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REPORT

Uptake of picophytoplankton, bacterioplankton and virioplankton by a fringing coral reef community (Ningaloo Reef, Australia)

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Abstract We examined the importance of picoplankton and virioplankton to reef trophodynamics at Ningaloo Reef, (north-western Australia), in May and November 2008. Picophytoplankton (*Prochlorococcus*, *Synechococcus* and picoeukaryotes), bacterioplankton (inclusive of bacteria and Archaea), virioplankton and chlorophyll *a* (Chl *a*) were measured at five stations following the consistent wave-driven unidirectional mean flow path of seawater across the reef and into the lagoon. *Prochlorococcus*, *Synechococcus*, picoeukaryotes and bacterioplankton were depleted to similar levels ($\sim$40% on average) over the fore reef, reef crest and reef flat (='active reef'), with negligible uptake occurring over the sandy bottom lagoon. Depletion of virioplankton also occurred but to more variable levels. Highest uptake rates, *m*, of picoplankton occurred over the reef crest, while uptake coefficients, *S* (independent of cell concentration), were similarly scaled over the reef zones, indicating no preferential uptake of any one group. Collectively, picophytoplankton, bacterioplankton and virioplankton accounted for the uptake of 29 mmol C m^{-2} day^{-1}, with *Synechococcus* contributing the highest proportion of the removed C. Picoplankton and virioplankton accounted for 1–5 mmol N m^{-2} day^{-1} of the removed N, with bacterioplankton estimated to be a highly rich source of N. Results indicate the importance of ocean–reef interactions and the dependence of certain reef organisms on picoplanktonic supply for reef-level biogeochemistry processes.

Keywords Coral reef · Picoplankton · Virus · Uptake · Ningaloo Reef · Indian Ocean

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Introduction

Picoplankton (cell size class 0.2–2 μm), comprising both photoautotrophic and heterotrophic microbes, are major contributors to biomass and productivity in oligotrophic oceanic systems (Stockner 1988). In oligotrophic waters characteristic of coral reefs, photoautotrophic phytoplankton (picophytoplankton) generally dominate phytoplankton biomass and primary production (Charpy and Blanchot 1999; Ferrier-Pagés and Furla 2001). Bacterioplankton generally account for a large fraction (>30%) of carbon biomass and are responsible for high rates of organic

matter recycling within coral reefs (Ferrier-Pagés and Gattuso 1998). Viruses further exceed bacterioplankton >tenfold, making them the most abundant cell type in coral reef waters. Through infection and lysis of their microbial hosts (see review by Weinbauer 2004), viruses likely play the same important role in coral reef biogeochemical processes (Patten et al. 2008) as they do in other marine systems (Suttle 2007).

The importance of picoplankton and virioplankton to coral reef trophodynamics has received attention only in recent years. Traditionally, studies of benthic-pelagic coupling in reef systems have focused on large particles as prey sources for benthic and cryptic coral reef organisms, i.e., zooplankton and microplankton (Glynn 1973; Sebens et al. 1996; Ferrier-Pagés et al. 1998) rather than picoplankton. Recently, however, flume and experimental studies have revealed that small particles encompassing the pico- and nano-fractions ($\sim$<10 μm) represent a significant food source for a range of benthic coral reef organisms including bivalves, sponges, ascidians, soft corals and scleractinian corals (Ferrier-Pagés et al. 1998; Ribes et al. 2003; Houlbrèque et al. 2004a). Viruses may also represent an additional energy source for reef sponges (Hadas et al. 2006). Estimates of in situ particle uptake by coral reef communities are, however, limited. Those studies showed that living particles in the <5 μm fraction, which accounted for more than 70% of carbon biomass, were significantly depleted during water passage across reefs (Ayukai 1995; Yahel et al. 1998; Fabricius and Dommisse 2000; Houlbrèque et al. 2006; Wyatt et al. 2010). When combined, these experimental and in situ studies indicate a strong dependency of benthic coral reef communities on the overlying water column, and subsequently that picoplankton represents a significant source of nutrition to coral reef benthic communities.

In this study, we examined the importance of picophytoplankton, bacterioplankton and virioplankton to reef energetics across a section of Ningaloo Reef in north-western Australia (Fig. 1). Ningaloo is a fringing reef, spanning a distance of approximately 260 km along the north-west coast of Australia and situated close to the continental shelf ($\sim$10 km at its narrowest point (Fig. 1)). Two ocean currents influence Ningaloo Reef: the Leeuwin Current (LC), a warm, low salinity, low nutrient current with southward flow that peaks in the austral autumn/winter and tends to suppress upwelling; and the Ningaloo Current (NC), a northward flowing current thought to promote transient and localised upwelling when the southerly winds increase during the austral spring/summer (Pearce 1991; Woo et al. 2006). In the austral spring/summer, elevated nitrate concentrations in the euphotic zone concomitant with increased phytoplankton biomass and primary production occur close to Ningaloo relative to offshore waters and have been attributed to

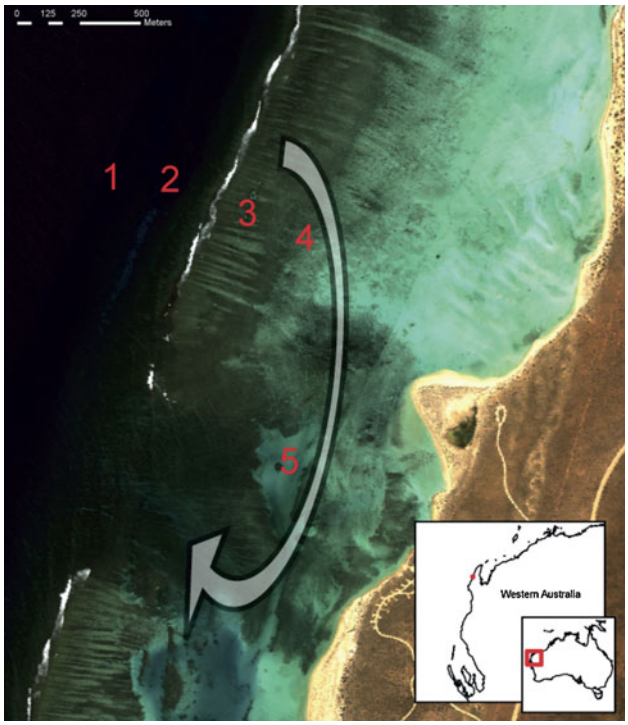

Fig. 1 Sandy Bay, Ningaloo Reef, Western Australia. Reef bathymetry and locations of water sampling stations (1 to 5). The *arrow* indicates the direction of water flow across the reef and out through the channel

upwelling associated with the NC (Hanson et al. 2005). A recent study by Wyatt et al. (2010) revealed, however, that winter phytoplankton biomass was higher in waters offshore of Ningaloo Reef in Autumn/Winter than in Spring/Summer, leading to greater removal of Chl *a* from the water column by the reef community. Regardless of the season, small phytoplankton (<5 μm) dominate the Chl *a* biomass in waters adjacent to Ningaloo (Wyatt et al. 2010). Given the dominance of particles <5 μm, the aim of this present study was to build on that of Wyatt et al. (2010) by examining in situ uptake of distinct groups of picoplankton and virioplankton at Ningaloo Reef. Independent of these being the first uptake measurements of picophytoplankton, bacterioplankton and virioplankton collectively by a reef community, these results represent, to our knowledge, the first measurements of picoplankton and virioplankton within a coral reef ecosystem within the East Indian Ocean Rim.

Methods

Study site

Sandy Bay, Ningaloo Reef, is situated on the north-west coast of Australia (22.23°S, 113.84°E) (Fig. 1). The fore reef slope ($\sim$1:30) rises to a shallow reef flat that stretches

Table 1 Dates in May 2008 and November 2008 when fixed stations (1–5) were sampled at Sandy Bay, Ningaloo

Month	Date	Station				
		1	2	3	4	5
May	11th	×				
	13th	×	×	×	×	×
	15th	×		×		
	16th			×	×	×
	17th				×	×
	22nd	×	×	×	×	×
November	7th			×	×	×
	8th	×	×	×		×
	9th	×	×	×	×	
	16th		×	×	×	
	17th	×		×	×	
	18th	×	×	×	×	×
	19th	×	×	×	×	

~500 m shoreward of the surf zone (Wyatt et al. 2010). The reef is separated from the shore by a 500-m-wide, 2–3-m-deep lagoon (Fig. 1). The hydrodynamics of Sandy Bay during the May and November 2008 study periods are discussed at length in Wyatt et al. (2010). Briefly, however, radiation stress gradients generated by wave breaking on the reef crest generate a consistent unidirectional mean flow across the reef flat towards shore, which then returns to the ocean through a channel (gap) in the reef; under typical wave conditions, this results in a residence time of ~2–6 h.

Sampling and measurements

Sampling was conducted over two, approximately 2-week periods in May and November 2008 (Table 1). These periods were chosen to coincide with times when regional ocean conditions offshore of Ningaloo Reef were expected to differ greatly, potentially resulting in differences in the concentrations of picoplankton and virioplankton delivered to the reef. In May, the strength of the LC should be at its strongest thereby suppressing upwelling, while in November, transient upwelling events may occur when LC transport is at its minimum and southerly winds are at their strongest (Smith et al. 1991; Feng et al. 2003). During each study period, seawater sampling was regularly conducted at five fixed stations, chosen to align with the dominant wave-driven mean flow path (Fig. 1). Wyatt et al. (2010) showed, using moored current measurements (supplemented with numerous drifter releases), that the flow between the sampling stations was extremely consistent, with the mean current vectors over the reef deviating by <10 degrees and never reversing due to the relatively weak tides. The benthic community composition along the transect varied from near 100% coral coverage across the fore reef and reef flat (stations 1–3), to patchy reef (station 4), to primary sand in the lagoon (station 5). In May 2008, it was not possible to sample all stations each day, so during this period some stations were sampled on alternate days (Table 1). In November 2008, however, simultaneous sampling of adjacent stations was conducted on most days (Table 1). At each station, surface seawater was collected using 2 × 20 l black carboys that were pre-rinsed 3 times in sample water prior to collection. Sampling was conducted during daylight hours with the maximum time taken to sample all stations on a given day of ~2 h.

Chl *a* concentrations were fluorometrically determined on duplicate 90% acetone extracts of 1-l samples filtered onto Whatman GF/F filters (Parsons et al. 1984). Samples were acidified with 10% HCl to correct for phaeopigments. Chl *a* >5 μm were also determined on 2-l duplicate samples filtered onto 5-μm nitex filters as above. Chl *a* <5 μm were then determined via subtraction (Chl *a* total—Chl *a* >5 μm).

Photosynthetic picophytoplankton (i.e. *Prochlorococcus*, *Synechococcus* and picoeukaryotes; collectively termed 'picophytoplankton' herein), bacterioplankton (inclusive of bacteria and Archaea) and virioplankton were enumerated by flow cytometry. Duplicate seawater samples (1.5 ml) were fixed in EM grade glutaraldehyde (0.5% final concentration) in the dark for 15 min and quick frozen in liquid nitrogen until analysis (Marie et al. 1999). For picophytoplankton, samples were thawed at 37°C, 1 μm fluorescent beads (Molecular Probes) added as an internal standard and samples were analysed using a FACSCANTO II (Becton–Dickinson) flow cytometer fitted with a 488 nm laser on high throughput mode at a flow rate of 60 μl min^{-1} for 2 min. *Prochlorococcus*, *Synechococcus* and picoeukaryotes were

discriminated on the basis of red and orange autofluorescence of chlorophyll and the accessory pigment phycoerythrin (Marie et al. 1999). Samples for bacterioplankton and virioplankton were thawed as above, diluted fivefold in 0.02-µm-filtered Tris EDTA buffer (pH 8, Sigma–Aldrich), stained with SYBR I Green (0.5×10^{-4} final concentration) in the dark at 80°C, and then 0.75-µm fluorescent beads (Molecular Probes) were added as an internal standard (Brussaard 2004). Bacterioplankton and virioplankton were analysed using the same flow cytometer, but at a flow rate of 30 µl min^{-1} for 2 min and discriminated based on side scatter and green (SYBR I) fluorescence. Virioplankton counts were corrected against a blank consisting of 0.02-µm-filtered TE buffer with 0.02-µm-filtered (5:1) seawater. Carbon (C) and nitrogen (N) biomass of picoplankton and virioplankton groups were estimated using conversion factors from the literature (Electronic Supplemental Material, ESM, Table 1).

Net picoplankton uptake rates

Net uptake rates by the reef community were estimated for each group based on the method described in Wyatt et al. (2010) for bulk phytoplankton. Briefly, the uptake rate, m_i, of different picophytoplankton groups, bacterioplankton and virioplankton (in units of cells m^{-2} day^{-1}) between each pair of sampling stations was estimated based on the measured cell concentrations C_i at each station i:

$$m_i = q(\Delta C_i / \Delta X_i) \quad (1)$$

where $\Delta C_i = \Delta C_i - C_{i+1}$ is the concentration difference between adjacent stations and $\Delta X_i = |X_i - X_{i+1}|$ is the distance between stations. The volumetric flow rate q (and not the current speed U) is roughly conserved between the stations, due to the simple wave-driven circulation patterns across this particular reef system (Wyatt et al. 2010). To compute q, a 2 MHz Nortek Aquadopp current profiler was deployed near station 3 (depth 1–2 m) during both study periods and recorded the mean current profiles every 5 min using 0.1 m bins (see Wyatt et al. 2010 for details). Note that we chose a convention consistent with Wyatt et al. (2010), where positive m_i values imply a net removal (uptake) of cells by the reef community, whereas negative values imply a net increase in cells (nevertheless, m_i will be referred to hereinafter as an 'uptake' rate).

To account for concentration-dependent uptake rates, uptake coefficients, S_i (in units of m day^{-1}), were also estimated for each group as:

$$S_i = m_i / \hat{C}_i \quad (2)$$

where m_i is the uptake rate defined in Eq. 1 and $\hat{C}_i$ can be estimated from the average concentration of cells between adjacent stations, i.e., $\hat{C}_i = (C_i + C_{i+1})/2$. Values for m and S were calculated for four distinct regions: 'fore reef' (stations 1–2), 'reef crest' including the surf zone (stations 2–3), 'reef flat' (stations 3–4) and 'lagoon' (stations 4–5).

Statistics

Multivariate analyses was performed in PRIMER Version 6 (PRIMER-E, Plymouth, UK) based on normalised euclidean distances of *Prochlorococcus*, *Synechococcus* and picoeukaryotes (all square root transformed) and bacterioplankton and virioplankton. A permutational multivariate analysis of variance (PERMANOVA) (see Anderson 2001; Anderson et al. 2008) of the resemblance matrix was used to test for differences in concentrations of picophytoplankton, bacterioplankton and virioplankton between seasons and stations using 9,999 permutations, with Type III (partial) sum of squares and permutation of residuals under a reduced model. Differences in cell concentrations, uptake rates, m, and uptake coefficients, S, between seasons and stations were tested as above but using unrestricted permutations of raw data. All values are reported as means ± standard error (SE) unless otherwise stated.

Results

Temporal variability of ocean-derived picophyto-, bacterio- and virioplankton

The biomass of Chl a <5 µm and concentrations of picophytoplankton at station 1 (outside the reef) showed large variations over scales of months to days (Fig. 2a). Temporal trends in total Chl a are provided in further detail in Wyatt et al. (2010). Briefly, total Chl a concentrations at station 1 were higher in May (averaging 0.52 µg l^{-1}) than November (averaging 0.36 µg l^{-1}), with Chl a <5 µm contributing ≥90% to the total Chl a during both seasons (Wyatt et al. 2010) (Fig. 2a). *Prochlorococcus* numerically dominated concentrations of picophytoplankton in May, comprising ~80% of the total picophytoplankton community at station 1 (Fig. 2b). Despite *Prochlorococcus* being approximately fivefold lower in November than in May ($F_{1,12} = 23.80$, $P = 0.003$), *Prochlorococcus* dominated concentrations of picophytoplankton on all occasions but one; where on the 17th November, *Prochlorococcus* comprised just 21%. Concentrations of *Synechococcus* in May also exceeded those in November ($F_{1,12} = 19.92$, $P < 0.002$) (Fig. 2c), but their contribution to total picophytoplanktonic concentrations scaled similarly between seasons (~20%). Picoeukaryotes were one to two orders of magnitude lower than *Synechococcus* or *Prochlorococcus*,

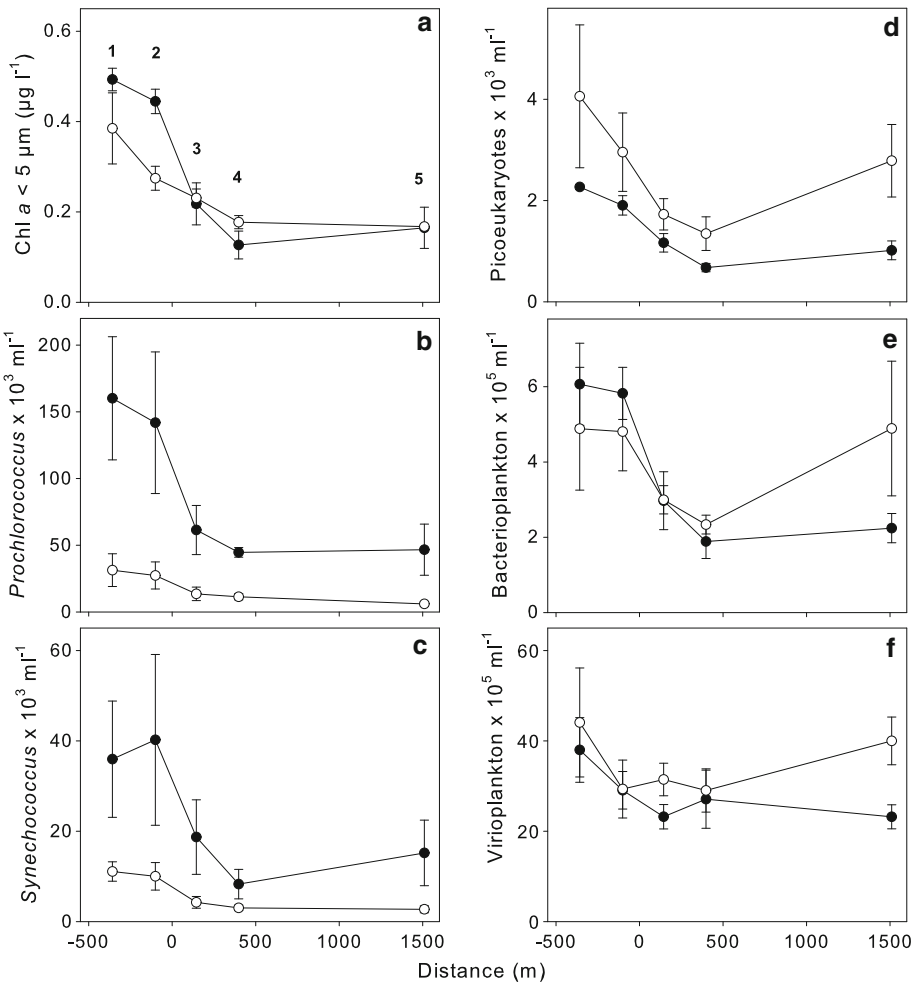

Fig. 2 Small chlorophyll *a* (Chl *a*) (<5 µm) and concentrations of picophytoplankton, bacterioplankton and virioplankton along fixed stations (1–5) (see Fig. 1) at Sandy Bay, Ningaloo, in May 2008 (*black closed circles*) and November 2008 (*open circles*). **a** Chl *a* <5 µm, **b** *Prochlorococcus*, **c** *Synechococcus*, **d** picoeukaryotes, **e** bacterioplankton and **f** virioplankton

respectively, and showed the opposite trend, with concentrations outside the reef ~2 times higher in November than in May (Fig. 2d). Bacterioplankton and virioplankton at station 1 further exceeded *Prochlorococcus* by one to two orders of magnitude, respectively (Fig. 2e, f), with no differences occurring between the two study periods (all $P > 0.05$).

Outside the reef, variability of picophytoplanktonic concentrations during May was relatively small (i.e. 2.3, 2.8 and 1.2-fold differences for *Prochlorococcus*, *Synechococcus* and picoeukaryotes respectively), however, in November, varied by up to a factor of 18, 5 and 11, respectively (data not shown), and coincided with largest Chl *a* fluctuations (Wyatt et al. 2010). Outside the reef, *Prochlorococcus*, *Synechococcus* and bacterioplankton contributed similarly to the combined picoplankton and virioplankton C biomass in May (on average, ~29% each), while in November, bacterioplankton (40 ± 5.6%) and *Prochlorococcus* (11 ± 3.3%) contributed the highest and lowest amount, respectively, to C biomass (data not shown). Outside the reef, bacterioplankton accounted for 53 ± 2.0% (May) and 62 ± 4.6% (November) of the combined picoplanktonic and virioplanktonic C biomass, while virioplankton contributed 3–5% (May) and 8–14% (November).

Temporal and spatial variability of picophyto-, bacterio- and virioplanktonic cell concentrations, uptake rates, *m*, and uptake coefficients, *S*

A sampling period × station PERMANOVA revealed significant differences in cell concentrations between May and November ($F_{1,31} = 33.89$, $P < 0.001$) and stations ($F_{4,31} = 86.19$, $P < 0.001$), with no interaction term ($F_{4,31} = 13.37$, $P = 0.114$). Pair-wise tests revealed that station differences were due to significantly higher cell concentrations occurring on the fore reef (station 1 and 2) than over the reef flat and lagoon (Stations 3, 4 and 5) (all $P < 0.01$) (Fig. 2).

Depletion of *Prochlorococcus*, *Synechococcus*, picoeukaryote and bacterioplankton occurred on the majority of sampling days in May and November over the fore reef

(stations 1–2), reef crest (stations 2–3) and reef flat (stations 3–4) (ESM, Table 2). Over the fore reef in May, *Prochlorococcus*, *Synechococcus*, picoeukaryotes and bacterioplankton exhibited similar levels of depletion, ranging between 4 and 23% (ESM, Table 2). Despite lower concentrations of *Prochlorococcus* and *Synechococcus* in November, both groups were depleted to similar levels (20–61%) over the fore reef in May and November. Depletion of virioplankton was more variable (5–59%) than for picoplankton (ESM, Table 2). Across the reef crest (stations 2–3), depletion levels for all groups of picoplankton were similar and further comparable to those changes occurring over the fore reef (ESM, Table 2). However, depletion of one group did not always coincide with a depletion of another. For example, on the 17th November, while there was a 44 and 32% depletion of *Synechococcus* and picoeukaryotes, respectively, over the reef crest, *Prochlorococcus* increased by 15%. Highly variable concentrations of virioplankton at stations 2 and 3 resulted in the depletion of virioplankton on two of the five sampling days. As water passed over the $\sim$250 m portion of reef flat (stations 3–4), concentrations of picoplankton were highly variable, resulting in both a depletion and an increase in cells. For example, *Synechococcus*, picoeukaryotes and bacterioplankton exhibited similar levels of depletion (on average, 35–52%) in May, while depletion of *Prochlorococcus* occurred on only 2 of 4 sampling days (ESM, Table 2). In November, cell depletion occurred for the different picoplankton groups over the reef flat on more than half of the sampling days. While depletion of virioplankton (16–60%) occurred on 2 of the 4 sampling days, an increase in virioplankton (7–109%) occurred on the other sampling days. Depletion of *Prochlorococcus* (10–65%) occurred on all but one day (May 22) in the lagoon (between stations 4 and 5) with no further depletion of *Synechococcus* or picoeukaryotes, consistent with the trends for total Chl *a* reported in Wyatt et al. (2010). Instead, increases in bacterioplankton, virioplankton, *Synechococcus* and picoeukaryotes occurred in the lagoon on some occasions, with lagoonal cell concentrations often equalling those occurring at the fore reef (Fig. 2, ESM Table 2).

The observed concentration differences for picophytoplankton, bacterioplankton and virioplankton, combined with the simultaneously measured flow rates q (via Eq. 1), were used to estimate uptake rates, m, of each group for the four zones. Apart from higher uptake rates, m, for picoeukaryotes occurring on the fore reef in November, uptake rates for *Prochlorococcus*, *Synechococcus* and bacterioplankton were significantly higher over the fore reef, reef crest and reef flat in May compared with November (all $P < 0.05$) (Fig. 3). Highest uptake rates, m, occurred for bacterioplankton and virioplankton due to their relatively high cell concentrations (Fig. 3). However, to account for the expected concentration dependency of uptake rates, m, uptake coefficients, S (Eq. 2), were also calculated (Fig. 4). Similarly scaled uptake coefficients, S, occurred for *Prochlorococcus*, *Synechococcus* and bacterioplankton over the fore reef in May, however, relatively lower and/or negative values of S occurred in November. In May, over the reef crest, uptake coefficients, S, for *Prochlorococcus*, *Synechococcus*, picoeukaryotes and bacterioplankton were not significantly different, ranging on average between 21.9 and 28.6 m day^{-1} (all $P < 0.01$). In November, uptake coefficients, S, of *Synechococcus* (26.9 $\pm$ 9.1 m day^{-1}) and picoeukaryotes (20.6 $\pm$ 8.10 m day^{-1}) were similar to those in May; however, those for *Prochlorococcus* (12.1 $\pm$ 6.6 m day^{-1}) and bacterioplankton (6.0 $\pm$ 6.1 m day^{-1}) were two to fourfold lower. Highest uptake coefficients, S, occurred on the reef flat in May for *Synechococcus* (54.9 $\pm$ 17.8 m day^{-1}), picoeukaryotes (39.7 $\pm$ 15.4 m day^{-1}) and bacterioplankton (33.0 $\pm$ 13.5 m day^{-1}) (Fig. 4). This contrasted with November, when uptake coefficients, S, for all picoplankton groups were low compared to May. In the lagoon, relatively low uptake coefficients occurred for *Prochlorococcus*, with low and/or negative uptake coefficients, S, occurring for *Synechococcus*, picoeukaryotes, bacterioplankton and virioplankton (Fig. 4).

Uptake rates, m, when plotted as a function of cell concentrations for the reef crest and reef flat, did not appear to reach saturation levels, as indicated by best fit positive linear relationships for *Prochlorococcus*, *Synechococcus* and picoeukaryotes (all $P < 0.001$) (ESM, Fig. 1a–c). No such clear relationships were evident for concentrations of bacterioplankton or virioplankton versus uptake rates (ESM, Fig. 1d, e). Uptake coefficients (S) were further plotted as a function of water velocity (U) for those occasions when positive uptake occurred over the reef crest and reef flat. Water velocity U alone explained 19, 63, 41 and 27% of the variation of uptake coefficients, S, for *Prochlorococcus*, *Synechococcus*, picoeukaryotes and bacterioplankton, respectively (all $P < 0.01$) (ESM, Fig. 2a–d). No linear relationship was evident for water velocity and uptake coefficients of virioplankton (ESM, Fig. 2e) ($P > 0.05$).

The fractional contribution of the five groups considered to C uptake varied seasonally and spatially over the reef (Fig. 5). Over the fore reef in May, *Prochlorococcus* accounted for 52 $\pm$ 3.8% of the removed C biomass, with *Synechococcus* and bacterioplankton each contributing a further 22 $\pm$ 12% and 11 $\pm$ 27%, respectively (Fig. 5a). In November, because cell concentrations were occasionally higher at station 2 than at station 1, subsequently resulting in an increase in *Prochlorococcus*-, *Synechococcus*- and bacterioplanktonic-derived C, picoeukaryote biomass accounted for 66% of the C uptake (Fig. 5b). Over the reef crest, *Prochlorococcus*, *Synechococcus* and bacterioplankton

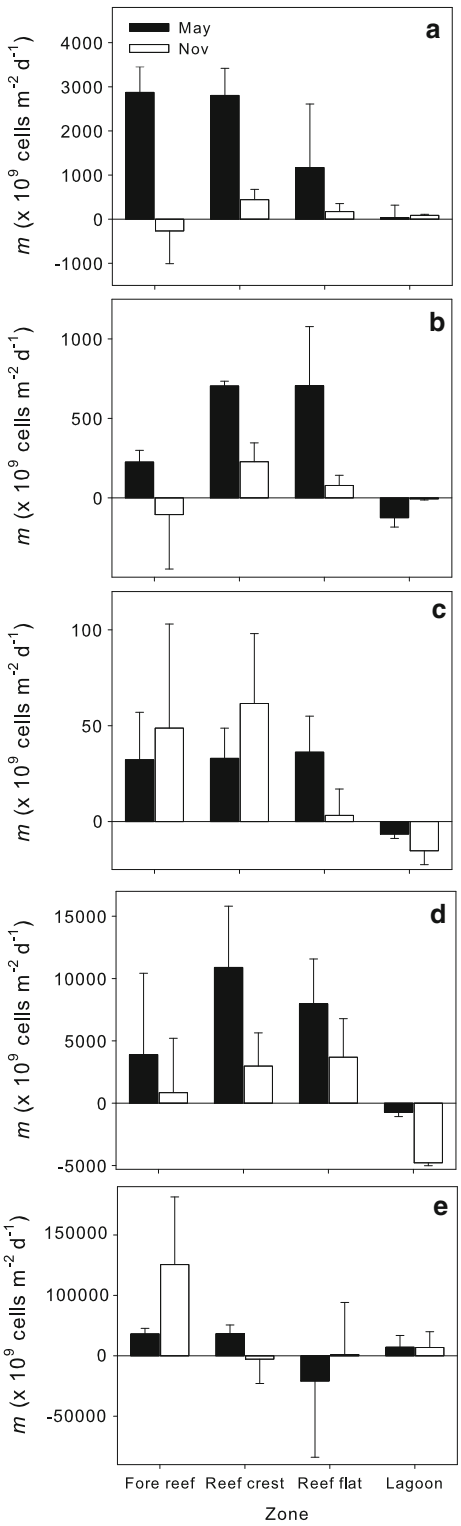

Fig. 3 Average uptake rates, m (1×10^9 cells m^{-2} day^{-1}), determined in each reef zone for **a** *Prochlorococcus*, **b** *Synechococcus*, **c** picoeukaryotes, **d** bacterioplankton and **e** virioplankton

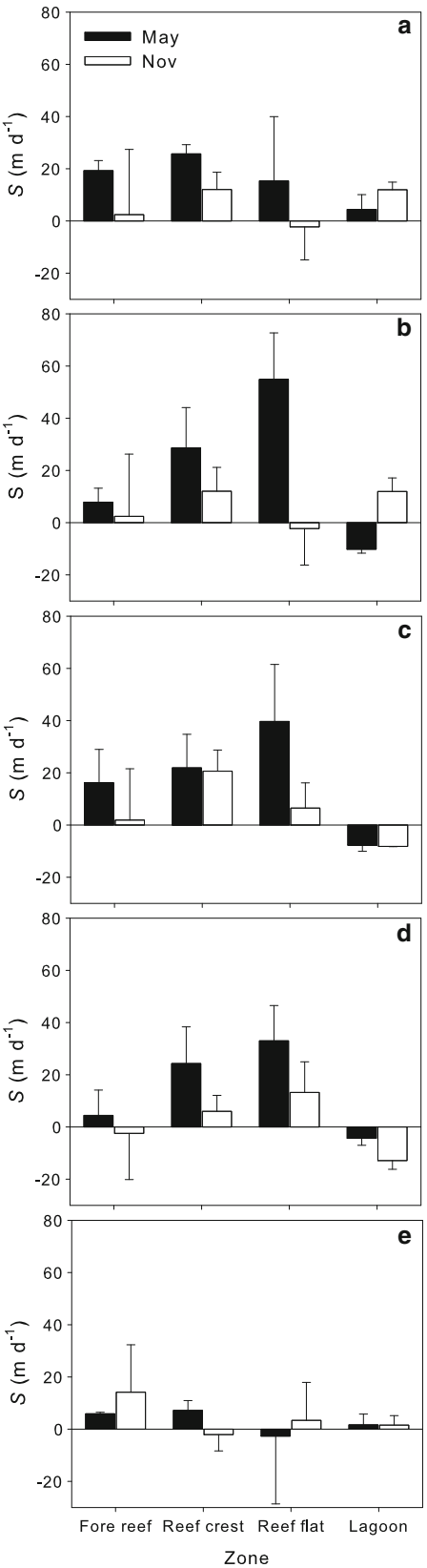

Fig. 4 Average uptake coefficients, S (m day^{-1}), determined in each reef zone for **a** *Prochlorococcus*, **b** *Synechococcus*, **c** picoeukaryotes, **d** bacterioplankton and **e** virioplankton

contributed similarly (on average, 28–34%) to C uptake in May (Fig. 5a), while in November; *Synechococcus*, bacterioplankton and picoeukaryotes contributed 28–30% to C

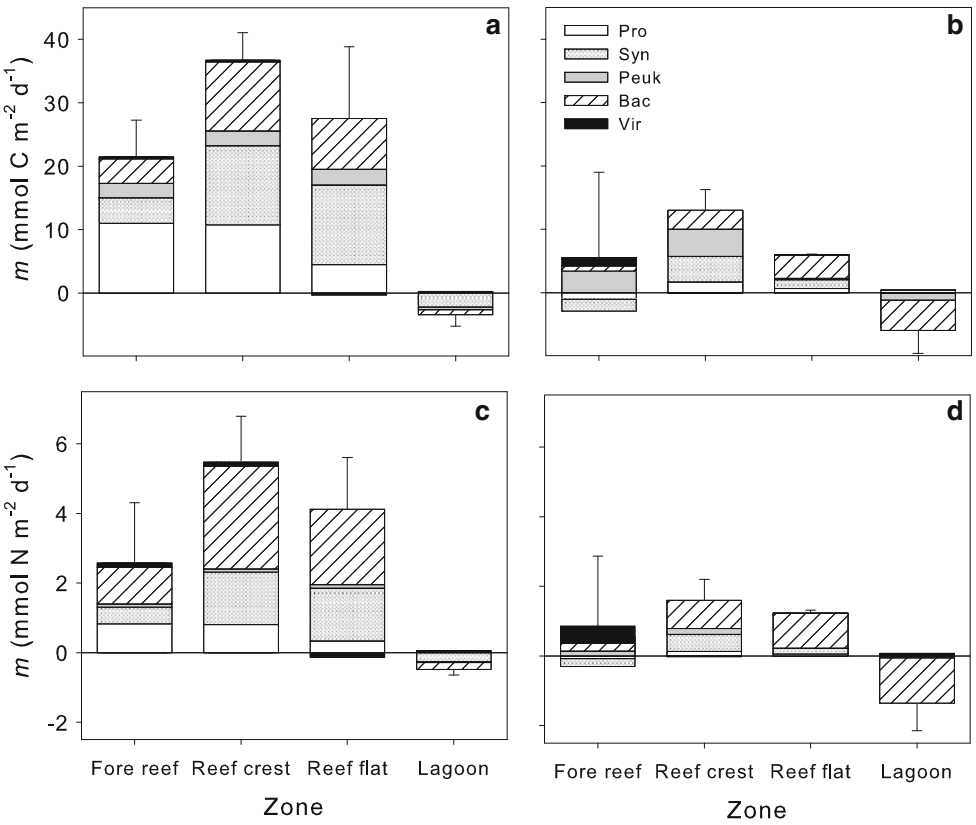

Fig. 5 Average fractional contribution of *Prochlorococcus* (*Pro*), *Synechococcus* (*Syn*), picoeukaryotes (*Peuk*), bacterioplankton (*Bac*) and virioplankton (*Vir*) to the uptake (*m*) (positive *m* values) and/or release (negative *m* values) of picoplanktonic- and viral-derived C (mmol N m^{-2} day^{-1}) and N (mmol C m^{-2} day^{-1}) at the fore reef, reef crest, reef flat and lagoon at Sandy Bay, Ningaloo. **a** and **b** represent C uptake *m* in May and November 2008, respectively. **c** and **d** represent N uptake *m* in May and November 2008, respectively. *Error bars* represent SE of the combined averaged picoplankton and virioplankton C and N uptake

uptake (Fig. 5b). Bacterioplankton accounted for ≥54% of the total N uptake in May and November over the reef crest and reef flat (Fig. 5c, d). Over the reef crest and reef flat, uptake of virioplankton-derived C or N was negligible (<1%), however over the fore reef in November when concentrations of picoplankton were sometimes higher at station 2 than at station 1, virioplankton accounted for 34 and 83% of the removed C and N, respectively (Fig. 5d).

Discussion

These are the first measurements of picoplanktonic and virioplanktonic concentrations at Ningaloo Reef and the first for a coral reef in the East Indian Ocean rim. In general, concentrations of picophytoplankton reflected those typical of oceanic waters (Partensky et al. 1999) rather those occurring in coral lagoons (Charpy and Blanchot 1999; Crosbie and Furnas 2001a), probably due to the close proximity of Ningaloo to the continental shelf break and associated offshore waters. Concentrations of bacterioplankton and virioplankton were similar to those occurring in near-shore through to oceanic coral reefs (Seymour et al. 2005; Dinsdale et al. 2008; Patten et al. 2008).

The delivery of ocean-derived picoplankton and virioplankton to Ningaloo was spatially and temporally variable. In May, *Prochlorococcus* and *Synechococcus* numerically dominated the picophytoplankton community, while in November picoeukaryotes contributed a higher proportion to the overall lower total cell concentrations. Potential regional physical oceanographic mechanisms accounting for differences in Chl *a* biomass off the Ningaloo coast are discussed in detail by Wyatt et al. (2010) and include acceleration of the LC in Autumn/Winter and local-scale upwelling events in November associated with the NC; both resulting in nutrient replenishment of surface waters in this region.

Despite these shifts in picophytoplankton community composition and biomass over scales of months to days, uptake, *m*, of picophytoplankton, bacterioplankton and, to a lesser extent, virioplankton occurred on the majority of sampling days in both May and November over all zones of the active reef (active reef = fore reef, reef crest and reef flat) (Fig. 3). In contrast, uptake of picoplankton or virioplankton was rarely evident over the sandy lagoon. Differences in picoplankton growth rates between reef zones would not explain the consistent uptake of cells, since picophytoplankton (~24 h) (Crosbie and Furnas 2001b) and bacterioplankton doubling times (>6–12 h) (Ferrier-Pagés and Furla 2001) in coral reefs waters exceed the lagoon residence time (~2–6 h). Instead, depletion of picophytoplankton, bacterioplankton and, on some occasions virioplankton, across the active reef suggests that the live reef community was responsible for the removal of

these ocean-derived particles—this is consistent with the decrease in total Chl *a* (Fig. 2a) and increase in phaeopigments (Chl *a* breakdown products) (see Fig. 4b in Wyatt et al. 2010).

Mechanisms for cell depletion

Isolating the specific mechanisms responsible for the observed depletion is beyond the scope of this present study. However, direct uptake of picoplankton by active (e.g. sponges) and passive (e.g. scleractinian corals) suspension feeding organisms in coral reefs is now well accepted (Fabricius and Dommisse 2000; Houlbrèque et al. 2004a). Indirect trapping of particles by organic material such as coral mucus (Naumann et al. 2009), coral spawn (Patten et al. 2008) and other organic particles could also potentially contribute to the removal of these cells from the water column. The fate of any trapped particles is not clear; however, sinking of particle-laden organic matter to the reef benthos may allow benthic reef organisms to access the picoplankton fraction from the water column (Wild et al. 2004; Naumann et al. 2009). Indeed, several coral reef benthic organisms such as gastropods (Kappner et al. 2000) and scleractinian corals (Goldberg 2002) feed on particulate material from the water column through mucocilary processes. Grazing by nanoplankton and microzooplankton (Ferrier-Pagés and Gattuso 1998) and planktivorous fish (Pinnegar and Polunin 2006), as well as viral lysis of picoplankton (Weinbauer 2004) could additionally account for the removal of some proportion of picoplankton and the subsequent increase in phaeopigments over the active reef. Regardless of the mechanism, our data, together with that of Wyatt et al. (2010), indicate that picoplankton and virioplankton are assimilated into the coral reef food web and are, as discussed below, likely to be instrumental in large scale coral reef biogeochemical cycling processes.

Comparisons of uptake rates, *m*, and coefficients, *S*, by different reef zones

Uptake rates, *m*, of picoplankton and virioplankton were highest overall, over the reef crest (Fig. 3). However, similarly scaled uptake rates, *m*, also occurred for *Synechococcus* and picoeukaryotes over the reef flat in May and for bacterioplankton in both May and November, despite comparatively lower concentrations of cells in these zones relative to the fore reef and reef crest (Fig. 3). To account for local concentration differences, estimated uptake coefficients, *S*, for *Prochlorococcus*, *Synechococcus*, picoeukaryotes and bacterioplankton on the reef flat were comparable and sometimes higher than those occurring on the fore reef and reef crest (Fig. 4). The variable, low and sometimes negligible uptake rates, *m*, and uptake coefficients, *S*, occurring at the fore reef should be interpreted with some caution given the complex flows along the fore reef at Ningaloo which includes an along reef component (see discussion in Wyatt et al. 2010).

The observed picophytoplankton uptake coefficients, *S*, were similar to total phytoplankton uptake coefficients at the fore reef, reef crest and reef flat at Ningaloo ($\sim$19, 9 and 21 m day^{-1}, respectively; Wyatt et al. 2010). In flume experiments with comparable flow speeds (13 cm s^{-1}) and with scleractinian coral cover >100%, in addition to the presence of cryptic coral-associated fauna, uptake coefficients, *S*, for *Synechococcus*, picoeukaryotes and bacterioplankton (6.2 $\pm$ 2.1, 7.2 $\pm$ 1.7 and 3.5 $\pm$ 1.7 m day^{-1} respectively; mean $\pm$ SD) (Ribes et al. 2003) are comparable to our field observations, albeit our measurements are roughly 2 times greater. Uptake coefficients more similar to those in this study occurred for *Synechococcus*, picoeukaryotes and bacterioplankton (20.8 $\pm$ 1.7, 11.3 $\pm$ 0.9 and 10.8 $\pm$ 1.22 respectively; mean $\pm$ SD) in flume experiments with a water velocity of 15 cm s^{-1} and with the benthic community predominantly comprised of sponges and ascidians (Ribes and Atkinson 2007). Ribes and Atkinson (2007) attributed these high uptake coefficients to active filtering of particles by filter feeders together with increased transport of particles into cryptic spaces. Over the reef crest and reef flat at Ningaloo, scleractinian corals visually dominate the benthic community. However, inner surfaces of cavities, crevices and cracks in the reef framework likely represent a significant proportion of the available reef surface (Ginsburg 1983). On other reefs, sponges alone cover >60% of internal surfaces with high densities of other filtering feeding organisms such as tunicates, bivalves and polychaetes (Richter et al. 2001). Significant depletion of Chl *a* and bacterioplankton relative to ambient water has been reported for coral reef cavities elsewhere (Richter and Wunsch 1999; Scheffers et al. 2004). It is likely that heterotrophic organisms within the reef framework also contribute to the relatively high uptake coefficients, *S*, of picoplankton at Ningaloo.

Processes occurring in the lagoon appeared to be different from those over the active reef. In contrast to consistent uptake of picoplankton by the active reef zones, increases in the concentration of bacterioplankton primarily, but also picophytoplankton and virioplankton, occurred within the lagoon (Figs. 3, 4). The release of nutrients (nitrate and ammonium) into the overlying water following high rates of remineralisation in highly permeable reef sediments (Miyajima et al. 2001) could potentially support high bacterioplanktonic biomass in lagoon waters. However, given that water residence time between station 4 and 5 ($\sim$1 h) exceeds bacterial doubling times in coral reef lagoons (Ferrier-Pagès and Furla 2001), this explanation seems unlikely. High concentrations of bacteria occur

within coral mucus relative to ambient water with coral mucus further scavenging particles from the water column (Wild et al. 2004). Therefore, detachment of reef surface-associated biofilms and coral mucus following water advection through the reef framework, as well as the release of sediment biofilms into lagoon waters, may be alternative mechanisms leading to relatively high cell concentrations of microorganisms reaching the lagoon. While we have not examined the potential exchange of microbial-enriched lagoon water with waters offshore of Ningaloo, Wyatt et al. (2010) point out that station 2 may at times be mixed (albeit to some small fraction) with re-circulated lagoon water. This process may account for the occasional negative uptake rates that occurred over the fore reef (Fig. 3).

Preferential uptake of different picoplankton/virus groups

Flume studies have noted preferential uptake of particular picoplankton types; *Synechococcus* uptake was higher than bacteria or picoeukaryotes (Ribes and Atkinson 2007) and picophytoplankton uptake higher than bacterioplankton or nanoplankton (Ribes et al. 2003). While the picoplankton size fraction appears to be preferred over larger cells by coral reef benthic communities, no clear selection for any individual group of picoplankton has been reported in situ (Ayukai 1995; Houlbrèque et al. 2006). In this study, despite high variability of cell concentrations delivered to the reef day to day, all groups of picoplankton were depleted to similar levels over the active reef (on average ~40%) (ESM, Table 2A). Similar depletion levels of picoplankton by coral reef communities have been reported for those few studies conducted to date (Ayukai 1995; Yahel et al. 1998; Houlbrèque et al. 2006).

There was evidence to suggest that virioplankton were also taken up by the benthic reef community, albeit to lower and more variable levels than picoplankton. Sponges are known to effectively remove large quantities of virioplankton from the water column; however, their overall contribution to sponge nutrition is thought to be low (Hadas et al. 2006). While there are no known studies documenting uptake of virioplankton by corals, scleractinian corals can effectively take up dissolved organic matter (DOM) in the form of dissolved nutrients, amino acids and carbohydrates from the water column even at nanomolar concentrations (Sorokin 1973; Ferrier 1991; Grover et al. 2003, 2006). Given that virioplankton fall within the operational definition of DOM (i.e. <0.45 μm in size), they occur ubiquitously at high concentrations in coral reefs with high turnover rates (relative to picoplankton), and given that many reef organisms are known to be able to utilise DOM as food source in coral reefs, it is possible that virioplankton represent an additional food source to benthic reef organisms.

Implications for picoplankton and virus uptake

A consistent feature of Ningaloo Reef and other coral reefs that have been studied worldwide is their capacity for removing ocean-derived microorganisms from the water column. The uptake of ocean living microorganisms by the reef benthos is suggested as one of the major ways in which coral reefs sustain high rates of productivity despite living in oligotrophic waters. At Ningaloo, the uptake of picophytoplankton accounted for the removal of 4 and 21 mmol C m^{-2} day^{-1} over the active reef in November and May, respectively (Fig. 5a, b). This compared well with the average value of ~20 mmol C m^{-2} day^{-1} estimated by Wyatt et al. (2010) using independent calculations of phytoplankton (Chl *a*) uptake (based on the conversion of Chl *a* to particulate organic carbon). Including bacterioplankton and virioplankton, 29 mmol C m^{-2} day^{-1} on average, was removed by the active reef. As discussed by Wyatt et al. (2010), this rate of removed C equated to a considerable (>20% on average) amount of reef net community productivity. *Synechococcus* generally contributed the highest proportion to the removed C; however, in November picoeukaryotes were also important contributors to C uptake. Carbon is, however, generally considered not to be limiting in coral reefs since most reefs are net autotrophic (Falter et al. 2011). Benthic organisms, such as corals do require additional nutrient sources such as nitrogen for tissue and skeletal growth, as well as photosynthesis and respiration (Houlbrèque et al. 2003, 2004b). Picoplankton and virioplankton accounted for ~1–5 mmol N m^{-2} day^{-1} of the removed N over the active reef (Fig. 5). These values align well with total phytoplankton (Chl *a*) N uptake estimates at Ningaloo during the same study period (~3.6 mmol N m^{-2} day^{-1}, Wyatt et al. 2010). They also compared well to other reported measurements, such as in the Red Sea (2.8 mmol N m^{-2} day^{-1}, Genin et al. 2009), but are lower than those N uptake *m* estimates (of total suspended organic matter) from a soft coral dominated community in the Great Barrier Reef (7–15 mmol N m^{-2} day^{-1}, Fabricius and Dommisse 2000). Bacterioplankton in particular were a highly rich source of N at Ningaloo, with bacterioplanktonic-derived N uptake exceeding the whole picophytoplanktonic N pool in both May and November (Fig. 5c, d). In addition to C and N, bacterioplankton have a high iron content relative to other picophytoplankton (Tortell et al. 1999) and are also sources of other essential elements (e.g. phosphorous (P), Fagerbakke et al. 1996) and micronutrients (e.g. B_{12}, Agostini et al. 2009); all of which are essential

for animal and algal (zooxanthellae) metabolism (Sorokin 1973). Against an often highly variable picophytoplankton community delivered to the reef, bacterioplankton exhibited only small temporal variability and thereby represent a consistent nutritive source to the benthic reef community at Ningaloo. While for the most part, the C and N contribution of virioplankton was small (<1%), their contribution was significant to total C and N uptake on the fore reef in November (35 and 83% of C and N uptake, respectively). With the flows somewhat more complex on the fore reef than inside the reef itself (Wyatt et al. 2010), these values should also be interpreted with some caution; however, this may suggest that virioplankton, at times, could contribute some N and P rich material to the reef benthos. Perhaps most importantly, virioplankton likely play other important roles in coral reef biogeochemistry through lysis and subsequent release of host cellular products (i.e. N, C, P, Fe and amino acids) into the water column, which can then be utilised by picoplankton communities (Gobler et al. 1997; Middelboe and Jorgensen 2006).

At seasonal scales, oceanographic conditions occurring offshore of Ningaloo result in a greater phytoplankton biomass delivered to the reef in the autumn/winter (Wyatt et al. 2010). Oceanographic conditions offshore are however further driven by interannual variability of current transport rates (e.g. of the LC (Feng et al. 2003)) influenced by the El Niño/Southern Oscillation (ENSO). The LC has a strong transport and a deep thermocline during La Nina years and weaker transport and shallower thermoclines during El Niño years (Feng and Wild-Allen 2009). These ENSO-related shifts in the LC could have major impacts on uptake rates of picoplankton by Ningaloo Reef. For example, any climate-related shifts towards more El Niño-like conditions (IPCC 2007) that reduce LC transport in austral Autumn/Winter would potentially limit picoplankton biomass delivered to the reef and could subsequently negatively affect the metabolism of benthic coral reef communities. Changes in ocean seawater physico-chemistry (e.g. increased seawater temperatures, increased CO_2 leading to ocean acidification) could further alter picoplankton community composition and/or the nutritional value of picoplankton cells (Fu et al. 2007) available to benthic coral reef communities. Uptake of living cells by the coral community is believed to be further critical for their resilience and recovery during climate driven stress events (e.g. coral bleaching, Grottoli et al. 2006). During periods when corals lose their zooxanthellae and become bleached, heterotrophic feeding on zooplankton can account for more than 100% of their daily metabolic demand (Grottoli et al. 2006). The role of picoplankton in such recovery has not been explored.

Uptake coefficients, *S*, exhibited a linear response with velocity *U* (ESM, Fig. 2), indicating that the uptake of picoplankton was primarily limited by hydrodynamic processes (i.e. mass transfer), at least across the range of concentrations and velocities we observed in the field. Interestingly, on the few occasions when uptake coefficients were negative, these values also exhibited linear increases with velocity (data not shown), suggesting that similar hydrodynamic processes may govern both the uptake and release of cells. However, the correlation of uptake rates, *m*, with cell concentrations (ESM, Fig. 1) implies physical control at low cell concentrations (linear response), up until the point at which biological uptake mechanisms for feeding are saturated (as indicated by the plateaux in the Michaelis–Menten-type hyperbola). While an outlier was responsible for driving the positive linear uptake–concentration relationship for picoeukaryotes (ESM, Fig. 2c), this high value is indicative of the natural variability of concentrations of picophytoplankton occurring offshore of Ningaloo Reef, which are dependent on offshore oceanographic conditions. Our results would be consistent with the initiation of saturation at the highest concentrations observed for *Prochlorococcus* and *Synechococcus*. This begs the question, at what cell concentration would this system saturate? Taken together, these results indicate an important interplay between physical (hydrodynamics of the system) and biological mechanisms (i.e. anatomical and physiological features of the benthic community) in controlling particle uptake at a range of scales from the individual organism, community and reef region. It is unclear at this stage, which members of the Ningaloo benthic community are the dominant consumers of the picoplankton and virus fraction and what mechanisms are operating to promote assimilation of the different microbial taxa into the coral reef food web. We believe priority should be given to better understanding the importance of ocean–reef interactions, particularly in terms of the significance of benthic-pelagic coupling processes in reef-level biogeochemistry and the dependence of certain reef organisms on picoplanktonic supply.

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