

Endolithic algae: an alternative source of photoassimilates during coral bleaching

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Recent reports of worldwide coral bleaching events leading to devastating coral mortality have caused alarm among scientists and resource managers. Differential survival of coral species through bleaching events has been widely documented. We suggest that among the possible factors contributing to survival of coral species during such events are endolithic algae harboured in their skeleton, providing an alternative source of energy. We studied the dynamics of photosynthetic pigment concentrations and biomass of endoliths in the skeleton of the encrusting coral *Oculina patagonica* throughout a bleaching event. During repeated summer bleaching events these endolithic algae receive increased photosynthetically active radiation, increase markedly in biomass, and produce increasing amounts of photoassimilates, which are translocated to the coral. Chlorophyll concentrations and biomass of endoliths were 4.6 ± 1.57 and $1570 \pm 427 \mu\text{g cm}^{-2}$ respectively, in skeletons of relatively healthy colonies (0–40% bleaching) but up to 14.8 ± 2.5 and $4036 \pm 764 \mu\text{g cm}^{-2}$ endolith chlorophyll and biomass respectively, in skeletons of bleached colonies (greater than 40% bleaching). The translocation dynamics of ^{14}C -labelled photoassimilates from the endoliths to bleached coral tissue showed significantly higher ^{14}C activity of the endoliths harboured within the skeletons of bleached corals than that of the endoliths in non-bleached corals. This alternative source of energy may be vital for the survivorship of *O. patagonica*, allowing gradual recruitment of zooxanthellae and subsequent recovery during the following winter.

Keywords: corals; *Oculina patagonica*; bleaching; endolithic algae; ^{14}C

1. INTRODUCTION

A central feature of shallow-water coastal ecosystems is the predominance of symbioses between invertebrates and dinoflagellate microalgae (zooxanthellae) (Odum & Odum 1955). Zooxanthellae photosynthesize while residing inside their hosts, continuously transferring to them up to 95% of their photosynthetic products (Muscatine 1990), thereby contributing to a variety of nutritional requirements, such as maintenance, synthesis of new cells, skeletal matrix, mucus, deposition of calcium carbonate, and the storage of energy-rich compounds for coral reproduction (Muscatine & Cernichiaro 1969; Crossland *et al.* 1980a,b; Muscatine *et al.* 1981, 1984; Rinkevich & Loya 1983, 1984; Kellogg & Patton 1983; Stimson 1987; Rinkevich 1989). Thus, when the coral loses its zooxanthellae, it loses its main energy resource, putting at risk its essential biological functions (Hoegh-Guldberg 1999; Wilkinson 1999, 2000). Reduced proteins and lipids (Porter *et al.* 1989; Michalek-Wagner & Willis 2001), lowered growth rate (Goreau & Macfarlane 1990), lower calcification and repair capabilities (Glynn 1993; Meesters & Bak 1993) and termination of gametogenesis (Szmant & Gassman 1990; Ward 2000; Fine *et al.* 2001) have all been reported following reduction in zooxanthellae densities (bleaching). Coral bleaching, the disruption of the symbiotic association between coral hosts and their symbiotic photosynthetic algal endosymbionts, is often linked to elevated seawater temperature (Glynn 1991, 1993; Brown 1997; Hoegh-Guldberg 1999) and high solar irradiance (Jokiel 1980; Lesser *et al.* 1990; Gleason & Wellington

1993; Glynn 1993). It threatens coral reefs throughout the world, causing mortality and, in some cases, local extinctions (Wilkinson 1999; Hoegh-Guldberg 1999). However, some coral species have been shown to survive severe bleaching events (Glynn 1993; Brown 1997; Hoegh-Guldberg 1999; Wilkinson 2000; Loya *et al.* 2001), leading to major structural shifts in some coral communities (Glynn 1993; Brown 1997; Ostrander *et al.* 2000; Loya *et al.* 2001). One of the most intriguing questions being asked by coral reef researchers is why some coral species, mostly of massive and encrusting growth forms, survive bleaching events, while others do not. The Mediterranean encrusting coral *Oculina patagonica* is one such surviving species. Although 80–90% of *O. patagonica* colonies along the Israeli coast bleach annually, more than 90% of the bleached colonies recover (Kushmaro *et al.* 1996, 1998).

During bleaching events of *O. patagonica*, we observed that 2–3 weeks after the onset of bleaching, green/red pigments of phototrophic endoliths become visible through the transparent coral tissue. The presence of these endolithic dwellers has been described in many scleractinians, especially massive and encrusting coral species (Highsmith 1981; Shashar & Stambler 1992; Shashar *et al.* 1997). The endolithic filamentous algae, usually siphonaceous chlorophytes of the genus *Ostreobium* (Jeffrey 1968; Lukas 1974; Le Campion-Alsumard *et al.* 1995), can appear as dense green bands or zones within the coral skeleton, underneath its tissue (Highsmith 1981). Odum & Odum (1955) suggested that endolithic algae are major contributors to the primary productivity of the coral reef. Kanwisher & Wainwright (1967) did not support this assumption, showing only slight oxygen production by these algae. Schlichter *et al.* (1995) were the first to demonstrate translocation of endolithic photoassimilates to the coral tissue,

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and contribution to growth, in the azooxanthellate coral *Tubastrea micranthus*. In a later study, Schlichter *et al.* (1997) studied the trophic potential of *Ostreobium quekettii* in two zooxanthellate coral species (*Mycedium elephantotus* and *Leptoseris fragilis*), pointing out their role in nutrient recycling and suggesting a minor importance in comparison with the contribution of zooxanthellae. Less than 5% of the photosynthetically active radiation (PAR) is able to penetrate and reach the zone of the green algae (Halldal 1968; Shibata & Haxo 1969; Schlichter *et al.* 1997), due to the absorbance by the unicellular endosymbiotic algae (zooxanthellae) and the inorganic skeleton itself (Kanwisher & Wainwright 1967). Three major factors appear to affect the intensity of light available to *Ostreobium* living within coral skeletons (Highsmith 1981): (i) 98% absorption of the incidental light by the zooxanthellae in the coral tissue; (ii) internal architecture of corals' skeleton, which affects the light transmission; and (iii) water depth. Low light intensities are expected to result in very low photosynthesis of the endolithic algae (Shashar & Stambler 1992). During bleaching, however, the loss of the shading effects of the zooxanthellae allows much higher light intensities to penetrate the skeleton, which can result in higher production of photoassimilates.

We studied the dynamics of photosynthetic pigment concentrations and biomass of the endoliths harbouring the skeleton of *O. patagonica*, and translocation of photoassimilates to the coral tissue, throughout a bleaching event and at different stages of bleaching.

2. MATERIAL AND METHODS

(a) *Endolith pigments and biomass*

Fresh coral cores ($r = 0.5$ cm, 0.5 cm thick) at different levels of bleaching were collected ($n = 37$ and 32 for pigment extraction and biomass quantification from the endoliths respectively). Determination of the rate of bleaching was performed by visual estimation of paleness before collection, followed by quantification of chlorophyll concentrations in the coral tissue. In each core, the tissue was removed from the imperforate skeleton using a WaterPik (Fort Collins, CO) and the skeleton was further cleaned using a brush, and inspected for tissue or zooxanthellae remnants. Extraction of the photosynthetic pigments from the tissue was by centrifugation of the resulting volume of tissue, zooxanthellae and seawater, whereas pigment extraction from the skeleton was carried out after grinding it using a stone mill. The skeleton powder containing endolithic algae, and the pellet containing the zooxanthellae, were individually assayed for chlorophyll by extraction in cooled 90% acetone overnight. The extracted chlorophyll was quantified spectrophotometrically. Chlorophyll *a* concentration was calculated using the equations of Jeffrey & Humphrey (1975).

To quantify biomass of endolithic algae within *O. patagonica* skeletons, the cleaned skeleton cores were dissolved in 7.5% nitric acid (v/v). The organic residues comprising the endoliths and the corals' organic matrices were dried overnight at 50 °C and weighed. In view of the thin tissue and thin skeleton, chlorophyll concentration and biomass were calculated per unit of surface area (cm^{-2}).

(b) *Pigments in partly bleached colonies*

Partly bleached colonies (where distinct areas of healthy, paled and totally bleached sections could be observed) were col-

lected ($n = 5$), photographed and the tissue was removed from the skeleton using a WaterPik. The bare skeleton was re-photographed. We compared pigmentation of the skeleton (resulting from the endolithic algae) at different bleaching stages of the tissue.

(c) *Translocation of photoassimilates*

To study translocation of photosynthetic products from the endolithic algae harboured in bleached and non-bleached *O. patagonica* skeletons to the coral tissue, totally bleached ($n = 15$) coral colonies were removed, including their substrate. We drilled a narrow hole (5 mm in diameter) underneath the coral skeleton up to the pigmented layer of the endoliths (figure 1). A ^{14}C -labelling cylinder (see Oren *et al.* 1997) was attached over the hole to enable point labelling of the endoliths in a restricted area. The colonies were then returned to their original location underwater (2–5 m depth), and the ^{14}C was injected into the cylinder (final concentration $0.01 \mu\text{Ci ml}^{-1}$) for an incubation period of 24 h (14 L : 10 D). At 24, 36 and 60 h after incubation (after the ^{14}C -labelling cylinder was removed), the coral tissue was removed from the skeleton using a WaterPik and the resulting volume was centrifuged to separate the tissue from the seawater. The skeleton was further cleaned of possible tissue remnants using a brush, and ground using a stone mill. Each sub-sample was acidified with 0.1 M HCl and left in a fume hood for 4 h to ensure that there was no remaining carbon dioxide. Tissue and skeleton powder were individually placed in a plastic vial and 8 ml of hydrogen peroxide (30%) was added in order to digest the tissues or organic components of the skeleton. After complete digestion (24 h), two replicates of 0.5 ml from each vial were sampled. Five millilitres of Biodegradable Counting Scintillation cocktail (BCS, Amersham) were added to each sample and ^{14}C activity was determined by a liquid scintillation counter (Packard & Tri-Carb 1500). Residual seawater after separation of the tissue showed negligible ^{14}C activity and thus was not added to the total tissue activity.

To study the tissue effect on the endoliths' ^{14}C incorporation within the coral skeleton, excluding the tissue (and possible zooxanthellae remnants) effect, a similar procedure was performed on nine bleached and nine healthy colonies, except that in this experiment the colonies were incubated after removal of their tissues. The clean skeletons, including the endolithic algae, were ^{14}C -incubated *in situ* for 24 h and sampled 12, 36 and 60 h after incubation.

Nine healthy colonies were labelled by mounting a labelling cylinder on the coral tissue (Oren *et al.* 1997) in order to compare the ^{14}C incorporation of the endolithic algae with that of the zooxanthellae.

Dark controls (incubation in the dark, $n = 9$), to prove light dependency of ^{14}C incorporation, were set by shading the colonies with 40 cm \times 40 cm black Plexiglass *in situ*.

3. RESULTS

(a) *Photosynthetic pigments and biomass*

Increasing bleaching (paleness) of the cores and a decrease in chlorophyll concentrations in the coral tissue produced an exponential increase in chlorophyll concentrations in the skeletons (figure 2a, $R^2 = 0.942$). Cores at low bleaching levels, with more than $4 \mu\text{g cm}^{-2}$ chlorophyll in their tissue (corresponding to less than 40% bleaching), had an average chlorophyll concentration in their skeleton of only $4.6 \pm 1.57 \mu\text{g cm}^{-2}$ ($n = 24$), whereas

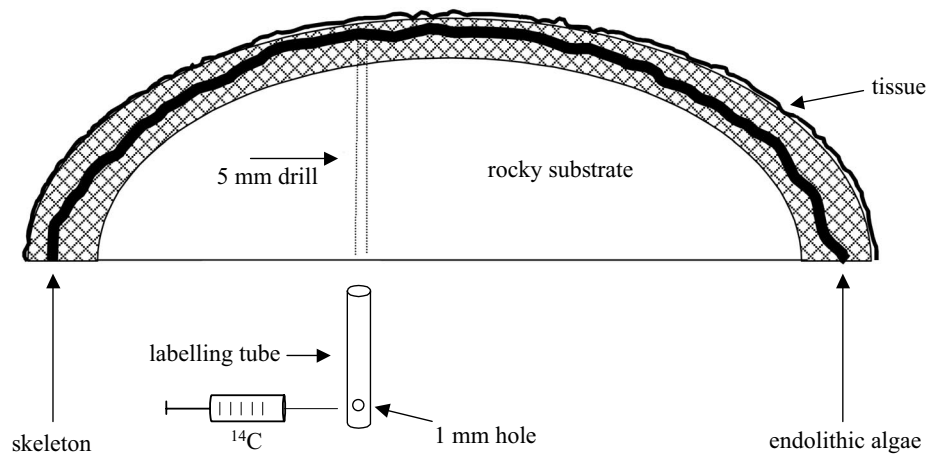


Figure 1. *Oculina patagonica*, schematic diagram of ^{14}C -labelling technique in bleached colonies.

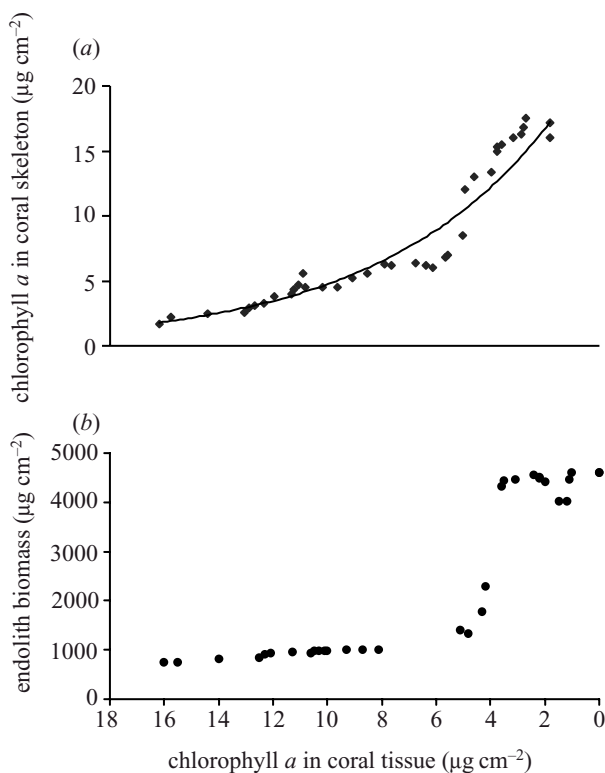


Figure 2. Dynamics of endolithic algae in *O. patagonica* skeletons during bleaching (levels of bleaching presented as chlorophyll *a* concentration in the coral tissue). (a) Chlorophyll concentration in the skeleton (originating from the endolithic algae) ($n = 37$); and (b) biomass of endolithic algae in coral skeletons at different bleaching levels ($n = 32$).

the average chlorophyll concentration in the skeleton of cores with less than $4 \mu\text{g cm}^{-2}$ chlorophyll in their tissue (corresponding to more than 40% bleaching) was $14.8 \pm 2.51 \mu\text{g cm}^{-2}$ ($n = 13$). Endolith biomass increased following a decrease in tissue chlorophyll concentrations (figure 2b), at a tissue chlorophyll concentration range of $8\text{--}16 \mu\text{g cm}^{-2}$ (corresponding to 0–20% bleaching), biomass values were up to $1012 \mu\text{g dry weight cm}^{-2}$. At a chlorophyll concentration range of $4\text{--}6 \mu\text{g cm}^{-2}$ (corresponding to 30–40% bleaching), biomass values ranged between 1403 and $2287 \mu\text{g dry weight cm}^{-2}$, and at a tissue chlorophyll concentration of less than

$4 \mu\text{g cm}^{-2}$ (greater than 40% bleaching), biomass values were up to $4612 \mu\text{g dry weight cm}^{-2}$ (figure 2b).

(b) Partly bleached colonies

After removal of the tissue from partly bleached colonies (figure 3), the skeleton under the zooxanthellate tissue (Z_1) was completely white (Z_2), whereas the skeleton under a bleached zone a few weeks old was heavily green pigmented, the pigment originating from the chlorophyll of endolithic algae. Under recently bleached areas (1–3 weeks), various levels of pigmentation were observed.

(c) Translocation of photoassimilates

^{14}C activity of the endoliths harboured within the skeletons of bleached corals ($n = 15$) was significantly higher than that of the endoliths in non-bleached corals ($n = 9$) (two-way ANOVA, $p_3 < 0.001$; figure 4 (S)). This result is consistent with the ^{14}C activity found in endoliths from bleached ($n = 9$) and non-bleached ($n = 9$) healthy colonies that were incubated after removal of their tissue (two-way ANOVA, $p_3 < 0.001$; figure 4 (SO)). Note that ^{14}C activity in (SO) was higher than that of corals incubated including their tissue (S).

^{14}C activity recorded in the tissues of healthy non-bleached ($n = 9$) colonies (incorporated by the zooxanthellae; figure 4a (T)) was 4–6-fold higher than the activity recorded in their skeleton (incorporated by the endolithic algae (S)), but only 1.5–3.5-fold higher than the activity recorded in skeletons of bleached ($n = 15$) colonies (figure 4b (S)).

Skeletons of bleached corals (figure 4a (S)) showed a significant decrease in ^{14}C activity, correlated with time ($r^2 = -0.92$, $p < 0.001$), while ^{14}C activity in their tissues (t) increased consistently and significantly 12, 36 and 60 h after incubation ($r^2 = 0.97$, $p < 0.001$; figure 4b).

By contrast, ^{14}C activity in healthy non-bleached skeleton (figure 4a (S)) and tissue (figure 4a (T)) was largely constant 12, 36 and 60 h after incubation. The same constant pattern of ^{14}C activity was recorded in skeletons of bleached and non-bleached corals that were incubated after removal of their tissue (figure 4 (SO)).

Dark control experiments demonstrated light-dependency of ^{14}C incorporation by the endoliths, with incorporation in the dark being less than 20% of that in the light.

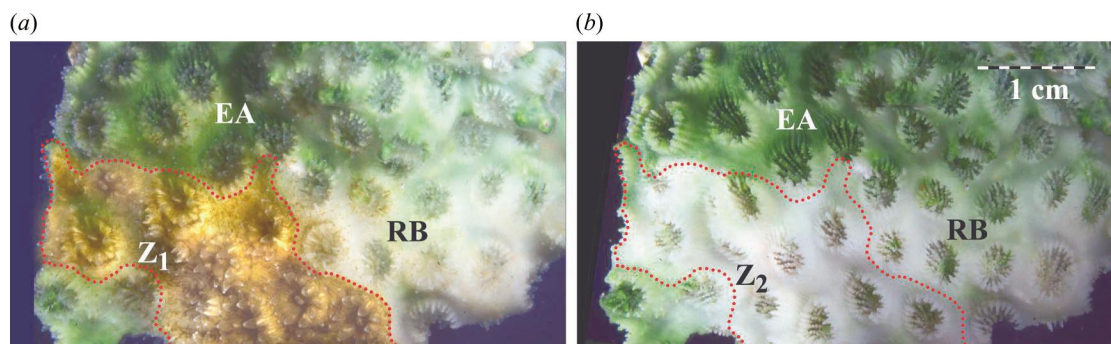


Figure 3. Distribution of endolithic algae during bleaching of the coral *O. patagonica* demonstrated on the same colony before and after removal of the tissue. (a) Prior to removal of the tissue, distinct stages of bleaching and tissue condition can be observed. Z_1 , area of healthy coral tissue; RB, an area of recently bleached and transparent coral tissue revealing skeleton free of pigmented endoliths; EA, an area of coral that was bleached for three weeks, showing the heavily pigmented endoliths beneath the transparent coral tissue. (b) After removal of the tissue, the endoliths condition can be detected and related to the pre-removed tissue condition. Z_2 : after removal of the living coral tissue from area Z_1 , no pigments were observed in the skeleton beneath the previously healthy tissue. Scale bar, 1 cm.

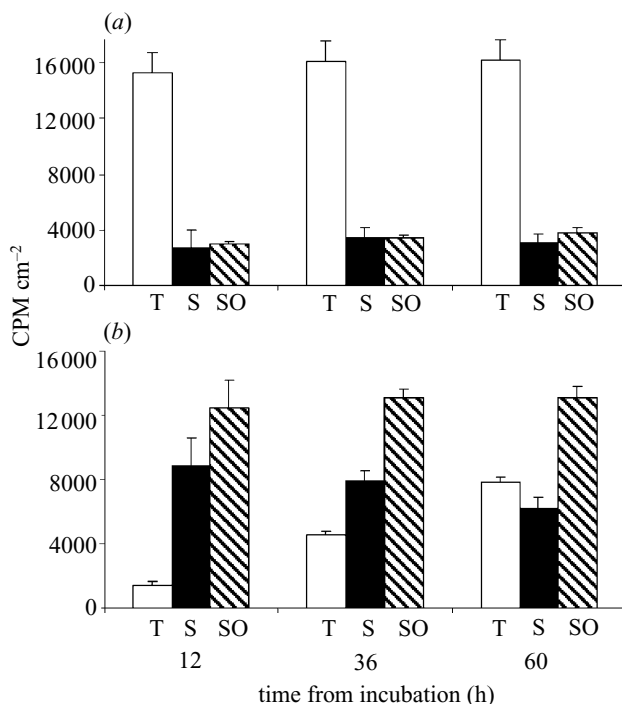


Figure 4. *Oculina patagonica*: ^{14}C activity of labelled photoassimilates recorded in the tissue (T), organic components of skeletons (S) and organic components of skeletons from colonies that were incubated after removal of their tissue (SO) 12, 36 and 60 h after incubation. (a) Healthy non-bleached colonies; (b) bleached colonies.

4. DISCUSSION

Much attention has been focused on bleaching in scleractinian corals due to mass mortality and local extinction, associated with large-scale bleaching episodes (Brown 1997; Glynn 1991, 1993; Hoegh-Guldberg 1999; Wilkinson 1999, 2000). However, bleaching may not always result in mortality (Hoegh-Guldberg 1999). In the present study we demonstrate that one of the mechanisms potentially assisting coral's survival through bleaching events may be the bloom of endolithic algae in the coral skeleton, with an increase in PAR penetrating it. Light levels set

the upper restriction on photosynthesis within the coral skeleton (Kanwisher & Wainwright 1967). In a healthy (non-bleached) colony, PAR reaching the endoliths within the coral skeleton is extremely low, because it is largely absorbed by the zooxanthellae, the coral tissue and the skeleton itself (Kanwisher & Wainwright 1967). However, during bleaching, with the loss of the zooxanthellae, absorbance of light by the coral tissue is low, allowing an increasing amount of PAR to reach the coral skeleton, resulting in a marked increase in biomass of the endolithic algae and increased production of photoassimilates. Photoassimilates released from the phototrophic endoliths reach the coral tissue, and due to the uptake of dissolved organic substances by the coral tissue, the photosynthesis products can be used (Schlichter *et al.* 1995). In the present study, translocation of photoassimilates from the coral skeleton (produced by the endolithic algae) to the tissue of bleached corals is revealed from the decreasing ^{14}C activity, over time, in the skeletons (figure 4b (S)) and increasing ^{14}C activity in the tissues (figure 4b (T)).

The rapid increase in biomass and chlorophyll concentration of the endoliths through increasing light intensities (figure 2) demands light acclimation capabilities from these algae, which usually inhabit very dark environments underneath the coral tissue (Shashar & Stambler 1992). While the energetic contribution of zooxanthellae to coral tissue decreases with increased bleaching, the contribution of the phototrophic endoliths increases. The translocation of endolith photoassimilates as an alternative energy source in these corals may explain the low mortality of *O. patagonica* following bleaching events. Schlichter *et al.* (1997) proposed that the coexistence of corals and endolithic algae is mutualistic ectosymbiosis. This symbiosis may be advantageous to the coral over endosymbiosis with zooxanthellae, during periods of environmental change (e.g. elevated seawater temperature). This advantage may be because the endoliths inhabit protected environments within the coral's skeletal compartments (Shashar *et al.* 1997) and thus are isolated from the ambient water. While this source of energy is nutritionally less important than the zooxanthellae (Schlichter *et al.* 1997), and is insufficient for sexual reproduction (Fine *et al.* 2001), it may

be vital for the survival of bleached colonies until the recruitment of zooxanthellae, resulting in recovery from bleaching during the following winter. This phenomenon may explain why massive and encrusting species, known to harbour dense populations of phototrophic endoliths in their skeleton (Highsmith 1981; Shashar & Stambler 1992; Shashar *et al.* 1997), are generally better survivors of mass bleaching events.

Differential susceptibility of corals to bleaching and survival following bleaching events were reported from many regions of the world, with evident lower susceptibility of massive and encrusting species, often explained by greater tissue thickness (Glynn 1988, 1993; Brown & Suharsono 1990; Hoegh-Guldberg & Salvat 1995; Kayanne *et al.* 1999; Hoegh-Guldberg 1999). Loya *et al.* (2001) reported that during the 1998 mass-bleaching event in Okinawa, Japan, branched corals were most susceptible while massive and encrusting colonies survived. They proposed that preferential survival of thick-tissued species, and shape-dependent differences in colony mass-transfer efficiency, were the reason for morphology-related survival.

We further propose that one of the mechanisms permitting survivorship of massive and encrusting coral species during bleaching events is their ability to utilize photoassimilates derived from their endolithic algae. This may explain, in part, the structural shifts that take place in some coral communities following mass-bleaching events.

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