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Seasonal and within-plant variation in fatty acid content and composition in the brown seaweed *Spatoglossum macrodontum* (Dictyotales, Phaeophyceae)

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Abstract We investigated seasonal and within-plant variation in total fatty acids (TFAs) and biomass increase in the tropical brown seaweed *Spatoglossum macrodontum* which was sampled from Magnetic Island (Queensland, Australia) at monthly intervals over 1 year. In this habitat, *S. macrodontum* is an annual species with a growth period from June to September where mean biomass changed from 8- to 136-g fresh weight. Although TFA content and fatty acid (FA) composition were not directly correlated to individual plant size, there was clear seasonal variation in TFA content with a peak in July (82.7 mg g^{-1} dry weight (dw)) followed by a 30 % decline in August and little subsequent variation from September to November (65.9–55.5 mg g^{-1} dw). The FA profile was rich in polyunsaturated FAs (PUFAs) (39 %); however, there was a change to a higher percentage of saturated FAs (SFAs) (42 %) and reduced PUFA (31 %) as plants reached the end of the growth period. Averaged across sampling periods, TFA content ranged from 77 mg g^{-1} dw in the tips to 30 mg g^{-1} dw in the base section. While PUFA content (37–38 %) was similar across sections, the base had less SFAs and a higher content of monounsaturated FAs (MUFAs) (29 %). These results are the first data on the seasonal biomass increase and the temporal and internal variations in FAs for this species with important implications when targeting large brown seaweeds as a source of FAs for nutraceuticals (PUFA(n-3), 21.8 % of TFA) or chemicals (C18:1 (n-9), 17.6 % of TFA).

Keywords Algae · *Spatoglossum* · Fatty acid · Omega-3 · Nutraceutical · Macroalgae

Introduction

There is an increasing focus on marine biomass as a renewable source of oils for foods, nutraceuticals and increasingly as a feedstock for a complex range of products including polymers, paints and solvents (Biermann et al. 2006; Stengel et al. 2011). Of particular importance for these applications is the 'quality' of oil, where the quantity of specific fatty acids determines the application of biomass for oil-based products. For example, nutraceuticals require a feedstock rich in polyunsaturated omega-3 fatty acids (PUFA(n-3)) (Gill and Valivety 1997), and even more specifically, the chemical industry has demands for fatty acids such as C18:1 (n-9) as precursors for biopolymers (Biermann et al. 2006; Biermann and Metzger 2008; Lligadas et al. 2010). Currently, the diversity of oil feedstock crops is mainly limited to soybean, oil palm and rape seed which compete with food crops (Pimentel et al. 2009) and have a narrow range of PUFA(n-3) (Dubois et al. 2007), limiting their use in health products. Oils from marine fish, which are traditionally utilised for the production of nutraceuticals, are seen as problematic as fish stocks are increasingly overfished and depleted (Pauly et al. 2005). Seaweed biomass is a novel choice as a bioresource for renewable oil because there is a broad biodiversity that is essentially untapped in terms of developing scalable bioresources for oil-based products. Furthermore, many species of seaweeds have high productivities under culture (Bolton et al. 2009; Lawton et al. 2013; Magnusson et al. 2014), some of which also have a relatively high oil content with a distinct and diverse composition of fatty

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acids (Gosch et al. 2012) making them targets for more in-depth investigation.

Importantly, the fatty acid content and composition of conspecific individuals of seaweed can vary considerably depending on geographies and time of sampling (Gosch et al. 2012; Hernández-Carmona et al. 2009; Nelson et al. 2002). Although there is potential for genotypic variation in the regulation of fatty acid content (Robinson et al. 2013), these spatial and temporal variations in fatty acid content and composition are generally linked to the environment particularly nutrient availability (Gómez and Wiencke 1998; Gordillo et al. 2001) and water temperature (Al-Hasan et al. 1991; Floreto et al. 1993) but also with changes in light level (Hotimchenko 2002) or salinity (Kumar et al. 2010). On a smaller scale, fatty acids also vary in their content and composition within individual plants, and this is potentially related to the morphological, functional and physiological differentiation of plant parts for growth, photosynthesis and energy storage (Gómez and Wiencke 1998; Lawrence and McClintock 1988; Stengel and Dring 1998). To date, only a limited number of species of brown seaweeds have been investigated for their internal fatty acid and lipid (oil) compositions with no consistent pattern in content and composition emerging. For example, *Sargassum confusum* has higher lipids in its main axis than in blades, while the main axis in *Cystoseira hakodatensis* has the lowest lipid content (Terasaki et al. 2009). *Postelsia palmaeformis* has more than double the lipid content in its fronds than in the holdfast (Lawrence and McClintock 1988). Therefore, it is expected that within-plant fatty acid distribution is species-specific and depends on the morphology of the species as well as its physiological and ecological circumstances. This inherent variability constitutes a challenge for the aquaculture of seaweeds for oils because a stable supply of extractable oils and fatty acids is preferable. However, and more importantly, it also provides the opportunity to exploit this natural variability and develop culture strategies that result in optimised yields of desired target fatty acids.

A critical first step, prior to the domestication of seaweeds for renewable oil-based products, is therefore the quantification of natural variation in total fatty acid (TFA) content and fatty acid composition and an understanding of the drivers thereof. Subsequently, culture conditions and harvest strategies for this new target species can be designed to predict the optimal TFA content and fatty acid composition for applications in specific oil-based products. In this study, we quantify the variation in TFA content and fatty acid composition of wild-collected *Spatoglossum macrodontum* J.Agardh (Dictyotales, Phaeophyceae). This species was selected because it is particularly rich in TFA (Gosch et al. 2012), with a wide distribution in the Pacific region. The first objective was to identify seasonal patterns in the content and composition of fatty acids within biomass and correlate this with plant size and sea surface temperature. The second objective was to identify potential within-plant variation of the content and composition in fatty acids between sections (tips, midsection and base section) of the seaweed. Together, this information will provide the fundamental data on which to develop culture and harvest strategies.

Materials and methods

Spatoglossum macrodontum was selected for this study because it is particularly rich in fatty acids and found along the Northern Queensland coast (Gosch et al. 2012). *S. macrodontum* has a broad distribution in the Pacific region including Queensland, Lord Howe Island, Samoa, French Polynesia, Hawaii and Japan (Guiry and Guiry 2014; Skelton et al. 2007). Samples were collected from Nelly Bay (19.16° S, 146.85° E), which is approximately 8 km from Townsville on Magnetic Island, Queensland, Australia. Samples were collected from the reef flat and fringing reef approximately 100 m from the shoreline. The reef flat is dominated by seaweed with increasing coral cover towards the reef slope.

Biomass and fatty acid analysis

Individual plants of *S. macrodontum* were haphazardly collected from Nelly Bay, for fatty acid and biomass size analysis, each month—when present, see "Results" section—from November 2011 to November 2012. In July, sampling was conducted at two occasions—'early July' and 'late July'—and specific sampling dates are provided in Table 2. During each sampling period, 15 plants were collected except in November 2011 ($n=14$) and early July ($n=9$). A plant was considered as an individual if it was clearly spatially isolated (>1 m) from other plants. Plants of different sizes were collected and transported on ice to James Cook University, Townsville, where they were rinsed in freshwater to remove debris, epiphytes and fauna. The total length and biomass of each individual were measured to correlate TFA content and fatty acid composition with plant size. A representative section of each individual plant, defined as a cutting that includes the tips, midsection and base section in a similar proportion to a whole plant, was removed to estimate TFA content and fatty acid composition of whole plants. Furthermore, to obtain a detailed understanding of the within-plant variation in fatty acid content and composition, three 1 cm^2 cuttings were taken respectively from the tips, midsection and base section from each plant (Online Resource 1). All samples were frozen to −20 °C, freeze-dried and milled to a fine powder. The seaweed powder was sealed in airtight jars and stored at −20 °C until fatty acid analysis.

Fatty acids were analysed for each replicate section and each representative section. A direct transesterification method was used to simultaneously extract and esterify the fatty

acids to fatty acid methyl esters (FAMEs) from 0.030 g dry weight (dw) subsamples for analysis by gas chromatography-mass spectrometry (GC-MS; 7890 GC, 5975 GC MS, DB-23 capillary column with 15 μm cyanopropyl stationary phase, 60 m length and 0.25 mm inner diameter (Agilent Technologies Australia Pty Ltd.)), as described in detail in Gosch et al. (2012). TFA content was determined as the sum of all FAMEs. Fatty acids are designated as CX:Y(n-z), where *X* is the total number of carbon, *Y* is the number of double bonds, and *z* is the position of the ultimate double bond from the terminal methyl group.

Biomass increase estimates

Based on average fresh weight (fw) and plant length data of each sampling period (n=15, exceptions: n=14 for November 2011, n=9 for early July 2012), specific growth rates were calculated with the following equation: specific growth rate (SGR) (% day^{-1})=100×[ln(W_f/W_i)] / t with W_f and W_i being the final and initial fresh weights or plant lengths, respectively.

Length and fw data of collected plants were used to create growth models (third order polynomial functions) to characterise the seasonal changes.

Proximate and ultimate analysis

Ash and elemental compositions (carbon (C), hydrogen (H), oxygen (O), nitrogen (N) and sulphur (S)) were analysed to compare the physiological state of whole plants and plant sections to fatty acid profiles in three random plants per section of the September collection period where plants reached their size maximum and are therefore of special interest for commercial applications. Because these analyses required more biomass than for fatty acid analysis alone (see "Biomass and fatty acid analysis" section), subsamples of pooled replicate sections (n=3 replicate cuttings) per plant were taken. Three random plants for each section and whole plant analysis were used. Ash content was determined by combustion in air at 550 °C (202C, SEM Ltd., Australia), and moisture content was measured on a moisture balance (MS70, A&D Company Ltd., Japan). Ultimate analysis (CHONS) was outsourced to OEA Laboratory Ltd., UK.

Statistical analysis

The effect of plant size (fw) on TFA content and fatty acid composition (saturated FA (SFA), monounsaturated FA (MUFA), and polyunsaturated FA (PUFA)) was analysed by correlations (Correlation, IBM SPSS version 21). The effects of sampling period on TFA content of whole plants were analysed by a one-way ANOVA and Tukey's honest significant difference (HSD) post hoc tests with 15 individual plants (exceptions: n=14 for November 2011, n=9 for early July 2012) for each sampling period (one-way ANOVA, Tukey's HSD, IBM SPSS version 21). Within-plant variation (tips, midsection and base section) in TFA content and interaction with sampling period was analysed with a two-way factorial ANOVA and Tukey's HSD post hoc tests with 15 individual plants per sampling period (exceptions: n=14 for November 2011, n=9 for early July 2012) and the mean of three cuttings per plant for each section (two-way ANOVA, Tukey's HSD, IBM SPSS version 21). TFA content, PUFA content and PUFA(n-3) content were correlated with water temperature data obtained from automated submerged water temperature loggers (NELFL 1, 2.4-m reef flat site 1) from the sampling site (AIMS 2013; correlation, IBM SPSS version 21). Variation in carbon, nitrogen, ash and C/N between different plant sections (tips, midsection and base section) (n=3) and whole plants (n=3) were analysed by one-way ANOVAs and Tukey's HSD post hoc tests (one-way ANOVA, Tukey's HSD, IBM SPSS version 21).

Results

Plant sizes and biomass productivity

Although sampling was conducted from January to May on a monthly basis, no plants were found until June (Fig. 1) when the first young plants were identified at an average length of 14.2 cm±0.9 standard error (SE) and a fresh weight of 8.4 g±1.3 SE. After an initial rapid increase in length to approximately 29 cm during the first 2 months, plant length remained relatively stable until September, while plant fresh weight increased from June to their peak weight (136.3 g±19.5 SE) in September. During this period, plants generally became 'bushier' as the number of branches increased. Both length and fresh weight decreased towards November 2012 (24.7 cm±1.9 SE, 61.5 g±9.0 SE) and were then similar to plants collected at the end of the previous growing season (November 2011) (23.4 cm±1.1 SE, 52.0 g±7.5 SE). Based on the size averages (Fig. 1), biomass of *S. macrodontum* changed from June to September at an average SGR of 2.49 % day^{-1}±0.99 SE with a range of SGR from −0.39 % day^{-1} (late July to August) to 3.78 % day^{-1} (early July to late July). From September to October, plant biomass changed at an SGR of −0.37 % day^{-1} and then rapidly declined from October to November at an SGR of −2.27 % day^{-1}. Although plant length followed the same growth pattern as biomass, the increase of length was comparably low with an average SGR of 0.66 % day^{-1}±0.46 SE (range −0.48 to 1.76 % day^{-1}) from June to September.

Annual size variation of *S. macrodontum* can be best described by a line of best fit of polynomial (third order)

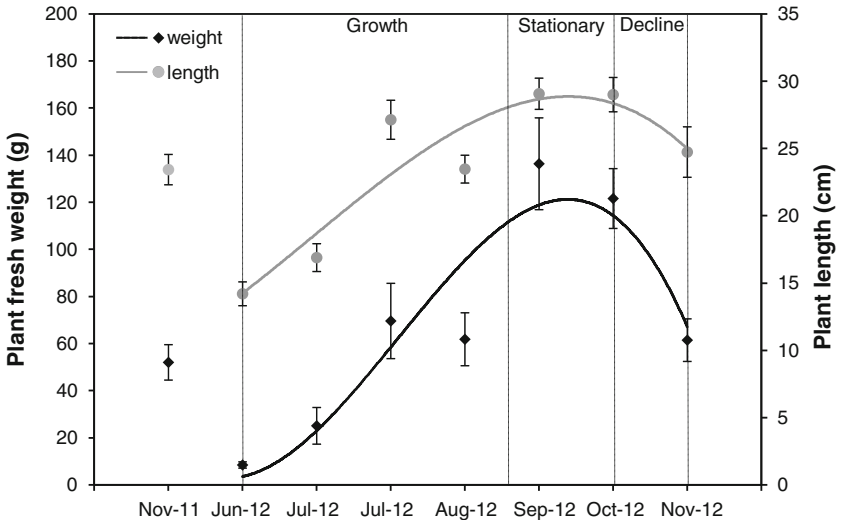

Fig. 1 Average length (cm±SE) and fresh weight (g±SE) of *S. macrodontum* plants collected over 1 year. Fifteen plants per sampling period were used except November 2011 (n=14) and 'early July' (n=9). No samples found from January to May 2012. Specific sampling dates are provided in Table 2. Polynomial (third order) estimate of plant length (cm, *grey line*) (R^2=0.85, y=−0.126 x^3+0.726 x^2+3.147 x+10.5) and plant fresh weight (g, *black line*) (R^2=0.87, y=−2.450 x^3+22.739 x^2+31.672 x +15) of plants collected from June to November 2012. *Vertical lines* define growth phases

functions for both length (R^2=0.85, y=−0.126 x^3+0.726 x^2 +3.147 x+10.5) and fresh weight (R^2=0.87, y=−2.450 x^3+ 22.739 x^2+31.672 x+15) illustrating a phase of rapid growth from June to September (growth phase) followed by a period of relative stable biomass size (stationary phase) and a prominent 'decline phase' from October to November (Fig. 1).

Total fatty acid content

There was clear seasonal variation in TFA content in *S. macrodontum* (ANOVA: $F_{7,104}$=4.906, p<0.001, Tukey's HSD) (Fig. 2a, Table 2). TFA content in whole plants increased by over 20 % from 65.4 mg g^{-1} dw±3.5 SE in June to its annual TFA maximum of 82.7 mg g^{-1} dw ±5.7 SE in late July. This was followed by a rapid decline in average TFA content by over 30 % in August (56.2 mg g^{-1} dw±2.3 SE). For the remainder of the year, TFA content varied between 65.9 mg g^{-1} dw±3.3 SE in September and 55.5 mg g^{-1} dw±4.2 SE in November. There was a negative trend but no significant correlation between TFA content and water temperature at the sampling site (r=−0.50, p=0.206, n=8; Online Resource 3a) and no correlation between TFA content and plant size (fw) (r=−0.001, p=0.991, n=112).

There was also distinct within-plant variation in TFA content depending on sampling date (two-way ANOVA: plant section×sampling date, $F_{14,319}$=7.781, p<0.001) (Fig. 2b). TFA content was significantly different between all plant sections (Tukey's HSD: p<0.001) with the base sections always having the lowest TFA content ranging from 20.9 mg g^{-1} dw±1.3 SE in November 2012 to 49.3 mg g^{-1} dw±4.6 SE in July (Online Resource 4). There was large annual variation in TFA content in the midsections with a peak period in July with over 100 mg g^{-1} dw. The tips had relatively stable TFA contents between 73.0 mg g^{-1} dw±1.9 SE in September and 79.7 mg g^{-1} dw±4.6 SE in November 2011 and were also the section with the highest TFA content except for the period from June to July when the midsections were richer in TFA.

Fatty acid composition

There was a clear seasonal variation in specific fatty acid composition expressed as changes in the proportions of PUFA, MUFA and SFA (Fig. 3a). At the start of the growth period in June, fatty acids of young plants consisted of 44 % PUFA, 21 % MUFA and 34 % SFA. During the initial growth phase from June to August, PUFA content declined to 41 % of TFA and further declined to 37 % of TFA towards September/ October when plants had reached their biomass peak. At the end of the life cycle in November, PUFA content further declined to 31 % of TFA. This general decline in PUFA is characterised by a 45 % decline of PUFA(n-3) particularly C18:4(n-3) which declined by over 60 % from June to November (Table 2). This decline in PUFA is generally mirrored by increasing saturation from 33 % in June to 42 % of TFA content in November.

Similar to TFA content, there was no clear relationship between plant size and fatty acid composition analysed for SFA (r=0.035, p=0.712, n=112), MUFA (r=0.073, p=0.442, n=112) and PUFA (r=−0.118, p=0.214, n=112) (Online Resource 2). Dominant SFA was C16:0 (24.64 % of TFA± 0.93 SE) and C14:0 (7.83 % of TFA±0.10 SE), while the most

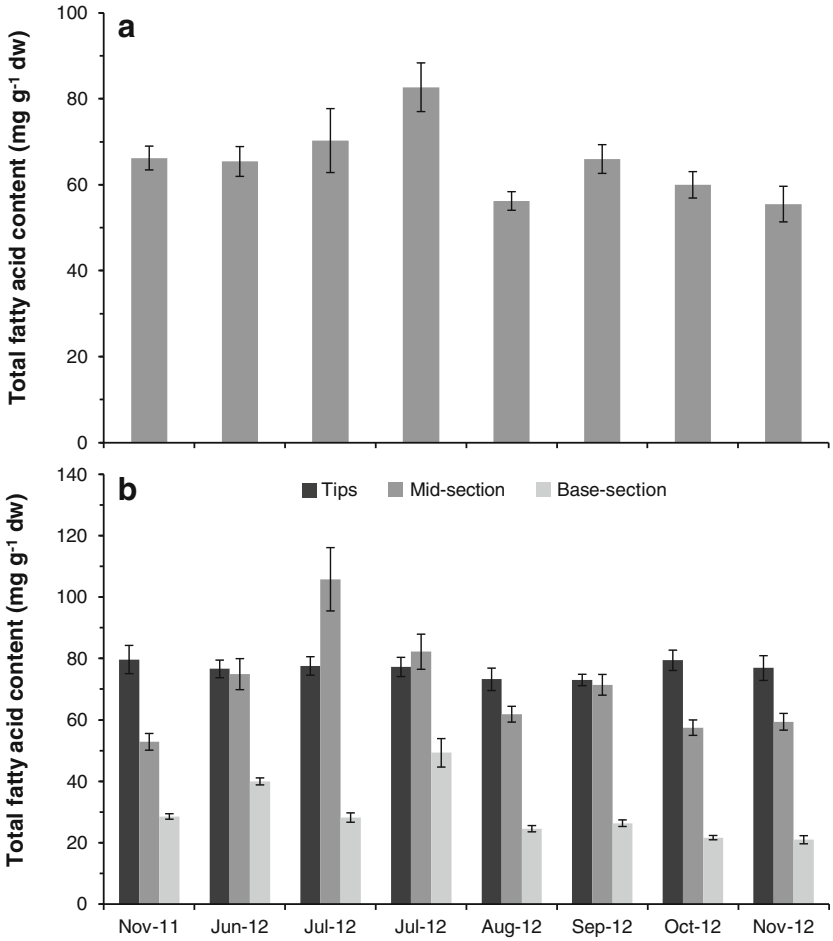

Fig. 2 Seasonal variation in mean total fatty acid (TFA) content (mg g^{-1} dw±SE) of *S. macrodontum* collected over the period of 1 year from November 2011 to November 2012 for **a** whole plants (one-way ANOVA: $F_{7,104}$=4.906, p<0.001) and **b** seasonal within-plant variation in TFA in the tips, midsection and base sections (two-way ANOVA: $F_{21,424}$= 5.232, p<0.001). Fifteen plants per sampling period were used except November 2011 (n=14) and 'early July' (n=9). Specific sampling dates are provided in Table 2

abundant MUFA was C18:1(n-9) (17.57 % of TFA±0.49 SE) (Table 2). PUFA(n-3) were more abundant than PUFA(n-6) with an n-6/n-3 ratio of 0.74. Of the PUFA(n-3), the most abundant fatty acids were C18:4(n-3) (8.44 % of TFA±0.74 SE), C18:3(n-3) (5.10 % of TFA±0.15 SE) and C20:4(n-3) (3.86 % of TFA±0.20 SE). There was, however, a strong negative correlation between water temperature and PUFA (r=−0.80, p=0.018, n=8; Online Resource 3b) and PUFA(n-3) (r=−0.81, p=0.015, n=8; Online Resource 3c).

Fatty acid composition also varied distinctly within plants with the base section having a less SFA profile (33 % SFA) than the midsections (38 % SFA) and tips (38 % SFA) (Fig. 3b–d, Online Resource 4). This low saturation of the base section is mainly a result of a relatively low content of C16:0 (21 % of TFA) compared to the midsections (26 % of TFA) and the tips (26 % of TFA). While the PUFA content was similar across plant sections (37–38 % of TFA), the base section had a relatively high content of MUFA (29 % of TFA) compared to the tips (23 % of TFA) and midsections (25 % of TFA). Similar to whole plants, PUFA content declined in all plant sections towards the end of the growth cycle with the largest decline from 46 to 27 % of TFA in the tips and the smallest decline from 44 to 32 % of TFA in the base sections.

Proximate and ultimate analysis

Ash content of the tips (7.9 % of dw±1.3 SE) and midsections (5.8 % of dw±1.2 SE) was similar, while the base section had more than three times this ash content (23.2 % of dw±8.5 SE) (Table 1; ANOVA: $F_{3,14}$=5.350, p=0.012). Although statistically not significant, nitrogen content tended to be higher in the tips (2.5 % of dw±0.2 SE), followed by the midsection (2.4 % of dw±0.3 SE) and base section (1.7 % of dw±0.3 SE) (Table 1; ANOVA: $F_{3,14}$=2.617, p=0.092). Carbon content was similar in the tips (42.4 % of dw±0.6 SE) and midsections (43.1 % of dw±1.5 SE) and significantly lower in the base sections (37.2 % of dw±1.4 SE) (Table 1; ANOVA: $F_{3,14}$=7.548, p=0.003). A similar pattern of carbon and nitrogen between the different plant sections was found when these values were expressed as proportions of ash-free dw (afdw) (Table 1).

Discussion

This study identified the brown seaweed *S. macrodontum* as an annual species which is apparent on the reef flat on Magnetic Island (Queensland, Australia) from June to November with a

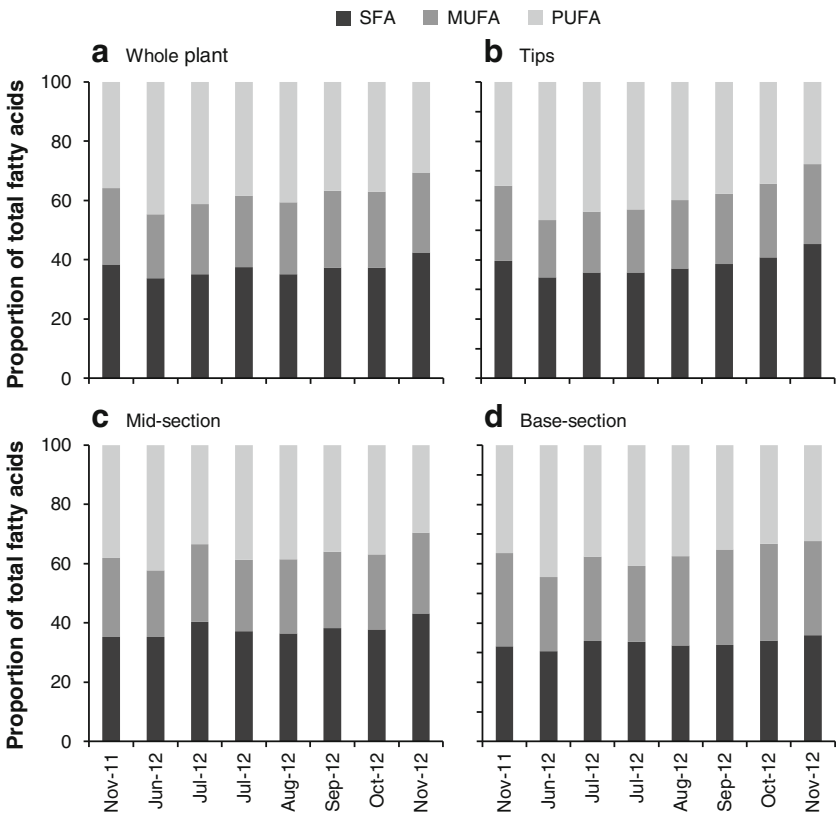

Fig. 3 Proportion of saturated fatty acids (SFAs), monounsaturated fatty acids (MUFAs) and polyunsaturated fatty acids (PUFAs) of total fatty acid (TFA) content of **a** whole plants and plant sections (**b** tips, **c** midsections, and **d** base sections) of *S. macrodontum* sampled over 1 year. Fifteen plants per sampling period were used except November 2011 (n=14) and 'early July' (n=9). Specific sampling dates are provided in Table 2

growth period from June to September. Its high TFA content and fatty acid composition make it a species of interest for the production of oil-based products particularly nutraceuticals and chemicals. This study also clearly identified seasonal variation in TFA content and composition that are linked to morphology and broad seasonal changes in water temperature. However, across all seasons, there was clear and consistent within-plant variation in TFA content and fatty acid composition, with the plant tips having higher overall TFA and a higher percentage of SFA, while the base section was richest in MUFA.

Plant sizes and biomass seasonality

S. macrodontum is an annual seaweed with macrothalli present from at least June to November at the sample site. Although sampling was conducted from January on a monthly basis, no macrothalli were found until June. This is potentially because of their small size and their cryptic location within dense stands of *Sargassum* species. Although many tropical brown seaweeds have no macrothalli present during the warmer summer, some *Dictyota* species survive as cryptic microthalli and start to grow once environmental conditions become favourable (Ateweberhan et al. 2005). In our study, it could not be determined whether individual *S. macrodontum* plants survived the summer as the dormant stage; however, it seems likely that populations were completely renewed every year from propagules as there was no evidence of microthalli.

The growth pattern of this species was characterised by a stage of rapid biomass increase from June to September followed by a stagnant phase and a subsequent biomass

Table 1 Elemental analysis of different plant sections and whole plants collected in September 2012 as means (wt%±SE, n=3) based on dry weight (dw) and ash-free dry weight (afdw)

	% dw		% afdw			
	Carbon	Nitrogen	Carbon	Nitrogen	Ash	C/N
Whole plant	41.9±0.5 a	2.3±0.1 a	44.6±0.3 a	2.4±0.1 a	9.4±0.9 a	18.2:1 a
Tips	42.4±0.6 a	2.5±0.2 a	45.3±0.9 a	2.7±0.1 a	7.9±1.3 a	16.8:1 a
Midsection	43.1±1.5 a	2.4±0.3 a	45.9±1.0 a	2.5±0.3 a	5.8±1.2 a	18.1:1 a
Base section	37.2±1.4 b	1.7±0.3 a	40.8±0.3 b	1.8±0.3 a	23.2±8.5 b	22.2:1 a

Significant and homogenous subsets (Tukey's HSD) are indicated by identical letters

decline towards the end of the life cycle. During the 'growth phase', average SGR of *S. macrodontum* (2.49 % day^{-1}±0.99 SE) was similar to other benthic brown seaweeds such as *Desmarestia viridis* (2.9 % day^{-1}) (Blain and Gagnon 2013) or *Sargassum hemiphyllum* (0.62–1.65 % day^{-1}) (Yu et al. 2013) but lower than common commercial species such as *Kappaphycus alvarezii* (3.72–7.17 % day^{-1}) (Hurtado-Ponce 1992) or various species of *Gracilaria* (2.5–7.8 % day^{-1}) (Skriptsova and Nabivailo 2009). Biomass increase in *S. macrodontum* occurred when both water temperature and incidental light were at their annual minimum (AIMS 2013; BOM 2013). Changes in water temperature and light govern the seasonal growth patterns of a range of seaweed species particularly brown seaweeds (Ateweberhan et al. 2005; Lüning 1990). For example, tropical *Spatoglossum asperum* (Ngan and Price 1980), temperate *Spatoglossum crassum* (Hwang et al. 2004), and other members of the Dictyotales (Ateweberhan et al. 2005) have a pattern of seasonal growth over the cooler winter. After the biomass peak in September, growth of *S. macrodontum* ceased, potentially triggered by increasing water temperatures and/or a reallocation of resources from growth towards reproduction as reported for other benthic brown seaweeds (Ateweberhan et al. 2005; Blain and Gagnon 2013; Díaz-Villa et al. 2005). Without any further growth, degenerative processes such as grazing, physical fragmentation and general tissue decomposition could explain the observed decline of biomass towards the end of the life cycle.

Fatty acids

This study confirms the high TFA content of *S. macrodontum* which ranged between 55.5 and 82.7 mg g^{-1} dw depending on the time of collection. These levels are within the range of fatty acid contents reported for this species sampled at the same location in September 2010 (57.40 mg g^{-1} dw±0.87 SE) (Gosch et al. 2012). The TFA content of *S. macrodontum* is approximately twice as high as that of the related species *Dictyota bartayresii* (35.15 mg g^{-1} dw±3.89 SE) (Gosch et al. 2012) and considerably higher than that of the common commercial seaweeds *Saccharina japonica* (15.91–30.63 mg g^{-1} dw) (Honya et al. 1994) and *Undaria pinnatifida* (total lipid 24 mg g^{-1} dw) (Herbreteau et al. 1997). This makes *S. macrodontum* an interesting target to investigate the production of oil-based products for the nutraceutical industry but also for targeted pre-cursors for biopolymers in the chemical industry.

S. macrodontum contains a diverse range of PUFA relevant to the nutraceutical market and is particularly rich in PUFA(n-3) with an n-6/n-3 ratio of 0.7, which is considerably lower than in most vegetable oils and similar to other seaweeds (Table 2; Dubois et al. 2007; Kumari et al. 2013; Schmid et al. 2014). A typical western diet with a high n-6/n-3 ratio has been linked to health problems including cancer and cardiovascular diseases (Russo 2009). The most abundant PUFA(n-3) in *S. macrodontum* is C18:4(n-3) which is an omega-3 fatty acid that is important for cardiovascular health (Guil-Guerrero 2007) and is a precursor for the nutritionally essential EPA C20:5(n-3) (Guil-Guerrero 2007). Notably, C18:4(n-3) is absent or present in only minute quantities in traditional terrestrial oil crops (Dubois et al. 2007), and alternative sources of this fatty acid are fish oils and genetically manipulated terrestrial crops, which are problematic because of increasingly depleted fish stocks (Pauly et al. 2005) and low consumer acceptance of genetically manipulated foods (Bredahl 2001). Other abundant and nutritionally important PUFA(n-3) in *S. macrodontum* are C20:4(n-3), C20:5(n-3) and particularly C18:3(n-3) which has been found to decrease blood pressure, improve heart and liver function and also redistribute body fat in animal trials (Poudyal et al. 2012, 2013).

S. macrodontum has a fatty acid profile with 33 to 42 % saturation, with the most abundant SFA being C16:0, followed by C14:0. Saturation in this species is within the range of several common seaweed species used for human consumption such as *Caulerpa lentillifera* and *Caulerpa racemosa* (40.8–43.3 % SFA; Paul et al. 2013) and *S. japonica* (26–48 % SFA; Honya et al. 1994) but higher than that of *U. pinnatifida* (20.4 % SFA; Sánchez-Machado et al. 2004). The fatty acid profile is also more saturated than that of common industrial oil crops such as rapeseed, soybean or sunflower but much less saturated than, for example, palm oil or coconut oils (Dubois et al. 2007; Table 2). A high degree of saturation in a diet is generally associated with negative health effects as SFA, in particular, C14:0 and C16:0 increase plasma cholesterol levels which contribute to cardiovascular diseases (Hunter 2001; Kris-Etherton and Yu 1997). However, the adverse effects of these SFA are generally associated with large quantities that are not usually consumed in the form of algal oils (Hayes and Khosla 1992). It is therefore likely that the effects of the PUFA content and the very low n-6/n-3 ratio of *S. macrodontum* will be beneficial.

S. macrodontum also has a high content of C18:1(n-9) (~18 % of TFA) which, for example, has demand in the chemical industry for the production of polyols and polyurethanes (Biermann et al. 2006; Lligadas et al. 2010). The relative and total content of this fatty acid is higher than that reported in most seaweed species (Gosch et al. 2012; Kumar et al. 2010; Schmid et al. 2014) highlighting the potential of *S. macrodontum* as a renewable feedstock for the manufacture and synthesis of chemical products. Although terrestrial crops such as palm oil have a more favourable fatty acid profile for such chemical processes (Table 2), environmental concerns and competition with food crops remain controversial (Tan et al. 2009).

This study also provides clear evidence of seasonal variation in fatty acids in *S. macrodontum* with a higher TFA

Table 2 Average content of fatty acids (% of TFA±SE) of *S. macrodontum* (whole plants) collected over 1 year and average of seasonal fatty acid content of *S. macrodontum* (% of TFA±SE) compared with typical fatty acid profiles of traditional oil feedstock plant species (% of TFA)

	Fatty acids (% of TFA) of *S. macrodontum*									Fatty acids (% of TFA) of oil crops			
	20/11/2011	4/6/2012	3/7/2012	30/7/2012	29/8/2012	26/9/2012	27/10/2012	26/11/2012	Annual average	Rapeseed	Palm oil	Soybean	Sunflower
C14:0	7.43±0.21	8.13±0.16	8.11±0.38	8.22±0.26	7.77±0.22	7.80±0.23	7.58±0.21	7.63±0.23	7.83±0.10	0.1	1.1	0.1	0.1
C14:1	0.43±0.03	0.48±0.03	0.53±0.04	0.35±0.03	0.43±0.02	0.45±0.02	0.45±0.04	0.43±0.06	0.44±0.02				
C15:0	0.49±0.04	0.47±0.02	0.66±0.03	0.59±0.02	0.77±0.03	0.62±0.02	0.65±0.03	0.75±0.03	0.63±0.04				
C16:0	26.93±0.80	21.94±0.77	21.48±1.58	24.74±1.21	22.57±0.89	25.10±0.78	25.14±0.58	29.20±0.78	24.64±0.93	5.1	43.8	10.8	6.4
C16:1(n-9)	0.37±0.02	0.37±0.02	0.65±0.05	0.46±0.03	0.62±0.03	0.59±0.03	0.60±0.03	0.58±0.05	0.53±0.04				
C16:1(n-7)	3.58±0.07	3.19±0.13	3.41±0.28	3.28±0.11	3.56±0.06	3.70±0.12	3.84±0.14	3.78±0.14	3.54±0.08	0.2	0.2	0.2	0.1
C16:1	0.61±0.03	0.60±0.05	0.69±0.05	0.49±0.04	0.63±0.03	0.69±0.03	0.77±0.03	0.93±0.05	0.68±0.05				
C16:2	0.23±0.04	0.33±0.03	0.41±0.09	0.25±0.05	0.46±0.02	0.47±0.02	0.42±0.06	0.18±0.07	0.34±0.04				
C17:0	0.38±0.04	0.32±0.04	0.59±0.03	0.39±0.03	0.50±0.01	0.49±0.04	0.40±0.07	0.47±0.08	0.44±0.03				
C16:3(n-4)	0.41±0.02	0.35±0.03	0.64±0.05	0.45±0.03	0.56±0.02	0.57±0.02	0.62±0.03	0.69±0.03	0.54±0.04				
C16:3(n-3)	0.46±0.02	0.47±0.03	0.62±0.05	0.49±0.03	0.57±0.02	0.57±0.03	0.62±0.03	0.57±0.05	0.55±0.02				
C16:4(n-3)	0.12±0.05	0.38±0.04	0.48±0.08	0.31±0.05	0.37±0.05	0.29±0.06	0.15±0.06	0.12±0.06	0.28±0.05				
C18:0	1.40±0.05	1.17±0.05	1.30±0.07	1.21±0.03	1.22±0.05	1.37±0.04	1.43±0.03	1.78±0.06	1.36±0.07	1.7	4.4	3.9	4.5
C18:1(n-9)	19.20±0.53	15.60±0.54	15.79±1.02	17.49±0.73	17.03±0.48	18.33±0.39	17.83±0.34	19.31±0.33	17.57±0.49	60.1	39.1	23.9	22.1
C18:1	0.83±0.05	0.58±0.06	1.04±0.03	0.90±0.03	1.00±0.03	0.94±0.05	1.10±0.05	1.23±0.06	0.95±0.07				
C18:1(n-5)	0.42±0.04	0.47±0.03	0.60±0.05	0.42±0.03	0.53±0.02	0.53±0.02	0.57±0.03	0.61±0.05	0.52±0.03				
C18:2(n-6)	2.94±0.05	3.03±0.06	2.67±0.08	2.73±0.05	2.54±0.05	2.48±0.04	2.75±0.07	2.78±0.06	2.74±0.06	21.5	10.2	52.1	65.6
C18:3(n-6)	1.28±0.03	1.55±0.06	1.12±0.04	0.99±0.04	0.90±0.02	0.92±0.02	1.07±0.04	0.98±0.03	1.10±0.08				
C18:3(n-3)	5.16±0.16	4.79±0.13	4.95±0.24	4.71±0.20	5.76±0.15	5.34±0.17	5.55±0.19	4.51±0.17	5.10±0.15	9.9	0.3	7.8	0.5
C18:4(n-3)	7.77±0.46	11.89±0.47	10.04±0.59	9.44±0.59	8.87±0.45	7.18±0.43	7.19±0.29	5.10±0.29	8.44±0.74				
C20:0	0.74±0.03	0.69±0.04	0.92±0.07	0.72±0.04	0.90±0.04	0.89±0.03	0.92±0.03	1.00±0.04	0.85±0.04	0.6	0.3	0.3	0.3
C20:1(n-9)	0.19±0.06	0.02±0.02	0.11±0.11	0.06±0.03	0.00±0.00	0.32±0.07	0.15±0.09	0.00±0.00	0.11±0.04	1.4	0.1	0.1	0.2
C20:2(n-6)	0.54±0.03	0.55±0.04	0.64±0.07	0.48±0.03	0.63±0.03	0.64±0.03	0.79±0.05	0.57±0.08	0.61±0.03	0.1			
C20:3(n-6)	2.64±0.08	4.46±0.10	4.39±0.21	4.34±0.17	3.50±0.07	3.08±0.11	2.74±0.10	2.16±0.03	3.41±0.32				
C20:4(n-6)	8.12±0.32	9.33±0.38	8.83±0.54	7.44±0.40	8.82±0.33	7.68±0.24	7.61±0.20	7.09±0.26	8.11±0.28				
C20:3(n-3)	0.09±0.05	0.00±0.00	0.19±0.10	0.45±0.03	0.47±0.04	0.38±0.06	0.43±0.08	0.04±0.04	0.26±0.07				
C20:4(n-3)	3.07±0.11	4.14±0.11	4.36±0.27	4.13±0.13	4.38±0.08	4.10±0.13	3.83±0.13	2.87±0.11	3.86±0.20				
C20:5(n-3)	3.24±0.11	3.80±0.08	3.38±0.14	3.51±0.07	3.30±0.12	3.11±0.06	3.26±0.06	3.14±0.09	3.34±0.08				
C22:0	0.00±0.00	0.00±0.00	0.00±0.00	0.02±0.02	0.13±0.09	0.09±0.06	0.00±0.00	0.06±0.06	0.04±0.02	0.3	0.1	0.2	0.8
C22:1(n-9)	0.00±0.00	0.00±0.00	0.00±0.00	0.01±0.01	0.18±0.08	0.22±0.07	0.25±0.09	0.00±0.00	0.08±0.04	0.1			0.1
C24:0	0.53±0.03	0.48±0.04	0.84±0.15	0.50±0.04	0.61±0.05	0.57±0.07	0.77±0.05	0.89±0.05	0.65±0.06	0.2	0.1	0.3	0.2

Table 2 (continued)

	Fatty acids (% of TFA) of *S. macrodontum*								Fatty acids (% of TFA) of oil crops			
	20/11/2011	4/6/2012	3/7/2012	30/7/2012	29/8/2012	26/9/2012	27/10/2012	26/11/2012	Annual average	Rapeseed	Palm oil	Soybean	Sunflower
Other FA	0.39±0.02	0.40±0.02	0.54±0.04	0.44±0.02	0.42±0.04	0.48±0.02	0.52±0.03	0.58±0.03	0.47±0.02	0.3	0.6		0.5
Total SFA	37.90±0.71	33.20±0.78	33.89±1.37	36.39±0.99	34.47±0.80	36.93±0.65	36.89±0.50	41.76±0.67	36.43±0.96	8	50.4	15.7	12.8
Total MUFA	25.63±0.52	21.32±0.42	22.83±0.86	23.47±0.66	23.96±0.36	25.79±0.37	25.57±0.41	26.87±0.30	24.43±0.65	62.4	39.4	24.2	22.4
Total PUFA	36.08±1.11	45.08±1.14	42.74±2.15	39.70±1.63	41.15±1.10	36.80±0.93	37.02±0.73	30.78±0.88	38.67±1.58	31.5	10.5	59.8	66
PUFA(n-3)	19.91±0.72	25.47±0.67	24.03±1.28	23.04±0.97	23.73±0.68	20.96±0.59	21.02±0.42	16.34±0.55	21.81±1.02	9.9	0.3	7.8	0.5
PUFA(n-6)	15.52±0.43	18.93±0.50	17.66±0.81	15.96±0.64	16.40±0.41	14.80±0.34	14.96±0.38	13.57±0.33	15.98±0.60	21.6	10.2	52.1	65.6
n-6/n-3	0.78±0.01	0.74±0.01	0.74±0.01	0.70±0.01	0.69±0.01	0.71±0.01	0.71±0.02	0.84±0.02	0.74±0.02	2.18	34.00	6.68	131.20
TFA (mg g^{-1} dw)	66.22±2.78 ab	65.42±3.47 ab	70.28±7.44 ab	82.69±5.66 b	56.22±2.32 a	65.99±3.34 ab	59.99±3.08 a	55.50±4.15 a	65.29±3.09				

Reviewed in Dubois et al. (2007). Total fatty acid (TFA) content is presented as means (mg g^{-1} dw±SE), and significant and homogenous subsets (Tukey's HSD) are indicated by identical letters. Fifteen plants per sampling period were used except November 2011 (n=14) and 'early July' (n=9). No samples found from January to May 2012

FA fatty acids, *TFA* total fatty acids, *SFA* saturated fatty acids, *MUFA* monounsaturated fatty acids, *PUFA* polyunsaturated fatty acids, *dw* dry weight

content during the colder winter months (June and July) and a general trend of increasing saturation and concomitant decrease of PUFA towards the end of the growth period. Seasonal variation in TFA content and fatty acid composition can be a response to changes in the key environmental parameters of temperature and light. For example, lower TFA during winter has been reported for various seaweeds (Honya et al. 1994; Nelson et al. 2002). Although there is limited data on the direct effect of temperature on the TFA in macroalgae (e.g. Al-Hasan et al. 1991), various seaweeds from cold water environments have a higher degree of unsaturation compared to seaweed from warm water environments (Pettitt et al. 1989; Nelson et al. 2002). This is possibly an environmental acclimatisation as PUFAs have a lower melting point than SFAs and therefore provide a physiological advantage in cold water environments by increased membrane lipid fluidity (Los et al. 2013; Thompson et al. 1992). This is supported by our study as PUFA and particularly PUFA(n-3) were negatively correlated with water temperature. In a similar manner, low light conditions not only lead to a higher TFA content in a range of seaweeds (Hotimchenko 2002) but also a higher degree of unsaturation (Klyachko-Gurvich et al. 1999). Previous work on marine microalgae suggests that this is a physiological response to improve the effectiveness of photosynthesis by increasing the fluidity of thylakoid membranes and thereby, electron flow in the chloroplast (Mock and Kroon 2002).

Although environmental variation provides an explanation for the observed fatty acid patterns, it is possible that saturation also increases with age or growth stage as proposed for the brown seaweeds *Costaria costata* (Gerasimenko et al. 2010) and *S. japonica* (Honya et al. 1994). This potentially relates to an increasing rate of PUFA oxidation in plants towards the end of their life cycle. Such an age/growth stage effect on fatty acids is unlikely in our study because plant size did not significantly explain fatty acid variability in *S. macrodontum*. However, it remains unclear whether plant size is an accurate measure of age and growth stage in this species due to potential grazing or fragmentation through physical disturbances, which is demonstrated by two distinct growth curves for length and weight at our study site.

In addition to this variation in fatty acids between whole plants, there was also internal within-plant variation in fatty acids with the tips and midsections having a higher TFA content and slightly more PUFA(n-3), while the base section was proportionally less saturated and richer in MUFA. This within-plant pattern is similar to those in the brown seaweeds *Sargassum miyabei* and *S. japonica* (Khotimchenko and Kulikova 2000; Kulikova and Khotimchenko 2000) and is likely related to the morphological, functional and physiological differentiation of plant parts required for growth, photosynthesis and energy storage (Gómez and Wiencke 1998; Lawrence and McClintock 1988; Stengel and Dring 1998). Generally, it can be expected that the thin and branched tips of

a seaweed such as *S. macrodontum* contain more photosynthetic tissue per unit biomass because of the higher surface area to volume ratio compared to the more compact holdfast region whose main function is structural support and attachment to the substratum (Arnold and Manley 1985; Littler and Littler 1985).

Functional differentiation between photosynthetic tips and structural base sections may also provide an explanation for the within-plant variation in TFA content of *S. macrodontum*. The lower measured TFA content of the base section can be a direct result of proportionally more carbohydrates than fatty acids in this region, reflecting its structural and energy storage function, while the photosynthetically active tips are richer in lipids that support photosynthetic activity. The major lipid class of brown seaweeds is the glycolipids which are directly associated with the light harvesting complex and are found in the photosynthetic membranes of algae and plants (Dembitsky et al. 1991; Dörmann and Hölzl 2010; Sanina et al. 2004) and dominate the upper sections of a range of seaweeds (Khotimchenko and Kulikova 2000; Kulikova and Khotimchenko 2000). Glycolipids of several seaweeds have a high concentration of PUFA(n-3) and particularly C18:4(n-3) and C20:5(n-3) (Khotimchenko 2003; Miyashita et al. 2013; Sanina et al. 2004). In *S. macrodontum*, however, there was no general dominance of PUFA(n-3) in the tips but a strong dependence on sampling time as PUFA(n-3) of the tips were generally more abundant from June to October, while there were no differences between tips and base sections during the decline phase in both November 2011 and 2012. It is possible that during the decline phase, there was a breakdown of tissue, oxidation of PUFA(n-3) and general physiological inactivity which together lead to a reduced PUFA(n-3) content in the tips. Although neither carbohydrates nor photosynthetic activity was measured per se in *S. macrodontum*, indirect evidence of the biochemical composition is provided in the form of a distinct within-plant variation in carbon and nitrogen content. The C/N ratio ranged from 16.8:1 in the tips to 22.2:1 in the base section (Table 1). Such C/N ratios are typical for tropical seaweeds (Atkinson and Smith 1983) and indicate nitrogen limitation. Within-plant variation in carbon and nitrogen content is documented for a range of seaweeds, such as *Macrocystis integrifolia* and *Nereocystis luetkeana* where the blades were richer in nitrogen than the stipes or bulbs across all seasons (Rosell and Srivastava 1985), or for *S. japonica* were the C/N ratio increased from the tips (7.87:1) to the basal parts (11.02:1) of the thallus (Wang et al. 2013). The proportionally higher N content in specific thallus regions is likely a consequence of a high concentration of photosynthetic pigments and associated proteins (Bird et al. 1982) as measured for *S. japonica* (Wang et al. 2013); also discussed by Rosell and Srivastava (1985). It is therefore likely that the proportionally higher N content in the tips of *S. macrodontum* is also related to the higher concentration of photosynthetic pigments in this plant section. Conversely, the higher proportion of carbon in the base is likely due to a high concentration of carbohydrates as means of energy storage (Percival 1979) but also due to the function of the holdfast in providing support, flexibility and firm attachment to the substratum rather than energy fixation (Littler and Littler 1985; Arnold and Manley 1985).

This study emphasises the suitability of *S. macrodontum* as a novel species for the production of oil-based products because of its high TFA content and a fatty acid composition that is suitable for nutraceuticals or chemicals. The high content of C18:1(n-9) make it a potential feedstock for the chemical industry. However, most importantly, the high and diverse content of PUFA(n-3) and its abundance of C18:4(n-3), which are absent in most traditional terrestrial oil crops, make it a suitable feedstock for the production of high value health products as nutraceuticals and a potential substitute for fish oil and terrestrial oil crops. Although this species is currently not cultured on a commercial scale and only limited experimental data has demonstrated its growth in tank-based cultures (Israel and Hophy 2002), its commercial potential is likely found in the South Pacific where it is abundant on islands such as Vanuatu or Samoa (Skelton et al. 2007). Extensive seaweed culture is an established industry in nearby Asia, providing the knowledge and infrastructure required for the aquaculture of brown seaweeds (Paul et al. 2012). Considering its morphology and benthic growth form, a culture method similar to other brown seaweeds such as kelps or *Sargassum* (Yu et al. 2013) might be successfully applied.

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