Variation in benthic primary production during tidal emersion within different intertidal habitats

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Abstract

Intertidal habitats provide a wealth of ecosystem services including fuelling oceanic food webs and processing nutrients however, understanding the response of these habitats to emersion has been largely overlooked. Increasing rates of terrestrial sediment reaching the coast is degrading the water column light climate and thus the productive capacity of benthic primary producers during immersion. As a result, low tide production may become more significant in the near future. There is currently little knowledge regarding how primary production changes over an emersion period, in particular how it varies with habitat type and the impacts of environmental stressors, such as desiccation.

This study explored the spatial (between habitats) and temporal (over austral summer and over individual emersion periods) variability in benthic primary production within a temperate barrier-enclosed estuary. Research was conducted in three intertidal habitats (encompassing differences in sediment properties, dominant primary producers, and macrofaunal communities) in Tauranga Harbour, New Zealand. Seagrass (*Zostera muelleri*), shellfish, and polychaete dominated habitats were chosen as they represent common intertidal habitats found in temperate regions. Emerged gross primary production (GPP), at the community scale, was quantified by measuring changes in carbon dioxide (CO_2) concentration over time during a series of successive three minute incubations spanning the entirety of the low tide period. This was achieved by measuring fluxes of CO_2 in benthic incubation chambers under both light and dark conditions, to derive net primary production (NPP) and sediment oxygen consumption (SOC) respectively. CO_2 fluxes were then analysed to determine whether sampling month or time exposed had a significant difference on the photosynthetic capacity of different intertidal habitats. Sedimentary and environmental variables were sampled to identify any key predictors of emerged primary production.

Primary production (both NPP and GPP) measured in the seagrass habitat exceeded both bare sediment habitats (by up to 11 times) due to inherent differences in the dominant primary producers (seagrass vs. microphytobenthos) and the associated photosynthetic biomass. Within bare sediment habitats, significant differences in

primary production were attributed to variation in sedimentary characteristics (particularly mud content) and macrofaunal communities. GPP was standardised for photosynthesising biomass to provide a measure of photosynthetic efficiency (GPP_{SG} and $GPP_{chl\ a}$). Once standardised, month to month differences within individual habitats disappeared, thus initial temporal differences measured over austral summer were primarily attributed to differences in biomass. Temporal trends over individual emersion periods were not consistent across all habitats. GPP_{SG} in the seagrass habitat increased hourly (from T1 to T4) on multiple sampling occasions, while no consistent trends were evident in either of the bare sediment habitats.

This study recognises that emerged primary production can equal, if not exceed, rates of production and carbon fixation during immersion. This reinforces the importance of including emerged intertidal habitats in global carbon budgets. Especially as the contribution of low tide production will become increasingly important as elevated turbidity levels may compromise the productive capacity of submerged habitats. Understanding the dynamics of intertidal habitats under emersion is valuable as they represent a significant proportion of coastal ecosystems in New Zealand and around the globe.

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Table of Contents

List of Figures

List of Tables

Chapter One

Introduction

1.1 Motivation

1.1.1 The intertidal environment

New Zealand has one of the longest coastlines in the world, amounting to 11,000 kilometres, encompassing a diverse range of coastal environments (Hume *et al.*, 1992). Coastal ecosystems are some of the most productive regions worldwide due to high nutrient loads, retention capabilities, and high light levels that facilitate primary production (Hopkinson *et al.*, 1999). Estuaries are one of these key coastal ecosystems, and typically exhibit spatial and temporal gradients in salinity, nutrients, terrestrially derived sediment and often community structure (Elliott & McLusky, 2002). New Zealand alone has over 400 estuaries (Thrush *et al.*, 2013) and intertidal regions contribute anywhere between 30 and 50% to the total estuarine area in New Zealand. Therefore, understanding the intertidal zone is relevant to a significant proportion of New Zealand's marine environment.

1.1.2 Benthic primary producers

Although many studies focus on the pelagic environment, the biomass of benthic primary producers often outweighs those in the overlying water column (Varela & Penas, 1985; Lukatelich & McComb, 1986; MacIntyre & Cullen, 1995). Coastal regions are often dominated by benthic primary production due to high nutrient concentrations in sediment porewaters and sufficient light levels reaching the benthos due to shallow waters (Ask et al., 2016). Additionally, many key ecological functions occur in the benthos and a significant proportion of coastal marine food webs rely on benthic primary production. Previous studies have recognised that benthic production drive approximately 80% of food webs in the coastal-marine environment (Christianen *et al.*, 2017). In just one example up to 95% of benthic macrofauna were dependent on the benthic primary producers present (Herman *et al.*, 2000). Thus, reinforcing how important benthic ecosystems are to the survival

of key basal resources and as a result a diverse and thriving aquatic ecosystem. New Zealand's temperate estuaries are dominated by two benthic primary producers, microphytobenthos (MPB), and a single seagrass species (*Zostera muelleri*) (Jones *et al.*, 2008).

MPB, the microscopic photosynthetic organisms that inhabit the sediments surface, are an integral component of shallow water coastal ecosystems (Middelburg *et al.*, 2000). There is significant focus on primary production within the scientific community however a large proportion concentrates on macroalgae and seagrasses while overlooking the importance of MPB production (Ask *et al.*, 2016). Within estuarine systems, MPB are a key energy source for coastal heterotrophs and have been known to contribute up to 50% of total production (Underwood & Kromkamp, 1999; Cahoon, 2006). It is this contribution that is heavily responsible for the autotrophic nature of these systems (Migné *et al.*, 2016). The organic carbon produced via algal primary production fuels aquatic food webs and is also often transported to adjacent ecosystems (Duarte & Cebrián, 1996; Herman *et al.*, 2000; Middelburg *et al.*, 2000; Ask *et al.*, 2016), thus, having a profound effect on a large spatial scale. Not only does MPB support significant secondary production, they also support many wider ecosystem services. This includes influencing the structure and function of benthic sediments, as well as facilitating nutrient cycling (MacIntyre & Cullen, 1995; Miller *et al.*, 1996; Cahoon, 2006). For example, MPB plays a key role in the removal of excess nutrients, and in facilitating remineralisation pathways in the coastal environment (Sakamaki *et al.*, 2006; Hochard *et al.*, 2010; Komorita *et al.*, 2012).

Microalgae in shallow water systems are influenced by numerous environmental factors including temperature, nutrients, tides, and grazing (Pniewski *et al.*, 2015). However, incident light remains the greatest control on MPB production, closely followed by photosynthesising biomass, which also appears to be a function of light (MacIntyre & Cullen, 1995; Underwood & Kromkamp, 1999). It is apparent that MPB have the ability to compensate reductions in biomass, due to unfavourable conditions (i.e. weather induced deposition), with short periods of rapid growth when conditions allow (Migné *et al.*, 2016). In addition, MPB exhibits significant spatial variation as a function of hydrodynamics, which in turn influences local sediment characteristics through erosion and deposition (Migné *et al.*, 2016). MPB biomass typically increases in regions of high mud content (MacIntyre & Cullen,

1995). However, this does not always result in increased production, as high mud content (25-30%) has been known to detrimentally affect ecosystem functioning (Pratt *et al.*, 2014a). As a result, it is expected that rates of emergent primary production are expected to vary across habitats of varying sediment characteristics (MacIntyre & Cullen, 1995). Literature also shows that the relationship between MPB biomass and sedimentary characteristics seems to be extremely complex (Yallop *et al.*, 1994; Cahoon *et al.*, 1999; Lelieveld *et al.*, 2003). Especially as macrofaunal community composition can regulate MPB biomass, both directly through grazing, as well as indirectly by influencing the sediment structure (i.e. through bioturbation). Bioturbation and irrigation by macrobenthos can influence the permeability of sediments and thus increase solute transport and gas diffusion rates which could otherwise limit photosynthesis and respiration processes (Christensen *et al.*, 1984). Consequently, the community type present within different intertidal habitats will exert a control on the potential productive capacity of the system.

MPB employ multiple techniques for photoregulation to ensure their success and survival in the dynamic and unstable environment the inhabit (Underwood *et al.*, 2005). The motile nature of MPB allow vertical migrations within the water and top sediment layers. In response to incident light individual cells will cycle positions at the surface and lower down, with upper cells shading those below to confer benefits for community production as a whole (Underwood *et al.*, 2005). Some studies have quantified this potential migration to a few centimetres in mud and up to 12 cm in sand flats (Kingston, 1999; Middelburg *et al.*, 2000). This reinforces that sediment photosynthesis largely depends on sediment composition as muddy sediments have a decreased sediment photic depth as firmly packed sediments attenuate light quicker than looser, sandier regions (Pniewski *et al.*, 2015). This micromigration adaptation is predicted to be a management strategy to avoid photoinhibition, overexposure, desiccation and grazing (Underwood *et al.*, 2005). Furthermore, different taxa of benthic microalgae are adapted to fill different light-related niches, with some lying at the surface under only low light conditions typically experienced at the start of the day before migrating downwards, and others favouring higher light conditions (Underwood *et al.*, 2005). These taxa-specific adaptations appears to benefit total biofilm productivity. As a result the proportions of different MPB taxa to the biofilm may determine potential photosynthetic capacity under different

light conditions (Underwood & Kromkamp, 1999). The possession of both physiological and behavioural adaptations of MPB to their environment is a key component dictating their success, especially in intertidal systems where abiotic conditions are more variable.

New Zealand's only primarily intertidal seagrass, *Zostera muelleri*, also plays a key role in primary production in temperate intertidal systems, especially during summer months (Jones *et al.*, 2008). Seagrass meadows are one of the most ecologically and economically valued marine ecosystems, facilitating carbon storage, providing habitat for juvenile fish, bird and invertebrate species, and playing a key role in nutrient cycling (Heck *et al.*, 2003; Fourqurean *et al.*, 2012; Costanza *et al.*, 2014; Parsons *et al.*, 2014). Since the 1950s *Z. muelleri* has declined by up to 90% in subtidal regions and by 38% in intertidal areas within Tauranga Harbour (Inglis, 2003; Park, 2016), this follows global trends in seagrass meadow decline (Waycott *et al.*, 2009). Reductions in the spatial extent of seagrass beds have been attributed to multiple causes including increased sedimentation, coastal development, and the expansion of mudflats that has reduced the amount of suitable habitat available to sustain seagrasses (Turner & Schwarz, 2006). In support of this, losses in seagrass biomass has been attributed to light limitations due to elevated levels of turbidity, as tested in pulsed suspended sediment events (Longstaff & Dennison, 1999; Ruiz Fernandez & Romero, 2001). The scientific literature lacks significant work surrounding the response of intertidal vegetation (seagrass) to the air exposure experienced during emersion periods (Ouisse *et al.*, 2011). Some evidence suggests that *Z. muelleri* possess a range of physiological adaptations to optimise photosynthesis and prevent photoinhibition, including modifying leaf shape or altering concentrations of light harvesting and protective pigments in response to incident light levels (Kohlmeier *et al.*, 2017). Despite this, more information regarding low tide stressors is needed as the high variability in abiotic factors within the intertidal environment is likely to influence biomass and productivity (Ouisse *et al.*, 2011; Bulmer *et al.*, 2016).

Seagrass meadows have been known to use low tide periods for the rapid uptake of atmospheric carbon dioxide (CO_2) (due to elevated assimilation in air compared to water), however long exposure periods increase the risk of desiccation and photoinhibition due to the lack of a protective layer of water (Bulthuis & Woelkerling, 1983; Adams & Bate, 1994; Leuschner *et al.*, 1998; Boese *et al.*,

2003). It is expected that the upper zonal limit of intertidal vegetation is defined by the distance from the low tide mark as this is a function of exposure time and thus desiccation (Leuschner *et al.*, 1998). It has been proposed that net photosynthesis rates, in European *Zostera* species, can drop by 50% following a 30% loss in leaf water content (Leuschner *et al.*, 1998). However, it is unknown if New Zealand *Zostera* respond in a similar way. Hydrodynamics and the fortnightly spring/neap cycle is likely a predictor in seagrass distribution on intertidal shores. However it is recognised that this capacity differs between species. Lower limits are expected to be determined by light availability as this is also a key determinant of photosynthesis (Leuschner *et al.*, 1998). Seagrasses have commonly been studied in isolation, such as at the leaf scale (Ouisse *et al.*, 2011), however this fails to recognise that they are part of a much wider community, in which species interactions can greatly modify a species productivity or response. Not only is light and the duration of exposure important for intertidal seagrass habitats, other key factors influencing the success of seagrass include sediment conditions, hydrodynamics, and nutrient concentrations (Koch, 2001; Matheson & Schwarz, 2007).

Primary producer type and biomass influences production within intertidal environments. However, the relationship between photosynthesising biomass and primary production is not always linear (Underwood *et al.*, 2005). In order to compare rates of gross primary production across habitats with the same dominant primary producers (i.e. bare sediment habitats dominated by microphytobenthos) a measure of photosynthetic efficiency can be calculated (Pratt *et al.*, 2014b). This is possible by normalising production estimates (i.e. GPP) by the amount of photosynthetic biomass, this is typically above-ground biomass in seagrass habitats and chlorophyll *a* concentration, a proxy for microphytobenthos, in bare sediment habitats. By removing biomass from the equation, other variables influencing production can be recognised.

1.1.3 Emerged primary production

Terrestrial influence on the coastal environment can have detrimental effects on primary production, typically due to water clarity issues, brought on by sedimentation events (Thrush *et al.*, 2004; Seers & Shears, 2015). This increased

turbidity, coupled with abiotic factors such as particle resuspension from wind-wave action and the influence of tidal cycles will likely begin to compromise the rate of benthic primary production during immersion (Green & Coco, 2007; Talke & Stacey, 2008). As a result the production by benthic microalgae is often assumed to be restricted to the emersion period, due to light limitation, owing to the turbidity during flood tides (Colijn & De Jonge, 1984; Guarini *et al.*, 2000; Migné *et al.*, 2004). This is supported by a study that named MPB as the major functional group in turbid estuaries with very small photic zones (~400 μm) and/or limited periods of production stimulating light levels (Underwood *et al.*, 2005). The acceleration of human-induced stressors such as eutrophication and turbidity affecting the coastal environment has shifted focus from the immersed environment to the emerged period, to determine if emergence can offer resilience in intertidal regions that are compromised during inundation (Drylie *et al.*, 2018). Therefore, benthic community metabolism must be measured during emergence, as well as in submerged conditions, in order to quantify the contribution of different tidal states to total benthic primary production.

Primary production under emerged conditions has been a recent focus of numerous studies as impacts on submerged productivity are discussed. Current research suggests there is potential for emerged microalgal production to be double that of high tide production (Asmus, 1982; Varela & Penas, 1985; Pinckney & Zingmark, 1991). An early study on intertidal macroalgae (Johnson *et al.*, 1974) has shown that production rates (mid-high intertidal zones) can be between 1.6 and 6.6 times higher in air than water, at the same irradiance and temperature (Johnson *et al.*, 1974). Additional studies (Migné *et al.*, 2016) have seen CO_2 fluxes, a measure of primary production, increase over the emersion period. This may be explained by the increased rate of gas exchange in air than water. As the reduction in sediment water content as the time of exposure increases would promote greater rates of CO_2 exchange across the sediment-air interface. The presence of low tide periods of higher CO_2 emission is estimated to contribute to a 30% increase in mineralisation of organic carbon when compared to submerged conditions alone (Sasaki *et al.*, 2009). Thus, tidal state plays a significant role in controlling the total gross primary production on intertidal flats.

Intertidal systems are highly stressful environments due to constant fluctuations in light availability, temperature and moisture (Thrush *et al.*, 2013). Additionally,

even fluctuations in the light regime reaching the benthos is a function of multiple other variables including cloud cover, tidal height, water depth and turbidity which all operate on different temporal scales ranging from tidal cycles to seasonal climatic changes (Kirk, 2011). The environmental variability experienced in these systems exerts a control on ecosystem functioning (Migné *et al.*, 2016). Short-term (over one low-tide period) changes in production are often a result of changes in incident light levels, attenuation, sedimentary photic depth and sun angle (Underwood *et al.*, 2005). Whereas, longer-term variation is typically due to local climates. It is valuable to assess primary production at a range of scales, not only seasonally, but within individual seasons (i.e. austral summer), to determine any episodic changes than may be overlooked if sampling only occurred once per season or year. Substantial data, collected over extended periods of time, is required in order to produce accurate annual estimates of production and carbon sequestration that can in turn be used in local and global carbon budgets.

A key stressor that has been disregarded in many low tide production studies is desiccation (Holmes & Mahall, 1982; Coelho *et al.*, 2009; Ouisse *et al.*, 2011). Current research suggests that natural desiccation rates appear to be reasonably low, allowing for photosynthetic capacity to remain high for the majority, if not the entirety, of the emersion period. In addition, most intertidal species can continue to assimilate carbon at a high rate even after 30-60% water loss. However the extent that desiccation influences GPP in temperate New Zealand estuaries is yet to be quantified. Desiccation does not only influence the benthic primary producers but also other organisms within the intertidal habitats. For example macrofauna are at the mercy of an ever changing environment, with potential risks including extremely high temperatures and the potential for desiccation during emersion (Migné *et al.*, 2009). Emerged respiration rates are therefore likely to vary from submerged rates due to differences in gas exchange as well as the changes in metabolic activity of benthic organisms (Migné *et al.*, 2009). Numerous studies have found benthic community respiration to decrease during low tide periods, as many species are inactive in the absence of the overlying water column (Asmus, 1982; Gribsholt & Kristensen, 2003; Cook *et al.*, 2004).

1.1.4 Methods for quantifying benthic primary production

Closed-chamber systems have been used in the past to measure CO_2 fluxes across benthic sediments (Migné *et al.*, 2002). CO_2 is measured as it is the waste product of photosynthesis and allows estimation of the rate of gross primary production. CO_2 fluxes are calculated by measuring the change in CO_2 concentration over time (Spilmont *et al.*, 2006). These methods facilitate the measure of CO_2 exchange across the sediment-air interface in situ, using an infrared gas analyser (Spilmont *et al.*, 2006). Thus, allowing estimates of primary production and respiration across benthic sediments, under respective light and dark conditions respectively. CO_2 (and O_2) fluxes are accepted by the scientific community as reliable measures of benthic metabolism at the community level as chambers encompass sediment, phyto- and zoobenthos (Migné *et al.*, 2002; Tang & Kristensen, 2007). This method causes minimal disturbance to the underlying sediment and integrates the heterogeneous nature of MPB cover over the chamber area (Migné *et al.*, 2002; Spilmont *et al.*, 2006). Therefore, flux approaches can increasingly be used in more heterogeneous environments where other methods would be impractical (Streever *et al.*, 1998)

This method is useful in estimating net and gross productivity as well as comparing production across multiple habitats, estuaries, or ecosystems (Streever *et al.*, 1998). The results from these systems can also be used in identifying the key factors controlling this production (Migné *et al.*, 2002). As well as assessing spatial variation, the short-term nature of incubation methods is beneficial in recognising the important variables controlling production (Streever *et al.*, 1998; Migné *et al.*, 2002). However, this can prove difficult in-situ as multiple environmental factors can vary simultaneously, making it hard to pinpoint cause and effect relationships (Darley *et al.*, 1976). This method also allows for a series of successive incubations to be conducted, producing a time series projection of how primary production changes over an emersion period. A benefit of using discrete measurements over the tidal cycle is that you can quantify temporal and spatial variation in production for a specific time of day, tide, and tidal regime (Migné *et al.*, 2009). This is often more beneficial than annual estimates which tend to integrate production and respiration variability, which can lead to an inaccurate image of daily, tidal, or seasonal estimates (Migné *et al.*, 2009). As this method is repeatable and it can also

be used as a measure of tracking ecosystem productivity, which could be used as a proxy for ecosystem health, through time.

Coastal environments are currently under threat as the amount of terrestrially derived sediment and nutrients reaching the coast has increased following urbanisation and the intensification of other land use practices (Bonsdorff *et al.*, 1997; Smith & W Schindler, 2009; Cosme & Hauschild, 2017). Detrimental ecosystem responses, such as eutrophication, are becoming increasingly prevalent, resulting in biodiversity loss, ecosystem instability and a simplification in community structure. All of these factors, directly or indirectly, affect the productive capacity of our coastal ecosystems. Thus, measuring and monitoring coastal productivity is important in determining how prevalent coastal stressors are affecting benthic communities (Bonsdorff *et al.*, 1997). Previous studies have used closed chamber methods to determine the fate of CO_2 in intertidal environments to help predict the future for global carbon cycles in the face of rapid environmental change (i.e. global warming) (Klaassen & Spilmont, 2012). Understanding the carbon balance of these crucial ecosystems may have a role in monitoring in the longer term and the transition of intertidal environments from sources to sinks of CO_2 may be a crucial tipping point. Consequently, understanding the nature and metabolic balance of intertidal ecosystems as either sinks or sources of CO_2 for the atmosphere requires quantifying both primary production and respiration (Heip *et al.*, 1995; Spilmont *et al.*, 2006; Migné *et al.*, 2016).

1.1.5 Knowledge gap

Quantifying benthic production during emersion has only been looked at three times in a New Zealand setting (Bulmer *et al.*, 2015; Bulmer *et al.*, 2017; Drylie *et al.*, 2018) and is yet to investigate how production may change over an individual low tide. By adapting previous methods (Migné *et al.*, 2002; Drylie *et al.*, 2018), by reducing incubation periods, a greater number of incubations can be conducted within a single tide (up to 48) providing time-series like data with replication and greater statistical power. This is advantageous when compared to overseas studies in which only one pair of incubations (one light and one dark) are conducted for extended durations (20-30 min) (Migné *et al.*, 2002; Migné *et al.*, 2009; Ouisse *et al.*, 2011). The longer an incubation, the more abnormal the situation will become,

when compared to initial in situ conditions, thus keeping incubations short is paramount in this study. In addition, environmental stressors present at low tide particularly desiccation has been given little attention within the literature, thus I aim to assess any effects of desiccation that may occur. This study will provide context for estimating primary production in New Zealand estuaries. This will be a useful addition to the scientific literature as many studies to date have not been replicated through time, and have been conducted in regions with relatively low light concentrations (not exceeding 600 μmol m^{-2} s^{-1}) which is a stark contrast to the austral summer conditions experienced in many New Zealand estuaries (Underwood *et al.*, 2005).

1.2 Study objectives

The key objective of this study is to determine if rates of GPP differ in different intertidal habitats and how rates of benthic GPP change between months in austral summer and over low tide exposure periods. I also wish to identify which environmental variables exert control on primary production and photosynthetic efficiency and whether or not these may change over the emersion period and between different intertidal habitats.

In reading the relevant literature, I conceptualised three goals:

1. To investigate whether the rates of emerged gross primary production vary in different intertidal habitats.
2. To explore how gross primary production changes over summer months and over an emersion period in different intertidal habitats.
3. To determine which environmental variables explain the most variation in emerged gross primary production in each of the intertidal habitats.

To achieve these goals, the chamber design and method used by Drylie *et al.* (2018) was adapted slightly to achieve the study objectives. A field experiment was then conducted, using the above method, to quantify how benthic primary production changes over low tide exposure periods. This was conducted in three intertidal habitats, a seagrass meadow, a shellfish bed, and a polychaete dominated region. Sites were visited monthly over the November 2018 to February 2019 period to span the duration of austral summer and identify any short-term climatic variations and their contribution to benthic primary production.

Chapter Two

Methodology

2.1 Study site

Tuapiro Point lies in the northern arm of Tauranga Harbour, located on the northeast coast of the North Island of New Zealand (**Figure 2.1**). Tauranga Harbour is a shallow (mean depth = 2.1 m), large (200 km^2), barrier-enclosed estuary. This tidally dominated estuary consists of extensive intertidal sand flats (66% of high tide area), connects to the Pacific Ocean by a northern and southern entrance, and experiences a diurnal tidal cycle. The study site has an expected emersion period for mid-intertidal zones of between three and five hours, with high tide depths between 1.2 and 1.6 meters. This site typically experiences annual mean (range) temperatures of 17ºC (0.3 – 32), daylight photosynthetically active radiation (PAR) of 638 µmol m^{-2} s^{-1} (5.98 – 2240), and relative humidity of 75% (21 – 100) (NIWA, 2019).

Seagrass, shellfish and polychaete dominated habitats were selected for sampling as they represent the major intertidal habitats found in Tauranga Harbour and other barrier-enclosed systems (**Table 2.1, Figure 2.2**). These habitats also distinguish between the two dominant primary producers found in intertidal environments, seagrass and microphytobenthos (MPB). Real time kinematic (RTK) surveying accurately (to 1 mm) identified the location and elevation of each habitat, to ensure the habitats were within close proximity, and of similar elevation, to minimise variation associated with broader scale environmental variables, such as immersion period, currents, catchment use and climate. An additional site visit on October 8th 2018 resulted in the selection of one relatively homogeneous area (9 m^2), within each habitat; with care taken to minimise intra-habitat variability (i.e. seagrass cover was a minimum of 65%).

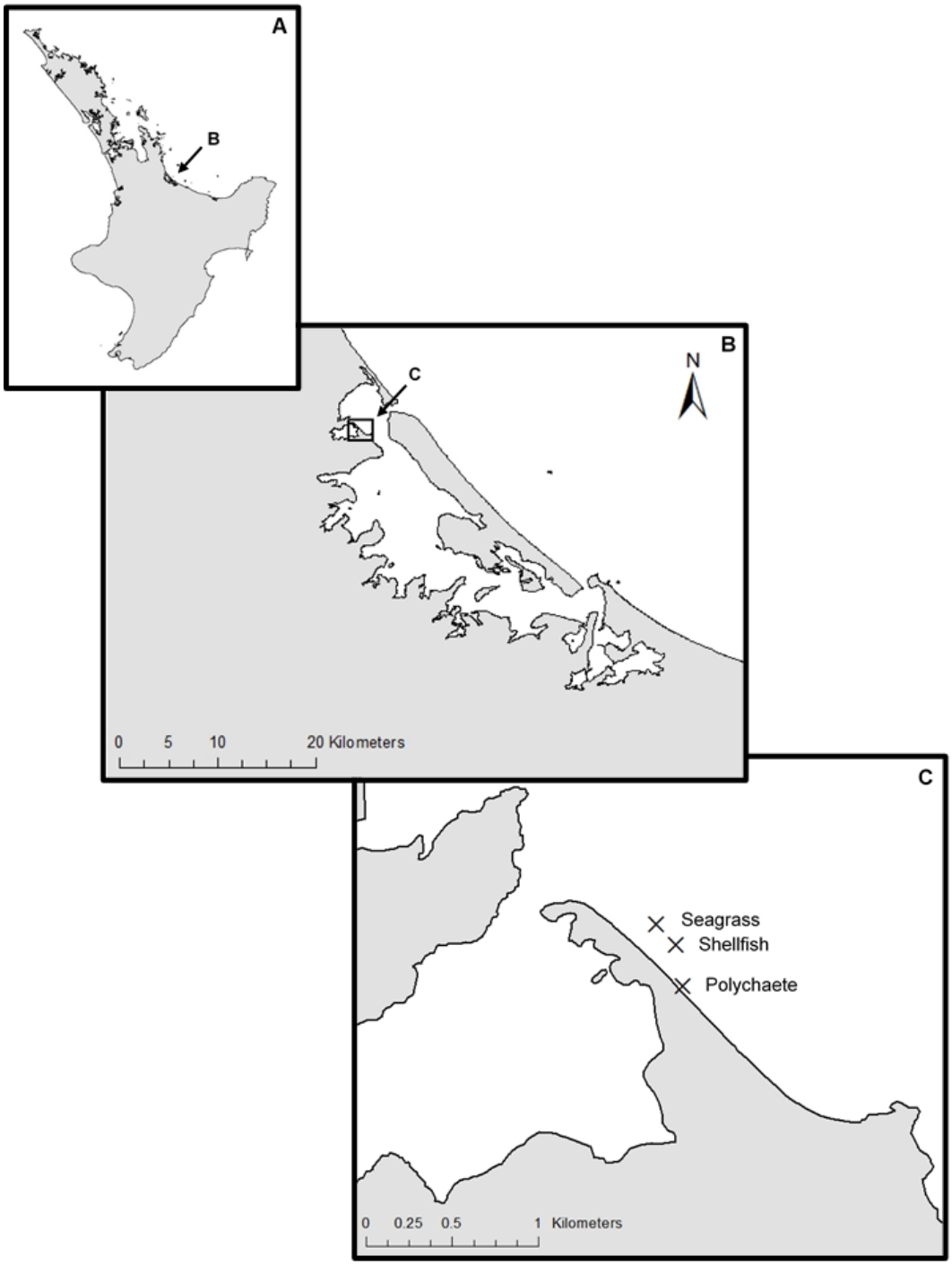

Figure 2.1. Map of North Island, New Zealand (A), Tauranga Harbour (B), and the location of the habitats sampled at Tuapiro Point (C).

Table 2.1. GPS coordinates of the three habitats (seagrass, shellfish, and polychaete) within Tauranga Harbour (NZGD2000).

Habitat	Latitude	Longitude	Elevation (MASL)
Seagrass	37°29'08.88"S	175°57'14.69"E	-0.378
Shellfish	37°29'12.61"S	175°57'19.92"E	-0.417
Polychaete	37°29'20.33"S	175°57'19.92"E	0.090

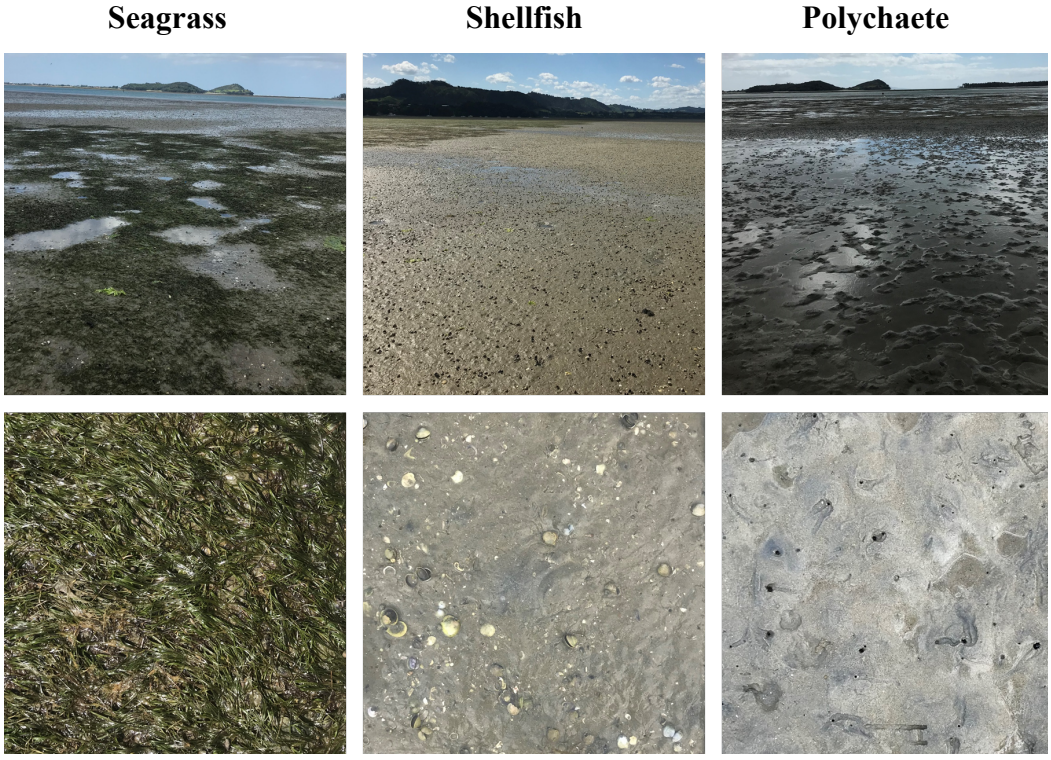

Figure 2.2. Site and detail photographs of the three sampled habitats at Tuapiro Point, Tauranga Harbour.

2.2 Field study

Initial sampling of emerged primary production took place in early November 2018, with repeated measurements occurring in the first week of each month, concluding in February 2019. This timeframe and frequency of sampling was chosen to capture the temperature extremes and environmental variation experienced in austral summer. During each campaign, the three habitats were measured on consecutive days with midday low tides (between 11:00 and 13:00 NZST) to minimise changes in weather and ensure exposure coincided with natural peaks in irradiance (Drylie *et al.*, 2018).

A Solinst level logger was introduced to each habitat for the duration of each sampling campaign (**Table 2.2**) to log tidal/water level fluctuations (1 Hz) below the sediment surface. This was used to understand the tidal cycle at the site and how the water table may be influencing gas exchange on the intertidal flats above.

To assess local environmental conditions (PAR, air temperature, sediment temperature and relative humidity) a weather station was set up once seawater drained from the site. A LICOR PAR logger was set up to measure incident light, near the sediment surface. Air temperature and relative humidity was measured approximately one metre above the sediment surface, with an apparatus that included a radiation shield to minimise the influence of heating from the sun. A temperature probe inserted to a depth of five centimetres measured sediment temperature throughout the day. Environmental data was recorded using a Campbell Scientific Data Logger (CR1000) at a frequency of 1 Hz, and was used to track what conditions were experienced during productivity measurements (**Table 2.2**). HOBO loggers were placed at the sediment surface near the weather station to provide a secondary measure of temperature and light, as well as inside each chamber to ensure that the temperature and light within the chambers during incubations were not significantly different from ambient conditions. Environmental variables were measured as they are likely to influence the low tide production monitored during the course of this study, and therefore will help to determine key controls on emerged primary production.

Once seawater had completely drained from the site, six benthic incubation chamber bases (L50 x W50 x H15 cm) were deployed to a depth of 5 cm. With lids fitted they encapsulated a volume of ~41 L over a sediment area of 0.25 m^2. Chamber placement was randomised within the 9 m^2 area on each sample date, given that chambers were at least 1 m apart and the same area was never sampled twice. A LiCOR 8100A Automated Soil CO_2 Flux System Infrared gas analyser (IRGA) measured CO_2 concentration (ppm) in a series of benthic incubations. For the duration of each incubation, the bases were fitted with a transparent domed lid, housing a thermocouple to measure air temperature within the chamber. The IRGA measured the CO_2 concentration of a continuous stream of air circulated through nylon tubing from the chamber to the Li-COR 8100A, at a frequency of 1 Hz (Drylie *et al.*, 2018). Measurements were made first under ambient light (net primary production (NPP)) in the 6 chambers and then in the dark (benthic

respiration or sediment oxygen consumption (SOC)). Immediately after each light incubation, a 100% shade cloth was fitted above the chamber base to darken the chamber area for a 30-min period, to ensure all photosynthetic processes had ceased prior to the dark incubation (Drylie *et al.*, 2018). Incubations were three and a half minutes in duration; with the initial 30 s period needed to stabilise the flux (this initial 30 s flux was removed from the data series prior to analysis). This was shorter than previous studies (Healy *et al.*, 1996; Streever *et al.*, 1998; Clavier *et al.*, 2011; Drylie *et al.*, 2018) but did not compromise the linear relationship between CO_2 concentration and time (tested in preliminary trials), and meant more replicate measurements could be completed during an emersion period. The shorter incubation period also minimised the potential for humidity and temperature changes to influence gas diffusion. Successive incubations, alternating between six in light and six in dark conditions, monitored gas exchange for the entire emersion period (~4 h) to determine how primary production changed over a low tide period (**Table 2.2**).

Prior to and at the end of all incubations, four small sediment cores (2.6 cm diameter x 2 cm deep) were collected from directly outside (before) and inside (after) each chamber (**Table 2.2**). Samples were pooled in whirl bags, stored in the dark, and frozen for later analysis of sediment properties (grain size, chlorophyll *a*, organic content) to characterise the sedimentary environment of each habitat. To calculate sediment water content and porosity, four 0-2 cm and four 5-7 cm cores were taken using a syringe corer (2.6 cm diameter) in the area surrounding the chambers, before the first incubation and following each series of six incubations. These were pooled into two pre-weighed containers (watertight plastic jars that could withstand being heated to 60 °C without losing weight), corresponding to the two depths. Containers were then stored upright, to prevent leakage, and in the freezer until analysis for percentage water content, and subsequent porosity calculations, could be completed. Porosity measurements provide useful information regarding sediment drainage which can influence rates of gas exchange and thus primary productivity.

At the seagrass habitat, quadrat photographs were taken of each seagrass chamber to facilitate percentage cover estimates using random count analysis (**Table 2.2**). After incubations, a large core (13 cm diameter x 15 cm deep) was taken from the centre of each chamber for calculation of seagrass biomass. This is important as primary production rates are often a function of biomass, and these measurements

will help account for this, separate from other environmental variables. Seagrass samples were sieved over a 1 mm mesh, in situ, and laid flat between foil sheets for freezing.

On initial (November) and final (February) sampling of emerged primary production in all habitats, a large macrofauna core (13 cm diameter x 15 cm deep) was taken in close proximity to each chamber and sieved in situ, over a 500 μm mesh. Resultant samples were preserved in 70% isopropyl alcohol and stored for later species identification. This allowed the macrofaunal community to be characterised and compared across the three habitats.

Table 2.2. The sampling frequency and number of CO_2 flux measurements, sediment, environmental and other variables sampled, when visiting intertidal habitats each month. Macrofauna was sampled at the chamber scale in November and February.

	T0	T1		T2		T3		T4		Scale	Total n	Frequency (Hz)
CO_2 fluxes												
Light (NPP)		✓		✓		✓		✓		Chamber	24	
Dark (SOC)			✓		✓		✓		✓	Chamber	24	
Sediment characteristics												
Grain size	✓								✓	Chamber	12	
Mud content	✓								✓	Chamber	12	
Organic matter	✓								✓	Chamber	12	
Chlorophyll *a*	✓								✓	Chamber	12	
Porosity	✓	✓	✓	✓	✓	✓	✓	✓	✓	Site	9	
Environmental variables												
PAR	→									Site		1
Air temperature	→									Site		1
Sediment temperature	→									Site		1
Relative humidity	→									Site		1
Water table level	→									Site		1
Other												
Seagrass									✓	Chamber	6	

2.3 Laboratory analysis

Sediment samples were thawed, homogenised, and divided into three subsamples corresponding to analysis of grain size, chlorophyll *a* and phaeopigment, and organic matter. Grain size samples were digested in 10% hydrogen peroxide until all organic matter had been removed (indicated by the ceasing of bubble formation) and particle size distribution determined with a Malvern Mastersizer 2000 (particle size range 0.05 – 2000 μm). Data was reported as median grain size (MGS) and % mud (< 63 μm) content. Pigment samples were freeze-dried to standardise sample water content prior to homogenising and subsampling. Pigment extraction was achieved by leaving 0.15 g subsamples to steep overnight following the addition of 10 mL of 90% buffered acetone. Samples were subsequently analysed on a Turner 10-AU fluorometer using an acidification step (1 mL hydrochloric acid) to separate chlorophyll *a* and phaeopigments (Arar & Collins, 1997) and reported as μg g^{-1} dw sediment. Organic content was determined by percent weight loss on ignition of a 10 g sediment sample, dried at 60°C until reaching a constant weight, then subsequently combusted at 550°C for 4 h (Heiri *et al.*, 2001). Sediment porosity was determined by measuring the water loss in the fixed volume sample after drying at 60°C (until constant mass), assuming a porewater density of 1 g cm^{-3} and following the equations of Danovaro (2009).

Seagrass percentage cover was estimated from quadrat photographs using a random count analysis program (CPCe v 4.1) (Kohler & Gill, 2006). This entailed the selection of 100 points per image and a manual assessment of whether they fell on live seagrass blades, dead blades or unvegetated sediment. Seagrass samples were defrosted and separated into above (AGB) and below-ground (BGB) tissues. Ten leaves were randomly selected from each sample and the leaf width (LW) and leaf length (LL) were measured using digital callipers. The number of shoots and an approximation of the number of leaves per shoot were used to estimate average leaf number (L#) per chamber (0.25 m^2). All seagrass roots and shoots were then dried at 60°C until constant weight for estimation of biomass and reported as g dw seagrass 0.25 m^{-2}, to allow comparisons with percentage cover which was reported at the chamber scale.

Macrofauna samples were stained with Rose Bengal dye 24 h prior to sorting. To begin, samples were washed through a series of four stacked sieves ranging from

5.6 – 0.5 mm. Macrofauna were then sorted and three samples from each habitat (from November and February) were randomly selected for identification. These samples were identified to the lowest possible taxonomic level (usually species) using a dissecting microscope and placed in 50% IPA for secondary identification checks.

2.4 Data analysis

Rates of primary production were determined from chamber CO_2 fluxes (µmol CO_2 m^2 h^{-1}) by regressing CO_2 concentrations against the incubation period. Subsequently, CO_2 consumption was converted to O_2 production using a respiratory quotient of 1 (Hopkins, 2006) and expressed as a flux (µmol m^{-2} h^{-1}) after normalising by the chamber area and volume. Fluxes resulting from light incubations provided information on net primary production (NPP) while dark incubations correspond to sediment community respiration (SOC). Gross primary production (GPP) was estimated from the difference between light and dark fluxes to quantify the rate of total carbon fixation.

Flux data was analysed in two steps to help elucidate the factors contributing to the variations in GPP. Initially, a two-way permutational multivariate analysis of variance (PERMANOVA) was conducted on GPP to determine the significance of habitat (fixed factor, 3 levels), month (fixed factor, 4 levels), and the habitat-month interaction. This study involved six replicate chambers, therefore the individual chamber measurements made during each hour of emersion (i.e. T1, T2, T3 and T4; **Table 2.2**) were averaged (n = 6). Secondly, each habitat was looked at individually to determine whether primary production varied between sampling months and within a low tide period. For these analyses all GPP flux measurements, calculated from each paired light and dark incubation, were used. Additionally, GPP fluxes were standardised by the dominant photosynthesising biomass (above-ground seagrass biomass for the seagrass habitat (GPP_{SG}), and chlorophyll *a* concentration for shellfish and polychaete habitats ($GPP_{chl\ a}$)), providing a measure of photosynthetic efficiency (Pratt *et al.*, 2015). A two-way repeated-measures PERMANOVA (with chamber as a random factor nested in month) were then run to identify any within habitat differences in $GPP_{chl\ a}$ or GPP_{SG} between sampling

months (fixed factor, 4 levels), exposure time (fixed factor, 4 levels), and the month-time interaction.

Multiple linear regression (using distance-based linear models, DistLM) was then used to identify which sediment characteristics or environmental variables (**Table 2.2**) explained the observed variation in GPP_{SG} or $GPP_{chl\ a}$. Continuous environmental data was converted to discrete measurements by taking averages of the environmental conditions experienced during each individual incubation period. DistLMs were performed on univariate Euclidean distance matrices and run for each habitat independently. Initially, models were run to identify significant predictors of GPP_{SG} or $GPP_{chl\ a}$ when fitted individually (marginal test) and then sequentially using a backwards elimination procedure and the corrected Akaike information criterion (AICc) to obtain the most parsimonious model. AICc was used as it is the most appropriate selection criterion when the number of variables is large compared to the sample size (Burnham & Anderson, 2002). Predictor variables were normalised to enable comparison among variables with different units, without altering the distribution. Where there was collinearity among variables ($r > 0.75$), the variable explaining the lesser amount of variability was omitted from full models (Dormann *et al.*, 2013).

A series of resemblance matrices were created for sediment characteristics (Euclidean) and environmental conditions (Euclidean) (**Table 2.2**) as well as above-ground seagrass biomass (Euclidean) and macrofaunal assemblages (Bray-Curtis). For this analysis environmental data was converted from continuous to discrete measurements by averaging the conditions experienced during each hour of sampling (i.e. T1, T2, T3 and T4; **Table 2.2**). Macrofauna data underwent a square-root transformation prior to this, to minimise instances of undue influence on the overall analysis and ensure that less abundant species were taken into account. Two-way PERMANOVAs were conducted on sediment characteristics and environmental variables to determine the significance of habitat, month, and the habitat-month interaction. While one-way PERMANOVAs were used to identify any significant differences in seagrass biomass between months, or in macrofaunal community between habitats. Post-hoc PERMANOVA pairwise tests were performed to discern effects at individual habitats where significant interactions between two factors had been detected. Multidimensional scaling analyses using principle coordinate ordinations (PCO) were used to illustrate differences in

sediment characteristics, environmental conditions, seagrass metrics, and macrofaunal community as a function of habitat and/or time. Vectors were overlain on plots to visualise variables correlated with the separation of habitats in multivariate space. A similarity percentage (SIMPER) analysis conducted on raw macrofauna data identified the taxa that contributed to dissimilarities in macrofaunal community assemblages between habitats.

All analyses were performed using PRIMER v7 PERMANOVA+ add on (Anderson, 2008; Clarke & Gorley, 2015) with untransformed data unless otherwise mentioned.

Chapter Three

Results

3.1 Site characteristics

3.1.1 Sediment properties

Sediment properties were notably different between habitats, and small-scale temporal variation was evident within habitats (**Table 3.1**). Sediment mud content measured in the seagrass and shellfish habitats was three-fold higher than in the polychaete dominated region. There was also temporal variation in sediment characteristics as they varied significantly across the four sampling months. This was largely driven by a decrease in percentage mud content in the two bare-sediment habitats in February. The results of a PERMANOVA analysis did reveal significant differences in a multivariate measure of sediment characteristics between habitats, sampling months and also the interaction term (**Table 3.2**). Indicating temporal variation in sediment characteristics was not consistent across all sites. Post-hoc pairwise tests showed that the multivariate measure of sediment characteristics was significantly different in all habitats in November and December, yet the seagrass and shellfish habitats were statistically similar in January and February. Additionally, within the shellfish and polychaete habitats sediment characteristics differed significantly between all sampling months, while sediment characteristics were similar in December and February in the seagrass habitat.

These trends are illustrated in a PCO ordination (**Figure 3.1**) with an overlay of sediment characteristics, where data points from each habitat are seen in distinguishable clusters. For example, samples from the polychaete habitat cluster to the left of the ordination, away from the other two habitats. It also illustrates that the sediment characteristics measured in the polychaete habitat are far less variable than those measured in the other two habitats.

Table 3.1. Sediment characteristics of each habitat as a function of sampling month, values are mean ± standard deviation (n = 6).

	MC (%)	MGS (µm)	OM (%)	Porosity (%)
Seagrass				
November	8.57 ± 1.01	175 ± 6.70	3.46 ± 0.61	45.7 ± 3.0
December	7.44 ± 0.78	170 ± 6.00	3.68 ± 0.65	43.1 ± 2.5
January	8.67 ± 0.86	167 ± 2.60	3.68 ± 0.65	48.1 ± 5.3
February	8.75 ± 1.31	168 ± 3.60	2.95 ± 0.42	43.5 ± 2.3
Shellfish				
November	8.79 ± 1.50	178 ± 5.00	2.75 ± 0.28	45.6 ± 2.7
December	9.53 ± 0.75	166 ± 4.40	2.10 ± 0.10	44.5 ± 2.6
January	8.89 ± 0.98	168 ± 2.80	2.09 ± 0.10	38.2 ± 8.7
February	5.08 ± 0.80	181 ± 3.50	2.32 ± 0.10	45.6 ± 3.5
Polychaete				
November	2.50 ± 0.54	193 ± 2.30	2.24 ± 0.14	45.0 ± 2.5
December	2.89 ± 0.40	185 ± 1.70	2.19 ± 0.18	43.7 ± 2.6
January	3.82 ± 0.69	184 ± 3.80	2.19 ± 0.18	43.9 ± 2.7
February	1.17 ± 0.61	196 ± 2.00	1.97 ± 0.07	45.0 ± 2.2

The abbreviations in the table represent the following: mud content (MC), median grain size (MGS), and organic matter (OM).

Table 3.2. Summary of two-way PERMANOVA (Euclidean) comparing sediment characteristics between habitats (SG = seagrass, SF = shellfish, P = polychaete), months (Nov, Dec, Jan, Feb) and habitat-month interaction. Significant P-values ($P < 0.05$) are shown in bold.

Source	Df	MS	Pseudo-F	P	Post-hoc pairwise tests
Habitat *X* Month	6	11.8	21.7	**0.001**	**Nov:** SG ≠ SF ≠ P **Dec:** SG ≠ SF ≠ P **Jan:** SG = SF, SG ≠ P, SF ≠ P **Feb:** SG = SF, SG ≠ P, SF = P **SG:** Nov ≠ Dec, Nov ≠ Jan, Nov ≠ Feb, Dec ≠ Jan, Dec = Feb, Jan ≠ Feb **SF:** Nov ≠ Dec ≠ Jan ≠ Feb **P:** Nov ≠ Dec ≠ Jan ≠ Feb
Habitat	2	76.3	140	**0.001**	
Month	3	9.22	16.9	**0.001**	
Residual	60	0.545			

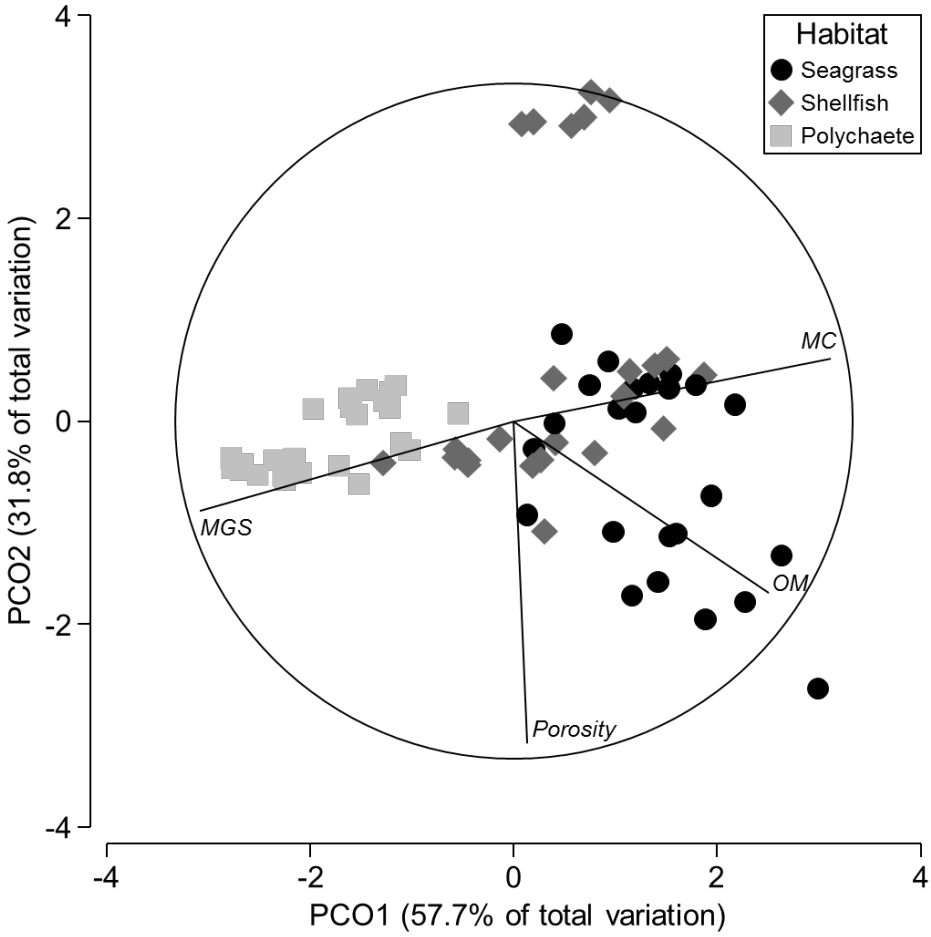

Figure 3.1. Non-metric PCO ordination (Euclidean) illustrating differences in sediment characteristics between intertidal habitats (see legend). The ordination has been overlaid with attributes of sediment characteristics in order to elucidate variation in plot distribution. See **Table 3.1** for a description of abbreviations used in the overlay.

3.1.2 Primary producer biomass

3.1.2.1 Microphytobenthos

A summary of sediment chlorophyll *a* content can be used as a proxy for microphytobenthos concentration to compare the photosynthesising capacity of the sediment within each habitat. Chlorophyll *a* concentration was greatest in the seagrass habitat on all occasions, and on average 1.4 – 2.0 times greater than in the shellfish bed and polychaete dominated habitat respectively (**Figure 3.2**). The results of a PERMANOVA analysis conducted on chlorophyll *a* concentration revealed a significant difference in chlorophyll *a* concentration between habitats, sampling months and also the interaction term (**Table 3.3**). A significant interaction term implies that the temporal trends are not consistent across all habitats. Post-hoc tests shown there are no significant differences in chlorophyll *a* concentrations with time in the shellfish habitat, yet there are in the seagrass and polychaete dominated sites. Overall, there was significant spatial variation between habitats and relatively small temporal differences with sampling month, within each habitat.

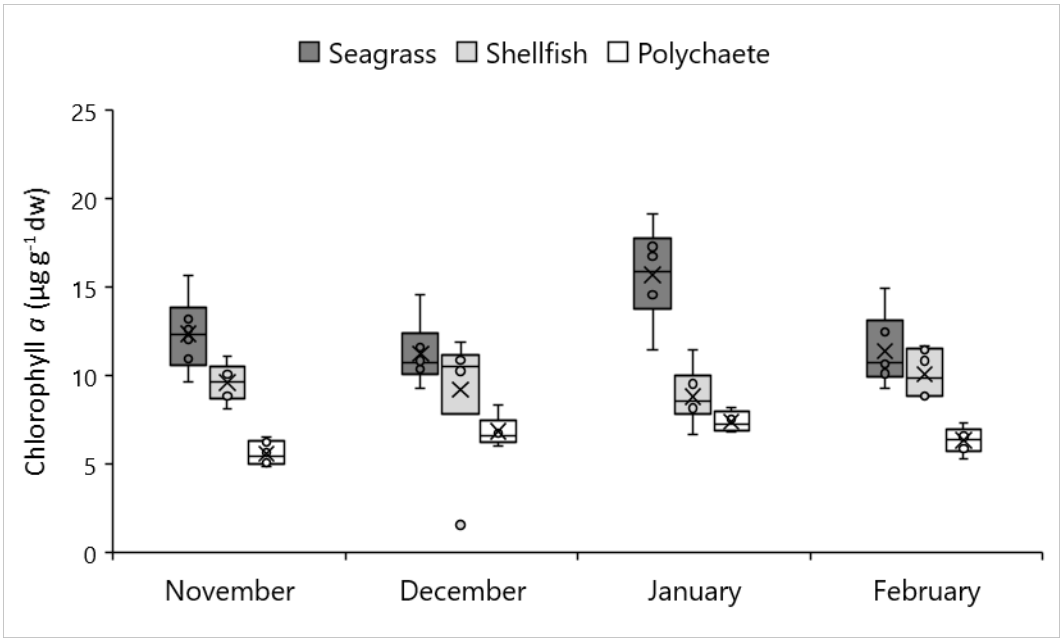

Figure 3.2. Sediment chlorophyll *a* concentration in seagrass, shellfish, and polychaete dominated habitats as a function of sampling month. Whiskers indicate maximum and minimum values with circles marking outliers. Box limits represent the 25th and 75th percentiles, solid lines within boxes are median values and crosses indicate means (n = 6).

Table 3.3. Summary of two-way PERMANOVA (Euclidean) comparing chlorophyll *a* concentration between habitats (SG = seagrass, SF = shellfish, P = polychaete), months (Nov, Dec, Jan, Feb) and habitat-month interaction. Significant P-values (P < 0.05) are shown in bold.

Source	Df	MS	Pseudo-F	P	Post-hoc pairwise tests
Habitat *X* Month	6	10.9	3.18	**0.008**	**Nov:** SG > SF > P **Dec:** SG = SF, SG > P, SF = P **Jan:** SG > SF, SG > P, SF = P **Feb:** SG = SF, SG > P, SF > P **SG:** Nov = Dec, Nov < Jan, Nov = Feb, Dec < Jan, Dec = Feb, Jan > Feb **SF:** Nov = Dec = Jan = Feb **P:** Nov < Dec, Nov < Jan, Nov = Feb, Dec = Jan, Dec = Feb, Jan > Feb
Habitat	2	226	66.2	**0.001**	
Month	3	9.61	2.81	**0.048**	
Residual	60	3.42			

3.1.2.2 Seagrass

A summary of seagrass morphology metrics can be used to recognise changes in the seagrass habitat over the study period (**Table 3.4**). Percentage cover estimates increased by 34% over the summer season, from November to January, before tailing off slightly in February. Leaf count, length and width all followed similar trends, increasing with time in the first three months, and decreasing in February (See Appendix 1; **Table A1.1**). The results of a PERMANOVA analysis, conducted on above-ground seagrass biomass, revealed a significant difference across sampling months (**Table 3.5**). A post-hoc pairwise test identified that above-ground seagrass biomass differed between all months, with the exception of November and December, and November and February.

These trends can be illustrated via PCO ordination (**Figure 3.3**), where data points from January and February are clustered towards the positive end of the seagrass attribute overlay. Earlier sampling points from November and December cluster further away from the overlay, indicating a negative trend due to relatively lower measures of many of the individual seagrass characteristics.

Table 3.4. Seagrass attributes as a function of sampling month, values are mean ± standard deviation (n = 6).

	Cover (%)	**AGB (0.25 m^2)**	**BGB (0.25 m^2)**	**TB (0.25 m^2)**
November	68 ± 2.0	14.3 ± 2.5	31.8 ± 10.3	46.1 ± 11.0
December	74 ± 7.0	15.5 ± 2.8	33.4 ± 6.5	48.8 ± 7.3
January	92 ± 4.0	24.7 ± 3.5	44.0 ± 9.5	68.8 ± 11.4
February	89 ± 3.0	17.2 ± 3.5	34.8 ± 4.0	52.1 ± 5.2

The abbreviations featured in the table represent the following: Seagrass percentage cover (Cover), above-ground biomass (AGB), below-ground biomass (BGB) and total biomass (TB).

Table 3.5. Summary of one-way PERMANOVA (Euclidean) comparing above-ground seagrass biomass between months (Nov, Dec, Jan, Feb). Significant P-values (P < 0.05) are shown in bold.

Source	Df	MS	Pseudo-F	P	Post-hoc pairwise tests
Month	3	0.110	13.5	**0.001**	Nov = Dec, Nov < Jan, Nov = Feb, Dec < Jan, Dec < Feb, Jan > Feb
Residual	20	0.008			

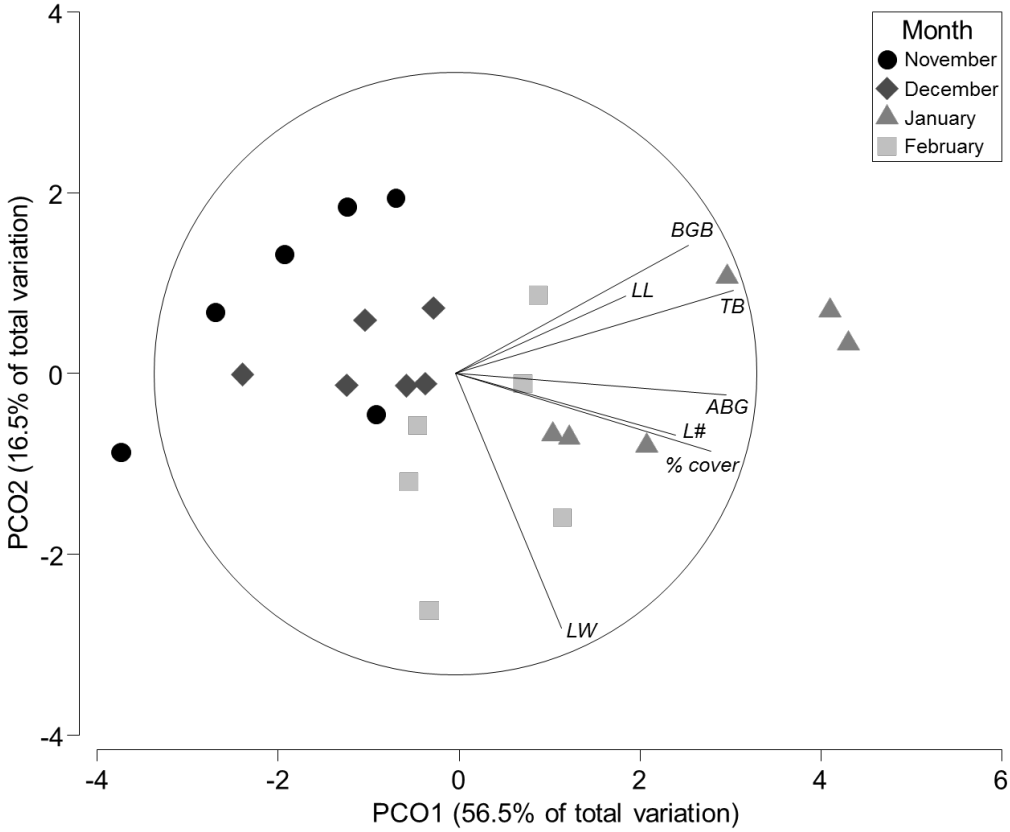

Figure 3.3. Non-metric PCO ordination (Euclidean) illustrating differences in seagrass health between sampling months (see legend). The ordination has been overlaid with attributes of seagrass biomass in order to elucidate variation in plot distribution. See **Table 3.4** for a description of abbreviations used in the overlay.

3.1.3 Macrofauna community assemblages

Abundance and taxa richness, both measures of macrofaunal community assemblages, varied between habitats (**Table 3.6**). The polychaete dominated habitat had the lowest average abundance and taxa richness per plot, being almost 40% less abundant and containing half the number of taxa found compared to the shellfish dominated habitat. The most abundant taxa found in the polychaete habitat were the predatory polychaete *Nereididae*, and the bivalve *Lasaea parengaensis*, in the shellfish habitat *the polychaete Prionospio aucklandica* and bivalve *Lasaea parengaensis* were dominant, and in the seagrass habitat the bivalve *Austrovenus stutchburyi*, and polychaetes *Nereididae,* and *Prionospio aucklandica*. Both average abundance and average taxa richness decreased between November and February sampling on all occasions, with the exception of the average total abundance in the seagrass habitat which remained constant. However, no conclusions can be drawn regarding differences between initial and final samples due to the low number of replicates (n = 3). A one-way PERMANOVA analysis conducted on a multivariate measure of macrofaunal community assemblages revealed a significant difference in community composition between habitats (**Table 3.7**). Post-hoc pairwise testing elucidated that all habitats differed significantly from each other (SF > SG > P) (**Table 3.7**). Examining plot configurations via PCO ordination (**Figure 3.4**) revealed a relationship between macrofaunal community assemblage and sediment characteristics. Median grain size was positively correlated with community composition in the polychaete habitat, while the other two habitats were positively correlated with mud content, organic matter and chlorophyll *a* concentration.

The number of species that contributed > 50% to the cumulative dissimilarity in community assemblages between the three habitats was assessed (**Table 3.8**). Five taxa were required to make up > 50% of the cumulative dissimilarity between the seagrass and shellfish habitats, while only three taxa contributed to the 50% limit in the seagrass-polychaete and shellfish-polychaete comparisons. This analysis outlines that comparatively the seagrass and shellfish habitats were more closely related to each other, by approximately 30%, than either were with the polychaete habitat.

Table 3.6. The abundance (average macrofauna count per core) and richness (average number of taxa per core) of macrofaunal communities in each habitat taken during initial (November) and final (February) site visits, values are mean ± standard deviation (n = 3).

Habitat	Seagrass	Shellfish	Polychaete
Abundance			
November	127 ± 19.7	142 ± 20.2	111 ± 35.5
February	127 ± 17.9	125 ± 28.6	79.0 ± 26.8
Mean	127 ± 0.00	134 ± 11.6	94.8 ± 22.4
Richness			
November	18.0 ± 4.04	25.0 ± 4.62	14.3 ± 1.15
February	16.3 ± 7.81	18.0 ± 7.23	10.0 ± 2.00
Mean	17.7 ± 1.41	21.7 ± 4.71	12.2 ± 3.06

Table 3.7. Summary of one-way PERMANOVA (Bray-Curtis) comparing macrofauna assemblages between habitats (SG = seagrass, SF = shellfish, P = polychaete). Significant P-values (P < 0.05) are shown in bold. Data was under square-root transformation.

Source	Df	MS	Pseudo-F	P	Post-hoc pairwise tests
Habitat	2	7410	10.8	**0.001**	SF > SG > P
Residual	15	685			

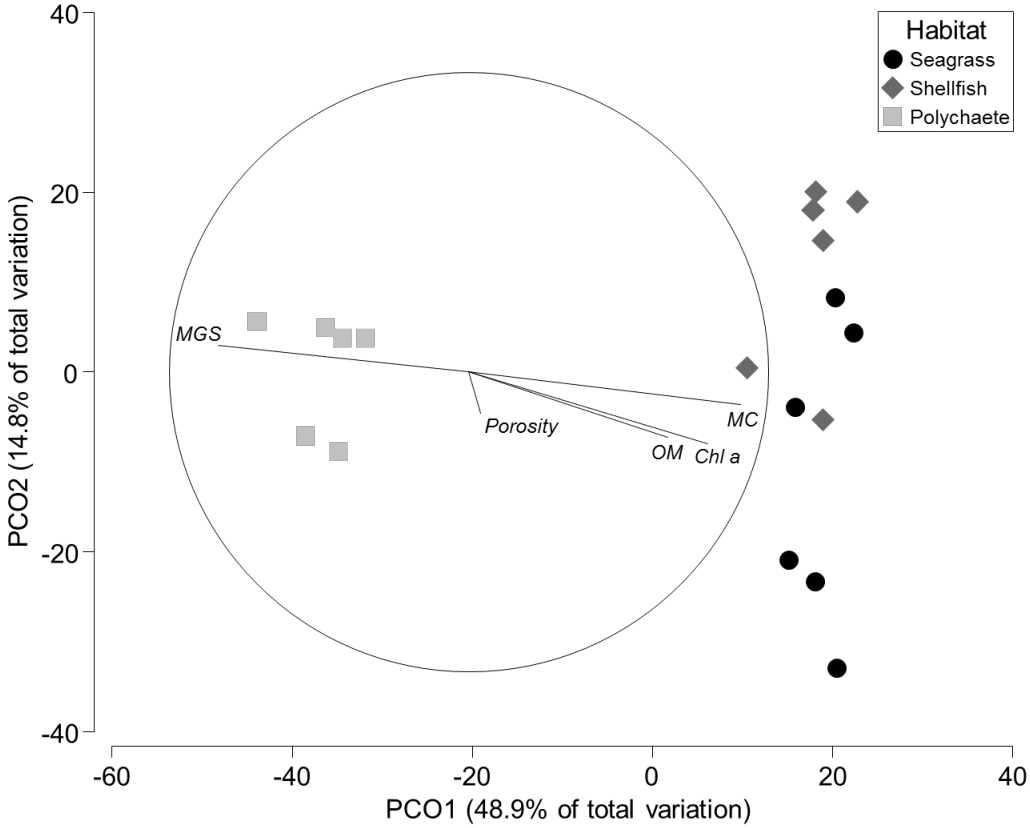

Figure 3.4. Non-metric PCO ordination (Bray-Curtis) illustrating differences in macrofauna community assemblages as a function of intertidal habitat (see legend). The ordination has been overlaid with sedimentary characteristics in order to elucidate variation in plot distribution. See **Table 3.1** for a description of abbreviations used in the overlay.

Table 3.8. Results of SIMPER analysis comparing taxa that contributed to > 50% of the cumulative dissimilarity in the macrofaunal community between habitats.

	Taxa	Mean Abundance		Contribution %	Dissimilarity %
Seagrass *X* Shellfish		Seagrass	Shellfish		**47.9**
	Prionospio aucklandica	11.7	34.3	19.6	
	Austrovenus stutchburyi	46.7	34.3	13.0	
	Zeacumantus subcarinatus	13.7	5.17	8.28	
	Aonides trifida	11.8	5.83	6.80	
	Phoxocephalidae	7.67	0.5	5.75	
Seagrass *X* Polychaete		Seagrass	Polychaete		**80.3**
	Nereididae	4.50	47	23.2	
	Austrovenus stutchburyi	46.7	6.5	22.0	
	Zeacumantus subcarinatus	13.7	0.00	8.14	
Shellfish *X* Polychaete		Shellfish	Polychaete		**76.9**
	Nereididae	8.00	47.0	21.5	
	Austrovenus stutchburyi	34.3	6.50	17.1	
	Prionospio aucklandica	34.3	5.83	16.1	

3.2 Environmental variability

The environmental conditions experienced at each habitat varied significantly over the study period, with less variation apparent between habitats within each sampling month (**Figure 3.5**). Air temperature and sediment temperatures were on average 5ºC higher in January when compared to November and December. PAR showed the greatest variability over the study period, with maximum mean PAR measured in the seagrass habitat in November (1640 µmol m^{-2} s^{-1}), in the shellfish habitat in December (1680 µmol m^{-2} s^{-1}), and in the polychaete habitat in February (1800 µmol m^{-2} s^{-1}). The results of a PERMANOVA analysis revealed a variation in environmental conditions between the three habitats, as well as between sampling months (**Table 3.9**). As expected, the environmental conditions, under which sampling took place, varied from month to month. However, it also indicates that environmental conditions varied significantly in consecutive days, during each sampling campaign, therefore the three habitats were not always sampled under similar conditions. The interaction term between habitat and sampling month was also significant, implying that differences in environmental conditions experienced by habitats within the same month were likely a result of short term weather patterns. Post-hoc pairwise tests identified that environmental conditions were significantly different across all habitats in November and December, and between seagrass and polychaete habitats in January and February. In the seagrass habitat, environmental conditions were statistically similar in November and December only, while conditions in January and February were similar in both the shellfish and polychaete habitats.

These trends are illustrated in a PCO ordination (**Figure 3.6**), grouped by sampling month, with an overlay of environmental variables. January and February appear closely related and to the left of the ordination, while the two earlier sampling months, November and December, are located to the right of the overlay. The overlay suggests that sediment and air temperature appear to be the key variables distinguishing differences across sampling months, with relative humidity and PAR being less deterministic.

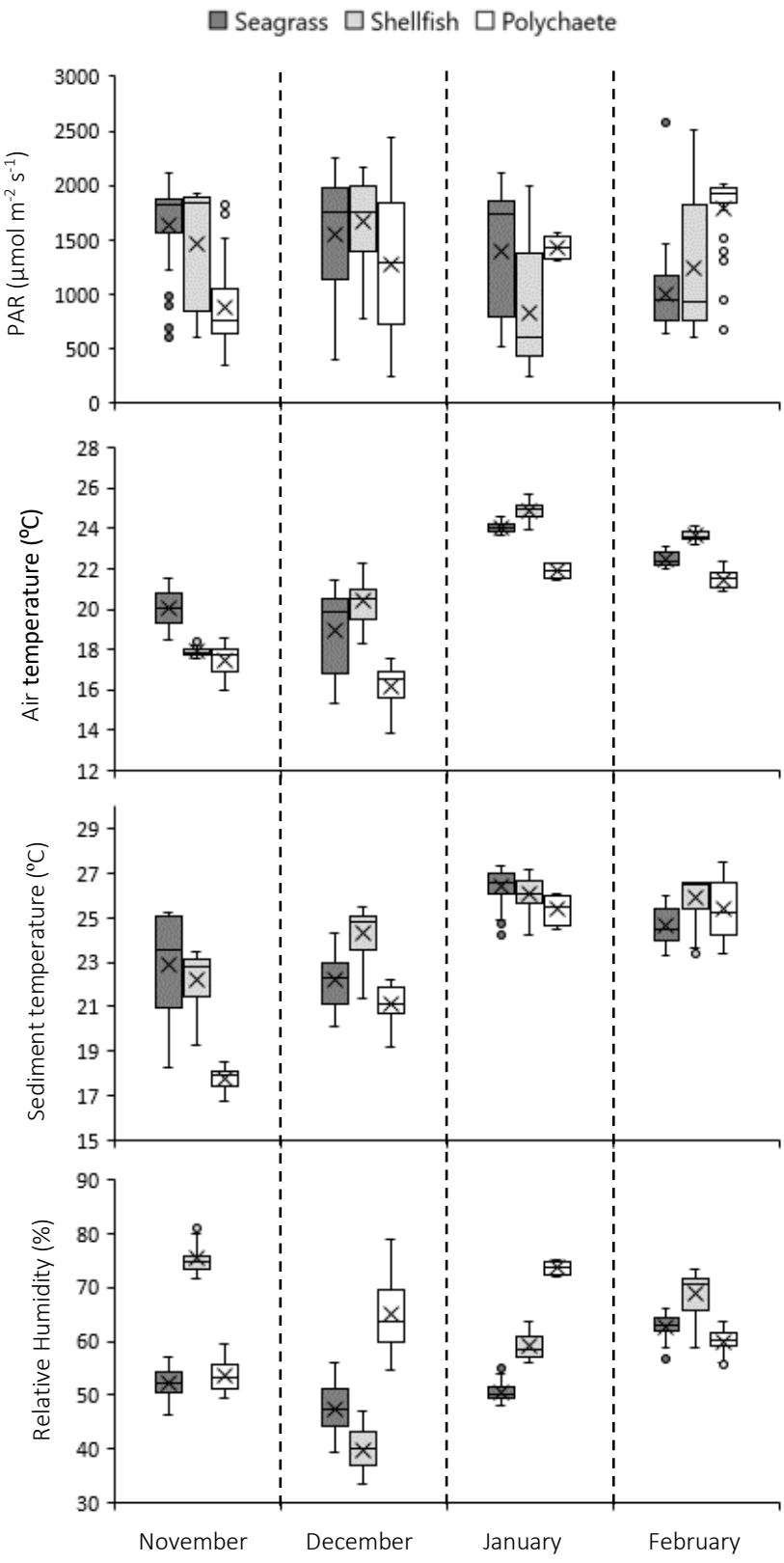

Figure 3.5. Surface incident photosynthetically active radiation (PAR), air temperature, sediment temperature, and relative humidity during measured monthly primary production measurements. Whiskers indicate maximum and minimum values with circles marking outliers. Box limits represent the 25th and 75th percentiles, solid lines within boxes are median values and crosses indicate means (n = 6). Note: January data for the polychaete habitat was sourced from the nearest climate station due to instrument error (NIWA, 2019). Note: Broken scales.

Table 3.9. Summary of two-way PERMANOVA (Euclidean) comparing environmental conditions between habitats (SG = seagrass, SF = shellfish, P = polychaete), months (Nov, Dec, Jan, Feb) and habitat-month interaction. Significant P-values ($P < 0.05$) are shown in bold.

Source	Df	MS	Pseudo-F	P	Post-hoc tests
Habitat *X* Month	6	10.1	22.8	**0.001**	**Nov:** SG ≠ SF ≠ P **Dec:** SG ≠ SF ≠ P **Jan:** SG = SF, SG ≠ P, SF ≠ P **Feb:** SG = SF, SG ≠ P, SF = P **SG:** Nov = Dec, Nov ≠ Jan, Nov ≠ Feb, Dec ≠ Jan, Dec ≠ Feb, Jan ≠ Feb **SF:** Nov ≠ Dec, Nov ≠ Jan, Nov ≠ Feb, Dec ≠ Jan, Dec ≠ Feb, Jan = Feb **P:** Nov ≠ Dec, Nov = Jan, Nov ≠ Feb, Dec = Jan, Dec ≠ Feb, Jan = Feb
Habitat	2	22.3	50.3	**0.001**	
Month	3	35.4	79.8	**0.001**	
Residual	60	0.444			

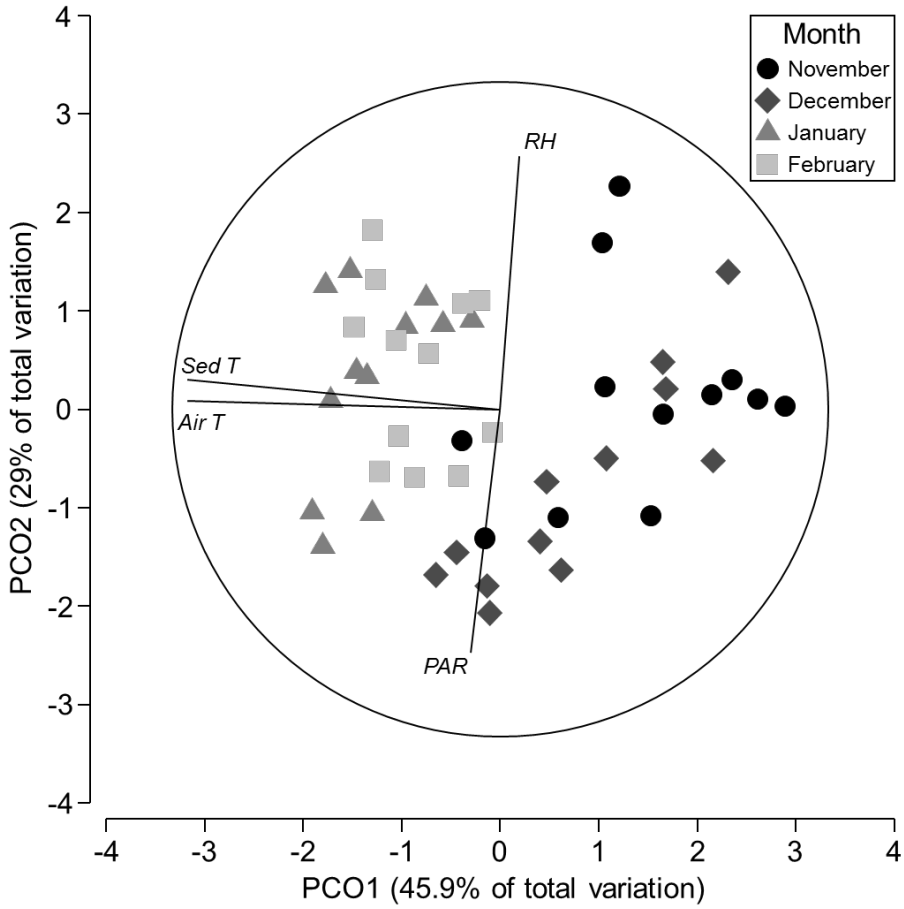

Figure 3.6. Non-metric PCO ordination (Euclidean) illustrating differences in environmental conditions between sampling months (see legend). The ordination has been overlaid with environmental variables in order to elucidate variation in plot distribution. The abbreviations featured in the overlay represent the following: Air temperature (Air T), sediment temperature (Sed T), photosynthetically active radiation (PAR) and relative humidity (RH).

3.3 Emerged primary production

Rates of primary production (both net and gross) appears to vary considerably in different habitat types, with slight temporal variation between sampling months (**Figure 3.7**). Maximum mean GPP of 5870, 702, and 1680 µmol O_2 m^{-2} h^{-1} was measured in the seagrass, shellfish and polychaete habitats respectively. Measurements of GPP were between three and 11 times higher in the seagrass dominated habitat than in the two unvegetated habitats (**Figure 3.7**). Average rates of NPP in the polychaete dominated habitat consistently exceeded that in the shellfish bed by approximately 25% in November, December and February, and by 75% in January. Rates of GPP were highest in January in all habitats, coinciding with maximum air and sediment temperatures (**Figure 3.5**). The seagrass habitat shows greater variation in most months, in comparison to the other two habitats.

The results of a PERMANOVA analysis revealed a significant difference in NPP and GPP between habitats, as well as between sampling months (**Table 3.10**). This indicates that there was a natural spatial and temporal variation in primary production occurring at the study site. The interaction term between habitat and sampling month was also significant, implying that temporal changes in NPP and GPP were habitat-specific and required pairwise tests to elucidate effects at each individual habitat. A post-hoc pairwise comparison of all habitats revealed that a significant difference between NPP and GPP measured in the two bare sediment habitats only occurred in January, with the remaining months being statistically similar (**Table 3.10**). NPP and GPP measured in the seagrass bed was statistically different to the other two habitats on all occasions. A further post-hoc pairwise comparison between sampling months identified that NPP and GPP readings were statistically similar in November and December, and again in January and February in the seagrass habitat (**Table 3.10**). In the shellfish habitat there were no significantly different responses in NPP or GPP with respect to sampling month. In the polychaete habitat NPP and GPP in November, December and February were statistically similar and all three were significantly different from primary production measures taken in January.

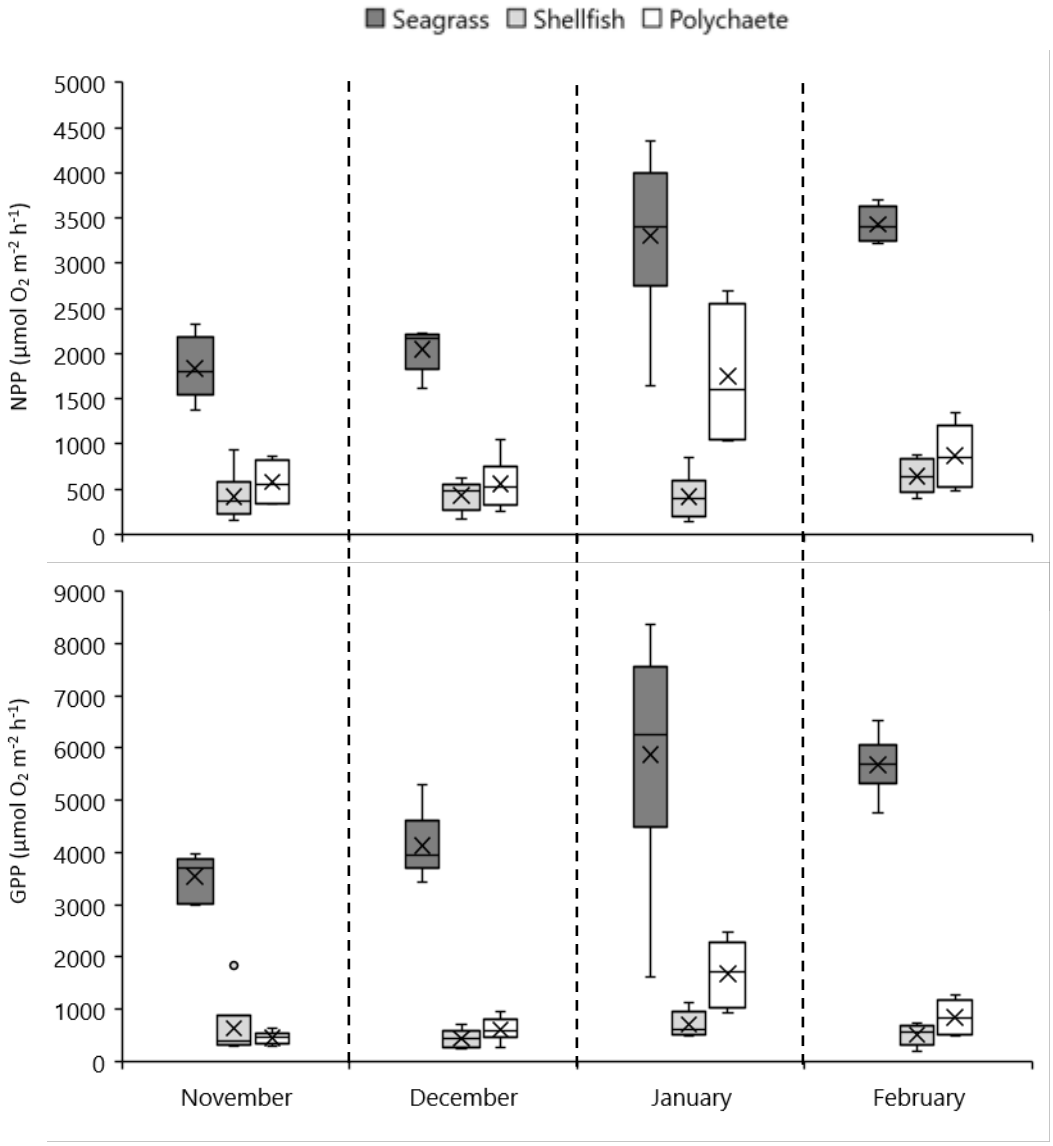

Figure 3.7. Net primary production (NPP) and gross primary production (GPP), during emersion in seagrass, shellfish, and polychaete dominated habitats as a function of sampling month. Whiskers indicate maximum and minimum values with circles marking outliers. Box limits represent the 25th and 75th percentiles, solid lines within boxes are median values and crosses indicate means (n = 6). Note: Scale changes between plots.

Table 3.10. Summary of two-way PERMANOVA (Euclidean) comparing net primary production (NPP) and gross primary production (GPP) between habitats, months, and the habitat-month interaction. Significant P-values ($P < 0.05$) are shown in bold.

Source	Df	MS	Pseudo-F	P	Post-hoc pairwise tests
NPP					
Habitat *X* Month	6	1260000	7.05	**0.001**	**Nov:** SG > SF, SG > P, SF = P **Dec:** SG > SF, SG > P, SF = P **Jan:** SG > SF, SG > P, SF < P **Feb:** SG > SF, SG > P, SF < P **SG:** Nov = Dec, Nov < Jan, Nov < Feb, Dec < Jan, Dec < Feb, Jan = Feb **SF:** Nov = Jan = Dec = Feb **P:** Nov = Dec, Nov < Jan, Nov = Feb, Dec < Jan, Dec = Feb, Jan > Feb
Habitat	2	31600000	177	**0.001**	
Month	3	3550000	19.9	**0.001**	
Residual	60	179000			

Table 3.10 (Continued). Summary of two-way PERMANOVA (Euclidean) comparing net primary production (NPP) and gross primary production (GPP) between habitats, months, and the habitat-month interaction. Significant P-values (P < 0.05) are shown in bold.

Source	Df	MS	Pseudo-F	P	Post-hoc pairwise tests
GPP					
Habitat *X* Month	6	2090000	3.34	**0.003**	**Nov:** SG > SF, SG > P, SF = P **Dec:** SG > SF, SG > P, SF = P **Jan:** SG > SF, SG > P, SF < P **Feb:** SG > SF, SG > P, SF < P **SG:** Nov = Dec, Nov < Jan, Nov < Feb, Dec < Jan, Dec < Feb, Jan = Feb **SF:** Nov = Jan = Dec = Feb **P:** Nov = Dec, Nov < Jan, Nov = Feb, Dec < Jan, Dec = Feb, Jan > Feb
Habitat	2	133000000	214	**0.001**	
Month	3	5640000	9.03	**0.001**	
Residual	60	624000			

Normalising GPP by photosynthesising biomass (above-ground seagrass biomass or sediment chlorophyll *a* content) provides a measure of photosynthetic efficiency (GPP_{SG} or $GPP_{chl\ a}$) and accounts for temporal variations in biomass (**Figure 3.8**). The increasing trend in gross primary production with sampling month in the seagrass bed seen in **Figure 3.7**, was far less clear once GPP has been standardised for photosynthesising biomass. The temporal trend was still apparent in the polychaete habitat, as well as the shellfish bed yet to a lesser extent.

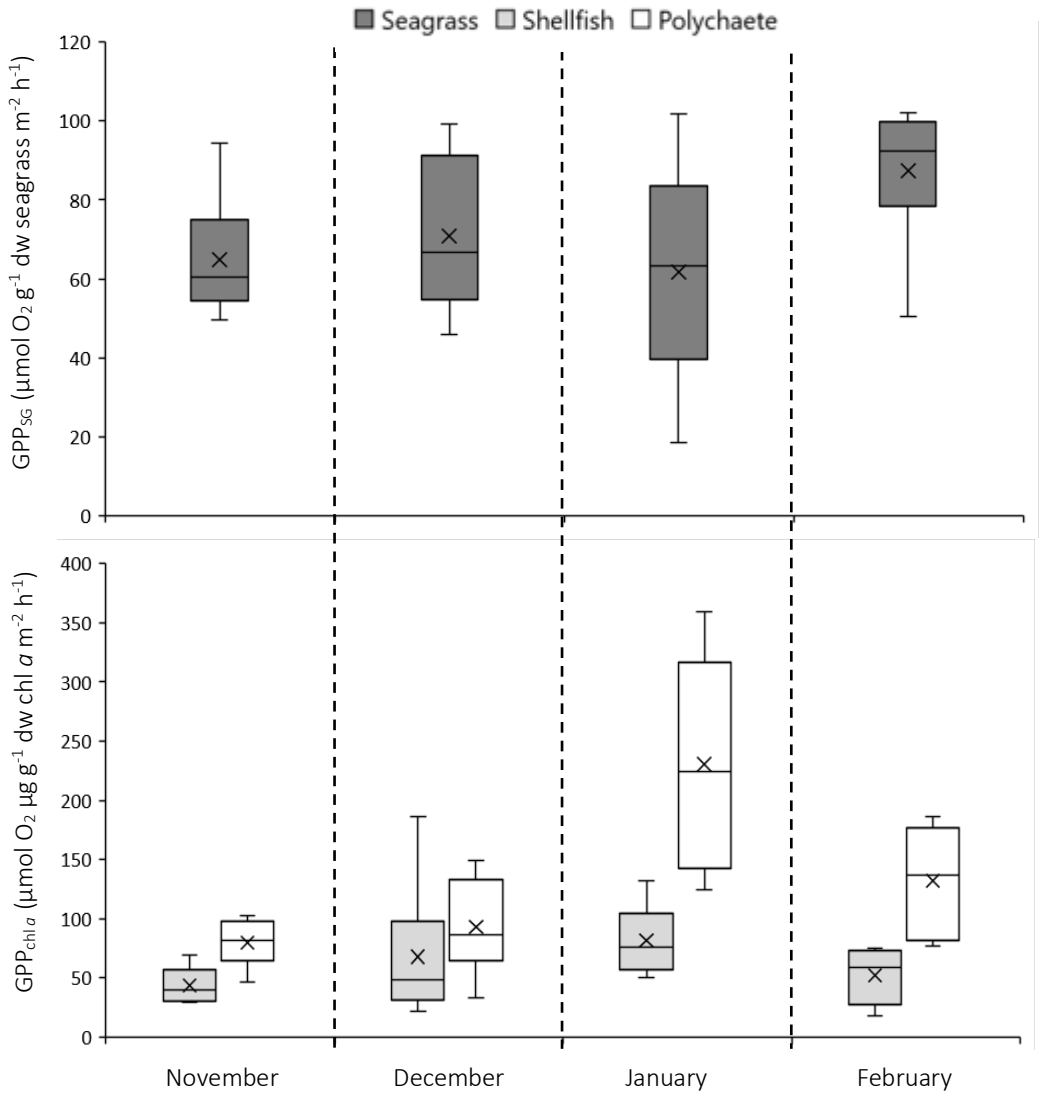

Figure 3.8. Gross primary production during emersion, standardised for photosynthetic biomass (seagrass above-ground biomass (GPP_{SG}) or sediment chlorophyll *a* content ($GPP_{chl\ a}$)) to provide a measure of photosynthetic efficiency in seagrass, shellfish, and polychaete dominated habitats as a function of sampling month. Whiskers indicate maximum and minimum values with circles marking outliers. Box limits represent the 25th and 75th percentiles, solid lines within boxes are median values and crosses indicate means (n = 6). Note: Scale changes between plots.

Rates of photosynthetic efficiency exhibit temporal variation, both with sampling month and over individual emersion periods (**Figure 3.9**). In the seagrass habitat (**Figure 3.9A**) GPP_{SG} appeared to increase with time exposed, from the first sampling round (T1) to the fourth (T4), this was particularly distinct in November and January. A similar trend was evident in the shellfish habitat in November and January also (**Figure 3.9B**). In the January sampling at the polychaete dominated habitat, $GPP_{chl\ a}$ appears to increase, from T1 up to a maximum at T3, before dropping off in the last round (T4) (**Figure 3.9C**). Uncharacteristically low measures of $GPP_{chl\ a}$ was measured in the polychaete habitat during the final two hours in February

A repeated measures PERMANOVA design was used to determine whether or not photosynthetic efficiency varied with month or exposure time in any of the three intertidal habitats (**Table 3.11**). Sampling month was only significant in the polychaete habitat and there was only a significant difference between exposure times in the seagrass dominated habitat. In the shellfish habitat a significant difference in the random factor (chamber) nested within sampling month was identified. In addition the interaction term was significant in both the seagrass and polychaete habitats indicating that emersion affects or trends were not consistent across all sampling months. Post-hoc tests conducted on the interaction term within the seagrass habitat show that there was no significant differences in GPP_{SG} with emersion in February, and in January the fluxes measured at the start of emersion (T1) were significantly different from any later measurements (T2, T3 and T4). GPP_{SG} measured during the first hour of emersion (T1) in February was significantly higher (up to 2 times greater) than that measured during T1 on the previous three visits, while GPP_{SG} measured in the last hour of emersion (T4) were statistically similar on all occasions. Post-hoc tests conducted on polychaete data outlined that $GPP_{chl\ a}$ measured in November was statically similar regardless of the hour sampled (T1, T2, T3 or T4), with the exception of a statistically different relationship between T2 and T4.

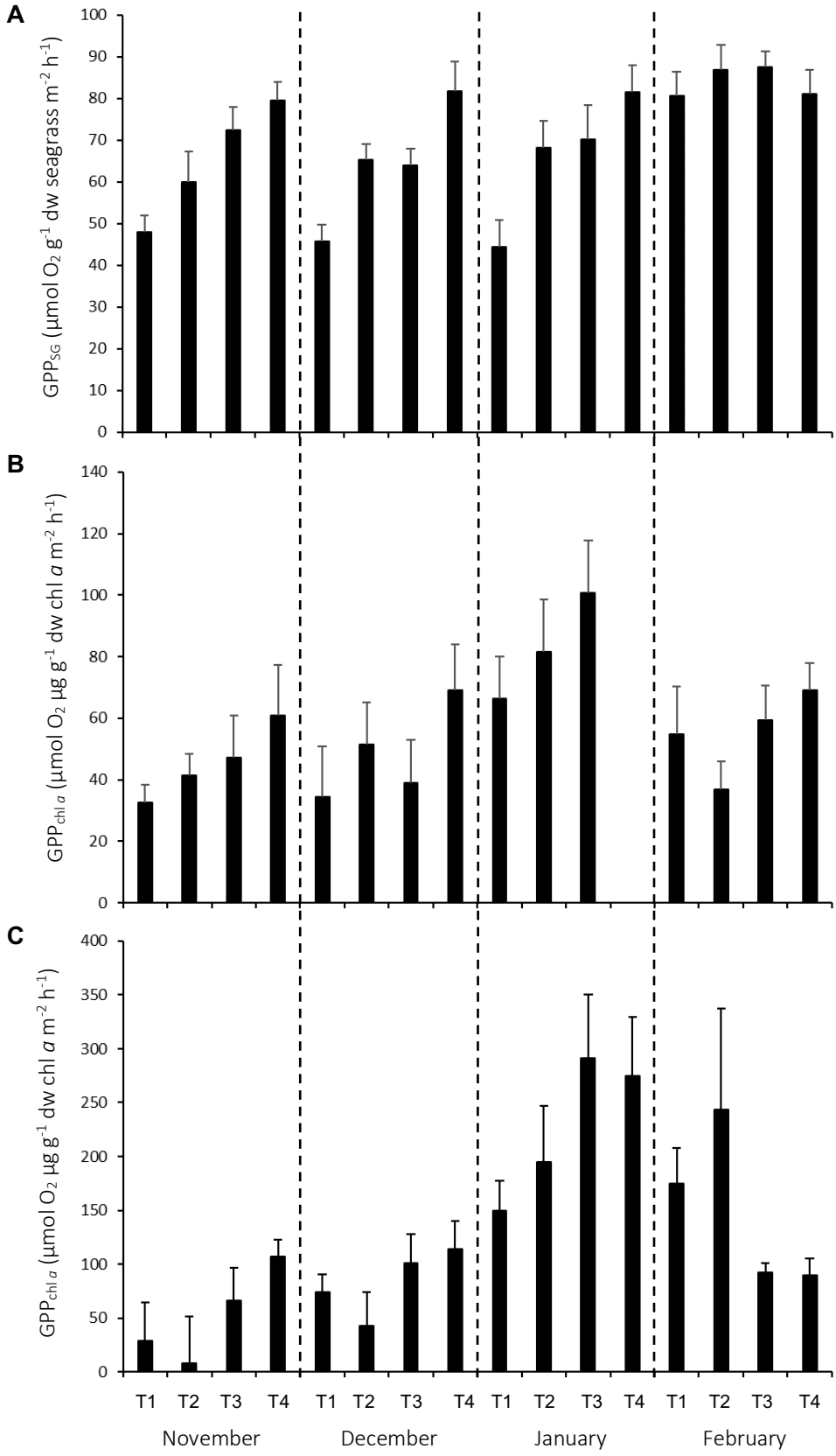

Figure 3.9. Rates of photosynthetic efficiency (GPP_{SG} or $GPP_{chl\ a}$) measured during emersion in a seagrass (A), shellfish (B), and polychaete (C) dominated habitats as a function of sampling month. Bars represent means (n=6) with standard error bars displayed. Note: Scale changes between plots.

Table 3.11. Summary of two-way repeated measures PERMANOVA (Euclidean) comparing photosynthetic efficiency (GPP_{SG} and $GPP_{chl\ a}$) between months, exposure time and the month-time interaction in each individual habitat. Significant P-values ($P < 0.05$) are shown in bold.

Source	Df	MS	Pseudo-F	P	Post-hoc pairwise tests
Seagrass					
Month *X* Time	9	707	3.09	**0.003**	**Nov:** T1 = T2, T1 < T3, T1 < T4, T2 = T3, T2 = T4, T3 = T4 **Dec:** T1 < T2, T1 < T3, T1 = T4, T2 = T3, T2 = T4, T3 = T4 **Jan:** T1 < T2, T1 < T3, T1 < T4, T2 = T3, T2 = T4, T3 = T4 **Feb:** T1 = T2 = T3 = T4 **T1:** Nov = Dec, Nov = Jan, Nov < Feb, Dec = Jan, Dec < Feb, Jan < Feb **T2:** Nov = Dec, Nov = Jan, Nov = Feb, Dec = Jan, Dec < Feb, Jan = Feb **T3:** Nov = Dec, Nov = Jan, Nov = Feb, Dec = Jan, Dec < Feb, Jan = Feb **T4:** Nov = Dec = Jan = Feb
Month	3	2840	1.66	0.211	
Time	3	3180	13.9	**0.001**	
Chamber (Month)	20	1730	7.55	**0.001**	
Residual	56	229			

Table 3.11 (Continued). Summary of two-way repeated measures PERMANOVA (Euclidean) comparing photosynthetic efficiency (GPP_{SG} and $GPP_{chl\ a}$) between months, exposure time and the month-time interaction in each individual habitat. Significant P-values ($P < 0.05$) are shown in bold.

Source	Df	MS	Pseudo-F	P	Post-hoc pairwise tests
Shellfish					
Month *X* Time	6	1010	2.41	0.054	
Month	3	4990	1.62	0.217	
Time	2	289	0.692	0.524	
Chamber (Month)	20	3170	7.59	**0.001**	
Residual	36	418			

Table 3.11 (Continued). Summary of two-way repeated measures PERMANOVA (Euclidean) comparing photosynthetic efficiency (GPP_{SG} and $GPP_{chl\ a}$) between months, exposure time and the month-time interaction in each individual habitat. Significant P-values (P < 0.05) are shown in bold.

Source	Df	MS	Pseudo-F	P	Post-hoc pairwise tests
Polychaete					
Month *X* Time	9	15000	7.76	**0.001**	**Nov:** T1 = T2, T1 = T3, T1 = T4, T2 = T3, T2 < T4, T3 = T4
					Dec: T1 = T2, T1 < T3, T1 < T4, T2 = T3, T2 < T4, T3 = T4
					Jan: T1 = T2, T1 < T3, T1 < T4, T2 = T3, T2 < T4, T3 = T4
					Feb: T1 = T2, T1 > T3, T1 > T4, T2 = T3, T2 = T4, T3 = T4
					T1: Nov = Dec, Nov < Jan, Nov < Feb, Dec < Jan, Dec < Feb, Jan = Feb
					T2: Nov = Dec = Jan = Feb
					T3: Nov = Dec, Nov < Jan, Nov = Feb, Dec < Jan, Dec = Feb, Jan > Feb
					T4: Nov = Dec, Nov < Jan, Nov = Feb, Dec < Jan, Dec = Feb, Jan > Feb
Month	3	108000	8.61	**0.001**	
Time	3	5480	2.83	0.058	
Chamber (Month)	20	13100	6.76	**0.001**	
Residual	71	1940			

3.4 Environmental predictors of emerged primary production

A correlation matrix was established to determine what abiotic variables may influence rates of photosynthetic efficiency in intertidal habitats (See Appendix 1). Some sedimentary and environmental variables showed significant correlations with GPP_{SG} and $GPP_{chl\ a}$, therefore multiple regression (using distance-based linear models; DistLM) was used to determine the drivers of this variability within each individual habitat.

In marginal tests for the seagrass habitat, variability in GPP_{SG} was significantly correlated with porosity and sediment temperature. Despite not being significant predictors, relative humidity, mud content, organic matter content and median grain size improved and therefore were included in the full regression model which explained 30% of the variation measured in GPP_{SG} in the seagrass habitat (**Table 3.12**). Photosynthetically active radiation was not a significant predictor in this model and air temperature was excluded from the model as it was significantly correlated with sediment temperature ($r > 0.75$) (See Appendix 1; **Table A1.2**).

In the shellfish habitat, marginal tests showed that variability in $GPP_{chl\ a}$ was significantly correlated with organic matter content, median grain size, porosity, sediment temperature, air temperature and PAR (**Table 3.12**). However, the most parsimonious model, explaining the greatest variation (17%) in $GPP_{chl\ a}$ in the shellfish habitat, only included organic matter and median grain size. Mud content, air temperature and relative humidity were excluded from the full regression model due to collinearity with other variables (See Appendix 1; **Table A1.3**).

In marginal tests, variability in $GPP_{chl\ a}$ in the polychaete habitat was significantly correlated with air temperature, median grain size, sediment temperature, relative humidity and mud content (**Table 3.12**). However, the full model, explaining 42% of the variation in $GPP_{chl\ a}$, only included air temperature and median grain size as key predictors. Sediment temperature, mud content, and porosity was excluded from the model due to significant correlations ($r > 0.75$) with other predictor variables (See Appendix 1;**Table A1.4**).

Table 3.12. Results of DistLM determining best combinations of predictor variables (using backwards elimination procedure and AICc criterion) explaining photosynthetic efficiency (GPP_{SG} or $GPP_{chl\ a}$) in intertidal habitats. Percentage gives the amount of variability explained by each variable when considered alone (marginal tests). Variables in bold were included in the best full model and total shows the total variation explained by the full model. Level of significance: *p < 0.1, ** p < 0.05, *** p < 0.01.

Habitat	Predictor	Pseudo-F	Percentage	Total
Seagrass				
	Porosity	5.42	**5.7****	
	Sediment Temp	4.28	**4.5****	
	Relative humidity	**3.37**	**3.6***	
	Mud content	**3.32**	**3.6***	
	Organic matter	**1.98**	**2.2**	
	Median grain size	**1.14**	**1.3**	
	PAR	0.63	0.7	
	Air Temp	0.51	0.6	
				30%
Shellfish				
	Organic matter	**9.98**	**12.7*****	
	Median grain size	**5.87**	**8.2****	
	Porosity	9.98	13.1***	
	Sediment Temperature	5.73	8.0**	
	Air Temperature	4.95	7.0**	
	PAR	4.79	6.8**	
	Relative humidity	2.59	3.8	
	Mud content	0.95	1.4	
				17%
Polychaete				
	Air Temperature	**30.0**	**26.1*****	
	Median grain size	**11.0**	**11.5*****	
	Sediment Temperature	24.8	22.6***	
	Relative humidity	20.6	19.5***	
	Mud content	16.8	16.5***	
	PAR	1.44	1.7	
	Organic matter	0.21	0.3	
	Porosity	4.50	5.0*	
				42%

Chapter Four

Discussion

This study was the first in the southern hemisphere to track gross primary production over an entire low tide period. The primary objective was to examine variations in the rate of primary production in response to emersion and to elucidate the effects of habitat, sampling month, and exposure time. The data collected was analysed to answer the following questions:

1. Do rates of emerged gross primary production vary in different intertidal habitats?
2. Do rates of emerged gross primary production change over summer months and/or over an emersion period in different intertidal habitats?
3. What environmental variables explain the most variation in emerged gross primary production?

4.1 Seasonal-spatial variation in emerged primary production

GPP significantly varied in each of the three habitats measured (**Table 3.10**). As expected, rates of GPP in the seagrass dominated habitat were significantly higher in all sampling campaigns, reaching up to 11 times greater, than the bare sediment habitats. This was due to the presence of seagrass, and the associated greater photosynthetic biomass with respect to MPB (Moncreiff *et al.*, 1992; Pratt *et al.*, 2015; Gustafsson & Norkko, 2016; Lohrer *et al.*, 2016). This is supported in many studies that recognise the role of seagrasses in carbon fixation (Fourqurean *et al.*, 2012; Ricart *et al.*, 2015)

In the seagrass habitat GPP varied significantly with sampling month. There was also significant variation in above-ground biomass and percentage cover in the present study which is expected as *Zostera muelleri* biomass is known to vary seasonally, often as a function of annual temperatures (Lee *et al.*, 2007). The apparent decrease in seagrass biomass between January and February could be due to senescence as the seagrass beds begin to deteriorate. Alternatively, reductions in biomass may be a result of temperatures exceeding conditions optimal for seagrass growth (11.5ºC - 26ºC), regularly in late summer (Lee *et al.*, 2007). However, once

GPP was standardised for photosynthetic biomass a lot of the variation through time was lost. Therefore, the amount of photosynthetic biomass present was the primary determinant of temporal changes in GPP rates in the seagrass habitat over the study period. A lack of significant temporal differences in GPP_{SG} between sampling months could be a result of limited variation in the key environmental predictors driving primary production as all sampling occurred in austral summer. If the study was conducted in all seasons, a greater variation in GPP_{SG}, and thus significant temporal differences could be expected (Vermaat & Verhagen, 1996; Lee *et al.*, 2007).

In this study the seagrass habitat did not significantly respond to the variation in PAR measured over the four sampling months. Despite this, previous studies on *Z. muelleri* have provided evidence for morphological plasticity as an adaptation to variable light climates (Peralta *et al.*, 2000; Hughes *et al.*, 2009; Vermaat, 2009). This variability has been reported in multiple forms, including a broadening and/or elongation of leaves in lower light conditions (Abal *et al.*, 1994; Peralta *et al.*, 2000), as well as changes in concentrations of light harvesting and protective pigments (Abal *et al.*, 1994; Peralta *et al.*, 2000; Kohlmeier *et al.*, 2014). It is expected that areas with high light intensity will have lower concentrations of light harvesting pigments and greater concentrations of protective (UV blocking) pigments, to protect against the high intensity environment (Abal *et al.*, 1994). Additionally, the risk of photoinhibition is reduced in seagrass canopies as the photic zone shifts further down into the canopy. Most intertidal seagrass habitats in New Zealand are not light limited, especially during austral summer, as only approximately 242 µmol m^{-2} s^{-1} is required for light saturation (Leuschner & Rees, 1993; Vermaat *et al.*, 1997; Ralph *et al.*, 2002; Schwarz, 2004). Despite this, the amount of incident light received is still expected to influence the morphometry and photophysiology of the seagrass (Kohlmeier *et al.*, 2014). Studies have shown that seagrass responses to light occur at all scales of plant structure and function, influencing pigments, anatomy, growth, biomass, isotope and tissue composition (Abal *et al.*, 1994). If this study was expanded to multiple sites in New Zealand, it would be expected that we would recognise differences in seagrass morphology as a function of local light climates (Kohlmeier *et al.*, 2014).

When comparing the two bare sediment habitats the polychaete dominated habitat appeared to consistently produce higher rates of GPP with respect to the shellfish

habitat (**Figure 3.7**). Post-hoc pairwise testing isolated that once normalised for biomass $GPP_{chl\ a}$ was significantly different between the two habitats in November, January and February. The greater photosynthetic efficiency measured in the polychaete habitat was not a function of higher temperatures as both air and sediment temperatures were higher in the shellfish habitat when the significant differences were measured (**Figure 3.5**). However, the polychaete habitat did receive higher PAR concentrations in January and February, although this should have little influence as both habitats were light saturated (>250 µmol m^{-2} s^{-1} for bare sediment) for the duration of the emersion period on all occasions (Barranguet *et al.*, 1998; Perkins *et al.*, 2001). Contrary to expectations once GPP was standardised for photosynthetic biomass the proportional differences between these two habitats were amplified as the shellfish habitat had consistently higher chlorophyll *a* concentrations.

Differences in MPB biomass was attributed to the sediment characteristics of each habitat, as the shellfish habitat was between 2 and 4 times muddier than the polychaete habitat (**Table 3.1**). The polychaete habitat was located slightly higher on the shore, with respect to the other two habitats, and therefore would have higher sediment turnover rates due to more wind-wave action reaching the bed (Green & Coco, 2007). This process, as well as the presence of many polychaete species, would result in keeping this habitat relatively free of mud, as supported by the low (1 - 4%) mud content measured. These trends in chlorophyll *a* concentration are consistent with numerous studies which recognise that MPB biomass is greater in muddy sediments, due to the greater surface area available for microalgae attachment (Pratt *et al.*, 2014a; Migné *et al.*, 2016). Additionally, diffusion rates are potentially higher in the polychaete habitat due to the lower mud content and greater median grain size, thus increasing rates of photosynthesis and respiration (**Table 3.1**). It has been recognised that muddier sediments constrain $GPP_{chl\ a}$ potential as biogeochemical processes are less efficient due to lower light, oxygenation depth and nutrient transport rates as a result of reductions in grain size and permeability (Pratt *et al.*, 2014a). A combination of these factors could explain the significant variation in the measured $GPP_{chl\ a}$ between the two bare sediment habitats in this study. Although significant differences were identified between the two bare sediment habitats, these habitats were not assessed simultaneously and instead were assessed on consecutive days, and at times under significantly different

environmental conditions. This may limit the validity of conclusions drawn regarding differences between habitats within each sampling month, as they may be a result of differing environmental conditions.

Similar to the seagrass habitat, the rates of emerged GPP in the shellfish and polychaete habitats also varied with sampling month (**Table 3.10)**. Once biomass normalised the temporal differences in the shellfish habitat were no longer significant. Temporal variation in MPB biomass has been reported in the literature (Orvain *et al.*, 2014; Migné *et al.*, 2016) and is likely responsible for the initial differences in GPP with sampling month. In contrast, the significant difference in $GPP_{chl\ a}$ between sampling months in the polychaete dominated habitat remained once normalised for MPB biomass. Within the polychaete habitat the persistence of significant differences can be attributed to the January sampling during which a much larger range of $GPP_{chl\ a}$ was measured, with respect to the other three sampling months (**Figure 3.8; Table 3.11**). There was no clear explanation for why this date produced a significantly larger variation term than all other occasions.

4.2 Variation in primary production within an emersion period

Vegetated and bare intertidal habitats respond differently to emersion. Photosynthetic efficiency appears to show significant trends within an emersion period in the seagrass habitat, yet no significant differences or consistent trends with time exposed in the bare sediment habitats (**Table 3.11**). The different temporal responses by each habitat implies that emersion affects different habitats in different ways, and recognises that the tidal flat does not respond in unison. Therefore, temporal variation within an emersion period is likely a function of multiple variables, including the adaptive ability of photosynthetic organisms to environmental stressors including desiccation and photoinhibition (Spilmont *et al.*, 2007; Drylie *et al.*, 2018).

In the seagrass habitat, photosynthetic efficiency (GPP_{SG}) during a single emersion period can be characterised as continually increasing from T1 to T4 (**Figure 3.9**). This can be explained by the enhanced rate of photosynthesis by seagrasses under short term exposure periods, as a result of reduced resistance to CO_2 diffusion (Beer & Rehnberg, 1997; Leuschner *et al.*, 1998; Silva *et al.*, 2005). Multiple studies have

shown macroalgae species (i.e. *Ulva* and *Ulvaria*) (van Hees & Van Alstyne, 2013) and other *Zostera* species (Leuschner *et al.*, 1998) reduce their photosynthetic rates in response to elevated desiccation stress. However, in this study desiccation does not appear to have a significant effect on photosynthesis in seagrass habitats. This may be due to a combination of the 'superficial cover' of *Zostera* spp. that essentially protects the remainder of the plant from desiccation (Ouisse *et al.*, 2011), as well as the limited exposure period to which *Z. muelleri* are accustomed to. If this period was prolonged it is likely that productivity would be compromised with potential for permanent cell damage (Beer & Eshel, 1983). This is supported by an Australian seagrass dieback event caused by unusually low spring tides coupled with extremely high temperatures (35ºC – 40ºC) (Seddon *et al.*, 2000). It is important to note that tolerance to desiccation is largely a function of temperature, and additional environmental conditions such a strong winds and low humidity may accelerate desiccation rates (Seddon & Cheshire, 2001). Hence, within typical conditions expected in New Zealand estuaries, seagrasses are tolerant to low tide exposure periods because of these adaptive abilities that prevent water loss and desiccation. However, risk of biomass losses due to dieback events may increase in future as the frequency of unpredictable climate extremes rises.

The increasing nature of GPP_{SG} through a low tide period may also be a result of different approaches to photoregulation. The risk of photoinhibition in seagrasses is greatly reduced due to self-shading, with top blades acting to reduce PAR concentrations reaching the bed underneath (Schwarz, 2004; Clavier *et al.*, 2011). Experimental studies have shown only 25% of incident PAR reached bottom leaves during low tide (Schwarz, 2004), this adaptation may consequently increase total productivity for the community as a whole. Furthermore, there is also evidence for short-term pigment cycling, at a daily scale, in response to tidal state and incident light conditions (Kohlmeier *et al.*, 2017). For example, photoprotective pigments were in significantly higher concentrations when low tide coincided with midday irradiance maxima, and pigment compositions fluctuate regularly in response to changing light conditions, reinforcing the dynamic nature of intertidal seagrasses (Chevalier *et al.*, 2010; Kohlmeier *et al.*, 2017). A combination of self-shading strategies and pigment cycling is likely to control trends in GPP_{SG} under emerged conditions.

In both bare sediment habitats there were no significant differences as a function of exposure time, and fluxes exhibit no consistent temporal trends (**Figure 3.9**). In contrast, previous studies on emerged production in bare intertidal habitats have recognised CO_2 fluxes increasing over individual emersion periods (Klaassen & Spilmont, 2012; Migné *et al.*, 2016). Migné *et al.* (2016) suggests that this is a result of non-biological processes occurring within the sediments, such as variations in pore-water chemistry. This can be compared to studies in other locations (i.e. Japan) that state GPP rates rapidly increase within the first hour of emersion (due to rapid drainage), followed by a stabilisation period of relatively constant fluxes (Sasaki *et al.*, 2009). Although none of these trends were apparent in the bare sediment habitats analysed in this study, a somewhat lack in consistent temporal variation may be due to the migration ability of MPB communities within top sediment layers. The migratory adaptation allows MPB to photoregulate and is predicted to be a management strategy to avoid photoinhibition, overexposure, desiccation and grazing (Underwood *et al.*, 2005). The vertical migration of these organisms in response to incident PAR levels can result in the maintenance of consistent rates of GPP through time and thus can explain the absence of significant differences in $GPP_{chl\ a}$ over a single low tide in either of the bare sediment habitats.

It has been suggested that regions of higher mud content may result in greater water retention abilities and thus decrease desiccation stress (Seddon & Cheshire, 2001; Boese *et al.*, 2003). This may also explain the inconsistent nature of CO_2 fluxes measured in the polychaete habitat, as it had an extremely low mud content (1-2%) and was slightly higher in elevation, resulting in a greater exposure time and thus potential for desiccation. Additionally, both bare sediment habitats lack the water retention capacity provided by the seagrass bed which also increases desiccation risk. Lastly, bare sediment habitats may have a quicker response time to short-term environment changes due to the absence of vegetation, this could also help explain the lack of a consistent pattern in $GPP_{chl\ a}$ through an emersion period.

The experimental design used imposes a risk that successive incubations may be influenced by previous incubations. For example, the continual alternating between light and dark conditions may have affected the physiological steady state of the organisms and thus influenced later dark acclimation periods. Statistical analyses accounted for replicates not being entirely independent by using a repeated

measures design. However, this does not compensate for the chambers being a potential artefact in this experiment.

4.3 Environmental predictors of emerged primary production

In this study, I investigated multiple environmental and sediment variables as predictors of photosynthetic efficiency (GPP_{SG} and $GPP_{chl\ a}$), a measure of ecosystem functioning. Variables were tested through multiple distLM models in order to find the best combination of variables that could predict responses in GPP_{SG} or $GPP_{chl\ a}$. While the distLM models did not account for large amounts of the variation, they did suggest some of the key variables explaining the observed variation in photosynthetic efficiency. Predictor variables varied in each of the three habitats. In the seagrass habitat, porosity (5.7%) and sediment temperature (4.5%) were the two significant predictors of variation in GPP_{SG}, while the full model (also including RH, MC, OM and MGS) explained 30% of the measured variation. In the shellfish habitat organic matter (12.7%) and median grain size (8.2%) were the only two variables included in the model, which explained just 17% of total variation in $GPP_{chl\ a}$. The environmental variables measured in the polychaete habitat explained 42% of the variation in $GPP_{chl\ a}$, with air temperature (26.1%) and median grain size (11.5%) being included in the most parsimonious model.

As light is a key prerequisite for primary production it is often assumed to control the rate of production and it has been widely propositioned that estuaries worldwide are heterotrophic systems, typically a result of limiting incident light concentrations (Heip *et al.*, 1995; Ouisse *et al.*, 2011). In light limited systems production can be predicted from biomass, incident irradiance and the attenuation coefficient or the light reaching the sediment surface (Heip et al., 1995). However, in temperate regions, especially during austral summer, light is almost never limiting during daylight hours and sediments are typically light saturated, especially during emersion. Surprisingly low light concentrations (0.4 – 5.1 µmol m^{-2} s^{-1}) are required to prompt photosynthesis and as mentioned earlier only ~250 µmol m^{-2} s^{-1} is required to saturate bare sediments (Barranguet *et al.*, 1998; Perkins *et al.*, 2001), and ~242 µmol m^{-2} s^{-1} in *Z. muelleri* beds (Leuschner & Rees, 1993; Vermaat *et al.*, 1997; Ralph *et al.*, 2002; Schwarz, 2004). In this study PAR was never measured

below these saturating light levels and thus was not identified as a significant predictor of GPP_{SG} or $GPP_{chl\ a}$ in distLM analyses in any of the three habitats.

Temperature (sediment or air) was recognised as a significant predictor in all three habitats yet was only included in the model in the seagrass and polychaete habitats. This is somewhat expected as temperature exerts a significant control on many biogeochemical processes acting in intertidal environments (Lee *et al.*, 2007). A study based in the subtropics revealed that a temperature increase of 10ºC would increase GPP by a factor of 4.8 (Lee *et al.*, 2011), while an early study suggested a temperature rise of 1ºC would accelerate GPP rates by 10% (Colijn & Van Buurt, 1975). Others suggest that maximum photosynthetic efficiency occurs at 25ºC and will begin to decline thereafter (Blanchard *et al.*, 1996). Early studies recognised the significant effect temperature has on primary production, particularly with respect to MPB communities at a number of temporal scales from season (Cadee & Hegeman, 1974; Admiraal & Peletier, 1980), to hourly during emersion (Admiraal, 1976; Rasmussen *et al.*, 1983). Furthermore, it is suggested that the short term effects of temperature affect all species differently (Admiraal, 1976), which would support the difference in key predictor variables as a function of habitat, as community composition and thus response significantly differs between the three habitats studied. The percentage of variation in photosynthetic efficiency explained by temperature is much higher in the polychaete habitat when compared to the other two habitats. This may suggest that temperature is more important in more permeable sediments. This could be explained by the accelerated draining in permeable habitats which removes any water layer that otherwise would buffer the sediment from temperature changes.

The 2011 study by Lee *et al.* also recognised a positive correlation between emerged GPP and grain size. Grain size was included in the most parsimonious models in the shellfish and polychaete habitat, while porosity (often highly correlated to median grain size) was significant in the seagrass habitat (Lee *et al.*, 2011). The physical structure of sediments is influenced during emersion due to the presence of air as opposed to water within pore spaces (Laima *et al.*, 2002). The positive relationship between grain size or porosity and primary production can be explained as the greater available pore space accelerates transport of solutes and enhances aerobic processes occurring in the sediments, which in turn increases total productivity (Laima *et al.*, 2002). This suggests that sediment traits (structure and

composition), such as mud content and median grain size, can play a key role in characterising environments as sinks or sources of CO_2 (Klaassen & Spilmont, 2012). Thus it is reasonable to infer that gas exchange and consequently photosynthetic efficiency is partly dependent on physio-chemical factors in the sedimentary environment, as well as biological factors.

In light saturated environments nutrient availability is likely to play a role in regulating production of both MPB and seagrass, thus influencing total productive capacities of intertidal flats (Lee *et al.*, 2007). Although this study did not assess sediment or water column nutrient concentrations it is important to note that they do have significant influence on primary production in estuarine environments. The significance of this relationship varies with habitat type, and seagrass meadows typically have a greater nutrient uptake and retention capacity with respect to bare sediment habitats (Thornton *et al.*, 2002; Rodil *et al.*, 2011). In temperate systems, like Tauranga Harbour, available nutrients tend to be the key factor limiting growth and thus production, therefore it could be expected to be a predictor variable of photosynthetic efficiency.

Lastly, macrofaunal community composition plays a key role in determining whether tidal flats are autotrophic or heterotrophic and thus are often assessed as predictors of ecosystem function. A 2007 study investigating infaunal influence stated that daily CO_2 exchange is often directly balanced by community respiration, however in defaunated sediment gross primary production can exceed microbial respiration by 40% (Tang & Kristensen, 2007). This describes the influence macrofaunal presence and functioning can have on benthic communities, even when inactive during low tide. Macrofaunal community composition was not assessed as an environmental predictor in this study as samples were only taken in during initial and final sampling campaigns, however it is likely to have explained a small percentage of the variation measured in GPP_{SG} and $GPP_{chl\ a}$.

As outlined in the distLM results, the environmental variables measured in the field did not account for much of the variation in GPP_{SG} or $GPP_{chl\ a}$. However, this was largely because a lot of the initial variation observed was accounted for by photosynthetic biomass and therefore removed once fluxes were standardised for biomass. The subsequent variation was minimal for several reasons. Firstly the photosynthetic organisms were adapted to maintain consistent productivity over a

summer period. Secondly, sampling did not occur over a large enough temporal gradient, as this study was conducted from November 2018 to February 2019, thus this data is restricted to austral summer periods. In future it would be great to expand this work to a seasonal study encompassing the broadest range of environmental conditions experienced by temperate estuaries in New Zealand. If a seasonal study was conducted it would be expected that greater variation in photosynthetic efficiency would be captured. Due to limitations imposed by the tide and due to the nature of the study (requiring high light conditions) GPP was only measured when low tide occurred around midday. Therefore, to assess the validity of my findings the environmental conditions measured during emerged GPP measurements were compared to the annual variation in environmental conditions measured from Tauranga Airport (NIWA, 2019). Despite constraints on appropriate field days GPP measurements were captured in light conditions (PAR) that represented 70% of annual variability, 56% of annual relative humidity, and 33% of annual air temperatures. As a result, the environmental conditions under which productivity was measured represents a relatively large percentage of annual conditions, especially considering the study was completed entirely in austral summer.

4.4 Research significance

The coastal ocean is often recognised as a key component within the global carbon cycle (Smith & Mackenzie, 1987; Smith & Hollibaugh, 1993; Gattuso *et al.*, 1998; Wollast, 1998; Bauer *et al.*, 2013). The high rates of GPP measured in seagrass habitats, ranging from 3000 to 8000 μmol O_2 m^{-2} h^{-1}, emphasise how important the contribution of seagrasses are to carbon fixation in coastal systems (Fourqurean *et al.*, 2012; Mazarrasa *et al.*, 2015; Röhr *et al.*, 2018). In contrast, MPB habitats are often discounted in local and global carbon budgets (Smetacek, 1999), however their potential resilience capacity (Drylie *et al.*, 2018) may support their future inclusion. It is predicted that emerged benthic habitats will contribute greater proportions to carbon sequestration in future as increasing levels of turbidity compromise the productive ability of benthos during immersion (Colijn, 1982). Investigation of this at both temporal and spatial scales is required due to the inherent variability of the intertidal environment as a result of the superimposition of diurnal, tidal and seasonal cycles (Migné *et al.*, 2009). However, studies looking

at either emerged or submerged in isolation, fail to recognise the inherent relationship between the two. Thus, there is a need to incorporate both tidal states (low & high) in determining the metabolic balance of benthic sediments.

A comparison between emerged GPP rates measured in this study and numerous previous studies regarding subtidal production in New Zealand estuaries was attempted (See Appendix 2; **Table A2.1**). GPP measurements conducted in this study (500 – 2500 μmol O_2 m^{-2} h^{-1}) in bare sediment habitats were with the range of reported rates of submerged GPP (18 – 3400 μmol O_2 m^{-2} h^{-1}). It is important to note that emerged and submerged GPP measurements are on the same scale, reinforcing that low tide production is significant and can contribute equal, if not more, to total coastal production. The great range of GPP may represent the wide range of environmental conditions experienced and in turn primary production rates found in New Zealand estuaries. Mud content exerts a control on these ecosystem functions with considerably lower measures of GPP and $GPP_{chl\ a}$ in sites with higher percentage mud (Needham *et al.*, 2011; Lohrer *et al.*, 2012). The breadth of these studies allows recognition that primary production and ecosystem functioning is extremely complex and is a function of many variables, thus deciphering cause-effect relationships proves difficult. Pratt *et al.* (2014b) quantified submerged NPP as a function of turbidity in Tauranga Harbour. During tidal submergence the light climate is influenced by an increased number of variables including water depth and suspended sediment concentrations (SSC), thus attributing responses to individual conditions proves difficult. Results showed a negative relationship between NPP and SSC, ranging from 1400 μmol O_2 m^{-2} h^{-1} under typical (20 mg L^{-1}) concentrations to 400 μmol O_2 m^{-2} h^{-1} under elevated (120 mg L^{-1}) concentrations. This highlights how high tide production may decrease as a result of the increased rate that terrestrial sediments are reaching the coast. This is an issue for MPB and seagrasses alike as high turbidity can affect growth rates ranging in extent from individual organisms to entire habitats, which will influence primary production and the photosynthetic efficiency of these important intertidal habitats.

The results discussed in this study will provide valuable information regarding sampling low tide production in future. For instance, in seagrass habitats the time in which sampling takes place (in relation to the tide) may dictate your results, while this appears to be less important in bare sediment habitats. Recognising that

different intertidal habitats respond in different ways to tidal emersion supports the need for habitat-specific sampling design.

4.5 Summary of major findings

This study compared the productive rates of three intertidal habitats within Tauranga Harbour, New Zealand to determine whether they are influenced by emersion in different ways. Abiotic and biotic variables were assessed as predictors of gross primary production.

The major findings of this study were:

1. Emerged GPP varies in different intertidal habitats, largely due to the dominant photosynthetic biomass. For instance GPP in the seagrass habitat significantly exceeded GPP in unvegetated sediments, which is as expected owing to the greater photosynthetic biomass associated with seagrass habitats (Moncreiff et al., 1992).

2. Rates of emerged GPP varied (by up to 40% (2300 µmol O_2 m^{-2} h^{-1}) in the seagrass habitat and by up to 70% (1200 µmol O_2 m^{-2} h^{-1}) in bare sediment habitats) over the austral summer period however, a large component of this variation is solely attributed to photosynthetic biomass.

3. Microphytobenthos and *Zostera muelleri* dominated habitats respond differently to emersion and employ different mechanisms to minimise chances of photoinhibition, desiccation, and grazing. Seagrass production increased during emersion while there was no consistent relationship in either of the bare sediment habitats.

4. Key environmental predictors of photosynthetic efficiency (GPP_{SG} and $GPP_{chl\ a}$) vary in different intertidal habitats. The most important common predictors are temperature and grain size/porosity.

5. Low tide production may become increasingly important in the future as the immersed period is compromised by light limitations.

4.6 Future research

To improve the scope of this study it would be beneficial to cover a broader range of environmental conditions, and account for other potential predictor variables. This could include encompassing a wider range of sites, spanning a gradient in environmental conditions (mud content, turbidity, trophic state). By exploring both turbid, pristine and the in-between environments we may be able to help predict ecosystem responses to further intensification/urbanisation and the resulting environmental degradation. Additionally, as the environmental/sediment variables measured did not explain a great deal of variation observed in gross primary production I would recommend exploring other potential variables such as porewater nutrient concentrations. In relation to desiccation stresses this may include measurements of leaf water content in seagrass habitats to isolate rates of water loss across the low tide period and how these may directly influence gross primary production. There is also potential to explore the influence of elevation, and how the rates of desiccation and the resulting stress may differ higher or lower within the intertidal zone. Repeating this study at higher intertidal elevations would provide an additional dataset to consider desiccation under extreme conditions, where emersion periods can reach over six hours.

This study was completed in a single location within a single harbour, thus extrapolating these results to a wider geographical scale proves difficult. In saying this, it is likely that the results in this study will be comparable to other barrier-enclosed systems in New Zealand. However, further research is required to fully understand low tide production in intertidal habitats and the dynamics of key stressors.

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Appendices

Appendix 1

Table A.1.1. Additional seagrass attributes as a function of sampling month, values are mean ± standard deviation (n = 6).

	L# (0.25 m^2)	**LL (mm)**	**LW (mm)**
November	3230 ± 410	67.6 ± 14.9	0.890 ± 0.19
December	3270 ± 230	72.5 ± 16.8	0.993 ± 0.13
January	5830 ± 1780	75.6 ± 18.1	1.04 ± 0.14
February	3820 ± 580	72.2 ± 18.3	1.10 ± 0.28

The abbreviations featured in the table represent the following: Leaf count (L#), leaf length (LL), and leaf width (LW).

Table A1.2. Pearson's correlation coefficient (r) between environmental variables in a seagrass dominated habitat. Significant P-values ($P < 0.05$) are shown in bold.

	MC	MGS	OM	Porosity	PAR	Air T	Sediment T	RH
(a) Environmental variables								
Mud Content	1.00							
Median Grain Size	**-0.30**	1.00						
Organic Matter	**0.31**	-0.17	1.00					
Porosity	**0.26**	-0.04	**0.43**	1.00				
PAR	-0.034	0.06	0.16	0.18	1.00			
Air Temperature	**0.29**	**-0.34**	0.06	**0.55**	**-0.25**	1.00		
Sediment Temperature	**0.21**	**-0.27**	0.07	**0.51**	-0.20	**0.76**	1.00	
Relative Humidity	**0.27**	-0.13	**-0.35**	**-0.23**	**-0.30**	**0.27**	0.12	1.00
(b) Ecosystem functions (response variables)								
NPP	0.073	**-0.241**	0.015	0.186	**-0.429**	**0.655**	**0.611**	**0.343**
SOC	0.067	-0.049	-0.160	-0.124	0.145	**-0.317**	**-0.398**	0.061
GPP	-0.004	-0.098	0.109	0.176	**-0.318**	**0.546**	**0.573**	0.143
GPP_{SG}	-0.189	0.112	-0.147	**-0.238**	-0.181	0.085	**0.209**	0.176

The abbreviations in the table represent the following: mud content (MC), median grain size (MGS), organic matter (OM), photosynthetically active radiation (PAR), air temperature (Air T), sediment temperature (Sediment T), relative humidity (RH), net primary production (NPP), sediment oxygen consumption (SOC), gross primary production (GPP) and photosynthetic efficiency (GPP_{SG}).

Table A.1.3. Pearson's correlation coefficient (r) between environmental variables in a shellfish dominated habitat. Significant P-values ($P < 0.05$) are shown in bold.

	MC	**MGS**	**OM**	**Porosity**	**PAR**	**Air T**	**Sediment T**	**RH**
(a) Environmental variables								
Mud Content	1.00							
Median Grain Size	**-0.76**	1.00						
Organic Matter	0.13	0.23	1.00					
Porosity	**-0.33**	**0.52**	**0.61**	1.00				
PAR	0.17	-0.00	**0.36**	**0.46**	1.00			
Air Temperature	**-0.36**	-0.09	**-0.78**	**-0.61**	**-0.53**	1.00		
Sediment Temperature	**-0.29**	-0.14	**-0.61**	**-0.46**	**-0.66**	**0.83**	1.00	
Relative Humidity	**-0.48**	**0.75**	0.13	0.22	-0.20	-0.04	-0.16	1.00
(b) Ecosystem functions (response variables)								
NPP	**-0.36**	0.19	**-0.24**	0.12	-0.02	**0.26**	0.20	0.05
SOC	**-0.36**	**0.37**	0.23	**0.66**	**0.43**	-0.18	-0.16	0.12
GPP	-0.05	-0.13	**-0.43**	**-0.43**	**-0.39**	**0.40**	**0.32**	-0.05
$GPP_{chl\ a}$	0.12	**-0.29***	**-0.36**	**-0.36**	**-0.25**	**0.28**	**0.27**	-0.21

The abbreviations in the table represent the following: mud content (MC), median grain size (MGS), organic matter (OM), photosynthetically active radiation (PAR), air temperature (Air T), sediment temperature (Sediment T), relative humidity (RH), net primary production (NPP), sediment oxygen consumption (SOC), gross primary production (GPP) and photosynthetic efficiency ($GPP_{chl\ a}$).

Table A.1.4. Pearson's correlation coefficient (r) between environmental variables in a polychaete dominated habitat. Significant P-values ($P < 0.05$) are shown in bold.

	MC	**MGS**	**OM**	**Porosity**	**PAR**	**Air T**	**Sediment T**	**RH**
(a) Environmental variables								
Mud Content	1.00							
Median Grain Size	**-0.65**	1.00						
Organic Matter	**0.71**	**-0.60**	1.00					
Porosity	**-0.57**	**0.90**	**-0.60**	1.00				
PAR	**-0.38**	0.17	-0.25	-0.02	1.00			
Air Temperature	**-0.80**	**0.74**	**-0.68**	**0.68**	**0.46**	1.00		
Sediment Temperature	**-0.63**	**0.28**	**-0.45**	0.10	**0.60**	**0.75**	1.00	
Relative Humidity	0.13	**-0.56**	**0.28**	**-0.72**	**0.37**	**-0.25**	**0.36**	1.00
(b) Ecosystem functions (response variables)								
NPP	**0.450**	**-0.37**	-0.11	**-0.22**	0.11	**0.54**	**0.45**	**0.49**
SOC	0.20	-0.03	-0.19	0.16	-0.18	0.04	-0.13	-0.10
GPP	**0.45**	**-0.38**	-0.05	**-0.29**	0.17	**0.54**	**0.51**	**0.55**
$GPP_{chl\ a}$	**0.41**	**-0.34**	-0.05	**-0.22**	0.15	**0.52**	**0.47**	**0.47**

The abbreviations in the table represent the following: mud content (MC), median grain size (MGS), organic matter (OM), photosynthetically active radiation (PAR), air temperature (Air T), sediment temperature (Sediment T), relative humidity (RH), net primary production (NPP), sediment oxygen consumption (SOC), gross primary production (GPP) and photosynthetic efficiency ($GPP_{chl\ a}$)

Appendix 2

An online literature search was conducted to find hourly rates of gross primary production and photosynthetic efficiency for intertidal sandflats under immersion. Literature-derived values were used to draw comparisons between submerged and emerged primary production within a New Zealand context.

Table A2.1. Summary of literature on submerged gross primary production (GPP) and photosynthetic efficiency ($GPP_{chl\ a}$) in mid-intertidal sandflats in temperate estuaries found in North Island, New Zealand. Abbreviations for chamber details: surface area (SA) and volume (V).

Location	Site	Mud content (%)	GPP (µmol O_2 m^{-2} h^{-1})	$GPP_{chl\ a}$ (µmol O_2 µg g^{-1} dw chl *a* m^{-2} h^{-1})	Chamber details	Reference
Tuapiro Point, Tauranga Harbour	1	10 - 22	1140 - 1520	-	SA: 0.114 m^2 V: 18 L	Sandwell *et al.* (2009)
Mahurangi Harbour	1 2 3	1.6 9.8 19	2100 1500 1400	263 188 175	SA: 0.016 m^2 V: 0.85 L	Lohrer *et al.* (2010)
Whangapoua Harbour	1 2 3	1.5 0.8 0.5	1950 2050 2500	195 293 357	SA: 0.016 m^2 V: 0.85 L	Rodil *et al.* (2011)
Waitemata Harbour	1 2	4 7	1600 750	95 110	SA: 0.016 m^2 V: 0.85 L	Lohrer *et al.* (2011)
Tauranga Harbour	1 2	0 13	- -	Summer: 600 - 900 Winter: 250 - 350 Summer: 200 Winter: 120 – 150	SA: 0.25 m^2 V: 35 L	Jones *et al.* (2011)
Tairua estuary, Coromandel Peninsula	1 2	13 37	- -	250 - 325 125 – 250	SA: 0.25 m^2 V: 35 L	Needham *et al.* (2011)

Table A.2.1 (Continued). Summary of literature on submerged gross primary production (GPP) and photosynthetic efficiency ($GPP_{chl\ a}$) in mid-intertidal sandflats in temperate estuaries found in North Island, New Zealand. Abbreviations for chamber details: surface area (SA) and volume (V).

Location	Site	Mud content (%)	GPP (µmol O_2 m^{-2} h^{-1})	$GPP_{chl\ a}$ (µmol O_2 µg g^{-1} dw chl *a* m^{-2} h^{-1})	Chamber	Reference
Waitemata Harbour	1	-	850	-	SA: 0.016 m^2 V: 0.85 L	Lohrer *et al.* (2012)
	2	5	900	-		
	3	-	1100	-		
Manukau Harbour	4	16	300	-		
Tamaki Estuary	5	13	800	-		
Whitford Embayment	6	5	1150	-		
North Island, NZ	1	0 – 14	-	100 – 325	SA: 0.016 m^2 V: 0.85 L	Pratt *et al.* (2014a)
Tuapiro Point, Tauranga Harbour	1	6.5	1000 – 3400	-	SA: 0.25 m^2 V: 35 L	Pratt *et al.* (2014b)
Whangapoua Harbour	1	< 5	-	450 - 620	SA : 0.016 m^2 V : 0.85 L	Gladstone-Gallagher *et al.* (2016)
Tuapiro Estuary, Tauranga Harbour	1	0-10	2500 – 5200	180 - 550	SA : 0.016 m^2 V : 0.85 L	Douglas *et al.* (2018)
Kaipara Harbour	1	8.1	200	17.9	SA: 0.25 m^2 V: 35 L	Drylie *et al.* (2018)
	2	4.0	1200	107		
	3	9.9	2000	274		
Tuapiro Point, Tauranga Harbour	1 (SF)	8.0	500 – 1800	20 – 200	SA: 0.25 m^2 V: 35 L	This study *
	2 (P)	2.5	900 - 2500	130 - 360		

* This study was conducted under emerged conditions, all others were conducted under submerged conditions