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Performance of Fast Repetition Rate fluorometry based estimates of primary productivity in coastal waters

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ABSTRACT

Capturing the variability of primary productivity in highly dynamic coastal ecosystems remains a major challenge to marine scientists. To test the suitability of Fast Repetition Rate fluorometry (FRRf) for rapid assessment of primary productivity in estuarine and coastal locations, we conducted a series of paired analyses estimating ^{14}C carbon fixation and primary productivity from electron transport rates with a Fast Repetition Rate fluorometer *MkII*, from waters on the Australian east coast. Samples were collected from two locations with contrasting optical properties and we compared the relative magnitude of photosynthetic traits, such as the maximum rate of photosynthesis (P_{max}), light utilisation efficiency (α) and minimum saturating irradiance (E_K) estimated using both methods. In the case of FRRf, we applied recent algorithm developments that enabled electron transport rates to be determined free from the need for assumed constants, as in most previous studies. Differences in the concentration and relative proportion of optically active substances at the two locations were evident in the contrasting attenuation of PAR (400–700 nm), blue (431 nm), green (531 nm) and red (669 nm) wavelengths. FRRF-derived estimates of photosynthetic parameters were positively correlated with independent estimates of ^{14}C carbon fixation (P_{max}: $n = 19$, $R^2 = 0.66$; α: $n = 21$, $R^2 = 0.77$; E_K: $n = 19$, $R^2 = 0.45$; all $p < 0.05$), however primary productivity was frequently underestimated by the FRRf method. Up to 81% of the variation in the relationship between FRRf and ^{14}C estimates was explained by the presence of pico-cyanobacteria and chlorophyll-*a* biomass, and the proportion of photoprotective pigments, that appeared to be linked to turbidity. We discuss the potential importance of cyanobacteria in influencing the underestimations of FRRf productivity and steps to overcome this potential limitation.

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1. Introduction

Primary production is a fundamental measure of an ecosystem's capacity to convert carbon dioxide into particulate organic carbon needed to fuel the foodweb, and thus underpins the regulation of trophic dynamics and carbon cycling (Falkowski, 2012). For decades, rates of marine primary productivity have been commonly measured using methods involving uptake of isotopically enriched inorganic carbon sources (Kaiblinger and Dokulil, 2006; Lawrenz et al., 2013a,b; Marra, 2002; Prieto et al., 2008; Steeman-Nielsen, 1952). Such methods have remained popular for a number of reasons, including their comparability with historic data. Additionally, the ^{14}C method is a sensitive technique which directly measures carbon assimilation that can be compared to standing stocks of organic carbon biomass. However, radioisotopes have become increasingly difficult to apply, largely due to greater health and safety regulations, and environmental restrictions limiting usage. This is of particular importance on small coastal vessels where the challenges of handling radioisotopes are greatest. This continues to present a major problem: the physical controls that underpin primary productivity in coastal waters are amongst some of the most dynamic over space and time, yet our understanding of how primary productivity varies in these waters remains largely unknown (Moore et al., 2006, 2006).

Active chlorophyll-*a* fluorometers have been designed to provide fast, non-invasive, accurate and accessible platforms to assess phytoplankton physiology and in turn determine photosynthetic rates (e.g. Kolber and Falkowski, 1993; Suggett et al., 2011) and hence overcome many of the limitations associated with radioisotope-based measurements. For oceanographic studies, Fast Repetition Rate-based fluorometers (FRRfs) have been most commonly used to quantify photosynthetic rates, specifically the rate of electron transport through photosystem II (PSII), ETR_{PSII} (Kolber et al., 1998; Oxborough et al., 2012). In principle, ETR_{PSII} measurements can be used to derive gross O_2 evolution or CO_2 uptake rates by applying a conversion factor that accounts for the various physiological pathways that effectively de-couple the ETR and O_2 evolution/CO_2 fixation from unity (Lawrenz et al., 2013a,b; Suggett et al., 2009a); these non-linear processes include alternate electron sinks such as nitrate reduction (see Suggett et al., 2011). The factor accounting for the conversion from ETR_{PSII} to CO_2 uptake has recently

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been termed the electron yield [or requirement] for carbon fixation, $\Phi_{E:C}$ (Kromkamp et al., 2008; Lawrenz et al., 2013a). Parallel measurements of ETR_{PSII} and O_2 production and/or CO_2 uptake can be correlated (Lawrenz et al., 2013a; Suggett et al., 2009a) suggesting that single values of $\Phi_{E:C}$ can be applied. Notwithstanding, $\Phi_{E:C}$ values appear to be highly dependent upon the phytoplankton taxa and/or specific physical conditions of the marine environment (Lawrenz et al., 2013a,b), and also potentially whether the phytoplankton are light-limited or light-saturated (Brading et al., 2013; Moore et al., 2006). Light-saturation requires that cells dissipate "excess" photochemical excitation pressure per unit of CO_2 fixed, therefore altering the conversion factor.

Methodological limitations associated with FRRF-based measures of ETR_{PSII}, as well as isotopically labelled carbon uptake, have been a major concern in reconciling the underlying factors that regulate $\Phi_{E:C}$ variability (Lawrenz et al., 2013a). Most notably, ETR_{PSII} is determined by applying FRRf-derived parameters that quantify the light absorption (σ_{PSII}) as well as the quantum yield of photochemistry for PSII to a biophysical model which describes the absolute electron transport rate (Kolber and Falkowski, 1993; Oxborough et al., 2012; see also Suggett et al., 2003). However, σ_{PSII} only describes the effective light absorption for PSII photochemistry relative to the number of active PSII "reaction centres" ([RCII]), i.e. those that can undergo photochemical charge separation, and thus [RCII] must be measured or assumed. Quantifying [RCII] is not straight-forward and only a handful of studies have simultaneously measured both [RCII] and ETR_{PSII} on natural samples (Moore et al., 2006; Oxborough et al., 2012; Suggett et al., 2006). Other studies have typically assumed a constant value weighted by a photoinactivation factor, but this approach is flawed (see Suggett et al., 2004, 2011). Recently, Oxborough et al. (2012) developed a method to empirically determine [RCII] directly from FRRf photophysiological parameters; however, this approach has not yet been applied to determine how [RCII] varies in nature and the associated effect upon ETR_{PSII}, and in turn $\Phi_{E:C}$.

Here we apply new developments in FRRf-based ETR_{PSII} algorithms (Oxborough et al., 2012) to explore variability of $\Phi_{E:C}$ in coastal phytoplankton communities. Despite past efforts to examine $\Phi_{E:C}$, few studies have applied them to coastal waters (Smyth et al., 2004; Raateoja et al., 2004; Melrose et al., 2006; Moore et al., 2006; see also Napoleon and Claquin (2012) using Pulse Amplitude Modulation (PAM) fluorometry) and it is still unclear to what extent phytoplankton composition and/or environment play in regulating $\Phi_{E:C}$ in such physically and bio-optically complex environments (Lawrenz et al., 2013a). Our study focused on two locations with distinct bio-optical properties, a nearshore coastal time-series monitoring station and an urbanised estuary, with clear differences in physicochemical properties and water column structure (Lee et al., 2011; Pritchard et al., 2001, 2003). We expected that the bio-optical properties would be markedly different between sites, with greater light attenuation in the turbid estuary due to the presence of dissolved materials and non-algal particles which attenuate and filter light and thus influence the wavelengths and intensity of light for photosynthesis. We also predicted a strong relationship between FRRf and ^{14}C estimates of primary production. Additionally we expected that physical factors such as high light intensity and nutrient availability may result in some variability in the relationship between FRRf and ^{14}C based estimates of carbon fixation, and applied multivariate analyses to identify key environmental and biological variables underlying the relationship between $\Phi_{E:C}$.

2. Methods

2.1. Water collection and measurement of environmental parameters

Phytoplankton assemblages were sampled from a historic time-series station at Port Hacking, NSW Australia (34°05′30″ S 151°15′30″ E) and in the Port Jackson Estuary (upper Parramatta River) (33°49′462″ S, 151°02′939″ E) through the lower estuary known as Sydney Harbour (33°51′001″ S, 151°12′086″ E) (Fig. 1). The coastal station (Port Hacking) is one of the longest biological time-series in the Southern Hemisphere (Thompson et al., 2011) and is located approximately 3 km offshore on the inner continental shelf. Here, water column stratification is seasonally dependent, where phytoplankton assemblages may be trapped in surface or sub-surface pycnoclines for days or weeks at a time (Pritchard et al., 2001). The Port Jackson estuary (approximately 30 km northwest of the coastal station) is a microtidal system, which is well mixed with semi-diurnal tides (Lee et al., 2011; Pritchard et al., 2003).

Maximum water depths at these sites were 100 m (Port Hacking, PH) and between 3 and 25 m (Sydney Harbour, SH). Water was collected at Port Hacking from the surface (3 m) and sub-surface fluorescence maximum (F_{max}; 35–45 m) during monthly intervals between May and August 2011, and in the Port Jackson estuary from 8 surface water (upper 1 m depth) stations in the same seasonal window during April and May 2011. Water was gently dispensed into 10 L polycarbonate bottles and stored in dim light (<10 μmol photons m^{-2} s^{-1}) at ambient temperature until returning to the laboratory, approximately 4 h after collection; these water samples were kept within 1–2 °C of ambient temperature during transport and laboratory sampling. A CTD sensor (SBE 911plus, Sea-bird Electronics, Washington, USA) provided vertical profiles of temperature, salinity, chlorophyll-*a* fluorescence and CDOM fluorescence at each sampling station.

Downwelled irradiance was measured in the water column with a hyperspectral spectroradiometer (Ramses, Trios, Rastede, Germany) according to Taylor et al. (2011) at 1 nm resolution between 344 and 750 nm. Photosynthetically active radiation (PAR 400–700 nm) was calculated using the following equation:

$$\mathrm{PAR} = \int_{400\,\mathrm{nm}}^{700\,\mathrm{nm}} E_d(z). \tag{1}$$

The diffuse attenuation coefficient K_d (m^{-1}) for PAR (i.e. the mean across 400–700 nm) and at specific wavelengths (443, 531 and 669 nm) was calculated by linear regression of the natural logarithm of light irradiances versus depth (Stramski et al., 2008; Kirk, 2011).

2.2. Phytoplankton pigments

Samples for photosynthetic and photoprotective pigment determination were filtered onto 25 mm glass fibre filters (Whatman GF/F,

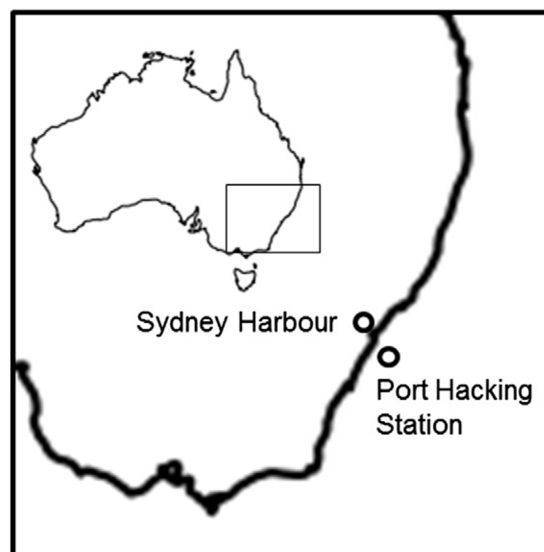

Fig. 1. Sampling locations, including the Port Hacking coastal time-series station and the Sydney Harbour (Port Jackson estuary) on the east coast of Australia.

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