REPORT

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Mass-transfer-limited nitrate uptake on a coral reef flat, Warraber Island, Torres Strait, Australia

Abstract Previous research has identified a relationship between the rate of dissipation of turbulent kinetic energy, ε, and the mass-transfer-limited rate of uptake by a surface, herein called the $\varepsilon^{1/4}$ law, and suggests this law may be applicable to nutrient uptake on coral reefs. To test this suggestion, nitrate uptake rate and gravitational potential energy loss have been measured for a section of Warraber Island reef flat, Torres Strait, northern Australia. The reef flat section is 3 km long, with a 3 m tidal range, and on the days measured, subject to 6 m s^{-1} tradewinds. The measured nitrate uptake coefficient, S, on two consecutive days during the rising tide was 1.23 ± 0.28 and $1.42 \pm 0.52 \times 10^{-4}$ m s^{-1}. The measured loss of gravitational potential energy across the reef flat, ΔGPE, on the same rising tides over a 178 m section was 208 ± 24 and 161 ± 20 kg m^{-1} s^{-2}. Assuming the ΔGPE is dissipated as turbulent kinetic energy in the water column, and using the $\varepsilon^{1/4}$ law, the mass-transfer-limited nitrate uptake coefficient, S_{MTL}, on the two days was 1.57 ± 0.03 and $1.45 \pm 0.04 \times 10^{-4}$ m s^{-1}. Nitrate uptake on Warraber Island reef flat is close to the mass-transfer limit, and is determined by oceanographic nitrate concentrations and energy climate.

Keywords Coral reefs · Friction · Nutrient uptake · Hydrodynamics · Torres Strait · Great Barrier Reef

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Introduction

Coral reef flats maintain a high rate of gross productivity per m^2 despite the relatively low nutrient concentration of the oceanic water that passes above their structures (Hatcher 1988). To explain this observation, a number of sources of nutrients have been proposed, including groundwater inputs, tidal mixing, and upwelling. Others have proposed that corals tightly recycle nutrients, and therefore do not require a large external supply of nutrients. A history of these ideas with references is detailed in Hatcher (1988, 1990) and Hearn et al. (2001).

In terms of the experiments detailed in this paper, the most significant historical studies consider coral reefs at an ecosystem scale. By measuring changing concentrations of biologically active water column constituents such as oxygen and phosphorus, early researchers were able to elucidate reef-scale phenomena such as gross and net community production and calcification rates (Sargent and Austin 1949; Odum and Odum 1955; Smith 1973). Following this work, Atkinson (1987) measured phosphate concentration along multiple transects across the Kaneohe Bay (Hawaii) reef flat in the direction of flow. These measurements showed that nutrients were removed from the water column and that the rate at which nutrients are taken up could account for the high productivity (Atkinson 1987; Atkinson and Smith 1987).

In a series of papers, it was further proposed that nutrient uptake by coral reefs is mass-transfer limited (Atkinson 1992; Bilger and Atkinson 1992; Atkinson and Bilger 1992). When the uptake is mass-transfer limited, the rate-limiting process governing uptake is the diffusion of nutrient ions across a diffusive boundary layer close to the surface of the corals. Coral communities not only take nutrients from the water column (Atkinson 1987), but it was proposed they were taking the nutrients at the fastest rate physically possible (Bilger and Atkinson 1992).

At the mass-transfer limit, uptake becomes dependent on hydrodynamic characteristics which affect the thickness of the diffusive boundary layer, such as water velocity, surface roughness, and viscosity. Experiments in laboratory flumes have demonstrated that nutrient uptake on experimental coral communities increases with increasing nutrient concentration, water velocity, and surface roughness (Thomas and Atkinson 1997).

As further evidence of mass-transfer limitation, gypsum dissolution from coral-shaped surfaces has been found to occur at a similar rate to ammonia uptake by live corals (Baird and Atkinson 1997). The energy dissipated by water scraping across a rough surface has long been recognized in the engineering literature as a convenient measure of the combined effects of hydrodynamic processes (Nikuradse 1933). Baird and Atkinson (1997) used an engineering relationship (Dipprey and Sabersky 1963) that correlates energy dissipation with heat transfer to accurately predict both the rate of gypsum dissolution from, and ammonia uptake by, coral surfaces.

While the above-mentioned experiments have convincingly demonstrated mass-transfer limitation of nutrient uptake in a laboratory setting, corresponding studies on natural coral reef flats have proven difficult. The laboratory experiments relied on elevated nutrient concentrations and techniques for measuring energy dissipation that cannot be applied in the field.

A more theoretical understanding of the relationship between energy dissipation and mass transfer is detailed in the fluid mechanics literature (Tennekes and Lumley 1972). Richardson (1922) introduced the idea of an inviscid cascade of turbulent kinetic energy from large to small scales of motion until it is dissipated as heat by molecular viscosity. The rate of this cascade of energy is called the turbulent energy dissipation rate, ε. In a classical paper in 1941, Kolmogorov proposed a statistical distribution of homogeneous turbulence with a spectrum uniquely characterized by the Kolmogorov length, $L = (v^3/\varepsilon)^{1/4}$ (Tennekes and Lumley 1972), where v is the kinematic viscosity.

Batchelor (1959) later showed that the corresponding spectrum of gradients in a tracer, such as a nutrient, is characterized by a length, $L_\theta = (D^2 v/\varepsilon)^{1/4}$, where D is the molecular diffusivity of the tracer, which bears his name (Tennekes and Lumley 1972). L and L_θ are the length scales at which there is an extremely rapid decrease in turbulent fluctuations (of either momentum or tracer), so that at smaller spatial scales, transport of these quantities can only occur by molecular processes.

Recently, Hearn et al. (2001) have used the Batchelor length to estimate nutrient uptake by coral reefs. Specifically, they assumed that the thickness of the diffusive boundary layer surrounding the corals, δ, is approximately equal to the Batchelor length, L_θ, for the particular nutrient. The nutrient uptake rate on a coral surface then follows directly from the values of ε, v, and D (for the ions of the nutrient). Hearn et al. (2001) showed that the uptake rate is proportional to the fourth root of ε and this is referred to as the $\varepsilon^{1/4}$ law (or the

'uptake-dissipation' law). Since the $\varepsilon^{1/4}$ law contains only three basic physical quantities and is derived from the physical arguments of Kolmogorov and Batchelor, it can be considered to be a fundamental law. Furthermore, the $\varepsilon^{1/4}$ law allows the mass-transfer-limited uptake rate of a nutrient to be found from purely physical measurements on a coral reef.

In order to apply the $\varepsilon^{1/4}$ law, the rate of dissipation of TKE in the water column must be determined. In some coral reef environments, loss of gravitational energy will be the main source of the energy dissipated (see Appendix A). The aim of this study is to use the loss of gravitational potential energy (GPE) as a measure of energy dissipation to determine if nutrient uptake on a natural coral reef flat is mass-transfer limited. To this end, nutrient uptake and GPE loss were measured on Warraber Island reef flat, Torres Strait (10°13'S, 142°50'E) on 2 days in August 2002. The measured nutrient uptake rates are compared to those predicted using the measured GPE loss and the $\varepsilon^{1/4}$ law. Assuming that all GPE is dissipated as TKE in the water column, this comparison provides a test of the mass-transfer-limitation hypothesis and the $\varepsilon^{1/4}$ law on a natural coral reef flat.

Study area

Torres Strait is a shallow (15–25 m deep) broad channel situated between the northern-most point of the Australian mainland, Cape York, and Papua New Guinea (Fig. 1). It is a region of large semi-diurnal tides, with tidal ranges of up to 3.5 m and strong tidal currents of up to 4 m s^{-1} (Woodroffe et al. 2000). The study was conducted during the dry winter period when strong southeasterly tradewinds blow continuously at approximately 6–8 m s^{-1}.

Warraber Island is a coral sand cay situated in the central Torres Strait (10°13'S, 142°50'E). The island occupies the western, leeward end of an elongated platform reef whose long axis extends over 5 km to the east (Fig. 1). The strongest wave action is on the southeast rim of the reef. The nutrient uptake and energy dissipation measurements were undertaken on a transect that extended in a northwest direction for 2 km from the southeast reef rim in the direction of flow during the flooding tide (Figs. 1, 2).

The reef flat to the south and east of the island is elevated and dry for much of the tidal cycle and is covered with sand with protrusions of dead and eroded coral colonies (Woodroffe et al. 2000). Coral outcrops increase in density and size towards the outer part of the reef flat.

Materials and methods

Warraber Island reef flat provides an ideal situation for measuring a loss in GPE, nutrient uptake and testing the $\varepsilon^{1/4}$ law. The reef flat is long, allowing sufficient
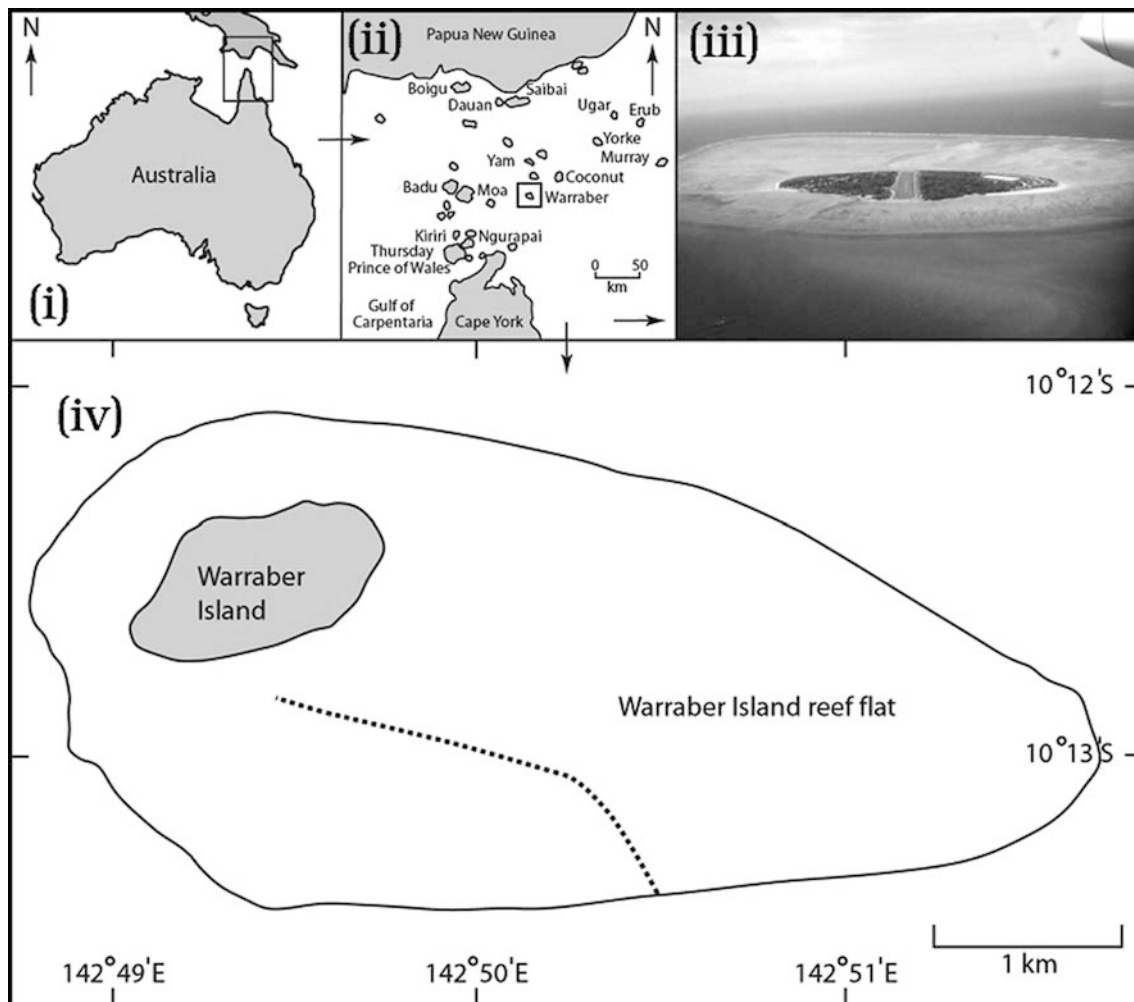
Fig. 1 Location of the study site showing (*clockwise from top left*): (**i**) and (**ii**) geographic location of Torres Strait and Warraber Island; (**iii**) an aerial photo of Warraber Island viewed from the northwest; and (**iv**) a detailed map of Warraber Island reef flat showing the approximate path of the water during nutrient sampling, and the extent of the reef flat from the reef crest to the island. See Fig. 2 for a more detailed path trajectory and location of instrument deployments

residence time for a measurable removal of nutrients from the water column. The tidal range is large, with significant periods of shallow water depth, when nutrients are most quickly depleted. During the dry season, meteorological conditions and the path of the water over the reef flat are predictable. This allows instruments to be deployed in locations well suited for the experiment, and facilitates the comparison of measurements on consecutive days. In particular, instruments can be deployed on flow streamlines. The rates of nutrient uptake and energy dissipation were measured on the reef flat, 400 to 1,300 m along the flow trajectory from the reef crest. In this region, the acceleration terms due to wave breaking are small, and the one-dimensional, depth-averaged flow becomes a simple balance between GPE loss and bottom friction (see Appendix A). This combination of experimental conditions allows a direct test of mass-transfer-limitation hypothesis and $\varepsilon^{1/4}$ law on a natural coral reef flat.

Measurement of nutrient uptake

Nutrient sampling was undertaken on 2 days (8th and 9th August 2002) during a flooding tide. Sampling began on the landward slope of the elevated reef crest. Samples were taken from an inflatable boat while following a neutrally buoyant drogue (filled 1-L plastic bottle) as it was advected from the start point across the reef flat, passed the instrument stations, and headed on towards the island (Fig. 2). A 9-L bucket was used to extract a water sample from the top 50 cm of the water column, and the time, total depth of water (using a tape measure), and position (using a Garmin GPS 45 Personal Navigator) of the sample were recorded. Two replicates were taken from the water sample and individually passed through a Sarstedt Filtropur S 0.45-μm filter into 10 mL vials. A fresh filter was used for each water sample. All samples were frozen within 4 h of collection. The water samples were analyzed for nitrate/nitrite and phosphate at the CSIRO Marine Research Laboratories, Hobart, between the 28th and 30th of August 2002. The
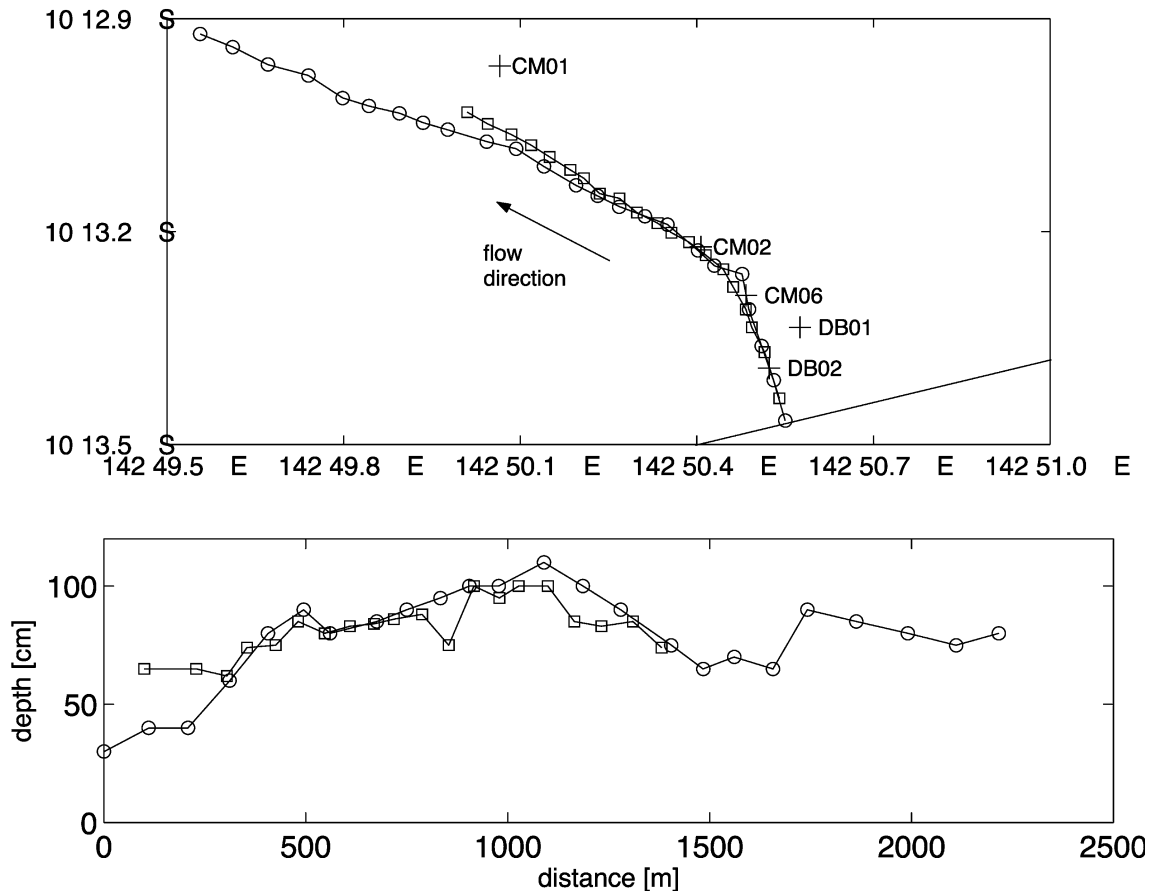
Fig. 2 The nutrient sampling transect on Warraber Island reef flat. The top panel shows the flow path of a drogue on two days (□ August 8, ○ August 9) from the reef crest (10°13.4'S, 142°50.5'E) past a wave gauge (*DB02*), and the two instrument stations (*CM06* and *CM02*). The *squares* and *circles* represent nutrient sampling locations on the 2 days. *DB01* and *CM01* were earlier deployments of *DB02* and *CM06*, respectively. *CM06* and *CM02* are 178 m apart. The *straight line* represents the reef crest (outer rim of the reef platform). The bottom panel shows the depth of water at the time of sampling against distance along the transect

replicates were averaged, and the results are plotted as a function of distance along the flow trajectory from the reef crest for August 8 and 9 (Figs. 3, 4).

The rate m at which nutrients are taken up by the benthos is given by:

$$m = S \, C \tag{1}$$

where C is the depth-averaged concentration of the nutrient in the water column, and S is the nutrient uptake coefficient. Note that m is a flux per unit projected area of benthos. Since the uptake rate is proportional to the concentration, the change in concentration of the nutrient as a result of uptake will be exponential.

In this paper, nutrient uptake rate is initially quantified by k, the gradient of the natural logarithm of the nutrient concentration against distance along the flow trajectory of water across the reef flat (Atkinson and Bilger 1992). The constant k is an exponential decay coefficient for concentration with distance, and has units

of length^{-1}. A type II linear regression is used to account for the error in measuring the distance across the reef (GPS maximum error ± 15 m) and the error in nutrient analysis (± 0.02 μM). The standard error in k given in the results accounts for both the errors in measurement and the uncertainty of the linear regression. A second measure of nutrient uptake used is the dimensionless Stanton number, St. The Stanton number is the ratio of the uptake rate of the nutrient to the rate of advection of the nutrient across the surface. The product of k and the mean depth, d, over the transect is used to obtain the observed Stanton number for the reef flat (Bilger and Atkinson 1992):

$$St = k \, d \tag{2}$$

The nutrient uptake coefficient, S, is given by:

$$S = St \, U \tag{3}$$

where U is the depth-averaged velocity of the water across the reef. The rate of removal of nutrient from the water column, m, can then be obtained from Eq. (1).

Measurement of gravitational potential energy loss

Measurements of water velocity and pressure were obtained at two sites (CM02 and CM06) on Warraber Island reef flat (Fig. 2). The stations were located

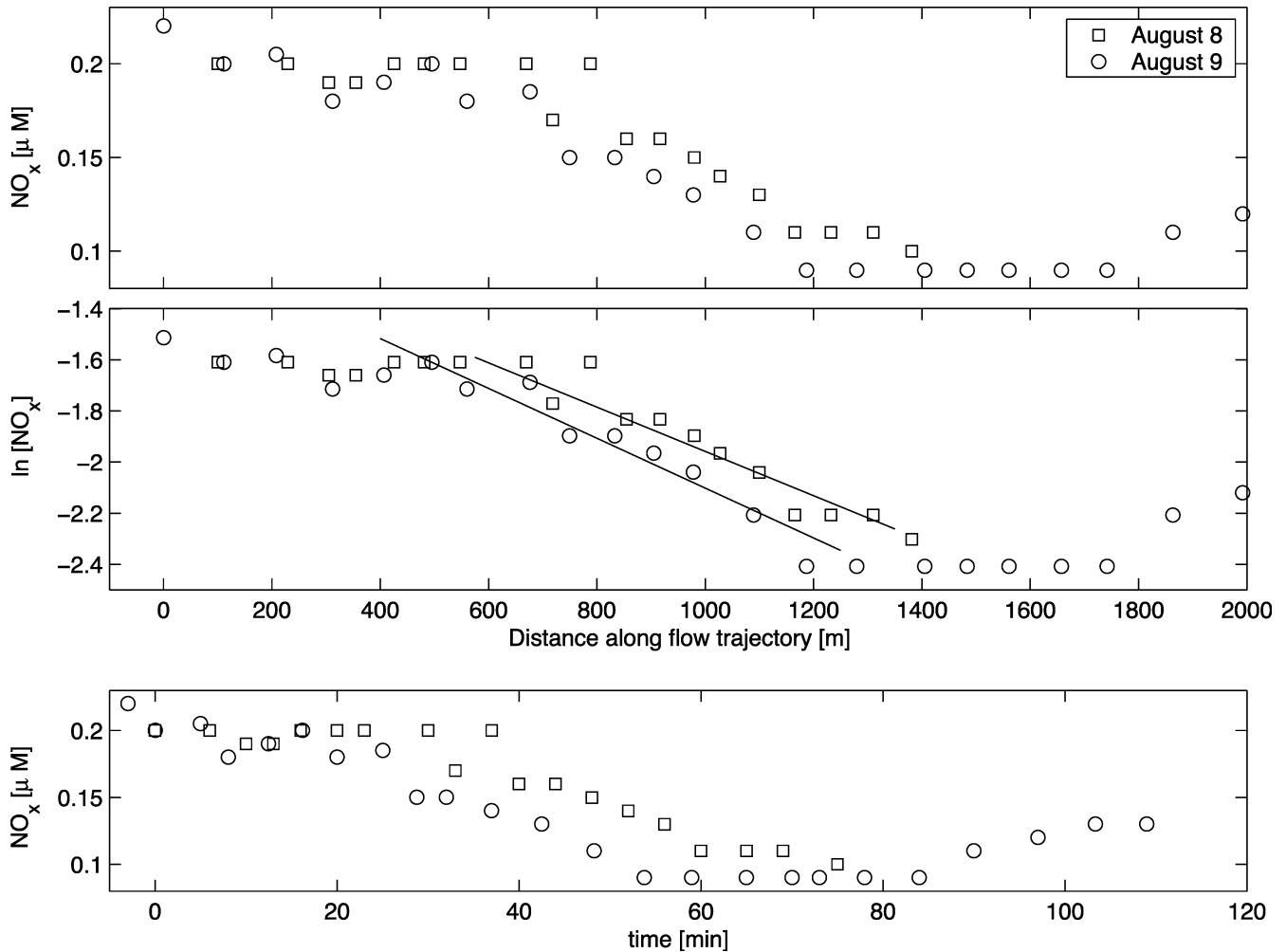**Fig. 3** Dissolved inorganic nitrogen ($NO_3^- + NO_2^-$) concentration (*top*) and the natural logarithm of dissolved nitrogen concentration (*center*) plotted against distance along the trajectory of the flow from the reef crest. The two lines represent a linear regression of the natural logarithm of dissolved inorganic nitrogen against distance over the section 400 to 1,300 m for August 8 and 9 ($r^2 = 0.92$ for both days). The constant k is given by the slope of the lines on each day. The bottom panel plots dissolved inorganic nitrogen concentration against time since the drogue was released at the reef crest

approximately 380 and 560 m along the flow trajectory from the reef crest. Water velocity was measured using a Falmouth Scientific Instruments two-dimensional Acoustic Current Meter (ACM), and pressure using a Honeywell Differential Pressure Sensor (DPS) logging to an auxiliary channel of the ACM. The ACM and DPS were mounted on a vertical 2 m aluminum pole that was supported at the base by a centered 30 cm crossbar, and at the top by four, approximately 5 m long guy ropes. The pole also supported a clear plastic tube 44 mm in internal diameter with a 4 mm diameter hole located 5 cm off the bottom, called a stilling well, which acts to damp out high-frequency wave motions. The distance between instrument stations and an estimate of the relative elevations of the pressure sensors was surveyed using an engineer level and stadia rod.

The ACM measures water speed to an accuracy of ± 0.01 m s^{-1} and direction to $\pm 2°$. The measuring volume was approximately 0.35 and 0.45 m above the reef surface, and located upstream of the instrument mounting. A differential pressure sensor was chosen to maximize accuracy. The Honeywell DPS has temperature compensation and maintains a linear relationship between port pressure difference and voltage output at pressures between 0 to 0.711 m of freshwater to within ± 1.8 mm, with a maximum response time of 10^{-3} s. One port of the DPS was exposed to atmospheric pressure approximately 3 m above the reef surface, while the other port was vented to the water contained within the stilling well. Water velocity and pressure were sampled every 0.5 s, and averaged every 60 s.

The measured pressure difference varied within a range approximately equal to the accuracy of the engineer level at resolving elevation differences. As a result, the level was not used to determine the absolute elevations of the pressure sensors. Instead, a type II linear regression was used to relate the mean water velocity and pressure difference between the two instrument locations. At zero current flow along a line in the direction of the current meters, the absolute water level height difference will be close to zero (wind and geostrophic setup being
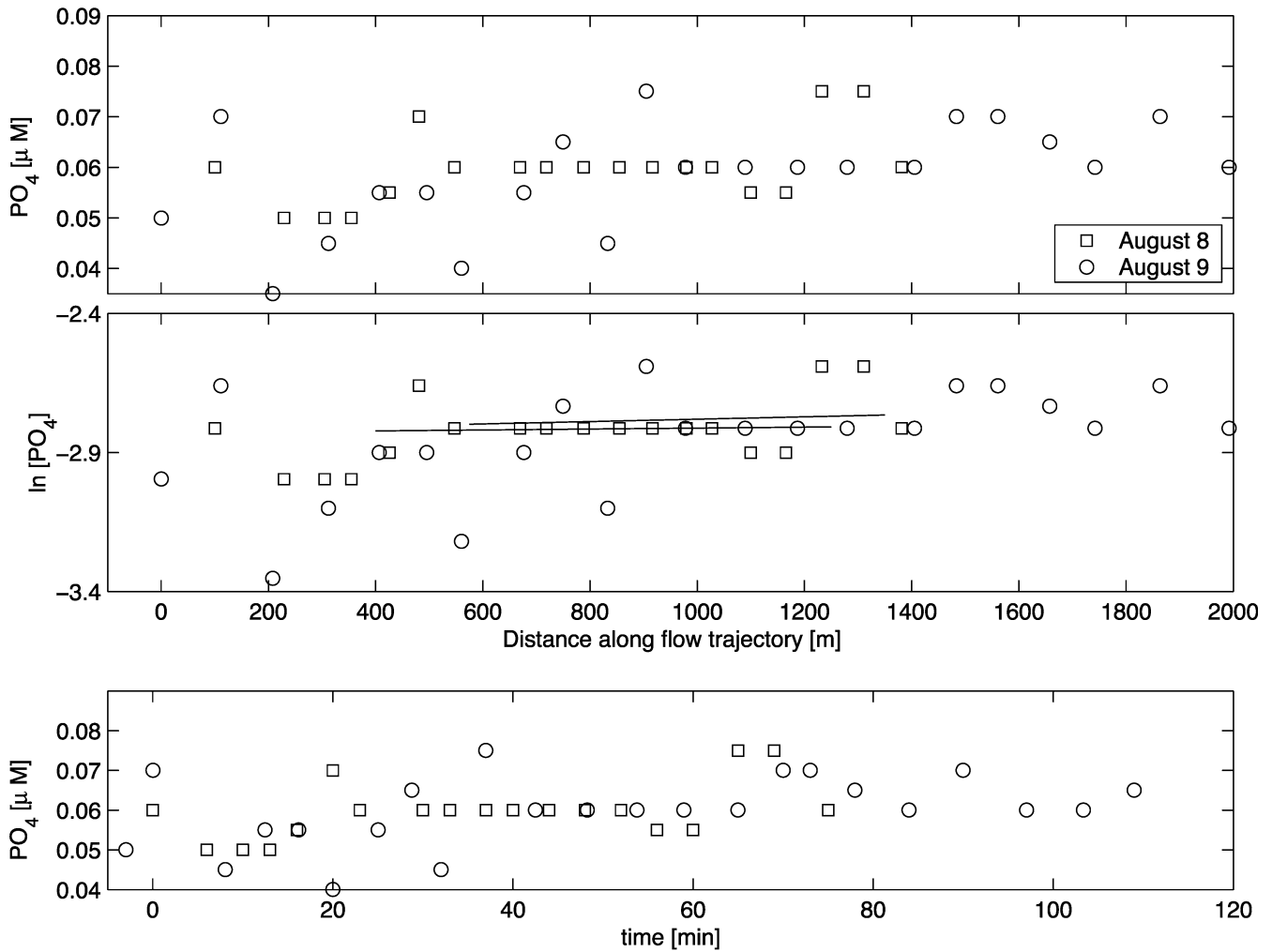
Fig. 4 Dissolved phosphate (PO_4^-) concentration (*top*) and the natural logarithm of dissolved phosphate concentration (*center*) plotted against distance along the trajectory of the flow from the reef crest. The bottom panel plots dissolved phosphate concentration against time since the drogue was released at the reef crest. Other details as per Fig. 3, with r^2 on both days less than 0.02

small – see Appendix A). A linear regression of the pressure difference and water velocity for 3 days of data has been used to obtain the relative height difference at zero flow of 1.489 ± 0.0157 cm ($n = 671$, $r^2 = 0.3416$, see Fig. 5). In other words, the linear regression indicates that the shoreward pressure sensor (CM02) was deployed at an elevation 1.489 cm lower than the seaward sensor (CM06). The mean height difference during the nutrient sampling, minus the height difference at zero flow, is used to calculate the loss in gravitational potential energy, ΔGPE, as the water moves the 178 m between the two instrument stations.

Measurement of meteorological conditions

An Oregon Scientific WM-918 Electronic Weather Station was installed on top of a water tower in the center of the island, approximately 2 km downwind of the transect. The weather station was situated 13 m above ground level ($\sim$18 m above sea level), and was 5 m higher than the top of the island vegetation. The station measured air temperature, wind speed, wind direction, humidity, and barometric pressure every 10 s, logging 5 min averages during the nutrient sampling period.

Results

Meteorological conditions

Nutrient samples were collected from 9:30–10:45 a.m. Eastern Standard Time on the 8th, and from 9:55–11:45 a.m. on the 9th of August 2002 in northern Australia's dry winter season. Unseasonably, August 6th was cloudy, and August 7th had considerable rain with low-lying thick cloud cover. The weather cleared on the night of August 7th, with the 8th and 9th being clear days. The weather conditions during the nutrient sampling periods were almost identical (Table 1) with a mean air temperature of 25.6 °C, a mean wind speed of 6.2 m s^{-1}, a mean wind direction of 116° (i.e., wind blew from ESE), a mean humidity of 75.0%, and a mean barometric pressure of 1,008 kPa.

Fig. 5 The relative surface height difference at the two instrument stations on Warraber Island reef flat as a function of flow velocity in the direction of a line between stations from August 8–10th. The intercept at zero velocity, 1.489 ± 0.0157 cm, is the absolute height difference between the sensors
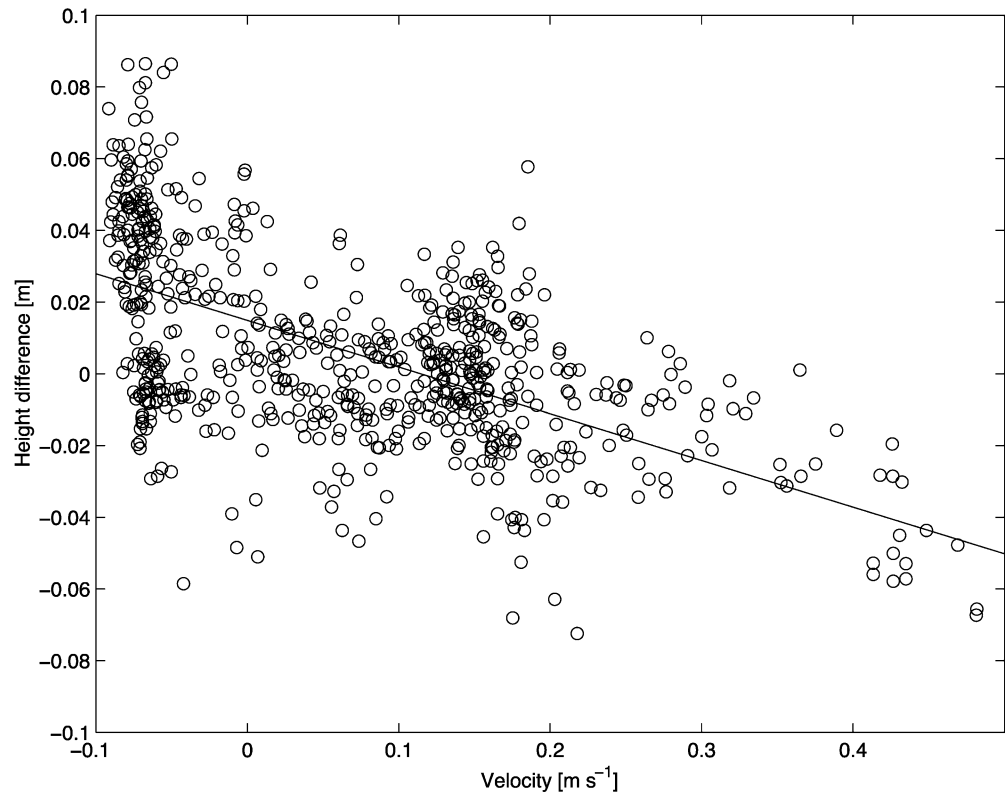

Table 1 Mean meteorological conditions at Warraber Island reef flat, Torres Strait on 8th August from 9:30–10:45 a.m. and on 9th August from 9:55–11:45 a.m.

	Air temp (°C)	Wind speed (m s^{-1})	Wind direction (°)	Barometric pressure (kPa)	Humidity (%)
Aug 8	25.5 ± 0.1	6.3 ± 0.1	118 ± 3	1008 ± 0.0	74.5 ± 0.2
Aug 9	25.6 ± 0.1	6.1 ± 0.1	114 ± 2	1008 ± 0.1	75.5 ± 0.2

Oceanographic conditions

The nitrate and phosphate concentrations in Torres Strait approximately 10 km northeast of Warraber Island (at 10°8'S 142°55'E) on the 3rd August were 0.24 and 0.06 μM, respectively. The flow of water over the experimental region was similar on both days (Fig. 2). When the tide level becomes higher than the reef crest, wave-breaking drives flow over the reef crest. After traveling approximately 400 m perpendicular to the reef rim, the flow is then topographically steered to the west, eventually passing the island to the west and re-entering the Torres Strait waters. Despite the relatively strong tradewinds, a force balance (Appendix A) and general observation of current direction throughout the tidal cycle suggests that winds do not play a significant role in forcing flow.

The water temperature on the reef flat and the wave climate on the reef crest (at DM02 in Fig. 2) on August 8 and 9 are given in Table 2. The water temperature, T, was a constant 25°C. The significant wave height, H_s, on both days was 0.15 m, and the wave period around 3 s.

Table 2 Mean temperature, T, depth, d, significant wave height, H_s, dominant wave period of the water column on 8th August between 10:10 and 10:27 a.m. and on 9th August between 10:45 and 11:03 a.m. Temperature was measured by the Falmouth Scientific Instruments ACM at CM06, while a DOBIE wave gauge at DM02 measured pressure. From the pressure record, d, H_s, and wave period are calculated

	T (°C)	d (m)	H_S (m)	Period (s)
August 8	25	0.93	0.15	2.3
August 9	25	0.97	0.15	3.7

Rate of nutrient uptake

The nitrate concentration decreased between 400 and 1,300 m along the flow trajectory from the reef crest (Fig. 3). The gradient of the natural logarithm of concentration against this distance, k, was determined as 8.65×10^{-3} and 9.74×10^{-3} m^{-1} for August 8 and August 9, respectively (the standard errors for all measurements relating to nitrate dynamics are given in results tables). The good fit for nitrate uptake ($r^2 = 0.92$ on both days, Table 3) is evidence of an exponential

Table 3 The gradient of the natural logarithm of concentration against distance, k, the mean depth, d, and the depth-averaged velocity, U, measured between 400 and 1,300 m along the transect on August 8 and 9. From the measured k, d, and U, the observed Stanton number, St (Eq. 2), and observed nutrient uptake coefficient, S (Eq. 3), are calculated

	k $\times 10^{-4}$ (m^{-1})	d (m)	St $\times 10^{-3}$	U $(m\ s^{-1})$	S $\times 10^{-4}$ $(m\ s^{-1})$
August 8	8.65 ± 1.59 $(r^2 = 0.92, n = 14)$	0.863 ± 0.023 $(n = 14)$	0.75 ± 0.16	0.164 ± 0.002 $(n = 77)$	1.23 ± 0.28
August 9	9.74 ± 2.94 $(r^2 = 0.92, n = 8)$	0.950 ± 0.037 $(n = 8)$	0.93 ± 0.32	0.153 ± 0.003 $(n = 97)$	1.42 ± 0.52

decay in nitrate concentration with distance along the flow trajectory.

The depth of the water was measured at each sampling point and the mean depth was 0.863 m on August 8, and 0.950 m on August 9. Using Eq. (2), the observed Stanton number for nitrate uptake, St, for August 8 is 0.75×10^{-3}, and is slightly higher at 0.93×10^{-3} for August 9. For the 8th August nutrient sampling period (9:30–10:45) average velocity, U, was 0.164 m s^{-1}, giving an observed nitrate uptake coefficient, S, using Eq. (3), of 1.23×10^{-4} m s^{-1}. For the 9th August nutrient sampling period (9:55–11:45), the velocity was slightly less ($U = 0.153$ m s^{-1}) and the uptake rate coefficient slightly greater ($S = 1.42 \times 10^{-4}$ m s^{-1}).

The phosphate concentration did not change significantly between 400 and 1,300 m along the flow trajectory. (Fig. 4). The gradient of the natural logarithm of concentration against distance, k, on August 8 and August 9 was measured as $0.0042 \pm 2.2 \times 10^{-3}$ m^{-1} ($r^2 = 0.014$, $n = 14$) and $0.0017 \pm 6.2 \times 10^{-3}$ m^{-1} ($r^2 = 0.0007$, $n = 8$). The observed Stanton number for phosphate uptake for August 8 was $0.00 \pm 2.90 \times 10^{-3}$, and for August 9 was $0.00 \pm 6.60 \times 10^{-3}$.

Rate of gravitational potential energy loss

The magnitude of the height difference between the two differential pressure sensors (DPS) at the instrument stations was positively correlated with water velocity between the two stations. For the duration for which the stations were in place (08:30, 8th August–10:10, 10th August), and for which the depth of water was within the calibrated range of the pressure sensors, a linear relationship between relative height difference and water velocity is given by $1.489 \pm 0.0157 - (0.130 \pm 0.014)\ U$ cm

($r^2 = 0.3416$, $n = 671$) (Fig. 5). A significant component of the height difference is correlated to water velocity, and can be accounted for by loss of energy due to friction on the bottom. Some of the remaining variability in height difference is a result of waves which are of low enough frequency not to be damped mechanically by the stilling wells. Although there is a relatively low correlation coefficient ($r^2 = 0.34$), the measurement used for subsequent calculations is the intercept, which is well constrained.

From the linear relationship between velocity, U, and absolute height difference between the two sensors, the intercept at $U = 0$ is determined as 1.489 cm. For the 8th August nutrient sampling period (9:30–10:45) the average height difference over 178 m, $\Delta\eta$, was 2.07 cm. For the 9th August nutrient sampling period (9:55–11:45) $\Delta\eta$ was 1.60 cm (Table 4).

The amount of gravitational potential energy (GPE) lost by 1 kg of water falling between the seaward and shoreward instrument stations, ΔGPE, is given by:

$$\Delta GPE = \rho g \Delta\eta \qquad (4)$$

where ρ is the density of seawater (1,023 kg m^{-3}), and g is the gravitational acceleration (9.81 m s^{-2}). For the 8th August sampling period $\Delta GPE = 208$ kg m^{-1} s^{-2}, while for 9th August $\Delta GPE = 161$ kg m^{-1} s^{-2}.

Comparison of energy dissipation rates and nutrient uptake rates

The $\varepsilon^{1/4}$ law given by Hearn et al. (2001) relates the mass-transfer-limited (MTL) nutrient uptake rate coefficient, S_{MTL}, to the rate of TKE dissipation, ε, the viscosity of the seawater, v, and the diffusivity of the dissolved nutrient ion, D:

Table 4 The measured change in elevation, $\Delta\eta$, and the travel time between instrument stations CM06 and CM02, Δt. Measured $\Delta\eta$ and Δt are used to calculated the loss of GPE, ΔGPE (Eq. 3), the rate of dissipation of TKE, ε (Eq. 6), the drag coefficient, C_D (Eq. 7), and the mass transfer limited nutrient uptake coefficient based on the $\varepsilon^{1/4}$ law, S_{MTL} (Eq. 5)

	$\Delta\eta$ $\times 10^{-2}$ (m)	Δt (s)	ΔGPE $(kg\ m^{-1}\ s^{-2})$	ε $\times 10^{-4}$ $(m^2\ s^{-3})$	C_D	S_{MTL} $\times 10^{-4}$ $(m\ s^{-1})$
August 8	2.07 ± 0.24 $(n = 77)$	$1,085 \pm 13$ $(n = 77)$	208 ± 24	1.87 ± 0.24	0.0366 ± 0.0061	1.57 ± 0.03
August 9	1.60 ± 0.20 $(n = 97)$	$1,163 \pm 23$ $(n = 97)$	161 ± 20	1.35 ± 0.19	0.0358 ± 0.0071	1.45 ± 0.05

$$S_{MTL} = \left(\frac{D^2}{v}\right)^{1/4} \varepsilon^{1/4} \tag{5}$$

For seawater at 25 °C, the molecular diffusivity of P ($HPO_4{}^{2-}$), D_P, is 7.0×10^{-10} m^2 s^{-1}, and the molecular diffusivity of N ($NO_3{}^-$), D_N, is 17.5×10^{-10} m^2 s^{-1} (Bilger and Atkinson 1992; Li and Gregory 1974). The molecular viscosity of seawater at 25 °C is approximately 9.4×10^{-7} m^2 s^{-1}.

For Warraber Island reef flat, it is assumed that the sea level changes between the two instrument stations can be accounted for by loss of GPE alone, and all the energy is dissipated as TKE in the water column (Appendix A). The rate of dissipation of TKE per kg, ε, becomes:

$$\varepsilon = \frac{\Delta GPE}{\rho \Delta t} \tag{6}$$

where Δt is the time the water parcel took to travel between instrument stations. For the 8th August, $\Delta t = 1{,}085$ s, and for the 9th August, $\Delta t = 1{,}163$ s. The dissipation rate of TKE, ε, for 8th August was 1.87×10^{-4} m^2 s^{-3}, and for the 9th August ε was 1.35×10^{-4} m^2 s^{-3}.

Using the 8th August measured GPE loss, the $\varepsilon^{1/4}$ law predicts a MTL nitrate uptake coefficient, S_{MTL}, of $1.57\pm0.03\times10^{-4}$ m s^{-1} (compared to a measured value of $S = 1.23\pm0.28\times10^{-4}$). On the 9th August, the $\varepsilon^{1/4}$ law predicts $S_{MTL} = 1.45\pm0.05\times10^{-4}$ m s^{-1} (compared to a measured value of $S = 1.42\pm0.52\times10^{-4}$). The observed nutrient uptake coefficient, S, was very close to the predicted MTL nutrient uptake coefficient, S_{MTL}, on both days. Note that the errors in S_{MTL} are small, due to the weak dependence of S_{MTL} on ε.

The rate of dissipation of TKE can also be used to determine the bottom drag coefficient of the reef flat, C_D. The drag coefficient reflects the average characteristics of the reef flat in terms of hydrodynamic drag. From Appendix A note that:

$$C_D = \frac{d\varepsilon}{U^3} \tag{7}$$

For the 8th August, C_D is 0.0366 and for the 9th August C_D is 0.0358 (Table 4). The relatively high values of C_D are consistent with high values reported for other small- (Hearn 1999) and large-scale studies of reef systems (Bode et al. 1997). The similarity of C_D between the 2 days provides a consistency check of the pressure difference measurements and illustrates the similarities between the two days.

Discussion

The observed exponential decay in N concentration with distance across the reef flat demonstrates that N is removed from the water column in proportion to the concentration. In contrast, there is no measurable change in P concentration. The removal of N from the water column demonstrates a significant supply of nitrate from the ocean which presumably drives new primary production on the reef flat. The N uptake coefficient, S, for Warraber Island reef flat on August 8 and 9 was 1.23 ± 0.28 and $1.42\pm0.52\times10^{-4}$ m s^{-1}.

The positive correlation between height difference and water velocity provides a measure of GPE loss and supports the assumption that GPE loss was balanced by bottom friction. Notably, this condition may not exist close to reef crest, where the effects of wave dissipation are likely to be important.

The measured nitrate uptake coefficients, S, were approximately equal to the MTL uptake coefficients, S_{MTL}, calculated from measured energy dissipation rates and the $\varepsilon^{1/4}$ law. On the 8th and 9th the uptake was 78 ± 19 and 98 ± 39%, respectively, of the mass-transfer limit. Using twice the standard error as a test for significant difference, S and S_{MTL} were not significantly different on either day.

The 6th and 7th August were cloudy days, with the 7th being especially dull, while the 8th and 9th were bright. The 2 days of low light preceding the August 8th measurements may have slowed the surface uptake reactions, which require energy, relative to the August 9th measurements. However, S and S_{MTL} were not significantly different on either the 8th or 9th, indicating no measurable reduction in nitrate uptake rates on the 8th, even after 2 days of dull winter weather. It is reasonable to conclude that the reef flat is taking up nitrate near the mass-transfer limit for most of the year.

The approximation that GPE loss is equal to TKE dissipation is unlikely to hold close to the reef crest, due to wave energy dissipation. Therefore the simple balance used on the reef flat cannot be applied on the reef crest. Nonetheless, it is surprising to see almost no reduction in nitrate concentration in the first 400 m along the flow trajectory. In this region the water is shallower and moving faster. The greater water velocity increases MTL uptake rates to the power 3/4, but residence time is reduced by a power of 1. As a result, for the same depth of water, the change in concentration with distance close to the reef crest should be slightly less than further from the crest. However, the shallower water of the first 400 m of the transect should be depleted at a greater rate for the same per m^2 flux than the deeper water encounter from 400 to 1,300 m. The slower reduction in nutrient concentration with distance in the first 400 m cannot be accounted for by changing depth, residence time, or water velocity. It could be that physical processes, such as the enhancement of across-reef eddy diffusion in the surf zone, or non-stationary characteristics of the flow counteract uptake. Alternatively, biological processes such as biologically limited nutrient uptake or the balanced release and uptake of nutrients may be important. Before any conclusions regarding nutrient uptake close to the rim of the reef can be made, direct energy dissipation measurements need to be undertaken.

The August 9th transect shows no measurable removal of N or P after 1,400 m. Lower turbulence and N

concentrations could in part explain reduced uptake rates. Additionally, the water was moving over coral sand areas that became dry when exposed at low tide, perhaps reducing biological demand for N. Thirdly, the water was beginning to mix with water that had taken different paths across the reef flat as it was advected around the island to drain out the leeward side channel.

A change in concentration of biologically active constituents in the water column can be used to estimate productivity (Odum and Odum 1955; Smith 1973). Phosphorus uptake, in particular, is tightly coupled to productivity in phosphate-limited coral reef systems (Atkinson 1992). With no significant change in phosphorus concentration along the flow transect, the following calculations relate nitrate uptake to productivity. Note that these calculations assume that (1) nitrate uptake is the primary source of N from the water column, and (2) that there is no significant nitrification or denitrification. These assumptions do not affect the conclusions made above regarding mass-transfer limitation of nitrate uptake.

At a nitrate concentration of 0.2 μM, with a Stanton number of 0.84×10^{-3} and water velocity of 0.16 m s^{-1}, the flux of N from the water column, $St\,UN$, is 2.7×10^{-8} mol N m^{-2} s^{-1}. Using an elemental C:N:P ratio of 550:30:1 for benthic macrophytes (Atkinson and Smith 1987), the N supply from the ocean accounts for an areal productivity of 0.5 g C m^{-2} d^{-1}. Using the Redfield ratio for unicellular algae (106:16:1), the areal productivity would be 0.2 g C m^{-2} d^{-1}. For the mixed community macrophyte – benthic microalgae on Warraber reef flat, the ocean nitrate contribution to areal productivity probably lies between 0.2 and 0.5 g C m^{-2} d^{-1}. Reported net productivity of reef flats vary between -1.7 and 27.0 g C m^{-2} d^{-1} (Hatcher 1990). Warraber reef flat may have been less productive than many reef environments, presumably because of the low amount of turbulent energy ($\varepsilon \sim1.5\times10^{-4}$ m^2 s^{-3}) relative to other reef environments such as Kaneohe Bay ($\varepsilon \sim10^{-2}$ m^2 s^{-3}, Hearn et al. 2001).

Nitrate uptake can be compared with phosphate uptake. For the reef flat to incorporate N at 2.7×10^{-8} mol N m^{-2} s^{-1}, and produce biomass at the C:N:P ratio of 550:30:1, would require the a flux of 0.1×10^{-8} mol P m^{-2} s^{-1}. Over the length of the transect (400 to 1,300 m), with a travel time of 5,625 s, a 0.1×10^{-8} mol P m^{-2} s^{-1} flux will reduce the concentration in 0.8 m depth of water by $(0.1\times10^{-8}\times5625\times1,000/0.8) = 0.007$ μM. This small reduction in P concentration across the reef is below the precision of the nutrient analysis technique used, making it impossible to determine by direct measurement whether N and P were taken up in a particular ratio, or whether P uptake proceeded at the mass-transfer limit.

The Stanton number is characteristic of a particular surface roughness, water velocity, and diffusivity of the nutrient. It is possible to use the measured Stanton number for nitrate, and an N:P ratio to calculate a theoretical Stanton number of P. This calculation requires the same assumptions as used above for productivity estimates. The Stanton number for P must be lowered to account for the slower diffusivity of P ions when compared to NO_3^- ions by multiplying by $(D_P/D_N)^{2/3} \sim0.53$ (Baird and Atkinson 1997). With a Stanton number for P of 0.45×10^{-3}, and an oceanic concentration of P of 0.06 μM, the MTL uptake of P is 0.43×10^{-8} mol P m^{-2} s^{-1}. The required P uptake rate to match the N uptake rate at ratio of 30:1 (0.1×10^{-8} mol P m^{-2} s^{-1} calculated above) is only $\sim23\%$ of the mass-transfer limit. It is reasonable to conclude, therefore, that P uptake is primarily determined by mass-transfer limitation of N and the biological constraint of a relatively fixed N:P ratio, rather than directly by diffusion limitation of PO_4^- ion transport.

In conclusion, measured nitrate uptake rates on Warraber Island reef flat were within measurement precision of those calculated using measured energy dissipation rates and the $\varepsilon^{1/4}$ law, demonstrating that on both days nitrate uptake rate was close to the mass-transfer limit. As such, it can be expected that nitrate uptake, and indirectly primary productivity and other ecological processes, will be a function of incoming oceanic nitrate concentrations and energy dissipation.

Appendix A

The one-dimensional equation for depth-averaged flow across the reef flat may be written as:

$$\frac{\partial U}{\partial t} + U\frac{\partial U}{\partial x} = g\frac{\partial \eta}{\partial x} + \frac{\tau_w}{\rho d} - \frac{\tau_b}{\rho d} \qquad (A1)$$

where U is the velocity across the reef flat, g is the gravitational acceleration, η is the sea level elevation, d is the depth, ρ is the density of water, τ_w is the wind stress in the x-direction, and τ_b is the bottom stress as a result of friction. A common relationship for the bottom stress is:

$$\tau_b = \rho C_D U^2 \qquad (A2)$$

where the coefficient of drag, C_D, depends on the roughness of the reef flat. The wind stress may be written in the same form:

$$\tau_{\mathrm{w}} = \rho_{\mathrm{a}} C_{\mathrm{a}} w^2 \qquad (A3)$$

where ρ_{a} is the air density (~1.2 kg m^{-3}), C_{a} is the drag coefficient of airflow over the ocean surface, and w is the wind speed. C_{a} depends on the roughness of the sea surface. A value of $C_{\mathrm{a}} = 1.0 \times 10^{-3}$ from offshore measurements in small seas (Smith et al. 1992) has been used.

With values typical of Warraber Island reef flat of $U \sim 0.2$ m s^{-1}, $d \sim 0.8$ m, $\partial\eta/\partial x \sim 10^{-4}$ and $w \sim 5$ m s^{-1}, a scaling analysis of Eq. (A1) shows that the two acceleration terms are of order 10^{-5}, the wind stress terms is of order 5×10^{-5}, and the pressure gradient term is of order 10^{-3}. Thus to within 5%, the balance between pressure gradient and bottom friction terms reflects a steady-state flow in which acceleration and wind stress terms play no significant role.

The balance can be written in the form:

$$gU\frac{\partial\eta}{\partial x} = \frac{C_{\mathrm{D}}U^3}{d} = \varepsilon \qquad (A4)$$

in which the left term represents the loss of gravitational potential energy and the right term the energy dissipation rate, where ε is the dissipation rate of TKE. Equation A4 can be used to obtain a value for C_{D}.

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