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Pelagic metabolism in the waters of the Great Barrier Reef

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Abstract

Pelagic metabolism (community respiration [CR] and net community production [NCP]) were measured in oxygen flux experiments at 14 locations in waters of the Great Barrier Reef (GBR) lagoon between 16°S and 23°S during the dry seasons of 2008 and 2009 and the wet seasons of 2009 and 2010. These were compared to similar experiments conducted in the wet season of 2005 in the far northern GBR (14°S). Seasonality (wet and dry season) was the greatest determinant of respiration rate, with median CR values of 1.85 mmol O_2 m^{-3} d^{-1} in the dry season and 2.87 mmol O_2 m^{-3} d^{-1} in the wet season. NCP normally ranged up to 9.16 mmol O_2 m^{-3} d^{-1}, depending on depth and phytoplankton biomass, though an extreme value of 14.96 mmol O_2 m^{-3} d^{-1} occurred during flood conditions. Cross-shelf effects had a strong influence on physicochemical variables but weaker effects on both CR and NCP, though both were higher inshore. All but two stations were net autotrophic, with a median ratio of gross primary production : CR of 1.5. Area-specific CR was 72 ± 23 standard deviation (SD) mmol O_2 m^{-2} d^{-1} in the dry season and 94 ± 27 SD mmol O_2 m^{-2} d^{-1} in the wet season. Area-specific NCP was lower in the dry season (41 ± 33 SD mmol O_2 m^{-2} d^{-1}) than in the wet season (55 ± 54 SD mmol O_2 m^{-2} d^{-1}). Peaks in area-specific NCP were associated with floods, intrusions of nutrient-rich sub-thermocline Coral Sea water, and localized phytoplankton blooms but otherwise showed few seasonal or spatial trends. Overall, CR in GBR lagoon waters was comparable to rates in oligotrophic oceanic waters, but NCP was more typical of shelf systems.

The Great Barrier Reef (GBR) is an iconic marine ecosystem 2300 km in length and up to 330 km in width, extending over 15° of latitude (9–24°S). All reefs south of Cape York (10°42′S) are contained within the Great Barrier Reef Marine Park (GBRMP), which includes approximately 3700 individual coral reefs (Hopley et al. 2007). Most reefs are located some distance from shore, and the body of water separating the reef matrix from the mainland is locally referred to as the GBR "lagoon." Approximately 90% of the shelf area within the GBRMP (238,700 km^2) is comprised of this lagoonal habitat. The GBRMP provides a global reference point for coral reef ecosystems facing threats from the combined effects of terrestrial runoff, overfishing, plagues of pest species such as Crown of Thorns (*Acanthaster planci*) starfish, and climate change (e.g., coral bleaching). However, inter-reefal and pelagic ecosystems of the GBRMP have received little scientific attention compared to the coral reefs themselves and pelagic process studies have largely focused on the central GBR (16–19°S; Furnas et al. 2005).

The GBR lagoon is bordered on the west by low-energy, mangrove-dominated ecosystems with turbid and chlorophyll-rich waters, and to the east it adjoins the matrix of mid- and outer-lagoon reefs perfused by clear oligotrophic waters originating from the Coral Sea. Overall, 73% of the volume of water within the GBRMP to the 150 m isobath is contained in depths of 40 m or less, and in most cases light can penetrate throughout the water column. In the central GBR coastal water moves north via wind-forced currents, but in the mid- and outer-lagoon movement is southward as a result of forcing by the East Australian Current. Southeast trade winds force surface waters onshore, suppressing upwelling on the outer margin of the GBR, but during the northwest monsoon these winds relax and episodic upwelling can occur. Patterns of water circulation in the GBR lagoon are complex and remain poorly understood. On the basis of radium isotope distribution, Hancock et al. (2006) estimated that waters within 20 km of the coast were flushed on timescales of 18–45 d. The numerical models of Luick et al. (2007) predicted flushing times for the GBR lagoon between 1 month and 1 yr, but the drifter studies of Choukroun et al. (2010) suggested this may be less than a month. More than 60% of regional rainfall occurs between the period January and March and is discharged to the coastal waters of the GBR lagoon by river flow. The largest river is the Burdekin River, which has a mean annual flow of 9.7×10^9 m^3, followed by the Normanby and Fitzroy Rivers. Between 17°S and 20°S Choukroun et al. (2010) estimated the daily exchange of GBR waters with the Coral Sea to be 23 km^3, which is approximately equal to the annual input by rivers in this section, though ocean exchange is likely to be threefold higher in the southern GBR and the influence of rivers proportionately lower.

Over an annual cycle, water temperatures in the GBR lagoon range between 20°C and 30°C. Concentrations of dissolved inorganic nutrients are low—total dissolved inorganic nitrogen (DIN) and phosphorus (DIP) are of the order of 0.1 μmol L^{-1} and show little spatial variation under "normal" circumstances (Furnas et al. 2005). Dissolved organic nutrients are consistently higher in concentration than inorganic forms (e.g., dissolved organic nitrogen [DON] ~ 4–6 μmol L^{-1}). Particulate nitrogen (PN), mainly in the form of detrital particles, is present in concentrations ~ 1 μmol L^{-1} (Furnas et al. 2005). Chlorophyll levels in the GBR are low compared to other parts of the world (0.2–0.8 μg L^{-1}) and are on average ~ 50% greater in the wet season (Brodie et al. 2007).

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Chlorophyll in inshore waters is up to fourfold higher than in offshore waters in the central region, and southern GBR waters are twofold higher than those in the north (De'ath and Fabricius 2010). All these indices of "water quality" can be exceeded during ephemeral event-driven regional phenomena such as floods and cyclones (Furnas et al. 2005, 2011). An approximately fourfold increase in nitrogen loads since pre-European times together with a change from predominately organic to inorganic species of nitrogen has resulted in the suggestion that inshore waters of the GBR lagoon south of Cooktown are eutrophic at some times of the year (Brodie et al. 2011).

Picoplankton accounts for 37–99% of primary production on the GBR shelf (Furnas and Mitchell 1987) with a "very productive and rapidly growing plankton community" despite low standing stocks of nutrients (Furnas et al. 2005). Growth rates of phytoplankton are high and are sustained by recycling and remineralization (Furnas et al. 2005). Both intrusive activity and floods have the capacity to change the size composition of phytoplankton communities in the GBR lagoon, from a picoplankton-dominated system to one in which cells > 10 μm, principally diatoms and dinoflagellates, ephemerally dominate phytoplankton biomass (Furnas et al. 2005). The nitrogen-fixing cyanobacterium *Trichodesmium* forms episodic blooms and may be an important source of new N to the GBR (Furnas et al. 2011). Area-specific pelagic primary production is higher during the wet season than during the dry season, but the cross-shelf gradient is strongest during the dry season (Furnas et al. 2005), with higher production offshore because of the combined effects of water transparency on phytoplankton growth and of depth in the calculation of area-specific measurements. Overall, Furnas and Mitchell (1987) estimated the total primary production of the GBR shelf at ~ 1 g C m^{-2} d^{-1}, of which 72% was attributable to phytoplankton.

In this paper we present the results of oxygen flux experiments conducted in the GBR lagoon from stations located nearshore, in mid-lagoon, and adjacent to the reef matrix between latitudes of 14°S and 23°S. To date, all measurements of pelagic primary production on the GBR have been conducted using the ^{14}C bicarbonate method, which reports values somewhere in between net and gross photosynthesis (Bender et al. 1999). The oxygen flux method has the advantage of resolving respiration rate, therefore separating net and gross production. Our study confirms the patterns of primary production of earlier studies but is the first to report pelagic respiration rates and to determine the P : R ratio of GBR waters.

Methods

Study area—This study combines the results of a 2 yr field campaign (2008–2010) with an earlier (2005) cruise to the Cape York section of the GBR. Between September 2008 and March 2010 we sampled at 14 stations between Cape Tribulation (16°S) in the north of the GBR lagoon and the Keppel Islands in the south (23°S; Fig. 1). Mid- and outer-lagoon stations were added to the inshore stations described by Schaffelke et al. (2011) on four cruises (Table 1), two of which were in the dry season (September–October) and two in the wet season (February–March). The station layout comprised four cross-shelf transects (inshore, mid-lagoon, and outer-lagoon) in four of the five Natural Resource Management (NRM) regions identified for the whole of GBR: Wet Tropics (two locations), Burdekin (three locations), Mackay Whitsunday (three locations), and Fitzroy (three locations). One mid-lagoon location was added approximately midway between each transect. The GBR lagoon is constricted near Cape Tribulation, and no mid-lagoon location was occupied for the Wet Tropics region. Inclement weather prevented us occupying two mid-lagoon and one outer-lagoon location in the Fitzroy region on our last cruise (February–March 2010). To extend the study domain to the Cape York NRM region as far north as 14°S, we included a set of five stations collected on an earlier cruise (N1–N5; Fig. 1).

For the purposes of spatial analysis of the 2008–2010 data set, we adopted the "across/along" coordinate system applied to water quality within the GBR by De'ath and Fabricius (2010). The value of along was set to 0 at 26°38′S and 1 at 10°42′N, and across set to 0 at the coast and 1 at the 80 m isobath along the shelf break.

Field sampling—With a few exceptions, sampling occurred during daylight hours at opportunistic times determined by the movement of the ship. Conductivity, temperature, and depth (CTD) casts at each station were made with a Seabird SBE19+ CTD (Sea-Bird Electronics) fitted with a Seabird SBE43 oxygen sensor, a Western Environmental Testing Laboratory (WET Lab) C-Star transmissometer (WET Labs), and a WET Labs fluorometer. Water transparency was measured with a Secchi disk, and the depth of the euphotic zone calculated on the basis of the Secchi depth with an empirically derived relationship for reef waters (M. Slivkoff pers. comm.). Water samples were collected with Niskin bottles from the depths corresponding to the light levels simulated by our on-deck incubators and used for oxygen flux measurements (*see* below), measurement of water column nutrients (2008–2010 samples only), and chlorophyll *a* (Chl *a*) concentration.

Water quality analyses—Analytical protocols for Chl *a* and nutrients are fully described in Schaffelke et al. (2011). Briefly, dissolved inorganic nutrient concentrations (Si, NH_4, NO_2, NO_3, and PO_4), DON, and dissolved organic phosphorus (DOP) were determined from frozen samples by segmented flow analysis using standard automated techniques. Water samples for dissolved organic carbon (DOC) analysis were collected in acid-rinsed syringes, and filtered through a 25 mm polycarbonate inline filter of 0.4 μm porosity into a 10 mL acid-washed tube. The sample was fixed by the addition of 100 μL of concentrated analytical reagent–grade HCl and refrigerated until subsequent analysis by high-temperature combustion in a Shimadzu TOC-5000 analyzer (Shimadzu Corporation).

Chl *a*, PN, particulate phosphorus (PP), particulate organic carbon (PC), and total suspended solids (TSS) were determined as described by Schaffelke et al. (2011).

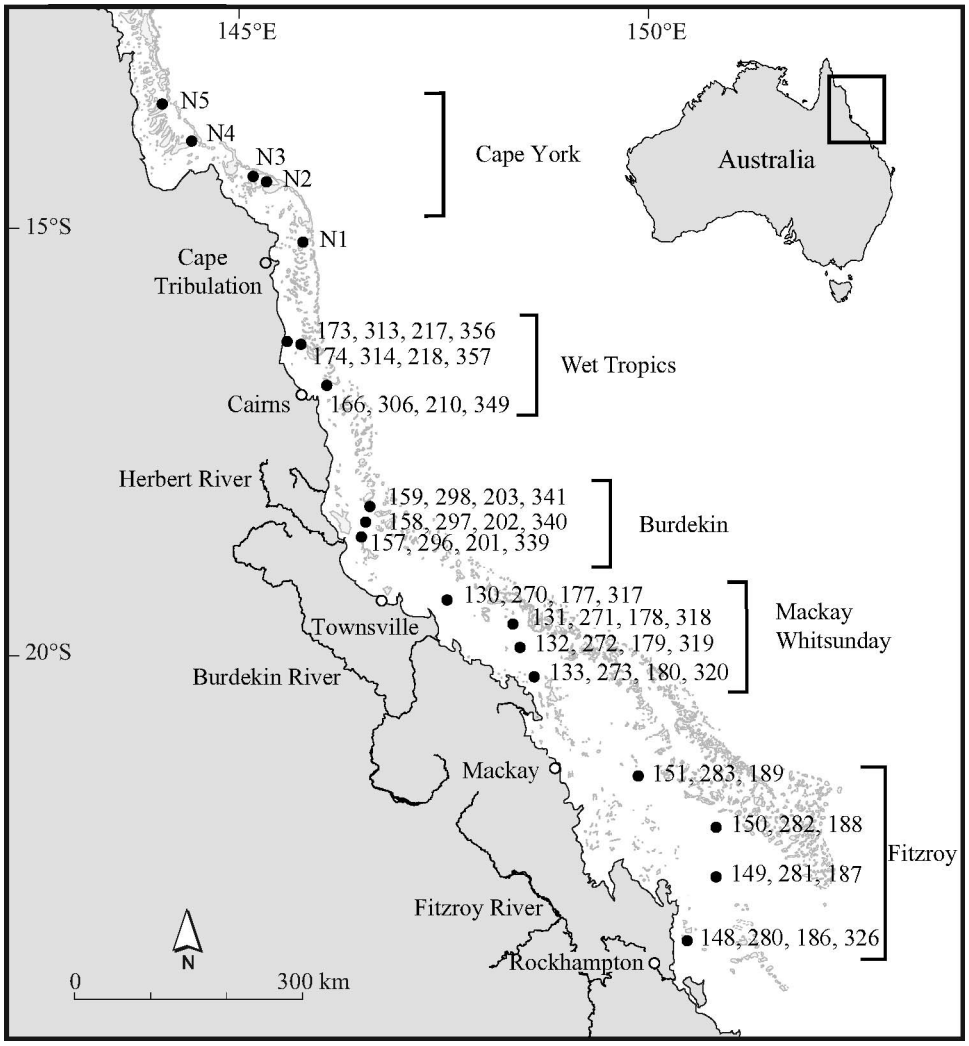

Fig. 1. Study area. Numbers refer to the station number, and the brackets to the approximate location of Natural Resource Management regions identified for the Great Barrier Reef Marine Park.

Determination of respiration and production rates—Immediately after retrieval onboard, seawater from the Niskin bottles was used to fill calibrated acid-washed iodine flasks with a nominal volume of 125 mL. Nine flasks were filled from each depth at every station: three were fixed immediately for Winkler titrations (zero-time samples); three were placed in a lightproof deck incubator (dark respiration); and three were placed in deck incubators with appropriate neutral-density mesh to simulate the light climate at the depth of collection. Surface seawater was continuously pumped through both light and dark incubators. The flasks were incubated at 3–4 light levels corresponding to 60%, 35%, and 15% of surface light (I_o), as well as either 100% or 5% I_o, depending on the light climate at the particular station. Samples were incubated for ~ 24 h, after which the flasks were fixed. The entire set of flasks from each experiment was titrated as a single batch within 24 h of completion of the experiment.

Table 1. Sampling dates and station numbers (number of station occupations).

Dates	Season	Stations
07–12 Feb 2005	Wet	N1–N5 (5)
30 Sep–12 Oct 2008	Dry	130–174 (14)
15–26 Feb 2009	Wet	177–218 (14)
29 Sep–12 Oct 2009	Dry	270–314 (14)
21 Feb–04 Mar 2010	Wet	317–357 (11)

Dissolved oxygen concentrations were determined with an automated high-precision Winkler titration system developed at the Oceanographic Data Facility, Scripps Institution of Oceanography, University of California, San Diego, and which uses the absorption of 365 nm ultraviolet light for endpoint detection. Net community production (NCP) and community respiration (CR) were estimated as the change in oxygen concentration during a 24 h period in flasks incubated in the light and dark, respectively. Gross primary production (GPP) was calculated as the sum of

Table 2. Mean (and 95% Bayesian highest posterior density [HPD]) effects on the CR associated with season (dry and wet), latitude and longitude (expressed as across and along shelf splines), observation depth, and a range of physicochemical parameters (centered and scaled separately for each season) combined by PCA (and expressed as the first two axes). Along is positive northward, and across is positive offshore. The probability from Markov chain Monte Carlo sampling (pMCMC) and anti-conservative p-values based on t-statistics ($pr > |t|$) are also indicated.

Source	Estimate	MCMC mean	HPD95 lower	HPD95 upper	pMCMC	$pr > \|t\|$
(Intercept)	−2.7050	−2.6587	−3.1751	−2.1715	0.0001	0.0000
Season	−0.5984	−0.6074	−0.8338	−0.3743	0.0001	0.0000
Across	1.1120	1.0754	0.1701	2.0341	0.0228	0.0385
Along	0.9863	0.9856	0.0332	1.9737	0.0462	0.0695
Depth*	0.0493	0.0391	−0.0268	0.1091	0.2550	0.1343
PC1	0.2834	0.2900	0.2266	0.3498	0.0001	0.0000
PC2	−0.0311	−0.0393	−0.1479	0.0730	0.4840	0.6022
Along : across	−2.8462	−2.7890	−4.6123	−1.0181	0.0028	0.0069

* Fourth-root transform.

NCP and CR, and the P : R ratio calculated as the ratio GPP : CR.

The average coefficient of variation of the replicate O_2 concentration measurements in the zero, dark, and light bottles was 0.09%, 0.20%, and 0.28%, respectively, and the mean of the standard errors of the CR and NCP rate measurements were 0.27 ($n = 276$) and 0.37 ($n = 276$) mmol $O_2\ m^{-3}\ d^{-1}$, respectively. We computed area-specific CR and NCP at each station by trapezoidal integration of volumetric data to either the sea bottom or the 1% isolume, depending on the total water depth at that station. The standard error (SE) of the estimate was calculated by propagating the depth-specific error as described in Serret et al. (2001).

Data analysis—Only the 2008–2010 sample series was analyzed statistically—the earlier 2005 sample set comprised only Chl *a*, CR, and NCP measurements and is included only to extend the latitudinal range of oxygen flux measurements to the Cape York region.

Broad spatial and temporal (seasonal) patterns in water quality were initially explored graphically via redundancy analysis (RDA) ordinations (Legendre and Legendre 1998) of fourth-root transformed physicochemical variables. RDA is a form of direct gradient analysis in which the multivariate (water quality) patterns are constrained by variation explained by a set of specific predictors (season, water depth, and across/along). Associated respiration and production patterns were then explored by overlaying correlation vectors of CR and NCP against the first two constrained ordination axes coordinates.

More specific spatial and temporal patterns of volume-specific CR and NCP were investigated using hierarchical mixed-effects models fitted via restricted maximum likelihood. Each model comprised the fixed effects of season, depth (normalized by fourth-root transformation), and the multiplicative natural spline terms of across and along, each of which were first centered to dampen the severity of multicollinearity. As both CR and NCP were directly influenced by the local physicochemical properties (*see* RDA above), additive water quality covariates (first two standardized axes from an unconstrained principal component analysis [PCA] comprising each of the physicochemical properties centered separately for each season, to ensure that PCA scores do not compete with season in the models) were also included in the models. Sampling station (nested within season by across/along) was included as a random effect to account for spatial variation, pseudoreplication, and temporal autocorrelation arising from multiple and repeated observations from the same stations. The influence of each sampling station was examined via case-deletion Cook's D diagnostics (Christensen et al. 1992) and models were refit following the omission of overly influential stations. Normality, homogeneity of variance, multicollinearity, intercept–slope correlations, and variance inflation diagnostics were also performed to ensure models were fitted appropriately.

Global mixed-effects models were constructed separately for CR and NCP and thereafter separately for each season (wet and dry). Inference was based on 95% Bayesian highest posterior density intervals of effect sizes predicted from posterior distributions of model parameters derived via Markov chain Monte Carlo sampling. Anti-conservative p-values based on t-statistics with upper bound degrees of freedom were also computed. Greater insights into the nature of spatial and temporal CR and NCP relationships were provided by examining partial dependency plots from aggregated boosted trees (De'ath 2007) of volume-specific CR or NCP against depth, across, and along for each season. A total of 5000 trees (shrinkage of 0.005, interaction depth of 5, and bag and training fractions of 50%) and five cross-validation folds were employed for each response and season combination. The optimum number of boosting iterations was estimated via cross-validation.

All mixed-effects modeling was performed using the lme4 package and pvals.fnc functions within R version 2.13.1 (R Development Core Team 2011).

Results

Water column structure—The greatest contrast in physicochemical variables was between wet and dry seasons (Table 2; Fig. 2). Temperatures were lower and more variable during the dry season (24.9°C ± 1.1°C standard deviation [SD]) than during the wet season (28.7°C ± 0.6°C SD; Fig. 2a). Conversely, during the dry season salinity was less variable (35.2 ± 0.2 SD) and higher than during the wet

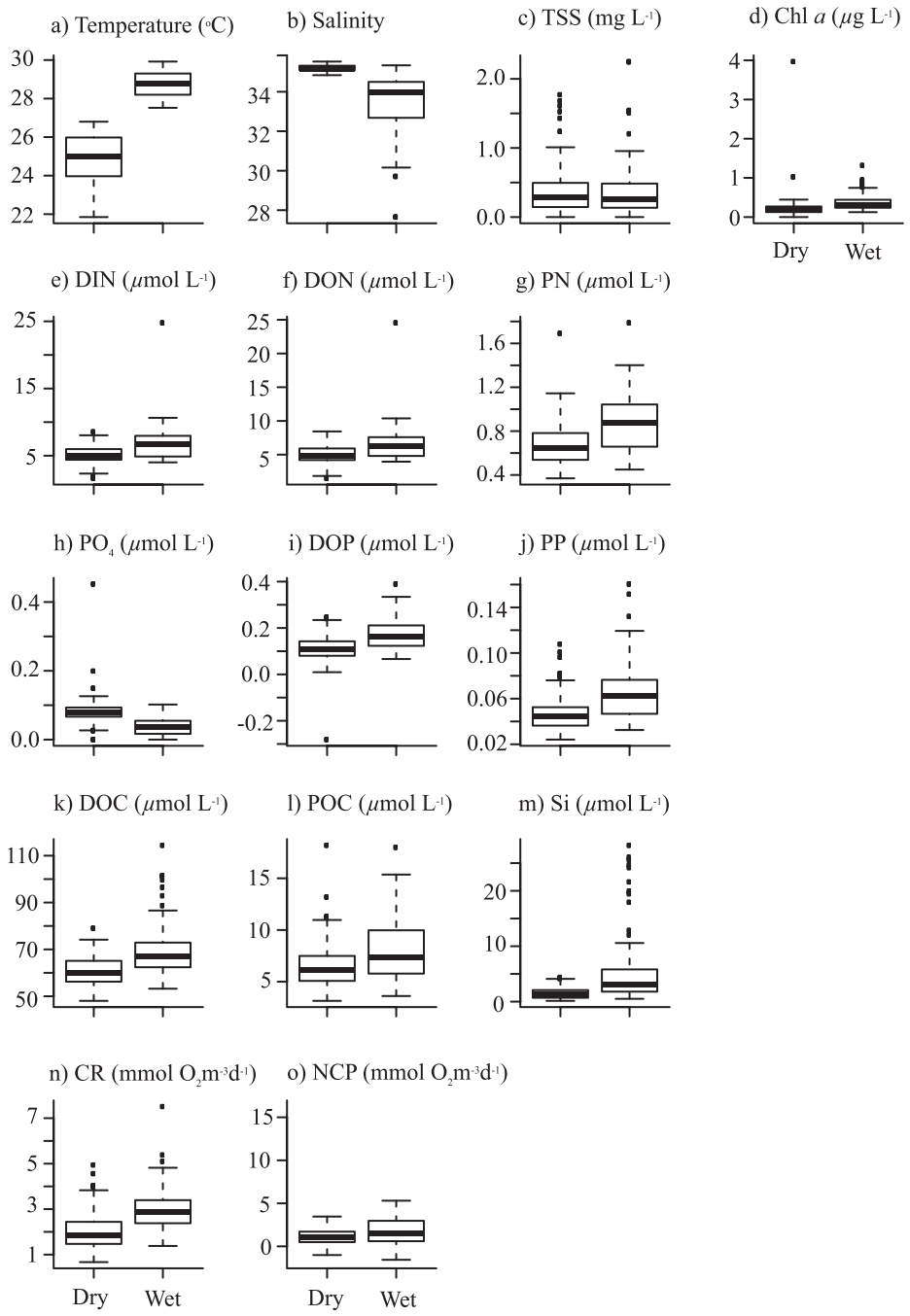

Fig. 2. Comparison of water column variables from the Great Barrier Reef lagoon in wet and dry seasons. The horizontal lines represent the quantiles of the data, i.e., the solid line is the median, the box represents 50% of the data, and in the absence of outliers, the whiskers represent a further 25% of the data. Outliers are defined as observations that are > 2 standard deviations from the mean.

season (33.6 ± 1.4 SD; Fig. 2b). For both dissolved nutrients (DIN, DON, PO_4, DOP, DOC, Si) and particulate nutrients (PN, PP, PC) as well as TSS and Chl *a*, there were no significant differences between wet and dry season means, though the wet season measurements were without exception more variable (Fig. 2). The average ratios of DIN : DIP were 1.89 at the inshore stations and 3.83 at mid- and outer-lagoon stations. Similarly, in the particulate fraction the ratio of C : N : P were 111 : 11 : 1 inshore, and 134 : 14 : 1 at mid- and outer-lagoon stations. Oxygen was close to saturation (mean = 102%), but on some occasions there was drawdown of oxygen saturation in the lower water column, particularly at inshore locations in the wet season. For instance, in the Wet Tropics at inshore stations

during the wet season oxygen fell to 88% saturation below 10 m depth at Sta. 201 (31 m total depth) and to 93% saturation below 12 m depth at Sta. 356 (19 m total depth).

During the dry season the water column was generally well mixed with respect to both temperature and salinity (Fig. 3a–c). Chlorophyll fluorescence was similar throughout the water column inshore, but typically increased in the lower half of the water column at mid-lagoon and outer-lagoon stations. During the wet season inshore stations often showed the influence of riverine discharges, indicated by lower salinity and higher temperature near the surface (Fig. 3d,e). The profile of chlorophyll fluorescence depended on the nature of the plume. For instance, the plume waters originating from the Herbert River in February 2009 (Sta. 201) were low in chlorophyll, which was higher in the underlying water column (Fig. 3d). In contrast, the plume of the Fitzroy River in February 2010 was turbid and phytoplankton rich, resulting in very high values of all measurements (Sta. 326; Fig. 3e). This station was so unusual that we have not included it in subsequent multivariate analyses.

During the wet season at outer-lagoon stations there were often indications of upwelling, with the intrusion of lower temperature–higher salinity water in a near-bottom layer, and a chlorophyll maximum in the lower water column. Interestingly, we did observe some upwelling events in the dry season, such as the outer-lagoon Sta. 298 in the Wet Tropics during October 2009 (Fig. 3h), which showed a clear temperature–salinity signal of the intrusion of Coral Sea water, again with a near-bottom chlorophyll maximum. In the mid-lagoon, a slight near-bottom chlorophyll maximum remained despite the water column being well-mixed with respect to temperature and salinity (Fig. 3f), either as a residual footprint of upwelling in the outer-lagoon or as a result of photoadaptation in situ.

The series of five stations occupied in the Cape York region (Sta. N1–N5; Fig. 1) were only occupied in the wet season of 2005, a year in which rainfall was below average. The water column in this area was isosaline but strongly thermally stratified (Fig. 3g) as a result of water ponding behind the hard line of the outer barrier reefs where there is little exchange with the Coral Sea and warming as a result of insolation. As was usually the case with other outer-lagoon stations (Fig. 3c,h), there was an accumulation of chlorophyll in the lower water column.

Oxygen fluxes—Measurements made in the plume of the Fitzroy River in March 2010 (Sta. 326) had extreme values of CR (11.12–14.96 mmol O_2 m^{-3} d^{-1}) and NCP (77 mmol O_2 m^{-3} d^{-1}) in the surface waters of the plume (Fig. 3e). Generally, CR was significantly higher in the wet season than in the dry season (Table 2; Fig. 2). In the dry season volume-specific CR ranged between 0.67 and 4.95 mmol O_2 m^{-3} d^{-1}, with a median value of 1.85 mmol O_2 m^{-3} d^{-1}; in the wet season these were 1.38, 7.51, and 2.87 mmol O_2 m^{-3} d^{-1}, respectively. The median value for the inshore stations during the wet season was somewhat higher: 3.43 mmol O_2 m^{-3} d^{-1}. At the 2005 Cape York region stations, CR was higher (4.09 ± 1.42 SD mmol O_2 m^{-3} d^{-1}) than observed at the 2008–2010 stations.

With the exception of Sta. 326, volume-specific NCP had a maximum of 9.16 mmol O_2 m^{-3} d^{-1}. During the dry season light bottle production was highest near-surface and decreased in parallel with light availability through the water column (Fig. 3a,b), except where chlorophyll maxima in the lower water column subsidized oxygen production at lower light levels (Fig. 3c,h). In the wet season the profiles of light bottle production through the water column were more variable (Fig. 3d,f,g). In some wet season experiments light bottle production in surface samples showed photoinhibition effects. For example, at Sta. 201 NCP was low at the surface and maximal at the intermediate depth that corresponded to the intersection of light penetration and subsurface chlorophyll (Fig. 3d). In contrast, Sta. 326 had extremely high measurements of NCP at the surface that rapidly decayed with light (Fig. 3e).

Redundancy analysis of water quality variables showed that CR and NCP accounted for $> 91\%$ of the constrained variance in the data (Fig. 4). There are two major environmental determinants of water quality: seasonality (strongly correlated to Axis 1) and location (across/along changes are correlated to Axis 2). The cross-shelf effect had the largest effect on physicochemical variables (higher values inshore), but within this gradient there was a very clear contrast between wet and dry seasons, probably forced by the resultant differences in temperature and salinity (Fig. 4). These variables also varied according to their latitude (along): directly in the case of temperature, and inversely in the case of salinity. All other physicochemical variables were correlated, with highest values inshore. Both CR and NCP were higher inshore than offshore, i.e., negatively correlated with position across the GBR lagoon. Accordingly, NCP and CR were highly correlated with nutrient concentrations and higher standing stocks of chlorophyll and suspended matter (Fig. 4).

While outliers did not appear to substantially influence the patterns from models incorporating season, they did skew effects in the models performed separately between seasons. Consequently, our conclusions are based on models for which highly influential stations have been removed. Since both CR and NCP appear to be directly influenced by local physicochemical variables, proxy variables (principal component [PC] 1 and PC2) comprising the first two axes from an unconstrained PCA of the physicochemical variables centered separately for each season were incorporated into a linear mixed-effects model with temperature, depth, across, and along as predictors and station as a random effect. PC1 was negatively aligned with TSS, Chl *a*, PN, and PP. PC2 was positively aligned with temperature and Si, and negatively with salinity.

In the wet season CR declined with depth, and was positively correlated with particulate matter (TSS, Chl *a*, PN, PP; i.e., negatively correlated to PC1; Table 3), reflecting the influence of inshore plumes. However, in the dry season this correlation was reversed with CR higher in water low in particulates (CR positively correlated to PC1). High values of dry-season CR were associated with cooler, more saline water (negatively correlated to PC2) and unrelated to depth. In the dry season NCP declined

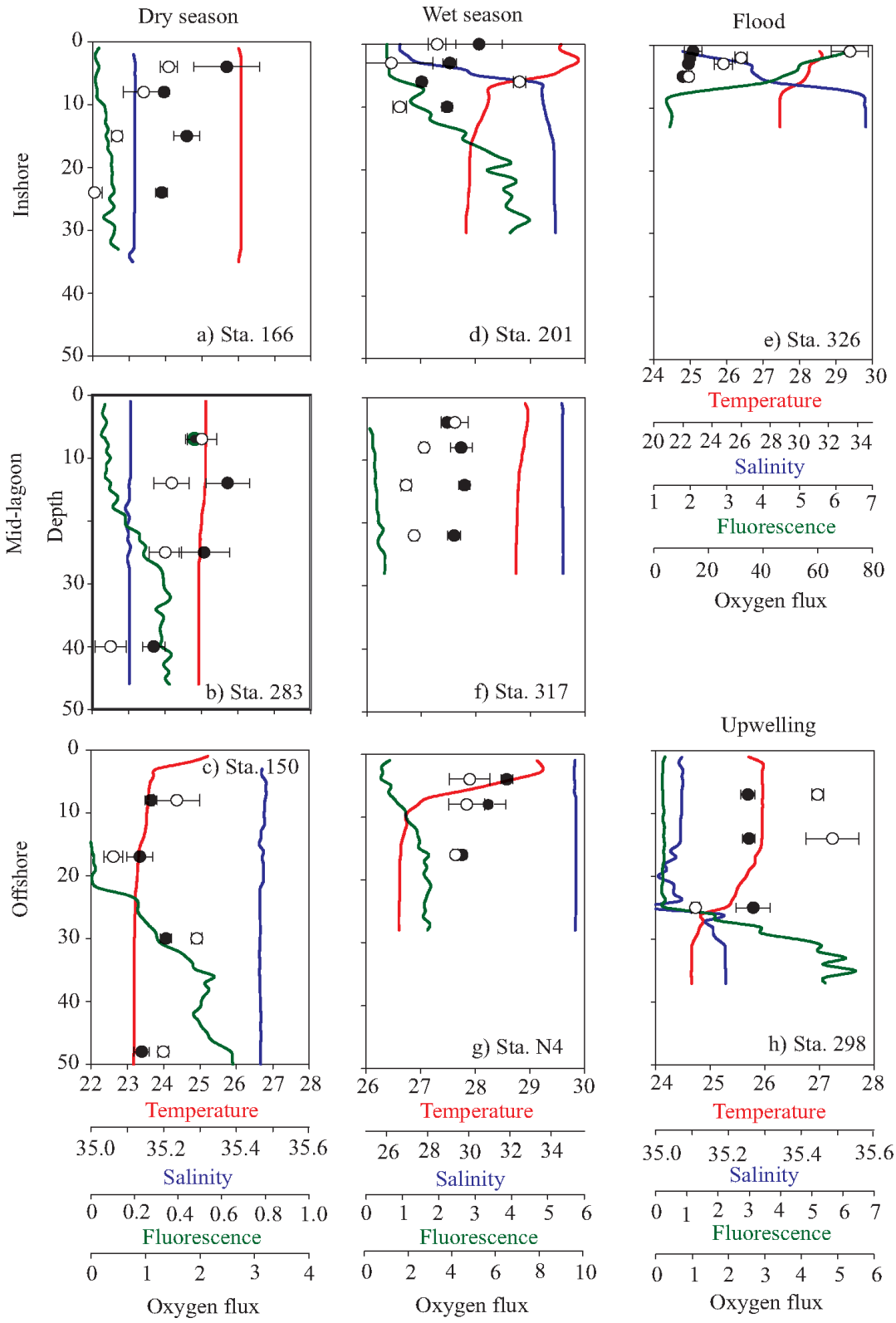

Fig. 3. Water column structure and oxygen flux measurements at representative stations. Temperature (red), salinity (blue), and chlorophyll fluorescence (green) is taken from CTD casts, and measurements of CR (solid circles) and NCP (open circles) from experimental incubations of water collected at the indicated depths. The error bars are standard errors (SE).

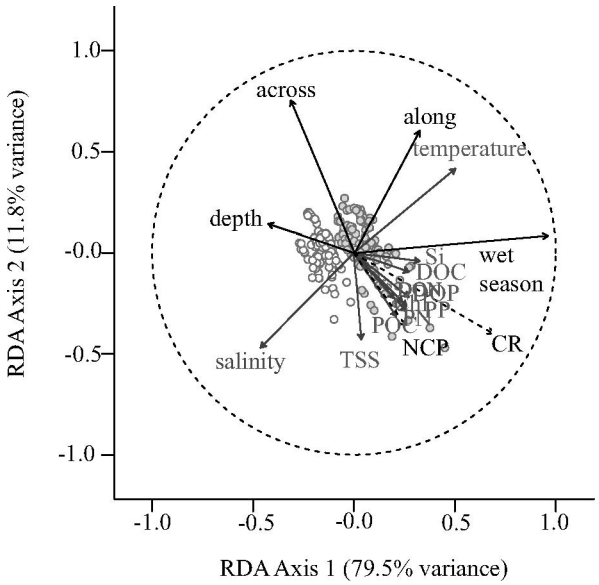

Fig. 4. Biplot from redundancy analysis (RDA) on water quality variables (gray arrows) constrained by spatial and temporal parameters (dark arrows) for samples collected in wet (solid circles) and dry (open circles) seasons with correlations between the first two RDA axes and CR and NCP.

with depth (reflecting the light profile) and was correlated with low temperature and high salinity (i.e., negatively correlated to PC2), reflecting higher values in the southern GBR (*see* below). In the wet season there was no relationship between NCP and depth, suggesting the compensating influence of subsurface chlorophyll maxima. Accordingly, NCP was associated with TSS, Chl *a*, PN, and PP (i.e., NCP was negatively correlated with PC1), indicating a correlation with phytoplankton biomass.

Spatial effects on CR and NCP were visualized using partial dependency plots, which allow the contribution of separate effects to be factored out (Fig. 5). CR was higher inshore than offshore (Fig. 5a,g). Spatial patterns in NCP were modest, with a tendency to be higher inshore than offshore (Fig. 5d,j) and higher in the south than the north (Fig. 5e,k). Cross-shelf patterns in both CR and NCP in the dry season were similar to those in the wet season (Fig. 5g,j), but the along-shelf patterns were quite different between seasons, with CR tending to be higher in the north in the dry season (Fig. 5h), despite being associated with cooler, more saline water (Table 3). In the wet season CR was higher in the Burdekin region than in the Wet Tropics or Fitzroy regions (Fig. 5b); the Mackay Whitsunday region was intermediate.

Area-specific respiration and production rates—For the 2008–2010 data set, area-specific GPP was 111 ± 47 SD mmol O_2 m^{-2} d^{-1} in the dry season (range 55–253 mmol O_2 m^{-2} d^{-1}), and 159 ± 63 SD mmol O_2 m^{-2} d^{-1} in the wet season (range 70–338 mmol O_2 m^{-2} d^{-1}). All but two stations were net autotrophic, with P : R ratios in the range of 0.8–4.5 and a median value of 1.5. Over all stations, area-specific CR was 72 ± 23 SD mmol O_2 m^{-2} d^{-1} in the dry season, and 94 ± 27 SD mmol O_2 m^{-2} d^{-1} in the wet season. Mean area-specific NCP was also lower in the dry season (41 ± 33 SD mmol O_2 m^{-2} d^{-1}) than in the wet season (55 ± 54 SD mmol O_2 m^{-2} d^{-1}), but NCP was more variable than CR (Fig. 6). In the dry season of 2009 two stations had particularly high NCP: Sta. 298, in the outer lagoon of the Burdekin region, which had a strong upwelling signature (Fig. 3h); and Sta. 280, in the Fitzroy region, possibly because of the presence of a *Trichodesmium* bloom. Similarly, in the wet season of 2009 two stations showed high rates of primary production (Sta. 179 in the Mackay Whitsunday region, and Sta. 189 to the north of the Fitzroy region), both of which were in the mid-lagoon. Station 179 had a lens of low-salinity water (salinity = 30) near surface that was not obvious in the innermost station on that transect, and NCP within that near-surface layer was particularly high (15.7 mmol O_2 m^{-3} d^{-1}). This may have originated from the plume of the Burdekin River, which was drawn offshore in that year because of calm conditions. Sta. 189 had a fluorescence peak at mid-water, with chlorophyll apparently in excess of 2 μg L^{-1}. In this case, calm conditions may have resulted in a stable water column that allowed a mid-water bloom to establish. The wet season of 2010 included the extremely high production at Sta. 326 in the plume of the Fitzroy River (Fig. 3e), where NCP approached 300 mmol O_2 m^{-2} d^{-1} and CR 169 mmol O_2 m^{-2} d^{-1}. Unfortunately, the three adjacent mid- and outer-lagoon stations in the southern section were not sampled on that cruise because of adverse weather conditions. Area-specific CR in the Cape York region was 103 ± 16 SD mmol O_2 m^{-2} d^{-1}, and NCP was 104 ± 63 SD mmol O_2 m^{-2} d^{-1}, with an average P : R of 1.87.

Discussion

This study has demonstrated that seasonality provides the greatest contrasts in both pelagic respiration and NCP in the GBR lagoon, and is the first to describe both pelagic respiration and NCP in the GBR lagoon. Stocks of all nutrient species and volume-specific CR tended to be higher in the wet season than in the dry season (Fig. 2). There was a consistent cross-shelf trend in CR, with inshore stations higher (Fig. 5a,g). The large range in CR reflects the diversity of water bodies and their constituent plankton communities found within the GBR lagoon, from eutrophic mangrove waterways and flood plumes to those from oligotrophic oceanic environments. This effect was not apparent for volume-specific NCP (with the exception of Sta. 326), probably because of the confounding effects on light climate of cloud cover and increased turbidity inshore as a result of rainfall during the wet season.

There is substantial agreement regarding the strong seasonal effect on physicochemical variables and chlorophyll concentration between our results and those of the 5-yr study of Schaffelke et al. (2011), though that study concentrated only on inshore locations. Our study was conducted on four of the 15 cruises described by Schaffelke et al. (2011), but added mid- and outer-lagoon stations. Major disturbance effects caused the most abrupt changes in water quality in the GBR lagoon, as was most noticeable during the Fitzroy River flood in 2010. Overall though, the

Table 3. Mean (and 95% Bayesian highest posterior density; HPD) effects on CR and NCP associated with season (dry vs. wet), latitude and longitude (expressed as across and along shelf splines), observation depth, and a range of physicochemical parameters (centered and scaled separately for each season) combined by PCA (and expressed as the first two axes). Along is positive northward, and across is positive offshore. Estimates were derived from 10,000 Markov chain Monte Carlo (MCMC) samples following linear mixed-effects modeling. The probability from anti-conservative *p*-values based on *t*-statistics ($pr > |t|$) are also indicated.

	Dry season				Wet season			
Source	MCMC mean	95% HPD	*p*MCMC	$pr > \|t\|$	MCMC mean	95% HPD	*p*MCMC	$pr > \|t\|$
CR								
(Intercept)	2.6850	(2.1805, 3.1928)	0.0001	0.0000	2.9006	(2.0844, 3.7284)	0.0001	0.0000
Across	−1.2595	(−2.2284, −0.3120)	0.0094	0.0131	−0.3388	(−1.8851, 1.3072)	0.6726	0.6210
Along	−1.4984	(−2.4118, −0.5616)	0.0024	0.0031	0.4568	(−1.1275, 1.8781)	0.5326	0.6682
Depth*	−0.0401	(−0.1144, 0.0371)	0.2998	0.2944	−0.1475	(−0.2666, −0.0200)	0.0198	0.0145
PC1	0.1936	(0.1176, 0.2711)	0.0001	0.0000	−0.2979	(−0.3857, −0.2048)	0.0001	0.0000
PC2	−0.1751	(−0.2513, −0.0990)	0.0001	0.0000	−0.1846	(−0.3436, −0.0075)	0.0322	0.0516
Along/across	3.1111	(1.1448, 5.2597)	0.0042	0.0058	2.0535	(−0.8754, 4.9064)	0.1612	0.1781
NCP								
(Intercept)	1.9664	(0.9534, 2.9344)	0.0002	0.0001	2.8950	(0.6468, 5.1379)	0.0160	0.0063
Across	−0.2099	(−1.8785, 1.5844)	0.8226	0.8063	−1.5418	(−5.4258, 2.7148)	0.4502	0.4090
Along	−1.0138	(−2.8110, 0.8693)	0.2816	0.2411	−1.4514	(−4.9314, 2.3673)	0.4190	0.3822
Depth*	−0.1841	(−0.3290, −0.0414)	0.0152	0.0098	0.0464	(−0.2519, 0.3602)	0.7556	0.7810
PC1	0.0434	(−0.0979, 0.1778)	0.5328	0.4825	−0.3050	(−0.5777, −0.0306)	0.0298	0.0223
PC2	−0.3066	(−0.4569, −0.1694)	0.0001	0.0000	−0.1195	(−0.5403, 0.3377)	0.5854	0.5972
Along/across	1.9573	(−1.8571, 5.6778)	0.3098	0.2765	1.1813	(−6.2194, 8.0101)	0.7376	0.7264

* Fourth-root transform.

stoichiometry of dissolved and particulate forms of C, N, and P accord with those from inshore waters of the GBR lagoon described by Schaffelke et al. (2011), except that the ratio of DIN : DIP was marginally higher (3.83) at mid- and outer-lagoon stations than the annual mean of 2.2 reported by Schaffelke et al. (2011), as was the PC : PN : PP ratio (134 : 14 : 1 cf. 121 : 12 : 1). In all cases these were elevated compared to the Redfield ratio (106 : 16 : 1), indicating nitrogen limitation of phytoplankton biomass in the first instance and a high contribution of detrital particles in the latter. The waters of the GBR lagoon were fully saturated with oxygen (mean of 102% saturation), aligning with values typical of the surface layers of the Pacific Ocean (Millero 2005).

Pelagic primary production of the GBR lagoon—In our study, the seasonally weighted (8 months dry, 4 months wet) estimates of median NCP are 0.60 g C m^{-2} d^{-1} and of GPP are 1.62 g C m^{-2} d^{-1}, assuming a photosynthetic quotient of 1.4 and a respiratory quotient (RQ) of 1.1 (Bender et al. 1999). All previous measurements of primary production in GBR waters have been made using the ^{14}C method, which on average represents ~ 45% of GPP (Bender et al. 1999). Accordingly, for purposes of comparison the corresponding mean value of primary production from our study is 0.73 g C m^{-2} d^{-1}. Our data are therefore in close agreement with those of Furnas et al. (2005), who estimated the mean primary production of the GBR lagoon over all regions and seasons to be 0.68 g C m^{-2} d^{-1}. However, it is important to note that event-driven pulses of NCP in the GBR lagoon can exceed 120 mmol O_2 m^{-2} d^{-1} (~ 2 g C m^{-2} d^{-1}), as they have done twice in 2005 and five times in 2008–2010 (Fig. 6), and events such as cyclones and upwelling can result in values in excess of 4 g C m^{-2} d^{-1} (Furnas and Mitchell 1987).

With one exception, the highest rates of area-specific productivity observed during the present study were at mid- and outer-lagoon stations, and were associated with intrusions of Coral Sea water. Primary production within flood plumes is very high—note the NCP as high as 77 mmol O_2 m^{-3} d^{-1} in the surface waters of Sta. 326—but this is limited to a very shallow lens of buoyant, turbid, and phytoplankton-rich water. Though volume-specific NCP is high near surface, this may not be reflected in area-specific estimates because of the shallow euphotic zone. The effect on primary production of lagoonal waters as the plume is mixed and diluted has not yet been measured but may be substantial. Nevertheless, during our study the elevation of primary production by flood plumes at shelf scale was of lesser magnitude than that of upwelling and intrusion because of the greater volumes of water within intrusions and the deeper euphotic zone in clear outer-lagoon waters (Furnas and Mitchell 1996).

How productive are the waters of the GBR when compared with shelf waters elsewhere? Our estimate of mean primary production of 0.73 g C m^{-2} d^{-1} is at the high end of the compilation of primary productivity in the Australian region given by Condie and Dunn (2006); only the Gulf of Carpentaria, the Northwest Shelf, Indonesian seas (Banda Sea, Makassar Strait), and the spring bloom in southeast Australia exceed the productivity of the GBR. Our data are similar to those measured in other subtropical and tropical coasts in Australia (Table 4); only the cryptic upwelling system in the vicinity of Northwest Cape is higher. From the few comparable data from tropical coastal waters elsewhere it seems that primary production

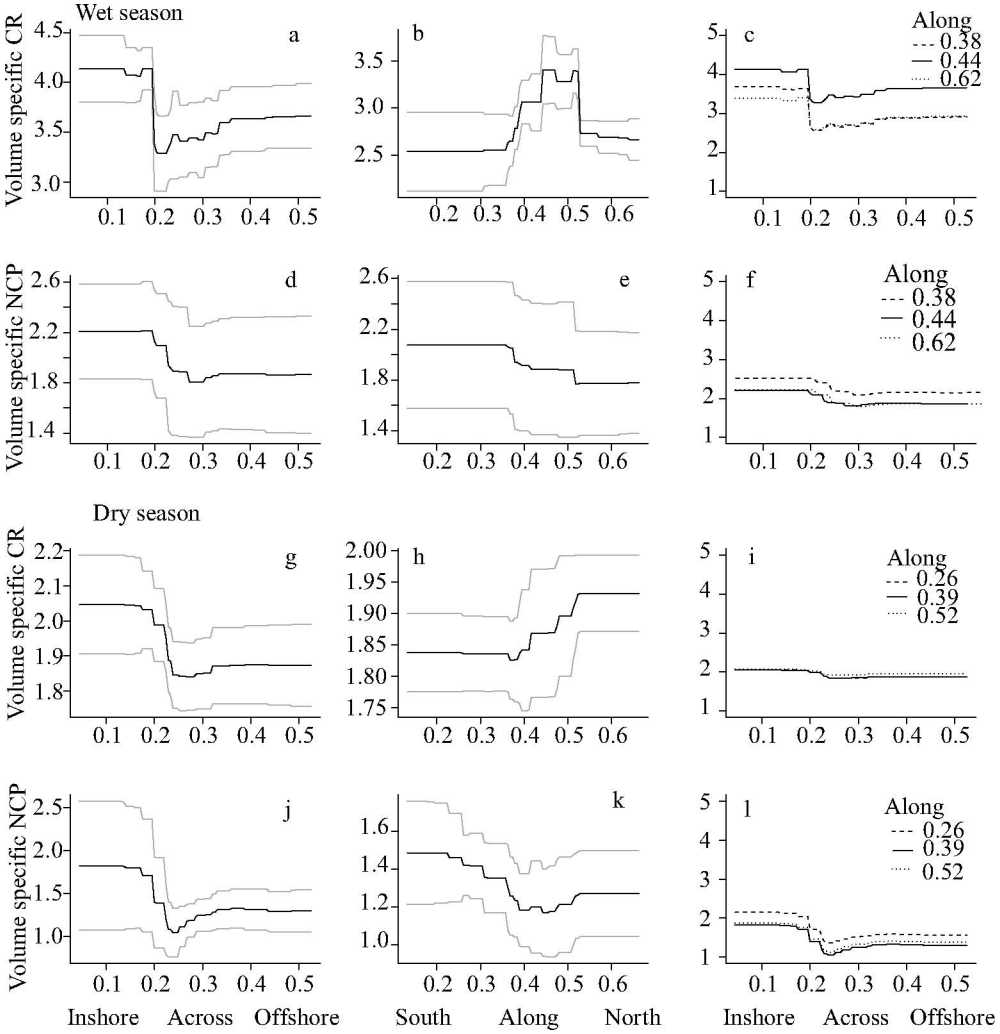

Fig. 5. (a–c, g–i) Partial-dependency plots of volume-specific CR and (d–f, j–l) volume-specific NCP with distance across the shelf (0 = coast to 1 = offshore) and along the shelf (0 = south to 1 = north) over (a–f) wet and (g–l) dry seasons. (a, b, d, e, g, h, j, k) show main effects, and (c, f, i, l) show the across/along interaction. Stippled bands in a, b, d, e, g, h, j, and k are 95% confidence intervals. The Fitzroy, Mackay Whitsunday, Burdekin, and Wet Tropics regions correspond to approximate values of along of 0.22, 0.41, 0.51, and 0.65, respectively.

in the GBR is on a similar scale to that in coastal waters of Kenya and Thailand, but lower than that in Indonesia (Table 4). By comparison, the tropical open ocean at the Bermuda Atlantic Time Series (BATS) and the Hawaii Ocean Time Series (HOT) stations have mean primary production of 0.50 ± 0.18 SD g C m^{-2} d^{-1} and 0.53 ± 0.14 SD g C m^{-2} d^{-1}, respectively (Saba et al. 2010).

Our data demonstrate that the GBR lagoon is moderately productive, but that GBR waters can become highly productive during periods of upwelling, cyclonic activity, or heavy rainfall. Such events usually, but not always, occur during the northwest monsoonal conditions experienced during the wet season.

Respiration and metabolic balance—Our median CR was 1.85 mmol O_2 m^{-3} d^{-1} in the dry season and 2.87 mmol O_2 m^{-3} d^{-1} in the wet season. CR data from the global respiration database (Robinson and Williams 2005) gives a median of 1.28 mmol O_2 m^{-3} d^{-1} for surface waters in tropical latitudes, all of which are from the open ocean. Coastal measurements from this database have a median of 3.21 mmol O_2 m^{-3} d^{-1}, but unfortunately none of these are from the tropics. Overall, our measurements of CR scale within the interquartile range (25th to 75th percentiles) of those for the surface marine waters of the world (fig. 9.9 of Robinson and Williams 2005). Inshore CR in the wet season was as high as 7.51 mmol O_2 m^{-3} d^{-1}, which is at the lower end of that found within the mangrove waterways of North Queensland (6.7–16.2 mmol O_2 m^{-3} d^{-1}; McKinnon et al. 2010). Only the single station occupied in the Fitzroy River plume (Sta. 326) approached those values, since in this case the plume of the river represented a seaward extension of the estuary itself. Within the GBR itself, Glud et al. (2008) measured CR of 2.25–4.07 mmol

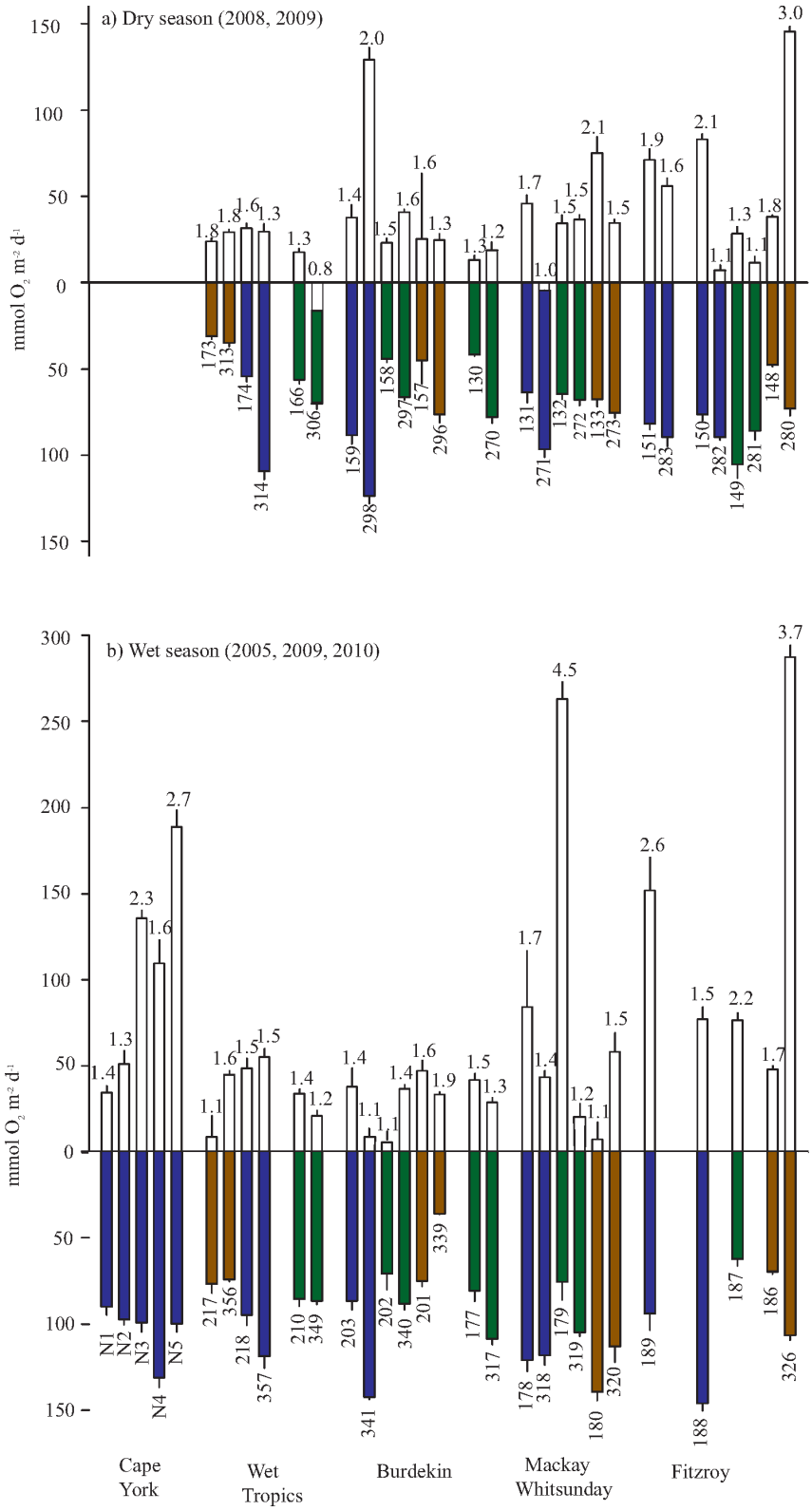

Fig. 6. Area-specific CR (colored bars) and NCP (white bars) in the (a) dry and (b) wet seasons throughout the GBR lagoon. Error bars represent standard errors of volumetric measurements propagated throughout sampled and integration depths. Numbers above bars indicate the ratio of GPP : CR. The station numbers are indicated below the bar. Bars occur as pairs, the left of which is from the first year of sampling and the right the second year. Inshore stations are indicated by brown, mid-lagoon stations by green, and outer-lagoon stations by blue.

Table 4. ^{14}C-based estimates of primary production (mg C m^{-2} d^{-1}) in tropical and subtropical coastal seas.

Location	Range (mg C m^{-2} d^{-1})	Mean	Source
Australia			
GBR	100–1500	680	Furnas and Mitchell 1989; Furnas unpubl.
Coral Sea	117–3033	599	Furnas and Mitchell 1996
Northwest Cape	356–8303	1962	Furnas 2007
Gascoyne Region, Western Australia	110–1310	560	Hanson et al. 2005
Gulf of Carpentaria*			Burford and Rothlisberg 1999
Wet season		950	
Dry season		560	
Tropical coasts			
Banda Sea, Indonesia	310–6830	1850	Gieskes et al. 1990
Eastern Indonesia	530–1230	1200	Kinkade et al. 1997
Gulf of Thailand	305–2440	821	Janekarm and Hylleberg 1989
Kenyan coast	120–3020		Kromkamp et al. 1997

* Stratified offshore waters.

O_2 m^{-3} d^{-1} in coral reef waters at Heron Island (23°S) during November 2005, which is comparable to our wet-season measurements. In similar water depths to those of the GBR on Australia's northwest shelf, McKinnon et al. (2011) measured mean values of CR of 3.2 ± 1.4 SD (Sahul Shelf), 2.3 ± 0.5 SD (Yampi Shelf), and 1.5 ± 0.7 SD mmol O_2 m^{-3} d^{-1} (Sahul Shoals). The close agreement of our results with those from northwest Australia indicates that these values may be representative of the shelf systems of tropical Australia.

Duarte and Regaudie-de-Gioux (2009) compiled all available data on the metabolic balance of marine planktonic communities, and concluded that, on average, a threshold GPP of 1–3 mmol O_2 m^{-3} d^{-1} was required for open-ocean planktonic communities to achieve metabolic balance (i.e., a P : R ratio of 1). The relationship between volume-based measurements of NCP and GPP on the GBR is highly significant ($p < 0.01$, $R^2 = 0.98$) and indicates that a threshold GPP of 2.15 mmol O_2 m^{-3} d^{-1} is required to achieve metabolic balance. There are few studies of tropical shelf areas with which to compare the GBR data (*see* Duarte and Regaudie-de-Gioux 2009; McKinnon et al. 2011). Our value of 2.15 mmol O_2 m^{-3} d^{-1} is intermediate between productive areas such as the northwest Indian Ocean (threshold GPP 4.2 mmol O_2 m^{-3} d^{-1}; Robinson and Williams 1999) and the oligotrophic subtropical North Pacific (threshold GPP 0.83 mmol O_2 m^{-3} d^{-1}; Williams and Purdie 1991) and higher than in the Timor Sea (threshold GPP 1.65 mmol O_2 m^{-3} d^{-1}; McKinnon et al. 2011).

Area-specific measurements of both CR and NCP broadly accord with those from tropical environments elsewhere (Table 5), bearing in mind that the integration depth differs between studies. Ningaloo Reef, between 21°47′S and 23°47′S on the western coast of Australia, appears to be more productive with higher estimates of both area-specific CR and NCP and a higher P : R ratio. The Timor Sea has a similar P : R ratio to the GBR, and the higher area-specific productivity results from the generally deeper water column, since volume-specific rates were broadly similar to the GBR (as above). The high P : R ratio of GBR waters is in contrast to the expectation that warm-water (> 21°C), picoplankton-dominated communities tend toward heterotrophy, at least in the open ocean (Regaudie-de-Gioux and Duarte 2012) as was the case for Sta. ALOHA (A Long-term Oligotrophic Habitat Assessment) in the Tropical Pacific (Williams et al. 2004; Table 5).

Drivers of metabolism—Our multivariate analyses were able to account for > 90% of the constrained variance in the data, and demonstrated that season was the greatest single determinant of pelagic metabolism in the GBR lagoon. Some insight into the underlying mechanisms was provided by our hierarchical mixed-effects models (Table 3),

Table 5. Comparison of area-specific CR, NCP, and the P : R ratio (i.e., GPP : CR) in tropical waters. Data are the mean ± standard error (SE). SATL, South Atlantic Gyral Province.

Location	CR (mmol O_2 m^{-2} d^{-1})	NCP (mmol O_2 m^{-2} d^{-1})	P : R	Reference
GBR	82±4	46±6	1.5	This study
Ningaloo Reef, Western Australia*	108±21	169±36	2.6	Hanson and McKinnon 2009
Timor Sea, northern Australia	141±17	88±24	1.6	McKinnon et al. 2011
Tropical Pacific	86±4	−24±5	~0.7	Williams et al. 2004
Subtropical North East Atlantic, SATL	40±10	20±3	1.7	Serret et al. 2006
Equatorial Atlantic	71±7	80±18	2.1	Perez et al. 2005

* Calculated from carbon units based on production quotient = 1.2 and RQ = 0.8 used in Hanson and McKinnon 2009.

which showed pronounced seasonal differences in the determinants of CR that were associated with particulate matter in the wet season, possibly reflecting microheterotrophic processes resulting from the introduction of labile allochthonous organic material. This did not appear to be the case in the dry season. Cross-shelf effects were the second greatest determinant of metabolism on the GBR, with highest rates of both volume-specific CR and NCP occurring in the coastal zone (Fig. 5). All available evidence points to nitrogen limitation of new biomass formation (Furnas et al. 2005). The formation of new biomass requires some external nutrient input, principally nitrogen. In the inshore zone, wet-season effects such as river floods are especially important as nitrogen sources within the coastal boundary zone (Alongi and McKinnon 2005). During the late summer (= wet season), upwelling and intrusion effects introduce new nitrogen, increasing primary production, especially in the outer lagoon but sometimes extending far inshore (Furnas and Mitchell 1996). In addition, there is some indication of limitation of production by iron (Entsch et al. 1983). The observation by Shaw et al. (2008) that aeolian dust increased remotely sensed phytoplankton biomass on the GBR suggests that the influence of trace elements on production may be worthy of further attention. However, in our study NCP tended to be highest in the southern GBR lagoon where the influence of aeolian dust is likely to be least (Fig. 5e,k), with this geographic effect stronger in the dry season as indicated by the comparatively strong negative correlation with temperature (PC2; Table 3). In the wet season NCP was more strongly correlated with phytoplankton biomass (PC1; Table 3) than with light (no correlation with depth; Table 3).

What proportion of CR might be attributable to heterotrophic bacteria? Calculating mean bacterial production (BP) rates of ~ 0.17 mmol C m^{-3} d^{-1} in the dry season and 0.92 mmol C m^{-3} d^{-1} in the wet season from the area-specific data given for inshore (10 m depth) and offshore (30 m depth) water columns by Furnas et al. (2011), and assuming bacterial respiration = $3.69 \times BP^{0.58}$ (Robinson 2008), mean bacterial respiration on the GBR would be 1.4 mmol O_2 m^{-3} d^{-1} during the dry season and 3.9 mmol O_2 m^{-3} d^{-1} during the wet season, RQ of 1.1 (Bender et al. 1999). Taking our seasonal means of CR, bacterial respiration therefore accounts for 77% of CR during the dry season and 135% in the wet season. Alternatively, taking the compilation of BP in Alongi and McKinnon (2005), most of which is from inshore and mangrove waterways, the mean BP is 0.92 mmol C m^{-3} d^{-1}, constituting 114% of our median inshore CR of 2.36 mmol O_2 m^{-3} d^{-1}. Obviously, comparisons between these measurements of BP and our values of CR are confounded by differences in methodological assumptions as well as the seasonal and site locations of each data set, but still point to BP accounting for a high proportion of CR in waters of the GBR. However, since phytoplankton biomass turns over up to twice daily but is constrained by grazing pressure as well as nutrient availability (Furnas et al. 2005), microbial heterotrophs such as heterotrophic nanoflagellates, ciliates, and heterotrophic dinoflagellates are also likely to be significant contributors to CR.

The contribution of pelagic production to the GBR ecosystem—For the GBR system as a whole, Furnas and Mitchell (1989) calculated that reef flats fixed 70.2×10^6 kg C d^{-1} and lagoons and back reef areas fixed 20.1×10^6 kg C d^{-1}. According to their calculations, phytoplankton fixed 126.9–170.1 $\times 10^6$ kg C d^{-1}, therefore contributing 58–65% of shelf primary production. Our equivalent estimate of 0.73 g C m^{-2} d^{-1} (taking into account methodological differences as described above) applied to a shelf area of 214,619 km^2 (238,700 km^2, less the 24,081 km^2 occupied by reefs; Hopley et al. 2007) results in a similar estimate of pelagic primary production to that of Furnas and Mitchell (1989): 157×10^6 kg C d^{-1}, accounting for 63% of shelf primary production. Alternatively, multiplying our estimate of GPP (1.62 g C m^{-2} d^{-1}) up to the scale of the whole GBR shelf less the area of reefs, results in an estimate of 127×10^9 kg C yr^{-1} gross production. Respiration by phytoplankton and other pelagic microbes accounts for 63%. What, then, is the fate of the 47×10^9 kg C yr^{-1} of net production?

Overall, coral reefs are net autotrophic by a factor of about 2–3% of GPP, and the nutrients necessary to provide this net production are derived from the pelagic (Kinsey 1991). Wyatt et al. (2010) estimated a Lagrangian flux of phytoplankton-derived particulate organic matter on to coral reefs of 16 mmol C m^{-2} d^{-1}. Applying this estimate to the total area of coral reefs within the GBRMP as above results in an estimate of carbon uptake by coral reefs of 1.69×10^9 kg C yr^{-1}, $< 4\%$ of our estimate of NCP. The high GPP of the coral reefs within the GBRMP (~ 7 g C m^{-2} d^{-1} on the reef flat) is largely sustained by internal processes, and our results confirm that there is more than ample pelagic production in surrounding waters to subsidize new production on coral reefs as originally suggested by Kinsey (1991). Admittedly, Atkinson (2011) provides an alternative explanation for the source of the new nutrients necessary to support net production of coral reefs based on a mass-balance approach involving the uptake of nutrients at low concentrations from the continuous flow of water on to the reactive surfaces of the reef face. In either case, to account for the fate of the comparatively high rates of NCP we have observed in this study, it is necessary to look elsewhere than to coral reefs themselves. Alongi et al. (2011) measured benthic respiration rates of 33 mmol C m^{-2} d^{-1} in inter-reef benthos (excluding highly productive reef passes). Assuming little net burial (Alongi and McKinnon 2005) this approximates benthic carbon demand, and translates to 66% of our estimate of mean areal NCP, making it the major sink for pelagic production. The balance of NCP remaining (30%) is likely to be entrained into pelagic food webs or exported.

The trophic status of the GBR—There has been increasing public concern about the extent of "eutrophication" on the GBR, not always with any clarity or precision about the use of the term. Eutrophication is most commonly taken to mean anthropogenically derived nutrient enrichment, resulting in increased phytoplankton growth and "undesirable disturbance" (Andersen et al. 2006). According to Nixon's (1995) definition of trophic states, the GBR lagoon is hypertrophic (> 500 g C m^{-2} yr^{-1}) on the basis of our median GPP, or mesotrophic (100–300 g C m^{-2} yr^{-1}) on the

basis of our median NCP. However, more modern definitions of eutrophication adopt the concept of "accelerated growth" and emphasize the need to measure primary production as part of normal monitoring activities. Using the most recent definition of eutrophication—*Eutrophication means the enrichment of water by nutrients causing an accelerated growth of algae and higher forms of plant life to produce an undesirable disturbance to the balance of organisms present in the water and to the quality of the water concerned, and therefore refers to the undesirable effects resulting from anthropogenic enrichment by nutrients* (Ferreira et al. 2011)—the only reasonable situation where GBR lagoon waters should be classified as eutrophic would be during flood periods when noticeable surface phytoplankton blooms occur (*see* Brodie et al. 2011). It is important to note, however, that accelerated growth has not been measured within flood plumes except in the case of our Sta. 326 in the Fitzroy River flood plume (Fig. 3e).

To adequately define the trophic state of aquatic food webs it is necessary to account for both respiration and primary production. The high P : R ratio (1.5 overall) of lagoonal waters of the GBR indicates these are strongly autotrophic. Also we found that oxygen is fully saturated throughout all GBR waters except for marginal local effects, and there was no evidence of the oxygen-depletion characteristic of truly eutrophied coastal zones (Howarth et al. 2011) though this may occur within adjacent estuarine systems during wet season low neap tides (McKinnon et al. 2010). Kroon et al. (2012) calculated that an anthropogenic load of 11×10^6 kg yr^{-1} of DIN, 6.9×10^6 kg yr^{-1} of DON and 52×10^6 kg yr^{-1} of PN enters the GBR. Though there is now a considerable body of evidence indicating local effects of nutrient loading (reviewed by Brodie et al. 2011), from a biogeochemical standpoint these loads are small. Assuming all of these forms of N were fully labile and taking the Redfield ratio for C : N of 6 : 62 and our pelagic primary production estimate of 118×10^9 kg C yr^{-1}, then the combined anthropogenic sources of N account for $< 0.4\%$ of the annual N demand of phytoplankton. If this N were taken up solely within the coastal zone (< 20 m depth) that comprises 17% of the shelf area (Hopley et al. 2007), then this source of N still only accounts for $< 3\%$ of demand. However, since these inputs are largely a result of short-lived events, they may be comparable to phytoplankton demand over short time periods (Furnas et al. 2005).

Our results echo those of previous studies in demonstrating the importance of short-lived climatic events in forcing pelagic processes in GBR waters. It is likely that changes in the frequency of climatic events such as cyclones, floods, and periods of strong wind, as well as potential changes to the physical oceanography will be the most important drivers of changes in pelagic metabolism, but it is not at all clear whether these effects will combine to result in elevated or reduced primary productivity in the GBRMP (McKinnon et al. 2007). To date, models of climate-driven changes in biogeochemical processes fail to account for pelagic respiration, which scales differently to temperature than primary production (López-Urrutia et al. 2006). The current worst-case prediction for the GBR is for a 3.3°C rise in water temperature by 2100 (Lough 2007). Regaudie-de-Gioux and Duarte (2012) predict a 25% decrease in P : R ratio will occur with a 4°C rise in temperature, though this may be offset to some extent by the higher concentrations of CO_2 increasing NCP. Given our GBR mean P : R of 1.5, the GBR lagoon is therefore likely to remain autotrophic well into the next century. For the time being, our data demonstrate that despite concerns regarding deterioration in water quality as a result of anthropogenic disturbances, the largest biome of the GBRMP is well oxygenated and autotrophic, with CR scaling with values typical of the oligotrophic ocean and NCP similar to other tropical shelf systems under "normal conditions," though event-driven pulses of productivity can approach those of productive upwelling systems.

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