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Patterns and controls of reef-scale production of dissolved organic carbon by giant kelp *Macrocystis pyrifera*

Daniel C. Reed,*[1] Craig A. Carlson,[1,2] Elisa R. Halewood,[1] J. Clinton Nelson,[1] Shannon L. Harrer,[1] Andrew Rassweiler,[1] Robert J. Miller[1]

[1]Marine Science Institute, University of California, Santa Barbara, California
[2]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California

Abstract

We investigated the patterns and controls of dissolved organic carbon (DOC) production by the giant kelp (*Macrocystis pyrifera*) using data from short-term in situ incubations of entire blades and portions of stipes. These data were incorporated into an empirical model of reef-scale net primary production (NPP) at Mohawk Reef in southern California, U.S.A. for an 8-yr period. Rates of DOC release of incubated blades varied unpredictably with time of year, but were significantly related to the irradiance at the sea surface during the incubations. The growth stage, C/N ratio, and epiphyte load of the blades and the temperature of the ocean during the incubations had no discernable effect on rates of DOC release. Blades produced on average 2–3 times more DOC than stipes, and stipes and blades produced on average 30% and 80% more DOC respectively during the day compared to the night. Modeled DOC NPP at the reef scale was on average highest in summer and spring ($\sim$0.5 g C m^{-2} d^{-1}) and lowest in winter and autumn ($\sim$0.31 g C m^{-2} d^{-1}), but it varied greatly among years for any given season as large oscillations in standing biomass led to corresponding fluctuations in reef-scale DOC NPP. The fraction of NPP released as DOC was highly variable when examined at the monthly time scale, but became much more stable at seasonal and annual time scales averaging 14% of total NPP.

Dissolved organic matter (DOM) in the ocean represents one of the largest exchangeable reservoirs of reduced carbon on Earth and its production and consumption is critically important to global carbon export and storage (Carlson and Hansell 2015). Marine DOM is a byproduct of primary production and food web interactions, and its decomposition is predominantly governed by the metabolism of heterotrophic bacterioplankton (Azam et al. 1983). The efficiency with which bacterioplankton utilize DOM determines whether it is repackaged as particles (bacterioplankton cells) and passed to higher trophic levels through a trophic pathway (Azam et al. 1983), remineralized to its dissolved inorganic constituents (Ducklow et al. 1986), or transformed into a recalcitrant state (Ogawa et al. 2001; Jiao et al. 2010) and made available for horizontal or vertical export (Carlson et al. 1994; Hansell et al. 2009). These pathways are quite different from those followed by particulate organic material (POM), and the degree to which primary production is partitioned into dissolved vs. particulate phases is a key determinant of biogeochemical cycling in marine ecosystems.

The vast majority of research examining the partitioning of primary production into dissolved and particulate phases has involved pelagic phytoplankton (Nagata 2000; Carlson and Hansell 2015). Much less is known about the dynamics of DOC production in shallow coastal waters where sources of DOC are more heterogeneous and include benthic macrophytes, freshwater and terrestrial autotrophs, and marine phytoplankton (Cauwet 2002; Wada and Hama 2013). Particularly noteworthy in this regard are marine habitats dominated by macroalgae and seagrasses, which are known to release a considerable amount of their production as DOC (Khailov and Burlakova 1969; Sieburth 1969; Lucas et al. 1980; Carlson and Carlson 1984; Wada et al. 2007).

Benthic assemblages of marine macroalgae and seagrasses may be a net source of DOC that helps fuel the microbial foodweb in the nearshore water column (Barrón et al. 2004; Wada and Hama 2013). For example, Halewood et al. (2012) found that bacterial carbon demand (BCD) in shallow coastal waters immediately offshore of a giant kelp (*Macrocystis pyrifera*) forest in southern California exceeded phytoplankton productivity during several periods throughout the year, indicating that sources of DOC other than phytoplankton production were used to support BCD. They hypothesized that *Macrocystis* may be an important source of DOC used to

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*Correspondence: dan.reed@lifesci.ucsb.edu

support BCD in many California near shore environments. Similar conclusions regarding the significance of kelp-derived DOC to microbial production have been reached for coastal waters in other regions (Newell et al. 1980; Newell and Lucas 1981; Wada et al. 2008; Wada and Hama 2013).

Kelp forests are among the most productive of all marine macrophyte communities (Reed and Brzezinski 2009), with reported estimates of net primary production (NPP) as high as 5662 g C m^{-2} yr^{-1} (Krumhansl and Scheibling 2012). In fact, kelp productivity may be substantially higher than many estimates because most calculations of kelp NPP are derived from measures of standing biomass and growth that do not account for production released as DOC (reviewed in Mann 2000). Studies that have measured production of DOC by kelps in situ using short-term incubations of individual blades or entire plants have found it to be highly variable, averaging between 13% and 62% of total NPP depending on species, time of year, growth stage, temperature, nutrients and light (Hatcher et al. 1977; Johnson et al. 1977; Abdullah and Fredriksen 2004; Wada et al. 2007; Wada and Hama 2013; however see Fankboner and de Burgh 1977). The extent to which this variability represents differences among species, environmental conditions or methodologies remains unclear.

The few attempts to estimate the contribution of kelp to the coastal DOC pool have involved scaling up mass-specific estimates of DOC release rates from short-term incubations to obtain reef-area estimates of DOC NPP (i.e., mass of kelp DOC produced per unit area of reef per unit time). This has been done by multiplying rates of DOC release (standardized per unit mass of kelp tissue) by static estimates of kelp standing biomass (standardized per unit area of reef) derived from a small number of samples covering small areas of reef (Abdullah and Fredriksen 2004), or by dividing measured rates of DOC release by previously published estimates of NPP (Wada et al. 2007). Such approaches assume that DOC release, standing biomass and NPP are relatively constant across time and space and are not appropriate for systems where these factors fluctuate widely. For example they would be difficult to apply to the giant kelp *M. pyrifera* (hereafter referred to as *Macrocystis*), a prominent surface canopy forming species whose biomass and NPP vary greatly in space and time in response to episodic wave disturbance, grazing, nutrient stress, and progressive senescence of fronds and blades (Reed et al. 2008; Parnell et al. 2010; Cavanaugh et al. 2013, Rodriguez et al. 2013). Consequently, understanding the dynamics of DOC production by *M. pyrifera* and the environmental factors that influence it requires dynamic estimates of POC and DOC production at the reef scale that account for its high spatial and temporal variability in standing biomass.

Here we examined the dynamics of DOC production by *Macrocystis* at the reef scale over an 8-yr period. We accomplished this using short-term in situ incubation experiments to determine the extent to which DOC release by *Macrocystis* varies as a function of tissue type, blade growth stage, epiphyte load, blade C : N ratio, sea surface irradiance, sea surface temperature, time of day, and day of year. We then incorporated the findings from these experiments into an existing reef-scale model of giant kelp NPP that previously did not include production released as DOM (Rassweiler et al. 2008). We applied this updated model to an 8-yr time-series of *Macrocystis* standing biomass, particulate losses (i.e., whole plants and individual fronds) and water column irradiance to examine temporal dynamics in the partitioning of giant kelp NPP into dissolved and particulate phases and the extent to which it varied as a function of total NPP and the time period considered.

Methods

In situ measurements of DOC release

We estimated rates of DOC release by *Macrocystis* using short-term (2–4 h) in situ incubations of entire blades and portions of stipes in the kelp forest at Mohawk Reef near Santa Barbara, California, U.S.A. (34° 23.660′ N, 119° 43.800′ W). Incubations of blades were conducted within 2 m of the sea surface at midday on eight dates between October 2007 and August 2011 to investigate the effects of blade growth stage, nutrient status (as indicated by C : N ratio determined using an Exeter Analytical CE-440 CHN/O/S elemental analyzer), epiphyte load, sea surface irradiance, and sea surface temperature on rates of DOC release from intact blades. The DOC produced by giant kelp may include active exudation as well as passive diffusion associated with tissue degradation and senescence. Because our in situ measurements did not distinguish between these processes we refer to them collectively as DOC release.

Blades were identified as growing (young blades located < 2 m from the tip of a growing frond), mature (older and larger robust blades located > 2 m from the tip of a growing frond), and senescent (eroded blades with $< 50\%$ of their initial blade margin intact). For each sampling date incubations were performed on 10–15 blades distributed across the three growth stages of blades with each blade being selected from a distinct kelp individual. Giant kelp blades in the Santa Barbara region are commonly encrusted with the bryozoan *Membranipora serrilamella* (Arkema 2009). A visual estimate of the percent cover of *M. serrilamella* on each blade was recorded and used to evaluate whether the amount of DOC produced by blades was related to epiphyte load, as previously suggested by Fankboner and de Burgh (1977). To evaluate the effects of tissue type (blade vs. stipe) and time of day (day vs. night) on DOC release by *Macrocystis*, we measured the amount of DOC released from 15 mature blades and portions of 15 intact stipes at Mohawk Reef during midday and near midnight in August 2011. During the entire study, photosynthetically active radiation

(PAR) at the sea surface was recorded once per min using an integrated spherical PAR sensor and data logger (MKV-L; Alec Electronics, Kobe, Japan) mounted above the sea surface on a vertical spar buoy moored in the kelp forest. Similarly, temperature was recorded every 10 min using automated loggers (Stowaway Onset tidbits; Onset Computer, Bourne, Massachusetts, U.S.A.) mounted to the spar buoy 1–2 m below the sea surface. Because temperature and nutrients are closely related in the study region (McPhee-Shaw et al. 2007), temperature also provided an estimate of the concentrations of nutrients in ambient seawater during the incubations. Irradiance (in units of μmol photons m^{-2} s^{-1}) and temperature (degrees Celsius) were averaged over each incubation to obtain mean values for each variable.

Incubations of intact blades were performed in clear plastic bags. The bags were 11 cm × 66 cm and constructed of 6 mm polyethylene. A two-piece threaded nylon barbed fitting was inserted through each bag as a sampling port with Teflon coated silicone septa on each side of the polyethylene to ensure a gas and water tight seal. Divers gently slipped a bag over each blade and sealed the bag at the base of the pneumatocyst where it attaches to the stipe using a nylon cable tie (Fig. 1a). Using this technique the volume of the water sealed within each bag varied among blades (generally between 0.3 L and 1.2 L). A second type of bag was constructed to sample DOC produced by stipes. For this we adapted a 3.8 L Ziploc polyethylene bag cut open on the two opposing sides (perpendicular to the zippered opening) with a built in sampling port as described above (Fig. 1b). An opened bag was zip locked around a portion of stipe extending between two blades and each end of the bag was then sealed around the stipe using a nylon cable-tie. Tests in the laboratory and field using rhodamine dye showed no detectable leakage from either type of bag. Samples were drawn with 60 mL polypropylene/polyethylene syringe (no black rubber plunger tip) using luer-lock syringe adaptors fitted to silicone tubing that was attached to the sampling ports (Fig. 1). All bags, sampling ports, tubing, and syringes were bathed in a 5% HCl solution, flushed with Nanopure water and dried prior to use in the field to minimize the leaching of organic material from bags during incubations.

Two replicate 60 mL syringe samples were extracted from each bag at the beginning and end of the incubation and the time of sample collection was recorded. Upon collection the syringes (with sample) were put into Ziploc bags, placed on ice in an insulated cooler and transported to the laboratory. The volume of water and mass of kelp tissue within each bag was determined at the end of the incubation and used to estimate the mass of DOC produced per dry mass of kelp tissue. Kelp tissue was returned to the laboratory where it was weighed wet then dried at 60°C for 3 d to determine dry mass.

Upon return to the laboratory the contents of each syringe were gently filtered through a GF/F filter (0.7 μm; pre-combusted at 450°C for a minimum of 4 h) housed in an acid-cleaned polycarbonate cartridge, collected into 40 mL combusted EPA vials, and stored frozen (−20°C) until analyzed.

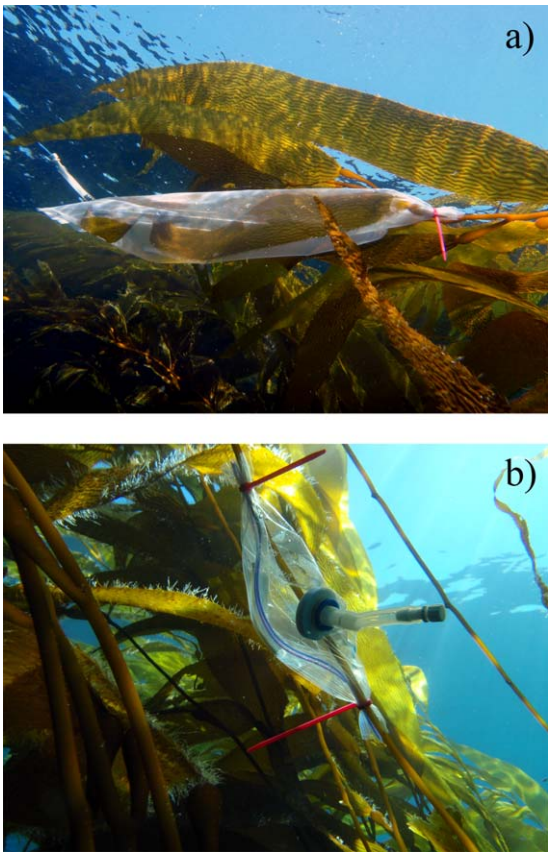

Fig. 1. Photographs showing the polyethene bags with sampling ports used to estimate DOC released by giant kelp in in situ incubations of (a) entire blades and (b) portions of stipes.

DOC analyses

DOC concentrations were determined via high temperature combustion using a Shimadzu TOC-V. The operating conditions of the Shimadzu TOC-V were slightly modified from the manufacturer's model system according to Carlson et al. (2010). CO_2 free carrier gas was produced with a Whatman gas generator. Sample was drawn into a 5 mL injection syringe, acidified with 2M HCL (1.5%) and sparged for 1.5 min with CO_2 free gas. Three to five replicate 100 μL aliquots of sample were injected into the combustion tube heated to 680°C. The resulting gas stream was passed through several water and halide traps, the CO_2 in the carrier gas was analyzed with a non-dispersive infrared detector and the resulting peak area was integrated with Shimadzu chromatographic software. Extensive conditioning of the combustion tube with repeated injections of low carbon water (LCW) and deep seawater was done to minimize the machine blanks. After conditioning, the system blank was assessed

with UV oxidized low carbon water. The system response was standardized daily with a four-point calibration curve of potassium hydrogen phthalate solution in LCW. All samples were systematically referenced against low carbon deep ocean reference water (>2600 m) and surface sea water every six to eight analyses (Carlson et al. 2010). The standard deviation of the deep and surface references analyzed throughout a run generally had a coefficient of variation ranging between 1% and 3% over the three to seven independent analyses (number of references depended on the number of samples in the run). Daily reference waters were calibrated with DOC consensus reference water provided by D. Hansell, University of Miami (Hansell 2005). The DOC concentrations were multiplied by the volume of each incubation bag to determine the grams of DOC produced during each incubation.

DOC release normalized by the mass of kelp tissue (in units of mg C (g dry mass)$^{-1}$ h^{-1}) was calculated as:

$$\text{DOC release} = \frac{(C_f - C_0)V}{TM}$$

where C_f is the final concentration of DOC (in units of mg C L^{-1}) measured as the mean of two syringe samples taken at the end of the incubation, C_0 is the initial concentration of DOC (in units of mg C L^{-1}) measured as the mean of two syringe samples taken at the beginning of the incubation, V is the volume (L) of water measured at the end of the incubation + volume (L) of the two syringe samples taken at the end of the incubation, T is incubation time (h) and M is dry mass (g) of kelp tissue used in the incubations.

Statistical analyses

Data collected from incubations performed on all sampling dates were used in an analysis of covariance (ANCOVA) to examine the effects of blade stage (growing, mature, senescent), sampling date, epiphyte load (percent of blade covered by *Membranipora*), and blade C : N ratio on rates of DOC release by *Macrocystis* blades. In this analysis blade stage was considered a fixed categorical factor, sampling date a random categorical factor, and epiphyte load and blade C : N ratio were used as covariates. A second ANCOVA was used to examine the roles of sea surface irradiance and sea surface temperature in accounting for the variation in the mean rate of DOC released by blades observed among sampling dates. In this analysis the response variable was the mean rate of DOC release averaged across all blades of a given stage on a given date. Blade stage was considered a fixed categorical factor and sea surface irradiance and sea surface temperature were used as covariates. Because the significance levels of all interactions involving the covariates were greater than 0.1 in both analyses they were not included in the final reduced models (Quinn and Keough 2002). Finally, the effects of time of day (midday vs. night) and type of tissue (blade vs. stipe) were evaluated with a two-way fixed factor analysis of variance (ANOVA) using data collected from incubations performed during August 2011. Data for all analyses were normalized by square root transformation, linear relationships between explanatory and predicted variables were verified via residual analysis, and multi-collinearity of covariates was low as determined by condition indices and tolerance values. There was a modest increase in the variance of DOC release with PAR, but the variance inflation factor (1.32) was still well below the commonly used cutoff values of 5 or 10 (Craney and Surles 2002). The variances of the class variables used in the ANCOVAs were heterogenous and transformations failed to homogenize them. This leads to excessive Type I errors, which are acceptable when results are non-significant (Underwood 1997).

Results

In situ measurements of DOC release

The effects of growth stage on the rate of DOC released by blades during the field incubations varied unpredictably among sampling dates (Fig. 2a, blade stage × date interaction in Table 1a). Differences among the three growth stages tended to be small when rates of DOC release were relatively low (e.g., November 2007, August 2011) and large and inconsistent when rates of DOC release were relatively high (e.g., May, August, and October 2008). The percent cover of the encrusting bryozoan *M. serrilamella* on incubated blades ranged from 0% to 95%; however, it did not explain any significant variation in the observed rates of DOC release, nor did the C : N ratio of the incubated blades, which ranged from 6 to 37 (Table 1a; Supporting Information Appendix A). The most significant factor contributing to the high temporal variation observed in rates of DOC released by *Macrocystis* blades was sea surface irradiance, which explained 13% of the variation observed among all incubated blades (Fig. 2b; Table 1b). By contrast, sea surface temperature and blade stage did not explain any significant variation in rates of DOC release, nor did interactions between blades stage and the two covariates (Table 1b).

DOC release was significantly affected by tissue type and time of day (Fig. 3). Blades produced on average 2–3 times more DOC than stipes ($F_{1,30} = 22.54$, $p < 0.001$) and stipes and blades produced on average 30% and 80% more DOC respectively during the day compared to the night ($F_{1,30} = 5.64$, $p = 0.024$). The effects of tissue type on DOC release did not vary significantly between day and night ($F_{1,30} = 2.78$, $p = 0.106$ for tissue type × time of day interaction).

Modeling the dynamics of DOC production at the reef scale

Model structure

We developed a reef scale model of DOC NPP to evaluate the dynamics of DOC production by *Macrocystis* per unit area of the sea floor at Mohawk Reef. This model works by integrating rates of DOC release per unit dry mass measured

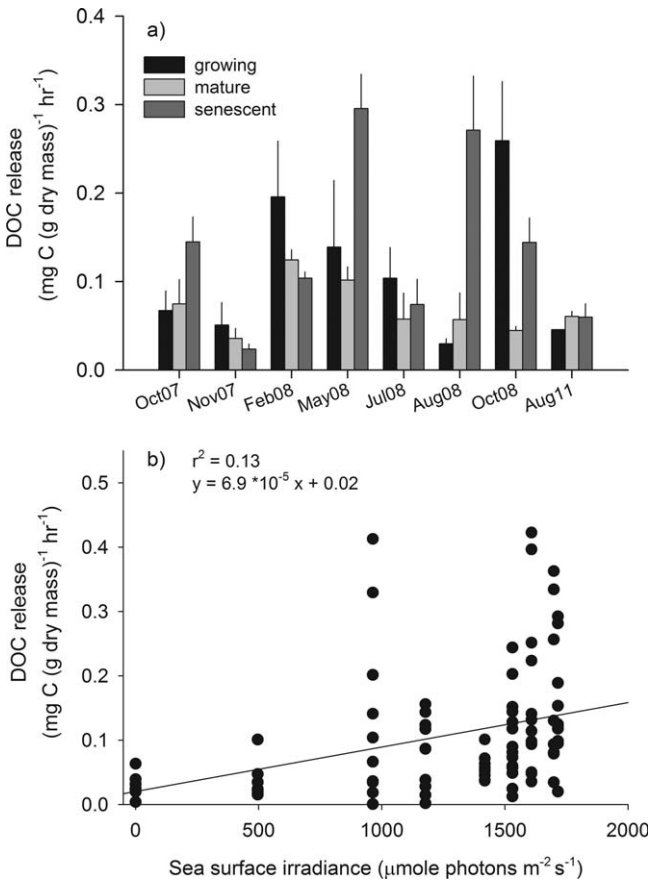

Fig. 2. (a) The effects of blade stage (growing, mature, senescent) and sampling date on rates of DOC release. Data are means (± SE) averaged over all incubations for each combination of blade stage and sampling date. (b) The relationship between the rate of DOC released from *Macrocystis* blades during in situ incubations and the mean photosynthetically active radiation (PAR) measured at the sea surface during the incubations.

in our experiments with an existing reef-scale model of particulate NPP by giant kelp. The existing model of particulate NPP was developed by the Santa Barbara Coastal Long Term Ecological Research program and has been used to estimate the particulate fraction of reef-scale NPP by giant kelp (in units of g C m^{-2} d^{-1}) based on monthly field measurements at Mohawk Reef since June 2002. The methods used to collect field data and the structure of the particulate NPP model are described in detail in Rassweiler et al. (2008) and Reed et al. (2008). Briefly, the model estimates particulate NPP by comparing giant kelp biomass at two time points (~1 month apart), calculating the growth rate implied by that change in biomass after accounting for independently measured loss rates of biomass, and integrating growth over the time period to give NPP. Prior to this study, the model did not account for dissolved losses of carbon, and so underestimated NPP by a fraction equivalent to this rate.

The standing biomass of giant kelp at each time point is calculated from morphometric measurements of all plants > 1 m tall within a 480 m^2 fixed plot. Three morphologically distinct sections of each plant are measured: (1) subsurface (immature fronds not long enough to reach the surface), (2) water column (the subsurface portion of surface reaching fronds), and (3) canopy (the surface portion of surface reaching fronds). Allometric relationships developed from 56 mature plants collected from the field on 42 dates and dissected, measured and weighed in the laboratory are used to convert linear measurements of each plant part into wet biomass. Loss rates of plants and fronds from surviving plants are calculated monthly based on ~15 tagged plants on which all fronds are individually tagged. Analyses of tissue samples collected from 15 plants each month are used to convert monthly estimates of wet biomass into dry mass and carbon mass.

We estimated DOC NPP at the reef scale (in units of g C m^{-2} d^{-1}) by combining the estimates of standing biomass produced by the model described above with mass-specific DOC release rates obtained from our in situ incubation experiments. We calculated DOC production by the stipe and blade portion of plants separately, converting estimates of biomass in the subsurface, water column, and canopy fractions into estimates of stipe and blade biomass based on blade/stipe biomass ratios developed from weights of blades and stipes from 292 fronds obtained from the 56 plants mentioned above that were collected from the field (Supporting Information Appendix B). This was done to account for temporal variation in the ratio of blade-to-stipe biomass

Table 1. Results of ANCOVA testing: (a) the effects of blade stage (growing, mature, senescent), sampling date, epiphyte load (percent of blade covered by *Membranipora serrilamella*), and blade C:N ratio on the rate of DOC release by *Macrocystis* blades, and (b) the effects of blade stage, sea surface irradiance and sea surface temperature. The significance levels of all interactions involving the covariates not shown here were > 0.1 and were not included in the final reduced ANCOVA models. Analyses were done on square root transformed values of DOC release in units of mg C (g dry $mass^{-1}$) h^{-1}

Source	DF	Mean Square	F-Value	P-Value
Blade stage	2	0.027	0.98	0.399
Date	7	0.060	5.54	<0.001
Epiphyte load	1	0.016	1.46	0.231
blade C:N	1	0.001	0.04	0.836
Blade stage * Date	14	0.028	2.57	0.006
Error	64	0.011		

Source	DF	Mean Square	F-Value	P-Value
Blade stage	2	0.014	1.86	0.180
Irradiance	1	0.077	9.92	0.005
Temperature	1	0.002	0.27	0.609
Error	22	0.008		

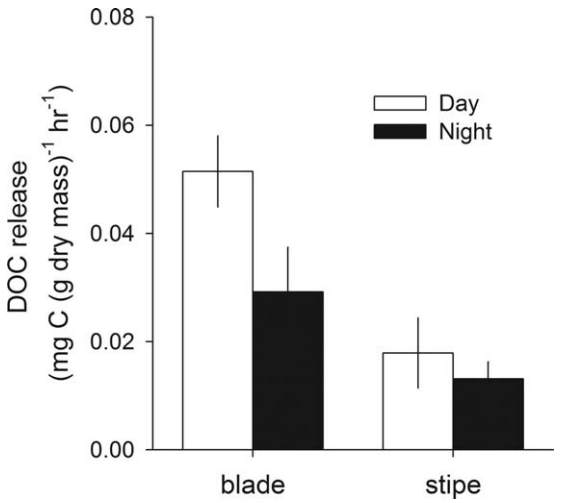

Fig. 3. The effects of time of day (midday vs. night) and tissue type (blade vs. stipe) on the rate of DOC release by *Macrocystis* during in situ incubations. Data are means (±1 SE).

due to changes in average plant morphology over time (e.g., changes in the fraction of biomass reaching the surface due to changes in size/age structure of fronds).

The effects of daily irradiance, and type of tissue (blade vs. stipe) on rates of DOC release per unit dry mass of *Macrocystis* were incorporated into our calculations of reef-scale DOC NPP. Measurements of irradiance began in 2007, hence we restricted our modeled estimates of DOC NPP to 2007–2014. The percent cover of the common epiphyte *Membranipora*, sea surface temperature, and blade growth stage were not considered in calculations of reef-scale DOC NPP because they did not account for a significant amount of the observed variation in rates of DOC release in field incubations.

DOC NPP by both blades and stipes was modeled as linear functions of irradiance at Mohawk Reef based on the relationship between the rate of DOC release and light observed in our incubation experiments (*see* Fig. 2b). When calculating DOC NPP, the effective PAR applied to the canopy section ($\text{meanPAR}_{\text{surf}}$) was the average PAR measured at the sea surface during the monthly sample period (including both day and night). Because the effect of light was linear, calculations based on daily average irradiance are identical to ones based on shorter term measurements of light. PAR for subsurface and water column sections of the kelp forest was calculated by combining measurements of PAR at the sea surface with measurements of PAR collected by an identical sensor moored 0.3 m above the bottom in the kelp forest. Sensors were retrieved monthly and replaced with clean calibrated sensors. Values obtained from the bottom sensor were adjusted for any biofouling that occurred during the month long deployment as per the methods of Harrer et al. (2013). For each hour during the 8-yr study period, the attenuation through the water column (K) was calculated as:

$$K=(-\ln(\text{PAR}_b/\text{PAR}_s))/D$$

where PAR_s is the average PAR measured at the sea surface during that hour, PAR_b is the average PAR measured at the bottom for the same hour, and D is the depth of the bottom sensor (7 m). Effective average subsurface irradiance (PAR_{sub}) was calculated by integrating light levels through the water column:

$$\text{PAR}_{\text{sub}}=((\text{PAR}_s-e^{(-KD)}\text{PAR}_s)/K)/D;$$

In calculations of DOC NPP, the effective PAR applied to the subsurface and water column sections of *Macrocystis* ($\text{meanPAR}_{\text{sub}}$) was the average PAR_{sub} calculated for the month (including both day and night). The slope and intercept of the relationship between PAR at the sea surface and DOC release in the canopy section were assumed to describe the relationship between PAR and mass specific DOC release by blade biomass throughout the plant, with biomass in subsurface and water column fronds experiencing lower PAR than the canopy as described above. Stipe biomass was assumed to respond to light in a similar way (consistent with our observations of stipe DOC release in the day and at night), but at only a fraction of the rate of release of blades.

Based on the above considerations, we calculated reef-scale DOC NPP (g C m^{-2} d^{-1}) by blades and stipes for each of the three plant sections each month from January 2007 through December 2014 as follows:

$$\text{DOC NPP}_{\text{blade\_can}}=B_{\text{blade\_can}}\times(c1+c2\times\text{meanPAR}_{\text{surf}})$$
$$\text{DOC NPP}_{\text{stipe\_can}}=B_{\text{stipe\_can}}\times(c1+c2\times\text{meanPAR}_{\text{surf}})\times c3$$
$$\text{DOC NPP}_{\text{blade\_wc}}=B_{\text{blade\_wc}}\times(c1+c2\times\text{meanPAR}_{\text{sub}})$$
$$\text{DOC NPP}_{\text{stipe\_wc}}=B_{\text{stipe\_wc}}\times(c1+c2\times\text{meanPAR}_{\text{sub}})\times c3$$
$$\text{DOC NPP}_{\text{blade\_sub}}=B_{\text{blade\_sub}}\times(c1+c2\times\text{meanPAR}_{\text{sub}})$$
$$\text{DOC NPP}_{\text{stipe\_sub}}=B_{\text{stipe\_sub}}\times(c1+c2\times\text{meanPAR}_{\text{sub}})\times c3$$

$\text{DOC NPP}_{\text{total}}$ was obtained by summing these terms. Here $B_{\text{blade\_can}}$ and $B_{\text{stipe\_can}}$ are the biomass densities of canopy blades and stipes respectively, in g dry mass m^{-2} of the sea floor, taken as an average between biomass densities measured at the start and end of each month. $B_{\text{blade\_wc}}$, $B_{\text{stipe\_wc}}$, $B_{\text{blade\_sub}}$, $B_{\text{stipe\_sub}}$, are similar values for the biomass of blade and stipe sections in the water column and subsurface parts of the plant (indicated by subscripts of "wc" and "sub" respectively). The terms $c1$ and $c2$ are the intercept and slope of the linear regression predicting blade DOC production (g C g dry kelp mass^{-1} d^{-1}) as a function of sea surface irradiance based on the incubation data, and $c3$ is the mean ratio of DOC production by stipes to the equivalent production by blades averaged over the day and night periods when measurements were obtained for stipes and blades (= 0.39). We compared this time-series of giant kelp DOC NPP to the amount of NPP partitioned into POC (= POC NPP) estimated from monthly measurements of changes in *Macrocystis*

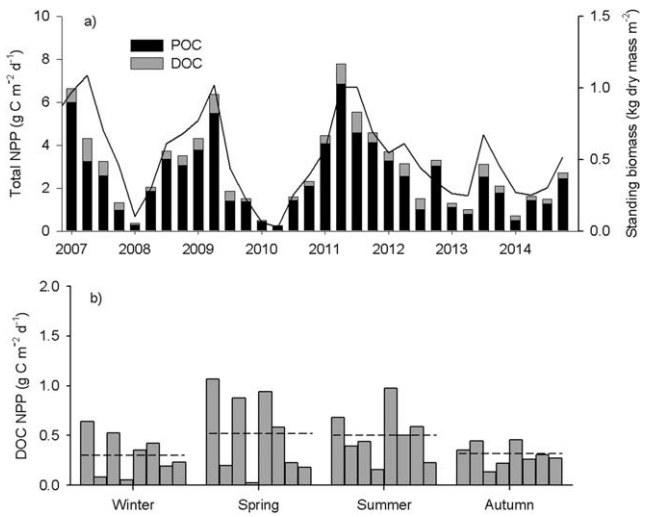

Fig. 4. (a) Stacked bar graph showing the seasonal contribution of POC and DOC to total NPP by *Macrocystis* and seasonal variation in standing biomass (solid line) during the 8-yr time series. (b) Inter-annual variability in DOC NPP by season. Data represent the mean daily values within a season for a given year from 2007 to 2014. Years are plotted chronologically from left to right within each season. Dashed lines represent the mean for each season averaged over all years.

biomass density and particulate loss rates of whole fronds and plants (Rassweiler et al. 2008).

We evaluated the importance of light in accounting for variation in modeled estimates of mass specific DOC production by examining the monthly variance among: (1) modeled estimates of DOC production for canopy biomass that assumed a constant value for PAR based on the long-term average, (2) modeled estimates of DOC production for the canopy biomass that incorporated our measurements of mean daily irradiance and (3) modeled estimates of DOC production for the entire plant (i.e., canopy, water column, and subsurface sections) that incorporated our measurements of mean daily irradiance. The first example allows for no variation in mass specific DOC release, the second allows for variation due to variation in the monthly light environment (both due to brightness and length of days), and the third example adds variation due to distribution of biomass throughout the plant (with resulting variation in the average light environment being experienced and the blade to stipe ratio).

The contribution of light to variation DOC NPP at the reef scale was assessed by regressing monthly estimates of reef-scale DOC NPP as a function of monthly standing biomass. There is necessarily a strong relationship between standing biomass and reef-scale DOC NPP (this is both a characteristic of our model and of nature), but the residual variation around this relationship is driven in part by temporal variation in light.

Propagation of uncertainty

Uncertainties underlying our calculations of biomass and particulate NPP are described in Harmon et al. (2007) and Rassweiler et al. (2008). New uncertainties involved in calculating reef scale DOC NPP include uncertainty in the relationship between PAR and mass specific DOC production, uncertainty in the ratio of stipe DOC production to blade DOC production, and uncertainty in the partitioning of biomass between stipes and blades for each section of the plant. We calculated the probability distribution for each of these parameters from our field measurements. We then propagated these uncertainties within the model using a Monte Carlo method in which we simulated 10,000 replicate runs of the model, in each run selecting a new value for each parameter at random from its associated probability distribution. The resulting distribution of output parameters (e.g., the slope of the relationship between total NPP and DOC NPP) allows us to place confidence intervals around our estimates of the contribution of DOC release to giant kelp NPP.

Model results

Total NPP (i.e., the sum of POC NPP and DOC NPP) varied substantially over time as the episodic loss and recovery of giant kelp biomass from wave disturbance in some winters led to large oscillations in standing biomass and total NPP with frequencies of 2–3 yr (Fig. 4a). Not surprisingly, POC dominated NPP throughout the time series averaging 2.46 g C m^{-2} d^{-1} compared to 0.41 g C m^{-2} d^{-1} for DOC NPP over the 8-yr study period. On average DOC NPP was highest in summer and spring (~0.5 g C m^{-2} d^{-1}) and lowest in winter and autumn (~0.31 g C m^{-2} d^{-1}; Fig. 4b). However, it varied greatly among years for any given season, especially winter and spring.

The proportions of the standing biomass contributed by the three morphologically distinct plant sections (which differ proportionally in the amount of biomass contributed by blades and stipes; Supporting Information Appendix B) varied substantially over time as well, but in different ways. The proportion contributed by subsurface fronds (61% blades by weight) fluctuated greatly from 0.12 to 0.94 over the 8-yr time series and varied inversely with standing biomass (Fig. 5a), while the proportion of standing biomass contributed by the canopy portion of fronds that reached the surface (which averaged 59% blades by weight) ranged from 0.15 to 0.59 and was positively related to standing biomass (Fig. 5b). By contrast the proportion of the standing biomass consisting of the water column portion of fronds that reach the surface (which averaged 37% blades by weight) varied much less over time (range = 0.05–0.39) and was relatively invariant to the large fluctuations in standing biomass (Fig. 5c). Despite these large fluctuations in forest morphology and standing biomass (Fig. 5a–c) the contributions of blades and stipes to the standing biomass were comparatively similar (53% vs. 47% for blades and stipes, respectively) and relatively constant over the 8-yr time series (Fig. 5d).

Temporal variation in modeled estimates of DOC NPP arise from variation in the light environment, variation in the ratio

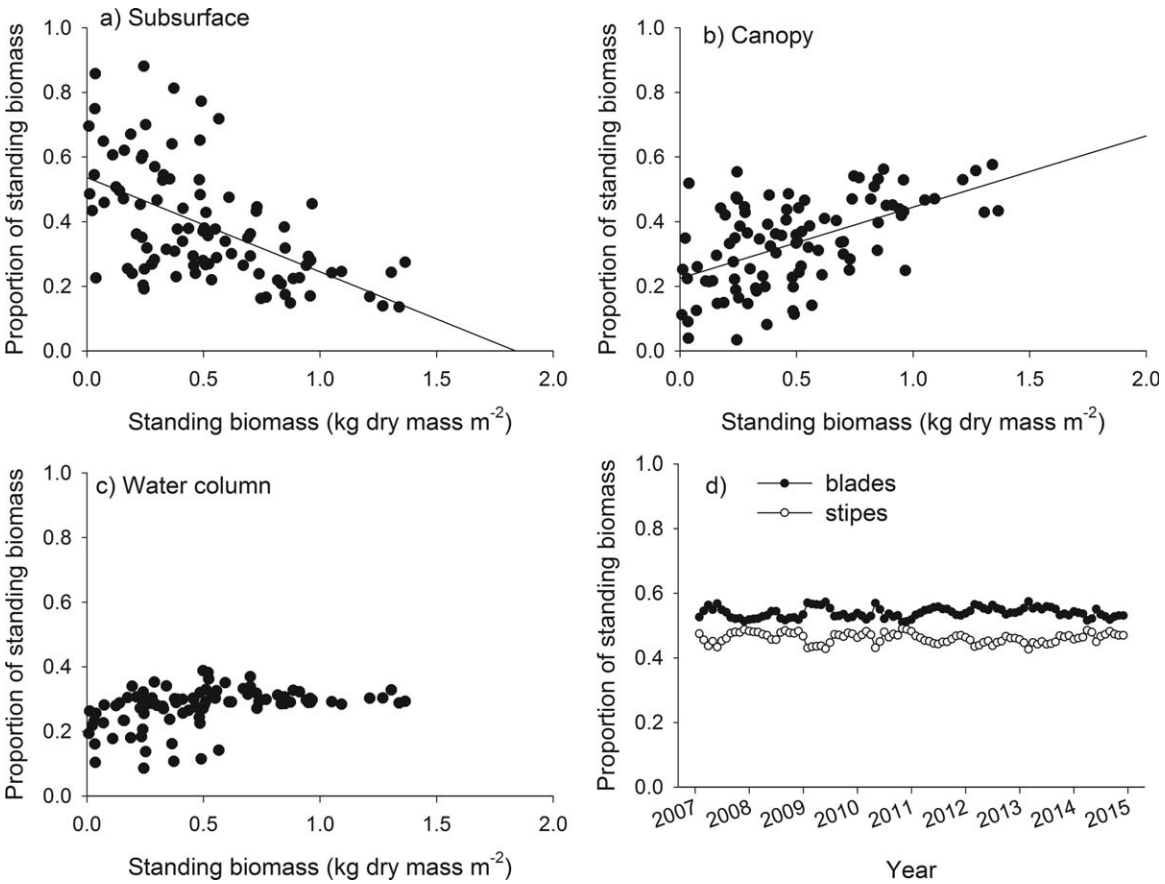

Fig. 5. The relationship between standing biomass and the proportion of standing biomass contributed by (a) subsurface fronds, (b) the canopy portion of fronds that reach the surface, and (c) the water column portion of fronds that reach the surface. (d) The proportion of standing biomass contributed by blades and stipes during the 8-yr time series. Data for all plots represent monthly values from January 2007 to December 2014.

of stipes to blades, and variation in standing biomass. Monthly variation in day length and cloud cover led to substantial variation in monthly estimates of mass specific DOC production (Fig. 6a, Canopy only constant PAR vs. Canopy only measured PAR). Adding consideration of water column attenuation and variation in stipe to blade ratio reduced the estimate of mass specific DOC production (due to lower average PAR level below the canopy), but did not add much variation from month to month (Fig. 6a, Canopy only measured PAR vs. Whole forest measured PAR). The limited role of variation in stipe to blade ratio was not surprising given how constant this ratio was over time (Fig. 5d). Taken together, monthly estimates of mass specific DOC release varied widely, with release rates in the brightest months nearly double those in the dimmest (Fig. 6a. Whole forest measured PAR). Nonetheless despite this high variation in mass specific DOC production, neither light nor tissue type had much effect on reef scale DOC NPP compared to the overwhelming effect of standing biomass which accounted for 90% of the variation in reef scale DOC NPP in our model (Fig. 6b). Variation in light and to a much lesser degree variation in tissue type led to the small amount of residual variation.

The relationship between total NPP and DOC NPP became more robust when considered over longer time periods. There was substantial variation in the ratio of DOC NPP to total NPP when measured monthly (Fig. 7a) compared to when measured at seasonal or annual scales (Fig. 7b,c). The slope as well as the scatter in this relationship was affected by time scale. At the monthly time scale DOC NPP averaged 10% of total NPP (as indicated by the slope of the relationship in Fig. 7a), whereas it converged to average 14% of total NPP when evaluated on a seasonal or annual basis (Fig. 6b,c). Accounting for uncertainties in our estimates of both total and DOC NPP revealed a relatively sharp limit on the lower bound of this relationship with a longer tail on the upper bound (Fig. 6d). The lower 95% confidence interval for the estimated slopes were 0.064, 0.092, and 0.097 (for monthly, seasonal and annual relationships respectively). The upper 95% confidence intervals for those same relationships were 0.155, 0.203, and 0.213. Thus we can say with confidence that when measured over timescales of a few months or longer DOC production made up at least 10% of total production, but possibly substantially more.

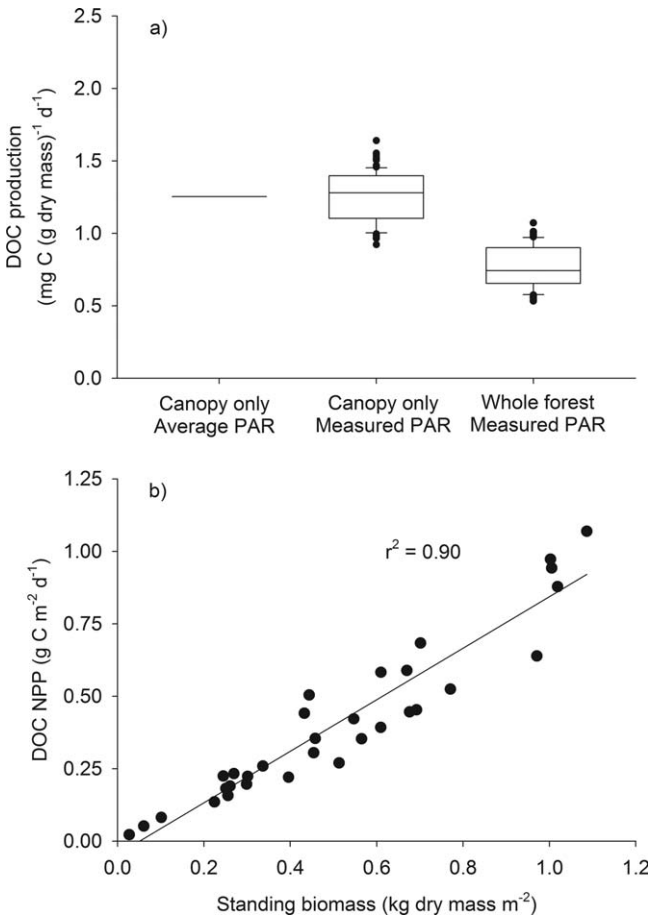

Fig. 6. Variation in modeled estimates of monthly DOC production. (a) Mass specific DOC production for the canopy assuming a constant light environment, for the canopy assuming the real measured light environment and for all plant parts assuming measured light environment. (b) Area specific DOC production based on the measured light environment as a function of standing biomass.

Discussion

The giant kelp forest at Mohawk Reef produced a substantial amount of DOC that comprised on average ~14% of the reef's total NPP when considered on a seasonal or annual basis. This fraction of NPP commonly exceeded 0.5 g C m^{-2} d^{-1} for an entire season, which is ~2 orders of magnitude greater than the rate of DOC production by phytoplankton measured by Halewood et al. (2012) in adjacent waters immediately offshore of the Mohawk kelp forest (0.5–2 μg C L^{-1} d^{-1}, equivalent to 0.005–0.02 g C m^{-2} d^{-1} in a 10 m water column, the approximate depth of the offshore edge of the Mohawk kelp forest). These results lend support to the hypothesis that BCD in the water column near *Macrocystis* forests can be subsidized by kelp-derived DOC (Halewood et al. 2012).

Our results show that prior studies of reef–scale NPP by *Macrocystis*, which did not account for the release of DOC (e.g., Gerard 1976; Reed et al. 2008), underestimated the contribution of this foundation species to the coastal carbon pool. The amount and predictability of this underestimation varies with the timescale over which NPP is examined. We found that on short time scales (i.e., days to months) the fraction of NPP partitioned into DOC by *Macrocystis* was ~10% on average, but highly variable, especially during periods of low productivity when exudation may continue even during periods of low POC NPP when kelp is not adding new tissue. Such short-term fluctuations in the fraction of NPP contributed by DOC are minimized when NPP is examined over longer periods (e.g., seasons or years). At these longer time scales, the contribution of DOC to *Macrocystis* NPP becomes more stable and increases to ~14%.

Similar to other studies (e.g., Johnson et al. 1977; Abdullah and Fredriksen 2004; Wada et al. 2007) we found the release of DOC from *Macrocystis* blades to be highly variable. Surface irradiance was the single most important factor accounting for this variation, as it explained 13% of the observed variability. Our finding that DOC release from blades was on average 80% higher during midday compared to night is consistent with the results of previous studies (Sieburth 1969; Abdullah and Fredriksen 2004; Maher and Eyre 2010), and reinforces the importance of light in regulating DOC production by macrophytes.

Production by *Macrocystis* occurs throughout the water column and irradiance varies tremendously in the water column particularly in giant kelp forests where light penetration varies not only with depth, but also with canopy density and position in the forest (Gerard 1984). Moreover, changes in the orientation of blades and the degree to which they are shaded by other blades on the same or adjacent fronds due to the vagaries of water motion can greatly influence the amount of light reaching blades and stipes at any point in time. Indeed, such variation in light undoubtedly accounted for some of the variation that we observed in DOC release among blades incubated on the same sampling date. Such high spatial variation in light is similar to that found in terrestrial forests and can be accounted for in part by averaging irradiance in different locations within the forest (Reifsnyder et al. 1971; Chazdon 1986). We accounted for variation in light within the canopy by sampling DOC release from multiple blades and stipes on different plants on each sampling date, effectively averaging a representative sample of light levels. For biomass below the canopy, we calculated effective light levels based on light measured at the surface and bottom of the forest and the assumption that attenuation is exponential with depth. This approach does not account for all the spatial variability in irradiance that exists within a given position in the water column in the forest due to shading and blade orientation. However, irradiance throughout the water column beneath the canopy is very low due to the exponential decline in light with depth and shading from surface canopy (Harrer et al. 2013). Therefore, errors associated with our estimates of DOC production

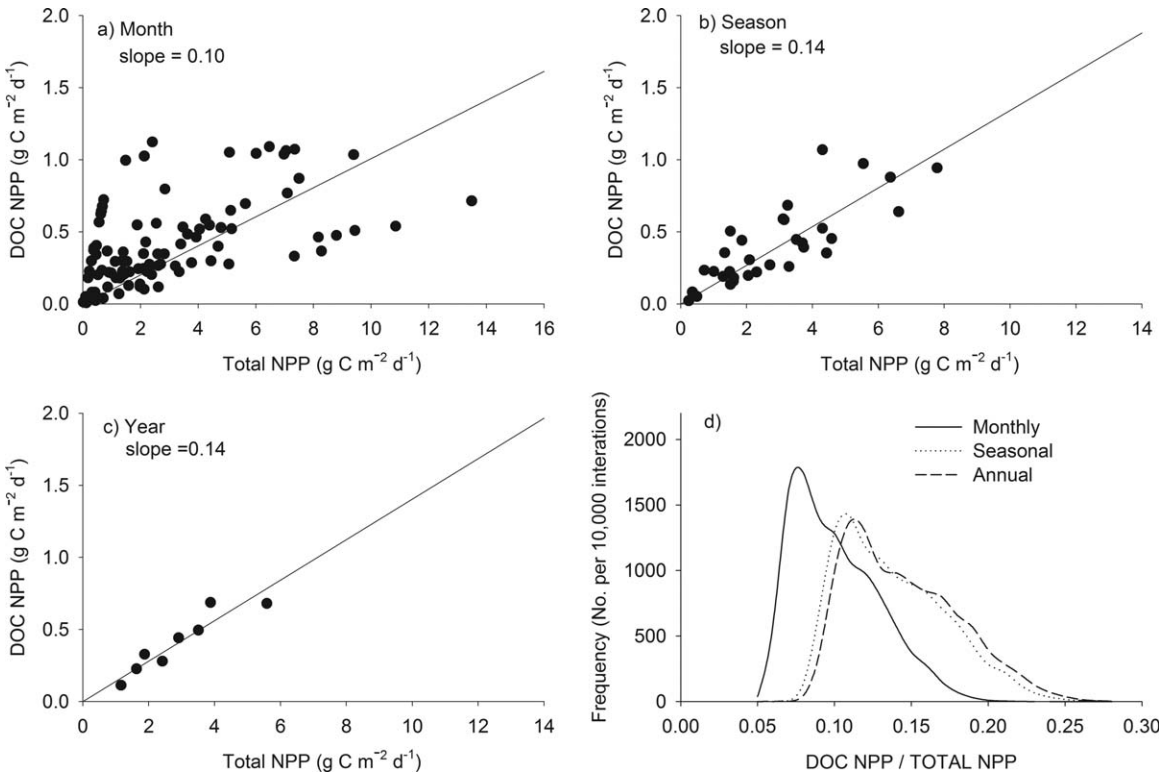

Fig. 7. The relationship between POC NPP and DOC NPP for mean daily values averaged over: (a) months, (b) seasons, and (c) years for January 2007 through December 2014.

beneath the canopy due to spatially variable irradiance are likely to be small in magnitude. Moreover, our finding that variation in DOC NPP is overwhelmingly driven by the massive temporal fluctuations in standing biomass suggest that such errors are likely to have little effect on spatial and temporal patterns of DOC NPP at the reef scale.

DOC exudation has been linked to the growth phase of juvenile *Laminaria hyperborea*, with higher DOC release during non-growth months as high requirements for growth lead to a lower proportion of fixed carbon being exuded (Abdullah and Fredriksen 2004). We did not find evidence that DOC release was linked to the growth phase of *Macrocystis* blades. Unlike *L. hyperborea* blade production and growth occur year round in *Macrocystis* (Reed et al. 2008; Stewart et al. 2009; Rodriguez et al. 2013) and the blades are short-lived (~50–100 d) and rapidly transition through growth, maturation and senescence (Rodriguez 2014). Such short life spans may make it more difficult to detect relationships between DOC exudation and the growth phase of blades in *Macrocystis*.

Rapidly growing phytoplankton populations also exude relatively little DOC (Nagata 2000), and exudation increases when nutrients become depleted (Goldman et al. 1992; Teira et al. 2001; Sintes et al. 2010). This has been interpreted as an energy dissipation strategy that allows the cell to keep the photosynthetic machinery active and ready to respond when nutrients become available (Ormerod 1983; Wood and Van Valen 1990). Our results suggest that this strategy is not commonly employed by *Macrocystis*, as we found no correlation between DOC release and blade C : N ratio, an indicator of nutrient condition of blades (Reed et al. 1996; Stewart et al. 2009) or sea surface temperature which is correlated with nutrient concentration (McPhee-Shaw et al. 2007). Moreover, we found little evidence for seasonality in DOC NPP by *Macrocystis* despite strong seasonality in seawater nitrate concentrations and blade C : N ratios during our 8-yr study period (Brzezinski et al. 2013). Thus, it does not seem that fluctuations in nutrient availability contributed significantly to the variation that we observed in DOC NPP.

The high levels of biomass production by kelps supports diverse assemblages of grazers, detritivores and microbes (Graham 2004; Michelou et al. 2013; Clasen and Shurin 2015; Schiel and Foster 2015). Most kelp biomass, however, is typically exported out of the forest to adjacent intertidal and deep sea ecosystems (Gerard 1976; Krumhansl and Scheibling 2012) where it can provide a significant trophic subsidy (Vetter 1995; Harrold et al. 1998; Dugan et al. 2003). Our results show that the magnitude of dissolved contributions from giant kelp can be substantial, and likely account for elevated levels of DOM observed in coastal waters

adjacent to giant kelp forests (Halewood et al. 2012). This is consistent with findings by Wada and Hama (2013) who suggested that benthic macroalgae could contribute up to 20% of the DOC in coastal waters. Bacterial consumption of kelp-derived DOM may thus represent an important path by which kelp-derived carbon re-enters the coastal food web (Newell and Lucas 1981). Conversely, kelp-derived DOC that resists rapid microbial degradation and persists could be exported from the nearshore reef environment and represent the major form of sequestered kelp carbon. Tracing the biochemical and trophic fate of kelp derived DOM is a challenge that promises new insight into the ecological role of microbial diversity within and adjacent to kelp forest ecosystems.

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