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Alternate coral–bryozoan competitive superiority during coral bleaching

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Abstract Bleaching of corals results from the loss of their symbiotic algae (zooxanthellae) and/or pigments. The supply of photoassimilates provided by the zooxanthellae to the coral declines during bleaching and reduces the ability to activate energy-costly processes such as maintenance, growth and reproduction. In the present study we compared the competitive outcomes, expressed as overgrowth and changes in colony sizes of *Oculina patagonica* (an encrusting Mediterranean stony coral) and the bryozoan *Watersipora* sp., growing in contact with each other, during and between bleaching events. Year-round observations of tagged colonies showed alternating competitive outcomes: *O. patagonica* wins over *Watersipora* sp. between bleaching events, but loses during bleaching events. Using the ^{14}C -point-labeling technique on coral tissue, we examined intra-colonial translocation of photosynthetic products from the point-tissue labeling towards interaction zones. In non-bleached *O. patagonica*, competition resulted in preferentially oriented translocation of ^{14}C products to the interaction zone located up to 8 cm away from the tissue-labeling site. Sites opposite the interaction zone received significantly less labeled photoassimilates compared to the interaction zone. In bleached colonies (40–85% bleached surface area), such translocation did not occur, probably explaining the failure to compete with the encrusting neighbor *Watersipora* sp. Our findings demonstrate the importance of colonial integration and resource orientation for the competitive superiority of *O. patagonica*.

Introduction

Coral bleaching results from the disruption of the symbiotic association between coral hosts and their symbiotic photosynthetic algal endosymbionts (Glynn 1993; Brown 1997; Hoegh-Guldberg 1999). During bleaching, hermatypic corals may occasionally suffer damage from a multitude of other agents (apart from the loss of their main energy source), such as storms, sedimentation, temperature fluctuations, emersion at low tide, diseases, anthropogenic stresses, predation and competitive interactions. The latter is of great importance (Chornesky 1989; Glynn 1993; Hoegh-Guldberg 1999), since competition for space on which to live is intense and is often the most important limiting resource in marine hard-substratum environments (Connell 1961; Dayton 1971). While the importance of competition to coral reef community structure is questionable (van Woesik 2002), in temperate zones competition has a major role in determining the structure of species assemblages in coastal habitats (Underwood 1979, 1992). Competition between individual colonies of different species has been shown to result in either a bilateral cessation of growth (“stand-off”) or a “win” for one competitor, when it damages and/or overgrows the opposing neighbor (Chornesky 1989). However, an overgrowing “winner” might later turn up overgrown and lose in the competition [“a reversal” sensu Buss and Jackson (1979) or “repeated reversals” sensu Chornesky (1989), when it occurs periodically]. Neighboring organisms may affect survival, shape, reproductive output and growth rate of sedentary organisms (Romano 1990; Alino et al. 1992).

In sessile invertebrate communities, the rate at which a species grows is an important factor influencing its competitive superiority (Sebens 1986; Nandakumar et al. 1993). Scleractinian corals are slow-growing organisms. Unless they possess some defensive mechanism for resisting invasion, corals would provide substrate, for sufficient periods of time, for settlement and growth by faster growing organisms (Porter 1974). The defensive

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mechanisms include the use of spines by bryozoans (Stebbing 1973; Harvell 1998), sweeper tentacles, mesenterial filaments (Lang and Chornesky 1990) and allelopathy (Sullivan et al. 1983; Koh and Sweatman 2000) by corals, all of which demand energetic input.

Essential life-preserving resources (amino acids, sugars, carbohydrates and small peptides) are supplied to the coral host from the zooxanthellae residing inside its tissue (Muscatine 1973; Trench 1979; Swanson and Hoegh-Guldberg 1998). In hermatypic corals up to 95% of the photosynthetic products are continuously translocated to the coral host (Muscatine 1990), where they contribute 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 and Cernichiaro 1969; Crossland et al. 1980; Muscatine et al. 1981, 1984; Kellogg and Patton 1983; Rinkevich and Loya 1984; Stimson 1987; Rinkevich 1989). Taylor (1977) reported a strong preferential movement and accumulation of ^{14}C -labeled compounds towards the tips in *Acropora cervicornis*. He further recorded an analogous pattern of photosynthate translocation in flat colonies of *Montastrea annularis*, where ^{14}C -labeled compounds were found at the growing edges up to 9 cm away from the incubation site.

Resources available to an organism are often limited and, therefore, must be allocated among competing biological functions, such as maintenance, somatic growth and reproduction (Bak and Steward-Van Es 1980; Bak 1983; Kozłowski and Wiegert 1986; Harrison and Wallace 1990). Consequently, intra-colonial resource integration is regarded as a basic life-preserving ability and one of the most important advantages of colonial organisms (Oren et al. 2001).

Oculina patagonica is an encrusting Mediterranean stony coral common along the Mediterranean coast of Israel at depths of 1–6 m (Fine et al. 2001). Bleaching of *O. patagonica* was first recorded in summer 1993 (Kushmaro et al. 1996), and has been continuously monitored since then. Bleaching of 70–80% of the population occurs annually, starting in late May with the rise in seawater temperature (Kushmaro et al. 1998). In contrast with reports from other regions of mass mortality following bleaching events, >90% of the bleached *O. patagonica* colonies fully recovers in the next winter (Kushmaro et al. 1998), through recruitment and/or cell division of their symbiotic zooxanthellae. In early observations we noticed that colonies of *O. patagonica* interact through direct aggression and overgrowth with other colonial organisms in their vicinity, mainly the bryozoan *Watersipora* sp. This encrusting cheilostome bryozoan (reaching a maximum size of 40 cm) and *O. patagonica* share the same habitat of vertical subtidal walls. While many *O. patagonica* colonies undergo bleaching during the summer, the bryozoan *Watersipora* sp. is an azooxanthellate species.

In the present study we focused on the effect of coral bleaching and colony integration on competitive

interactions of *O. patagonica* with the bryozoan *Watersipora* sp. We followed *O. patagonica*'s competitive performance during and between bleaching events, as well as the resource orientation and translocation associated with it. Recently we demonstrated an oriented translocation of ^{14}C -labeled materials towards regenerating areas in *O. patagonica* (Fine et al. 2002). We showed that in bleached corals, no such translocation occurred. We found the existence of a bleaching threshold of ca. 40% that terminates intra-colonial resource translocation in *O. patagonica*. In the present study, we examined the competitive capabilities of the species in view of the previously found bleaching threshold.

Materials and methods

Measurement of overgrowth interactions

Coral–bryozoan overgrowth interactions were analyzed along the vermetid reefs of Sdot-Yam, Israel (32°29.77'N; 34°54.23'E), at depths of 1–6 m. All the colonies inhabit vertical walls of the vermetid reefs, a shaded environment of variably low irradiance, according to sea conditions. Tagged colonies of *Oculina patagonica* ($n=200$) were surveyed to assess the number of competitive interactions between *O. patagonica* and *Watersipora* sp. These colonies were randomly chosen from an area of 500 m² that was under continuous observation during the *O. patagonica* bleaching study (1993–2000, Fine et al. 2001). All *O. patagonica*–bryozoan interactions, as well as interactions with other encrusting organisms were recorded. When the growing edge of a competitor was seen to overgrow and cover parts of the living surface area of the other competitor it was determined to be a “winner”. Direct settlement onto one of the competitors was not counted as overgrowth (see Turner and Todd 1994; Barnes and Rothery 1996).

Twenty tagged interactions between *O. patagonica* and *Watersipora* sp. (out of 30 interactions recorded in the above-mentioned survey) were studied in detail during 2000–2001. The competitors were observed and photographed monthly (January 2000–December 2001) using a Nikonos-V camera, with a close-up apparatus mounted on a 28 mm lens. Size of competitors (surface area) and percentage of bleaching (portion of bleached area from total colony area) of *O. patagonica* colonies were analyzed from the color slides using a computerized image analyzer (Olympus CUE-3). Growth rate of non-interacting colonies of *O. patagonica* ($n=9$) and *Watersipora* sp. ($n=9$) was calculated in a similar manner (photography and image analyzing), to allow comparison of growth rate between interacting and non-interacting colonies.

Radioactive labeling procedure

In order to study patterns of intra-colonial translocation of photosynthetic products within colonies of *O. patagonica*, we used ^{14}C -labeling cylinders (see Oren et al. 1997) that enabled coral tissue labeling on a restricted colony portion of 5 cm². To achieve a firm seal with the coral tissue, the opening of each cylinder was glued to a section of self-adhesive isolation foam. Final attachment of the cylinders to the coral surface was accomplished by wires anchored to a firm hard substrate or pre-prepared screws mounted near the colony. A 0.5 mm hole covered with rubber enabled injection of the radioactive carbon into each cylinder (final concentration: 0.01 $\mu\text{Ci ml}^{-1}$). ^{14}C -labeling of all experimental colonies was initiated at 0900 hours for a total period of 24 h, after which the cylinders were removed. Coral cores of 1 cm² and 0.5 cm thickness (tissue + skeleton) were sampled, using a stainless-steel corer, 48 h after removal of the labeling cylinders. Each core was individually placed in a plastic vial and transferred to the

laboratory. The seawater from each vial was drained, and 8 ml of hydrogen peroxide (30%) was added in order to digest the tissues. After complete tissue digestion (24 h), two 0.5 ml replicates from each vial were sampled. Then, 5 ml of biodegradable counting scintillation cocktail (BCS, Amersham) was added to each sample. Activity of ^{14}C was determined by liquid scintillation counter (Packard, Tri-Carb 1500).

Intra-colonial translocation in non-bleached versus bleached colonies during competition

To examine possible intra-colonial translocation of photosynthetic products towards the coral–bryozoan interaction zone, we conducted ^{14}C labeling in ten healthy colonies of *O. patagonica* (five pre-bleached in April and five non-bleached in July 2001), five partly bleached colonies with < 40% bleached surface area and seven partly bleached colonies with > 40% bleached surface area (July 2001, 12–18 cm in diameter) that were found adjacent to and in contact with *Watersipora* sp. (5–15 cm in diameter). The bleaching percentage groups were selected according to Fine et al. (2002). In partly bleached colonies the labeling cylinder was attached on a non-bleached section of the colony. In each of the colonies, the labeling cylinder was attached at a distance of 4–8 cm from the interaction (coral–bryozoan) line (Fig. 1). Using a stainless-steel corer, seven coral cores (0.5 cm radius, 0.5 cm thickness, tissue + skeleton) were sampled from each labeled colony 48 h after removal of the labeling cylinder: one core from the labeling point (L), two cores from the colony edges at the interaction zone (IZ, 4–8 cm from L), two cores opposite the interaction zone (OIZ, 3–5 cm from L) and two cores on the colony edges opposite the interaction zone (CE, up to 8 cm from L, Fig. 1). Six additional intact unlabeled colonies (three non-bleached and three bleached) were sampled for control background ^{14}C -activity measurements.

Results

Overgrowth interactions

Bleaching of *Oculina patagonica* was observed in late May and beginning of June (1993–2000), with a rise in seawater temperature to ca. 26°C. Recovery of the colonies, determined by the regaining of pigmentation, started with a decrease in seawater temperature in

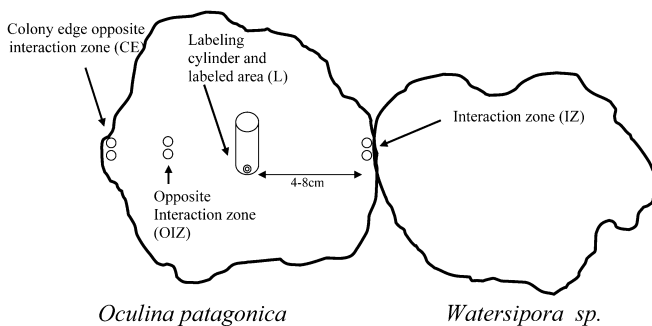


Fig. 1 *Oculina patagonica*. Schematic diagram of ^{14}C labeling and sampling locations in colonies during competitive interactions with the bryozoan *Watersipora* sp. [L labeled area; IZ interaction zone, located 4–8 cm away from labeled area; OIZ sites opposite the interaction zone, 4–8 cm away from labeled area; CE colony edge opposite IZ, located 4–8 cm away from labeled area; open circles locations from which cores (tissue and skeleton) were sampled for examination of ^{14}C activity]

October (Fig. 2). Seawater temperature along the Mediterranean coast of Israel ranges from a minimum of 16°C in March to a maximum of 30°C in August (Fig. 2). Out of the 200 *O. patagonica* colonies examined, 41 were found in close contact with encrusting organisms: 30 with the bryozoan *Watersipora* sp., six with sponges, three with ascidians and two intraspecific interactions. All interactions recorded were between colonies inhabiting vertical (wall) substrates in relatively shaded areas (overhangs and north-facing walls).

Out of the 20 photographed interactions between *O. patagonica* and *Watersipora* sp. the win/lose ratio was significantly correlated with bleaching percentage (portion of bleached area from the total colony surface area, $r^2=0.85$, $P<0.001$). With an increase in the bleaching percentage during the bleaching season (June–September, Fig. 2) there was an increase in the number of losses in competition with *O. patagonica* (Fig. 3a). In all observations of the tagged colonies, non-bleached and partly bleached (< 40% bleached surface area of the total colony area) colonies were winners, while colonies with > 40% bleached surface area lost in competition with *Watersipora* sp. During January–April, 95 ± 10% ($n=20$) of the *O. patagonica* colonies were winners. Only 5% of the colonies that were still bleached (> 40% bleached surface area) lost in competition with *Watersipora* sp. During May–September, the peak of the bleaching period, only 30 ± 5% ($n=20$) of the *O. patagonica* colonies (non-bleached colonies and colonies with < 40% bleached surface area), won, while 70 ± 5% (> 40% bleached surface area) lost. During October–December, with a gradual recovery from bleaching (Fig. 2), 55 ± 10% ($n=20$) of the colonies (non-bleached colonies and colonies with < 40% bleached surface area) were winners in competition (Fig. 3a).

Growth rate (linear extension) attained by interacting *O. patagonica* and *Watersipora* sp. according to analysis of the monthly photos was 0.6 ± 0.3 and 0.7 ± 0.5 cm month⁻¹ ($n=20$), respectively, during winter months

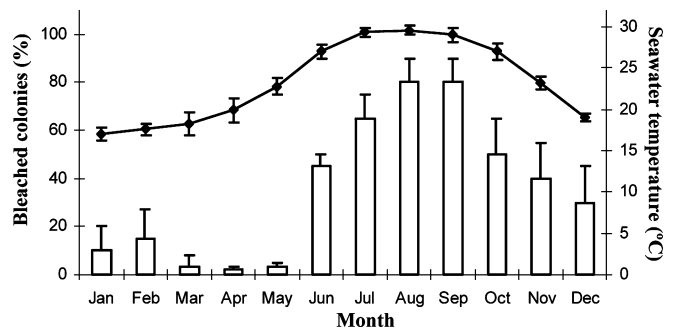


Fig. 2 *Oculina patagonica*. Monthly bleaching percentages of 200 tagged colonies (±SD) (bars, visual estimates), and monthly average of seawater temperatures recorded from 1993 to 2000 (line, ±SD). During the summer, with an increase in seawater surface temperatures (SST), a peak in the number of bleached colonies is evident, while during the winter, with a decrease in SST, coral recovery takes place (less bleached colonies)

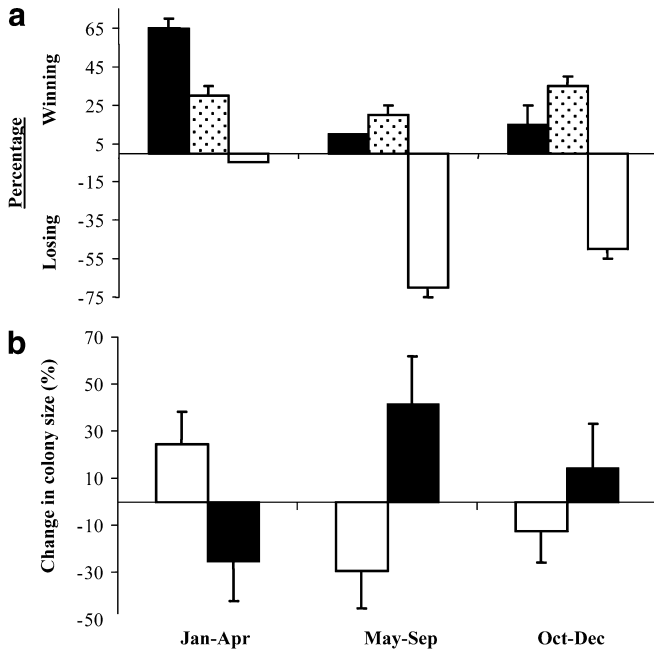


Fig. 3a, b *Oculina patagonica*. **a** Percentage of interactions (winning or losing) between *O. patagonica* and *Watersipora* sp. throughout January–December, 2000–2001 (solid bars non-bleached colonies; dotted bars and open bars colonies of <40% or >40% bleached surface area, respectively). **b** Net growth percentage of *O. patagonica* (open bars) and *Watersipora* sp. (solid bars) during periods between bleaching events (January–April) during bleaching events (May–September) and during recovery from bleaching (before full recovery, October–December)

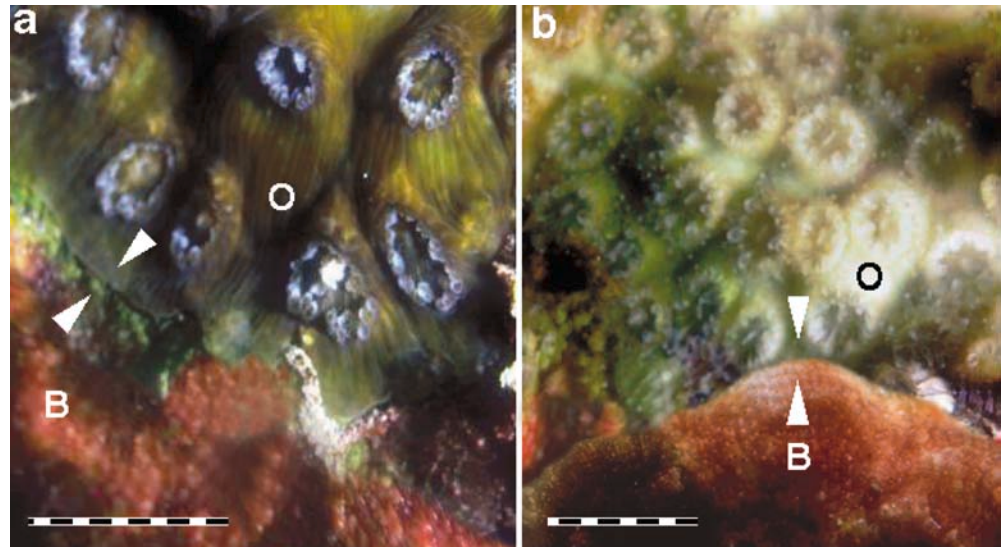
(November–April). During summer (May–October), growth rate of non-bleached and partly bleached (<40% bleached surface area) *O. patagonica* colonies decreased to 0.3 ± 0.2 cm month⁻¹ ($n=12$) and that of bleached colonies (>40% bleached surface area) decreased to 0.0 cm month⁻¹ ($n=8$). In contrast, *Watersipora* sp. colonies maintained a summer growth rate of 0.6 ± 0.3 cm month⁻¹ ($n=20$) (similar to winter growth rate).

Non-interacting colonies of *O. patagonica* and *Watersipora* sp. attained a significantly lower growth rate than interacting colonies [one-way ANOVA, least significant difference (LSD) $P < 0.001$]. Colony size was not a determinant of competitive ability ($r^2 = 0.01$, $P > 0.05$). During January–April *O. patagonica* overgrew *Watersipora* sp. gaining $24.3 \pm 14.0\%$ ($n=20$) of its initial size (average size during October–December) at the expense of the latter (Figs. 3b, 4a). During May–September (bleaching season), *Watersipora* sp. overgrew $29.7 \pm 15.7\%$ ($n=20$) of *O. patagonica*'s surface area and gained (including growth in non-interacting zones of the colony) $41.4 \pm 20.2\%$ ($n=20$) of its initial size (Figs. 3b, 4b). During recovery from bleaching (October–December) *O. patagonica* overgrew $12.6 \pm 13.0\%$ ($n=20$) of *Watersipora* sp. surface area and gained (including growth in non-interacting zones of the colony) $14.3 \pm 18.6\%$ of its initial size (Fig. 3b).

Intra-colonial translocation in non-bleached versus bleached colonies during competition

Forty-eight hours after ¹⁴C-labeling treatments, the 5 cm² labeled areas (L) in all experimental colonies demonstrated high ¹⁴C activity (9087.8 ± 2743.2 CPM cm⁻², $n=22$) compared to background (¹⁴C activity in healthy randomly sampled intact *O. patagonica* colonies = 25.8 ± 6.7 and 24.6 ± 5.4 CPM cm⁻², $n=6$, for non-bleached and bleached intact colonies, respectively). ¹⁴C incorporation to healthy non-bleached *O. patagonica* colonies did not differ significantly from that incorporated to healthy non-bleached parts of partly bleached colonies (one-way ANOVA with repeated measures, LSD, $P > 0.05$). ¹⁴C incorporation and translocation rates of non-bleached colonies in April did not differ significantly from that found in July (one-way ANOVA with repeated measures, LSD, $P > 0.05$, $n=10$).

Fig. 4a, b *Oculina patagonica*. Competitive interactions showing: **a** a healthy non-bleached *O. patagonica* (*O*) colony overgrowing the bryozoan *Watersipora* sp. (*B*) and **b** *Watersipora* sp. overgrowing a bleached *O. patagonica* colony. Scale bars: 5 mm



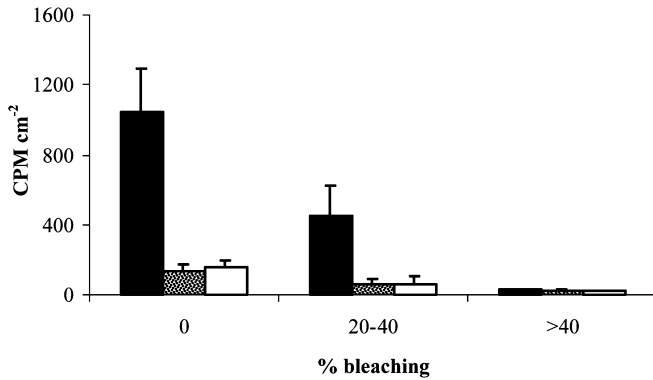


Fig. 5 *Oculina patagonica*. Average activity of ¹⁴C in the coral tissues (CPM cm⁻²) recorded in non-bleached colonies ($n=10$), with 20–40% bleached surface area ($n=5$) and colonies with >40% bleached surface area ($n=7$) (solid bars coral tissue from interaction borders, located 4–8 cm from the labeled site; dotted bars coral tissue from sites opposite to the interaction borders, 4–8 cm from the labeled site; open bars colony edges opposite to the interaction zone). Average ¹⁴C activity recorded in the labeling area (L) was 9087.8 ± 2743.2 CPM cm⁻², $n=22$. Background ¹⁴C activity recorded in randomly sampled intact *O. patagonica* colonies was 25.8 ± 6.7 and 24.6 ± 5.4 CPM cm⁻², $n=6$, for non-bleached and bleached intact colonies, respectively

Coral samples taken from the colony edge within the interaction zone (IZ) of non-bleached colonies ($n=10$) exhibited ¹⁴C activity significantly higher than that of samples opposite the interaction zone (OIZ) and of samples from the colony edges (CE) opposite IZ (one-way ANOVA with repeated measures, $P < 0.001$; Fig. 5). In non-bleached colonies, minor translocation was detected also to the site opposite the interaction zone (OIZ) and to the colony edges opposite the interaction zone (CE). We detected a sub-group of colonies, with 20–40% bleached surface area ($n=5$), that showed significant ¹⁴C translocation to the interaction zone (one-way ANOVA with repeated measures, LSD, $P < 0.001$; Fig. 5), but non-significant translocation to OIZ and CE (one-way ANOVA with repeated measures, LSD, $P > 0.05$; Fig. 5).

In bleached colonies (>40% bleached surface area, $n=7$), samples taken from the colony edges within the interaction zone (IZ) exhibited ¹⁴C activity that did not differ significantly from that of OIZ, CE or even the intact control samples (one-way ANOVA with repeated measures, LSD, $P > 0.05$; Fig. 5).

Discussion

Shifts in species composition and community structure following bleaching events in coral reefs have been reported (Glynn 1988; Brown and Suharsono 1990; Gleason 1993; Guzman and Cortes 2001; Loya et al. 2001) and widely discussed (Glynn 1993; Brown 1997; Done 1999; Hoegh-Guldberg 1999; Wilkinson 2000). One of the factors shaping communities during and following bleaching events is inter-specific competition,

as it is well understood that corals under severe competition from other organisms during bleaching have reduced recovery potential (Done 1999).

However, in temperate non-reef environments, no reports are available as to the consequences of coral bleaching on community structure in general and competition in particular. On temperate infralittoral shores, such as the environment studied in the present study site, coralline algae cover almost all available space and sedentary animals are usually restricted to shaded or vertical substrates. The latter tend to be completely overgrown by organisms, especially colonial forms (see Peres 1967; Sara and Vacelet 1973), resulting in competition for space (Connell 1961; Dayton 1971).

Zibrowius and Ramos (1983) reported the high competitive competence of *O. patagonica* through overgrowth of mussels, oysters, barnacles and ascidians. In the present study we demonstrate the effect of bleaching events on the competitive ability of the scleractinian Mediterranean coral *O. patagonica*. The competitive superiority of *O. patagonica* over the bryozoan *Watersipora* sp. during winter months is expressed by its high win/lose ratio as well as by an increase in colony size of *O. patagonica* and a decrease in colony size of its competitor *Watersipora* sp. (Fig. 3b). However during summer, when the coral population undergoes bleaching, with the loss of its zooxanthellae, it ceases to grow and becomes susceptible to overgrowth by competing species, in this case mainly by *Watersipora* sp. (Figs. 3, 4).

The importance of colony size on the competitive success of sessile organisms has been well documented by Buss (1980), who demonstrated that larger colonies possess higher competitive capabilities. However, the opposite is true in competitive interactions between *O. patagonica* and *Watersipora* sp.; since very small (<12.5 cm²) colonies have a lower tendency to bleach (Levin, Fine and Loya, unpublished data), they are likely to avoid overgrowth by *Watersipora* sp. or even overgrow it and win in competition.

During bleaching, reduced growth (Goreau and Macfarlane 1990), calcification and repair capabilities (Glynn 1993; Meesters and Bak 1993) may translate into a reduced ability to compete for space with other organisms, such as algal turf, coralline algae, macroalgae, sponges, bryozoans and tunicates (Glynn 1993; Hoegh-Guldberg 1999). The growth rates of competing *O. patagonica* colonies as presented in this study are higher than those reported previously (Fine et al. 2001) for non-competing colonies. A similar case was reported for a bryozoan by Buss (1980). This suggests that a higher than usual growth rate is needed to win competition. Indeed more resources (¹⁴C-labeled compounds) were found to be translocated to the forward-growing edges of *O. patagonica* (see also Taylor 1977). It also suggests that when no competitors are encountered, the colony will not use its maximal growth potential, and the growth–reproduction trade-off (Loya 1976; Szmant-Froelich 1985; Glynn 1993) will tilt towards investing

resources in sexual reproduction (increasing the number of genets rather than increasing in size). An important consequence of modularity is reflected in the colony's ability to continually re-allocate resources among its units in response to environmental changes and various stresses caused by biotic or abiotic factors. Intra-colonial transport of organic compounds within hermatypic coral colonies is in fact a well-known phenomenon (Muscatine and Porter 1977; Taylor 1977; Muscatine et al. 1981). Pearse and Muscatine (1971) have already suggested that symbiont photosynthates are translocated throughout the coral tissue towards regions of maximal demand. In bryozoans too, newly developing zooids at the colony edge are initially unable to feed and must therefore be subsidized by feeding zooids in the center of the colony (Harvell 1990). Miles et al. (1995) suggested that translocation in a bryozoan is controlled by a source-sink process: inner zooids act as source, while zooids on edges act as sink.

The ^{14}C -fixation rate and translocation recorded in the present study for *O. patagonica* are much lower than those recorded for reef coral species such as *Stylophora pistillata* (Gattuso et al. 1993), *Platygyra lamellina* and *Favia fava* (Oren et al. 1997) and *Porites* sp. (Oren et al. 1998). This may imply to lower metabolism of *O. patagonica* during the time of the experiment and thus reduced uptake, or a weaker alga-coral symbiotic relationship resulting in reduced release of photosynthetic products by the algae. *O. patagonica* showed translocation of ^{14}C -labeled materials toward regions of competitive interaction (IZ) and also (although to a lesser extent) to other zones of the colony (OIZ, CE). These results demonstrate the ability of non-bleached *O. patagonica* colonies to translocate photosynthetic products towards areas of contact with competing neighboring organisms. Furthermore, the fact that the interaction zone, demonstrated significantly higher ^{14}C activity when compared with the opposite sites (OIZ and CE) indicates that the translocation was oriented. These findings coincide with our previous findings on translocation of ^{14}C -labeled materials towards regenerating areas in *O. patagonica* Fine et al. (2002). Another noteworthy result that correspond with (Fine et al. 2002) is that colonies with >40% bleached surface area showed no translocation of ^{14}C toward the interaction zone (nor to other parts of the colony). This may explain the inferior competition capabilities demonstrated by bleached colonies of *O. patagonica*. Colonies with 20–40% bleached surface area demonstrated oriented translocation to the interaction zone, but negligible translocation to OIZ or to CE. This may imply preferential translocation toward regions of competition, causing the colony to shut down translocation to non-competing edges and, hence, maintaining life-preserving functions (i.e. preventing overgrowth by competing neighbors).

In the present study we have shown that competitive competence of *O. patagonica* is coupled with resource

translocation to the interaction zones. During bleaching, lower metabolic capacity of the colony results in lower resource translocation capabilities, explaining the alternate competitive superiority or inferiority of *O. patagonica* between and during bleaching events, respectively.

We assume that the current competitive steady state of *O. patagonica*, as shaped by the annual bleaching events, may change in accordance with the frequency and intensity of the bleaching events. Increasing incidents and severity of coral bleaching in the future and subsequent failures to out-compete other sessile organisms might end up in the exclusion of the currently most abundant coral species along the eastern Mediterranean coast.

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