



## Fatty acid profiling of tropical marine macroalgae: An analysis from chemotaxonomic and nutritional perspectives

Puja Kumari, A.J. Bijo, Vaibhav A. Mantri, C.R.K. Reddy\*, Bhavanath Jha

Discipline of Marine Biotechnology and Ecology, CSIR – Central Salt and Marine Chemicals Research Institute, Bhavnagar, Gujarat 364002, India

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### ABSTRACT

The lipid and fatty acid (FA) compositions for 100 marine macroalgae were determined and discussed from the context of chemotaxonomic and nutritional perspectives. In general, the lipid contents in macroalgae were low (2.3–20 mg/g fr. wt.) but with substantially high amounts of nutritionally important polyunsaturated fatty acids (PUFAs) such as LA, ALA, STA, AA, EPA and DHA, that ranged from 10% to 70% of TFAs. More than 90% of the species showed nutritionally beneficial *n*6/*n*3 ratio (0.1:1–3.6:1) ( $p \leq 0.001$ ). A closer look at the FA data revealed characteristic chemotaxonomic features with C18 PUFAs (LA, ALA and STA) being higher in Chlorophyta, C20 PUFAs (AA and EPA) in Rhodophyta while Phaeophyta depicted evenly distribution of C18 and C20 PUFAs. The ability of macroalgae to produce long-chain PUFAs could be attributed to the coupling of chloroplastic FA desaturase enzyme system from a photosynthetic endosymbiont to the FA desaturase/elongase enzyme system of a non-photosynthetic eukaryotic protist host. Further, the principal component analysis segregated the three macroalgal groups with a marked distinction of different genera, families and orders, Hierarchical cluster analyses substantiated the phylogenetic relationships of all orders investigated except for those red algal taxa belonging to Gigartinales, Ceramiales, Halymeniales and Rhodymeniales for which increased sampling effort is required to infer a conclusion. Also, the groups deduced from FA compositions were congruent with the clades inferred from nuclear and plastid genome sequences. This study further indicates that FA signatures could be employed as a valid chemotaxonomic tool to differentiate macroalgae at higher taxonomic levels such as family and orders.

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### 1. Introduction

Benthic marine macroalgae, commonly known as seaweeds are multicellular photosynthetic organisms with considerable potentials for using as a source of bioactive compounds of immense pharmaceutical and nutraceutical importance. They are rich sources of nutritionally beneficial components such as proteins, carbohydrates, polyunsaturated fatty acids (PUFAs), antioxidants, minerals, dietary fibers and vitamins (Chandini et al., 2008; Mohamed et al., 2011) and are thus consumed as functional foods. There are 250 macroalgal species commercially utilized worldwide, of which 150 are consumed as human food (Barrow, 2007). The macroalgal species, in general, are low in lipids and contain 1–5% on dry wt. basis. Nevertheless, the nutritionally important C18 and C20 PUFAs including *n*3 PUFAs are present in substantially high amounts with anti-inflammatory, anti-thrombotic and anti-arrhythmic responses (Kumari et al., 2010; Gillies et al., 2011). The *n*-3 PUFAs are of particular importance as they cannot be

synthesized by humans and are thus obtained only through dietary sources.

Fatty acids (FAs) being metabolites of conserved acetyl-CoA pathway have been extensively studied from the context of chemotaxonomic perspectives in higher plants (Mongrand et al., 2001, 2005; Dussert et al., 2008), cyanobacteria (Shukla et al., 2011), bacteria (Malviya et al., 2011; Núñez-Cardona, 2012), microalgae (Dunstan et al., 2005; Lang et al., 2011) and fungi (Mishra et al., 2010). Further, Dunstan et al. (2005) deciphered the evolutionary relationship between the FA composition of Rhodophyceae and Cryptophyceae microalgae and the endosymbiotic theory. According to the endosymbiotic theory, the micro- and macroalgae of both Chlorophyceae and Rhodophyceae have been originated from primary endosymbiosis of photosynthetic cyanobacteria and eukaryotic host while Phaeophyta diverged from red algae via secondary (or tertiary) endosymbiosis along with other chlorophyll *c* bearing algae such as Cryptophytes, Haptophytes, diatoms, Dinoflagellates and non-photosynthetic Apicomplexans, ciliates and oomycetes, forming the super-group Stramenopiles at the base of the tree of life (Baldauf et al., 2000; Baldauf, 2008; Archibald, 2009, 2012; Dorrell and Smith, 2011; Baurain et al., 2012; De Clerck et al., 2012; Green, 2010; Woehle et al., 2012).

\* Corresponding author. Tel.: +91 278 256 5801x614; fax: +91 278 2567562/2566970.

E-mail address: [crk@csmcri.org](mailto:crk@csmcri.org) (C.R.K. Reddy).

But, there is no consensus among the researchers regarding the number of secondary endosymbiosis and whether the endosymbiotic event involved different red algae and/or different heterotrophic hosts including the number of plastid losses in algae containing chlorophyll *c* (Green, 2010; Archibald, 2012; Baurain et al., 2012; De Clerck et al., 2012). Further, these endosymbiont cyanobacteria that exhibited the capability of synthesizing C18 *n*-3 and *n*-6 PUFAs, finally resulted into double membrane chloroplasts in green and red algae, the main sites of FA biosynthesis in photosynthetic eukaryotes (Sperling et al., 2003). Similarly, the red algal endosymbiont formed 3–4 membrane bound plastids in stramenopiles. Numerous studies and available EST databases of algae have revealed that the evolution of green, red and brown algae has undergone multiple endosymbiotic and horizontal gene transfer of plastidial and nuclear genomes, gene duplication and losses, including those of FA metabolism (Domergue et al., 2003; Ryall et al., 2003; Bowler et al., 2008; John et al., 2008; Le Corguillé et al., 2009; Michel et al., 2010; Coelho et al., 2012; Chan et al., 2012; Chen and Smith, 2012; Cock et al., 2010; Dittami et al., 2012). Further, it is well known that *de novo* FA biosynthesis takes place in chloroplast up to C16:0/C18:0/C18:1, after which these FAs are attached to phosphatidylcholine (PC). They are then either desaturated and utilized for the synthesis of glycerolipids of chloroplast membrane or transported to ER for further chain elongation and desaturation and thereafter utilized for the synthesis of membrane lipids, storage lipids or transported back to the chloroplast for membrane biosynthesis (Ohlrogg and Browse, 1995; Uttaro, 2006; Joyard et al., 2010; Huerlimann and Heimann, 2012). As cyanobacteria can produce FAs only up to C18 (Liu et al., 2010; Iliev et al., 2011), Dunstan et al. (2005) hypothesized that Rhodophytes inherited the capability of synthesizing C20 PUFAs from the coupling of elongase and desaturase enzyme system of the eukaryotic host with the photosynthetic *n*-3 C18 PUFA-producing prokaryote (cyanobacteria) during the primary endosymbiosis. Similarly, the secondary endosymbiosis of the photosynthetic *n*-3 C20 PUFA-producing eukaryote and the eukaryotic host capable of further chain elongation and desaturation resulted in the *de novo* production of C22 PUFAs along with C20 PUFAs in Cryptophytes. However, a few studies are available where FA composition of macroalgae has been investigated in correlation to the endosymbiotic history. Understanding the FA profiles in the light of endosymbiotic evolution of different lineages of macroalgae could be an important prerogative for gaining insights into the algal lipid metabolism.

Furthermore, FA compositions of numerous macroalgae have been reported world-wide for their nutritional potential but their chemotaxonomic implications gained importance only in the last decade. Recently, Galloway et al. (2012) reported FA signatures of 40 temperate macrophytes (both seaweeds and sea grasses) from San Juan Archipelago, USA. But the diversity of macroalgal species investigated for FA composition is still low, approximated to be <200 (Gosch et al., 2012) which is minuscule against total estimated species of 9255, to date (Guiry and Guiry, 2012).

In our previous study, the FA profiles of 27 macroalgal species have been reported from Gujarat coast, India (Kumari et al., 2010) but the study was limited to the understanding of chemotaxonomic relationships among few commercially important macroalgae. In the present study, we analyzed total lipid (TL) and FA compositions of 100 macroalgae belonging to 46 different genera, 30 families and 18 orders encompassing samples from northern and central west coast of India. An attempt was made to understand their chemotaxonomic relationships at different taxonomic levels using multivariate principal component and hierarchical cluster analysis and compared with the available phylogenetic data. Furthermore, the results were also correlated with the endosymbiotic origin of three extant macroalgal lineages besides mapping the algal species rich in nutritionally essential *n*-3 PUFAs that

could possibly be cultivated for utilizing in various food and nutraceutical formulations.

## 2. Results and discussion

### 2.1. Lipids

The total lipid (TL) contents investigated in this study varied significantly ( $p \leq 0.001$ ) among different algal species (Table 1). The brown algae showed the highest TL contents (5.7–20.1 mg/g fr. wt.), followed by green algae (3.1–20 mg/g fr. wt.) and red algae (2.3–12.2 mg/g fr. wt.). The Dictyotales and Bryopsidales (except *Caulerpa microphysa*, *Caulerpa racemosa* v. *occidentalis*) had higher TL contents that corroborate with the recent findings of Gosch et al. (2012). Further, *Ulva* spp. (except *Ulva erecta*), *Monostroma oxyspermum* and *Sargassum cinereum* also showed high contents of TL (10–20 mg/g fr. wt.) in the present study. The variations observed between different species of the same genus was more likely to be due to the inter-specific/intra-generic variations rather than the geographical and environmental conditions as apparent from the minor variations found in the environmental parameters for the studied collection sites. Also, there was no trend observed between TL contents of macroalgal species belonging to the same genus and collection sites. Further, the lipid contents of the present study were lower than those reported for the same or related species (such as *Acrosiphonia* sp., *Cystoseira* sp., *Laurencia* sp., *Polysiphonia* sp. and *Scytosiphon* sp.) from Caspian Sea (Dembitsky et al., 1993), Sea of Japan (Khotimchenko, 1998), Bohai Sea (Li et al., 2002) and Seribu Island, Indonesia (Santoso et al., 2006). However, the lipid contents of *C. racemosa*, *Caulerpa sertularioides*, *Cladophoropsis javanica*, *S. cinereum*, *Padina* spp. and *Ulva* spp. reported either similar or 1.2–2.0-fold higher values with an exception of *U. erecta* that showed equal content to the sibling species of *Ulva intestinalis* studied from Bohai Sea (Li et al., 2002). These variations could be attributed to the interplay of inter- or intra-specific variations along with the spatiotemporal variations in environmental parameters across the world (Chandini et al., 2008).

Moreover, it is evident from this study that macroalgae contained lipids as high as 2% on fresh weight basis that diminishes their prospects for biodiesel production. On the contrary, microalgae especially *Chlorella*, *Botryococcus*, *Chaetoceros* and *Phaeodactylum* are promising sources of biodiesel as they contain lipids more than 40% on dry weight basis (Becker, 2007; Ryckebosch et al., 2012; Yang et al., 2012). However, recently Gosch et al. (2012) studied the macroalgae of genus *Dictyota*, *Spatoglossum*, *Derbesia* and *Caulerpa* for lipids and reported a range from 10% to 12% on dry wt. basis that is quite comparable with those reported for several microalgal species such as *Tetraselmis*, *Rhodomonas*, *Scendesmus* and a few strains of *Skeletonema* and *Isochrysis* (Huerlimann et al., 2010; Mata et al., 2010), and thus emphasized the need for considering macroalgae as a promising resource for production of oil-based bioproducts.

### 2.2. Fatty acid composition

#### 2.2.1. Chlorophyta

The FA compositions of 33 species belonging to the orders of Ulvales, Ulotrichales, Bryopsidales, Siphonocladales and Cladophorales are presented in Table 2 and Supplementary Table 1. The green algal samples showed higher contents of unsaturated fatty acids (UFAs) with the exception of *Ulva lactuca*, *C. racemosa* v. *occidentalis*, *C. racemosa* v. *corneophora*, *Codium dwarkense*, *Bryopsis plumosa* and *M. oxyspermum* which had 1.1–1.4-fold higher contents of saturated fatty acids (SFAs) ( $p \leq 0.001$ ). The PUFA contents in them ranged between 28% (*U. lactuca*) and 71% (*Caulerpa veravalensis*) of total

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