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Differences in growth, morphology and tissue carbon and nitrogen of *Macrocystis pyrifera* within and at the outer edge of a giant kelp forest in California, USA

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ABSTRACT: To investigate the extent to which alteration of physical factors by giant kelp beds affects the growth of kelp within the bed, we conducted analyses of frond morphometrics at 2 mo intervals, elongation rates and tissue chemistry of individuals of *Macrocystis pyrifera* on the interior and edge of a kelp bed off the coast of Santa Barbara, California, USA. The density of the kelp canopy varied greatly during the 13 mo study, ranging from 0.03 to 8.03 m² blade tissue m⁻² sea surface. Time series analysis of flow velocity, light, temperature and seawater nitrate concentrations inside and outside of the bed indicated that when canopy density was high (May to September) current speeds in the bed were 25 % of incident flow, and light below the canopy (at 1 m depth) was reduced to 10 % surface irradiance. Nitrate concentrations were highly variable and similar between inside and outside moorings. When the canopy was well developed, kelp fronds on the seaward edge of the bed had faster elongation rates and larger blades, resulting in higher overall growth rates (mass added per day) than interior fronds. Carbon and nitrogen accumulation by edge fronds was also higher during this period, which fueled growth rates of edge fronds that were nearly twice as high as interior fronds when the canopy was densest. Thus, the growth and tissue chemistry of *M. pyrifera* within the kelp bed depended on the extent to which the bed modified ambient physical conditions.

KEY WORDS: Kelp bed · *Macrocystis pyrifera* · Ecosystem engineering · Growth · Morphology · Nitrogen · Carbon · Light · Water flow

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INTRODUCTION

The giant kelp *Macrocystis pyrifera* forms large beds in shallow temperate waters along the Pacific coasts of North and South America, Africa, Southern Australia and New Zealand (Abbott & Hollenberg 1976). It

anchors to rocky substratum from depths of 20 m and extends through the water column forming dense canopies at the surface. Light under kelp canopies can be reduced to less than 5 % of surface irradiance (Foster 1975, Heine 1983, Gerard 1984, Reed & Foster 1984, Dean 1985), and the mechanical interaction of kelp

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with flow can attenuate currents and internal waves (Jackson & Winant 1983, Jackson 1984, 1997, Gaylord et al. 2007, Rosman et al. 2007, Fram et al. 2008). As such, giant kelp is a classic autogenic ecosystem engineer (sensu Jones et al. 1994), altering physical conditions by its presence and creating habitats very distinct from adjacent waters. However, giant kelp beds are dynamic systems, and the extent to which they modify their surrounding physical environment is a function of their areal extent and the density of individuals within them, which change with seasonal and inter-annual variability in nearshore physical conditions.

Patterns of productivity and abundance of *Macrocystis pyrifera* off the coast of California are influenced by seasonal changes in light, water motion and nitrate availability (Dayton & Tegner 1984, Dayton et al. 1992, Edwards & Estes 2006, Reed et al. 2008). The abundance of kelp in turn influences these physical processes in and around a kelp bed. For example, giant kelp canopies, which in southern California tend to be densest in summer when ambient seawater nitrate concentrations are typically lowest, can retard currents and reduce the amount of nitrate delivered to the bed interior (Jackson 1997, Gaylord et al. 2007, Fram et al. 2008). Similarly, light availability within a kelp bed may be as much a function of canopy density as it is ambient sunlight. As a result, light in the interior of a kelp bed may be reduced to levels that inhibit nutrient uptake and photosynthesis in *M. pyrifera* (Gerard 1986, Colombo-Pallotta et al. 2006) and understory macrophytes (Stewart & Carpenter 2003). Such effects caused by the kelp canopy are reduced by winter storms that thin or remove the canopy, thereby increasing light and nutrient penetration into the bed, and allowing for recruitment and growth of young kelp that would otherwise be out-competed for light by the surface canopy (Reed & Foster 1984, Dean et al. 1989, Watanabe et al. 1992). Thus, there are important interactions between giant kelp and the environmental factors that drive its abundance and growth, and the strength of these interactions varies among seasons and years.

Like many seaweeds, kelp can mitigate its ambient light and nutrient environment by storing carbon (C) and nitrogen (N) taken up in excess of what is required for growth, and use of stored photosynthate and nutrients can effectively uncouple growth from its external light and nutrient environment (e.g. Chapman & Craigie 1977, Hatcher et al. 1977, Gerard 1982, Gomez & Wiencke 1998, Phillips & Hurd 2003). For example, when light is abundant and growth is limited by nitrogen, excess photosynthate is stored as mannitol and laminarin, which are mobilized to support growth when conditions switch to nutrient sufficiency but light limitation. Mannitol stores are labile and used first to

support growth; laminarin is a longer-term carbohydrate storage compound that must be converted to mannitol prior to translocation and use (Chapman & Craigie 1978). Low levels of this carbohydrate may result from low rates of photosynthesis, generally a result of light limitation, or rapid growth (Chapman & Craigie 1978). Similarly, when external supplies of nitrogen are replete, nitrogen taken up in excess of growth demands are stored in vacuoles as nitrate reserves (Young et al. 2007), and growth can be sustained by stored nitrate under conditions of high light but low ambient nitrogen availability. Information on the availability of kelp storage compounds is critically important when assessing the environmental causes for differences in growth, and the degree to which kelp can de-couple growth from ambient conditions through nutrient storage varies. Arctic kelp *Laminaria solidungula* can effectively de-couple growth from the external environment by storing nutrients for up to 6 mo (Chapman & Lindley 1980), while *Macrocystis pyrifera* can use up nutrient reserves within 2 to 4 wk (Gerard 1982).

We investigated the extent to which modification of physical factors by a kelp bed over the course of 1 yr affected the growth of giant kelp within the bed. Specifically, we asked: (1) To what extent are ambient light, flow and modeled nitrate availability altered by changes in the density of a kelp bed over 1 yr? (2) Does the growth and internal tissue chemistry of kelp fronds in the interior and at the edge of a kelp bed differ in response to modification of physical conditions by the bed?

MATERIALS AND METHODS

System description. *Macrocystis pyrifera* is the world's largest alga and among the fastest growing autotrophs, attaining lengths in excess of 25 m and exhibiting daily elongation rates in excess of 0.5 m d^{-1} (Clenndenning 1971). An individual consists of a tangle of vine-like fronds arising from a single basal holdfast. Each frond consists of a rope-like stipe that is buoyed by many leaf-like blades attached by small gas bladders. The buoyant fronds extend through the water column forming a dense canopy at the sea surface. Nutrient uptake and photosynthesis occur throughout the entire organism.

This study was conducted at the Mohawk kelp bed ($34^{\circ} 23' 38.7'' \text{ N}$, $119^{\circ} 43' 44.8'' \text{ W}$), off the coast of Santa Barbara in southern California, USA. The reef is ~300 and 120 m in the alongshore and cross-shelf directions, respectively (Gaylord et al. 2007). The region has a Mediterranean climate characterized by relatively calm, dry summer and autumn months, upwelling-

favorable winds in the spring, and episodic rainstorms in the winter. This setting creates strong seasonality in the supply of nutrients from upwelling, internal waves and terrestrial runoff, and in the frequency of physical disturbance from storm-generated surface waves (McPhee-Shaw et al. 2007, Fram et al. 2008). Wind-driven upwelling during spring supplies 70% of the nitrate delivered on an annual basis. Internal waves are the dominant mechanism of nitrate delivery to nearshore kelp beds in summer when surface waters may be nutrient-depleted. Storm-generated waves in winter routinely tear kelp holdfasts from the substratum and effectively thin or remove kelp beds (Reed et al. 2008). Gaylord et al. (2007) and Fram et al. (2008) provide detailed nutrient and flow analyses in and around the Mohawk kelp bed during the course of the present study. Reed et al. (2008) provide a 4 yr time course of wave height, kelp standing crop and net primary productivity of giant kelp in this region, including the Mohawk kelp bed.

Kelp canopy density. Kelp canopy density was quantified as the area (m^2) of blade tissue in the surface canopy per m^2 of sea surface. We chose this metric to characterize kelp bed density because the majority of the biomass of *Macrocystis pyrifera* is contained in the canopy where most nitrate uptake and photosynthesis occur (Towle & Pearse 1973, Wheeler & Srivastava 1984, Colombo-Pallotta et al. 2006). The density of canopy fronds in the Mohawk kelp bed was measured monthly in the center of the kelp bed as part of an ongoing monitoring program by the Santa Barbara Coastal Long Term Ecological Research project (SBC-LTER; Rassweiler et al. 2008). Canopy fronds were defined as fronds that extended throughout the water column and were at least 1 m in length at the sea surface. We measured the blade area per unit length of frond for 10 of the canopy fronds in each sampling period and used these data to convert the density of canopy fronds to the mean area of blade tissue in the surface canopy per m^2 of sea surface.

Although a variety of factors can cause the density of kelp to vary within a bed, measurements of frond density in the center of the Mohawk kelp bed appeared to be a reasonable estimate of the density of the canopy throughout the bed during our study. Frond densities measured in a uniform grid over the entire Mohawk kelp bed (including interior and edge

locations) in March through April 2005 and again in August through September 2005 (Gaylord et al. 2007) were nearly identical to densities recorded in the center of the bed by SBC-LTER (mean number of fronds per m^2 in entire bed vs. center of bed = 2.71 vs. 2.72 in April 2005 and 5.46 vs. 4.96 in August 2005).

Physical variables inside and at the edge of the kelp bed. Environmental data were collected from May 2005 to May 2006 at and around 2 moorings: one inside the kelp bed at 8.0 m depth 190 m from shore, and one outside of the kelp bed at 10.4 m depth 300 m from shore (Fig. 1). Water column irradiance was measured as photosynthetic photon flux density (PPFD) at the surface and 1 m below the surface inside and outside the kelp bed near, but not shaded by, the moorings. PPFD was recorded using a Li-250A light meter and a Li-192 cosine corrected quantum sensor. The averages of 5 spot readings at each depth (i.e. surface and 1 m) over 5 min were recorded between 11:00 and 13:00 h in each month of the study. Data are presented as the proportion of surface irradiance at 1 m depth inside the bed relative to the outside the bed. Beginning in August 2007 SBC-LTER began collecting PPFD data near our inside and outside moorings at the Mohawk kelp bed once per minute using hemispherical collectors (MKV-L, Alec Electronics) mounted ~50 cm above the sea floor. We used these more continuous measurements of PPFD to evaluate the validity of our spot measurements in determining the effects of



Fig. 1. *Macrocystis pyrifera*. Aerial view of the Mohawk kelp bed off the coast of Santa Barbara, California, USA, in May 2005 and the positions of the inside and outside moorings. Interior fronds were sampled in the vicinity of the inside mooring and edge fronds were sampled at the seaward margin of the bed, which moved as the bed expanded and contracted

the surface canopy on light reduction. The density of the kelp canopy during the period of high frequency PPFD measurements (August 2007 to May 2008) was comparable with that during the period of this study (May 2005 to April 2006; see 'Results')

Water velocities during the 13 mo study were measured at the inside mooring with a bottom-mounted upward-looking 1200 kHz acoustic Doppler current profiler (ADCP, RD Instruments) and at the outside mooring with a 600 kHz ADCP. Velocity data were collected every 2 min in 0.5 m vertical bins, extending from 1.5 m above the bottom to 1.5 m below the surface. Depth-averaged hourly means of 2 min samples were calculated for each sampling period over which kelp growth was measured (see section 'Kelp frond growth').

An array of multiple RBR TR-1050 thermistors (Richard Branker Research TR-1050) was attached to a vertical PVC spar buoy located 10 m south (offshore) of each ADCP mooring. Thermistors in each chain array were spaced 1 m apart, from 0.6 m above the substratum to just above mean sea level, and sampled every 10 s at a resolution of 0.002°C. We estimated seawater nitrate concentrations from temperature–nitrate relationships established from nitrate and temperature data collected by a single nitrate autosampler (analyzing sensor (Envirotech model NAS) mounted 4 m above the bottom near the outside mooring (Fram et al. 2008). We compared temperature-derived concentrations of seawater nitrate in the top 1 m of the water column at the interior and outside moorings.

Response of kelp in the interior and at the edge of the bed. Kelp frond growth: Elongation rates of 7 to 25 fronds at the offshore edge and in the interior of the Mohawk kelp bed were recorded every 2 mo from May 2005 to May 2006 by measuring the length of tagged fronds at the beginning and end of 8 to 14 d sample periods. Fronds were selected haphazardly from different kelp plants. From the surface, individual fronds with intact growing tips were pulled into upright positions in the water column, and the depth of the water column was measured and used as an estimate of the length of the subsurface portion of the frond. The length of the frond at the water surface was measured from the point at which the frond reached the water surface to the end of its growing tip. The sum of the subsurface and surface lengths was used as the total length of the frond. Frond length measurements were only acquired on calm days to minimize error associated with swell.

We estimated the precision of our measurements of frond length from 3 repeated measurements of 4 separate fronds from different kelp plants during each sampling period. The mean (\pm SD) deviation of these measurements was 0.14 ± 0.09 m (range = 0.020 to

0.30 m) for the canopy portion, and 0.09 ± 0.06 (range = 0.0 to 0.25 m) for the water column portion for fronds that ranged from 8.9 to 17.1 m total length. Lengths obtained for the water column portion of fronds using this technique were checked against measurements made by divers and found to be within 2.5% of each other.

To examine the effects of location within the bed on frond morphology we collected a variety of morphological measurements of fronds. Divers collected 10 to 20 actively growing surface fronds at the edge and in the interior of the kelp bed during our sampling periods and returned them to the laboratory, where we measured their length, wet weight, stipe diameter, blade density (i.e. number of blades per unit length of stipe) and blade area (estimated from 5 blades in the midwater and canopy portions of the frond). The depth at which the fronds were collected was recorded and the length corresponding to the depth was used to distinguish the water column and canopy portions of the frond. The ratio of frond mass: frond length was used as an indication of frond bushiness. Frond growth, estimated in terms of the amount biomass added per frond per day, was calculated as the product of frond elongation (increase in frond length per day) and frond bushiness.

Kelp tissue chemistry analysis: Carbon and nitrogen storage products are informative metrics used to determine how kelp integrates changes in their physiochemical environment over weeks to months (Chapman & Craigie 1978). Total C and N content and concentrations of mannitol, laminarin and soluble nitrate were determined for each sample period from mature canopy blades collected from fronds used in elongation measurements. Kelp tissue used for these analyses was dried to a constant mass at 60°C, and then ground to a fine powder in a plant mill. We determined the C and N content using a Carlo-Erba Flash EA 1112 series elemental analyzer (Thermo-Finnigan Italia), calibrated against an aspartic acid standard. Mannitol was isolated by conducting 3 successive 5 min extractions of 0.5 to 0.9 g dry kelp with 5 ml of 100% ethanol in a water bath at 80°C, decanting after each extraction. We evaporated 1 ml sub-samples of the extract, reconstituted them with de-ionized water, and analyzed for mannitol using a periodate-chromotropic acid assay (Lambert & Neish 1950). Laminarin was extracted from the remaining algal tissue after it was soaked in 0.1 N NaOH overnight and homogenized in a tissue grinder. Alginates were precipitated by adding 2 N HCl. The supernatant containing the laminarin was assayed as glucose following the anthrone reagent method of Yemm & Willis (1954).

To determine the amount of soluble nitrate in kelp tissue, we macerated 2 to 5 g blade tissue in 90%

ethanol and extracted it overnight in 50 ml of 90% ethanol (Williams & Herbert 1989). The supernatant was analyzed for nitrate concentration on a QuickChem FIA 8500 autoanalyzer (Lachat Instruments). Sample absorbances were corrected for chlorophyll absorbances by repeating the spectrometric analysis without reagents. Concentrations were standardized to dry mass.

Statistical analysis. Statistical analyses were conducted using JMP (v6.0.3, SAS Institute). Two-way fixed factor ANOVAs were used to compare the main and interactive effects of date and location (inside and edge) on frond elongation rates, bushiness, growth (both as kilograms kelp biomass added per day and grams C and N added per day) and all tissue chemistry variables. Date was considered a fixed factor because we expected responses to vary seasonally. Comparisons between inside and edge locations on specific dates were conducted using post-hoc least square means (LSM) pairwise comparisons. Principal component analyses were used to determine whether frond morphometrics differed between the interior and edge portions of the kelp bed. The effects of position within the water column (surface canopy and water column) and location within the bed (inside and edge) on 2 principal components were evaluated using 2-way fixed factor ANOVAs that included measurements from all dates. Significance was determined as $\alpha < 0.05$.

RESULTS

Physical conditions in and around the kelp bed

Canopy density of the Mohawk kelp bed was highest in summer (June to August) and lowest in winter and spring (November to May; Fig. 2). The dense canopy in summer 2005 ($8.03 \pm 1.158 \text{ m}^2 \text{ blade area m}^{-2} \text{ sea surface}$) reflected high plant survivorship during the preceding winter followed by spring growth (Reed et al. 2008). A series of large storms in December 2005 severely reduced the density of the kelp bed to $0.03 \pm 0.007 \text{ m}^2 \text{ blade area m}^{-2} \text{ sea surface}$ (Fig. 2).

Light intensities and current speeds at the Mohawk kelp bed were generally lower inside the bed com-

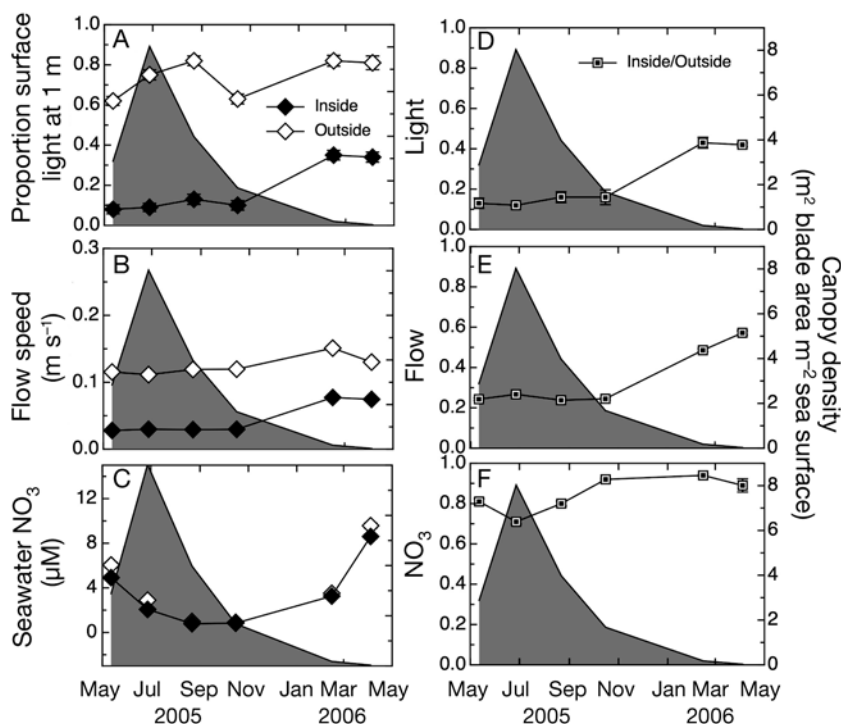


Fig. 2. *Macrocystis pyrifera*. Time series of light, water flow and nitrate conditions inside and outside of the Mohawk kelp bed. (A) Proportion of surface irradiance at 1 m depth in the interior of the bed and outside the bed ($n = 5$ observations). (B) Depth-averaged flow speeds inside and outside the bed averaged over 1 h intervals for the duration of each sampling period ($n \geq 1440$ observations). (C) Temperature-derived nitrate concentrations inside the bed in the canopy at the outside mooring ($n \geq 1440$ observations). (D–F) Inside/outside ratios of light, flow speed and seawater nitrate, respectively (all mean values \pm SE). The right-hand y-axis and the shaded area in all panels represent the density of the kelp bed canopy

pared with outside (Fig. 2A,B); however, increases in kelp density amplified these differences (Fig. 2D,E). Correlations between canopy density and the ratio of light penetrating to 1 m below the surface inside the bed relative to outside the bed showed a logarithmic decline with increasing canopy density ($y = -0.1623\ln(x) + 0.4252$, $R^2 = 0.74$). Light measurements inside the kelp bed were always made adjacent to a kelp frond, so the effect of shading created by individual kelp fronds was detectable at low canopy densities. At its densest (July 2005), the canopy reduced the light penetrating through it to $\sim 10\%$ of ambient levels (Fig. 2D). With 2 exceptions, PPFD from our spot measurements outside the bed at mid-day exceeded the $500 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ required to saturate photosynthesis of *Macrocystis pyrifera* in southern California (Gerard 1986). However, inside the Mohawk kelp bed, light was potentially limiting to photosynthesis, with our readings ranging from 32 to $386 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. The proportional decrease between light inside and outside the bed from these spot measurements ($\sim 10\%$ reduction when canopy is densest,

Fig. 2D) is similar to those based on higher frequency data obtained from moored sensors in 2007 to 2008 (Fig. 3). When the canopy was densest during this time (August 2007), light in the interior of the bed was reduced to ~10% of that outside the bed. Removal of the canopy by winter storms in 2005 and in 2007 dramatically increased the amount of light in the interior of the bed to 45 and 50% of outside levels, respectively (Figs. 2D & 3). Current velocities averaged throughout the water column also displayed a logarithmic decline with kelp canopy density ($y = -0.0603\ln(x) + 0.3466$, $R^2 = 0.85$). In the virtual absence of the kelp canopy (March to May 2006) there was still a difference between the flow velocities recorded at the inside and outside moorings reflecting the effect of a very sparse bed and the fact that current speed increases modestly with water depth (Gaylord et al. 2007). Ambient sea-water nitrate concentrations were highest in May of 2005 and 2006, and were similar inside and outside the bed (Fig. 2C,F).

Kelp growth

Differences in frond growth and morphology between the interior and edge of the kelp bed were most evident when the canopy was dense, as edge fronds elongated significantly faster and displayed greater bushiness and higher growth rates in summer (July to September) 2005 than did fronds growing in the interior of the bed (Fig. 4). As the density of the canopy decreased in October, growth rates slowed and differences in elongation, bushiness and growth between inside and edge fronds declined and eventually disappeared in subsequent sample periods.

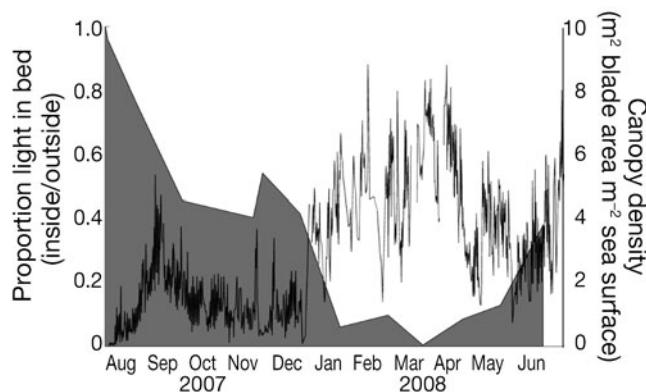


Fig. 3. *Macrocystis pyrifera*. Ratio of photon flux densities obtained at the inside and outside mooring of the Mohawk kelp bed and kelp canopy density from August 2007 to June 2008. The right-hand y-axis and the shaded area represent the density of the kelp bed canopy

Frond elongation ($F_{5,114} = 13.38$, $p < 0.01$; Fig. 4A) and bushiness ($F_{5,99} = 9.55$, $p < 0.01$; Fig. 4B) varied temporally across our year-long sampling effort, but edge fronds always had higher values than did inside fronds (elongation $F_{1,114} = 6.47$, $p < 0.05$; bushiness $F_{1,99} = 12.35$, $p < 0.01$; Fig. 4A,B). Differences in growth rates between edge and interior fronds varied over time (Fig. 4C, $F_{5,84} = 3.51$, $p < 0.01$ for date \times site interaction). Fronds at the edge of the kelp bed grew markedly more than did fronds in the interior of the

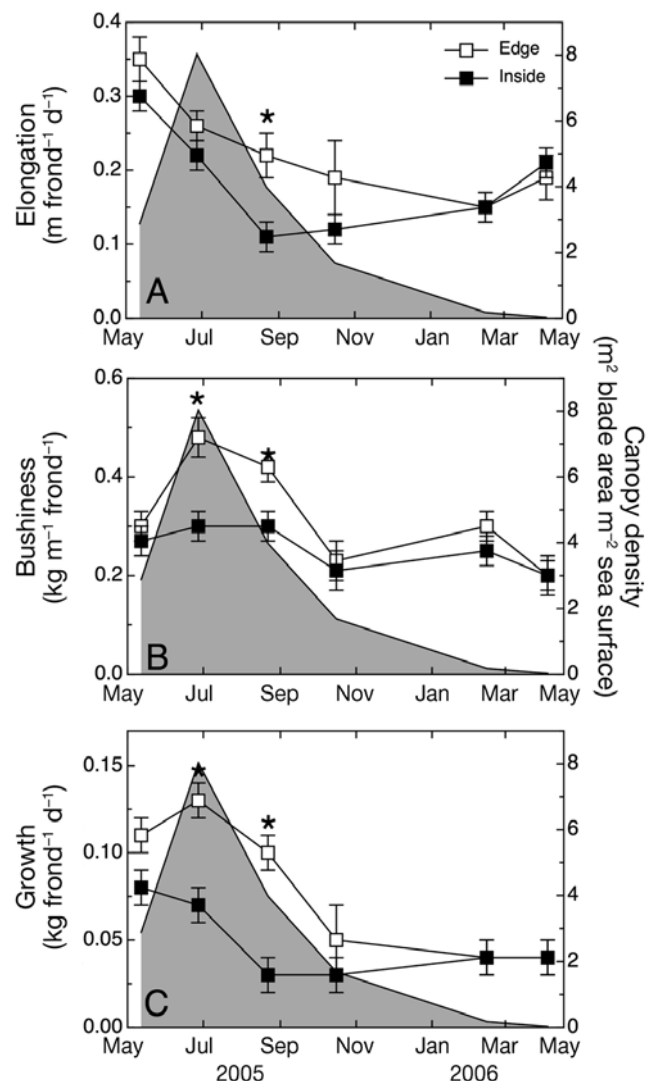


Fig. 4. *Macrocystis pyrifera*. Frond (A) elongation rate, (B) bushiness and (C) growth rates of kelp fronds inside and at the edge of the Mohawk kelp bed from May 2005 to May 2006 (mean \pm SE; bushiness, $n \geq 10$ fronds; elongation and growth, $n \geq 10$ fronds except for October edge when $n = 7$; May 2006 edge, $n = 8$; inside, $n = 7$). The right-hand y-axis and the shaded area in all panels represent the density of the kelp bed canopy. Asterisks (*) indicate inside and edge values differed significantly from one another as determined by post-hoc least square means pairwise comparisons

bed during all sample periods in 2005, but these differences disappeared after the kelp bed was decimated by storms in December 2005 (Fig. 4C).

Frond shape

Differences in frond bushiness between edge and interior portions of the kelp bed were greatest in July 2005 relative to other sampling periods. At this time edge fronds had $\sim 1.5 \times$ mass m^{-1} than did interior fronds, and differences in morphology were primarily due to larger blades on edge fronds (Fig. 5). Principal component analysis of morphometric measurements for all measurements taken over the course of the year indicated that principal component 1 (PC1) accounted for 55% of the variation in morphology between interior and edge fronds over the course of the year. PC1 had high loadings on bushiness, blade density and mean blade area (Table 1). Results from ANOVA and Tukey's post-hoc analyses on the PC1 loadings for all dates indicated significant

Table 1. Loadings of principal components 1 (PC1) and 2 (PC2) of morphometrics of fronds from the edge and interior of the Mohawk kelp bed from May 2005 to May 2006

Eigenvector	PC1	PC2
Length (m)	-0.51645	0.34832
Mass (kg m^{-1})	0.49185	0.29102
Stipe diameter (mm)	-0.08118	0.80121
No. of blades m^{-1}	0.54508	-0.2000
Mean blade area (m^2)	0.43319	0.32852
Eigenvalue	2.7726	1.3496
Percent	55.45	26.99
Cumulative percent	55.45	82.44

differences in canopy portions of edge and inside fronds, but not for water column portions of fronds (Fig. 6; $F_{1,222} = 6.08$, $p < 0.02$ for position \times location interaction). No differences were found for PC2 ($F_{1,222} > 3.8$, $p > 0.05$ for the main and interactive effects of position and location).

Carbon and nitrogen reserves

All chemical constituents (except soluble nitrate) showed significant differences between inside and edge at some point during the year (Fig. 7; $F_{5,215} > 2.60$ and $p < 0.026$ for all date \times location interactions excluding soluble nitrate). The amount of soluble nitrate varied significantly over time (Fig. 7E; $F_{5,215} = 24.34$, $p < 0.001$), but was consistently similar between inside and edge fronds ($F_{1,215} < 0.01$, $p > 0.99$ for location; $F_{5,215} = 24.31$, $p > 0.01$ for date; $F_{1,215} = 0.50$, $p > 0.77$ for date \times location interaction). Carbon concentration was higher in edge fronds when the canopy was most dense and differences in light between inside and outside the bed were greatest. Nitrogen content was similar for both edge and interior fronds and varied with the ambient concentration of nitrate in seawater (as determined from temperature). When the surface canopy of kelp was dense (May to September 2005), fronds growing at the edge of the kelp bed had higher carbon content than did fronds growing in the interior of the kelp bed (Fig. 7A). Carbon storage of inside fronds (and to a lesser extent, edge fronds) showed a transition from mostly laminarin in July to October 2005, to primarily mannitol in winter 2006.

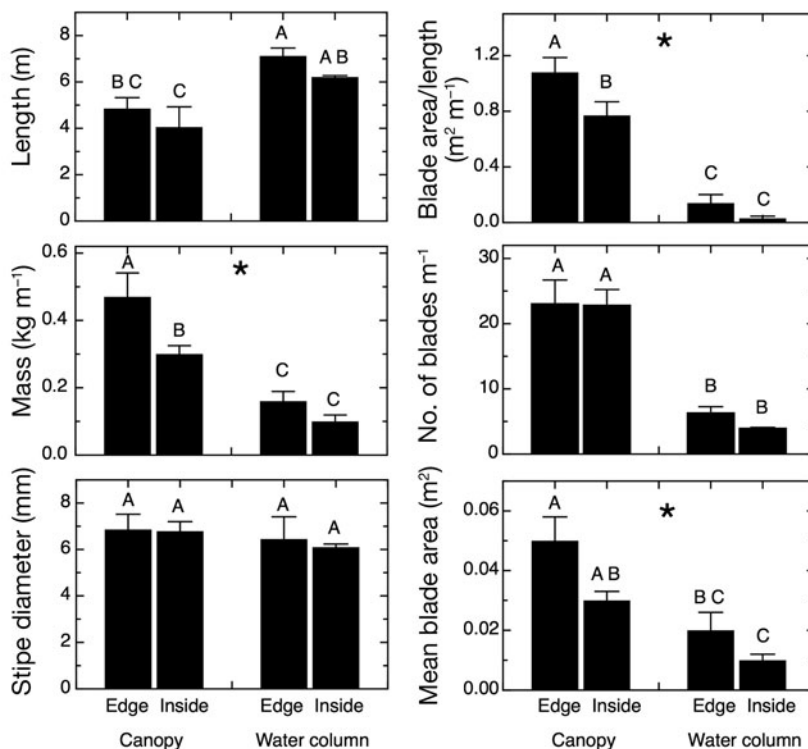


Fig. 5. *Macrocystis pyrifera*. Morphometrics of canopy and water column portions of edge ($n = 19$) and interior ($n = 16$) fronds in July 2005, the month with the largest difference in bushiness and growth between interior and edge fronds. Data are mean \pm SE. Different letters above bars indicate significant differences between measurements, as determined by post-hoc least square means pairwise comparisons. Asterisks (*) indicate differences between inside and edge fronds (incorporating water column and canopy measurements)

The total nitrogen content of inside and edge fronds was similar on all dates except August, when inside fronds had slightly (but significantly) higher values than edge fronds (Fig. 7D). Soluble nitrate concentrations of fronds were highest in the spring of 2005 and

2006 and similar between the inside and edge portions of the kelp bed on all dates (Fig. 7E). Patterns of the C:N ratio reflected the high nitrogen content (%N and nitrate) in the spring of 2005 and 2006, and low nitrogen content in the summer and winter. C:N ratios were not different for interior and edge fronds except in August, when values for edge fronds were higher (Fig. 7F), which reflected the high mannitol concentrations for edge fronds and high nitrogen content for inside fronds observed during this period (Fig. 7B,D).

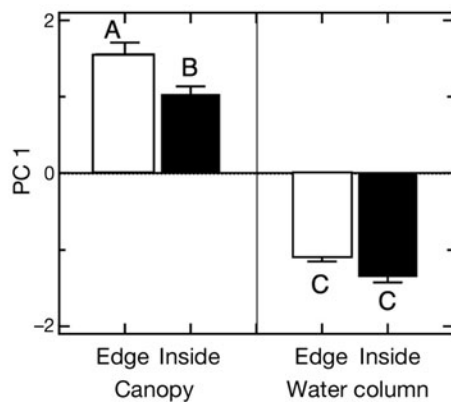


Fig. 6. *Macrocystis pyrifera*. Principal component 1 (PC 1) for canopy and water column portions of edge and inside fronds (mean \pm SE; edge, $n = 56$ fronds; inside, $n = 55$ fronds). Different letters indicate significant differences as indicated by Tukey's post-hoc comparisons

Growth rates expressed as carbon and nitrogen production

We estimated the mass of carbon and nitrogen added per frond per day from the total nitrogen and carbon content of kelp tissue, and frond growth rates. Edge fronds added more mass of both carbon and nitrogen when the canopy was dense (Fig. 8), which is consistent with increased access to light and nitrate flux. Date and location within the kelp bed independently affected the production of kelp nitrogen as the rate of nitrogen added per frond was greatest at the beginning of the study and consistently higher at the edge of the bed (Fig. 8A; $F_{5,84} = 21.24$, $p < 0.01$ for date; $F_{1,84} = 10.44$, $p < 0.01$ for location). In contrast, the effects of location within the kelp bed on the production of kelp carbon varied depending on the date; the rate of carbon added per frond was only greater in edge fronds in May to September (Fig. 8B; $F_{5,84} = 4.57$, $p < 0.01$ for date \times location interaction).

DISCUSSION

The results of the present study indicate that modification of ambient physical conditions by the Mohawk kelp bed reduced the growth and altered the morphology and chemical composition of giant kelp within the bed when the canopy was well developed. In July and September, fronds at the edge of the kelp bed grew faster, were bushier and had higher carbon and nitrogen incorporation rates than did those in the interior of the bed, possibly in response to increased light (due to less shading) at the edge versus the

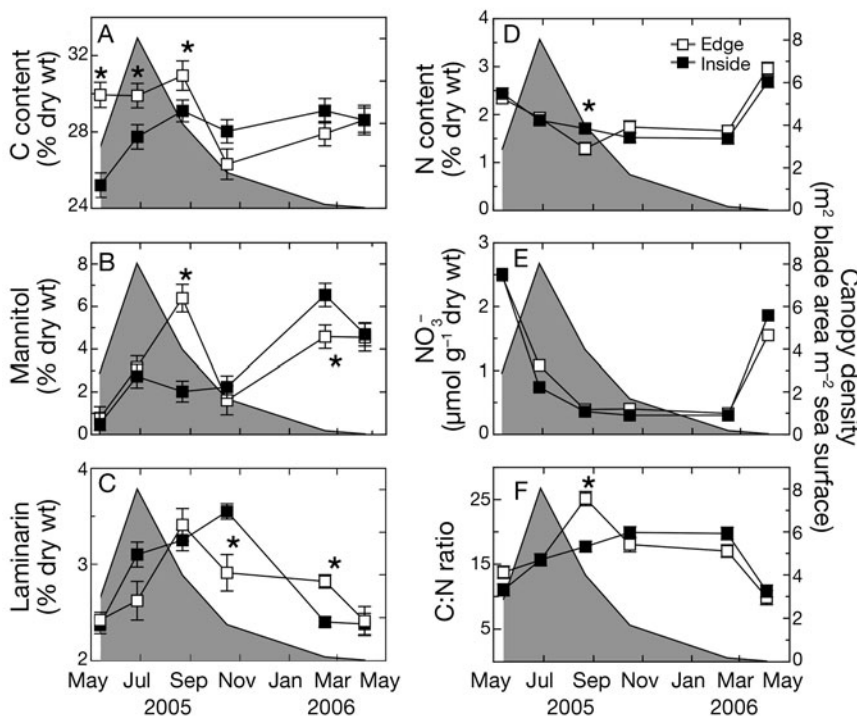


Fig. 7. *Macrocystis pyrifera*. Tissue chemistry of growing kelp fronds from the edge and inside of the Mohawk kelp bed from May 2005 to May 2006; (A) carbon, (B) mannitol, (C) laminarin, (D) nitrogen, (E) soluble nitrate and (F) total carbon: nitrogen (mean \pm SE, $n \geq 10$ fronds for all). The right-hand y-axis and the shaded area in all panels represent the density of the kelp bed canopy. Asterisks (*) indicate inside and edge values significantly different from one another as determined by post-hoc least square means pairwise comparisons

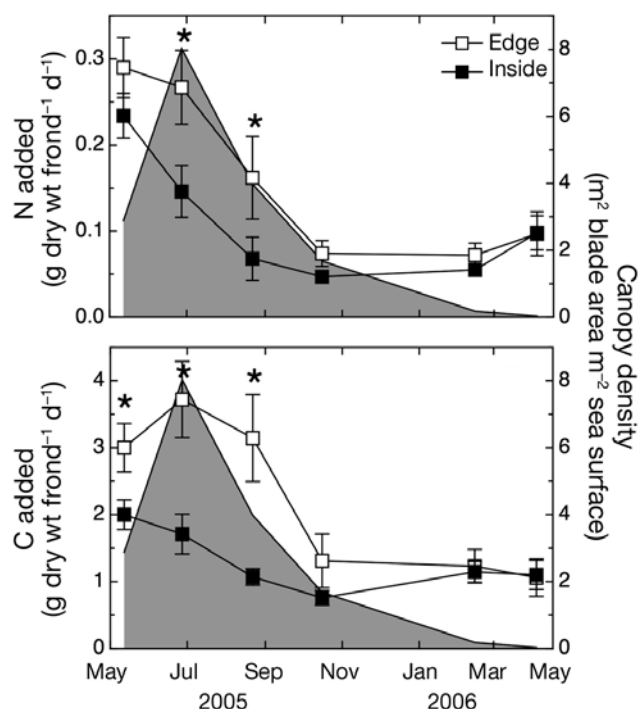


Fig. 8. *Macrocyctis pyrifera*. Nitrogen and carbon uptake by interior and edge fronds estimated from measurements of %N and %C of kelp tissue and frond growth (mean \pm SE; $n \geq 10$ except for October edge when $n = 7$; May 2006 edge, $n = 8$; inside, $n = 7$). The right-hand y-axis and the shaded area in both panels represent the density of the kelp bed canopy. Asterisks (*) indicate inside and edge values differed significantly from one another as determined by post-hoc least square means pairwise comparisons

interior of the bed. These differences were reduced or eliminated as the canopy density thinned in fall and winter of 2005.

Qualitatively kelp at both the edge and interior of the bed responded similarly to seasonal patterns in resource availability although the amplitude of the kelp response was reduced in the interior. Fronds at both the interior and edge of the kelp bed had high rates of elongation following spring upwelling in May 2005 (see Fram et al. 2008 for data on nitrate supplied by upwelling at this time). Elongation rates declined in fall as ambient nitrate levels decreased, and winter storms decimated the bed. Growth rates and bushiness were highest for both inside and edge fronds in May and July, but dropped for inside fronds in September and for edge fronds in November.

Nitrate availability is an important factor affecting the growth of giant kelp (Jackson 1977, North & Zimmerman 1984, Zimmerman & Kremer 1986), and nitrate stores can be used to fuel kelp growth for up to 1 mo in the absence of an external nitrogen supply (Zimmerman & Kremer 1986, van Tussenbroek 1989).

We observed the fastest elongation rates and highest concentrations of internal stores of nitrate in spring 2005 when seawater nitrate was high. The high nitrate stores observed in May 2005 were reduced by more than half over the next 2 mo during a period of rapid growth. High concentrations of seawater nitrate in spring 2006 did not result in high growth rates because kelp in the bed had not recovered from winter storms. Rates of nitrogen accumulation were elevated for edge fronds during July to September (Fig. 8), the period when edge fronds experienced higher growth than did interior fronds (Fig. 4). The more rapid accumulation of nitrogen for edge fronds was a consequence of their higher growth rate as tissue nitrogen content was similar between edge and interior fronds (Fig. 7), causing the increase in nitrogen accumulation rates to be proportional to changes in growth rate. This finding supports the model results of Fram et al. (2008), who found that edge fronds in the Mohawk kelp bed experienced 22% higher net nitrogen accumulation (mmol N g^{-1} wet wt) than did interior fronds during the period of our study; however, that those differences were not due to differences in rates of resource supply as the supply of nitrogen to interior and edge fronds was nearly the same, despite reduced flow velocities within the bed. They hypothesized that nitrogen accumulation rates are driven indirectly via processes that affect overall growth rate, and this is consistent with our findings. Fronds in both the interior and edge of the bed appeared N-replete from July to September as soluble nitrate was still detected in kelp tissue from both locations (although at very low concentrations), suggesting N-replete conditions at both locations.

Differences in the carbon content and rates of carbon accumulation between interior and edge fronds during the spring period of maximum growth and canopy density suggest that light is the main variable affecting these differences, given that ambient and stored nutrients appeared to be plentiful and similar between interior and edge fronds. Not only were fronds on the edge of the bed growing faster than were those in the interior, but their carbon content was higher as well, leading to differences in carbon accumulation rates that exceeded the differences in growth rate. We suggest that the edge fronds experience a more favorable light environment, which allows for both more rapid growth and carbon storage. Differences in the light environment between the interior and edge of the bed are mainly biologically driven functions of canopy density and the degree of self-shading among individual kelp. Shading would be maximal at this time due to high canopy densities that prevailed for much of this period. Of the physical factors quantified in this study, light was most strongly correlated with canopy density and

was reduced within the bed below levels required to saturate photosynthesis (Gerard 1984, Colombo-Pallotta et al. 2006). The carbon content of interior fronds was significantly lower than that of edge fronds from May to September 2005, when the surface canopy was most dense. Differences in %C of inside fronds disappeared as the canopy began to decline in October 2005 (Fig. 7A).

However, not all the differences in light and flow between inside and outside the kelp bed were caused by the kelp canopy, as the amount of light 1 m below the surface, and the mean flow velocity were lower inside the kelp bed even after the kelp canopy was removed by winter storms (see also Fram et al. 2008). In the case of light, this reduction may have been due to higher levels of wave-induced turbidity at the inside site, which was 110 m shoreward of the outside mooring. As noted previously, the differences in flow may also be attributed to bathymetry as depth-averaged flow speeds increase modestly with depth (Gaylord et al. 2007). Nonetheless, our finding shows that the differences in growth between interior and edge fronds largely disappeared following the dramatic decline in the surface canopy and suggest that differential access to light is responsible for these differences. Additionally, in a detailed study of flow and nitrate supply to the Mohawk kelp bed during the period of this study, Fram et al. (2008) found that nitrate flux was similar for edge and interior kelp.

Differences in resource availability and allocation between interior and edge kelp fronds may result in trade-offs in performance for kelp at different positions within the bed. Reduced biomass of inside fronds may have important consequences on kelp spore production, which in *Macrocystis pyrifera* is related to vegetative biomass (Neushul 1963, Reed 1987). However, the hydrodynamic force drag scales with surface area and the effect of larger blades of edge fronds may result in higher rates of damage and detachment in powerful swells that pass through the kelp bed (B. Gaylord unpubl.). The differences in growth and morphology that we observed between interior and edge fronds at the Mohawk kelp bed are similar to the response of understory macroalgae to variation in light availability caused by fluctuations in the surface canopy. Experimental manipulations of *M. pyrifera* canopy led to significant increases in growth and lateral production of blades in the understory kelp *Pterygophora californica* due to increased light interception (Watanabe et al. 1992). Similar responses to edges have been examined in terrestrial forests systems to understand the effect of patch creation by logging on wood production (Law et al. 1992, McDonald & Urban 2004). Persistent gaps in forests typically result in increased height, lateral

growth and expansion of adjacent trees in northern hardwood stands (Frelich & Martin 1988, Wardman & Schmidt 1998, York et al. 2003). Given such patterns, the geometry of the kelp bed, particularly perimeter to area ratio, is likely to have a major influence on composition, abundance and growth of species that inhabit the kelp bed.

This study has shown that engineering by a small kelp bed has implications for the growth and chemical composition of the kelp itself. Reduction of flow and light in the interior of the bed is a general feature of kelp beds, and this work highlights the differential response of *Macrocystis pyrifera* to a range of physical conditions, through variation in growth, morphology and tissue chemistry. Throughout its range, modification of ambient conditions within kelp beds probably plays an important role in structuring these habitats, particularly at the edges of its distribution where ambient physical conditions approach limiting levels. As *M. pyrifera* is the foundation species for one of the most productive ecosystems on earth (Mann 2000), variability in its growth and morphology can have profound ecological consequences via the extent to which it modifies its habitat, as has been shown in cordgrass *Spartina anglica* and eelgrass *Zostera marina* (Bouma et al. 2005, Van Hulzen et al. 2007). Understanding the causes of such variability in giant kelp provides much needed insight into the mechanisms structuring this important marine ecosystem.

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