Plankton Respiration, Production, and Trophic State in Tropical Coastal and Shelf Waters Adjacent to Northern Australia

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In a changing ocean, tropical waters can be instructive as to the potential effects of climate induced changes on marine ecosystem structure and function. We describe the relationships between planktonic community respiration (CR), net community production (NCP), gross primary production (GPP), and environmental variables in 14 regions and three ecosystem types (coastal, coral reef, and open sea) from Australia, Papua New Guinea, and Indonesia. The data are compiled from separate studies conducted between 2002 and 2014 with the goal of better parameterizing the metabolic balance in tropical marine waters. Overall, these regions were strongly autotrophic (average GPP:CR ratio: 2.14 ± 0.98), though our dataset of 783 paired measurements did include some oceanic stations where heterotrophy (GPP:CR < 1) was predominant, and some coastal stations that were intermittently heterotrophic. Our statistical analysis suggested that temperature was the most important determinant of CR in coral reef and ocean ecosystems but less so in coastal ecosystems, where chlorophyll concentration was more important. In contrast, chlorophyll and sampling depth were more important in regulating GPP than temperature. The relationships between temperatures and metabolic rates showed that these were ecosystem-dependent, with coastal ecosystems showing less response to temperature than coral reef and open sea sites. The threshold of GPP to achieve metabolic balance fell in a range between 0.715 mmol O_2 m^{-3} d^{-1} in the Coral Sea to 10.052 mmol O_2 m^{-3} d^{-1} in mangrove waterways of Hinchinbrook Channel. These data allow regions in and around northern Australia to be ranked in terms of trophic state, ranging from the oligotrophic Scott Reef (GPP:CR = 0.84 ± 0.08) to productive surface waters of the Kimberley coast (GPP:CR = 5.21 ± 0.62). The measurement of pelagic metabolism shows potential as a quantitative tool to monitor the trophic state of coastal waters.

Keywords: plankton respiration, primary production, metabolic balance, trophic state, tropical coastal waters

INTRODUCTION

Sixty years ago the concept of net community production (NCP), the difference between gross primary production (GPP), and the community (autotrophic plus heterotrophic) respiration (CR) was framed by Odum (1956). Despite this, it is only within the last two decades that the oceanographic community has intensively studied the metabolic balance of the ocean (Ducklow and Doney, 2013). "Metabolic state" is defined as the ratio between GPP and CR at the scale of the

ecosystem, with a system being autotrophic if it produces more organic matter than it consumes (GPP:CR > 1) and heterotrophic if organic matter consumption exceeds *in situ* production (GPP:CR < 1). This ratio therefore describes the balance between the flow of organic matter required to maintain community metabolic balance (GPP:CR = 1) and that available for growth or export away from the ecosystem (NCP) (Platt et al., 1992).

Globally, coastal waters account for 14–33% of total oceanic production and ∼80% of organic matter burial, making them amongst the most productive and biogeochemically active zones of the biosphere (Gattuso et al., 1998). While some studies suggest that these systems are net heterotrophic due to the delivery of large amounts of continentally derived organic matter (Smith and Mackenzie, 1987; Smith and Hollibaugh, 1993), others have found that globally the coastal ocean is autotrophic, exporting 15% of its NCP to the open ocean (Ducklow and McAllister, 2005). These differences could be due to differences in methodology or to spatio-temporal variation in metabolic balance. Spatio-temporal variation has been attributed to factors such as (1) changes in environmental conditions (e.g., temperature: Regaudie-de-Gioux and Duarte, 2012); (2) differences in the input and composition of nutrients (Martínez-García et al., 2010); (3) changes in plankton abundance and productivity of primary producers (Gasol and Duarte, 2000); (4) variation in the phytoplankton size structure and growth rate (Marañón, 2015); and (5) the amount and reactivity of the locally produced (autochthonous) and imported (allochthonous) organic matter (e.g., Serret et al., 1999; Robinson et al., 2002; Lønborg and Álvarez-Salgado, 2012).

Tropical coastal waters receive approximately one order of magnitude more input of continental derived carbon, nitrogen, and phosphorus than temperate and arctic regions (Brunskill, 2010). The phytoplankton production rates in tropical coastal waters are high and can in some instances match some of the most productive areas of the global ocean (e.g., upwelling areas), with these high rates being sustained by high temperatures and a constant supply of nutrients and solar radiation (Nittrouer et al., 1995). In tropical coastal systems with a narrow shelf (e.g., coastal waters of the Bismarck Sea) most terrestrial material, together with the organic matter produced *in situ*, is exported to the open ocean (Burns et al., 2008). By contrast, in systems with a broad shelf (e.g., Great Barrier Reef), most organic matter is consumed within the continental shelf (Brunskill et al., 2010). The few published measurements of pelagic metabolism from coastal tropical waters suggest that these are mainly net autotrophic (GPP:CR > 1) but that the metabolic balance varies both temporally and spatially (McKinnon et al., 2007, 2013).

Robinson and Williams (2005) reviewed all the measurements of pelagic respiration available to that date, and identified a shortfall of data from tropical regions. Paired measurements of production and respiration are even fewer. Here, we present the results of metabolism (i.e., respiration and production) experiments conducted in 14 study regions of tropical Australia, Papua New Guinea, and Indonesia spanning latitudes from 5 to 23°S, collected in the course of numerous studies using similar experimental designs and methodologies. Collectively, these studies make a sizable contribution to the data deficit

from tropical waters, but more importantly allow comparisons of production, respiration, and metabolic balance in tropical habitats ranging from turbid inshore waters to the oligotrophic waters of the tropical ocean.

Our objective is three-fold: (1) to compare tropical ecosystems by partitioning our data into different ecosystem types (coastal waters, coral reef waters, and open sea); (2) to rank regions in order of metabolic activity, an approach we consider useful for understanding and managing coastal waters increasingly threatened by anthropogenic influences on ecosystem productivity mediated by environmental variables such as nutrients and light, and; (3) to identify factors influencing metabolism that have the potential to shift the trophic state of these ecosystems as a result of environmental changes. All data has been made available as Supplementary Material. Measurements are in Supplementary Data Sheet 2, and station data in Supplementary Data Sheet 3.

MATERIALS AND METHODS

Study Areas
This study is based on both published and unpublished data on NCP, dark Community Respiration (CR), and GPP collected between 2002 and 2014 from field campaigns conducted in tropical coastal and shelf waters of northern Australia, Indonesia, and Papua New Guinea (**Table 1**, **Figure 1**). The studies were undertaken in 14 regions characterized by high water temperatures (22–34°C), low dissolved nutrient concentrations and low plankton biomass (Furnas et al., 2011; Supplementary Material). The climate in these areas is typically monsoonal, with a wet summer season (December–March) and a dry winter season (April–November). Climatic events can result in elevations of nutrient and phytoplankton biomass during periods of strong vertical mixing (e.g. storms, cyclones) or from land runoff, particularly during the wet season (e.g., McKinnon et al., 2007; Furnas et al., 2011).

Sample Collection
Full-depth continuous conductivity-temperature-depth (CTD) profiles were recorded (Seabird SBE19Plus) at each sampling site to determine water depths for subsequent biological sampling. Following the CTD cast, water samples were taken with Niskin bottles at depths spanning the euphotic zone (defined here as extending to the 1% light level), with sampling depths determined as those best simulated by our on-deck incubators on the basis of the light profile either from CTD casts or from secchi depths. Therefore, the discrete sampling depths depended on the water depth and light profile at the particular study site, and ranged from the surface to a maximum depth of 100 m (Scott Reef; Supplementary Figure 1). In some studies an additional near-bottom sample was taken to identify potentially higher respiration rates associated with the presence of nepheloid layers generated by near-bottom resuspension. Immediately after retrieval on board, seawater from the Niskin bottles was used to fill calibrated acid-washed iodine flasks with a nominal volume of 125 mL for oxygen production and respiration experiments. For all studies a minimum of three replicate flasks were filled for measurement of initial oxygen concentration (zero-time

TABLE 1 | Summary of data sources.

Region	Ecosystem	Abbreviation	Start Date	End Date	Reference	*n*
Arafura Sea	O	ARA	2 Dec 2011	7 Dec 2011	McKinnon unpublished data	20
Bathurst Island	C	BHI	18 Aug 2005	26 Feb 2006	McKinnon unpublished data	15
Coral Sea	O	COR	25 May 2004	26 May 2004	McKinnon unpublished data	8
Darwin Harbour	C	DHB	14 Feb 2004	22 Feb 2006	Burford et al., 2008	47
Exmouth Gulf	C	EXM	3 Apr 2002	22 Apr 2003	McKinnon unpublished data	19
Great Barrier Reef	R	GBR	5 Feb 2005	5 Mar 2010	McKinnon et al., 2013; Alongi et al., 2015	300
Gulf of Papua	C	GOP	8 May 2004	25 May 2004	McKinnon et al., 2007	48
Gove	C	GOV	26 Jun 2007	2 Jul 2007	Alongi and McKinnon, 2011	6
Hinchinbrook Channel	C	HIN	16 Oct 2007	28 Feb 2008	McKinnon et al., 2010	32
Indonesia	C	IND	23 Aug 2006	20 Mar 2007	Alongi et al., 2009	35
Kimberley Coast	C	KIM	23 Jan 2011	22 Mar 2014	McKinnon unpublished data	46
Ningaloo Reef	R	NIN	11 Apr 2002	30 Apr 2002	Hanson and McKinnon, 2009	17
Scott Reef	O	SCT	25 Jun 2008	4 Dec 2009	McKinnon unpublished data	107
Timor Sea	O	TIM	5 Mar 2004	22 Jun 2005	McKinnon et al., 2011	83

Regions are allocated to three ecosystem types (O, Open Sea; C, Coastal; R, Coral Reef). Studies were conducted between the start and end dates, and where these data sets have been published the corresponding reference is given. The number of paired measurements (n) of volume-specific community respiration (CR) and gross primary production (GPP) is also shown.

FIGURE 1 | Map of Northern Australia, showing the regions where metabolism studies were conducted. Regional abbreviations are given in **Table 1**.
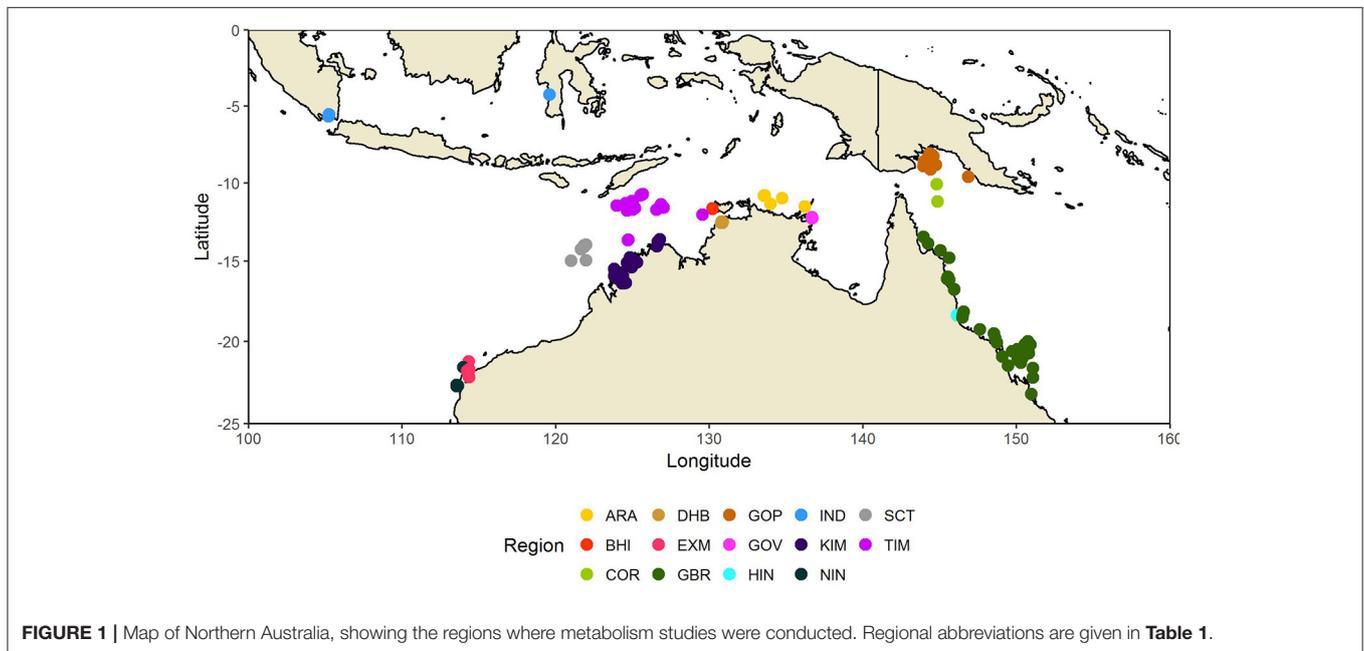
samples), respiration (incubated in the dark for 24 h), and production (placed in deck incubators for 24 h under neutral density mesh to simulate light levels occurring at discrete depths throughout the euphotic zone). Surface seawater was continuously pumped through the incubators to approximate temperatures *in situ*. In the Arafura Sea the number of replicates was increased to 4, and at Scott Reef to 5.

We have compiled a total of 783 pairs of concurrent measurements of NCP, CR, and (GPP, as the sum of CR and NCP) based on changes in oxygen concentration in light and dark bottle incubations (**Table 1**). There were an additional 67 measurements of CR alone. In all, the data was derived from 12 regions in northern Australia, one in Papua New Guinea, and two in Indonesia. Data from the two Indonesian regions have been pooled because both originated from shallow bays containing sea cages for finfish aquaculture, and there was insufficient data density to establish any clear differences between them (for details see Alongi et al., 2009). The number of paired measurements varies greatly between regions: the smallest data set is from Gove (*n* = 6), and the largest from the waters of the Great Barrier Reef region (*n* = 300; **Table 1**).

Immediately after filling the iodine flasks, samples were taken from the same Niskin bottles for the analysis of total suspended solids (TSS), chlorophyll *a* (chl *a*), dissolved inorganic

nutrients (NH_4^+, NO_3^-/NO_2^-, HPO_4^{2-}, and SiO_4), particulate organic carbon (POC), nitrogen (PN) and phosphorus (PP), dissolved organic carbon (DOC), total dissolved nitrogen (TDN) and phosphorus (TDP) (**Table 2**). The filtration and processing of these water samples started immediately after collection. Sample water (1 L) for TSS analysis was collected on pre-weighed $0.4\,\mu m$ polycarbonate filters (47 mm diameter). After filtration, filters were rinsed with 50 mL of deionized water to remove salt. TSS concentrations were determined gravimetrically from the mass difference between loaded and unloaded filters after drying overnight at $60°C$. Chl *a* samples were collected by filtering between 100 and 200 mL of the sampled water through precombusted ($450°C$, 4 h) GF/F filters (pore size $\sim0.7\,\mu m$), which were frozen ($-20°C$) until analysis. Suspended matter was collected under low-vacuum on precombusted GF/F filters for particulate organic matter (250 mL) analysis. All filters were kept frozen ($-20°C$) until analysis. The samples for the dissolved phase (inorganic nutrients, DOC, TDN, and TDP) were immediately filtered through a $0.45\,\mu m$ filter cartridge (Sartorius MiniSart) into acid-washed 10 mL HDPE plastic containers. Duplicate water samples (10 mL) for inorganic nutrients, TDN and TDP, were kept frozen ($-20°C$) until analysis. Ten milliliters sub-samples for DOC were collected in duplicate and preserved by adding $100\,\mu L$ 32% AR-grade HCl and stored in the dark at $4°C$ until analysis.

Sample Analysis

Dissolved oxygen concentrations were determined with an automated high-precision Winkler titration system which uses the absorption of 365 nm ultraviolet light for endpoint detection. The entire set of flasks from each experiment was titrated as a single batch within 24 h of completion of the experiments. NCP was calculated as the difference in dissolved oxygen concentration between light-incubated samples and zero time samples; dark CR was defined as the change in oxygen concentration between dark-incubated samples and zero samples. GPP was calculated as the sum of NCP and CR, and the P:R ratio as the GPP:CR ratio. Where near-bottom samples were taken, these were not included in production calculations since only CR was measured. Coefficients of variation of the replicate O_2 concentration measurements in the zero, dark, and light bottles were typically 0.09, 0.20, and 0.28%, respectively. In this manuscript we report area-specific metabolic rates by trapezoidal integration of volumetric values of NCP and CR.

Chl *a* was determined with a Turner Designs 10 AU fluorometer after 90% acetone extraction (Yentsch and Menzel, 1963). Inorganic nutrients (NH_4^+, NO_3^-/NO_2^-, HPO_4^{2-}, and SiO_4) were determined using standard segmented flow analysis (Hansen and Koroleff, 1999). The precisions of replicate samples were $\pm0.01\,\mu mol\,L^{-1}$ for NH_4^+, $\pm0.1\,\mu mol\,L^{-1}$ for NO_3^-/NO_2^-, $\pm0.02\,\mu mol\,L^{-1}$ for HPO_4^{2-}, and $\pm0.05\,\mu mol\,L^{-1}$ for SiO_4.

Particulate organic carbon and nitrogen content (POC and PN) were measured by high temperature combustion ($950°C$) using a Shimadzu TOC-V carbon analyser fitted with a SSM-5000A solid sample module, after the inorganic carbon on the filters (e.g., $CaCO_3$) had been removed by acidification of the sample with 2M HCl (Nieuwenhuize et al., 1994).

TABLE 2 | Environmental properties of water used in metabolism experiments (see Materials and Methods for definitions) and summary of volumetric CR, NCP, and GPP by ecosystem type.

Variable	Unit	Coastal	Open Sea	Coral Reef
Temperature	$°C$	28.62 ± 0.12	28.42 ± 0.08	26.44 ± 0.11
Salinity	PSU	32.34 ± 0.24	34.28 ± 0.02	34.44 ± 0.09
DIN	$\mu mol\,L^{-1}$	0.47 ± 0.04	0.45 ± 0.09	0.08 ± 0.01
DON	$\mu mol\,L^{-1}$	6.54 ± 0.21	7.21 ± 0.32	6.63 ± 0.17
PN	$\mu mol\,L^{-1}$	2.62 ± 0.12	0.74 ± 0.04	0.86 ± 0.03
DIP	$\mu mol\,L^{-1}$	0.28 ± 0.01	0.12 ± 0.01	0.09 ± 0.01
DOP	$\mu mol\,L^{-1}$	0.35 ± 0.02	0.17 ± 0.01	0.13 ± 0.01
POC	$\mu mol\,L^{-1}$	17.27 ± 1.60	5.92 ± 0.33	7.78 ± 0.29
PP	$\mu mol\,L^{-1}$	0.21 ± 0.01	0.03 ± 0.01	0.06 ± 0.01
DOC	$\mu mol\,L^{-1}$	71.91 ± 1.29	70.86 ± 1.28	67.66 ± 1.39
SiO_4	$\mu mol\,L^{-1}$	15.18 ± 1.56	3.08 ± 0.12	3.85 ± 0.62
TSS	$mg\,L^{-1}$	8.57 ± 0.83	0.81 ± 0.10	0.63 ± 0.05
Chl a	$\mu g\,L^{-1}$	1.11 ± 0.05	0.30 ± 0.03	0.43 ± 0.04
CR	$mmol\,O_2\,m^{-3}\,d^{-1}$	4.85 ± 0.21	1.84 ± 0.06	2.53 ± 0.09
NCP	$mmol\,O_2\,m^{-3}\,d^{-1}$	6.61 ± 0.53	0.65 ± 0.17	2.92 ± 0.35
GPP	$mmol\,O_2\,m^{-3}\,d^{-1}$	11.78 ± 0.60	2.49 ± 0.20	5.46 ± 0.42

Data are mean ± SE.

The analyser was calibrated using AR Grade EDTA for the 5 point standard curve. Particulate phosphorus (PP) was determined spectrophotometrically as inorganic P after digesting the particulate matter in 5% potassium persulphate. The method was standardized using orthophosphoric acid as the standard for the 4 point calibration. We compared peak areas of the filter blanks and standard solutions to ensure consistency between runs with no major deviations found.

Dissolved organic carbon (DOC) concentrations were measured by high temperature combustion ($680°C$) using a Shimadzu TOC-5000A carbon analyser. Concentrations were determined by subtracting a Milli-Q blank and dividing by the slope of a daily 4 points standard curve made from potassium hydrogen phthalate and glycine. The consistency between runs was verified by comparing peak areas of standard solutions with no major deviations found. Analyses of total dissolved nitrogen (TDN) and phosphorus (TDP) were determined by oxidation ($121°C$, 70 min) in alkaline conditions by persulphate digestion of water samples (Valderrama, 1981), which were then analyzed for inorganic nutrients, as described above. Dissolved organic nitrogen (DON) concentrations were calculated as the difference between TDN and dissolved inorganic nitrogen (DIN; $NH_4^+ + NO_3^-/NO_2^-$) (DON = TDN–DIN) and dissolved organic phosphorus (DOP) as the difference between TDP and dissolved inorganic phosphorus (DIP; HPO_4^{2-}) (DOP = TDP–DIP).

Statistical Analysis

We first explored the distribution of the data using Cleveland dotplots of all variables (**Table 2**) individually by sampling location, alongside box, and whisker plots categorized by season, since in previous studies there were strong contrasts between wet (December–March) and dry seasons (April–November).

Our dataset includes a range of ecosystem types. In addition to conducting statistical analyses on the entire dataset, we also conducted analyses grouped by ecosystem type. Regional data were classified into three ecosystem types: Coral Reef (GBR, NIN); Open sea (ARA, COR, SCT, TIM); and Coastal (BHI, DHB, EXM, GOP, GOV, HIN, IND, KIM). Of these, the coral reef ecosystems are most clearly defined as the waters surrounding the two largest coral reef systems in Australia. The open sea ecosystems were characterized as being primarily in open ocean water out of sight of land. The Scott Reef region was classified as oceanic because most sampling took place in Indian Ocean waters on the shelf edge. The coastal ecosystem includes regions that were all estuarine to some degree, though there is a gradation in the extent of fresh water influence. For example, the Hinchinbrook Channel (HIN) was strongly influenced by freshwater in the wet season, and the innermost stations of the Gulf of Papua (GOP) were influenced by the Fly River. At the other extreme, Exmouth Gulf is a tropical embayment in which inshore waters can be hypersaline, and is best described as a negative estuary. Moreover, the coastal regions were all characterized by the presence of mangrove forests on their shores.

Physical, chemical, and biological variables potentially influencing CR and GPP were explored via Gradient Boosted Regression Tree (BRT) Models (Ridgeway, 2017). We chose to use BRT's because of their ability to accommodate missing data by imputation, their suitability to independently estimate the effects of predictors that are themselves correlated, and their ability to estimate the relative importance of predictors in complex systems. BRT models combine two machine learning methodologies; regression trees and boosting. Regression trees are hierarchical models that recursively partition the data on the basis of minimizing prediction errors and in so doing provide a powerful framework that is insensitive to outliers and missing data, unaffected by monotone transformations and scales of covariates and naturally accommodate non-linearity and complex interactions (Hastie et al., 2011). Boosting in a regression tree context is a numerical optimization technique for minimizing deviance (a measure of the difference between observed and predicted) at each step of a sequential series of trees, each of which focuses on the most poorly predicted components of the preceding tree (De'ath, 2007; Elith et al., 2008). BRT models are typically encouraged to "learn" slowly and thoroughly by constructing very large numbers of small regression trees, training each tree on a random subset of the residuals from the proceeding tree and "shrinking" the contribution of each tree. Finally, over-fitting can be countered through one of a number of regularization techniques (such as cross-validation) that serve to strike a balance between predictive performance and model fit (Hastie et al., 2011). Collectively, this stochasticity and sequential slow learning through large numbers of small regression trees typically yield predictions that are superior to regular linear modeling approaches.

BRT models for log-transformed CR and GPP included the covariates listed in **Table 2**. A total of 5,000 trees were fit to an interaction depth of 5, bag fraction of 0.5 and shrinkage rate of 0.001. The optimal number of boosting iterations was determined by the "out-of-bag" method. The relative importance of each predictor was calculated as the frequency of splits involving each variable weighted by the associated square improvement in the model averaged over all trees and scaled out of 100 such that larger values signify stronger influence. Uncertainty in partial effects and relative importance estimates was incorporated by bootstrapping (sampling with replacement) each BRT 100 times. All BRT models were fit via the gbm package (Ridgeway, 2017) within the R Statistical and Graphical Environment (R Core Team, 2016).

To examine the role of temperature in regulating metabolic rates it is necessary to account for the co-variance between temperature and plankton biomass. We, therefore, standardized CR and GPP to Chl a concentration, the only index of plankton biomass available in our dataset. The data was then averaged within 1°C data bins to provide an average response to a given temperature. This procedure also forces that all bins have the same weight in the subsequent statistical analyses, independent of the amount of data that they initially contain.

The relationship between temperature and biological activity is normally modeled using an Arrhenius-type relationship, assuming that chemical kinetics control the observed rates (Ahlgren, 1987). The Arrhenius equation is defined as:

$$k = A \cdot e^{-E_a/R \cdot T} \qquad (1)$$

where k is the enzyme activity; A is the theoretical enzyme activity in the absence of activation energy (E_a): E_a is the energy barrier to be surpassed in order for the reaction to take place (in J mol^{-1}); R is the universal gas constant (8.314 J mol^{-1} K^{-1}); and T is the temperature in Kelvin (K). The factor is known as the Boltzmann expression, which shows the fraction of the reactive molecules having energy in excess of E_a (Arrhenius, 1889). An estimate of E_a can be derived from the slope of an Arrhenius plot of natural logarithm of activity (CR and GPP) vs. the reciprocal of absolute temperature (T). The E_a, can thereafter be calculated by multiplying the regression slope by R, the gas constant.

Regression analyses of CR, NCP, GPP, and Chl a (total dataset and by ecosystem type) were performed using the best–fit between the two variables X and Y obtained by Model II regression as described in Sokal and Rohlf (1995) using the package lmodel2 within R (R Core Team, 2016).

RESULTS

Environmental Conditions

Salinity varied overall from a minimum of 18.5 to a maximum of 36.6, with the lowest values taken from waters close to shore influenced by wet season runoff (Supplementary Figure 2). Temperature varied between 22 and 34°C, with highest levels found in surface waters during the wet season (Supplementary Figure 3). Overall, there was little difference in temperature and salinity between ecosystems (**Table 2**). TSS concentrations varied between 0.01 and 67.92 mg L^{-1} with highest levels in the Gulf of Papua and at nearshore stations in Darwin Harbour and on the Kimberley Coast (Supplementary Figure 4). The coastal ecosystems had an order of magnitude higher TSS than the open sea or coral reef ecosystems. Chlorophyll a (Chl a) concentrations

ranged between 0.02 and 8.26 μg L^{-1}, with highest levels in the mangrove waterways of Bathurst Island during the wet season (Supplementary Figure 5), with coastal ecosystems having ~3-fold higher concentrations than the other ecosystem types. The dissolved inorganic nitrogen (DIN) and phosphorus (DIP) concentrations varied between levels below detection limit up to 8.2 and 1.50 μmol L^{-1}, respectively (Supplementary Figures 6, 7). Generally, DIN and DIP concentrations of surface waters were close to the detection limits of standard methods, but occasionally higher levels were found at stations closer to shore directly affected by river runoff. DIN concentrations were similar in coastal and open sea ecosystems, but lower in the coral reef ecosystem, whereas DIP was highest in the coastal ecosystems (**Table 2**). Dissolved silicate (SiO$_4$) concentrations were highest in the coastal ecosystems (**Table 2**), but was always detectable in all ecosystems with levels between 0.2 and 121.4 μmol l^{-1} (Supplementary Figure 8), suggesting that in all regions there was mostly sufficient silicate present to support growth of diatom populations.

Concentrations of particulate organic matter (POM) were elevated in surface waters during the wet season and at stations closer to shore, as indicated by POC (Supplementary Figure 9), PN (Supplementary Figure 10), and PP (Supplementary Figure 11), and all of which were highest in the coastal ecosystems (**Table 2**). The average C: N: P stoichiometry of the suspended particulate fraction was 150:10:1, which is slightly higher but not different to the Redfield ratio and ratios found for recently produced organic matter (106:16:1, Redfield et al., 1963), suggesting a predominantly planktonic origin of this material.

Higher levels of dissolved organic matter (DOM) were observed in surface waters during the wet season and closer to shore. Dissolved organic carbon (DOC) was similar in all ecosystems, with a tendency to be higher in the wet season (Supplementary Figure 12). Dissolved organic nitrogen (DON) was similar in all ecosystems (**Table 2**), and slightly higher in the wet season in some regions (Supplementary Figure 13). DOP was highest in the coastal ecosystems (**Table 2**), with seasonal differences in some regions (Supplementary Figure 14). The average C:N:P stoichiometry of the DOM pool was 367:49:1, which was higher than the Redfield ratio but comparable with ratios reported for coastal waters worldwide (Lønborg and Álvarez-Salgado, 2012).

Oxygen Fluxes

CR ranged from 0.12 to 16.67 mmol O$_2$ m^{-3} d^{-1} and was highest in the coastal ecosystems [mean 4.22 $\pm$ 0.17(SE) mmol O$_2$ m^{-3} d^{-1}]; for the coral reef ecosystems it was 2.53 $\pm$ 0.09 mmol O$_2$ m^{-3} d^{-1} and for the open sea 1.77 $\pm$ 0.90 mmol O$_2$ m^{-3} d^{-1}. Ranking regions by median CR (**Figure 2**) illustrated the variation within the coastal ecosystem group, with lowest CR in the Gulf of Papua (2.36 $\pm$ 0.24 mmol O$_2$ m^{-3} d^{-1}) and highest in Bathurst Island (6.70 $\pm$ 0.84 mmol O$_2$ m^{-3} d^{-1}). Overall, CR was lowest in the oceanic waters of the Coral Sea (0.76 $\pm$ 0.07 mmol O$_2$ m^{-3} d^{-1}) (**Figure 2**, Supplementary Figure 15).

Most experiments were conducted in shallow waters (Supplementary Figure 1): 79% of measurements were made in 25 m or less. Because the water column was generally well
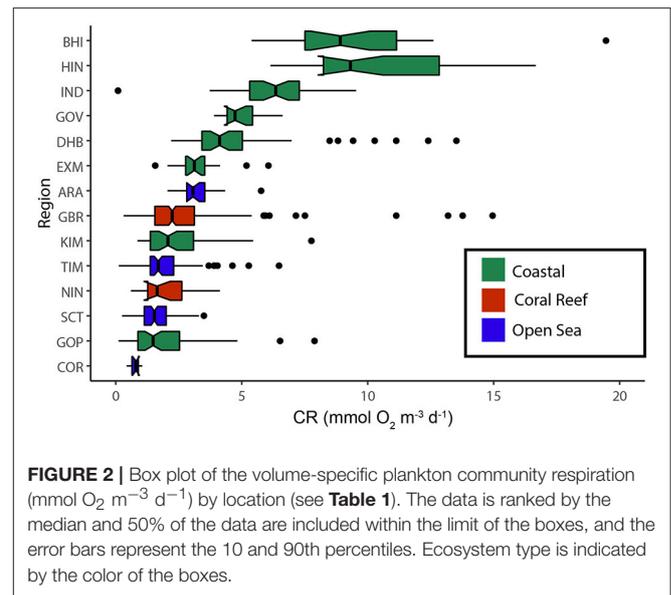
FIGURE 2 | Box plot of the volume-specific plankton community respiration (mmol O$_2$ m^{-3} d^{-1}) by location (see **Table 1**). The data is ranked by the median and 50% of the data are included within the limit of the boxes, and the error bars represent the 10 and 90th percentiles. Ecosystem type is indicated by the color of the boxes.

mixed over this depth range there were negligible vertical differences in CR, and where near-bottom samples were taken these did not differ from rates higher in the water column. In the oceanic waters adjacent to Scott Reef, however, experiments were conducted at six depths through the euphotic zone down to 100 m in both the wet and dry seasons of 2008 and 2009 (**Figure 3**). In the dry season there was a well-defined mixed layer to about 90 m; in the wet season the mixed layer was less well-defined and confined to the top 35 m. Even over the 100 m depth range of the Scott Reef experiments there was no indication of vertical differences in CR in either season (**Figure 3**).

In our dataset the volume-specific NCP varied between −9.34 to 76.99 mmol O$_2$ m^{-3} d^{-1}. NCP was highest in the coastal ecosystems (6.61 $\pm$ 0.53 mmol O$_2$ m^{-3} d^{-1}) followed by coral reef waters (2.92 $\pm$ 0.35 mmol O$_2$ m^{-3} d^{-1}) and the open sea (0.65 $\pm$ 0.17 mmol O$_2$ m^{-3} d^{-1}; **Table 2**). On average, Darwin Harbour had the highest volume-specific NCP (10.71 $\pm$ 0.88 mmol O$_2$ m^{-3} d^{-1}). Scott Reef was the only dataset to be heterotrophic on average (NCP of −0.25 $\pm$ 0.09 mmol O$_2$ m^{-3} d^{-1}).

GPP was highest in the coastal ecosystems (11.89 $\pm$ 0.86 mmol O$_2$ m^{-3} d^{-1}), followed by reef ecosystems (5.46 $\pm$ 0.68 mmol O$_2$ m^{-3} d^{-1}) and the open sea (2.57 $\pm$ 0.28 mmol O$_2$ m^{-3} d^{-1}). The maximum volume-specific GPP of 91.95 mmol O$_2$ m^{-3} d^{-1} occurred in flood waters in the inshore waters of the Great Barrier Reef, but otherwise GPP was highest in the Hinchinbrook Channel (19.71 $\pm$ 1.21 mmol O$_2$ m^{-3} d^{-1}), Darwin Harbour (15.85 $\pm$ 0.88 mmol O$_2$ m^{-3} d^{-1}) and Bathurst Island (15.03 $\pm$ 0.65 mmol O$_2$ m^{-3} d^{-1}) (Supplementary Figure 16).

Relationships between Production and Respiration

On a volumetric basis, all regions were mean autotrophic except for Scott Reef (GPP:CR = 0.84 $\pm$ 0.08; **Table 3**), though
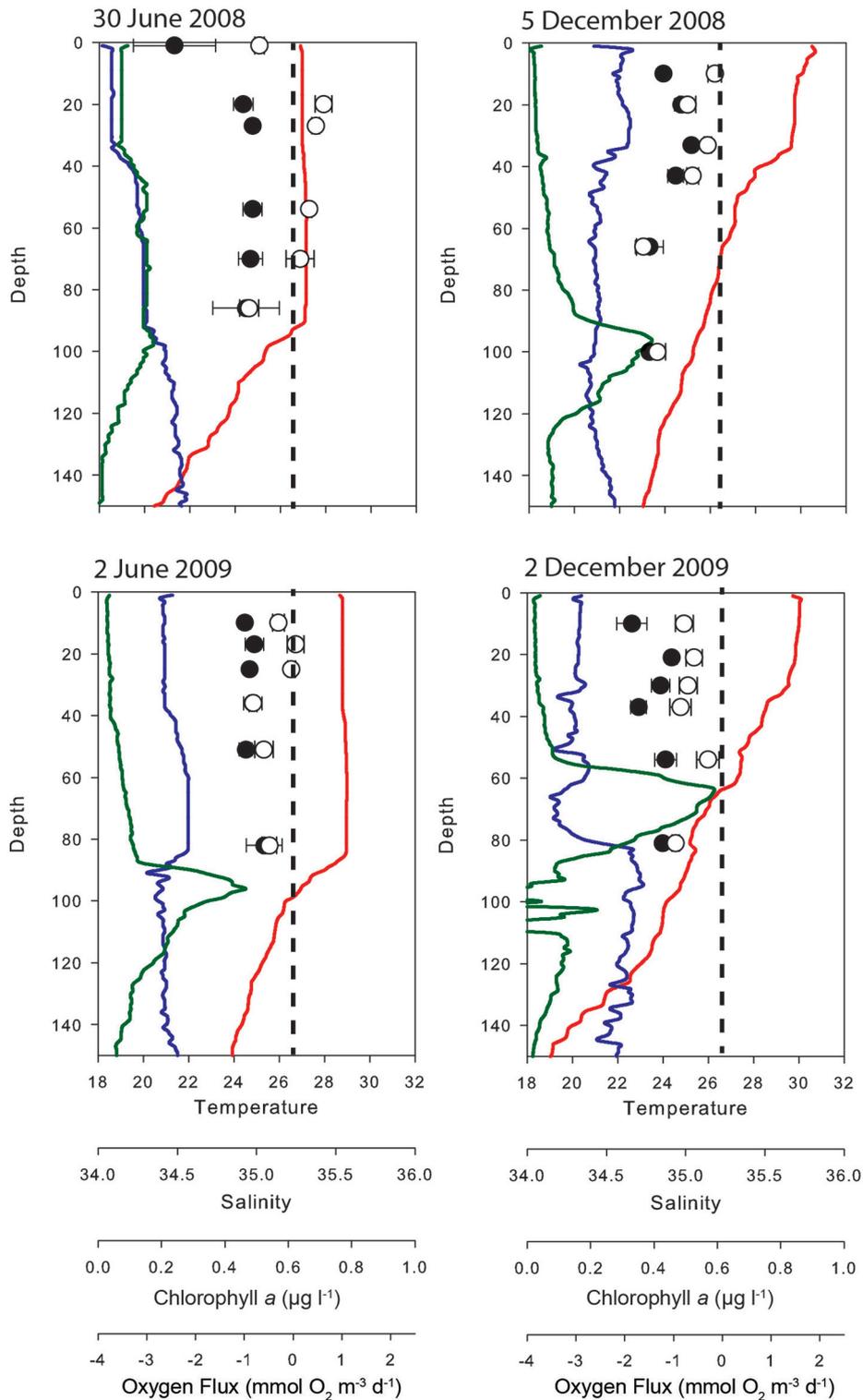
FIGURE 3 | Vertical patterns of CR (filled symbols) and NCP (open symbols) as measured in dark and light bottles respectively, at an oceanic station SW of Scott Reef. Oxygen flux are reported as mmol O_2 m^{-3} d^{-1}. The vertical dashed line is the compensation point (i.e., NCP = CR). Vertical profiles of temperature (red), salinity (blue), and chlorophyll fluorescence μg L^{-1} (green) are derived from the CTD data.

TABLE 3 | The mean ratio (±SE) of volumetric GPP:CR for each study area, ranked in ascending order.

Region	GPP:CR
Scott Reef	0.84 ± 0.08
Indonesia	0.98 ± 0.56
Coral Sea	1.20 ± 0.19
Bathurst Island	1.49 ± 0.18
Arafura Sea	1.64 ± 0.12
Gulf of Papua	1.86 ± 0.23
Hinchinbrook Channel	1.89 ± 0.18
Timor Sea	1.93 ± 0.21
Great Barrier Reef	2.08 ± 0.09
Gove	2.67 ± 0.34
Ningaloo Reef	2.93 ± 0.42
Exmouth Gulf	2.93 ± 0.45
Darwin Harbour	3.51 ± 0.34
Kimberley Coast	5.21 ± 0.62
Average	2.09 ± 0.08

FIGURE 4 | The relationship between the means of volume-specific GPP and CR (both mmol O_2 m^{-3} d^{-1}) for each location (**Table 1**). Error bars correspond to the SE and are within the symbol size in some cases.

TABLE 4 | Significant regressions of the relationship between net community production (NCP) and gross primary production (GPP) to determine the threshold necessary for metabolic balance for regions reported in **Table 1**.

Region	Intercept	95% CI	Slope	95% CI	R^2	Threshold GPP mmol O_2 m^{-3} d^{-1}
OPEN SEA						
Coral Sea	−0.55	0.89	0.77	0.59	0.83	0.71
Scott Reef	−1.61	0.37	1.03	0.26	0.67	1.57
Timor Sea	−1.38	0.33	0.84	0.08	0.95	1.63
Arafura Sea	−2.53	2.23	0.87	0.33	0.84	2.92
COASTAL						
Gulf of Papua	−1.61	0.87	0.83	0.18	0.87	1.94
Kimberley Coast	−2.14	0.34	0.97	0.08	0.98	2.20
Exmouth Gulf	−4.85	2.35	1.20	0.26	0.95	4.05
Darwin Harbour	−5.07	2.60	1.00	0.16	0.93	5.09
Indonesia	−4.87	2.24	0.88	0.21	0.89	5.54
Gove	−6.16	8.87	1.07	0.65	0.96	5.78
Bathurst Island	−9.29	4.37	0.95	0.25	0.95	9.79
Hinchinbrook Channel	−9.45	3.33	0.94	0.15	0.95	10.05
CORAL REEF						
Ningaloo Reef	−1.63	2.39	0.94	0.38	0.86	1.73
Great Barrier Reef	−1.68	0.17	0.84	0.03	0.97	2.01
Whole dataset	−1.94	0.24	0.82	0.04	0.91	2.38

Slope, intercept, and standard error are values found by Model II regression (RMA). R^2, coefficient of determination.

threshold of GPP to achieve metabolic balance fell in a range between 0.715 mmol O_2 m^{-3} d^{-1} in the Coral Sea to 10.052 mmol O_2 m^{-3} d^{-1} in mangrove waterways of Hinchinbrook Channel (**Table 4**). There was a considerable range of threshold values within the coastal group. The mean threshold of GPP over the whole dataset was 2.38 mmol O_2 m^{-3} d^{-1} and 5.56, 1.87, and 1.71 mmol O_2 m^{-3} d^{-1} for the coastal, and coral reef open sea ecosystems, respectively.

CR scaled with both GPP and CR, with CR scaling at the 0.77 power of GPP, and the 0.47 power of NCP (**Figure 5**; **Table 5**). In the open sea, CR scaled at the 0.22 power of NCP, lower than the other ecosystems (**Table 5**).

Environmental Predictors of Metabolism

We used Boosted Regression Trees to compare the relative importance of individual physico-chemical and biological variables as well as Region, Sampling depth, and Season as predictors of both volumetric CR and GPP. For CR in the whole dataset, regional differences were the most important determinant, closely followed by Chl *a* with minor effects of temperature and depth (Supplementary Figure 17). In the case of Chl *a* there is a threshold at ~1.0 µg L^{-1} above which CR increases markedly (Supplementary Figure 17E). In the case of GPP (Supplementary Figure 18), Chl *a* was the most important predictor (Supplementary Figure 18Q),

heterotrophy was also observed in some experiments in the Hinchinbrook Channel and in the Timor Sea. Darwin Harbour and the Kimberley coast had disproportionally high GPP:CR ratios (3.51 ± 0.34 and 5.21 ± 0.62 respectively; **Table 3**). Overall, volume-specific CR scaled with GPP in our dataset (**Figure 4**). Model II regression (RMA) between CR and GPP for the entire dataset results in a slope of 0.42 ± 0.06 (95% C.I.), with an R^2 of 0.43.

Examination of the relationship between NCP and GPP using Model 2 Regression allows the estimation of the threshold values of GPP necessary to achieve metabolic balance (GPP:CR = 1) (**Table 4**). The resulting metabolic thresholds rank all regions in order of trophic state, within the allocated ecosystem type. The

FIGURE 5 | Log-log relationships of GPP and CR **(Top)** and NCP and CR **(Bottom)**, as mmol O_2 m^{-3} d^{-1}. Symbol colors correspond to the location of the measurement as indicated in **Figure 1**, and the regression line for each group is plotted as: A, entire data set; C, coastal ecosystems; O, open sea ecosystems; R, coral reef ecosystems. Model 2 regression statistics are given in **Table 5**.

TABLE 5 | Model 2 Regression statistics (RMA) for the relationship between $\log_{10}$ transformed volumetric CR, and GPP, and NCP respectively (see **Figure 5**).

Ecosystem	Intercept	95% CI	Slope	95% CI	R^2	p	n
GPP							
All	0.01	0.06	0.66	0.11	0.42	0.01	783
Open Sea	0.10	0.05	0.56	0.30	0.21	0.01	218
Coastal	−0.28	0.35	0.98	0.39	0.55	0.01	248
Coral Reef	−0.11	0.12	0.77	0.21	0.39	0.01	317
NCP							
All	0.25	0.04	0.47	0.13	0.24	0.01	607
Open Sea	0.22	0.01	0.31	0.24	0.18	0.01	119
Coastal	0.06	0.46	0.78	0.67	0.11	0.01	210
Coral Reef	0.22	0.10	0.53	0.40	0.10	0.01	278

the coastal ecosystems, regional differences in CR outweighed other environmental predictors (**Figures 6K–O**) with Chl *a* concentration of secondary importance, showing a marked increase in CR above 0.7 µg L^{-1}. Conversely, there was a decrease in CR at POC concentrations between 6 and 12 µmol L^{-1}, while a slight increase was found for temperatures above ∼28.5°C.

For GPP, Chl *a* was the most important predictor in coral reef ecosystems, with smaller effects of TSS, PN and depth (**Figures 7A–E**). There was a pronounced increase in GPP at Chl *a* concentrations between 0.3 and 0.5 µg L^{-1}, and moderate increases at TSS > 1.0 mg L^{-1} and PN above 1.3 µmol L^{-1}. GPP declined at depths between 10 and 35 m. In the open sea, Chl *a* was again the best predictor, with depth second. DOP had a smaller impact, while there was no difference between the four open sea regions (**Figures 7F–J**). GPP increased with Chl *a* concentrations between 0.07 and 0.40 µg L^{-1} and slightly decreased at depths >30 m. Regional differences remained the most important predictor of GPP in the coastal ecosystems, with Chl *a* and depth also being important (**Figures 7K–O**). GPP increased at Chl *a* concentrations >0.4 µg L^{-1} and stabilized at >1.2 µg L^{-1}. The GPP was highest in surface waters, and stabilized at depths >15 m. Dissolved silicate, an index of terrestrial influence, had little effect on GPP.

The relationship between CR and GPP with temperature, described by the Arrhenius equation, showed only significant impacts of temperature for CR in the coral reef ecosystems and for GPP in the open sea ecosystems. This yielded apparent activation energies (E$_a$) of 127 ± 45 kj mol^{-1} for CR in the coral reef and 266 ± 56 kj mol^{-1} for GPP in the open sea ecosystems, respectively.

GPP scaled with Chl *a* to the power of 1.017, and CR scaled with Chl *a* to the power of 0.645 (**Figure 8**).

Productivity of Waters Adjacent to Northern Australia

On an area-specific basis, all locations were predominately autotrophic (**Figure 9**), though some stations in mangrove waterways were heterotrophic in the wet season. In the case of Scott Reef, however, there was positive NCP in only one season (June 2008), and the system was heterotrophic on all other occasions.

with region and depth the only other variables exerting any influence.

The importance of region in the analysis of the whole dataset suggested differences in trophic functioning across the different ecosystem types. Accordingly, we repeated our analysis for the three ecosystem types (coastal, coral reef and open sea) as shown in **Table 1**. The coral reef dataset comprised 317 paired measurements of CR and GPP, and the open sea and coastal ecosystems 218 and 248 paired measurements, respectively (**Table 1**).

Considering the environmental variables that best predicted CR in coral reef ecosystems, temperature and POC were selected as most important, with a lesser effect of season and PP (**Figures 6A–E**). There was a pronounced increase in CR in waters with temperatures between 25 and 28°C, and POC levels between 8 and 15 µmol L^{-1}. There was also a slight tendency for CR to be higher in the wet season, and a gradual increase in CR above PP concentrations of 0.07 µmol L^{-1}. In the open sea, temperature, Chl *a*, salinity and POC were the best predictors of CR, with a minor effect of sampling depth (**Figures 6F–J**). CR increased above temperatures of 28°C and Chl *a* concentrations of 0.3 µg L^{-1}. The effects of salinity and depth are more subtle, with a slight decrease in CR with depths between 10 and 50 m and salinity >33.8. Within

FIGURE 6 | Partial-dependency plots (based on Boosted Regression Tree analysis – see Methods) of the response of CR to the most important predictors. Coral Reef Ecosystems, **(A)** relative importance of predictors for coral reef ecosystems; **(B)** temperature; **(C)** POC; **(D)** season; **(E)** PP; Open Sea Ecosystems **(F)** relative importance of predictors for open sea ecosystems; **(G)** temperature; **(H)** Chl *a*; **(I)** salinity; **(J)** depth; Coastal Ecosystems, **(K)** the relative importance of predictors for coastal ecosystems; **(L)** Region; **(M)** Chl *a*; **(N)** POC; and **(O)** temperature. Regional abbreviations are defined in **Table 1**, and Covariate labels are defined in the Materials and Methods section. Each graph represents the modeled effect of each covariate holding all other covariates constant. Since the relative importance of a covariate is the percentage of all node splits involving that covariate, a simple critical threshold (indicated by the vertical dashed line) can be established as 100/n (where n is the number of covariates) since if all covariates where equally important, they would each have a relative importance of 100/n. Therefore, the relative importance of covariates above this threshold can be interpreted as more important than would be expected by pure chance alone.

Comparison of the regional area-specific data reveals a quite different ranking in the scale of metabolic rates to that derived from the volume-specific data (**Figure 9**), in large part due to the effects of depth (i.e., a deep location with low volume-specific production may have higher area-specific production than a shallow location with very high volume-specific production).
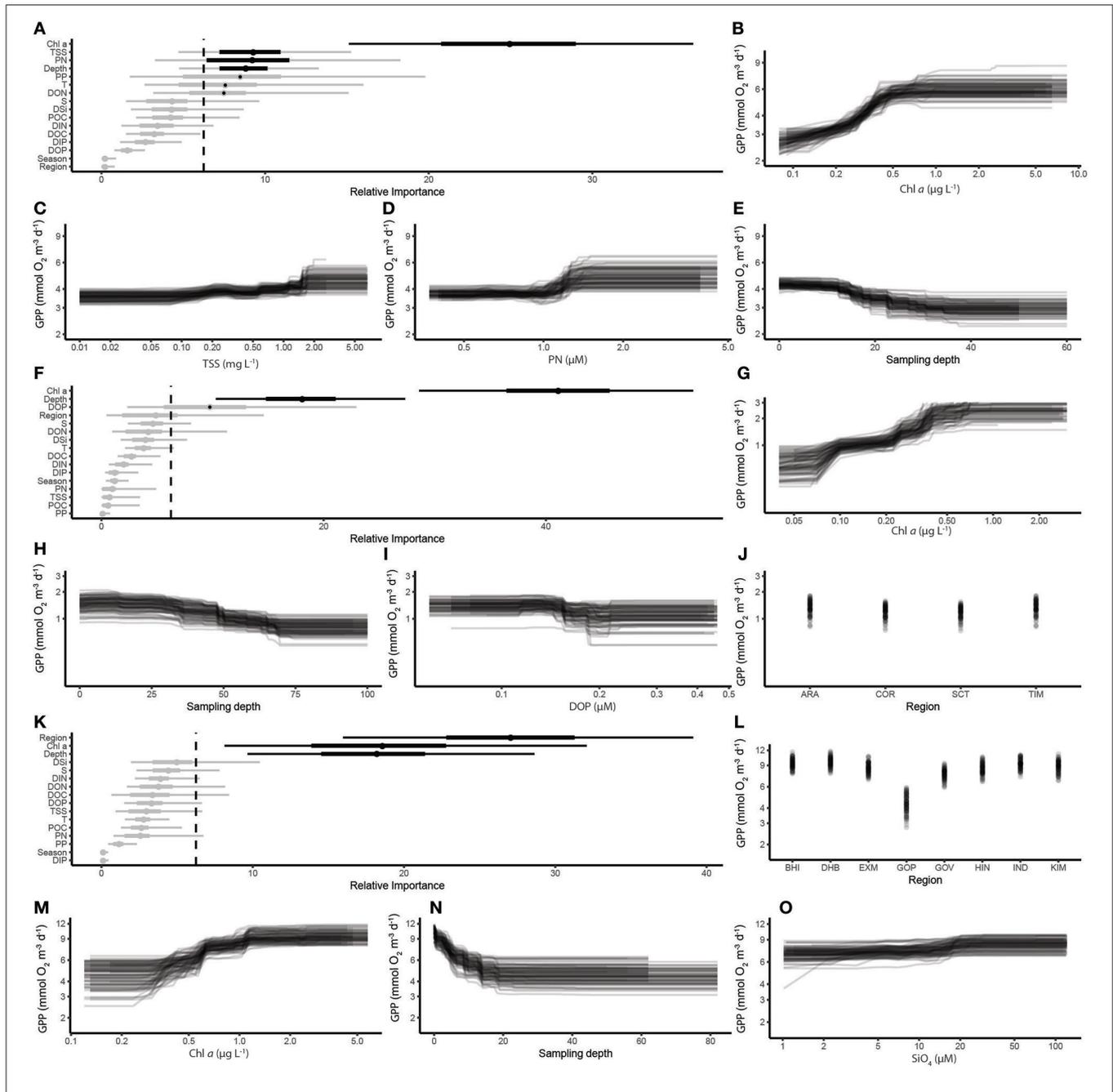
FIGURE 7 | Partial-dependency plots of the response of GPP to the most important predictors based on BRT statistics, as for **Figure 6**. Coral Reef Ecosystems, **(A)** relative importance of predictors for coral reef ecosystems; **(B)** Chl a; **(C)** TSS; **(D)** PN; **(E)** depth; Open Sea Ecosystems **(F)** relative importance of predictors for open sea ecosystems; **(G)** Chl a; **(H)** depth; **(I)** DOP; **(J)** region; Coastal Ecosystems **(K)** relative importance of predictors for coastal ecosystems; **(L)** region; **(M)** Chl a; **(N)** depth; **(O)** SiO$_4$.

Moreover, the ranking of regions varied depending on the variable; for instance, the Arafura Sea ranked highest in terms of area-specific CR whereas Ningaloo ranked highest in NCP, GPP, and GPP:CR. The highest area-specific CR occurred in the Arafura Sea (206 mmol O$_2$ m^{-2} d^{-1}; **Figure 9**), where high volume specific CR and a comparatively large depth range (up to 45 m) combined to yield a high area-specific rate.

The locations with the highest values of area-specific NCP include blue-water locations such as Ningaloo (169 mmol O$_2$ m^{-2} d^{-1}, equivalent to about 2 g Cm^{-2} d^{-1}), which is fueled by virtue of upwelling jets of nutrient-rich water, and turbid inshore waters such as Darwin Harbour and the Kimberley coast where very high rates of production in a very shallow euphotic zone serve to subsidize respiration throughout the

FIGURE 8 | Log-log relationships of GPP (mmol O_2 m^{-3} d^{-1}) and chlorophyll a (µg L-1) **(Top)** and CR (mmol O_2 m^{-3} d^{-1}) and chlorophyll a (µg L^{-1}) **(Bottom)**. Symbol colors correspond to the location of the measurement as indicated on **Figure 1**, and regression lines indicated as for **Figure 5**. Model 2 regression statistics are given in **Table 6**.
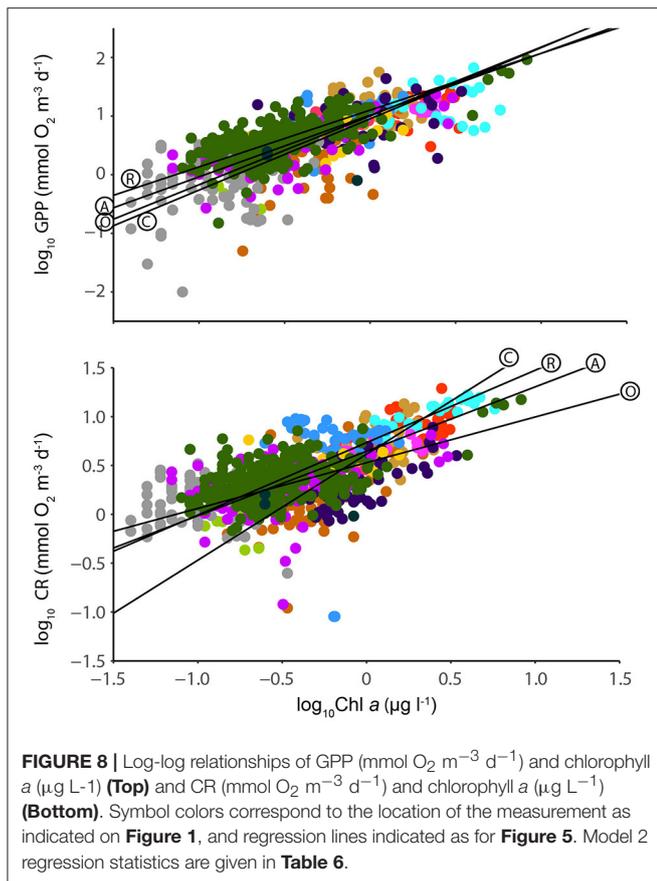
water column. The trophic state of these regions, as indicated by the GPP:CR ratio, reflecting very high rates of autotrophy at Ningaloo, Darwin Harbour and Exmouth Gulf (average ratio ~1.5), and heterotrophy at Scott Reef (average ratio ~0.79) (**Figure 9**). Heterotrophic stations (ratio below 1) were intermittently observed at Exmouth Gulf, the Timor Sea, the Gulf of Papua, and Hinchinbrook Channel.

DISCUSSION

Plankton CR, NCP, and GPP are key factors in controlling the response of the marine carbon cycle to global ocean warming and eutrophication. Few measurements of plankton CR are available for the tropical ocean and from the southern hemisphere in general (Robinson and Williams, 2005; Regaudie-de-Gioux and Duarte, 2013). Our data greatly expand the information available for shelf seas but include only a few oceanic data points. The mean CR for surface marine waters globally is 3.5 ± 0.13 (SE) mmol O_2 m^{-3} d^{-1}, 4.9 ± 0.23 mmol O_2 m^{-3} d^{-1} for depths < 10 m, 7.4 ± 0.74 mmol O_2 m^{-3} d^{-1} for coastal waters and 3.3 ± 0.15 mmol O_2 m^{-3} d^{-1} for the open ocean (Robinson and Williams, 2005). By comparison, our data have regional means ranging from 0.76 mmol O_2 m^{-3} d^{-1} in the Coral Sea to 10.62 mmol O_2 m^{-3} d^{-1} in the mangrove waterways of Hinchinbrook Island (**Figure 2**).

Our data are derived from experiments from a potpourri of seasons and oceanographic conditions; for example our Coral Sea measurements comprise only 2 experiments conducted on an opportunistic basis, whereas other studies include seasonal and spatial contrasts. The larger studies have been published separately, and the reader is referred to those publications for full discussion of pelagic metabolism and the environmental correlates of metabolism in each system (Great Barrier Reef; McKinnon et al., 2013), Gulf of Papua (McKinnon et al., 2007), Timor Sea (McKinnon et al., 2011). The oceanographic setting of the Scott Reef stations (on the margin of the Indian Ocean) places these measurements of metabolism in the same context as those used to support the theory that the open ocean is heterotrophic (Duarte et al., 2013).

Unfortunately, we have very little idea of the organisms responsible for the metabolic activity in our study areas. That said, in pelagic systems generally photosynthetic bacteria and algae are primarily responsible for the formation of organic material (i.e., GPP), but both autotrophic and heterotrophic organisms contribute to CR. Robinson and Williams (2005) noted that organisms <10 µm in size are responsible for at least 75% of CR, and that 99% occurs in organisms <50 µm in size. Respiration by >73 µm zooplankton from the Kimberley coast and the GBR accounted for only 1% of the seasonally averaged whole water respiration (McKinnon et al., 2015). In the tropical coastal waters described in our study picoplankton contributed the overwhelming majority of primary production (Furnas et al., 2005; Furnas and Carpenter, 2016) and there is a rich community of heterotrophic microbes (Alongi et al., 2015). However, coastal waters have a greater proportion of larger cells such as diatoms (e.g., Revelante et al., 1982), though the sporadic occurrence of the diazotrophic cyanobacterium *Trichodesmium* is common to all regions.

The GPP:CR ratio ranged between 0.84 ± 0.08 and 5.21 ± 0.62 depending on region (**Table 3**) with an average GPP:CR ratio of 2.09 ± 0.08, which is greater than on most other continental margins (Mackenzie et al., 2005; Jahnke, 2010; Liu et al., 2010; Bauer et al., 2013) (**Table 3**; **Figure 4**). Differences in GPP:CR ratios can be caused by differences in (1) light and nutrient availability; (2) food web organization; (3) changes in phytoplankton community structure and cell sizes; and/or (4) bioavailability of the organic matter pool which varies over both seasonal and spatial scales (Mallin and Paerl, 1992; Lønborg and Álvarez-Salgado, 2012; Marañón, 2015). Due to our current limited understanding of plankton community composition and the supply mechanisms of nutrients and organic matter in these waters means it is difficult to account for the main driving force of the variable GPP: CR ratio. The water clarity is high in most of the investigated areas and the shelves are on average shallower than in other systems (Liu et al., 2010), so these factors would tend to foster naturally high rates of autotrophic production in relation to CR. Accordingly, we suggest that the tropical estuarine and coastal regions considered here are mainly autotrophic and do not support the widely held premise that the coastal ocean is heterotrophic (GPP:CR < 1). However, we acknowledge that as this is based on the measurement of dark respiration only, and it is likely that light respiration is higher than in the dark,
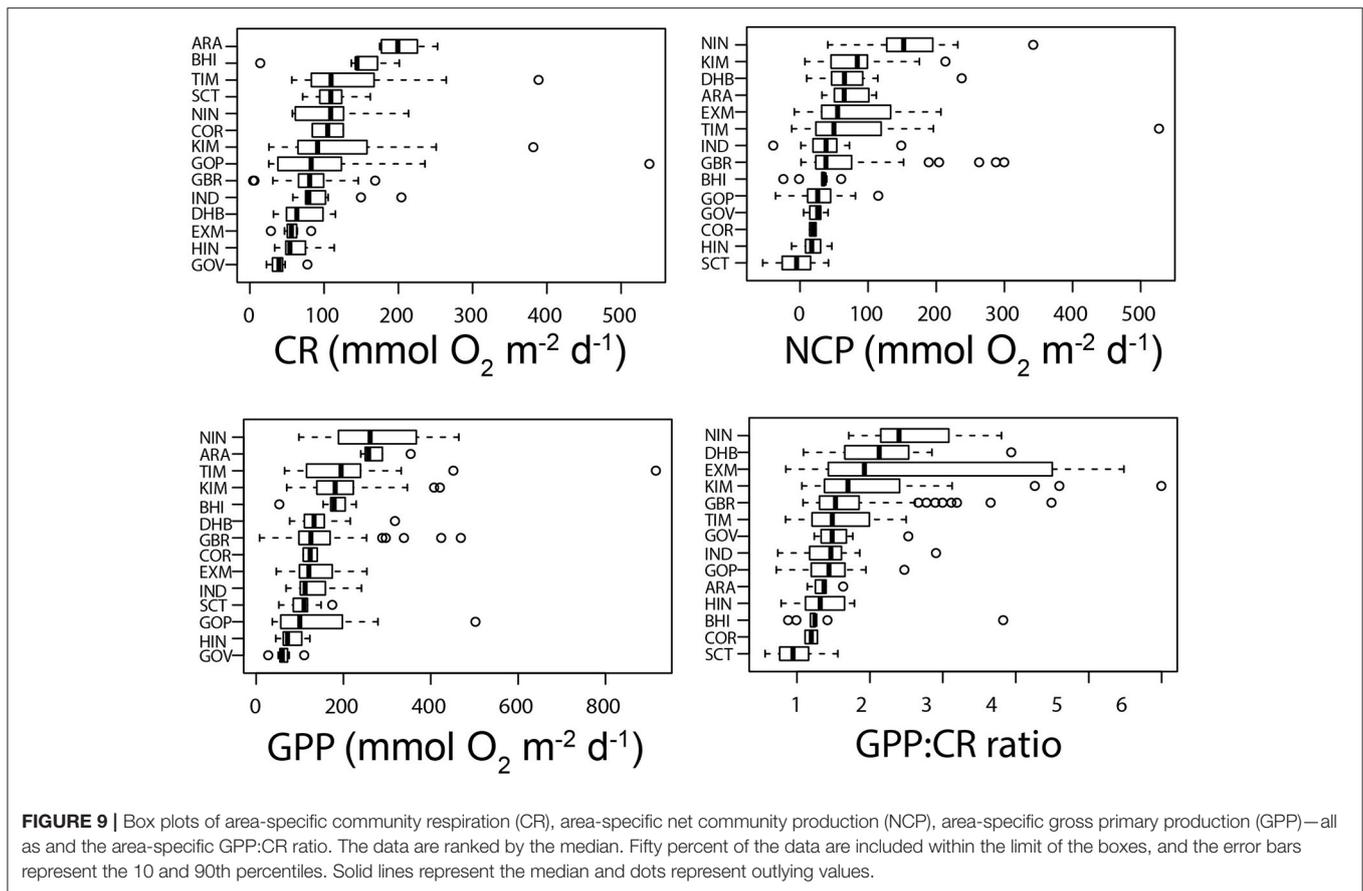
FIGURE 9 | Box plots of area-specific community respiration (CR), area-specific net community production (NCP), area-specific gross primary production (GPP)—all as and the area-specific GPP:CR ratio. The data are ranked by the median. Fifty percent of the data are included within the limit of the boxes, and the error bars represent the 10 and 90th percentiles. Solid lines represent the median and dots represent outlying values.

TABLE 6 | Model 2 Regression statistics (RMA) for the relationship between $\log_{10}$ transformed volumetric GPP and CR with $\log_{10}$ transformed chlorophyll respectively (see **Figure 8**).

Ecosystem	Intercept	95% CI	Slope	95% CI	R^2	p	n
GPP							
All	1.017	0.065	1.054	0.153	0.50	0.01	738
Open Sea	1.002	0.274	1.174	0.399	0.39	0.01	216
Coastal	0.953	0.025	1.215	0.544	0.25	0.01	233
Coral Reef	1.102	0.135	0.969	0.251	0.45	0.01	289
CR							
All	0.645	0.049	0.660	0.118	0.40	0.01	806
Open Sea	0.528	0.207	0.468	0.299	0.15	0.01	224
Coastal	0.616	0.024	1.085	0.337	0.36	0.01	286
Coral Reef	0.733	0.169	0.741	0.319	0.23	0.01	296

our values of GPP may be underestimated (Pringault et al., 2007).

In this study we have measured the organic matter fraction that is produced and degraded within a 24 h cycle, but in reality the organic matter pool contains labile compounds with short turnover times (from hours to days), a semi-labile pool with longer turnover times (from weeks to months) and a recalcitrant background pool (Boudreau and Ruddick, 1991; Hansell, 2013).

Therefore, estimates of both organic matter degradation rates and water residence time are needed to determine if the organic matter in a water sample is degraded within the shelf or exported to the open ocean. In one of the regions included in our study (the Great Barrier Reef), a geochemical estimate of the carbon balance using radioisotopes suggested a near balance between production and respiration with only minor export of labile organic matter (Brunskill et al., 2010). Our data suggest that tropical coastal waters are indeed exporting organic matter (potentially both particulate and dissolved) to adjacent marine ecosystems.

Environmental Determinants of Metabolism

Our BRT analysis illustrates the relative importance of different environmental variables as predictors of metabolism in the three ecosystem types. For CR, temperature was selected as the most important in coral reef and open ocean ecosystems, while it was less important in coastal ecosystems. Chl a was an important predictor of CR in coastal and open sea ecosystems, but not in coral reef ecosystems, where other variables associated with particulate material (POC, PP) were more important. Regional differences remained the most important predictor of both CR and GPP in the coastal ecosystems, indicating that some communities were more productive than others. The only ecosystem where depth had an important effect on CR

was in the open sea ecosystem. This may be related to the differences in temperature through the water column, which was most pronounced in these regions because of the greater depth range. In contrast, Chl *a* and depth were among the most important determinants of GPP in all three ecosystem types, which is unsurprising given the importance of biomass and light availability in regulating primary production.

In our dataset, volumetric CR scaled as the 0.66 power of GPP overall (0.56, 0.77, and 0.98 powers in open sea, coral reef, and coastal ecosystems respectively; **Table 5**), in good agreement with previous estimates: 0.79 reported by Regaudie-de-Gioux and Duarte (2013), 0.50 by Duarte and Agustí (1998), and 0.62 by Robinson and Williams (2005). For the relationship between CR and NCP the scaling factors were all lower, confirming the pattern that CR increases more slowly with overall productivity than NCP (Duarte and Agustí, 1998). The scaling factors between CR and both GPP and NCP were highest in coastal ecosystems, and lowest in the open sea (**Table 5**; **Figure 5**). Overall, in our dataset the regression of GPP on Chl *a* explained 50% of the variance across all study regions (**Table 6**), in contrast to the study of Regaudie-de-Gioux and Duarte (2013) where only 30% of the variance (from mostly oceanic stations) was explained.

Our studies did not show large differences in CR through the water column since depth was only found as a minor influence in open sea ecosystems (**Figure 6F**) and had no impact in the other ecosystem types. This was not the case for GPP or NCP since these are light dependent and the light climate varied enormously between regions. Some of our regions (Hinchinbrook Channel, Bathurst Island, and some on the Kimberley coast) have highly turbid water where light is virtually extinguished in the top meter of the water column. In these conditions, phytoplankton are distributed throughout the water column by turbulence and adapt to low light conditions by increasing the Chl *a* concentration per cell (Demers et al., 1986). Under our experimental protocol these cells were maintained in constant light rather than continuously circulated through the range of light climates in the water column, which may inflate the productivity values by holding light-adapted cells in a high light environment, or alternatively deflate them by photoinhibition. Mallin and Paerl (1992) simulated the effects of a variable light climate in a shallow estuary and demonstrated that phytoplankton cells moved rapidly through light-limited conditions as a result of mixing which allowed them sufficient light to maintain high productivity.

The temperature dependence of the ocean's metabolism has been explained using the Arrhenius law within the framework of the metabolic theory of ecology (MTE) (López-Urrutia et al., 2006). This theory scales the metabolic rates by combining the effects of body size and temperature, suggesting that autotrophic and heterotrophic processes in marine systems will react differently to ocean warming, thus possibly changing the metabolic balance and leading to a more heterotrophic ocean (Yvon-Durocher et al., 2010). In accordance with the MTE, Regaudie-de-Gioux and Duarte (2012) found that temperature exerted a strong influence on Chl *a* -specific metabolic rates. In a similar fashion, we examined the relationship between temperature and Chl *a* -specific metabolic rates assuming an Arrhenius-type relationship (linearity of the natural logarithm of a rate process vs. inverse absolute temperature). Our analysis showed temperature dependence of CR in the coral reef and GPP in the open sea ecosystems. These disparate responses to temperature may be related to differences in the supply of nutrients, availability of organic matter, and/or food web community composition and structure (Sarmento et al., 2010; López-Urrutia and Morán, 2015; Lønborg et al., 2016). These results are also slightly at odds with our BRT analysis, where temperature was an important predictor of CR in both coral reef and open sea ecosystems, and was not selected as a predictor of GPP in any. These disparities occur because the BRT analysis considered the effects of multiple predictors in parallel. For example, depth was selected as an important predictor of GPP, in large part because of the covariance of temperature (and indeed other variables, e.g., light in the case of GPP) with depth. In combination, our analyses suggest differences in how the metabolic rates in the three ecosystems types will be impacted by increasing ocean temperatures, with least impact found in coastal ecosystems.

Productivity of Coastal Waters Adjacent to Northern Australia

On an area-specific basis, GPP was highest off Ningaloo Reef and in the Arafura Sea. Furnas (2007) showed sporadically very high production rates as a result of cryptic upwelling off Australia's NW Cape, just north of Ningaloo Reef. Furnas and Carpenter (2016) found that the highest primary production in the shelf seas of northern Australia occurred in the Arafura Sea. The water column in the Arafura Sea has a depth of about 65 m and was strongly stratified during the wet season conditions at the time of sampling, with a mixed layer of about 30 m. The bottom layer is sourced from sub-thermocline water in the Timor Trough and the widespread undercurrent-driven upwelling and tidal stirring persistently pump nutrient-rich sub-surface water into the region (Rochford, 1966; Condie, 2011; Kampf, 2015a,b), in turn contributing to rapid phytoplankton growth in the well-insolated surface layers. The high standing stocks of diazotrophs including blooms of *Trichodesmium* (Montoya et al., 2004) hint at the regional importance of N_2 fixation in driving phytoplankton growth and productivity. Very high rates of productivity (up to 7 g C m^{-2} d^{-1}) are also known to occur in the nearby Banda Sea (Gieskes et al., 1990). At the other end of the productivity spectrum, Scott Reef, on the outer edge of the continental shelf of NW Australia, was the only region that was consistently heterotrophic, though heterotrophy was also observed in the Timor Sea (McKinnon et al., 2011), Hinchinbrook Channel at low tide during the wet season (McKinnon et al., 2010), and in the Coral Sea. Stations at Bathurst Island, Hinchinbrook, and in Indonesia were part of studies of the environmental effects of sea cage aquaculture, and were to some extent enriched by organic wastes from the farms. Despite this, these locations were mainly autotrophic. Our finding of net heterotrophy at the most oceanic stations (Coral Sea, Scott Reef) is in alignment with other studies of the tropical ocean (e.g., Viviani et al., 2011), and fuel the wider debate on the heterotrophy of the global ocean (Duarte

et al., 2013). These results furthermore support the idea that the net heterotrophic conditions in more offshore regions could be driven by the export of excess autotrophic production from inshore waters.

Productivity data are usually expressed in units of carbon, since the ^{14}C method has by far the largest number of measurements. Our oxygen-based measurements can be converted to carbon equivalents assuming respiratory and photosynthetic quotients of 1.2 and 1.4 respectively (Bender et al., 1999). On this basis, the locations with the highest GPP (Ningaloo Reef, Arafura Sea) have C-specific CR of 1.3 and 2.5 g C m^{-2} d^{-1}, and C-specific NCP of 2.0 and 4.3 g C m^{-2} d^{-1} respectively. Summing these gives GPP values for Ningaloo Reef of 3.3 g C m^{-2} d^{-1} and Arafura Sea of 6.8 g C m^{-2} d^{-1}. Assuming ^{14}C measurements are 45% of GPP (Bender et al., 1999), then these approximate primary production rates of 1.5 and 3.1 g C m^{-2} d^{-1}, which are comparable to the ^{14}C measurements at shelf stations near NW Cape (the northern extent of Ningaloo Reef) but about 50% higher than those from the Arafura Sea (Furnas, 2007; Furnas and Carpenter, 2016).

Furnas and Carpenter (2016) reviewed ^{14}C measurements of primary production taken in northern Australian waters over a period of 23 years. Their study domain is very similar to that of the present study, but includes a greater proportion of shelf as opposed to coastal stations. Two of the stations sampled by Furnas and Carpenter (2016) are also included in our data set (Scott Reef and the Arafura Sea), and in fact the water used for both productivity measurements was taken from the same bottle casts. Estimates of total areal production based on ^{14}C from those experiments (Furnas and Carpenter, 2016) account for 41% (Ordinary Least Squares) or 52% (Model 2 regression, Ranged Major Axis) of our estimated GPP ($R^2 = 0.63$), which is in good agreement with the conclusion of Bender et al. (1999) that ^{14}C measurements account for 45% of GPP.

Ranking the Trophic State of Coastal and Shelf Pelagic Ecosystems

Inorganic nutrients turn over very quickly in the tropical coastal waters adjacent to northern Australia. For instance, in the Great Barrier Reef DIN are so rapidly acquired by microbiota as to be fully depleted within hours (Furnas et al., 2005) resulting in standing stocks of nutrients being close to the detection levels of the analytical methods. Despite this, a great deal of research effort has gone into monitoring of "water quality," especially in the coastal waters of the Great Barrier Reef, primarily by measuring inorganic and organic nutrient species as well as Chl a. The nutrient data have overall proved of very limited use in understanding human impacts because nutrients are so rapidly transformed and have low and invariant standing stocks. In partial recognition of this, increased emphasis has been placed upon the use of Chl a as an index to detect spatial and temporal changes in water quality resulting from increased nutrient loads (e.g., Brodie et al., 2007).

We believe indices of the formation and decay of organic matter are crucial to measure ecosystem health and make informed management decisions. Strictly speaking, the "trophic status" of a water body is defined by the GPP:CR ratio ("P:R

ratio"), with a ratio greater than unity denoted autotrophic because there is net production of organic matter, and those less than unity said to be heterotrophic, in which case there is net degradation of organic matter. Therefore, in theory the degree of "eutrophication" of a water body can be quantified by measurement of the GPP:CR ratio, and regions ranked in order of trophic state.

An even better way to rank regions by trophic state may be to use the thresholds necessary to achieve metabolic balance. The threshold GPP below which plankton communities tend to be heterotrophic scales from 0.71 mmol O$_2$ m^{-3} d^{-1} in the Coral Sea to 10.05 mmol O$_2$ m^{-3} d^{-1} in Hinchinbrook, thus ranking each region on a scale from oligotrophic to eutrophic (**Table 4**). For comparison, Duarte and Regaudie-de-Gioux (2009) found a global ocean average of 1.07, 1.33 for the Pacific Ocean, and 4.16 mmol O$_2$ m^{-3} d^{-1} for the Mediterranean Sea. Comparing our thresholds it is clear that mangroves have a high threshold GPP because of the contribution of labile organic matter from the mangrove forests themselves, but also from tidal resuspension of fine sediments, settled detritus and microphytobenthos (for instance, Bathurst Island has a tidal range of 8 m, some parts of Kimberley coast over 10 m). By contrast, the waters of the central Coral Sea are some of the most oligotrophic in the world ocean, and have a comparatively low threshold GPP. It is also noteworthy that our ranking of regions by trophic state bears little resemblance to that derived on the basis of Chl a alone (Supplementary Table 1).

Phytoplankton growth depends on light availability, which is influenced by cloud cover and turbidity arising from turbulence as a result of wind and tides, all of which can vary on time scales of hours to days. For example, consecutive cloudy and cloud-free days and the resulting changes in irradiance may change the scale of production measured, resulting in high variability in the GPP:CR ratio. Also, if incubation techniques are employed the light climate in experimental containers needs to reflect that in the field, which can be challenging. For example, it has recently been demonstrated that borosilicate flasks widely used for experimental incubations filter out UV light resulting in overestimation of production (Agustí et al., 2014). Moreover, the use of incubators allowing the passage of UV light may also mistakenly include the UV photo-oxidation (oxygen sink) in their plankton productivity term, which can lead to an underestimation of NCP (Kitidis et al., 2014; Gieskes et al., 2015). For a routine and repeatable index of trophic state, we therefore conclude that including production measurements that are light dependent is adding errors that are difficult to control.

The measurement of dark CR is comparatively straightforward and does not have the problems associated with variation in light climate. CR ranks in accordance with what might reasonably be expected of the trophic status of marine ecosystems in northern Australia (**Figure 2**) and closely resembles the ranking of the threshold necessary to achieve metabolic balance (**Table 4**). Highest rates are found in the "ultratrophic" (sensu; Burford et al., 2003) mangroves such as those in creeks running into Hinchinbrook Channel, lowest rates in the oligotrophic Coral Sea. Our regression analyses indicate that the measurement of CR accounts for 42% of the variance

in GPP, reinforcing the point made by Robinson and Williams (2005) that respiration, rather than primary production, is a both practical and reliable measurement of trophic state. On this basis, we advocate the adoption of measurements of CR as a quantitative tool to monitor the trophic state of coastal waters (Dodds and Cole, 2007).

In conclusion, this study demonstrates that: (1) the tropical coastal waters studied are overall strongly autotrophic (average GPP:CR ratio 2.14 ± 0.98); (2) CR scaled according to the 2/3 power of GPP, and accounted for 42% of the variance in GPP; (3) temperature, Chl *a* (phytoplankton biomass) and regional differences were the main factors influencing both CR and GPP; (4) the impact of temperature on metabolic rates is ecosystem-dependent, with coastal ecosystems showing least response; and (5) measurements of pelagic metabolism could be used as a quantitative tool to monitor the trophic state of coastal waters.

AUTHOR CONTRIBUTIONS

AM designed the study. AM and SD collected and processed samples, performed experiments and laboratory assays, and analyzed and interpreted the data. ML conducted statistical analyses. AM and CL wrote the manuscript, with input from all authors. All authors approved the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2017.00346/full#supplementary-material

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