Marine Biology (2006)
DOI 10.1007/s00227-006-0269-5

RESEARCH ARTICLE

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Fatty acid composition of flora and fauna associated with *Sargassum* mats in the Gulf of Mexico

Received: 22 December 2004 / Accepted: 12 December 2005

Abstract Feeding ecology of organisms associated with floating *Sargassum* in the northwestern Gulf of Mexico was assessed using fatty acids. Nineteen groups were collected from the *Sargassum* community including four autotrophs, eight invertebrates, five juvenile fishes, and two adult fishes. Spatial and temporal variability in polyunsaturated fatty acid (PUFA) signatures of selected taxa (*Sargassum fluitans* [autotroph], *Leander tenuicornis* [primary heterotroph], *Balistes capriscus* [secondary heterotroph]) was examined to quantify natural variation within these dietary tracers. Although PUFA signatures varied seasonally for all three taxa, no differences were detected between samples collected in year 2000 and 2001 or from different sample locations in the northwest Gulf. PUFA signatures made up 16.3–62.3% of the total fatty acid composition of main autotrophs present in the pelagic environment [particulate organic matter (POM), epiphytic algae, *S. fluitans, S. natans*], and PUFA profiles of selected primary producers were distinct. Specifically, levels of 20:5*n*−*3*, 22:5*n*−*3*, and 22:6*n*−*3* were significantly higher in POM than *Sargassum* spp. or epiphytic algae (*Cladophora* sp.). Dominant PUFA in the tissue of invertebrate and vertebrate consumers were 18:2*n*−*6*, 20:4*n*−*6*, 20:5*n*−*3*, 22:5*n*−3, 22:6*n*−3 and multivariate analyses indicated that PUFA signatures of all consumers were highly similar to POM. As a result, heterotrophs utilizing the *Sargassum* complex may rely heavily on phytoplankton production rather than production by *Sargassum* or associated epiphytic algae.

Communicated by P.W. Sammarco, Chauvin

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Introduction

Food webs tie biological organisms to surrounding physical environments linking population management with ecosystem ecology (Crowder et al. 1996). Studies in feeding ecology have been used to determine overall ecosystem productivity and assist in identification of source(s) of organic matter (Pringle et al. 1999; Paine 2002; Worm et al. 2002). Comprehensive data on food web structure can be used to delineate natural pathways of energy flow through an ecosystem (Vander Zanden and Rasmussen 2001; Lorrain et al. 2002). In addition, data on temporal and spatial variation in trophic relationships can be used to assess short and long-term stability and complexity of food webs (Winemiller and Polis 1996). As a result, assessments of food web structure and trophic relationships are critical for understanding ecosystem performance and energetic relationships of associated taxa.

Due to inherent problems associated with conventional measures of diet (e.g., gut content analysis), considerable effort has been afforded to the development of alternative approaches (e.g., stable isotopes, fatty acids) to identify trophic links and determine food web structure within marine systems (Fry and Sherr 1988; Iverson et al. 1997). Stable carbon and nitrogen isotopes have been used extensively to identify source(s) of primary production within marine food webs, as well as the trophic position of associated fauna (e.g., Fry and Sherr 1988; Hobson and Wassenaar 1999). Although the approach has provided important insights on feeding histories of marine fauna, primary producers and secondary consumers often have similar isotopic signatures, thus limiting the usefulness of the approach for examining trophic relationships. In recent years, fatty acid signatures have increasingly been used as natural

dietary tracers for a variety of aquatic organisms including invertebrates, fishes, sea turtles, and marine mammals (e.g., Fraser et al. 1989; Graeve et al. 1994; Iverson et al. 1997; Kirsch et al. 1998), and the approach has been shown to overcome deficiencies often associated with stable isotope analysis (Kiyashko et al. 1998; Kharlamenko et al. 2001). Due to biochemical limitations in marine organisms, polyunsaturated fatty acids (PUFAs) are rarely modified or synthesized de novo, especially in marine vertebrates (Raclot et al. 1998; Hastings et al. 2001; Graeve et al. 2002; Gurr et al. 2002). Therefore, PUFAs present in the tissue of marine consumers are often obtained exclusively from dietary sources and useful for reconstructing feeding histories (e.g., Iverson et al. 1997; Graeve et al. 2002; Turner and Rooker 2005a).

Sargassum is a pelagic, brown algae that dominates a section of the western North Atlantic known as the Sargasso Sea and is present throughout the Caribbean and Gulf of Mexico (Butler et al. 1983). Two species of *Sargassum, S. fluitans*, and *S. natans*, support a large diversity of marine invertebrates and vertebrates, including several commercially, recreationally, and ecologically important fishes (Fine 1970; Dooley 1972; Bortone et al. 1977; Coston-Clements et al. 1988; Settle 1993). *Sargassum*, like most drifting macrophytes, provides complex habitat in surface waters for epipelagic species and thus may affect survival of species that rely on this unique habitat for food and refuge (Fine 1970; Kingsford 1995). In fact, fauna within the *Sargassum* complex are often several orders of magnitude higher than in oligotrophic waters of the Gulf of Mexico (Dooley 1972; Kingsford 1993; Lambert et al. 1999), further indicating the importance of the mat community as critical habitat of pelagic species. Although *Sargassum* is recognized as essential fish habitat (EFH) by the National Marine Fisheries Service (SAFMC 1998), the role of *Sargassum* has yet to be determined, and data regarding trophic relationships of associated fauna is clearly needed to fully understand its importance within pelagic ecosystems.

In the present study, we examined the feeding ecology of fauna associated with free-floating, pelagic *Sargassum* mats in the northwest Gulf of Mexico using PUFAs. Results of a previous study utilizing stable isotopes (Rooker et al. in press) indicated that organic matter supplied to heterotrophs inhabiting the mat community might not originate from either *Sargassum* species. However, due to similarities in isotopic signatures of associated autotrophs (phytoplankton and epiphytic algae) this study did not assess the relative importance of producers other than *Sargassum*. Therefore, the aim of the present study was to use fatty acid signature analysis to trace source(s) of primary production to consumers using the *Sargassum* complex and to determine feeding histories of associated fauna. Specific objectives of the present study were to (1) examine spatial and temporal variation of PUFAs in a representative autotroph, primary heterotroph, and secondary heterotroph, (2) characterize PUFAs of autotrophs and consumers, and (3) determine the source of organic matter to heterotrophs by comparing their signatures to those derived for autotrophs.

Materials and methods

Sample collection

Samples were collected from three sites within the northwestern Gulf of Mexico including one inshore and two offshore sites stratified into a northern and southern region (Fig. 1). The inshore and offshore sites were < 30 and 30–60 nm from shore, respectively. Collections were conducted monthly from May through August in 2000 and 2001. *Sargassum* mats were chosen at random within each region during each collection. A 20 m (*L*)×3.3 m (*H*) purse seine with 1,000-μm mesh was deployed around individual mats to collect flora and fauna. In addition, larger fishes were collected by hook and line opportunistically at each sample site. Samples of particulate organic matter (POM) was collected from seawater pre-filtered through a 125-μm sieve (to reduce the risk of sample contamination) then collected in a 25-μm sieve before being filtered onto 0.7-μm Whatman glass fiber filters for analysis. Samples for zooplankton were collected from seawater in a 125-μm sieve before being filtered onto 0.7-μm Whatman glass fiber filters for analysis. Epibiota (including flora and fauna) were removed from thallus, blades, and pneumatocysts of *Sargassum* using forceps. Muscle tissue from fish in the present study was collected via two different methods:

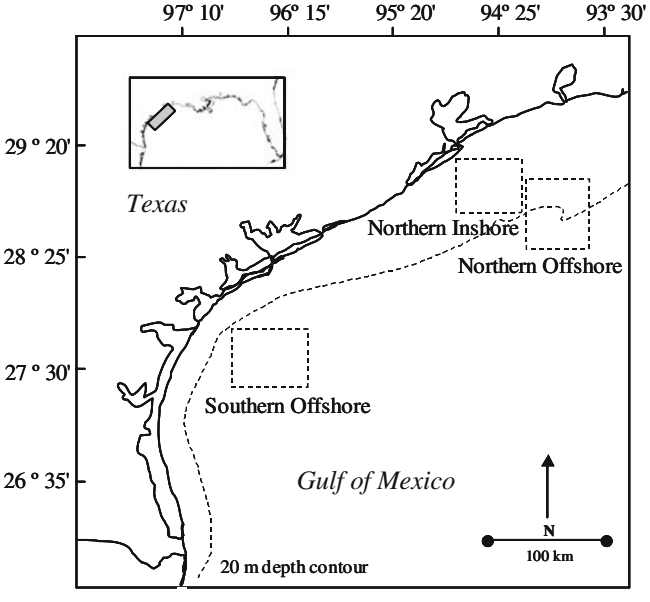

Fig. 1 Location of sampling sites in the northwestern Gulf of Mexico

5–10 g of lateral muscle was collected from large (> 50 mm) specimens, which small specimens (< 50 mm) were homogenized and processed whole. To evaluate the degree of variability among sample tissues individual PUFAs of muscle (white and red) collected from different body locations (dorsal, lateral-surface, lateral-deep, ventral, red muscle) and organ tissues (liver, gonad, viscera, fins) were examined in juvenile dolphinfish (*Coryphaena hippurus*) ($n = 38$), a species included in the present study. Although significant differences (MANOVA, $P < 0.001$) were identified among tissue types using the same five PUFAs utilized in the present study, further examination revealed these differences as being primarily based upon the type of tissue (e.g., muscle, liver, fins, etc.). Further, levels of individual PUFAs within white muscle along the body surface of a pelagic fish (lateral muscle tissue) were essentially homogeneous and representative of the whole carcass. Therefore based upon these data, lateral muscle tissue was used in fishes included in the present study.

Sample preparation and analysis

Whole samples of autotrophs, invertebrates, and juvenile fishes, and lateral muscle tissue from adult fishes were homogenized thoroughly with blenders and mixing mills. Lipid was then extracted in duplicate aliquots in chloroform:methanol (2:1; v:v) after Folch et al. (1957) as modified by Iverson et al. (2001). Fatty acid methyl esters were prepared by transesterification directly from ≤ 100 mg of pure extracted lipid (filtered and dried over anhydrous sulfate), with 0.5 N sulfuric acid in methanol plus dichloromethane following the Hilditch procedure (Iverson et al. 1992). Analysis of methyl esters was run using temperature-programmed gas chromatography according to Iverson (1993) on a Perkin Elmer Autosystem II Capillary FID Gas Chromatograph fitted with a 30 m×0.25 mm internal diameter column coated with 50% cyanopropyl polysilohexane (0.25 µm film thickness, J&W DB-23, Folsom, CA, USA) and linked to a computerized integration system (Turbochrome 4 software, PE Nelson). Identification of fatty acids and isomers was determined by calibrating gas chromatography data with known standards (Nu Check Prep., Elysian, MN, USA). Individual fatty acids were converted to mass percent of total fatty acids using conversion factors from Ackman (1972, 1991) after accounting for the contribution of BHT.

Statistical analyses

Multivariate analysis of variance (MANOVA) and analysis of variance (ANOVA) were used to examine differences in composition of PUFA signatures and individual PUFAs, respectively among autotrophs and consumers. Further, MANOVA and ANOVA were used to assess spatial and temporal variability among an autotroph (*S. fluitans*), primary heterotroph (*Leander tenuicornis*), and secondary heterotroph (*Balistes capriscus*). Tukey's honestly significant difference (HSD $\alpha = 0.05$) test was used to find a posteriori difference among groups. Normality and homogeneity of variances were verified using Kolmogorov–Smirnov and Bartlett tests, respectively. Fatty acid data were arcsine-transformed before parametric tests were run to correct for their binomial distribution (percentages) (Zar 1998). Principal components analysis (PCA) was used to examine distance relationships among autotrophs and subsequent consumers based on PUFA signatures. Factors were extracted using a correlation matrix with minimum eigenvalues of 1.0. Hierarchical cluster analysis was used to identify natural associations of invertebrates and fishes using PUFA signatures. Euclidean distances were calculated using complete linkages among species and identified three natural groupings of invertebrates and two groups of fishes based upon similarity of PUFA signatures. Cluster groupings were identified by the distance at which groups were clearly related to the variables of interest in a manner such that the samples were relatively constant within clusters (Williams 1971). Clusters were tested using discriminant classification scores to determine if they represented natural groupings of species/taxa based upon PUFA signatures (Mojena 1977; Cuevas et al. 2000). Since similar PUFA signatures should represent common feeding pathways, invertebrate and fish groups were maintained for further analysis to simplify trophic interactions among consumers. Classification and regression tree (CART) analysis was used to predict membership of individuals within categories based upon PUFA signatures of trophic groups identified through cluster analysis (Johnson and Wichern 2002). Trees were constructed using the twoing procedure for splitting criteria due to the large number of independent groupings (SPSS 1998). PUFAs involved with each split and the direction were determined from the position of the PUFA label. For example, if the left side of the split had a reported value of 22:6*n*−3 < 26.3, then levels of 22:6*n*−3 in individuals to the left of the split were < 26.3% of the total fatty acid composition, while those along the right split had values > 26.3 %. Cross-validated (jackknifed) classification scores were used to calculate classification success at each terminal node.

Results

Sixty-seven individual fatty acids were identified during analysis. The five PUFAs [18:2*n*−6 (linoleic acid), 20:4*n*−6 (arachidonic acid, AA), 20:5*n*−3 (eicosapentaenoic acid, EPA), 22:5*n*−3 (docosapentaenoic acid, DPA), and 22:6*n*−3 (docosahexaenoic acid, DHA)], were used to assess temporal and spatial variation within the system and determine trophic relationships of the

associated community fauna to reduce the number of variables because they were (1) the most abundant and (2) were found to be indicators of diet in previous studies of estuarine and marine consumers (Turner and Rooker 2005a, b). Further uses of the term 'PUFA signatures' is based upon these five fatty acids.

Nineteen groups were selected as representatives of the *Sargassum* community including four autotrophs, eight invertebrates, five juvenile fishes, and two adult fishes (Table 1). PUFAs comprised the largest percent composition of all fatty acid groups (i.e., saturated, monounsaturated, polyunsaturated) in most samples (16.3–62.3% of the total fatty acid composition). Furthermore, the five most abundant PUFAs made up 54.1–95.9% of the PUFAs and 9.6–44.9% of the total fatty acid composition of the samples processed and were used exclusively for further characterization of trophic relationships.

Spatial and temporal variation

Spatial and temporal variation in PUFA signatures was investigated at three distinct levels in the *Sargassum* mat community: autotroph (*S. fluitans*), primary heterotroph (*L. tenuicornis*), secondary heterotroph (*B. capriscus*) (Table 2). Significant seasonal differences in PUFA signatures were identified for *S. fluitans* and *B. capriscus* using MANOVA, but not *L. tenuicornis* (Table 3) (Fig. 2a). Univariate comparisons revealed that significant monthly variation in PUFAs was driven by differing levels of 22:5*n*−*3* in both *S. fluitans* and *B. capriscus*, while no effect was observed in 18:2*n*−*6*, 20:4*n*−*6*, 20:5*n*−*3*, or 22:6*n*−*3* (Table 4). Tukey's HSD indicated that levels of 22:5*n*−*3* in *S. fluitans* and *B. capriscus* differed between May–June and July–August (Table 4). However, no significant differences in PUFA signatures were detected between samples of *S. fluitans*, *L. tenuicornis*, and *B. capriscus* collected in 2000 and 2001 (Fig. 2b, Table 3) or among regions sampled (Fig. 2c, Table 3) based upon MANOVA. To ensure that seasonal variation in PUFA signatures did not confound our characterization of trophic relationships, only samples from May and June 2000 were used for further assessments.

Table 1 Representative species of the *Sargassum* community

Species	*n*	Length (mm)
Autotrophs		
Cladophora sp. (green epiphytic algae)[a]	10	n/a
Sargassum fluitans (brown algae)[a]	36	n/a
Sargassum natans (brown algae)[a]	24	n/a
POM[b]	25	n/a
Invertebrates		
Zooplankton[a]	15	n/a
Membraniporum sp. (bryozoan)[a]	6	n/a
Algaophenia latecarinata (hydroid cnidarian)[a]	6	8–12
Spirorbis sp. (serpulid polychaete)[a]	6	1–2
Latruetes fucorum (hippolytid shrimp)[a]	12	8–16
Leander tenuicornis (palaemonid shrimp)[a]	12	21–36
Portunus sayi (portunid crab)[a]	12	17–39
Scyllaea pelagica (nudibranch gastrpod)[a]	12	57–76
Fishes		
Balistes capriscus (gray triggerfish)[a]	27	61–99
Caranx crysos (blue runner)[a]	18	46–58
Histrio histrio (sargassum fish)[a]	19	66–90
Monocanthus hispidus (planehead filefish)[a]	20	65–91
Seriola dumerili (greater amberjack)[a]	20	92–145
Coryphaena hippurus (dolphinfish)[ab]	9	330–487
Acanthocybium solandri (wahoo)[a]	3	1,035–1,115

All specimens collected from Northern Offshore location during May[a] or June[b] 2000. Length represents total length for fishes, carapace length for shrimps, and carapace width for crabs

Table 2 Species used for analyses of temporal and spatial variability in *Sargassum* communities

Species	*n*	Length (mm)
Sargassum fluitans (brown algae)	72	n/a
May 2000–Northern Offshore	36	n/a
May 2000–Northern Inshore	6	n/a
May 2000–Southern Offshore	6	n/a
May 2001–Northern Offshore	6	n/a
June 2000–Northern Offshore	6	n/a
July 2000–Northern Offshore	6	n/a
August 2000–Northern Offshore	6	n/a
Leander tenuicornis (palaemonid shrimp)	48	17–36
May 2000–Northern Offshore	12	15–26
May 2000–Northern Inshore	6	27–33
May 2000–Southern Offshore	6	18–29
May 2001–Northern Offshore	6	16–20
June 2000–Northern Offshore	6	25–33
July 2000–Northern Offshore	6	20–31
August 2000–Northern Offshore	6	19–36
Balistes capriscus (gray triggerfish)	63	53–103
May 2000–Northern Offshore	27	68.5–102.6
May 2000–Northern Inshore	6	56–102
May 2000–Southern Offshore	6	65–99
May 2001–Northern Offshore	6	53–88
June 2000–Northern Offshore	6	78–100
July 2000–Northern Offshore	6	76–90
August 2000–Northern Offshore	6	64–102

Length represents total length in *B. capriscus* and carapace length in *L. tenui*cornis

Table 3 Multivariate analysis of variance results for spatial and temporal variability in PUFA signatures of *S. fluitans*, *L. tenui cornis*, and *B. capriscus*

Species	Variable	*F*	*P*
S. fluitans	Season	6.875	0.029
L. tenuicornis	Season	17.831	0.176
B. capriscus	Season	7.015	0.025
S. fluitans	Year	15.544	0.183
L. tenuicornis	Year	16.255	0.182
B. capriscus	Year	17.727	0.176
S. fluitans	Region	18.534	0.215
L. tenuicornis	Region	24.912	0.586
B. capriscus	Region	16.557	0.176

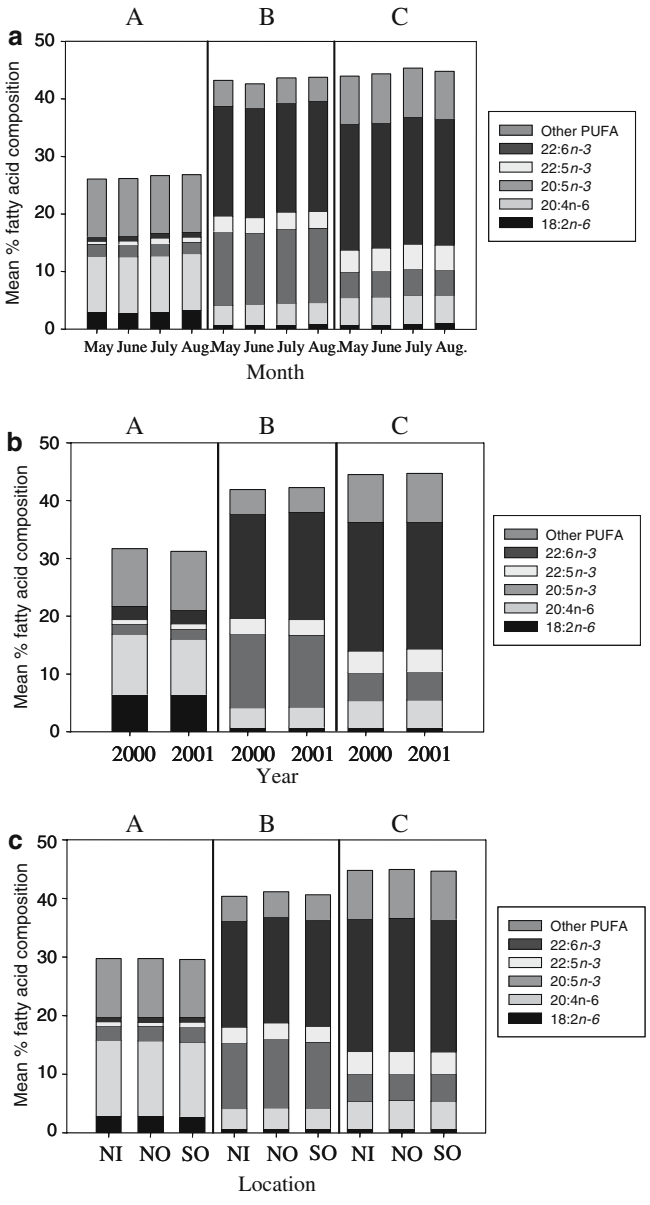

Fig. 2 Percent composition of five abundant polyunsaturated fatty acids (*PUFAs*) for an autotroph (**a** *Sargassum fluitans*), primary heterotroph (**b** *Leander tenuicornis*), and secondary heterotroph (**c** *Balistes capriscus*) from *Sargassum* communities in the northwest Gulf of Mexico. Mean values are reported for 18:2*n*−6, 20:4*n*−6, 20:5*n*−3, 22:5*n*−3, 22:6*n*−3, and all other PUFAs by **a** month (May, June, July, August), **b** year (2000, 2001), and **c** location (*NI* northern inshore, *NO* northern offshore, *SO* southern offshore)

Autotrophs

Significant differences in PUFA signatures of four autotrophs were identified (MANOVA, $P < 0.001$). Levels of 18:2*n*−6, 20:4*n*−6, 20:5*n*−3, and 22:6*n*−3 were significantly different among autotrophs (ANOVA, $P < 0.001$), although levels of 22:5*n*−3 were similar in all autotrophs sampled ($P = 0.094$). Tukey's HSD tests indicated that levels of 20:5*n*−3, 22:5*n*−3, and 22:6*n*−3 were found in significantly higher concentrations in POM than in *S. fluitans, S. natans*, or *Cladophora* sp. (Fig. 3). Additionally, levels of 18:2*n*−6 were significantly higher in *Cladophora* sp. than in *S. fluitans*, *S. natans*, or POM, while levels of 20:4*n*−6 were significantly higher in *S. fluitans* and *S. natans* than in *Cladophora* sp. or POM.

Invertebrates

PUFA signatures of eight invertebrates included in the present study were significantly different (Fig. 4a; MANOVA, $P < 0.001$), and univariate contrasts indicated that levels of all five PUFAs were significantly different among taxa examined. Levels of 18:2*n*−6 were significantly different among invertebrates (ANOVA, $P < 0.001$), but Tukey's HSD test showed that overall significant differences were driven by differences among three groups: crustaceans (*L. tenuicornis*, *Latruetes fucorum*, *Portunus sayi*), epibionts-nudibranch (*Membraniporum* sp., *Spirorbis* sp., *Algaophenia latecarinata*, and *Scyllaea pelagica*) and zooplankton. Similar trends were observed for three of the other four individual PUFAs, as levels of 20:4*n*−6 (ANOVA, $P < 0.001$), 20:5*n*−3 (ANOVA, $P < 0.001$), and 22:6*n*−3 (ANOVA, $P < 0.001$) were significantly different in invertebrates overall. However, Tukey's HSD test showed that significant differences were again driven by differences among three groups: crustaceans, epibionts-nudibranch, and zooplankton. Levels of 22:5*n*−3 (ANOVA, $P < 0.001$) were also significantly different among invertebrates, but Tukey's HSD test showed that significant differences were driven by differences between two groups: crustaceans-epibionts-nudibranch and zooplankton. Hierarchical cluster analysis identified three natural groupings of invertebrates based upon PUFA signatures: crustaceans (invertebrate group A = IA), epibiota and an associated nudibranch (invertebrate group B = IB), and zooplankton (invertebrate group C = IC) at a euclidean distance of 4.0 (Fig. 4b).

Fishes

Significant differences in PUFA signatures of fish taxa were also observed (Fig. 5a; MANOVA, $P < 0.001$). Univariate contrasts indicated 18:2*n*−6, 20:4*n*−6, 20:5*n*−3, and 22:6*n*−3 were significantly different among fishes (ANOVA, $P < 0.001$), while no effect was observed for 22:5*n*−3 (ANOVA, $P = 0.336$). Tukey's HSD tests indicated that levels of 18:2*n*−6 were not significantly different among species within two groups: (a) *Caranx crysos*, *Seriola dumerili*, *C. hippurus*, *Acanthocybium solandri*, (b) *B. capriscus*, *Monocanthus hispidus*, *Histrio histrio*. Tukey's HSD tests also showed that levels of 20:4*n*−6 and 22:6*n*−3 differed between these two groups but were similar among taxa within the group. In contrast, Tukey's HSD tests for the PUFA 20:5*n*−3 revealed significant differences among three groups: *C. crysos* and *S. dumerili*, *C. hippurus* and *A. solandri*,

Table 4 Analysis of variance and Tukey HSD results for seasonal variability in PUFA signatures of *S. fluitans*, *L. tenuicornis*, and *B. capriscus*

Species	Variable	*F*	*P*	May	June	July	Aug
S. fluitans	18:2*n*−6	0.784	0.245	a	a	a	a
L. tenuicornis	18:2*n*−6	0.690	0.582	a	a	a	a
B. capriscus	18:2*n*−6	5.489	0.060	a	a	a	a
S. fluitans	20:4*n*−6	0.361	0.782	a	a	a	a
L. tenuicornis	20:4*n*−6	2.551	0.103	a	a	a	a
B. capriscus	20:4*n*−6	2.481	0.145	a	a	a	a
S. fluitans	20:5*n*−3	0.430	0.736	a	a	a	a
L. tenuicornis	20:5*n*−3	2.997	0.095	a	a	a	a
B. capriscus	20:5*n*−3	2.515	0.120	a	a	a	a
S. fluitans	22:5*n*−3	38.927	> 0.001	a	a	b	b
L. tenuicornis	22:5*n*−3	2.055	0.185	a	a	a	a
B. capriscus	22:5*n*−3	7.549	0.013	a	a	b	b
S. fluitans	22:6*n*−3	0.111	0.952	a	a	a	a
L. tenuicornis	22:6*n*−3	0.730	0.563	a	a	a	a
B. capriscus	22:6*n*−3	0.152	0.925	a	a	a	a

Within a variable row, months sharing the same letters are not significantly different. In all cases $P < 0.05$

and *B. capriscus*, *M. hispidus*, *H. histrio*. Similar to univariate contrasts, hierarchical cluster analysis indicated PUFA signatures of the two groups were distinct at a Euclidean distance of 3.0: Fish Group A (FA) (*H. histrio*, *B. capriscus*, and *M. hispidus*), Fish Group B (FB) (*C. crysos*, *S. dumerili*, *A. solandri*, and *S. cavalla*) (Fig. 5b).

Trophic interactions

Levels of PUFA signatures of consumers were similar to levels found in POM, while significantly different from quantities found in either *Sargassum* species or *Cladophora* sp. (Figs. 3, 6; MANOVA, $P < 0.001$). PCA was performed using averaged individual PUFA values including all autotrophs, invertebrates, and fishes, and over 68% of the variation in composition of PUFA signatures could be explained by principal components 1 and 2. Scatterplots of components 1 and 2 revealed similarities among individual invertebrates and fishes with POM and separation from other autotrophs (Fig. 6).

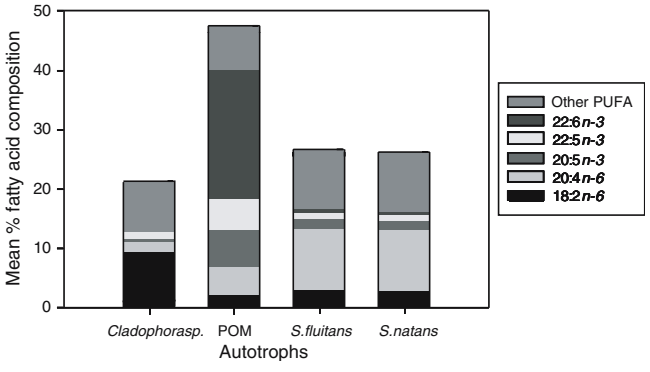

Fig. 3 Percent composition of five abundant polyunsaturated fatty acids (*PUFAs*) within autotrophs. Mean values are reported for 18:2*n*−6, 20:4*n*−6, 20:5*n*−3, 22:5*n*−3, 22:6*n*−3, and of all other PUFAs

As with PCA, CART results demonstrated that individuals from higher trophic levels consistently grouped with POM, rather than *Sargassum* spp. or *Cladophora* sp., but included an analysis of the individual PUFAs most influential in each classification event. Overall, CART classified POM and consumers from *Sargassum* sp. and *Cladophora* sp. by levels of 22:6*n*−3 (Fig. 7). Further, CART analysis successfully classified invertebrate groups IA, IB, and IC using PUFA signatures. Based upon these results it appears that 18:2*n*−6 was most influential in separating groups IB and IC, while 22:6*n*−3 was the most important PUFA for separating groups IA and IB. Additional members of IC were separated from POM by levels of 18:2*n*−6. CART analysis also successfully classified fish groups using PUFA signatures; FA was classified with a subset of individuals from IB, and FA and IB were further separated by levels of 18:2*n*−6, FB was classified with IA and further separated by levels of 20:4*n*−6. Although it appears that 22:6*n*−3 was an important PUFA in most consumers, levels of 18:2*n*−6 varied considerably among invertebrate groups, and 20:4*n*−6 among fish groups, possibly indicating subtle differences in their individual feeding patterns.

Discussion

Results suggest that PUFA signatures of autotrophs and heterotrophs from *Sargassum* mat communities remain fairly stable across spatial and annual scales. Although significant differences were detected in PUFA signatures of *S. fluitans* and *B. capriscus*, variability was driven by levels of a single PUFA (22:5*n*−3). Seasonal variation in PUFA signatures may be a result of changes in PUFA composition of autotrophs, as signatures in macro and micro algae have been linked to light intensity, salinity,

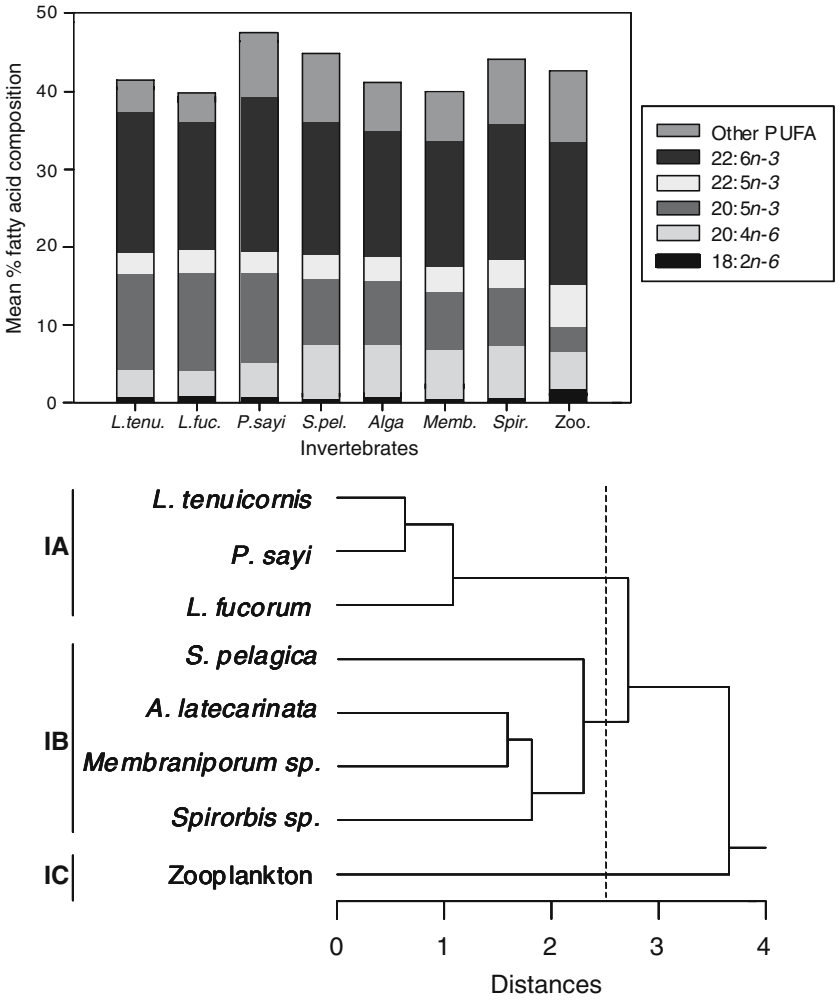

Fig. 4 Polyunsaturated fatty acid (*PUFA*) data for invertebrates included in the present study including 18:2*n*−*6*, 20:4*n*−*6*, 20:5*n*−*3*, 22:5*n*−*3*, 22:6*n*−*3*, and of all other PUFAs. In **a**, mean values of percent composition are reported for *L. tenu. Leander tenuicornis*, *L. fuco. Latruetes fucorum*, *P. sayi Portunus sayi*, *S. peal Scyllaea pelagica*, *Alga. Algaophenia latecarinata*, *Memb. Membraniporum* sp., *Spir. Spirorbis* sp., *Zoo.* zooplankton. In **b**, these values are used to construct a hierarchical cluster plot separating groups IA (*Leander tenuicornis*, *Latruetes fucorum*, *Portunus sayi*), IB (*Scyllaea pelagica*, *Algaophenia latecarinata*, *Membraniporum* sp., *Spirorbis* sp.), and IC (zooplankton). *Dashed lines* represent splits between groups at a Euclidean distance of 4.0

temperature, and available nutrients (Thompson et al. 1990, 1992; Elenkov et al. 1996; Graeve et al. 2002). For example, Floreta and Teshima (1998) found that increasing light intensities increased levels of most fatty acids in Chlorophyta and Rhodophyta species and decreased levels in *Sargassum piluliferum*, while higher salinities caused an increase in levels of fatty acids in all species. Moreover, phytoplankton community structure and distribution is also affected by oceanographic conditions (Boehlert and Mundy 1994), and thus observed seasonal patterns for Gulf taxa may be a function of both changes in PUFA production by autotrophs as well as changes in the community composition of autotrophs.

Fatty acid signatures of POM were significantly different than signatures of *Sargassum* spp. or *Cladophora* sp., and contained high levels of PUFAs including 20:5*n*−*3*, 22:5*n*−*3*, and 22:6*n*−*3*, while levels of 18:2*n*−*6* and 20:4*n*−*6* were more abundant in both macroalgae (*Sargassum* spp. and *Cladophora* sp.). These results were not unexpected since concentrations of some long-chain PUFAs (22:5*n*−*3*, 22:6*n*−*3*) are found in many phytoplankton species, although levels of these fatty acids are often minimal or absent in macroalgae (Herbretau et al. 1997; Graeve et al. 2002). Phytoplankton is typically the largest component of POM, though smaller amounts of bacteria and non-living particles are present (Hama 1999), and it often contains substantial amounts of long-chain PUFAs like 20:5*n*−*3* and 22:6*n*−*3* (Pedersen et al. 1999; Graeve et al. 2002). As previously reported, large concentrations of long-chain PUFAs including 20:5*n*−*3*, 22:5*n*−*3*, and 22:6*n*−*3* are often found in diatoms, dinoflagellates, and haptophytes (Harrington et al.1970; Henderson et al. 1988; Pedersen et al. 1999). Strains of *Crypthecodinium cohnii*, a heterotrophic dinoflagellate found closely associated with *Sargassum* spp. in both the Atlantic and Gulf of Mexico (Beam and Himes 1982) contain such large amounts of 22:6*n*−*3* that they are cultured to produce quantities commercial grade PUFAs for use in nutritional supplements and aquaculture feeds (Henderson et al. 1988; Jiang et al. 1999). Conversely, macroalgae typically contain very low quantities of long-chain PUFAs, especially 22:6*n*−*3*. Graeve et al. (2002) demonstrated that several genera of macroalgae from both Arctic and Antarctic biomes contained large quantities of 18:2*n*−*6* and 20:4*n*−*6*; however, levels of 22:6*n*−*3* were negligible in most species. In addition,

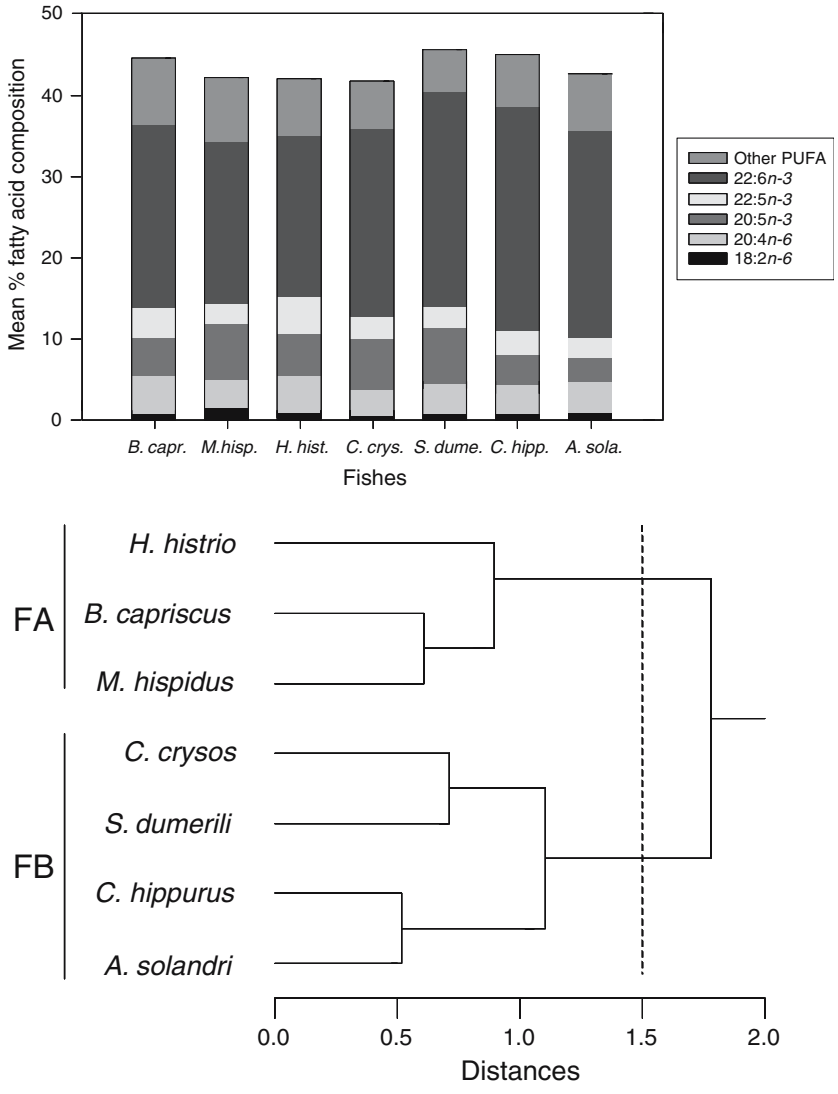

Fig. 5 Polyunsaturated fatty acid (*PUFA*) data for fishes included in the present study including 18:2*n*−*6*, 20:4*n*−*6*, 20:5*n*−*3*, 22:5*n*−*3*, 22:6*n*−*3*, and of all other PUFAs. In **a**, mean values of percent composition are reported for *B. capr*. *Balistes capriscus*, *M. hisp*. *Monocanthus hispidus*, *H. hist*. *Histrio histrio*, *C. crys*. *Caranx crysos*, *S. dume*. *Seriola dumerili*, *C. hipp*. *Coryphaena hippurus*, *A. sola*. *Acanthocybium solandri*. In **b**, these values are used to construct a hierarchical cluster plot separating groups FA (*Balistes capriscus*, *Monocanthus hispidus*, *Histrio histrio*) and FB (*Caranx crysos*, *Seriola dumerili*, *Coryphaena hippurus*, *Acanthocybium solandri*). The dashed line represents a split between groups at a Euclidean distance of 3.0

Herbretau et al. (1997) identified similar trends in brown and green algae which were comparable to findings from the present study, as high levels of 20:4*n*−*6* (19.2–31.8% total fatty acid composition), low levels of 20:5*n*−*3* (2.5–3.6%), and trace amounts of 22:6*n*−*3* (0–1.8%) were found in *Sargassum muticulum* and three other brown alga, whereas *Codium fragile* (green algae) contained lower levels of 20:4*n*−*6* (4.2%), and no 20:5*n*−*3* or 22:6*n*−*3*. Conversely, Khotimchenko et al. (2002) found substantial quantities of 20:4*n*−*6* and 20:5*n*−*3* in species of Rhotophyta and Phaetophyta, although these levels were not identified in *Sargassum* ssp. in the present study. Therefore, PUFA signatures of phytoplankton in POM are most likely contributing to signatures found in the *Sargassum* food web indicating that phytoplankton is the likely source of organic matter in this complex.

Organic matter incorporated into invertebrates appears to have originated from phytoplankton in POM rather than *Sargassum* spp. or *Cladophora* sp. based upon PUFA signatures. High levels of long-chain PUFA signatures, apparently derived from phytoplankton, were identified in all invertebrates included in the present study. For example, copepods, the most abundant marine zooplankton in pelagic waters, are highly associated with *Sargassum* and typically feed upon diatom and dinoflagellate species (Yeatman 1962; Cowles et al. 1988; Xu and Wang 2001). As a result, food chains utilizing organic matter from marine phytoplankton tend to be exceptionally enriched in levels of 20:5*n*−*3* and 22:6*n*−*3* (Sargent 1978; Pedersen et al. 1999; Domiazon et al. 2000). PUFA signatures of invertebrates were similar to phytoplankton in POM, indicating that phytoplankton appears to be the source of organic matter in the system. Zooplankton, crustaceans, and epibiotic-nutibranchs groups all had relatively high levels of 20:4*n*−*6*, 20:5*n*−*3*, and 22:5*n*−*3* and extremely high levels of 22:6*n*−*3*, and each of the three taxa were strongly associated with phytoplankton in multivariate assessments of PUFA signatures.

Similar to invertebrates, PUFA signatures of fish groups were similar to POM, suggesting that organic matter supplied to these taxa originates principally from

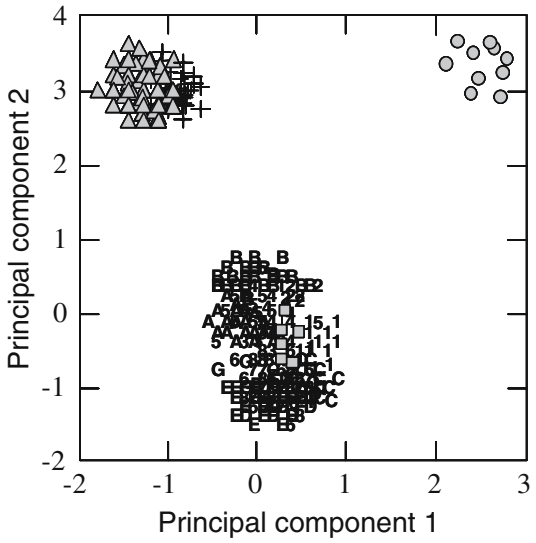

Fig. 6 Plot of principal components 1 and 2 for polyunsaturated fatty acid (*PUFA*) signatures of autotrophs (*filled square* POM, *filled triangle Sargassum fluitans*, + *Sargassum natans*, *filled circle Cladophora* sp.), invertebrates (*1* zooplankton, *2 Membraniporum* sp., *3 Spirorbis* sp., *4 Algaophenia latecarinata*, *5 Scyllaea pelagica*, *6 Leander tenuicornis*, *7 Latruetes fucorum*, *8 Portunus sayi*), and fishes (*A Monocanthus hispidus*, *B Balistes capriscus*, *C Histrio histrio*, *D Caranx crysos*, *E Seriola dumerili*, *F Coryphaena hippurus*, *G Acanthocybium solandri*) in the *Sargassum* community

phytoplankton. High levels of long-chain PUFAs, including 20:4*n*−*6*, 20:5*n*−*3*, and 22:5*n*−*3* and extremely high levels of 22:6*n*−*3*, apparently derived from phytoplankton, were identified in all fishes included in the present study. PUFA signatures of fish group FA were similar to invertebrate groups IB and IC. Similar finding were reported by Dooley (1972), noting that stomachs of *B. capriscus* and *H. histrio* within the *Sargassum* community contained primarily copepods, and macro invertebrates and juvenile fishes, respectively, whereas *M. hispidus* target an assortment of micro invertebrates including hydroids and copepods. PUFA signatures of fish group FB, which represents more mobile taxa, were similar to levels identified in IA, indicating that the two groups share a common source of organic matter. Similarly, Dooley (1972) indicated that *C. crysos* and *S. dumerili* fed upon crustaceans including *L. tenuicornis*, and small fishes including juvenile *C. crysos*. Additionally, stomach contents analysis and stable isotope analysis have revealed that *C. crysos* and *S. dumerili* comprise a large portion of the diet in large *C. hippurus* (> 700 mm) and while *A. solandri* have been shown to feed upon *B. capriscus* and *C. crysos* (Magnuson and Heitz 1971; Manooch and Hogarth 1983; Manooch et al. 1984; Rooker et al. 2004).

Every effort was made during the present study to control the quality of sample collection and processing; however, possible biases still exist primarily in relation to POM collection and muscle tissue sampling. Due to inherent difficulties associated with sampling phytoplankton for tissue analysis, PUFA signatures of POM, rather than of phytoplankton, were used to describe planktonic sources of organic matter. Although phytoplankton is typically the largest component of POM, it often contains other particles including metazooplankton, protozooplankton, bacteria, and various non-living particles (Hama 1999; Iken et al. 2001; Schmidt et al. 2003). In the present study, POM was classified as sample material collected between 25 and 125 μm, encompassing a large size-range of organisms, which may actually confound the true PUFA signature of phytoplankton (e.g., del Giorgio and France 1996; Grey et al. 2000). For example, a parallel study conducted using natural nitrogen ($\delta^{15}N/^{14}N$) isotope ratios from the same samples indicated that trophic position of phytoplankton (POM) and first order consumers were not as distinct as expected (2–3 ppt shift not observed), indicating the POM signature may include proto and metazooplankton or particulate matter of other heterotrophs (Rooker et al. in press). Nevertheless, this "trophic contamination effect" should not confound our analysis of PUFA signatures for several reasons: (1) phytoplankton is the dominant component of POM, including the size-range sampled during the present study (Carpenter 1970; Lambert et al. 1999), (2) PUFA signatures of Gulf of Mexico phytoplankton species match levels present in POM from the present study (Beam and Himes 1982; Henderson et al. 1988; Jiang et al. 1999; Pedersen et al. 1999), and (3) PUFA signatures of consumers within the *Sargassum* community were significantly different from PUFA signatures from all other primary producers except the POM sample. Therefore, the identity of the organisms comprising POM (whether phytoplankton or other) is not critical to this assessment and the quality of our POM sample is sufficient to characterize the PUFA signatures of phytoplankton and track the flow of phytoplankton-derived organic matter though this system.

In summary, high concentrations of PUFAs found in POM more closely match levels in higher trophic groups of the *Sargassum* community than signatures of *S. fluitans, S. natans*, or *Cladophora* sp., suggesting that phytoplankton is the major source of organic matter entering this food web. Organic matter incorporated into invertebrates including crustaceans, nudibranch, epibionts, and zooplankton, appears to have originated from phytoplankton in POM based upon PUFA signatures. PUFA signatures of juvenile and adult fishes in the complex are similar to prey taxa and thus utilization of *Sargassum* mats is in part may be linked to their value as feeding grounds. Although *Sargassum* does not appear to directly contribute nutrients to the food web, it may play important roles in nutrient recycling, aggregation mechanisms, as substrate, and increasing habitat complexity in pelagic environments.

Acknowledgements The authors would like to thank two anonymous reviewers and D. Wells, J. Harper, B. Geary, and M. Lowe

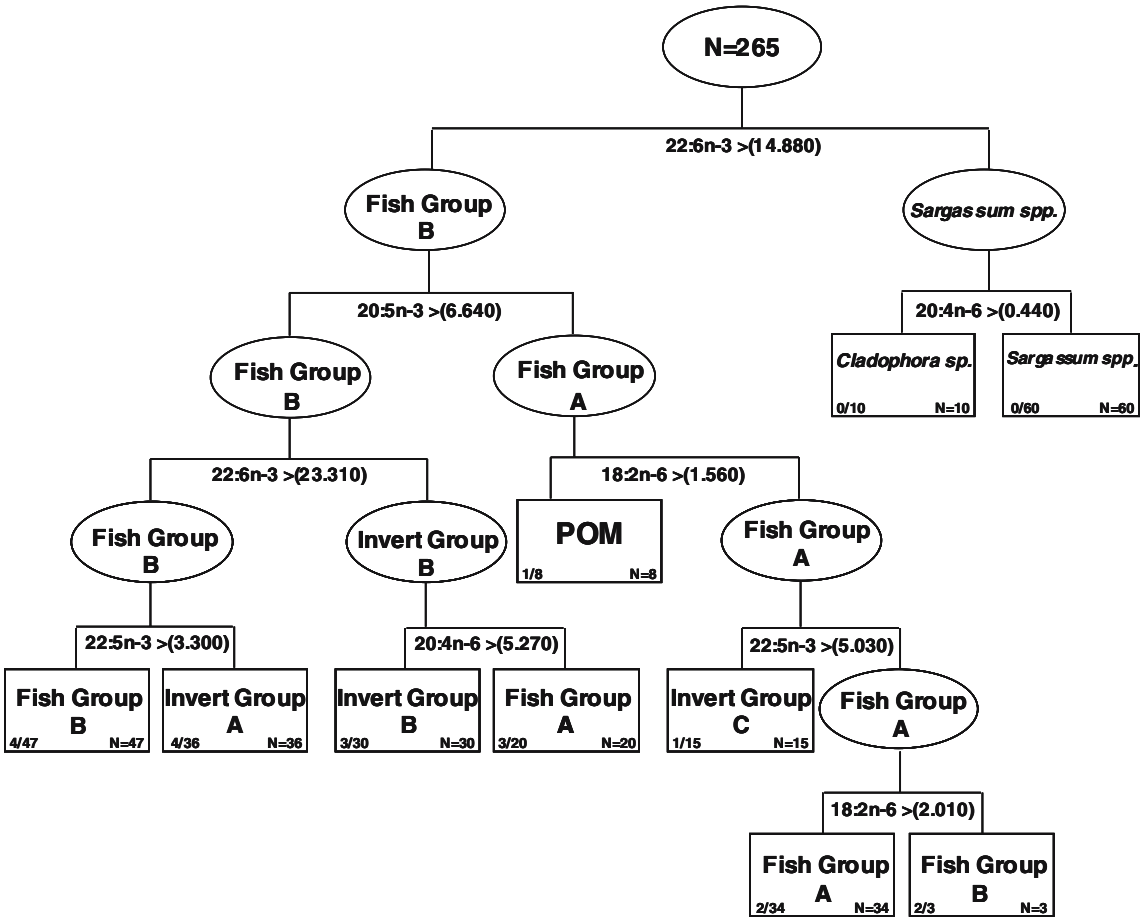

Fig. 7 Classification and regression tree of all *Sargassum* community species. *Ellipses* indicate intermediate splitting nodes and *rectangles* indicate terminal node with classifications. *Labels* indicate the group with the largest number of samples at each node, except the initial node which gives the overall sample size of analysis. Within each terminal node are both fractions indicating number of misclassifications and sample size. Fatty acids are listed at each split with concentrations. Label position indicates value of associated polyunsaturated fatty acid (*PUFA*) at each split; label on side with $< X\%$ total PUFA composition, opposite side of the split represents individuals with $> X\%$ total PUFA composition

for assistance in the field. This project was funded by the Aquarium at Moody Gardens, Galveston, Texas.

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