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$\delta^{13}C$ and $\delta^{15}N$ in tissue of coral polyps and epilithic algae inhabiting damaged coral colonies under the influence of different light intensities

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Abstract Studies were performed of the carbon and nitrogen stable isotope ($\delta^{13}C$ and $\delta^{15}N$) composition ($\delta^{13}C$ and $\delta^{15}N$) of the corals *Porites cylindrica* and *P. lutea* (5 years after damaging the colonies by the bleaching events) and of epilithic algae settled onto damaged areas of coral colonies. Coral polyps and three epilithic algal communities ('red algal turf, green algal turf and red calcified crusts') were sampled along the boundary between communities of coral polyps and algal colonizers from differently illuminated habitats from 2 to 90% of incident surface photosynthetically active radiation (PAR_0). It was found that communities with a predominance of red algae significantly differed from communities with a predominance of green algae in $\delta^{13}C$ but not in $\delta^{15}N$ values. An influence of habitat irradiance was found only for communities of coral polyps for $\delta^{13}C$ and $\delta^{15}N$ values: under bright light (70–90% PAR_0) polyp tissues of both coral species were significantly enriched in heavy carbon isotopes and insignificantly in nitrogen isotopes ($\delta^{13}C$ values difference $\sim$4‰) relative to tissues of corals under lower light 15–50% PAR_0. On the basis of these results we assumed that differences in light intensities in the habitat ranging from 15 to 90% PAR_0 do not influence on accessibility of the main carbon and nitrogen sources for corals and algae, and exchange by these elements between organisms. We also assumed that the relative enrichment in the heavy carbon isotopes of coral tissues in high light is a result of decreased isotope fractionation (or the absence of fractionation in photosynthesis of their zooxanthellae).

Keywords Carbon · Corals · Epilithic algae · Irradiance · Isotope composition · Nitrogen

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Introduction

Field observations and experiments, conducted in the sea and in outdoor aquaria (Diaz-Pulido and McCook 2002, 2003, 2004; Titlyanov et al. 2005, 2006), showed that communities of algal turf were formed on lesions of damaged colonies of scleractinian corals during 6–8 months of succession, varying with conditions. Such damaged colonies occupied with algae are convenient objects for the study of relationships

between coral polyps and epilithic algae living in the same colony. These relationships could be competitive, mutualistic, or parasitic (Nabivailo and Titlyanov 2006). The study of food relations, the use of common sources of biogenic elements by coral and algae, the exchange with biogenic elements between these organisms can help to elucidate character of relationships between the organisms. For instance, this method has been used in the study of carbon and nitrogen exchange between coral polyps and their symbiotic zooxanthellae (Muscatine et al. 1989; Muscatine and Kaplan 1994) in determination of biogenic elements sources for corals in oligotrophic and eutrophic environments (Risk et al. 1993; Mendes et al. 1997; Heikoop et al. 2000), in the study of trends in $\delta^{13}C$ and $\delta^{15}N$ composition in corals across the continental shelf (Risk et al. 1994) and in determining natural inter-reef variability in $\delta^{13}C$ and $\delta^{15}N$ of shallow reef corals as a foundation for investigating variations in sources of carbon and nitrogen available to corals (Heikoop et al. 2000).

In our previous analyses (Titlyanov et al. 2008) of carbon and nitrogen isotopic composition in tissues of coral polyps of hermatypic corals and of epilithic algae (taken from the same coral colony) showed that epilithic algae and coral polyps mainly use different sources of these biogenic elements. This give the basis to assume that adjoining associations of epilithic algae and coral polyps do not exchange nitrogen-containing metabolites to a significant extent under optimum light intensity (about 60–70% PAR_0) (Titlyanov et al. 2008). At the same time, it is well known that when even one of the symbionts is photosynthetic organism, character of their relationships directly depends on light conditions (Nabivailo and Titlyanov 2006). For instance, under bright (90% PAR_0) and moderate (30% PAR_0) light, the main source of carbon for polyps of the scleractinian coral *Stylophora pistillata* is products of photosynthesis of their zooxanthellae (Titlyanov et al. 2000). At the same time, under low light ($\sim$2% PAR_0) zooplankton (product of predation) is the main source of carbon and nitrogen (Titlyanov et al. 2000). More over, under extremely low light less than 1% PAR_0, cells of polyps partially digest and assimilate their own zooxanthellae (Titlyanov et al. 1996).

The study of carbon and nitrogen isotope composition in tissues of corals and epilithic algae living in the same colony under differently lighted sites of coral reef can help to elucidate the main sources of these elements for these organisms and also to elucidate the degree of metabolite exchanges between the organisms.

In this work, the natural stable isotope ratios of organic carbon and nitrogen in polyp tissues and epilithic algae taken from the same damaged colonies of scleractinian corals dwelling under different irradiances—in bright (70–90 PAR_0), moderate (20–30% PAR_0) and low (2–5% PAR_0) light—were analyzed. The study used colonies of the massive coral *Porites lutea* and the branching coral *P. cylindrica*, which were damaged by the bleaching events in the summer of 1998 and were partially overgrown with algae at the time of sampling (the summer of 2003).

The aim of the study was to elucidate the influence of PAR_0 on carbon and nitrogen nutrition of coral polyps and epilithic algae living within the same coral colony in habitat and to elucidate how change food relationships between algae and corals are dependent upon light factor.

Materials and methods

Collection site

The study was carried out at the fringing reef of Sesoko Island (Okinawa, Japan, 26°38′N, 127°52′E) in August 2003. Colonies of the hermatypic massive coral *Porites lutea* Edwards and Haime 1860 and the branched coral *Porites cylindrica* (Dana 1846) weighing 1–2 kg each were collected from open sites at a depth of 1–1.5 m (70–90% PAR_0) and from shaded sites at a depth of 2–2.5 m (15–30% PAR_0) from the same locality. Two coral colonies of each species were taken from each collection site. Coral colonies taken for analysis were partially damaged and had old lesions overgrown by epilithic algae represented mainly by algal turf communities and by communities of red crust algae. Turf consisting mainly of red algae was termed as "red turf", those with a predominance of green algae were called "green turf", while communities of encrusting red algae were named "red crusts". Carbon and nitrogen stable isotope samples taken from the upper part of colonies at a depth of 1–1.5 m and from the differently lighted upper and lower parts of coral colonies taken from a depth of 2–2.5 m. The upper portions of colonies in

open sites at a depth of 1–1.5 m were exposed to 70–90% of PAR_0, which in the middle of a sunny day was 1,269–1,620 μmol m^{-2} s^{-1}, while the upper portions of colonies in shaded sites at a depth of 2–2.5 m were exposed to 15–30% PAR_0 (270–540 μmol m^{-2} s^{-1}) and the lower portions of shaded 2–10% PAR_0 (36–180 μmol m^{-2} s^{-1}).

Coral fragments representing three or four polyp rows directly adjacent to the boundary with algal communities were cut from the colony with a delicate handsaw. The height of sawed out mini-block was approximately equal to the height of a corallite (3 mm); the mini block was of four corallite rows (5–6 mm) wide and 1–2 cm long (Titlyanov et al. 2008). Associations of epilithic algae such as red turf, green turf and red crusts living along the boundary of coral polyps were considered for analysis. Algae living along the boundary (a strip 5 mm wide) were collected under a stereoscopic microscope or a magnifying glass (Titlyanov et al. 2008). By four samples of coral polyps and epilithic algal communities were taken from different illuminated portions of colonies.

Species compositions of epilithic algae were studied under light microscope with magnifications 10, 20, 60 and 100×. Species abundance was studied under stereoscopic microscope for three random areas (each 5 cm^2) (Titlyanov et al. 2008).

Measurement of irradiance

Irradiance was measured at the water surface and near the upper parts and the base of colonies in their habitat before sampling with a Li-Cor radiation sensor (Model LI-192 SB) at three time intervals: 9:00–10:00 h, 13:00–14:00 h and 17:00–18:00 h. Relative photosynthetically active radiation at each sampling location was derived from these measurements and presented as a percentage of the incident photosynthetically active radiation ($PAR_0 = 100\%$).

$\delta^{13}C$ and $\delta^{15}N$ analyses

All samples of coral fragments with coral tissue and thalli of epilithic algae were treated with acid (1N HCl) for decalcifying of the coral (Risk et al. 1994) and occasional skeletal particles on the algal thalli. After that the samples were rinsed with distilled water and dried at 60°C. Heikoop et al. (1998) have shown that such an acid treatment does not affect the isotope composition of carbon and nitrogen of coral samples.

The natural isotope to stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) of the samples were determined using a mass spectrometer (MAT 253, Finnigan) coupled online via Finnigan ConFlo III interface with elemental analyzer (FlashEA 1112, ThermoQuest). Results are expressed in the standard δ unit notation as:

$\delta X(‰) = \left[\left(R_{\text{sample}}/R_{\text{reference}}\right) - 1\right] \times 10^3$, where X is ^{13}C or ^{15}N and R is $^{13}C/^{12}C$ for carbon, and $^{15}N/^{14}N$ for nitrogen.

These values are reported relative to the Vienna Pee Dee Belemnite (PDB) standard for carbon and to air N_2 for nitrogen.

Statistical analysis

Data were used with statistical package Statistica v.6.0 (StatSoft Inc., Tulsa, OK, USA) for data analysis, and One-way ANOVA to evaluate inter-species differences in isotopic signatures. One-way ANOVA Tukey HSD test was used to compare mean isotopic signatures of different species. The influence of irradiance on the $\delta^{13}C$ and $\delta^{15}N$ values of the coral samples were estimated using factorial 2-way ANOVA (fixed factors = irradiance and coral species). Prior to statistical analyses, normality and homogeneity of variance were checked for all data (Kolmogorov–Smirnov test and Cochran's test, respectively).

Results

Algal species composition and abundance from habitats with different irradiances

The "red turf" (RT) community colonizing the upper portions of damaged colonies dwelling under light intensity from 15 to 90% PAR_0, consisted of 37 algal species: Rhodophyta, with 25 species were the most abundant (Table 1). Under both light intensities (70–90% PAR_0 and 15–30% PAR_0), the following red algae dominated: *Jania capillacea, Hypnea pannosa, Gelidiopsis intricata, Ceramium procumbens* and *Herposiphonia secunda*.

Communities of "green turf" (GT) and accompanying algae dwelling in the light range from 15 to

Table 1 Species composition and abundance of three different algal communities growing close to coral polyps of *Porites cylindrica* and *P. lutea* taken from habitats with irradiances of 70–90, 15–30 and 2–10% PAR_0

Species of algae	% PAR_0					
	70–90 RT	15–30	70–90 GT	15–30	15–30 RC	2–10
Bacillariophyta						
Licmophora abbreviata Agardh	+	+	+	+		
Cyanobacteria						
Chroococcus turgidus (Kützing) Nägeli	+	+	+	+		
Lyngbya limnetica Hieronymus			++	++		
Lyngbya polychroa (Meneghini) Rabenhorst	+	+				
Lyngbya semiplena (C. Agardh) J. Agardh			+	+		
Oscillatoria spp.			+			
Phormidium spp.			+			
Spirulina tenerrima Kützing			+			
Nostoc commune Vaucher			+			
Hormothamnion sp.	++					
Dichothrix sp.	+					
Chlorophyta						
Verdigellas sp.			+			
Acrochaete viridis (Reinke) Nielsen (*Entocladia viridis* Reinke)	+					
Rhizoclonium implexum (Dillwyn) Kützing	+		++	+++		
Rhizoclonium sp.			+			
Cladophora laetevirens (Dillwyn) Kützing				+		
Cladophora sp.			+			
Boodlea composita (Harvey) Brand		+				
Cladophoropsis membranacea (Hofman Bang ex C. Agardh) Børgesen				+		
Ventricaria ventricosa (J. Agardh) Olsen and J. West		+				
Valonia macrophysa Kützing	+	+				
Caulerpa sertularioides (S. Gmelin) Howe			+	+		
Derbesia sp.			+++	++		
Phaeophyta						
Ectocarpus sp.			+	+		
Hincksia mitchelliae (Harvey) P·C. Silva			+			
Sphacelaria novae-hollandiae Sonder	+					
Sphacelaria rigidula Kützing			++	++		
Dictyota plaffii Schnetter?	+	+				
Dictyota sp.				+		
Lobophora variegata (Lamouroux) Womersley ex Oliveira				+		
Rhodophyta						
Erythrotrichia carnea (Dillwyn) J. Agardh		+				
Acrochaetium virgatulum (Harvey) Bornet		+				
Acrochaetium sp.	+	+	+	+		
Fosliella sp.						
Hydrolithon farinosum (J.V. Lamouroux) Penrose and Y.M. Chamberlain	+	++	+		+	+
Hydrolithon sp.		+			+	+

Table 1 continued

Species of algae	% PAR_0					
	70–90 RT	15–30	70–90 GT	15–30	15–30 RC	2–10
Neogoniolithon sp.	+	+				
Jania capillacea Harvey	++	+			+	
Gelidium pusillum (Stackhouse) Le Jolis		+				
Hypnea pannosa J. Agardh	+	++				
Hypnea spinella (C. Agardh) Kützing	+	+				
Peyssonnelia conchicola Piccone and Grunow					+	+
Peyssonnelia sp.					+	+
Rhodymenia sp.	+					
Champia parvula (C. Agardh) Harvey		+				
Gelidiopsis intricata (C. Agardh) Vickers	++	+++				
Lomentaria corallicola Børgesen		+				
Centroceras clavulatum (C. Agardh) Montagne	+	+	+		+	+
Corallophila apiculata (Yamada) R. Norris	+	+			+	
Ceramium procumbens Setchell and Gardner	++	+				
Spermothamnion sp.	+	+				
Griffithsia subcylindrica Okamura		+				
Herposiphonia secunda (C. Agardh) Ambronn f. *secunda* M.J. Wynne	++	++				
Chondrophycus parvipapillatus (Tseng) Garbary and Harper (*Laurencia parvipapillata* Tseng)	+	+				
Laurencia sp.	+					
Polysiphonia sp.	+	+	+	+		
Tolypiocladia glomerulata (C. Agardh) Schmitz		+				
Digenea simplex (Wulfen) C. Agardh	+					

GT Turf consisting of green algae, *RC* red algae forming calcified crusts, *RT* turf consisting of red algae

+++, Abundant occurrence or more than 10 individuals per cm^2; ++, less than 10 individuals per cm^2; +, less than 1 individual per cm^2 for fleshy and other large forms of macrophytes

90% PAR_0 consisted of 25 algal species (8 Chlorophyta, 7 Cyanobacteria, 5 Phaeophyta, 4 Rhodophyta and 1 Bacillariophyta). Under bright and moderate light, algal species compositions were 44% similar with *Rhizoclonium implexum*, *Derbesia* sp. (Chlorophyta), *Lyngbya limnetica* (Cyanobacteria) and *Sphacelaria rigidula* (Phaeophyta) dominating.

The "red crusts" (RC) that contained 7 species were predominantly calcareous forms: *Peyssonnelia* spp. and *Hydrolithon farinosum*.

$\delta^{13}C$, $\delta^{15}N$ in coral and epilithic algae tissues

All coral samples studied represent combined host coral tissues and intracellular symbiotic zooxanthelae. The mean $\delta^{13}C$ value of *Porites lutea* polyps was -12.6 ± 1.8(SD)‰ and the mean $\delta^{15}N$ value was 5.3 ± 0.4(SD)‰. The corresponding values for *Porites cylindrica*, were -13.6 ± 1.5 and 5.2 ± 0.3(SD)‰, respectively. The mean carbon and nitrogen isotope signatures for the two coral species did not differ significantly ($p > 0.5$, ANOVA Tukey HSD test).

For the red algal turf communities, the mean values were: -16.8 ± 1.4(SD)‰ for $\delta^{13}C$; and 3.3 ± 1.1(SD)‰ for $\delta^{15}N$. When compared with the red turf, green algal turf communities had significantly higher mean $\delta^{13}C$ values (-12.0 ± 2.3(SD)‰) ($p = 0.0002$, ANOVA Tukey HSD test), but similar mean $\delta^{15}N$ value, 3.0 ± 1.1(SD)‰). The red crust algal community had mean $\delta^{13}C$ value of -18.3 ± 1.6(SD)‰ similar to that of red turf, and $\delta^{15}N$ values

Table 2 $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SD; $n = 4$) of coral polyp and epilithic algae from differently illuminated parts of (70–90, 15–30 and 2–10% PAR_0) of damaged colonies of scleractinian corals

Species	$\delta^{13}C$				$\delta^{15}N$			
	% PAR_0			*p*-level	% PAR_0			*p*-level
	70–90	15–30	2–10		70–90	15–30	2–10	
Porites lutea	−10.3 ± 0.6	−13.7 ± 0.7	−13.5 ± 0.7	<0.001	5.4 ± 0.6	5.5 ± 0.1	5.1 ± 0.3	NS
Porites cylindrica	−11.7 ± 0.6	−14.4 ± 0.6	−14.8 ± 0.3	<0.0001	5.5 ± 0.1	5.1 ± 0.2	5.5 ± 0.2	<0.01
Red algal turf	−16.0 ± 1.5	−17.5 ± 0.9		NS	3.2 ± 1.4	3.4 ± 0.9		NS
Green algal turf	−10.6 ± 2.4	−13.4 ± 1.3		NS	3.2 ± 0.6	3.1 ± 1.4		NS
Red algal crusts		−18.3 ± 2.1	−18.4 ± 1.4	NS		4.0 ± 0.6	3.9 ± 0.5	NS

Results of one-way ANOVA are shown for each species; NS, not significant

3.9 ± 0.5(SD)‰ insignificantly higher than that of red algal turf ($p = 0.228$, ANOVA Tukey HSD test).

Carbon isotopic compositions in green algal turf coral polyps were similar. Red algal turf and red crust algal community are significantly depleted in $\delta^{13}C$ comparing with corals and green algal turf ($p < 0.002$, ANOVA Tukey HSD test). All $\delta^{15}N$ values for algae were significantly lower than for coral polyps ($p < 0.001$, ANOVA Tukey HSD test).

The influence of irradiance on $\delta^{13}C$, $\delta^{15}N$ in coral and algal tissues

With a decrease in irradiance from 70–90% to 15–30% PAR_0, the $\delta^{13}C$ of coral polyps decreased significantly i.e. by more than 3‰: the $\delta^{13}C$ values decreased from −10.3 to −13.7‰ in *Porites lutea*, and from −11.7 to −14.4‰ in *P. cylindrica* (Table 2). Further decrease in irradiance from 15–30% to 2–10% PAR_0 did not influence coral $\delta^{13}C$ values (Table 2). More over, the $\delta^{15}N$ values of the two coral species were changed with a decrease in irradiance by no more than 0.5‰ and only for *P. cylindrica* these changes (decrease) were significant (Table 3). However, the results of factorial 2-way ANOVA (Table 3) showed that $\delta^{13}C$ and $\delta^{15}N$ signatures of coral polyps were clearly and consistently different between localities with different irradiances. The influence of light intensity on $\delta^{13}C$ and $\delta^{15}N$ values in two coral species did not differ significantly (Table 3).

In contrast to corals, there were no significant differences in carbon and nitrogen isotopic signatures of epilithic algal associations colonizing damaged corals at different irradiances (Table 2).

Table 3 Summary of factorial 2-way ANOVA to assess significant differences in isotopic signatures between irradiance at sampling sites (70–90, 15–30 and 2–10% PAR_0) and coral species (*Porites lutea* and *Porites cylindrica*)

Variable	Effect	*df*	MS	*F*	*p*-level
$\delta^{13}C$	Irradiance	2	26.618	51.588	<0.000001*
	Species	1	6.510	12.618	0.002*
	Irradiance × species	2	0.213	0.413	0.668
	Error	18	0.516		
$\delta^{15}N$	Irradiance	2	0.3907	4.538	0.025*
	Species	1	0.0864	1.004	0.330
	Irradiance × species	2	0.1486	1.727	0.206
	Error	18	0.0861		

Asterisk indicate significant *p*-levels

Discussion

Stable isotope compositions in coral tissues and the colonizing algae

Carbon and nitrogen stable isotope compositions of coral polyps from *Porites lutea* and *P. cylindrica* colonies did not differ in light regime (70–90%, 15–30% and 2–10% PAR_0) (Table 2) from those of hermatypic corals taken from coral reefs of Ishigaki Island (Ryukyu Archipelago), Zanzibar Island, Palau Island, the Great Barrier Reef of Australia and Florida Reef, which varied from −15.1 to −14.0‰ for carbon, and from 2.6 to 8.9‰ for nitrogen (Yamamuro et al. 1995; Heikoop et al. 1998, 2000; Sammarco et al. 1999; Risk et al. 1994; Reynaud et al. 2002). Such a similarity between the $\delta^{13}C$ and

$\delta^{15}N$ for different geographical locations suggests that corals of Sesoko Island have similar sources of carbon and nitrogen and paths of metabolism as those from coral reefs in the tropics and subtropics.

Also, our study shows that stable isotope content from the 2 species of *Porites* living under different light regimes do not differ. However, Muscatine et al. (1989) showed that carbon isotope composition of coral animal tissue and zooxanthellae among corals species from shallow water differ significantly: the fleshy *Montastrea* spp. and the perforate non-branching *Porites astreoides* were isotopically heavier than the perforate branching *Acropora* spp. and the branching *Madracis mirabilis*. The difference in isotope compositions in dependence on colony morphology displays probably only in different genera but not in species of the same genus as like in our case.

Our range of $\delta^{13}C$ values (−10.6 to −18.4‰) for epilithic algal communities, inhabiting under different light intensities, are very much within the range of values (−35 to −3‰) found by other researchers (Yamamuro et al. 1995; Raven et al. 2002; Wang and Yeh 2003; Titlyanov et al. 2006). Carbon isotope compositions of red or green algae clearly differ: the red algal turf has mean $\delta^{13}C$ value −16.8‰, the red crusts −18.3‰, and the green algal turf −12.0‰. This implies that the green algae are more enriched in ^{13}C than the red algae, which is also consistent with the literature data (Raven 2003; Raven et al. 2002, 2005; Wang and Yeh 2003; Giordano et al. 2005). It is likely that the differences in carbon stable isotope compositions of different algal tissues and coral polyps depend on carbon intake source of these algae. Thus, green algae are more rich in ^{13}C than red algae (irrespective of the light conditions in habitat) probably because they possess a mechanism to accumulate the carbon assimilated as both HCO_3 and CO_2 by restricting leakage of inorganic carbon from their intracellular pool, decreasing the capacity for assimilation by Rubisco (ribulose bisphosphate carboxylase-oxygenase) to result in large carbon isotope fractionation (Raven et al. 2002, 2005; Giordano et al. 2005; Kevekordes et al. 2006).

It is known that zooxanthellae use carbon of the "internal CO_2 pool" of corals in photosynthetic process (Muscatine et al. 1989). The principal source of carbon in the internal CO_2 pool is mainly animal metabolism (CO_2 released in the process of dark respiration of the animal) (Muscatine et al. 1989). Moreover, the part of carbon (~20%) comes to coral tissue during the assimilation of ingested zooplankton (McAuley 1994). This possibly explains the presence of more heavy carbon in coral tissue compared with algal tissues that use CO_2 and HCO_3 during photosynthesis.

The $\delta^{15}N$ mean values in red turf, green turf and red crusts were 3.3, 3.2‰, and 3.9‰ respectively. Low $\delta^{15}N$ values of algal turfs probably were a result of the presence of some species of Cyanobacteria fixing their nitrogen from the atmosphere (e.g., *Lyngbya* spp. or *Hormothamnion* sp.). Samples of red crusts did not contain Cyanobacteria (Table 1). Yamamuro et al. (1995) reported low $\delta^{15}N$ values close to 0.0‰ for Cyanobacteria at Ishigaki and Palau Islands.

Influence of irradiance on $\delta^{13}C$, $\delta^{15}N$ on coral tissue and algae

We did not find the average $\delta^{13}C$ and $\delta^{15}N$ values of algal associations living at various irradiances to differ. However, it is known that marine autotrophs living at high irradiances have a high rate of photosynthesis and nitrogen assimilation and can be limited by the supply of carbon and nitrogen. Moreover, frequently there is a mechanism of concentrating inorganic carbon. As a result, these marine autotrophs can only weakly fractionate the isotopes, and consequently, they might have relativly more heavy isotopes in their tissue (Johnston et al. 1992; Raven et al. 2002).

The absence of significant difference in isotope composition of algae growing under different irradiances (70–90% or 15–30% PAR_0) implies that algae can acclimate to light in the range from 15 to 90% PAR_0 This confirm our previous studies (Titlyanov et al. 1983; Titlyanov 1991), where scleractinian corals and Sargassaceae algae growing at irradiances from 20 to 80% PAR_0 showed maximum rates of photosynthesis and daily primary production at midday. In all probabilities, in localities with high and moderate light intensities and with the same concentration of inorganic carbon and nitrogen in seawater, algae with close photosynthetic rates have similar extents of carbon and nitrogen isotope discrimination and isotope compositions of these elements in tissues.

Muscatine et al. (1989) found an essential difference in $\delta^{13}C$ of zooxanthellae and animal tissues of colonies of the same coral species dwelling at different depths (different light quantity). As the reason for depletion of ^{13}C in corals at larger depth the authors suggest an increase in isotopic discrimination with decreased rates of photosynthesis by the zooxanthellae in low light. However, with changes in depth, not only does the light intensity change, but also concentration and composition of zooplankton as well as isotope composition of dissolved inorganic carbon (DIC) changes. Therefore, deepwater corals in experimental studies of Muscatine et al. (1989) were probably depleted of heavy carbon not only as a result of the decrease in isotopic discrimination but also because of their greater heterotrophy compared with shallow water corals or because of greater content of light isotopes in DIC at depth compared with that of at shallows. Our analyses show that coral polyps living at the same depth but in shaded sites (15–30% PAR_0) had lower $\delta^{13}C$ (difference ca. 4‰) values than in those sites with relatively more light (70–90% PAR_0) probably because of the increase in carbon isotope discrimination under low light.

Conclusion

We show that light intensity in the range from 2 to 90% PAR_0 does not influence isotope compositions of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of red and green epilithic algal settlers on *Porites lutea* and *P. cylindrica* colonies. In contrast, coral polyps living under bright (70–90% PAR_0) light were significantly enriched in heavy isotopes of carbon (ca. 4‰ more) and of nitrogen (ca. 0.5‰ more) compared with polyps dwelling under low light (2–5% PAR_0). The latter, probably depend on decreasing isotopic discrimination or its complete absence in reactions of photosynthesis and nitrogen assimilation in zooxanthellae of corals in bright light, but not with changes in carbon and nitrogen sources or with metabolite exchange with neighboring associations of red and green epilithic algae.

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