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# The source and fate of organic matter and the significance of detrital pathways in a tropical coastal ecosystem

*Tak-Cheung Wai,*[1] *Jasmine S. S. Ng, and Kenneth M. Y. Leung*
The Swire Institute of Marine Science and Division of Ecology and Biodiversity, School of Biological Sciences,
The University of Hong Kong, Pokfulam Road, Hong Kong, P.R. China

*David Dudgeon*
Division of Ecology and Biodiversity, School of Biological Sciences, The University of Hong Kong, Pokfulam Road,
Hong Kong, P.R. China

*Gray A. Williams*
The Swire Institute of Marine Science and Division of Ecology and Biodiversity, School of Biological Sciences,
The University of Hong Kong, Pokfulam Road, Hong Kong, P.R. China

*Abstract*

Stable isotope analysis (SIA) and fatty acid profiling were used to elucidate the supply and fate of energy in a tropical coastal ecosystem in Hong Kong, southern China. To investigate seasonal changes in source supply on the diets of different trophic guilds, measurements were taken in three rocky bays before and after the onset of the summer monsoon, when supply of both marine macroalgal and streamborne terrestrial detritus increases. Particulate organic matter, comprising a mixture of marine and terrestrial sources, was the ultimate food source (>60%) for suspension feeders, which were the major prey items of a predatory gastropod (*Thais*). Increased levels of bacterial fatty acid biomarkers (BaFA) were recorded after the onset of the summer monsoon, indicating amplified dependence on detrital materials in both primary and secondary consumers. The considerable increase in the detritus fraction of sedimentary organic matter at the onset of the summer monsoon was reflected by enhanced levels of BaFA, possibly due to the degeneration of macroalgae. Significant contributions of this marine algal detritus to deposit feeders (*Holothuria*, 36%) and of terrestrial detritus to an echinoid grazer (*Salmacis*, 14%) were revealed by SIA mixing models as well as elevated BaFA concentrations. These results indicate a higher dependence on heterotrophic food chains based on decomposing marine algae and terrestrial detritus after the onset of the summer monsoon. Such seasonal variation in the importance of detrital energy sources is, therefore, likely to be important to coastal ecosystem functioning in the monsoonal tropics.

Most primary production is not consumed directly, and dead autotrophic material becomes an important energy and nutrient source for organisms via detrital pathways (Mann 1988; Moore et al. 2004). Dual stable isotope ratios and fatty acid signatures have been used as tracers to show how detritus from a variety of origins can serve as an energy source for marine communities (e.g., riverine discharges—Paterson and Whitfield 1997; seagrass beds—Boschker et al. 2000; macroalgae—Norderhaug et al. 2003; phytoplankton and mangroves—Bouillon et al. 2004; Mfilinge et al. 2005). These studies show that the relative importance of energy from terrestrial- and marine-derived detritus vs. energy from phytoplankton and benthic algae is highly variable within and among coastal marine ecosystems. High spatial variation in detrital availability and composition has made it difficult to generalize about the importance of detrital pathways, and complexity is added in instances where the relative contributions of different energy sources are influenced by tidal exchange and seasonal changes (Guest et al. 2004; Doi et al. 2005). The relative importance of these food sources to secondary production in a particular system is, therefore, predicted to be case specific.

On seasonal, tropical shores in Hong Kong, monsoons have an important effect on the supply of detritus (Dudgeon 1982; Kaehler and Williams 1996). During the cool, dry northeastern monsoon (December–March), extensive beds of erect macroalgae (especially *Sargassum* spp.) develop along rocky coasts, but these die back when water temperatures rise in May to June as the warmer, southwestern monsoon begins to dominate (Hodgkiss 1984; Kaehler and Williams 1996). As a result, large quantities of detached and decomposing macroalgae are exported by the tides to other intertidal and subtidal habitats (Kaehler and Williams 1996), creating a potential trophic link between these different habitats. During the hot, wet southwestern monsoon (June–September), rainfall increases significantly and contributes to ~70% of the average annual rainfall

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[1] Corresponding author (waitakcheung@hotmail.com).

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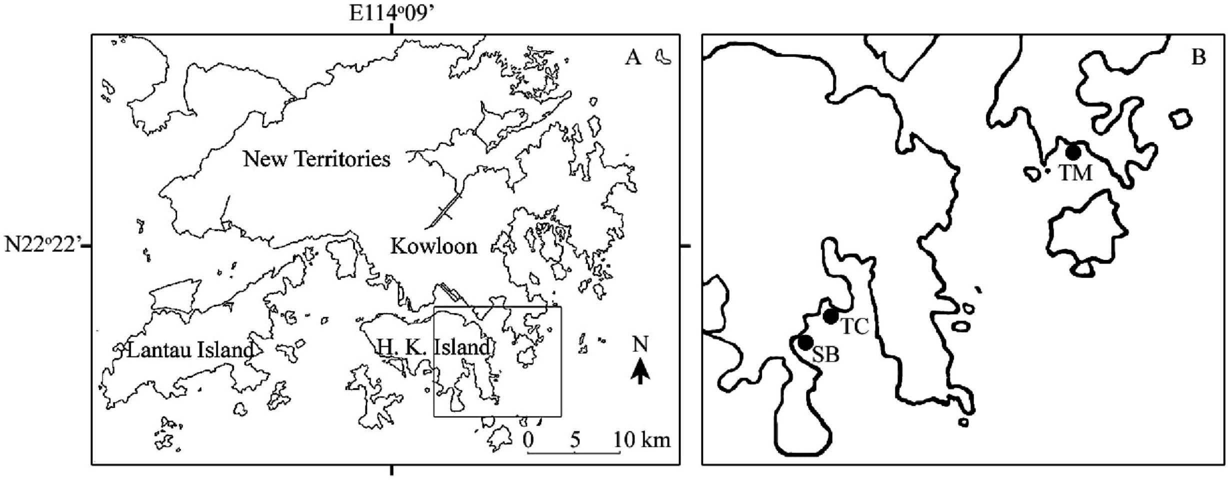

Fig. 1. (A) Map of Hong Kong and (B) the study sites, Turtle Cove (TC), Stanley Bay (SB), and Tai Mui Wan (TM).

(2,589 mm; Hong Kong Observatory 1997–2006 (www.hko.gov.hk); *see* also Dudgeon and Corlett 2004). Litter fall in Hong Kong is higher than in northern temperate latitudes, and Hong Kong's hill streams appear to be relatively poor at retaining detritus (Dudgeon 1982; Lam and Dudgeon 1985). Terrestrial-derived detritus (in the form of dissolved organic matter, particulate organic matter [POM], and leaf litter) is transported by streams to coastal waters during spates and typhoons, providing an additional source of energy to marine consumers. While factors influencing the structure and seasonality of rocky shore communities in Hong Kong have been investigated (e.g., Kaehler and Williams 1996; Wai and Williams 2006; and references therein), little is known about the supply and relative importance of exogenous and endogenous organic sources or the degree to which intertidal and subtidal food webs are dependent on them.

The present study of a coastal ecosystem in the monsoonal tropics aims to identify the potential sources and fate of organic matter using a combination of stable isotope analyses and fatty acid profiles, taking account of potential spatial (between sites) and temporal (before and after the onset of the summer monsoon) variation in supply and utilization. The availability and utilization of algal food sources (phytoplankton, benthic microalgae, and macroalgae), detritus (terrestrial- and macroalgae-derived detritus), and particulate and sedimentary organic matter were investigated in intertidal and subtidal assemblages to reveal the main trophic pathways and determine the relative importance of different energy sources.

## Methods

*Study sites and period*—Sampling was conducted at three semiexposed bays—Turtle Cove (TC), Stanley Bay East (SB), and Tai Mui Wan (TM)—in southeastern Hong Kong (22°22′N, 114°09′E, Fig. 1). Each site received drainage from small hill streams that flowed through shrubland and secondary forest. Samples were collected before and after the onset of the southwestern (summer) monsoon in 2005. During the summer monsoon (June–September), the mean seawater temperature (28°C) and monthly total rainfall (683.6 mm) were much higher than during the northeastern (winter) monsoon (December–March; 17°C and 27.5 mm, respectively; Hong Kong Observatory 2004, 2005 (www.hko.gov.hk)).

*Sampling protocols*—Samples of potential food sources, namely, POM, plankton (a mixture of phytoplankton and zooplankton with size $> 125$ $\mu$m), and sedimentary organic matter (SOM), were collected at each site within 20 m from the shore and streams at each site once before (early May) and monthly after the onset of the summer monsoon (June, July, and August 2005). POM was defined as a mixture of suspended organic materials with particle size $<125$ $\mu$m. Four POM samples were collected by filtering 12 liters of surface seawater through a 125-$\mu$m mesh (to remove zooplankton), followed by a precombusted GF/C filter paper (1.2-$\mu$m pore size, Whatman). Four plankton samples were collected using a plankton net (50-cm diameter, 125-$\mu$m mesh size), towed along the water column, parallel to the shore, for 10 min. Sixteen SOM samples (area $\sim$10 $\times$ 20 cm, depth top 5 cm of the sediments) were collected by scuba divers at approximately 3–5-m water depth at each site; four samples were then pooled (to minimize small-scale spatial variation, which was not of interest in this study) to form replicates for analyses (i.e., $n = 4$ for each site).

The dominant macroalga, *Sargassum hemiphyllum*, was collected in December 2004 and August 2005 representing winter and summer monsoon samples, respectively. For each sampling period, thalli from different individuals were pooled to form replicates for analyses ($n = 4$). *Sargassum* detritus (degrading thalli, $n = 4$) was collected once at two sites (TC and SB) at the onset of the summer monsoon (late May 2005), when the algae started to degrade and the thalli readily detached during gentle wave action. At Turtle Cove, terrestrial detritus (leaf litter, $n = 4$) was collected once by hand at stream outflows after rain in June. All samples were frozen at $-20$°C prior to analysis.

Six species of common, widely distributed consumers, representing four different trophic guilds (grazers, suspension feeders, deposit feeders, and predators), were collected at each site before (early May) and 4 months after (late August) the onset of the summer monsoon. A grazer, *Lunella coronata* (Turbinidae); suspension feeders, *Saccostrea cucullata* (Ostreidae) and *Septifer virgatus* (Mytilidae); and a predator, *Thais clavigera* (Muricidae), were collected at mid–low shore. An echinoid grazer, *Salmacis sphaeroides* (Temnopleuridae), and a deposit feeder, *Holothuria leucospilota* (Holothuriidae), were collected at ~3–5-m depth by scuba divers. Whole-body tissues (with gut contents removed) of bivalves, muscle tissues of gastropods and sea cucumbers, and gonads of sea urchins were used for analysis. Except for the relatively large *Holothuria* where single individuals were used as replicates ($n = 6$), five to six individuals of each species were pooled as a replicate ($n = 4$) for analyses. All samples were frozen at −20°C prior to analysis.

*Stable isotope analysis (SIA)*—Animal tissues were oven dried (for 72 h at 45°C) and ground to a fine powder. Prior to analyses, SOM samples for carbon isotope analysis were treated with an excess volume of 5% HCl to remove carbonates and then dried (for 72 h at 45°C). Aliquots of untreated SOM samples were used for nitrogen isotope analysis. Animal and autotroph samples were not acid treated, as this procedure has been shown to be inappropriate for taxa with low carbonate contents (Ng et al. 2007). The isotopic ratios of dried samples (R = $^{13}C : ^{12}C$ or $^{15}N : ^{14}N$) were determined by the UC Davis Stable Isotope Facility (Department of Plant Sciences, University of California at Davis, Davis, California) and reported in standard delta ($\delta$) notation ($\delta^{13}C$ or $\delta^{15}N$), defined as parts per thousand (‰) deviation from a standard (Vienna Pee Dee belemnite for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$): $\delta^{13}C$ or $\delta^{15}N = ((R_{\text{sample}} : R_{\text{standard}}) - 1) \times 1{,}000$ (Peterson and Fry 1987). The analytical precision (as standard deviation for repeated measurements of the internal standards, $n = 10$) for the measurement was 0.02‰ and 0.17‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Molar carbon to nitrogen (C : N) ratios were also calculated for each sample.

*Fatty acid profiling (FAP)*—Lipids were extracted from aliquots of the samples following the 2 : 1 (volume : volume, v : v) chloroform-methanol method modified from Bligh and Dyer (1959). Fatty acids of total lipids were transesterified to methyl esters with 6% (v : v) sulfuric acid ($H_2SO_4$) in methanol, and all prepared fatty acid methyl esters (FAMEs) were stored in nitrogen at −20°C before analysis. FAP of POM was not performed because of small sample mass. FAMEs were analyzed using gas chromatography equipped with mass spectrometry (GC-MS; Hewlett Packard 6890 series) and separated within a capillary column (Agilent DB-225, 30-m × 0.25-mm inner diameter, 0.25-$\mu$m film thickness). Helium was used as the carrier gas at a constant inlet flow of 1.1 mL min$^{-1}$. After injection (1-$\mu$L sample each time; split ratio = 2 : 1) at 60°C for 3 min, the column temperature was raised to 220°C at 40°C min$^{-1}$ and then held at 220°C for 6 min. The detector and injector were held at 120°C and 220°C, respectively. FAMEs were identified by the GC-MS and also by comparison of GC peaks with the retention times of authentic standards (Supelco and Alltech) using the fatty acid 19 : 0 as an internal standard. Each fatty acid is expressed as a relative percentage of the total fatty acids identified in a sample and designated by shorthand nomenclature X : YnZ, where X is the number of carbon atoms, Y is the number of double bonds, and Z is the position of the ultimate double bond from the terminal methyl group.

*Statistical analyses*—Spatial and temporal differences in stable isotopic values ($\delta^{13}C$ and $\delta^{15}N$) and molar C : N ratios were compared using two-way analysis of variance (ANOVA), followed by Student–Newman–Keuls (SNK) tests for multiple comparisons. For POM, SOM, and plankton, both sampling date (four levels) and site (three levels) were treated as random factors. For *Sargassum* and consumers, sampling period (two levels, winter and summer monsoons, and before and 4 months after the onset of the summer monsoon, respectively) and site (three levels) were treated as fixed and random factors. Prior to analysis, raw data were tested for homogeneity of variance using Cochran's test. If data showed heterogeneous variances and could not be stabilized by transformation, ANOVA was performed on untransformed data, but results were interpreted with a conservative significance level ($\alpha = 0.01$). Simple linear regression analyses, using $\delta^{13}C$, $\delta^{15}N$ values, and C : N ratios as dependent variables and time as a predictor variable, were carried out to investigate the temporal changes in POM, SOM, and plankton over the summer monsoon.

Multiple-source stable isotope mixing models (IsoSource version 1.3.1; Phillips and Gregg 2003) were used to quantify the contribution of various potential food sources to the diet of consumers after the onset of the summer monsoon. The food sources used in each calculation were selected according to the feeding mode of the consumers and the polygon defined by their potentially important foods (Phillips et al. 2005). For POM, SOM, and plankton, mean values of three sampling dates (June, July, and August) were used, which represented the summer monsoon samples. The SIA values of some potential food items, including the mixture of microalgae, cyanobacteria, and bacteria on rock (i.e., biofilm) and on sediment surfaces (i.e., biomat); crustose algae (*Hildenbrandia* spp.); coralline algae; and barnacles (*Tetraclita squamosa*) were obtained from Ng et al. (2007) and Wai et al. (unpubl.). Before calculations, $\delta^{13}C$ and $\delta^{15}N$ values of the consumers were corrected for isotope fractionations of 1‰ and 3‰, respectively (McCutchan et al. 2003). The source increment value was set at 1%. For consumers with mixture isotope values inside the polygon, mass balance tolerance was set at 0.1‰. If the mixture isotopic values of the consumers were at the edge or out of the polygon, tolerance was gradually increased by 0.1‰ up to a maximum of 1.0‰. Feasible contributions of each food source were reported as mean and 1st- and 99th-percentile ranges, where narrow ranges represent better-constrained estimates of source contribution (Phillips and Gregg 2003).

Multivariate analyses were performed to determine spatial and temporal variations in fatty acid compositions

Table 1. Mean values (±SD, $n$=4; except for *Holothuria*, where $n$=6) of $\delta^{13}$C, $\delta^{15}$N, and molar C : N ratio of different groups of food sources and consumers at different sites (Turtle Cove [TC], Stanley Bay [SB], and Tai Mui Wan [TM]), sampled before and 4 months after the onset of the summer monsoon. Particulate organic matter (POM) and sedimentary organic matter (SOM) were sampled monthly from May to August, but only data from May (before) and August (after) are shown. *Sargassum* was sampled in December and August, representing winter (before) and summer (after), respectively. *Sargassum* detritus was sampled in late May and terrestrial detritus in June.

| | Before | | | After | | |
|---|---|---|---|---|---|---|
| | TC | SB | TM | TC | SB | TM |
| $\delta^{13}$C (‰) | | | | | | |
| POM | −17.32±0.21 | −17.20±0.17 | −18.01±0.19 | −21.91±0.36 | −21.35±0.40 | −22.45±0.72 |
| Plankton | −18.48±0.17 | −18.34±0.13 | −16.93±1.23 | −19.35±0.74 | −19.09±0.21 | −22.30±0.59 |
| SOM | −19.32±0.58 | −18.63±0.44 | −19.27±0.60 | −21.71±0.77 | −20.00±1.05 | −19.55±0.37 |
| *Sargassum* | −18.40±0.64 | −17.12±0.29 | −15.39±0.79 | −13.58±0.15 | −13.50±0.23 | −12.10±0.20 |
| *Sargassum* detritus | −17.90±0.08 | −16.27±0.55 | — | — | — | — |
| Terrestrial detritus | — | — | — | −29.93±0.05 | — | — |
| *Saccostrea* | −17.39±0.48 | −18.15±0.26 | −16.26±0.95 | −17.68±0.35 | −17.44±0.10 | −16.70±0.22 |
| *Septifer* | −18.05±0.26 | −18.30±0.35 | −18.31±0.23 | −17.81±0.60 | −17.72±0.30 | −18.04±0.28 |
| *Thais* | −14.57±0.10 | −14.72±0.07 | −14.23±0.09 | −14.55±0.06 | −15.53±0.24 | −14.60±0.20 |
| *Lunella* | −12.53±0.09 | −12.01±0.17 | −11.80±0.20 | −11.61±0.37 | −12.34±0.17 | −11.49±0.28 |
| *Salmacis* | −16.81±0.17 | −17.54±0.18 | −15.86±0.22 | −15.65±0.15 | −15.10±0.53 | −15.48±0.11 |
| *Holothuria* | −13.70±038 | −13.24±0.42 | −13.09±0.44 | −13.04±0.61 | −13.16±0.53 | −12.92±0.44 |
| $\delta^{15}$N (‰) | | | | | | |
| POM | 9.01±0.40 | 8.50±0.33 | 6.44±0.22 | 8.25±1.49 | 6.86±2.33 | 1.48±0.41 |
| Plankton | 12.43±0.52 | 10.92±0.43 | 6.37±0.63 | 9.35±0.19 | 9.02±0.08 | 7.68±0.10 |
| SOM | 6.42±0.51 | 7.48±0.19 | 3.92±2.22 | 6.50±0.46 | 6.61±0.49 | 3.74±1.43 |
| *Sargassum* | 7.65±0.10 | 7.23±0.19 | 7.80±0.14 | 7.23±0.09 | 7.62±0.07 | 7.02±0.20 |
| *Sargassum* detritus | 8.86±0.63 | 8.71±0.36 | — | — | — | — |
| Terrestrial detritus | — | — | — | 0.83±0.27 | — | — |
| *Saccostrea* | 8.23±0.31 | 8.44±0.12 | 8.46±0.47 | 8.68±0.13 | 8.94±0.24 | 8.15±0.09 |
| *Septifer* | 8.14±0.07 | 8.34±0.18 | 8.09±0.21 | 8.60±0.38 | 8.59±0.53 | 8.35±0.28 |
| *Thais* | 11.83±0.14 | 12.17±0.13 | 12.38±0.09 | 11.91±0.26 | 12.44±1.31 | 12.16±0.28 |
| *Lunella* | 10.56±0.12 | 10.28±0.12 | 10.63±0.36 | 10.41±0.24 | 10.21±0.12 | 10.58±0.17 |
| *Salmacis* | 8.40±0.08 | 8.63±0.08 | 8.57±0.14 | 8.56±0.91 | 9.16±0.24 | 8.75±0.24 |
| *Holothuria* | 11.00±0.54 | 11.29±0.48 | 12.02±0.66 | 11.53±1.30 | 10.96±0.53 | 11.53±0.37 |
| C : N ratio | | | | | | |
| POM | 5.70±0.15 | 4.72±0.17 | 4.99±0.09 | 4.07±0.18 | 4.04±0.54 | 4.09±0.80 |
| Plankton | 6.03±0.33 | 6.01±0.25 | 6.44±0.47 | 5.68±0.24 | 5.37±0.10 | 10.05±0.65 |
| SOM | 115.63±30.38 | 93.88±6.40 | 35.73±19.35 | 112.46±13.61 | 90.29±19.26 | 25.56±11.45 |
| *Sargassum* | 18.98±1.29 | 19.79±0.34 | 22.59±2.45 | 20.79±0.91 | 20.60±0.29 | 21.11±0.30 |
| *Sargassum* detritus | 10.66±0.64 | 11.62±0.39 | — | — | — | — |
| Terrestrial detritus | — | — | — | 36.48±2.50 | — | — |
| *Saccostrea* | 5.35±0.60 | 6.52±0.29 | 4.85±0.50 | 5.66±0.30 | 5.35±0.30 | 6.17±0.30 |
| *Septifer* | 5.52±0.37 | 5.59±0.38 | 5.69±0.69 | 5.09±0.67 | 5.25±0.55 | 5.85±0.53 |
| *Thais* | 5.75±0.16 | 5.25±0.16 | 5.49±0.41 | 5.14±0.39 | 6.01±1.82 | 5.45±0.08 |
| *Lunella* | 3.87±0.03 | 3.88±0.05 | 3.90±0.06 | 3.85±0.11 | 3.89±0.07 | 3.83±0.07 |
| *Salmacis* | 7.48±0.68 | 7.69±0.85 | 7.60±0.57 | 5.45±0.40 | 5.21±0.57 | 4.59±0.29 |
| *Holothuria* | 4.16±0.13 | 4.16±0.08 | 4.01±0.09 | 4.03±0.24 | 4.03±0.13 | 3.96±0.16 |

(relative % weight of 36 fatty acids from three sites, $n$ = 4 for each site) of food sources (no data for POM) and consumers. Plankton and SOM were analyzed separately. All benthic consumers were analyzed as a whole group to produce a generalized picture of the spatial and temporal variations in FAP compositions of the consumers. All multivariate analyses were based on Bray–Curtis dissimilarity matrices calculated from square-root-transformed data. To visualize multivariate patterns, nonmetric multidimensional scaling (nMDS) ordinations were performed on FAP composition data of the groups using PRIMER 6 (PRIMER-E Ltd). Two-way crossed analysis of similarities (ANOSIM) was used to investigate the observed patterns of spatial and temporal variation (as described previously), with test statistics computed after 4,999 permutations. FAP biomarkers used to identify food sources were based on the reviews by Meziane et al. (1997), Kharlamenko et al. (2001), and Mfilinge et al. (2005). Spatial and temporal differences in the FAP biomarkers were compared using two-way ANOVA as described previously.

## Results

*SIA of food sources*—The $\delta^{13}$C values of SOM were within a range from −21.71 to −17.52‰, while $\delta^{15}$N values ranged from 3.74‰ to 7.54‰ and C : N ratios from 35.73 to 137.76 (Table 1). The $\delta^{13}$C, $\delta^{15}$N, and molar C : N ratio of SOM showed significant interactions between sampling date and site (Table 2). Regression analyses revealed a significant negative relationship between $\delta^{13}C$ of SOM and time ($r^2 = 0.16$, $F_{1,46} = 8.69$, $p < 0.01$) but no clear relationship for $\delta^{15}N$ or C : N ratio with time.

Mean values of $\delta^{13}C$, $\delta^{15}N$, and C : N ratio of POM were spatially and temporally variable, ranging from −22.45‰ to 16.65‰, 1.48‰ to 9.01‰, and 3.49 to 4.88, respectively (Table 1). All values of POM showed significant interactions between sampling date and site and decreased significantly after the onset of the summer monsoon (Tables 1, 2). The depletion in $\delta^{13}C$ values of POM coincided with higher total rainfall before sampling in August (Fig. 2). There was a gradual decrease in $\delta^{13}C$, $\delta^{15}N$, and C : N ratio of POM after the onset of the summer monsoon, and significant negative relationships with time were detected (regression analyses, all with $p < 0.01$: $\delta^{13}C$, $r^2 = 0.606$, $F_{1,46} = 70.68$; $\delta^{15}N$, $r^2 = 0.156$, $F_{1,46} = 8.47$; C : N ratio, $r^2 = 0.185$, $F_{1,\,46} = 10.46$).

Values of $\delta^{13}C$, $\delta^{15}N$, and C : N ratios of plankton were highly variable, ranging from −22.30‰ to −16.93‰, 6.37‰ to 12.43‰, and 5.37 to 10.05, respectively; all values showed significant interactions between sampling date and site (Tables 1, 2). Regression analyses revealed a significant negative relationship between plankton $\delta^{13}C$ and time ($r^2 = 0.24$, $F_{1,46} = 14.79$, $p < 0.001$) but no clear relationship for $\delta^{15}N$ or C : N ratio.

The $\delta^{13}C$ values of SOM, POM, and plankton were within the same range from −22.45‰ to −16.65‰ and positively correlated with each other. The $\delta^{13}C$ values of POM were correlated with plankton (Spearman's correlation coefficient [$r_s$] = 0.545, $p < 0.001$) and SOM ($r_s$ = 0.619, $p < 0.001$), which was also correlated with plankton ($r_s$ = 0.453, $p < 0.001$).

Terrestrial detritus had the most depleted $\delta^{13}C$ (−29.93‰, mean) and $\delta^{15}N$ values (0.83‰), with relatively high C : N ratios (36.48; Table 1). The marine macroalga *Sargassum* exhibited intermediate $\delta^{13}C$ (−18.40‰ to −12.10‰) and $\delta^{15}N$ values (7.02–7.80‰) when compared with other sources (Table 1). Values of $\delta^{13}C$, $\delta^{15}N$, and C : N ratio of *Sargassum* showed significant interactions with sampling period and site (Table 2). SNK tests showed that the $\delta^{13}C$ value of *Sargassum* was significantly enriched (by ~4‰) at all sites after the onset of the summer monsoon, while no consistent pattern was observed for values of $\delta^{15}N$ and C : N ratio (Tables 1, 2). *Sargassum* detritus was more enriched in $\delta^{13}C$ (by ~0.5–0.9‰) and $\delta^{15}N$ (by ~0.5–1.2‰) but greatly depleted in C : N ratio (by ~8 units) when compared with fresh *Sargassum* from the same site (Table 1).

*SIA of consumers*—The suspension feeders *Septifer* and *Saccostrea* showed the most depleted $\delta^{13}C$ values among consumers, followed by *Salmacis*, *Thais*, *Holothuria*, and *Lunella* (Table 1; Fig. 3). The predatory gastropod, *Thais*, had the most enriched $\delta^{15}N$ values, followed by *Holothuria*, *Lunella*, *Salmacis*, *Saccostrea*, and *Septifer*, and their C : N ratios ranged from 3.83 (*Lunella*) to 7.69 (*Salmacis*; Table 1). Of these, only *Holothuria* showed no spatial or temporal differences in $\delta^{13}C$, $\delta^{15}N$, and C : N ratio (Table 2). For $\delta^{13}C$ values, *Lunella*, *Salmacis*, and *Thais*

Table 2. *F*-ratios from analysis of variance (ANOVA) to investigate variation in $\delta^{13}C$, $\delta^{15}N$, and C : N ratios of different groups of food sources and consumers between sampling period (Se) and site (Si). For particulate organic matter (POM), plankton, and sedimentary organic matter (SOM), data for Se comparison were four random dates (May–August); degrees of freedom (df) for Se, Si, Se × Si, and residual are 3, 2, 6, and 36, respectively. For *Sargassum*, data used for Se comparison were winter (December) and summer (August). For the consumers, data used for Se comparison were before (early May) and 4 months after (late August) the onset of summer monsoon. For *Sargassum* and all consumers (except *Holothuria*), df for Se, Si, Se × Si, and residual are 1, 2, 2, and 18, respectively. For *Holothuria*, df for Se, Si, Se × Si, and residual are 1, 2, 2, and 30, respectively. Significant differences between sites are indicated by bold and asterisk(s): * ($p<0.05$); ** ($p<0.01$); *** ($p<0.001$). Data were not transformed prior to analysis. If Cochran's test for homogeneity: # indicates the test was violated, $p<0.05$. Results of ANOVA and Student–Newman–Keuls tests were interpreted at a significance level of $p = 0.01$.

| | Source of variation | | |
|---|---|---|---|
| | Se | Si | Se × Si |
| Food source variables | | | |
| POM | | | |
| $\delta^{13}C$ | **18.88**** | 0.47 | **18.80***** |
| $\delta^{15}N$ | 1.12 | 0.63 | **19.75***** |
| C : N | 4.46 | 0.10 | **8.92***** |
| Plankton | | | |
| $\delta^{13}C$ | 3.36 | 0.01 | **20.56***** |
| $\delta^{15}N$ | 0.80 | 0.61 | **74.16***** |
| C : N | 0.45 | 1.40 | **29.32***** |
| SOM | | | |
| $\delta^{13}C$ | **5.46*** | **9.18*** | **4.11**** |
| $\delta^{15}N$ | 1.75 | #8.13* | **3.40**** |
| C : N | 0.97 | **11.05**** | **5.28***** |
| *Sargassum* | | | |
| $\delta^{13}C$ | **70.75*** | **51.69***** | **6.33**** |
| $\delta^{15}N$ | 0.64 | 0.09 | **37.02***** |
| C : N | 0.20 | **6.48**** | #3.57* |
| Consumer variables | | | |
| *Saccostrea* | | | |
| $\delta^{13}C$ | 0.00 | **16.80***** | 3.38 |
| $\delta^{15}N$ | 0.66 | **4.46*** | **6.19**** |
| C : N | 0.04 | 3.03 | **19.29***** |
| *Septifer* | | | |
| $\delta^{13}C$ | 11.33 | 0.98 | 0.55 |
| $\delta^{15}N$ | **21.31*** | 1.27 | 0.30 |
| C : N | 1.21 | 1.58 | 0.69 |
| *Thais* | | | |
| $\delta^{13}C$ | 2.58 | **53.57***** | **16.40***** |
| $\delta^{15}N$ | 0.09 | 1.45 | 0.38 |
| C : N | 0.01 | 0.13 | 1.57 |
| *Lunella* | | | |
| $\delta^{13}C$ | 0.67 | **12.08***** | **14.74***** |
| $\delta^{15}N$ | 9.64 | **6.15**** | 0.14 |
| C : N | 1.39 | 0.40 | 0.58 |
| *Salmacis* | | | |
| $\delta^{13}C$ | 4.95 | **13.98***** | **30.20***** |
| $\delta^{15}N$ | 5.99 | **9.04**** | 2.27 |
| C : N | **76.90*** | 1.04 | 1.42 |
| *Holothuria* | | | |
| $\delta^{13}C$ | 2.91 | 1.78 | 1.28 |
| $\delta^{15}N$ | 0.09 | 2.77 | 1.79 |
| C : N | 12.58 | 3.00 | 0.25 |

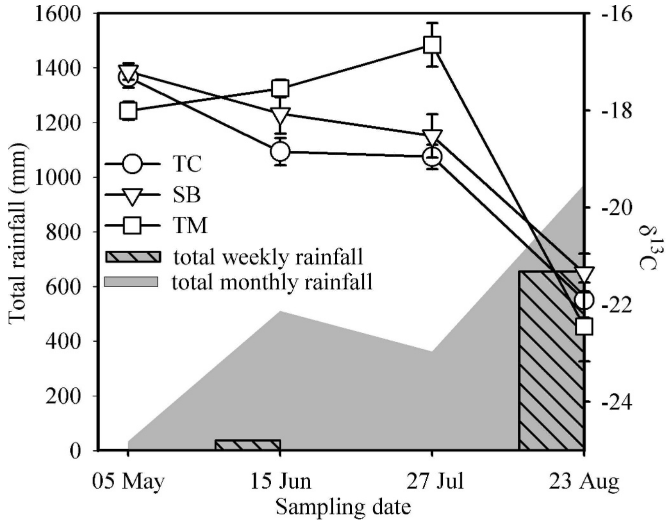

Fig. 2. Mean $\delta^{13}C$ values (‰, ±SD, $n = 4$) of particulate organic matter (POM) and mean total rainfall (mm) monthly and a week before the sampling dates during the study period.

exhibited a significant interaction between time (Se) and site (Si), while *Saccostrea* showed a significant site difference, and *Septifer* showed no difference with site or time (Table 2). The significant Se × Si interaction was mainly a result of variable patterns of $\delta^{13}C$ enrichment at different sites. SNK tests showed that *Lunella* (in TC) and *Salmacis* (in TC and SB) were more enriched in $\delta^{13}C$ after the onset of the summer monsoon (Tables 1, 2). *Thais*, in contrast, had more depleted $\delta^{13}C$ values (in SB and TM) (Table 1). Only *Saccostrea* (in TC and SB) and *Septifer* (in all sites) showed significant enrichment in $\delta^{15}N$ values after the onset of the summer monsoon, while C : N ratios of *Salmacis* declined at all sites over the same period (Tables 1, 2).

Four months after the onset of the summer monsoon, the SIA mixing models (i.e., IsoSource) estimates of feasible contribution of POM to the suspension feeders, *Saccostrea* and *Septifer*, were similar (between 36% and 93%, 1st–99th-percentile ranges), followed by plankton, *Sargassum* detritus, and terrestrial detritus (Fig. 3A,B). Isotope ratios suggest that *Thais* gained energy mainly from *Saccostrea*, *Septifer*, and *Tetraclita* (between 0% and 55%; Fig. 3C). The feasible contributions of *Sargassum* and biofilm were similar for the grazer *Lunella* (between 0% and 83%), while noncoralline crustose algae played a lesser role (0–64%), followed by smaller contributions of terrestrial detritus, *Sargassum* detritus, and crustose coralline algae (Fig. 3D). The feasible contributions of biomat to the echinoid grazer *Salmacis* were the highest (19–71%), followed by *Sargassum* and its detritus (cumulatively 13–60%), terrestrial detritus, and SOM (Fig. 3E). Deposit-feeding *Holothuria* evidently relied mainly on biomat (47–71%) and *Sargassum* detritus (26–52%), followed by SOM and terrestrial detritus (Fig. 3F).

*FAP of food sources*—A relatively high proportion of saturated fatty acids (SFA) was observed in plankton (~45%), SOM (55%), *Sargassum* detritus (~40%), and terrestrial detritus (~71%; Table 3). All but plankton were characterized by high percentages of bacterial (detrital) biomarkers (BaFA), including odd-branched carbon fatty acids (i15:0, a15:0, and i17:0) and 18:1n7. The mean percentages of BaFA in these three sources were 17.1%, 11.6%, and 8.3%, respectively, and monounsaturated fatty acids (MUFA) made up ~17–30% of the total fatty acids. Low percentages (<10%) of polyunsaturated fatty acids (PUFA) were detected in both SOM and terrestrial detritus, while a higher abundance (~25%) was found in *Sargassum* detritus (Table 3). Fresh *Sargassum* was characterized by a high proportion of PUFA (~50%), of which 20:4n6 contributed ~19%, followed by essential fatty acids (EFA; 18:2n6 and 18:3n3) and 20:5n3 (Table 3). The mean total percentage of PUFA, EFA, and 20:4n6 in fresh *Sargassum*, however, significantly decreased from ~50% to ~25%, ~16% to ~10%, and ~19% to ~12% after the onset of the summer monsoon (Tables 3, 4). When compared with fresh *Sargassum*, SFA, MUFA, and BaFA were, nevertheless, significantly enriched in *Sargassum* detritus ($t$-tests, df = 6, $p < 0.001$).

FAP of SOM and plankton before (i.e., in May) were distinct from those after the onset of the summer monsoon, but site differences in FA compositions were inconsistent over these periods (Fig. 4A,B). There were significant temporal (SOM, ANOSIM Global $R = 0.755$, $p < 0.001$; plankton, $R = 0.982$, $p < 0.001$) and spatial (SOM, $R = 0.558$, $p < 0.001$; plankton $R = 0.711$, $p < 0.001$) variations in FA composition of both SOM and plankton. BaFA, SFA, PUFA, and 22:6n3 of SOM exhibited significant temporal variation (Table 4). While a relatively higher percentage of PUFA was found before the summer monsoon in May, higher percentages of BaFA and SFA were observed in SOM in June and subsequently (Fig. 5A).

The percentage of various FA biomarkers or ratios in plankton were highly variable (significant interactions; Table 4) but showed no general trends. While the FAP of plankton samples from June and July were characterized by a high abundance of diatom biomarkers (16 : 1 and 20 : 5), those taken in August had a relatively high percentage of BaFA, dinoflagellate biomarker (22:6n3), and zooplankton biomarkers (20 : 1 and 22 : 1; Fig. 5B).

*FAP of consumers*—SFA made up ~23–40% of the total fatty acids of consumers (Table 3), with 16 : 0 being dominant, followed by 14 : 0 and 18 : 0. MUFA constituted ~35% of the total fatty acids of *Holothuria* (Table 3) but only 10–20% in the other consumers in which 20 : 1 and 18:1n9 were the most abundant MUFA. Long-chain MUFA (24:1n9) were abundant (~10%) in *Holothuria* but present only in trace amounts in other consumers. All consumers exhibited high levels of PUFA (>35%; Table 3) and especially high levels of C20 and C22 PUFA. PUFA 22:6n3, which is specific to dinoflagellates, was abundant in the suspension feeders *Saccostrea* and *Septifer* and their predator *Thais*. The *Holothuria*, *Lunella*, and *Thais* exhibited high levels of PUFA, 20:4n6, specific to macroalgae and protozoa. Both PUFA 20:4n6 and 20:5n3 (the latter of which is a diatom biomarker) were abundant in the sea urchin, *Salmacis* (Table 3).

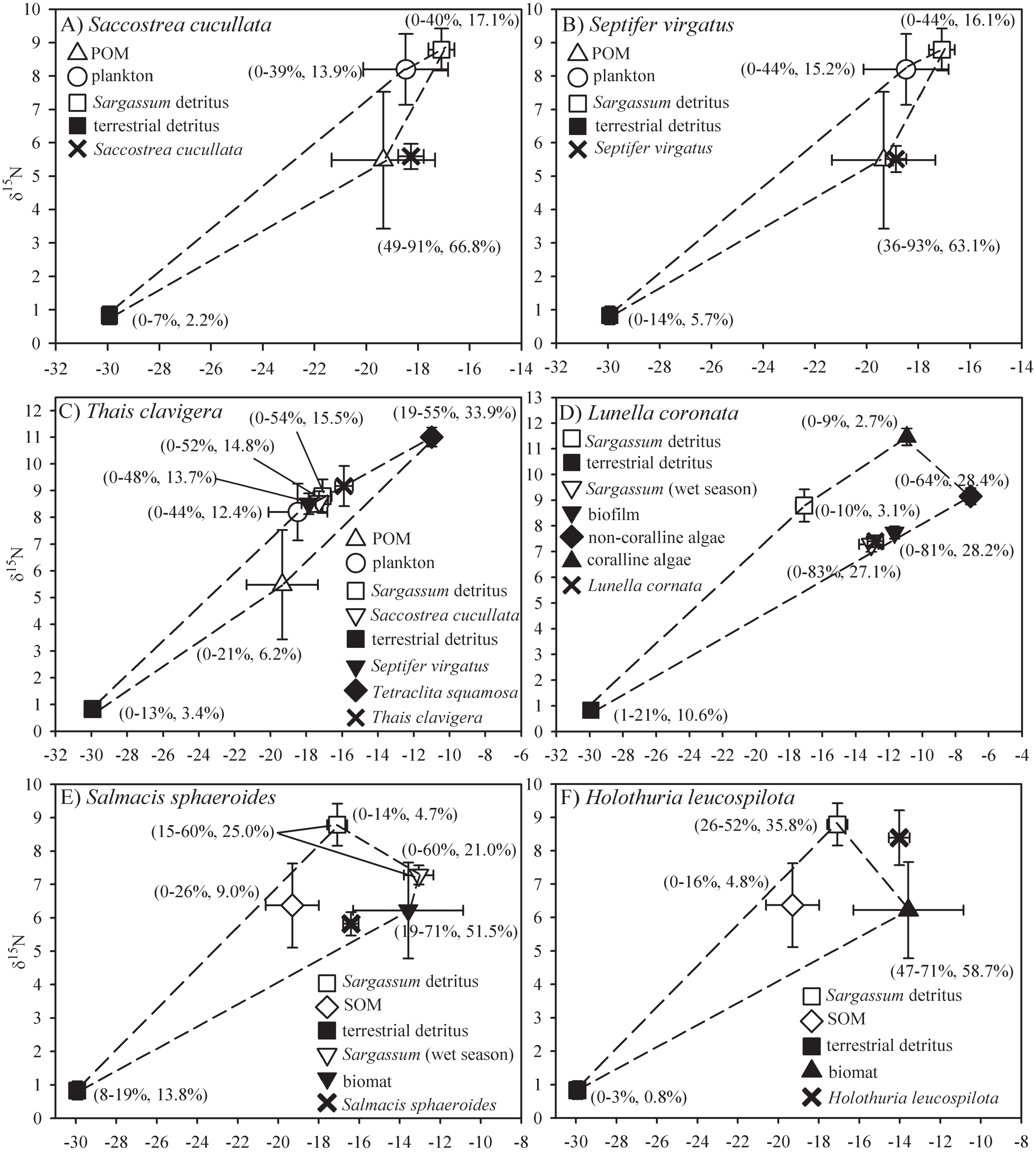

Fig. 3. Mean $\delta^{13}$C and $\delta^{15}$N values (‰, ±SD) of the potential sources for (A) *Saccostrea cucullata*, (B) *Septifer virgatus*, (C) *Thais clavigera*, (D) *Lunella coronata*, (E) *Salmacis sphaeroides*, and (F) *Holothuria leucospilota* during the summer monsoon. $\delta^{13}C$ and $\delta^{15}$N values of the consumers are corrected by 1‰ and 3‰ trophic fractionation, respectively (McCutchan et al. 2003). The values of contribution (1st–99th percentiles, mean) calculated from the IsoSource program are shown in parentheses. For particulate organic matter (POM), plankton, and sedimentary organic matter (SOM), mean values from June, July, and August were used for calculation. Note scales of axis are different.

Table 3. Mean weight % (±SD, $n=4$ for *Sargassum* detritus and terrestrial detritus; $n=18$ for *Holothuria*; and $n=12$ for the other groups) of selected fatty acid variables in total lipids of different groups of food sources and consumers before (early May) and after (late August) the onset of the summer monsoon. Sum of saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), polyunsaturated fatty acids (PUFA), and individual fatty acids (FA), which made up the FA biomarkers in Fig. 5, are shown. *Sargassum* detritus was sampled in late May and terrestrial detritus in June. SOM = sedimentary organic matter.

| Fatty acid biomarkers | | Plankton | SOM | *Sargassum* | *Saccostrea* | *Septifer* | *Thais* | *Lunella* | *Salmacis* | *Holothuria* | *Sargassum* detritus | Terrestrial detritus |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Before the summer monsoon | | | | | | | | | | | | |
| ΣSFA | | 54.46±2.63 | 52.44±3.24 | 29.05±1.42 | 37.77±2.92 | 39.92±2.17 | 31.42±0.98 | 41.27±1.02 | 33.10±0.88 | 24.06±1.88 | — | — |
| ΣMUFA | | 23.02±3.85 | 29.42±2.96 | 21.23±1.50 | 14.88±1.08 | 19.97±1.11 | 11.46±0.50 | 11.42±0.58 | 20.69±1.08 | 37.17±1.22 | — | — |
| ΣPUFA | | 20.36±6.34 | 9.22±2.73 | 49.58±1.87 | 45.61±3.53 | 37.56±2.56 | 56.05±1.30 | 44.29±0.82 | 44.43±1.42 | 35.33±2.36 | — | — |
| Diatom FA | 16:1 | 11.97±3.27 | 10.43±2.28 | 7.41±0.34 | 2.05±0.63 | 4.84±0.90 | 0.61±0.08 | 1.46±0.17 | 4.46±0.43 | 3.75±2.48 | — | — |
| | 20:5n3 | 4.20±0.86 | 1.39±0.55 | 10.63±3.26 | 6.26±0.96 | 7.78±1.43 | 5.80±0.32 | 6.61±0.51 | 13.36±2.71 | 7.29±6.57 | — | — |
| Bacterial FA (BaFA) | i15:0 | 0.71±0.27 | 3.73±0.46 | 0.09±0.03 | 0.38±0.08 | 0.55±0.09 | 0.22±0.11 | 0.31±0.02 | 0.54±0.06 | 1.09±1.14 | — | — |
| | a15:0 | 0.46±0.17 | 2.09±0.38 | 0.00±0.00 | 0.32±0.10 | 0.00±0.00 | 0.04±0.10 | 0.25±0.02 | 0.29±0.02 | 0.62±0.71 | — | — |
| | i17:0 | 0.53±0.14 | 1.52±0.20 | 0.02±0.04 | 0.65±0.09 | 1.36±0.23 | 0.50±0.05 | 1.71±0.17 | 0.50±0.10 | 0.95±1.01 | — | — |
| | 18:1n7 | 1.99±0.36 | 8.19±1.51 | 0.33±0.17 | 1.61±0.28 | 3.59±0.39 | 0.50±0.05 | 2.23±0.35 | 3.69±0.14 | 2.25±2.03 | — | — |
| Essential FA (EFA) | 18:2n6 | 1.19±0.23 | 1.13±0.21 | 5.35±0.18 | 1.53±0.49 | 1.92±0.41 | 2.10±0.17 | 3.89±0.16 | 1.00±0.09 | 0.98±0.88 | — | — |
| | 18:3n3 | 0.84±0.20 | 0.45±0.08 | 11.20±0.84 | 1.35±0.56 | 2.43±0.59 | 0.91±0.19 | 2.03±0.51 | 1.18±0.11 | 0.59±0.55 | — | — |
| Dinoflagellate FA | 22:6n3 | 11.42±6.10 | 1.80±2.21 | 0.00±0.00 | 24.99±3.22 | 16.56±2.22 | 17.95±1.68 | 3.07±0.56 | 7.80±3.38 | 1.59±1.43 | — | — |
| Zooplankton ΣFA | 20:1 | 1.61±0.29 | 2.26±0.76 | 2.05±0.34 | 5.78±0.53 | 7.59±0.65 | 5.52±0.20 | 2.68±0.19 | 6.36±0.27 | 12.65±13.13 | — | — |
| | Σ22:1 | 0.79±0.18 | 0.23±0.22 | 1.42±0.11 | 0.30±0.15 | 0.42±0.21 | 1.00±0.27 | 0.41±0.43 | 2.44±0.24 | 5.16±4.84 | — | — |
| FA for macroalgae and protozoa | 20:4n6 | 0.75±0.09 | 1.88±0.65 | 19.36±1.14 | 3.08±1.50 | 2.28±0.52 | 12.73±0.81 | 16.38±1.44 | 10.17±0.36 | 19.75±22.61 | — | — |
| After the onset of the summer monsoon | | | | | | | | | | | | |
| ΣSFA | | 35.86±7.20 | 61.87±6.01 | 45.57±2.66 | 37.89±1.88 | 38.68±1.59 | 33.26±1.10 | 41.07±1.19 | 32.85±1.83 | 23.11±1.16 | 39.53±1.02 | 71.33±0.86 |
| ΣMUFA | | 44.94±5.37 | 25.85±5.71 | 23.13±1.97 | 17.54±1.05 | 21.56±1.65 | 14.99±0.83 | 13.41±0.61 | 21.13±0.75 | 35.80±1.67 | 29.34±0.81 | 17.70±0.42 |
| ΣPUFA | | 17.51±3.38 | 2.41±0.47 | 30.98±3.48 | 42.69±2.85 | 36.78±2.83 | 50.30±1.60 | 42.49±0.87 | 44.15±1.85 | 37.21±1.87 | 25.00±0.27 | 5.80±0.31 |
| Diatom FA | 16:1 | 36.28±8.16 | 11.50±2.91 | 10.01±3.18 | 4.04±0.86 | 5.80±0.84 | 0.77±0.22 | 1.40±0.29 | 3.96±0.69 | 2.48±0.81 | 6.77±0.15 | 6.05±0.29 |
| | 20:5n3 | 8.90±3.51 | 0.17±0.19 | 3.75±0.24 | 7.82±2.11 | 8.57±1.56 | 4.83±1.49 | 4.54±0.41 | 12.79±3.43 | 6.57±1.28 | 3.07±0.05 | 0.95±0.08 |
| BaFA | i15:0 | 0.59±0.26 | 4.34±0.37 | 0.00±0.00 | 0.40±0.03 | 0.61±0.07 | 0.29±0.03 | 0.30±0.03 | 0.55±0.07 | 1.14±0.23 | 2.41±0.04 | 1.90±0.15 |
| | a15:0 | 0.38±0.11 | 2.22±0.29 | 0.00±0.00 | 0.27±0.03 | 0.00±0.00 | 0.28±0.03 | 0.20±0.06 | 0.31±0.03 | 0.71±0.12 | 2.00±0.03 | 1.04±0.05 |
| | i17:0 | 0.38±0.12 | 1.67±0.22 | 0.22±0.52 | 0.81±0.06 | 1.66±0.26 | 0.57±0.07 | 1.86±0.15 | 0.55±0.07 | 1.01±0.15 | 0.98±0.02 | 1.18±0.04 |
| | 18:1n7 | 3.06±1.40 | 7.44±2.37 | 0.69±0.09 | 2.79±0.50 | 3.85±0.29 | 1.01±0.33 | 2.71±0.40 | 4.52±0.68 | 2.03±0.41 | 5.29±0.22 | 3.14±0.57 |
| EFA | 18:2n6 | 1.72±0.35 | 1.03±0.29 | 4.57±0.77 | 1.37±0.18 | 1.62±0.13 | 1.98±0.20 | 3.55±0.29 | 0.77±0.11 | 0.88±0.15 | 1.72±0.10 | 2.46±0.12 |
| | 18:3n3 | 0.56±0.06 | 0.35±0.12 | 6.25±1.56 | 0.96±0.13 | 1.71±0.19 | 0.93±0.23 | 2.10±0.46 | 0.85±0.17 | 0.55±0.09 | 2.47±0.05 | 1.35±0.09 |
| Dinoflagellate FA | 22:6n3 | 3.08±0.80 | 0.00±0.00 | 0.99±0.65 | 20.97±3.85 | 14.91±3.45 | 13.50±2.16 | 2.01±0.72 | 6.68±1.29 | 1.43±0.16 | 9.96±0.17 | 0.00±0.00 |
| Zooplankton FA | Σ20:1 | 1.18±0.31 | 0.68±0.28 | 2.31±0.33 | 6.55±0.25 | 7.66±0.76 | 8.27±0.46 | 4.48±0.16 | 6.67±0.61 | 13.13±0.91 | 3.07±0.08 | 0.00±0.00 |
| | Σ22:1 | 0.05±0.17 | 0.04±0.11 | 1.24±0.20 | 0.42±0.04 | 0.56±0.49 | 0.90±0.29 | 0.57±0.47 | 2.62±0.24 | 4.84±0.44 | 3.09±0.13 | 0.00±0.00 |
| FA for macroalgae and protozoa | 20:4n6 | 0.94±0.27 | 0.41±0.10 | 12.44±1.76 | 2.94±0.21 | 2.85±0.31 | 11.86±0.60 | 16.22±0.83 | 11.99±2.05 | 22.61±1.75 | 4.83±0.11 | 1.04±0.12 |

Table 4. *F*-ratios from ANOVA to investigate variation in weight percentage of total fatty acid (FA) of sum of (A) saturated fatty acids (SFA), (B) monounsaturated fatty acids (MUFA), (C) polyunsaturated fatty acids (PUFA), (D) diatom FA (Σ[16 : 1 and 20:5n3]), (E) bacterial FA(BaFA, Σ[i- and a15:0, i17:0, and 18:1n7]), (F) essential FA (EFA, Σ[18:2n6 and 18:3n3]), (G) dinoflagellate FA (22:6n3), (H) zooplankton FA (Σ[20 : 1 and 22 : 1]), and (I) 20:4n6. NA = not applicable. SOM = sedimentary organic matter. Significant differences between sites are indicated by bold and asterisk(s): * ($p<0.05$); ** ($p<0.01$); *** ($p<0.001$). *See* Table 2 for symbols, abbreviations, and details in ANOVA.

| | Source of variation | | |
|---|---|---|---|
| Variables | Se | Si | Se × Si |
| Plankton | | | |
| (A) SFA | #7.14* | 0.25 | **8.23*** ** |
| (B) MUFA | **28.74*** ** | 1.99 | **7.45*** ** |
| (C) PUFA | **17.05** ** | 0.62 | **19.65*** ** |
| (D) Diatom FA | **15.98** ** | 0.98 | **20.37*** ** |
| (E) BaFA | 9.44 | 3.14 | **11.97*** ** |
| (F) EFA | **16.67** ** | 2.67 | **7.01*** ** |
| (G) Dinoflagellate FA | **6.04*** | 0.37 | **51.31*** ** |
| (H) Zooplankton FA | **320.27*** ** | 1.09 | #3.01* |
| (I) 20:4n6 | **62.03*** ** | 0.04 | **8.03*** ** |
| SOM | | | |
| (A) SFA | **18.01** ** | **15.38** ** | 1.25 |
| (B) MUFA | 3.88 | **10.33*** | 1.65 |
| (C) PUFA | **86.15*** ** | **6.96*** | 0.62 |
| (D) Diatom FA | 1.78 | **11.54** ** | 1.97 |
| (E) BaFA | **8.78*** | 3.55 | 1.32 |
| (F) EFA | 3.55 | **6.02*** | 0.59 |
| (G) Dinoflagellate FA | **10.02** ** | 1.52 | 0.73 |
| (H) Zooplankton FA | **12.45** ** | 2.10 | **3.70** ** |
| (I) 20:4n6 | **19.78** ** | **6.35*** | **2.71*** |
| *Sargassum* | | | |
| (A) SFA | **165.79** ** | #4.04* | 3.21 |
| (B) MUFA | 4.31 | **26.70*** ** | **6.28** ** |
| (C) PUFA | #90.26* | **9.53** ** | **6.79** ** |
| (D) Diatom FA | NA | NA | NA |
| (E) BaFA | NA | NA | NA |
| (F) EFA | #21.05* | **48.17*** ** | **21.47*** ** |
| (G) Dinoflagellate FA | NA | NA | NA |
| (H) Zooplankton FA | NA | NA | NA |
| (I) 20:4n6 | #30.13* | 0.64 | **9.05** ** |
| *Saccostrea* | | | |
| (A) SFA | 0.00 | 3.37 | **6.21** ** |
| (B) MUFA | **23.31*** | **8.47** ** | 2.97 |
| (C) PUFA | 1.69 | 3.44 | **4.55*** |
| (D) Diatom FA | 3.82 | **15.71*** ** | **12.57*** ** |
| (E) BaFA | **44.98*** | **8.61** ** | 3.23 |
| (F) EFA | 1.11 | **54.39*** ** | **21.59*** ** |
| (G) Dinoflagellate FA | 3.10 | **13.98*** ** | **6.71*** ** |
| (H) Zooplankton FA | 9.28 | 0.87 | **3.95*** |
| (I) 20:4n6 | 0.03 | **13.79*** ** | **13.37*** ** |
| *Septifer* | | | |
| (A) SFA | 8.87 | **4.61*** | 0.57 |
| (B) MUFA | 4.42 | **5.06*** | 2.87 |
| (C) PUFA | 0.28 | **7.59** ** | 2.11 |
| (D) Diatom FA | 2.35 | **9.40** ** | 3.38 |
| (E) BaFA | 2.36 | **6.99** ** | **12.28*** ** |
| (F) EFA | 3.39 | **48.59*** ** | **27.34*** ** |
| (G) Dinoflagellate FA | 1.44 | **30.11*** ** | **5.04*** |
| (H) Zooplankton FA | 0.57 | 2.75 | 0.96 |
| (I) 20:4n6 | 7.18 | **24.81*** ** | **5.27*** |
| *Thais* | | | |
| (A) SFA | **751.89*** ** | **4.59*** | 0.01 |
| (B) MUFA | **148.76** ** | **25.88*** ** | **3.73*** |
| (C) PUFA | **622.03** ** | **12.53*** ** | 0.30 |
| (D) Diatom FA | 0.41 | **40.30*** ** | **66.60*** ** |
| (E) BaFA | 16.54 | **7.62** ** | **17.55*** ** |
| (F) EFA | 0.76 | **107.05*** ** | **8.19** ** |
| (G) Dinoflagellate FA | **69.37*** | **60.29*** ** | 3.01 |
| (H) Zooplankton FA | **876.32*** ** | **10.73*** ** | 0.15 |
| (I) 20:4n6 | 3.33 | **7.24** ** | #5.20* |
| *Lunella* | | | |
| (A) SFA | 0.14 | **6.53** ** | 2.42 |
| (B) MUFA | **126.99** ** | **4.22*** | 0.68 |
| (C) PUFA | **24.03*** | 2.07 | 1.28 |
| (D) Diatom FA | **524.54** ** | **14.25*** ** | 0.42 |
| (E) BaFA | 7.16 | **22.82*** ** | 3.55 |
| (F) EFA | 0.30 | **68.99*** ** | **37.21*** ** |
| (G) Dinoflagellate FA | 2.71 | 1.89 | **12.56*** ** |
| (H) Zooplankton FA | **66.21*** | 0.12 | 1.82 |
| (I) 20:4n6 | 0.03 | **4.34*** | **6.97** ** |
| *Salmacis* | | | |
| (A) SFA | 0.04 | **13.65*** ** | **17.45*** ** |
| (B) MUFA | 1.04 | **20.50*** ** | **3.90*** |
| (C) PUFA | 0.03 | **7.99** ** | **22.31*** ** |
| (D) Diatom FA | **70.40*** | **79.59*** ** | 0.08 |
| (E) BaFA | 5.99 | **9.30** ** | **12.47*** ** |
| (F) EFA | 7.25 | 1.37 | **10.75*** ** |
| (G) Dinoflagellate FA | 0.15 | **30.04*** ** | **103.61*** ** |
| (H) Zooplankton FA | 2.01 | **6.10** ** | 2.82 |
| (I) 20:4n6 | 1.59 | **33.85*** ** | **47.68*** ** |
| *Holothuria* | | | |
| (A) SFA | 2.19 | 1.73 | 1.66 |
| (B) MUFA | **19.30*** | **4.74*** | 0.48 |
| (C) PUFA | 3.83 | 0.96 | 1.92 |
| (D) Diatom FA | **153.92*** ** | **7.76** ** | 0.01 |
| (E) BaFA | 0.00 | **9.98** ** | **4.53*** |
| (F) EFA | 0.67 | **22.75*** ** | **9.02*** ** |
| (G) Dinoflagellate FA | **19.86*** | 2.99 | 0.55 |
| (H) Zooplankton FA | 0.28 | **5.50** ** | 0.82 |
| (I) 20:4n6 | 6.96 | 1.67 | 2.34 |

The FAP of all consumers before the summer monsoon were clearly separated from those after the onset of the summer monsoon in nMDS ordinations (ANOSIM Global $R = 1$, $p < 0.001$; Fig. 4C). Samples from TM were also separated from samples collected at the other two sites, which were relatively similar ($R = 0.929$, $p < 0.001$; Fig. 4C). Six FAP biomarkers with different origins were further analyzed using ANOVA, that is, diatom FA (16 : 1 and 20:5n3), essential fatty acids (EFA 18:2n6 and 18:3n3 as biomarkers of fresh autotrophic materials), BaFA (i- and a15:0, i17:0, and 18:1n7 indicating detrital sources), dinoflagellate FA (22:6n3), zooplankton FA (20 : 1 and 22 : 1), and 20:4n6 (indicative of protozoan or macroalgal sources). The percentage of these biomarkers was spatially and

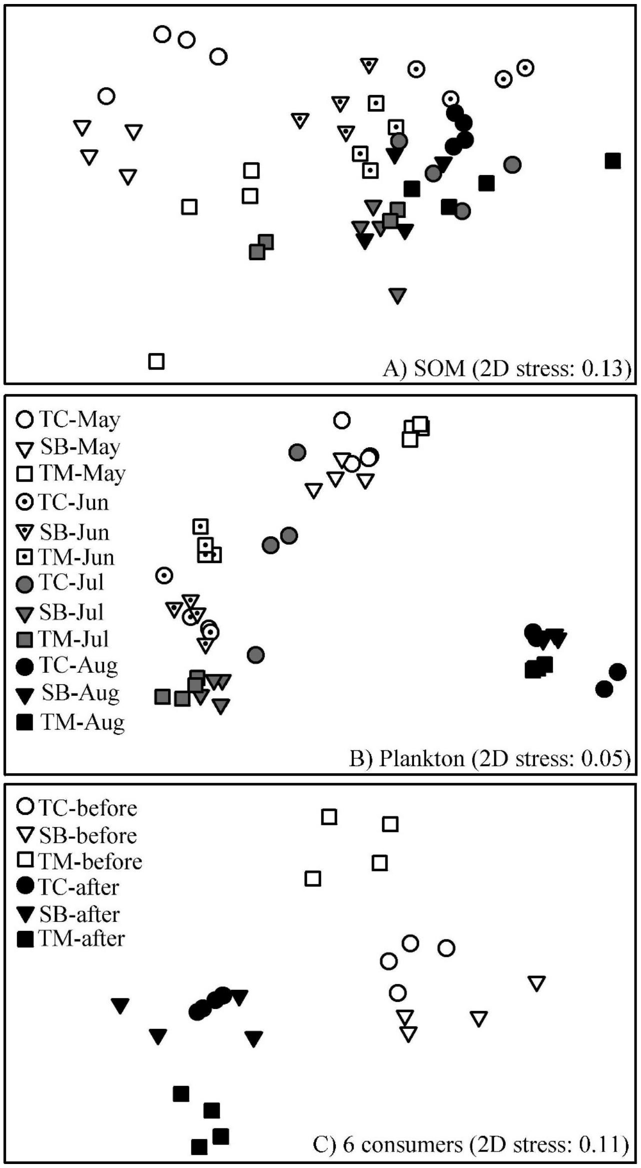

Fig. 4. nMDS ordinations of fatty acid compositions in total lipids of (A) SOM, (B) plankton, and (C) six consumers sampled from the three sites, Turtle Cove (TC), Stanley Bay (SB), and Tai Mui Wan (TM), at different sampling periods. Ordinations were based on the square-root-transformed Bray–Curtis similarity matrix.

temporally variable in different groups of consumers (Table 4). The significant Se × Si interaction was mainly a result of variable patterns of change at different sites. SNK tests showed that all consumers at all sites, except *Lunella* and *Holothuria*, showed significant increases in BaFA after the onset of the summer monsoon. Significant decreases in EFA were shown by *Septifer* (in SB and TM), *Lunella* (in SB and TM), *Salmacis* (at all sites), and *Holothuria* (in TC and SB) in this period (Table 4; Fig. 5C–H). *Saccostrea* (in TC and TM), *Septifer* (in SB and TM), *Lunella* (in SB and TM), and *Thais* (at all sites) showed significant reductions in dinoflagellate FA after the onset of the summer monsoon. Zooplankton FA in *Saccostrea*, *Thais*, and *Lunella* at all sites significantly increased after the onset of the summer monsoon, while all consumers, except *Saccostrea* and *Septifer*, showed a reduction in diatom FA over this period (Table 4; Fig. 5C–H).

## Discussion

*Assimilation of marine- and terrestrial-derived detritus during the summer monsoon as traced by SIA and FAP*—While SIA was useful to reveal trophic pathways, FAP clearly showed diet shifts in consumers during the summer monsoon. Temporal patterns of variation in SIA and FAP of food sources and consumers were consistent at all sites, although the extent of temporal change varied among sites. Site differences were probably related to local differences in physical variables, such as tidal currents, rainfall and sediment characteristics, and nutrient availability and retention time of detritus. While the supply of both algal- and terrestrial-derived detritus and their utilization by consumers increased after the onset of the summer monsoon, algal-derived materials (phytoplankton, benthic algae, and detritus derived from both) were generally the major food source for both pelagic and benthic trophic pathways. In the pelagic pathway, POM formed the base of the food chain, and the coupling of $\delta^{13}C$ values of plankton and POM indicated the utilization of POM by plankton (Bouillon et al. 2004; Martinetto et al. 2006). These items were consumed by suspension feeders (*Septifer* and *Saccostrea*), which, the SIA mixing model confirmed, were a major prey of *Thais* (Taylor 1980).

POM can be derived from both phytoplankton and algal- and terrestrial-derived detritus. These sources can be highly variable with season in tropical marine ecosystems, and it is important to understand the relative contributions of these sources to POM when investigating the trophic base of assemblages relying on pelagic food chains (e.g., Kaehler et al. 2000). The abundance of phytoplankton, particularly diatoms, is elevated during the summer monsoon in Hong Kong (Huang et al. 2004) and could account for the higher abundance of diatom biomarkers (16 : 1 and 20:5n3) and the relative scarcity of dinoflagellate (22:6n3) biomarkers (Meziane et al. 1997; Kharlamenko et al. 2001; Mfilinge et al. 2005) in plankton and suspension feeders during this period. The enhanced supply of phytoplankton during the summer monsoon may provide suspension feeders with phytodetritus. The more enriched $\delta^{15}N$ values of consumers after the summer monsoon

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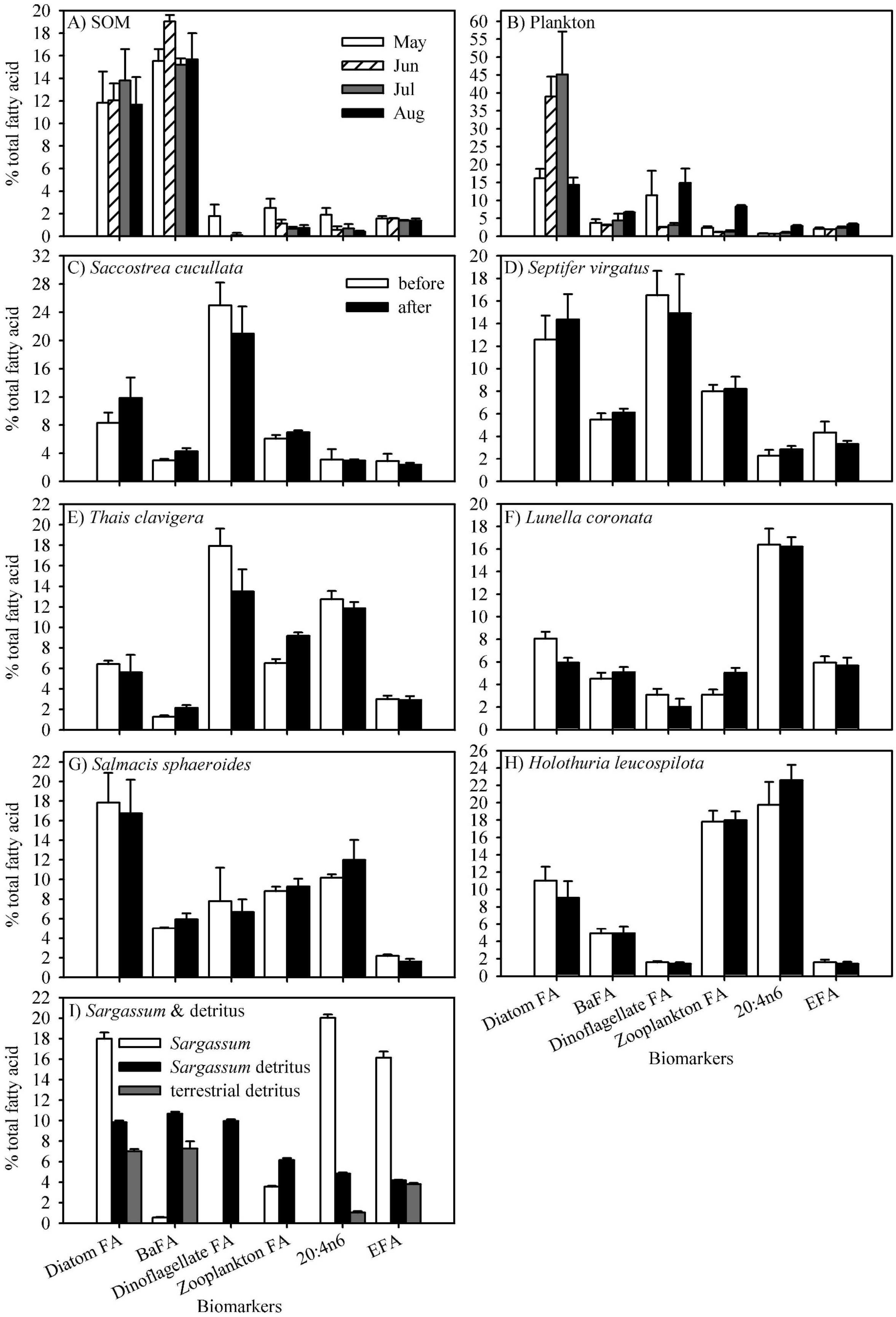
Fig. 5. Mean weight % (+SD) of fatty acid biomarkers of total lipids of (A) SOM, (B) plankton, (C) *Saccostrea cucullata*, (D) *Septifer virgtus*, (E) *Thais clavigera*, (F) *Lunella coronata*, (G) *Salmacis sphaeroides*, (H) *Holothuria leucospilota*, and (I) *Sargassum* and detritus at different sampling periods. *See* Table 4 for abbreviations. Each bar represents the pooled data of three sites ($n$ = 18 for *Holothuria leucospilota*; $n$ = 12 for others). Note scales of y-axis are different.


A) SOM
May
Jun
Jul
Aug
B) Plankton
C) *Saccostrea cucullata*
before
after
D) *Septifer virgatus*
E) *Thais clavigera*
F) *Lunella coronata*
G) *Salmacis sphaeroides*
H) *Holothuria leucospilota*
I) *Sargassum* & detritus
*Sargassum*
*Sargassum* detritus
terrestrial detritus
% total fatty acid
Diatom FA
BaFA
Dinoflagellate FA
Zooplankton FA
20:4n6
EFA
Biomarkers

indicate that there may have been a dietary shift to a greater dependence on detritus rather than phytoplankton (France et al. 1998). The higher abundance of BaFA (i- and a15:0, i17:0, and 18:1n7) and zooplankton biomarkers (20 : 1 and 22 : 1) but lower levels of diatom biomarkers (16 : 1 and 20:5n3) in *Thais* indicates increased use of energy derived from detritus and zooplankton during the summer monsoon. This dietary shift was not closely coupled with utilization of suspension feeders as prey by *Thais*; instead, it probably reflects the ability of these snails to assimilate soluble and suspended organic matter from the water column (Lau and Leung 2004).

While both suspension feeders and *Thais* relied on energy derived from POM and plankton and were characterized by depleted $\delta^{13}$C values (−14‰ to −18‰), benthic consumers (*Lunella*, *Salmacis*, and *Holothuria*) depended mainly on energy derived from benthic algae and algal-derived detritus. Consequently, they had more enriched $\delta^{13}$C signatures (−12‰ to −17‰). *Lunella* fed mainly on benthic algae, crustose *Hildenbrandia*, and biofilm. The $\delta^{13}$C values of these energy sources become more enriched during the summer monsoon (Ng et al. 2007) and would account for the elevated $\delta^{13}$C values of *Lunella* and *Salmacis*.

SIA mixing models demonstrated that the biomat (i.e., the mixture of benthic microalgae, cynobacteria, and bacteria, >50% contribution) was the major food source for *Salmacis* and *Holothuria*, followed by macroalgal-derived organic matter during the summer monsoon. Terrestrial detritus may also provide an alternative energy source for *Salmacis*, as indicated by the ~14% contribution of such detritus in the mixing model, although it is a more refractory food source with lower nitrogen and higher C : N ratio than macroalgal detritus (Buchsbaum et al. 1991; Bouillon et al. 2004). *Sargassum* detritus appeared to be one of the major food sources of *Holothuria*. SIA and FAP signatures of this consumer, however, did not vary over the study period. Such consistency could result from selective ingestion of organic matter from the sediment surface (Jangoux and Lawrence 1982), implying that macroalgal detritus in forms that *Holothuria* can ingest are available over much of the year. While *Salmacis* and *Holothuria* often inhabit the same benthic habitats, algal debris and fecal pellets generated by sea urchin feeding may be consumed by the sea cucumbers with the combined action of these echinoderms playing an important role in subtidal nutrient recycling (Mamelona and Pelletier 2005).

Although SIA mixing models can help elucidate trophic pathways, this method has a number of sources of uncertainty. The choice of diet-consumer fractionation values, for example, is crucial in the mixing model. As no explicit data of isotopic fractionation of Hong Kong marine species were available, the values used in this study were based on literature estimates (Vander Zanden and Rasmussen 2001; Post 2002; McCutchan et al. 2003). By using the same estimates for different species of consumers, the corrected SIA values of some species, such as *Holothuria*, are at the margins of the mixing polygons, indicating that not all potential sources were included in the model or that the SI signatures of food sources were highly variable (e.g., POM and biomat). The estimates of the SIA mixing model are conservative in such cases (Phillips and Gregg 2003). The use of specific tissues for analysis in different species may also confound the application of $\Delta\delta^{13}$C, given that lipid-rich tissues (e.g., urchin gonads) generally have more depleted $\delta^{13}$C than tissues with fewer lipids (e.g., gastropod foot muscle; Post et al. 2007).

FAP offers a valuable alternative dietary tracer to SIA. The greater availability of, and dependence of consumers on, detrital food sources during the summer monsoon was confirmed by FAP biomarkers. The higher percentages of SFA but lower proportions of PUFA in SOM during the summer monsoon indicated a faster degradation of newly deposited organic matter (Canuel and Martens 1996). The contribution of detritus to SOM was reflected in the abundance of BaFA in SOM (e.g., Saliot et al. 2001) throughout the study. After the onset of the summer monsoon, however, a dramatic increase in the abundance of BaFA in SOM occurred as a result of bacterial growth on degenerating *Sargassum* tissues (Lee 2000). Macroalgal detritus has a more enriched nitrogen content and hence a lower C : N ratio (*see* Kaehler et al. 2000; Norderhaug et al. 2003) because of the assimilation of exogenous nitrogen sources by bacteria (Machás et al. 2006). Such bacteria—and thus energy-rich SOM and detritus—are a valuable food for benthic consumers as confirmed by the increase in detritally derived BaFA and the reduction in diatom (20:5n3) and fresh autotrophic material (EFA) sources assimilated by *Salmacis* and other consumers after the onset of the summer monsoon.

The significant depletion of diatom biomarkers in *Holothuria* may indicate reduced utilization of algal sources (e.g., microalgae in biomat and sediments) during the summer monsoon, whereas the abundance of 20:4n6 could be explained by inputs derived from protozoan and also endosymbiotic bacterial production (Howell et al. 2003). The same pattern was seen in *Salmacis*, suggesting that this seasonal transition may be specific to echinoderms, which often possess endosymbionts (Jangoux and Lawrence 1982).

Although FAP could identify most autotrophic and heterotrophic energy sources, detrital sources could not be separated and hence are collectively expressed as BaFA. In this case, a more specific method, for example, compound-specific isotope analysis of BaFA, which eludicates the utilization of the detritial materials by bacteria, would be useful to identify the availability, source, and fate of suspended particulate detritus (i.e., POM and SOM; *see* Gacia et al. 2002).

*Potential trophic links between terrestrial and marine food webs*—The $\delta^{13}$C values of POM were intermediate between those of terrestrially derived organic carbon (−27‰ to −29‰ for C3-plants and POM derived from them; Yam and Dudgeon 2005) and marine carbon sources (−15‰ to −19‰; Ng et al. 2007), indicating that the POM consisted of both terrestrial POM and marine phytoplankton (Hellings et al. 1999). The $\delta^{13}$C-depleted terrestrial detritus may also contribute to marine food chains as dissolved organic matter (leaf leachate) that can be easily assimilated by heterotrophic bacteria (Rochelle-Newall et al. 2004) and subsequently consumed by plankton and detritivores (Hall and Meyer 1998). The utilization of terrestrial detritus was also shown by an enrichment of $\delta^{13}$C values (relative to terrestrial materials) in POM and plankton, as the isotopically lighter carbon in the dissolved inorganic matter can be utilized by phytoplankton for carbon production (Hellings et al. 1999). This trophic pathway was also confirmed by the high abundance of FAP biomarkers of bacteria (BaFA), dinoflagellates (22:6n3), and zooplankton (20 : 1 and 22 : 1) in marine consumers (such as *Septifer* and *Saccostrea*) after the onset of the summer monsoon. A pelagic–benthic coupling of the food web was evident, as shown by the correlated $\delta^{13}$C values of POM and SOM, indicating a pathway by which phytodetritus contributes to benthic food chains (Bouillon et al. 2004; Martinetto et al. 2006).

In this seasonally variable, tropical ecosystem, algae (as phytoplankton, benthic microalgae, and macroalgae) formed the base of both pelagic and benthic food chains at the three study sites. Consumers, however, became more dependent on marine-derived and terrestrially derived detritus after the onset of the summer monsoon. This seasonal change in availability and utilization of organic matter by major feeding groups highlights the importance of detrital food chains in supporting intertidal and subtidal assemblages during the hot summer monsoon in tropical Asian coastal ecosystems.

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