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Mass-transfer gradients across kelp beds influence *Macrocystis pyrifera* growth over small spatial scales

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ABSTRACT: Nitrogen is essential for algal productivity but often reaches limiting concentrations in temperate ecosystems. Increased water motion enhances nitrogen uptake by decreasing the thickness of the diffusion boundary layer surrounding algal surface tissue, allowing for increased nitrogen mass-transfer across this boundary. *Macrocystis pyrifera* forms large beds that span the water column and can alter the surrounding physical environment by creating bed-wide boundaries that may reduce current and wave propagation to the bed interior; reduced water motion may decrease mass-transfer rates and therefore alter nitrogen uptake. We investigated whether a water mass-transfer gradient across *M. pyrifera* beds exists by identifying 3 bed types likely to experience different water motion intensities (open, shoreline exterior and shoreline interior) and whether this gradient influenced heterogeneity in *M. pyrifera* growth and tissue status during low nitrogen (summer) and high nitrogen (winter) conditions. Gypsum dissolution suggested that mass-transfer significantly increased across beds; open bed dissolution rates were approximately 6% higher than the shoreline exterior, which exhibited mean dissolution rates 17% higher than the shoreline interior. Summer kelp growth, pigmentation, tissue %N and C:N paralleled mass-transfer, where exterior kelp exhibited higher values than interior kelp. The same trends did not exist during the winter, when ambient nitrogen concentrations were high, suggesting that mass-transfer is an important mechanism for nitrogen acquisition during limitation events. This study highlights mass-transfer variability across relatively small macroalgal beds and the corresponding effects on kelp growth and nitrogen status, which previously might have been assumed as uniform due to the general wave exposure.

KEY WORDS: Water motion · Algae · Nitrogen · Limitation · Hydrodynamic · Nutrient

INTRODUCTION

Marine primary productivity is fundamentally governed by light (Dayton et al. 1999), nutrient supply (Foley & Koch 2010) and temperature (Dayton et al. 1992). These factors vary over space and time, influencing the distribution, growth rate and physiology of macroalgal populations (Dayton et al. 1999). During the summer, temperate coastal waters typically have low nitrogen concentrations, which can reduce algal growth and overall productivity (Hanisak 1979, Zimmerman & Kremer 1986, Brown et al. 1997) because nitrogen is essential for tissue and pigment construction and maintenance (Shivji 1985). *Macrocystis pyrifera* is the world's largest and fastest growing alga; it thus has a high nutrient demand (Gerard 1982a). Changes in kelp growth or competitive strategy as a result of reduced nitrogen availability may have large-scale ecological consequences, as kelp forms conspicuous beds that provide food and shelter to numerous temperate invertebrates (Estes et al. 2004, Christie et al. 2009), coastal fishes (Anderson

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1994, Norderhaug et al. 2005) and other vertebrates — i.e. marine mammals and birds (Graham et al. 2008) — in both hemispheres.

Water motion can ameliorate nutrient limitation events by providing enhanced nitrogen uptake via increased water mass-transfer rates (Hurd 2000, Kregting et al. 2008). As water flows over kelp, a concentration gradient in dissolved metabolic products and wastes forms between the bulk seawater and the surface tissue (Hurd et al. 1996, Sanford & Crawford 2000, Hurd & Pilditch 2011). In this region, the movement of dissolved substances is predominately through molecular diffusion, and it is known as the diffusion boundary layer (DBL). Thicker DBLs can lead to slower nutrient uptake (mass-transfer), whereas increased water motion decreases the DBL thickness, increasing the relative concentrations of nutrients at the blade surface compared to under slower flows (Hurd 2000). Mass-transfer is faster through turbulent boundaries (i.e. wave induced) than laminar boundaries (i.e. current induced) (Anderson & Charters 1982) and may be a critical mechanism increasing nutrient acquisition in nutrient-limited conditions (Gerard & Mann 1979).

Both laboratory experiments and *in situ* studies have described enhanced nutrient uptake and growth rates in macroalgae and seagrass exposed to increased water motion (Hurd et al. 1996, Thomas et al. 2000). Hepburn et al. (2007) found that *M. pyrifera* in wave-exposed sites displayed higher growth rates and higher tissue nitrogen concentrations than did individuals growing in wave-sheltered sites. Furthermore, *M. pyrifera* is unique in that it is an ecosystem engineer (Jones et al. 1994) and has the ability to alter the physical environment in which it lives by modifying light penetration to understory algae (Reed & Foster 1984, Stewart et al. 2009) and by slowing water motion by up to 70% (Jackson & Winant 1983, Gaylord et al. 2007). Such water-motion buffering may increase the thickness of the DBL above *M. pyrifera* blades for individuals located in the interior of the kelp bed, thus reducing mass-transfer rates. Stewart et al. (2009) showed that *M. pyrifera* growing on the edge of a kelp bed displayed higher growth rates and higher tissue carbon and nitrogen concentrations than kelp found in the interior of the same bed but attributed these differences primarily to edge individuals receiving more light than interior individuals; water mass-transfer was not measured. Besides water motion and light, nutrients and temperature are other primary factors that influence macroalgal growth; however, with regular wave- and current-induced water exchange, ambient nutrient concentrations within a kelp bed are not expected to differ from those outside the bed (Fram et al. 2008). Using the same logic, water temperature inside and outside a given bed should also be similar. Therefore, intra-bed variability in nutrient uptake and productivity may be driven by variability in mass-transfer rates. Jackson (1977) reported that cross-shore water motion penetrates 400 m into Californian kelp beds. Not all algal beds occupy such a large area, and it is unclear whether smaller beds experience uniform or heterogeneous mass-transfer rates; research is therefore warranted to investigate whether intra-specific differences in kelp growth, physiology and tissue chemistry can be attributed to differences in mass-transfer within the same bed.

In this study, we investigated whether a mass-transfer gradient across *M. pyrifera* kelp beds exists, and then whether this exposure gradient influences growth, erosion, pigment concentrations, tissue nitrogen and C:N ratios. To test whether a mass-transfer gradient is a general phenomenon that occurs in different habitats with similar algal structure, we selected 2 regions within southeast New Zealand that differ in light and fluvial regimes: the Otago coast and NE Stewart Island. All sites were established on points or small headlands sheltered from prevailing wind and swell and therefore were moderately exposed to waves and currents. The Otago coast is subject to increased freshwater input via larger rivers; these rivers deliver fine sediments to the nearshore and thus increase water turbidity and decrease light penetration (Pritchard et al. 2013). Nearshore Stewart Island experiences diffuse freshwater input from small streams, and light penetrates deeper (N. Desmond, D. W. Pritchard, C. Hepburn unpubl. data). The mass-transfer gradient was identified in relatively small fringing beds (10 to 20 m wide), which paralleled the rocky shoreline, and also in small open kelp beds (20 to 30 m diameter), which grew on isolated reefs not directly linked to the shore. Two subsites were established in fringing beds (interior and exterior), and 1 subsite was established in open beds (exterior); these 3 subsites were expected to experience a range of water motion intensity and therefore vary in water mass-transfer. This study includes 2 observation periods, one during low-nitrogen (summer) and the other during high-nitrogen conditions (winter). We analysed seawater nitrate (NO_3^-) and ammonium (NH_4^+) and tissue stable nitrogen isotopes ($\delta^{15}N$), which can give insight into nitrogen utilisation in conjunction with nitrogen availability; lighter nitrogen isotopes are preferentially assimilated over heavier isotopes (Sigman et al. 1999), so a lighter signature

may indicate exposure to a larger nitrogen pool. We first anticipated that mass-transfer rates would increase across the kelp bed exposure gradient (fringing interior < fringing exterior < open bed). Because nitrogen concentrations were likely to be low or limiting, we expected that summer observations of growth rate, total tissue nitrogen and pigment concentrations would increase with increasing mass-transfer across this gradient and that $\delta^{15}N$ would be lighter in bed types with increased mass-transfer because those kelp were likely to have access to more nitrogen and thus preferentially assimilate more ^{14}N. Finally, because higher C:N molar ratios suggest nitrogen limitation, we expected summer values to reflect lower C:N in bed types with increased water mass-transfer (i.e. open beds). We did not expect that growth and tissue chemistry would differ across the exposure gradient during the winter because light would be more limiting than nitrogen for all bed types.

MATERIALS AND METHODS

Study sites

This study was conducted along Otago and Stewart Island coastlines, which are situated in southeast New Zealand (Fig. 1A). Three replicate sites per region were selected, all with east-facing aspects on small headlands, and were not directly exposed to prevailing southerly wind or swell. Each site is characterized by *Macrocystis pyrifera*-dominated beds reaching 10 to 13 m (below mean low water) in depth; rocky reefs in these regions meet an expansive and uniform sandy benthos at such depths; therefore, the depths kelp-dominated beds can reach are physically restricted (Hepburn et al. 2011, authors' pers. obs.). Within each site, 3 subsites were established to test a gradient of exposure and kelp-bed position: fringing reef interior, fringing reef exterior and open reef (Fig. 1B).

Light, temperature and seawater nutrients

For the duration of the study, light and temperature loggers (HOBO® Pendant 64K–UA-002-64) were deployed at 2 m (below mean low water) at each site; this depth was chosen because 75% of the kelp biomass and productivity occurs in the top 2 m of the water column (North 1971). To prevent shading, algae were removed around the logger every 3 mo. Separate temperature loggers (HOBO® Water Temperature Pro v2 U22-001) were also deployed across

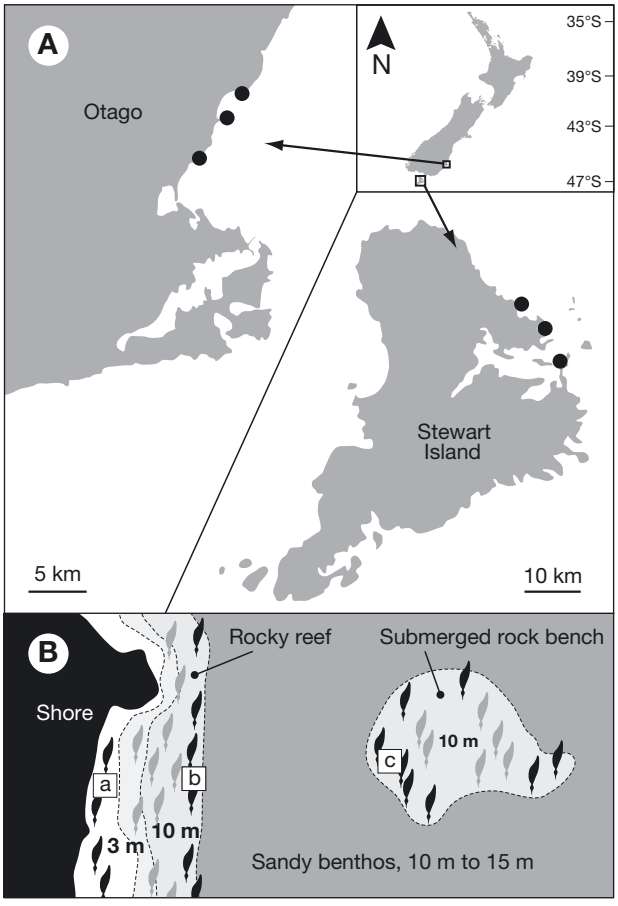

Fig. 1. (A) Study regions and associated sites within New Zealand. All sites are listed from north to south: Otago — Matainaka, Karitāne and Black Rocks; Stewart Island — West Head, Horseshoe Point and High Point. (B) Typical spatial and depth arrangement of subsites of *Macrocystis pyrifera* within a given site; open bed distance from shore ranged from 0.29 to 0.52 km. All kelp blades show typical bed coverage, while the black kelp blades indicate where tagging occurred in each bed type: (a) fringing interior, (b) fringing exterior and (c) open bed

the kelp beds; these were attached to kelp individuals at 2 m depth in each subsite. Due to risk of thallus loss, these loggers were deployed for only 1 wk in April 2013. Seawater nitrate (NO_3^-) and ammonium (NH_4^+) concentrations were determined at the beginning and end of each growth observation period. Seawater samples, in replicates of 3, were collected from 2 m below the surface at each subsite. In both regions, all samples were collected within a 1 h time frame to minimize any temporal influence on nutrient concentrations. HCl-washed equipment was used throughout sampling, and seawater was immediately filtered (Whatman™ GF/C) and frozen. Samples were analysed using a Lachat® QuikChem 8500 automated ion analyser.

Water mass-transfer

Gypsum dissolution rates were used to quantify water mass-transfer in *M. pyrifera* canopies at each of the 18 subsites. This is an appropriate technique to measure mass-transfer in environments subject to different flow regimes (Porter et al. 2000). Blocks were prepared using gypsum (Calcium Sulphate Hemihydrate 100%) mixed with Milli-Q water in a ratio of 3:2 (w:w). This mixture was then transferred into 3 cm^2 moulds, and each block received a looped cable tie for attachment purposes before the mixture set. The blocks were dried at 65°C, and the initial weight was recorded. Ten blocks were attached to 10 separate *M. pyrifera* canopy fronds (1 m below the surface) in each subsite. After approximately 48 h, blocks were re-collected, dried at 65°C and final weights were recorded. Dissolution rates were expressed as weight (g) lost per hour.

M. pyrifera growth and erosion rates

Growth rates for *M. pyrifera* were determined during nutrient-limited and nutrient-saturated events, which coincided with summer (mid-December 2012 to mid-January 2013) and winter (mid-July 2013 to mid-August 2013), respectively. Growth rates were determined using methods modified from Hepburn et al. (2007). Thirty *M. pyrifera* individuals were haphazardly selected at each of the 18 subsites; the top 1 to 2 m of an adult frond from each was pulled aboard a small boat and tagged at the pneumatocyst-stipe joint using labelled flagging tape; tape was fluorescent pink and approximately 1 m long to facilitate re-location. In each tagged blade, a disc of tissue (1.5 cm diameter) was removed approximately 100 mm from the blade meristem to monitor blade growth. Four growth metrics were then collected (Fig. 2): blade elongation, blade erosion, stipe elongation and new blade production. Kelp fronds were returned to the sea, and about 1 mo after tagging events, the fronds were relocated via snorkelling, cut below the tagged blade and held in opaque plastic bags for transport to a laboratory. The 4 growth metrics were re-measured, and any fronds that were compromised (i.e. broken stipe) were not included in growth analysis. Daily relative growth and erosion rates (RGR, d^{-1}) were calculated using methods from Evans (1972). Tissue replacement rates were calculated by subtracting Δ erosion from the Δ blade elongation raw values; these were also converted into RGRs.

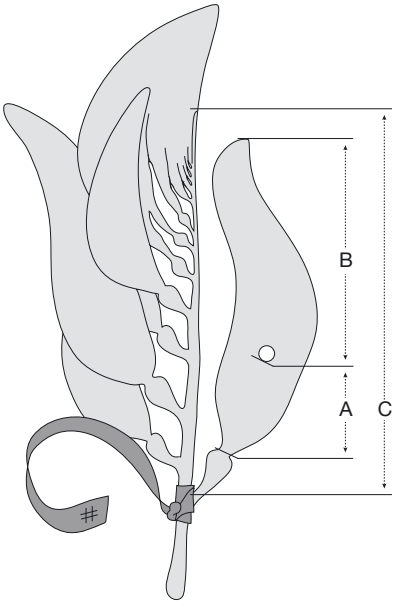

Fig. 2. Measurement strategy for *Macrocystis pyrifera* fronds. (A) Blade elongation — distance between the top of the pneumatocyst and bottom of the hole on the tagged blade, (B) blade erosion — distance from the bottom of the hole to the blade's distal tip, (C) stipe elongation — distance from the tagged joint to the stipe apical tip; new blade production was measured by counting the number of blades within this stipe segment

Pigmentation and tissue carbon, nitrogen and isotopic status

After frond collection, the blade below the tagged pneumatocyst-stipe joint was removed and tissue that had grown during the duration of the study's seasonal periods (circa basal: 85 mm) was excised. A leaf corer was used to remove discs of tissue (1.5 cm diameter), which were immediately frozen, before storage at –80°C until pigment extraction; these discs were also used to measure blade wet weight (g cm^{-2}). Pigment concentrations (chlorophyll *a*, chlorophyll *c* and fucoxanthin) were determined using methods modified from Seely et al. (1972) and Duncan & Harrison (1982), where DMSO was used for the primary extraction and acetone for the secondary. Results were expressed in micrograms per square centimetre of tissue.

The remainder of the excised blade tissue was freeze-dried and ground into a fine powder using a ball mill (Retsch® MM400), then stored in 5 ml tubes. Samples for C, N, $\delta^{13}C$ and $\delta^{15}N$ were prepared by weighing 1.5 mg of homogenised tissue into tin foil capsules (n = 3 $subsite^{-1}$). Nitrogen and carbon isotopes were assayed by combustion of the whole material in a Carlo Erba NC2500 elemental analyser (CE Instruments) and measured using a Europa Sci-

entific '20/20 Hydra' (Europa Scientific) isotope ratio mass spectrometer (IRMS) in continuous flow mode. Raw isotope ratios were normalised to the international scales using the IAEA (International Atomic Energy Agency) reference and the standards USGS-40 and USGS-41. C:N data are represented in the form of molar ratios instead of total carbon and nitrogen ratios.

Statistical analyses

The differences in means of selected categories of data (gypsum dissolution rates, seawater nutrients, growth rates, erosion rates, tissue chemistry, pigmentation, tissue wet weight) from each subsite (fringing interior, fringing exterior, open bed) were determined using a hierarchical linear model (HLM). The HLMs included a fixed factor (region), random factors (subsite nested within site) and the dependent variable (i.e. growth rate or %N). These models were run separately for each season because we expected that the mechanism of interest (cross-bed mass-transfer gradient) would not be present during the winter due to high ambient seawater nitrogen concentrations. The differences in means of data from the light + temperature loggers were determined using a 1-way ANOVA, while the means of the data from the temperature-only loggers were tested using nested ANOVA. Differences in means were determined using Tukey's honestly significantly different (HSD) post hoc test. Significance was set at the 5% level ($\alpha = 0.05$). Temperature and light data fulfilled prerequisites of normality (Kolmogorov-Smirnov test with Lilliefors correction) and equal variance (Levene median test) for parametric tests; HLMs do not require homogeneity or independence (Field 2012) and were therefore not tested for such. All statistical analyses were carried out using the software package R© Version 3.0.2.

Table 1. Statistical values derived from hierarchical linear models (HLMs) testing for differences of means across the mass-transfer gradient (bed type affect) for listed parameters. Otago and Stewart Island, New Zealand, were pooled into the same HLM, with region was included as a fixed factor. Significant results are highlighted in bold. na: not applicable; data not collected

Factor	Summer			Winter		
	df	*F*	p	df	*F*	p
Abiotic						
Nitrate (NO_3^-)	3,201	1.01	0.39	3,191	1.43	0.23
Ammonium (NH_4^+)	3,201	0.09	0.97	3,190	2.38	0.069
Temperature[a]	2,1240	1.55	0.212	na	na	na
Block dissolution[b]	2,78	21.38	**<0.001**	2,52	15.78	**<0.001**
Growth/erosion						
Blade	2,8	9.14	**0.009**	2,9	2.42	0.143
Stipe	2,8	8.22	**0.012**	2,9	0.38	0.698
New blades	2,8	2.18	0.175	2,9	0.70	0.520
Erosion	2,8	6.07	**0.025**	2,9	1.91	0.203
Tissue replacement	2,8	12.3	**0.004**	2,9	3.04	0.098
Tissue wet weight	2,8	7.67	**0.014**	2,9	8.51	**0.008**
Pigmentation						
Chlorophyll *a*	2,8	7.98	**0.012**	2,9	0.49	0.629
Chlorophyll *c*	2,8	5.28	**0.036**	2,9	1.50	0.274
Fucoxanthin	2,8	8.29	**0.011**	2,9	0.42	0.669
Total pigments	2,8	8.24	**0.011**	2,9	0.28	0.760
Tissue chemistry						
% C	2,8	0.32	0.733	2,9	0.13	0.878
% N	2,8	5.63	**0.029**	2,9	5.89	**0.023**
C:N	2,8	8.88	**0.009**	2,9	5.57	**0.027**
Isotopic signatures						
$\delta^{13}C$	2,8	4.74	**0.044**	2,9	0.02	0.983
$\delta^{15}N$	2,8	4.70	**0.045**	2,9	0.35	0.712

[a]As described in the text, temperature logger deployment across the mass-transfer gradient was limited
[b]December 2013 and August 2013 dissolution rates used for summer and winter, respectively; the third month fell between seasons

RESULTS

Light, temperature and seawater nutrients

Otago and Stewart Island had similar mean daily quantum doses during the summer, averaging 2.88 ± 0.19 and 3.23 ± 0.18 mol photons m^{-2} d^{-1}, respectively (df = 1,184; $F = 1.64$; p = 0.202). Winter light was lower in Otago, averaging 0.48 ± 0.04 mol photons m^{-2} d^{-1}; Stewart Island light levels averaged 0.92 ± 0.02 mol photons m^{-2} d^{-1} (df = 1,121; $F = 91.97$; p < 0.001). Temperatures in Otago and Stewart Island waters were significantly different during both seasons (summer: df = 1,184; $F = 375.3$; p < 0.001; winter: df = 1,121; $F = 1175.0$; p < 0001); Otago waters were warmer than those at Stewart Island during the summer (15.23 ± 0.06 and 13.92 ± 0.03°C, respectively) but colder during the winter (9.69 ± 0.04 and 11.10 ± 0.02°C, respectively). Temperature data from secondary loggers did not vary across bed type (Table 1). Both NO_3^- and NH_4^+ showed seasonal patterns, with low concentrations during

the summer and high concentrations in the winter (Fig. 3), and there was no significant difference in these nutrient concentrations across bed type (Table 1).

Water mass-transfer

The dissolution rates of the gypsum blocks significantly varied across the exposure gradient (Table 1), and the regions did not significantly differ from each other (df = 1,4; $F = 6.02$; p = 0.070). The pattern of dissolution rate was consistent, where blocks in fringing interior beds had lower rates than blocks in the fringing exterior, which had lower rates than the open beds (Fig. 4). The mean dissolution rate of the open bed blocks was approximately 6.0% (±2.4%) higher than that of the fringing exterior blocks, which exhibited a mean dissolution rate of 17.4% (±2.7%) higher than that of the fringing interior blocks.

M. pyrifera growth, tissue weight and pigmentation

Bed type (fringing interior, fringing exterior, open) significantly influenced all growth and pigment parameters during both seasons (Table 1); however, summer patterns were different from winter patterns. During the summer, when ambient nitrogen concentrations were low, blade elongation, stipe

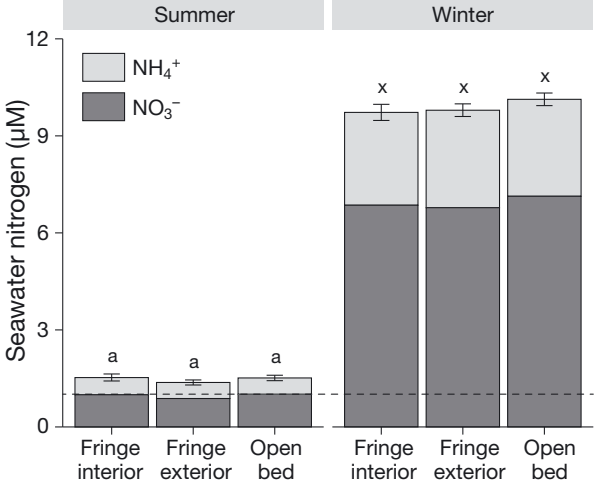

Fig. 3. Mean nitrate and ammonium seawater concentrations from Otago and Stewart Island, New Zealand. Samples of *Macrocystis pyrifera* were collected at the beginning and end of each observation period: December 2012–January 2013 (summer) and July 2013–August 2013 (winter). Dashed line indicates the 1 µM level, which indicates the concentration described as limiting kelp growth. Error bars: SE (n = 6). Letters above the bars represent post hoc grouping

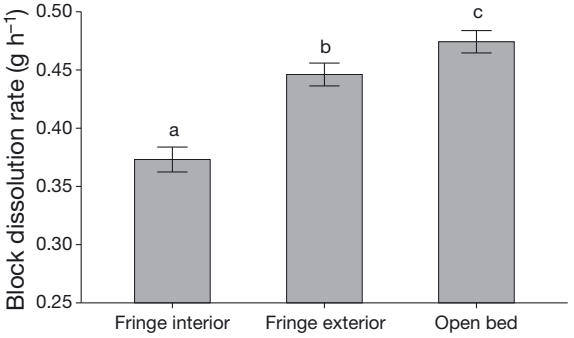

Fig. 4. Mean gypsum block dissolution rates from different types of kelp beds (*Macrocystis pyrifera*) at both Otago and Stewart Island, New Zealand. Blocks were deployed/received in August 2013, October 2013 and December 2013. Error bars: SE (n = 4). Letters above the bars represent post hoc grouping

elongation and tissue replacement rates increased across the mass-transfer gradient (increasing towards open beds) (Fig. 5). Blade erosion followed an inverse pattern, where erosion rates were lowest in the open beds and highest in the fringing interior. Summer blade production was the only growth parameter to not align with the mass-transfer gradient pattern seen in other parameters. During the winter, growth and erosion rates did not follow a consistent trend. Summer pigment concentrations significantly increased across the mass-transfer gradient, while bed type had no effect on winter concentrations (Fig. 6, Table 1). Total pigment concentration was much higher during the winter (df = 1,153; F = 653.91; p < 0.001).

Bed type also affected blade tissue wet weight. Summer blade wet weight increased across the mass-transfer gradient (Table 1): fringing interior weights were consistently lighter than fringing exterior, which were lighter than open bed values (0.039 ± 0.002, 0.045 ± 0.002, 0.052 ± 0.002 g cm^{-2}, respectively). Although bed type also had an effect on winter weights (Table 1), the pattern was not consistent with the mass-transfer gradient; the fringing subsites were grouped together and lighter than the open bed subsites (interior, exterior, open: 0.048 ± 0.003, 0.047 ± 0.003, 0.057 ± 0.004 g cm^{-2}, respectively). Mean winter tissue weights were not heavier than summer weights (df = 1,154; $F = 3.69$; p = 0.0566).

M. pyrifera tissue chemistry

During the summer, the nitrogen status of *M. pyrifera* blade tissue, indicated by %N and C:N, increased significantly with mass-transfer rates (Fig. 7,

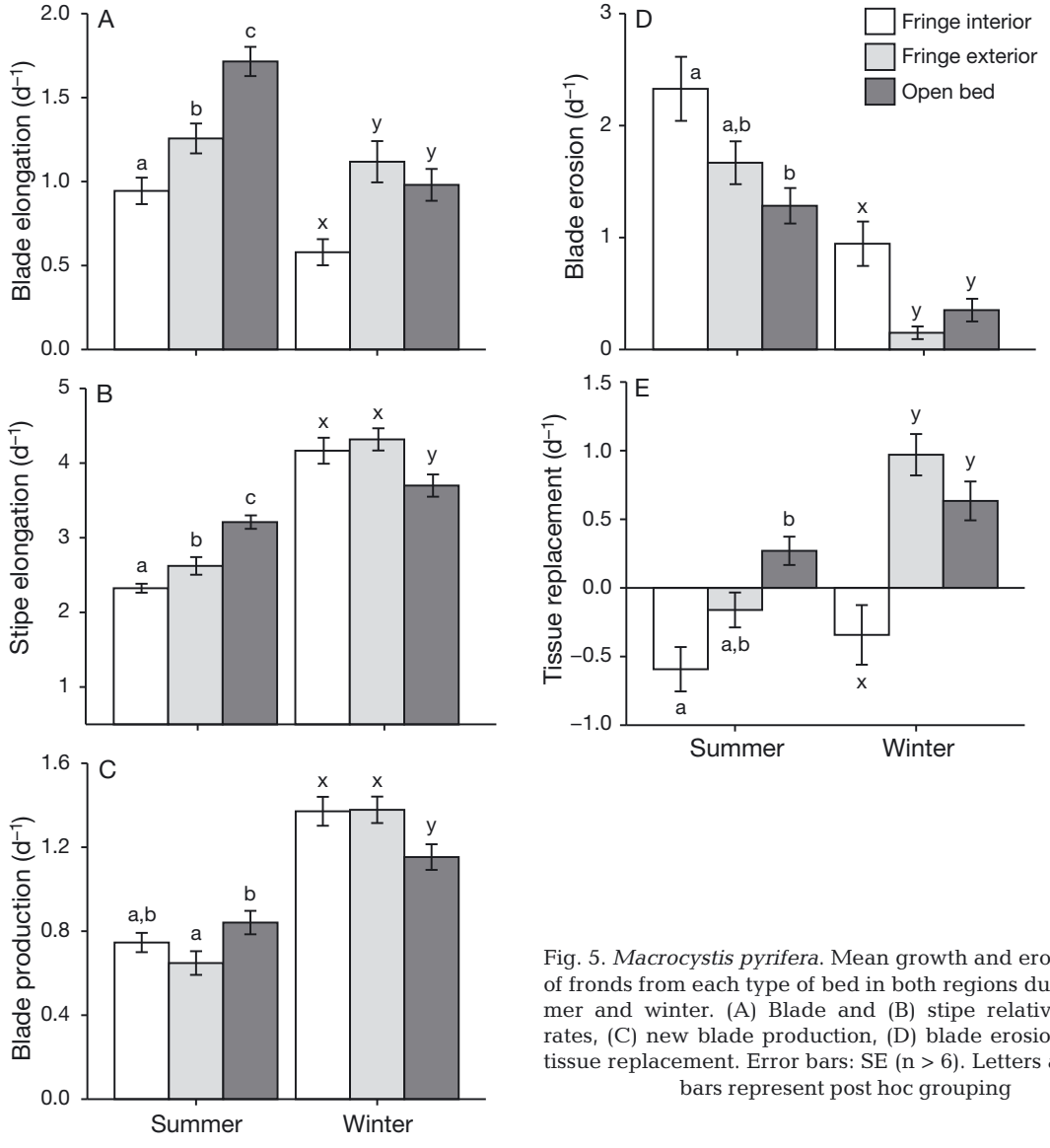

Fig. 5. *Macrocystis pyrifera*. Mean growth and erosion rates of fronds from each type of bed in both regions during summer and winter. (A) Blade and (B) stipe relative growth rates, (C) new blade production, (D) blade erosion and (E) tissue replacement. Error bars: SE (n > 6). Letters above the bars represent post hoc grouping

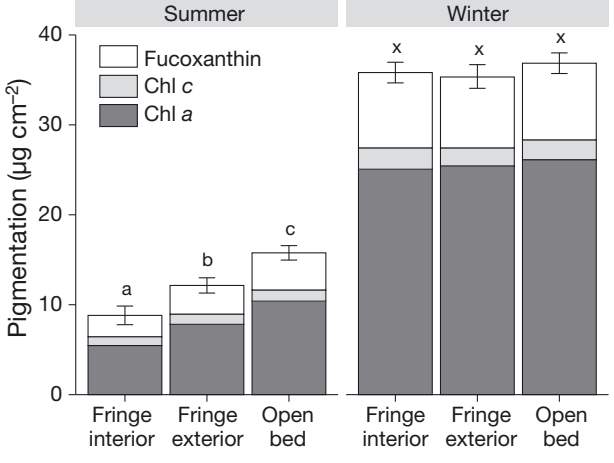

Fig. 6. *Macrocystis pyrifera*. Mean pigment concentrations in adult, surface canopy blades during the summer and winter from type of bed in both regions; all tissue was collected in the basal 100 mm of each blade. Error bars: SE of total pigments (n = 6). Letters above the bars represent post hoc grouping

Table 1). During the winter, %N significantly decreased with increasing mass-transfer rates and C:N significantly increased (Table 1), i.e. the opposite of the trend observed in summer. Summer $\delta^{13}C$ and $\delta^{15}N$ values were significantly heavier than winter values ($\delta^{13}C$: df = 1, 93; $F = 145.5$; $p < 0.001$; $\delta^{15}N$: df = 1, 92; $F = 208.0$; $p < 0.001$). Otago summer isotopic signatures (Fig. 8) were collectively lighter than Stew-

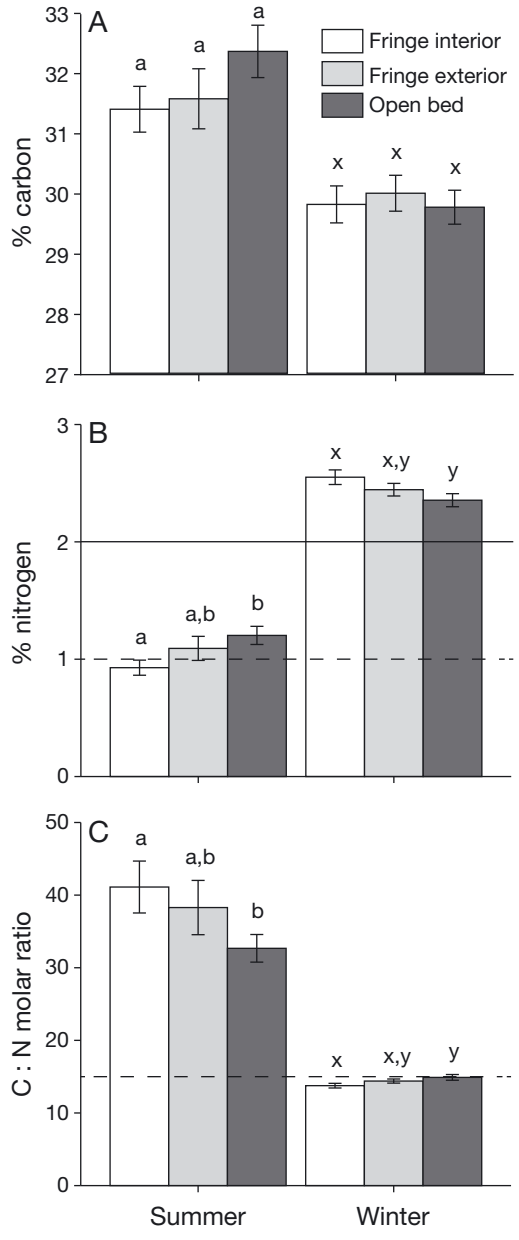

Fig. 7. *Macrocystis pyrifera*. Tissue chemistry from adult canopy blades collected from each type of bed in both regions. (A) %C. (B) %N. Solid line indicates the concentration necessary to support sustained growth; dashed line indicates the level thought to inhibit/reduce growth. (C) C:N molar ratios; dashed line is set at 15 and values ≥15 are expected to indicate nitrogen exhaustion. Error bars: SE (n = 6). Letters above the bars repre-sent post hoc grouping

art Island values ($\delta^{13}C$: df = 1,43; $F = 12.78$; $p < 0.001$; $\delta^{15}N$: df = 1,41; $F = 54.66$; $p < 0.001$). Bed type had an effect on both summer and winter $\delta^{13}C$ and $\delta^{15}N$ values (Table 1), perhaps surprising as it appears that Otago summer $\delta^{15}N$ values are similar (Table 2); however, p-values are close to the 0.05 level.

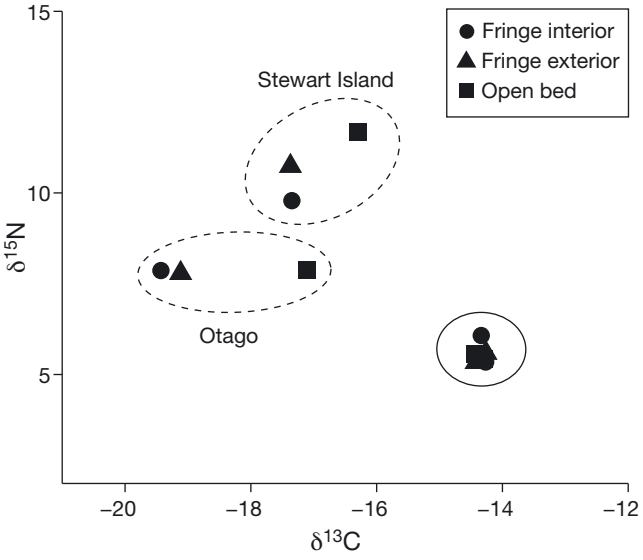

Fig. 8. *Macrocystis pyrifera*. Nitrogen and carbon stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) determined for adult blades in the surface canopy from each type of bed in both regions. Dashed ovals represent summer values; solid circle represents winter values

DISCUSSION

Macroalgal productivity is dependent on the physical and chemical properties of the surrounding environment. While variation in kelp growth has been previously demonstrated to occur between beds (Gerard & Mann 1979, Hepburn et al. 2007), this study provides the first evidence that *Macrocystis pyrifera* growth within a singular site is not uniform and that the differences in growth rates presented here can be attributed to hydrodynamic gradients over relatively small spatial scales (tens of metres). Other dominant factors that influence productivity are light, temperature and ambient nitrogen. Stewart et al. (2009) reported within-bed growth patterns akin to those described in this study but proposed light attenuation due to self-shading as the mechanism behind this variability. Because of logistical difficulties, this study did not measure light attenuation in the top 2 m of the water column at all of the 18 subsites. However, if light was a significant variable in determining intra-site growth rates, we would expect: (1) equivalent frond growth rates between fringing exterior and open bed types because these kelp were tagged along both bed edges and should experience similar light conditions, and (2) higher growth rates along the bed edge compared to the interior during winter because ambient light is limiting during this period — exterior kelp would benefit from increased light availability from a theoretical decrease of shading. Furthermore,

Table 2. Mean (±SE) summer and winter $\delta^{13}C$ and $\delta^{15}N$ values across bed type for Otago and Stewart Island, New Zealand

	Summer		Winter	
	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Otago				
Fringe interior	−17.12 ± 0.41	7.87 ± 0.13	−13.82 ± 0.31	6.07 ± 0.30
Fringe exterior	−19.11 ± 0.58	7.90 ± 0.12	−14.42 ± 0.47	5.34 ± 0.23
Open bed	−17.43 ± 0.38	7.86 ± 0.06	−14.44 ± 0.30	5.56 ± 0.17
Stewart Island				
Fringe interior	−17.35 ± 0.36	9.79 ± 0.41	−14.26 ± 0.17	5.35 ± 0.26
Fringe exterior	−17.37 ± 0.34	10.74 ± 0.27	−14.26 ± 0.26	5.59 ± 0.32
Open bed	−16.30 ± 0.57	11.09 ± 0.21	−13.96 ± 0.29	5.43 ± 0.24

according to Falkowski & LaRoche (1991), algae acclimatised to lower mean light should have higher pigment concentration per unit area, but this study found that summer exterior kelp tissues had higher pigmentation than interior tissues. Pigment differentiation across the canopy of the bed during this season is likely due to differences in tissue %N, where interior kelp could not assimilate enough nitrogen to properly maintain pigmentation and/or tissue structure. This is consistent with other studies describing that chlorophyll *a* and accessory pigments were positively responsive to external NO_3^- assimilation potential (Smith et al. 1983, Shivji 1985). It is also possible that a decline in photopigments is an indication of internal nitrogen reserve depletion because pigments have been suggested as another form of internal nitrogen pools in *M. pyrifera* (Chin 1989, Kopczak 1994, Hepburn 2003). The higher pigment concentrations observed in winter are likely a seasonal response to both high nitrogen (Boussiba et al. 1999) and low light (Lapointe & Ryther 1979, Aguilera et al. 2002).

Ambient seawater nitrogen concentrations were unlikely to directly contribute to the observed heterogeneity in growth because concentrations within and outside of kelp beds were statistically similar, as predicted by Fram et al. (2008). However, because the rate of nutrient uptake is dependent on both ambient nutrient concentration and water motion (Gerard 1982a, Zimmerman & Kremer 1986), low summer nitrogen concentrations likely had an important interaction with mass-transfer and total nitrogen assimilated. In fact, summer tissue %N did significantly increase with increasing mass-transfer. Summer %N and seawater NO_3^- values were around 1% and 1 µM, respectively, which are described as inhibiting and/or reducing *M. pyrifera* growth (Hanisak 1979, Gerard 1982b). However, ambient NH_4^+ levels raised the total seawater nitrogen above 1 µM, and it is therefore possible that total seawater nitrogen was high enough to ameliorate severe nitrogen limitation, as suggested in other *M. pyrifera* studies (Hepburn et al. 2006, Brzezinski et al. 2013). C:N values decreased with increasing mass-transfer and corroborate the apparent summer nitrogen depletion as the values in both regions exceed 15, values ≥15 are thought to indicate nitrogen exhaustion (Hanisak 1983). Despite signs of nitrogen exhaustion, summer growth rates were sustained in both regions, especially for blade elongation. These findings are consistent with those of Gerard (1982b) and Brzezinski et al. (2013), who both found that overall algal growth did not decline as a result of low nitrate levels. *M. pyrifera* is a species with high morphological, physiological and life-history plasticity, allowing it to adapt to different nitrogen environments around the globe (for more details see Graham et al. 2008, Buschmann et al. 2014). Specific to wave exposure, Hurd & Pilditch (2011) describe that *Macrocystis* blades from wave-exposed locations have thicker tissue and are more narrow than blades collected from wave-sheltered locations; furthermore, exposed blades exhibited surface corrugations, while sheltered blades were smooth. They found that because sheltered blades lacked surface corrugations — therefore less structure to create drag — the DBLs were generally thinner than those associated with wave-exposed morphologies. Understanding the morphological variation/adaptation in *M. pyrifera* and other macrophytes presented in this study has important implications for further research investigating intra-site nutrient acquisition and the excretion of wastes and, therefore, for primary productivity.

It cannot be overlooked that the interior kelp reside at shallower depths than the other 2 bed types, as is the nature of these reefs. Is it possible that the growth of interior kelp is depth limited? Current literature concerning the direct relationship between depth and adult *M. pyrifera* frond growth is sparse. Jackson (1987) presents a model that predicts higher *M. pyrifera* biomass in shallower water (6 to 12 m) compared to deeper water (15 to 18 m) and assumes that frond length is 40% greater than depth. Our data suggest that growth was not depth limited. We do not expect that depth would reduce blade elongation because these tissues have the highest contribution to photosynthesis and therefore productivity (Colombo-Pallotta et al. 2006), and it is not logical that blade surface area potential would be inhibited by depth,

especially when considering the high plasticity of this species. However, if depth were important, we would expect interior kelp to have higher %N in tissues or lower C:N ratios because nitrogen could be allocated to tissue maintenance instead of new tissue generation; our data do not reflect this. It is conceivable that depth could influence stipe elongation, but, by comparing summer and winter values, it is clear that summer growth of interior fronds did not reach maximum rates, as observed during winter. Not only were interior growth rates higher during the winter, but they were also equivalent and/or higher than rates measured in fronds growing at 10 m depth. Furthermore, we did not observe increased indeterminate growth occurrences — where the end of the stipe has a bladder instead of an active meristem — in interior kelp (present study, T. A. Stephens unpubl. data), which would be expected if growth were triggered to cease.

Nitrogen assimilated during summer was most likely used for rapid growth rather than for the maintenance of existing tissue. This is supported by positive growth for blades despite high blade erosion rates during summer. Blade erosion was highest in interior individuals, where nutrient uptake potential is lower due to thicker DBLs; these individuals would then uptake less nitrogen and have less to allocate to tissue maintenance. It is interesting to note differences in tissue integrity: when handling blades belonging to interior kelp during the summer, the distal tissue appeared frayed and would disintegrate if not handled with care; winter interior blades were much more robust and the distal tissues still relatively thick but appeared fractured or torn (T. A. Stephens pers. obs.). It is possible that water motion has a secondary effect on blade erosion for kelp located directly adjacent to shore; waves may throw the interior kelp against the rocky shoreline and cause blade damage beyond passive erosion. These 2 forms of erosion reduce the amount of photosynthetic active tissues, which further reduces productivity of interior individuals to a point where new blade growth cannot keep up with tissue loss, therefore producing negative net tissue replacement rates throughout the year. This might also explain the low blade growth rate of interior kelp observed during the winter if the blades are indeed subject to tear; mechanical damage stresses have been described as reducing biomass production in terrestrial ecosystems (Zangerl et al. 1997). It is a curious thing that interior kelp manage to persist with apparent negative tissue replacement values, the mechanism behind such survival is unclear. Perhaps a growth strategy reminiscent to that of a conveyor belt is involved — where younger, smaller blades replace older, larger blades as the frond grows. During fieldwork, it was noted that basal blades on interior kelp were missing or partially missing; with less biomass in the basal section, the individual might allocate more of its internal resources to new blade growth because older tissue is compromised. This could explain why new blade production in interior kelp was higher than predicted (by water mass-transfer patterns) during the summer (Fig. 5C).

Nutrient availability, ambient productivity and nutrient origin influence isotopic signatures. Otago and Stewart Island neritic waters are primarily resupplied by cross-shelf transport of subantarctic surface water (SASW) (Van Hale & Frew 2010) and Tasman Sea surface water (TSSW) (Jillett 1969, Heath 1985), respectively, and do not experience typical large-scale coastal upwelling events (Heath 1985, Greig et al. 1988). Otago and Stewart Island $\delta^{13}C$ and $\delta^{15}N$ values group together during the winter because nutrient availability is high and allows both populations to preferentially select lighter isotopes (^{12}C and ^{14}N). Summer signatures are heavier because autotrophic plankton populations bloom and lower ambient NO_3^- concentrations to near depletion levels and thus reduce $^{14}NO_3^-$ availability. Otago and Stewart Island summer values group separately because of their source of nutrients (subsidy pool). SASW has high nitrogen and low chlorophyll (HNLC), and has a $\delta^{15}N\text{-}NO_3^-$ of 8‰ (Van Hale & Frew 2010). TSSW is not HNLC and thus likely has a $\delta^{15}N\text{-}NO_3^-$ closer to 14‰, as seen in other Pacific regions (Wankel et al. 2007). We expected that bed type would influence isotopic signatures, in that kelp exposed to increased mass-transfer would have lighter signatures because of higher potential for preferential selection, but our data do not support this hypothesis. Instead, summer $\delta^{13}C$ signatures were heavier in open beds of both regions compared to fringing kelp, and Stewart Island summer $\delta^{15}N$ signatures were also heavier, with increased mass-transfer rates. These results are difficult to interpret, but might highlight a bias of our tissue sampling design that could impact isotope values. By removing a standard basal 85 mm of tissue from all blades, we possibly excised tissue grown over a longer temporal scale from interior individuals (due to slower growth rates) and a shorter temporal scale in more exterior blades. We would expect lighter $\delta^{13}C$ and $\delta^{15}N$ values before summer productivity (as seen in winter values); therefore, if excess tissue was excised from interior blades, our results might partially reflect pre-summer isotopic values and thus bias the values towards lighter signatures. Oceanographic parame-

ters are also a likely explanation for the differences in mean seawater temperature between Otago and Stewart Island. Otago neritic waters are constrained by a dominant front (Southland Front; Burling 1961), while Stewart Island waters are not (Heath 1985); therefore, Otago water masses have a relatively long nearshore residency time, which results in higher summer and lower winter temperatures (Jillett 1969). Although kelp productivity is known to have a positive relationship with seawater temperature (Dayton et al. 1992), regional differences in temperature did not affect the cross-bed patterns in growth and tissue status seen in this study.

We propose that the bed-wide boundary layers created by kelp — i.e. along-shore and cross-shore (Jackson 1977, Gaylord et al. 2007, 2012) — induce variation in water mass-transfer within a given kelp bed, which induces intra-bed heterogeneity in the growth and tissue status of the *M. pyrifera* individuals observed in this study. Such heterogeneity in biomass and/or tissue %N could influence mobile herbivore feeding behaviour or bed position occupied because nitrogen is important for growth and reproduction (Mattson 1980) and some fishes actively pursue nitrogen-rich algae (Goecker et al. 2005). Understanding mass-transfer patterns and the consequences due to decreased rates is also critical for algal aquaculture endeavours, where the layout and density of deployed macroalgal lines would likely influence mass-transfer and therefore productivity, especially if ambient nitrogen concentrations reach seasonal lows. In addition, this study may help correct estimates of total macroalgal carbon production and biomass estimates in a defined area, which are potentially over-estimated if models are based on the offshore/high-flow studies that dominate the literature. Finally, although decreased mass-transfer reduces kelp growth and productivity, such a hydrodynamic regime could increase population resilience to changes in seawater chemistry associated with climate change, such as ocean acidification (Cornwall et al. 2013a). The chemical environment within the DBL can be very different from that of the ambient environment (Hurd et al. 2011), where increased pH is associated with slower water motion (Cornwall et al. 2013b). This effect was measured just millimetres above the tissue surface, but similar properties may occur in large-scale macrophyte canopies that experience reduced flow (Okubo et al. 2002, Kregting et al. 2008). Therefore, although self-buffering by *M. pyrifera* may reduce water mass-transfer and also nitrogen uptake, this mechanism may alleviate the effects of ocean acidification via increased pH within boundary layers.

SUMMARY

This study highlights hydrodynamic variability within and across relatively small macroalgal beds that, previously, may have appeared uniform in exposure due to bed locality (i.e. open coasts versus bays) and/or shoreline aspect (i.e. exposure to prevailing swell). This fine-scale variability has important implications for key processes surrounding nutrient uptake and for photosynthesis and primary productivity. *Macrocystis pyrifera* is a large and complex organism that can alter the surrounding physical environment and buffer interior kelp individuals from wave and current movement, leading to higher growth in individuals from open beds compared to those from within kelp beds. These bed types directly influence nutrient uptake rates due to DBL kinetics. It is clear that kelp individuals growing in open beds have higher productivity rates, supported by the growth, tissue wet weight, pigmentation and %N data presented in this study. The disparity in growth and tissue status between interior and exterior fronds across ecosystems will likely be driven by individual and frond density at the edge of the kelp bed — higher densities should equate to even less water motion to the interior. More research is warranted to investigate how algal productivity and nutrient utilization under such exposure regimes affect macrophyte distribution, ecology and resilience to perturbation within reef ecosystems over various spatio-temporal scales.

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