



Phytoplankton absorption predicts patterns in primary productivity in Australian coastal shelf waters

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ABSTRACT

The phytoplankton absorption coefficient (α_{PHY}) has been suggested as a suitable alternate first order predictor of net primary productivity (NPP). We compiled a dataset of surface bio-optical properties and phytoplankton NPP measurements in coastal waters around Australia to examine the utility of an *in-situ* absorption model to estimate NPP. The magnitude of surface NPP ($0.20\text{--}19.3 \text{ mmol C m}^{-3} \text{ d}^{-1}$) across sites was largely driven by phytoplankton biomass, with higher rates being attributed to the microplankton ($>20 \mu\text{m}$) size class. The phytoplankton absorption coefficient α_{PHY} for PAR (photosynthetically active radiation; α_{PHY}) ranged from 0.003 to 0.073 m^{-1} , influenced by changes in phytoplankton community composition, physiology and environmental conditions. The α_{PHY} coefficient also reflected changes in NPP and the absorption model-derived NPP could explain 73% of the variability in measured surface NPP ($n = 41$; RMSE = 2.49). The absorption model was applied to two contrasting coastal locations to examine NPP dynamics: a high chlorophyll-high variation (HCHV; Port Hacking National Reference Station) and moderate chlorophyll-low variation (MCLV; Yongala National Reference Station) location in eastern Australia using the GLOP-DC satellite α_{PHY} product. Mean daily NPP rates between 2003 and 2015 were higher at the HCHV site ($1.71 \pm 0.03 \text{ mmol C m}^{-3} \text{ d}^{-1}$) with the annual maximum NPP occurring during the austral winter. In contrast, the MCLV site annual NPP peak occurred during the austral wet season and had lower mean daily NPP ($1.43 \pm 0.03 \text{ mmol C m}^{-3} \text{ d}^{-1}$) across the time-series. An absorption-based model to estimate NPP is a promising approach for exploring the spatio-temporal dynamics in phytoplankton NPP around the Australian continental shelf.

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1. Introduction

Estimates of net primary productivity (NPP, photosynthetically produced organic carbon after respiratory losses) from marine phytoplankton provide information about the rate of carbon

production for the marine food web (Cloern et al., 2014; Finkel, 2014; Westberry and Behrenfeld, 2014). Coastal shelf waters generate 29% of the world's marine NPP within an area of just 11% of the ocean's surface area (Finkel, 2014; Gazeau et al., 2004; Pauly and Christensen, 1995; Wollast, 1998). In the global context, average NPP in Australian coastal waters is low (Chavez et al., 2011; Cloern et al., 2014). However, our understanding of the temporal and spatial dynamics in NPP and its absolute magnitude is limited to a small number of studies involving traditional measurements made on board ships and in the laboratory (Everett and Doblin, 2015; Furnas and Carpenter, 2016 and references therein).

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Satellites provide the opportunity to fill the vast temporal and spatial gaps in conventional measurements of phytoplankton NPP in Australian waters due to their near synoptic capture of ocean colour data (Hayes et al., 2005). However, algorithms are required to transform maps of ocean colour, the result of the absorption and scattering of light by water, phytoplankton and non-phytoplankton material, to a description of phytoplankton physiology (Barnes et al., 2014; Bouman et al., 2000) and an estimate of NPP in ocean ecosystems (Sathyendranath et al., 2009).

Empirical relationships or mechanistic models are used to link phytoplankton biological rates (such as growth rate and NPP) and photosynthetic parameters (carbon-to-chlorophyll-*a* ratio) with “more-easily” measured satellite products such as sea-surface temperature, irradiance or chlorophyll-*a* (via the assimilation number). These physical and biological proxies have proven to be highly variable in their efficacy for coastal waters (Everett and Doblin, 2015; Mélin and Vantrepotte, 2015). This is largely due to the multivariate nature of environmental and seasonal influences on phytoplankton physiology, that cannot always be summarised to a constant value needed for empirical relationships (Behrenfeld et al., 2016). In addition, the satellite retrieval of the commonly used biological parameter, chlorophyll-*a* (Chl-*a*), using model inversion of satellite remote sensing reflectance (R_{rs}) is highly unreliable in coastal waters (Tilstone et al., 2011). The inversion method is complicated due to the interference of other optically active substances (suspended organic and inorganic matter, and coloured dissolved organic matter) in the water-leaving reflectance (Aurin and Dierssen, 2012; Odermatt et al., 2012) and variable atmospheric aerosols contributing to the top of the atmosphere reflectance (Wang et al., 2007). Uncertainties with respect to chlorophyll-*a* retrievals in coastal waters globally are a significant problem where the concentration of optically active constituents, and hence inherent optical properties (IOPs) and specific inherent optical properties (SIOPs; normalised to constituent concentration), are highly variable, both temporally and spatially (Brando et al., 2012; Cherukuru et al., 2014; Qin et al., 2007). In contrast, the phytoplankton absorption coefficient (α_{PHY}) can be more reliably inverted from R_{rs} using deconvolutions of total absorption (α_{TOT}) using semi-analytical algorithms (Barker et al., 2007; Moore et al., 2009; Sauer et al., 2012). The Generalised IOP model is one such algorithm which allows a high percentage (>80%) of valid retrievals of α_{PHY} in waters of all trophic levels and across all seasons (Werdell et al., 2013).

Replacement of the chlorophyll-*a* parameter with the phytoplankton absorption coefficient (α_{PHY}) has been proposed as a viable alternative for estimating NPP in oceanic and coastal waters (Barker et al., 2007; Barnes et al., 2014; Marra et al., 2007; Silsbe et al., 2016). This is because the concentration of pigments within a cell changes in predictable ways with the composition and abundance of phytoplankton and environmental conditions (light, temperature, nutrients etc; Bouman et al., 2000; Marra et al., 2007; Aiken et al., 2008). Furthermore, variation in the α_{PHY} coefficient at different wavelengths (e.g. 440 nm vs 676 nm) or chlorophyll-specific phytoplankton absorption coefficient ($\alpha^*_{PHY}(\lambda)$) are due to changes in the physiology or composition of the phytoplankton community. Such changes include taxonomic or pigment composition, cell size, pigment packaging or intracellular pigment concentration (Aiken et al., 2008; Bouman et al., 2000; Bricaud et al., 2004). Although phytoplankton absorption is a relatively inexpensive and simple parameter to measure in marine sampling programs (Sathyendranath et al., 2009), there has been limited application of this approach because of the lack of absorption data coupled with primary productivity measurements (Barnes et al., 2014; Everett and Doblin, 2015; Marra et al., 2007).

Absorption based models of primary productivity use the

phytoplankton absorption coefficient ($\alpha_{PHY}(\lambda)$) as a first order predictor of NPP or as a light capture term to quantify the absorption of photosynthetically active radiation (400–700 nm; PAR or E) which is then utilised to fix inorganic carbon. The maximum efficiency of photon capture to carbon conversion (ϕ_m) varies with nutrient concentration and PAR (sometimes parameterised as ϕ_E ; Kiefer and Mitchell, 1983). Generally, the absorption coefficient is measured directly using an *in-situ* absorption meter, in the laboratory using a filter pad technique (Lee et al., 1996; Oubelkheir et al., 2006; Tassan and Ferrari, 1995) or indirectly via inversion of in-water and/or above-water radiance (Qin et al., 2007). The parameters describing the partitioning and utilisation of light by the photosynthetic apparatus for photochemistry and carbon fixation (e.g. ϕ_m and ϕ_E) are often estimated from laboratory based studies with algal monocultures (Marra et al., 2007, 2003). Despite the limited data from mixed natural assemblages, absorption-based NPP models have reliably estimated NPP with low error, using *in-situ* data in the Equatorial Pacific, Southern Ocean, Western English Channel, California coast, North Atlantic, and North Pacific (Barnes et al., 2014; Ma et al., 2014; Marra et al., 2007). Absorption-based models have also been applied to satellite inverted α_{PHY} coefficient to study the dynamics of NPP in the Southern Ocean and global eastern boundary upwelling regions (Hirata et al., 2009; Shang et al., 2010) and provide global estimates of annual NPP (Ma et al., 2014).

To assess the utility of an absorption-based approach to estimate surface NPP in Australian coastal waters, this study compiled bio-optical and NPP data from tropical to temperate Australian locations. Using this unique dataset, we tested the hypothesis that light absorption by phytoplankton is a strong first-order predictor of surface phytoplankton NPP. The absorption-based model was then used to examine NPP dynamics in two contrasting regions on the East Australian coast – one in an area with low chlorophyll-*a* variation and another with relatively high chlorophyll-*a* variation (Jones et al., 2015).

2. Methods

2.1. Sampling sites

Coastal waters around Australia were sampled during four oceanographic research voyages (V1–V4) and at a coastal time-series station (PHNRS) between 2010 and 2014. Sampling locations included the north-west Kimberley region (V1), eastern Australia (V2), northern Australia (V3), the Great Barrier Reef inner-reef (GBR; V4) and in south-eastern Australia at the Port Hacking National Reference Station (PHNRS; see Fig. 1 and Table 1 for station locations). Water was collected at depths of up to 5 m (within the first optical depth) for surface measures of NPP, physico-chemical, biogeochemical, and bio-optical parameters (Table 1).

2.2. *In-situ* sampling

2.2.1. Net primary productivity

Samples (0.5–4.0 L) of surface seawater were incubated at *in-situ* temperature and light to estimate surface NPP. Stations sampled during V2, V3 and PHNRS were incubated for 24 h and stations sampled during V1 and V4 were incubated during the light period (1–6 h; Table 1). Water was dispensed into 0.5–4.0 L polycarbonate bottles and inoculated with $100 \mu\text{mol L}^{-1} \text{NaH}^{13}\text{CO}_3$ (V3 and V4) to achieve <5% enrichment (Burford et al., 2011) or $\text{NaH}^{14}\text{CO}_3$ (V1, V2 and PHNRS) to achieve 20 μCi activity (Knap et al., 1996). After incubation, samples were filtered onto 25 mm glass fibre filters (Whatman GF/F 0.7 μm pore size; pre-combusted for ^{13}C assays).

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