and PO_4^{3-} fluxes was not significant (p = 0.12). Across sites, net denitrification was also positively correlated with increasing SCR in seagrass habitats (r = 0.42, p = 0.015, Figure 4.5e; see Appendix Table D.4). However, there was no significant relationship between net denitrification and SCR in the unvegetated habitat (p = 0.13; Figure 4.5e; see Appendix Table D.5). DE showed no significant correlation with SCR for either habitat (p = 0.24-0.74; see Appendix Table D.4 & D.5).

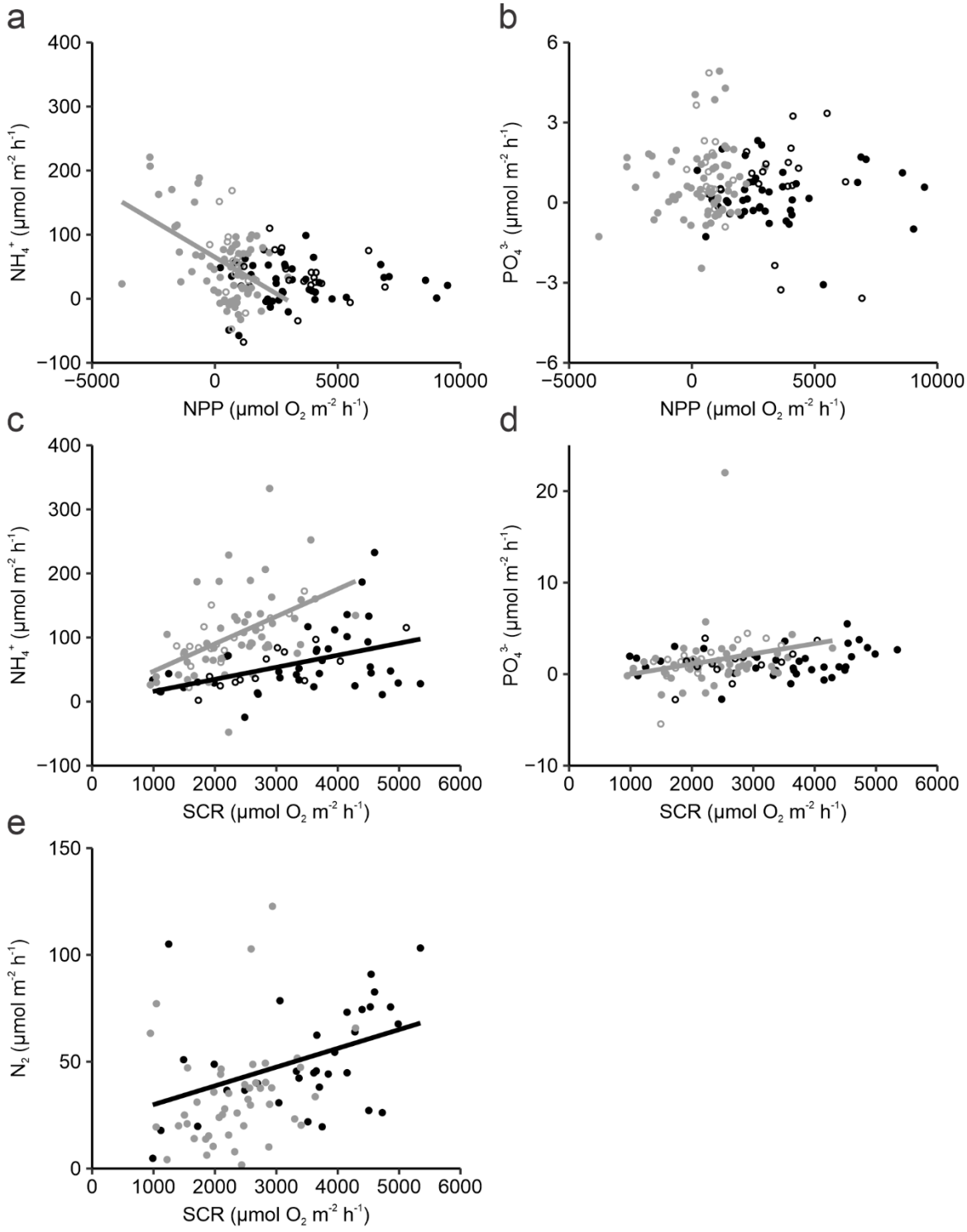


Figure 4.5 Variation in NH_4^+ (a & c), PO_4^{3-} (b & d) and N_2 fluxes (net denitrification; e) and oxygen fluxes (net primary production (NPP) & sediment community respiration (SCR)) during light (NPP; a & b) and dark (SCR; c, d & e) conditions in the seagrass (black) and unvegetated (mudflat plots included; grey) habitats. NH_4^+ (a & c) and PO_4^{3-} (b & d) flux plots incorporate data from summer 2019 spatial sampling (closed circles) and from seasonal TUA sampling (open circles). Trendlines fitted represent significant linear correlations (Pearson's r = -0.26-0.50, p = 0.035-0.00001; black = seagrass; grey = unvegetated habitat). See Appendix Table D.4 & D.5 for Pearson correlations and p-values, and correlation between denitrification efficiency and SCR.

Across the combined spatial and seasonal datasets, few environmental variables were significantly correlated to NH_4^+ and PO_4^{3-} fluxes in both the seagrass and unvegetated (including mudflat) habitats regardless of treatment (see Appendix Table D.4 & D.5). Where significant correlations did occur, these were generally weak (r = -0.30-0.44). In both habitats, porewater NH_4^+ concentrations were positively correlated to NH_4^+ fluxes. However, this correlation was not consistent across both light and dark conditions; seagrass – only in light conditions ($r = 0.25$, $p < 0.05$); unvegetated – only in dark conditions ($r = 0.26$, $p < 0.05$). Additionally, in the unvegetated habitat, NH_4^+ fluxes during dark conditions were negatively correlated with median grain size ($r = -0.30$, $p < 0.05$) and positively correlated with mud content and temperature ($r = 0.25$ & 0.27, respectively, $p < 0.05$; see Appendix Table D.5). During light conditions, light availability was positively correlated with PO_4^{3-} fluxes in the unvegetated habitat ($r = 0.22$, $p < 0.05$), but not significantly correlated with PO_4^{3-} fluxes in the seagrass habitat, nor with the NH_4^+ fluxes in either habitat ($p > 0.05$; see Appendix Table D.4 & D.5). In the unvegetated habitat, PO_4^{3-} fluxes during light conditions was most strongly correlated to salinity ($r = 0.28$, $p < 0.05$; see Appendix Table D.5). In the seagrass habitat, NH_4^+ fluxes during dark conditions, and PO_4^{3-} fluxes during both dark and light conditions, were not significantly correlated with any of the measured environmental variables (see Appendix Table D.4).

Across the spatially resolved data, in both the seagrass and unvegetated habitats, net denitrification was negatively correlated with mud content ($r = -0.42$ & -0.29, respectively, $p < 0.05$; see Appendix Table D.4 & D.5). Net denitrification was most strongly correlated to adult *M. liliana* count in the seagrass habitat ($r = -0.57$; $p < 0.001$), and chlorophyll *a* concentration in the unvegetated habitat ($r = -0.31$; $p < 0.05$). DE was most strongly correlated with porewater PO_4^{3-} concentrations in the seagrass habitat ($r = 0.42$; $p < 0.05$), and mud content in the unvegetated habitat ($r = -0.36$; $p < 0.05$).

4.4 Discussion

Within a large oligotrophic estuary, I examined how nutrient cycling differed across two key estuarine habitats (seagrass and unvegetated flats) incorporating a range of sedimentary conditions (5-33 % mud content). Seasonal patterns, at one of the relatively sandy sites (TUA), was also evaluated. By working in adjacent seagrass and unvegetated plots with similar sediment properties and macrofaunal community structure (see Appendix Table D.1, D.2 & D.3), I was able to directly compare the influence of the benthic primary producer communities on nutrient exchange. The two additional unvegetated mudflat plots also enabled an extension of the sedimentary gradient for the unvegetated site (up to 49 %).

The prominent role photosynthesis has on ammonium (NH_4^+) fluxes was highlighted in my results. Firstly, during light conditions, less NH_4^+ was released from the sediment compared to under dark conditions, indicating an uptake of nutrients for photosynthesis by seagrass and microphytobenthos (MPB). Secondly, compared to the unvegetated habitat, NH_4^+ fluxes were lower in the seagrass habitat which are generally reported to have higher rates of primary production (Clavier *et al.*, 2014; Drylie *et al.*, 2018; Gustafsson & Norkko, 2016). This is likely owing to the greater amounts of benthic photosynthesising biomass in the seagrass habitat (i.e., seagrass, MPB and in some cases also epiphytes (Moncreiff *et al.*, 1992)). Net primary production (NPP) in the seagrass habitat remained positive during all spatial and seasonal sampling, while 24 % of the unvegetated habitat samples had negative NPP. Accordingly, during light conditions NH_4^+ fluxes declined with increasing NPP in the unvegetated habitat. Whereas, due to there being a net production of oxygen in the light chambers in the seagrass habitat, NPP did not affect NH_4^+ fluxes (where fluxes were approximately half that of the adjacent habitat). Alongside high photosynthetic rates, the ability for seagrass to release oxygen from their roots likely contributes to the higher sediment redox potential of seagrass habitats compared to unvegetated sediments (Enríquez *et al.*, 2001; Marbà *et al.*, 2010). This increased

oxygen availability may also have enhanced the transformation of NH_4^+ via nitrification, reducing the overall NH_4^+ pool (Caffrey & Kemp, 1990; Lin *et al.*, 2021b). This was not supported by the porewater NH_4^+ concentrations, which did not differ between adjacent habitats for all but one site (WPA). Although, the methodology I used to measure porewater nutrient concentrations may not have been sensitive enough to detect these changes.

Despite light being considered the main driver of benthic primary production (Lee *et al.*, 2007; MacIntyre *et al.*, 1996), chamber light availability was not correlated with the NH_4^+ fluxes under light conditions in both habitats. Although, during chamber incubations, seafloor light availability was above saturating levels for photosynthesis measured in Tauranga Harbour (see Chapter 2, Flowers *et al.*, 2023) for all but one site (WPA). Nevertheless, the lower efflux of NH_4^+ found in seagrass, unvegetated and mudflat habitats in the presence of light indicates that if light availability is reduced via increased concentrations of suspended sediment (Kirk, 1985; Thrush *et al.*, 2004) and/or water-column algae (Nielsen *et al.*, 2002), photosynthetic rates will be decreased and NH_4^+ effluxes may increase. This effect was demonstrated by Pratt *et al.* (2014b) who saw that declines in NPP and increases in NH_4^+ efflux occurred in association with increased suspended sediment concentrations on an unvegetated sandflat. In oligotrophic estuaries, this reduction in seafloor light availability could result in a feedback loop, whereby reduced light availability increases the export of nutrients from sediments, therefore reducing sediment nutrient availability. This may in turn, further restrict benthic primary production and fuel more frequent phytoplankton blooms causing further reductions in seafloor light availability (Duarte, 1995; Vahtera *et al.*, 2007). This ultimately reinforces the negative eutrophication feedback spiral causing oligotrophic estuaries to shift to a more degraded state (Duarte, 1995; Vahtera *et al.*, 2007).

Even in the absence of photosynthesis (i.e., dark conditions) NH_4^+ effluxes were lower in the seagrass compared to the unvegetated habitat. As suggested by Bulmer *et al.* (2018),

particularly in low nutrient systems, the higher rates of productivity in seagrass habitats could deplete the nutrients available to be released into the water-column, resulting in lower NH_4^+ effluxes during dark conditions. Furthermore, during relatively short periods of darkness (i.e., < 8 h), *Zostera* species have also been shown to uptake nutrients by catabolizing starch reserves (Alexandre *et al.*, 2016; Touchette & Burkholder, 2000). This could contribute to the reduced efflux of NH_4^+ seen in the seagrass habitat during the ~4-5 h dark incubation. Overall, as porewater NH_4^+ concentrations were similar in both habitats, seagrass habitats appear to play a more prominent role in reducing the release of NH_4^+ into the water-column.

Measurements of net denitrification (di-nitrogen (N_2) effluxes) were similar in the adjacent seagrass and unvegetated habitats with the exception of two sites (ATH & OTU). Comparisons of denitrification in seagrass and unvegetated habitats have shown mixed results with some studies showing similar rates across habitats (e.g., Russell *et al.*, 2016), whilst others with higher rates in seagrass (e.g., Eyre *et al.*, 2011; Smyth *et al.*, 2013), and in unvegetated sediments (e.g., Ottosen *et al.*, 1999; Risgaard-Petersen *et al.*, 1998). In the seagrass habitat, net denitrification increased with increasing sediment community respiration (SCR). Although this trend was not evident in the unvegetated habitats, positive correlations between net denitrification and SCR in unvegetated habitats have previously been observed (e.g., O'Meara *et al.*, 2020; Piehler & Smyth, 2011; Zimmerman & Benner, 1994). As nitrifying bacteria consume oxygen to convert NH_4^+ to nitrate (NO_3^-), this relationship could be an indication of nitrification. Although not investigated in this study, SCR can also be driven by organic matter remineralisation and benthic community respiration (Glud, 2008; Sandwell *et al.*, 2009). Bioturbating and burrowing activities by benthic macrofauna can increase the area of the oxic-anoxic interface, and thereby the area available for coupled nitrification-denitrification processes to be undertaken (Aller, 1988; Woodin *et al.,* 2016). These activities as well as bioirrigation by benthic macrofauna (e.g., hydraulic pumping by *M. liliana*) can influence the

transport of nutrients and oxygen within the sediment that can be used to fuel nitrification and denitrification (Eyre & Ferguson, 2009; Woodin *et al.*, 2010). SCR was also positively correlated with NH_4^+ fluxes in both habitats, and PO_4^{3-} fluxes in the unvegetated habitat, during dark conditions. The remineralisation of organic matter, which releases NH_4^+ and PO_4^{3-} as biproducts, and/or the excretory release of NH_4^+ by benthic organisms (Magni *et al.*, 2000), may enhance the coupled nitrification-denitrification processes by augmenting the availability of NH_4^+ for nitrifying bacteria. Although, the influence of organic matter on denitrification has been shown to be dependent on the organic matter source and quality (Eyre *et al.*, 2013). As porewater NH_4^+ concentrations did not differ between the adjacent seagrass and unvegetated habitats, this may have contributed to the similar net denitrification rates measured across habitats.

Mud content negatively impacted net denitrification rates in both the seagrass and unvegetated habitats (with mudflat plots included). In the unvegetated habitat, dark NH_4^+ fluxes also increased in sediments with higher mud content. As there was no significant difference in NH_4^+ fluxes and net denitrification between the unvegetated habitats and the mudflat plots, this indicates relationships were not solely driven by the high mud measurements. The large surface area of mud particles enables more organic matter to bind (Huettel *et al.*, 2014). As a result, mud and organic content are generally positively correlated, as observed in this study. The release of NH_4^+ with organic matter remineralisation may have contributed to the high porewater concentrations measured in the mudflat plots. While higher rates of denitrification have been found in sediments with greater amounts of organic matter (Crawshaw *et al.*, 2019), increased mud content can limit nitrification-denitrification processes as it reduces sediment permeability and the oxic layer depth (Glud, 2008; Huettel *et al.*, 2014; Huettel *et al.*, 2003). These effects can reduce the area available for nitrifying bacteria (Henriksen & Kemp, 1988) and also restrict the diffusion of solutes in the sediment, leading to an excess of porewater NH_4^+

concentrations which can limit nitrification (Anthonisen *et al.*, 1976). This secondary effect may be indicated by the strong correlations between mud content and porewater NH_4^+ and PO_4^{3-} concentrations in both habitats. While mud content was identified to be related with nutrient cycling in my analyses, with the use of linear correlations the effect of some environmental variables on nutrient cycling may be dampened or missed. For example, linear correlations may be working in opposing directions for different environmental variables, or there may be interactions and feedbacks between environmental variables that are influencing nutrient cycling (e.g., Thrush *et al.*, 2012; Vieillard & Thrush, 2021).

Across my study sites in Tauranga Harbour, water-column NO_3^- concentrations were close to or below detection limits, supporting the estuaries' low-nutrient oligotrophic status (Plew *et al.*, 2020). My measurements of NH_4^+ fluxes and net denitrification were similar to those in other low-nutrient systems (e.g., Eyre & Ferguson, 2002; O'Meara *et al.*, 2020). Additionally, similar average rates of net denitrification have been found in unvegetated sediments of eutrophic estuaries (e.g., 80 (this study) vs. 76-103 μmol N_2-N m^{-2} h^{-1} (Cornwell *et al.*, 2016; Fear *et al.*, 2005)). Although, compared to this study, maximum denitrification rates were ~1.5 times higher in the eutrophic sediments measured by Cornwell *et al.* (2016) (246 vs. 364 μmol N_2-N m^{-2} h^{-1}). Previous studies have demonstrated that the contribution of coupled nitrification-denitrification increased with decreasing water-column NO_3^- concentrations in unvegetated habitats (Bartoli *et al.*, 2008; Deek *et al.*, 2013). Thus, in eutrophic unvegetated sediments, a greater proportion of denitrification is likely to be fuelled directly from high water-column NO_3^- concentrations. Furthermore, average NH_4^+ fluxes during dark conditions measured by Cornwell *et al.* (2016) are 2 times higher than the average NH_4^+ measurement in the unvegetated habitats (including mudflats) in this study (201 vs. 101 μmol NH_4^+ m^{-2} h^{-1}, respectively). Therefore, while denitrification may be contributing to a greater removal of bioavailable nitrogen in eutrophic estuaries, the loss of seagrass and consequential reductions

in benthic primary production means fewer nutrients are being taken up to fuel benthic photosynthesis. This in turn, leads to more nutrients being released from the sediment. Without management to reduce nitrogen loading, this will continue to fuel the eutrophication spiral (Cloern, 2001; Vahtera *et al.*, 2007).

Despite the similarity in net denitrification rates across the soft sediment habitats, the ability for seagrass habitats to reduce the release of NH_4^+ into the water-column led to higher denitrification efficiency (DE; i.e., a greater proportion of the total inorganic nitrogen is released as N_2), compared to the unvegetated habitats. Other studies have positively correlated DE to a system's trophic state (i.e., daily ratio of photosynthesis to respiration; Eyre & Ferguson, 2002; Eyre *et al.*, 2011; Mangan *et al.*, 2022). This is consistent with the positive NPP measured for all samples in the seagrass habitat. In contrast, in the unvegetated habitat, DE declined with increasing mud, owing to a greater NH_4^+ efflux during dark conditions, likely driven by reduced rates of primary production (see Chapter 3, Flowers *et al.*, *in review*). Thus, an increase in the proportion of unvegetated habitats with seagrass decline will reduce denitrification efficiency as more NH_4^+ is released from the sediment, especially in muddier habitats. Regardless of the denitrification rate, the more NH_4^+ and PO_4^{3-} that is released into the water-column, the more nutrients become available to fuel pelagic production. This increases the potential risk of algal blooms that could ultimately cause estuaries to degrade (Cloern, 2001; Cooper & Brush, 1993; Munkes, 2005).

Soft sediment coastal habitats play an important role as nutrient filters (McGlathery *et al.*, 2004). Specifically, this *in situ* study highlights that benthic primary producers are key regulators of nutrient cycling within soft sediment habitats in oligotrophic systems. In seagrass habitats, less inorganic nitrogen is released from the sediment, resulting in a higher denitrification efficiency compared to unvegetated habitats. However, increased mud content can reduce the rates of denitrification in both seagrass and unvegetated habitats. Therefore, if

seagrass meadows continue to decline (Dunic *et al.* 2021; Waycott *et al.*, 2009) and shift to unvegetated habitats, there are likely to be consequences on the ability of sediments to reduce the release of inorganic nutrients and remove them from the system, especially in muddier sediments. Effective management decisions to reduce seagrass decline and the input of sediments and nutrients will therefore be vital to retaining the resilience of oligotrophic estuaries to eutrophication.

Chapter 5: General discussion

The three interlinked research chapters of my thesis involved *in situ* measurements to investigate how benthic primary production and nutrient cycling in seagrass meadows (*Zostera muelleri*) and unvegetated sediment habitats may respond to the effects of elevated terrestrially derived sediment inputs into estuaries. Specifically, this thesis investigated the effects of elevated terrestrial sediment inputs in the short-term while they are held in suspension (Chapter 2) and the long-term consequences of increasing mud content (Chapter 3 & 4). Collectively, these research chapters highlight the value of working across multiple habitats and the importance of incorporating measurements across spatial and temporal scales.

5.1 Summary of major findings and implications

Chapter 2 of this thesis was conducted to assess how rates of benthic primary production in seagrass and unvegetated habitats may be affected by reductions in seafloor light availability resulting from increasing water-column turbidity. To achieve this, I used benthic incubation chambers during submerged and emerged periods to derive *in situ* seasonal photosynthesis-irradiance (P-I) curves in a seagrass meadow and an unvegetated sandflat. The construction of P-I curves for both tidal states that incorporate seasonally derived data is a unique aspect of my research. These P-I curves allow for the identification of saturating irradiances that incorporates the temporal variability shown in my results. My P-I curves showed strong light responses during submergence in both habitats and seagrass during emergence, but in the exposed sandflat there was little relationship between light availability and photosynthesis. I also demonstrated that light-saturated gross primary production (GPP) in both habitats was higher during submerged than emerged periods, and that this difference was most pronounced in the sandflat habitats. Overall, owing to higher rates of light-saturated GPP

during both tidal states, daily rates of GPP were higher in the seagrass habitat compared to the sandflat (Figure 5.1a).

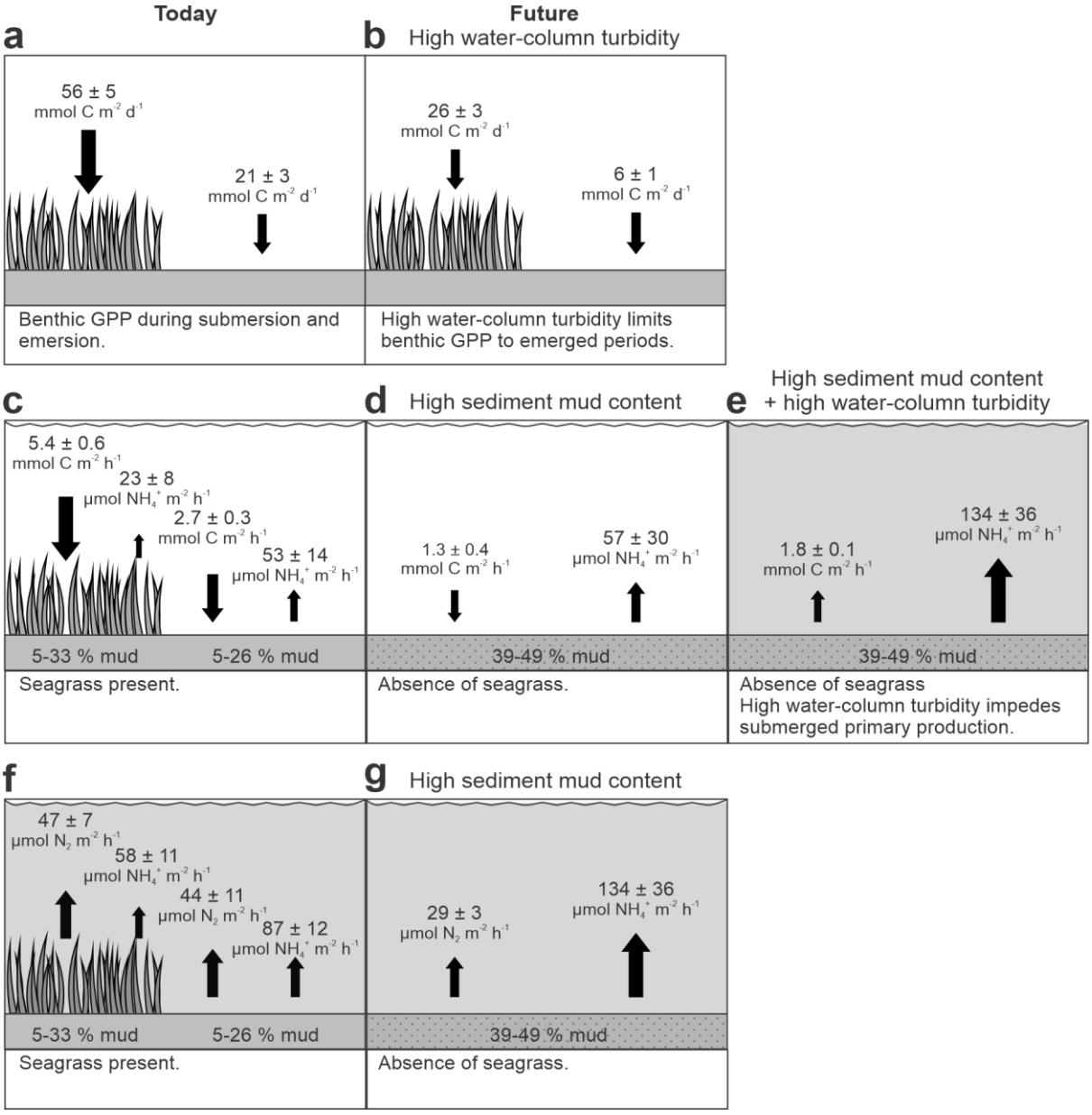


Figure 5.1 Conceptual diagram demonstrating both the current and potential future implications of (a→b) high water-column turbidity (impeding submerged production) on seasonally-averaged daily rates of light-saturated gross primary production (GPP; mmol C m^{-2} d^{-1}; ± 1 SE; see Chapter 2 for calculation), (c→d) high sediment mud content, (d→e) and the combined effects of high sediment mud content and high water-column turbidity on hourly rates of carbon uptake/release (GPP in light conditions (c & d), sediment community respiration in dark conditions (e); mmol C m^{-2} h^{-1}) and effluxes of NH_4^+ (µmol NH_4^+ m^{-2} h^{-1}) during submerged periods, and (f→g) high sediment mud content on hourly rates of denitrification (µmol N_2 m^{-2} h^{-1}) and effluxes of (µmol NH_4^+ m^{-2} h^{-1}) during dark conditions and submerged periods based on data collected throughout this thesis (a & b – Chapter 2; c, d & e – Chapters 3 & 4; f & g – Chapter 4). Values presented in c, d, e, f & g represent averages across sites (adjacent habitats – c & f, mudflat plots – d, e & g) sampled in austral summer 2019 (± 1 SE).

Globally, in areas of high water-column turbidity, benthic primary production can be limited to emerged periods only (e.g., Guarini *et al.*, 2002; Lin *et al.*, 2020; Migné *et al.*, 2004). Based on my results in Chapter 2, assuming rates of emerged productivity remain constant, the limitation of production to emerged periods only, could result in reductions of daily rates of GPP by 2.2 and 3.1 times in the seagrass and unvegetated habitats, respectively (Figure 5.1a → b). Increased water-column turbidity could therefore have severe consequences on the productive capacity for intertidal environments.

Using a natural sedimentary gradient (5-33 % mud content), in Chapter 3 I aimed to investigate how benthic primary production in seagrass and unvegetated habitats may be affected by increased mud content due to long-term elevated inputs of terrestrial sediments. To the best of my knowledge, this is the first *in situ* assessment of seagrass primary production across a gradient in mud content. Consistent with my results in Chapter 2, seagrass net primary production (NPP) and GPP was greater than the adjacent unvegetated habitat (Figure 5.1c). In both adjacent habitats, NPP and GPP did not vary with mud content. However, with the inclusion of additional mudflat sites (39-49 % mud content), which expanded the mud gradient outside the distribution of *Z. muelleri* in Tauranga Harbour, NPP and GPP in the unvegetated habitat declined with increasing mud content. The results of this chapter suggest that if seagrass habitats continue to decline, the loss of primary production resulting from a shift to unvegetated habitats will be magnified in areas with high mud content (≥ 39 %; Figure 5.1c → d). Furthermore, the loss of seagrass habitats will also have consequences for other ecosystem functions they undertake (e.g., habitat provision (Parsons *et al.*, 2013), carbon sequestration (Duarte *et al.*, 2005b; Mcleod *et al.*, 2011), improved water clarity (reviewed by de Boer, 2007)).

Alongside mud content being a strong driver of GPP in the unvegetated habitat, Chapter 3 also revealed a strong relationship between photosynthesis and light availability in both habitats, as

identified in Chapter 2. Consequently, if increased sediment mud inputs and high water-column turbidity co-occur and impede submerged primary production, this will likely cause a shift from carbon uptake to fuel photosynthesis (i.e., GPP), to sediment carbon release, through benthic respiration (Figure 5.1d → e).

In Chapter 4, I assessed temporal and spatial variations in nutrient processing in seagrass and unvegetated habitats. By taking measurements of dissolved inorganic nutrients and di-nitrogen (N_2) gas from the submerged incubations undertaken for Chapters 2 and 3, I was able to demonstrate the tight coupling between benthic primary production and biogeochemical nutrient cycling. Specifically, ammonium (NH_4^+) fluxes were consistently lower during light conditions compared to dark in both habitats (Figure 5.1c & d vs. f & g). Additionally, compared to the unvegetated habitats, NH_4^+ effluxes were lower in the seagrass (Figure 5.1c & f) which, as shown in Chapters 2 & 3, have higher photosynthetic rates. Owing to the lower release of NH_4^+, I demonstrated that denitrification efficiency (DE; i.e., the proportion of total inorganic nitrogen released as N_2 gas) was highest in the seagrass habitat. However, my results showed that increased mud content reduced the ability for both the seagrass and unvegetated habitats to remove excess nitrogen (i.e., net denitrification). Increasing mud also reduced DE in the unvegetated habitat. These results highlight that seagrass loss and increased mud content will likely lead to a more substantive rise in NH_4^+ release from the sediment and a reduction in the removal of excess nitrogen (Figure 5.1f → g). Alongside any suspended sediments, increased phytoplankton concentrations fuelled by increased water-column nutrient availability will further reduce seafloor light availability (Duarte, 1995; Vahtera *et al.*, 2007) which, as highlighted in Chapter 2, will cause further declines in benthic primary production. Ultimately, these findings indicate that the loss of benthic primary production will reduce the resilience of estuaries to eutrophication.

Findings across the three research chapters have important implications for the management of sedimentation which is threatening estuarine habitats globally. In the future, the input of terrestrial sediments is likely to increase with greater intensification of anthropogenic activities and more frequent severe weather events as a result of climate change, highlighting the need for effective management actions (Seneviratne *et al.*, 2012; Thrush *et al.*, 2004). Furthermore, with climate change, sea-level is projected to rise by 1.4 m by 2100 (Rahmstorf, 2007) and will result in an increase in the proportion of time current intertidal areas are submerged. The seasonally integrated P-I curves I constructed in Chapter 2 reveal that the consequences of sea-level rise on daily GPP, and subsequently ecosystem trophic state (i.e., daily ratio of production to respiration), are highly dependent on the clarity of the water. If the water-column remains clear, increasing submergence time could increase daily GPP in both habitats. However, the negative effects of water-column turbidity on submerged GPP will be exacerbated as sea-level rises and cause declines in trophic state. Alongside the decline of submerged GPP, more NH_4^+ is likely to be released into the water-column, especially in muddier sediments (Figure 5.1f vs. g). Consequently, the results of my thesis highlight that if sea-level rise occurs in combination with increased water-column turbidity and mud content, this will increase the vulnerability of estuarine ecosystems to declines in benthic primary production and eutrophication.

5.1.1 Scaling up the loss of seagrass decline

Worldwide, it is estimated that ~7 % of seagrass habitats are being lost each year (Waycott *et al.*, 2009). In New Zealand, declines in seagrass meadows have been reported in numerous estuaries (Inglis, 2003; Matheson *et al.*, 2011; Park, 2016; Turner & Schwarz, 2006). In a few areas in New Zealand, seagrass cover has increased through natural recolonisation and restoration efforts (Lundquist *et al.*, 2018; Matheson *et al.*, 2017; Park, 2016). However, these gains are minimal compared to what has historically been lost.

In Tauranga Harbour, long-term areal assessments of *Z. muelleri* cover have shown its distribution has reduced by 69 % (3,063 ha) from 1959 to 2022 (Park, 2016; Shao *et al.*, 2024). To demonstrate the potential consequences of this seagrass decline, I scaled rates of carbon uptake and sediment NH_4^+ release based on the intertidal area occupied by the seagrass and unvegetated habitats in 1959 and in 2022. To do this, I used the average GPP (photosynthetic quotient of 1.2 used to convert dissolved oxygen fluxes to carbon (Ryther, 1956)) and average NH_4^+ flux rates under light conditions for each habitat across all sites sampled during austral summer 2019 (see Chapter 3 & Chapter 4). This change in intertidal habitat area equated to a 30 % reduction in carbon uptake (318,757 vs. 222,221 mol C h^{-1}) and a 32 % increase in the release of NH_4^+ (2,963 vs. 3,909 mol NH_4^+ h^{-1}). While these estimations incorporate data measured across ≥ 9 sites, it should be recognised that these values do not incorporate the temporal variability in GPP and NH_4^+ fluxes (as demonstrated in Chapter 2 & 4) and therefore should be used cautiously. Additionally, a small proportion of seagrass loss in Tauranga Harbour was from subtidal areas (Park, 2016). Nevertheless, these values highlight the possible magnitude of the consequences of the seagrass decline that has already occurred in Tauranga Harbour and also demonstrate the potential productive and nutrient processing gains that could be achieved through seagrass restoration efforts.

5.2 Future research considerations and concluding remarks

Future research could help to further our understanding of how estuarine degradation may impact the ecosystem functions of soft sediment habitats. This will help pave the way for the development of effective management decisions to reduce the impact humans are having on the services they rely on.

5.2.1 Methodological considerations

Shading experiments provide a direct measure of the relationship between primary production and light availability (as demonstrated in Chapter 2). These measurements thereby allow us to assess the potential effects of increased suspended sediment concentrations. However, suspensoids are also likely to have other effects including reducing feeding rates of suspension feeders (Ellis *et al.*, 2002; Hewitt & Norkko, 2007), which are known to have a strong influence on ecosystem functions including primary production (Sandwell *et al.*, 2009; Thrush *et al.*, 2006; Woodin *et al.*, 2016). A study by Pratt *et al.* (2014b) investigated the effects of increased water-column turbidity on primary production by experimentally increasing suspended sediment concentrations within benthic chambers. A promising avenue of future research would be to undertake a methodological comparison of experimental shading and induced suspended sediment concentrations: the results of which could help to de-couple the potential effects of reduced light availability and the physical effect of suspended sediment on primary production.

The use of membrane inlet mass spectrometry (MIMS) using the N_2:Ar method to measure N_2 fluxes allowed me to determine net denitrification rates in the seagrass and unvegetated habitats during dark conditions (Chapter 4). Due to the high rates of primary production in both habitats, I restricted these measurements to the dark chambers only, to avoid the potential effects that oxygen saturation can have on the accuracy of the measurement of N_2 fixation/denitrification (Eyre *et al.*, 2002). However, the N_2:Ar method has previously been used to determine denitrification during light conditions (e.g., Eyre *et al.*, 2011; O'Meara *et al.*, 2020). If accurate assessments of N_2 fixation/denitrification during light conditions can be undertaken, this could enhance the findings of my Chapter 4 results by demonstrating the potential influence of photosynthesis on denitrification rates. By only measuring net denitrification, I was also unable to determine the potential contributions of direct denitrification (using water-column NO_3^-),

coupled nitrification-denitrification, annamox or N_2 fixation to nitrogen cycling in our soft sediment habitats (Seitzinger *et al.*, 2006). Isotopic tracers have previously been used to assess different nitrogen cycling pathways in seagrass and unvegetated habitats (e.g., Bartoli *et al.*, 2008; Chen *et al.*, 2021; Garcias-Bonet *et al.*, 2018). However, isotopic tracers can underestimate rates of denitrification, particularly in areas where the distribution of NO_3^- within the sediment can be non-homogenous (e.g., due to burrowing macrofauna and coupled nitrification-denitrification processes (Ferguson & Eyre, 2007)). A combined use of the N_2:Ar method and isotopic tracer techniques (as undertaken by An *et al.* (2001)) may improve our understanding of nitrogen cycling and the role of benthic primary producers in soft sediment habitats. Future research should continue to focus on underrepresented systems including oligotrophic estuaries, especially as an understanding of the controls of nutrient cycling in 'healthy' systems will provide important information for restoration of eutrophic systems (Vieillard & Thrush, 2021).

5.2.2 Multiple effects of terrestrial sediment inputs

When elevated levels of terrestrial sediment enter estuaries they can have a multitude of effects on ecosystem function (Thrush *et al.*, 2004). In Chapter 3, I identified a reduction in submerged primary production with increasing mud content in unvegetated habitats. Although, in the study by Lin *et al.* (2021a), higher rates of emerged primary production were found in muddier sediments (0.1-77 % mud content). However, due to high water-column turbidity, primary production was limited to the emerged period only (Lin *et al.*, 2021a). To expand on these findings, in an oligotrophic system like Tauranga Harbour, where seafloor light is not limited, an assessment of benthic primary production during both tidal states across a mud content gradient could be undertaken. This research may indicate whether primary production during emerged periods can compensate for declines experienced during submerged periods in muddier habitats. This would further expand on my findings in Chapter 2 which showed that

at a site with low mud content, light-saturated primary production during emerged periods was lower than during submerged in both the seagrass and unvegetated habitat.

The spatial mud content gradient used in Chapter 3 & 4 was not combined with a gradient in water-column turbidity (as demonstrated by the sites generally having light-availability above saturating levels (Chapter 2)). Within published literature, saturating irradiances in soft sediment habitats are highly variable (reviewed by Lee *et al.*, 2007; Mangan *et al.*, 2020a), demonstrating that they are dependent on site-specific conditions. As such, an interesting avenue of future research could be to investigate how P-I relationships may be related to mud content. A meta-analysis investigating previously reported saturating irradiance values and the environmental variables of the habitats in which they were recorded would be a promising start. However, this can be complicated with the different techniques used to derive *in situ* P-I curves (i.e., benthic chambers (this study) vs. oxygen microprofiles (e.g., Guarini *et al.*, 2002)) and those used to measure sediment grain size (i.e., laser diffraction (this study) vs. dry/wet sieving (e.g., Clavier *et al.*, 2014)). Measuring P-I curves during submergence in sites of differing mud content would also be valuable and enable a more direct comparison of saturating irradiances. If muddier habitats have higher saturation irradiances, this will indicate that increases in mud content are likely to make soft sediment habitats more vulnerable to declines in water-column turbidity.

5.2.3 Adaptability to future change

By deriving *in situ* P-I curves during both tidal states, I was able to illustrate how daily rates of GPP may change in response to reductions in seafloor light availability and altered submergence periods: both of which will be amplified with sea-level rise. However, as sea-level rise is relatively slow (i.e., ~1.3 cm yr^{-1} based on the eustatic estimate by Rahmstorf (2007) for a rise of 1.4 m from 1990 to 2100), benthic primary producers may be able to adapt and/or evolve to the gradual increase in submergence. For example, in response to changing

light availability, seagrass can undergo pigment alterations (Kohlmeier *et al.*, 2014), morphological changes (Ralph *et al.*, 2007) and upregulate primary production during emergence (Drylie *et al.*, 2018). Additionally, microphytobenthos (MPB) can shift community composition to be dominated by vertically-migrating diatoms when sediment light penetration is reduced (Consalvey *et al.*, 2004). To provide further insight into how sea-level rise may influence soft sediment ecosystem functions, future studies could use a space for time approach (Pickett, 1989) and measure submerged and emerged primary production along a tidal gradient. While space for time approaches can provide an indication of potential changes in ecosystem function with changing environmental conditions that may occur over long timescales, differences in environmental properties between locations (e.g., hydrodynamic condition that can influence mud accretion) can drive location-specific differences in ecosystem function. As such, extrapolating results from space for time approaches to predict future change should be taken with caution.

In Chapter 3, I found that despite an increase in chlorophyll *a* concentration (an indicator of MPB biomass) with sediment mud content, there was a decline in biomass-standardised GPP in the unvegetated habitat. While shifts in MPB community composition have been observed with changes in sediment mud content (Consalvey *et al.*, 2004), it is unclear whether changes in MPB community structure, as a response to environmental change, affects ecosystem functioning in soft sediment habitats. In a study by Hope *et al.* (2020a), the effects of nutrient enrichment and turbidity on the quality of MPB as a food source for *Macomona liliana* was investigated using lipid biomarkers. Future research could also expand on this to increase the understanding of changes in MPB quality with increasing mud content and the potential consequences of changes in MPB to coastal foodwebs. The information gained from future research could be highly valuable, as shifts in community structure and/or the quality of MPB could be occurring prior to broader-scale implications on ecosystem functions. If this is the

case, monitoring of MPB community structure and/or quality could be used as a tool for monitoring environmental degradation from elevated terrestrial sediment inputs. Environmental DNA (eDNA) is a promising technique that could be used to assess this and has previously demonstrated changes in the community compositions of eukaryotes, diatoms and bacteria in soft sediment habitats in response to nutrient enrichments (Clark *et al.*, 2020).

As terrestrial sediment deposition in coastal environments will vary across spatial and temporal scales, many areas are likely to differ in fine sediment accumulation rates. In Chapters 3 & 4, biotic environmental variables (e.g., macrofaunal community composition, primary producer biomass) differed across the mud content gradient. Additionally, previous studies have found that sediment depositions of as little as 7.5 mm have been shown to cause seagrass mortality (reviewed by Zabarte-Maeztu *et al.*, 2021a), with depositions of 5 mm shown to impact macrofaunal community structure and cause shifts in ecosystem functioning (Lohrer *et al.*, 2004b; Rodil *et al.*, 2011). To build on my findings from Chapters 3 & 4, future research could investigate if the rate of sediment deposition influences soft sediment ecosystem functioning. This could be determined through the use of a variety of techniques including sediment plates and isotope dating (Woods & Kennedy, 2011). This research would help provide more understanding about whether the effects of increasing mud content on soft sediment habitats are dependent on the rate of fine sediment accumulation. This type of research could also increase our understanding around the potential effects stochastic terrigenous sediment dumps (from severe weather events) may have on soft sediment primary production and nutrient cycling.

5.2.4 Limitations of seagrass distribution

Seagrass distribution is often associated with seafloor light availability (and accordingly water depth), wave exposure and thermal tolerances (Bulmer *et al.*, 2016; Downie *et al.*, 2013; Schubert *et al.*, 2015; Short *et al.*, 2007). However, levels of mud content as a driving factor of

seagrass distribution is less often considered (Koch, 2001). *Z. muelleri* has been found in sediments with up to 72 % mud content (Edgar & Shaw, 1995), but in Tauranga Harbour its distribution appears to be restricted to ≤ 35 % mud content (Crawshaw, 2020). Although, an assessment of the controls of *Z. muelleri* distribution has also not yet been undertaken in New Zealand. Previous studies have demonstrated that sedimentary conditions can reduce the growth and depth limits of seagrass species within the *Zostera* genus (Ferguson *et al.*, 2016; Krause-Jensen *et al.*, 2011; Zabarte-Maeztu *et al.*, 2021b). These results indicate that sediment mud content could be imposing some limitation to the distribution of *Zostera* species. As continued elevated terrestrial sediment inputs are causing more sandy estuarine habitats to become muddier (Jaffe *et al.*, 2007; Thrush *et al.*, 2004), information on whether mud content is limiting seagrass distribution will be vital to reducing seagrass decline. Furthermore, an understanding of the environmental drivers of seagrass distribution and ecosystem functioning, such as that gained from my thesis, could help inform seagrass restoration efforts. For example, the mud content limits of seagrass distribution alongside saturating-irradiances calculated from my photosynthesis-irradiance curves could be used to prioritise locations for seagrass restoration.

5.2.5 Ecosystem interaction networks and tipping points

Using ecosystem interaction networks could further build on the understanding of the environmental drivers of benthic primary production and nutrient cycling in soft sediment habitats identified in my thesis. Interaction networks can demonstrate the presence of potential feedbacks between environmental components that were not fully captured in the statistical analyses I undertook (e.g., Thrush *et al.*, 2021; Vieillard & Thrush, 2021). Furthermore, interaction networks can provide insight into how ecosystem resilience may be eroded through environmental stress imposed by elevated terrestrial sediment inputs (as previously demonstrated in unvegetated habitats by Gammal *et al.* (2022) & Thrush *et al.* (2021)). This

information is important as when an ecosystem's resilience to anthropogenic pressure is reduced, it can make ecosystems more vulnerable to reaching tipping points and undergoing a regime shift (Folke *et al.*, 2004; Walker *et al.*, 2004). In Chapter 3, a significant decline in NPP and GPP in the unvegetated habitats occurred only when the mudflat sites were included in the analysis. This suggests a possible threshold in production capacity at 35 % mud content. Once tipping points are crossed, it is generally difficult for systems to return back to 'healthy' states with the same degree of ecosystem functionality (Duarte *et al.*, 2009; Munkes, 2005). To ensure precautionary management actions can be undertaken that avoid ecosystems shifting to more degraded states, it is vital that environmental thresholds are identified and the effects of anthropogenic pressure on the resilience of soft sediment habitats is understood.

5.2.6 Effects from multiple stressors

With the intensity of climate change and land-use changes increasing globally, estuarine soft sediment habitats are more likely to be impacted simultaneously by multiple anthropogenic stressors (Halpern *et al.*, 2019; Halpern *et al.*, 2008; Hewitt *et al.*, 2016). While my thesis primarily focused on the effects of elevated terrestrial sediment inputs, future research should investigate the potential cumulative effects of multiple stressors on soft sediment ecosystem function. Research on multiple stressors is important due to the way in which stressors can interact and create 'surprising' responses in soft-sediment systems (Folt *et al.*, 1999). For example, the interaction between two or more stressors can result in an additive (combined effect is the sum of the individual effect of the stressors), antagonistic (combined effect is less than the sum of the individual effects), or synergistic (combined effect is greater than the sum of the individual effects) responses (Folt *et al.*, 1999). Some research investigating how the effects of terrestrial sediment inputs on ecosystem function can vary when combined with other stressors has been undertaken in unvegetated habitats, but this has mainly focused on the combined effects with nutrient enrichment (e.g., Douglas *et al.*, 2018; Gammal *et al.*, 2022;

Mangan *et al.*, 2020b). Moreover, research on the effects of multiple stressors on seagrass meadows are often focused on biomass, growth and survival responses (reviewed by Stockbridge *et al.*, 2020), with limited research investigating effects on ecosystem functioning (e.g., York *et al.*, 2013).

5.2.7 Scaling-up ecosystem functioning

Scaling-up field studies into models of ecosystem functions over large spatial scales is a valuable tool for the development of management strategies to combat future anthropogenic pressure (Thrush & Lohrer, 2012). The construction of reliable system-scale models of ecosystem functions is dependent on data collected over different temporal and spatial scales. The extensive spatial and temporal data I have collected within Tauranga Harbour, a large, temperate, oligotrophic estuary, throughout my three research chapters is highly valuable for model parameterisation. The P-I curves collected in Chapter 2 were recently combined with satellite estimates of intertidal seagrass percent cover and unvegetated tidal flat distributions (determined using remote sensing and machine learning), and diffuse attenuation coefficients for PAR (photosynthetically-active radiation), to provide estuary-wide estimates of benthic primary production in seagrass meadows and unvegetated habitats (Shao *et al.*, 2024). The utility of my data for ecosystem-scale models could additionally be used to identify hotspots of ecosystem functions. However, as my study was confined to one harbour, the relevance of my results to other estuaries may be limited. Integrating my data with that collected from different estuaries around New Zealand could further enhance the generality of my findings and strengthen our knowledge on the environmental variables controlling ecosystem function. Additionally, when scaling-up measurements over large spatial scales, other variables that may influence changes in environmental properties or ecosystem function should also be considered. For example, estuarine hydrodynamics can influence rates of sediment accretion and large seagrass meadows have the potential to improve sea-floor light availability by

altering rates of sediment deposition and resuspension (reviewed by Adams *et al.,* 2016; de Boer, 2007). This could also help to identify current knowledge gaps, providing a pathway for future research.

5.2.8 Conclusion

My thesis demonstrates the potential future impacts elevated terrestrial sediment inputs may have on benthic primary production and nutrient cycling in intertidal seagrass meadows and unvegetated habitats. By incorporating environmental variability over temporal and spatial scales, I have provided a significant contribution to the current knowledge of soft sediment ecosystem functioning. The knowledge gained throughout my thesis on the drivers of ecosystem functions in intertidal soft sediment habitats will help support the quantification of ecosystem services which is important for highlighting the benefits that will be lost with future ecosystem degradation and those that could be gained with restoration. I have highlighted that the continuing loss of seagrass habitats could have serious consequences on rates of estuarine benthic primary production and nutrient processing. Additionally, my results have demonstrated that the capacity for soft sediment habitats to undertake primary production and nutrient cycling can be eroded with continued anthropogenic pressure from elevated terrestrial sediment inputs. With the inevitability of climate change, this pressure is likely to intensify as sea-level rises and the input of terrestrial sediments (and other contaminants) are accelerated (Seneviratne *et al.*, 2012). Empirical field-based studies, such as those undertaken for this thesis, will provide vital knowledge of the potential future effects that anthropogenic stressors could have on ecosystem functions. This knowledge will be invaluable for informing future management decisions to reduce inputs of terrestrial contaminants which will help mitigate against further seagrass decline and ensure that the functional capacity of estuaries is maintained.

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Appendices

Appendix A

Table A.1 Summary of gross primary production (GPP; mmol C m^{-2} h^{-1}) in seagrass and unvegetated habitats measured using whole-community sampling techniques found within published literature.

Location	Reference	Tidal State	Method		Seagrass species	**GPP** (mmol C m^{-2} h^{-1}) Seagrass	Unvegetated sediment	
Lake Illawarra, Australia	Qu *et al.* (2005)	Submerged	Core incubations	*Ex situ*	*Ruppia megacarpa*	7.6	0.2-1.4	d, e
Sydney, Australia	Eyre *et al.* (2002)	Submerged	Core incubation	*Ex situ*	*Zostera capricorni*	1.0	0.8	a, e
Moreton Bay, Australia	Eyre *et al.* (2011)	Submerged	Core incubation	*Ex situ*	*Zostera capricorni*	13.0-16.7	2.4-3.0	a, e
Kaomei Wetland, Taiwan	Lee *et al.* (2011)	Emerged	Benthic chamber	*In situ*	*Zostera japonica*	1.0-1.8	0.6-5	d
Tairua Estuary, New Zealand	Drylie *et al.* (2018)	Submerged	Benthic chamber	*In situ*	*Zostera muelleri*	0.4-7.6	0.2-1.9	a, f
		Emerged	Benthic chamber	*In situ*	*Zostera muelleri*	6.1-10.3	1.2-3.4	a, f
Ria Formosa lagoon, Portugal	Bahlmann *et al.* (2015)	Submerged	Dyanamic flux chamber	*In situ*	*Zostera noltii*	36.5	8.4	b, c
		Emerged	Dyanamic flux chamber	*In situ*	*Zostera noltii*	17.5	2.1	b, c
Banc d'Arguin, Africa	Clavier *et al.* (2014)	Submerged	Benthic chamber	*In situ*	*Zostera noltii*	36.0-47.7	7.1-8.1	b, d
		Emerged	Benthic chamber	*In situ*	*Zostera noltii*	4.7-8.0	0.3-1.4	b, d
Arcachon Bay, France	Delgard *et al.* (2016)	Submerged	Core incubation	*Ex situ*	*Zostera noltii*	0.4-7.3	0.0-2.1	a, e
Arcachon Bay, France	Migné *et al.* (2016)	Emerged	Benthic chamber	*In situ*	*Zostera noltii*	3.8-8.4	0.7-4.4	b, d
Bay of Morlaix, France	Ouisse *et al.* (2010)	Emerged	Benthic chamber	*In situ*	*Zostera noltii*	8.2-10	0.5-2.7	

[a]Average values obtained from figure. [b]GPP calculated from net primary production and community respiration. [c]Average value reported in text.
[d]Photosynthetic maximum values obtained from photosynthesis-irradiance curves. [e]Values converted to mmol C m^{-2} h^{-1} from mmol O_2 m^{-2} h^{-1} using a photosynthetic quotient of 1.2 (Ryther, 1956).
[f]Values converted to mmol C m^{-2} h^{-1} from mmol O_2 m^{-2} h^{-1} using the photosynthetic quotient reported by the study.

Table A.2 Summary of average net denitrification rates (i.e., N_2 release via denitrification and/or anammox pathways; µmol N_2-N m^{-2} h^{-1}) in seagrass and unvegetated habitats measured using whole-community sampling techniques found within published literature.

						Denitrification (µmol N_2-N m^{-2} h^{-1})		
Location	**Reference**	**Technique**			**Seagrass species**	**Seagrass**	**Unvegetated sediment**	
Pensacola Bay System, Gulf of Mexico	Fulford *et al.* (2022)	Benthic chamber	*In situ*	N_2:Ar	*Halodule* spp. & *Thalassia* spp.	0-372	0-314	[a]
Wallis Lake, Camden Haven, and Hastings River Estuary	Eyre *et al.* (2013)	Benthic chambers & Core incubations	*In situ* & *Ex situ*	N_2:Ar	*Halophila ovalis*, *Zostera capricorni*, *Posidonia australis*, & *Ruppia megacarpa*	51-445	4-227	
Valli di Comacchio lagoon, Italy	Bartoli *et al.* (2008)	Core incubation	*Ex situ*	Isotope pairing	*Ruppia cirrhosa*	2-24	2-101	[a]
St. Joseph Bay, Florida, USA	Hoffman *et al.* (2019)	Core incubation	*Ex situ*	Isotope pairing	*Thalassia testudinum*	89-213	127-205	[a]
Sydney, Australia	Eyre & Ferguson (2002)	Core incubation	*Ex situ*	N_2:Ar	*Zostera capricorni*	88	138	[a, b]
Moreton Bay, Australia	Eyre *et al.* (2011)	Core incubation	*Ex situ*	N_2:Ar	*Zostera capricorni*	56-84	6-54	[a, b]
South Bay, Virginia	Aoki & McGlathery (2018)	Push-pull deployment	*In situ*	N_2:Ar	*Zostera marina*	20	5	
Limfjorden, Denmark	Ottosen *et al.* (1999)	Core incubation	Ex situ	Isotope pairing	*Zostera marina*	1.4	4.2	[a, c]
Shinnecock Bay, New York, USA	Zarnoch *et al.* (2017)	Core incubation	*Ex situ*	N_2:Ar	*Zostera marina*	0-28	0-65	[a]
Western Port, Australia	Russell *et al.* (2016)	Core incubations	*Ex situ*	Isotope pairing	*Zostera muelleri*	0-22	0-10	[a]
Bogue Sound, North Carolina, USA	Piehler & Smyth (2011)	Core incubation	*Ex situ*	N_2:Ar	NR	29-156	13-92	[a]
Bogue Sound, North Carolina, USA	Smyth *et al.* (2013)	Core incubation	*Ex situ*	N_2:Ar	NR	0-162	0-143	[a]

[a]Average values obtained from figure. [b]Values converted to µmol N_2-N m^{-2} h^{-1} from µmol N_2 m^{-2} h^{-1}. [c]Values reported as coupled nitrification-denitrification measurements. NR = not reported.

Appendix A References

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Appendix B [3]

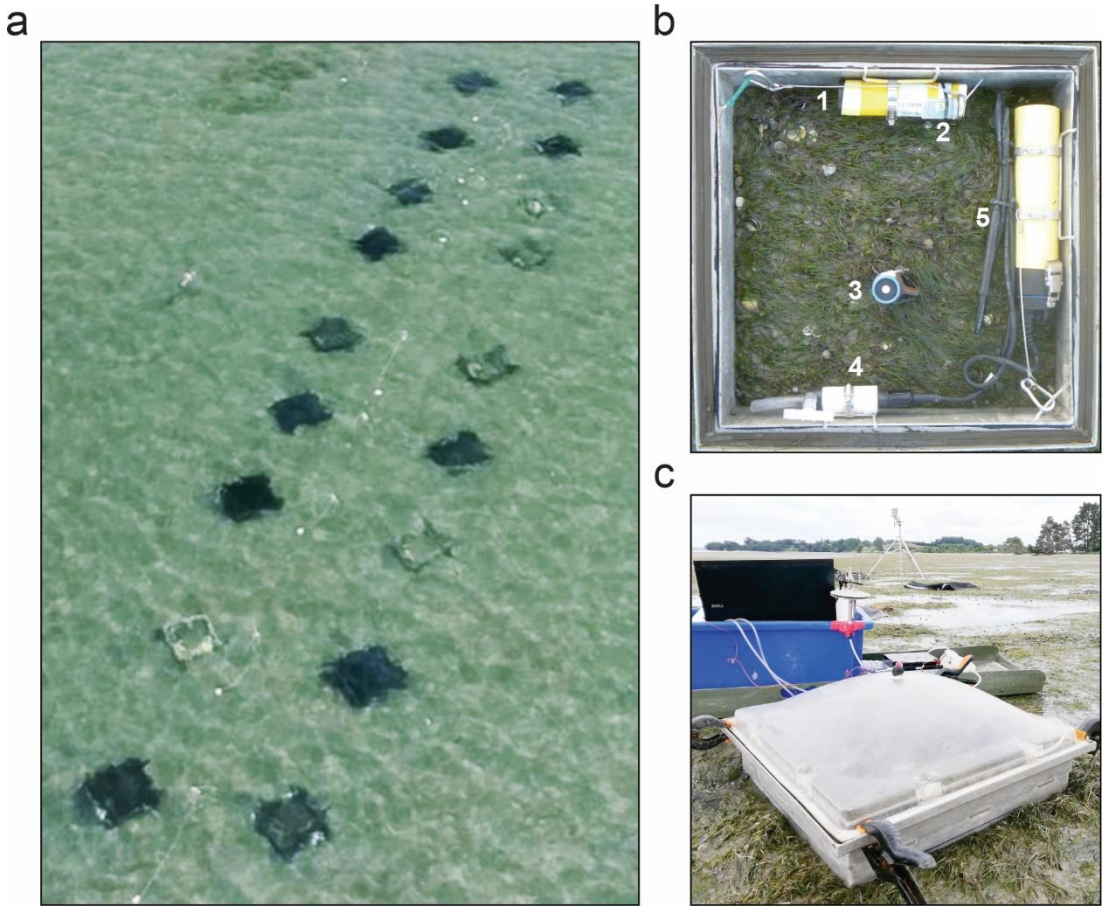


Figure B.1 (a) Submerged benthic incubation chamber deployment with shade treatments in the sandflat habitat (photo credit: Jack Massuger). (b) Benthic chamber base (0.5×0.5 m) and instruments configured for submerged incubations (chamber lid not shown); (1) Dissolved oxygen logger, (2) HOBO light and temperature logger, (3) Odyssey light logger and (4) pump connected to (5) battery pack. (c) A benthic chamber configured for emerged incubations connected to CO_2 analyser (in blue bin).

[3] This chapter has been published in the journal *Limnology and Oceanography* Volume 68: 1301-1315 (2023), under the title "Going under: the implications of sea-level rise and reduced light availability on intertidal primary production" by G.J.L. Flowers, H.R. Needham, R.H Bulmer, A.M. Lohrer and C.A. Pilditch. DOI: 10.1002/lno.12347.

Table B.1 Site sediment and adult bivalve characteristics for seagrass and sandflat habitats for each sampling event (mean ± 1 SD, n = 18-22). Data grouped by austral season.

			Sediment Characteristics				**Adult Bivalves (> 10 mm)**			
	Date	Habitat	Mud content (%)	Median grain size (µm)	Water content (%)	Organic content (%)	Aus. count (# core^{-2})	Mac. count (# core^{-2})	Aus. size (mm)	Mac. size (mm)
Spring	Oct-18	Seagrass	7.8 ± 1.6	173 ± 7	29.3 ± 2.1	3.3 ± 0.7	18 ± 8	2 ± 1	17 ± 1	23 ± 6
		Sandflat	7.6 ± 1.0	175 ± 5	26.5 ± 1.4	2.5 ± 0.2	19 ± 7	2 ± 1	18 ± 1	23 ± 4
	Oct-19	Seagrass	6.3 ± 0.9	176 ± 4	25.0 ± 1.2	2.5 ± 0.2	21 ± 8	3 ± 1	17 ± 1	22 ± 5
		Sandflat	8.8 ± 0.7	172 ± 4	27.2 ± 1.5	2.9 ± 0.2	21 ± 10	3 ± 1	18 ± 1	23 ± 3
Summer	Jan-19	Seagrass	5.9 ± 1.0	176 ± 8	27.3 ± 1.5	2.7 ± 0.3	18 ± 9	2 ± 1	16 ± 1	23 ± 4
		Sandflat	6.0 ± 1.1	181 ± 7	24.9 ± 1.3	2.4 ± 0.2	17 ± 5	3 ± 1	19 ± 1	22 ± 3
	Jan-20	Seagrass	6.7 ± 0.9	178 ± 5	26.1 ± 1.1	2.6 ± 0.2	16 ± 9	1 ± 1	18 ± 1	23 ± 4
		Sandflat	8.3 ± 1.0	175 ± 6	26.9 ± 1.2	2.6 ± 0.2	15 ± 7	2 ± 1	19 ± 1	23 ± 4
Autumn	Apr-19	Seagrass	6.9 ± 0.7	170 ± 5	27.8 ± 1.7	3.0 ± 0.3	19 ± 11	2 ± 1	16 ± 1	22 ± 4
		Sandflat	9.4 ± 1.0	170 ± 6	27.4 ± 0.9	3.1 ± 0.6	21 ± 8	3 ± 1	18 ± 1	23 ± 3
Winter	Jul-19	Seagrass	5.3 ± 0.6	177 ± 5	26.6 ± 1.0	2.4 ± 0.2	30 ± 14	2 ± 1	17 ± 1	22 ± 3
		Sandflat	6.5 ± 0.9	174 ± 5	28.2 ± 1.2	2.9 ± 0.2	20 ± 10	4 ± 2	19 ± 1	21 ± 3
	Jul-20	Seagrass	5.7 ± 0.9	177 ± 7	25.8 ± 1.3	2.8 ± 0.2	20 ± 7	1 ± 1	18 ± 1	24 ± 3
		Sandflat	5.4 ± 0.8	178 ± 5	25.3 ± 1.2	2.5 ± 1.4	19 ± 8	2 ± 1	20 ± 1	23 ± 3

Mud – sediment mud content (% < 63 µm), Aus. – *Austrovenus stutchburyi*, Mac. – *Macomona liliana.*

Table B.2 Community photosynthesis-irradiance (P-I) curve parameters (± 95% CI) for seagrass and sandflat habitats under submerged and emerged conditions for each sampling event. Data grouped by austral season.

		Submerged					**Emerged**				
	Date	*Pmax*	*α*	*Ik*	R^2	*n*	*Pmax*	*α*	*Ik*	R^2	*n*
	Seagrass										
Spring	Oct-18	6589 ± 1766	24.1 ± 9.5	274	0.82	15	4555 ± 292	14.7 ± 3.5	309	0.90	15
	Oct-19	4349 ± 512	32.0 ± 9.4	136	0.90	15	2311 ± 253	17.0 ± 5.4	136	0.87	15
Summer	Jan-19	7236 ± 1933	34.9 ± 21.0	208	0.51	17	7333 ± 549	27.6 ± 6.1	266	0.90	15
	Jan-20	6636 ± 927	24.7 ± 7.3	269	0.90	15	4245 ± 400	15.7 ± 6.4	271	0.73	15
Autumn	Apr-19	5103 ± 1260	40.1 ± 11.6	127	0.92	15	11167 ± 15090	29.1 ± 13.6	384	0.89	15
Winter	Jul-19	5068 ± 1250	58.9 ± 25.7	86	0.83	15	4527 ± 555	18.1 ± 6.0	250	0.85	15
	Jul-20	6346 ± 1842	35.6 ± 15.1	178	0.86	15	3100 ± 703	15.4 ± 9.4	201	0.63	15
	Sandflat										
Spring	Oct-18	2854 ± 290	13.9 ± 3.2	205	0.93	15	919 ± 291	9.9 ± 19.7	93	0.07	13
	Oct-19	2662 ± 440	17.7 ± 7.0	150	0.83	15	1133 ± 73	8.7 ± 3.3	131	0.45	15
Summer	Jan-19	4330 ± 913	27.1 ± 16.5	160	0.52	17	1227 ± 141	9.3 ± 6.1	132	0.26	15
	Jan-20	3666 ± 1423	8.1 ± 3.2	455	0.89	15	1920 ± 222	7.3 ± 3.6	261	0.55	15
Autumn	Apr-19	2798 ± 787	10.4 ± 2.8	270	0.95	15	1097 ± 147	5.0 ± 2.6	220	0.58	15
Winter	Jul-19	2524 ± 1078	17.2 ± 7.4	147	0.89	15	929 ± 152	99.4 ± 161.6	9	0.04	15
	Jul-20	2775 ± 5273	15.7 ± 12.3	177	0.64	14	835 ± 83	4.6 ± 1.6	183	0.78	15

Pmax – photosynthetic maximum (µmol C m^{-2} h^{-1}), *α* – photosynthetic efficiency (alpha; µmol C m^{-2} h^{-1} (µmol photons m^{-2} s^{-1})$^{-1}$), *Ik* – saturation irradiance (PAR, µmol m^{-2} s^{-1}).

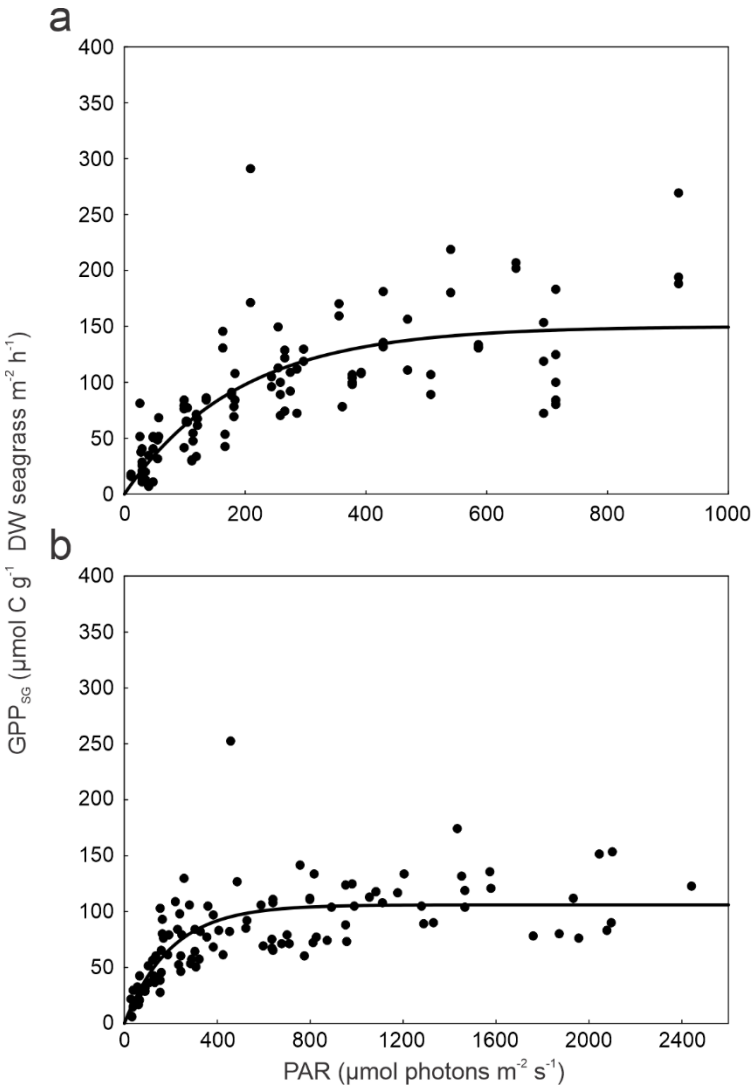


Figure B.2 Seasonally averaged photosynthesis-irradiance (P-I) curves for intertidal seagrass under (a) submerged and (b) emerged conditions (see Table B.3 for parameter estimates). Curves were constructed using gross primary production standardised by seagrass above-ground biomass (GPP_{SG}) from seven seasonal sampling events (austral spring (October) 2018 – winter (July/August) 2020; PAR – photosynthetically active respiration). Note the difference in X-axis scale between submerged and emerged conditions.

Table B.3 Seasonally averaged photosynthesis-irradiance curve parameters (± 95% CI) for seagrass habitats under submerged and emerged conditions using gross primary production standardised for seagrass above-ground biomass.

	Pmax	*α*	*Ik*	R^2	*n*
Submerged	150 ± 20	0.78 ± 0.18	193	0.58	107
Emerged	106 ± 9	0.53 ± 0.13	199	0.51	105

Pmax – photosynthetic maximum (µmol C g^{-1} DW seagrass m^{-2} h^{-1}), *α* – photosynthetic efficiency (µmol C g^{-1} DW seagrass m^{-2} h^{-1} (µmol photons m^{-2} s^{-1})$^{-1}$), *Ik* – saturation irradiance (µmol photons m^{-2} s^{-1}).

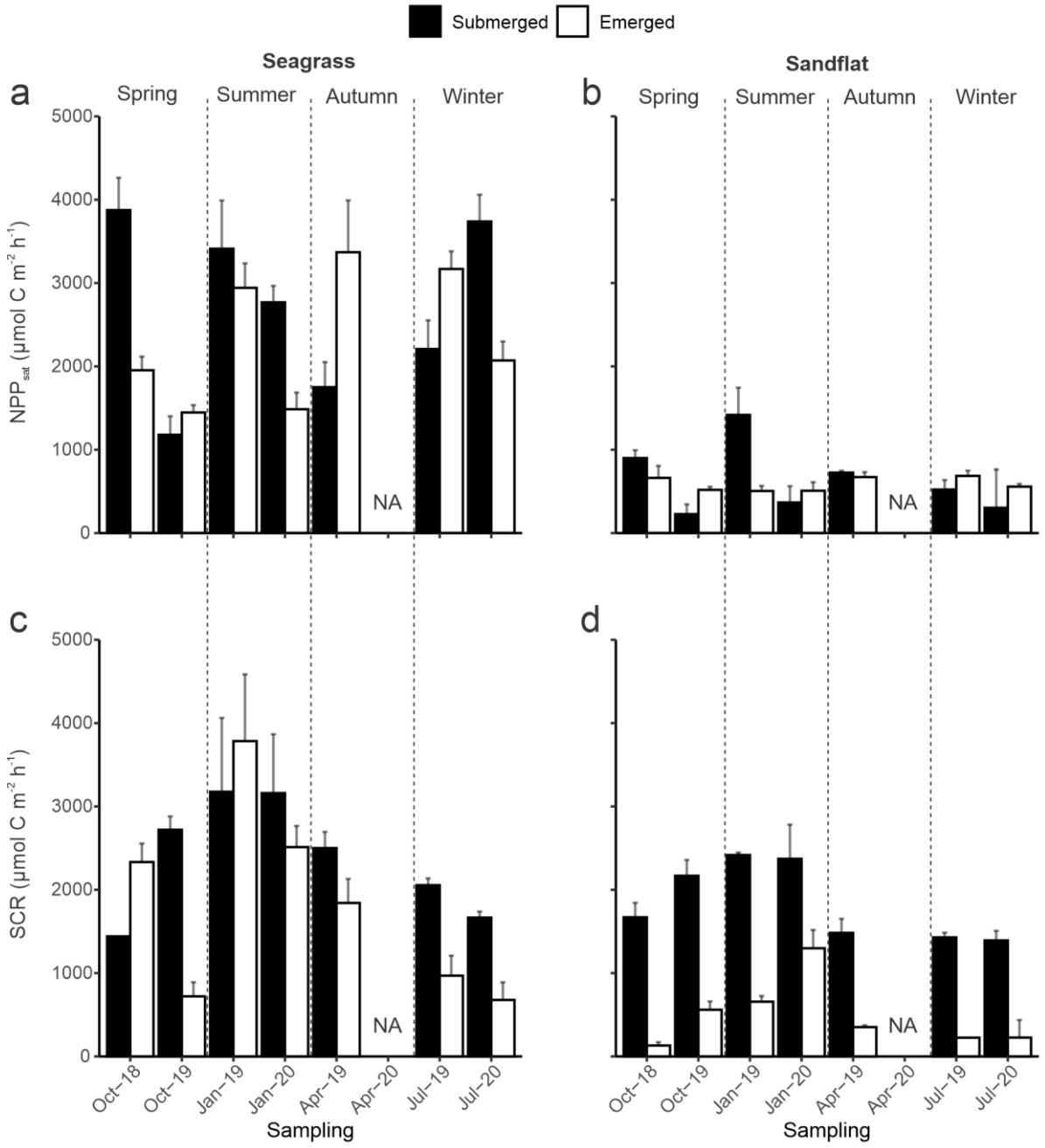


Figure B.3 Seasonal variations in light-saturated net primary production (NPP_{sat} – a & b; n = 3-15) and sediment community respiration (SCR – c & d; n = 1-3) as a function of habitat (a & c – seagrass, b & d – sandflat) during submerged (black bars) and emerged (white bars) conditions. Bars (mean + 1 SE) arranged by austral season (indicated by the dashed line).

Table B.4 Results from a three-way fixed factor PERMANOVA (999 permutations; Euclidean distance-based matrices) comparing light-saturated gross (GPP_{sat}) and net primary production (NPP_{sat}), and sediment community respiration (SCR) between season (4 levels; spring (Sp), summer (Su), autumn (A), winter (W)), habitat (2 levels: seagrass (SG) & sandflat (SND)) and tidal state (2 levels: submerged (SUB) & emerged (EMG)). Models were run with all possible interactions and where significant interactions (p-perm < 0.05) occurred, main effects (and two-way interactions in the presence of a three-way interaction) were ignored (PERMANOVA+, PRIMER v7). Significant effects ($p < 0.05$) are given in bold.

	Term	**df**	**Pseudo-F**	**p-perm**	**Post-hoc pairwise tests**		
					Season	Tidal state	Habitat
GPP_{sat}	Season x Tidal state x Habitat	3	2.86	**0.032**	**SUB; SG,** Su > (Sp = A = W) **SUB; SND,** Su > (Sp = A) > W **EMG; SG,** (Su = A) > (Sp = W) **EMG; SND,** Su > ((A > W) = Sp)	**SG; Sp Su & W,** SUB > EMG **A,** SUB = EMG **SND; Sp Su A & W,** SUB > EMG	**SUB & EMG; Sp Su A &W,** SG > SND
	Tidal state x Habitat	1	6.52	**0.016**			
	Season x Habitat	3	4.91	**0.002**			
	Season x Tidal state	3	3.13	**0.039**			
	Habitat	1	397	**0.001**			
	Tidal state	1	53.4	**0.001**			
	Season	3	35.73	**0.001**			
NPP_{sat}	Season x Tidal state x Habitat	3	2.77	**0.044**	**SUB; SG,** (Su > A) = W = Sp **SUB; SND,** (A > W) = Su = Sp **EMG; SG,** Su = A = W, (A = W) > Sp, Su = Sp **EMG; SND,** Sp = Su = A = W	**SG; Sp & Su,** SUB > EMG **A & W** SUB = EMG **SND; Su** SUB > EMG **W** EMG > SUB **Sp & A,** SUB = EMG	**SUB & EMG; Sp Su A & W,** SG > SND
	Tidal state x Habitat	1	0.01	0.908			
	Season x Habitat	3	1.70	0.164			
	Season x Tidal state	3	4.96	**0.005**			
	Habitat	1	198	**0.001**			
	Tidal state	1	0.52	0.454			
	Season	3	2.45	0.060			

Table B.4 Cont.

	Term	df	Pseudo-F	p-perm	Post-hoc pairwise tests		
					Season	Tidal state	Habitat
SCR	Tidal state x Habitat	1	5.55	**0.016**		**SG & SND,** SUB > EMG	**SUB & EMG,** SG > SND
	Habitat	1	41.7	**0.001**			
	Tidal state	1	43.8	**0.001**			
	Season	3	16.7	**0.001**	Su > (Sp = A) > W		

Table B.5 Distance-based Linear Model marginal test results for light-saturated fluxes of gross primary production (GPP_{sat}), light-saturated net primary production (NPP_{sat}) and sediment community respiration (SCR) as a function of habitat and tidal state. Results give the individual proportion (Prop.) of variance explained by each predictor that was significantly (≤ 0.1) correlated to the response variable (Corr. = correlation direction).

		Seagrass								**Sandflat**							
		Submerged				**Emerged**				**Submerged**				**Emerged**			
	Predictor	Pseudo-F	p-value	Prop.	Corr.	Pseudo-F	p-value	Prop.	Corr.	Pseudo-F	p-value	Prop.	Corr.	Pseudo-F	p-value	Prop.	Corr.
GPP_{sat}	PAR	27.88	0.001	0.35	+	12.38	0.002	0.17	+	16.11	0.001	0.26	+	12.96	0.002	0.13	+
	Temperature	24.25	0.001	0.32	+	56.84	0.001	0.48	+	35.57	0.001	0.43	+	21.11	0.001	0.19	+
	Chl *a*									4.17	0.063	0.08	-	4.94	0.035	0.05	-
	Mac. count	4.47	0.037	0.08	-												
	Mac. size	3.59	0.489	0.07	+					3.47	0.079	0.07	-				
	SG %	4.33	0.054	0.08	+	29.05	0.001	0.32	+								
	SG AGB	10.55	0.041	0.17	+	43.46	0.001	0.42	+								
NPP_{sat}	PAR	10.87	0.002	0.18	+	3.04	0.083	0.05	+	9.96	0.004	0.17	+				
	Temperature	5.30	0.030	0.09	+					13.40	0.001	0.22	+	3.63	0.059	0.04	-
	Chl *a*													6.13	0.018	0.07	+
	Mac. count	5.30	0.029	0.09	-												
	Aus. size													8.82	0.004	0.09	-
	Mac. size	6.20	0.015	0.11	+									3.61	0.054	0.04	-
	SG %	7.75	0.011	0.13	+	14.99	0.001	0.20	+								
	SG AGB	9.71	0.007	0.16	+	16.69	0.001	0.21	+								
SCR	Temperature					53.10	0.001	0.76	+	6.40	0.021	0.27	+	5.30	0.042	0.29	+
	Chl *a*													6.09	0.021	0.32	-
	Mac. count					10.32	0.007	0.38	+								
	Aus. size									3.19	0.081	0.16	-				
	Mac. size	4.03	0.088	0.24	+												
	SG AGB					10.65	0.006	0.39	+								

PAR – photosynthetically-active radiation, Chl *a* – sediment chlorophyll *a* content, Mac. – *Macomona liliana*, Aus. – *Austrovenus stutchburyi*, count – average count, size – average size, SG % - live seagrass percentage cover, SG AGB – seagrass above-ground biomass.

Table B.6 Distance-based Linear Model stepwise results for net primary production (NPP_{sat}) and sediment community respiration (SCR) as a function of habitat and tidal state. Significance levels of marginal tests of individual predictors: *p ≤ 0.1, **p ≤ 0.05, p ≤ 0.01***. See Table B.5 for full marginal test results.

		Seagrass		**Sandflat**	
	Predictor	**Submerged**	**Emerged**	**Submerged**	**Emerged**
NPP_{sat}	PAR	0.18***		0.05***	
	Temperature			0.22***	
	Chl *a*				0.04**
	Mac. count	0.04**			
	Aus. size				0.09***
	Mac. size				0.05*
	SG %	0.14**			
	SG AGB		0.21***		
	Total	0.36	0.21	0.27	0.18
	AICc	-15.75	-12.04	-10.12	-10.27
SCR	Temperature		0.76***	0.27**	
	Chl *a*				0.32**
	Mac. count		0.03***		
	Mac. size	0.24*			
	SG AGB	0.34	0.09***		
	Total	0.57	0.88	0.27	0.32
	AICc	-5.60	-30.23	-2.35	-1.79

PAR – photosynthetically-active radiation, Chl *a* – sediment chlorophyll *a* content, Mac. - *Macomona liliana*, Aus. – *Austrovenus stutchburyi*, count – average count, size – average size, SG % - live seagrass percentage cover, SG AGB - seagrass above-ground biomass.

Appendix C [4]

[4] This chapter is under review in the journal Estuaries and Coasts under the title "The effect of sediment mud content on primary production in seagrass and unvegetated intertidal flats" by G.J.L. Flowers, H.R. Needham, R.H Bulmer, A.M. Lohrer and C.A. Pilditch. DOI: 10.21203/rs.3.rs-3315615/v1.

Table C.1 Site sampling date, location, water depth, wind-wave exposure and variation in macrofaunal community composition (mean ± 1 SD; n = 3-5). See Table C.5 for site variation in taxa abundance.

								Macrofauna				
Site	Site name	Habitat	Sampling date	Latitude	Longitude	Depth HT (m)	Exposure	Aus. count (# core^{-1})	Mac. count (# core^{-1})	Sp (# core^{-1})	N (# core^{-1})	H' (# core^{-1})
ATH	Athenree	Seagrass	13/03/2019	-37.4489	175.9692	1.11	578	2 ± 1	2 ± 1	16 ± 3	128 ± 21	1.7 ± 0.2
		Unveg.						3 ± 3	3 ± 3	16 ± 1	155 ± 14	1.9 ± 0.0
BRW	Burrows Street	Seagrass	12/02/2019	-37.7083	176.1683	0.97	2,750	3 ± 3	1 ± 0	16 ± 3	103 ± 18	1.9 ± 0.3
		Unveg.						2 ± 2	2 ± 1	14 ± 2	89 ± 33	2.0 ± 0.2
MAT	Matahui	Seagrass	25/02/2019	-37.5845	175.9844	0.80	10,499	0 ± 0	3 ± 1	17 ± 3	94 ± 35	2.3 ± 0.4
		Unveg.						0 ± 1	3 ± 1	11 ± 3	106 ± 23	2.0 ± 0.3
OMK	Omokoroa	Seagrass	24/01/2019	-37.6408	176.0469	1.28	3,215	13 ± 5	2 ± 1	17 ± 1	196 ± 19	2.1 ± 0.0
		Unveg.						13 ± 5	2 ± 1	19 ± 1	198 ± 43	2.1 ± 0.2
ONG	Ongare	Seagrass	12/03/2019	-37.5019	175.9706	1.02	3,233	12 ± 3	4 ± 2	21 ± 2	263 ± 93	1.9 ± 0.2
		Unveg.						7 ± 4	6 ± 1	19 ± 7	157 ± 76	2.2 ± 0.3
OTU	Otumoetai	Seagrass	13/02/2019	-37.6653	176.1558	1.21	4,137	26 ± 7	1 ± 1	21 ± 2	375 ± 31	2.1 ± 0.0
		Unveg.						24 ± 11	2 ± 1	20 ± 1	278 ± 75	2.1 ± 0.1
TPU	Te Puna	Seagrass	25/01/2019	-37.6617	176.0450	1.23	771	6 ± 3	1 ± 2	18 ± 2	282 ± 67	1.5 ± 0.0
		Unveg.						11 ± 3	2 ± 1	17 ± 3	211 ± 31	1.9 ± 0.3
TUA	Tuapiro Point	Seagrass	10/01/2019	-37.4853	175.9539	0.89	5,745	18 ± 9	2 ± 1	20 ± 1	167 ± 29	2.2 ± 0.1
		Unveg.	11/01/2019					18 ± 5	4 ± 1	16 ± 3	153 ± 57	2.0 ± 0.2
URE - Mud	Uretara-Mudflat	Plot1	11/03/2019	-37.5364	175.9348	1.09		0 ± 0	1 ± 1	7 ± 2	57 ± 10	1.0 ± 0.3
		Plot2		-37.5365	175.9340	1.04		0 ± 0	1 ± 1	6 ± 2	32 ± 7	1.1 ± 0.3
WMA - Mud	Waimapi-Mudflat	Plot1	11/02/2019	-37.7185	176.1531	1.09		0 ± 0	0 ± 0	6 ± 2	9 ± 2	1.6 ± 0.4
		Plot2		-37.7187	176.1534	1.10		0 ± 0	1 ± 1	5 ± 2	9 ± 2	1.5 ± 0.5
WPA	Waipapa	Seagrass	26/02/2019	-37.6263	176.0064	1.33	6,597	1 ± 1	2 ± 1	23 ± 3	253 ± 61	1.8 ± 0.1
		Unveg.						0 ± 0	2 ± 1	14 ± 3	141 ± 24	1.6 ± 0.2

Depth HT – mean high tide water depth, Exposure – mean wind-wave exposure, Aus. – adult *Austrovenus stutchburyi*, Mac. – adult *Macomona liliana*, Sp – number of species, N – number of organisms (excl. large bivalves), H' – Shannon Weiner diversity index.

Table C.2 Intra-habitat Pearson correlation coefficients (r) between (a) environmental variables (seagrass habitat not shaded (n = 9); unvegetated habitat grey shading (n = 13)) and (b) environmental variables and measures of seagrass condition.

		Light	Temp.	Mud	MGS	WC	OC	Chl *a*	Phaeo	Aus.	Mac.	Sp	N	H'
a.	*Environmental*													
	Light		0.326	-0.722	0.570	-0.583	-0.543	-0.106	-0.327	0.676	0.428	0.667	0.718	0.498
	Temp.	0.525		0.114	-0.215	0.095	0.046	-0.040	0.070	0.285	-0.080	0.013	-0.030	0.046
	Mud	-0.599	-0.484		-0.880	0.900	0.890	0.502	0.705	-0.528	-0.561	-0.763	-0.688	-0.711
	MGS	0.127	0.299	-0.624		-0.903	-0.863	-0.341	-0.645	0.275	0.464	0.610	0.536	0.555
	WC	-0.111	-0.318	0.772	-0.687		0.957	0.434	0.652	-0.331	-0.503	-0.654	-0.554	-0.741
	OC	-0.084	-0.221	0.684	-0.533	0.746		0.579	0.719	-0.364	-0.461	-0.619	-0.513	-0.760
	Chl *a*	-0.066	-0.096	0.491	-0.017	0.573	0.615		0.768	-0.139	-0.331	-0.149	-0.023	-0.286
	Phaeo	-0.320	-0.411	0.745	-0.296	0.734	0.691	0.832		-0.221	-0.396	-0.366	-0.283	-0.366
	Aus.	0.617	0.451	-0.384	-0.212	-0.006	-0.015	-0.050	-0.199		0.250	0.675	0.811	0.492
	Mac.	-0.426	-0.342	0.364	-0.350	0.161	0.134	-0.026	0.101	-0.141		0.557	0.394	0.536
	Sp	0.332	0.015	0.062	-0.176	0.262	0.523	0.392	0.371	0.353	0.254		0.857	0.803
	N	0.337	0.245	0.256	-0.354	0.461	0.661	0.529	0.423	0.505	-0.089	0.604		0.591
	H'	0.171	-0.179	-0.487	0.092	-0.410	-0.257	-0.378	-0.375	0.331	0.091	0.097	-0.294	
b.	*Seagrass*													
	AGB	0.344	0.342	0.109	-0.179	0.279	0.298	0.307	0.229	0.292	0.104	0.430	0.547	-0.225
	BGB	0.554	0.442	-0.348	0.068	-0.037	-0.029	0.035	-0.155	0.544	-0.003	0.440	0.528	0.026
	TB	0.510	0.432	-0.196	-0.022	0.081	0.094	0.141	-0.018	0.483	0.038	0.458	0.561	-0.067
	AGB:BGB	-0.160	-0.125	0.577	-0.334	0.469	0.452	0.376	0.514	-0.243	0.092	0.112	0.124	-0.271
	Cover	0.597	0.302	-0.391	0.026	-0.048	0.039	0.118	-0.029	0.568	-0.200	0.477	0.428	0.378
	Width	-0.405	-0.123	0.520	0.052	0.313	0.205	0.281	0.370	-0.589	0.028	-0.257	-0.051	-0.596
	Length	0.124	0.178	0.338	-0.162	0.448	0.477	0.425	0.357	-0.004	0.028	0.140	0.493	-0.436
	SA	-0.206	-0.002	0.532	-0.085	0.446	0.370	0.370	0.414	-0.391	0.018	-0.147	0.195	-0.635
	Count	0.755	0.339	-0.439	-0.061	-0.064	0.039	0.032	-0.173	0.695	-0.101	0.571	0.439	0.323
	C:N AGB	-0.390	-0.336	0.217	0.116	0.117	-0.036	-0.068	0.150	-0.545	0.086	-0.474	-0.507	-0.107
	C:N BGB	-0.174	-0.223	0.506	-0.527	0.520	0.375	0.090	0.283	-0.250	0.140	0.082	0.143	-0.346

Light – chamber light (Lux), Temp. – chamber temperature (°C), Mud – sediment mud content (% < 63 µm), MGS – median grain size (µm), WC – sediment water content (%), OC – sediment organic content (%), Chl *a* – sediment chlorophyll *a* content (µg g^{-1} DW), Phaeo – sediment phaeopigment content (µg g^{-1} DW), Aus. – adult *Austrovenus stutchburyi* count (# $core^{-1}$), Mac. – adult *Macomona liliana* count (# $core^{-1}$), Sp – number of species (# $core^{-1}$), N – number of organisms (excl. large bivalves; # $core^{-1}$), H' – Shannon diversity index (# $core^{-1}$), AGB – seagrass above ground biomass (g DW m^{-2}), BGB – seagrass below ground biomass (g DW m^{-2}), TB – total seagrass biomass (g DW m^{-2}), Cover – total seagrass percentage cover (%), Width – blade width (mm), Length – blade length (mm), SA – blade surface area (mm^2), Count – blade count (# $core^{-1}$), C:N – carbon-nitrogen content ratio. Data used from light chambers (n = 5) with the exception of sediment variables (MGS, mud, WC and OC (n = 5)) and macrofaunal community variables (number of species and organisms, Shannon Weiner diversity index (n = 3)).

Table C.3 P-values of intra-habitat Pearson correlation coefficients between (a) environmental variables (seagrass habitat not shaded (n = 9); unvegetated habitat grey shading (n = 13)) and (b) environmental variables and measures of seagrass condition.

		Light	Temp.	Mud	MGS	WC	OC	Chl *a*	Phaeo	Aus.	Mac.	Sp	N	H'
a.	*Environmental*													
	Light		0.0081	<0.0001	<0.0001	<0.0001	<0.0001	0.4010	0.0079	<0.0001	0.0004	<0.0001	<0.0001	0.0012
	Temp.	0.0002		0.3674	0.0861	0.4504	0.7170	0.7498	0.5819	0.0215	0.5288	0.9361	0.8572	0.7818
	Mud	<0.0001	0.0008		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	MGS	0.4075	0.0459	<0.0001		<0.0001	<0.0001	0.0055	<0.0001	0.0268	0.0001	<0.0001	0.0004	0.0002
	WC	0.4671	0.0331	<0.0001	<0.0001		<0.0001	0.0003	<0.0001	0.0072	<0.0001	<0.0001	0.0003	<0.0001
	OC	0.5839	0.1447	<0.0001	0.0002	<0.0001		<0.0001	<0.0001	0.0029	0.0001	<0.0001	0.0008	<0.0001
	Chl *a*	0.6645	0.5319	0.0006	0.9102	<0.0001	<0.0001		<0.0001	0.2693	0.0070	0.3667	0.8872	0.0775
	Phaeo	0.0321	0.0051	<0.0001	0.0483	<0.0001	<0.0001	<0.0001		0.0767	0.0011	0.0219	0.0804	0.0220
	Aus.	<0.0001	0.0019	0.0092	0.1612	0.9686	0.9230	0.7456	0.1891		0.0442	<0.0001	<0.0001	0.0015
	Mac.	0.0035	0.0216	0.0139	0.0183	0.2909	0.3818	0.8657	0.5094	0.3562		0.0002	0.0131	0.0004
	Sp	0.0905	0.9404	0.7587	0.3787	0.1871	0.0052	0.0434	0.0567	0.0710	0.2016		<0.0001	<0.0001
	N	0.0857	0.2177	0.1968	0.0704	0.0154	0.0002	0.0046	0.0280	0.0072	0.6579	0.0008		0.0001
	H'	0.3940	0.3707	0.0100	0.6489	0.0338	0.1963	0.0520	0.0536	0.0917	0.6508	0.6303	0.1363	
b.	*Seagrass*													
	AGB	0.0205	0.0216	0.4758	0.2397	0.0639	0.0465	0.0404	0.1301	0.0514	0.4973	0.0250	0.0032	0.2590
	BGB	0.0001	0.0024	0.0191	0.6578	0.8114	0.8497	0.8176	0.3093	0.0001	0.9850	0.0217	0.0047	0.8994
	TB	0.0003	0.0030	0.1963	0.8863	0.5953	0.5389	0.3547	0.9043	0.0008	0.8060	0.0162	0.0023	0.7400
	AGB:BGB	0.2935	0.4124	<0.0001	0.0250	0.0012	0.0018	0.0110	0.0003	0.1083	0.5468	0.5783	0.5364	0.1720
	Cover	<0.0001	0.0441	0.0080	0.8649	0.7530	0.8003	0.4398	0.8493	<0.0001	0.1885	0.0118	0.0260	0.0517
	Width	0.0058	0.4202	0.0003	0.7334	0.0366	0.1759	0.0614	0.0124	<0.0001	0.8563	0.1954	0.8023	0.0010
	Length	0.4161	0.2418	0.0233	0.2881	0.0020	0.0009	0.0036	0.0160	0.9812	0.8536	0.4876	0.0089	0.0232
	SA	0.1751	0.9873	0.0002	0.5796	0.0021	0.0124	0.0124	0.0047	0.0079	0.9091	0.4640	0.3285	0.0004
	Count	<0.0001	0.0229	0.0025	0.6910	0.6776	0.8006	0.8366	0.2559	<0.0001	0.5083	0.0019	0.0220	0.1001
	C:N AGB	0.0080	0.0240	0.1529	0.4481	0.4439	0.8152	0.6579	0.3250	0.0001	0.5749	0.0124	0.0070	0.5945
	C:N BGB	0.2521	0.1403	0.0004	0.0002	0.0002	0.0110	0.5564	0.0600	0.0980	0.3593	0.6840	0.4753	0.0775

Light – chamber light (Lux), Temp. – chamber temperature (°C), Mud – sediment mud content (% < 63 µm), MGS – median grain size (µm), WC – sediment water content (%), OC – sediment organic content (%), Chl *a* – sediment chlorophyll *a* content (µg g^{-1} DW), Phaeo – sediment phaeopigment content (µg g^{-1} DW), Aus. – adult *Austrovenus stutchburyi* count (# $core^{-1}$), Mac. – adult *Macomona liliana* count (# $core^{-1}$), Sp – number of species (# $core^{-1}$), N – number of organisms (excl. large bivalves; # $core^{-1}$), H' – Shannon diversity index (# $core^{-1}$), AGB – seagrass above ground biomass (g DW m^{-2}), BGB – seagrass below ground biomass (g DW m^{-2}), TB – total seagrass biomass (g DW m^{-2}), Cover – total seagrass percentage cover (%), Width – blade width (mm), Length – blade length (mm), SA – blade surface area (mm^2), Count – blade count (# $core^{-1}$), C:N – carbon-nitrogen content ratio. Data used from light chambers (n = 5) with the exception of sediment variables (MGS, mud, WC and OC (n = 5)) and macrofaunal community variables (number of species and organisms, Shannon Weiner diversity index (n = 3)).

Table C.4 Pearson correlation coefficients (r; with p-values in parentheses) between site averages of mud content, light, water depth and porewater nutrient concentrations for the seagrass (n = 9) and all unvegetated habitats (n = 9-13).

	Mud	PAR – Site	PAR – Seafloor	%Attenuation	PAR – HT	PAR – LT	Depth - HT	Porewater NO_x	Porewater PO_4^{3-}	Porewater NH_4^+
Mud		0.436 (0.1368)	-0.349 (0.2429)	0.511 (0.0743)	-0.609 (0.0820)	-0.771 (0.0149)	0.191 (0.5311)	-0.487 (0.0917)	-0.182 (0.5524)	0.910 (<0.0001)
PAR – Site	0.134 (0.7304)		0.129 (0.6750)	0.343 (0.2512)	0.131 (0.7361)	0.096 (0.8058)	0.424 (0.1489)	-0.614 (0.0257)	0.401 (0.1506)	0.401 (0.1748)
PAR – Seafloor	-0.610 (0.0814)	0.333 (0.3816)		-0.873 (0.0001)	0.656 (0.0551)	0.742 (0.0222)	-0.049 (0.8727)	-0.252 (0.4069)	0.661 (0.0139)	-0.158 (0.6071)
%Attenuation	0.689 (0.0402)	0.175 (0.6526)	-0.853 (0.0035)		-0.578 (0.1034)	-0.645 (0.0606)	0.199 (0.5142)	0.021 (0.9460)	-0.413 (0.1609)	0.312 (0.2999)
PAR – HT	-0.552 (0.1231)	0.112 (0.7737)	0.649 (0.0587)	-0.573 (0.1071)		0.835 (0.0051)	-0.503 (0.1675)	-0.366 (0.3323)	0.443 (0.2326)	-0.040 (0.9194)
PAR – LT	-0.696 (0.0373)	0.084 (0.8300)	0.748 (0.0205)	-0.647 (0.0596)	0.835 (0.0051)		-0.480 (0.1905)	-0.251 (0.5147)	0.609 (0.0819)	-0.183 (0.6375)
Depth – HT	0.513 (0.1580)	0.534 (0.1387)	-0.059 (0.8807)	0.270 (0.4822)	-0.503 (0.1675)	-0.480 (0.1905)		-0.001 (0.9979)	0.221 (0.4682)	0.082 (0.7909)
Porewater NO_x	0.034 (0.9299)	-0.386 (0.3046)	-0.202 (0.6027)	0.117 (0.7650)	-0.502 (0.1686)	-0.100 (0.7980)	-0.122 (0.7539)		-0.321 (0.2851)	-0.584 (0.0362)
Porewater PO_4^{3-}	-0.484 (0.1859)	0.471 (0.2004)	0.656 (0.0551)	-0.392 (0.2961)	0.321 (0.4004)	0.535 (0.1376)	0.230 (0.5510)	0.047 (0.9048)		0.118 (0.7008)
Porewater NH_4^+	0.514 (0.1580)	-0.031 (0.9379)	-0.374 (0.3214)	0.412 (0.2710)	-0.705 (0.0340)	-0.358 (0.3436)	0.342 (0.3676)	0.678 (0.0449)	0.027 (0.9459)	

Mud – sediment mud content (% < 63 µm), PAR - Photosynthetically active radiation (µmol photons m^{-2} s^{-1}), PAR-Site & -Seafloor – sampling day, %Attenuation - percent water-column light attenuation (Site vs. Seafloor PAR), PAR – HT - median incident high tide PAR, PAR – LT - median incident low tide PAR, Depth – HT – mean high tide water depth (m), Porewater - porewater nutrient concentration (µg L^{-1}).

Table C.5 Site average abundance (# core^{-1}) of taxa (n = 3) in seagrass (SG) and unvegetated (UV) habitats.

Site	ATH		BRW		MAT		OMK		ONG		OTU		TPU		TUA		URE		WMA		WPA	
Habitat	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**Plot 1**	**Plot 2**	**Plot 1**	**Plot 2**	**SG**	**UV**
Anthozoa																						
Anthopleura aureoradiata	2.7	16.0	0.0	0.3	1.7	0.3	1.0	9.0	0.7	5.7	0.0	0.7	2.3	22.7	0.3	1.0	0.3	0.0	0.0	0.0	7.0	1.0
Edwardsia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Asteroidea																						
Patiriella regularis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bivalvia																						
Arthitica bifurca	1.0	0.0	0.3	0.0	1.3	1.0	3.3	0.3	0.7	0.7	0.0	0.0	1.7	0.3	0.0	0.0	8.3	2.3	1.3	0.3	5.7	2.0
Austrovenus stutchburyi	2.3	1.3	8.3	10.3	0.3	0.3	21.3	32.0	15.7	10.0	61.7	44.7	19.0	22.0	43.0	35.0	0.3	0.0	0.0	0.0	1.3	0.0
Lasaea parengaensis	0.3	0.7	1.7	2.0	0.0	0.3	0.0	0.3	0.3	0.7	0.0	0.0	0.0	0.0	1.3	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Linucula hartvigiana	0.0	0.3	0.0	0.0	0.0	0.0	20.0	11.3	8.0	1.7	49.0	38.0	18.3	10.7	0.7	1.3	0.0	0.0	0.0	0.0	33.0	20.0
Macamona liliana	3.3	3.0	1.3	2.7	4.0	4.7	5.3	4.3	6.0	9.3	0.7	3.3	2.7	5.0	3.7	6.7	1.0	1.0	0.7	1.0	4.3	3.3
Paphies australis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Zemysia	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Clitellata																						
Oligochaeta	5.0	30.0	7.0	1.7	9.7	1.7	0.0	2.3	17.7	9.0	7.3	17.7	1.7	3.7	6.3	14.7	0.7	2.3	0.7	1.3	2.3	0.0
Gastropoda																						
Cominella glandiformis	0.0	1.3	0.7	1.0	0.7	1.3	2.7	1.3	3.3	1.0	5.7	0.7	0.3	1.7	0.7	2.3	0.0	0.0	0.0	0.0	2.7	1.3
Diloma subrostrata	0.0	0.0	1.0	0.0	0.0	0.0	3.0	0.3	4.0	0.0	2.3	0.0	0.7	1.7	5.0	0.3	0.0	0.0	0.0	0.0	2.3	0.0
Eatoniella sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Haminoea zelandiae	0.3	0.3	0.0	0.0	0.0	0.0	0.3	0.7	0.0	0.0	0.0	0.0	0.7	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Micrelenchus huttoni	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	5.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.3	0.0
Neoguraleus sinclairi	0.3	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.3	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Notoacmea scapha	0.7	0.0	6.0	0.0	0.3	0.3	10.0	2.3	2.7	0.0	9.0	2.3	5.0	5.7	14.0	0.0	0.0	0.0	0.0	0.0	4.3	0.0
Pisinna zosterophila	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Zeacumantus lutulentus	0.0	0.7	6.3	3.7	3.7	3.0	0.7	2.0	0.7	0.7	0.7	0.7	3.0	6.7	2.3	0.3	0.0	0.0	0.0	0.0	0.7	9.7
Zeacumantus subcarinatus	0.0	0.0	2.0	0.0	1.0	0.0	0.0	0.3	5.3	0.0	22.0	7.0	0.0	0.0	14.0	6.7	0.0	0.0	0.0	0.0	2.7	0.0

Table C.5 cont.

Site	ATH		BRW		MAT		OMK		ONG		OTU		TPU		TUA		URE		WMA		WPA	
Habitat	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**Plot 1**	**Plot 2**	**Plot 1**	**Plot 2**	**SG**	**UV**
Malacostraca																						
Alpheus sp.	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Austrohelice crassa	0.7	0.0	0.0	0.0	0.3	0.0	0.7	0.7	0.3	0.0	1.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0
Autrominius modestus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Colorostylis lemurum	0.0	1.3	0.7	2.7	0.0	0.0	0.0	2.3	0.0	1.3	0.0	28.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.7
Corophium sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Eurylana arcuata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
Filhollianassa filholi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Halicarcnius varius	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Halicarcnius whitei	0.3	0.7	0.7	1.0	1.7	0.7	2.0	0.3	1.3	0.3	1.3	0.0	0.3	0.3	2.0	0.3	0.0	0.0	0.0	0.0	0.3	0.7
Hemigrapsus crenulatus	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hemigrapsus sexdentatus	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	1.3	0.0
Hemiplax hirtipes	1.0	0.0	0.7	0.3	0.7	0.0	0.3	0.0	0.0	1.0	0.3	0.0	0.0	0.3	0.0	0.0	1.7	1.7	1.0	0.3	1.0	0.3
Lysianassidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	2.7	0.7	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Melita awa	0.0	0.0	0.3	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paracalliope novizealandiae	2.7	0.7	2.3	0.3	7.7	0.0	2.7	6.0	13.0	1.7	42.3	15.0	3.3	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.3	0.7
Paramoera chevreuxi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Philocheras australis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phoxocephalidae	0.3	0.0	0.7	0.0	2.7	0.0	17.7	6.3	4.3	0.3	40.3	22.3	2.7	1.0	4.0	0.0	0.0	0.0	0.0	0.0	3.3	0.3
Protorchestia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Squilla sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Torridoharpinia hurleyi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3
Nemertea (phylum)	0.7	2.7	0.3	0.3	0.7	0.3	0.0	1.0	0.0	2.0	0.0	2.0	1.0	1.3	2.0	1.7	0.0	0.0	0.0	0.0	0.0	0.3
Platyhelminthes (phylum)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Polychaeta																						
Aonides trifidia	0.3	1.0	0.0	0.3	25.3	30.7	0.0	0.3	0.3	2.0	2.3	0.7	0.0	0.0	10.0	34.3	0.0	0.0	0.0	0.0	1.3	1.3
Aricidia sp.	0.0	0.0	0.0	0.0	0.0	0.0	1.7	5.3	0.3	10.3	0.0	1.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.7	9.3

Table C.5 cont.

Site	ATH		BRW		MAT		OMK		ONG		OTU		TPU		TUA		URE		WMA		WPA	
Habitat	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**Plot 1**	**Plot 2**	**Plot 1**	**Plot 2**	**SG**	**UV**
Boccardia	0.0	3.0	0.0	0.0	0.3	0.0	0.0	0.0	0.3	0.7	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
Capitella sp.	1.0	1.3	2.7	1.3	0.3	0.0	0.0	0.0	1.0	0.3	0.0	0.0	0.3	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.7	0.0
Ceratonereis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dorvilleidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Glycera americana	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Hesionidae (family)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Heteromastus filiformis	28.0	10.0	0.3	0.0	16.7	24.7	55.3	76.7	31.7	42.0	6.3	7.7	186	84.3	3.7	3.3	39.3	21.3	1.0	1.3	141	79.7
Macroclymenella stewartensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Magelona dakini	0.7	0.3	0.0	0.0	0.0	0.0	0.0	2.0	0.3	6.7	0.0	0.0	0.0	0.0	1.3	3.3	0.0	0.0	0.0	0.0	0.0	0.0
Microspio maori	0.0	0.0	0.3	3.0	0.0	13.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nereididae (family)	10.7	9.7	8.7	16.3	9.0	15.3	6.3	4.3	9.3	4.3	8.0	2.0	6.0	9.3	5.7	10.7	5.0	1.7	2.7	3.7	4.3	4.0
Orbinia papillosa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.3	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Owenia petersenae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.3	1.3	0.0	0.0	0.0	0.0	0.0	0.0
Paradoneis lyra	1.7	2.7	0.0	1.0	0.0	0.0	0.0	0.0	7.0	17.3	0.3	0.0	1.0	0.7	1.7	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Platynereis sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Prionispio aucklandica	66.3	66.0	48.3	34.3	2.0	0.0	52.7	39.7	138	35.0	123	96.7	32.0	43.7	61.3	47.3	0.3	0.0	0.3	0.3	12.0	3.3
Prionispio yuriel	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudopolydora corniculata	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudopolydora paucibranchiata	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scalibregmatidae (family)	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scolecolepides benhami	0.0	0.3	1.0	2.3	1.0	1.0	0.0	1.0	0.7	0.7	0.0	0.0	1.0	0.3	0.3	1.0	0.7	1.7	1.7	1.7	1.0	0.7
Scoloplos cylindrifer	1.7	3.0	4.7	9.7	2.7	11.0	0.0	0.0	0.3	0.0	0.3	0.3	1.3	0.0	0.0	2.7	0.0	0.0	0.0	0.0	1.0	0.3
Sphaerosyllis semiverrucosa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.3	0.3	0.7	0.3	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Syllinae (Subfamily)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polyplacophora																						
Chiton glaucus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table C.6 Results of one-way PERMANCOVA (9999 permutations; Euclidean distance-based matrices) comparing sediment community respiration (SCR) between habitats (fixed factor; 2 levels: seagrass and unvegetated sediment) with sediment mud content as a covariate. Significant effects ($p < 0.05$) are given in bold.

	Term	df	SS	MS	Pseudo-F	p-perm	Habitat effect
SCR	Mud x Habitat	1	0.11	0.11	0.12	0.7258	
	Mud	1	0.02	0.02	0.02	0.8764	
	Habitat	1	10.02	10.02	11.39	**0.0010**	Seagrass > Unvegetated

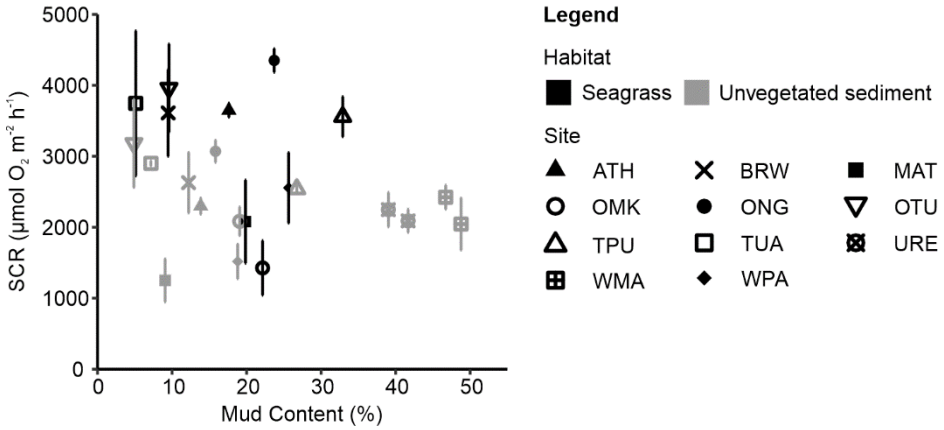


Figure C.1 Variation in sediment mud content (% < 63 µm) and sediment community respiration (SCR) in seagrass (black) and unvegetated sediment (grey) habitats. Data represent the site average (n = 2-5) ± 1 SE and symbols are indicative of site locations presented in Figure 3.1. There were no significant linear relationships in the seagrass habitat ($p = 0.46$, $n = 9$) nor in the unvegetated habitat for both the adjacent and extended (i.e., mudflat plots included) datasets ($p = 0.57$ & 0.46, $n = 9$ &13, respectively).

Table C.7 Distance-based Linear Model (DistLM) marginal test results for net primary production (NPP), gross primary production (GPP) and biomass-standardised GPP in seagrass (n = 9) and all unvegetated habitats (n = 13). Proportion (Prop.) results give the variance explained by the environmental predictors individually (Corr. = correlation direction). Shaded variables were not included in the step-wise DistLM model due to high collinearity (Pearson's r > 0.8) with other variables.

			Seagrass				**Unvegetated**			
	Predictor group	Predictor	Pseudo-F	p-value	Prop.	Corr.	Pseudo-F	p-value	Prop.	Corr.
NPP	*Physicochemical*	Site light	17.89	0.0003	0.2938	+	1.78	0.1879	0.0275	-
		Chamber light	25.37	0.0001	0.3711	+	47.80	0.0001	0.4314	+
		Temperature	8.18	0.0060	0.1598	+	3.24	0.0791	0.0490	-
		PW NO_x	1.19	0.2811	0.0270	-	0.34	0.5723	0.0053	+
		PW PO_4^{3-}	33.89	0.0001	0.4408	+	8.83	0.0054	0.1229	+
		PW NH_4^+	0.09	0.7617	0.0022	+	23.71	0.0001	0.2734	-
	Sediment	Mud	1.13	0.2987	0.0256	-	34.99	0.0001	0.3571	-
		MGS	0.02	0.8817	0.0005	+	21.73	0.0003	0.2565	+
		WC	0.87	0.3513	0.0198	+	12.88	0.0005	0.1698	-
		OC	3.38	0.0743	0.0730	+	9.49	0.0035	0.1310	-
		Chl *a*	1.93	0.1696	0.0430	+	0.04	0.8501	0.0007	-
		Phaeo	0.19	0.6638	0.0043	+	5.36	0.0239	0.0784	-
	Macrofauna	Aus. count	17.95	0.0002	0.2945	+	16.62	0.0003	0.2088	+
		Mac. count	7.41	0.0089	0.1470	-	5.66	0.0171	0.0824	+
		Sp	5.27	0.0254	0.1092	+	25.79	0.0001	0.2905	+
		N	20.00	0.0002	0.3174	+	42.23	0.0001	0.4013	+
		H'	0.12	0.7363	0.0028	-	4.71	0.0335	0.0696	+
	Seagrass	SG Cond1	12.47	0.0012	0.2249	+				
		SG Cond2	0.13	0.7263	0.0029	-				
		C:N AGB	1.60	0.2068	0.0359	-				
		C:N BGB	0.63	0.4315	0.0145	-				

Biomass-standardised GPP: Seagrass – seagrass above-ground biomass-standardised GPP, Unvegetated - chlorophyll *a* biomass-standardised GPP. Site & Chamber light – Lux, PW – porewater nutrient concentrations*, Mud – sediment mud content, MGS – median grain size, WC – sediment water content, OC – organic content, Chl *a* – sediment chlorophyll *a* content, Phaeo - sediment phaeopigment content, Aus. – adult *Austrovenus stutchburyi*, Mac. – adult *Macomona liliana*, Sp – number of species*, N – number of organisms (excl. large bivalves)*, H' – Shannon Weiner diversity index*, SG Cond1 & SG Cond2 - seagrass morphology PCO1 & PCO2 coordinates (see Fig. 2), C:N – carbon to nitrogen content ratio, AGB – above-ground biomass, BGB – below-ground biomass. *Average value per plot used in analyses.

Table C.7 cont.

			Seagrass				Unvegetated			
	Predictor group	Predictor	Pseudo-F	p-value	Prop.	Corr.	Pseudo-F	p-value	Prop.	Corr.
GPP	*Physicochemical*	Site light	11.80	0.0010	0.2153	+	0.52	0.4731	0.0082	-
		Chamber light	27.77	0.0001	0.3924	+	98.42	0.0001	0.6097	+
		Temperature	20.31	0.0001	0.3208	+	1.02	0.3201	0.0159	+
		PW NO_x	0.11	0.7425	0.0027	-	<0.0001	0.9971	<0.0001	-
		PW PO_4^{3-}	23.10	0.0001	0.3495	+	23.19	0.0001	0.2690	+
		PW NH_4^+	0.94	0.3423	0.0214	+	20.40	0.0002	0.2446	-
	Sediment	Mud	1.48	0.2266	0.0332	-	35.30	0.0001	0.3591	-
		MGS	0.12	0.7350	0.0028	+	14.22	0.0004	0.1841	+
		WC	0.58	0.4522	0.0133	+	10.81	0.0025	0.1464	-
		OC	1.90	0.1749	0.0424	+	9.03	0.0043	0.1254	-
		Chl *a*	1.60	0.2095	0.0358	+	0.20	0.6494	0.0032	-
		Phaeo	0.002	0.9642	0.0001	+	4.79	0.0304	0.0706	-
	Macrofauna	Aus. count	16.36	0.0002	0.2756	+	39.01	0.0001	0.3824	+
		Mac. count	4.36	0.0462	0.0920	-	8.04	0.0062	0.1132	+
		Sp.	4.69	0.0360	0.0983	+	41.01	0.0001	0.3943	+
		N	16.94	0.0004	0.2826	+	58.58	0.0001	0.4819	+
		H’	1.06	0.3170	0.0240	-	10.84	0.0022	0.1468	+
	Seagrass	SG Cond1	18.54	0.0001	0.3013	+				
		SG Cond2	1.21	0.2739	0.0274	-				
		C:N AGB	2.06	0.1650	0.0458	-				
		C:N BGB	0.39	0.5305	0.0089	-				

Biomass-standardised GPP: Seagrass – seagrass above-ground biomass-standardised GPP, Unvegetated - chlorophyll *a* biomass-standardised GPP. Site & Chamber light – Lux, PW – porewater nutrient concentrations*, Mud – sediment mud content, MGS – median grain size, WC – sediment water content, OC – organic content, Chl *a* – sediment chlorophyll *a* content, Phaeo - sediment phaeopigment content, Aus. – adult *Austrovenus stutchburyi*, Mac. – adult *Macomona liliana*, Sp – number of species*, N – number of organisms (excl. large bivalves)*, H’ – Shannon Weiner diversity index*, SG Cond1 & SG Cond2 - seagrass morphology PCO1 & PCO2 coordinates (see Fig. 2), C:N – carbon to nitrogen content ratio, AGB – above-ground biomass, BGB – below-ground biomass. *Average value per plot used in analyses.

Table C.7 cont.

			Seagrass				**Unvegetated**			
			GPP_{SG}				$GPP_{Chl\text{-}a}$			
	Predictor group	Predictor	Pseudo-F	p-value	Prop.	Corr.	Pseudo-F	p-value	Prop.	Corr.
Biomass-standardised GPP	*Physicochemical*	Site light	0.01	0.9445	0.0001	+	8.07	0.0047	0.1136	-
		Chamber light	0.84	0.3662	0.0192	+	72.81	0.0001	0.5361	+
		Temperature	1.98	0.1670	0.0440	+	1.64	0.2044	0.0254	+
		PW NO_x	0.16	0.6918	0.0036	-	0.48	0.4876	0.0076	+
		PW PO_4^{3-}	0.77	0.3874	0.0176	+	20.67	0.0003	0.2559	+
		PW NH_4^+	4.82	0.0363	0.1009	-	22.27	0.0002	0.2611	-
	Sediment	Mud	2.23	0.1401	0.0492	-	73.14	0.0001	0.5372	-
		MGS	0.64	0.4247	0.0147	+	22.77	0.0001	0.2654	+
		WC	1.46	0.2343	0.0238	-	24.74	0.0001	0.2820	-
		OC	0.96	0.3358	0.0218	-	32.96	0.0001	0.3435	-
		Chl *a*	0.82	0.3706	0.0186	-	27.32	0.0001	0.3025	-
		Phaeo	2.11	0.1498	0.0468	-	36.53	0.0001	0.3671	-
	Macrofauna	Aus. count	2.94	0.0913	0.0640	+	28.32	0.0001	0.3101	+
		Mac. count	8.56	0.0061	0.1661	-	13.39	0.0003	0.1753	+
		Sp.	3.64	0.0652	0.0781	-	31.61	0.0001	0.3341	+
		N	0.36	0.5514	0.0083	-	30.72	0.0001	0.3278	+
		H’	0.83	0.3733	0.0189	+	22.41	0.0001	0.2624	+
	Seagrass	SG Cond1	3.60	0.0603	0.0773	-				
		SG Cond2	14.73	0.0006	0.2551	+				
		C:N AGB	0.39	0.5332	0.0091	-				
		C:N BGB	0.03	0.8609	0.0007	-				

Biomass-standardised GPP: Seagrass – seagrass above-ground biomass-standardised GPP, Unvegetated - chlorophyll *a* biomass-standardised GPP. Site & Chamber light – Lux, PW – porewater nutrient concentrations*, Mud – sediment mud content, MGS – median grain size, WC – sediment water content, OC – organic content, Chl *a* – sediment chlorophyll *a* content, Phaeo - sediment phaeopigment content, Aus. – adult *Austrovenus stutchburyi*, Mac. – adult *Macomona liliana*, Sp – number of species*, N – number of organisms (excl. large bivalves)*, H’ – Shannon Weiner diversity index*, SG Cond1 & SG Cond2 - seagrass morphology PCO1 & PCO2 coordinates (see Fig. 2), C:N – carbon to nitrogen content ratio, AGB – above-ground biomass, BGB – below-ground biomass. *Average value per plot used in analyses.

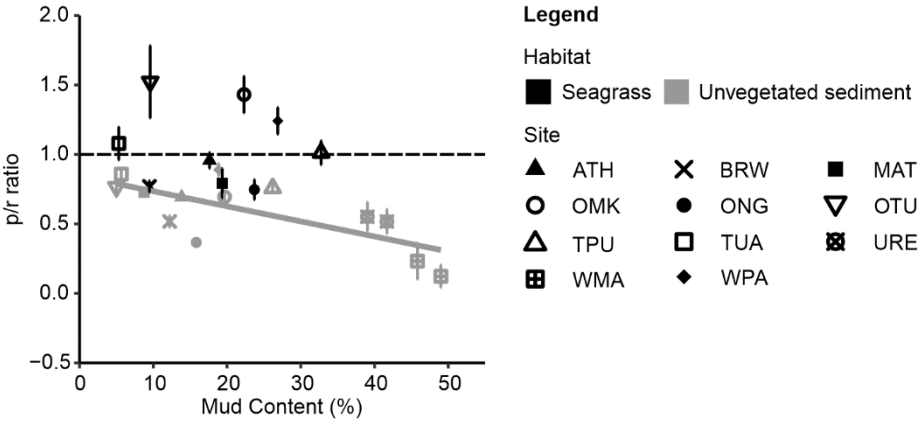


Figure C.2 Variation in sediment mud content (% < 63 µm) and photosynthesis-respiration (p/r) ratio in seagrass (black) and unvegetated sediment (grey) habitats. Sites above the dotted line (p/r = 1) are net autotrophic while those below are heterotrophic. Data represent the site average (n = 5) ± 1 SE and symbols are indicative of site locations presented in Figure 3.1. The grey trendline highlights a significant linear correlation (Pearson's r = -0.72, p = 0.006, n = 13) in the unvegetated sediment which was absent when 'mud' only sites/plots (i.e., > 35 %) were excluded (p = 0.84, n = 9). There was no significant relationship in the seagrass habitat (p = 0.87, n = 9).

Appendix D

Table D.1 Site locations and variability in light availability, physicochemical variables (n = 1-10), porewater nutrient concentration (n = 3-5), sedimentary variables (n = 5-10*), indicators of primary producer biomass (microphytobenthos and seagrass; n = 10) and macrofauna variables (large bivalves (n = 10) and community composition (n = 3)) in the seagrass, unvegetated sediment (Unveg.) and mudflat ('Mud') habitats (mean ± 1 SD).

		GPS Location		**Light availability**		**Physicochemical**		**Porewater Nutrients**		**Sediment**		
Site	Habitat	Latitude	Longitude	PAR - Site ($\mu mol\ m^{-2}\ s^{-1}$)	PAR - SF ($\mu mol\ m^{-2}\ s^{-1}$)	Temperature (°C; chamber)	Salinity (psu)	NH_4^+ ($\mu mol\ L^{-1}$)	PO_4^{3-} ($\mu mol\ L^{-1}$)	Mud content (% < 63 µm)	MGS (µm)	OC (%)
ATH	Seagrass	-37.4489	175.9692	1191 ± 458	481 ± 144	22.9 ± 0.5	34.08	21.0 ± 31.4	0.8 ± 0.3	17.6 ± 1.8	217 ± 12	2.9 ± 0.3
	Unveg.					22.8 ± 0.5		13.5 ± 13.5	0.9 ± 0.3	13.8 ± 2.2	209 ± 19	2.4 ± 0.3
BRW	Seagrass	-37.7083	176.1683	1564 ± 675	516 ± 218	24.2 ± 0.4	29.43	2.2 ± 1.6	0.6 ± 0.05	9.5 ± 0.8	251 ± 8	2.3 ± 0.1
	Unveg.					24.0 ± 0.4		5.2 ± 6.5	0.5 ± 0.1	12.2 ± 3.7	208 ± 17	2.1 ± 0.2
MAT	Seagrass	-37.5845	175.9844	1240 ± 405	257 ± 116	19.2 ± 0.2	32.55	7.5 ± 9.4	0.5 ± 0.1	19.4 ± 1.5	172 ± 7	3.0 ± 0.3
	Unveg.					19.2 ± 0.2		2.8 ± 2.1	0.3 ± 0.05	8.8 ± 2.9	211 ± 11	1.7 ± 0.2
OMK	Seagrass	-37.6408	176.0469	1350 ± 853	399 ± 231	21.0 ± 0.3	34.25	18.4 ± 6.9	1.3 ± 0.3	22.3 ± 2.2	122 ± 5	3.8 ± 0.3
	Unveg.					21.0 ± 0.4		33.6 ± 38.9	1.5 ± 0.3	19.7 ± 1.1	126 ± 5	3.5 ± 0.2
ONG	Seagrass	-37.5019	175.9706	1285 ± 470	256 ± 198	23.2 ± 0.5	33.76	57.3 ± 40.8	1.0 ± 0.3	23.7 ± 1.7	135 ± 10	4.0 ± 0.4
	Unveg.					23.0 ± 0.4		3.6 ± 3.2	0.5 ± 0.1	15.8 ± 1.6	169 ± 7	2.9 ± 0.2
OTU	Seagrass	-37.6653	176.1558	2070 ± 171	754 ± 17	23.8 ± 0.8	33.03	22.3 ± 9.9	2.9 ± 0.9	9.6 ± 1.6	198 ± 14	3.8 ± 1.7
	Unveg.					23.6 ± 0.7		12.2 ± 7.8	3.5 ± 0.4	5.0 ± 0.8	216 ± 10	2.0 ± 0.3
TPU	Seagrass	-37.6617	176.0450	2089 ± 477	535 ± 141	22.0 ± 0.6	33.51	23.6 ± 24.1	0.8 ± 0.4	32.8 ± 1.2	113 ± 6	5.0 ± 0.2
	Unveg.					22.0 ± 0.5		10.5 ± 9.5	0.9 ± 0.2	26.2 ± 2.1	131 ± 7	4.6 ± 0.2
TUA	Seagrass	-37.4853	175.9539	1621 ± 566	656 ± 226	22.7 ± 0.8	34.53	6.3 ± 6.8	2.0 ± 1.0	5.6 ± 0.8	178 ± 6	2.8 ± 0.3
	Unveg.			1678 ± 540	702 ± 208	23.0 ± 0.7	34.48	17.8 ± 10.7	2.2 ± 0.5	5.8 ± 1.2	182 ± 7	2.4 ± 0.2
URE - Mud	Plot1	-37.5364	175.9348	1838 ± 177	443 ± 85	22.0 ± 0.3	31.24	70.4 ± 76.7	1.7 ± 1.9	41.7 ± 1.6	82 ± 4	6.2 ± 0.2
	Plot2	-37.5365	175.9340			22.0 ± 0.2		62.4 ± 78.0	1.2 ± 1.9	39.0 ± 0.6	91 ± 2	5.7 ± 0.3
WMA - Mud	Plot1	-37.7185	176.1531	1994 ± 437	255 ± 64	23.9 ± 0.2	30.26	73.8 ± 22.9	0.9 ± 0.5	49.0 ± 2.7	65 ± 6	4.8 ± 0.3
	Plot2	-37.7187	176.1534			23.7 ± 0.2		76.0 ± 22.7	1.2 ± 0.4	45.8 ± 4.6	72 ± 10	4.6 ± 0.4
WPA	Seagrass	-37.6263	176.0064	1990 ± 194	139 ± 186	20.2 ± 0.5	32.53	26.7 ± 12.8	1.0 ± 0.4	26.9 ± 7.0	204 ± 42	5.1 ± 1.5
	Unveg.					20.0 ± 0.4		8.6 ± 8.8	0.6 ± 0.2	18.9 ± 1.5	248 ± 38	2.8 ± 0.1

PAR – photosynthetically active radiation, SF – seafloor, MGS – median grain size, OC – organic content. *TUA n = 10, all remaining sites n = 5.

Table D.1 cont.

		Microphytobenthos		Seagrass			Macrofauna				
Site	Habitat	Chl *a* ($\mu g\ g^{-1}$ DW)	Phaeo ($\mu g\ g^{-1}$ DW)	AGB ($g\ DW\ m^{-2}$)	BGB ($g\ DW\ m^{-2}$)	AGB:BGB	Aus. count (# $core^{-1}$)	Mac. count (# $core^{-1}$)	Sp. (# $core^{-1}$)	N (# $core^{-1}$)	H' (# $core^{-1}$)
ATH	Seagrass	16.1 ± 1.2	8.6 ± 1.1	68 ± 23	122 ± 32	0.6 ± 0.2	2 ± 1	2 ± 1	16 ± 3	128 ± 21	1.7 ± 0.2
	Unveg.	13.0 ± 1.6	6.3 ± 0.8				3 ± 3	3 ± 3	16 ± 1	155 ± 14	1.9 ± 0.0
BRW	Seagrass	15.2 ± 0.7	6.9 ± 0.5	31 ± 4	67 ± 13	0.5 ± 0.1	3 ± 3	1 ± 0	16 ± 3	103 ± 18	1.9 ± 0.3
	Unveg.	13.9 ± 3.1	6.0 ± 0.8				2 ± 2	2 ± 1	14 ± 2	89 ± 33	2.0 ± 0.2
MAT	Seagrass	12.1 ± 1.4	8.4 ± 1.7	41 ± 11	98 ± 24	0.5 ± 0.2	0 ± 0	3 ± 1	17 ± 3	94 ± 35	2.3 ± 0.4
	Unveg.	8.0 ± 0.8	3.7 ± 0.5				0 ± 1	3 ± 1	11 ± 3	106 ± 23	2.0 ± 0.3
OMK	Seagrass	16.1 ± 1.5	10.4 ± 1.4	26 ± 9	60 ± 23	0.4 ± 0.1	13 ± 5	2 ± 1	17 ± 1	196 ± 19	2.1 ± 0.0
	Unveg.	14.7 ± 0.5	8.7 ± 0.6				13 ± 5	2 ± 1	19 ± 1	198 ± 43	2.1 ± 0.2
ONG	Seagrass	17.5 ± 1.5	11.4 ± 2.0	90 ± 29	148 ± 39	0.6 ± 0.1	12 ± 3	4 ± 2	21 ± 2	263 ± 93	1.9 ± 0.2
	Unveg.	10.9 ± 0.9	6.3 ± 1.0				7 ± 4	6 ± 1	19 ± 7	157 ± 76	2.2 ± 0.3
OTU	Seagrass	21.5 ± 3.3	10.2 ± 1.1	85 ± 18	192 ± 62	0.5 ± 0.1	26 ± 7	1 ± 1	21 ± 2	375 ± 31	2.1 ± 0.0
	Unveg.	12.6 ± 1.8	5.5 ± 0.8				24 ± 11	2 ± 1	20 ± 1	278 ± 75	2.1 ± 0.1
TPU	Seagrass	22.0 ± 1.8	15.8 ± 2.7	56 ± 23	63 ± 23	1.0 ± 0.7	6 ± 3	1 ± 2	18 ± 2	282 ± 67	1.5 ± 0.0
	Unveg.	27.9 ± 1.2	13.6 ± 2.3				11 ± 3	2 ± 1	17 ± 3	211 ± 31	1.9 ± 0.3
TUA	Seagrass	13.0 ± 1.7	6.2 ± 1.0	65 ± 22	140 ± 23	0.5 ± 0.2	18 ± 9	2 ± 1	20 ± 1	167 ± 29	2.2 ± 0.1
	Unveg.	10.7 ± 1.2	5.7 ± 0.8				18 ± 5	4 ± 1	16 ± 3	153 ± 57	2.0 ± 0.2
URE - Mud	Plot1	18.2 ± 0.8	10.1 ± 0.8				0 ± 0	1 ± 1	7 ± 2	57 ± 10	1.0 ± 0.3
	Plot2	16.3 ± 0.9	9.7 ± 0.8				0 ± 0	1 ± 1	6 ± 2	32 ± 7	1.1 ± 0.3
WMA - Mud	Plot1	17.4 ± 1.5	10.3 ± 1.3				0 ± 0	0 ± 0	6 ± 2	9 ± 2	1.6 ± 0.4
	Plot2	16.9 ± 2.0	13.3 ± 2.7				0 ± 0	1 ± 1	5 ± 2	9 ± 2	1.5 ± 0.5
WPA	Seagrass	32.7 ± 6.6	19.6 ± 4.7	62 ± 23	94 ± 41	0.8 ± 0.5	1 ± 1	2 ± 1	23 ± 3	253 ± 61	1.8 ± 0.1
	Unveg.	21.8 ± 1.5	8.5 ± 0.3				0 ± 0	2 ± 1	14 ± 3	141 ± 24	1.6 ± 0.2

Chl *a* – sediment chlorophyll *a* content, Phaeo – sediment phaeopigment content, AGB – above-ground biomass, BGB - below-ground biomass, Aus. – adult *Austrovenus stutchburyi*, Mac. – adult *Macomona liliana*, Sp. – number of species, N – number of organisms (excl. large bivalves), H' – Shannon Weiner diversity index.

Table D.2 Site average abundance (# core^{-1}) of taxa (n = 3) in seagrass (SG) and unvegetated (UV) habitats.

Site	ATH		BRW		MAT		OMK		ONG		OTU		TPU		TUA		URE		WMA		WPA	
Habitat	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**Plot 1**	**Plot 2**	**Plot 1**	**Plot 2**	**SG**	**UV**
Anthozoa																						
Anthopleura aureoradiata	2.7	16.0	0.0	0.3	1.7	0.3	1.0	9.0	0.7	5.7	0.0	0.7	2.3	22.7	0.3	1.0	0.3	0.0	0.0	0.0	7.0	1.0
Edwardsia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Asteroidea																						
Patiriella regularis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bivalvia																						
Arthitica bifurca	1.0	0.0	0.3	0.0	1.3	1.0	3.3	0.3	0.7	0.7	0.0	0.0	1.7	0.3	0.0	0.0	8.3	2.3	1.3	0.3	5.7	2.0
Austrovenus stutchburyi	2.3	1.3	8.3	10.3	0.3	0.3	21.3	32.0	15.7	10.0	61.7	44.7	19.0	22.0	43.0	35.0	0.3	0.0	0.0	0.0	1.3	0.0
Lasaea parengaensis	0.3	0.7	1.7	2.0	0.0	0.3	0.0	0.3	0.3	0.7	0.0	0.0	0.0	0.0	1.3	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Linucula hartvigiana	0.0	0.3	0.0	0.0	0.0	0.0	20.0	11.3	8.0	1.7	49.0	38.0	18.3	10.7	0.7	1.3	0.0	0.0	0.0	0.0	33.0	20.0
Macamona liliana	3.3	3.0	1.3	2.7	4.0	4.7	5.3	4.3	6.0	9.3	0.7	3.3	2.7	5.0	3.7	6.7	1.0	1.0	0.7	1.0	4.3	3.3
Paphies australis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Zemysia	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Clitellata																						
Oligochaeta	5.0	30.0	7.0	1.7	9.7	1.7	0.0	2.3	17.7	9.0	7.3	17.7	1.7	3.7	6.3	14.7	0.7	2.3	0.7	1.3	2.3	0.0
Gastropoda																						
Cominella glandiformis	0.0	1.3	0.7	1.0	0.7	1.3	2.7	1.3	3.3	1.0	5.7	0.7	0.3	1.7	0.7	2.3	0.0	0.0	0.0	0.0	2.7	1.3
Diloma subrostrata	0.0	0.0	1.0	0.0	0.0	0.0	3.0	0.3	4.0	0.0	2.3	0.0	0.7	1.7	5.0	0.3	0.0	0.0	0.0	0.0	2.3	0.0
Eatoniella sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Haminoea zelandiae	0.3	0.3	0.0	0.0	0.0	0.0	0.3	0.7	0.0	0.0	0.0	0.0	0.7	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Micrelenchus huttoni	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	5.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.3	0.0
Neoguraleus sinclairi	0.3	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.3	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Notoacmea scapha	0.7	0.0	6.0	0.0	0.3	0.3	10.0	2.3	2.7	0.0	9.0	2.3	5.0	5.7	14.0	0.0	0.0	0.0	0.0	0.0	4.3	0.0
Pisinna zosterophila	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Zeacumantus lutulentus	0.0	0.7	6.3	3.7	3.7	3.0	0.7	2.0	0.7	0.7	0.7	0.7	3.0	6.7	2.3	0.3	0.0	0.0	0.0	0.0	0.7	9.7
Zeacumantus subcarinatus	0.0	0.0	2.0	0.0	1.0	0.0	0.0	0.3	5.3	0.0	22.0	7.0	0.0	0.0	14.0	6.7	0.0	0.0	0.0	0.0	2.7	0.0

Table D.2 cont.

Site	ATH		BRW		MAT		OMK		ONG		OTU		TPU		TUA		URE		WMA		WPA	
Habitat	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**Plot 1**	**Plot 2**	**Plot 1**	**Plot 2**	**SG**	**UV**
Malacostraca																						
Alpheus sp.	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Austrohelice crassa	0.7	0.0	0.0	0.0	0.3	0.0	0.7	0.7	0.3	0.0	1.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0
Autrominius modestus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Colorostylis lemurum	0.0	1.3	0.7	2.7	0.0	0.0	0.0	2.3	0.0	1.3	0.0	28.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.7
Corophium sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Eurylana arcuata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
Filhollianassa filholi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Halicarcnius varius	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Halicarcnius whitei	0.3	0.7	0.7	1.0	1.7	0.7	2.0	0.3	1.3	0.3	1.3	0.0	0.3	0.3	2.0	0.3	0.0	0.0	0.0	0.0	0.3	0.7
Hemigrapsus crenulatus	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hemigrapsus sexdentatus	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	1.3	0.0
Hemiplax hirtipes	1.0	0.0	0.7	0.3	0.7	0.0	0.3	0.0	0.0	1.0	0.3	0.0	0.0	0.3	0.0	0.0	1.7	1.7	1.0	0.3	1.0	0.3
Lysianassidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	2.7	0.7	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Melita awa	0.0	0.0	0.3	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paracalliope novizealandiae	2.7	0.7	2.3	0.3	7.7	0.0	2.7	6.0	13.0	1.7	42.3	15.0	3.3	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.3	0.7
Paramoera chevreuxi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Philocheras australis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phoxocephalidae	0.3	0.0	0.7	0.0	2.7	0.0	17.7	6.3	4.3	0.3	40.3	22.3	2.7	1.0	4.0	0.0	0.0	0.0	0.0	0.0	3.3	0.3
Protorchestia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Squilla sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Torridoharpinia hurleyi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3
Nemertea (phylum)	0.7	2.7	0.3	0.3	0.7	0.3	0.0	1.0	0.0	2.0	0.0	2.0	1.0	1.3	2.0	1.7	0.0	0.0	0.0	0.0	0.0	0.3
Platyhelminthes (phylum)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Polychaeta																						
Aonides trifidia	0.3	1.0	0.0	0.3	25.3	30.7	0.0	0.3	0.3	2.0	2.3	0.7	0.0	0.0	10.0	34.3	0.0	0.0	0.0	0.0	1.3	1.3
Aricidia sp.	0.0	0.0	0.0	0.0	0.0	0.0	1.7	5.3	0.3	10.3	0.0	1.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.7	9.3

Table D.2 cont.

Site	ATH		BRW		MAT		OMK		ONG		OTU		TPU		TUA		URE		WMA		WPA	
Habitat	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**SG**	**UV**	**Plot 1**	**Plot 2**	**Plot 1**	**Plot 2**	**SG**	**UV**
Boccardia	0.0	3.0	0.0	0.0	0.3	0.0	0.0	0.0	0.3	0.7	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
Capitella sp.	1.0	1.3	2.7	1.3	0.3	0.0	0.0	0.0	1.0	0.3	0.0	0.0	0.3	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.7	0.0
Ceratonereis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dorvilleidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Glycera americana	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Hesionidae (family)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Heteromastus filiformis	28.0	10.0	0.3	0.0	16.7	24.7	55.3	76.7	31.7	42.0	6.3	7.7	186	84.3	3.7	3.3	39.3	21.3	1.0	1.3	141	79.7
Macroclymenella stewartensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Magelona dakini	0.7	0.3	0.0	0.0	0.0	0.0	0.0	2.0	0.3	6.7	0.0	0.0	0.0	0.0	1.3	3.3	0.0	0.0	0.0	0.0	0.0	0.0
Microspio maori	0.0	0.0	0.3	3.0	0.0	13.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nereididae (family)	10.7	9.7	8.7	16.3	9.0	15.3	6.3	4.3	9.3	4.3	8.0	2.0	6.0	9.3	5.7	10.7	5.0	1.7	2.7	3.7	4.3	4.0
Orbinia papillosa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.3	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Owenia petersenae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.3	1.3	0.0	0.0	0.0	0.0	0.0	0.0
Paradoneis lyra	1.7	2.7	0.0	1.0	0.0	0.0	0.0	0.0	7.0	17.3	0.3	0.0	1.0	0.7	1.7	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Platynereis sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Prionispio aucklandica	66.3	66.0	48.3	34.3	2.0	0.0	52.7	39.7	138	35.0	123	96.7	32.0	43.7	61.3	47.3	0.3	0.0	0.3	0.3	12.0	3.3
Prionispio yuriel	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudopolydora corniculata	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudopolydora paucibranchiata	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scalibregmatidae (family)	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scolecolepides benhami	0.0	0.3	1.0	2.3	1.0	1.0	0.0	1.0	0.7	0.7	0.0	0.0	1.0	0.3	0.3	1.0	0.7	1.7	1.7	1.7	1.0	0.7
Scoloplos cylindrifer	1.7	3.0	4.7	9.7	2.7	11.0	0.0	0.0	0.3	0.0	0.3	0.3	1.3	0.0	0.0	2.7	0.0	0.0	0.0	0.0	1.0	0.3
Sphaerosyllis semiverrucosa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.3	0.3	0.7	0.3	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Syllinae (Subfamily)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polyplacophora																						
Chiton glaucus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table D.3 Seasonal variability in light availability, physicochemical variables (n = 1-10), porewater nutrient concentrations (n = 5), sedimentary variables (n = 6-10), indicators of primary producer biomass (microphytobenthos and seagrass; n = 6-10) and macrofauna variables (n = 6-10) in the seagrass and unvegetated sediment (Unveg.) habitats at TUA (mean ± 1 SD).

			Light availability		**Physicochemical**		**Porewater nutrients**		**Sediment**		
Season	Sampling	Habitat	PAR-Site ($\mu mol\ m^{-2}\ s^{-1}$)	PAR-SF ($\mu mol\ m^{-2}\ s^{-1}$)	Temperature (°C; chamber)	Salinity (psu)	NH_4^+ ($\mu mol\ L^{-1}$)	PO_4^{3-} ($\mu mol\ L^{-1}$)	Mud content (% < 63 µm)	MGS (µm)	OC (%)
Spring	Oct-18	Seagrass	1925 ± 89	711 ± 86	17.9 ± 0.7	35.6	12.8 ± 3.0	2.6 ± 0.6	8.1 ± 2.0	173 ± 8	3.1 ± 0.5
		Unveg.	1823 ± 363	785 ± 145	17.9 ± 0.8	35.6	7.3 ± 6.9	2.6 ± 0.6	7.9 ± 1.2	174 ± 2	2.4 ± 0.2
	Oct-19	Seagrass	1463 ± 501	548 ± 167	14.3 ± 0.8	36.1	5.5 ± 4.7	2.5 ± 1.7	6.8 ± 1.2	175 ± 1	2.6 ± 0.2
		Unveg.	1689 ± 498	601 ± 188	14.9 ± 0.8	34.9	8.4 ± 7.2	3.0 ± 0.4	8.9 ± 0.9	172 ± 1	2.9 ± 0.2
Summer	Jan-19	Seagrass	1641 ± 585	666 ± 236	22.7 ± 0.8	34.5	6.3 ± 6.8	2.0 ± 1.0	5.6 ± 0.8	178 ± 6	2.8 ± 0.3
		Unveg.	1671 ± 538	698 ± 208	23.0 ± 0.7	34.5	17.8 ± 10.7	2.2 ± 0.5	5.8 ± 1.2	182 ± 7	2.4 ± 0.2
	Jan-20	Seagrass	2232 ± 146	905 ± 103	20.8 ± 1.0	35.8	10.4 ± 13.1	4.0 ± 1.6	6.5 ± 1.0	181 ± 1	2.6 ± 0.3
		Unveg.	2202 ± 170	846 ± 86	20.9 ± 0.7	35.9	25.4 ± 25.5	4.6 ± 1.5	8.0 ± 0.7	178 ± 1	2.6 ± 0.1
Autumn	Apr-19	Seagrass	567 ± 403	250 ± 159	20.0 ± 0.3	32.3	12.7 ± 11.7	2.3 ± 0.6	7.0 ± 0.6	171 ± 1	3.0 ± 0.2
		Unveg.	1000 ± 362	421 ± 145	19.6 ± 0.6	33.9	13.6 ± 3.8	2.6 ± 0.2	9.9 ± 0.9	169 ± 1	3.4 ± 0.9
Winter	Jul-19	Seagrass	652 ± 371	244 ± 125	14.2 ± 0.4	33.4	9.3 ± 10.7	1.6 ± 0.4	5.4 ± 0.5	179 ± 1	2.4 ± 0.2
		Unveg.	771 ± 314	256 ± 98	14.3 ± 0.4	34.1	19.5 ± 18.6	1.7 ± 0.5	6.8 ± 1.0	176 ± 1	2.9 ± 0.2
	Jul-20	Seagrass	1295 ± 149	454 ± 58	14.8 ± 0.7	33.1	38.4 ± 17.4	2.3 ± 0.6	5.4 ± 0.8	176 ± 1	2.7 ± 0.2
		Unveg.	262 ± 92	150 ± 61	13.8 ± 0.2	32.2	41.2 ± 7.8	2.0 ± 0.6	5.2 ± 1.0	180 ± 1	2.3 ± 0.1

PAR – photosynthetically active radiation, SF – seafloor, MGS – median grain size, OC – organic content.

Table D.3 cont.

			Microphytobenthos		**Seagrass**			**Macrofauna**	
Season	Sampling		Chl *a*	Phaeo	AGB	BGB	AGB:BGB	Aus. count	Mac. count
			(µg g^{-1} DW)	(µg g^{-1} DW)	(g DW m^{-2})	(g DW m^{-2})		(# $core^{-1}$)	(# $core^{-1}$)
Spring	Oct-18	Seagrass	15.5 ± 3.2	9.1 ± 3.8	56 ± 18	107 ± 34	0.6 ± 0.3	16 ± 8	2 ± 1
		Unveg.	12.8 ± 1.2	7.4 ± 1.5				19 ± 7	2 ± 1
	Oct-19	Seagrass	14.6 ± 2.1	8.4 ± 2.3	37 ± 6	82 ± 18	0.5 ± 0.1	21 ± 7	2 ± 1
		Unveg.	15.5 ± 1.5	9.1 ± 0.6				24 ± 11	3 ± 2
Summer	Jan-19	Seagrass	13.0 ± 1.7	6.2 ± 1.0	65 ± 22	140 ± 23	0.5 ± 0.2	18 ± 9	2 ± 1
		Unveg.	10.7 ± 1.2	5.7 ± 0.8				18 ± 5	4 ± 1
	Jan-20	Seagrass	12.4 ± 1.7	6.8 ± 1.1	34 ± 11	77 ± 21	0.4 ± 0.1	12 ± 7	2 ± 1
		Unveg.	10.4 ± 1.0	6.6 ± 0.7				15 ± 6	2 ± 1
Autumn	Apr-19	Seagrass	14.0 ± 1.5	7.5 ± 0.8	52 ± 10	80 ± 38	1.1 ± 1.1	21 ± 10	2 ± 1
		Unveg.	14.3 ± 1.7	7.8 ± 0.8				21 ± 6	4 ± 1
Winter	Jul-19	Seagrass	14.7 ± 1.2	8.9 ± 1.4	42 ± 4	58.7 ± 17	0.7 ± 0.2	27 ± 14	2 ± 1
		Unveg.	12.5 ± 3.9	8.3 ± 2.8				24 ± 9	5 ± 1
	Jul-20	Seagrass	14.8 ± 1.7	8.9 ± 1.6	35 ± 15	70 ± 22	0.5 ± 0.1	18 ± 4	1 ± 1
		Unveg.	10.7 ± 0.8	8.2 ± 0.7				19 ± 6	2 ± 1

Chl *a* – sediment chlorophyll *a* content, Phaeo – sediment phaeopigment content, AGB – above-ground biomass, BGB - below-ground biomass, Aus. – adult *Austrovenus stutchburyi*, Mac. – adult *Macomona liliana.*

Table D.4 Pearson correlation coefficients between (a) environmental variables and (b) nutrient cycling during light and dark conditions in the seagrass habitat (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Data from spatial and TUA seasonal datasets combined for environmental and fluxes of NH_4^+ and PO_4^{3-}, while N_2 efflux and denitrification efficiency (DE) measurements are only from the spatial dataset.

	Light[a]	Temp	Salinity[b]	Mud[c]	MGS[c]	OC[c]	Chl *a*	Phaeo	AGB	BGB	Aus.	Mac.	PW PO_4^{3-}[b]	PW NH_4^+[b]	NPP	SCR
(a) Environmental																
Temp	0.22															
Salinity[b]	0.50***	-0.34***														
Mud[c]	-0.45***	0.29**	-0.08													
MGS[c]	0.11	0.14	-0.46***	-0.50***												
OC[c]	-0.17	0.19*	0.03	0.74***	-0.49***											
Chl *a*	-0.14	0.14	-0.16	0.56***	-0.03	0.69***										
Phaeo	-0.33**	0.02	-0.06	0.73***	-0.30***	0.75***	0.84***									
AGB	0.17	0.35***	0.09	0.19*	-0.08	0.32***	0.30***	0.26**								
BGB	0.41***	0.38***	0.11	-0.08	0.08	0.08	0.09	-0.05	0.70***							
Aus.	0.26*	-0.25**	0.31***	-0.52***	-0.14	-0.18*	-0.18*	-0.23**	0.10	0.21*						
Mac.	-0.30*	-0.03	0.16	0.18*	-0.24**	0.04	-0.08	0.03	0.08	0.01	-0.02					
PW PO_4^{3-}[b]	0.71***	-0.24**	0.53***	-0.61***	-0.003	-0.18*	-0.16	-0.26**	0.02	0.19*	0.60***	-0.17				
PW NH_4^+[b]	-0.19	0.14	0.10	0.45***	-0.38***	0.44***	0.34***	0.40***	0.44***	0.25***	-0.01	0.31***	-0.12			
(b) Nutrient cycling (response variables)																
Light																
NH_4^+	-0.06	0.05	0.05	0.08	-0.18	0.10	0.03	0.09	0.11	-0.04	0.09	0.11	0.08	0.25*	0.03	
PO_4^{3-}	0.01	-0.01	0.12	0.03	-0.17	0.08	-0.03	0.06	-0.04	-0.03	0.11	0.11	0.23	0.04	-0.03	
Dark																
NH_4^+	-	0.23	-0.27	0.00	0.19	-0.16	-0.13	-0.06	-0.09	-0.17	-0.22	0.04	-0.16	-0.17	-	0.46***
PO_4^{3-}	-	0.14	0.21	-0.16	-0.26	0.06	-0.06	-0.11	-0.02	0.10	0.25	0.00	0.44*	-0.06	-	0.23
N_2[c]	-	0.53**	-0.37*	-0.42*	0.29	-0.17	-0.07	-0.15	0.22	0.26	0.25	-0.57***	0.36*	-0.32	-	0.42*
DE[c]	-	0.10	0.08	-0.25	0.18	0.04	0.20	0.01	0.26	0.39*	0.29	-0.36*	0.42*	0.05	-	0.07

Light – chamber lux, Temp – chamber temperature, Mud – sediment percent mud content, MGS – median grain size, OC – sediment organic content, Chl *a* – sediment chlorophyll *a* content, Phaeo – sediment phaeopigment content, AGB – seagrass above-ground biomass, BGB – seagrass below-ground biomass, Aus. – adult *Austrovenus stutchburyi* count, Mac. – adult *Macomona liliana* count, PW – porewater concentration, NPP – net primary production (light O_2 fluxes), SCR – sediment community respiration (dark O_2 fluxes).

[a] Light chamber measurements only. [b] Single measurement per plot per site/season (PW = plot averages). [c] Spatial measurements dark chamber measurements replicated for light chamber measurements.

Table D.5 Pearson correlation coefficients between (a) environmental variables and (b) nutrient cycling during light and dark conditions in the unvegetated habitat (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Data from spatial and TUA seasonal datasets combined for environmental and fluxes of NH_4^+ and PO_4^{3-}, while N_2 efflux and denitrification efficiency (DE) measurements are only from the spatial dataset.

	Light[a]	Temp	Salinity[b]	Mud[c]	MGS[c]	OC[c]	Chl *a*	Phaeo	Aus.	Mac.	PW PO_4^{3-}[b]	PW NH_4^+[b]	NPP	SCR
(a) Environmental														
Temp	0.03													
Salinity[b]	0.69***	-0.40***												
Mud[c]	-0.64***	0.42***	-0.63***											
MGS[c]	0.49***	-0.25**	0.38***	-0.85***										
OC[c]	-0.50***	0.24**	-0.41***	0.87***	-0.85***									
Chl *a*	-0.14	0.16*	-0.23**	0.52***	-0.32***	0.58***								
Phaeo	-0.29**	0.06	-0.27***	0.66***	-0.65***	0.69***	0.72***							
Aus.	0.63***	-0.42***	0.60***	-0.59***	0.28***	-0.38***	-0.22**	-0.17*						
Mac.	0.33**	-0.18*	0.47***	-0.48***	0.33***	-0.36***	-0.33***	-0.33***	0.34***					
PW PO_4^{3-}[b]	0.61***	-0.21**	0.54***	-0.37***	0.08	-0.17*	-0.26***	-0.13	0.67***	0.02				
PW NH_4^+[b]	-0.59***	0.23**	-0.55***	0.85***	-0.85***	0.78***	0.21**	0.55***	-0.37***	-0.49***	-0.05			
(b) Nutrient cycling (response variables)														
Light														
NH_4^+	0.07	0.22*	0.03	0.13	-0.17	0.02	0.03	0.16	0.11	0.06	0.08	0.04	-0.46***	
PO_4^{3-}	0.22*	-0.04	0.28*	-0.08	-0.004	-0.001	0.18	0.25*	0.23*	0.03	0.22	-0.13	0.08	
Dark														
NH_4^+		0.27*	-0.15	0.25*	-0.30*	0.07	-0.09	0.20	-0.01	-0.004	0.02	0.26*		0.50***
PO_4^{3-}		0.09	0.08	0.09	-0.16	0.18	0.04	0.13	0.08	-0.09	0.24	0.12		0.26**
N_2		0.16	-0.12	-0.29*	0.16	-0.25	-0.31*	-0.19	0.27	0.20	0.08	-0.21		0.22
DE		-0.25	-0.03	-0.36*	0.32*	-0.25	-0.20	-0.29*	0.12	0.24	-0.01	-0.33*		-0.18

Light – chamber lux, Temp – chamber temperature, Mud – sediment percent mud content, MGS – median grain size, OC – sediment organic content, Chl *a* – sediment chlorophyll *a* content, Phaeo – sediment phaeopigment content, Aus. – adult *Austrovenus stutchburyi* count, Mac. – adult *Macomona liliana* count, PW – porewater concentration, NPP – net primary production (light O_2 fluxes), SCR – sediment community respiration (dark O_2 fluxes).

[a] Light chamber measurements only. [b] Single measurement per plot per site/season (PW = plot averages). [c] Spatial measurements dark chamber measurements replicated for light chamber measurements.

Table D.6 Results from fixed factor PERMANOVAs (9999 permutations; Euclidean distance-based matrices) comparing the effects of habitat (2 levels; seagrass (SG) & unvegetated (Unveg)), site (9 levels; see Figure 4.1) and where applicable treatment (2 levels; dark & light) on porewater (PW) NH_4^+ and PO_4^{3-} concentrations, fluxes of NH_4^+, PO_4^{3-} and N_2, and denitrification efficiency (DE) measured in summer 2019. For NH_4^+ and PO_4^{3-} fluxes, a three-way fixed factor PERMANOVA was undertaken, while two-way fixed factor PERMANOVAs were undertaken for porewater NH_4^+ and PO_4^{3-} concentrations, N_2 effluxes (net denitrification) and DE. Significant effects ($p \leq 0.05$) are given in bold.

					Post-hoc	
	Term	**df**	**Pseudo-F**	**p-perm**	**Habitat**	**Treatment**
PW NH_4^+	Site × Habitat	8	2.59	**0.0132**	**WPA** SG > Unveg **all remaining sites** SG = Unveg	
	Habitat	1	4.86	**0.0306**		
	Site	8	2.09	**0.0466**		
PW PO_4^{3-}	Site × Habitat	8	1.10	0.3764		
	Habitat	1	0.41	0.5185		
	Site	8	41.63	**0.0001**		
NH_4^+	Treatment × Site × Habitat	8	0.90	0.5277		
	Treatment × Site	8	1.29	0.2647		
	Treatment × Habitat	1	0.004	0.9483		
	Site × Habitat	8	3.33	**0.0026**	**BRW, MAT, TPU** SG = Unveg, **all remaining sites** SG < Unveg	
	Treatment	1	32.96	**0.0001**		Dark > Light
	Site	8	10.10	**0.0001**		
	Habitat	1	124.75	**0.0001**		
PO_4^{3-}	Treatment × Site × Habitat	8	0.71	0.6736		
	Treatment × Site	8	4.36	**0.0002**		**OTU & TUA** Dark > Light, **all remaining sites** Dark = Light
	Treatment × Habitat	1	6.32	**0.0133**	**Dark** SG = SND, **Light** SG < SND	**SG** Dark > Light, **SND** Dark = Light
	Site × Habitat	8	0.77	0.6338		
	Treatment	1	15.81	**0.0004**		
	Site	8	8.08	**0.0001**		
	Habitat	1	1.42	0.2390	.	
N_2	Site × Habitat	8	2.99	**0.0103**	**ATH & OTU** SG > Unveg. **all remaining sites** SG = Unveg.	
	Site	8	7.26	**0.0001**		
	Habitat	1	0.37	0.5584		
DE	Site × Habitat	8	1.81	0.1014		
	Site	8	1.89	0.0892		
	Habitat	1	7.06	**0.0117**	SG > Unveg.	

Table D.7 Results from fixed factor one-way PERMANOVAs (9999 permutations; Euclidean distance-based matrices) comparing the effects of habitat (2 levels: unvegetated & mudflat) on porewater (PW) NH_4^+ and PO_4^{3-} concentrations, fluxes of NH_4^+, PO_4^{3-} and N_2, and denitrification efficiency (DE) measured in summer 2019. Significant effects ($p < 0.05$) are given in bold.

	Term	df	Pseudo-F	p-perm
PW NH_4^+	Habitat	1	3.48	**0.0030**
PW PO_4^{3-}	Habitat	1	5.17	**0.0002**
NH_4^+ dark	Habitat	1	3.19	0.0788
NH_4^+ light	Habitat	1	0.06	0.8090
PO_4^{3-} dark	Habitat	1	1.05	0.3714
PO_4^{3-} light	Habitat	1	2.61	0.1155
N_2	Habitat	1	1.31	0.2732
DE	Habitat	1	3.23	0.0773

Table D.8 Results from fixed factor PERMANOVAs (9999 permutations; Euclidean distance-based matrices) comparing the effects of habitat (2 levels; seagrass (SG) & unvegetated sediment (Unveg.)), season (4 levels; spring (Sp), summer (Su), autumn (A), winter (W)) and where applicable treatment (2 levels; dark & light) on porewater (PW) NH_4^+ and PO_4^{3-} concentrations, and fluxes of NH_4^+ and PO_4^{3-} measured at TUA from spring 2018 to winter 2020. For NH_4^+ and PO_4^{3-} fluxes, a three-way fixed factor PERMANOVA was undertaken, while two-way fixed factor PERMANOVAs were undertaken for porewater NH_4^+ and PO_4^{3-} concentrations. Significant effects ($p \leq 0.05$) are given in bold.

					Post-hoc		
	Term	**df**	**Pseudo-F**	**p-perm**	**Habitat**	**Treatment**	**Season**
PW NH_4^+	Season × Habitat	3	1.01	0.3954			
	Habitat	1	1.96	0.1658			
	Season	3	6.37	**0.0006**			W > (Sp = Su = A)
PW PO_4^{3-}	Season × Habitat	3	0.17	0.9185			
	Habitat	1	0.69	0.4033			
	Season	3	4.67	**0.0062**			W < (Sp = Su = A)
NH_4^+	Treatment × Season × Habitat	3	0.13	0.9435			
	Treatment × Season	1	1.01	0.4050			
	Treatment × Habitat	3	1.83	0.1761			
	Season × Habitat	3	0.46	0.7050			
	Treatment	1	11.83	**0.0018**		Dark > Light	
	Season	3	1.13	0.3435			
	Habitat	1	13.79	**0.0005**	SG < Unveg.		
PO_4^{3-}	Treatment × Season × Habitat	3	0.68	0.5814			
	Treatment × Season	1	0.99	**0.0497**		**Su** Dark > Light, **all other seasons** Dark = Light	**Light** Su > (Sp = A = W) **Dark** Sp = Su = A = W
	Treatment × Habitat	3	0.79	0.3774			
	Season × Habitat	3	0.99	0.4086			
	Treatment	1	4.71	**0.0335**			
	Season	3	4.87	**0.0040**			
	Habitat	1	0.45	0.5119			

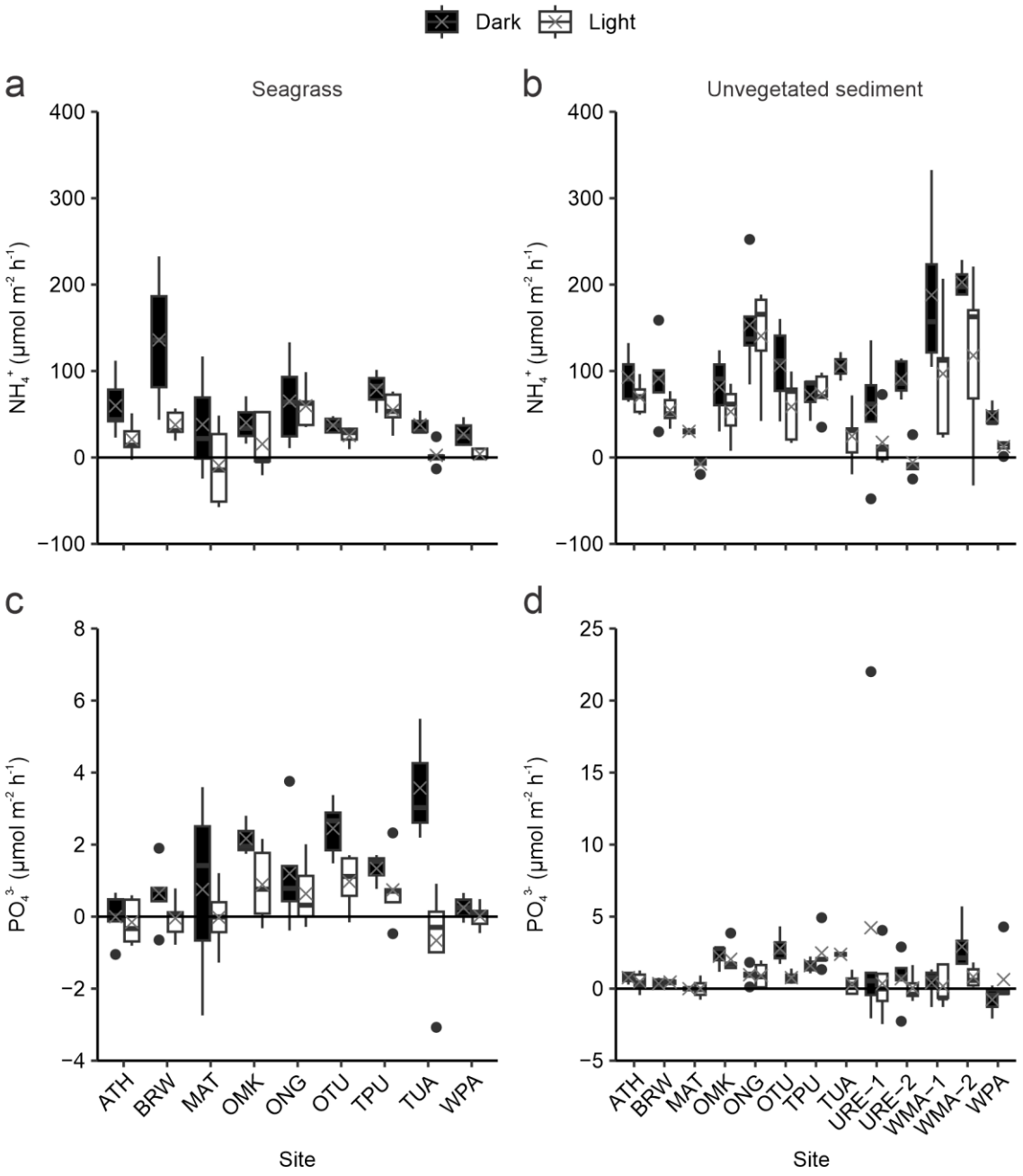


Figure D.1 Inter-site variability in NH_4^+ (a & b) and PO_4^{3-} (c & d) fluxes during dark (black) and light (white) conditions (positive = efflux, negative = influx) in the seagrass (a & c) and unvegetated sediment (b & d) habitat (n = 2-5). Crosses indicate mean values. Note differences in y-axes scale between plots.

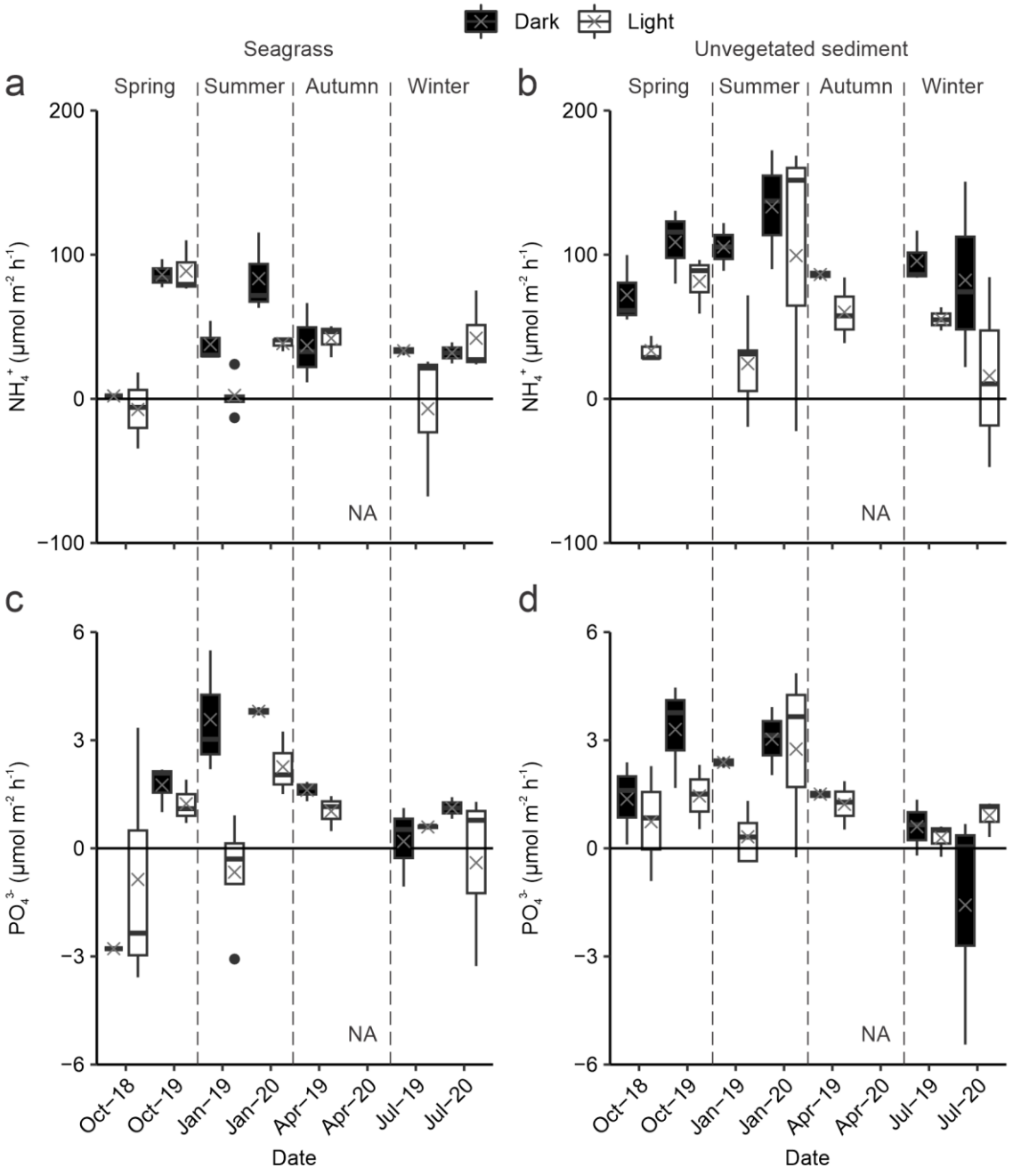


Figure D.2 TUA inter-seasonal variability in NH_4^+ (a & b) and PO_4^{3-} (c & d) fluxes during dark (black) and light (white) conditions (positive = efflux, negative = influx) in the seagrass (a & c) and unvegetated sediment (b & d) habitat (n = 1-5). Boxes arranged by austral season (indicated by the dashed line). Crosses indicate mean values. Note differences in y-axes scale between NH_4^+ and PO_4^{3-} flux plots.

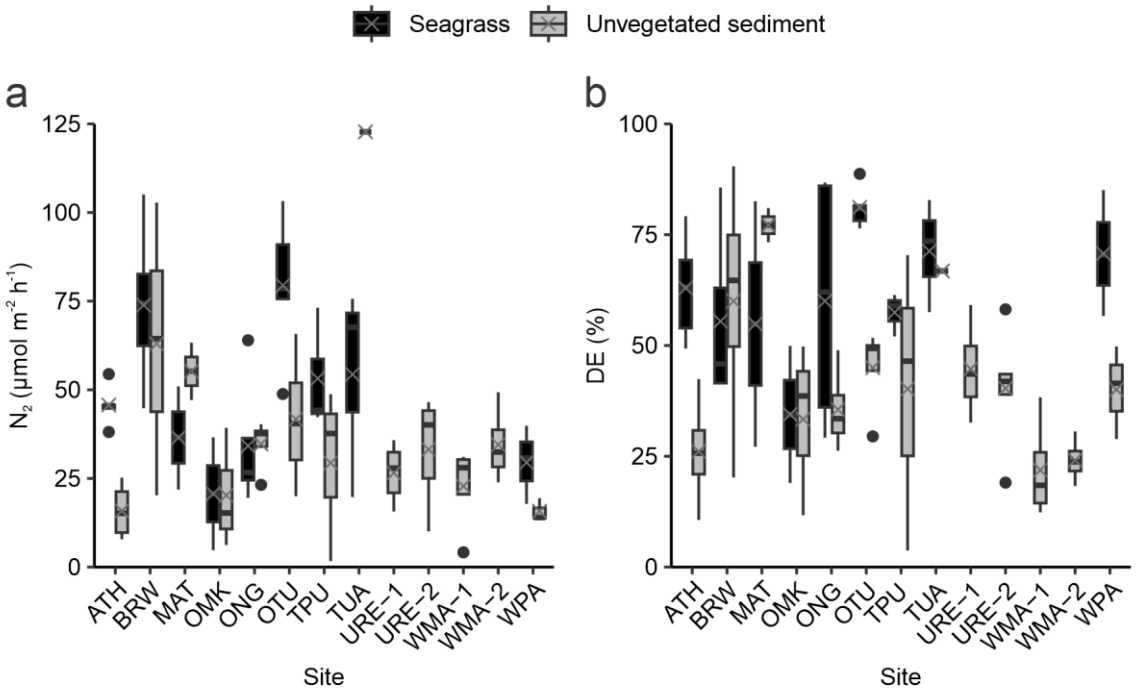


Figure D.3 Inter-site variability in N_2 effluxes (net denitrification) and denitrification efficiency (DE) as a function of habitat (seagrass – black; unvegetated sediment – grey; n = 1-5). Crosses indicate mean values.