Tidal and seasonal forcing of dissolved nutrient fluxes in reef communities

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Abstract. Benthic fluxes of dissolved nutrients in reef communities are controlled by oceanographic forcing including local hydrodynamics ~~regime~~ and seasonal changes in oceanic nutrient supply. Up to a third of reefs worldwide can be characterised as having circulation that is predominantly tidally-forced, yet almost all previous research on reef nutrient fluxes has focused on systems with wave-driven circulation. Fluxes of dissolved nitrogen and phosphorus were measured on a strongly tide-dominated reef platform with a spring tidal range exceeding 8 m. Nutrient fluxes were estimated using a one-dimensional control volume approach, combining flow measurements with modified Eulerian sampling of waters traversing the reef. Measured fluxes were compared to theoretical mass-transfer-limited uptake rates derived from flow speeds. Reef communities released ~~a moderate amount of~~2.3 mmol m^{-2} d^{-1} of nitrate, potentially derived from the remineralization of phytoplankton and dissolved organic nitrogen. Nutrient concentrations and flow speeds varied between the major benthic communities (coral reef and seagrass), resulting in spatial variability in estimated nitrate uptake rates. Rapid changes in flow speed and water depth are key characteristics of tide-dominated reefs, which caused mass-transfer-limited nutrient uptake rates to vary by an order of magnitude on time scales of ~minutes – hours. Seasonal nutrient supply was also a strong control on reef mass-transfer-limited uptake rates, and increases in offshore dissolved inorganic nitrogen concentrations during the wet season caused an estimated twofold increase in uptake.

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1 Introduction

Reef organisms remove nutrients from overlying waters for essential metabolic and biogeochemical processes, which enable them to accumulate biomass and ultimately support broader marine food webs (McMahon et al., 2016;Parrish, 1989). 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 (Atkinson and Falter, 2003;Larned, 1998;Smith, 1984). Suspended N and P can be categorized in 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_x), ammonium (NH_4^+), and phosphate (DIP), which are found at low concentrations in reef waters.

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;Baird et al., 2004;Falter et al., 2016;Reidenbach et al., 2006;Thomas and Atkinson, 1997), and these uptake rates can be predicted for a particular reef 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).

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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 and 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), corals (Grover 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 (< 2μm) and bacterial cells, and are an important source of nutrients for reef suspension and filter-feeding organisms (Houlbrèque et al., 2006;Ribes et al., 2005;Wyatt et al., 2010).

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~~2004;Falter et al., 2016;Reidenbach et al., 2006;Thomas and Atkinson, 1997), and these uptake rates can be predicted for a particular reef 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).~~

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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 (Cuet et al., 2011a;Furnas, 2003;Paytan et al., 2006;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;Stuhldreier et al., 2015;Wyatt et al., 2012) or internal waves (Green et al., in press;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 annual mean significant wave height (offshore of the reef) is less than the mean tidal range (Lowe and Falter, 2015). Reefs that are strongly tide-dominated can experience substantial variability in flow speeds and water depths over a single semidiurnal tidal cycle (Lowe et al., 2015), which suggests that mass-transfer-limited nutrient uptake rates (and other biological processes) would also vary throughout the tidal cycle.

The Kimberley coastal region (located in remote northwest Australia) has a macrotidal regime where spring tidal ranges can reach 12m in some locations (Kowalik, 2004). The region contains thousands of islands with a total reef area estimated to be ~2000 km^2 (Kordi and O'Leary, 2016) inhabited by diverse coral reef and seagrass communities (Richards et al., 2015;Wells et al., 1995). Recent work has revealed the strongly tide-dominated circulation that can occur on Kimberley 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 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 measurements of coral calcification (Dandan et al., 2015), seagrass productivity (Pedersen et al., 2016), reef community metabolism (Gruber et al., 2017), and particulate nutrient uptake (Gruber et al., 2018) have been published from tide-dominated systems, yet little is currently known about how these large tides control fluxes of dissolved nutrients. The objectives of this study were to: 1) measure fluxes of dissolved N and P on a tidally-forced reef, 2) compare measured rates to maximum potential uptake predicted by mass-transfer theory, and 3) compare tidal forcing (velocity and water depth changes) and oceanic forcing (seasonal changes in nutrient concentration) of 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.

2 Methods

2.1 Field site

A series of field experiments were conducted in the western Kimberley region at Tallon Island, which contains a large intertidal reef platform (surface area 2.2 x 10^6 m^2) on its eastern side (Figure 1~~Figure 1~~). The platform is elevated slightly (25 cm) above mean sea level, and the seaward rim is 10 cm shallower than the rest of the platform; this feature, coupled with bottom friction, prevents reef benthic communities from becoming emersed during low tide (Lowe et al., 2015). 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 coral reef outer zone (200 m wide extending shoreward from the crest). Between these distinct communities, a 200 m zone of rubble and sand occurs where the seagrass and coral reef communities mix (Figure 1~~Figure 1~~). *Enhalus acoroides* is found with *Thalassia hemprichii* in the seagrass zone (Wells et al., 1995). The coral community contains brown foliose macroalgae (predominantly *Sargassum* spp.), a diverse assemblage of small hard corals (~5-10% cover), soft coral, coralline macroalgae, and crustose coralline algae.

The Kimberley region experiences a sub-tropical climate, so field experiments at Tallon reef were conducted during the dry (5 – 20 October 2013) and wet seasons (4 – 9 February 2014). Nutrient concentrations were measured from duplicate filtered water samples (Table 1~~Table 1~~) and were collected around hydrodynamic instrumentation, forming a one-dimensional control volume as detailed below (see also Gruber et al., 2017). This approach~~ed~~ allowed estimation of dissolved nutrient~~s~~ fluxes (the net uptake or release of nutrients) across the reef benthos~~, which represent the net uptake or release of nutrients~~. Estimates of uptake of DIN and DIP at the limits of mass-transfer were made using hydrodynamic data over a spring-neap cycle (~15 days) collected during the hydrodynamic study of Lowe et al. (2015) and nutrient concentrations from water sampling during the Oct and Feb field experiments. ~~Current speed was not measured at CR during the Oct 2013 field experiment, so measurements from a detailed hydrodynamic study (which included instruments positioned at SG and CR) during Apr 2014 were used (Lowe et al., 2015).~~ Flows on the reef platform are strongly tide-driven, and can be predicted based on water depth and tidal phase (Lowe et al., 2015); 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. This manuscript presents tidal phase-averaged data as a way to visualize hydrodynamic and biogeochemical measurements that tend to fluctuate with the phase of tide. Phase-averaged values in this study are ensemble averages of all measurements ~~from every~~occurring at a given point in the semidiurnal (M2) tidal cycle (e.g., average of all measurements taken during low tide).

2.2 Dissolved nutrient sampling

Water samples were collected during both field experiments for analysis of dissolved nutrient concentrations in offshore and reef flat waters. Eulerian sampling occurred at three stations (Figure 1~~Figure 1~~): the coral zone ('CR'), the seagrass zone ('SG'), and offshore of the reef in adjacent waters ('Off'). Offshore samples were collected ~~from just beneath the water surface~~ throughout the semidiurnal tidal cycle on days of sampling (Table 1~~Table 1~~). Collecting water samples on the reef platform was not feasible during periods of peak flood and ebb, which occurred 0 – 1 and 4 – 6 hours, respectively, after the onset of reef flooding (when offshore waters first overtopped the reef crest). Rapid changes in water depth during these tidal phases caused current speeds exceeding 0.8 m s^{-1} (Figure 2~~Figure 2~~), which made for unsafe conditions for sampling by foot or boat. Reef sampling was conducted during the remaining 9 hours of each tidal cycle, either by foot when water depths were low (~0.4 – 0.6 m) or by boat during high tide (1 – 4 hours from the onset of reef flooding).

Water samples were collected from just beneath the water surface for analysis of dissolved nutrients. ~~with a~~A 50 mL syringe (pre-rinsed with reef water) was used to collect water, which was~~and~~ immediately filtered (Minisart, pore size 0.45 μm) into 30 mL pre-rinsed tubes. These samples were placed in darkness on ice and were frozen upon return to the field station (several hours); samples were transported and stored frozen until analysis at the laboratory (<4 weeks from the end of the field experiment). 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 estimated from the total dissolved nitrogen less NO_x and NH_4^+. All nutrient concentrations presented are the mean of duplicate samples.

2.3 Control volume approach

The control volume (CoVo) technique utilises flow measurements and modified Eulerian sampling of solutes or particles to derive in situ benthic flux estimates. Tallon reef platform is well-suited to a one-dimensional CoVo approach due to long periods (approximately 10 h of each semidiurnal tidal cycle) of consistent flow direction; nutrient sampling may thus be conducted at 'upstream' and 'downstream' sites during these periods. A similar approach has previously been used on Tallon reef to estimate its benthic metabolism (Gruber et al., 2017) and particulate material uptake (Gruber et al., 2018) rates. A bottom-mounted acoustic Doppler current profiler (Nortek Aquadopp HR) was stationed near SG (Figure 1~~Figure 1~~) and measured current velocity and water depth (h) at 1 Hz and 0.03 m bins. Depth-averaged flow speeds (u) were ~~bin-~~averaged at 5 min intervals. During the reef's extended ~10 hour ebb tide, water drained off the platform in a consistent northeast direction (80° ± 30°, mean ± standard deviation), along which the water sampling stations were aligned. Depth-averaged current velocity was rotated in this ebb flow direction (u_x) and transport q_x was estimated as

$$q_x = u_x h, \tag{1}$$

assuming negligible horizontal dispersion. The net flux J_{net} (in mmol N or P m^{-2} d^{-1}) of each nutrient species (NO$_x$, NH$_4^+$, DIP, and DON) into the benthos was estimated as

$$-J_{\mathrm{net}} = \bar{h}\frac{d\bar{C}}{dt} + q_x\frac{(C_{\mathrm{CR}} - C_{\mathrm{SG}})}{dx}, \qquad (2)$$

where the distance between sampling stations dx was 540 m and $\bar{h}$ was the mean water depth along dx. Nutrient concentrations at CR and SG are represented by C_{CR} and C_{SG}, respectively; $\bar{C}$ is the mean of C_{CR} and C_{SG} ~~concentrations at both stations~~at a given time-step (Genin et al., 2002). Positive values of J_{net} represent net benthic nutrient uptake and negative J_{net} indicates net release of nutrients to the water column; these fluxes are the net result of all biogeochemical processes occurring between SG and CR, and thus represent fluxes from a combination of seagrass and coral reef communities. The 'local' benthic flux (i.e., nutrient uptake or release occurring ~~at~~ in the reference frame of ~~a~~ the sampling stations) is represented by the first right-side term of Eq. (2), and was estimated at hourly intervals when water sampling occurred. The second term of Eq. (2) represents the 'advective' flux (i.e., nutrient uptake or release during transit between sampling stations). ~~,~~ Transit time between stations changed throughout the tidal cycle, and could be on the order of hours during periods of slow flow (<5 cm s^{-1}). To better represent the advective component, ~~and was~~advective fluxes were calculated at every point where nutrient concentrations were available and were then bin-averaged over a time interval that ~~fluctuated with changing flow speeds~~approximated the transit time. These estimates were then linearly interpolated to times where local estimates existed~~; this method is described in greater detail in Gruber et al. (2017)~~.

2.4 Uptake rates at the limits of mass-transfer

For comparison with the field observations, the theoretical uptake rates of DIN and DIP at the limits of mass-transfer (J_{MTL}) were calculated for each of the measurements of J_{net} above. Assuming nutrient concentrations at the tissue surface of benthic organisms were near zero, J_{MTL} was estimated along the study transect (from SG to CR) as (Falter et al., 2004)

$$J_{\mathrm{MTL}} = S\bar{C}, \qquad (3)$$

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

$$S = u_x \cancel{u} C_D^{0.5}/(\mathrm{Re_k}^{0.2}\mathrm{Sc}^{0.6}), \qquad (4)$$

where C_D is the drag coefficient, Re$_k$ is the roughness Reynolds number, and Sc is the Schmidt number. Mass-transfer velocity 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 (through the Schmidt number) yet is unrelated to nutrient concentration (see below). The Schmidt number is defined as the kinematic viscosity ~~(v)~~ divided by the ~~diffusivity~~ diffusion coefficient D of the nutrient species, which were 19.05, 19.80, and 7.00 x 10^{-6} cm^2 s^{-1} for NO$_x$, NH$_4^+$, and PO$_4^{3-}$, respectively (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 an empirical relationship~~s~~ ~~using~~ between h and the mean height of reef ridges h_r as (McDonald et al., 2006)

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$$C_D = 1.01(h/h_r)^{-2.77} + 0.01, \qquad (5)$$

~~, following the same approach as used in estimates of reef metabolism (Gruber et al., 2017)~~where h_r was determined by measuring the mean height (vertical distance between the crest and trough of a reef ridge) of all ridges along a 50 m transect. The roughness Reynolds number $\mathrm{Re_k}$ is defined as

$$\mathrm{Re_k} = u_* k_s / \nu,$$

(~~5~~6)

where k_s, a hydraulic roughness length scale, was 0.5 m (Lowe et al., 2015) and the shear velocity u_* is a function of bottom shear stress τ_b and seawater density ρ as

$u_* \equiv \sqrt{\tau_b/\rho} =$ u_x~~u~~$\sqrt{C_D/2}$.

(~~6~~7)

Estimates of maximum potential nutrient release ($J_{release}$) represent the flux of NO_x, NH_4^+, and DIP necessary to match the observed J_{net} assuming uptake occurred at mass-transfer-limited rates, and were estimated as (Wyatt et al., 2012)

$$J_{release} = J_{net} - J_{MTL}$$

(~~7~~8)

for each of the intervals over which J_{net} was calculated.

Large changes in water depth, flow speed, and nutrient concentration occurred during each tidal cycle, yet measurements of J_{net} could only be made during ebb tide (generally 6 – 12 hours after onset of reef flooding). In order to understand how the range of flow speeds experienced by this reef platform could influence maximum potential nutrient uptake rates, we calculated J_{MTL} continuously over a full ~15 day spring-neap cycle at individual stations ~~at~~ SG and CR. Flow speed measurements from an April 2014 experiment were used, which included an ADP and ADV located at SG and CR, respectively; as discussed previously, flows on Tallon reef can be predicted based on water depth and tidal phase (Lowe et al., 2015), so measurements from April would be representative of flows during Oct and Feb experiments. Calculations were made as above (Eq. 3-7) with the exception of using u instead of u_x (Eq. 4, 7), as we are now estimating fluxes over the full tidal cycle rather than only the ~unidirectional ebb tide portion. ~~Current speed was not measured at CR during the Oct 2013 field experiment, so measurements from a detailed hydrodynamic study (which included instruments positioned at SG and CR) during Apr 2014 were used (Lowe et al., 2015). Flows on the reef platform are strongly tide-driven, and can be predicted based 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 (CR and SG) and field experiments (Oct and Feb) using measured concentrations (Figure 3~~Figure 3~~) where available. As it was not possible to collect water samples during peak ebb tide (due to hazardous conditions), nutrient concentrations in offshore waters (Table 1~~Table 2~~) were assumed to be representative of concentrations on the reef platform during those times.

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In a strongly tide-dominated system such as Tallon reef, each tidal cycle ‘refills’ the reef by flushing it with fresh oceanic water. In order to conceptualise the net biogeochemical fluxes that occur over this cycle, we used tidal cycle averages. Tidal cycle averages of mass-transfer velocities (S_{cyc}) and mass-transfer-limited nutrient flux (J_{cyc}) were calculated as the mean of all S and J_{MTL}, respectively, occurring within an individual semidiurnal tidal cycle beginning when water flooded the reef platform.

Uncertainties in estimates of S, J_{net}, and J_{MTL} were estimated by propagating standard deviations using Monte Carlo simulation (10,000 iterations). Error terms for hydrodynamic variables were derived from bin-averaged data (Lehrter and Cebrian, 2010) and were 0.01 m for h, 0.03 m s^{-1} for u, 0.05 μM for concentrations of NO_x and NH_4^+, 0.01 μM for DIP, 1.0 μM for DON. Tidal phase-averaged concentrations of NO_x and DIP used in J_{MTL} estimates were assigned standard deviations of 0.5 μM and 0.05 μM, respectively.

3 Results

3.1 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~~2° C warmer during the wet season in Feb, and levels of DIN were elevated, with NO_x concentrations approximately double those measured during the dry season in Oct (Table 1~~Table 2~~). Salinity and concentrations of DIP and DON were ~~slightly lower during the wet season in Feb~~similar between seasons. Reef platform nutrient concentrations were similar to offshore concentrations during flood tide and the start of ebb tide (~3 – 6 hours after reef flooding, Figure 3~~Figure 3~~); during the remaining 6 hours of ebb tide, the concentrations of DIN changed dramatically depending on the reef zone (benthic community type). In the case of NO_x, concentrations decreased in the seagrass zone (SG) but increased in the coral zone (CR) by up to five times compared to offshore levels (Figure 3~~Figure 3~~a,b). Increases in NH_4^+ occurred at both SG and CR during ebb tide (Figure 3~~Figure 3~~c,d), while DIP was generally lower than offshore concentrations but tended to increase at CR during the final few hours of ebb tide (Figure 3~~Figure 3~~e,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~~Figure 4~~a), 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~~Figure 4~~b,c), and J_{net} for DIP tended to transition from net uptake to net release over the duration of ebb tide. There were no substantial differences in overall mean J_{net} of dissolved inorganic nutrients between Oct and Feb field experiments (Table 2~~Table 3~~). Fluxes of DON did differ between seasons; J_{net} varied between net uptake and net release during Oct (Figure 4~~Figure 4~~d) although mean J_{net} was negligible (Table 2~~Table 3~~).

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During Feb, J_{net} of DON transitioned from net uptake to net release over the ebb tide (Figure 4~~Figure 4~~d), but showed a large uptake on average (Table 2~~Table 3~~).

3.2 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).~~ For simplicity, only values of *S* for NO$_x$ are shown, as the values of other species (NH$_4^+$, DIP) differ only in magnitude by a constant factor (due to diffusivity). Although temperature influences *S* through viscosity, changes in temperature on the reef platform had a negligible effect on *S* (<0.01%) compared to reef hydrodynamics. The tidal phase-averages of *S* on the reef platform (Figure 5~~Figure 5~~) 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 largest *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 2~~Figure 2~~); values of *S* during flood tide were ~30% greater at CR compared to SG, which was due to the larger flow speeds and slightly shallower (10 cm) water depths that occurred near the reef crest~~ (Figure 2)~~. Lowest *S* each tidal cycle (Figure 5~~Figure 5~~) occurred at high tide when flow speeds became negligible and reef water depths were comparatively large (~2.5 m). Values of *S* were relatively small (~5 m d^{-1} for NO$_x$) later in ebb tide (8 – 12 hours after reef flooding) and were similar between SG and CR. As *S* was estimated over a full spring-neap tidal cycle, the ranges of values shown (Figure 5~~Figure 5~~) are from the most (spring) and least (neap) energetic tidal cycles, which ~~differ~~ cause *S* to vary by a factor of <4.

The mass-transfer-limited nutrient fluxes J_{MTL} were a function of both *S* as well as the local nutrient concentrations (Eq. 3). Fluxes showed variability over the tidal cycle associated with *S*, but also showed prominent differences between benthic communities and seasons related to nutrient concentrations. Elevated NO$_x$ concentrations at CR (Figure 3~~Figure 3~~a,b) resulted in rising J_{MTL} during the final 6 hours of ebb tide, while low NO$_x$ concentrations at SG resulted in low J_{MTL}, especially during ebb tide (Figure 6~~Figure 6~~). Similar concentrations of DIP (Figure 3~~Figure 3~~e,f) ~~and NH$_4^+$~~ between sites resulted in similar J_{MTL} between CR and SG ~~for both nutrient species~~ (Figure 6~~Figure 6~~c,d). ~~The influence of s~~Seasonal changes in offshore nutrient concentrations~~ was evident~~, particularly for NO$_x$, have the potential to enhance nutrient uptake rates. ~~where e~~Elevated ~~levels~~ offshore NO$_x$ during Feb (Table 1~~Table 2~~) resulted in a doubling of estimated J_{MTL} during ~~the first 6 hours~~flood and high tide portions of each tidal cycle, compared to Oct (Figure 6~~Figure 6~~a,b). 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 1~~Table 2~~, Figure 6~~Figure 6~~c,d). The maximum potential release of DIN and DIP to the water column assuming uptake was mass-transfer-limited ($J_{release}$, Eq. ~~7~~8), was calculated for every instance of measured J_{net} (Figure 4~~Figure 4~~). In the case of NO$_x$, $J_{release}$ was roughly double J_{net} (Figure 4~~Figure 4~~a) due to the large net NO$_x$ release measured on the reef platform. Whereas for NH$_4^+$ and DIP, $J_{release}$ was on the order of J_{MTL} due to negligible values of J_{net} (Figure 4~~Figure 4~~b,c). Overall mean

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rates of J_{MTL} and J_{release} for DIN did not show seasonal differences (Table 2~~Table 3~~), which was likely a function of these estimates only occurring during a portion (ebb) of the tidal cycle.

When S was averaged over individual semidiurnal tidal cycles (e.g., mean of all S within a tidal cycle, beginning with reef flooding), the difference between SG and CR was only ~1 m d^{-1} (Figure 7~~Figure 7~~). Mass-transfer velocities for NO_x and NH_4^+ were of similar magnitude over the tidal cycle, while those for DIP were ~50% lower (Figure 7~~Figure 7~~); this was a function of the diffusivity of each of these solutes (Li and Gregory, 1974). When J_{MTL} was similarly averaged over individual tidal cycles (Figure 8~~Figure 8~~), community and seasonal differences in J_{MTL} described previously (Figure 6~~Figure 6~~) were prominent. Uptake of NO_x showed the greatest differences between seasons and sites, with uptakes rates during the wet season greater than dry season rates by a factor of ~2. Similarly, estimates of DIP uptake were slightly enhanced during the dry season compared to wet season rates, while uptake of NH_4^+ was similar between seasons and sites (Figure 8~~Figure 8~~).

4 Discussion

4.1 Oceanic nutrient supply

The measurements of offshore nutrient concentrations presented in Table 1~~Table 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 μM common in reef waters (Atkinson and Falter, 2003). Measurements from the coastal Kimberley (Table 1~~Table 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 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., 2018) relative to ‘typical’ oligotrophic reef waters, suggest that some coastal Kimberley reefs may experience naturally mesotrophic conditions.

Wet season terrestrial discharge events deliver sediment and nutrients to coastal waters of northern Australia (Brodie et al., 2010;Devlin and Schaffelke, 2009;Schroeder et al., 2012). Offshore concentrations of NO_x and NH_4^+ measured in our study approximately doubled during the Feb field experiment compared to Oct, whereas DIP and DON were similar between seasons (Table 1~~Table 2~~). Whether this increase is due to river discharge or coastal oceanographic processes is not presently clear in the Kimberley region, and warrants future study. Ratios of offshore DIN:DIP were 4.3 and 10.7 in Oct and Feb, respectively (Table 1~~Table 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;McKinnon et al., 2013;Schaffelke et al., 2012). This suggests that N-limitation may be less severe in the Kimberley than in GBR waters, particularly during the wet season.

4.2 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~~Figure 4~~a), while NH_4^+ and DIP fluxes varied between uptake and release (Figure 4~~Figure 4~~b,c) but overall were negligible during the ebb tide (Table 2~~Table 3~~). Previous studies of reef nutrient fluxes in flumes or other controlled environments have generally shown uptake approaching the limits of mass-transfer for NH_4^+ (e.g., Atkinson et al., 1994;Cornelisen and Thomas, 2009;Larned and Atkinson, 1997;Thomas and Atkinson, 1997), DIP (reviewed in Cuet et al., 2011b), and less frequently for NO_x (e.g., Baird et al., 2004); these controlled environments lack some of the confounding processes present in natural reef communities.~~.~~ Yet net release of ~~all three species~~nutrients (especially NO_x) clearly occurs in situ as concentrations on many reefs exceed those offshore (e.g., Hatcher and Frith, 1985;Leichter et al., 2013;Rasheed et al., 2002), 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 with 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., 1990) and N_2 fixation adds to the NH_4^+ pool, it seems unlikely that either of these processes dominate the observed nutrient fluxes.

If we assume that the fluxes discussed above (J_{net}) simultaneously occur with uptake of DIN and DIP near the limits of mass-transfer, this gives a gross release ($J_{release}$) of ~10 mmol N m^{-2} d^{-1} and ~0.5 mmol P m^{-2} d^{-1} (Table 2~~Table 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., 2018) is on the order of $J_{release}$ in the case of P, but is much smaller than $J_{release}$ of N. Large particles (such as entire fronds of macroalgae) are rare but can form a major component of the particulate organic pool on some reefs (Alldredge et al., 2013); remineralisation of similar material (rather than small particles like phytoplankton) may be the source of the observed DIN release on Tallon. Finally, fluxes of DON on the order of J_{net} were measured on Tallon, with net uptake occurring during the Feb experiment (Figure 4~~Figure 4~~d). The dynamics of DON in reef systems have been addressed in a few studies (e.g., Haas and Wild, 2010;Thibodeau et al., 2013;Ziegler and Benner, 1999), 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 phytoplankton uptake on Tallon reef, but released DIN exceeds phytoplankton inputs and is likely derived from additional sources including remineralisation of large particles and DON.

4.3 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 (Wyatt et al., 2012;Zhang et al., 2011). In wave-dominated systems, *S* would be expected to be reasonably consistent while offshore wave forcing remain similar (e.g., at scales of days – weeks). Estimates of *S* from Tallon reef show uptake rates varying rapidly on the scale of hours or even minutes; for instance, uptake rates for NO_x decreased by an order of magnitude (~30 – 3 m d^{-1}) over the period of an hour during flood tide (Figure 6~~Figure 6~~a). When averaged over longer time-scales (i.e., over individual semidiurnal tidal cycles), estimates of *S* for DIN and DIP (~9 and ~5 m d^{-1}, respectively) were similar to the mean of those measured in previous studies and only differed slightly between seagrass and coral reef zones (Figure 7~~Figure 7~~). Tallon reef platform experiences flows and water depths particular to its geometry and position relative to mean sea level; therefore, *S* (and accordingly nutrient uptake) will vary in other tide-dominated reef communities as a function of these factors.

Estimates of mass-transfer-limited uptake of DIN and DIP varied over a tidal cycle with *S*, but also showed differences in uptake with reef zone and season (Figure 6~~Figure 6~~). Reef zones were similar in DIP uptake rates, but rising concentrations of NO_x in the coral zone during ebb tide caused estimates of J_{MTL} to increase compared to the seagrass zone (Figure 6~~Figure 6~~a,b). Previous work on Tallon reef has shown that the coral 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_x and NH_4^+ were elevated in the wet season, while DIP declined compared to the dry season (Table 1~~Table 2~~); these seasonal differences were evident in the mass-transfer-limited nutrient fluxes even when integrated over individual semidiurnal tidal cycles (Figure 8~~Figure 8~~). Ratios of DIN:DIP mass-transfer-limited uptake during Oct were 8.6 and 10.8 for seagrass and coral zones, respectively (Figure 8~~Figure 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 8~~Figure 8~~), which suggests that N-limitation may be somewhat alleviated due to increases in oceanic DIN during the wet season.

4.4 Comparison of wave and tidal forcing

This study suggests several important differences between wave- and tide-dominated reef biogeochemistry, which are controlled by the hydrodynamic regime. Firstly, the 'source' of a water parcel overlying a particular benthic community differs between wave- and tide-dominated systems. In a simplified wave-driven reef, offshore (oceanic) water moves from reef crest to back reef roughly unidirectionally, generally exiting the reef through channels. Thus, benthic communities are subjected to the physico-chemical water properties present in offshore waters modified by the communities 'upstream' of them. In a simplified tide-driven reef, flow direction changes throughout the tidal cycle; during flood tide, offshore waters enter the reef, while during ebb tide, waters from the backreef traverse all 'downstream' communities. These flow patterns control water residence times within the reef community. In wave-dominated reefs, flow speeds are driven by wave-breaking on the reef, creating residence times on the scale of ~hours; wave energy can be generally consistent in time over ~days – weeks (Lowe and Falter, 2015). In tide-dominated systems, reef waters exchange with offshore waters at timescales ≤ a semidiurnal (or diurnal) tidal cycle; this residence time will vary depending on the reef vertical position relative to mean sea level and its morphology. Finally, there are marked differences in nutrient uptake rates between wave- and tide-dominated reefs. The consistency of wave energy at scales of ~days – weeks likely drives similarly consistent mass-transfer-limited nutrient uptakes rates on wave-dominated reefs. On reefs with strong tidal forcing however, flow speeds are highly variable throughout the tidal cycle and mass-transfer-limited uptake can vary by an order of magnitude within ~hours - minutes. Flow speeds also change over the spring-neap tidal cycle (~15 days); on Tallon reef, mass-transfer-limited uptake rates were ~2-4 fold greater during spring tides relative to neap tides.

The ~8 m tidal range of Tallon reef is typical of tidal ranges in the Kimberley region, and thus the results presented here are likely to be broadly representative of conditions experienced by many reefs (~2000 km^2 of total reef area) in this region. Most reefs globally do not experience such an 'extreme' tidal regime, and therefore some aspects of this study (such as benthic fluxes varying by an order of magnitude on scales of minutes to hours) would not necessarily represent conditions on meso- or microtidal reefs. However, approximately 30% of reefs worldwide have tide-dominated circulation, including iconic systems such as much of the southern Great Barrier Reef (Lowe and Falter, 2015); such reefs likely experience a similar, though more moderated, version of the physical processes that occur in macrotidal systems. Our work therefore provides some insight into other researchers may relate benthic fluxes to tidal processes on other reef systems. ~~Further work on tidally-forced reefs is necessary to understand the morphological and hydrodynamic properties that distinguish them from wave-driven reef systems. Such~~ Further process-based studies that incorporate tidal forcing will improve predictions of reef water temperatures (and coral bleaching), in situ calcification rates, and many other physically-linked biological processes that ~~determine~~ affect the health and resilience of coral reef communities.

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Conclusions

In conclusion, this study was one of the first to measure rates of in situ benthic nutrient uptake and release on a tidally-forced reef. We found that reef communities released a moderate amount of DIN, potentially derived from the remineralization of phytoplankton, large organic material, and DON. The strong tidal forcing of this reef drives large variability (an order of magnitude) 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 relieved during the wet season; seasonal increases in offshore nitrate concentrations increased mass-transfer-limited uptake rates by a factor of ~2. This work identifies some hydrodynamic properties of tide-dominated reefs that control their biogeochemistry and help define them in comparison to wave-dominated reefs.

Author contribution

Field experiments were designed by RKG, RJL, and JLF. Fieldwork was conducted by RKG and RJL. RKG analysed the results and prepared the manuscript with contributions from RJL and JLF.

Competing interests

The authors declare that they have no conflict of interest.

Acknowledgements

This work was conducted on Bardi Jawi sea country and we acknowledge the Traditional Owners past, present, and emerging who care for this country. We thank the Bardi Jawi Rangers and Kimberley Marine Research Station staff for providing assistance and local knowledge during field experiments. We thank Michael Cuttler, Jordan Iles, Miela Kolomaznik, and Leonardo Ruiz-Montoya for helping with fieldwork. Three anonymous reviewers gave helpful comments that improved earlier versions of this manuscript. Funding was provided by the Western Australian Marine Science Institution's Kimberley Marine Research Program (Project 2.2.3), an Australian Research Council Future Fellowship (FT110100201) to RJL, and the ARC Centre of Excellence for Coral Reef Studies (CE140100020).

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Figure captions

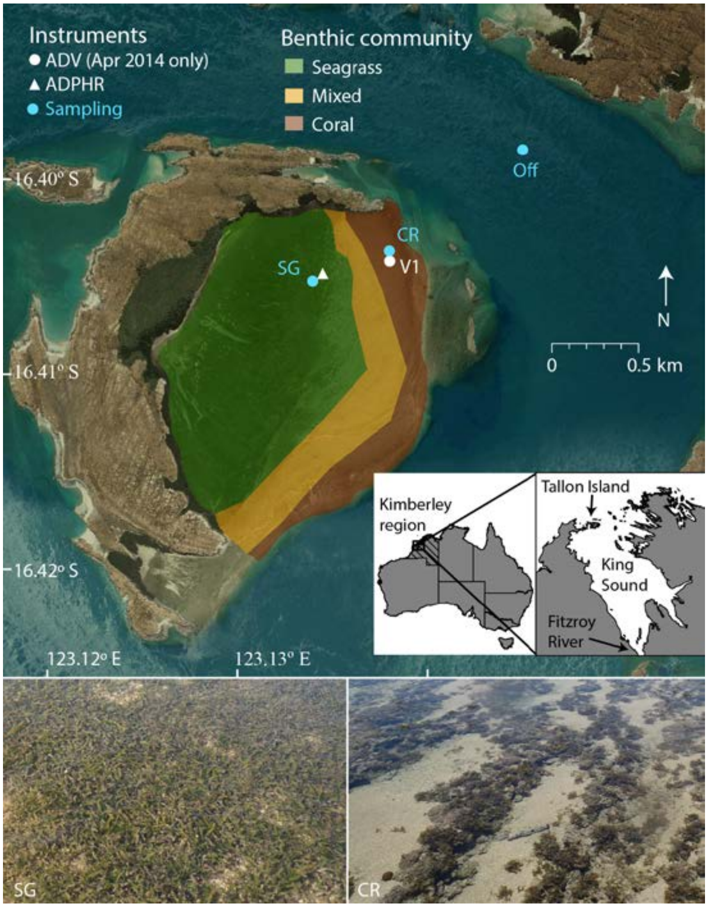

Figure 1. Deployment locations of hydrodynamic instrumentation and water sampling locations on Tallon reef platform and offshore. Inset shows Tallon Island location in the west Kimberley region of Australia. ADV refers to acoustic Doppler velocimeter and ADPHR refers to acoustic Doppler profiler.

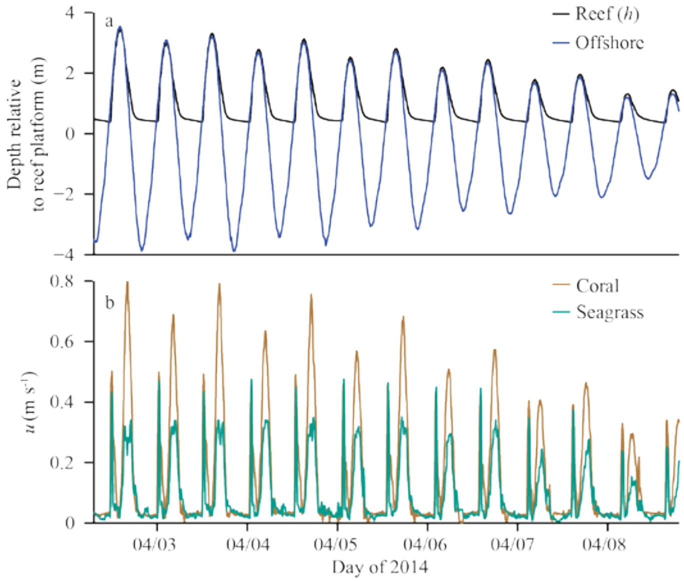

Figure 2. Selected time-series of spring-neap transition showing a) water depths (*h*) on the reef ~~(*h*)~~(measured in the seagrass zone) and offshore, with depth-averaged flow speed *u* in b) coral and seagrass-dominated zones.

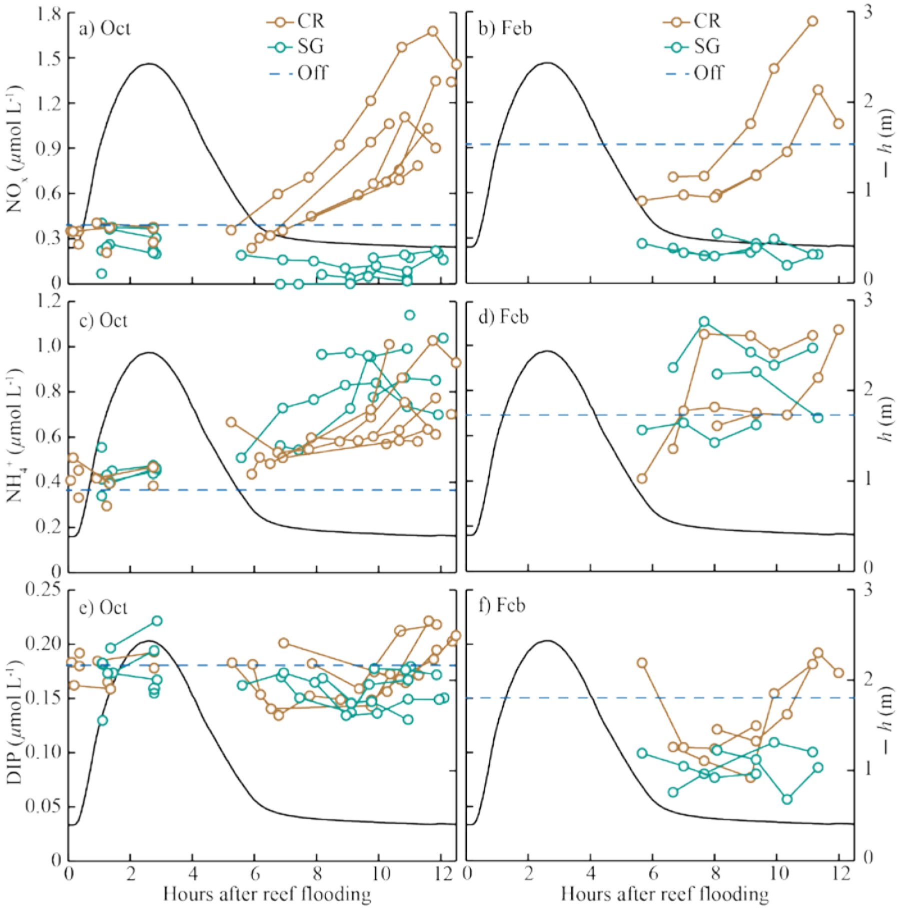

Figure 3. Measurements of a,b) nitrate (NO_x), c,d) ammonium (NH_4^+), and e,f) dissolved inorganic phosphorus (DIP) from water samples during Oct (left column) and Feb (right column) field experiments. Samples were taken at two reef stations [coral (CR) and seagrass (SG) dominated zones] and mean offshore nutrient concentrations are shown (blue dashed line). Tidal phase-averaged water depth *h* is also shown (black line).

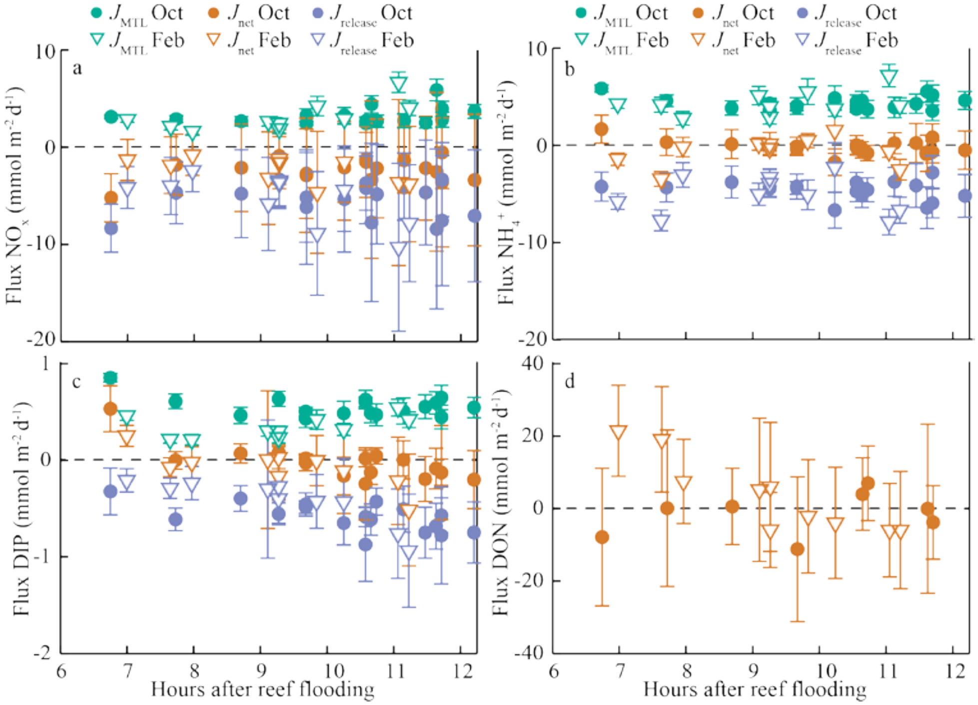

Figure 4. Fluxes (± standard deviation) of a) nitrate (NO_x), b) ammonium (NH_4^+), c) dissolved inorganic phosphorus (DIP), and d) dissolved organic nitrogen (DON) along the study transect during both field experiments. Net benthic fluxes (J_{net}) were estimated using the CoVo approach, while mass-transfer-limited uptake (J_{MTL}) was calculated (Eq. 3) from reef platform flow and nutrient concentrations, and nutrient release ($J_{release}$) was estimated from net and MTL fluxes.

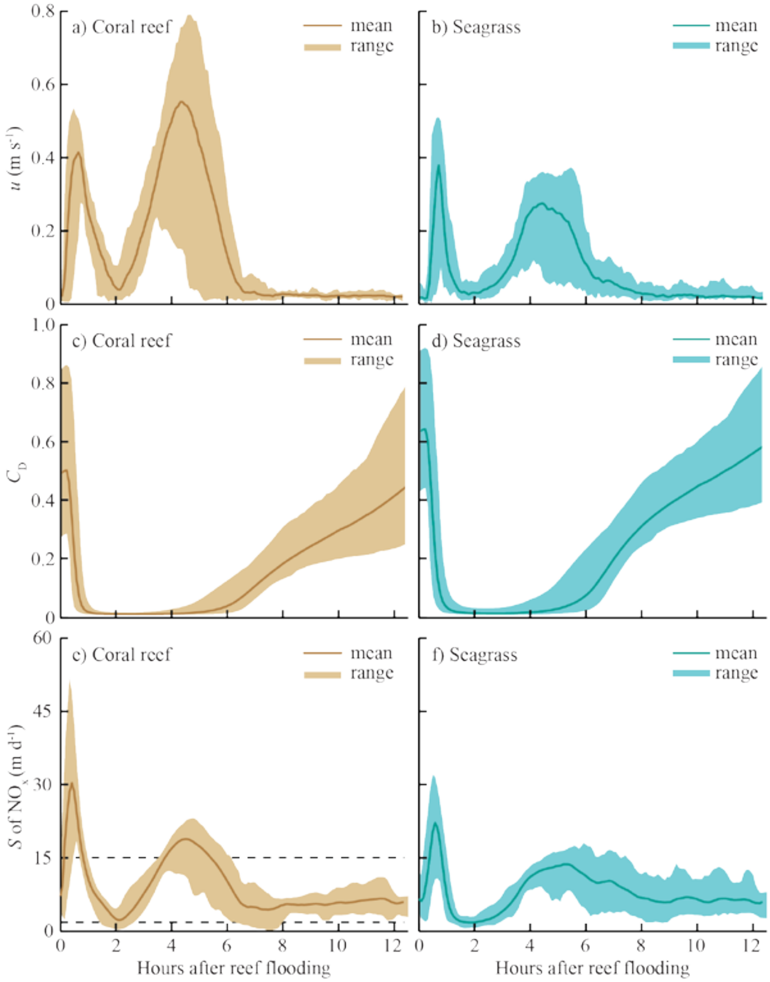

Figure 5. Tidal phase-~~averaged~~ averages of flow speed u, drag coefficient C_D, and mass-transfer velocity S for nitrate (NO$_x$) in ~~a)~~ coral ~~(CR)~~ and ~~b)~~ seagrass ~~(SG)~~-dominated zones. Phase-averages are the mean of all measurements occurring at the same point in the tidal cycle (i.e., mean of all S at high tide), and the range represents conditions during spring and neap tidal cycles. Hydrodynamic data are from April 2014. Dashed lines in panel (e) indicate upper and lower limits of S measured from previous studies of reef communities reviewed by Atkinson and Falter (2003).

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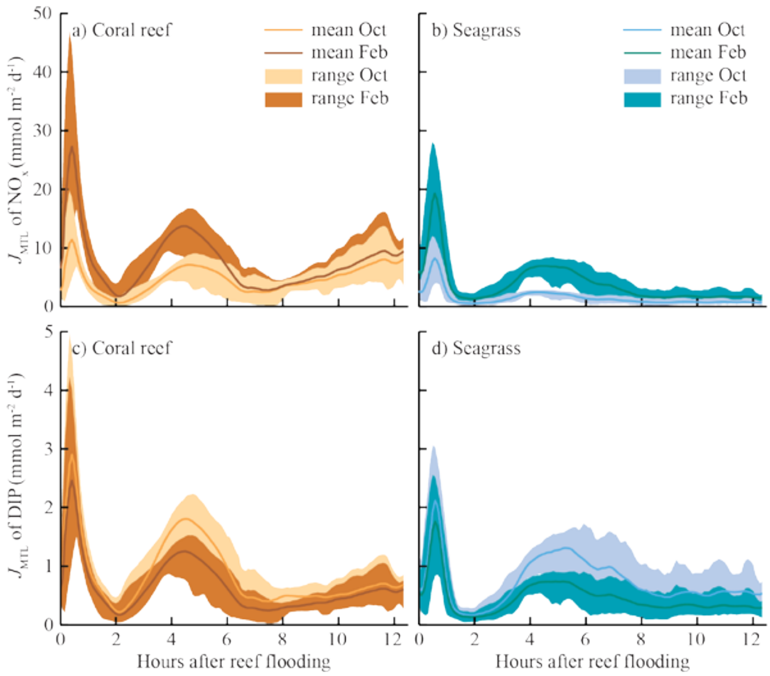

Figure 6. Tidal phase-averaged mass-transfer-limited uptake rates of J_{MTL} for a,b) NO_x and c,d) DIP in both coral and seagrass-dominated zones over a full spring-neap cycle. Phase-averages are the mean of all measurements occurring at the same point in the tidal cycle (i.e., mean of all J_{MTL} at high tide). Shaded areas of J_{MTL} indicate the range, where maximum values approximate uptake during spring tides and minimum values during neap tides. Estimates of J_{MTL} were calculated using tidal phase-averaged nutrient concentrations from Oct and Feb field experiments (Figure 3~~Figure 3~~) and mass-transfer velocity *S* (Figure 5~~Figure 5~~).

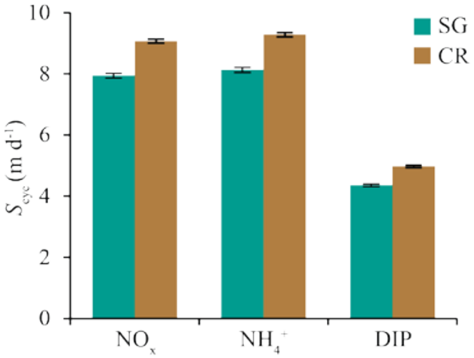

Figure 7. Means (± standard deviation) of mass-transfer velocity *S* for all individual semidiurnal tidal cycles (*n* = 23) for nitrate (NO$_x$), ammonium (NH$_4^+$), and dissolved inorganic phosphorus (DIP). Values are from seagrass (SG) and coral (CR)-dominated communities.

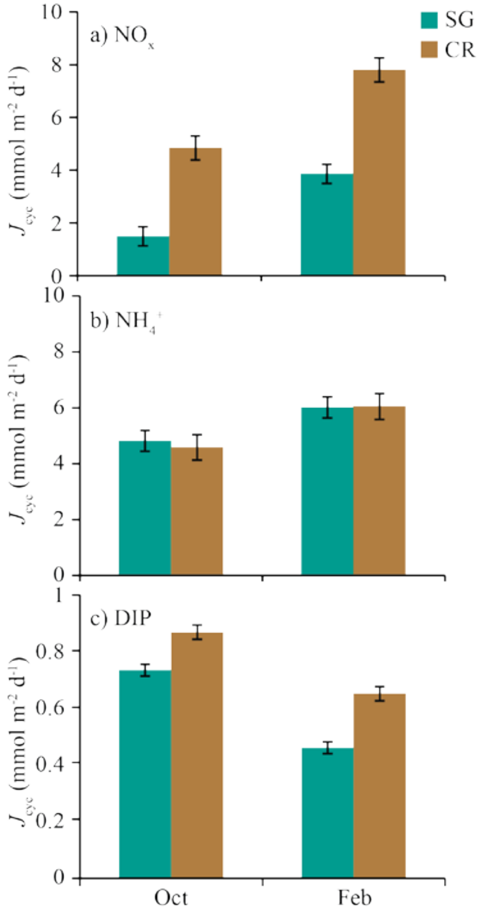

Figure 8. Means (± standard deviation) of mass-transfer-limited uptake J_{MTL} for all individual semidiurnal tidal cycles (n = 23) for a) nitrate (NO$_x$), b) ammonium (NH$_4^+$), and c) dissolved inorganic phosphorus (DIP). Values are from seagrass (SG) and coral (CR)-dominated communities during Oct and Feb field experiments.

Tables

~~**Table 1. Number of duplicate water samples collected during both field experiments at offshore (Off), coral (CR), and seagrass (SG)-dominated sites for analysis of dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP), and dissolved organic nitrogen (DON).**~~

~~Dates~~	~~Season~~	~~Sites~~	~~DIN/DIP~~	~~DON~~
~~5 - 20 Oct 2013~~	~~Dry~~	~~Off~~	~~26~~	~~26~~
		~~CR~~	~~36~~	~~36~~
		~~SG~~	~~33~~	~~32~~
~~4 - 9 Feb 2014~~	~~Wet~~	~~Off~~	~~15~~	~~15~~
		~~CR~~	~~14~~	~~14~~
		~~SG~~	~~13~~	~~13~~

Table 1. Summary of mean (*standard deviation*) conditions in offshore waters ~~(Off)~~ during Oct and Feb field experiments. ~~Number of samples represented by each mean is shown in Table 1.~~ Nutrient species measured are nitrate/nitrite (NO$_x$), ammonium (NH$_4^+$), dissolved inorganic phosphorus (DIP), and dissolved organic nitrogen (DON). Number of duplicate nutrient samples collected is shown for offshore (Off), coral (CR), and seagrass (SG) sites.

	Tide range (m)†				Concentration (µM)				
	Spring	Neap	Salinity	Temp (°C)	NO$_x$	NH$_4^+$	DIP	DON	Number of samples (site)
5-20 Oct 2013	6.7	2.6	34.7 (*0.02*)	27.8 (*0.29*)	0.40 (*0.09*)	0.37 (*0.12*)	0.18 (*0.02*)	12.7 (*2.4*)	26 (Off), 36 (CR), 33 (SG)
4-9 Feb 2014	7.0	2.1	34.2 (*0.06*)	30.1 (*0.06*)	0.92 (*0.19*)	0.69 (*0.23*)	0.15 (*0.03*)	10.7 (*2.5*)	15 (Off), 14 (CR), 13 (SG)

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[†] Difference between max and min water levels

Table 2. Mean (*standard error*) 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 nitrate/nitrite (NO$_x$), ammonium (NH$_4^+$), dissolved inorganic phosphorus (DIP), and dissolved organic nitrogen (DON). Mean net (J_{net}), mass-transfer-limited (J_{MTL}), and release ($J_{release}$) fluxes are from samples taken during the final 6 hours of ebb tide and do not represent fluxes at all phases of the semidiurnal tidal cycle.

		Oct 2013	Feb 2014
NO$_x$	J_{net}	-2.3 (*0.29*)	-2.4 (*0.47*)
	J_{MTL}	3.3 (*0.04*)	3.1 (*0.20*)
	$J_{release}$	-5.5 (*0.30*)	-5.5 (*0.47*)
NH$_4^+$	J_{net}	-0.06 (*0.07*)	-0.6 (*0.11*)
	J_{MTL}	4.6 (*0.05*)	4.5 (*0.09*)
	$J_{release}$	-4.6 (*0.09*)	-5.0 (*0.14*)
DIP	J_{net}	-0.03 (*0.013*)	-0.08 (*0.038*)
	J_{MTL}	0.56 (*0.006*)	0.35 (*0.007*)
	$J_{release}$	-0.59 (*0.014*)	-0.43 (*0.039*)
DON	J_{net}	-1.6 (*2.07*)	3.4 (*1.50*)

MS No.: bg-2018-413
Anonymous Referee #1
Reviewer comments are included below denoted as “Ref1”.
Author response to each comment is given below the comment denoted as “Authors”.
Please note that page/line numbers correspond to the revised version of the manuscript rather than the original version.

Ref1: Gruber et al. present measurements of nutrient concentrations and dissolved nutrient flux rates from a macro tidal reef in the Kimberley region of Australia. They compare net rates of dissolved nutrient uptake to the theoretical mass transfer-limited uptake rates.
They conclude that the reef acts as a source of DIN and DIP to the water column. I find this manuscript well-written with good logic and structure. I have some comments to help improve the readability, especially for readers unfamiliar with the sequences of papers that have come from this group of authors on reef physics-biogeochemistry at this site. Overall, I would classify these comments as minor-to-moderate.

Authors: We thank the reviewer for their supportive and constructive comments on this manuscript (ms).

Ref1: I do have one over-arching question/comment: Tallon reef, and the macrotidal Kimberley, seem like end-members on the spectrum of hydrodynamic conditions experienced on reefs. The authors do a good job referencing the Lowe and Falter (2015) paper highlighting the ubiquity of tidal-dominated reefs (even though most research has gone into studying wave-dominated systems), but how applicable do you think the results here are to other systems? Not many other systems feature large amounts of aerial exposure, asymmetric phase duration, and the massive velocities associated with drainage of the platform. How do these conditions affect the applicability of Tallon reef as a model biogeochemical system whose results can be generalized?

Authors: The tidal range at Tallon reef (~8 m) is typical of ranges experienced by other Kimberley reefs, and our results are likely fairly representative of the ~2000 km^2 of total reef area in this region. An ~8 m tidal range is indeed extreme compared to most reefs worldwide; however, tidal forcing acting as the dominant process in reef circulation is quite common (for example, most of the Great Barrier Reef has tide-dominated circulation). While the large degree of variability in benthic fluxes presented in this paper would not necessarily be representative of most reef systems, the patterns caused by tides are likely to be common among tide-dominated reefs (~30% of reefs worldwide). We have added some text to Discussion Section 4.4 to clarify this, as multiple reviewers had similar comments.

Here are some more detailed comments broken down by sections of the paper.

Abstract:
Ref1: L15-“moderate amount”, replace with an actual quantity of nitrate

Authors: We have added this value to the Abstract.

Introduction:
Ref1: I recommend the authors reverse the ordering of their discussion of organic and inorganic nutrients. Since the manuscript focuses on DIN and DIP, it stands to reason that they should be discussed before the refractory DON and DOP pools. I recommend

that you move the paragraph discussion inorganic nutrients (p. 2, L 10-23) ahead of the discussion of organic nutrients (p. 2, L 1-8).

Authors: We have changed the order of these paragraphs.

Methods:
Section 2.1:
Ref1: Please insert your well-worded definition of “tidal phase-averaging” from the Fig. 5 caption into p. 4, L 10-13. The current wording in this paragraph is ambiguous about whether data are averaged within the phases of a tidal cycle or across tidal cycles. The definition in the figure caption relieves this ambiguity.

Authors: We agree this wording was ambiguous and have revised that sentence for clarity.

Section 2.2.
Ref 1: How were water samples collected exactly? Did you hold the syringe at the surface and draw up the water? Or was it just above the benthos? Did you directly collect the water with the syringe? Or did you use some auto-sampler to sample the water, and then draw up into a syringe? A few more details would be helpful for conveying you’re sampling plan to readers.
Authors: We have added some wording to make Section 2.2 p4 L25-26 clearer.

Section 2.3
Ref1: As it stands now, I think this paragraph could benefit for a few clarifications. First, I think the authors need to be more explicit that the J_net estimate is not for the seagrass site, nor for the coral site, but is the average flux rate along the transect moving from the seagrass to the coral site. Even though this may be obvious for people experienced in control volume approaches, I think it is less intuitive for people without control volume backgrounds.

Authors: We agree with the reviewer and have added a sentence to p5 L19 to clarify this point.

Ref1: When the authors write “C_bar is the mean of concentrations at both stations”, do you mean that you average C_bar between the seagrass and coral site at each time-step? If so, say so. I find the current wording confusing.

Authors: We agree with the reviewer and have added text to p5 L17 to clarify.

Ref1: Please either provide more explanation for why you use “local benthic flux” to describe the unsteadiness term on the RHS of Eq. 2.

Authors: This is a naming convention that illustrates we are working in the frame of reference of the sampling stations. We have modified some text to p5 L21 to clarify.

Ref1: At the end of this paragraph, the authors state “… this method is described in greater detail in Gruber et al. (2017).”. Is this in reference to your interpolation of advective estimates to when you have nutrient samples? I think the authors need to be clear about how the interpolation proceeds, and do so in a manner which does not require reading Gruber et al. (2017) to understand the interpolation.

Authors: We agree and have added an explanation that clarifies this (p5 L23-27).

Section 2.4
Ref1: There is no equation for C_D (p. 6, L 3-5). Instead the authors state "…following the same approach as used in estimates of reef metabolism (Gruber et al. 2017).". Please give additional information on C_D so that interested readers could evaluate your C_D model without having to read Gruber et al. (2017).

Authors: This was an omission and we have added an equation and explanation for calculating C_D (p6 L8-10). It actually wasn't the same method as Gruber et al. 2017 as we found a more realistic (we think) way of estimating the drag coefficient during the time between that article's publication and the submission of this ms.

Minor comments for the Methods:
Ref1: Please add in some information about the precision of your nutrient measurements. Please list Sc value numbers for your inorganic nutrients (or at least diffusion coefficients) (p. 6, L 1-2).

Authors: We have added values for diffusion coefficients to p6 L5-6.

Ref1: Please quantify all error terms that went into your Monte Carlo simulations (p. 6, L 30)

Authors: We have added these terms to p7 L6.

Results:
Ref1: p. 7, L 26: Quantify changes in S due to diffusivity

Authors: This should now be clear to readers as we have added values for diffusion coefficients as above, and the differences in *S* between DIN and DIP species are a proportion of *D*.

Ref1: p. 7, L 27: Quantify temperature effects on S (don't need a lot here, but something to give readers a sense if the error from ignoring temperature variability is on the order of 0.01%, 0.1%, 1%, 10%, etc. would be useful).

Authors: Keeping temperature constant rather than allowing it to vary (and change viscosity) would change values of *S* by 0.009%. We have added this value to the ms (p8 L2).

Figures:
Ref1: Fig 1: Do you have example photos from the SG and CR sites that could be added to this figure to help convey the communities described in the 1st paragraph of the Methods? I think this visual representation would help readers understand the two sites.

Authors: We have added two photos from the sampling sites to Figure 1.

Ref1: Fig. 4: Please describe the error bars (e.g., SD, SE, 95% CI, etc.)

Authors: Thanks for picking that up! Those are standard deviation, which has been added to the figure caption.

Ref1: Fig. 5: I think it would be interesting to put dashed lines on these plots to show the range of S estimates from flume and wave-driven field system studies (p. 10, L 24-28). These would really help show that the variability in S in tidal-dominated systems is far larger than in previously studied systems.

Authors: We have added some lines on Figure 5 and some explanatory text in the figure caption showing a range of *S* values from previous work.

Ref1: Figs. 5 and 6: I think these two figures should be combined, and it would really help readers to see them as a multi-panel plot so that they can understand how closely the J_MTL estimates mirror the S estimates (or alternatively, depart from each other).

Authors: Earlier versions of this ms had Figs 5 and 6 combined, but we found it confusing as *S* could get mistaken for a benthic flux estimate since the phase averages look fairly similar. We prefer to leave these figures separate and no changes have been made to the ms.

Tables:
Ref1: Table 1: "Number of duplicate samples"- does this mean the total number of replicates analyzed? Or the total number of unknown water samples collected, each of which were duplicated? Please clarify. Tables 1 and 2: I think these tables can be combined. This would streamline the manuscript by reducing the number of tables (as it stands right now, Table 1 adds little unique information).

Authors: We have combined Tables 1 and 2 together and clarified the distinction about duplicates in the table caption.

Grammar/typos:
Ref1: p. 1, L 30: Correct subscripting/superscripting of NOx and NH4+

Authors: Thanks for picking that up! Addressed.

Ref1: p. 7, L 24: "through" (though)

Authors: Thanks for picking that up! Addressed.

MS No.: bg-2018-413, Anonymous Referee #2

Referee comments are included below denoted as “Ref2”.

Author response to each referee comment is given below the comment denoted as “Authors”. Please note that page/line numbers correspond to the revised version of the manuscript rather than the original version. Please also note that this version of the manuscript contains corrections from Referee #1.

Ref2: This MS reports fluxes of dissolved inorganic nitrogen and phosphorus and theoretical mass-transfer-limited uptake rates on a strongly tide-dominated reef platform. The amount of nutrients that is released in the water column is calculated from these two data sets.

General evaluation:
Overall, this is a very interesting paper, showing that mass-transfer-limited uptake rates may vary by an order of magnitude on the scale of minutes to hours on tide-dominated reefs, due to substantial variability in flow speeds and water depths over the tidal cycle. Differences between wave- and tide-dominated reef biogeochemistry that are due to the hydrodynamic regime are nicely highlighted. I have a number of relatively minor comments aimed at clarifying the methods and results (detailed below), which the authors should be able to answer easily. The main concern is that nutrient concentrations were not measured in Feb during the first 6 hours of the tidal cycle. Missing data were replaced by nutrient concentrations in offshore waters, which is maybe not perfectly supported by the data, particularly with regard to NOX (Figure 3). I would therefore recommend more caution in the conclusions regarding seasonal differences in JMTL (see below). The discussion about the implications in terms of nutrient limitation is worthwhile, however.

Authors: We thank the referee for their supportive and thorough comments on this manuscript (ms). We address the concerns about using offshore waters for nutrient concentrations in specific comments below.

Comments in detail: Introduction

Ref2: p. 2 Line 5: you could add a reference about corals: Grover, R., Maguer, J. F., Alle- mand, D., & Ferrier-Pagès, C. (2008). Uptake of dissolved free amino acids by the scleractinian coral Stylophora pistillata. Journal of Experimental Biology, 211(6), 860-865.

Authors: This reference has been added to p2 L21.

Methods

2.1 Field site

Ref2: p. 4 Lines 8-10: The hydrodynamic study of Lowe at al. (2015) was performed in March-April 2014, while the MS reports nutrient concentrations from October 2013 and February 2014. Although this is justified later in the MS, the reason why hydrodynamic data collected at the same time as nutrients were not used to calculate mass-transfer-limited uptake rates is unclear at this point.

Authors: We moved an explanatory sentence from p6 to p4 L10-13 to clarify this point earlier in the Methods section for readers.

Ref2: p. 4 Lines 11-13: It is unclear if this concerns mass-transfer-limited uptake rates only, or nutrient fluxes as well.

Authors: We have added clarification to p4 L14 to indicate that this applies to all data.

2.3 Control volume approach

Ref2: Line 8: “Depth-averaged flow speeds were bin-averaged”: do you mean that you first averaged flow speeds in each bin (at 5 min intervals) before depth averaging?

Authors: We think the word “bin-averaged” may have been confusing, so we have clarified the wording on p5 L11.

Ref2: Lines 13-21: I think this paragraph needs some clarification. You are using the mean of concentrations at both stations to calculate the local benthic flux, but you explain then that this local term represents nutrient uptake or release occurring at a sampling station (in my mind, CR or SG, while you are calculating Jnet on the transect). The advective flux is described as nutrient uptake or release during transit between sampling stations, which I also find very confusing. Should not it be what is added or subtracted to the transect due to water transport?

Authors: A control volume approach comes from fluid dynamics and is using both Eulerian (the “local” flux term) and Lagrangian (the “advective” flux term) frames of reference. Basically, when you take samples at fixed positions in a moving fluid, the changes that you see are always a balance of changes in situ (i.e., nutrient uptake at your sampling station) and changes due to water masses advecting into your sampling station. Depending on the flow speed, one term may dominate over another (e.g., in fast flow, the “advective” term will dominate, while in slow flow the “local” term will dominate). Control volumes are used to estimate net fluxes over the entire volume (so a mix of coral and seagrass on the reef flat). We have clarified this on p5 L22-23.

Ref2: The minus sign in front of Jnet is also surprising at first glance. It might be more understandable to state that the sign of Jnet was reversed so that uptake is positive and release negative.

Authors: The minus sign is typical of benthic flux studies, as it is used to define the frame of reference. There is an explanation of the sign convention on p5 L21-22.

2.4 Uptake rates at the limits of mass-transfer

Ref2: p.5 Lines 25-30: In the results, JMTL is first calculated for both CR and SG (Figure 6), not along the study transect. Maybe the reasoning would be easier to follow if there was first a paragraph about the calculation of mass-transfer velocity and JMTL at each one of the two stations, and then, a new paragraph explaining the calculation of Jrelease.

Authors: In Section 2.4, JMTL is first calculated along the study transect (p6 L4) similarly to how Jnet integrates fluxes along the study transect. Addition of text to p5 L22-23 should clarify that Jnet is an integrated measurement over the transect, which should alleviate confusion. On p6 L23-26, Jrelease is calculated using Jnet and JMTL. At the end of this section (p6 L28-p7 L6), we calculate JMTL over the full tidal cycle at both stations individually; we have added some text to this section to clarify these calculations.

Ref2: p.5 Line 30 to p.6 Line 9: This, although necessary, is really hard to follow. There are very nice explanations given in the results (p. 7 Lines 23-27) that might help the reader to go through the equations. Would it be possible to integrate these explanations into this paragraph, specifying the parameters whose variability has the most influence?

Authors: We have moved some text from the Results to p6 L9-12 to give a simpler explanation of mass transfer velocity.

Ref2: Maybe, in a second step, you could simplify equation 4, as some parameters are constants (or nearly constant). This would highlight the influence of flow speed (and possibly water depth: the drag coefficient CD was taken as 0.02 in Gruber et al. (2017), but I didn’t understand if this is the case here) and nutrient diffusivity?

Authors: We prefer to leave Eq. 4 as it is; constant variables are defined in the text below each equation, so it should be clear which variables are constant (very few in Section 2.4 – just density, kinematic viscosity, and diffusivity). We have added the constant values for diffusivity to p6 L13 to make this easier for readers to use.

Ref2: In Gruber et al. (2017), u* is a function of ux, not u (this MS). Is there an explanation? I would also suggest that you explain why you are using u in S calculation, and not ux.

Authors: Ux is used when we make estimates (such as with the CoVo) during the ~unidirectional ebb tide period (since ux is flow speed along the axis of the transect). When we calculate JMTL over the full tidal cycle (no longer ~unidirectional, but rather with large changes in direction), we use u (non-rotated flow speed). We clarified this by using ux in Eqn 4,7 and then explaining the difference in text p7 L1-3.

Ref2: Lines 16-28: I would suggest to give these informations before Line 10 (calculation of Jrelease). Could you please clarify which instruments were deployed exactly? On Figure 1, a velocimeter is shown at CR, but you are not using the data, right? Jnet was calculated from the ADCP data at SG, are you using the same current speed data for the calculation of JMTL and then Jrelease, or the data from Lowe et al. (2015)?

Authors: We think this should now be clarified due to clarification of JMTL calculation at the beginning of Section 2.4 (see responses above). ADP data were used to calculate Jnet, JMTL, and Jrelease as this instrument was deployed in Oct, Feb, and Apr. ADV data were only available from April, so were used only to calculate the full tidal cycle version of JMTL (last part of Section 2.4). We have added explanation of which velocity data were used on p6 L31-p7 L1 and added a comment about ADV deployment time into Figure 1.

Ref2: Lines 29-30: This deserves more explanations. Do you mean, for example, that error bars on Figure 4 are uncertainties in estimates of each one of the calculated fluxes? Please add this information in the caption.

Authors: Indeed, the error bars in Figure 4 are standard deviations of each calculated flux. We have added this information to the caption. Good catch!

Results

3.1 Nutrient concentrations and measured fluxes

Ref2: Line 4: From Table 2, water temperature is about 2◦C warmer in Feb (not 3◦C). Some observations could be supported by statistics: line 6 (DIP and DON are slightly lower in Feb); lines 6-7 (concentrations are similar on the reef and offshore until 6 hours after flooding); lines 18-19 (no difference between Oct and Feb for NH4?).

Authors: Good observation about temperature, we have corrected this. We don’t think statistics on nutrient concentrations or fluxes would add very much to this ms. The purpose of this ms is not to determine whether seasons are significantly different from one another. If that were our purpose, we would need to replicate by season (at least 3 dry seasons and at least 3 wet seasons, which we did not do). Doing statistics would give you some p-values, but it wouldn’t actually give you any truth about seasonality.

3.2 Mass-transfer velocity and nutrient uptake

Ref2: It is unclear from p. 6 lines 3-5 that the drag coefficient was calculated as a function of water depth to draw Figure 5 (the drag coefficient was taken as 0.02 in Gruber et al., 2017). Please clarify in the Methods.

Authors: We actually used a variable form of CD (from McDonald et al. 2006), which was an accidental omission from the ms. We have added an equation and explanation for calculating CD (p6 L14-18). Between the publication of Gruber et al. 2017 and the submission of this ms, we found a more realistic (we believe) way of estimating the drag coefficient. Drag in shallow reef environments is very much an ongoing field of research!

Ref2: p. 7 Lines 26-27: Can you roughly quantify the effect of temperature on S?

Authors: Temperature changes alter S by <0.01%, and we have added this value to p8 L12.

Ref2: p. 7 Line 28: Could you add on Figure 5 the drag coefficient as a function of hours after reef flooding (and maybe flow speed as well, to avoid having to go back to Figure 2). Also state in the caption that hydrodynamic data (and presumably water depth?) are from March-April 2014 (Lowe et al., 2015), while temperature and salinity from Oct 2013 and Feb 2014 (is that right?).

Authors: We have added 4 more panels to Figure 5, which now shows tidal phase-averages of CD and u for both communities. We have also added the clarification that hydrodynamic data are from April 2014 to the caption. Temperature is from April as well, but as discussed above, temperature affects S by a negligible amount (<0.01%); salinity is not part of these calculations, except in the viscosity of seawater, which effectively a constant over the range of salinities measured in the coastal ocean.

Ref2: p. 7 Line 32: Figure 2 doesn’t show water depth at SG and CR. Could you add tidal phase-averaged water depth at each site on Figure 3?

Authors: Figure 2 shows water depth at SG, and we have added this clarification to the caption of this figure. Water depth at CR is indistinguishable from SG as the reef platform is basically flat (there is a 10 cm vertical difference between SG and CR, which would not be visible in these figures). Tidal phase-averaged water depth is already shown in Figure 3 as a black line.

Ref2: p. 8 Line 4: Could you explain “which differ by a factor of <4”? Is it the ratio of the flow speeds?

Authors: This statement refers to S, and we have added this clarification to p8 L21.

Ref2: Figure 6: There are missing nutrient data, especially in Feb (0-6 hours after reef flooding; Figure 3). I understand from p. 6 Lines 24-26 that missing data were replaced by nutrient concentrations in offshore waters. From Figure 3, this looks acceptable in Oct, but maybe less in Feb, especially for NOx. Could you show on Figure 6 the time periods during which nutrients were actually measured?

Authors: As the referee points out, we did not collect water samples during flood/high tide in Feb. However, from the samples collected in Oct, it can be seen that water flooding the reef (i.e. at 0-1 hours after reef flooding in Figure 3) has nutrient concentrations very close to offshore waters. This is because this flooding water is offshore water – flow is occurring across the entire reef flat, which is why seagrass and coral nutrient concentrations are similar during this time. As can be seen in Oct, sometime around high tide (~3 h after reef flooding) concentrations begin slowly diverging from those in offshore waters. This same pattern of reef concentrations roughly matching offshore concentrations from 0-3 h would almost certainly occur in Feb as well, since the hydrodynamics of the reef remain the same. We agree that there is a period of 2.5 hours (3 – 5.5 hours after reef flooding) when concentrations were not measured but are likely diverging from those offshore. Rather than make assumptions about what nutrient concentrations were during those 2.5 hours, we applied rather large error terms to tidal phase-averaged concentrations of NOx and DIP (standard deviations of 0.5 uM and 0.05 uM, respectively). These values are given on p7 L17-18. This error was then propagated (via Monte-Carlo) through all estimates of JMTL.

Ref2: p. 8 Line 10: JMTL is not shown for ammonia. Why?

Authors: JMTL isn’t shown in the large multi-panel figures (Figs 4, 5, and 6) because it looks very similar to NOx (being concentration and flow-dependent) and we were trying to minimize the size and complexity of figures (there are quite a few figures already). The reference to NH4 on p8 L27 has been removed to clarify this sentence.

Ref2: p. 8 Lines 11-13: This looks speculative, as nutrient concentrations were not measured in Feb during the first 6 hours of the tidal cycle (see previous comment on Figure 6). Please state clearly that you are assuming that NOx concentrations are similar on the reef and offshore during this period and add some comment in the Discussion.

Authors: We are confident that for the period from flood to high tide (0-3 h after reef flooding in Fig 6), offshore nutrient concentrations are representative of concentrations on the reef for reasons discussed above. We have made the wording more cautious on p8 L28-30.

Ref2: Figure 4: I assume that JMTL is the mean of the values shown on Figure 6 for SG and CR?

Authors: JMTL shown there was calculated along the transect (SG to CR). We have added a note in Figure 4 caption to clarify.

Ref2: p. 8 Line 17: Is “NOx release” “net NOx release”?
Seasonal differences: could you add your stats as a column in Table 3?

Authors: We have added “net” to NOx release as suggested.

p. 8 Line 19: This comment refers to Lines 11-13 (see above). I would suggest to simply state that, contrary to DIP, DIN concentrations are similar at both seasons during the part of the tidal cycle studied.

Ref2: P 8 from Line 21, and Figures 7 and 8: I understand that you averaged S and JMTL over each one of the 12-hours period available, and then averaged these averages. If that’s right, first you should explain why, and then, I don’t think averaging averages is the best way to assess standard deviations (they also appear very small in Figure 7, given the range in Figure 5).

Authors: That is correct. We thought this would be an interesting way to conceptualise the data in a ‘bigger picture’ sense given that tide-dominated systems are so physically controlled by the tide. We could have just averaged all the data together, but we were trying to be creative (and more physically-focused) since tide-dominated systems have never really been studied before! We have added explanation to p7 L8-9. Standard deviations are not averaged, but are generated by running the entire calculation (as shown in the Methods) with 10,000 sets of noise-corrupted data using Monte-Carlo simulations. The range you see in Figure 5 is not standard deviations, but are values from the spring vs neap cycle (see Fig 5 caption). Standard deviations are relatively small for our estimates because S is so closely controlled by flow speed (as you can see in Fig 5); as a result, JMTL is also closely controlled by flow speed. Flow speed has a small standard deviation thanks to the accuracy and precision of ADPs/ADVs, which is then propagated through our estimates.

Ref2: Lines 21-24 and Figure 7: I’m not sure this is very useful. The two points about S are: (1) the small difference between SG and CR, which is already described p. 7 Lines 31-32 and p. 8 Line 3, and (2) the difference between DIN and DIP which you can easily talk about after p. 7 Lines 25-26.

Authors: Figure 7 does add to the story because it is showing the ‘bigger picture’ of mass transfer velocity. The first discussion of S (p7 L31-32 in the referree’s comment) talks about how it varies within a tidal cycle (at times 30% greater at CR vs SG). Figure 7 (and Lines 21-24 in the referee’s comment) show the ‘bigger picture’ that when averaged over longer time periods, differences between SG and CR are actually fairly small. We prefer to leave this as is.

Ref2: From Line 24 and Figure 8: Again, I would not recommend using all data from Figure 6 due to missing nutrient values. Differences between seasons and sites are already described (p. 8 Lines 6-14).

Authors: We believe we are representing missing nutrient values in a reasonable way through: assumptions based on hydrodynamics (described previously) and relatively large error terms (standard deviation of 0.5 uM for NOx), which are propagated through these calculations. We would prefer to leave this figure as is.

Discussion

Ref2: p. 9 Line 17 (DIP and DON): DIP and DON are “slightly lower (. . .) in Feb” p. 7 Line 6 and “similar between seasons” p. 9 Line 17. One of these two sentences needs to be re-written after stats are performed.

Authors: We have changed p7 L24 to read “similar between seasons”. Our response to stats is discussed previously.

Ref2: Line 28 to p.10 Line 2: Do you mean that mass-transfer-limited uptake was demonstrated in controlled environments because nutrient release was negligible compared to uptake?

Authors: That is the most likely explanation why flume experiments show uptake near mass-transfer limits. Whereas, in natural reef environments, a host of other processes (detrital remineralisation, phytoplankton grazing, etc) are occurring that confound uptake measurements (as discussed in the following paragraph in Section 4.2). We have added text (p10 L12) to clarify this.

Ref2: p. 10 Line 4: overestimation of DIN release on Tallon: I don’t understand your point. Whatever the source, I think that your calculation of DIN release is fine. Could you clarify?

Authors: This line is simply addressing the question of other DIN inputs to the CoVo that may not be accounted for in our calculations (like N2-fixation and porewater advection, on which there is some existing literature). We think this text is fine as written.

Ref2: References
There are two papers by Lowe et al., 2015. Please use 2015a and 2015b throughout the text.

Authors: There is only one Lowe et al., 2015 paper. The other paper is Lowe and Falter 2015.

MS No.: bg-2018-413, Anonymous Referee #3

Referee comments are included below denoted as “Ref3”.

Author response to each referee comment is given below the comment denoted as “Authors”. Please note that page/line numbers correspond to the revised version of the manuscript rather than the original version. Please also note that this version of the manuscript contains corrections from Referees #1 and 2.

Ref3: The study reports results from measurements of dissolved nitrogen and phosphorus fluxes in a tide-dominated reef. The fluxes were estimated using a one-dimensional control volume method, i.e. nutrient concentrations were measured on the reef platform at two points along the flow path of the tidal currents, and from the concentrations changes occurring between the two points, fluxes were estimated. The measurements suggest a release of nitrate, while fluxes of NH4+ and DIP varied between net uptake and release. The results are interesting and produce new insights into the functioning of tide- dominated reefs.

Authors: We thank the referee for their supportive comments and review of this manuscript (ms).

Ref3: A few points need clarification and revision: This is a subtropical environment with healthy seagrass and coral cover. Nutrients in the water column are low and it is surprising that the reef platform with seagrass and healthy coral releases nitrate during low tide. Assuming that during the low water phase photosynthesis of vascular and unicellular plants reaches a maximum, one would expect nutrient uptake of the benthic community resulting in a net uptake.

Authors: Actually, it is common for in situ reef studies communities to measure a release of nitrate. There are many references cited in the Discussion that have also found nitrate release on reefs (p10 L12-16). This is thought to be due to processes such as grazing of benthic filter-feeders and other reef organisms on phytoplankton and detrital remineralisation. To our knowledge, no one has yet conclusively showed why nitrate release occurs, so this is very much an open question! We would guess that this release is not coming from the seagrass community; based on nutrient concentrations at the end of ebb tide (when advection was negligible) shown in Figure 3, nitrate is quite low in the seagrass community. It is important to note that the control volume (CoVo) method provides estimates of benthic fluxes over the length of the transect (thus a function of all ecological communities along the transect), rather than separate fluxes for seagrass and coral communities. This point has been clarified on p5 L22-23.

Ref3: Tidal current vector fields previously published by the authors for this study site (Lowe et al. 2015) revealed that the tidal water in and outflow is not symmetrical, resulting in a residual current entering the reef at its southeastern edge and leaving at its northeastern edge. These residual currents include flows parallel to the reef, which may cause that the two sampling stations measure some waters that took different pathways over the reef platform. It is conceivable that the residual currents transport water with different nutrient concentrations to the two measuring stations and that the observed difference in nitrate concentration between the two stations is a function of the pathways of the residual currents.

Authors: We are confident that ‘current pathways’ are not the cause of the observed nitrate release. The CoVo approach is only used when the direction of flow aligns with the sampling transect (during ebb tide), and not when flow vectors are moving perpendicular to the transect (this is described on p5 L6-8). Nitrate concentrations become most elevated at the end of ebb tide, when flow is very slow ~2 cm/s. During this period, the “local” flux term will dominate our estimates of Jnet, meaning that local processes (nutrient release in the vicinity of the station) are causing these changes rather than advection of water parcels.

Ref3: The reef lagoon appears to be lined by mangrove forest and the seagrass community accumulates organic-rich sediments. The mixed zone between seagrass and coral has pockets of sediment and a porous structure. Could release of fluid from the sediments and the porous structure of the mixed zone explain the nutrient increase during decreasing water level as the path of the residual currents is along the mixed zone? This should be clarified.

Authors: There may be porewater advection occurring on Tallon reef, which we discuss on p10 L16-18. However, we doubt this is the cause of increases in nitrate, as porewater tends to have very low nitrate concentrations (near detection limit). The cause of net nitrate release is most likely the processes discussed in Section 4.2.

Ref3: The tidal range exceeding 8 m is unusual. This is not a typical scenario, which needs to be considered and pointed out when generalizing the results.

Authors: We agree with this comment and have added a new paragraph to the Discussion to help readers understand how our results can perhaps be generalised to other reefs that are tide-dominated but not necessarily macrotidal. See p12 L19-28.

Minor comments.

Ref3: P1L9 a “forcing” is not a “regime”, please rephrase.

Authors: We have rephrased this statement.

Ref3: P1L25 “Reef waters have carbon concentrations that are orders of magnitude greater than nitrogen (N) and phosphorus (P)”. If a ratio close to Redfield is applicable here, C concentrations order(s) magnitudes higher than those of the nutrients can be expected. Benthic communities would not be nutrient limited. If carbon is way higher, please rephrase.

Authors: I’m not sure I understand this comment. P1 L25 is referring to the fact that benthic organisms tend to be N and/or P limited rather than C-limited. The Redfield ratio is a C:N:P ratio that is often used to infer phytoplankton nutrient limitation, and I’m not sure how this is related to the line in our ms?

Ref3: P2L10 “labile dissolved inorganic species”. “Labile” here seems the wrong word as some of these inorganic species can be very stable in the marine environment.

Authors: “Labile” is a term commonly used to refer to NOx, NH4, and PO4, as these nutrient species can be readily utilised by organisms. In contrast, DON and DOP are often called “refractory” meaning less-readily utilised by organisms.

Ref3: P2L16 “turbulent transport” should be added to the list of the controls of nutrient transfer

Authors: This sentence is referring to the relationship derived from fluid dynamics that controls benthic nutrient uptake and is not a ‘list of controls of nutrient transfer’. Later in the ms (Eqns 3 and 4), these relationships are defined mathematically, and do not include turbulence.

P4L8 “reef benthos, which represent the net uptake or release of nutrients”. Please add information on nutrient uptake/release of water column organisms

Authors: This statement has been rephrased (p4 L7-8) for clarity.

Ref3: P4L32 “All nutrient concentrations presented are the mean of duplicate samples” why didn’t you take triplicate samples, which would have allowed calculation of standard deviation, opening up other options for statistical analysis?

Authors: Triplicate samples weren’t part of this study design, as we weren’t attempting to determine statistically whether one nutrient measurement was significantly different to another nutrient measurement. Error estimates, however, are central to this study as described on p7 L14-18.

Ref3: P5L8 How large is the error introduced by using depth-averaged current velocity instead

Authors: Instead of…? Depth-averaged current velocity is fairly ubiquitous in studies of shallow water environments.

Ref3: P11L8 If the coral zone is 20% more productive than the seagrass zone (Gruber et al., 2017), one would expect an increasing N consumption during decreasing water level as light intensity at the reef surface increases, with higher N demands in the coral zone. The results suggest the opposite, how is this explained?

Authors: As mentioned above, the CoVo approach gives flux estimates over the full transect (incorporating seagrass and coral communities). This release of nitrate is most likely coming from the reef community, for reasons that are discussed above (phytoplankton grazing and remineralisation) and in detail in Section 4.3 of the Discussion.

Ref3: P11L20 “In a simplified wave-driven reef, offshore (oceanic) water moves from reef crest to back reef roughly unidirectionally. Thus, benthic communities are subjected to the physico-chemical water properties present in offshore waters modified by the communities ‘upstream’ of them.” This should be explained in more detail, as water transported into the reef also has to leave the reef, irrespective of the transport process. This release may traverse the communities that contacted this water before as in the tidal dominated reef.

Authors: On wave-driven reefs, water tends to cross the reef flat and then travel alongshore and eventually exit the reef through channels. This is a well-established transport process (see Monismith, S. (2007): Hydrodynamics of coral reefs, Annu Rev Fluid Mech, 39, 37-55 for more details and references therein). We have added some text (p12 L5) to clarify this.