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Repetitive harvesting of *Macrocystis pyrifera* (Phaeophyceae) and its effects on chemical constituents of economic value

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Abstract: Kelp harvesting has increased globally in recent decades and is expected to continue rising as the demand for kelp-derived products for use in aquaculture and industrial applications increases. In response, numerous studies have examined how harvesting impacts kelp populations and their associated communities, but the effects of repeated harvesting of the same individuals on the chemical properties for which they are extracted remain poorly understood. This knowledge gap may be especially crucial in areas where the same kelps are necessarily harvested multiple times per year due to their overall low abundance. To address this, we examined how repetitive harvesting of the same individuals of giant kelp, *Macrocystis pyrifera*, over a 3-month period influences tissue chemical properties (i.e. alginate yield, viscosity and strength, nutritional quality, such as protein, carbohydrate, lipid, crude fiber, ash and energy content, and tissue carbon/nitrogen ratios). Our results indicate that, while these properties vary over time, presumably due to variability in oceanographic conditions, repetitive harvesting of the same individuals does not significantly impact these properties.

Keywords: alginate; harvesting; kelp; *Macrocystis*; nutritional value.

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Introduction

The potential for harvesting kelp (large brown seaweeds in the Order Laminariales) has been explored worldwide for numerous economic reasons. These include using kelp and/or chemicals extracted from kelp for human food, animal fodder and the chemical industry (Buschmann et al. 2014, Schiel and Foster 2015). One of the most economically important activities has been the extraction of alginic acid (also referred to as alginate), which is the most abundant structural component of kelp cell walls (McHugh 2003). Due to its mechanical strength, viscosity and ability to absorb water, alginic acid is used in a wide range of markets (Schiel and Foster 2015), and therefore approximately 66% of the global kelp harvest has been conducted for its extraction (McHugh et al. 2001). Additionally, kelps are also used as food in abalone aquaculture facilities in places such as CA, USA and Chile (Buschmann et al. 2014) and, as the number of these facilities increases to supply a growing world demand, the need for fresh kelp to feed the abalone is also growing.

The giant kelp, *Macrocystis pyrifera*, is the most common kelp species harvested for use in abalone aquaculture facilities because it is a good source of fiber, protein and carbohydrates (Lahaye 1991, Cruz-Suárez et al. 2000). As a result, demand for *M. pyrifera* biomass has also increased, raising concerns about populations that currently occur in a diminished state. Consequently, efforts have been made to identify harvesting methods that are not only sustainable, but also allow enough kelp biomass to be harvested to meet the needs of these industries (Borrás-Chavez et al. 2012, Vásquez et al. 2012, Westemeier et al. 2014). For example, for *M. pyrifera* in deeper water, such as in CA, USA and Baja California, México, the entire floating portion to a depth of 1 m is generally removed, thereby leaving the meristems near the holdfast undisturbed and allowing regrowth of the harvested individuals (Kelco 1976). In contrast, for *M. pyrifera* in shallower water, such as along much of central and northern Chile, the entire thallus is often removed (Borrás-Chavez

et al. 2012, Westermeier et al. 2014), in some cases resulting in strong negative impacts on the populations and endangering the sustainability of the industry. To address this, recent studies have explored the sustainability of existing harvesting techniques that involve either harvesting tissues from different individuals from a single population several times each year (Westermeier et al. 2014), or repeatedly harvesting tissues from the same individuals each year (Borrás-Chavez et al. 2012).

The impacts of harvesting on the growth and physiological condition of kelps have been broadly studied (Bartsch et al. 2008) but the physiological effects of harvesting on the internal tissue chemistry remain poorly understood. Indeed, repeated harvesting of large amounts of biomass (and therefore removal of photosynthetic tissue) may constrain the allocation of resources and energy throughout the kelp thallus. This can reduce the production of alginic acid and other macromolecules, and result in the allocation of resources to traits such as growth and spore production, especially during periods when energy is limited (Wiener 1992, Vrede et al. 2004). Therefore, repetitive harvesting of the same individuals may contribute to changes in the quality and quantity of the products extracted, likely reducing their final market price.

The goal of this study was to examine if repetitive harvesting of *M. pyrifera* individuals over several months has a significant effect on alginate properties (i.e. yield, viscosity and strength) or on nutritional quality (i.e. protein, lipid, fiber and carbohydrate content, and carbon/nitrogen ratios). Our hypothesis was that repetitive harvesting of the same individuals during a single season would result in less photosynthetic tissue, and that the lowered amount of energy produced would be allocated, therefore, to growth and reproduction and away from the production of structural components such as alginate and other macromolecules.

Materials and methods

Harvesting

The study was conducted at the Point Loma kelp forest, CA, USA (32° 40' 57.6" N and 117° 15' 58.5" W) during the summer, 2010. SCUBA divers tagged 45 haphazardly selected individuals of *Macrocystis pyrifera* (Linnaeus) C. Agardh occurring within a ~1200-m² area with plastic numbers for later identification (all fronds emerging from

coalescent holdfasts were considered as one "individual"). Tagged individuals were separated from one another by at least 3 m. One-half of the fronds on each tagged individual were then removed by cutting them near the holdfast but above the meristems. To simulate repeated harvesting on these individuals, divers relocated these individuals every 15 days for 15 weeks and again removed half of their fronds, which were a mixture of old and new tissues. In addition, one-half of the fronds were removed from 45 previously un-harvested *M. pyrifera* individuals on each harvesting date as described above. To ensure these individuals had not been harvested previously, they were selected at random from nearby areas that were located at least 30 m from the perimeter of the harvested area. These areas were marked with GPS points to ensure future harvesting did not occur there, and a new un-harvested area was selected on each subsequent harvesting date.

All fronds were brought back to the laboratory on each sampling date and air-dried before being prepared for analysis. Because the biomass needed for adequate alginate extraction exceeded the amount that could be collected from individual kelps, and because homogenizing the tissues from multiple individuals most closely represents how these kelps are processed by the industry prior to extraction, the fronds collected from within each harvest treatment were also homogenized on each date to obtain a single sample from each treatment. From these homogenized samples, three technical replicates were separated and proximate, alginate and C:N (carbon/nitrogen ratio) analyses were conducted on them as suggested in previous studies (e.g. Hernández-Carmona 1996). Consequently, our study did not examine variation in tissue properties among kelp individuals, but rather assessed variation within each sample of the homogenized tissues, and therefore reflects variability due to our analytical techniques. To address this, we collected tissues from a sufficiently large number of individuals (45) over a large enough area (1200 m²) to encompass the expected variation in the relatedness among individuals within the larger Point Loma population (Carney et al. 2013). Therefore, while our results do not describe how individual kelps vary in their tissue properties, they do provide insight into how these properties vary within a larger pooled sample of kelps. Lastly, ocean sea surface temperature data were obtained for the Point Loma area (Buoy 46231, SCRIPPS Research Institute) from the NOAA National Buoy Data Center (<http://www.ndbc.noaa.gov/>) for each day of the study, and ocean temperatures near the benthos were recorded on each harvesting date using dive computers.

Alginate quality

All kelp tissue samples were sun-dried before being ground to a particle size of 0.1 cm² with a Wiley Mill Grinder (Thomas Scientific, Swedesboro, NJ, USA). 200 g of each sample were then transported to Centro Interdisciplinario de Ciencias Marinas (CICIMAR) La Paz, México for chemical analysis. Alginic acid (hereafter alginate) was extracted following the methodology of Arvizu-Higuera et al. (2002), with all analyses done in triplicate. Specifically, 20 g per sample were hydrated in 180 ml of 0.1% formaldehyde solution (Mallinckrodt, KY, USA) overnight. Samples were then rinsed with distilled water, placed in beakers with 300 ml of distilled water, and washed with 1N HCl (JT Baker, Center Valley, PA, USA) at pH 4 and stirred constantly for 15 min. The alginate was extracted using Na₂CO₃ (JT Baker, Center Valley, PA, USA) at pH 10 in a 80°C water bath (Precision Scientific, Chicago, IL, USA) for 2 h. The resulting paste was diluted in distilled water and filtered using a low-pressure vacuum pump (General Electric, Benton Harbor, MI, USA), with diatomaceous earth (JT Baker, Center Valley, PA, USA) as filter aid to facilitate the process. Finally the clarified solution was precipitated with EtOH (AZ, Zapopan, Jalisco, MEX). The resulting alginate fibers were placed in Petri dishes and dried at 50°C for 12 h. Alginate yield was calculated as the ratio between the final (post-extraction) weight of the alginate and the initial (pre-extraction) dry weight of the kelp samples, and expressed as a percentage of total sample weight. Alginate viscosity was measured in a 1% (w/v) solution using a viscosimeter LVT (Brookfield, Middleboro, MA, USA), set at 22°C at 60 rpm, following the addition of 0.5% sodium hexametaphosphate (Spectrum, Gardena, CA, USA) as calcium sequester (Rodríguez-Montesinos et al. 2008). The alginate gel strength was measured by preparing calcium alginate gels. Specifically, dialysis tubes (8 cm×4.5 cm) (Spectrum Laboratories, INC., Rancho Dominguez, CA, USA) were filled with 1% sodium alginate solution and immersed in a 10% calcium chloride solution overnight to convert the sodium alginate to calcium alginate. Tubes were carefully cut in half and gel strength was measured with a texturometer TA.XT plus (Stable Micro Systems, Godalming, Surrey, UK), programmed to perform a penetration of 2 cm over a 5-s period in order to break the gel.

Nutritional quality

The nutritional quality of the dried kelp samples was assessed at CIBNOR (Centro de Investigaciones

Biológicas del Noroeste), La Paz, México by proximate analysis. However, due to technical problems associated with samples obtained on days 45, 75 and 105, nutritional quality was only determined for kelps harvested on days 1, 15, 30, 60 and 90. Specifically, tissue moisture, ash, crude protein, ether-extractable lipid content, crude fiber, total carbohydrates, and calorific content were estimated according to the methods of the Association of Official Agriculture Chemists (AOAC 1995) and expressed as percentage dry weight (except for calorific content that was expressed in calories g⁻¹). Dry weights of each tissue component were obtained as follows: Ash was determined as the weight difference after calcination of the samples at 600°C for 5 h. Crude protein was obtained using the Micro-Kjeldahl method where the total nitrogen content was determined and then multiplied by 6.25 to obtain the amount of crude protein. Ether-extractable lipid content was determined by the ether-extraction method using a Soxtec-Avanti, Tecator apparatus (FOSS Analytical AB, Höganäs, Sweden). A successive hydrolysis (acid/alkali) was performed to extract and determine crude fiber. Energy, expressed in calories, was obtained by calorimetry. The nitrogen-free extract (carbohydrate fraction of the total sample) was obtained by subtracting the mean percentages of each compound (protein, ash, lipids and crude fiber) from 100 for the total dry weight and, therefore, no standard error could be obtained for carbohydrates (see AOAC 1995 for further details). Finally, a portion of each *Macrocystis pyrifera* (Linnaeus) C. Agardh sample was dried and ground as described above, and taken to the Ecology Analytical Laboratory at San Diego State University where the concentrations of carbon and nitrogen were determined using a Costech ECS 4010 Elemental Analyzer (Costech Analytical Technologies, Inc., Valencia, CA, USA). A standard curve was created using acetanilide ($r^2 > 0.998$), and carbon to nitrogen ratios (C:N) were calculated as [moles carbon]/ [moles nitrogen].

Statistical analysis

All multivariate analyses of tissue components were performed using PRIMER 6.1.11 (Primer-E Ltd., Plymouth, UK), and all univariate analyses were done using Systat version 12 (Systat Software Inc., San Jose, CA, USA). Prior to testing, data were checked for normality by graphical examination of the residuals (univariate tests) and bivariate Draftsman plots (multivariate tests), and for equality of variances using Bartlett's test. Data for kelp tissue lipid content, crude fiber, crude protein, carbohydrates, minerals (ash), gross energy, gel strength, alginate

yield and alginate viscosity were normalized, and differences between harvesting treatments were assessed using a two-way mixed-model permutational analysis of variance (PERMANOVA), with time (week) as a random factor and harvesting treatment (repeatedly harvested vs. Un-harvested) as a fixed factor. To determine the relative importance of each factor to the overall variation in tissue properties, the magnitude of effect for each factor was determined using variance partitioning (Graham and Edwards 2001). When there was significant variation among levels in one of the factors, a SIMPER analysis was done to identify the percent contribution of each tissue component to the overall observed difference. Finally, an analysis of covariance (ANCOVA) was used to test for changes in the carbon/nitrogen (C:N) ratios between the two harvest treatments and over time.

Results

Total *Macrocystis pyrifera* tissue properties (alginate and nutrition combined) did not differ significantly between the two harvest treatments (PERMANOVA: $p=0.206$), but did vary through time ($p<0.001$; Table 1). In fact, differences between the two harvest treatments accounted for only 2% of the total variation in the combined tissue properties while variation through time accounted for 55% of the total variation in the combined tissue properties. These factors, however, interacted such that the temporal changes in tissue properties differed between the harvest treatments and accounted for 35% of the total variation, but no consistent differences in their temporal patterns could be identified. Unexplained (error) variation accounted for 8% of the total variation in tissue properties. Together, this indicated that most of the variation in combined tissue properties was due to changes in time, with little influence of harvest method.

Table 1: *Macrocystis pyrifera*.

Sources	df	SS	MS	Pseudo-F	p (Perm)
Treatment (Tr)	1	14.228	14.228	1.524	0.206
Time (Ti)	4	109.430	27.358	42.033	0.001^a
Tr×Ti	4	37.322	9.330	14.336	0.001^a
Residual	20	13.017	0.650		

Results of a mixed-model, two-factor PERMANOVA testing differences in alginate and nutritional tissue components between “un-harvested” and “repeatedly harvested” populations in the Point Loma kelp forest, CA, USA. Harvest treatments were considered as a fixed factor and time was considered as random factor. Bold-faced type denotes significant differences ($p<0.05$).

When values for the different tissue properties were considered separately, alginate yield, expressed as the weight of alginate extracted relative to the total weight of each sample, ranged from 9 to 17% in the fronds of the un-harvested samples and from 11 to 19% in the fronds of the repeatedly harvested samples (Figure 1A). Similarly, values for alginate viscosity ranged from 360 to 1880 mPa s for un-harvested fronds, and 341–2280 mPa

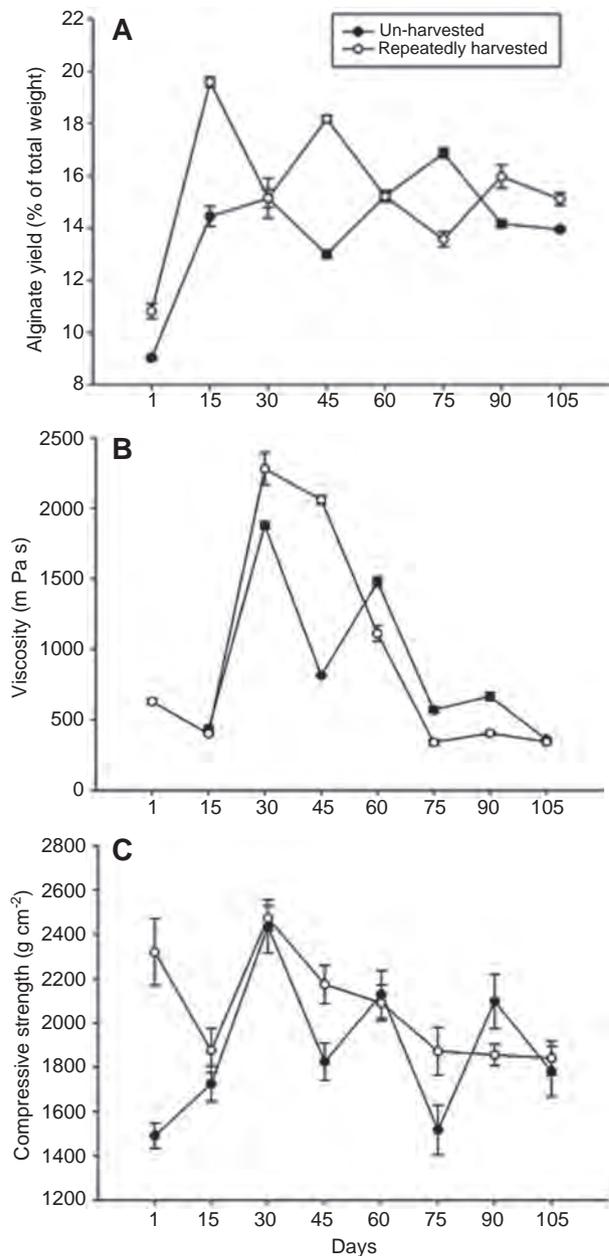


Figure 1: *Macrocystis pyrifera*. Temporal variation in alginate properties. (A) Alginate yield (% of total weight), (B) viscosity (m Pa s) and (C) alginate compressive strength (g cm^{-2}) in tissues harvested from the Point Loma kelp forest, CA, USA. Error bars show within-sample standard errors from three technical replicates.

s for repeatedly harvested fronds (Figure 1B), and compressive gel strength ranged from 1491 to 2435 g cm² for un-harvested fronds, and from 1840 to 2474 g cm² for repeatedly harvested fronds (Figure 1C). Protein content ranged from 13 to 16% for un-harvested fronds, and from 12 to 15% for repeatedly harvested fronds (Figure 2A). Lipids, which are often low in abundance in brown algae, ranged from <0.1 to 0.3% in the fronds from both treatments (Figure 2B). Ash content ranged from 30 to 44% for un-harvested fronds, and from 35 to 38% for repeatedly harvested fronds (Figure 2C). Fiber content ranged

from 5 to 7% for un-harvested fronds, and from 5 to 8% for repeatedly harvested fronds (Figure 2D). The remaining tissue was mostly composed of carbohydrates, which ranged from 34 to 50% for un-harvested fronds, and 40–53% for repeatedly harvested fronds (Figure 2E). Tissue energy content ranged from 2317 to 2642 cal g⁻¹ in the un-harvested fronds, and from 2330 to 2530 cal g⁻¹ in the repeatedly harvested fronds (Figure 2F). Lastly, like other tissue properties, C:N ratios did not differ significantly between the homogenized kelp tissues from the two harvest treatments (ANCOVA: $p=0.421$), but they did

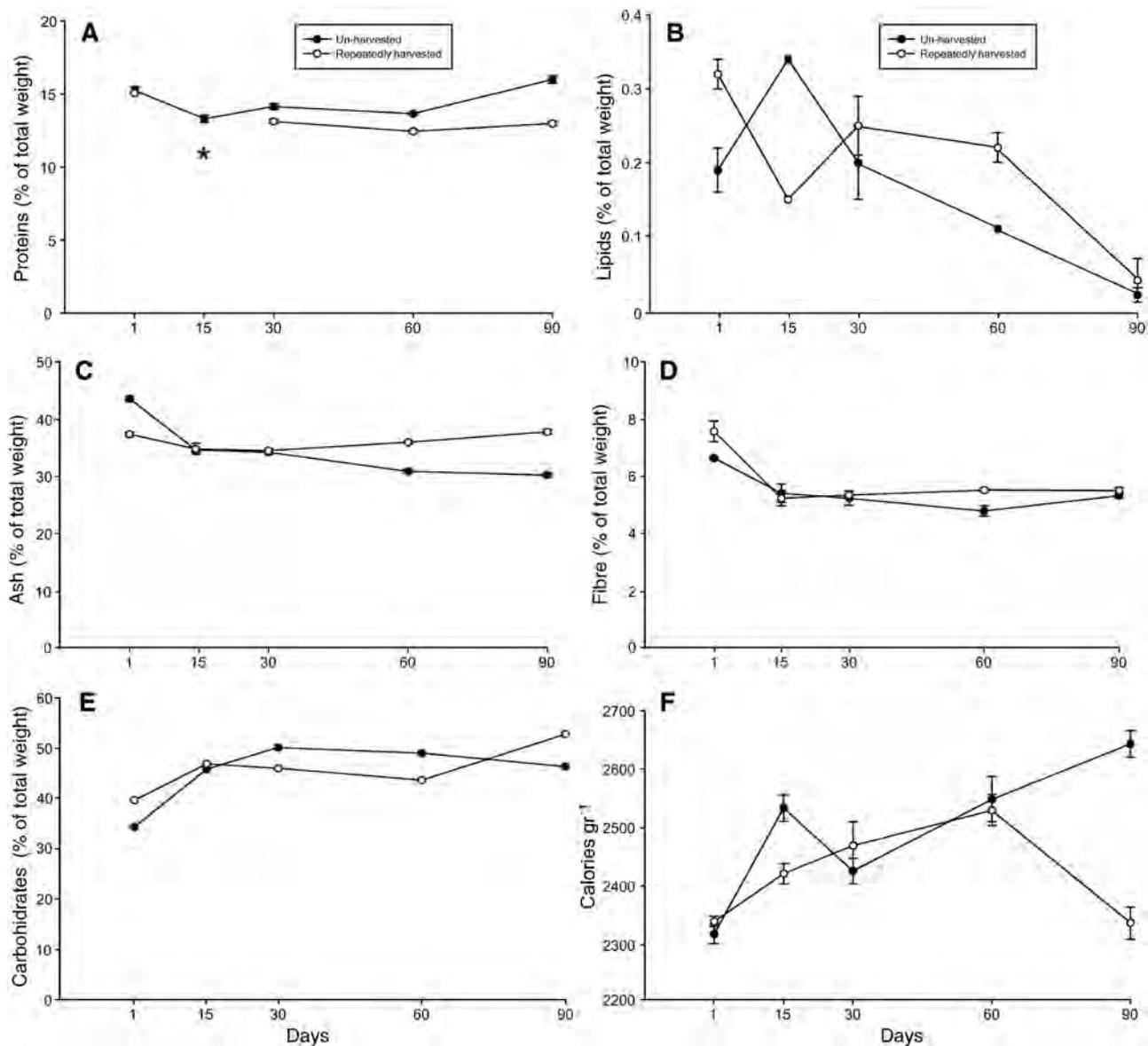


Figure 2: *Macrocystis pyrifera*. Temporal variation in nutritional components, expressed as percent of total tissue weight, for (A) protein, (B) lipid, (C) ash (salts), (D) fibre, (E) carbohydrate, and (F) energy content expressed as calories per gram, in tissues harvested from the Point Loma kelp forest, CA, USA. Error bars (A, B, C, D, F) show within-sample standard errors from 3 technical replicates. *=No data for day 15 in the repeatedly harvested treatment.

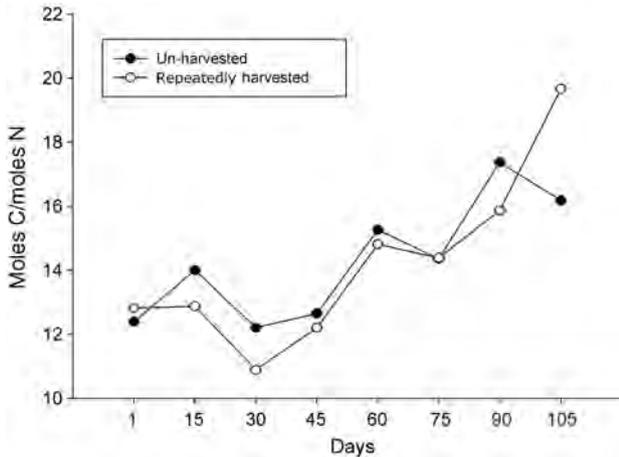


Figure 3: *Macrocystis pyrifera*. Temporal variation in mean C:N ratios in tissues from the Point Loma Kelp forest, CA, USA. All error bars (standard errors from three technical replicates) are smaller than symbols.

vary through time ($p < 0.001$; Figure 3) with no interaction between harvest treatment and time ($p = 0.390$).

Ocean bottom temperature in the Point Loma kelp forest measured at the time of each harvesting bout exhibited little difference throughout the 3-month experiment (average temperature = $11.8 \pm 0.6^\circ\text{C}$). Likewise, sea surface temperatures (SST) measured offshore did not vary substantially throughout the experimental period (average temperature = $19.23 \pm 0.7^\circ\text{C}$).

Discussion

Kelp harvesting has been increasing worldwide in recent decades for the extraction of alginates and for use as fodder in aquaculture industries. As a consequence, researchers have sought to identify new harvesting techniques and/or validate existing ones that are not only sustainable, but also satisfy the increasing demands for the products extracted (Borrás-Chavez et al. 2012, Vásquez et al. 2012, Guiry and Morrison 2013, Vega et al. 2014, Westermeier et al. 2014). However, none of these harvesting methods incorporates assessments of how they affect the final products for which the kelps are harvested. This knowledge gap may be crucial given that repeated removal of biomass from the same individuals could reduce the production and quality of alginates and/or lower the nutritional quality of their tissues. Previously, variability in tissue chemistry has been attributed to oceanographic factors such as nutrient availability, currents, depth, temperature, and/or latitudinal distribution (reviewed in

Schiel and Foster 2015). We found that repeated harvesting of the same individuals over time periods of a few months had little-to-no impact on any of the economically relevant chemical constituents for which they are harvested (see also Westermeier et al. 2012). Indeed, while temporal variability explained the largest amount (55%) of the total variation in the combined tissue properties, differences between the harvest treatments explained little to no variation (2%).

Alginate yield in the harvested *Macrocystis pyrifera* tissues ranged from 9 to 20% of the tissue dry weight, which is slightly lower than but similar to values observed for *M. pyrifera* harvested commercially along the coasts of Baja California, Mexico (19–22%; Rodríguez-Montesinos and Hernández-Carmona 1991). The temporal variation in alginate yield was again not the result of repeated harvesting, as no differences between the harvesting treatments were detected, but was probably due to seasonal variability in environmental factors such as temperature and nutrient availability (Schiel and Foster 2015), or possibly differences in the age structure of the harvested populations (Jones 1956, McKee et al. 1992, Westermeier et al. 2012). However, only temperature was measured in this study and it exhibited so little variation that we cannot attribute any of the variation in tissue characters to this factor. Likewise, alginate viscosity and gel strength, which are measures of overall alginate quality and are related to the enhanced flexibility and mechanical resistance in the kelp tissues (reviewed in Schiel and Foster 2015), were also unaffected by repeated harvesting.

Two of the most important kelp tissue components needed for abalone aquaculture are proteins and fiber, and neither of these was impacted by repeated harvesting. Specifically, lipids, which make up a small fraction (i.e. 0.5–2%) of the total tissue mass in *M. pyrifera* (North 1971, Kelco 1976, Rodríguez-Montesinos and Hernández-Carmona 1991) ranged from < 0.01 to 0.35%, the lowest values observed during the late summer, but again did not differ between the two harvest treatments. This is consistent with the findings of Westermeier et al. (2012) who also observed that lipid content in *M. pyrifera* tissues from natural populations decreases during summer.

As with other tissue properties, carbohydrates, tissue ash and gross energy did not differ between the harvest treatments. Indeed, tissue ash, which includes various minerals, cations, anions and chloride (Larsen 1975, Rodríguez-Montesinos and Hernández-Carmona 1991, Ortiz et al. 2009), and gross energy were both similar to values reported by Westermeier et al. (2012) for *M. pyrifera*, with gross energy also being similar to values reported for other kelps such as *Eisenia arborea* (Areschoug) (Hernández-Carmona

et al. 2009). Lastly, protein production in kelp tissues is closely related to overall tissue nitrogen content (Gorham and Lewey 1984), and therefore tissue nitrogen and carbon ratios can provide an estimate of kelp physiological performance and protein production (Gerard and North 1984, Henley and Dunton 1995, Korb and Gerard 2000, Gevaert et al. 2008). Here, C:N ratios did not differ between the two harvest treatments, suggesting that repeated harvesting of *M. pyrifera* does not impact them.

In addition to exploring ways to increase the sustainability of kelp harvesting techniques, other avenues, such as long-line, spore-based cultures and the isolation of high-performance *M. pyrifera* genotypes appear to be promising avenues for the future exploitation of farmed populations (Vásquez 2008, Westermeier et al. 2012, Buschmann et al. 2014). However, while these techniques are being explored for use in aquaculture and food industries worldwide (Gojón-Baez et al. 1998, Dworjanyn et al. 2007, Cruz-Suárez et al. 2009, Buschmann et al. 2014), harvesting of natural populations still remains the best source for kelp tissues and provides a viable industry for local communities in many areas of the world. Further, recent work by Borrás-Chavez et al. (2012) suggests that repeatedly harvesting tissues from the same kelp individuals over time provides a sustainable way to maintain kelp populations, especially when the kelps are in low abundance. Results from our current study indicate that this method of repeated harvesting tissues from the same *M. pyrifera* individuals does not impact the final products for which they are harvested, and therefore should not impact their economic worth. However, we are aware that complex synergies between variation in oceanographic factors and different internal physiological constraints associated with different ecomorphs of the species (e.g. Kopczak et al. 1991) may result in variable responses by different populations around the world, and care must be taken when policy decisions are made even though the same species is being considered worldwide. Future studies should be directed to evaluate if our short-term (weeks) results can be extended to also describe long-term (years) impacts of repeated harvesting. We believe that an effort to measure these chemical components every time a new harvesting strategy is tested should be a mandatory step in the process of identifying sustainable alternatives, and this should also be a priority for the industry, especially if the goal is to maintain the quality of the products and its economic value in the market.

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