Importance of kelp detritus as a component of suspended particulate organic matter in giant kelp *Macrocystis pyrifera* forests

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ABSTRACT: To determine the potential of giant kelp *Macrocystis pyrifera* detritus as a food resource for coastal suspension feeders, we quantified the production and size distribution of small particulate (<1 cm) kelp detritus in relation to water motion, state of kelp blade erosion, and percent cover of the bryozoan *Membranipora serrilamella* on blades. We enclosed kelp blades in the laboratory and in the field to collect detritus particles, which we then fractionated by size. Carbon and nitrogen content were quantified for each size fraction. Suspension feeders typically consume particles up to 250 µm in size, and most kelp detritus particles that we collected were within this size range. Blade degradation state and blade mass were found to be weak but significant predictors of detrital generation. We used the data from our laboratory and field experiments combined with 5 yr of monthly biomass measurements of giant kelp and suspended particulate organic matter (POM) to estimate the contribution of kelp detritus to suspended particulate organic carbon (POC) and nitrogen (PON) in the kelp forest at Mohawk Reef off Santa Barbara. Results showed that detrital kelp carbon contributed <0.2% of total suspended reef POC and PON. Therefore, despite the high production rate of kelp and the importance of exported kelp detritus to intertidal and deep-water ecosystems, our results suggest that small kelp detrital particles do not represent a significant food source to kelp forest suspension feeders.

KEY WORDS: Kelp detritus· Suspension feeders · POM · Stable isotopes · Phytoplankton · *Macrocystis pyrifera* · Giant kelp forest

INTRODUCTION

Carbon can be regarded as a tracer of energy exchange pathways within and across ecosystems; quantifying these pathways is necessary to understand changes in ecosystem structure and function (Mann 1988, Valiela et al. 2001). In near-shore marine ecosystems, detrital exchange pathways are significant and can be larger than those associated with grazing (Mann 1988, Rothäulser & Thiel 2006). High C:N ratios and polyphenolic content in living macrophyte tissues lessens their palatability and nutritive value to grazers (Duggins & Eckman 1997, Norderhaug et al. 2003), and consequently many macrophyte-dominated marine ecosystems tend to be rich

in detritus (Mann 1988, Cebrian 1999). Examples include salt marshes (Teal 1962, Mann 1988), seagrass beds (Zieman & Zieman 1989), and mangrove forests (Robertson et al. 1988). On temperate shallow rocky reefs, the large brown macroalgae known as kelps may be significant contributors to detrital food webs (Stuart et al. 1982, Duggins et al. 1989, Norderhaug et al. 2003), but the quantities and physical and biochemical characteristics of detritus produced by kelps are poorly known (Krumhansl & Scheibling 2012).

Macrocystis pyrifera (giant kelp) is abundant in shallow temperate waters across the globe (Graham et al. 2007), and is regarded as a foundation species (sensu Dayton 1972) due to its profound effects on eponymous kelp forest ecosystems (Foster & Schiel

1985, Graham et al. 2007). Giant kelp is thought to shape the ecosystem through 2 fundamentally different processes: (1) effects of its physical presence or structure, and (2) provision of food to higher trophic levels. Unequivocal evidence for these processes is scarce, however, because most studies that have examined the effects of kelp were not designed to distinguish between these 2 processes (reviewed by Graham et al. 2007). Nevertheless, evidence for the effects of kelp's provision of physical structure to kelp forest ecosystems is strong. *Macrocystis* canopies decrease light to the benthos by up to 90% (Pearse & Hines 1979, Reed & Foster 1984), leading to reductions in understory macroalgal abundance and primary production, and phytoplankton production (Miller et al. 2011). Kelp-induced reductions in understory algal abundance may decrease competition for space in the forest and lead to an increased abundance of sessile invertebrates (Arkema et al. 2009). Kelp forests act as baffles, slowing water currents (Jackson & Winant 1983, Gaylord et al. 2007, Rosman et al. 2007) and potentially affecting fluxes of particulate organic matter (POM), larvae, and nutrients inside the forest (Eckman et al. 1989, Hurd 2000). Although *Macrocystis* is highly productive, producing 600 to 1300 g C m^{-2} yr^{-1} (Reed & Brzezinski 2009), evidence for its influence as an important energy source to the kelp forest food web is more equivocal.

Macrocystis is available to the food web as living tissue attached to the plant, as detached detritus, and as dissolved organic matter (DOM) exuded by living plants or detritus. The importance of kelp-derived DOM to reef food webs is virtually unknown, although current work suggests it can be used by bacterioplankton (C. Carlson pers. comm.). Diverse species graze on *Macrocystis* directly, including snails, crustaceans, echinoderms, and fish (reviewed by Foster & Schiel 1985, Dayton 1985, Graham 2004). However, grazers are thought to consume relatively little *Macrocystis* production; estimates have been between 3 and 12% (Gerard 1976), including consumption of recently detached drift kelp. The majority of giant kelp production apparently ends up as detritus (Mann 1988). Despite this, we have little understanding of the character and fate of this detritus and its role in subtidal food webs. Several studies using stable isotopes have postulated that smaller fragments of kelp detritus comprise an important constituent of the suspended POM consumed by kelp forest suspension feeders. These studies have estimated that kelp-derived material could comprise from ~20 to 80% of the diet of some reef sessile suspension feeders, including bivalves, sponges, bryozoans, as-

cidians, and barnacles (Dunton & Schell 1987, Duggins et al. 1989, Kaehler et al. 2000, Fredriksen 2003), although patterns of variability in the isotope values of these consumers and phytoplankton suggest that these are overestimates (Nadon & Himmelman 2006, Miller & Page 2012). There are few studies that have directly examined the rates of production or physical characteristics of kelp-derived POM.

In this study, we measured the particle size distribution and quantity of kelp detritus produced by *Macrocystis pyrifera* blades both in the laboratory and in the field. We hypothesized that detritus was produced largely through erosion at the distal end of the blade, and that water motion and blade condition would affect this process. Consequently, water motion, blade mass, blade perimeter, and distal erosion perimeter were evaluated as potential predictors of the production and size distribution of kelp detritus. We hypothesized that increased water motion and highly eroded blades would produce more detritus, and proportionally more detritus in larger particle size classes. To estimate the potential importance of *Macrocystis* detritus as a component of POM and potential food source for reef suspension feeders, we used field measurements of kelp biomass and POM collected monthly in a kelp forest off Santa Barbara, California, to estimate the production of detritus by giant kelp seasonally and inter-annually for 5 yr. These data allow estimation of the abundance of kelp detritus relative to the total POM pool in coastal waters within size ranges relevant to benthic and pelagic suspension feeders.

MATERIALS AND METHODS

Kelp detritus characteristics and production

We measured the production, particle size distribution, and chemical composition of detritus produced from blades of *Macrocystis pyrifera* incubated in plastic bags in the laboratory and field. For laboratory incubations, blades were collected from a kelp bed located in 5 to 6 m of water offshore of Goleta Beach, California. Kelp fronds (2 to 3) were harvested by swimmers on the morning before each laboratory incubation (26 Jul, 2 Aug, and 9 Aug 2011). Within 30 min of collection, the fronds were transferred to a filtered sea water table from which individual blades were chosen for the incubation. Blades were cut from the fronds by snipping the frond's stipe above and below the target blade, leaving the pneumatocysts intact. Mobile epifauna present on

the blades, such as snails and amphipods, were removed, but epiphytes and sessile epifauna (which were not abundant on the blades) were not. Before incubation, each blade was carefully blotted and weighed (wet weight). Using a digital camera, photographs were taken of each blade adjacent to a ruler. Blade perimeter, length along the distal eroding edge, and percent of blade area covered by bryozoans were measured by tracing the images using ImageJ software (Version 1.46); the ruler was used to calibrate the software measurements. After photographing, each blade was placed in a 20 × 76 cm transparent plastic bag with 5 l of filtered seawater (0.22 µm), and the bag was secured around the base of the pneumatocyst with 2 plastic cable ties, allowing the blade to sit in a position similar to that when it was attached to a frond. Blades were then placed on a platform shaker table that caused the kelp blades to undulate similarly to those observed in the field. Incubations were conducted in a temperature-controlled room under cool white fluorescent lights (14 h light:10 h dark, 200 to 220 µmol m^{-2} s^{-1}) at 16°C, which are typical conditions experienced by canopy blades of *Macrocystis* in the summer off Santa Barbara.

The effect of 2 factors, blade condition and water motion, on detrital production were evaluated in the laboratory incubation experiments. Blades become smaller in area as they senesce and degrade over time, and the end of the blade becomes ragged in appearance. To evaluate the effect of blade condition on detrital production, mature blades were chosen at 3 levels of degradation based on the area of intact blade remaining (>75% intact, 50–75% intact, and <50% intact). To explore the effect of water motion on detrital production, separate experiments were run at 3 levels of water motion created by the platform shaker (30, 35, and 40 revolutions per minute, RPM). Each level of water motion was replicated in 3 separate trials, with 24 kelp blades per replicate trial (n = 8 for each of the 3 levels of degradation: low, medium and high). Controls (n = 2 per trial) consisted of 5 l of filtered seawater in plastic bags without a kelp blade. At 24 and 48 h after the start of each experiment, 4 of the 8 incubation bags of each of the 3 degradation levels were collected and sampled for POM. The 2 control bags lacking blades were sampled for POM after 48 h.

To characterize the size fractions of POM produced, the contents of each bag were gently poured through sequential sieves of 1 mm, 250 µm, 125 µm, and 25 µm mesh size. Particles larger than 1 cm diameter and visible epifauna and epiphytes were removed from the 1 mm sieve and the smaller kelp particles were retained. After gently rinsing the sieves with filtered seawater (0.22 µm) to ensure size fractionation was complete, we filtered a subsample (630 ml) of the 5 l of sieved water (total volume measured for each bag to include rinse water) onto a precombusted (450°C for 2 h) glass fiber filter (GFF, 0.7 µm nominal pore size) to quantify particles <25 µm. The contents of each sieve fraction were also rinsed onto precombusted GFF filters with filtered seawater. Filtered samples were dried for 3 d at 50°C, acidified with 2 to 3 drops of concentrated HCl to remove carbonates, stored in a desiccator, and analyzed for carbon and nitrogen content using a CHN elemental analyzer (Carlo-Erba Flash EA 1112 series, Thermo-Finnigan Italia) in the Marine Science Institute's Analytical Laboratory at the University of California Santa Barbara. Kelp particles >1 cm were dried for 3 d at 50°C and weighed, and their carbon and nitrogen content was estimated using mean mass-specific conversion factors for *Macrocystis pyrifera* (C = 30.6 ± 0.2% dry mass, N = 2.3 ± 0.03% dry mass; Santa Barbara Coastal Long Term Ecological Research project [SBC LTER] unpubl. data). For the no-kelp controls, only the <25 µm size class was analyzed for C and N content. For each experiment, the mean C and N values of the controls was subtracted from the <25 µm size class to correct for non-kelp sources of POM.

A similar experiment to that described above was performed in the field for comparison to the laboratory measurements of detritus production. Swimmers filled 20 × 76 cm bags with surface seawater, and carefully enclosed haphazardly selected blades, still attached to fronds, for each of the 3 levels of degradation described above (n = 3 for each degradation level). The bags were closed around the bases of pneumatocysts using the same methods as above. Six control bags containing only seawater were attached to a thin nylon line with floats to hold them at approximately the same depth (~0.3 m) as the kelp-containing bags. Five bags, 1 from each degradation category and 2 controls, were collected on each of the following 3 d. Blades were removed immediately and retained, and the incubation bags were then sealed with cable ties, brought back to the laboratory, size-fractionated and filtered, and analyzed for carbon and nitrogen content using the same methods as in the laboratory experiments. To evaluate whether detrital production was related to blade mass and epiphyte load, we weighed each blade and took photographs to measure percent of blade area covered by bryozoans. All handling and size fractionation were completed on the same day samples were collected from the field.

Water motion

Clod cards were used to compare the relative water motion produced by each RPM setting of the shaker table in the laboratory to that experienced by blades in nature. Following the methods of Thompson & Glen (1994), 250 g batches of plaster of Paris (DAP) were mixed slowly with 187.5 ml of deionized water. The resulting slurry was poured into small plastic cups, and bubbles were tapped out. After 20 to 30 min, the cups were cut away from the hardened mixture, which was dried in an oven for 3 d at 60°C. The blocks were sanded to approximately the same size and attached with Sea Goin' Poxy Putty brand epoxy to 5 cm acrylic squares. After weighing, each clod card with attached acrylic square was fastened to one end of a thin, 6.25 mm diameter fiberglass rod using nylon cable ties. A rod with attached clod card was then placed in a plastic bag containing 5 l of filtered seawater identical to those used for incubating kelp blades. Cable ties were used to close the bags around the free end of the fiberglass rod (opposite the clod card) to keep the clod card near the center of the bag and prevent it from rubbing on the bag sides.

Clod cards were incubated in the laboratory at each RPM setting for 24 h (n = 3 replicates per RPM setting). To assess water motion in the field, clod cards were also deployed in the kelp canopy at 2 reefs (Arroyo Quemado and Mohawk Reef, n = 12 per reef) for 2 d (22 to 24 Aug 2011). The acrylic squares were affixed with cable ties at to a nylon line strung at ~0.3 m depth between 2 floats and anchored to the bottom. On retrieval, clod cards were dried for a minimum of 1 wk at 60°C and weighed to the nearest mg.

Data analysis

We used a 1-way fixed factor ANOVA to compare particle generation rates between laboratory and field experiments. Levene's test was used to test for heteroscedasticity prior to ANOVA, and as a result all dependent variables were natural log transformed. t-tests were used to compare particulate organic carbon (POC) and nitrogen (PON) generation rates from field versus laboratory experiments for each particle size class (>25 µm, 25–125 µm, 125–250 µm, 0.25–1 mm, 1–10 mm, and >10 mm). Data from laboratory incubations were analyzed with ANCOVA to test the hypothesis that blades at higher levels of degradation and in more turbulent water would generate more particles; treatments were

water motion (fixed, 3 levels: 30, 35, and 40 RPM), and blade degradation level (fixed, 3 levels: <50, 50–75%, and >75% whole). Blade mass served as the covariate in this analysis. We used stepwise regression (with inclusion criteria 0.25 probability to enter and 0.1 probability to leave the model) to evaluate the amount of variation in POM production explained by the percent of the blade covered by the bryozoan *Membranipora serrilamella*, blade mass, blade perimeter and distal erosion length (defined as the traced length along the distal eroding edge of each blade), water motion and blade degradation level. Multicollinearity between predictor variables was evaluated using bivariate correlation (Quinn & Keough 2002). All statistical analyses were conducted using JMP (SAS Institute, Windows version 10.0). Results are given as means ± SE.

Seasonal and interannual estimates of detrital production

We estimated the amount of particulate C and N produced by kelp, and the kelp-derived suspended detrital carbon and nitrogen pool, using a 5 yr time series (2007 to 2011) of *Macrocystis* biomass at Mohawk Reef off Santa Barbara, California (34° 23′38″N, 119°43′45″W), and compared these estimated kelp inputs to the total POC and PON pool, measured concurrently at the same kelp forest. Mohawk Reef is a shale reef at 5 to 9 m depth that supports a giant kelp forest with an average area of 21 000 m^2 (Cavanaugh et al. 2010). We calculated the average rate of detrital C input in each season to the Mohawk kelp forest, KDC$_{in}$, in units of mg C m^{-2}, as:

$$KDC_{in} = KB_{blade} \times KDC_{shed} \qquad (1)$$

where KB$_{blade}$ is the average biomass of kelp blades during each season in units of g dry mass m^{-2}, and KDC$_{shed}$ is the average rate of production of detrital C by kelp blades in particle size classes below 250 µm across all our blade incubation experiments, in units of mg C g^{-1} blade dry weight. We focused on smaller particles because they are within the size class generally consumed by suspension feeders (Self & Jumars 1988). SBC LTER estimates the standing biomass of giant kelp at Mohawk Reef monthly using morphometric measurements taken by divers (detailed methods available in Rassweiler et al. 2008). To convert these whole-plant biomass measurements to blade biomass, we multiplied by the average fraction of *Macrocystis* plant biomass comprising blades (0.53 ± 0.01), which was measured for 55 plants collected at

3 reefs (including Mohawk Reef) between June 2002 and June 2003 (Reed et al. 2008). We then estimated average kelp detrital C concentration, in units of mg C m^{-2}, assuming steady state, for each season as:

$$[KDC] = KDC_{in} \times \tau \qquad (2)$$

where τ is the average residence time of seawater within the kelp forest at Mohawk Reef: 1.1 h (Fram et al. 2008). Our approach ignores removal processes within the forest, which we assume are negligible at timescales smaller than this rather short residence time. As a simple sensitivity analysis, we varied kelp biomass, KDC$_{shed}$, and residence time by 25% to evaluate their effect on the final estimate of kelp detrital C concentration. In an additional exercise to explore the effect of residence time on the magnitude of the kelp detrital carbon pool, we used a longer residence time of 6 h to calculate [KDC]. We used the same methods as above to estimate PON contributions by *Macrocystis*. Errors were propagated through all calculations using the quadratic method. We compared [KDC] and [KDN] with depth-integrated measurements of total POC and PON measured monthly at Mohawk Reef to estimate the relative contribution of kelp-derived detritus to the total POM pool. POM samples were collected monthly at Mohawk Reef at 1 m and 5 m depth during the same time interval as kelp biomass density was measured; methods are described in detail at http://sbc. lternet.edu/external/Ocean/Protocols/Brzezinski_2009-01-01_C_N_filtration.pdf.

Briefly, POC and PON concentrations were measured using 630 ml water samples filtered through precombusted glass fiber filters and analyzed with a CHN elemental analyzer (Leeman Labs Model 440 or Carlo-Erba Flash EA 1112 series) in the Marine Science Institute Analytical Laboratory at the University of California Santa Barbara. Concentrations were integrated through the 5 m water column to obtain estimates of POC and PON in units of mass m^{-2} in the Mohawk kelp forest.

RESULTS

Kelp blade characteristics

The wet mass of *Macrocystis* blades sampled for the experiments averaged 22.0 ± 0.8 g; (range = 13.6 to 39.9 g). Length of the distal erosion perimeter averaged 307 ± 23 mm (range = 37 to 1169 mm). Distal erosion perimeter as a percentage of total blade perimeter increased across the 3 blade condition cat-

egories (mean = 18 ± 5% for >75% intact blades, 31 ± 4% for 50–75% intact blades and 43 ± 4% for <50% intact blades). Percent cover of the epiphytic bryozoan *Membranipora serrilamella* on the experimental kelp blades was low, averaging 2.3 ± 0.6% among blades with *M. serrilamella* present, and ranged from 0 to 14% across all experimental blades. *M. serrilamella* was absent on 46% of blades.

Water motion

Clod card dissolution rate was strongly correlated with the motion settings on the orbital shaker table (Fig. 1; least-squares regression, $F_{1,7} = 36.9$, p < 0.001, $r^2 = 0.84$), and dissolution was 3 times higher at the highest agitation level compared to the lowest. In the field, the dissolution rate of clod cards fell within the range of the laboratory rates, and the level of water motion, as indicated by the dissolution rate, was similar across the 2 sites (Fig. 1).

Correlates of kelp detritus production

POC and PON production per blade were highly correlated (least-squares linear regression, $r^2 = 0.86$, p < 0.0001). Therefore, we only present results pertaining to carbon; analyses for nitrogen showed virtually identical results. Blade age category was a significant positive predictor of kelp detritus production in laboratory experiments, but the regression
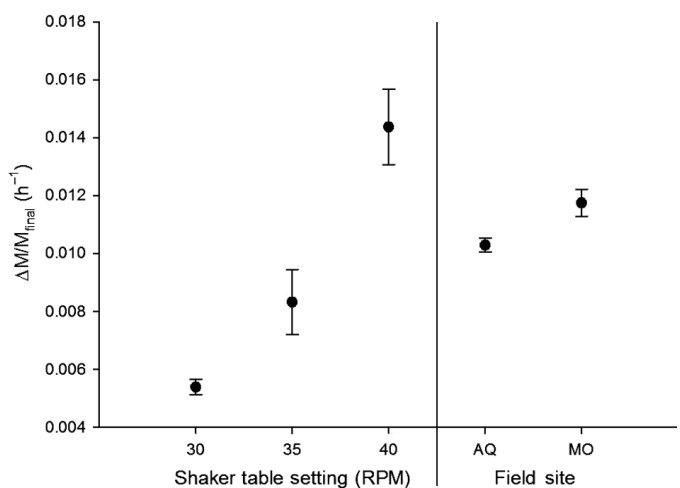

Fig. 1. Mean dissolution rates (±SE) of plaster clod cards on the shaker table in the laboratory at 30, 35, and 40 rotations per minute (RPM; n = 3 per setting), and in the field at Arroyo Quemado (AQ, n = 9) and Mohawk (MO, n = 8) Reefs. Dissolution rates are expressed as the proportional change in mass, $\Delta M/M_{final}$ (h^{-1})

Table 1. *Macrocystis pyrifera.* ANCOVA analysis of total detrital carbon production (ln transformed) by the factors blade condition (fixed, 3 levels: <50, 50–75%, and >75% whole), water motion (fixed, 3 levels: 30, 35, and 40 RPM), and covariate blade mass (g wet mass)

Source	df	SS	F	p
Blade condition	2	3.599	4.621	0.01
Water motion	1	0.432	1.111	0.30
Blade mass (g)	1	0.958	2.460	0.12
Blade condition × water motion	1	1.850	2.376	0.10
Error	65	25.31		
Adjusted r^2				0.14

Table 2. *Macrocystis pyrifera.* Stepwise multiple regression analysis investigating the relative contributions of (1) blade condition, (2) blade wet mass, (3) blade perimeter, (4) distal erosion length and (5) water motion to variation in the amount of detritus produced from *Macrocystis* blades incubated in enclosed bags in the laboratory per day, ln(C d^{-1}). Only those independent variables that met the inclusion criteria for entering into the model are shown

Source	df	SS	F	p
Blade condition	1	2.351	10.33	0.002
Distal erosion	1	0.396	1.738	0.19
Wet mass	1	1.296	5.695	0.02
Error	68	15.47		
Adjusted r^2				0.16

model explained only 14% of the observed variation (Table 1, adjusted r^2 = 0.14, SS = 3.69, F = 2.93, p = 0.01). Significantly more particulate carbon was shed by the 2 classes of degraded blades (50–75% and <50% intact) compared to the >75% intact blades (Tukey's HSD, p < 0.05), but there was no difference between the 50–75% and <50% categories (Tukey's HSD, p = 0.6). Stepwise multiple regression showed that blade mass, blade age category, and distal erosion perimeter best explained the mass-specific production of detrital POM in laboratory experiments, but again the model explained relatively little of the observed variation (Table 2, adjusted r^2 = 0.16, df = 3, SS = 3.80, F = 5.56, p < 0.001). Water motion and blade perimeter were not significant predictors of detrital production.

Kelp detritus production and characteristics: carbon

Kelp blades shed an average 842.9 ± 115 µg POC g^{-1} blade dry mass d^{-1} when averaged across both the laboratory and field experiments (Fig. 2). Most (70 ± 2%) of this carbon was in the <250 µm size fractions that are available to suspension feeders (Fig. 1). Laboratory-incubated blades generally shed more particulate carbon than field-incubated blades ($F_{1,79}$ = 7.80, p < 0.01). These differences were significant in 2 size fractions: 25–125 µm (t = 2.08, df = 79, p < 0.05) and 0.25–1 mm (t = 5.29, df = 79, p < 0.001; Fig. 2). Overall, successively larger size fractions produced
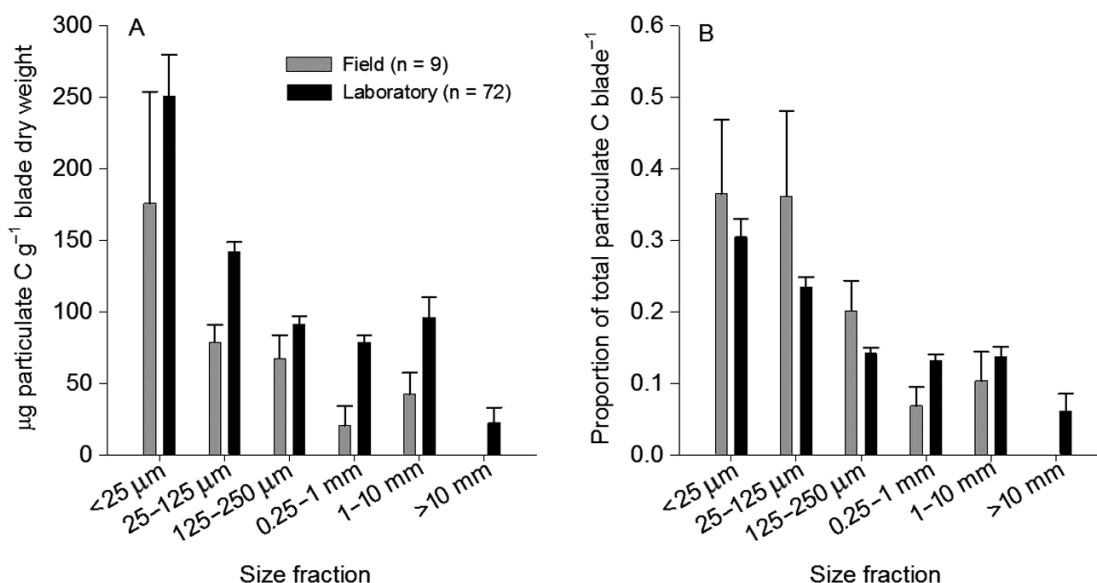

Fig. 2. (A) Mean (±SE) size-fractionated mass of detrital carbon produced per g blade dry weight during 24 h laboratory and *in situ* incubations. (B) Mean proportion (±SE) of total detrital carbon in different size fractions produced by *Macrocystis* blades during laboratory (black bars) and field (grey bars) incubations

less C. The largest size fraction (>10 mm) was completely absent in the field experiment and contributed the smallest proportion of carbon in the laboratory experiment.

Kelp detritus production and characteristics: nitrogen

PON produced by the kelp blades averaged 108.7 ± 18 µg N g^{-1} blade dry weight d^{-1} when averaged across both the field and laboratory experiments (Fig. 3). Like POC, most ($73 \pm 2\%$) of the PON was found in the <250 µm size classes (Fig. 3), and laboratory-incubated blades shed more PON than field-incubated blades ($F_{1,79} = 9.15$, p < 0.01), differences significant for the 25–125 µm ($t = 2.07$, df = 79, p < 0.05), 0.25–1 mm ($t = 3.79$, df = 79, p < 0.001), and 1–10 mm size classes ($t = 2.23$, df = 79, p < 0.05; Fig. 3A). Larger size fractions contributed successively less PON to the total pool, as was the case for POC. The carbon to nitrogen ratio of kelp POM averaged 7.54 ± 0.2 and ranged between 5.0 and 17.3.

Reef-scale estimates of detrital production

The calculated contribution of kelp-derived POM to the total pool of POC and PON at Mohawk Reef was found to be negligible. Applying our detrital production rates to the 5 yr monthly time series of

kelp biomass yielded an average *Macrocystis* contribution of 131.9 ± 16 mg POC m^{-2} d^{-1} and 18.8 ± 2 mg PON m^{-2} d^{-1} to the suspended POM pool at Mohawk Reef. The suspended POM pool during this time averaged 3982.7 ± 389 mg POC m^{-2} and 678.2 ± 70 mg PON m^{-2}. Using a water residence time of 1.1 h (Fram et al. 2008), this translates to a *Macrocystis* contribution of 0.18% of the POC and 0.15% of the PON present on the reef during the 5 yr period. Kelp biomass, KDC$_{shed}$, and residence time all contributed equally to the calculated POC/PON; i.e. a 25% increase in any of these factors resulted in a 25% increase in POC/PON. Using a longer residence time of 6 h, which may better characterize a larger kelp forest (Fram et al. 2008), resulted in increased contributions that were nevertheless still quite small: 0.96% of reef POC and 0.80% of PON. Seasonally, kelp detritus contributions to POC and PON varied with kelp biomass, reaching lows in winter 2008 and winter-spring 2010 (Fig. 4). Highest contributions were generally during spring through autumn. Total POC peaked in spring for all years (Fig. 4), most likely reflecting the spring phytoplankton bloom in the Santa Barbara Channel driven by seasonal upwelling (Brzezinski & Washburn 2011). PON followed a similar pattern, although in 2011 PON remained similar from spring-autumn (Fig. 4). Lowest abundance of POC and PON was generally in winter, although this pattern was most consistent for PON (Fig. 4).
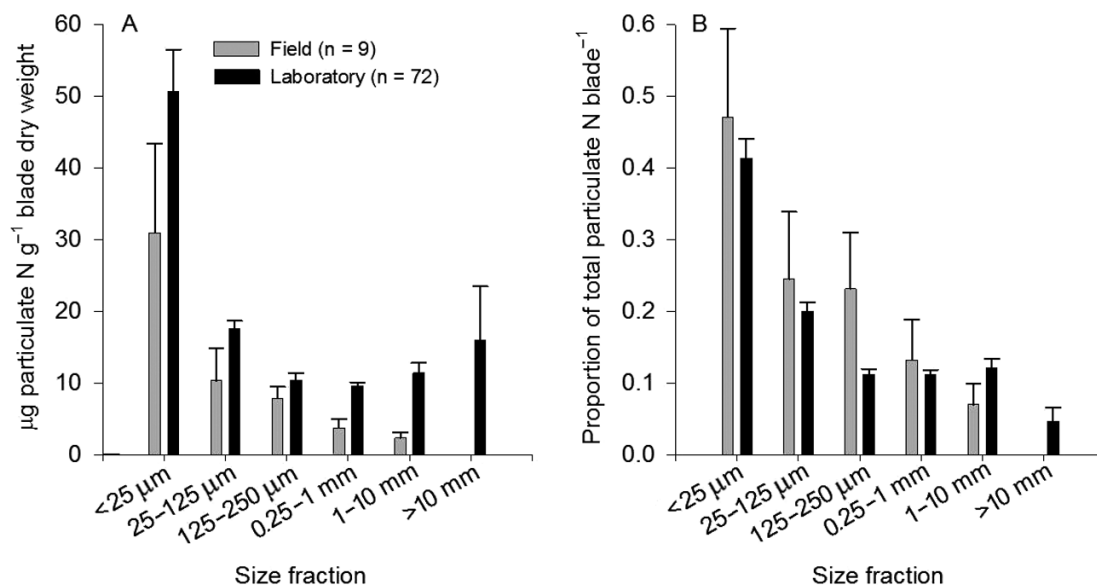

Fig. 3. (A) Mean (±SE) size-fractionated mass of detrital nitrogen produced per g blade dry weight during 24 h laboratory (black bars) and *in situ* (grey bars) incubations. (B) Mean proportion (±SE) of total detrital nitrogen produced within different size fractions by *Macrocystis* blades during laboratory (black bars) and *in situ* (grey bars) incubations
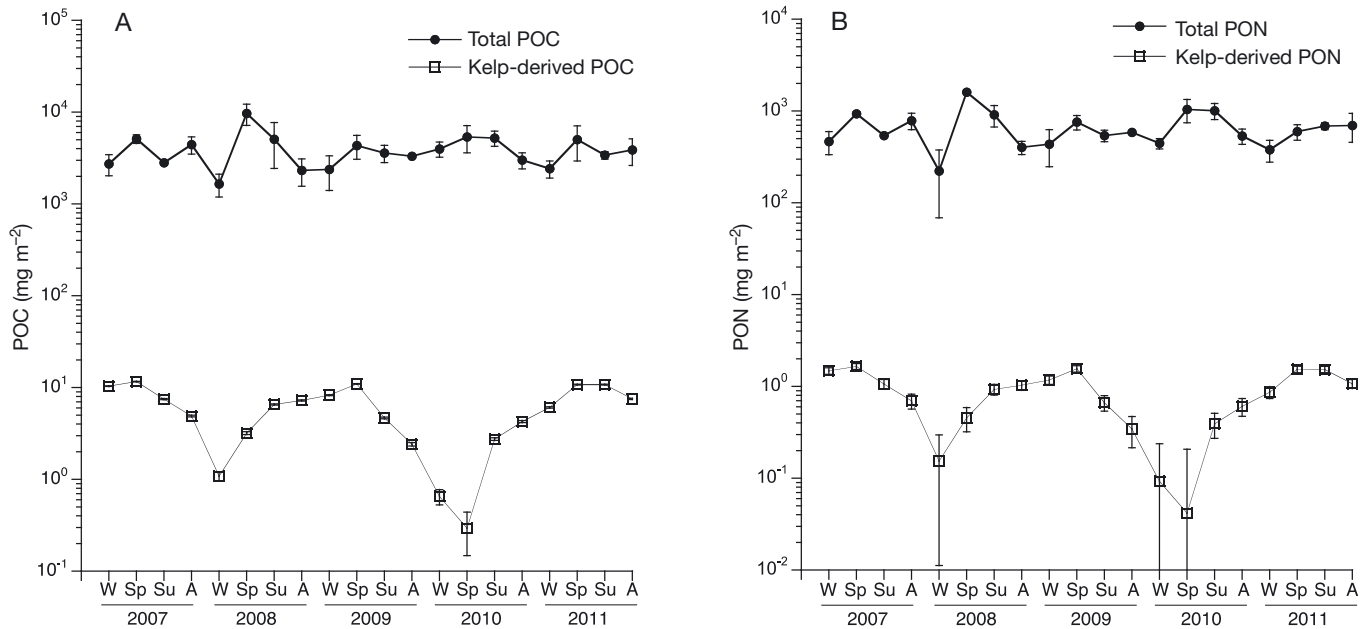
Fig. 4. Time series of (A) particulate organic carbon (POC) and (B) particulate organic nitrogen (PON) at Mohawk Reef from 2007 to 2011. Solid symbols: total POM pool measured monthly and averaged by season; open symbols: kelp-derived detritus estimated using experimentally measured rates of detritus generation combined with monthly kelp biomass measured on the reef and assuming a reef water residence time of 1.1 h

DISCUSSION

Potential importance of kelp detritus as a trophic resource

Kelp detritus has been argued to be a significant food source to kelp forest suspension feeders based largely on stable isotope evidence (reviewed by Miller & Page 2012), implying that kelp detritus is (1) within the size spectrum of particles consumed by suspension feeders, and (2) abundant enough to be a significant component of suspended POM. Thus far, however, no quantitative estimates have been made of the size spectrum of suspended kelp detritus, and estimates of production quantities of suspended kelp detritus have relied on indirect measures such as rates of blade erosion (Newell et al. 1982, Krumhansl & Scheibling 2011, 2012). Suspension feeders consume particles across a wide size spectrum, ca. <1 to 300 µm (reviewed by Shimeta & Jumars 1991, Ward & Shumway 2004), and the majority of detrital particles produced by *Macrocystis* blades were within this range. Over 70% of detrital kelp carbon and 60% of nitrogen were partitioned in particles ≤250 µm, which encompasses the size range of most phytoplankton as well as bacterioplankton—the major food sources of most suspension feeders. Furthermore, the C:N ratio of kelp detritus particles was relatively low, averaging 7.5, which is at the extreme low end of the wide

range reported for living kelp blades in the Santa Barbara Channel (7% to 38%; Brzezinski et al. 2013). This low C:N ratio could be due to the presence of microbial biomass on decaying kelp particles, and might make kelp detritus a relatively high quality food source (Duggins & Eckman 1997). However, the contribution of kelp detrital carbon and nitrogen relative to the total suspended POM pool was small, comprising <1% even when assuming a long (6 h) seawater residence time in the kelp forest and zero removal. Furthermore, if any of the variables in our calculations, including detrital generation rates, were off by an order of magnitude, the resulting particulate C or N contributions of kelp detritus would still amount to less than 2% of the total POM pool. Even this small value is an overestimate of the amount of kelp POM available to a typical suspension feeder, since most ingest particles only 1 to 10 µm in diameter (LaBarbera 1984). This paucity makes it unlikely that kelp detritus comprises a significant source of food for benthic suspension feeders. Some suspension-feeding species attach directly to *Macrocystis* blades and stipes, and these animals could conceivably use kelp detritus as a food source before it is diluted throughout the water column. In kelp forests of southern California, for example, bryozoans (e.g. *Membranipora* spp.) and hydroids (e.g. *Sertularia* spp.) commonly grow on kelp. Indeed, there is evidence that *Membranipora* may rely on kelp-derived

DOM as a source of nutrition (De Burgh & Fankboner 1978). Suspension-feeding crustaceans, including the kelp canopy mysid *Holmesimysis costata*, amphipods, ostracods, and copepods, are also common in the kelp forest canopy (Coyer 1984) and could exploit kelp detritus as food. However, the biomass of suspension feeders is much larger on the benthos, where most work on the contribution of kelp as a food source has focused. Our results indicate that giant kelp detritus is not abundant enough at any time of the year to be a significant food source for these reef suspension feeders. This conclusion is reinforced by experimental feeding studies that have shown some suspension feeders actively select against kelp detritus in the presence of phytoplankton (Cranford & Grant 1990, Levinton et al. 2002), suggesting it is unlikely that the importance of kelp detritus as a food source is magnified relative to its abundance through selective feeding by suspension feeders.

These results conflict with the body of work reporting large contributions of kelp carbon in both POM and the tissues of suspension feeders inferred using stable isotope distributions. Using stable isotope data and mixing models, 20 to >80% of the diets of suspension feeders have been asserted to consist of kelp-derived particles on shallow rocky reefs across the world (Dunton & Schell 1987, Duggins et al. 1989, Kaehler et al. 2000, Fredriksen 2003, Tallis 2009). What explains this discrepancy? Two factors influence the possible importance of kelp detritus as a POM source: the production of kelp detritus and the total quantity of POM available from all sources. Our study was done in the Santa Barbara Channel in forests of *Macrocystis*, while other published studies encompass many different locations and kelp species, some of which may generate more significant quantities of detritus. It is unlikely that location and species identity fully account for this discrepancy, however, as the standing biomass and production of *Macrocystis* are comparable to that measured for other species of kelp at other locations (Reed & Brzezinski 2009). Concentrations of POC and PON in the Santa Barbara Channel, an upwelling region, are relatively high due to phytoplankton production (Brzezinski & Washburn 2011), but this is similar to other upwelling zones where kelps thrive (Bracken et al. 2012). It is noteworthy that patterns of stable isotope data obtained from Mohawk Reef and other kelp forests in the Santa Barbara Channel were very similar to those observed in other kelp forest isotope studies: $\delta^{13}C$ values of suspension feeders reflected those of bulk POM, which had a $\delta^{13}C$ signature that was between that of kelp and offshore phytoplankton

(Page et al. 2008). Previous studies interpreted this pattern as a high contribution of kelp carbon to reef POM as well as to suspension-feeder diets. Isotope values of POM at the Santa Barbara sites, however, were unrelated to kelp biomass and instead were correlated with chlorophyll concentration and phytoplankton production, suggesting that enriched isotope values of POM were driven by phytoplankton (Page et al. 2008, Miller & Page 2012, Miller et al. 2013). Increased growth rates can drive ^{13}C enrichment of phytoplankton (Laws et al. 2002), and this process likely leads to POM $\delta^{13}C$ enrichment during phytoplankton blooms (Miller & Page 2012, Miller et al. 2013). Our results indicate that kelp detritus makes up a tiny fraction of total POC and PON in the kelp forest, which is consistent with the conclusions of Page et al. (2008) and Miller et al. (2013) that phytoplankton, rather than kelp detritus, drives temporal variability of suspended POM $\delta^{13}C$ in the Santa Barbara Channel.

Using blade loss rate measurements, Krumhansl & Scheibling (2011) estimated the rate of detrital production in Nova Scotian kelp beds as 150 to 513 g C m^{-2} yr^{-1}. Comparing this rate with phytoplankton production off Nova Scotia, cited as 190 g C m^{-2} yr^{-1} (Platt 1971), Krumhansl & Scheibling (2011) asserted that detritus produced by kelps *Saccharina longicruris* and *Laminaria digitata* might be the main food source for suspension and deposit feeders in the region. No measurements of particle size distribution were done. Our rates of particulate detritus generation by attached blades of *Macrocystis,* combined with the mean blade biomass of *Macrocystis* in the kelp forest at Mohawk Reef averaged over 5 yr, yielded an estimate of detrital production by blades of 48.5 ± 10 g C m^{-2} yr^{-1}. This value is surprisingly close to the Nova Scotia range, given that it only includes particles ≤250 µm, and it is well within the range cited in a recent review of kelp detritus generation rates (Krumhansl & Scheibling 2012). In the Santa Barbara Channel, phytoplankton production is somewhat higher than that in Nova Scotia, averaging ~260 to 690 g C m^{-2} yr^{-1} (Shipe & Brzezinski 2003, Brzezinski & Washburn 2011) suggesting that the production of kelp detritus ≤250 µm in size can be nearly 20% of that by phytoplankton. Two considerations are likely to substantially reduce the importance of kelp detritus despite its seemingly significant rate of production on reefs. First, because kelps are restricted to shallow reefs within the photic zone, the area of the coastal ocean that supports kelp production is substantially smaller than that which supports phytoplankton production. Detritus generated

by kelps will be dispersed and diluted to non-reef areas by physical processes governing along- and cross-shore transport, greatly lowering the biomass of kelp detritus in the water column relative to its production. Phytoplankton production, on the other hand, occurs across a more expansive habitat—the photic zone across the entire ocean—and phytoplankton biomass and production can be uniformly high in shallow coastal waters (Lucas et al. 2011a,b, Goodman et al. 2012). Secondly, phytoplankton grow and divide in the water column where they accumulate in typically nonequilibrial fashion as living cells. Kelp detritus, on the other hand, does not have the capacity to self propagate, as it is presumably shed as moribund or senescing cells that begin rapid decay (Newell et al. 1982).

Factors affecting kelp detritus production

As *Macrocystis* blades age, they tend to erode from the tip, and the eroding edge is tattered and soft. Therefore, we, like others, hypothesized that most detritus generated from kelp blades would be produced from the eroding edge of the blade. However, little variation in the rate of detrital shedding was explained by a regression model that included the length of eroding blade perimeter, as well as the overall state of blade degradation. This could be due to detrital production by the interior of the blade, away from the edge. *Macrocystis* blades are typically pitted with small holes and cavities, and these may be significant sources of detritus in addition to the eroding edge of the blade. Nevertheless, the blade degradation categories probably captured the overall state of blade grazing, pitting, and senescence, and did not substantially improve our model fit. Another possibility is that loss of detritus from gross blade erosion may be mostly in the form of larger pieces, or in some cases from direct grazing (Dixon et al. 1981), which are not relevant to consideration of suspended POM pools, and are detectable only over longer time scales than our 24 to 48 h incubations.

Water motion was not a significant predictor of the production of small particles of detritus by kelp blades in our study. This cannot be attributed to artificially low rates of water motion, since clod card dissolution rates in the experiments bracketed those measured *in situ* (Fig. 3). Storm disturbance has often been implicated in loss of *Macrocystis* biomass, but this loss primarily results from the removal of whole plants and fronds (Dayton & Tegner 1984, Seymour et al. 1989, Reed et al. 2008, 2011). Despite this noticeable episodic effect of waves, most seasonal variation in the dynamics of *Macrocystis* biomass is explained by the progressive senescence of fronds on attached plants (Rodriguez et al. 2013). Our results suggest that lower levels of water motion, while influencing nutrient availability and gas exchange of kelps (Hurd 2000), may not significantly affect production of small suspended detrital particles.

Other factors that may influence rates of detrital production by kelps include temperature and grazing. Hobday (2000) found that detached, floating *Macrocystis pyrifera* plants degrade at a constant rate of 0.64 cm d^{-1}, with rates increasing sharply above a 20°C threshold. Similarly, Rothäusler et al. (2009) found a positive relationship between temperature and degradation of *Macrocystis* across a latitudinal gradient, and this was exacerbated by increases in grazing under warm conditions. Krumhansl & Scheibling (2011) also found that rates of blade erosion in kelps *Laminaria digitata* and *Saccharina longicruris* were positively related to temperature. Our experiments were done at ~16°C, slightly above the mean of 15.3°C for the Santa Barbara Channel for the period 1997 to 2000 (Otero & Siegel 2004). Maximum mean sea surface temperatures in the Channel typically reach ~19°C (Otero & Siegel 2004), with higher temperatures occurring during El Niño Southern Oscillation (ENSO) events. Rates of blade degradation may be higher during such conditions (Hobday 2000), which could lead to increased detrital production. Any such increases, however, are likely to be temporary since such warm temperatures are accompanied by declines in kelp abundance (Parnell et al. 2010).

Few large organisms graze directly on kelp; sea urchins occasionally cause whole plants to break free from the bottom, but typically subsist on drift kelp that sinks to the bottom (Harrold & Reed 1985, Watanabe & Harrold 1991). Small invertebrate grazers, including small crustaceans and gastropods, however, are common in the *Macrocystis* canopy (Coyer 1984, 1987). Although their abundance is apparently regulated by fish predation (Davenport & Anderson 2007), these small grazers may reach larger abundances during ENSO events, causing declines in kelp biomass and recruitment (Tegner & Dayton 1987, Graham 2002). When their abundance is lower, the feeding activity of small grazers could enhance the production of small kelp detrital particles. A similar mechanism, 'sloppy feeding' by copepods, has been implicated as a major source of DOM to marine food webs (Møller et al. 2003, Steinberg et al. 2004).

Seasonal variation in kelp detrital production is unlikely to influence its importance to the POM pool (see above), but is worth discussion in the context of kelp population dynamics. *Macrocystis* fronds are initiated continuously throughout the year as older fronds are shed when they approach a terminal age (Gerard 1976, Rodriguez et al. 2013). This pattern likely drives the declines in kelp abundance often seen during summer and autumn, as springtime surges in frond initiation are followed by senescence 3 to 4 mo later (Rodriguez et al. 2013). Winter storms also typically remove large amounts of kelp biomass from California kelp forests, but most of these losses are in the form of whole plants or fronds (Reed et al. 2008). The resulting low winter standing biomass of kelp underlies the low detrital production we estimated for winter (Fig. 4). Therefore, in California we may predict that detrital generation may peak in summer and autumn given seasonal patterns of growth and senescence in *Macrocystis*.

The high productivity of *Macrocystis* results from rapid growth of a relatively small standing biomass that turns over multiple times per year (Reed et al. 2008). This growth strategy produces large amounts of detritus in the absence of massive grazing. Nevertheless, our results suggest that although the bulk of small kelp detrital particles lie well within the size range consumed by suspension feeders, their biomass relative to the total POM pool is low, making them an unlikely source of nutrition for these consumers. The restricted depth range of kelps, the degradation of detritus by microbes, and the relatively rapid flux of water and particulates through kelp forests is likely to reinforce this conclusion. This certainly does not imply that *Macrocystis* is a trophic dead end. Kelp detritus may comprise an important part of the 'microbial loop' in the kelp forest and surrounding coastal waters (Newell et al. 1982). Larger pieces of kelp detritus, however, provide an important food source to detritivores in the kelp forest and in adjacent intertidal and deep water ecosystems, and likely constitute the most important contribution of kelp detritus to marine food webs.

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