

Annual plankton community metabolism in estuarine and coastal waters in Perth (Western Australia)

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The planktonic metabolic balance, that is the balance between gross primary production (GPP) and community respiration (CR), was determined in Matilda Bay (estuarine) and Woodman Point (coastal) in Perth, Western Australia. The rates of net community production ($NCP = GPP - CR$) and the ratio between GPP and CR (P/R) were assessed to evaluate whether the metabolic balance in the two coastal locations tend to be net autotrophic (production exceeding community respiration) or net heterotrophic (respiration exceeding production). We also analyzed environmental variability by measuring temperature, salinity, heterotrophic bacterial abundance and chlorophyll *a* concentration. Samples were collected fortnightly from March to October of 2014. During the study period the metabolic rates were three times higher in Matilda Bay than in Woodman Point. The predominant metabolism was the net autotrophic at both sites with P/R ratios higher than one in the majority of the sampling dates. In Matilda Bay the metabolic rates were negatively correlated with salinity and positively with chlorophyll *a*. In Woodman Point only the GPP was positively correlated with chlorophyll *a*. The positive correlation between P/R ratio and GPP in Matilda Bay and the positive correlations between the metabolic rates and chlorophyll *a* suggest that factors controlling autotrophic processes are modulating the planktonic metabolic balance in the coastal marine ecosystem in Perth. Not significant correlations were found between the metabolic rates and the temperature and heterotrophic bacterial abundance. However, in Matilda Bay the metabolic rates were negatively correlated with salinity, denoting river dynamics influence. The net autotrophic metabolic balance indicates that in both ecosystems planktonic communities are acting as a sink of CO₂ and as a source of organic matter and oxygen to the system and are able to export organic matter to other ecosystems.

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Abstract

The planktonic metabolic balance that is the balance between gross primary production (GPP) and community respiration (CR) was determined in Matilda Bay (estuarine) and Woodman Point (coastal) in Perth, Western Australia. The rates of net community production ($NCP = GPP - CR$) and the ratio between GPP and CR (P/R) were assessed to evaluate whether the metabolic balance in the two coastal locations tend to be net autotrophic (production exceeding community respiration) or net heterotrophic (respiration exceeding production). We also analyzed environmental variability by measuring temperature, salinity, heterotrophic bacterial abundance and chlorophyll *a* concentration. Samples were collected fortnightly from March to October of 2014. During the study period the metabolic rates were three times higher in Matilda Bay than in Woodman Point. The predominant metabolism was the net autotrophic at both sites with P/R ratios higher than one in the majority of the sampling dates. In Matilda Bay the metabolic rates were negatively correlated with salinity and positively with chlorophyll *a*. In Woodman Point only the GPP was positively correlated with chlorophyll *a*. The positive correlation between P/R ratio and GPP in Matilda Bay and the positive correlations between the metabolic rates and chlorophyll *a* suggest that factors controlling autotrophic processes are modulating the planktonic metabolic balance in the coastal marine ecosystem in Perth. Not significant correlations were found between the metabolic rates and the temperature and heterotrophic bacterial abundance. However, in Matilda Bay the metabolic rates were negatively correlated with salinity, denoting river dynamics influence. The net autotrophic metabolic balance indicates that in both ecosystems planktonic communities are acting as a sink of CO₂ and as a source of organic matter and oxygen to the system and are able to export organic matter to other ecosystems.

Introduction

Plankton metabolism is a fundamental property of marine ecosystem driving the flux of gases and the transference of organic matter to the food web (Duarte et al. 2011). The metabolism of plankton communities in the open ocean is in approximate balance, i.e. with gross primary production (GPP) similar to community respiration (R) and a P/R ration close to 1.0, or experiences small deviations from this balance (Williams et al. 2013, Duarte et al. 2013), because deviations from such balance require external inputs of nutrients or organic carbon, which are small in the open ocean. In contrast, coastal plankton communities, which typically present higher metabolic rates (Duarte and Agustí, 1998), may present large deviations from metabolic balance with either excess respiration over production when the ecosystem receives large inputs of labile organic carbon (e.g. Mediterranean coastal areas, Duarte et al., 2004, Vidussi et al., 2011) or gross primary production in excess of respiration when the ecosystem receives large inputs of dissolved inorganic nutrients (e.g. Agusti et al., 2004).

The metabolic balance of coastal ecosystems plays an important role in determining their role as CO₂ sources or sinks. What the role of coastal ecosystems is as CO₂ sources or sinks is uncertain (Borges 2005, Cai 2011). Recently, a contrasting role between continental shelves acting as sinks and near-shore ecosystems as sources of atmospheric CO₂ was proposed to reconcile opposing views on the role of coastal ecosystems as CO₂ sources or sinks (Chen and Borges, 2009; Cai, 2011). In particular, inner estuaries are believed to act as sources of CO₂ to the atmosphere due to a prevalence of heterotrophic ecosystem metabolic status fuelled by land-derived inputs of organic carbon (Odum and Hoskin, 1958; Odum and Wilson, 1962; Heip et al., 1995; Kemp et al., 1997; Gattuso et al., 1998; Hopkinson and Smith, 2005).

However, virtually all of the results from near-shore and open coastal ecosystems thus far refer to those in the northern hemisphere, particularly Europe, the USA and Asia (Borges, 2005; Chen and Borges, 2009; Cai, 2011). As these typically represent highly populated areas with watersheds supporting intense agricultural practices, the results may not be directly transferable to coastal areas in the southern hemisphere. In particular, we are only aware of one published study assessing plankton metabolism in Australian coastal waters, conducted in the Great Barrier

region (McKinnon et al., 2013). This study concluded that autotrophic plankton metabolism prevails in this coastal zone (McKinnon et al., 2013), despite being located in the wet Australian tropics with a distinct rainy season. Moreover, the inshore area was even more strongly autotrophic than the offshore region of the GBR, which is in contrast to the expectation that inshore coastal waters should be heterotrophic. Whether this is specific of the Great Barrier Reef or autotrophic metabolism is prevalent in other regions of Australia is, thus far, unresolved.

Here we report plankton metabolic rates for two contrasting coastal sites in the Perth area in temperate Western Australia, Matilda Bay, an inshore-site in the Swan river estuary, and Woodsman Point, an open coastal site. Specifically, we assessed fortnightly during a year (March 2014 to March 2015) community respiration (CR), gross primary production (GPP) and net community production (NCP), along with temperature, salinity, dissolved inorganic nutrient concentration, chlorophyll a and bacterial abundance.

Methods

Matilda Bay is located in the lower reaches of the Swan River, one of the main rivers in Western Australia with an extension of more than 50 Km and a catchment area about 190,000 Km² (Thomson, 1998). The estuary is permanently open to the ocean since 1987 when a rocky bar near to the mouth of the estuary in Fremantle was removed, and has a seasonal cycle influenced by rainfall seasonal variations with hot and dry summers and wet and cool winters with about 90% of the annual rain (Thomson, 1998; Hamilton et al., 2006). During winter most of the water body is fresh because of the rainfall and runoff but the salinity increases upstream when the rainfall decreases and the system receive a significant flow of oceanic waters (Thompson 1998). The estuary has received anthropogenic pressure because of land clearing for agricultural purposes, increase of urbanization and construction of dams for water supply among others (Chan et al. 2002; Thompson 1998). Consequently, nutrient inputs and sedimentation rates have increased and the water quality has decreased (Chan et al. 2002; Hamilton et al. 2006). Gedaria (2012) reported that salinity and temperature are the main drivers of the abundance of phytoplankton species in the Swan River estuary. Woodman Point is located in the Owen

Anchorage in the Coast of Cockburn Sound (Perth, Western Australia), and, in contrast with Matilda Bay, represents an open shoreline with no direct freshwater influence.

Sub-surface water samples were collected at fortnightly intervals between March 2014 to March 2015 in Matilda Bay (Latitude -31.990496 °S, longitude 115.818182 °E) and the Ammunition Jetty, Woodman Point Latitude -32.124124 °S, longitude 115.75868 °E). Samples were then transported to incubated and processed at the University of Western Australia (UWA). Temperature (°C), Salinity and dissolved oxygen were measured through the water column by deploying a calibrated YSI EXO1 Multi-parameter Water Quality Sonde fitted with a pressure sensor (± 0.04 m), temperature ($\pm 0.01^\circ\text{C}$) and conductivity sensor, as well as an optode dissolved oxygen sensor. In addition, surface water temperature was measured from the water collected by a digital thermometer.

Net community production (NCP), gross primary production (GPP) and community respiration (CR) were quantified by changes in dissolved oxygen using micro-Winkler techniques by the use of a precise automatic titration based on redox potentiometric endpoint. Water collected in each site was siphoned into 21 calibrated glass borosilicate Winkler bottles. Seven bottles were fixed immediately to measure initial oxygen, another seven bottles were incubated in the light and the last seven bottles were incubated in the dark (Fig. 2). The incubation was run for 24 hours in situ conditions of temperature and natural solar radiation in an outdoor, temperature controlled tank. After the incubation, samples were fixed and the final oxygen was measured using a high-precision autotitrator (Compact Titrator G20, Mettler Toledo). NCP rates were determined from the oxygen change in the clear bottles (oxygen clear – initial oxygen), CR rates were determined from the oxygen change in the dark bottles (Initial oxygen – dark oxygen) and GPP rates were calculated as the sum of CR and NCP (Duarte et al., 2011).

Aliquots of 200 ml of water samples were used for chlorophyll *a* analyses using acetone extraction and fluorometric determination after Parsons et al. (1984). Subsamples were filtered through Whatman grade GF/F glass microfiber filters of 25 mm diameter. Filters were placed in plastic tubes of 1 ml and stored at -20°C until their analysis. Filters were immersed in acetone at 90% during 24 hours for chlorophyll *a* extraction. After that period, chlorophyll *a* fluorescence

was measured by the use of a Trilogy Laboratory Fluorometer (Turner Designs) equipped with a module of Chlorophyll a Non-Acidification Fluorescent Module (CHL-A NA) at UWA. The fluorometer was calibrated with pure chlorophyll a (Sigma- Aldrich C6144-1mg) solution.

Samples for dissolved inorganic nutrient analyses were collected during transportation to the laboratory and kept frozen until analysis in a segmented flow autoanalyzer following standard procedures Samples (Hansen and Koroleff, 1999).

The temperature response of plankton communities was described by fitting, using least squares regression analysis, the Arrhenius equation,

$$\ln Y = A \exp^{-AE/kT}$$

where Y is the property of interest, AE is the activation energy (eV), k is the Boltzmann's constant ($8.617734 \times 10^{-5} \text{ eV } ^\circ\text{K}^{-1}$) and T is the sea-surface water temperature ($^\circ\text{K}$), and A is a fitted intercept (Regaudie-de-Gioux and Duarte, 2012).

Results

Surface water temperature ranged from 12 to 27.4 $^\circ\text{C}$ and 15.1 to 25 $^\circ\text{C}$ (Fig. 1a) and salinity ranged from 22.03 to 36.97 units and 31.62 to 37.12 units (Fig. 1b) in Matilda Bay and Woodman Point, respectively. The minimum salinity was reached in late winter and spring in Matilda Bay, following river discharge, whereas the pattern was less clear, with low salinity also concentrated in winter and early spring, in Woodman Point (Fig. 1b). Dissolved inorganic nitrogen concentration was highest in winter, but phosphate concentration was highest in late summer in Matilda Bay (Fig. 2a-c). In contrast, nitrate and phosphorus concentrations in Woodman Point were lower ($P < 0.05$) than those in Matilda Bay (Table 1) and dissolved inorganic nitrogen concentration showed two maxima, winter and summer, while phosphate concentrations showed a summer minima (Fig. 2a-c). Chlorophyll *a* concentration was significantly higher and more variable in Matilda Bay than in Woodman Point (Table 1, Fig. 2d), and reached the highest values in winter, at the time of peak nitrate concentration (Fig. 2d), as

there was a significant, positive, relationship between chlorophyll *a* concentration and nitrate concentration ($r = 0.67$, $P < 0.0001$).

Respiration rates were, on average, twice as high in Matilda Bay as in Woodman Point (Table 1), and increased strongly toward summer in Woodman Point whereas it shows a less seasonal variability in Matilda Bay (Fig. 3a). Gross primary production was also much higher in Matilda Bay than in Woodman Point (Table 1), with no clear seasonal pattern at either site (Fig. 3b). The communities were generally autotrophic, with GPP about twice as high as R (NCP and P/R > 1 , Table 1), with NCP being three times higher, on average, at Matilda Bay than at Woodman Point (Table 1, Fig. 3c), and neither community displaying any clear seasonal trend in net community production along the year (Fig. 3c). GPP was significantly correlated with CR ($r = 0.68$, $P < 0.0001$), but NCP increased strongly with increasing GPP (Fig. 4). Net community production and gross primary production increased with increasing chlorophyll *a* concentration, with the relationship between community respiration rate and chlorophyll *a* being much weaker, albeit also significant (Fig. 5a,c).

Respiration rates increased with increasing temperature, resulting in an activation energy of 0.76 ± 0.21 (Fig. 6a). GPP showed, in contrast, no significant temperature-dependence ($P > 0.05$), possibly due to large variability in chlorophyll *a*, masking the effect of temperature on GPP. Indeed, when standardized to chlorophyll *a*, as observed in previous studies (e.g. Regaudie de Gioux and Duarte, 2012; Garcia-Corral et al., 2017), there was a significant temperature-dependence of gross primary production, with an activation energy of 0.69 ± 0.12 (Fig. 6b), comparable to that of community respiration.

Discussion

Chlorophyll *a* values were higher in Matilda Bay than in Woodman point, which values ranged within those reported for coastal waters around Perth (Pearce et al., 2006). The highest chlorophyll *a* concentration in both Matilda Bay and Woodman point occurred at the low salinity winter events. Chlorophyll *a* concentration in the Swan River has been reported to vary seasonally showing large interannual variability (Thompson, 1998). The mean and highest values

observed in Matilda Bay were consistent with the highest chlorophyll *a* reported previously for the estuary (Thompson, 1998). Both coastal ecosystems, but particularly Matilda Bay, supported productive communities, as reflected in relatively high GPP rates.

Community Respiration rates was less variable than GPP, particularly at Matilda Bay, but GPP sufficed to support all carbon demands from the community and generate excess organic matter, resulting in a prevalence of autotrophic communities at both sites, with average P/R ratios above 2.0 similar across both sites. This is expected from relatively productive sites with GPP well above the threshold previously determined to delineate autotrophic from heterotrophic communities (Duarte & Agustí, 1998; Duarte & Regaudie-de-Gioux, 2009). Net community production was strongly correlated with chlorophyll *a* concentration, accounting for the much higher NCP in eutrophic Matilda Bay compared to Woodman Point plankton communities, suggesting that the metabolic balance of plankton communities in the coast of Perth is regulated by factors controlling autotrophic processes, such as nutrient inputs, salinity regimes and temperature. In coastal waters of Northern Australia, McKinnon et al (2017) observed also that the metabolism and community respiration were also positively related to chlorophyll concentration.

The results presented here contribute to address a paucity of studies of plankton community metabolism in the Indian Ocean (Regaudie-de-Gioux & Duarte, 2013). Robinson and Williams (1999) studied the planktonic metabolic balance during a research cruise in the Gulf of Oman, reporting P/R ratios for surface waters between 1.17 and 2.43, with the highest ratio near to the Omani coast (Regaudie-de-Gioux & Duarte, 2013; Robinson & Williams, 1999). Indeed, the P/R ratio of the station closer to the Omani coast, 2.43 (Robinson & Williams, 1999) was similar to the P/R ratio for our study sites in the Western Australia coast.

Our results indeed showed a prevalence of net autotrophic metabolism in plankton communities of the Coast of Perth (Western Australia), both at the eutrophic estuarine waters at Matilda Bay and the open coastal Indian Ocean waters at Woodman Point. This indicates that planktonic communities in these coastal location act as strong CO₂ sinks and sources of organic matter and oxygen to the system. This is in contrast to the expectation that near-shore ecosystems act as

sources of atmospheric CO₂, proposed to reconcile opposing views on the role of coastal ecosystems as CO₂ sources or sinks (Chen & Borges, 2009; Cai, 2011). Indeed, the pattern showed here, with higher net community production in the inner waters of Matilda Bay compared to the more open waters at Woodman Point are in agreement with prior findings for Australia of prevalence of autotrophic metabolism, with inshore areas being more strongly autotrophic than offshore waters of the Great Barrier Reef (McKinnon et al., 2013).

The plankton communities in the coastal waters of Perth showed increased metabolic rates with increasing temperature, as expected from metabolic theory of ecology (Brown et al., 2004). However, the activation energy for gross primary production of 0.69 ± 0.12 eV found here was well below that found in previous analyses of Indian Ocean communities, focused on open-ocean waters, reporting a E_a for gross primary production, standardized to chlorophyll *a*, of 1.70 eV (Garcia-Corral et al., 2017). Also, whereas, consistent with other assessments (e.g. Regaudie de Gioux & Duarte 2012; Garcia-Corral et al., 2017), the activation energy for community respiration was higher than that for gross primary production, this difference was small and not statistically significant. This is important as it predicts that warming events, such as the heat wave that impacted on marine ecosystems across Western Australia in 2011 (Wernberg et al., 2016), will affect gross primary production and respiration rates of plankton communities in a similar way.

Conclusions

Our results indicated that planktonic communities in the two coastal Western Australia locations studied act as strong CO₂ sinks and sources of organic matter and oxygen to the system. The plankton communities of the Coast of Perth (Western Australia) showed net autotrophic metabolism both at the eutrophic estuarine waters at Matilda Bay and the open coastal Indian Ocean waters at Woodman Point. This result is in contrast to the expectation of net heterotrophic balance for near-shore ecosystems, but in agreement with the few metabolic balance assessments from Australian coastal waters. The thermal relationships indicated that warming may decrease the strong capacity observed for CO₂ sinks. Our study is based on two

contrasting plankton communities in Western Australia and, while useful to address the absence of reports on plankton community metabolism in the Indian Ocean coast of Australia, and the paucity of reports across the Indian Ocean (Regaudie de-Gioux & Duarte 2013), a broader analyses of coastal plankton communities across Western Australia is required to confirm the patterns revealed here and diagnose the role of plankton communities in across Western Australia in carbon fluxes and their likely response to future warming.

Acknowledgement

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Figure Headings

Figure 1: Temporal variability in seawater temperature and salinity. Changes in surface seawater temperature and salinity in Matilda Bay are shown as blue line and symbols, and in Woodman Point as red line and symbols, along the study period.

Figure 2: Nutrient variability. Changes in (a) nitrate, (b) ammonium, (c) phosphate and (d) chlorophyll *a* concentration in Matilda Bay (blue line and symbols) and Woodman Point (red line and symbols) along the study period.

Figure 3: Planktonic metabolism. Changes in (a) community respiration rate, (b) gross primary production, and (c) net community production in Matilda Bay (blue line and symbols) and Woodman Point (red line and symbols) along the study period.

Figure 4. The relationship between net community production and gross primary production. The solid line shows the fitted regression equation: $NCP \text{ (mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}) = -2.65 + 0.65 (\pm 0.05) GPP \text{ (mmol O}_2 \text{ m}^{-3} \text{ d}^{-1})$ ($R^2 = 0.75$, $P < 0.0001$). Blue symbols and red symbols correspond to Matilda Bay and Woodman Point, respectively.

Figure 5. Plankton metabolism and phytoplankton. The relationship between (a) net community production, (b) gross primary production and (c) community respiration and chlorophyll *a* concentration. The solid lines shows the fitted regression equations: (a) $NCP \text{ (mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}) = -1.54 + 2.29 (\pm 0.19) Chl \text{ } a \text{ (}\mu\text{g Chl } a \text{ L}^{-1})$ ($R^2 = 0.73$, $P < 0.0001$); (b) $GPP \text{ (mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}) = 2.93 + 3.03 (\pm 0.05) Chl \text{ } a \text{ (}\mu\text{g Chl } a \text{ L}^{-1})$ ($R^2 = 0.69$, $P < 0.0001$); and (c) $R \text{ (mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}) = 4.45 + 0.74 (\pm 0.24) Chl \text{ } a \text{ (}\mu\text{g Chl } a \text{ L}^{-1})$ ($R^2 = 0.15$, $P = 0.0036$). Blue symbols and red symbols correspond to Matilda Bay and Woodman Point, respectively.

Figure 6: Thermal relationships. Arhenius plots showing the relationship between the natural log of (a) community respiration and (b) gross primary production standardized to chlorophyll *a*, and $1/kT$, where *k* is the Boltzmann' s constant ($8.617734 \times 10^{-5} \text{ eV } ^\circ\text{K}^{-1}$) and *T* is the sea-surface water temperature ($^\circ\text{K}$) in Matilda Bay (blue symbols) and Woodman Point (red symbols). The

395 solid lines show the fitted equations: $\ln R \text{ (mmol O}_2 \text{ mg m}^{-3} \text{ d}^{-1}) = 31.87 - 0.76 (\pm 0.21) 1/kT$ (R^2
 396 $= 0.21$, $P = 0.0008$) and $\ln \text{GPP/Chl a (mmol O}_2 \text{ mg Chl a}^{-1} \text{ d}^{-1}) = 28.8 - 0.69 (\pm 0.12) 1/kT$ ($R^2 =$
 397 0.41 , $P < 0.0001$).

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Table 1(on next page)

Mean (\pm SE) of the variables measured in Matilda Bay and Woodman Point (Western Australia).

NCP = net community production, GPP = gross primary production and P/R = is the ratio of GPP over R. Asterisks denotes statistically significant difference (t-test, $P < 0.05$).

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	Matilda Bay		Woodman Point	
	Mean	± SE (N = 33)	Mean	± SE (N = 27)
Temperature (°C)	20.90	0.66	20.79	0.57
Salinity	32.09	0.95	35.13*	0.29
Ammonia (μmol N L ⁻¹)	2.68	0.30	2.17	0.29
Nitrate (μmol N L ⁻¹)	2.32	0.71	0.56*	0.08
Phosphate (μmol P L ⁻¹)	0.52	0.06	0.20*	0.02
Chlorophyll a (μg Chl <i>a</i> L ⁻¹)	4.05	0.47	1.68*	0.14
Respiration (μmol O ₂ L ⁻¹ d ⁻¹)	8.81	0.76	4.33*	0.48
NCP (μmol O ₂ L ⁻¹ d ⁻¹)	7.21	1.29	2.32*	0.61
GPP (μmol O ₂ L ⁻¹ d ⁻¹)	16.05	1.56	6.23*	0.60
P/R	1.91	0.14	2.05	0.27

2

3

Figure 1(on next page)

Temporal variability in seawater temperature and salinity.

Changes in surface seawater temperature and salinity in Matilda Bay are shown as blue line and symbols, and in Woodman Point as red line and symbols, along the study period.

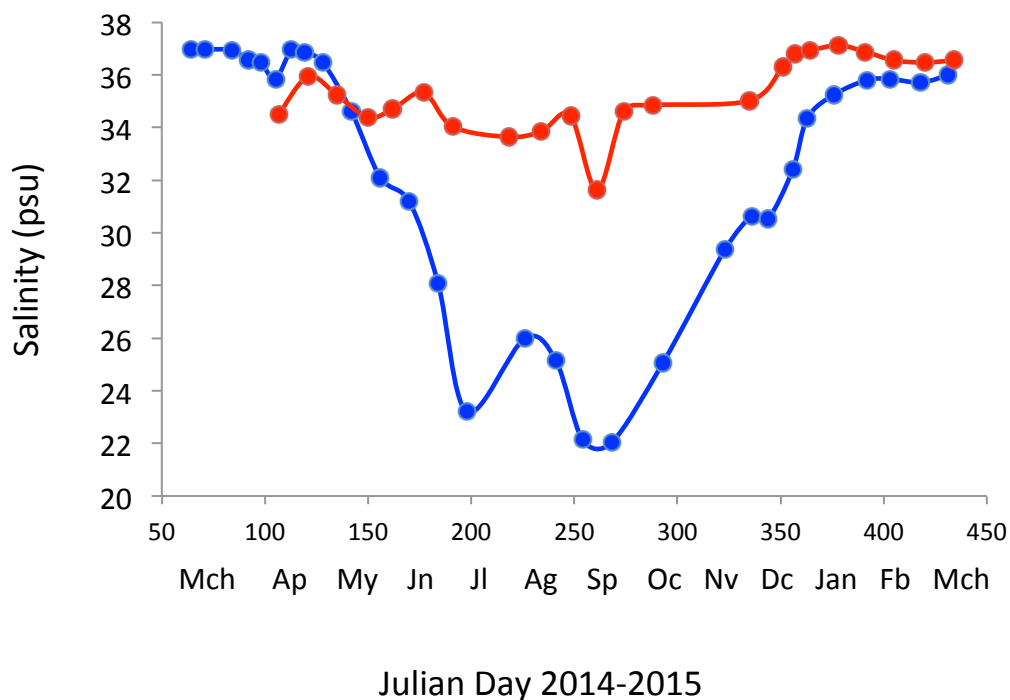
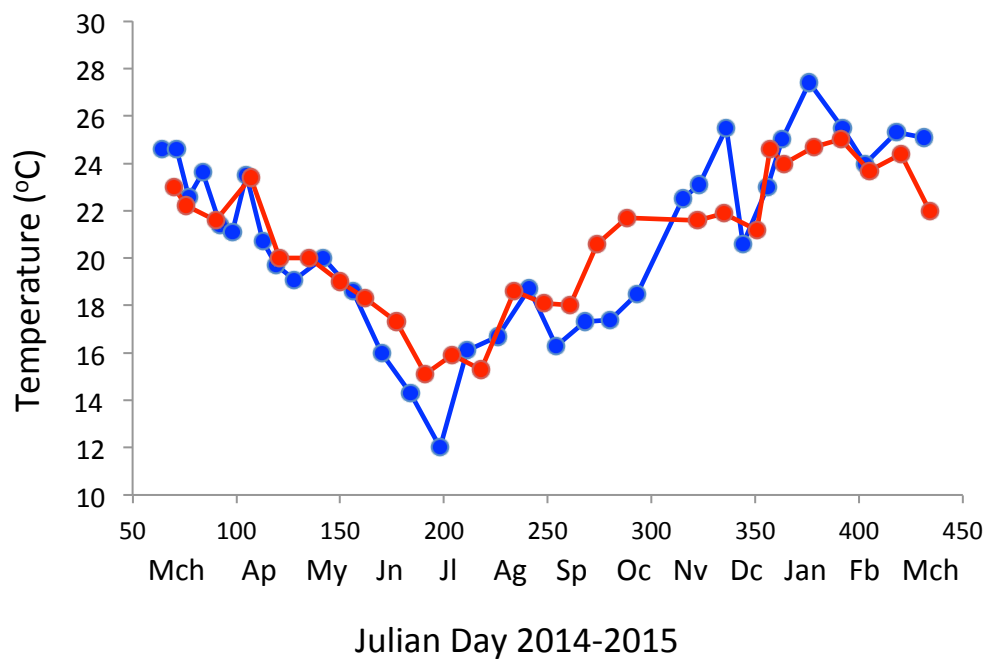


Figure 2 (on next page)

Nutrient variability

Changes in (a) nitrate, (b) ammonium, (c) phosphate and (d) chlorophyll *a* concentration in Matilda Bay (blue line and symbols) and Woodman Point (red line and symbols) along the study period.

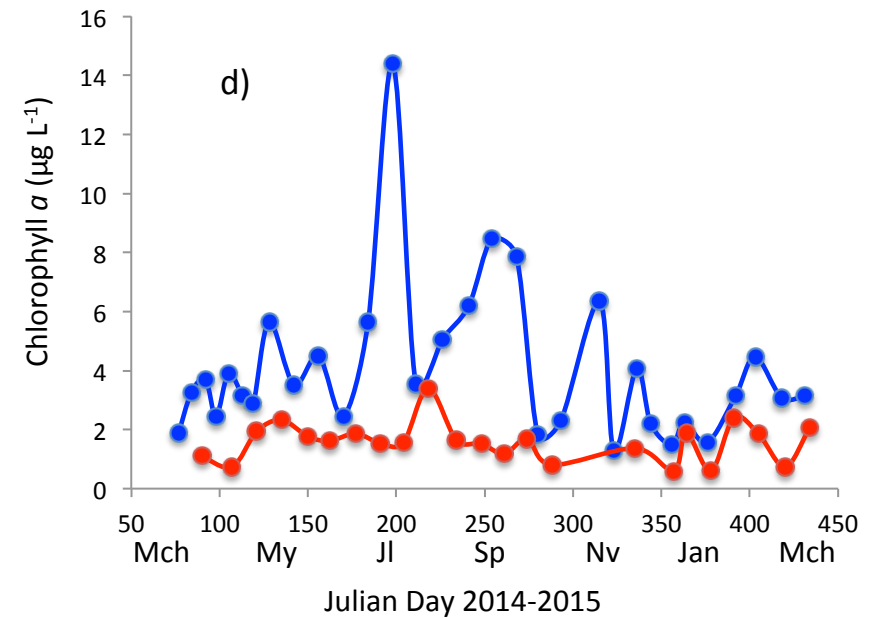
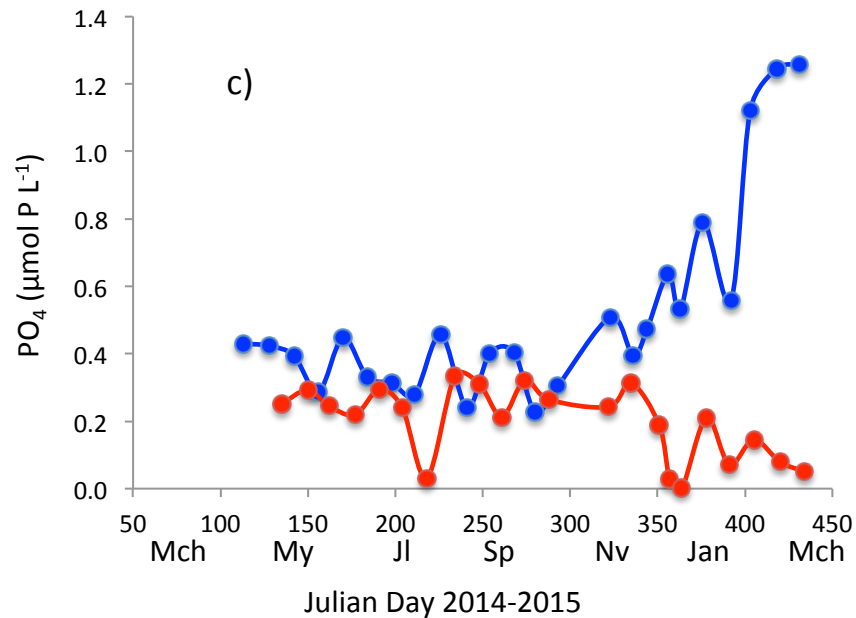
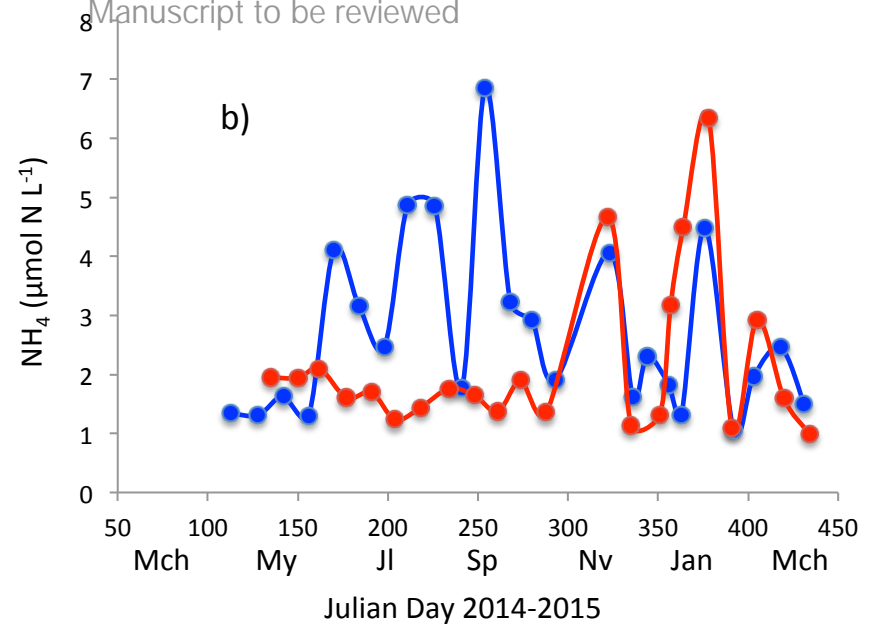
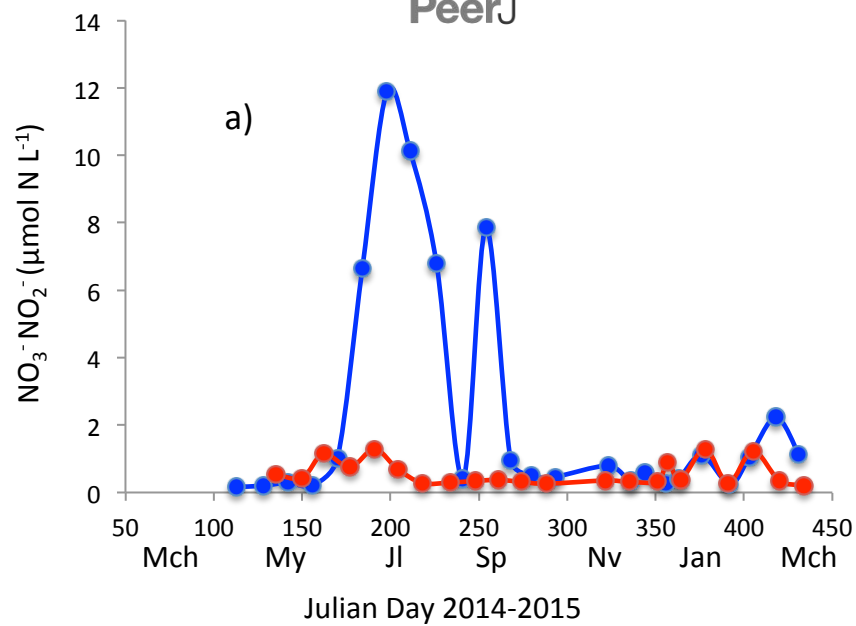
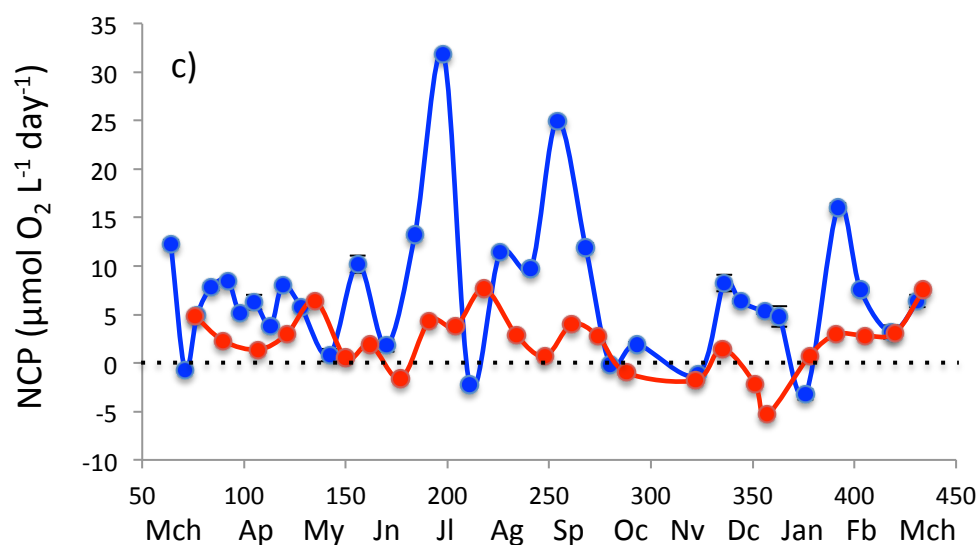
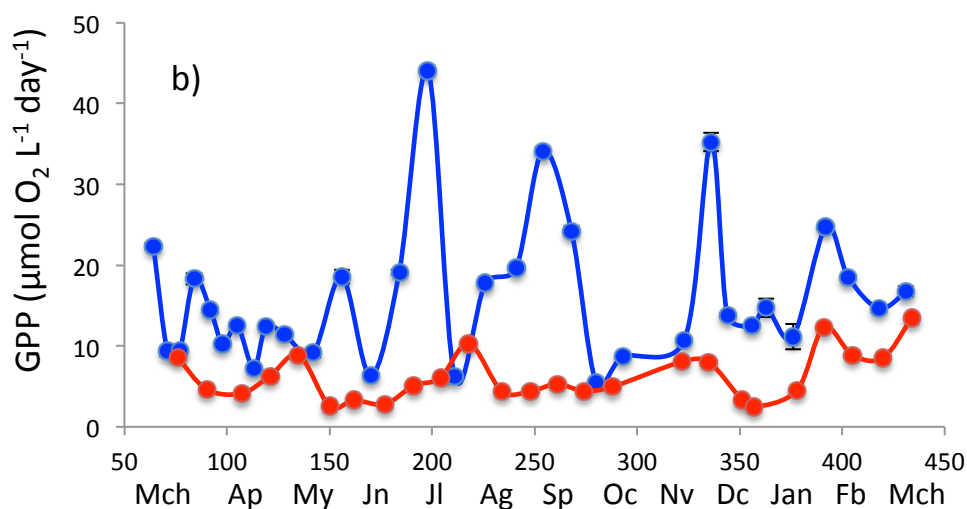
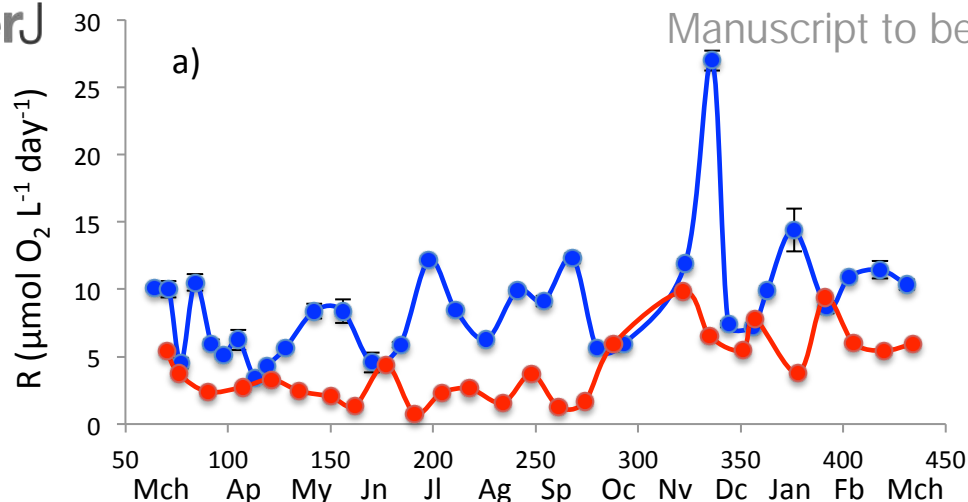


Figure 3(on next page)

Planktonic metabolism

Changes in (a) community respiration rate, (b) gross primary production, and (c) net community production in Matilda Bay (blue line and symbols) and Woodman Point (red line and symbols) along the study period.



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Figure 4(on next page)

The relationship between net community production and gross primary production.

The solid line shows the fitted regression equation: $NCP \text{ (mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}) = -2.65 + 0.65 (\pm 0.05) GPP \text{ (mmol O}_2 \text{ m}^{-3} \text{ d}^{-1})$ ($R^2 = 0.75$, $P < 0.0001$). Blue symbols and red symbols correspond to Matilda Bay and Woodman Point, respectively.

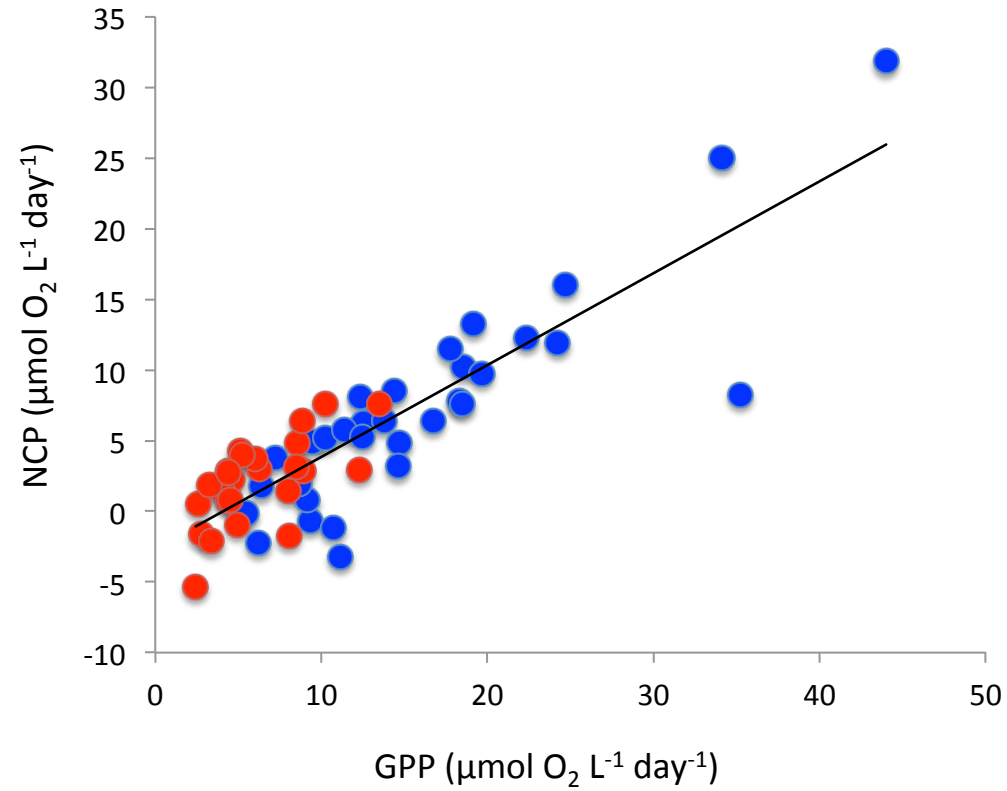


Figure 5(on next page)

Plankton metabolism and phytoplankton.

The relationship between (a) net community production, (b) gross primary production and (c) community respiration and chlorophyll *a* concentration. The solid lines shows the fitted regression equations: (a) NCP ($\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$) = $-1.54 + 2.29 (\pm 0.19) \text{ Chl } a (\mu\text{g Chl } a \text{ L}^{-1})$ ($R^2 = 0.73$, $P < 0.0001$); (b) GPP ($\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$) = $2.93 + 3.03 (\pm 0.05) \text{ Chl } a (\mu\text{g Chl } a \text{ L}^{-1})$ ($R^2 = 0.69$, $P < 0.0001$); and (c) R ($\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$) = $4.45 + 0.74 (\pm 0.24) \text{ Chl } a (\mu\text{g Chl } a \text{ L}^{-1})$ ($R^2 = 0.15$, $P = 0.0036$). Blue symbols and red symbols correspond to Matilda Bay and Woodman Point, respectively.

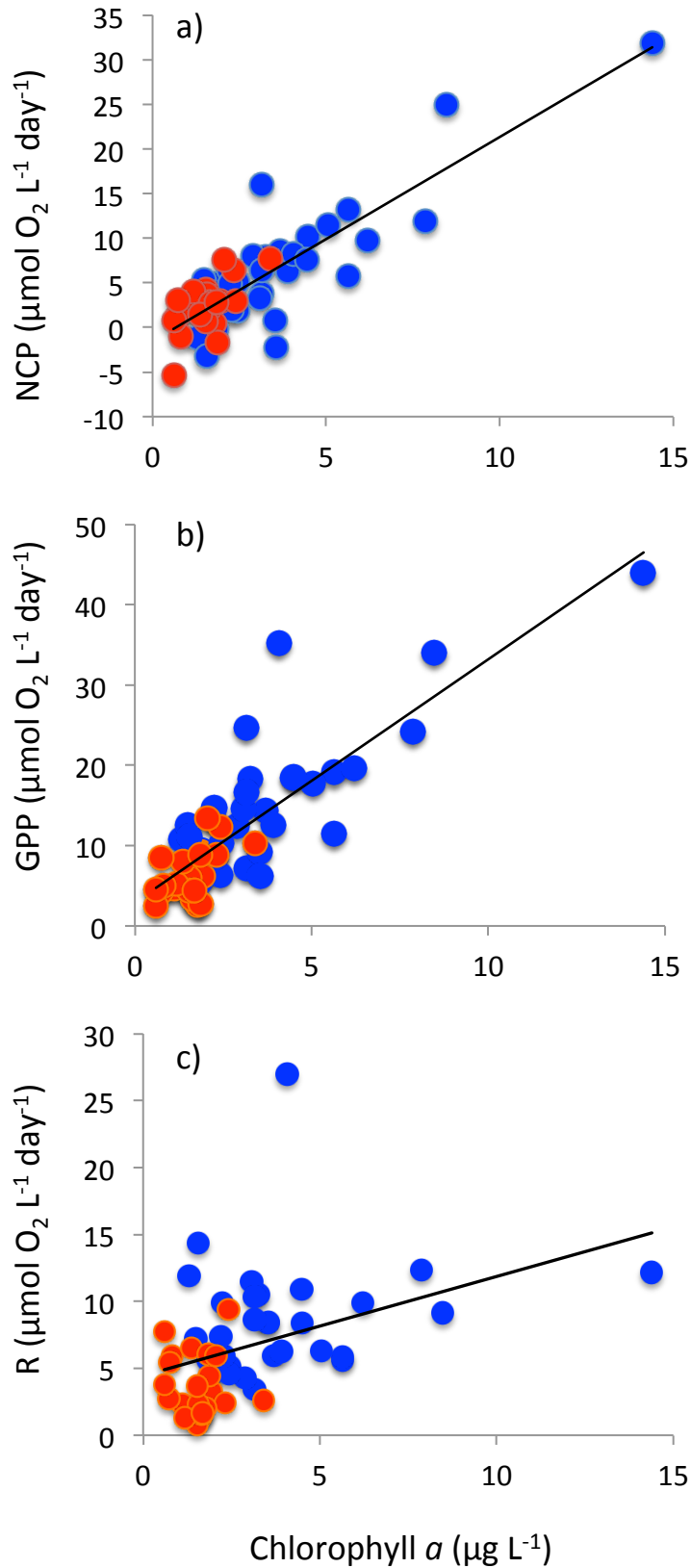


Figure 6 (on next page)

Thermal relationships.

Arrhenius plots showing the relationship between the natural log of (a) community respiration and (b) gross primary production standardized to chlorophyll *a*, and $1/kT$, where *k* is the Boltzmann's constant ($8.617734 \times 10^{-5} \text{ eV } ^\circ\text{K}^{-1}$) and *T* is the sea-surface water temperature ($^\circ\text{K}$) in Matilda Bay (blue symbols) and Woodman Point (red symbols). The solid lines show the fitted equations: $\ln R \text{ (mmol O}_2 \text{ mg m}^{-3} \text{ d}^{-1}) = 31.87 - 0.76 (\pm 0.21) 1/kT$ ($R^2 = 0.21$, $P = 0.0008$) and $\ln \text{GPP/Chl } a \text{ (mmol O}_2 \text{ mg Chl } a^{-1} \text{ d}^{-1}) = 28.8 - 0.69 (\pm 0.12) 1/kT$ ($R^2 = 0.41$, $P < 0.0001$).

