J Appl Phycol (2015) 27:1297–1306
DOI 10.1007/s10811-014-0415-2

Seasonal and interannual variation of fatty acids in macrophytes from the Pacific coast of Baja California Peninsula (Mexico)

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Received: 9 April 2014 / Revised and accepted: 15 September 2014 / Published online: 17 October 2014

Abstract The fatty acid composition of macrophytes is usually quite stable among different taxonomic groups, and thus, several fatty acids can been used as biomarkers. However, variations between species can be affected by seawater temperature and other ambient factors. With higher annual temperatures, we expect less polyunsaturated fatty acids, and changes in the fatty acid signature of algae. Here we analyzed seasonal and interannual variations, in two species of red (*Gelidium robustum* and *Gracilaria* sp.), two brown (*Eisenia arborea* and *Macrocystis pyrifera*), and two green macroalgae (*Ulva lactuca* and *Ulva* sp.), and one species of seagrass (*Phyllospadix torreyi*) sampled in a subtropical climate (Bahía Tortugas and Bahía Asunción, BCS, Mexico) from 2002 to 2004. We found that the fatty acid signatures of the red and brown algae were quite stable among seasons and years, in contrast to those of the green algae, which showed a strong annual variation in their fatty acid signature that affected their annual segregation in the factor analysis and are probably a result of net primary production (NPP), which was strongly correlated to individual fatty acids. The fatty acid signature in brown algae is affected by photosynthetically active radiation (PAR), but their variation in the factor analysis is fairly stable despite seasonal or interannual differences. The polyunsaturated fatty acids (PUFAs) were correlated to sea surface temperature (SST) in seagrass. The differences in fatty acid variations between macrophyte groups can provide useful biomarker information for use in trophic analyses.

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Keywords Arachidonic acid · Environmental variability · Lipids · Macroalgae · Seagrass

Introduction

Macrophytes are the primary producers of food in the marine ecosystems; they supply oxygen through photosynthesis and provide support and hideout for many organisms. As primary producers, they provide the basic fatty acid patterns in the marine food webs (Bergé and Barnathan 2005). The fatty acid composition of macrophytes is usually quite stable among different taxonomic groups, and thus, several fatty acids can been used as biomarkers. Red algae and brown algae show high proportions of 20:4n-6 and 20:5n-3, but red algae have more 20:5n-3 than 20:4n-6 (Alfaro et al. 2006), and brown algae have also a high proportion of 18:4n-3. The green algae are characterized by high proportions of 16:0, 18:3n-3, and the C16 polyenoic fatty acids 16:4n-3 or 16:3n-3 (Khotimchenko 1993), and higher levels of 18:1n-7 compared to 18:1n-9 (Vaskovsky et al. 1996; Li et al. 2002). The fatty acid profile of seagrass is mainly 18:3n-3, 18:2n-6, 16:3n-3, and 16:0 (Gillan et al. 1984; Vaskovsky et al. 1996; Hanson et al. 2010).

As concluded by Dethier et al. (2013), "studies that use fatty acids as biomarkers may often assume that these profiles or signatures are relatively invariant in space and time." However, variations between species can be strong. Red algae of the genus *Gracilaria* have been found to have either very high levels of 20:5n-3, high levels of both 20:5n-3 and 20:4n-6, or only very high levels of 20:4n-6, and it has been proposed that the species can be identified by their 20:4n-6/20:5n-3 ratio (Khotimchenko and Gusarova 2004; Imbs et al. 2012). Other red algae, such as *Gracilaria corticata* (J. Agardh) J. Agardh have been found to contain high levels of 16:0 and 18:1n-9, but no 20:5n-3 (Gressler et al. 2010; Rohani-Ghadikolaei et al. 2012). Some brown algae do not

contain 18:4n-3 (Dawczynski et al. 2007). Yazici et al. (2007) found that the signature fatty acids from green algae can be absent, as is the case of 16:3n-3 and 16:4n-3, and a ratio of 18:1n-7/18:1n-9 of lower than 1 for *Codium fragile* (Suringar) Harriot or that a replacement of 18:3n-3 for 18:4n-3 occurred in *Ulva* (*Enteromorpha*) *linza* Linnaeus.

Besides differences between species or geographic locations, differences in fatty acids in some particular species from the same location in natural beds have been described (Nelson et al. 2002; Hernández-Carmona et al. 2009), mainly in relation to seasonal variations of seawater temperature (Dawes et al. 1993; Floreto et al. 1993a), but also under culture and, particularly, light intensity (Floreto and Teshima 1998; Khotimchenko and Yakovleva 2005), availability of nutrients (Floreto et al. 1993b, 1996), photoperiod (Floreto et al. 1993a, 1994), and salinity (Dawes et al. 1993; Floreto and Teshima 1998). In addition, sampling different stages of growth or reproduction of the algae might also produce variation in fatty acid metabolism and accumulation (Khotimchenko 2006).

Most of these studies have been made on macroalgae sampled in temperate climates. Higher annual temperatures and more stable seasonal temperatures of tropical and subtropical areas, falling between 19 and 27 °C throughout a year for the sea surface temperature (SST) in the North Pacific Ocean (LLuch 2011), might decrease the levels of polyunsaturated fatty acids in algae, and this can affect their use as biomarkers. Here we analyzed variations in fatty acids, particularly those used as biomarkers, as a result of seasonal and interannual variations, in two species of red, two brown, and two green macroalgae and one species of seagrass sampled in a subtropical climate, which can be used for identification of trophic interactions in a marine food web.

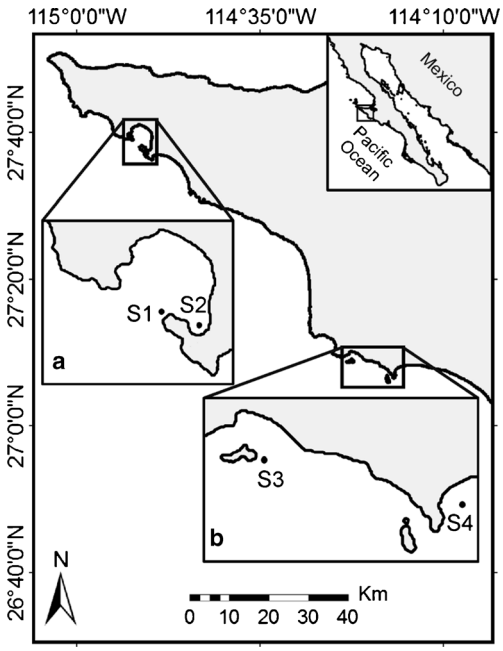

Fig. 1 Sampling locations. **a** *S1*=Los Morros and *S2*=El Rincón in Bahía Tortugas and **b** *S3*=Bahía Asunción and *S4*=San Roque, Baja California Sur, Mexico

Materials and methods

Sampling

In Bahía Tortugas, BCS, Mexico, the red algae *Gelidium robustum* (N. L. Gardner) Hollenberg & I. A. Abbott, brown algae *Eisenia arborea* Areschoug and *Macrocystis pyrifera* (Linnaeus) C. Agardh, and the seagrass *Phyllospadix torreyi* S. Watson were collected at Los Morros. The red algae *Gracilaria* sp., and green algae *Ulva lactuca* Linnaeus and *Ulva* sp. were collected at El Rincón (Fig. 1a) in 2003 and

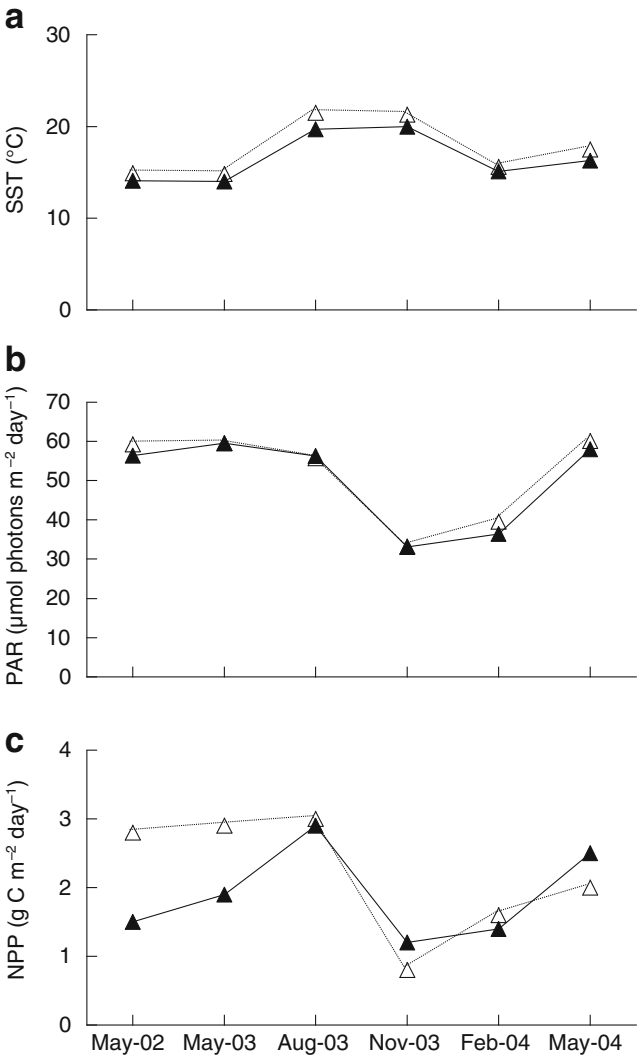

Fig. 2 **a** Average sea surface temperature (SST; °C), **b** photosynthetically active radiation (PAR; µmol photons m^{-2} day^{-1}), and **c** net primary production (NPP; g C m^{-2} day^{-1}) obtained at sampling locations, Baja California Sur, Mexico. Sampling location A is represented by *filled triangles*, and sampling location B by *open triangles*

2004. Samples of *G. robustum*, *E. arborea*, *U. lactuca*, and *P. torreyi* were collected in Bahía Asunción, and *M. pyrifera* in San Roque (Fig 1b) on May 2002. The first two sites (S1 and S2) and the last two sites (S3 and S4) were very similar in relation to environmental parameters, but there was a difference in net primary production (NPP; g C m^{-2} day^{-1}), between the first two and the last two sites, so S1 and S2 are referred to as sampling location A, and S3 and S4 are referred to as sampling location B (Fig. 2). Specimens were transported on ice to the laboratory at Centro de Investigaciones Biológicas del Noroeste (CIBNOR) in La Paz, BCS, Mexico.

Fatty acid analyses

Upon arrival, samples were cleaned from epibionts under running tap water. Lipids were extracted with 2:1 chloroform/methanol (2:1 *v*/*v*) according to Folch et al. (1957), and extracts were stored for less than 3 months in chloroform in a Teflon-lined screw-cap glass vial at 20 °C under a nitrogen atmosphere until further analysis. Fatty acids were transesterified with boron-trifluoride methanol (BF_3 14 % methanol, Supelco), and methyl esters were analyzed in a gas chromatograph (GC Agilent Technologies 6890 M) equipped with DB-23 Silica column (30 m×0.25 mm ID×0.25 μm film thickness), flame ionization detector with helium as the carrier gas (0.7 mL min^{-1}), and a temperature ramp from 110 to 220 °C. Fatty acids were identified by comparing their retention times with those of standards (Sigma, Bellefonte, PA, USA) with the concentration of each fatty acid corrected by correlation with the response of the corresponding standard. Data were analyzed using GC ChemStation Rev. A .10.02 (1757, Agilent Technologies, 2003).

Satellite-derived data

As a proxy of the state of the environment, net primary production (NPP)—i.e., total primary production minus the losses due to respiration of the phytoplankton—was calculated with a NPP model based on the Vertically Generalized Production Model (VGPM) by Behrenfeld and Falkowski (1997) and matchups with in situ NPP measurements collected by the CalCOFI program (VGPM-CAL model; see Kahru et al. (2009)). Satellite estimates of Chl *a*, photosynthetically active radiation (PAR), and sea surface temperature (SST) were used as input. Mean values were calculated in an 18×18 pixel window in the study areas. The VGPM-CAL model was applied to monthly satellite images using full resolution (1 km) merged data from multiple sensors (SeaWiFS, MODISA, and MODIST) for Chl *a*, MODISA and

Table 1 *Gelidium robustum* fatty acid proportion (n=3/sampling date, means ± SE)

	May 2002	May 2003	Aug 2003	Nov 2003	Feb 2004	May 04	*P*
14:0	6.20±0.76 ab	3.91±0.17 b	5.30±0.28 ab	5.31±0.13 ab	6.32±0.46 a	4.70±0.22 ab	<0.01
16:0	38.3±2.04 a	28.3±0.32 b	29.5±0.94 b	31.7±0.46 b	40.9±1.46 a	29.9±0.82 b	<0.001
18:0	1.17±0.03 ab	0.92±0.11 bc	0.97±0.08 bc	1.06±0.03 abc	1.33±0.08 a	0.84±0.04 c	<0.01
16:1n-9	1.11±0.07 a	0.35±0.03 b	0.39±0.01 b	0.42±0.08 b	0.59±0.12 b	0.37±0.07 b	<0.001
16:1n-7	7.70±0.42 a	1.79±0.10 b	1.84±0.04 b	2.01±0.08 b	1.88±0.15 b	1.52±0.12 b	<0.001
16:4n-3	0.20±0.04 c	0.76±0.07 a	0.61±0.08 ab	0.64±0.05 ab	0.46±0.02 bc	0.46±0.07 bc	<0.001
18:1n-9	5.11±0.43	4.95±0.19	4.99±0.09	5.44±0.13	4.82±0.15	4.74±0.06	N.S.
18:1n-7	3.00±0.20 a	1.9±0.2 b	2.1±0.1 ab	2.3±0.2 ab	2.4±0.2 ab	2.1±0.2 ab	<0.05
18:2n-6	1.36±0.14 a	0.64±0.07 b	0.55±0.02 b	0.69±0.01 b	0.69±0.01 b	0.60±0.01 b	<0.001
18:3n-6	0.32±0.02 b	0.20±0.01 c	0.31±0.02 b	0.43±0.02 a	0.22±0.01 c	0.26±0.01 bc	<0.001
18:3n-3	0.13±0.01 bc	0.18±0.05 bc	0.23±0.02 b	0.49±0.01 a	0.18±0.01 bc	0.11±0.01 c	<0.001
18:4n-3	0.19±0.01 b	0.35±0.12 ab	0.35±0.03 ab	0.61±0.02 a	0.28±0.02 b	0.20±0.02 b	<0.01
20:4n-6	14.7±0.91 d	27.1±1.50 a	21.9±0.90 b	19.3±0.37 bc	16.4±1.16 cd	17.5±0.33 cd	<0.001
20:5n-3	19.1±0.60 c	26.7±0.44 b	29.4±0.67 b	27.3±0.81 b	22.3±1.16 c	36.0±1.35 a	<0.001
22:6n-3	1.49±0.15	1.21±0.90	1.25±0.19	2.09±0.19	0.88±0.07	0.36±0.03	N.S.
SAT	45.4±1.46 a	33.1±0.44 b	35.8±1.3 b	38.0±0.60 b	48.6±1.97 a	35.5±1.05 b	<0.001
MUFA	16.9±0.97 a	9.1±0.53 b	9.5±0.13 b	10.3±0.34 b	9.9±0.28 b	8.9±0.25 b	<0.001
PUFA	37.7±0.64 c	57.8±0.45 a	54.7±1.37 ab	51.7±0.85 b	41.6±2.08 c	55.7±1.04 ab	<0.001
n-3/n-6	1.29±0.05 bc	1.03±0.09 c	1.41±0.03 b	1.53±0.07 b	1.40±0.08 b	2.03±0.10 a	<0.001
PUI	215±3.5 b	260±1.4 a	252±5.5 a	241±3.9 a	195±8.7 b	261±5.6 a	<0.001

Unifactorial ANOVA followed by Tukey *post-hoc* analyses were applied to assess differences among means. Means sharing different superscript in a row were significantly different (P<0.05)

N.S. not significant

Table 2 *Gracilaria* sp. fatty acid proportion (n=3/sampling date, means ± SE)

	May 2003	Feb 2004	May 04	*P*
14:0	3.84±0.16	4.85±0.49	3.49±1.56	N.S.
16:0	33.4±0.79	42.0±4.59	37.6±2.35	N.S.
18:0	1.27±0.02 ab	1.80±0.27 a	0.96±0.10 b	<0.05
16:1n-9	0.33±0.05	0.24±0.08	0.26±0.08	N.S.
16:1n-7	0.26±0.02 b	0.30±0.02 b	0.47±0.02 a	<0.001
16:4n-3	0.54±0.01	0.63±0.06	0.54±0.05	N.S.
18:1n-9	5.45±0.27	4.27±0.51	4.61±0.17	N.S.
18:1n-7	0.51±0.02 b	0.71±0.09 b	1.33±0.09 a	<0.001
18:2n-6	0.43±0.02	0.53±0.09	0.46±0.02	N.S.
18:3n-6	0.41±0.03 a	0.31±0.04 ab	0.27±0.01 b	<0.05
18:3n-3	0.13±0.08	0.56±0.40	0.37±0.04	N.S.
18:4n-3	0.09±0.03 b	0.17±0.04 b	0.35±0.02 a	<0.001
20:4n-6	52.9±1.14 a	42.9±5.05 b	48.7±0.73 ab	<0.05
20:5n-3	0.28±0.03	0.30±0.06	0.24±0.01	N.S.
22:6n-3	0.20±0.04	0.32±0.02	0.21±0.08	N.S.
SAT	38.4±0.92	48.7±5.33	42.1±0.90	N.S.
MUFA	6.55±0.24	5.51±0.57	6.66±0.34	N.S.
PUFA	55.1±1.03	45.8±4.76	51.3±0.59	N.S.
n-3/n-6	0.03±0.00	0.05±0.02	0.03±0.01	N.S.
PUI	226±3.8 a	186±18.9	208±2.8	N.S.

Unifactorial ANOVA, followed by Tukey *post hoc* analyses, was applied to assess differences among means. Means sharing different letters in a row were significantly different (P<0.05)

N.S. not significant

MODIST for SST, and remapped 4-km images from SeaWiFS for PAR. Time series for NPP, SST, and PAR were calculated for two study areas (sections A and B, Fig. 1). Merged satellite data were provided by Dr. Mati Kahru (Scripps Institution of Oceanograpy, UCSD).

Statistical analysis

Fatty acid proportions are reported as mean ± standard error. One-way ANOVA, followed by Tukey tests, was used to assess significant differences (P<0.05) between sampling months. A Spearman correlation was calculated among all variables. Factor analysis (Varimax normalized using principal component extraction) was used to extract the maximum variance from data sets with each principal component as a linear combination of individual fatty acids of seaweeds, considering a factor loading ≥0.7 and eigenvalues >1.0. Signature fatty acids from the seven species were compared in samples obtained in May, August, November 2003, and February 2004 for the seasonal comparison, and from samples obtained in May 2002, May 2003, and May 2004 for the interannual comparison. Not all species were found on all dates. All statistical analyses were made using Statistica v. 6.0.

Results

Sea surface temperature (SST), photosynthetically active radiation (PAR), and net primary production (NPP)

The SST was 14–15 °C in May and increased to 20–21 °C in August and November of 2003. It decreased to 16 °C in February–May 2004 (Fig. 2a). The PAR was stable at 56 mol photons m^{-2} day^{-1} in May 2002, 2003, and 2004. It decreased to 51 mol photons m^{-2} day^{-1} in August 2003 and decreased further until reaching 35–36 photons $m^{-2}day^{-1}$ in November 2003 and February 2004 (Fig. 2b). The NPP was higher in May 2002 and 2003 (2.5±0.5 g C m^{-2} day) at sampling location A compared to that at sampling location B. The values of NPP at both sampling locations were similar in August 2003 and decreased in both sampling locations in November 2003, increased slightly in February 2004, and started to diverge in May 2004 between sampling locations.

Fatty acid composition

The red alga *G. robustum* (Table 1) had as major fatty acids 16:0 (26.9–38.7 %), followed by 20:5n-3 (18.3–34.4 %) and 20:4n-6 (14.1–26.3 %), while *Gracilaria* sp. (Table 2) had mainly 20:4n-6 (40.2–50.1 %) and 16:0 (31.6–39.2 %).

The brown alga *E. arborea* (Table 3) contained as major fatty acids 20:4n-6 (16.2–22.1 %), 16:0 (10.3–17.9 %), 18:4n-3 (8.6–17.0 %), 18:1n-9 (7.9–14.4 %), and 20:5n-3 (8.6–10.5 %). The major fatty acids for *M. pyrifera* (Table 4) were 16:0 (19.2–27.1 %). 18:3n-3 (3.6–16.2 %), 20:4n-6 (9.9–16.7 %), and 20:5n-3 (6.9–11.2 %).

The green alga *U. lactuca* (Table 5) had as major fatty acids 16:0 (28.5–30.6 %), 18:1n-7 (11.0–15.7 %), 18:3n-3 (10.8–14.4 %), and 18:4n-3 (13.4–16.7 %). In May 2002, a decrease of 18:3n-3 (4.6 %) and 18:4n-3 (2.2 %) in favor of 16:0 (45.1 %) was found. The other green alga analyzed, *Ulva* sp. (Table 6), had a high proportion of 16:0 (23.0–33.1 %), 18:3n-3 (16.8–27.1 %), and 16:4n-3 (6.7–13.2 %).

The seagrass *P. torreyi* (Table 7) had a very high proportion of 18:3n-3 (52.3–56.4 %), followed by 18:2n-6 (11.4–15.4 %) and 16:0 (11.0–11.4 %).

Correlations

We found significant negative correlations for SST with 18:2n-6 (r=+0.76; P<0.05) and the n-3/n-6 ratio in *E. arborea* (r=−0.77; P<0.05), and with 18:3n-3 (r=0.92; P<0.05) in *M. pyrifera*. SST also correlated to SAT (r=+0.93; P<0.05), PUFA (r=−0.87; P<0.05), and the 20:4n-6/20:5n-3 ratio (r=+0.81; P<0.05) in *P. torreyi*.

PAR had an effect only in brown algae, with a correlation found with 20:4n-6 (r=−0.89; P<0.05) and MUFA (r=−0.90;

Table 3 *Eisenia arborea* fatty acid proportion (n=3/sampling date, means ± SE)

	May 2002	May 2003	Aug 2003	Nov 2003	Feb 2004	May 04	*P*
14:0	6.90±0.18 a	4.50±0.08 b	3.85±0.12 b	4.01±0.10 b	4.45±0.27 b	4.53±0.13 b	<0.0001
16:0	22.9±0.77 a	11.1±0.45 d	15.8±0.94 b	17.6±0.41 b	15.1±0.97 bc	12.4±0.31 cd	<0.0001
18:0	3.06±0.25 a	0.47±0.04 c	1.31±0.27 bc	1.53±0.03 b	1.38±0.39 bc	0.53±0.02 bc	<0.0001
16:1n-9	0.87±0.32	0.60±0.07	0.62±0.02	0.48±0.01	0.47±0.10	0.45±0.17	N.S.
16:1n-7	10.9±0.51 a	6.0±0.45 b	5.1±0.35 bc	5.2±0.20 bc	3.6±0.47 c	4.7±0.31 bc	<0.0001
18:1n-9	12.3±0.43 abc	8.4±0.48 c	12.4±1.28 ab	15.3±0.32 a	13.2±1.41 a	9.2±0.19 bc	<0.001
18:1n-7	2.78±0.18 a	0.40±0.03 b	0.45±0.04 b	0.42±0.02 b	0.27±0.06 b	0.27±0.02 b	<0.0001
16:4n-3	0.57±0.01 b	0.96±0.09 a	0.91±0.07 ab	0.61±0.03 ab	0.68±0.12 ab	0.82±0.08 ab	<0.05
18:2n-6	4.28±0.12 c	5.30±0.25 bc	5.97±0.20 ab	6.65±0.24 a	4.47±0.19 c	5.54±0.52 abc	<0.001
18:3n-6	0.44±0.09 b	1.84±0.46 a	1.39±0.06 ab	2.10±0.16 a	1.24±0.17 ab	1.38±0.10 ab	<0.001
18:3n-3	5.65±0.21 b	9.20±0.47 a	6.99±0.44 b	5.61±0.47 b	7.47±0.69 ab	9.09±0.24 a	<0.001
18:4n-3	8.15±0.66 d	18.3±0.99 a	13.3±0.97 bc	9.20±0.08 cd	13.6±1.1 b	18.2±0.97 a	<0.0001
20:4n-6	12.5±0.26 c	21.4±0.59 ab	20.5±0.10 b	22.0±0.50 ab	23.5±1.09 a	22.0±0.43 ab	<0.0001
20:5n-3	8.6±0.42 b	11.3±0.58 a	11.2±0.76 a	9.1±0.25 ab	10.4±0.47 ab	10.5±0.44 ab	<0.05
22:6n-3	0.0±0.0	0.05±0.02	0.03±0.01	0.03±0.01	0.04±0.02	0.12±0.09	N.S.
SAT	32.9±0.66 a	16.1±0.56 d	21.0±1.12 bc	23.2±0.50 b	20.9±1.14 bc	17.5±0.45 cd	<0.0001
MUFA	26.9±0.44 a	15.5±0.81 c	18.6±0.91 bc	21.4±0.28 b	17.6±1.94 bc	14.7±0.29 c	<0.0001
PUFA	40.3±0.66 d	68.5±1.4 a	60.4±2.03 bc	55.4±0.30 c	61.5±3.1 abc	67.8±0.55 ab	<0.0001
n-3/n-6	1.33±0.10 a	1.40±0.04 a	1.17±0.15 a	0.80±0.04 b	1.10±0.05 ab	1.35±0.10 a	<0.0001
PUI	206±9.9 c	270±2.1 a	245±7.4 ab	226±0.8 bc	250±10.5 ab	266±2.6 a	<0.001

Unifactorial ANOVA, followed by Tukey *post hoc* analyses, was applied to assess differences among means. Means sharing different letters in a row were significantly different (P<0.05)

N.S. not significant

Table 4 *Macrocystis pyrifera* fatty acid proportion (n=3/sampling date, means ± SE)

	May 2002	May 2003	Aug 2003	Nov 2003	Feb 2004	May 04	*P*
14:0	13.9±0.57 a	5.73±0.26 c	5.63±0.16 c	5.78±0.05 c	7.28±0.33 b	5.84±0.27 bc	<0.0001
16:0	21.5±1.39 a	9.76±0.59 b	11.1±0.70 b	11.6±0.14 b	11.3±0.35 b	9.2±1.39 b	<0.0001
18:0	1.67±0.29 a	0.35±0.02 b	0.42±0.04 b	0.44±0.01 b	0.40±0.01 b	0.29±0.02 b	<0.0001
16:1n-9	0.94±0.22 a	0.59±0.27 b	0.70±0.21 b	0.44±0.17 b	0.21±0.16 b	0.43±0.24 b	N.S.
16:1n-7	3.43±0.21 a	0.53±0.07 c	1.24±0.26 b	0.68±0.01 bc	0.79±0.10 bc	0.57±0.04 bc	<0.0001
16:4n-3	1.55±0.27 b	0.97±0.18 a	1.22±0.18 ab	0.93±0.01 ab	0.94±0.13 ab	1.06±0.09 b	N.S.
18:1n-9	2.63±0.11 d	7.65±0.38 bc	6.41±0.35 c	8.29±0.07 b	10.1±0.67 a	6.53±0.22 c	<0.0001
18:1n-7	0.18±0.05 ab	0.12±0.01 b	0.25±0.06 a	0.13±0.01 b	0.12±0.00 b	0.10±0.02 b	<0.05
18:2n-6	7.46±0.22 a	4.6±0.26 b	6.95±0.53 a	7.34±0.03 a	4.23±0.11 b	3.86±0.28 b	<0.0001
18:3n-6	1.43±0.18 b	1.17±0.12 b	2.25±0.11 a	2.45±0.02 a	1.11±0.11 b	1.18±0.02 b	<0.0001
18:3n-3	5.09±0.28 d	10.0±0.46 a	8.46±0.33 bc	7.83±0.10 c	7.09±0.42 c	9.64±0.15 ab	<0.0001
18:4n-3	11.1±1.87 c	22.6±1.95 ab	19.6±1.51 ab	19.2±0.22 ab	17.2±1.01 bc	25.3±0.42 a	<0.0001
20:4n-6	18.3±1.13 b	18.1±1.13 b	19.1±0.16 b	20.3±0.46 ab	23.6±0.36 a	17.2±0.74 b	<0.0001
20:5n-3	10.8±0.55 c	17.3±1.16 a	16.5±0.3 ab	14.5±0.12 b	14.8±0.53 b	18.4±0.93 a	<0.0001
22:6n-3	0.07±0.04 b	0.03±0.02 b	0.11±0.02 b	0.08±0.06 b	0.43±0.10 a	0.09±0.03 b	<0.01
SAT	37.1±2.03 a	15.8±0.73 b	17.1±0.76 b	17.8±0.10 b	19.0±0.68 b	15.3±0.4 b	<0.0001
MUFA	7.17±0.29 d	8.88±0.48 bc	8.61±0.06 bcd	9.54±0.15 b	11.2±0.49 a	7.6±0.04 cd	<0.001
PUFA	55.8±2.21 c	75.3±1.15 ab	74.3±0.73 ab	72.7±0.09 ab	69.8±1.16 b	77.1±0.4 a	<0.0001
n-3/n-6	1.06±0.04 c	2.16±0.22 ab	1.63±0.09 bc	1.42±0.03 c	1.40±0.05 c	2.46±0.17 a	N.S.
PUI	158±16.7 b	239±7.5 a	224±10.2 a	229±8.2 a	214±8.4 a	236±11.2 a	<0.0001

Unifactorial ANOVA, followed by Tukey *post hoc* analyses, was applied to assess differences among means. Means sharing different letters in a row were significantly different (P<0.05)

N.S. not significant

Table 5 *Ulva lactuca* fatty acid proportion (n=3/sampling date, means ± SE)

	May 2002	May 2003	Aug 2003	Nov 2003	Feb 2004	May 04	*P*
14:0	2.72±0.08 a	0.60±0.14 b	1.14±0.29 b	0.98±0.37 b	0.67±0.18 b	0.51±0.05 b	<0.0001
16:0	50.1±4.26 a	34.7±0.81 b	34.2±0.54 b	32.0±1.47 b	32.0±0.47 b	36.5±1.00 b	<0.0001
18:0	3.23±0.17 a	0.69±0.03 bc	1.05±0.19 b	0.53±0.02 c	0.72±0.02 bc	0.74±0.02 bc	<0.0001
16:1n-9	1.03±0.22 a	0.20±0.04 b	0.59±0.22 ab	0.65±0.21 ab	0.37±0.08 ab	0.29±0.02 ab	<0.05
16:1n-7	11.4±0.75 a	2.36±0.34 b	4.56±0.25 b	4.58±0.45 b	4.06±0.13 bc	4.61±0.02 b	<0.0001
16:4n-3	0.49±0.12 c	8.57±0.38 a	8.39±0.52 ab	9.94±0.28 a	6.58±0.12 ab	4.22±2.03 bc	<0.0001
18:1n-9	4.40±0.61 a	0.85±0.26 b	1.46±0.22 b	0.97±0.05 b	1.15±0.02 b	1.52±0.04 b	<0.0001
18:1n-7	11.5±0.12 c	12.4±0.73 c	13.7±0.44 bc	14.8±0.44 b	15.6±0.30 b	17.8±0.45 a	<0.0001
18:2n-6	3.20±0.49	3.37±0.61	3.38±0.14	2.65±0.04	3.71±0.04	3.10±0.13	N.S.
18:3n-6	0.73±0.08 a	0.32±0.04 b	0.34±0.03 b	0.27±0.02 b	0.22±0.01 b	0.27±0.02 b	<0.0001
18:3n-3	3.75±0.54 d	16.2±0.61 a	12.1±0.34 c	13.4±0.25 bc	15.3±0.15 ab	13.5±0.41 bc	<0.0001
18:4n-3	1.84±0.28 c	18.7±1.13 a	15.0±0.48 b	17.4±0.72 ab	18.3±0.32 a	16.0±0.54 ab	<0.0001
20:4n-6	1.99±0.55 a	0.16±0.04 b	0.64±0.22 b	0.13±0.01 b	0.14±0.03 b	0.22±0.01 b	<0.0001
20:5n-3	3.05±0.63 a	0.46±0.12 c	1.97±0.25 ab	1.39±0.31 bc	0.48±0.02 c	0.48±0.05 c	<0.0001
22:6n-3	0.0±0.00 b	0.11±0.02 b	1.39±0.32 a	0.25±0.01 b	0.10±0.01 b	0.14±0.03 b	<0.0001
SAT	56.0±4.03 a	36.0±0.74 b	36.4±0.42 b	33.6±1.29 b	33.4±0.59 b	37.7±0.98 b	<0.0001
MUFA	28.4±1.48 a	15.8±0.78 c	20.3±0.75 bc	21.0±0.19 bc	21.2±0.44 bc	24.2±0.46 b	<0.001
PUFA	15.6±2.56 c	48.2±0.59 a	43.4±0.43 ab	45.5±1.12 aa	45.5±0.55 a	38.1±1.44 b	<0.0001
n-3/n-6	1.56±0.03 c	12.2±2.08 ab	8.94±0.39 b	13.8±0.52 a	10.0±0.17 ab	9.6±0.71 ab	<0.0001
PUI	96.0±9.6 c	194±1.6 a	184±1.1 ab	187±5.2 ab	189±1.8 ab	165±6.7 b	<0.0001

Unifactorial ANOVA, followed by Tukey *post hoc* analyses, was applied to assess differences among means. Means sharing different letters in a row were significantly different (P<0.05)

N.S. not significant

Table 6 *Ulva* sp. fatty acid proportion (n=3/sampling date, means ± SE)

	May 2003	May 2004	*P*
14:0	0.77±0.24	1.39±0.06	<0.05
16:0	25.8±1.49	37.1±2.39	<0.05
18:0	0.45±0.11	1.08±0.03	<0.01
16:1n-9	0.24±0.04	0.32±0.01	N.S.
16:1n-7	0.94±0.07	1.56±0.06	<0.05
16:4n-3	14.8±0.73	6.99±0.20	<0.0001
18:1n-9	0.60±0.04	2.03±0.39	<0.05
18:1n-7	6.94±0.21	8.73±0.22	<0.001
18:2n-6	4.56±0.15	5.83±0.12	<0.001
18:3n-6	1.22±0.16	1.29±0.05	N.S.
18:3n-3	30.5±0.59	18.8±0.37	<0.0001
18:4n-3	8.32±0.56	5.79±0.21	<0.05
20:4n-6	1.33±0.07	1.78±0.10	<0.05
20:5n-3	1.21±0.11	2.65±0.35	<0.05
22:6n-3	0.24±0.10	3.45±1.40	N.S.
SAT	27.1±1.26	39.5±2.42	<0.05
MUFA	8.73±0.15	12.7±0.22	<0.001
PUFA	64.2±1.35	47.8±2.23	<0.001
n-3/n-6	7.76±0.33	4.23±0.16	<0.0001
PUI	217±6.1	183±12.1	N.S.

Unifactorial ANOVA analyses were applied to assess differences among means

N.S. not significant

P<0.05) in *M. pyrifera*, and n-3/n-6 (r=+0.85; P<0.05) and 20:4n-6/20:5n-3 (r=−0.82; P<0.05) in *E. arborea*.

NPP was correlated to several fatty acids in most of the algae analyzed here: the MUFA (r=−0.83; P<0.05) and the 18:1n-7/18:1n-9 ratio (r=+0.84; P<0.05) in *M. pyrifera*; 16:1n-9 (r=+0.83; P<0.05) and 20:4n-6 (r=−0.82; P<0.05) in *E. arborea*; 16:0 (r=+0.80; P<0.05), 18:0 (r=+0.78; P<0.05), 18:1n-9 (r=+0.77; P<0.05), 18:3n-6 (r=+0.81; P<0.05), 18:3n-3 (r=−0.77; P<0.05), 20:4n-6 (r=+0.83; P<0.05), 20:5n-3 (r=+0.74; P<0.05), and n-3/n-6 (r=−0.81; P<0.05) in *U. lactuca*; and 18:3n-6 (r=−0.83; P<0.05) and 18:4n-3 (r=+0.83; P<0.05) in *P. torreyi.* The red macroalgae showed no correlation to NPP in this work.

Seasonal and interannual variation

Two factor analyses were applied; one to assess the seasonal variation and the other to assess the interannual variation (Table 8). Most (92 %) of the seasonal variation was described by two principal components; the first factor explained 51.8 % of the variance, with significant but negative contributions of 18:2n-6 (−0.96) and 18:3n-3 (−0.96). The second factor explained 40.2 % and had significant but negative contributions of 16:4n-3 (−0.98) and the 18:1n-7/18:1n-9 ratio (−0.97). In the interannual comparison, 85.4 % of the variation was given by two factors, with the first accounting for 52.1 % and

Table 7 *Phyllospadix torreyi* fatty acid proportion (n=3/sampling date, means ± SE)

	May 2003	Aug 2003	Nov 2003	Feb 2004	May 04	*P*
14:0	0.97±0.10	1.03±0.10	1.08±0.23	1.00±0.12	0.95±0.06	N.S.
16:0	12.5±1.03	13.0±0.15	12.7±0.17	12.3±0.22	12.4±0.28	N.S.
18:0	0.52±0.02 c	0.90±0.01 a	0.85±0.03 a	0.67±0.02 b	0.73±0.02 b	<0.0001
16:1n-9	1.18±0.19	0.75±0.38	0.91±0.30	0.87±0.22	0.73±0.29	N.S.
16:1n-7	0.23±0.02 b	0.52±0.09 a	0.34±0.03 ab	0.24±0.02 b	0.26±0.01 b	<0.01
16:4n-3	1.78±0.12	2.07±0.28	1.89±0.20	1.80±0.19	1.81±0.06	N.S.
18:1n-9	0.91±0.08 b	1.21±0.03 a	1.24±0.06 a	0.82±0.06 b	1.07±0.05 ab	<0.001
18:1n-7	0.64±0.02 b	0.90±0.05 a	0.70±0.02 b	0.68±0.02 b	0.73±0.02 b	<0.001
18:2n-6	16.8±1.68 a	13.0±0.81 b	17.7±0.90 a	13.3±1.01 b	14.5±0.40 ab	<0.05
18:3n-6	0.0±0.0 c	0.06±0.01 a	0.0±0.0 c	0.0±0.0 c	0.02±0.0 b	<0.0001
18:3n-3	59.5±2.14	62.0±1.28	60.2±0.62	62.6±1.13	61.8±0.75	N.S.
18:4n-3	0.17±0.05 a	0.33±0.01 b	0.19±0.01 a	0.18±0.04 a	0.24±0.06 ab	N.S.
20:4n-6	0.02±0.01 b	0.24±0.05 a	0.09±0.02 b	0.02±0.00 b	0.05±0.02 b	<0.001
20:5n-3	0.46±0.22 ab	0.90±0.22 a	0.45±0.08 ab	0.13±0.03 b	0.24±0.06 b	<0.05
22:6n-3	0.05±0.01	0.17±0.09	0.20±0.08	0.07±0.01	0.18±0.05	N.S.
SAT	14.0±0.96	14.9±0.24	14.6±0.12	13.9±0.31	14.1±0.32	N.S.
MUFA	2.97±0.12	3.38±0.27	3.19±0.30	2.61±0.21	2.79±0.29	N.S.
PUFA	83.1±0.97	81.7±0.12	82.2±0.41	83.5±0.52	83.1±0.41	N.S.
n-3/n-6	3.77±0.47 ab	4.96±0.34 b	3.56±0.23 a	4.93±0.46 ab	4.43±0.18 ab	N.S.
PUI	214±3.6	214±0.2	213±0.8	215±1.7	212±1.5	N.S.

Unifactorial ANOVA, followed by Tukey *post hoc* analyses, was applied to assess differences among means. Means sharing different letters in a row were significantly different (P<0.05)

N.S. not significant

composed by 18:2n-6 (0.97) and 18:3n-3 (0.94), and the second accounting for 33.3 % and composed of 16:4n-3 (−0.91) and 20:4n-6 (−0.94). The factor analysis showed that 18:1n-7/18:1n-9 was better for differentiating seasonal variation, while 20:4n-6 was better to differentiate macrophytes when comparing for interannual variation (Table 8).

Table 8 Factor loadings (Varimax normalized) using principal component extraction

Variation	Seasonal		Interannual	
	Factor 1	Factor 2	Factor 1	Factor 2
16:4n-3	**−0.98**	0.04	−0.13	**−0.90**
18:2n-6	0.12	**0.96**	**−0.97**	0.10
18:3n-3	−0.08	**0.96**	**−0.94**	−0.16
20:4n-6	**0.70**	0.65	0.63	0.56
18:1n-7/18:n-9	**−0.95**	−0.08	0.03	**−0.95**
Explained Variance	2.35	2.32	2.25	2.06
Prp.Total	0.47	0.46	0.45	0.41
Eigenvalue	2.69	1.97	2.67	1.65
% Total variance	53.72	39.31	53.32	33.05
Cumulative Eigenvalue	2.69	4.65	2.67	4.32
Cumulative %	53.72	**93.03**	53.32	**86.37**

Bold loadings are >0.70

G. robustum, *E. arborea*, and *M. pyrifera* had a consistent fatty acid signature when analyzed in a seasonal cycle (February, May, August, November of 2003; Fig. 3a) or among years (May of 2002, 2003, 2004; Fig 3b), while *U. lactuca* and *Ulva* sp. had a tendency to differ in its fatty acid signature between years (Fig. 3b).

Discussion

There were strong variations in the fatty acid profile of each macrophyte in relation to environmental conditions. For example, *G. robustum* had more 20:5n-3 (36 %) in May 2004, compared to the other sampling dates (19–29 %), while *U. lactuca* had a different profile in May 2002, with lower 18:3n-3 (3.8 %) and 18:4n-3 (1.8 %) and higher 20:4n-6 (2 %) and 20:5n-3 (3.1 %) in May 2002, compared to the other sampling dates (12–16 %, 15–19 %, 0.1–0.6 %, 0.5–1.9 %, respectively). Since these fatty acids are considered biomarkers for each taxonomic group, such variations in the same site and intra-species can produce erroneous interpretations, particularly when elucidating consumer diets. Using a few fatty acids in a PCA or factorial analysis, instead of individual fatty acids, allows discriminating up to family levels.

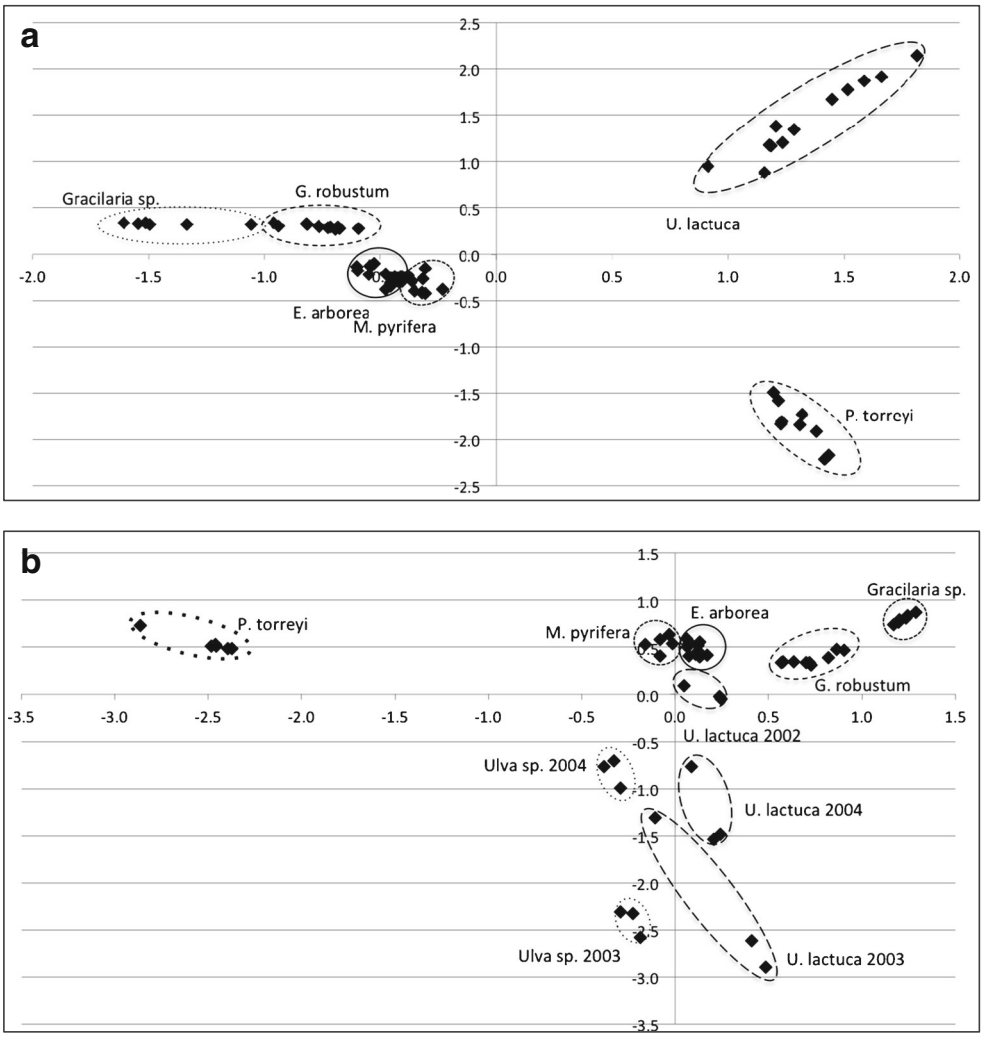

Fig. 3 Seasonal variation (**a**) and interannual variation (**b**) using factor scores with five fatty acids for seven macrophytes species. Each *point* is a replicate sample

Galloway et al. (2012) proposed the use of 18:2n-6, 18:3n-3, 18:3n-6, 18:4n-3, 20:4n-6, 20:5n-3, and 22:6n-3, and Dethier et al. (2013) the use of 18:2n-6, 18:3n-3, 18:4n-3, 20:4n-6, and 20:5n-3. We used 16:4n-3, 18:2n-6, 18:3n-3, 20:4n-6, and the 18:1n-7/18:1n-9 ratio to differentiate among macrophytes sampled during spring, summer, autumn, and winter of a selected year (2003–2004) or in May of three different years (2002, 2003, 2004) and found that brown, red algae, and *P. torreyi* had a consistent seasonal and annual distribution, while green algae had a tendency to differ in its fatty acid signature between years. However, brown algae tended to overlap both annually or seasonally. Intermingling of signatures among brown algae was also reported by Dethier et al. (2013). *U. lactuca* showed a wide variation among seasons and years (Fig. 3a, b). Differences among years for the green algae were mainly driven by 16:4n-3. The factor analysis showed that 18:1n-7/18:1n-9 and 20:4n-6 can be used to differentiate macrophytes when comparing for seasonal variation, while 18:2n-6 and 18:3n-3 were better for differentiating annual variation (Table 8).

The seasonal and annual variation is given by changes in environmental conditions. We were expecting less PUFA in all macrophytes because of the high SST that can be reached in this region. In accordance, we found significant negative correlations for temperature and PUFA (r=−0.87; P<0.05) and 20:4n-6/20:5n-3 ratio (r=+0.81; P<0.05) in *P. torreyi*, and the n-3/n-6 ratio in *E. arborea* (r=−0.77; P<0.05). Similarly, Dawes et al. (1993) found higher values of PUFA found in *Gracilaria tikvahiae* cultured at lower temperature (10–18 vs 20–26 °C). Negative correlations with temperature denote a decrease in PUFA when temperature increases, as expected, but it only occurred in *P. torreyi. P. torreyi* also had an increase in ARA with higher temperatures, and higher n-6 was also found in *E. arborea*. In spite of a higher interannual temperature for the sampled zone compared to temperate climates, the fatty acid composition of macrophytes analyzed in this work coincided with what has been previously described for each taxonomic group.

All algae analyzed here, except the red algae, had an influence of marine net primary production (NPP) on fatty

acid composition. The NPP is a key metric of the ecosystem health and carbon cycling and is usually estimated as the product of plant biomass, an incident solar flux, and a scaling parameter that accounts for variations in the plant physiology (Behrenfeld et al. 2001). The phytoplankton and macrophytes interact, directly and indirectly, through their impact on the use of light, oxygen flux, and nutrient turnover (Sunbäck and McGlathery 2005). These parameters interact and their individual effects on fatty acids, which are also dependent as substrate-product, are difficult to separate.

Light has a marked effect but only in brown algae, and particularly a negative effect on 20:4n-6 in both brown algae. An increase in 20:5n-3 in relation to 20:4n-6 can be indicating an increase in desaturation activity in red or brown algae (Kim et al. 1996). Brown algae have complex plastids derived by secondary endosymbiosis of a red alga and can also synthetize 20:4n-6 and 20:5n-3 and accumulate 18:4n-3 (Graeve et al. 2002), but there is much smaller evolutionary distances among genera of the brown algae than among genera of red or green algae, in accordance to the intermingling in the PCA of both brown algae analyzed. Galloway et al. (2012) concluded that this similarity is carried on to the fatty acid signatures, with brown algae more difficult to separate, and brown and red algae closer together than to green algae or to seagrass, which is, again, similar to the results obtained here by PCA. Green algae and seagrass are in the same lineage, having chloroplasts with similar biochemical pathways, accumulating more C_{18} fatty acids, while red algae have rhodoplasts and are able to elongate to 20:4n-6 and 20:5n-3 (Graeve et al. 2002). Seagrass are well separated from green algae as they only recently colonized the marine environment (Galloway et al. 2012).

Another possibility is that 20:4n-6 are being used to form prostaglandins (PG). However, very little 20:4n-6 is used to synthetize PG, and in general, an increase in 20:4n-6 has been reported when red algae are submitted to stressful condition such as changes in temperature (Imbs et al. 2001), desiccation (Kumar et al. 2011), decreased solar irradiation (Imbs et al. 2001), or even biotic interactions, as red and brown algae react with an oxidative burst to epiphytes that can be used to produce oxylipins belonging to the PG and leukotriene series, and sulfated compounds from short-chain fatty acids can be used as sexual pheromones or herbivore deterrents (Potin et al. 2002).

On the other hand, differences between years and seasons could be the result of different life stages. Photosynthesis and lipid biosynthesis in algae are controlled by environment conditions such as light, temperature, salinity, depth, and availability of nutrients (Guschina and Harwood 2006), but less studies have focused on different life stages. There are striking differences in the fatty acid signature in sporophyte and gametophyte stages of the brown alga *Desmarestia muelleri*, including the levels of 20:5n-3, which are doubled in sporophytes compared to those in gametophytes (Graeve et al. 2002). Seaweeds with life stages that differ in ploidy level might express recessive traits during haploid stages, including differences in the fatty acid composition as was found for a red algae by Tasende (2000). In Baja Califonia, reproductive thalli of *Gracilaria vermiculophylla* were collected during March, April, May, July, and November, but not in August (Bellorin et al. 2004), suggesting that *Gracilaria* in this location has different morphology of phases. These diverse fatty acid signatures in different reproductive stages can be a result of changes in the capability of desaturation and elongation.

In conclusion, biomarkers may often assume that these profiles or signatures are relatively invariant in space and time; however, the fatty acid composition significantly differed among sampling dates for the species analyzed here, as a result of SST, NPP, and PAR. Some of these algae had a consistent fatty acid signature when analyzed in a seasonal or annual cycle, as was the case of red and brown algae, which can be useful in trophic analyses to a certain level, but other biomarkers have to be used to achieve more segregation. However, green algae were well separated interannually and between the two species analyzed using a factorial analysis.

Acknowledgments This research was supported by SEP-CONACYT 2002-C01-41410 and 156118.

References

Alfaro AC, Thomas F, Sergent L, Duxbury M (2006) Identification of trophic interactions within an estuarine food web (northern New Zealand) using fatty acid biomarkers and stable isotopes. Estuar Coast Shelf Sci 70:271–286

Behrenfeld MJ, Falkowski PG (1997) Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnol Oceanogr 42:1–20

Behrenfeld MJ, Randerson JT, McClain CR, Feldman GC, Los SO, Tucker CJ, Falkowski PG, Field CB, Frouin R, Esaias WE, Kolber DD, Pollack NH (2001) Biospheric primary production during an ENSO transition. Science 291:2594–2597

Bellorin AM, Oliveira MC, Oliveira EC (2004) *Gracilaria vermiculophylla*: a western Pacific species of Gracilariaceae (Rhodophyta) first recorded from the eastern Pacific. Phycol Res 52:69–79

Bergé JP, Barnathan G (2005) Fatty acids from lipids of marine organisms: molecular biodiversity, roles as biomarkers, biologically active compounds, and economical aspects. Adv Biochem Eng Biotechnol 96:49–125

Dawczynski C, Schubert R, Jahreis G (2007) Amino acids, fatty acids, and dietary fibre in edible seaweed products. Food Chem 103:891–899

Dawes CJ, Kovach C, Friedlander M (1993) Exposure of *Gracilaria* to various environmental conditions II. The effect on fatty acid composition. Bot Mar 36:289–296

Dethier MN, Sosik E, Galloway AWE, Duggins DO, Simenstad CA (2013) Addressing assumptions: variation in stable isotopes and

fatty acids of marine macrophytes can confound conclusions of food web studies. Mar Ecol Prog Ser 478:1–14

Floreto EAT, Teshima S (1998) The fatty acid composition of seaweeds exposed to different levels of light intensity and salinity. Bot Mar 41: 467–481

Floreto EAT, Hirata H, Ando S, Yamasaki S (1993a) Fatty acid composition of *Ulva pertusa* Kjellman (Chlorophyta) and *Gracilaria incurvata* Okamura (Rhodophyta) in Japanese coastal waters. Bot Mar 36:217–222

Floreto EAT, Hirata H, Ando S, Yamasaki S (1993b) Effects of temperature, light Intensity, salinity and source of nitrogen on the growth, total lipid and fatty acid composition of *Ulva pertusa* Kjellman (Chlorophyta). Bot Mar 36:149–158

Floreto EAT, Hirata H, Yamasaki S, Castro SC (1994) Influence of light intensity on the fatty acid composition of *Ulva pertusa* Kjellman (Chlorophyta). Bot Mar 37:143–149

Floreto EAT, Teshima S, Ishikawa M (1996) Effects of nitrogen and phosphorus on the growth and fatty acid composition of *Ulva pertusa* Kjellman (Chlorophyta). Bot Mar 39:69–74

Folch J, Lees M, Sloane Stanley GH (1957) A simple method for the isolation and purification of total lipides from animal tissues. J Biol Chem 226:497–509

Galloway AWE, Britton-Simmons KH, Duggins DO, Gabrielson PW, Brett MT (2012) Fatty acid signatures differentiate marine macrophytes at ordinal and family ranks. J Phycol 48:956–965

Gillan FT, Hogg RW, Drew EA (1984) The sterol and fatty acid compositions of seven tropical seagrasses from North Queensland. Aust Phytochem 23:2817–2821

Graeve M, Kattner G, Wiencke C, Karsten U (2002) Fatty acid composition of Arctic and Antarctic macroalgae: indicator of phylogenetic and trophic relationships. Mar Ecol Prog Ser 231:67–74

Gressler V, Yokoya NS, Fujii MT, Colepicolo P, Filho JM, Torres RP, Pinto E (2010) Lipid, fatty acid, protein, amino acid and ash contents in four Brazilian red algae species. Food Chem 120:585–590

Guschina IA, Harwood JL (2006) Lipids and lipid metabolism in eukaryotic algae. Prog Lipid Res 45:160–186

Hanson CE, Hyndes GA, Wang SF (2010) Differentiation of benthic marine primary producers using stable isotopes and fatty acids: Implications to food web studies. Aquat Bot 93:114–122

Hernández-Carmona G, Carrillo-Domínguez S, Arvizu-Higuera D, Rodríguez-Montesinos YE, Murillo-Álvarez JI, Muñoz-Ochoa M, Castillo-Domínguez RM (2009) Monthly variation in the chemical composition of *Eisenia arborea* J.E. Areschoug. J Appl Phycol 21: 607–616

Imbs AB, Vologodskaya AV, Nevshupova NV, Khotimchenko SV, Titlyanov EA (2001) Response of prostaglandin content in the red alga Gracilaria verrucosa to season and solar irradiance. Phytochemistry 58:1067–1072

Imbs AB, Latyshev NA, Svetashev VI, Skriptsova AV, Le T, Pham M, Nguyen V, Pham L (2012) Distribution of polyunsaturated fatty acids in red algae of the genus *Gracilaria*, a promising source of prostaglandins Russ J. Mar Biol 38:339–345

Kahru M, Kudela R, Manzano-Sarabia M, Mitchell BG (2009) Trends in primary production in the California Current detected with satellite data. J Geophys Res 114:1–7

Khotimchenko SV (1993) Fatty acids of green macrophytic algae from the Sea of Japan. Phytochemistry 32:1203–1207

Khotimchenko SV (2006) Variations in lipid composition among different developmental stages of *Gracilaria verrucosa* (Rhodophyta). Bot Mar 49:34–38

Khotimchenko SV, Gusarova IS (2004) Red algae of Peter the Great Bay as a source of arachidonic and eicosapentaenoic acids. Russ J Mar Biol 30:183–187

Khotimchenko SV, Yakovleva IM (2005) Lipid composition of the red alga *Tichocarpus crinitus* exposed to different levels of photon irradiance. Phytochemistry 66:73–79

Kim MK, Dubacq JP, Thomas JC, Giraud G (1996) Seasonal variations of triacylglycerols and fatty acids in *Fucus serratus*. Phytochemistry 43:49–55

Kumar M, Gupta V, Trivedi N, Kumari P, Bijo AJ, Reddy CRK, Jha B (2011) Desiccation induced oxidative stress and its biochemical responses in intertidal red alga *Gracilaria corticata* (Gracilariales, Rhodophyta). Environ Exp Bot 72:194–201

Li X, Fan X, Han L, Lou Q (2002) Fatty acids of some algae from the Bohai Sea. Phytochemistry 59:157–161

LLuch D (2011) Informe del Proyecto PEACC Baja California Sur Pesca. http://www.spyde.bcs.gob.mx/cgds/files/proyectos/PEACC/Reporte_Final_PESCA_PEACC-BCS.pdf. Accessed 1 April 2014

Nelson MM, Phleger CF, Nichols PD (2002) Seasonal lipid composition in macroalgae of the northeastern Pacific Ocean. Bot Mar 45:58–65

Potin P, Bouarab K, Salaün JP, Pohnert G, Kloareg B (2002) Biotic interactions of marine algae. Curr Opin Plant Biol 5:308–317

Rohani-Ghadikolaei K, Abdulalian E, Ng WK (2012) Evaluation of the proximate, fatty acid and mineral composition of representative green, brown and red seaweeds from the Persian Gulf of Iran as potential food and feed resources. J Food Sci Technol 49:774–780

Sunbäck K, McGlathery K (2005) Interactions between benthic macroalgal and microalgal mats. In: Kristensen E, Haese RR, Kostka JE (eds) Interactions between macro and microorganisms in marine sediments. American Geophysical Union, Washington, pp 7–29

Tasende MG (2000) Fatty acid and sterol composition of gametophytes and sporophytes of *Chondrus crispus* (Gigartinaceae, Rhodophyta). Sci Mar 64:421–426

Vaskovsky VE, Khotimchenko SV, Bangmei X, Li H (1996) Polar lipids and fatty acids of some marine macrophytes from the yellow sea. Phytochemistry 42:1347–1356

Yazici Z, Aysel V, Öksüz E, Köse A, Cumali S, Güven KC (2007) Fatty acid composition of marine macroalgae from the Black Sea and Dardanelles. Toxicol Environ Chem 89:371–379