METABOLISM, PARTICLE UPTAKE, AND
NUTRIENT FLUXES ON A TIDE-DOMINATED
FRINGING REEF

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THESIS DECLARATION

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Approval to access Bardi Jawi lands was given through a Kimberley Traditional Owner agreement, facilitated by the Kimberley Land Council and the Bardi Jawi Prescribed Body Corporate.

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This thesis contains published work and/or work prepared for publication, some of which has been co-authored.

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Reef organisms are strongly dependent on the physical and chemical conditions of surrounding ocean waters, which influence rates of key metabolic and biogeochemical processes such as primary production, respiration, nutrient uptake, and grazing on suspended particulate matter. Flows driven by currents and waves interact with reef topography to determine the delivery rate of dissolved and particulate material to the surfaces of reef organisms. Reef circulation also controls the temperature and light availability at the reef surface, which in turn influence broader-scale ecological processes, especially rates of community primary production. Tide-dominated reefs are reefs that experience mean tidal ranges in excess of local mean significant wave heights. Despite being common (~one third of all reefs worldwide), almost no studies have focused on how the large tidal forcing of these systems controls the physical and chemical properties of overlying waters and, in turn, community ecological processes.

This study was conducted in the remote and near-pristine Kimberley region of northwest Australia at Tallon Island. This reef platform is strongly forced by semidiurnal tides (spring range >8 m) and experiences highly asymmetric tidal phase durations, with ebb tides lasting ~10 hours. The reef itself has distinct benthic zonation, with a seagrass-dominated community inhabiting the inner portion of the platform and a macroalgal-dominated community (including small corals, ~5-10% cover) on the outer seaward zone. Three field experiments (each lasting 2-3 weeks) were conducted in Oct 2013 (dry season), Feb 2014 (wet season), and Apr 2014 (late wet season). Hydrodynamic instrumentation, in situ calibrated fluorometers, and dissolved oxygen (DO) loggers deployed on the reef platform provided continuous measurements of flow...
speed, chlorophyll $a$ (chl $a$), DO, and water temperature, while concentrations of dissolved and particulate nutrients were repeatedly measured with strategic water sampling. A one-dimensional control volume approach was used to estimate: 1) community production and respiration; 2) benthic chl $a$ and particulate nutrient fluxes; and 3) dissolved nutrient uptake and release within the two major reef zones.

Temperature and DO variations measured on the reef platform were among the most extreme recorded for reefs worldwide, with diel ranges of ~11°C and 440 $\mu$M DO. Hypoxic conditions (DO < 63 $\mu$M) occurred when low water depth coincided with nighttime, and could last for up to 7 hours each night. Estimates of productivity suggest that benthic communities were not negatively affected by short-term (~hours) extremes in light (up to 1800 $\mu$mol m$^{-2}$ s$^{-1}$) and temperature (>35°C), and were moderately productive compared to similar communities worldwide. The reef alternated between net autotrophy and heterotrophy over a ~15 day cycle, which was related to the phase difference between the solar and tidal cycles.

Suspended particulate nutrients and chl $a$, food sources for benthic filter-feeders, were depleted towards the end of ebb tide. Flood tides then ‘refreshed’ these pools by delivering a pulse of oceanic water onto the reef platform. Rates of benthic chl $a$ uptake measured on Tallon were lower than previous studies of many reef communities, and the reef was a net source of particulate nutrients to the surrounding ocean waters, with particulate organic carbon exports comprising ~3% of the reef’s daily production. Potential uptake rates of dissolved inorganic nutrient species varied over a tidal cycle as a function of flow conditions and water column nutrient concentrations, with fluxes varying by an order of magnitude over the range of flow speeds naturally occurring on this reef platform. Fluxes were also forced by offshore nutrient concentrations, which
increased during the wet season. A net release of inorganic nutrients was balanced by an uptake of dissolved organic nutrients on the reef platform, suggesting that organic species may be an important nutrient source.
# Table of Contents

Thesis Declaration ................................................................. ii  
Abstract ....................................................................................... iii  
List of Tables .................................................................................. ix  
List of Figures ............................................................................... xii  
Acknowledgements ......................................................................... xx  
Authorship Declaration: Co-Authored Publications .................. xxii

## 1. Introduction ........................................................................ 1  
1.1. Importance of reefs ...................................................... 1  
1.1.2. Developments in reef studies ....................................... 2  
1.1.3. Reef circulation and physical forcing ............................. 4  
1.1.4. Introduction to the Kimberley region ............................. 6  
1.1.5. Organization and objectives ......................................... 10

## 2. Metabolism of a tide-dominated reef platform subject to extreme diel temperature and oxygen variations ................................................................. 13

2.1. Abstract ........................................................................... 13  
2.2. Introduction ...................................................................... 15  
2.3. Methods ........................................................................... 17  
2.3.1. Study site .................................................................. 18  
2.3.2. Field measurements ................................................... 21  
2.3.3. Community productivity ............................................. 23  
2.4. Results .............................................................................. 29  
2.4.1. Environmental conditions ........................................... 29  
2.4.2. Benthic productivity .................................................... 32  
2.5. Discussion ......................................................................... 40  
2.5.1. Extreme conditions on the reef flat ............................ 40  
2.5.2. Eulerian decomposition of benthic oxygen fluxes .......... 41  
2.5.3. Dissolved oxygen drives community respiration .......... 43  
2.5.4. Response of community metabolism .......................... 46
3. Benthic uptake of phytoplankton and ocean-reef exchange of particulate nutrients on a tide-dominated reef .......................................................... 50
  3.1. Abstract .............................................................................................................. 50
  3.2. Introduction ....................................................................................................... 52
  3.3. Methods ............................................................................................................. 54
    3.3.1. Field site .................................................................................................... 54
    3.3.2. Water sampling ........................................................................................ 59
    3.3.3. Control volume approach ....................................................................... 61
    3.3.4. Reef-scale mass balance ......................................................................... 63
    3.3.5. Statistics and error propagation ............................................................. 68
  3.4. Results .............................................................................................................. 68
    3.4.1. Chlorophyll $a$ and particulate nutrients .............................................. 68
    3.4.2. Benthic chl $a$ fluxes ............................................................................. 74
    3.4.3. Benthic fluxes of total POC and PON .................................................. 78
  3.5. Discussion ....................................................................................................... 80
    3.5.1. Offshore chl $a$ and particulate nutrients ............................................ 80
    3.5.2. Size-dependent deposition and resuspension of POM ....................... 84
    3.5.3. Benthic fluxes of chl $a$ and phytoplankton-derived nutrients .......... 86
    3.5.4. Benthic fluxes and reef zonation ............................................................ 88
    3.5.5. Net export of particulate nutrients ......................................................... 89

4. Dissolved nutrient fluxes over a tide-dominated tropical fringing reef ......... 92
  4.1. Abstract .............................................................................................................. 92
  4.2. Introduction ....................................................................................................... 94
  4.3. Methods ............................................................................................................. 98
    4.3.1. Field site .................................................................................................... 98
    4.3.2. Water sampling ........................................................................................ 100
    4.3.3. Control volume approach ....................................................................... 102
    4.3.4. Uptake rates at the limits of mass-transfer ............................................ 104
  4.4. Results .............................................................................................................. 108
    4.4.1. Nutrient concentrations and measured fluxes .................................... 108
    4.4.2. Mass-transfer velocity and nutrient uptake .......................................... 111
  4.5. Discussion ....................................................................................................... 115
    4.5.1. Oceanic nutrient supply ......................................................................... 115
4.5.2. Rates and sources of benthic release of DIN and DIP ......................... 117
4.5.3. Tidal and seasonal forcing of mass-transfer-limited fluxes ................ 120

5. General discussion and conclusions ......................................................... 122
   5.1.1. Overview .......................................................................................... 122
   5.1.2. Summary of major findings .............................................................. 122
   5.1.3. Effects of wave vs tidal forcing on metabolism and biogeochemistry .. 126
   5.1.4. Broader implications for the region ..................................................... 127
   5.1.5. Future research directions ................................................................. 128

References ........................................................................................................... 129
LIST OF TABLES

Table 2.1. Summary of mean (SD) and ranges of environmental conditions on Tallon reef platform during both field experiments. DO refers to dissolved oxygen, $u_{10}$ refers to wind speed at 10 m, and (--) indicates no available data. ......................30

Table 2.2. Summary of net community production ($NCP$), community respiration ($R$), and gross primary production ($P$) during the wet season. Fluxes (mean of $n$ days) are in units of mmol O$_2$ m$^{-2}$ d$^{-1}$ (± SE). Ratio between gross production and respiration is $P:R$. .................................................................38

Table 3.1. Number of chl $a$ samples taken each field experiment at each site, including during Lagrangian drifts and large (>5 µm) chl $a$ fractions. Number of particulate organic carbon (POC), nitrogen (PON), and phosphorus (PP) samples are also indicated. Tide stages (ebb, flood) refer to tides on the reef platform, (--) indicates no samples available, and values are the number of duplicate samples. ........................................................................................................58

Table 3.2. Summary of mean (SD) concentrations and stoichiometry of particulate organic carbon (POC), nitrogen (PON), and phosphorus (PP) from all field experiments. Reef zone [macroalgal (MA), mixed (Mix), and seagrass (SG)] values are from final 6 hours of ebb tide, and offshore (Off) values are from all stages of the tide. Number of samples represented by each mean are shown in Table 3.1, and (--) indicates no data available. .................................................................71

Table 3.3. Mean (SD) net benthic fluxes of chl $a$ and phytoplankton-derived particulate organic carbon (POC$_p$) and nitrogen (PON$_p$) determined by the mass balance (MB) and CoVo approaches during the Apr field experiment. Values for this...
study are overall means of all tidal cycle means \((n = 17)\). Also shown are estimates [mean \((SE)\) or range] of the same variables from previous studies of reef communities................................................................. 79

Table 3.4. Estimates of particulate organic carbon (POC) and nitrogen (PON) fluxes using the mass balance approach (Figure 3.11, Table 3.3) for Tallon reef during the Apr field experiment. All values are means \((SD)\) in mmol m\(^{-2}\) d\(^{-1}\). Detrital release is sinks of organic material (off-reef flow and chl \(a\) uptake) less the oceanic inputs................................................................. 82

Table 4.1. Number of duplicate water samples collected during both field experiments at offshore (Off), macroalgal (MA), and seagrass (SG)-dominated sites. Water quality variables include dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP), dissolved organic nitrogen (DON), and particulate organic nitrogen (PON) and phosphorus (PP). ................................................. 100

Table 4.2. Summary of mean \((SD)\) conditions in offshore waters (Off) during Oct and Feb field experiments. Number of samples represented by each mean is shown in Table 4.1. Water quality variables are nitrate (NO\(_x\)), ammonium (NH\(_4^+\)), dissolved inorganic phosphorus (DIP), and dissolved organic nitrogen (DON). ........................................................................................................................... 108

Table 4.3. Mean \((SE)\) net fluxes (in mmol m\(^{-2}\) d\(^{-1}\)) of nutrients determined by the CoVo approach during the Oct and Feb field experiments. Nutrient species include dissolved inorganic nitrogen (DIN) and phosphorus (DIP); dissolved organic nitrogen (DON); particulate organic nitrogen (PON); and particulate phosphorus (PP). Net \((J_{net})\), mass-transfer-limited \((J_{MTL})\), and release \((J_{release})\) fluxes are from the final 6 hours of ebb tide................................................................. 110
LIST OF FIGURES

Figure 1.1. Locations in the west Kimberley region mentioned in this thesis, including the Tallon Island study site. Image courtesy of Chelys. .............................................. 6

Figure 1.2. A small section of the reef crest of Tallon Island near a) the beginning and b) the middle of ebb tide (note the person for scale in bottom photograph). During ebb tide, the crest becomes a hydraulic control and restricts water flow off Tallon reef. ........................................................................................................ 8

Figure 1.3. Scaffolding (4 m tall) with instrumentation in the centre of the Tallon Island reef platform during a) high tide and b) end of ebb tide. During ebb tide, a minimum water depth (~0.4 m) is maintained on the reef platform. .................. 10

Figure 2.1. Location of Tallon Island in the west Kimberley region of northwestern Australia. .............................................................................................................. 18

Figure 2.2. Instrument deployment locations on Tallon reef flat and benthic community zones determined by photographic survey. Images of benthic communities at dissolved oxygen (DO) loggers sites 1 (DO1) and 3 (DO3) during low tide are shown on the right. ADPHR refers to the acoustic Doppler current profiler..... 19

Figure 2.3. Length of reef represented in productivity measurements for both communities (dashed line) and mean (± standard error) flow $u_x$ (black dots) with water depth $h$ on the reef flat. Times shown at the top of the figure indicate the time interval at which the advective component of $J_{O2}$ was estimated. A longer interval (80min, indicated by shaded box) was used as flow on the reef slowed, which allowed estimates of the advective term over each community.......... 26
Figure 2.4. Time-series of conditions on Tallon reef during a portion of the wet season field experiment including: a) depth-averaged current velocity in the along-transect direction ($u_x$) and water depth on the reef platform ($h$); b) wind speed and direction at 10 m ($u_{10}$); c) photosynthetically active radiation (PAR) at the reef surface; d) dissolved oxygen (DO) concentration at DO1 (seagrass site) with hypoxia (DO < 63 µM) indicated by dashed line; and e) water temperature ($T$) at DO1 (seagrass site).

Figure 2.5. A one-day sample of the total time-series of local, advective, and air-sea components of benthic oxygen flux ($J_{O2}$) for a) seagrass and b) macroalgal communities during the wet season field experiment with water depth $h$. Hourly fluxes of c) net primary production ($np$) and community respiration ($r_{night}$) in both communities are shown with grey boxes indicating nighttime periods.

Figure 2.6. Relationships of community respiration ($r_{night}$) to a) temperature ($T$) and b) dissolved oxygen (DO). Relationships between DO and c) temperature-normalized $r_{night}$ ($r_{Tref}$) also shown for seagrass and macroalgal communities during the wet season field experiment. Monod relationships (dashed lines) used to predict daytime respiration ($r_{day}$) and nighttime respiration ($r_{night}$) for periods when oxygen fluxes were not available are shown where $r_{Tref} = 59.1\text{DO} / (432.6 + \text{DO})$ for seagrass ($R^2 = 0.72$) and $r_{Tref} = 42.6\text{DO} / (125.5 + \text{DO})$ for macroalgal communities ($R^2 = 0.63$).

Figure 2.7. Relationship between flow speed ($u_x$) and first-order uptake rate coefficients of oxygen in seagrass and macroalgal communities ($k_{SG}$ and $k_{MA}$), and coefficients estimated from mass transfer limits ($S_{MTL}$).
Figure 2.8. Photosynthesis-irradiance curves for hourly net production $np$ in a) seagrass and b) macroalgal communities during the wet season field experiment. Water column dissolved oxygen (DO) for each measurement is shown in the color bar.

Figure 2.9. Photosynthesis-irradiance curves for hourly rates of gross primary production $p$ in seagrass and macroalgal communities during the wet season field experiment. The best hyperbolic tangent fit of each dataset (solid lines) are shown with 95% confidence intervals (dashed lines).

Figure 2.10. Daily mean ($\pm$ SD) a) temperature ($T$), b) dissolved oxygen (DO), and rates of net community production ($NCP$) in c) seagrass and d) macroalgal communities during both seasons. Values are shown as a function of difference between high tide and solar noon expressed in hours. Zero hours indicates the alignment of high tide and solar noon, while negative hours indicate high tide occurring prior to solar noon.

Figure 3.1. Deployment locations of hydrodynamic instrumentation and hand sampling locations on Tallon reef platform. Inset shows Tallon Island location in the west Kimberley region of Australia. ADV refers to acoustic Doppler velocimeters, ADPHR refers to acoustic Doppler current profilers, and FLNTU refers to fluorometers.

Figure 3.2. Tidal phase-averaged hydrodynamic conditions on Tallon Reef including a) water depth at SG ($h$) and offshore; b) current speed at five hydrodynamic instruments (V1 – V4 are acoustic Doppler velocimeters and ADP is acoustic Doppler profiler); and current vectors from c) flood tide, d) start of ebb tide, and e) middle of ebb tide. All values are means from a full spring-neap cycle.
scale changes on current vectors to emphasize flow patterns. Crosses indicate periods when water depth was too low to measure flow. Length of reef crest ($l_r$) used for discharge estimates (see Methods) is coloured to correspond with associated hydrodynamic instrumentation.

Figure 3.3. Relationship between chlorophyll $a$ measured from filtered water samples and concurrent measurements from fluorometers (FLNTU) (solid line, $R^2 = 0.74$). The dashed line shows a 1:1 relationship. Regression coefficients derived from the data shown were used to adjust FLNTUs to in situ conditions.

Figure 3.4. Mean ($\pm$ SE) chlorophyll $a$ (a,b) and ratio of phaeopigments:chlorophyll $a$ (c,d) from water samples at offshore (Off) and reef stations [macroalgal (MA), mixed (Mix), and seagrass (SG) dominated zones] during all field experiments. Samples are categorized as taken during flood tide or during ebb tide (final 6 hours) on the reef platform. The number of samples represented by each mean is shown in Table 3.1.

Figure 3.5. Mean (with 95% confidence limits) chlorophyll $a$ concentration (a,b) and ratio of phaeophytin:chl $a$ (c,d) from water samples in small ($<5 \mu m$) and large ($>5 \mu m$) fractions at offshore (Off) and reef stations [macroalgal (MA) and seagrass (SG) dominated zones]. All samples taken during the Oct field experiment during final 6 hours of ebb tide on the reef (Table 3.1). Asterisks (*) denote means which are significantly different ($p < 0.05$) to offshore means.

Figure 3.5. Relationship between chlorophyll $a$ measured from filtered water samples and concurrent measurements from fluorometers (FLNTU) (solid line, $R^2 = 0.74$). The dashed line shows a 1:1 relationship. Regression coefficients
derived from the data shown were used to adjust FLNTUs to in situ conditions.

Figure 3.6. Reef flat a) depth $h$ (tidal phase-averaged) shown with all chlorophyll $a$ measurements from fluorometers in b) macroalgal and c) seagrass-dominated zones shown with hour after reef flooding during the Apr field experiment. Color indicates the flow speed $u$ adjacent to each fluorometer. Chl $a$ values shown were corrected according to regressions shown in Figure 3.5. Note that different limits are used in the color scale of each plot in order to accommodate differences in the range of flow speeds at each station.

Figure 3.7. Tidal phase-averaged chl $a$ (lines) and standard deviation (shaded areas) from a) macroalgal and b) seagrass-dominated zones is shown for daytime (coloured) and nighttime (black) periods during the Apr field experiment.

Figure 3.8. All estimates of benthic flux of chlorophyll $a$ using the one-dimensional control volume technique ($JcHlaCoVo$). Positive values indicate net uptake by the reef and negative values indicate net release to overlying waters. Individual estimates (black dots) shown with tidal phase-averaged flux (line) and flux estimates from drifter releases ($JcHlaDrift$) in macroalgal (MA) and seagrass (SG) -dominated zones.

Figure 3.9. Tidal phase-averaged (lines) and ranges (shaded areas) of a) discharge and b) net rate of chlorophyll $a$ transfer $F_{net}$ onto (positive) and off of (negative) Tallon reef platform are shown with hours after reef flooding. Discharges are onto ($Q_{in}$) and off of ($Q_{out}$) the reef platform.

Figure 3.10. Mean ($\pm$ SD) vertical flux of chlorophyll $a$ over each tidal cycle determined by the mass balance technique ($JcHlaMB$) for the Apr field
experiment. Positive values indicate net uptake of chl $a$ on the reef platform, while negative values indicate net release of chl $a$ to the overlying waters. ....78

Figure 3.11. Concentrations of particulate organic a) carbon (POC) and b) nitrogen (PON) on the reef (station Mix) during the Apr field experiment, shown as a function of hours after reef flooding. Mean tidal phase-averaged water depth $h$ shown in black. Coloured lines, which indicate the relationship between POC and PON with time after reef flooding ($R^2 = 0.46$ and 0.57, respectively), were used to estimate nutrient concentration in off-reef discharge during ebb tide. Dashed lines represent 95% confidence limits of the mean. Coloured circles on the x-axis denote mean concentration offshore..................................................81

Figure 4.1. Deployment locations of hydrodynamic instrumentation and water sampling locations on Tallon reef platform and offshore. Inset shows Tallon Island location in the west Kimberley region of Australia. ADV refers to acoustic Doppler velocimeters and ADPHR refers to acoustic Doppler profiler. ............99

Figure 4.2. Selected time-series of spring-neap transition showing a) water depths on the reef platform ($h$) and offshore, with depth-averaged flow speed $u$ in b) macroalgal and c) seagrass-dominated zones. Times of water sampling are indicated by black circles in subplot a. .............................................................103

Figure 4.3. Measurements of nitrate (NO$_x$) (a,b), ammonium (NH$_4^+$) (c,d), and dissolved inorganic phosphorus (DIP) (e,f) from water samples during Oct (left column) and Feb (right column) field experiments. Samples were taken at two stations [macroalgal (MA) and seagrass (SG) dominated zones], and the tidal phase-averaged mean from each station is shown with dashed lines. Phase-averaged concentrations are fixed at the y-axis at the concentration of waters
flooding the reef (offshore nutrient concentration shown in Table 4.2). Phase-averaged water depth $h$ is also shown (black line). ........................................... 107

Figure 4.4. Fluxes of a) nitrate (NO$_3^-$), b) ammonium (NH$_4^+$), and c) dissolved inorganic phosphorus (DIP) along the study transect during both field experiments shown with water depth on the reef flat ($h$). Net benthic fluxes ($J_{net}$, in blue) were estimated using the CoVo approach, while mass-transfer-limited uptake ($J_{MTL}$, in green) was calculated from reef platform flow and nutrient concentrations, and nutrient release ($J_{release}$, in red) was calculated from net and MTL fluxes. ....... 109

Figure 4.5. Net benthic fluxes ($J_{net}$) of a) dissolved organic nitrogen (DON), b) particulate nitrogen (PN), and c) particulate phosphorus (PP) along the study transect during both field experiments shown with water depth on the reef flat ($h$). Fluxes were estimated using the CoVo approach. ............................................. 112

Figure 4.6. Tidal phase-averaged mass-transfer velocity $S$ for a) nitrate (NO$_3^-$), c) ammonium (NH$_4^+$), and e) dissolved inorganic phosphorus (DIP) calculated in both macroalgal (MA) and seagrass (SG)-dominated zones over a full spring-neap cycle. These coefficients were used to estimate the mass-transfer-limited uptake rates $J_{MTL}$ of b) NO$_3^-$, d) NH$_4^+$, and f) DIP using phase-averaged nutrient concentrations from Oct and Feb field experiments (Figure 4.3). Phase-averages are the mean of all measurements occurring at the same point in the tidal cycle (i.e., mean of all $S$ at high tide). ........................................................................ 114

Figure 4.7. Means ($\pm$ SE) of mass-transfer velocity $S$ from all tidal cycles ($n = 23$) for nitrate (NO$_3^-$), ammonium (NH$_4^+$), and dissolved inorganic phosphorus (DIP). Values are from seagrass (SG) and macroalgal (MA) dominated communities. .................................................................................................................................................. 116
Figure 4.8. Tidal cycle averages (± SE) of mass-transfer-limited uptake $J_{MTL}$ for a) nitrate (NO$_3$), b) ammonium (NH$_4^+$), and c) dissolved inorganic phosphorus (DIP) in seagrass (SG) and macroalgal (MA)-dominated zones during Oct and Feb field experiments. Values are means of all tidal cycle means ($n = 23$) over a full spring-neap cycle.

Figure 5.1. Fitzroy River discharge measured at Willare (site 802008 Dept. of Water) from 1998 – 2014. Upper right inset shows years ranked by annual discharge, with 2013/2014 wet season highlighted in red.
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This thesis contains work that has been previously published and is currently in review for publication.

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| Student contribution to work: Fieldwork, labwork, data analysis, and writing (80% overall) |

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I, Ryan Lowe certify that the student statements regarding their contribution to each of the works listed above are correct

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1. **INTRODUCTION**

1.1.1. **Importance of reefs**

   Tropical reefs are among the most iconic and vibrant of all ecological systems, and provide food and shelter for diverse assemblages of marine life (Bellwood and Hughes 2001; Hughes et al. 2002). Although often associated with corals that contribute to building reef frameworks, reefs are more generally biogenic structures built by a number of calcifying organisms such as crustose coralline algae (Goreau 1963) and can contain a broad mixture of habitat-forming organisms such as corals, macroalgae, and seagrasses. Reefs provide many ecosystem services to local communities, including support of fisheries, coastal protection, and tourism (Moberg and Folke 1999). As an example, Australia’s Great Barrier Reef World Heritage Area is estimated to generate about $15-20 billion per year from tourism, fishing, boating, and social values (Stoeckl et al. 2014).

   Reefs worldwide have undergone drastic losses in coral cover and biodiversity in recent decades (Bellwood et al. 2004), largely due to anthropogenic activity (Bryant et al. 1998). The global effects of climate change are expected to continue adding pressure on reefs through chronic ocean warming (Hughes et al. 2003), marine heat waves (Hughes et al. 2017) and ocean acidification (Hoegh-Guldberg et al. 2007). Issues affecting reefs at a local scale include overfishing (Pandolfi et al. 2003), direct destruction, and reduced water quality from increases in sediment and nutrient loading in coastal catchments (Furnas 2003; Fabricius 2005). Unlike climate change, local issues can be addressed with regional management actions, and substantial research has
focused on how water quality affects the health of coral reefs (Szmant 2002; Fabricius 2005; De'ath and Fabricius 2010). This work has shown that the baseline conditions, key environmental forcing variables, and inherent variability of the ecosystem must be understood in order to develop effective management strategies for reefs into the future (Hughes et al. 2005; Wooldridge et al. 2006).

1.1.2. Developments in reef studies

Aside from the early observations of Pacific reefs by Darwin and Cook (Stoddart 1976), some of the most influential reef research occurred in the 1940s and 50s immediately prior to the use of atolls as bomb testing sites (Stoddart 1968). These studies focused on Indo-Pacific atolls such as Bikini and Eniwetok, which were oligotrophic, wave-forced, and exposed to minimal terrestrial inputs. These reefs had high coral cover, abundant light, and experienced relatively stable environmental conditions. Their morphology consisted of a steeply-sloping forereef; an energetic reef crest dominated by coralline algae; a reef flat dominated by a mosaic of coral, algae, and sand patches; and a sandy back-reef slope with scattered coral heads and outcrops (Tracey et al. 1948). Measurements of high rates of benthic gross productivity in such nutrient and phytoplankton-poor surrounding waters led scientists to conclude that coral reefs recycled nutrients tightly and were likely nitrogen-limited (Sargent and Austin 1949; Odum and Odum 1955).

During the following decades, much scientific effort was focused on measuring net production and calcification of reef systems (Kinsey 1985; Crossland et al. 1991) and identifying external sources of nutrients to reefs (Wiebe 1987; D'Elia and Wiebe 1990). Primary producers of oligotrophic reef communities were found to have low
demand for nitrogen and phosphorus relative to phytoplankton, based on tissue C:N:P ratios (Atkinson and Smith 1983). Researchers found that episodic processes such as wind-driven upwelling (Andrews and Gentien 1982), internal waves (Andrews 1983), or terrestrial discharge events (Wolanski and van Senden 1983) could transport large amounts of ‘new’ nutrients to reefs. Additionally, evidence of direct inputs of nitrogen from groundwater discharge (Simmons Jr 1992) or nitrogen fixation (Larkum et al. 1988) on the reef flat were found in particular systems. More recently, researchers found that the smallest plankton (pico- and nanoplankton, < 2 µm) had been overlooked in earlier studies due to sampling protocols. These small organisms constituted an important nutrient source for sessile suspension and filter-feeders including corals, sponges, tunicates, and bivalves (Ayukai 1995; Ferrier-Pagès and Gattuso 1998).

Over the last few decades, researchers have used laboratory techniques and concepts from engineering mass-transfer theory to show that nutrient uptake on reefs is physically limited by mass-transfer, the movement of material through the thin diffusive boundary layer surrounding the surface of an organism (Bilger and Atkinson 1992). Mass-transfer theory postulates that uptake rates of dissolved inorganic nitrogen and phosphorus are a function of flow speed, bottom friction, nutrient concentration, and diffusion characteristics of the solute (Atkinson and Falter 2003). Feeding on particulate nutrient sources such as phytoplankton is similarly enhanced as a function of water velocity (Fabricius et al. 1995; Genin et al. 2009; Jones et al. 2009). Mass-transfer theory provides an explanation for the apparent incongruity between high rates of reef productivity and oligotrophic waters observed in early reef studies; reef organism nutrient requirements are low (high tissue C:N:P ratios), and nutrient uptake occurs at rates limited by mass-transfer (Atkinson 2011).
Many excellent studies have related rates of productivity and nutrient uptake to hydrodynamic forcing in controlled conditions such as flumes (reviewed in Atkinson and Falter 2003), and validating these studies with field observations of natural in situ populations remains a challenge (Lowe and Falter 2015). Hydrodynamic conditions vary over the different zones of a reef system (such as forereef, crest, reef flat, and lagoon), thereby influencing rates of productivity, nutrient uptake, and particle trapping (e.g., Carpenter and Williams 2007; Ribes and Atkinson 2007; Cuet et al. 2011b). Estimates are also just beginning to represent variability in offshore forcing conditions, such as seasonal variations in phytoplankton or nutrient inputs (e.g., Wyatt et al. 2010; Wyatt et al. 2012). The experimental method predominantly used in this thesis is the ‘control volume’ (CoVo) approach (Genin et al. 2002), which allows in situ measurement of fluxes in natural reef communities without obstructing water flow with barriers such as submersible chambers. This method combines Eulerian sampling (i.e., water samples taken at a fixed location over time), with a modified Lagrangian (i.e., following a water parcel as it traverses the area of interest) approach. The CoVo is enclosed by several loggers or water samplers, which measure changes in the variable of interest as water passes through the volume; thus, this method is best suited to environments where benthic fluxes are sufficiently great and advection sufficiently slow that changes can be detected between sampling events. The size of the CoVo and sampling frequency required may therefore differ for each variable of interest depending on the magnitude of its benthic flux.

1.1.3. Reef circulation and physical forcing

From the classical reef studies in the Indo-Pacific up to the present day, research has mainly focused on reefs where circulation is forced by waves (Monismith 2007;
Waves interact with the steep forereef causing wave setup that provides pressure gradients to drive flow across reef flats; these wave-driven mean flows enter a back reef or lagoon, and then exit the system through deep channels (Symonds et al. 1995; Hearn 1999). On these reefs, tides have some secondary importance to circulation by controlling the magnitude of wave set-up (Gourlay 1996), changing water depth that influences bottom drag (McDonald et al. 2006), and controlling the exchange rate of water exiting the reef system (Kench 1998; Taebi et al. 2011). The residence time and depth of water over reef communities exert strong physical controls on environmental conditions experienced by the benthos, and for typical wave-dominated reefs, residence time across the reef flat is on the order of a few hours or less (Hatcher et al. 1987). Given their rapid flushing, wave-dominated reefs are strongly controlled by changes to temperature, dissolved oxygen (DO), dissolved CO₂, and nutrients in offshore waters (e.g., Wyatt et al. 2012; Falter et al. 2013; Zhang et al. 2013).

Despite this focus on wave-forced reefs, recent work has shown that up to a third of reefs worldwide have hydrodynamic forcing that can be considered tide-dominated, defined as the situation where mean tidal range exceeds annual mean significant wave height (Lowe and Falter 2015). These systems are common in east Africa, parts of the Indo-Pacific, and northern Australia, and have received very limited attention in the scientific literature thus far. Strongly tidally-forced reefs can experience asymmetry in tidal phase durations and flow speeds as a function of reef morphology, bottom roughness, and reef elevation relative to mean sea level (Lowe et al. 2015). Reef communities can experience long (~several hours) periods of isolation from offshore waters when water level drops below the reef crest. This may occur every tidal cycle or
less frequency for portions of the ~fortnightly spring-neap cycle, and can result in
dramatic changes in temperature (>10° C), dissolved CO₂, DO (up to ~450 µM), and
pH over several hours (Ohde and van Woesik 1999; McCabe et al. 2010; Silverman et
al. 2012; Dandan et al. 2015). Very few studies have assessed how the productivity or
biogeochemical cycling on tide-dominated reefs responds to the physical or
environmental variability characteristic of these systems.

1.1.4. Introduction to the Kimberley region

By any estimation, the Kimberley region of northwestern Australia (Figure 1.1)
contains one of the most pristine coastal zones in the world (Bryant et al. 1998; Halpern
et al. 2008). At roughly the size of California in the USA, the region is sparsely
populated containing only ~50,000 people, located mainly in the towns of Broome, Derby, Halls Creek, Fitzroy Crossing, and Kununurra. The coastal Kimberley contains an array of habitats including mangroves, mudflats, seagrass meadows, and fringing reefs surrounding many of the region’s ~2500 islands (Government of Western Australia 2011). Due to its remoteness and difficult working conditions, very few scientific studies had been conducted until recently, though surveys from various agencies had been conducted over the years (reviewed in Waples 2007). Additionally, indigenous Traditional Owner groups have maintained knowledge and active management of the region for tens of thousands of years (Horstman and Wightman 2001), and are presently helping plan the region’s future (NKSCSC 2010; Oades and Meister 2013). Interest in formal recognition and conservation of the coastal Kimberley led to the creation of the Kimberley Marine Research Program in 2011, a $12 M research funding initiative through the WA state government’s Western Australian Marine Science Institution (Simpson 2011), which partially funded this thesis among dozens of other research projects. This program had objectives that included collecting information on key ecological processes in the coastal Kimberley, as well as informing the creation and management of 5 million hectares of state marine park (Moore et al. 2016).
The Kimberley coast is macrotidal, with spring tidal ranges reaching 12 m in some locations (Kowalik 2004). Recent mapping has shown that the region contains ~2000 km² of reef area occurring mainly as fringing and planar reefs (Kordi and O’Leary 2016). These reefs contain diverse assemblages of coral, macroalgae, and crustose coralline algae, with seagrasses found in some back reef areas (Walker and Prince 1987; Wells et al. 1995); limited information from surveys suggests that Kimberley coral diversity is generally high and is equivalent to that of the inshore Great Barrier Reef (GBR) (Richards et al. 2015). Many reef platforms sit at or just above mean sea level (Solihuddin et al. 2016), and thus the reef crest can become emersed during portions of each tidal cycle. Intertidal reefs such as Tallon Island (Buccaneer

Figure 1.2. A small section of the reef crest of Tallon Island near a) the beginning and b) the middle of ebb tide (note the person for scale in bottom photograph). During ebb tide, the crest becomes a hydraulic control and restricts water flow off Tallon reef.
Archipelago), the study site for this thesis, and the 400 km$^2$ Montgomery Reef (Camden Sound) have reef crests that form a hydraulic control during ebb tide (Lowe et al. 2015) (Figure 1.2), restricting the flow of water off the reef platform, and allowing the platform to maintain a shallow water depth even when tidal elevation has fallen far below the reef crest (Figure 1.3).

The Kimberley region experiences a dry monsoonal climate, where precipitation occurs during the wet season (roughly November to March), with generally little rain during the dry season (roughly April to October). The Kimberley’s large and relatively pristine river systems transport fresh water laden with terrestrial material to the coastal ocean during wet season rain events and generally recede to intermittent pools during the dry season (Kennard 2010). The river system closest to Tallon Island is the Fitzroy River, one of the largest rivers in Australia, with a catchment of 85,000 km$^2$ and annual discharge ranging from 300 -25,000 GL depending on the amount of wet season rainfall (Pusey and Kath 2015). The Fitzroy River discharges into King Sound, a large shallow gulf ~100 km long; islands of the Buccaneer Archipelago (including Tallon Island) sit at the mouth of King Sound (Figure 1.1). In other tropical monsoonal regions such as the northern GBR, seasonal river discharge is a significant feature of the region that strongly influences coastal water quality (Schaffelke et al. 2012). With the exception of a few studies during the dry season (Wolanski and Spagnol 2003; Jones et al. 2014), almost nothing is known about seasonal changes in Kimberley coastal water quality or its influence on marine ecological communities (Masini et al. 2009).
As reviewed above, there are substantial gaps in scientific understanding of how key metabolic and biogeochemical processes in reef communities are influenced by tidal and seasonal forcing. This study is among the first worldwide to examine such ecological processes on strongly tidally-forced reefs. Additionally, it is one of the first scientific studies in the entire coastal Kimberley region.

This thesis is organized as a set of Chapters in the form of three journal articles (Chapters 2 – 4), each with a separate introductory and discussion section. In order for Chapters 2 – 4 to stand as publishable units, some repetition of introductory and
methodological material was necessary. All field research was conducted on Tallon Island reef platform in the west Kimberley, and Chapter 2 presents environmental conditions on Tallon reef platform and discusses the degree to which extremes in temperature and DO influence reef metabolism. Chapter 3 presents a study of benthic particle uptake by reef communities and assesses the contribution of this process to reef nutrient cycling. Chapter 4 presents a study of dissolved nutrient fluxes on the reef platform and assesses the role of tidal forcing in reef nutrient uptake. A final conclusion chapter (Chapter 5) is included to discuss the overarching relevance of this thesis to reef metabolism and biogeochemistry research as well as to the state of reef science in the Kimberley region. The broad research questions of this study are:

Chapter 2

i) How are environmental conditions (temperature, dissolved oxygen, and light) on a tide-dominated reef platform related to daily tidal and spring-neap cycles?

ii) How are community-scale (100s m) rates of productivity and respiration influenced by extreme variability in flow, temperature, light, and dissolved oxygen?

Chapter 3

i) What are the net benthic fluxes of phytoplankton and particulate nutrients on a strongly tide-dominated reef and how are fluxes related to the tidal cycle?

ii) How do seasonal changes in phytoplankton and particulate nutrients in offshore waters influence particle fluxes?
iii) How does the retention of particulate nutrients relate to overall reef nutrient cycling?

Chapter 4

i) What are the theoretical and measured fluxes of dissolved nutrients on the reef platform?

ii) How does tidal forcing (velocity and water depth changes) and oceanic forcing (seasonal changes in nutrient concentration) influence nutrient uptake?

iii) What role do dissolved nutrients play in the overall reef nutrient budget, and how do they relate to the productivity of reef communities?
2. Metabolism of a Tide-Dominated Reef Platform Subject to Extreme Diel Temperature and Oxygen Variations

2.1. Abstract

Benthic dissolved oxygen fluxes were measured on the reef flat of Tallon Island, an intertidal reef platform in the Kimberley region of northwestern Australia, for periods of two weeks in the wet and dry seasons. This reef flat is strongly tidally forced by semidiurnal tides (spring range >8 m) and experiences highly asymmetric water level variability, with ebb durations lasting ~10 hours; this results in diel variations in water temperature and dissolved oxygen (DO) concentration (up to ~11°C and 440 µM, respectively) that are among the most extreme recorded for reefs worldwide. Given the consistent tidal flow patterns, a one-dimensional control volume approach was used to make continuous Eulerian measurements of net production and community respiration from observed changes in DO within two zones: an inner zone dominated by seagrass and an outer zone dominated by macroalgae. Community respiration (R) was controlled primarily by DO concentration; however, fluxes approached the limits of DO mass transfer at low flow speeds. Estimates of gross primary production (P) suggested that

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reef communities were able to fix carbon at rates comparable to other tropical seagrass and mixed reef flat communities despite short-term (~hours) extremes in light (up to 1800 µmol m$^{-2}$ s$^{-1}$) and temperature (>35°C). Daily net community production fluctuated between net autotrophy and heterotrophy over a ~15 day period depending on the phase difference between the solar and tidal cycles but was nonetheless metabolically balanced on time scales greater than weeks ($P/R = 1.0 - 1.1$).
2.2. Introduction

The global distribution of tropical reefs is related to the physico-chemical properties of the ocean waters in which they live (Kleypas et al. 1999); the composition of which can influence rates of organismal metabolic and biogeochemical processes including primary production (Carpenter 1985; Lee et al. 2007), respiration (Berry and Raison 1981), calcification (Gattuso et al. 1999), and nutrient uptake (Atkinson 2011). Temperature and light availability exert a particularly strong influence on net community production, which represents the net sum of primary production (the process by which autotrophs fix dissolved inorganic carbon through photosynthesis) and respiration (the oxidation of organic carbon compounds to create energy) (Odum and Odum 1955; Smith 1973; Gattuso et al. 1998). Although seasonal and latitudinal gradients determine temperature and light availability at a regional scale, waters overlying reefs often have substantially different physico-chemical properties than the surrounding offshore ocean, due to the combined effects of local reef circulation patterns, net atmospheric heating, and benthic production (Lowe and Falter 2015). Reef morphology and local hydrodynamic regime dictate flow speed, inputs of oceanic waters, and residence time on the reef (Monismith 2007). Living benthic communities then alter the spatial and temporal distribution of the products and reactants of production including dissolved oxygen (DO) (Long et al. 2013), dissolved CO₂ (Falter et al. 2013), alkalinity (Zhang et al. 2012), dissolved nutrients (Zhang et al. 2011), and plankton (Wyatt et al. 2010). Thus, the dynamic nature of the habitat in which a reef community lives depends greatly on the prevailing physics driving the circulation of reef waters and heat exchange across the air-sea interface, as well as the collective metabolism of the organisms present.
The majority of research on reef circulation to date has focused on wave-driven systems, where wave breaking in the surf zone induces wave forces that drive circulation (Monismith 2007). However, for a large proportion of reefs (up to a third worldwide), the mean tidal range exceeds the local significant wave height; these reefs can be considered tide-dominated (Lowe and Falter 2015). Tide-dominated reefs can experience dramatic changes in water depth, flow speed, and direction over a single tidal cycle (Lowe et al. 2015), and water levels can fall below portions of the reef on a daily to fortnightly basis, isolating reef waters from offshore (McCabe et al. 2010) or aerially exposing benthic organisms (Richards et al. 2015). This class of reef is common throughout the Indo-Pacific, east Africa, and northern Australia; yet tide-dominated reefs have received little scientific attention to date.

Reef morphology coupled with a strong macrotidal regime result in large and rapid changes in physico-chemical conditions in reef waters. This daily variability is among the most extreme that has been documented on reefs worldwide (Dandan et al. 2015; Pedersen et al. 2016). Reef systems in the Kimberley region of northwestern Australia experience tidal ranges that are among the largest in the world: up to 12 m in some locations (Kowalik 2004). Due to its complex coastline formed by drowned river valleys (Brocx and Semeniuk 2011), this region contains over 2600 islands, many with associated fringing reefs. Community zonation on these fringing reefs is often distinct, with macroalgal-dominated communities (including corals and coralline algae) occurring on the outer zone, and seagrass-dominated communities on the inner zone (Wells et al. 1995). Large diel temperature variations in the Kimberley have been recorded around living corals (range ~7°C with max temps ~35°C, Dandan et al. 2015) and seagrass beds (range up to 12°C with max temps ~38°C, Pedersen et al. 2016),
along with high irradiances (up to 2400 $\mu$mol m$^{-2}$ s$^{-1}$, Dandan et al. 2015) and large diel changes in DO concentration (range up to 450 $\mu$M O$_2$, Pedersen et al. 2016). Variability in these and other physico-chemical properties may influence or even constrain the productivity and resilience of benthic communities (Smith and Birkeland 2007; Comeau et al. 2014; Schoepf et al. 2015). The goal of this study is to investigate how the community production of nearshore fringing reefs in the Kimberley responds to these environmental extremes. The aims of this study were to: 1) assess the community scale (100s m) rates of productivity and respiration on a tide-dominated reef flat using a control volume method, 2) relate rates of photosynthesis and respiration to extreme variability in flow, temperature, light, and DO concentration, and 3) compare the metabolism of two major reef zones: macroalgal-dominated and seagrass-dominated.

2.3. Methods

The in situ production and respiration of reef communities has been measured since the 1940s using a wide range of methods (Staehr et al. 2012). Historically, reef flats have received the majority of attention due to their shallow depths and high biomass densities that provide the biogeochemical signals necessary to support conventional respirometry techniques (Gattuso et al. 1998). Lagrangian drifters (Barnes 1983) have been used extensively, and Eulerian methods can also be useful when flow patterns are well-established (Koweek et al. 2015a) or when the community of interest is isolated from surrounding waters (Ohde and van Woesik 1999; Shaw et al. 2012). More recently, methods utilizing rates of vertical turbulent convection (McGillis et al. 2011; Long et al. 2013) have resulted in productivity estimates from the energetic
forereef and reef crest zones. The control volume approach (e.g., Genin et al. 2002), combines Eulerian and Lagrangian techniques and has subsequently been applied to a variety of reef systems (Falter et al. 2008; Genin et al. 2009; Falter et al. 2012; Teneva et al. 2013). This method is useful for the tide-dominated reef flat chosen for this study, as it allows estimation of metabolism over a range of flow speeds and integrates productivity estimates on the scale of benthic communities (100s of m).

2.3.1. Study site

The Kimberley region is located in northwestern Australia (Figure 2.1) and has a dry monsoonal climate, with rain occurring primarily from November to March (the ‘wet season’) and absent during the rest of the year (the ‘dry season’). Human populations are sparse throughout the Kimberley; thus, it is among the few marine areas worldwide experiencing minimal human impact (Halpern et al. 2008). These reef systems represent a unique opportunity to study near-pristine reef communities in a strongly tidally-forced setting. Although Australia’s indigenous Traditional Owners
have maintained their own observational knowledge of these reefs for tens of thousands of years (Horstman and Wightman 2001), no studies have previously assessed the in situ productivity of Kimberley reefs.

The field experiments took place at Tallon Island (Figure 2.1), an intertidal fringing reef located in the western Buccaneer Archipelago (Solihuddin et al. 2016). It is a large reef platform (~1.5 km cross-shore) that sits slightly above mean sea level (+0.25 m AHD) and experiences semidiurnal tidal ranges in excess of 8 m during spring.

Figure 2.2. Instrument deployment locations on Tallon reef flat and benthic community zones determined by photographic survey. Images of benthic communities at dissolved oxygen (DO) loggers sites 1 (DO1) and 3 (DO3) during low tide are shown on the right. ADPHR refers to the acoustic Doppler current profiler.
phases (Collins et al. 2015). The platform is nearly flat and its offshore boundary is sharply delineated by a steep crest, over which water cascades during ebb tide (Lowe et al. 2015). Both this reef crest and the bottom friction from benthic organisms on the platform reduce flow draining off the reef at low tide, which results in the platform remaining submersed over a tidal cycle despite the water level offshore falling several meters below the elevation of the reef (Lowe et al. 2015). Tidal durations are thus highly asymmetric on the reef platform with ebb tides lasting approximately 10 hours regardless of position in the spring-neap cycle.

Tallon reef flat supports both macroalgae- and seagrass-dominated communities that occur in distinct zones (Figure 2.2). The seagrass community is larger in area, stretching from the shoreline to approximately 400 m from the reef crest, and is dominated inshore by *Enhalus acoroides* (L.f.Royle) and offshore by *Thalassia hemprichii* (Ehrenb.) Aschers (Wells et al. 1995). The macroalgal community covers a band approximately 200 m wide at the reef crest and is dominated by brown macroalgae (*Sargassum* spp.) but also contains many other fleshy macroalgal species, coralline algae, and coral coverage of 5-10% (Wells et al. 1995). A small amount of sparse *Thalassia* was present in the otherwise *Sargassum*-dominated ~200 m ‘mixed’ band separating seagrass and macroalgal zones (Figure 2.2). Although previous studies have noted these zones (Wells et al. 1995), no map of benthic communities was available. Community coverage on the reef flat was determined by photographic transects conducted on foot during low tide. In the cross-reef direction, the community composition changed rapidly, so a 10-30 m spatial resolution was used, whereas a 100-200 m resolution was sufficient in the along-reef direction.
2.3.2. Field measurements

Field studies, each lasting two weeks, were conducted during the dry season (5 to 20 October 2013), with a second study at the end of the wet season (27 March to 9 April 2014). The hydrodynamics of this reef have already been investigated in detail (Lowe et al. 2015), and our study was situated on the northern end of the reef flat (near site A1 described in that paper). The northern reef flat experiences a consistent northeastwardly flow off the reef during ebb tide (towards 80° ± 30°, mean ± standard deviation) for approximately 10 hours during each tidal cycle, with flow speeds becoming negligible as water depth becomes sufficiently low (<0.4 m) (Lowe et al. 2015). This prolonged period of unidirectional flow provides an interesting natural setting to quantify community-scale (100s of meters) benthic oxygen fluxes. A one-dimensional control volume approach was applied with instruments placed in a transect along the major axis of ebb tide flow.

Water depth and current velocities were sampled at 1 Hz by an upward-looking Nortek Aquadopp HR (Nortek AS) affixed to the bed (Figure 2.2). A small bin size (0.03 m) and low blanking distance (0.1 m) captured the current velocities even when water depth at the sensor ($h$) reached minimum values (~0.4 m) at the end of low tide. Depth-averaged flow speed along the major axis of ebb tide flow ($u_x$) was available for all but 5% of the field study, only excluding periods when the water depth approached the minimum measurement depth ($h < 0.4$ m). A small neutrally-buoyant drifter (a mandarin) was used to estimate flow velocity during these slow, nearly stagnant periods of flow. The drifter was released near the Aquadopp and tracked on foot for 30 min during both the dry and wet season studies ($n = 25$ and 16, respectively). Approximately 50% of drifter releases occurred when Aquadopp measurements were also available for
comparison. For periods of low \( h \) (<0.4 m), \( u_t \) was estimated from a significant linear relationship \((p<0.001, R^2 = 0.79)\) between along-transect transport \( q_x \) where

\[
q_x = u_t h,
\]

and change in depth \( dh/dt \) (implied from conservation of mass, assuming horizontal dispersion was negligible) for 30-min bin-averaged data from the Aquadopp and drifters.

Water column DO concentrations were measured every 5 min using Troll 9500 LTS equipped with an RDO dissolved oxygen optode and temperature sensor (InSitu Inc.). One DO sensor was placed in each reef zone (DO1 in seagrass and DO3 in macroalgae), and a third sensor (DO2) was positioned between these in the narrow mixed zone (Figure 2.2); this arrangement allowed measurement of DO in both reef zones simultaneously. The sensors were calibrated before deployment using a two-point method of 100% (aerated with pump) and 0% (deoxygenated with 1 M sodium sulphite solution) saturation. Minor drift in DO measurements (<10 µM) was corrected by placing all loggers together for two 30 min periods during each deployment, and then deriving a small correction factor with linear regression. Although the reef platform as a whole was nearly level, it was populated with a series of near-parallel ridges 15 - 25 cm high that ran parallel to the crest and were spaced 1 - 1.5 m apart (Figure 2.2), thus creating quasi-sinusoidal variations in local water depth. Mean water depth \( \bar{h} \) was estimated by adjusting \( h \) with an offset derived from depth measurements every 20 cm along a portion of the instrument transect (made with a ruler at low tide) in both communities.
Light levels (downwelling photosynthetically active radiation, PAR) were recorded at the surface of the reef platform at 5 min intervals using a QCP-2300 cosine collector (Biospherical Instruments Inc.). Wind speed and direction were recorded at a 1 min interval 10 m above the reef platform using a Wind Sentry 03002-L anemometer (Campbell Scientific) during the wet season field experiment only.

2.3.3. Community productivity

Time-series of benthic oxygen flux ($J_{O2}$ in mmol O$_2$ m$^{-2}$ hr$^{-1}$) were computed for each community zone (macroalgal- and seagrass-dominated) using an Eulerian approach as (Falter et al. 2008)

$$J_{O2} = \frac{d\bar{c}}{dt} + q_x \frac{dc}{dx} - k_{O2}(C_{sat} - \bar{c}). \quad (2)$$

The first term on the right side of Eq. (2) represents local accumulation of oxygen, where $\bar{c}$ is mean oxygen concentration along the transect (mean of DO1 and DO2 for seagrass, DO2 and DO3 for macroalgae). The second term is the advective oxygen flux, where $dC/dx$ is the change in oxygen concentration over the transect (difference of DO1 to DO2 for seagrass, DO2 to DO3 for macroalgae) and transect length ($dx$) was 270 m for both communities. The final term is the air-sea gas flux, where $k_{O2}$ is the gas transfer velocity and $C_{sat}$ is oxygen saturation estimated from water temperature and salinity (Weiss 1970). Tallon reef was not exposed to wave action due to sheltering by nearby islands (Figure 2.1), so estimates of gas transfer velocity that describe turbulent open channel flow were deemed more analogous to the reef platform than open-ocean studies. The reference gas transfer velocity $k_{O2ref}$ was
\[ k_{O2ref} = k_w + k_a, \]  

the sum of gas transfer velocities due to water flow \( k_w \) and wind \( k_a \) (Chu and Jirka 2003). Flow-induced gas transfer was estimated as (Chu and Jirka 2003)

\[ k_w = 2.15(u^3_{*w}/h)^{0.25}, \]  

where \( u_{*w} \) is the bottom shear velocity

\[ u_{*w} = u_{x} \sqrt{C_D/2}, \]  

and the drag coefficient \( C_D \) for the reef platform was taken as 0.02 following Lowe et al. (2015). Wind-induced gas transfer velocity \( k_a \) is estimated as (Chu and Jirka 2003)

\[ k_a = 0.00183 u^2_{*a}, \]  

where \( u_{*a} \) is the air shear velocity

\[ u_{*a} = 0.01 u_{10} \sqrt{(8 + 0.65 \times u_{10})}, \]  

estimated from wind speed at 10 metres \( (u_{10}) \) (Chu and Jirka 2003). The reference gas transfer \( k_{O2ref} \) was corrected to in situ conditions using estimated Schmidt numbers for oxygen under reference \((Sc_{O2ref})\) and in-situ \((Sc_{O2})\) conditions as

\[ k_{O2} = k_{O2ref} (Sc_{O2ref}/Sc_{O2})^w. \]  

where \( w = 2/3 \) for a smooth air-water interface (Wanninkhof 1992). Schmidt numbers were estimated from a linear relationship with temperature from Ramsing and Gundersen (1994), given that commonly-used estimates (Wanninkhof 1992) are only valid for temperatures <30° C. Wind speed measurements were not available for the dry season field study, so the median wind speed from the wet season field study was
used to estimate $k_{O_2}$. Previous work (Zappa et al. 2003; Borges et al. 2004) has shown that $k_{O_2}$ tends to be small when wind speeds are low ($<4 \text{ m s}^{-1}$), which occurred during the majority (75%) of the wet season field study (wind speed was not available for the dry season). Air-sea gas fluxes were therefore expected to be a minor contribution to $J_{O_2}$, but were retained for completeness.

The raw instrument data were bin-averaged at 30 min intervals for calculation of the local and gas flux terms contributing to the calculation of $J_{O_2}$ (Eq. 2). The time-scale for averaging the advective flux term needed to reflect the transit time of a water parcel between oxygen loggers, the length of which increased over the ebb tide period as $u_x$ slowed and $h$ decreased. When $h > 0.90 \text{ m}$ (around the peak of high tide), differences in DO concentrations between sensors and changes with time were too small to generate reliable estimates of $J_{O_2}$, so estimates were not made during these periods. For $0.90 > h > 0.70 \text{ m}$, individual calculations of the advective flux term made every five minutes were bin-averaged over 30 min intervals (Figure 2.3), roughly corresponding to the estimated transit time between loggers. As $u_x$ slowed when $0.70 > h > 0.50 \text{ m}$, calculations of the advective flux term were averaged over 80 min intervals and interpolated onto the common 30 min interval used to calculate the local and gas flux terms (Figure 2.3). Towards the end of ebb tide, water depths were shallow ($h < 0.5 \text{ m}$) and $u_x$ became very slow (of order 1 cm s$^{-1}$); although the advective term was expected to be small, it was retained for completeness at a 30 min interval. By organizing our calculations this way, we were able to estimate $J_{O_2}$ for roughly half the time during each field experiment. Due to the daily advancement of the dominant semidiurnal (M2) tides by 50 min each day and the length of the field experiments, $J_{O_2}$
estimates covered a range of temperature and light conditions characteristic of this reef platform.

Daytime net production rate \( (np \text{ in mmol O}_2 \text{ m}^{-2} \text{ hr}^{-1}) \) was defined as hourly \( J_{O_2} \) occurring between sunrise and sunset \( (\text{PAR} \geq 5 \mu\text{mol m}^{-2} \text{ s}^{-1}) \), while nighttime community respiration rate \( (r_{\text{night}} \text{ in mmol O}_2 \text{ m}^{-2} \text{ hr}^{-1}) \) was defined as hourly \( J_{O_2} \) occurring between sunset and sunrise \( (\text{PAR} < 5 \mu\text{mol m}^{-2} \text{ s}^{-1}) \). Gross primary production rate \( (p \text{ in mmol O}_2 \text{ m}^{-2} \text{ hr}^{-1}) \) was defined as

\[
p = np + \hat{r}_{\text{day}}, \tag{9}
\]

where \( \hat{r}_{\text{day}} \) was the predicted hourly daytime respiration rate (Staehr et al. 2012).

Although it is common practice in metabolism studies to assume that \( r_{\text{night}} = \hat{r}_{\text{day}} \) (Odum and Odum 1955), this assumption is unlikely to be valid given the extreme
The dependency of \( r_{\text{nigh}} \) on flow was examined with the maximum uptake rate coefficient of oxygen from mass transfer limitation (\( S_{\text{MTL}} \)) as (Falter et al. 2004),

\[
S_{\text{MTL}} = \frac{\sqrt{c_f/2}}{\text{Re}_k^{0.2} \text{Sc}_{\text{O}_2}^{0.6}} u_x,
\]

(10)

where \( c_f \) is the friction coefficient, the Schmidt number of oxygen (\( \text{Sc}_{\text{O}_2} \)) is the kinematic viscosity (\( v \)) divided by the diffusion constant, and the roughness Reynolds number (\( \text{Re}_k \)) is

\[
\text{Re}_k = u_* w k_s / v,
\]

(11)

where \( k_s \) is a hydraulic roughness length scale, assumed to be 0.5 m for the reef platform (Lowe et al. 2015). In reef systems where water depth approaches the maximum reef organism height, \( c_f \) increases dramatically and can be estimated from empirical relationships of the ratio of \( h \) and maximum reef height (McDonald et al. 2006). First-order oxygen uptake rate coefficients (in m day\(^{-1}\)) for measured fluxes of \( r_{\text{nigh}} \) [where \( i = \text{SG} \) (seagrass) or MA (macroalgae)] were then estimated from Bilger and Atkinson (1992)

\[
k_i = r_{\text{nigh}} / \dot{C} \times 24,
\]

(12)

and could be compared to \( S_{\text{MTL}} \) to assess whether the fluxes approached mass transfer limits.

The respiration of organisms (and communities as a whole) is known to follow an Arrhenius relationship with temperature that can be described by \( Q_{10} \), the factor by
which rates would increase if temperature increased by 10°C (Berry and Raison 1981). An assumption of \( Q_{10} = 2 \) is commonly made in most aquatic systems (Valiela 1995), and \( Q_{10} \) has also previously been shown to be 2.0 for *T. hemprichii* living on the Tallon reef platform (Pedersen et al. 2016). The degree to which temperature (\( T \)) changes likely affected community respiration was assessed by computing a version of \( r_{\text{night}} \) (\( r_{\text{Tref}} \)) normalized to constant temperature \( T_{\text{ref}} \) as Berry and Raison (1981)

\[
r_{\text{Tref}} = r_{\text{night}} Q_{10}^{(T_{\text{ref}}-T)/10},
\]

where \( T_{\text{ref}} \) is equal to the mean offshore water temperature during each study period, and \( Q_{10} \) is 2.

After adjusting for the effects of changing temperature on community respiration (Eq. 13), we found that there were significant relationships between DO and \( r_{\text{Tref}} \) in both seagrass (\( R^2 = 0.72 \)) and macroalgal (\( R^2 = 0.63 \)) communities (see Results). We then estimated a temperature-normalized version of \( r_{\text{night}} \) (\( \hat{r}_{\text{Tref}} \), where the overhat represents a predicted rate rather than observed measurement) as a Monod function of DO

\[
\hat{r}_{\text{Tref}} = \frac{r_{\text{max}} \tilde{C}}{K_s + \tilde{C}},
\]

where \( r_{\text{max}} \) and \( K_s \) were the maximum respiration rate and half-velocity constant, respectively, of the relationship with DO concentration (see Results). Estimates of \( \hat{r}_{\text{Tref}} \) were then re-adjusted to observed in situ temperatures (Eq. 13) to generate predictions of in situ dark respiration (\( \hat{r}_{\text{night}} \)) when direct measurements of \( J_{O2} \) were not possible (i.e., during flooding tides or when \( h > 0.9 \) m). We followed a similar approach to estimate \( \hat{r}_{\text{day}} \) using in situ DO concentration and temperatures (Eqs. 13, 14)
rather than simply assuming that \( \hat{r}_{day} \) was equal to the mean of \( r_{night} \). Daily rates of community respiration (\( R \), in mmol O\(_2\) m\(^{-2}\) d\(^{-1}\)) were then estimated as the sum of direct measurements (\( r_{night} \)) and predicted rates (\( \hat{r}_{day} \) and \( \hat{r}_{night} \)) from midnight on the previous day to midnight on the following day.

To estimate daily rates of community gross primary production (\( P \), in mmol O\(_2\) m\(^{-2}\) d\(^{-1}\)) from hourly rates (\( p \)), we either used direct measurements when available (Eq. 9), or predicted rates (\( \hat{p} \)) assuming that the dependence of gross primary production on irradiance (PI curve) had a hyperbolic tangent form (Jassby and Platt 1976) as

\[
\hat{p} = p_{\max} \tanh\left( \alpha \frac{P}{p_{\max}} \right),
\]

where \( \alpha \) is the initial slope of the curve and \( p_{\max} \) is the production rate at saturating light levels (see Results). Daily rates of gross primary production were then calculated as the sum of all \( p \) and \( \hat{p} \) between sunrise and sunset. Net community production (\( NCP \), in mmol O\(_2\) m\(^{-2}\) d\(^{-1}\)) was calculated as the difference between \( P \) and \( R \) (\( NCP = P - R \)).

Uncertainty in metabolism estimates due to uncertainties in various input variables was calculated via Monte Carlo simulations using 10,000 sets of noise-corrupted data (Falter et al. 2008).

2.4. Results

2.4.1. Environmental conditions
Each field study captured at least one combined spring-neap tidal cycle with offshore tidal ranges of ~7 m during springs and ~2.5 m during neaps (Table 2.1). Water depth on the reef flat ranged between ~0.4 and 3.4 m during spring tides and from ~0.4 to 1.3 m during neap tides (Figure 2.4a). Due to the elevation of the reef flat above mean sea level, there were large asymmetries in the duration of tidal phases resulting in a form of ‘tidal truncation’ whereby the minimum depth during low tides remained fixed on the reef platform at a well-defined threshold of around 0.4 m (Lowe et al. 2015). The ebb tide was elongated to 10 h of the total 12.4 hour semidiurnal cycle, with flow speeds tapering from >0.4 m s\(^{-1}\) to 0.02 m s\(^{-1}\) during the ebb period (Figure 2.3). Wind speeds during the wet season field study were generally low (mean = 3.3 m s\(^{-1}\), Table 2.1, Figure 2.4b) due to the sheltering of Tallon Island by surrounding islands to the east of the Dampier Peninsula (Figure 2.1).
Water quality on Tallon reef flat was characterised by large diel changes in physico-chemical properties, the magnitudes of which were determined by the phase difference (or time lag) between the solar and tidal cycles (Lowe et al. 2016). Light levels on the reef platform could be quite high, reaching $>1800 \mu$mol m$^{-2}$ s$^{-1}$ when...
minimum water depths \((h < 0.4 \text{ m})\) occurred around midday (Figure 4c). Water temperatures on the reef flat were on average \(\sim 2^\circ \text{C}\) warmer during experiments conducted in the wet season than those conducted during the dry, although a similar wide range of temperatures was recorded during both seasons (Table 2.1). Temperature variations of up to \(11^\circ \text{C}\) over a single 10 hour ebb period occurred when low \(h\) coincided with high light levels (Figure 2.4e). Warm water on the reef flat could persist for several hours, especially during the wet season, when temperatures exceeded \(32^\circ \text{C}\) for up to six hours a day. Diel oxygen concentrations varied by up to \(440 \mu \text{M}\) over each ebb tide (Figure 2.4d) and reached saturation levels of up to \(280\%\) when low tide coincided with high light levels. Water column hypoxia (defined as \(\text{DO} < 63 \mu \text{M}\)) developed on the reef platform nightly for 1 to 7.5 hours each day (Figure 2.4d), depending on the overlap of low tide and nighttime, or equivalent to \(\sim 15\%\) of each field study period.

Given that reef flat water quality was similar between wet and dry seasons (Table 2.1), it was not surprising that diel variations in benthic community metabolism were also similar. Because our primary interest was in determining community response to diel extremes in environmental conditions, most results that are presented focus on the more comprehensive measurements collected during the wet season. Nonetheless, we compare differences in overall rates of gross primary production and respiration between the wet and dry seasons following our examination of metabolism at diel timescales.

2.4.2. Benthic productivity
The relative importance of the three Eulerian flux components (local, advective,
and air-sea exchange) to the total flux of DO differed between the seagrass (inner zone) and macroalgal (outer zone) communities. In the seagrass-dominated inner zone, $J_{O2}$ estimates were usually dominated by the local accumulation term, with advective and air-sea components each contributing <10% to the total flux (Figure 2.5a). In contrast,

![Figure 2.6. Relationships of community respiration $r_{\text{night}}$ to a) temperature ($T$) and b) dissolved oxygen (DO). Relationships between DO and c) temperature-normalized $r_{\text{night}}$ ($r_{\text{Tref}}$) also shown for seagrass and macroalgal communities during the wet season field experiment. Monod relationships (dashed lines) used to predict daytime respiration $r_{\text{day}}$ and nighttime respiration $r_{\text{night}}$ for periods when oxygen fluxes were not available are shown where $r_{\text{Tref}} = 59.1 \text{DO} / (432.6 + \text{DO})$ for seagrass ($R^2 = 0.72$) and $r_{\text{Tref}} = 42.6 \text{DO} / (125.5 + \text{DO})$ for macroalgal communities ($R^2 = 0.63$).]
both local and advective flux terms were important contributors to total $J_{O2}$ estimates within the macroalgal-dominated outer zone (~55% and 35%, respectively), while air-sea exchange again contributed <10% (Figure 2.5b). Despite playing a minor role in overall $J_{O2}$ estimates, air-sea exchange occasionally accounted for more than 30% of the total $J_{O2}$ for periods of several hours (about 10% of field studies) when water column DO became supersaturated and flows were > 2 cm s$^{-1}$ (Figure 2.5b).

The daily advance of the dominant lunar semidiurnal (M2) tidal cycle by 50 min combined with the roughly two-week duration of both field studies provided us with the opportunity to measure net community production over a wide range of flow, temperature, DO, and PAR conditions found on this reef platform. Rates of $r_{night}$ tended to decline through the night, and approached zero when the ebb tide was fully synchronized with the nighttime period (Figure 2.5c). Reef flat water temperatures cooled by up to 4°C (from temperature at sunset) during these periods due to air-sea heat exchange. However, estimates of temperature-normalized $r_{night}$ (or $r_{Tref}$, Eq. 13) demonstrated that less than 8% of the pattern of decline observed in $r_{night}$ could be attributed to falling temperatures (Figure 2.6a). Having removed this minor temperature dependency, we found a significant non-linear dependency of $r_{Tref}$ on ambient DO concentrations in seagrass and macroalgal zones ($p < 0.0001$, $R^2 = 0.72$ and 0.63, respectively) over the range of nighttime DO (7 – 300 µM O$_2$ or 10 – 150% saturation, Figure 2.6c). To assess whether depletion of dissolved organic carbon substrate (photosynthesis-derived carbohydrates) over the night may have contributed to the falling $r_{night}$ (Figure 2.5c), the DO and $r_{Tref}$ relationship was also limited to estimates from only the first 2 hours after sunset; yet, the coefficients derived from this relationship remained similar.
Comparison of the derived first-order dissolved oxygen uptake rate coefficients for the seagrass ($k_{SG}$) and macroalgal ($k_{MA}$) communities against the maximum benthic mass transfer velocity for DO ($S_{MTL}$) showed that $J_{O2}$, and therefore $r_{night}$, would often approach the physical limit allowed by convective mass transfer when flow speeds were low (< 2 cm s$^{-1}$, Figure 2.7). Benthic oxygen flux was not particularly dependent on flow speed ($R^2 = 0.07$) over the full range of flow speeds measured (0 – 20 cm s$^{-1}$).
Due to the phase difference (or daily time lag) between light and tidal cycles, we were able to make an equal number of estimates of productivity at all light levels over each field period ($n = 20$ for each of seven $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ bins of PAR values spanning 0 to 1750 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Photosynthesis-irradiance curves made using estimates of hourly net production from field measurements revealed patterns related to DO (Figure 2.8). PI curves for both communities showed downward concavity, or declining rates of $np$ when temperature and DO were high ($>350 \mu\text{M}$), which typically occurred in the afternoon. Similarly to $np$, the macroalgal community showed greater rates of gross primary production than seagrass at all light levels (Figure 2.9). Photosynthesis-irradiance relationships using $p$ exhibited a more conventional hyperbolic tangent form, especially in the seagrass community (Figure 2.9); this indicated that some of the observed downward concavity in $np$ at high light levels (Figure 2.8) was related to DO-driven increases in daytime respiration relative to
production. The initial slopes of these curves ($\alpha$) were 0.095 and 0.15 for seagrass and macroalgal zones, respectively (Figure 2.9); the production rates at saturating light levels ($p_{\text{max}}$) were 47 and 61 mmol O$_2$ m$^{-2}$ hr$^{-1}$ for seagrass and macroalgal zones, respectively.

Mean daily rates of metabolism (the combination of direct and predicted)

Table 2.2. Summary of net community production ($NCP$), community respiration ($R$), and gross primary production ($P$) during the wet season. Fluxes (mean of $n$ days) are in units of mmol O$_2$ m$^{-2}$ d$^{-1}$ ($\pm$ SE). Ratio between gross production and respiration is $P:R$.

<table>
<thead>
<tr>
<th>Community</th>
<th>$n$</th>
<th>$NCP$</th>
<th>$R$</th>
<th>$P$</th>
<th>$P:R$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seagrass</td>
<td>12</td>
<td>50 ($\pm$ 8)</td>
<td>380 ($\pm$ 4)</td>
<td>430 ($\pm$ 5)</td>
<td>1.1</td>
</tr>
<tr>
<td>Macroalgae</td>
<td>12</td>
<td>10 ($\pm$ 5)</td>
<td>570 ($\pm$ 5)</td>
<td>580 ($\pm$ 6)</td>
<td>1.0</td>
</tr>
</tbody>
</table>
measurements) showed similar net community production in seagrass and macroalgal zones (Table 2.2). The macroalgal community had higher overall rates of both $P$ and $R$ than seagrass, yet both communities had balanced $P:R$ ratios (Table 2.2).

Nonetheless, $NCP$ varied on a daily basis as a function of the mismatch between the length of tidal and solar cycles (Figure 2.10). The solar (light) cycle occurs at a 24 hr period, while the dominant semidiurnal M2 tide occurs at a ~12.4 hr period. This difference results in a low frequency modulation in the daily mean and range of

![Figure 2.10. Daily mean (± SD) a) temperature ($T$), b) dissolved oxygen (DO), and rates of net community production ($NCP$) in c) seagrass and d) macroalgal communities during both seasons. Values are shown as a function of difference between high tide and solar noon expressed in hours. Zero hours indicates the alignment of high tide and solar noon, while negative hours indicate high tide occurring prior to solar noon.](image-url)
temperature (Figure 2.10a) and DO (Figure 2.10b) lasting ~15 days (Lowe et al. 2016) as periods of shallow water coincide with a range of light intensities (Figure 2.4). A time lag of 0 hours denotes a day when high tide was aligned with solar noon, and thus ebb tide occurred from ~12:00 – 22:00 and 0:00 – 10:00. A time lag of ±6 hours denotes a day when high tide was aligned with ~6:00/18:00, and thus ebb tide occurred from ~6:00 – 16:00 and ~18:00 – 04:00. A sinusoidal pattern was observed in both the wet and dry seasons, with maximum NCP occurring just after 0 hours (Figure 2.10). A time lag of ±6 hours meant water depth on the reef flat was low when the highest light levels occurred, resulting in large increases in DO and temperature.

2.5. Discussion

2.5.1. Extreme conditions on the reef flat

The physico-chemical properties of reef flat waters measured in this study rank among the most extreme recorded for reef systems worldwide (Kleypas et al. 1999). When low water depths occurred around solar noon, temperatures on the reef platform exceeded 36°C and showed a large range (up to 11°C) over a single 10 h ebb tide period (Figure 2.4e). Such extreme reef temperatures (>36°C) have been observed in a few other parts of the world including the Red Sea and the Arabian Gulf (Coles and Fadlallah 1991; Ateweberhan et al. 2006). Furthermore, diel fluctuations of ~8°C can occur in the Gulf of Oman (Coles 1997), in the backreef pools of fringing reefs of Ofu in American Samoa (Craig et al. 2001), and on reef flats at One Tree Island in the central Great Barrier Reef (Silverman et al. 2012). Similar variations have been additionally recorded in a small number of shallow nearshore habitats where seagrasses
are found. In particular, the species present on Tallon reef (*E. acoroides* and *T. hemprichii*) are known to occur in other intertidal environments that experience elevated temperatures (>35°) on diel timescales (Bridges and McMillan 1986; Collier and Waycott 2014).

In addition to extremes in water temperatures, this study also documented large diel variability in dissolved oxygen saturation: supersaturation when low tide occurred at midday (up to 280%) and up to 7.5 hours of hypoxia when shallow water depths occurred in the middle of the night (Figure 2.4d). A small number of previous studies have recorded large changes in DO concentration in shallow backreef areas (Piniak and Brown 2009; Koweek et al. 2015b) and shallow reef flat waters isolated during low tides (Ohde and van Woesik 1999; Silverman et al. 2012). However, while hypoxia has been reported at the surface of reef organisms and in organism tissue when subjected to low flow speeds under experimental conditions (Kühl et al. 1995; Ulstrup et al. 2005), it is rarely reported for reef water columns under in situ conditions. Although temperature and DO extremes over the year undoubtedly exceed what we present here, the diel patterns in water quality we observed can nonetheless be considered representative for this reef (Lowe et al. 2016). More importantly, these extreme conditions are likely representative of many other fringing reef platforms found throughout the 13,000 km of coastline within the Kimberley region.

2.5.2. **Eulerian decomposition of benthic oxygen fluxes**

The local component of the non-conservative transport equation (Eq. 2) was greater in magnitude than either the advective or gas flux terms for both benthic communities (Figure 2.5). This was likely due to the relatively homogeneous and dense
cover of primary producers in their respective zones, the shallow water depths (<0.5 m), and the slow flows (<5 cm s\(^{-1}\)) during large portions of ebb tide. However, the advective component was relatively larger in the macroalgal zone, likely due to the location of this zone between the inner seagrass community and the reef crest (Figure 2.2). Water flowing across the macroalgal community (and off the reef) during the ebb tide originated from the less productive seagrass community where oxygen concentrations did not increase as rapidly with time thereby creating a spatial gradient in dissolved oxygen that, acting in combination with the cross-reef advection, contributed substantially to the total calculated benthic flux. In contrast, water that flowed across the oxygen sensors within the seagrass zone had previously overlain seagrass communities of similar percent cover further upstream; thus, a substantial spatial gradient in oxygen concentration did not develop. Our results therefore show that slow flow alone does not guarantee that the advective component of the non-conservative Eulerian transport calculations will be negligible (Eq. 2), but rather the combination of slow flow and spatially homogenous benthic fluxes upstream of the point of measurement. In addition, our results suggest that metabolism on similar reef flats may be estimated for portions of the tidal cycle using Eulerian methods provided that the flow patterns are relatively consistent, the community of interest is of sufficient size, and the spatial position and patchiness of the community relative to key morphological boundaries are carefully considered. For other tide-dominated reefs where flow speeds remain greater throughout the tidal cycle (e.g., ≥ 5 cm s\(^{-1}\)) and transit times are short, advective components may be the dominant contributor to \(J_{O2}\) (Falter et al. 2012). Regardless, any measurement of community metabolism under such shallow conditions (\(h \leq 0.4\) m) will require very accurate measurements of water depth.
throughout the area of interest (Shaw et al. 2014; Kwiatkowski et al. 2016). For example, every 1 cm inaccuracy in water depth on the Tallon reef platform translated into a ≥5% change in estimated rates of hourly metabolism during low tide.

2.5.3. **Dissolved oxygen drives community respiration**

Nighttime community respiration in both the seagrass and macroalgal communities showed a regular diel pattern whereby rates were greatest directly after sunset and declined through the night; greatest declines (up to 90%) occurred when the ebb tide began after sunset. Previous studies have observed similar patterns in in situ community respiration throughout the night [~30% by Falter et al. (2011) and ~60% by Long et al. (2013)], which the authors generally attributed to a steady reduction in the supply of photosynthate once daytime primary production had ceased. The wide range of nighttime environmental variability on Tallon reef flat that included temperature (28.5 – 32.5°C), flow speed (0.01 – 0.20 m s⁻¹), and DO (7 – 300 µM) provided an opportunity to explore possible mechanisms for changing $r_{night}$ including: 1) falling nighttime temperatures, 2) slowing flow speeds, 3) falling oxygen concentrations, and 4) limitation in the supply of photosynthetically fixed carbon.

The first mechanism was the simplest to assess, as the temperature dependency of respiration has been well-studied in aquatic systems (Valiela 1995), and $Q_{10}$ values specific to *T. hemprichii* on Tallon reef have already been quantified via controlled incubations (Pedersen et al. 2016). We found that nighttime temperature declines could explain only ~8% of the observed decline in $r_{night}$. The second possible mechanism was investigated by comparing the first-order uptake rate coefficients for nighttime respiration ($k_{SG}$ and $k_{MA}$) to flow speed to assess mass transfer limitation of oxygen.
fluxes to the benthos. The absence of a relationship between uptake rate coefficients and $u_e$ indicated that $r_{\text{night}}$ was not generally controlled by flow speed, perhaps with the exception of low flows ($<3$ cm s$^{-1}$) under which it approached the limits of convective oxygen mass transfer (Figure 2.7). Previous studies examining the relationship between productivity and flow have shown mixed results. Some studies have shown that the diffusive boundary layer thickness decreases with flow speed under very slow experimental flows, thus indicating higher rates of oxygen mass transfer (Shashar et al. 1993; Kühl et al. 1995; Larkum et al. 2003; Mass et al. 2010), yet others have demonstrated no change in respiration with flow speed (Newton and Atkinson 1991; Lesser et al. 1994; Schutter et al. 2010). Our findings thus suggest that extreme changes in dissolved oxygen concentration were a dominant factor controlling rates of community respiration on Tallon reef flat, as $r_{\text{night}}$ showed a strong dependency on dissolved oxygen concentration in both seagrass and macroalgal communities (Figure 2.6). The coefficients of these Monod relationships did not change when only the first two hours after sunset were considered, suggesting that carbon limitation (the fourth potential mechanism) was not the primary control on dark respiration. Some previous work has documented how rates of nighttime respiration in coral (Newton and Atkinson 1991) and seagrass (Zimmerman et al. 1989) can be controlled by dissolved oxygen concentrations. It is therefore likely that regulation of community respiration by dissolved oxygen levels may be important in other reef communities that experience extremes in oxygen saturation; however, further work addressing the combined influence of flow, dissolved oxygen, and carbon limitation on respiration is warranted.

It is common practice in metabolism studies to estimate daytime respiration as a constant mean of nighttime respiration despite evidence that daytime respiration rates
can greatly exceed nighttime rates (Kühl et al. 1995; Langdon et al. 2003). This assumption is made mainly out of computational convenience since measuring daytime respiration independently of net production is logistically challenging, and requires the introduction of tracers, inhibitors, or complete control over the light cycle, none of which is practical to do at the community scale under in situ conditions (Kemp and Testa 2011). In the case of Tallon reef flat, an assumption of a constant daytime respiration equal to mean nighttime respiration would have resulted in the underestimation of daily respiration rates by ~30%. More importantly, modelling daytime respiration as a function of dissolved oxygen concentration could explain some of the apparent hysteresis in the dependency of net production on light (Figure 2.8). Estimates of community gross primary production that accounted for enhanced daytime respiration due to elevated dissolved oxygen levels showed reduced hysteresis at high light intensities (Figure 2.9). These results suggest that high dissolved oxygen concentration, rather than temperature, was the primary control on daytime respiration; however, high temperatures or high irradiance levels may still influence primary production in other ways (e.g., damage to photosystem II, photoinhibition), which may explain residual hysteresis in PI curves (Figure 2.9). The estimates presented here do not attempt to account for photorespiration (Buapet et al. 2013), the process whereby O₂ is consumed in place of CO₂ during the daytime in seagrasses (Larkum et al. 2007) and some macroalgae (Reiskind et al. 1989), and more research is necessary to gain an understanding of the importance of this process in systems that experience extremes in oxygen saturation. Overall, these results suggest that primary producers are well-adapted to the extreme ranges of environmental conditions on the reef flat and can
maintain high rates of photosynthetic carbon fixation despite short-term (~hours) periods of high temperature and light (Carpenter 1985).

2.5.4. Response of community metabolism

Despite the diel extremes in temperature, irradiance, and dissolved oxygen measured in our study, benthic communities approached or exceeded mean metabolism rates published in previous reef studies \( P = 580 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1} \) for the macroalgal community, Table 2.2, versus \( 640 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1} \) for an average reef flat (Falter et al. 2013). Evidence suggests that productivity of reef algal communities can become compromised when temperatures exceed 32°C (Hwang et al. 2004; Sinutok et al. 2011); however, prior studies have not generally focused on species already adapted to high temperatures (Schoepf et al. 2015). Although there have been numerous studies of how environmental drivers affect rates of calcification in coral and other reef calcifiers (Kleypas et al. 2005), studies of environmental controls on the productivity of reef algal communities are less common (Hurd 2000; Koch et al. 2013).

In the case of the seagrass community, rates of \( P \) and \( R \) (Table 2.2) were well above the global means for tropical seagrass systems [252 and 217 mmol O\(_2\) m\(^{-2}\) d\(^{-1}\), respectively, from Duarte et al. (2010)]. Studies of \( T. \) hemprichii productivity are relatively limited in the seagrass literature, especially compared to northern hemisphere species such as \( T. \) testudinum (Lee et al. 2007). Previous work assessing the effect of thermal stress on \( T. \) hemprichii has shown that short-term (~2 hr) temperature extremes (>35°C) can cause photoinhibitory effects for several days (Campbell et al. 2006), yet, other work has shown no indication of reduced productivity (Collier and
Waycott 2014). At any rate, it is clear that this species is capable of maintaining high rates of production despite exposure to temperature extremes.

Productivity rates estimated for wet and dry seasons were nearly identical, which was likely due to similar environmental conditions on the reef flat during both field experiments (Table 2.1). The wet season field experiment coincided with a nearly two-week high pressure system and generally low cloud cover. However, storms with heavy rainfall and high cloud cover occur frequently during the wet season and typically last ~1 week. A period of high cloud cover would likely reduce the diel variability in environmental conditions on the reef flat, yet it is not clear what effect this would have on net community production.

The main driver of variations in reef flat NCP at weekly time-scales was the timing of low tide relative to the solar cycle. As discussed above, this low-frequency modulation is due to the phase difference between solar and semidiurnal M2 tidal cycles and has a ~15 day period (Lowe et al. 2016), which is similar to (but not the same as) the ~15 day period defining the spring-neap tidal cycle. When the semidiurnal high tides occurred at midday and midnight, benthic communities were able to fix carbon in excess of what was respired over the course of a day (NCP > 0, Figure 2.10c,d). When low tides coincided with solar noon, high oxygen saturation (Figure 2.10b) and temperature (Figure 2.10a) occurred on the reef flat, which drove increased rates of respiration relative to production and NCP thus became negative (Figure 2.10c,d). Nonetheless, when averaged over the course of two weeks, the macroalgal and seagrass communities of Tallon exhibited the kind of balanced P:R ratio (1.0 and 1.1, respectively) that is typical for a wide range of shallow reefs worldwide (Odum 1956; Kinsey 1985; Falter et al. 2013). This tight coupling between photosynthetic production
and respiration is likely the result of low nutrient concentrations (<1 µM, Schoepf et al. 2015) and frequent periods of low flow, which result in mass transfer-limited rates of nutrient uptake. This stoichiometrically limits the amount of carbon used by reef primary producers to synthesize new biomass relative to the high rates of carbon being fixed (Falter et al. 2001; Falter et al. 2011). Our results suggest that productivity studies conducted over short time scales (i.e., less than two weeks) may grossly over- or under-estimate net community production and P:R on similar tide-dominated reefs.

This study was conducted on a strongly tide-dominated reef, yet the diel and fortnightly patterns in physico-chemical parameters and productivity can be found on other reefs with much smaller tidal ranges. Tidal asymmetry, in this case the extension of ebb tide to ~10 hours, can occur when the height of the reef platform (relative to mean sea level) is less than half the mean tidal range (mean of spring and neap ranges) (Lowe et al. 2016). Shallow waters on the reef are also required to create large diel changes in water quality; on Tallon this occurs due to its reef morphology (a wide platform with a shallower crest relative to the reef flat) as well as bottom friction from the reef communities present (Lowe et al. 2015). Recent work by Lowe et al. (2016) has shown how diel temperature fluctuations can be tidally-regulated, even in reef systems with spring tidal ranges of only ~1 m. Additionally, ~fortnightly modulations in temperature and DO have been measured at One Tree Island, which experiences tidal asymmetry due to reef rim control and a spring tidal range of 3.5 m (Silverman et al. 2012). Thus, even reefs with even a modest tidal range may to some degree be experiencing low frequency changes in net production similar to what has been described on Tallon reef flat.
In summary, this study showed that Tallon reef flat experiences diel variability in flow, temperature, light, and dissolved oxygen concentrations that is among the most extreme in the world. Reef community respiration was generally unrelated to flow speed, but was instead controlled by water column oxygen concentration; this constituted an interesting finding that may be important in other systems experiencing diel extremes in oxygen saturation. Productivity did not appear to be greatly reduced by short-term exposure to temperatures as high as 37°C, and the reef flat showed levels of productivity that were nonetheless similar to more energetic, wave-driven reef systems subject to far more modest variability in environmental conditions. The surplus or deficit in daily net community production appeared to be dependent on the phase difference between the solar and tidal cycles, likely because extremes in light, temperature, and oxygen occurred when the semi-diurnal low tides coincided with midday and midnight. Nonetheless, the production and consumption of fixed carbon was well-balanced \( \frac{P}{R} \approx 1 \) in both communities and in both seasons when averaged over the ~fortnightly period. The results of this study demonstrate how two entirely different communities of primary producers (seagrass and macroalgae) were able to produce (and consume) large amounts of fixed carbon under extreme environmental conditions. Future work will focus on the relationship of benthic fluxes of nutrients to the physical processes driving water quality on the Tallon reef platform and the linkage between oceanic boundary conditions and net productivity of reef communities.
3. Benthic Uptake of Phytoplankton and Ocean-Reef Exchange of Particulate Nutrients on a Tide-Dominated Reef

3.1. Abstract

Benthic fluxes of chlorophyll $a$ (chl $a$) and particulate organic carbon (POC) and nitrogen (PON) were quantified on Tallon reef, a strongly tide-dominated (spring range >8 m) reef located in the Kimberley region of northwestern Australia, over a 2 week period. Extensive hydrodynamic observations were used to construct a reef-scale mass balance to estimate material exchange between the reef and ocean over individual tidal cycles. Additionally, a one-dimensional control volume approach was used to estimate fluxes of chl $a$ in waters traversing the reef platform. Particulate material was delivered to the reef platform in a pulse during flood tide, and benthic uptake of chl $a$ declined to negligible values towards the end of ebb tide. On the scale of tidal cycles, a net uptake of chl $a$ was observed on the reef platform (on average 1.3 mg chl $a$ m$^{-2}$ d$^{-1}$), which was lower than previous studies of many reef communities. Fluxes showed variability depending on the magnitude of individual tidal cycles, which was likely related to volumes of oceanic chl $a$ inputs. Tallon reef was a net source of detrital POC and PON to the surrounding coastal ocean, with average POC exports ~3% of the reef’s benthic...
gross primary production. Seasonal measurements of water quality reported here are among the first records for the coastal Kimberley, and suggest that reefs in the west Kimberley may experience naturally elevated levels of phytoplankton and particulate nutrients, especially during the wet season.
3.2. Introduction

Marine particulate organic matter (POM) is an important component of the coastal nutrient pool that includes bacteria, phytoplankton, zooplankton, and detrital matter (Volkman and Tanoue 2002). POM is a major nutrient source for many reef organisms including active filter-feeders such as sponges (Bell 2008) and passive suspension feeders such as corals (Houlbrèque and Ferrier-Pagès 2009). In oligotrophic reef waters, the smallest fraction of phytoplankton (the picoplankton) generally dominate the pool of “living” POM (Charpy 2005); therefore, most recent studies on reef community grazing have focused on the uptake of small particles (e.g., Ayukai 1995; Patten et al. 2011). Yet, coastal waters have variable concentrations and forms of POM, given that they receive nutrient-rich waters from terrestrial sources in the form of river discharge (Brodie et al. 2010) and oceanic sources via such mechanisms as coastal upwelling (Zhang et al. 2016) or transport and mixing from internal waves (Wang et al. 2007). POM can also be created in situ by reef organisms such as sponges (the ‘sponge loop’) as a consequence of feeding on dissolved organic compounds (de Goeij et al. 2013). It has been suggested that elevated levels of POM may increase reef heterotrophy, especially in low-light environments (Fabricius 2005), but very few studies have quantified reef-scale fluxes of organic particles (e.g., Fabricius and Dommasse 2000; Cuet et al. 2011a; Wyatt et al. 2013).

Previous work has demonstrated that reef community grazing rates are a function of both POM concentration and flow conditions, the latter of which enhances rates of particle delivery to the benthos through vertical turbulent convection (Ribes and Atkinson 2007; Jones et al. 2009; Monismith et al. 2010). Thus, measurements of both
the oceanic supply of particles to reefs and the local flow conditions are necessary to explain observed rates of community grazing. Many previous studies on particle uptake by benthic communities have been conducted on wave-dominated reef systems where wave-breaking on the forereef drives mainly unidirectional currents across the reef flat (Monismith 2007). The input of oceanic POM to such wave-dominated systems is generally consistent on the scale of days and is controlled by offshore supply and local hydrodynamic conditions (Wyatt et al. 2012). However, there are many other reefs (up to a third worldwide) where the mean tidal range exceeds the local significant wave height and are thus considered to be ‘tide-dominated’ (Lowe and Falter 2015). These reefs experience rapid changes in water depth and flow speed (Lowe et al. 2015) that, in turn, could increase the delivery rate of particle-rich waters to grazing organisms as a function of the tidal phase. Thus, tide-dominated reefs are expected to show large changes in benthic POM fluxes over a tidal cycle, with maximum rates of uptake occurring when flow velocities and oceanic inputs are greatest.

Controlled flume studies have been important in identifying the roles of grazer assemblage (Yahel et al. 2006) and flow speed (Ribes and Atkinson 2007) on grazing rates, but estimates are mainly relevant for the specific experimental grazing community being examined (Ribes et al. 2005). Methods such as Lagrangian sampling of waters following drogue tracks (Yahel et al. 1998; Cuet et al. 2011a) or control volume (CoVo) approaches that utilize continuous velocity measurements and Eulerian sampling to estimate fluxes over a volume of interest (Genin et al. 2009; Monismith et al. 2010) have provided researchers with direct in situ estimates of grazing rates by reef communities; however, only a limited number of these studies have been conducted to date. Indirect estimates of particle uptake rates derived from mass budgets of
particulate organic carbon or chl a (Ayukai 1995; Cuet et al. 2011a) have also been useful, but these techniques have limited applicability and may introduce large errors if local flow conditions are not well-constrained. Though a moderate number of studies have examined in situ grazing by reef communities, no studies have yet addressed the influence of tidal forcing on the supply or uptake rates of phytoplankton or particulate nutrients on reefs.

In this study, we examine the net benthic fluxes of phytoplankton, POC, and PON on a strongly tide-dominated reef. Two complementary approaches were used given the complex and rapidly-varying flows of such systems: a one-dimensional control volume and a mass balance. These results will help identify how tidal forcing, the dominant hydrodynamic process for many reefs worldwide, can control inputs of oceanic material to reef communities and can influence benthic fluxes of organic particles within and over tidal cycles. These results will also be compared to rates of reef metabolism to estimate the contribution of reef-scale benthic particle uptake to net community production.

3.3. Methods

3.3.1. Field site

The Kimberley region is a remote and near-pristine portion of northwest Australia, containing thousands of islands and ~2000 km$^2$ of total reef area (Kordi and O’Leary 2016). Its coast is macrotidal, experiencing spring tide ranges of up to 12 m (Kowalik 2004), and thus its reef systems are strongly tide-dominated (Lowe and Falter
Tallon Island, located in the Buccaneer Archipelago of the west Kimberley, contains a large (surface area $2.2 \times 10^6$ m$^2$) intertidal fringing reef platform that sits just above mean sea level (+0.25 m AHD [Australian height datum]) and is bounded on its seaward edge by a slightly shallower (+0.35 m AHD) crest (Figure 3.1).

These features result in strong tidal asymmetry on the reef platform (Lowe et al. 2015), where the ebb phase of the dominant semi-diurnal tide is elongated to ~10 hours and the flood phase is truncated to ~2 hours (Figure 3.2). Although offshore water
levels fall well below the reef platform during ebb tide, reef communities remain submerged through the ebb phase due to the shallower crest and friction from the benthos, with minimum water depths of ~0.4 m occurring at the end of the ebb phase (Figure 3.2a).

The detailed hydrodynamics (Lowe et al. 2015), thermodynamics (Lowe et al. 2016), and community productivity (Gruber et al. 2017) of Tallon reef have already been reported elsewhere. The platform contains two types of benthic community: a seagrass-dominated inner zone and a macroalgal-dominated outer zone that are separated by a zone ~200 m wide where the two community types become mixed within a sand and coral rubble substrate (Figure 3.1). The inshore seagrass meadow stretches from the fringing mangrove shoreline to 400 m landward of the reef crest and contains *Enhalus acoroides* and *Thalassia hemprichii* growing on sand (Wells et al. 1995). The macroalgal zone is 200 m wide extending shoreward from the reef crest and is dominated by the brown macroalgae *Sargassum* spp. growing on mostly lithified reef framework that also contains a diverse assemblage of foliose brown macroalgae, red corallines, and crustose coralline algae. Filter feeding organisms found in the macroalgal-dominated zone include sponges, giant clams (*Tridacna* and *Hippopus* spp.), soft corals, small hard corals (5-10% cover), and likely cryptic filter feeders within the porous reef framework (Richter et al. 2001). Sponges were the main filter feeder found in the seagrass and mixed zones, with a large number of detritivorous sea cucumbers observed at densities of ~0.5 individuals m$^{-2}$, although organism densities were not quantified through randomized sampling.
Three field experiments were conducted at Tallon reef with each lasting one to
two weeks: 5 – 20 October 2013 (dry season), 4 – 9 February 2014 (wet season), and 27 March – 9 April 2014 (late wet season) (Table 3.1). Fixed volumes of water were filtered to determine chl $a$ and particulate nutrient concentrations during all field experiments according to the protocols below. The final field experiment coincided with the detailed hydrodynamic study reported in Lowe et al. (2015). By deploying in situ-calibrated fluorometers and an automated sampler among hydrodynamic instrumentation, we were able to estimate benthic fluxes of POM on the reef platform using two approaches: a one-dimensional control volume technique and a mass balance, as detailed below. Throughout this manuscript we refer to ‘benthic fluxes’ (the ‘net uptake’ or ‘net release’) of chl $a$ and particulate nutrients, rather than ‘grazing’.

Table 3.1. Number of chl $a$ samples taken each field experiment at each site, including during Lagrangian drifts and large (>5 µm) chl $a$ fractions. Number of particulate organic carbon (POC), nitrogen (PON), and phosphorus (PP) samples are also indicated. Tide stages (ebb, flood) refer to tides on the reef platform, (--) indicates no samples available, and values are the number of duplicate samples.

<table>
<thead>
<tr>
<th>Dates</th>
<th>Season</th>
<th>Site</th>
<th>Ebb</th>
<th>Flood</th>
<th>Drifts</th>
<th>&lt;5µm</th>
<th>POC/PON</th>
<th>PP</th>
</tr>
</thead>
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<tr>
<td>5 - 20 Oct 2013</td>
<td>Dry</td>
<td>Off</td>
<td>9</td>
<td>7</td>
<td>--</td>
<td>9</td>
<td>4</td>
<td>6</td>
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<tr>
<td></td>
<td></td>
<td>MA</td>
<td>22</td>
<td>10</td>
<td>8</td>
<td>12</td>
<td>--</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SG</td>
<td>6*</td>
<td>10</td>
<td>8</td>
<td>4</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>4 - 9 Feb 2014</td>
<td>Wet</td>
<td>Off</td>
<td>14</td>
<td>3</td>
<td>--</td>
<td>--</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MA</td>
<td>14</td>
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<td>11</td>
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<tr>
<td></td>
<td></td>
<td>SG</td>
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<td>10</td>
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<tr>
<td>27 Mar - 9 Apr 2014</td>
<td>Late Wet</td>
<td>Off</td>
<td>13</td>
<td>11</td>
<td>--</td>
<td>--</td>
<td>3</td>
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<td></td>
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</tr>
</tbody>
</table>

*Indicates samples from the final 6 hours of ebb tide.
Due to the rapidly varying flows characteristic of Tallon reef and the design of this study, it was not possible to delineate between rates of grazing by benthic organisms and net deposition (or resuspension). However, we will demonstrate that grazing is likely the dominant process driving observed benthic fluxes, especially for small particles (see Discussion).

3.3.2. Water sampling

Extensive water sampling was conducted during each field experiment to determine concentrations of chl \(a\) and particulate organic nutrients offshore and on the reef. The majority of our sampling efforts were conducted at four fixed (Eulerian) stations: the channel adjacent to the reef (‘Off’), and on the reef platform in the macroalgal-dominated zone (‘MA’), the mixed zone (‘Mix’), and the seagrass-dominated zone (‘SG’) (Figure 3.1). Offshore samples from just below the water surface, were collected by boat at roughly one hour intervals on the days when water sampling occurred (Table 3.1). Samples from the reef were collected on foot during the middle to end of ebb tide (6-12 hours after reef flooding, Figure 3.2) and by boat when water levels were higher (1-4 hours after reef flooding). Sampling by boat or on foot was not possible during peak flood and ebb periods (0-1 and 4-6 hours after reef flooding, respectively, Figure 3.2) due to the hazardous flow conditions on the reef. Thus, an ISCO automated water sampler (Teledyne Isco, Inc.) was placed on a 4 m high scaffolding at Mix (Figure 3.1) during the Apr field experiment and sampled hourly during the first few hours after reef flooding (Table 3.1). Lagrangian sampling of changes in water quality following water masses traversing over the reef was also conducted during ebb tides of the Oct field experiment. A small neutrally-buoyant drogue (mandarin) with GPS tracker attached was released at SG or MA (\(n = 4\) for
each) and allowed to drift for 30 min. Water samples were collected at the start and end locations of each drift (Table 3.1). Sampling for chl $a$ and all suspended particulates was done in duplicate, and values presented are the mean of duplicates.

Water samples for analysis of chl $a$ concentration were collected in 2 L plastic bottles and filtered under vacuum onto 47 mm (pore size 0.7 $\mu$m) glass fiber filters (Whatman GF/F) within 1 hour of collection. The concentration of the large size-fraction chl $a$ (>5 $\mu$m) was determined by filtration through 47 mm (pore size 5 $\mu$m) polycarbonate filters (Nuclepore). Filters were folded in aluminum foil and placed on ice until return to the field station (several hours) where they were frozen until analysis. Water samples for analysis of particulate organic carbon and nitrogen and particulate phosphorus were filtered onto 25mm GF/Fs that had been pre-combusted (4 hours at 550°C). The volume filtered varied between 0.5 – 2 L, or when sufficient material was collected on each filter. Filters were then rinsed with a small amount (5-10 mL) of ultrapure water, dried under gentle vacuum, placed in pre-combusted aluminum foil packets, and stored frozen until analysis.

All laboratory analyses were conducted within a few weeks of returning from the field. Filters for chl $a$ analysis were placed in 90% acetone, sonicated, and allowed to extract overnight at 4°C. The following day, samples were centrifuged and the supernatant was read on a fluorometer (Turner Designs Trilogy) for total chl $a$. Samples were then acidified with 0.1N hydrochloric acid for determination of phaeophytin $a$ and chl $a$ correction (Arar and Collins 1997). Particulate organic carbon and nitrogen analysis was conducted using a Shimadzu TOC-V carbon analyzer fitted with solid sample combustion (SSM-5000A) and total nitrogen units; filters were acidified pre-combustion to remove inorganic carbonates. A hot acid digestion in 5%
persulfate was performed on filters for particulate phosphorus analysis (Menzel and Corwin 1965), and the resulting concentration of liberated phosphate was determined spectrophotometrically (Parsons et al. 1984) with a Shimadzu UV-1601.

3.3.3. Control volume approach

A one-dimensional control volume (CoVo) approach was used to estimate the net benthic flux of chl $a$ during the Apr field experiment. This method utilizes flow velocity and modified Eulerian sampling of chl $a$ at upstream and downstream points, and we have already used a similar approach to estimate the net community productivity of the seagrass and macroalgal zones on Tallon reef (Gruber et al. 2017). Current velocity ($u$) and water depth ($h$) were recorded at 1 Hz by a bottom-mounted acoustic Doppler current profiler (Nortek Aquadopp HR AS) with 0.03 m bin size, located near SG (Figure 3.1). Towards the end of ebb tide, the water depth reached a minimum on the reef platform ($h \approx 0.4$ m, Figure 3.2), and in the rare instances (5% of the total field study) where water depth encroached on instrument blanking distance, the flow speed was estimated from drifter releases (Gruber et al. 2017). Tidal phase-averaging is used throughout this manuscript to present patterns in hydrodynamic and other continuous data related to the phase of tide. Phase-averages are ensemble averages of a given variable at each point in the semi-diurnal (M2) tidal cycle (e.g., mean of all values measured at high tide).

Fluorometers (Wetlabs FLNTUSB) were deployed at MA and SG (Figure 3.1) at 20 cm above the bed, and were configured to burst-sample at 1 Hz for 10 sec every 5 min, yielding data over 17 complete tidal cycles. Fluorometers were placed together for 30 min periods during the start, middle, and end of the field experiment to check for
drift, which was negligible. Instrument output was bin-averaged at 5 min intervals and calibrated to in situ conditions using regressions with chl $a$ samples taken during the experiment and during water sampling at the offshore station (see Results). Water samples were collected over the wide ranges of irradiance and temperature that naturally occurred on the reef platform, so we are confident that the fluorometers provided a close approximation of in situ chl $a$ concentrations.

During each 10 hour ebb tide, water drained off the northern portion of the reef platform in the northeasterly direction ($80^\circ \pm 30^\circ$, mean $\pm$ standard deviation; Figure 3.2d,e), aligned with the instrument transect. Depth-averaged flow speed along the instrument transect ($u_x$) was bin-averaged at 5 min intervals and used to estimate transport $q_x$ as

$$q_x = u_x h,$$

assuming horizontal dispersion was negligible. The benthic flux of chl $a$ ($J_{\text{chl} a}^{\text{CoVo}}$ in mg chl $a$ m$^{-2}$ h$^{-1}$) was estimated as (Genin et al. 2009)

$$-J_{\text{chl} a}^{\text{CoVo}} = \bar{h} \frac{d\bar{C}}{dt} + q_x \frac{(C_{MA} - C_{SG})}{dx},$$

where $C_{MA}$ and $C_{SG}$ are the chl $a$ concentrations at MA and SG, respectively, and $\bar{C}$ is the mean of both. The transect length $dx$ was 540 m and $\bar{h}$ represents mean water depth along the transect. Note that a sign convention is assumed where positive $J_{\text{chl} a}^{\text{CoVo}}$ indicates net uptake of chl $a$ by the benthos while negative values indicate net release to the water column. The first term on the right side of Eq. (2) represents the mean local benthic flux of chl $a$ (i.e., uptake or release in the vicinity of the loggers), while the second term refers to the uptake or release of chl $a$ during advection between loggers.
This formulation assumes that rates of phytoplankton growth and pelagic grazing of phytoplankton were balanced on the timescale of hours (Genin et al. 2009). The local term was bin-averaged into 30-min increments, beginning at peak high tide. As flow speeds change throughout ebb tide, a varying averaging interval must be used for the advective term; estimates were bin-averaged based on transit time between SG and MA and then linearly interpolated onto a common 30 min interval (Gruber et al. 2017). The CoVo approach was relevant for ebb tide periods (~10 hours each semidiurnal tidal cycle) when flow vectors were aligned with the instrument transect.

The Lagrangian measurements following drifters provided an independent estimate of benthic chl \(a\) flux during ebb tides. Fluxes (in mg chl \(a\) m\(^{-2}\) h\(^{-1}\)) were estimated as

\[
J_{\text{chla}}^{\text{drift}} = \frac{\Delta C}{\Delta t},
\]

(3)

where \(\Delta C\) was the change in chl \(a\) concentration from water samples taken at the start and end of the drift, \(\Delta t\) was drift time, and \(h_{\text{drift}}\) was the mean water depth along the drifter track.

3.3.4. Reef-scale mass balance

Though useful for determining benthic chl \(a\) fluxes during ebb tides, the CoVo approach could not account for fluxes during flood tides, as flow direction changed rapidly and was generally not aligned with the instrument transect. In order to understand how representative the CoVo estimates were during a full tidal cycle and at the larger reef platform scale, we also utilized a second approach: a mass balance that combined measurements of exchange across the reef crest with oceanic and reef chl \(a\)
values. A similar approach has previously been used to construct a heat budget for Tallon reef to assess temperature variability (Lowe et al. 2016). Flow velocities and water depths were recorded at 2 Hz by four upward-looking acoustic Doppler velocimeters (Nortek Vector) evenly spaced along the reef crest (V1-4, Figure 3.1) at the same deployment locations as in Lowe et al. (2015). Raw data were despiked (Goring and Nikora 2002), filtered for instances when water depth approached the sampling volume (0.4 m above the bed), and averaged at 5 min intervals. Cross-shore transport \( q_i \), where \( i = 1:4 \) corresponding to instruments V1-4) was defined for each instrument as the transport component normal to the reef crest, with the convention that onshore flow was positive and offshore flow negative. Low water depth affected instruments V1 and V4 towards the end of ebb tide (Figure 3.2b), when flows were slow (<0.05 m s\(^{-1}\)); for these instances, \( q_1 \) was assumed to equal \( q_x \) (i.e., transport was conserved), and \( q_4 \) was assumed to be similar in magnitude to all other \( q_i \); this assumption was confirmed with drifter releases described above. The integrated discharge across each of the four segments of reef crest \( Q_i \) (in m\(^3\) s\(^{-1}\)) was estimated as

\[
Q_i = q_i l_i, \tag{4}
\]

where \( l_i \) is the length of crest represented by each of the four cross-reef transport terms (shown in color Figure 3.2c,d,e). Total discharge in the onshore direction \( Q_{in} \) was the sum of all positive (i.e., shoreward) \( Q_i \) each time step, while discharge offshore \( Q_{out} \) was the sum of all negative (i.e., seaward) \( Q_i \). In order to estimate the rate of phytoplankton import into the reef system, we assumed water crossing the reef crest at flood tide \( Q_{in} \) had a constant chl \( a \) concentration equal to the mean at Off during the Apr field experiment (0.60 \( \mu \)g L\(^{-1}\), Figure 3.4a). Offshore chl \( a \) concentrations were relatively constant (standard error of the mean = 0.04 \( \mu \)g L\(^{-1}\)), but uncertainty was nonetheless
incorporated into error estimates (described below). The rate of chl $a$ import from offshore waters ($F_{in}$, in mg chl $a$ s$^{-1}$) was estimated each time step as

$$F_{in} = Q_{in} C_o,$$

(5)

where $C_o$ was offshore chl $a$ concentration. We assumed that water exiting the reef during ebb tide ($Q_{out}$) would have chl $a$ concentrations equivalent to those measured at MA ($C_{MA}$), the fluorometer closest to the reef crest (~100 m). This assumption was based on the observations that: (1) during the early portion of ebb tide (when the majority of $Q_{out}$ occurs), offshore discharge mainly crosses $l_1$, the boundary associated with $C_{MA}$ (Figure 3.2d); and (2) towards the end of ebb tide (when $Q_{out}$ is very low), all flow streamlines (Figure 3.2e) pass over benthic communities of similar composition (Figure 3.1). Despite several assumptions associated with the mass balance, we will show that estimates from this method compared well to estimates made using the entirely different CoVo approach (see Results), which gives us confidence that these assumptions are reasonable.

The rate of chl $a$ export from the reef platform ($F_{out}$) during each time step was then estimated as

$$F_{out} = Q_{out} C_{MA},$$

(6)

and the net rate ($F_{net}$) of chl $a$ import or export each time step was then

$$F_{net} = F_{in} + F_{out}.$$  

(7)

In order to represent the overall balance between oceanic inputs and off-reef exports, estimates of $F_{net}$ were integrated over each semidiurnal tidal cycle, where $F_{cyc}$ was the sum of all $F_{net}$ occurring from the start of flood tide (zero hours after flooding)
to the end of ebb tide (~12.4 hours after reef flooding) for each of the 17 tidal cycles where continuous chl \( a \) values were available. We then calculated a mean net benthic flux \( J_{\text{chl}a}^{MB} \) (in mg chl \( a \) m\(^{-2}\) d\(^{-1}\)) for each tidal cycle as

\[
J_{\text{chl}a}^{MB} = F_{\text{cyc}} / (A_{\text{reef}} \ t_{\text{cyc}}),
\]

where \( t_{\text{cyc}} \) is the tidal cycle length (in days), and \( A_{\text{reef}} \) is the reef platform surface area. Positive values indicate net uptake of chl \( a \) on the reef, while negative values indicate net chl \( a \) release to offshore waters. In order to compare benthic fluxes estimated with the CoVo and mass balance approaches, \( \overline{J_{\text{chl}a}^{CoVo}} \) (in mg chl \( a \) m\(^{-2}\) d\(^{-1}\)) was calculated as the mean of all \( J_{\text{chl}a}^{CoVo} \) during each tidal cycle.

The input of phytoplankton-derived particulate nutrients on the reef was estimated using significant linear relationships (\( p < 0.01 \)) between concentrations (in \( \mu \)g L\(^{-1}\)) of POC and chl \( a \) \( (R^2 = 0.61) \) and PON and chl \( a \) \( (R^2 = 0.80) \) during the Apr field experiment. The flux of phytoplankton-derived POC with each tidal cycle (POC\( p \)) could then be estimated as the product of the regression coefficient, 36.7 ± 21.8 (mean ± 95% confidence interval), and \( J_{\text{chl}a}^{MB} \). Note that this empirically-derived conversion factor is very similar to the carbon:chl \( a \) ratio of 30:1 commonly assumed in phytoplankton studies (Cloern et al. 1995). The flux of phytoplankton-derived PON (PON\( p \)) could be similarly estimated as the product of 10.10 ± 3.78 and \( J_{\text{chl}a}^{MB} \). This empirically-derived ratio of nitrogen:chl \( a \) is at the upper end of the range \( (1.70 – 14.7) \) reported in previous studies (Yentsch and Vaccaro 1958; Wyatt et al. 2010) and implies a C:N ratio below Redfield, yet within the range found in natural populations (Geider and La Roche 2002).
Using a mass balance approach similar to the above for chl \(a\) (Eqs. 4 – 7), benthic fluxes of total POC and PON were estimated over a mean tidal cycle using phase-averaged versions of discharges \(Q_{in}\) and \(Q_{out}\). Water sampling on the reef platform occurred over multiple tidal cycles, so POC and PON concentrations, while variable, could be considered representative of a mean tidal cycle (average of full spring/neap cycle). Oceanic inputs of POC and PON during flood tide were assumed to be at the same concentrations as the mean values at Off (Eq. 5). Significant nonlinear relationships, commonly observed in reef particulate uptake studies (Ribes et al. 2003; Ribes et al. 2005), were fit to POC and PON measurements \((R^2 = 0.46\) and 0.57, respectively) to estimate concentrations over a full ebb tide at Mix (see Results), which was assumed to be similar to POC and PON in water exiting the reef platform (Eq. 6). Finally, mean benthic fluxes of total POC and PON were calculated as the balance between oceanic inputs and off-reef export during ebb tide (Eqs. 7, 8).
3.3.5. Statistics and error propagation

The chl $a$ concentrations recorded by factory-calibrated fluorometers were highly correlated with direct measurements of chl $a$ from water samples ($R^2 = 0.74, p < 0.001$; Figure 3.5); however, they did slightly underestimate in situ chl $a$ by ~25% on average. Regression of laboratory versus in situ field measurements of chl $a$ were therefore used to calibrate fluorometer estimates of chl $a$ concentrations.

Significant differences among means of water quality variables were assessed with one-way ANOVAs using SAS statistical software (v9.4). The assumption of homoscedasticity was met with Levene’s test, and normality of residuals was assessed both visually and through the Shapiro-Wilk normality test. Tukey-Kramer adjusted least-squared means were calculated, and all pair-wise comparisons were computed. In cases where data required transformation to meet assumptions, uncertainty around the mean was represented by back-transformed 95% confidence limits. Uncertainties in estimates of $J_{chla}^{Cov}$ and $J_{chla}^{MB}$ were calculated via Monte Carlo simulation ($n = 10,000$) where input variances were drawn from bin-averaged data (Lehrter and Cebrian 2010).

3.4. Results

3.4.1. Chlorophyll $a$ and particulate nutrients

Offshore chl $a$ concentrations were similar between the first two field experiments during the dry and early wet seasons (~0.45 $\mu$g L$^{-1}$), and were elevated by the end of the wet season in Apr (0.60 $\mu$g L$^{-1}$); offshore chl $a$ values were similar during flood and ebb tidal phases during all field experiments (Figure 3.4a, b). Ratios of
phaeophytin to chl \( a \), with phaeophytin a degradation product of chl \( a \) whose production is most often associated with phytoplankton grazing (Lorenzen 1967), were \( \sim 0.6 \) for offshore waters (Figure 3.4c, d).

Size-fractionated chl \( a \) values showed that the offshore phytoplankton pool contained comparable amounts of both ‘small’ (< 5 \( \mu \)m) and ‘large’ (> 5 \( \mu \)m) cell sizes, at least as inferred from chl \( a \) concentrations (Figure 3.5a, b). The large fraction also tended to contain comparatively more degraded chl \( a \) than the small fraction, with
phaeo:chl ratios of 0.9 and 0.3, respectively (Figure 3.5c, d). Unlike chl $a$, offshore particulate nutrient concentrations were lowest during the final field experiment; the low values for ratios of POC:chl $a$ and PON:chl $a$ suggested that phytoplankton comprised a larger proportion of total POC and PON at the end of the wet season than during other field experiments (Table 3.2).

In contrast to offshore waters, chl $a$ and particulate nutrient concentrations on the reef platform were highly dependent on the tidal phase. For samples taken around high tide, chl $a$ and phaeo:chl were similar to offshore measurements (Figure 3.4b,d). During ebb tide, however, chl $a$ on the reef platform declined, reaching less than half of offshore levels by the end (final 6 hours) of ebb tide (Figure 3.4a); this trend was observed during all three field experiments. In general, minimum levels of chl $a$ were found at either MA or Mix (Figure 3.4a). Ratios of phaeo:chl on the reef increased by the end of ebb tide, up to a factor of 3 during the Feb field experiment; in all field experiments, maximum values of phaeo:chl were found at MA (Figure 3.4c). Both large (>5 $\mu$m) and small (<5 $\mu$m) size fractions of chl $a$ were significantly reduced ($p < 0.003$) by the end of ebb tide on the reef relative to offshore waters (Figure 3.5a,b). Ratios of phaeo:chl were also significantly elevated ($p < 0.005$) in both small (Figure 3.5c) and large (Figure 3.5d) size fractions on the reef relative to offshore.
Table 3.2. Summary of mean (SD) concentrations and stoichiometry of particulate organic carbon (POC), nitrogen (PON), and phosphorus (PP) from all field experiments. Reef zone [macroalgal (MA), mixed (Mix), and seagrass (SG)] values are from final 6 hours of ebb tide, and offshore (Off) values are from all stages of the tide. Number of samples represented by each mean are shown in Table 3.1, and (--) indicates no data available.

<table>
<thead>
<tr>
<th></th>
<th>Concentration (μM)</th>
<th>Ratio (μg μg$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Off* Oct 2013</td>
<td>14.6 (3.1)</td>
<td>2.77 (0.61)</td>
</tr>
<tr>
<td>MA</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>SG</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Off* Feb 2014</td>
<td>14.6 (5.9)</td>
<td>1.71 (0.25)</td>
</tr>
<tr>
<td>MA</td>
<td>9.2 (3.7)</td>
<td>0.95 (0.39)</td>
</tr>
<tr>
<td>SG</td>
<td>12.3 (4.7)</td>
<td>1.19 (0.21)</td>
</tr>
<tr>
<td>Off* Apr 2014</td>
<td>6.5 (1.3)</td>
<td>1.10 (0.22)</td>
</tr>
<tr>
<td>MA</td>
<td>3.7 (1.3)</td>
<td>0.49 (0.22)</td>
</tr>
<tr>
<td>Mix</td>
<td>7.2 (2.5)</td>
<td>0.99 (0.27)</td>
</tr>
<tr>
<td>SG</td>
<td>--</td>
<td>--</td>
</tr>
</tbody>
</table>

*Samples are from all stages of tide
Towards the end of ebb tide on the reef platform (final 6 hours of the ~10 hours of ebb tide), suspended particulate nutrient concentrations on the reef were depressed by up to ~50% relative to offshore values (Table 3.2). Concentrations of POC, PON, and PP were consistently lowest at MA (compared to Off and SG) during each field experiment. The stoichiometry of particulate nutrients differed between the reef and offshore waters (Table 3.2), with elevated PON:PP and POC:PP observed at MA and SG. Ratios of particulate nutrients to chl $a$ showed that chl $a$ declined relative to total

Figure 3.5. Mean (with 95% confidence limits) chlorophyll $a$ concentration (a,b) and ratio of phaeophytin:chl $a$ (c,d) from water samples in small (<5 $\mu$m) and large (>5 $\mu$m) fractions at offshore (Off) and reef stations [macroalgal (MA) and seagrass (SG) dominated zones]. All samples taken during the Oct field experiment during final 6 hours of ebb tide on the reef (Table 3.1). Asterisks (*) denote means which are significantly different ($p < 0.05$) to offshore means.
POC, PON, and PP on the reef; highest ratios of POC:chl $a$ and PON:chl $a$ were observed in the MA and Mix zones during the Feb and Apr field experiments (Table 3.2).

Continuous chl $a$ measurements on the reef showed distinct features related to phases in the tidal cycle (Figure 3.6); chl $a$ concentrations rose sharply during flood tide

![Figure 3.6](image)

Figure 3.6. Reef flat a) depth $h$ (tidal phase-averaged) shown with all chlorophyll $a$ measurements from fluorometers in b) macroalgal and c) seagrass-dominated zones shown with hour after reef flooding during the Apr field experiment. Color indicates the flow speed $u$ adjacent to each fluorometer. Chl $a$ values shown were corrected according to regressions shown in Figure 3.5. Note that different limits are used in the color scale of each plot in order to accommodate differences in the range of flow speeds at each station.
(0 – 3 h after reef flooding) when high chl $a$ offshore waters inundated the reef platform. During each tidal cycle, maximum chl $a$ concentrations occurred in conjunction with high flow velocities produced by each peak flood and peak ebb ($\sim$0 – 1.5 h and 4 – 6 h after reef flooding, respectively), and could reach $\sim$1.0 $\mu$g L$^{-1}$ during the highest spring tides (Figure 3.6b,c). Chl $a$ concentrations declined as water levels on the reef platform became low, and chl $a$ generally remained low for the remainder of ebb tide (final 6 hours), as was independently observed in the water samples (Figure 3.4a). Chl $a$ at MA was stable $\sim$0.1 – 0.2 $\mu$g L$^{-1}$ during this late ebb tide period (Figure 3.6b), while concentrations were slightly higher ($\sim$0.3 – 0.4 $\mu$g L$^{-1}$) and more variable at SG (Figure 3.6c). Tidal phase-averaging showed chl $a$ values were $\sim$0.5 $\mu$g L$^{-1}$ during peak ebb and flood periods (Figure 3.7), with high variability due to changes in flow velocity related to the spring-neap cycle. During the final 6 h of each tidal cycle, low chl $a$ concentrations were seen at MA during both day and night (Figure 3.7a), while elevated chl $a$ ($\sim$0.3 $\mu$g L$^{-1}$) occurred at SG during the daytime only (Figure 3.7b).

### 3.4.2. Benthic chl $a$ fluxes

Benthic fluxes of chl $a$ estimated using the control volume approach ($J_{chla}^{CoVo}$) displayed rapid variations during the early portion of ebb tide, 3 – 6 h after reef flooding (Figure 3.8). A net release of chl $a$ into the water column ($J_{chla}^{CoVo} < 0$) occurred during peak ebb (4 h after reef flooding), which coincided with high flow velocities (Figure 3.6) and was likely related to the resuspension of large detrital material containing chl $a$ (see Discussion). Net uptake of chl $a$ ($J_{chla}^{CoVo} > 0$) occurred during the rest of ebb tide, reaching a maximum 6 h after reef flooding, and tapering to zero by the end of ebb tide (Figure 3.8). The Lagrangian estimates of the benthic fluxes from drifter releases at
MA closely matched the tidal phase-average of $J_{\text{chl}a}^{\text{CoVo}}$; whereas $J_{\text{chl}a}^{\text{Drift}}$ from the seagrass zone was basically negligible (Figure 3.8).

The flow discharges on and off the reef platform were approximately ‘balanced’ (i.e., water volumes from flood and ebb tides were equal for each tidal cycle), with residual errors of less than 5%. The fact that our water mass balance was so accurately closed also gave us confidence that this approach could therefore be used to estimate the net uptake or release of POM by the Tallon reef platform over an entire tidal cycle.
Tidal phase-averaged plots of discharge showed that oceanic inputs ($Q_{in}$) peaked during flood tide and continued for ~3 hours of ebb tide (Figure 3.9a), due to on-reef flows along the reef platform’s southern boundary (Figure 3.2d). The majority of off-reef discharge ($Q_{out}$) occurred at the beginning of ebb tide, 3 – 6 h after reef flooding, with negligible discharge during the final 6 h of ebb tide. Net transfer of chl $a$ onto the reef ($F_{net} > 0$) was greatest during peak flood (Figure 3.9b). During the beginning of ebb tide (3 – 6 h after reef flooding), chl $a$ inputs from $Q_{in}$ (Figure 3.9a) partially balanced the large chl $a$ exports due to high chl $a$ concentrations in $Q_{out}$ (Figure 3.6b). Transport of chl $a$ off the reef platform ($F_{net} < 0$) became negligible during the final 6 hours of ebb tide (Figure 3.9b).
Positive values of $J_{chl}^{MB}$ indicated net uptake of chl $a$ over each tidal cycle, suggesting that the reef was generally a sink for suspended chl $a$, although estimates of $J_{chl}^{MB}$ for some tidal cycles were not significantly different to zero (Figure 3.10). Large variability in $J_{chl}^{MB}$ between tidal cycles was evident, and $J_{chl}^{MB}$ appeared to have a long-term periodicity on the order of weeks (Figure 3.10).

Figure 3.9. Tidal phase-averaged (lines) and ranges (shaded areas) of a) discharge and b) net rate of chlorophyll $a$ transfer $F_{net}$ onto (positive) and off of (negative) Tallon reef platform are shown with hours after reef flooding. Discharges are onto ($Q_{in}$) and off of ($Q_{out}$) the reef platform.
Overall mean benthic fluxes of chl $a$ estimated from the mass balance and CoVo (means of $J_{chl_a}^{MB}$ and $J_{chl_a}^{CoVo}$, respectively) were similar despite being made on entirely different spatial and temporal scales (Table 3.3). These estimates demonstrate that Tallon reef platform was a net sink to suspended chl $a$ during the Apr field experiment. For further discussion, we will focus on mass balance estimates of chl $a$ flux ($J_{chl_a}^{MB}$) since these account for processes occurring over the entire tidal cycle, rather than only ebb tide.

### 3.4.3. Benthic fluxes of total POC and PON
Measurements of POC and PON concentration occurred over multiple tidal cycles; therefore, exponential decay relationships (see Methods) represented phase-averaged particulate concentrations at Mix during the Apr field study (Figure 3.11). By using a mass balance approach similar to that of chl a, we were further able to estimate mean fluxes of total POC and PON on the reef platform (Table 3.4). Phytoplankton-

### Table 3.3. Mean (SD) net benthic fluxes of chl a and phytoplankton-derived particulate organic carbon (POCp) and nitrogen (PONp) determined by the mass balance (MB) and CoVo approaches during the Apr field experiment. Values for this study are overall means of all tidal cycle means (n = 17). Also shown are estimates [mean (SE) or range] of the same variables from previous studies of reef communities.

<table>
<thead>
<tr>
<th>Study</th>
<th>Method</th>
<th>Flux (mg chl a m⁻² d⁻¹)</th>
<th>Flux POCp (mmol C m⁻² d⁻¹)</th>
<th>Flux PONp (mmol N m⁻² d⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>This study</td>
<td>MB</td>
<td>1.31 (0.25)</td>
<td>4.0 (1.4)</td>
<td>0.95 (0.26)</td>
</tr>
<tr>
<td></td>
<td>CoVo</td>
<td>1.58 (0.18)</td>
<td>4.8 (1.7)</td>
<td>1.14 (0.31)</td>
</tr>
<tr>
<td>Yahel et al. 2006</td>
<td>Flume</td>
<td>0.36 - 1.4</td>
<td></td>
<td>1.3 - 5.2</td>
</tr>
<tr>
<td>Cuet et al. 2011</td>
<td>MB</td>
<td>1.21*</td>
<td>3.04*</td>
<td>0.32</td>
</tr>
<tr>
<td>Ayukai 1995</td>
<td>MB</td>
<td>3*</td>
<td>7.5*</td>
<td></td>
</tr>
<tr>
<td>Genin et al. 2009</td>
<td>CoVo</td>
<td>3.69 (1.18)</td>
<td>18.3 (8.3)</td>
<td>2.8</td>
</tr>
<tr>
<td>Wyatt et al. 2010</td>
<td>Eulerian</td>
<td>5.67 (0.77)</td>
<td>19.6 (2.7)</td>
<td>3.43 (0.47)</td>
</tr>
<tr>
<td>Patten et al. 2011</td>
<td>Eulerian</td>
<td>4 - 20</td>
<td></td>
<td>0.2 - 1.9</td>
</tr>
<tr>
<td>Monismith et al. 2010</td>
<td>CoVo</td>
<td>9.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fabricius and Domnisse 2000</td>
<td>Eulerian</td>
<td>11 (2.5)</td>
<td>28.3 (6.2)</td>
<td></td>
</tr>
<tr>
<td>Ribes and Atkinson 2007</td>
<td>Flume</td>
<td>28 - 42*</td>
<td>70 - 105</td>
<td>7 - 10</td>
</tr>
<tr>
<td>Ribes et al. 2005</td>
<td>Flume</td>
<td>31 (2)*</td>
<td>77.5 (5)</td>
<td>7.3 (0.5)</td>
</tr>
<tr>
<td>Yahel et al. 1998</td>
<td>MB</td>
<td>65.6*</td>
<td>164</td>
<td></td>
</tr>
</tbody>
</table>

*Includes microbial community
*Assuming C:chl a of 30
*Assuming mean chl a = 0.2 mg m⁻³
*Assuming C:N of 9.5 based on cell data from Houlbrèque et al. (2006)
derived particulate nutrients (POC<sub>p</sub> and PON<sub>p</sub>) that were retained on the reef represented ~7% and ~10%, respectively, of the total POC and PON inputs during each tidal cycle; however, we measured the net release of total POC and PON to the coastal ocean during the Apr field experiment, as off-reef exports exceeded oceanic inputs (Table 3.4).

A release of detrital material (non-phytoplanktonic) by the reef platform can be invoked to explain the difference between net uptake of POC<sub>p</sub> and PON<sub>p</sub> (a sink) and net export of total POC and PON. This release term is simply the sinks of POM (off-reef flow and chl <i>a</i> uptake) less the oceanic inputs (Table 3.4). Detrital export is estimated to have exceeded POC<sub>p</sub> by a factor of ~4 and was of similar magnitude to PON<sub>p</sub>; thus, exported material would have a high C:N ratio (~15:1 compared to ~7:1 commonly found for phytoplankton).

3.5. Discussion

3.5.1. Offshore chl <i>a</i> and particulate nutrients
The southwest coast of the Kimberley is among the most pristine marine areas in the world (Halpern et al. 2008); however, water quality sampling from the three field studies reported here showed similarities between Tallon reef and reefs experiencing elevated nutrient inputs from anthropogenic sources (Schaffelke et al. 2012). Chlorophyll \( a \) concentrations offshore of Tallon reef (Figure 3.4) were roughly double those in the macrotidal northern GBR (Brodie et al. 2007), where coastal catchments have had relatively low anthropogenic pressure over the last 150 years (Furnas 2003;
Wooldridge et al. 2006); instead, our offshore measurements were at or greater than the chl a threshold (0.45 µg L⁻¹) used to indicate water quality favorable for high coral diversity in the GBR (De'ath and Fabricius 2010). Particulate organic carbon concentrations measured during our study (Table 3.2) were similar to typical values for coral reef waters during all field experiments (Atkinson and Falter 2003; Schaffelke et al. 2012). Particulate organic nitrogen concentrations were elevated (especially during Oct) relative to < 1 µM typical of reef waters (Atkinson and Falter 2003; Schaffelke et al. 2012) and were similar to nearshore reefs subject to elevated turbidity (Fabricius and Dommisse 2000). These observations further agree with other recent studies of the broader coastal Kimberley region (Thompson and Bonham 2011; Jones et al. 2014), suggesting that nearshore Kimberley reefs may naturally experience generally ‘meso’-trophic conditions, at least with regard to the concentration of particulate nutrients and phytoplankton.

Large seasonal differences in coastal water quality can occur in regions with a monsoonal climate as delivery of terrestrial sediment and nutrients to coastal waters occurs primarily during wet season pulsed events (Furnas 2003; Devlin and Brodie 2003).
Our study is one of the first to measure wet season chl $a$ and particulate nutrients in the coastal Kimberley (e.g., McKinnon et al. 2015a; McKinnon et al. 2015b; Furnas and Carpenter 2016). Concentrations of chl $a$ (Figure 3.4) were 50% greater by the end of the wet season (Apr), relative to dry (Oct) and mid-wet (Feb) field experiments, while POC and PON values declined (Table 3.2). Changes in nearshore water quality associated with terrestrial discharge during the wet season can be highly variable between events and years given that rates of terrestrial runoff are themselves highly variable (Schroeder et al. 2012). Based on monitoring data from the Fitzroy River, the largest coastal river in the west Kimberley (Figure 3.1), the 2013-2014 wet season was characterized by below-average freshwater discharge (Willare station, http://water.wa.gov.au). Thus, the seasonal changes in water quality presented in this study may very well under-represent most other years when rates of precipitation during the wet season are much higher.

A substantial body of evidence has accumulated over the last 20 years indicating that the majority of chl $a$ present in the tropical ocean water surrounding reefs (usually ~80%) is contained within picophytoplankton defined by cell sizes <2 $\mu$m (Charpy 2005). Studies of some coral reefs have shown that picophytoplankton can also be the largest contributor to the particulate carbon (Yahel et al. 1998; Patten et al. 2011) and nitrogen (Ribes et al. 2003) grazed by reef organisms. In our study, smaller phytoplankton (<5 $\mu$m) comprised only ~45% of total chl $a$ in the vicinity of Tallon reef (Figure 3.5a,b), which is similar to what has been found in shallow macrotidal waters such as the northern GBR and Torres Strait (Furnas and Carpenter 2016) and inshore Kimberley waters (Thompson and Bonham 2011; Jones et al. 2014). Previous work has
suggested that the prevalence of larger suspended particles containing chl $\alpha$ in the coastal Kimberley is due to particle flocculation (Jones et al. 2014), which is enhanced in the presence of suspended silt/clays (Deng et al. 2015) and strong vertical mixing (Wolanski and Spagnol 2003). Depletion of both large and small chl $\alpha$ pools on Tallon reef coincided with significantly elevated ratios of phaeo:chl (Figure 3.5c,d), which suggests that this depletion was at least partly due to grazing (Welschmeyer and Lorenzen 1985). Therefore, large particles (nanoplankton or flocculated material) could be an important component of nutrients grazed by reefs in shallow macrotidal waters. Further work incorporating flow cytometry and microscopy would help elucidate the nature of suspended particles in the coastal Kimberley. Only a handful of published studies have occurred in this region, and a great deal of further field research is required to determine representative values and scales of variability of water quality parameters.

3.5.2. Size-dependent deposition and resuspension of POM

Given the nature of our bulk measurements of chl $\alpha$ and flow, it was not possible to discriminate between grazing by benthic organisms and net deposition in this study. However, we can estimate the likelihood of suspended particle deposition using the Rouse number ($P$), the ratio of a particle’s settling velocity $w_s$ to the shear velocity $u^*$ as (Eisma 2012) $P = w_s/(\kappa u^*)$ where $\kappa$ is the von Karman constant (0.40) and $u^*$ is estimated from depth-averaged velocity at SG (Gruber et al. 2017); when $P \ll 1$, deposition does not occur and particle concentration is uniform with depth. Previous work has shown that POC/PON particles (and large phytoplankton) in King Sound (our ‘offshore’ waters) were mostly in the 10 – 64 $\mu$m size range as (Wolanski and Gibbs 1995; Wolanski and Spagnol 2003). For particles in this size range, $w_s$ would be $\sim$0.002 cm s$^{-1}$ (Burns and Rosa 1980), and thus negligible settling would occur ($P \ll 1$) over
the entire tidal cycle. Very large POC/PON (> 500 µm) with a much greater $w_s \sim 0.3$ cm s$^{-1}$ (Jähmlich et al. 2002) would have a low Rouse number (< 0.7) during peak flood and ebb (0 – 1.5 and 4 – 6 h after reef flooding, respectively). However, $P$ would exceed 1 once depth-averaged flow speeds slowed to ~0.10 m s$^{-1}$, which occurred during high tide and the final 6 h of ebb (Figure 3.2). Therefore, settlement of large particles likely occurs during high tide (at least temporarily) and for several hours towards the end of ebb tide after the majority of off-reef discharge has already occurred (Figure 3.9). This POC/PON pool, while not grazed in suspension, would nonetheless be available for grazing by abundant benthic detritivores (such as sea cucumbers and some polychaetes) observed on Tallon (e.g., Uthicke 1999).

With flow speeds generally high (0.3 – 0.4 m s$^{-1}$) during peak flood and ebb periods (Figure 3.2b) and exceeding 0.8 m s$^{-1}$ during spring tides, resuspension clearly plays a role in benthic fluxes of large particles on Tallon reef. In a sense, each tidal cycle serves to ‘flush’ these larger particulates from the reef platform, as flood tide resuspends large particles that have settled during the final ~6 h of ebb tide and ‘new’ particulate material such as detritus generated in benthic communities during this period. This can be seen in particulate nutrient and chl $a$ concentrations during high tide and peak ebb in excess of offshore means (Figure 3.6, Figure 3.11) as well as negative benthic fluxes of chl $a$ during peak ebb (Figure 3.8). Resuspension during peak ebb coincides with high levels of off-reef discharge (Figure 3.9), so it seems likely that the majority of resuspended particles are exported off-reef each tidal cycle.
3.5.3. Benthic fluxes of chl a and phytoplankton-derived nutrients

Net benthic fluxes of chl a for Tallon reef were on the lower end (but within the range) of previous estimates of chl a uptake by reef communities (Table 3.3). Low grazing estimates ($\leq 4 \text{ mg chl a m}^{-2} \text{ d}^{-1}$) have been found for a few reef communities; but most previous estimates are an order of magnitude larger than Tallon (Table 3.3). However, unlike previous studies, we cannot isolate benthic grazing on Tallon from resuspension of large particles containing chl a, which partially ‘masks’ grazing and results in observed low net uptake over a tidal cycle. Our measurements showed variability between tidal cycles, with a possible ~fortnightly periodicity (Figure 3.10). Previous work on Tallon has shown that daily temperature variability (Lowe et al. 2016) and net community production (Gruber et al. 2017) can vary over a ~15 day period driven by the differences in the phasing of the solar and semi-diurnal tidal cycle periods. In the case of chl a uptake, the mechanism is more likely to be related to the volume of offshore water flooding the reef platform and flow speeds during peak ebb; these are a function of the spring-neap tidal cycle, which also occurs at a similar fortnightly period but is not related to the solar-tidal cycle offset described above. Our results thus emphasize that short term experiments lasting a few days may greatly over- or under-estimate fluxes of particles on tide-dominated reefs. Future research in these systems should occur on scales that capture the variability in hydrodynamic processes related to the ecological or biogeochemical rates of interest.

Estimates of fluxes of carbon (POC$_p$, 4.0 mmol C m$^{-2}$ d$^{-1}$) and nitrogen (PON$_p$, 0.95 mmol N m$^{-2}$ d$^{-1}$) from benthic chl a uptake were lower than most previous work, and were in some cases two orders of magnitude lower (Table 3.3). Our study may have underestimated nitrogen fluxes as we only considered particles with chl a, thus
neglecting the heterotrophic bacterial community, which can be abundant in coral reef waters (Ribes et al. 2003; Houlbrèque et al. 2006) and contributes disproportionately to fluxes of PON due to low C:N ratios (Patten et al. 2011). Few studies have compared the magnitude of in situ benthic fluxes of phytoplankton-derived POC and PON to reef community productivity. Studies at the organism-scale show large variability in the influence of heterotrophy on nutrient budgets (Houlbrèque and Ferrier-Pagès 2009), with some estimating that grazing can supply ~50% and ~30% of carbon and nitrogen requirements for coral growth (Anthony 1999), while others find that coral uptake of POC\textsubscript{p} is a small fraction (< 7%) of its gross primary production (Houlbrèque et al. 2004). Sponges, which are highly efficient filter-feeders (Reiswig 1971), can supply the majority of carbon for their respiratory demands with grazed POC (Hadas et al. 2009). Other in situ studies similarly conducted over reef scales have found grazed POC\textsubscript{p} to be on the order of reef net primary production (Ayukai 1995; Wyatt et al. 2010) or a small fraction (~1%) of reef gross primary production (Ribes et al. 2005).

Assuming a photosynthetic quotient of 1 (Kinsey 1985), gross and net production for Tallon reef platform (mean of seagrass and macroalgal communities) was ~500 and ~30 mmol C m\textsuperscript{-2} d\textsuperscript{-1}, respectively, during the Apr experiment (Gruber et al. 2017). Thus, benthic fluxes of POC\textsubscript{p} (Table 3.3) were <1% of gross production, but were also much lower (<15%) than rates of net production, unlike many previous studies. Primary producers on the reef had relatively high tissue N and P concentrations, with mean C:N:P values of 251:16:1 found in \textit{T. hemprichii} leaves (N. Cayabyab, unpubl.), which is well below typical values of 550:30:1 found in seagrasses and marine macroalgae (Atkinson and Smith 1983). Using tissue stoichiometry and rates of net production, nitrogen demand by primary producers could be roughly
estimated as 1.9 mmol N m$^{-2}$ d$^{-1}$; thus, reef PON$_p$ fluxes (Table 3.3) represent roughly half of the nitrogen demand.

### 3.5.4. Benthic fluxes and reef zonation

The mass balance and one-dimensional control volume approaches used on Tallon reef platform do not distinguish between benthic fluxes occurring in seagrass and macroalgal communities. Previous work has shown that grazing rates can vary by two-fold from forereef to back reef communities (Wyatt et al. 2010; Patten et al. 2011), which may be related to differences in grazer assemblages or densities (Ribes et al. 2005). Grazer densities on Tallon were observed to be higher in MA and Mix compared to SG (though this was not quantified), and there are multiple lines of evidence to suggest that particle uptake may be concentrated in macroalgal and mixed zones. Chlorophyll $a$ concentrations toward the end of ebb tide (final ~6 h) tended to be greater at SG than MA/Mix, with much lower ratios of phaeo:chl (Figure 3.4). Time-series of chl $a$ showed that this elevation only occurred during the day (Figure 3.7b); given that ebb tide duration was sufficiently long for measurable phytoplankton growth to occur (Furnas et al. 1990), these higher chl $a$ values may represent phytoplankton growth in the absence of strong grazing. Additionally, estimates of benthic chl $a$ uptake from drifter releases in the macroalgal zone were closely matched to the mean of control volume estimates (Figure 3.8), whereas drifter releases in the seagrass zone showed no net flux. Macroalgal and mixed zones occupy ~50% of Tallon reef platform; if chl $a$ uptake occurred only in those zones, our estimates would roughly double, but would still be on the lower end of previous estimates (Table 3.3).
3.5.5. Net export of particulate nutrients

Unlike phytoplankton, rates of particulate nutrient uptake or release by reef communities are generally difficult to determine in situ, as concentrations of POC and PON do not typically change across the reef relative to natural variability among samples (Crossland and Barnes 1983; Houlbrèque et al. 2006); this does not necessarily indicate a lack of uptake, but rather a change in the composition of POM as water traverses the reef (Wyatt et al. 2013). To our knowledge, only one example of a reef acting as a net sink to POC (208 mmol C m$^{-2}$ d$^{-1}$) and PON has been reported, which occurred in a soft coral community under elevated particulate loads (Fabricius and Dommasse 2000). A few sediment trap studies have estimated net export of POC from reefs, and generally found rates to be 4 – 7% of reef GPP (Delesalle et al. 1998; Hata et al. 1998; Hata et al. 2002); however, these studies quantified POC deposited offshore, and did not account for particulates in suspension.

In the case of Tallon reef, a water balance combined with measurable temporal changes in POC and PON concentrations allowed us to estimate the net export of particulate organic matter over a tidal cycle (Table 3.4). Net export (the difference between oceanic inputs and off-reef exports) of POC was 13.6 mmol C m$^{-2}$ d$^{-1}$, or just ~3% of mean reef gross primary production, while export of PON was 0.2 mmol N m$^{-2}$ d$^{-1}$. These values likely underestimate total particulate export, as they only consider particles up to ~3 mm in diameter (as determined by the diameter of water sampling tubing) and thus neglect large and rare particles, which may comprise up to two-thirds of reef POC export (Alldredge et al. 2013). Our results suggest that Tallon reef platform was both a net sink for oceanic phytoplankton and a net source of mostly detrital POC and PON to coastal waters, similar to results from a few previous field
studies (Prins et al. 1996; Cuet et al. 2011a; Wyatt et al. 2013). A ‘detrital release’ term was invoked to represent the rate of (non-chl a-associated) POC and PON export (17.6 mmol C and 1.15 N mmol m\(^{-2}\) d\(^{-1}\), respectively) needed to balance POC\(_p\) and PON\(_p\) uptake (Table 3.4). These detrital terms are similar to what has been found for other seagrass and reef communities (25 and 8.3 mmol C m\(^{-2}\) d\(^{-1}\), respectively), and may constitute a source of organic material for pelagic consumption just offshore of the reef (Cuet et al. 2011a; Säwström et al. 2016).

In conclusion, although Tallon reef seems to experience water quality conditions similar to inshore tropical reefs subject to nutrient loading, it does not display the reef-scale net heterotrophy that has been suggested for such reefs (Fabricius 2005). Instead, uptake rates of oceanic phytoplankton on the reef were very low and the platform acted as a net source of particulate organic carbon and nitrogen to the coastal ocean. This may be related to periods of high light availability when water depth is low, as well as offshore dissolved inorganic nutrient concentrations on the high side of reef habitats worldwide (Atkinson and Falter 2003), that enable moderate rates of reef-scale net production (Gruber et al. 2017). Deeper reefs of the coastal Kimberley (and other tide-dominated reefs with elevated POM loads) may display low rates of primary production due to reduced light availability, and thus depend more on grazing to meet the energetic needs of the reef community. Of course, fluxes of particulate nutrients to and from other tide-dominated reefs may differ with bathymetry, oceanic nutrient inputs, tidal range, and a whole suite of other factors. Thus, there is considerable room for future research to examine how the prevailing physics of water transport, mixing, and heating more generally control biogeochemical and ecological processes in tide-dominated reef communities.
4. DISSOLVED NUTRIENT FLUXES OVER A TIDE-DOMINATED TROPICAL FRINGING REEF

4.1. Abstract

Benthic fluxes of dissolved nutrients on reef communities are controlled by oceanographic forcing including hydrodynamic regime and seasonal changes to nutrient concentrations. Nutrient dynamics have mainly been studied on reefs with wave-driven circulation, yet up to a third of reefs worldwide can be characterised as tide-dominated. Fluxes of dissolved nitrogen and phosphorus were measured on a strongly tide-dominated (spring range >8 m) reef platform located in the Kimberley region of northwestern Australia. A one-dimensional control volume approach was used, which combines continuous measurements of flow with modified Eulerian sampling of waters traversing the reef. Measured fluxes were compared to theoretical mass-transfer-limited uptake derived from flow speeds. Reef communities released a moderate amount of dissolved inorganic nitrate, possibly derived from the remineralization of phytoplankton and dissolved organic nitrogen. Rapid changes in flow speed and water depth characteristic of this reef caused large variations in mass-transfer-limited nutrient uptake rates up to an order of magnitude on time scales of ~minutes – hours. Upstream nitrate release and higher flow speeds enhanced potential dissolved inorganic nitrogen uptake in downstream reef zones. Reef primary producers displayed indications of nitrogen-

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3 This chapter is an adapted version of: Gruber, R.K., R.J. Lowe, and J.L. Falter. (prepared for submission to Coral Reefs). Dissolved nutrient fluxes over a tide-dominated tropical fringing reef.
limitation during the dry season, which may be somewhat relieved by seasonal increases in offshore dissolved inorganic nitrogen during the wet season.
4.2. Introduction

Reef organisms remove nutrients from overlying waters for essential metabolic and biogeochemical processes, which enables them to accumulate biomass and ultimately support broader marine food webs (Parrish 1989; McMahon et al. 2016). Reef waters have carbon concentrations that are orders of magnitude greater than nitrogen (N) and phosphorus (P), and thus benthic community productivity is generally limited by the rates at which organisms can acquire N and P (Smith 1984; Larned 1998; Atkinson and Falter 2003). Suspended N and P can be categorized into dissolved inorganic (DIN, DIP), dissolved organic (DON, DOP), and particulate organic (PON, PP) fractions, which are generally utilized by different groups of organisms. Primary producers take up labile (readily reduced and incorporated into new tissue) dissolved inorganic nutrients in the forms of nitrate/nitrite (NO$_3^-$), ammonium (NH$_4^+$), and phosphate (DIP), which are consequently found at low concentrations in reef waters. Ocean-derived dissolved organic N and P compounds are generally thought to be refractory or energetically-intensive for organisms to utilise (Knapp et al. 2005); thus, DON tends to dominate the nitrogen pool in reef waters, although DOP concentrations are generally low and similar to DIP (Furnas et al. 2011). However, studies on DON uptake have provided mixed results: some have measured a net production of DON by reef communities (Cuet et al. 2011a; Tanaka et al. 2011), while others have found evidence that primary producers (Vonk et al. 2008) and filter-feeders (Rix et al. 2017) can directly utilize some DON compounds. Finally, particulate N and P pools in reef waters are generally dominated by small phytoplankton and bacterial cells, and are a major nutrient source for reef suspension and filter-feeders (Ribes et al. 2005; Houlbrèque et al. 2006; Wyatt et al. 2010).
The majority of studies on reef nutrient dynamics have focused on the labile dissolved inorganic species as these are tightly coupled to reef productivity (D'Elia and Wiebe 1990; Szmant 2002). Research over the last two decades has shown that the upper limit of DIN and DIP uptake on reefs is physically constrained by mass-transfer, a term that refers to the transfer of solutes in the water column across diffusive boundary layers surrounding the tissue surface of an organism (Bilger and Atkinson 1992; Hurd 2000). Nutrient uptake in reef waters is typically mass-transfer limited (i.e. the biological demand for nutrients is higher than the physical rate at which they can be supplied). Therefore, the uptake rate has a first-order relationship with nutrient concentration and is a function of water velocity, bottom roughness properties, and diffusion characteristics of the solute (Atkinson 2011). Due to dependency of mass-transfer-limited nutrient uptake on flow speed, the local hydrodynamic conditions within a reef directly affect uptake rates of DIN and DIP (Atkinson and Bilger 1992; Thomas and Atkinson 1997; Baird et al. 2004; Reidenbach et al. 2006; Falter et al. 2016), and these uptake rates can now be predicted for a particular reef and given sufficient information (Falter et al. 2004; Zhang et al. 2011). However, validating these models with observations from living systems remains a major challenge as measurements must occur at spatial and temporal scales relevant to reef circulation, and in situ uptake is often confounded by simultaneously-occurring biogeochemical processes that release DIN and DIP to the water column (Atkinson and Falter 2003; Wyatt et al. 2012).

Accurate measurements of nutrient uptake in natural reef communities are still relatively limited, and are just beginning to incorporate spatial and temporal variability in forcing conditions (Lowe and Falter 2015), such as gradients in wave energy across a
reef or seasonal changes in local oceanic nutrient concentrations (e.g., Wyatt et al. 2012). While many studies have assessed nutrient dynamics in reefs experiencing long-term nutrient enrichment [e.g., due to anthropogenic changes to river discharge (Furnas 2003) or submarine groundwater inputs (Paytan et al. 2006; Cuet et al. 2011a; Tait et al. 2014)], relatively little work has focused on systems experiencing natural pulses in nutrient delivery from processes such as coastal upwelling (Andrews and Gentien 1982; Wyatt et al. 2012; Stuhldreier et al. 2015) or internal waves (Leichter et al. 2003; Wang et al. 2007). Additionally, the majority of reef research to date has occurred on reefs whose circulation patterns and residence times are mainly driven by wave-breaking on the forereef (Monismith 2007). However, the circulation of up to a third of reefs worldwide has been estimated to be tide-dominated, defined as the case where the offshore mean tidal range exceeds the annual mean significant wave height (Lowe and Falter 2015). Reefs that are strongly tide-dominated can experience substantial variability in flow speeds and water depths over a tidal cycle (Lowe et al. 2015), which implies that mass-transfer-limited nutrient uptake rates would also vary substantially in response to this tidal forcing.

The Kimberley coastal region is a remote and near-pristine portion of northwestern Australia with a macrotidal regime where spring tidal ranges can reach 12 m in some locations (Kowalik 2004). The region contains thousands of islands with a total reef area of ~2000 km² (Kordi and O’Leary 2016) inhabited by diverse communities of corals (Richards et al. 2015), macroalgae (Wells et al. 1995), and seagrasses (Pedersen et al. 2016). Recent studies have documented the strongly tide-dominated circulation that can occur on Kimberley intertidal reef platforms (Lowe et al. 2015). When the tidal amplitude (half the tidal range) is greater than the reef elevation
relative to mean sea level, water levels drop below the reef for portions of each tidal
cycle, and this “truncation” of the semi-diurnal tide results in asymmetric phase
durations (~10 hour ebb and ~2 hour flood) and flow speeds (Lowe et al. 2015).
Extended periods of low water depth on reef platforms such as Tallon Island (located in
the west Kimberley) can cause communities to experience high irradiances that result in
diel temperature changes up to 11° C (Lowe et al. 2016) and dissolved oxygen
fluctuations among the most extreme measured worldwide (Gruber et al. 2017). Recent
work has documented rates of coral calcification (Dandan et al. 2015), thresholds of
coral thermal tolerance (Schoepf et al. 2015), seagrass productivity (Pedersen et al.
2016), reef community production (Gruber et al. 2017), and reef particulate nutrient
uptake (Gruber et al. (in review)) in tide-dominated systems, yet nothing is currently
known about how these strong tides control uptake of dissolved nutrients. The
objectives of this study were to: 1) measure benthic fluxes of dissolved N and P on a
tide-dominated reef, 2) compare measured rates to maximum potential uptake predicted
by mass-transfer theory, and 3) determine the influence of tidal forcing (velocity and
water depth changes) and oceanic forcing (seasonal changes in nutrient concentration)
on mass-transfer-limited uptake rates. This work will provide some preliminary insight
into the magnitudes, variability, and temporal scales of nutrient cycling on tide-
dominated reefs.
4.3. Methods

4.3.1. Field site

A series of field experiments were conducted in the western Kimberley region of the Buccaneer Archipelago at Tallon Island, which contains a large intertidal reef platform (surface area 2.2 x 10^6 m^2) on its eastern side (Figure 4.1). The platform is elevated just slightly above mean sea level [+0.25 m Australian Height Datum (AHD)]; its seaward edge consists of a slightly shallower (+0.35 m AHD) crest, which, coupled with bottom friction prevents reef benthic communities from becoming emersed during low tide. The platform is covered with a series of regular shore-parallel ridges ~0.15 - 0.25 m in height and contains two benthic communities: a seagrass-dominated inner zone (from the fringing mangrove shoreline to 400 m landward of the reef crest), and a macroalgae-dominated outer zone (200 m wide extending shoreward from the crest). These are separated by a zone ~200 m wide where the two community types become mixed on sand and coral rubble (Figure 4.1). The seagrass community contains *Enhalus acoroides* and *Thalassia hemprichii* (Wells et al. 1995), and the macroalgal zone is dominated by the brown macroalgae *Sargassum* spp. and contains a diverse assemblage of foliose brown macroalgae, red corallines, crustose coralline algae, and small corals (~5-10% cover).

Two field experiments were conducted at Tallon reef with each lasting two weeks: 5 – 20 October 2013 (dry season) and 4 – 9 February 2014 (wet season). Duplicate water samples were filtered to determine nutrient concentrations during both field experiments (Table 4.1) according to the protocols below. Hydrodynamic instrumentation placed among water sampling stations allowed us to measure benthic
fluxes of dissolved nutrients on the reef platform using a one-dimensional control volume approach as detailed below (see also Gruber et al. 2017); these fluxes represent the net uptake or net release of nutrients.

Figure 4.1. Deployment locations of hydrodynamic instrumentation and water sampling locations on Tallon reef platform and offshore. Inset shows Tallon Island location in the west Kimberley region of Australia. ADV refers to acoustic Doppler velocimeters and ADPHR refers to acoustic Doppler profiler.

Fluxes of particulate nutrients were the subject of previous work on this reef (Gruber et al. (in review)), but were also measured in this study to assess potential relationships with dissolved fluxes and to give dissolved fluxes a greater reef nutrient budget context. To estimate the gross uptake of DIN and DIP at the limits of mass-
transfer, we used hydrodynamic data from a full spring-neap (~15 day) cycle collected during the detailed hydrodynamic study reported in Lowe et al. (2015) and nutrient concentrations from water sampling during the Oct and Feb field experiments. Tidal phase-averaging is used in this manuscript to present patterns in hydrodynamic and other continuous data related to the phase of tide. Phase-averages are ensemble averages of a given variable at each point in the semidiurnal (M2) tidal cycle (e.g., mean of all values measured at high tide).

4.3.2. Water sampling

Extensive water sampling was conducted during both field experiments to determine the concentrations of dissolved nutrients offshore and on the reef platform. Sampling occurred at three fixed (Eulerian) stations (Figure 4.1): the deep channel adjacent to the reef (‘Off’), and on the reef platform in the macroalgal-dominated zone (‘MA’), and the seagrass-dominated zone (‘SG’). Offshore samples were collected from just beneath the water surface at roughly one hour intervals on the days when

<table>
<thead>
<tr>
<th>Dates</th>
<th>Season</th>
<th>Site</th>
<th>DIN/DIP</th>
<th>DON</th>
<th>PON/PP</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 - 20 Oct 2013</td>
<td>Dry</td>
<td>Off</td>
<td>26</td>
<td>26</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MA</td>
<td>36</td>
<td>36</td>
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<tr>
<td></td>
<td></td>
<td>SG</td>
<td>33</td>
<td>32</td>
<td>--</td>
</tr>
<tr>
<td>4 - 9 Feb 2014</td>
<td>Wet</td>
<td>Off</td>
<td>15</td>
<td>15</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MA</td>
<td>14</td>
<td>14</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SG</td>
<td>13</td>
<td>13</td>
<td>10</td>
</tr>
</tbody>
</table>
water sampling occurred (Table 4.1). Samples from the reef platform were collected on foot during the middle to end of ebb tide (6 – 12 hours after reef flooding) when water depths were low (~0.4 – 0.6 m) and by boat when water levels were higher (1 – 4 hours after reef flooding). Sampling by boat or on foot was not possible during peak flood and ebb periods (0 – 1 and 4 – 6 hours after reef flooding, respectively) due to hazardous conditions on the reef platform, when current speeds could reach 0.8 m s\(^{-1}\) (Figure 4.2).

Water samples were collected for analysis of dissolved nutrients with a 50 mL syringe (pre-rinsed with reef water) and immediately syringe-filtered (Minisart, pore size 0.45 µm) into 30 mL tubes. These samples were placed in darkness on ice until return to the field station (several hours) where they were frozen until analysis at the laboratory. Water samples for analysis of particulate organic nitrogen and particulate phosphorus were filtered onto 25mm GF/Fs that had been pre-combusted (4 hours at 550°C). The volume filtered varied between 0.5 – 2 L, or when sufficient material was collected on each filter. Filters were then rinsed with a small amount (5-10 mL) of ultrapure water, dried under gentle vacuum, placed in pre-combusted aluminium foil packets, and stored frozen until analysis.

All laboratory analyses were conducted within a few weeks of returning from the field. Analyses of nitrate and nitrite (NO\(_x\)), ammonium (NH\(_{4}^+\)), and inorganic phosphorus (DIP) concentrations were determined on a flow-injection autoanalyzer (Lachat QuikChem 2500) using standard methods (Strickland and Parsons 1972). Total dissolved nitrogen was determined by persulfate oxidation of filtered samples (Valderrama 1981) followed by analysis of nitrate as above. Dissolved organic nitrogen (DON) was inferred from the total dissolved nitrogen less NO\(_x\) and NH\(_{4}^+\). Analysis of
particulate organic nitrogen collected on filters was conducted using a Shimadzu TOC-V carbon analyzer fitted with solid sample combustion (SSM-5000A) and total nitrogen units. A hot acid digestion in 5% persulfate was performed on filters for particulate phosphorus analysis (Menzel and Corwin 1965), and the resulting concentration of liberated phosphate was determined spectrophotometrically (Parsons et al. 1984) with a Shimadzu UV-1601. All nutrient concentrations presented are the mean of duplicate samples.

4.3.3. Control volume approach

A one-dimensional control volume (CoVo) approach was used to estimate the net benthic flux of nutrients. This method utilizes flow information and modified Eulerian sampling of nutrient concentrations at upstream and downstream points. Tallon reef platform is well-suited to the CoVo approach due to long periods (~10 h each tidal cycle) of consistent flow direction, and we have already used a similar approach to estimate the net community productivity (Gruber et al. 2017) and particle uptake (Gruber et al. (in review)) on this reef. Current velocity vectors and water depth \( h \) were recorded at 1 Hz by a bottom-mounted acoustic Doppler current profiler (Nortek Aquadopp HR) with 0.03 m bin size, located near SG (Figure 4.1). Towards the end of ebb tide, the water depth reached a minimum on the reef platform \( h \approx 0.4 \) m, and in the rare instances (5% of the total field study) where water depth encroached on instrument blanking distance, the flow speed was estimated from drogue releases. Depth-averaged flow speeds \( u \) were bin-averaged at 5 min intervals.
During the extended 10 hour ebb tide period on the reef, water drained off the northern portion of the reef platform in a consistent northeasterly direction (80° ± 30°, mean ± standard deviation), aligned with the water sampling transect. Depth-averaged current velocity was rotated into the along-transect direction \((u_x)\) and used to estimate transport \(q_x\) as

\[
q_x = u_x h,
\]

\(1\)
assuming horizontal dispersion was negligible. The net benthic flux $J_{\text{net}}$ (in mmol N or P m$^{-2}$ d$^{-1}$) of each nutrient species (NO$_x$, NH$_4^+$, DIP, DON, PON, and PP) was estimated as (Genin et al. 2002)

$$-J_{\text{net}} = \bar{h} \frac{d\bar{C}}{dt} + q_x \frac{(C_{\text{MA}} - C_{\text{SG}})}{dx},$$

(2)

where $C_{\text{MA}}$ and $C_{\text{SG}}$ are the nutrient concentrations at MA and SG, respectively, and $\bar{C}$ is the mean of both locations. The transect length $dx$ was 540 m and $\bar{h}$ represents mean water depth along the transect. Note that a sign convention is assumed where positive $J_{\text{net}}$ indicates net nutrient uptake by the benthos while negative values indicate net release to the water column. The first term on the right side of Eq. (2) represents the mean local nutrient flux (i.e., uptake or release in the vicinity of sampling stations), while the second term refers to the uptake or release during advection between stations. The local term was estimated when water sampling occurred (~hourly). The advective term was averaged over a longer time interval (based on the transit time between SG and MA), and estimates were then linearly interpolated to times when local estimates occurred; this method is described in greater detail in Gruber et al. (2017).

4.3.4. Uptake rates at the limits of mass-transfer

For comparison with the field observations, we also calculated the theoretical uptake rates of DIN and DIP at the limits of mass-transfer ($J_{\text{MTL}}$) for each of the measurements of $J_{\text{net}}$ above. Assuming nutrient concentrations at the surface of benthic organisms were near zero, $J_{\text{MTL}}$ was estimated along the study transect (from SG to MA) as (Falter et al. 2004)
\[ J_{\text{MTL}} = S \bar{C}, \]  

where \( S \) is the mass-transfer velocity (in \( \text{m d}^{-1} \)). Estimates of \( J_{\text{MTL}} \) and \( S \) were made for NO\(_x\), NH\(_4^+\), and DIP, and were averaged over the same time intervals as \( J_{\text{net}} \). Mass-transfer velocity \( S \) was estimated as (Falter et al. 2004)

\[ S = u C_D^{0.5} / (R_{ek}^{0.2} S_c^{0.6}), \]  

where \( C_D \) is the drag coefficient, \( R_{ek} \) is the roughness Reynolds number, and \( S_c \) is the Schmidt number. The Schmidt number is defined as the kinematic viscosity \( v \) divided by the diffusivity of the nutrient species (Li and Gregory 1974). The drag coefficient \( C_D \) increases dramatically as reef water depth decreases (Lentz et al. 2017), and so was estimated from empirical relationships using \( h \) and maximum reef height (McDonald et al. 2006), following the same approach as used in estimates of reef metabolism (Gruber et al. 2017). The roughness Reynolds number \( R_{ek} \) is defined as

\[ R_{ek} = u_* k_s / v, \]  

where \( k_s \) is a hydraulic roughness length scale, assumed to be 0.5 m for the reef platform (Lowe et al. 2015) and the shear velocity \( u_* \) is a function of bottom shear stress \( \tau_b \) and seawater density \( \rho \) as

\[ u_* \equiv \sqrt{\tau_b / \rho} = u \sqrt{C_D / 2}. \]  

Estimates of maximum potential nutrient release (\( J_{\text{release}} \)) represents the flux of NO\(_x\), NH\(_4^+\), and DIP necessary to match the observed \( J_{\text{net}} \) assuming uptake occurred at mass-transfer-limited rates, and were estimated as (Wyatt et al. 2012)
\[
J_{\text{release}} = J_{\text{net}} - J_{\text{MTL}}.
\] (7)

for each of the intervals over which \(J_{\text{net}}\) was calculated.

Large changes in water depth, flow speed, and nutrient concentration occurred during each tidal cycle and over the ~fortnightly spring-neap cycle, and measurements of \(J_{\text{net}}\) occurred during ebb tide (generally 6 – 12 hours after reef flooding). In order to understand how the range of flow speeds experienced by this reef platform could influence nutrient uptake rates, we calculated \(J_{\text{MTL}}\) continuously over a full ~15 day spring-neap cycle at SG and MA. Current speed was not measured at MA during the Oct 2013 field experiment, so measurements from a detailed hydrodynamic study (which included instruments positioned at SG and MA) during Apr 2014 were used (Lowe et al. 2015). Flows on the reef platform are completely tide-driven, and can be predicted based on information on water depth and tidal phase; given that spring and neap tidal ranges were very similar between Oct and Apr experiments, velocity measurements from Apr can be considered representative of velocities in Oct. Tidal phase-averaged concentrations of NO\(_x\), NH\(_4^+\), and DIP were approximated for both sites (MA and SG) and field experiments (Oct and Feb) with second-order polynomial curve-fitting (Figure 4.3) where the value of the y-intercept was the nutrient concentration in offshore waters (Table 4.2). These curves were used to estimate \(\bar{C}\) at each point in the tidal cycle, as it was not possible to continuously collect water samples due to hazardous conditions during peak ebb and flood. Tidal cycle averages of mass-transfer velocities (\(S_{\text{cyc}}\)) and mass-transfer-limited nutrient flux (\(J_{\text{cyc}}\)) were calculated as the mean of all \(S\) and \(J_{\text{MTL}}\), respectively, occurring within a tidal cycle beginning when water flooded the reef platform.
Uncertainties in estimates of $J_{\text{net}}$ and $J_{\text{MTL}}$ were estimated by propagating standard deviations via Monte Carlo simulation ($n = 10,000$). Input error terms were drawn from bin-averaged data (Lehrter and Cebrian 2010).
4.4. Results

4.4.1. Nutrient concentrations and measured fluxes

Characteristics of offshore water (temperature, salinity and nutrient concentrations) showed some differences between dry and wet season field experiments. Water temperature was ~3° C greater during the wet season in Feb, and levels of DIN were elevated, with NO₃ concentrations approximately double those measured during the dry season in Oct (Table 4.2). Salinity and concentrations of DIP and DON were slightly lower during the wet season in Feb. Nutrient concentrations on the reef platform were similar to offshore concentrations during flood tide and the beginning of ebb tide (~3 – 6 hours after reef flooding, Figure 4.3); however, during the remainder of ebb tide (~6 – 12 hours after reef flooding) the concentrations of DIN changed dramatically depending on the reef zone (benthic community type). In the case of NO₃, concentrations decreased in the seagrass zone (SG) but increased at MA by up to five times compared to offshore levels (Figure 4.3a,b).

<table>
<thead>
<tr>
<th>Date</th>
<th>Tidal range (m)</th>
<th>Salinity</th>
<th>Temp (°C)</th>
<th>NO₃</th>
<th>NH₄⁺</th>
<th>DIP</th>
<th>DON</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oct 2013</td>
<td>6.7</td>
<td>34.7</td>
<td>27.8</td>
<td>0.40</td>
<td>0.37</td>
<td>0.18</td>
<td>12.7</td>
</tr>
<tr>
<td></td>
<td>(0.02)</td>
<td>(0.29)</td>
<td></td>
<td>(0.09)</td>
<td>(0.12)</td>
<td>(0.02)</td>
<td>(2.4)</td>
</tr>
<tr>
<td>Feb 2014</td>
<td>7.0</td>
<td>34.2</td>
<td>30.1</td>
<td>0.92</td>
<td>0.69</td>
<td>0.15</td>
<td>10.7</td>
</tr>
<tr>
<td></td>
<td>(0.06)</td>
<td>(0.06)</td>
<td></td>
<td>(0.19)</td>
<td>(0.23)</td>
<td>(0.03)</td>
<td>(2.5)</td>
</tr>
</tbody>
</table>

°Difference between max and min water levels offshore
Increases in $\text{NH}_4^+$ were seen at both SG and MA during ebb tide (Figure 4.3c,d), while DIP was generally lower than offshore concentrations but tended to increase at

Figure 4.4. Fluxes of a) nitrate ($\text{NO}_3^-$), b) ammonium ($\text{NH}_4^+$), and c) dissolved inorganic phosphorus (DIP) along the study transect during both field experiments shown with water depth on the reef flat ($h$). Net benthic fluxes ($J_{\text{net}}$, in blue) were estimated using the CoVo approach, while mass-transfer-limited uptake ($J_{\text{MTL}}$, in green) was calculated from reef platform flow and nutrient concentrations, and nutrient release ($J_{\text{release}}$, in red) was calculated from net and MTL fluxes.
MA during the final few hours of ebb tide (Figure 4.3e,f).

Fluxes of DIN and DIP estimated using the CoVo technique were generally negative, indicating a net efflux (release) of nutrients from the benthos to the water column. This was especially true for NO$_x$, where net nutrient release ($J_{net} < 0$) reached 5 mmol m$^{-2}$ d$^{-1}$ (Figure 4.4a), and net uptake ($J_{net} > 0$) was not observed during any point in either field experiment. Fluxes of NH$_4^+$ and DIP varied between net uptake and release (Figure 4.4b,c), and $J_{net}$ for DIP tended to transition from net uptake to net release over the course of ebb tide.

There were no substantial differences in mean $J_{net}$ of DIN or DIP between Oct

<table>
<thead>
<tr>
<th></th>
<th>Oct 2013</th>
<th>Feb 2014</th>
</tr>
</thead>
<tbody>
<tr>
<td>DIN</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$J_{net}$</td>
<td>-2.3 (0.3)</td>
<td>-2.9 (0.6)</td>
</tr>
<tr>
<td>$J_{MTL}$</td>
<td>7.8 (0.3)</td>
<td>7.6 (0.6)</td>
</tr>
<tr>
<td>$J_{release}$</td>
<td>-10.2 (0.5)</td>
<td>-10.6 (1.0)</td>
</tr>
<tr>
<td>DIP</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$J_{net}$</td>
<td>-0.03 (0.04)</td>
<td>-0.08 (0.06)</td>
</tr>
<tr>
<td>$J_{MTL}$</td>
<td>0.56 (0.02)</td>
<td>0.35 (0.04)</td>
</tr>
<tr>
<td>$J_{release}$</td>
<td>-0.59 (0.03)</td>
<td>-0.43 (0.08)</td>
</tr>
<tr>
<td>DON</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$J_{net}$</td>
<td>-1.6 (2.1)</td>
<td>3.4 (3.3)</td>
</tr>
<tr>
<td>PON</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$J_{net}$</td>
<td>--</td>
<td>0.5 (0.6)</td>
</tr>
<tr>
<td>PP</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$J_{net}$</td>
<td>--</td>
<td>0.02 (0.03)</td>
</tr>
</tbody>
</table>

Table 4.3. Mean (SE) net fluxes (in mmol m$^{-2}$ d$^{-1}$) of nutrients determined by the CoVo approach during the Oct and Feb field experiments. Nutrient species include dissolved inorganic nitrogen (DIN) and phosphorus (DIP); dissolved organic nitrogen (DON); particulate organic nitrogen (PON); and particulate phosphorus (PP). Net ($J_{net}$), mass-transfer-limited ($J_{MTL}$), and release ($J_{release}$) fluxes are from the final 6 hours of ebb tide.
and Feb field experiments (Table 4.3), as estimates differed by less than one standard error. Fluxes of DON did differ between seasons; \( J_{\text{net}} \) varied between net uptake and net release during Oct (Figure 4.5a) although mean \( J_{\text{net}} \) was negligible (Table 4.3). During Feb, \( J_{\text{net}} \) of DON transitioned from net uptake to net release over the ebb tide (Figure 4.5a), but showed a large uptake on average (Table 4.3). Fluxes of PON and PP were variable during Feb (Figure 4.5b,c), and mean \( J_{\text{net}} \) was negligible (Table 4.3).

### 4.4.2. Mass-transfer velocity and nutrient uptake

The mass-transfer velocity \( S \) is a function of flow speed and is indirectly related to water depth through the drag coefficient; the magnitude of \( S \) depends on the diffusivity of the nutrient species of interest (though the Schmidt number) yet is unrelated to nutrient concentration (Eq. 4). Although temperature influences \( S \) through viscosity, changes in temperature on the reef platform had a negligible effect on \( S \) compared to the physical forcing. The tidal phase-averages of \( S \) on the reef platform (Figure 4.6a,c,e) demonstrate the strong influence of flow speed and water depth on \( S \).

Mass-transfer velocities rose sharply during the peak flood and ebb periods (0 – 1.5 and 4 – 6 h after reef flooding, respectively). The maximum \( S \) each tidal cycle occurred at the beginning of flood tide, characterized by high flow speeds (~0.5 m s\(^{-1}\)) and minimum water depths (~0.4 m) on the reef platform (Figure 4.2); maximum values of \( S \) were 30% greater at MA compared to SG, which was a function of the greater flow speeds that occurred near the reef crest (Figure 4.2). Minimum \( S \) each tidal cycle (Figure 4.6a,c,e) occurred at high tide when flow speeds became negligible and reef water depths were comparatively large (~2.5 m).
Values of $S$ were relatively low (~5 m d$^{-1}$ for DIN and ~3 m d$^{-1}$ for DIP) later in ebb tide (8 – 12 hours after reef flooding) and were similar between SG and MA (Figure 4.6a,c,e). When $S$ was averaged over complete tidal cycles, the difference between SG and MA was negligible for all three nutrient species (Figure 4.7). Mass-transfer

**Figure 4.5.** Net benthic fluxes ($J_{net}$) of a) dissolved organic nitrogen (DON), b) particulate nitrogen (PN), and c) particulate phosphorus (PP) along the study transect during both field experiments shown with water depth on the reef flat ($h$). Fluxes were estimated using the CoVo approach.
velocities for NOx and NH4⁺ were of similar magnitude over the tidal cycle, while those for DIP were a constant ~50% lower (Figure 4.6, Figure 4.7); this was a function of the diffusivity of each of these solutes (Li and Gregory 1974).

The mass-transfer-limited nutrient fluxes $J_{MTL}$ were a function of both $S$ as well as the local nutrient concentrations (Eq. 3). $J_{MTL}$ showed variability over the tidal cycle associated with $S$, but also showed prominent differences between benthic communities and seasons. Elevated NOx concentrations at MA during Oct and Feb (Figure 4.3a,b) resulted in rising $J_{MTL}$ towards the end of ebb tide (6 – 12 h after reef flooding), while low NOx concentrations at SG resulted in low $J_{MTL}$, especially during ebb tide (Figure 4.6b). Whereas, similar concentrations of NH4⁺ (Figure 4.3c,d) and DIP (Figure 4.3e,f) between sites resulted in similar $J_{MTL}$ between MA and SG for both nutrient species (Figure 4.6d,f). The influence of seasonal changes in offshore nutrient concentrations could be seen, particularly for NOx, where elevated levels during Feb (Table 4.2) resulted in a doubling of $J_{MTL}$ during the first 6 hours of each tidal cycle, compared to Oct (Figure 4.6b). Seasonal differences in $J_{MTL}$ were also found for DIP, where elevated fluxes occurred during Oct (compared to Feb) due to higher DIP concentration in the dry season (Table 4.2, Figure 4.6f). These community and seasonal differences in $J_{MTL}$ were particularly obvious when averaged over full tidal cycles. Uptake of NOx showed the greatest differences between seasons and sites, while NH4⁺ was the most similar between seasons and sites (Figure 4.8).
Finally, the maximum potential release of DIN and DIP to the water column assuming uptake was mass-transfer-limited ($J_{\text{release}}$, Eq. 7), was calculated for every

Figure 4.6. Tidal phase-averaged mass-transfer velocity $S$ for a) nitrate ($\text{NO}_x$), c) ammonium ($\text{NH}_4^+$), and e) dissolved inorganic phosphorus (DIP) calculated in both macroalgal (MA) and seagrass (SG)-dominated zones over a full spring-neap cycle. These coefficients were used to estimate the mass-transfer-limited uptake rates $J_{\text{MTL}}$ of b) $\text{NO}_x$, d) $\text{NH}_4^+$, and f) DIP using phase-averaged nutrient concentrations from Oct and Feb field experiments (Figure 4.3). Phase-averages are the mean of all measurements occurring at the same point in the tidal cycle (i.e., mean of all $S$ at high tide).

Finally, the maximum potential release of DIN and DIP to the water column assuming uptake was mass-transfer-limited ($J_{\text{release}}$, Eq. 7), was calculated for every
instance of $J_{\text{net}}$ (Figure 4.4). In the case of NO$_x$, $J_{\text{release}}$ was roughly double $J_{\text{net}}$ (Figure 4.4a) due to the large NO$_x$ release measured on the reef platform. Whereas for NH$_4^+$ and DIP, $J_{\text{release}}$ was on the order of $J_{\text{MTL}}$ due to negligible values of $J_{\text{net}}$ (Figure 4.4b,c). At the scale of tidal cycles, overall rates of $J_{\text{MTL}}$ and $J_{\text{release}}$ for DIN did not show seasonal differences (Table 4.3). However, the mass-transfer-limited uptake and release of DIP were enhanced in Oct as compared to Feb (Table 4.3).

4.5. Discussion

4.5.1. Oceanic nutrient supply

The measurements of offshore nutrient concentrations presented in Table 4.2 are among the first published for the Kimberley region (Jones et al. 2014) and are the only (to our knowledge) published record that includes measurements during the wet season. Concentrations of dissolved nutrients (NO$_x$, NH$_4^+$, DIP, and DON) were at the upper end of typical values in coral reef waters worldwide, especially in the case of DON, which far exceeded the $<5 \mu$M common in reef waters (Atkinson and Falter 2003). Measurements from the coastal Kimberley (Table 4.2) also exceeded long-term mean values from inshore waters of the Great Barrier Reef (GBR) during both the wet and dry seasons (Furnas et al. 2005; Schaffelke et al. 2012). The Kimberley region shares similar rainfall patterns, tidal ranges, and low levels of catchment alteration with the northern wet tropics region of the GBR (at a similar latitude to the Kimberley), yet concentrations of DIN and DIP measured in this study were an order of magnitude greater than those from the wet tropics (Furnas et al. 2005; Schaffelke et al. 2012). These observations, coupled with elevated concentrations of chlorophyll $a$ and
particulate nutrients (Gruber et al. (in review)) relative to ‘typical’ oligotrophic reef waters, suggest that coastal Kimberley reefs may experience naturally mesotrophic conditions throughout the year.

Wet season terrestrial discharge events deliver sediment and nutrients to coastal waters of northern Australia (Devlin and Schaffelke 2009; Brodie et al. 2010; Schroeder et al. 2012). Offshore concentrations of NO\textsubscript{x} and NH\textsubscript{4}\textsuperscript{+} measured in our study ~doubled during the Feb field experiment compared to Oct, whereas DIP and DON were similar between seasons (Table 4.2). However, river discharge for the 2013-2014 wet season was below-average (monitoring data from Fitzroy River, Willare station, http://water.wa.gov.au), suggesting that the seasonal changes observed in dissolved nutrients may under represent those of an ‘average’ wet season. Ratios of offshore DIN:DIP were 4.3 and 10.7 in Oct and Feb, respectively (Table 4.2), with the value during Oct similar to the DIN:DIP ratio of ~3:1 previous found in coastal Kimberley
waters during the dry season (Jones et al. 2014). These values are below the Redfield ratio (16:1), suggesting that pelagic production may be N-limited. This is common for reef waters generally, although long-term averages of inshore GBR waters are generally <3:1 even during the wet season (Furnas et al. 2005; Schaffelke et al. 2012; McKinnon et al. 2013). This suggests that N-limitation may be less severe in the Kimberley than in GBR waters, particularly during the wet season.

4.5.2. Rates and sources of benthic release of DIN and DIP

Benthic nutrient fluxes measured using the control volume technique ($J_{net}$) showed net release of NO$_x$ on Tallon (Figure 4.4a), while NH$_4^+$ and DIP fluxes varied between uptake and release (Figure 4.4b,c) but overall were negligible during the ebb tide (Table 4.3). Previous studies of reef nutrient fluxes have generally shown uptake approaching the limits of mass-transfer for NH$_4^+$ (e.g., Atkinson et al. 1994; Larned and Atkinson 1997; Thomas and Atkinson 1997; Cornelisen and Thomas 2009), DIP (reviewed in Cuet et al. 2011b), and less frequently for NO$_x$ (e.g., Baird et al. 2004); for example, in controlled experimental conditions simulated in flumes. Yet net release of all three species (especially NO$_x$) occurs in situ as inferred from concentrations in many reefs that exceed those offshore (e.g., Hatcher and Frith 1985; Rasheed et al. 2002; Leichter et al. 2013) and release rates up to ~20 mmol NO$_x$ m$^{-2}$ d$^{-1}$, ~12 mmol NH$_4^+$ m$^{-2}$ d$^{-1}$, and ~2 mmol DIP m$^{-2}$ d$^{-1}$ have been measured in in situ studies (Miyajima et al. 2007a; Miyajima et al. 2007b; Silverman et al. 2012; Wyatt et al. 2012). We have not considered nitrogen inputs from other sources such as N$_2$ fixation (Cardini et al. 2014) or reef porewater advection during ebb tide (Santos et al. 2011), which may result in an overestimation of DIN release on Tallon. However, given that NO$_x$ concentrations generally approach detection limits in reef porewater (Sansone et al. 1990; Tribble et al. 117
1990) and N₂ fixation adds to the NH₄⁺ pool, it seems unlikely that either of these processes dominate the observed nutrient fluxes.

If we assume that the fluxes discussed above (\(J_{\text{net}}\)) simultaneously occur with uptake of DIN and DIP near the limits of mass-transfer, this gives a gross release
(\(J_{\text{release}}\)) of \(\sim 10\ \text{mmol N m}^{-2}\ \text{d}^{-1}\) and \(\sim 0.5\ \text{mmol P m}^{-2}\ \text{d}^{-1}\) (Table 4.3). Previous work has attributed inorganic nutrient release to remineralization of particulate material by benthic filter-feeders (Ribes et al. 2005; Wyatt et al. 2012) and detritivores (Silverman et al. 2012), which can graze PON on the order of DIN release rates, as well as nitrification by sponge communities (Southwell et al. 2008). In the case of Tallon reef, uptake of phytoplankton (0.95 mmol N and 0.20 mmol P m\(^{-2}\) d\(^{-1}\)) (Gruber et al. (in review)) is on the order of \(J_{\text{release}}\) in the case of P, but is much smaller than \(J_{\text{release}}\) of N. Additionally, fluxes of \(J_{\text{net}}\) or \(J_{\text{release}}\) on Tallon were not correlated with particulate nutrient uptake as some other studies have demonstrated (Wyatt et al. 2012). Large particles (such as fragments of macroalgae) would not have been collected by our water sampling due to the width of bottle mouths (diam. \(\sim 5\ \text{cm}\)), nor would particles with very rapid sinking speeds such as faecal pellets. Such large and rare particles can comprise the majority of particulate organic material on reefs (Alldredge et al. 2013), and remineralisation of similar material may be the source of the observed DIN release on Tallon. Finally, fluxes of DON on the order of \(J_{\text{net}}\) were measured on Tallon, with net uptake occurring during the Feb experiment (Figure 4.5a). The dynamics of DON in reef systems have been addressed in a few studies (e.g., Ziegler and Benner 1999; Haas and Wild 2010; Thibodeau et al. 2013), and there is some evidence that reef organisms including corals (Ferrier 1991), sponges (Rix et al. 2017), and seagrasses (Vonk et al. 2008) can directly utilise DON. In summary, gross release of DIP may be derived from remineralised P from phytoplankton uptake on Tallon reef, but released DIN is likely derived from other sources including remineralisation of large particles and DON.
4.5.3. Tidal and seasonal forcing of mass-transfer-limited fluxes

Few estimates of nutrient uptake rate $S$ exist for in situ reef communities; the majority of previous estimates come from controlled flume experiments and are in the range of 2 – 15 m d$^{-1}$ (reviewed in Atkinson and Falter 2003). Uptake rates are strongly dependent on flow and roughness characteristics (Falter et al. 2016), and in wave-dominated systems $S$ can vary by an order of magnitude across the reef (e.g., from 25 m d$^{-1}$ on the forereef to 5 m d$^{-1}$ in the backreef) as bottom stress from wave forcing declines (Zhang et al. 2011; Wyatt et al. 2012). In wave-dominated systems, $S$ would be expected to be reasonably consistent while wave conditions remain similar (e.g., at scales of days – weeks). Estimates of $S$ from Tallon reef suggest that on tide-dominated reefs, uptake rates can vary rapidly on the scale of hours or even minutes; for instance, uptake rates for DIN decreased by an order of magnitude ($\sim$30 – 3 m d$^{-1}$) over the period of an hour during flood tide (Figure 4.6a,c). When averaged over longer time-scales (i.e., over full tidal cycles), estimates of $S$ for DIN and DIP ($\sim$9 and $\sim$5 m d$^{-1}$, respectively) were similar to the mean of those measured in previous studies and did not differ between seagrass and macroalgal reef zones (Figure 4.7). Tallon reef platform experiences flows and water depths particular to its geometry and position relative to mean sea level, yet $S$ (and accordingly nutrient uptake) may vary more substantially over tide-dominated reef communities that occur at different elevations or below mean sea level (Solihuddin et al. 2016).

Estimates of mass-transfer-limited uptake of DIN and DIP varied over a tidal cycle with $S$ (Figure 4.6b,d,f), but also showed differences in uptake with reef zone and season. Reef zones were similar in terms of NH$_4^+$ and DIP uptake, but rising concentrations of NO$_x$ in the macroalgal zone during ebb tide caused estimates of $J_{MTL}$
to rise compared to the seagrass zone (Figure 4.6b, Figure 4.8a). Previous work on Tallon reef has shown that the macroalgal zone is ~20% more productive than the seagrass zone (Gruber et al. 2017), which may be related to this difference in potential nitrate fluxes. Concentrations of NO\textsubscript{x} and NH\textsubscript{4}\textsuperscript{+} were elevated in the wet season, while DIP declined compared to the dry season (Table 4.2); these seasonal differences were evident in the mass-transfer-limited nutrient fluxes even when averaged over tidal cycles (Figure 4.8). Ratios of DIN:DIP mass-transfer-limited uptake during Oct were 8.6 and 10.8 for seagrass and macroalgal zones, respectively (Figure 4.8). These ratios are well below the tissue N:P ratio of 30:1 typical of reef primary producers (Atkinson and Smith 1983) and suggest that producers on Tallon reef may be strongly N-limited (at least during the dry season). This is supported by low N:P ratios (14:1) measured in *Thalassia* leaf tissue from Tallon reef during Oct (N. Cayabyab, unpubl.). During Feb, ratios of DIN:DIP mass-transfer-limited uptake were 21.5 and 21.3 for seagrass and macroalgal zones, respectively (Figure 4.8), which suggests that N-limitation may be somewhat alleviated due to increases in oceanic DIN during the wet season.

In conclusion, this study was one of the first to measure rates of benthic nutrient uptake and release on a strongly tidally-forced reef. We found that reef communities released a moderate amount of DIN, possibly derived from the remineralization of phytoplankton, large organic material, and DON. The strong tidal forcing of this reef can drive large variability in mass-transfer-limited nutrient uptake rates at short time scales (minutes – hours), and uptake can be enhanced in reef zones downstream of where DIN release occurs. Tallon reef displays some indications of nitrogen-limitation during the dry season, which may be somewhat relieved during the wet season due to seasonal increases in oceanic DIN.
5. GENERAL DISCUSSION AND CONCLUSIONS

5.1.1. Overview

The overarching goals of this research were to investigate rates of benthic metabolism and nutrient cycling in a tide-dominated reef system and investigate how these ecological processes are linked to the physical environmental conditions. In Chapter 2, the response of benthic metabolism to the extreme environmental conditions that reef organisms experience daily on Tallon reef were assessed in two distinct habitat zones. Chapter 3 describes seasonal changes in offshore water quality and presents a study of phytoplankton and particulate nutrient uptake on Tallon reef. Finally, Chapter 4 compared fluxes of dissolved nutrients measured on the reef with theoretical fluxes derived from reef hydrodynamics. This final discussion chapter will summarize the major findings from the chapters described above and will discuss the implications of these findings for future research of tide-dominated reefs as well as research in the coastal Kimberley region.

5.1.2. Summary of major findings

Our findings show that Tallon reef experienced some of the most extreme conditions yet recorded for tropical reef systems worldwide. Extreme daily variability in temperature and dissolved oxygen occurred on the reef platform, and was related to the semidiurnal tidal and solar (light) cycles. The geometry, bottom roughness properties, and position of the platform relative to mean sea level caused water to ‘pond’ on the reef for up to 10 hours during each ebb tide (twice daily). When these extended low tide periods occurred near noon, the reef warmed rapidly with
temperatures rising by 10°C over several hours, reaching values up to 38°C. This high light availability also drove moderate rates of community benthic primary production, which released oxygen into the water column and resulted in extremes in oxygen saturation (~270%). When low tide periods occurred near midnight, community respiration caused oxygen levels to plummet, resulting in hypoxia (DO <63 µM) for up to 7.5 hours every night or ~15% of the total time-series. Low oxygen levels are known to harm or kill organisms in other ecosystems, and are not typically recorded on reefs.

Rates of gross primary production of the dominant communities (macroalgae and seagrass) did not decline at high temperatures or show signs of photoinhibition, emphasising the resilience of these organisms to extreme conditions. Large variability in nighttime community respiration appeared to be driven by oxygen concentration rather than temperature; such behaviour has been previously measured in controlled laboratory studies, but has not been described in situ. Net community production oscillated over a ~15 day cycle with environmental variability (temperature, light, and DO), depending on the timing of noon relative to low tide. Finally, the overall rates of productivity were similar to the global mean for tropical reefs, demonstrating that tide-dominated reefs can maintain moderate rates of production despite the environmental extremes they experience.

Water quality offshore of Tallon reef showed minor seasonal changes over the 2013/2014 wet season, suggesting that waters at the mouth of King Sound are mildly influenced by river discharge from the Fitzroy River during wet seasons with below-average rainfall (Figure 5.1). Chlorophyll a (chl a) concentrations increased in waters surrounding the reef from the end of the dry season (Oct) through the wet season (Apr), while particulate nutrient concentrations declined. Water quality on the reef platform
displayed large variability over a tidal cycle, as pulses of particulate nutrients and chl $a$ transported onto the reef during flood tide were then depleted by benthic grazing towards the end of ebb tide; thus, flood tide is a key process that replenishes food sources for certain reef organisms. Reef uptake of phytoplankton showed a periodicity on the scale of weeks similar to that observed in net production, which may be a function of chl $a$ input related to spring-neap changes in flood tide water volumes.

Overall, net benthic uptake of chl $a$ on Tallon reef was much lower than most previous reefs studied, and the reef was a net source of particulate nutrients to surrounding waters due to resuspension and export of particulate detritus during peak ebb tide. Therefore, grazing of the benthos on chl $a$ is not likely to be a substantial source of nutrients for Tallon reef communities, although grazers may still play a key

Figure 5.1. Fitzroy River discharge measured at Willare (site 802008 Dept. of Water) from 1998 – 2014. Upper right inset shows years ranked by annual discharge, with 2013/2014 wet season highlighted in red.
role in other biogeochemical pathways such as the uptake of pico/nanoplankton and dissolved organic compounds.

Concentrations of dissolved nutrients were highly variable on Tallon reef, rising by several times offshore levels during ebb tide. Measurements of dissolved nutrient fluxes showed that the reef released a moderate amount of dissolved inorganic nitrogen, which was likely derived from the remineralization of phytoplankton, large organic detritus, and dissolved organic nitrogen. Theoretical estimates of dissolved inorganic nutrient uptake assuming mass-transfer-limitation of the benthos showed that uptake velocities on Tallon were large and highly variable over a tidal cycle. Nutrient uptake velocities were calculated as a function of flow speed and bottom drag (estimated from roughness characteristics and water depth), and increased by an order of magnitude during times of rapid flow and shallow water. This tidally-forced variability in uptake rates occurred at short time scales (minutes – hours) in contrast to uptake rates on wave-dominated reefs, which vary on scales of days – weeks as a function of offshore wave conditions. Mass-transfer-limited fluxes of ammonium and phosphate were similar between benthic communities (macroalgae and seagrass), but fluxes of nitrate were distinctly different between zones due to nitrate concentrations. Enhancement of nitrate uptake in the macroalgal zone may explain why this community is ~20% more productive than the seagrass zone. Mass-transfer theory suggests that Tallon reef is nitrogen-limited, which was corroborated by nutrient ratios in seagrass tissue. Wet season increases in nitrate in offshore waters may somewhat relieve this nitrogen-limitation.
5.1.3. Effects of wave vs tidal forcing on metabolism and biogeochemistry

The magnitudes and time-scales of variability in physical and biogeochemical conditions on Tallon reef were considerably different than on previously-studied wave-driven reefs, and this section will provide a general comparison between the two forcing conditions. Large changes in flow speed, water depth, temperature, DO, chl \( a \), and nutrient concentrations occurred on Tallon reef platform every tidal cycle, with conditions changing on scales of minutes – hours. This variability dwarfed seasonal changes in temperature, chl \( a \), and nutrient concentrations in offshore waters. Reef zones showed some differences in flow speeds, and chl \( a \) and nutrient concentrations differed between zones during ebb tide. Tallon reef displayed low-frequency variations in mean temperature, DO, and net productivity that occurred over ~fortnightly scales related to the offset between the semidiurnal M2 tide and the solar cycle. Similarly, a low-frequency modulation in chl \( a \) uptake was observed on the reef platform. More research is necessary to determine the forcing of such variability and if such oscillations are a common feature of tide-dominated reefs.

In contrast, wave-dominated reefs experience fairly consistent physical and biogeochemical conditions on scales of days – weeks. Changes in water quality can occur due to episodic events such as wind-driven upwelling and generally have a smaller magnitude (e.g., temperature change of a few degrees) than what can occur each tidal cycle on tide-dominated reefs. Ecological processes such as chl \( a \) grazing or nutrient uptake are also linked to episodic events. However, wave-dominated reefs generally have differences between reef zones (i.e., reef crest vs backreef) that are consistent in time, such as chl \( a \) and nutrient concentrations decreasing across the reef.
5.1.4. Broader implications for the region

Although our study was conducted on a single reef, intensive measurements of physical conditions (e.g., hydrodynamics, reef morphology, platform height above sea level) allow some generalization of results to other Kimberley reefs. Recent work has documented the morphology and height relative to sea level of many Kimberley reefs (Kordi et al. 2016). These characteristics determine the duration of ebb tide on the reef, and thus control the extremes in environmental conditions such as water flow, temperature, light, DO, and pH that will develop there. Environmental extremes and productivity measured on other high intertidal reefs such as Montgomery, a large reef (400 km²) important for tourism, would likely be very analogous to those measured on Tallon. Reefs growing below sea level (Solihuddin et al. 2016) such as on Cockatoo Island, would experience shorter ebb tide periods, reduced environmental variability, and would be more closely linked to oceanographic conditions.

These results can be used to help inform future monitoring and scientific studies of Kimberley reefs. For reefs above mean sea level, the spring-neap tidal cycle does not affect temperature, DO concentration, or productivity; instead, these are driven by the timing of noon relative to ebb tide. This cycle is ~15 days in length and is an important consideration for future studies, as those shorter than ~15 days may greatly over-or under-estimate the quantity or process of interest. Additionally, a high-frequency record of water depth at the study site is a key component of any future work, as inaccuracies in depth on the order of decimetres can substantially alter estimates of productivity and nutrient uptake.
5.1.5. Future research directions

This work raises many interesting questions for future research efforts. Other ecological and biogeochemical processes of interest, such as coral calcification, predator-prey interactions, or spawning of benthic organisms are likely to show dependency on tidal forcing on similar reefs. Reef position relative to sea level controls some environmental conditions not explored in this work including turbidity and light availability. Although this work found reef heterotrophy (grazing on suspended particles) to be a relatively minor component of the overall reef nutrient budget, this may not be the case for subtidal reefs experiencing elevated turbidity and reduced light penetration throughout the tidal cycle.

Our study was conducted during the 2013-2014 wet season, which experienced relatively low rainfall levels compared to the previous 20 years (Figure 5.1). Some differences in offshore water quality were observed between seasons, but there is presently no record of water quality during a wet season with average or above-average rainfall. Additionally, Tallon reef is relatively far (~100 km) from the mouth of the closest major river (Fitzroy River), but other Kimberley reefs are much closer to river mouths, especially in the northern part of the region. Inter-annual and cross-shelf differences in water quality and its effect on reefs remains a substantial knowledge gap for the region.
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136


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