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Temporal variation in lipid, protein and carbohydrate content in the Red Sea soft coral *Heteroxenia fuscescens*

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Heteroxenia fuscescens is a common zooxanthellate soft coral on the shallow reefs of the Gulf of Eilat, northern Red Sea. Its main nutritional sources are the uptake of dissolved organic material (DOM) and carbon fixation by its symbiotic algae (zooxanthellae). Recent studies have indicated that although colonies of *H. fuscescens* release planulae all year round, their fecundity was subject to seasonal changes. In this study the monthly per cent of ash, lipid, protein and carbohydrate in the coral tissue over a three year period was determined. It was found that the tissues of colonies of *H. fuscescens* contained a monthly per cent mean of 8.8 ±4 ash (without sclerites), 11 ±3.5 lipid, 19.2 ±6.4 protein, and 0.6 ±0.01 carbohydrate (N=36). This study is the first to present such values based on long term investigation of the biochemical profile of a coral, thus enabling an examination of temporal variability in biochemical composition among seasons and successive years. The results indicated seasonal fluctuations in lipid and protein content, while variation in the biochemical composition among years was expressed only in the protein content. The mean energetic content of *H. fuscescens* was relatively high at 23.3 ±1.2 kJ g^{-1} dry weight (DW). A significant difference in the energetic content of *H. fuscescens* was found among seasons. It is suggested that the increase in nutrient levels following the annual mixing event at the Gulf of Eilat and the raised light levels led to high energetic content during summer, which may reflect the increase in the number of embryos and developing planulae in *H. fuscescens* colonies. Furthermore, it is suggested that in the Gulf of Eilat seasonal fluctuations in the abiotic features of the water may have an impact on the biochemical composition and energetic content of the studied species.

INTRODUCTION

Soft corals (Octocorallia: Alcyonacea) are common throughout the Indo-Pacific region, and hundreds of different species occupy a range of reef habitats across a wide depth gradient. In the Red Sea, soft corals, after the scleractinians, are the most abundant benthic group occupying space on the reef, and are represented by more than 180 species (Benayahu, 1985, 1990). Colonies of *Heteroxenia fuscescens* (Ehrenberg, 1834) of the family Xeniidae are common zooxanthellate soft corals on shallow reefs of the Gulf of Eilat, northern Red Sea (Benayahu, 1985). Their main nutritional source is derived from the uptake of dissolved organic material (DOM) and carbon fixation by its symbiotic algae (zooxanthellae), whereas particulate food is of lesser importance (Schlichter & Liebezeit, 1991). Colonies of *H. fuscescens* display continuous gametogenesis and planulation throughout the year (Benayahu, 1991). In the Red Sea this species is subjected to a seasonal environmental regime that alternates between stratified warm waters in summer, which are poor in nutrients, and in winter upwelling of low temperature waters, which are rich in nutrients (Reiss & Hottinger, 1984; REEFLUX, 1991; Erez et al., 1991; Genin et al., 1995; Lindell & Post, 1995). These seasonal changes in the abiotic features of the water may cause temporal changes in the reproductive processes of these corals (see below).

The resources available to an organism are often limited, and must be allocated among various processes essential for survival and reproduction (Ward, 1995a; Rinkevich, 1996). The accepted paradigm is that reproduction, growth and regeneration in corals are 'energy-costly' processes, and thus there should be a trade-off in resource allocation among them (Harrison & Wallace, 1990; Ward, 1995a; Rinkevich, 1996). The main energetic source for many corals is derived from carbon fixation by their zooxanthellae. Consumption of plankton or particulate and dissolved organic materials increase their total carbon input (Harrison & Wallace, 1990; Rinkevich, 1996). Colonies of *H. fuscescens* gain nutrition from both the uptake of DOM and from carbon fixation by their zooxanthellae (Schlichter & Liebezeit, 1991). Understanding the biochemical composition of organisms is crucial to the understanding of energy transfer within an ecological community (Lucas, 1994). However, there have been few biochemical studies of corals in general, and of soft corals in particular. Most of the studies deal with lipid composition of the coral tissue and its symbionts, and with the lipid relationship to coral growth and reproduction (Meyers, 1977; Patton et al., 1977; Stimson, 1987; Latyshev et al., 1991; Harland et al., 1992, 1993; Ward, 1995a,b). The findings of the above studies indicate that the large amount of lipid present in corals constitutes an energy reserve which is partitioned between growth and reproduction. To date only a few studies have dealt with the entire biochemical profile (lipid, protein and carbohydrate) of

scleractinian corals (Szamant-Froelich & Pilson, 1980; Fitt et al., 1993; Achituv et al., 1994) or of soft corals (Slattery & McClintock, 1995).

Previous studies have indicated that although colonies of *H. fuscescens* release planulae all year round, their reproductive features are subject to seasonal changes (Ben-David-Zaslow & Benayahu, 1996; Ben-David-Zaslow et al., 1999). During summer (June–September) and autumn (October–November) fecundity is greater and more colonies released planulae. In addition, summer planulae are longer and almost all of them are competent to metamorphose. Recently, we have suggested that these temporal fluctuations in the species' reproductive processes are related to seasonal changes in nutrient and light levels in the Gulf of Eilat (Ben-David-Zaslow et al., 1999), which consequently derive from annual changes in water stratification (Reiss & Hottinger, 1984; REEFLUX, 1991; Erez et al., 1991; Genin et al., 1995). Therefore, it is hypothesized that the biochemical composition of colonies of *H. fuscescens* reflect temporal fluctuations in the ambient abiotic regime. In this study the monthly per cent of ash, lipid, protein and carbohydrate in the coral tissue for a three year period have been determined and the findings evaluated in relation to seasonal fluctuations in the water temperature.

MATERIALS AND METHODS

Sampling

Sexually mature colonies of *Heteroxenia fuscescens* were sampled monthly over a three year period (October 1994 to September 1997) from the reef near the Marine Biology Laboratory at Eilat (MBL) at 3–6 m deep. Each month samples from five colonies were taken, and the seawater temperature was recorded *in situ* at 6 m deep. The whole-body coral samples were fixed in 4% formalin in seawater for 24 h, and then transported to Tel Aviv for biochemical testing. The samples were rinsed in distilled water, lyophilized, and placed in pre-weighed glass vials. Each vial and its tissue sample was weighed. For each colony one sample was taken of dry tissue of ~1 g for lipid extraction and ~0.01 g for protein and carbohydrate analyses. Lipid, protein and carbohydrate concentrations were expressed as percentages of the dry coral tissue weight for each colony sampled. An average of each biochemical component was calculated monthly for each five colonies.

Ash analysis

The tissue samples were decalcified in a mixture of equal volumes of formic acid (50%) and sodium citrate (50%) for 30 min. Per cent ash was determined gravimetrically by placing pre-weighed, decalcified whole-body dry tissue samples in a muffle furnace at 500°C for 4 h (see Slattery & McClintock, 1995).

Lipid analysis

The coral dry tissue samples were placed in individual vials containing 5 ml ethyl acetate and sonicated for 5 min, capped and left for 24 h at room temperature. The extract was filtered through a Whatman no. 1 filter paper directly into a pre-weighed glass tube. The filter paper was then rinsed three times with 2 ml ethyl acetate. This procedure was repeated three times, and the filtered extracts were evaporated to dryness under N_2 atmosphere at 25°C. Total lipid was determined by weighing the vials on a Mettler AE50 balance.

Protein analysis

Protein was measured using a modification of the micro-Lowry spectrophotometric technique (Peterson, 1977), with bovine serum albumin (Sigma) as a standard protein.

Carbohydrate analysis

Carbohydrate was measured by the phenol-sulphuric acid method of Dubois et al. (1956), using D-glucose (Sigma) as a standard. This method is particularly suitable because of its sensitivity to micro-quantities of sugar (Lucas, 1994).

Refractory calculations

The refractory material of each sample was estimated by subtracting the combined per cent composition of all constituents (ash, lipid, protein and carbohydrate) from 100%, and for the purposes of energetic quantification it was assumed to represent insoluble protein (Slattery & McClintock, 1995).

Energetic content

The energetic composition of the colonies was calculated indirectly by multiplying appropriate coefficients (Fruton & Simmonds, 1953) by each of the organic components: 9.46, 5.65, 4.1 cal g^{-1} for lipid, protein, and carbohydrate respectively, converted to joules. The total energy content of 1 g whole-body tissue was then calculated as the sum of the energy values attributed to each component.

Statistical analysis and definitions

The seasons were defined in this study according to the stratification of the water column at Eilat, following Lindell & Post (1995). 'Winter' refers to December–March; 'spring' to April and May; 'summer' to June–September; and 'autumn' to October and November. We considered an annual cycle to commence from October, when the thermocline starts to break, till September of the following year, when it is still in evidence. All analyses of temporal changes in biochemical composition of *H. fuscescens* were performed according to these definitions. Statistical procedures were carried out after arcsine-transformation to satisfy the conditions of normality and equal variance. Variation around means is given as standard deviation (SD).

RESULTS

Ash analysis

There were no significant differences in percentage ash in coral tissue samples among seasons (Table 1) and years

Table 1. *Biochemical composition (percentage dry weight; mean ±SD) of whole-body tissues of sexually mature colonies of* Heteroxenia fuscescens *in the different seasons over three years.*

	Autumn (N=6 months)	Winter (N=12 months)	Spring (N=6 months)	Summer (N=12 months)
Ash	10.3 ±3.7	9.9 ±5.1	8.5 ±2.5	7.3 ±2.7
Lipid	11.6 ±2.2	7.9 ±1.2	9.5 ±2	14.5 ±2.6
Protein	18.9 ±9.7	22.8 ±21.1	20.3 ±16.4	15.3 ±12.2
Carbohydrate	0.62 ±0.01	0.57 ±0.01	0.69 ±0.02	0.62 ±0.01
Refractory	58.6 ±6.5	58.8 ±10.8	61 ±9.4	62.3 ±7.9

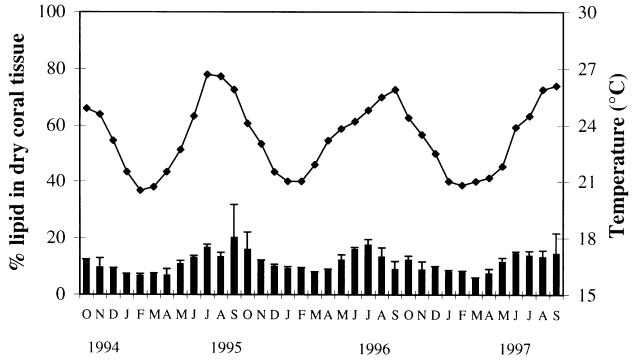

Figure 1. Lipid content (% dry weight; mean ±SD, N=5) of whole-body sample of sexually mature colonies of *Heteroxenia fuscescens* in each month over three years represented by bars. Line represents water temperature.

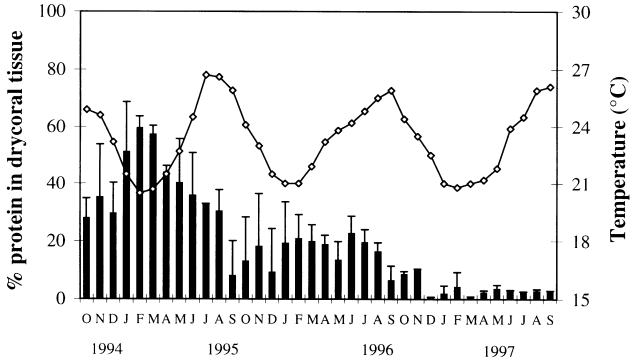

Figure 2. Protein content (% dry weight; mean ±SD, N=5) of whole-body sample of sexually mature colonies of *Heteroxenia fuscescens* in each month over three years represented by bars. Line represents water temperature.

(two-way analysis of variance (ANOVA), $P<0.05$). In the course of the entire study period a monthly mean of 8.8 ±4% ash (without sclerites) was found in the samples (N=36 months).

Lipid analysis

Significant differences (one-way ANOVA, $P<0.05$, least significant difference (LSD)-test, $P<0.001$) were found in the mean percentage of lipid in dry coral tissue among the different seasons (Table 1). During summer it was significantly higher (14.5 ±2.6%, N=12 months) than in the other seasons, followed by autumn (11.6 ±2.2%, N=6 months), spring (9.5 ±2.0%, N=6 months) and winter (7.9 ±1.2%, N=12 months). There was no significant difference in percentage lipid in dry coral tissue among the years (one-way ANOVA, $P>0.05$). The mean monthly lipid content corresponded to the water temperature, i.e. a higher percentage of lipid was noted when the water temperature was high and vice versa (Figure 1). In the course of the entire study period a monthly mean of 11.0 ±3.5 percentage of lipid was found in the samples (N=36 months).

Protein analysis

There was a significant difference among the three years in percentage protein in coral tissue (Figure 2, one-way ANOVA, $P<0.05$, LSD-test, $P<0.001$). The monthly mean protein content during the first year (October 1994–September 1995) was significantly higher (37.6 ±13.6%, N=12 months) than in the last two. A decrease in protein level was recorded in the second year (October 1995–September 1996; 16.4 ±4.7%, N=12 months), followed by the third (October 1996–September 1997; 3.6 ±2.8%, N=12 months). Throughout the first two years of the study the monthly mean percentage protein in coral tissue was higher when the water temperature was low, and vice versa. The only significant difference among seasons was recorded between summer and winter of the first year (one-way ANOVA, $P<0.05$). In the course of the entire study period a monthly mean of 19.2 ±16.4 percentage protein was found in the samples (N=36 months).

Carbohydrate analysis

There was no significant difference in percentage carbohydrate of tissue samples among seasons (Table 1) and years (two-way ANOVA, $P>0.05$). In the course of the entire study period a monthly mean of 0.61 ±0.01 percentage carbohydrate was found in the samples (N=36 months).

Energetic content

Significant differences (one-way ANOVA, $P<0.05$, LSD-test, $P<0.05$) were found in the mean energetic content among the different seasons (Table 2). During summer it was significantly higher (24.6 ±0.9 kJ g^{-1} DW, N=12 months) than in the other seasons, followed by autumn (23.1 ±0.8 kJ g^{-1} DW, N=6 months), spring (22.9 ±0.2 kJ g^{-1} DW, N=6 months) and winter (22.5 ±1.1 kJ g^{-1} DW, N=12 months). There was no significant difference in percentage lipid in dry coral tissue

Table 2. *Energetic composition ($kJ\,g^{-1}$ dry weight; mean ±SD) of whole-body tissues of sexually mature colonies of* Heteroxenia fuscescens *in the different seasons over three years.*

	Autumn (N=6 months)	Winter (N=12 months)	Spring (N=6 months)	Summer (N=12 months)
Lipid	4.6 ±0.9	3.2 ±0.5	3.8 ±0.8	5.7 ±1.0
Protein	4.5 ±2.3	5.3 ±4.9	4.8 ±3.9	3.6 ±2.9
Carbohydrate	0.10 ±0.02	0.10 ±0.03	0.12 ±0.04	0.11 ±0.02
Refractory	13.8 ±1.3	13.9 ±3.0	14.4 ±0.5	14.7 ±2.3
Total	23.1 ±0.8	22.5 ±1.1	22.9 ±0.2	24.6 ±0.9

among the years (one-way ANOVA, $P > 0.05$). In the course of the entire study period the monthly mean energetic content was 23.3 ±1.2 kJ g^{-1} DW (N=36 months).

DISCUSSION

Seasonal changes in the biochemical composition of various marine invertebrates have been well documented (Thompson et al., 1992; Lucas, 1994; Mourente et al., 1994; Sree et al., 1994; Chanas & Pawlik, 1995; Navarro & Thompson, 1995). Among the cnidarians there have been such reports for sea anemones (Ortega et al., 1988; McManus et al., 1997). Although various studies have provided coral concentration values of constituents such as ash, lipid, protein and carbohydrate (see below), no study has ever examined seasonal changes in the biochemical composition of either stony or soft corals. Tropical stony corals and sea anemones have often been regarded as lipid-rich (Patton et al., 1977; Spencer-Davies, 1991; Harland et al., 1993). Patton et al. (1977) reported that dry tissue of the scleractinian coral *Pocillopora capitata* contained 34% lipid of the total organic matter. Stimson (1987) found lipid content ranging from 30 to 40% in the tissue of six Hawaiian species: *Cyphastrea ocellina*, *Montipora verrucosa*, *Pocillopora compressa*, *Pocillopora damicornis* (Y and B types) and *Pocillopora meandrina*. Harland et al. (1992) reported the lipid content for some Caribbean corals: *Porites porites* (8.5–11%), *Montastrea annularis* (29%) and *Siderastrea siderea* (26–35%). In a later study Harland et al. (1993) reported a lipid content of 32% for the Caribbean species *Montastrea annularis* and lower values of 11–17% for *Porites porites* and the Red Sea species *Pocillopora verrucosa*, *Stylophora pistillata* and *Goniastrea retiformis*. Ward (1995b) reported a range of 29–46% lipid concentration for the Australian species *Pocillopora damicornis*, while Szamant-Froelich & Pilson (1980) found a mean lipid content of 3 mg cm^{-2} for *Astrangia danae*. Fitt et al. (1993) found 1.8 mg lipid cm^{-2} for *Montastrea annularis* and Achituv et al. (1994) found 0.17 mg lipid cm^{-2} for the Hawaiian *Pocillopora damicornis*. Harland et al. (1992) concluded that a difference of about 30% found in various coral lipid concentrations could be attributed to the analysis technique used.

There is only sparse information available on protein content in stony corals. Using the Lowry assay, Patton et al. (1977) found that *Pocillopora capitata* had a protein concentration of 33% of the organic matter. The same assay yielded 1 mg cm^{-2} for the Pacific *Fungia scutaria* (Johannes, 1974) and 4.38 mg cm^{-2} for *Montastrea annularis* (Fitt et al., 1993). Achituv et al. (1994) found a concentration of 900 $\mu g\,cm^{-2}$ for Hawaiian *P. damicornis*. Goreau & Goreau (1959) reported nitrogen values per cm^2 for the Caribbean species *Acropora cervicornis*, *Colpophyllia natans* and *M. annularis*. Later Szamant-Froelich & Pilson (1980) converted the values to protein, obtaining 4 mg cm^{-2} for the first species and 48 mg cm^{-2} for other two. In addition, they reported a mean protein content of 10 mg cm^{-2} for *Astrangia danae*, and suggested that differences in protein content among species may relate to polyp size and arrangement, as well as being a consequence of the technique used.

The only studies dealing with carbohydrate concentration in corals are those of Fitt et al. (1993), who reported 0.34 mg cm^{-2} for *Montastrea annularis*; Szamant-Froelich & Pilson (1980), who found 6 mg cm^{-2} for *Astrangia danae*; and Achituv et al. (1994), who found a value of 275 $\mu g\,cm^{-2}$ for Hawaiian *Pocillopora damicornis*.

Prior to the present study, the only reference dealing with the biochemical profile of a soft coral was that of Slattery & McClintock (1995), reporting the composition of the three shallow water Antarctic soft coral species *Alcyonium paessleri*, *Clavularia frankliniana* and *Gersemia antarctica*. In their study, the mean percent values ranged from 30.2–47.0% ash (including sclerites), 5.2–12.6% lipid, 10.4–23.9% protein, and 0.5–0.7% carbohydrate. We found that the tissues of *Heteroxenia fuscescens* contained a monthly percent mean of 8.8 ±4.0% ash (without sclerites), 11.0 ±3.5% lipid, 19.2 ±16.4% protein, and 0.61 ±0.01% carbohydrate (N=36). Our study is the first to present a long term mean of the biochemical profile of a soft coral. This enabled us to examine temporal variability in biochemical composition of a soft coral among seasons and successive years. Throughout the three years of the study, lipid concentration was found to be greater during summer, when the temperature was high, than during the other seasons (Figure 1, Table 1).

During the first two years protein concentration decreased when water temperature increased and vice versa. However, the difference in protein concentration in the soft coral among seasons was significant only in the first year (Figure 2). Variation in the biochemical composition among years was expressed only in the protein content. In the first year this value was the highest, and it gradually decreased in the following years (Figure 2). We suggest that in the Gulf of Eilat seasonal fluctuations in the abiotic features of the water may have an impact on the biochemical composition of *Heteroxenia fuscescens*. The vertical mixing during the cold months transports nutrients from the depths and enriches the upper water layers, which are poor in nutrients during the hot summer (Reiss & Hottinger, 1984; REEFLUX,

1991; Erez et al., 1991; Genin et al., 1995). Since colonies of *H. fuscescens* gain nutritional benefit both from the uptake of DOM and by carbon fixation by zooxanthellae (Schlichter & Liebezeit, 1991), we suggest that the seasonal fluctuations in its biochemical composition are related to respective changes in ambient nutrient and light levels. In the present study we measured the biochemical composition of whole-body samples, including somatic tissue, gonads, developing planulae and zooxanthellae. It has been reported that ammonium enrichment of the water cause a significant increase in the biochemical composition and densities of the symbiotic algae (Muscatine et al., 1989; Achituv et al., 1994; Muller-Parker et al., 1994). Muller-Parker et al. (1994) reported that both the coral animal and the zooxanthellae respond to the addition of exogenous dissolved inorganic nitrogen provided as 20 μM ammonium. Achituv et al. (1994) found that in 20 μM ammonium enrichment algal lipid and protein content increased. In recent studies (Ben-David-Zaslow & Benayahu, 1996; Ben-David-Zaslow et al., 1999) we found seasonal and year to year variation in reproductive processes of *H. fuscescens*. During summer and autumn the percentage of planulating colonies was significantly higher than in winter and spring, fecundity was greater during summer than in the rest of the year, and summer planulae were larger (Ben-David-Zaslow et al., 1999). A prolonged competence period for planulae was recorded for summer as compared to winter, and almost all of the former were competent to metamorphose, as opposed to the winter when only 52% metamorphosis was found (Ben-David-Zaslow & Benayahu, 1996). The temporal changes in the biochemical composition reported in the current study may therefore reflect changes in the zooxanthellae, somatic tissue and planulae, and not only in the coral tissue itself.

Most shallow-water reef inhabiting corals are abundant in many areas of nutrient depleted waters (Trench, 1979). The energy available to an organism is often limited and must be allocated among various vital processes, such as repair, maintenance, reproduction and growth. It has been shown that all are 'energy-costly' processes (Harrison & Wallace, 1990; Ward, 1995a; Rinkevich 1996). The energetic content of colonies of *H. fuscescens* found in this study was relatively high, 23.3 $\pm$1.2 kJ g^{-1} DW. Slattery & McClintock (1995) reported on energy content ranging from 14.5 to 17.3 kJ g^{-1} DW for three Antarctic soft coral species, and concluded that soft corals probably account for the highest energetic standing crop in the shallow waters of McMurdo Sound. A significant difference in the energetic content of *H. fuscescens* was found among seasons (Table 2): in summer the energetic content was the highest, followed by spring, autumn and winter. This pattern corresponds to temporal changes in the coral fecundity (Ben-David-Zaslow et al., 1999). Thus, it is suggested that the increase in energetic content in colonies of *H. fuscescens* during the summer, when nutrient and light levels are the highest, is due to the increasing number of embryos and developing planulae. However, further studies are needed in order to evaluate the temporal aspects of energy content and its allocation in corals, in order to assess its contribution to the available standing crop of coral reefs.

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