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Size matters: bleaching dynamics of the coral *Oculina patagonica*

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ABSTRACT: A 2-yr continuous photographic monitoring of a tagged population of the encrusting coral *Oculina patagonica* in the Mediterranean was conducted to study intra-colonial bleaching dynamics and the relationship between bleaching, mortality, and colony size. Surveys of non-tagged colonies showed that during the peak bleaching season (August, sea surface temperature = 31°C), non-bleached colonies were frequently found to be small colonies averaging 4.6 ± 2.3 cm in diameter. Within tagged colonies, percent bleached surface area was correlated to water temperature. In colonies that underwent bleaching, the perimeter of the colony was affected first, and, as water temperatures increased, bleaching progressed toward the colony center. During the summer months, partial mortality occurred in the perimeter region of bleached colonies in 22% of the tagged colonies and 25% of the tagged colonies died; 40% of the colonies that died belonged to the largest size group. This partial mortality caused an average decline of 46 ± 27% in the average colony size, resulting in a shift to a smaller size group within the monitored population. Since in this species, colonies as small as 2 cm in diameter are reproductive, bleaching may have a less significant effect on the reproductive fitness of the small size groups in the population. The high mortality of large colonies, high survivorship of the small colonies, and the decline in colony size, due to partial mortality, suggest that, in the case of bleaching in populations of *O. patagonica*, small colony size is advantageous.

KEY WORDS: Coral bleaching · Mediterranean Sea · Population dynamics · *Oculina patagonica*

INTRODUCTION

Coral bleaching, the whitening of corals due to loss of their symbiotic algae (zooxanthellae) and/or their pigments (Hoegh-Guldberg & Smith 1989, Glynn 1993, Brown 1997), has affected extensive reef areas around the world (Hoegh-Guldberg 1999). Bleaching is deleterious for corals, resulting in reduced growth rates (Goreau & MacFarlane 1990), suppression of sexual reproduction (Szmant & Gassman 1990, Fine et al. 2001), impaired healing following damage (Meesters & Bak 1993), increased susceptibility to disease (Harvell et al. 1999), and, occasionally, mass mortality (Wilkinson 1999, Glynn et al. 2001, Loya et al. 2001). Mortality in corals is generally size specific, and rates of whole-colony mortality decrease as the size of the colony increases (Connell 1973, Sakai 1998). However, mortality following bleaching events is believed to be independent of colony size (Baird & Marshall 2002). Nevertheless, field evidence indicates that mortality rates of coral recruits are unaffected by bleaching (Mumby 1999) and show high recovery by recently settled juveniles compared with adults (Edwards et al. 2001). Moreover, both experimental and theoretical works predict that large size may actually be a disadvantage when corals are exposed to thermal stress (Nakamura & Van Woesik 2001). Loya et al. (2001) reported that small colonies of acroporid corals had higher survivorship than large colonies in the same habitat, following a mass bleaching event in Okinawa,

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Japan. This phenomenon reoccurred following a bleaching event at the same site 3 yr later, when small colonies of *Acropora* were least affected (Bena & Van Woesik 2004). Similar results were found following a bleaching event in the Java Sea, when the smallest mushroom corals (fungiids) were the least affected (Hoeksema 1991). Thus, the accumulating evidence raises the question of a possible relationship between colony size and bleaching.

While large-scale bleaching patterns of coral reefs have been studied extensively (Hoegh-Guldberg 1999), little is known about within-colony bleaching patterns (spatial distribution of bleached patches over the surface of a colony). The manner in which colonies bleach is considered species specific (Lasker et al. 1984, Gates 1990). For example, within the Fungiidae, some species were affected over their whole upper surface during a bleaching event, while other species showed a mosaic pattern (Hoeksema 1991). In *Agaricia* spp. the ridges of the colonies appeared white, while *Montastrea annularis* colonies had a 'blotchy' appearance, and in *Porites porites* bleached tissue was restricted to 1 or 2 branches of the top of the colony (Gates 1990). Lasker et al. (1984) described a similar bleaching pattern for the hydroids *Millepora alcicornis* and *M. complanata*, where colonies first whitened at their tips and the bleached area then extended toward the colony base. Brown et al. (2000) reported intercolonial bleaching patterns in *Goniastrea aspera* and explained it by differential exposure to solar radiation between east- and west-facing surfaces.

Every summer since 1996, 80 to 90% of the colonies of the encrusting coral *Oculina patagonica* undergo bleaching in the Mediterranean Sea, off the coast of Israel (Israely et al. 2001). This occurs when surface seawater temperatures (SST) rise over 26°C to a maximum of 30 to 31°C. It was shown that the causative agent for bleaching in this coral was the bacterium *Vibrio shiloi* (Kushmaro et al. 1996, 1997) and that seawater temperature is a contributing factor (Rosenberg & Ben-Haim 2002). In contrast to reports of post-bleaching mass mortality from other regions, most of the *O. patagonica* colonies recover during the winter months. Bleaching then re-occurs as the water temperatures rise the following summer (Kushmaro et al. 1998, Fine et al. 2001). The repeated and high incidence of these bleaching events in *O. patagonica* colonies along the Israeli Mediterranean shore makes this coral a model organism for studying the dynamics of bleaching at both population and individual colony levels. This study is the first to conduct continuous monitoring of the same coral population during 2 consecutive bleaching events in order to examine within-colony bleaching patterns and to ascertain the relationship between bleaching, colony size, and partial mortality.

MATERIALS AND METHODS

The study was performed from 2000 to 2003 at Sdot-Yam (Mediterranean coast of Israel: 32° 29.77' N, 34° 53.23' E) along the 'vermetid reefs' at a depth range of 3 to 6 m. Observations were performed by SCUBA diving. Ambient seawater temperatures were obtained using an Onset Stow Away data-logger placed at the study site at a depth of 1.5 m.

Survey. During August and November 2001 and August and September 2002, bleaching surveys were conducted at Sdot-Yam. A defined area of 500 m^2 was examined extensively by SCUBA diving. The diameter of each *Oculina patagonica* colony observed in the study area was measured to the nearest millimeter using a ruler, and the percentage of the bleached surface area was estimated visually.

Photographic monitoring. A total of 62 colonies of *Oculina patagonica* were tagged (31 in December 2000 and 31 in October 2001) at the study site. During the research all examined colonies were photographed monthly using a Nikonos-V camera or a digital Sony DSC P-9 camera. The photographs were transferred to JPEG format to enable further analysis. Bleaching progression (increase in the colony bleached surface area) was examined using the PHOTOSHOP 7 (Adobe) program by laying several consecutive photographs one on top of another. Total colony area and bleached surface area were measured using the INSPECTOR 2.1 (Matrox Electronic Systems) program. This allowed the calculation of bleaching percentage and progression.

In order to examine whether colony size plays a role in bleaching, the tagged colonies were divided at the beginning of the monitoring period into 3 size classes, with respect to their maximal live surface area (MLSA) as follows: small (MLSA < 16 cm^2), medium (MLSA > 16 cm^2 and < 60 cm^2), and large (MLSA > 60 cm^2).

Zooxanthella density and chlorophyll measurements. In order to ascertain whether the within-colony bleaching pattern is due to a possible difference between the initial density of zooxanthellae and the chlorophyll *a* concentration in the colony center versus its margins, equal-sized core samples (1 cm diameter and 2 to 3 mm thick) from the center and the perimeter were sampled (May 2003) from 8 randomly selected healthy colonies. Coral tissue was removed from the skeleton using a jet of re-circulated, 0.45 µm filtered seawater (FSW) using a WaterPik (Teledyne, Johannes & Wiebe 1970) and centrifuged at 4500 × *g* for 20 min in 50-ml tubes. In order to separate host tissue from zooxanthellae, the liquid extract was discarded and the pellet was re-suspended in 1 ml FSW, homogenized, and transferred to 1.5-ml Eppendorf tubes. Following centrifugation at 20 000 × *g* for 10 min, the liquid extract was discarded and the pellet was re-suspended in 1 ml FSW. This step was repeated twice in order to obtain a clean sample. Density of zooxanthellae in each sample was determined from counts of 3 sub-samples (10 µl each), which were viewed using an improved Neubauer hemocytometer (Weber). Counts were normalized to coral surface area.

To quantify chlorophyll *a* concentration the pellet containing the zooxanthellae was further assayed by extraction in 1 ml of chilled 90% acetone overnight. The extracted chlorophyll was quantified spectrophotometrically, and the chlorophyll *a* concentration was calculated using the equations of Jeffery & Humphrey (1975) and normalized to coral surface area.

Statistical analysis. All statistical analyses were carried out using Statistica 6.1. The data were tested for normality and homogeneity of variances, when required arcsine transformations were obtained. Fisher's LSD (least significant differences) tests were used as post hoc comparisons when significant differences were detected using ANOVAs (analyses of variance). Results are presented as averages (± standard deviations) throughout the text.

RESULTS

Seasonal bleaching of *Oculina patagonica* colonies in the Mediterranean Sea

A correlation ($r^2 = 0.49$, $p < 0.01$) between seawater temperature and percent bleached surface area of the coral *Oculina patagonica* (Fig. 1) was found. Monthly photographs revealed that the percentage of bleached surface area of the tagged colonies increased rapidly in the summer following a rise in seawater temperatures. Colony bleached surface area reached a maximum average of 42 ± 20% in August 2001 and 30 ± 22% in August 2002, when water temperature reached 30°C (Fig. 1). As water temperature decreased during the winter months, the bleached colony surface area decreased, reaching a minimum of 4.0 ± 9% in April 2001 and May 2002, when water temperature reached 20 to 22°C.

Bleaching progression within colonies of *Oculina patagonica*

Monthly monitoring revealed that bleaching appeared first at the perimeter of the colony. As the temperature continued to rise, bleaching progressed toward the center of the colony, resulting in the center being the last area within the colony to undergo bleaching (Fig. 2). This phenomenon was observed in 94% of the tagged colonies.

Zooxanthella density and chlorophyll concentrations

No significant difference in zooxanthella density and chlorophyll concentration (n = 8 Wilcoxon matched pairs test, $p > 0.05$) was found between the edge and center of non-bleached colonies. Zooxanthella density at the colony edge was $6.24 \pm 1.8 \times 10^6$ cells cm^{-2} and chlorophyll concentration was 16.76 ± 5.02 µg chl *a* cm^{-2} versus $5.8 \pm 2.2 \times 10^6$ cells cm^{-2} and 16.67 ± 6.7 µg chl *a* cm^{-2}, respectively, at the colony center.

Mortality, bleaching, and colony size

During the summer months partial mortality of the perimeter occurred in 22% of the tagged colonies (n = 62 colonies). This resulted in an average decline of 46 ±

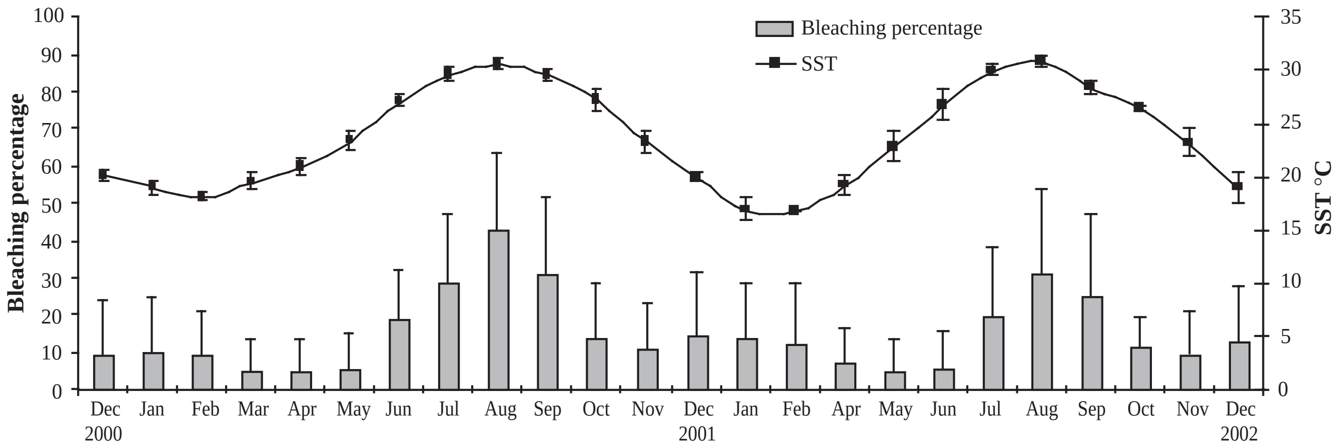

Fig. 1. *Oculina patagonica.* Mean percentage (±SD) of bleached surface area relative to whole colony surface from December 2000 to December 2002 (SST: sea surface temperature)

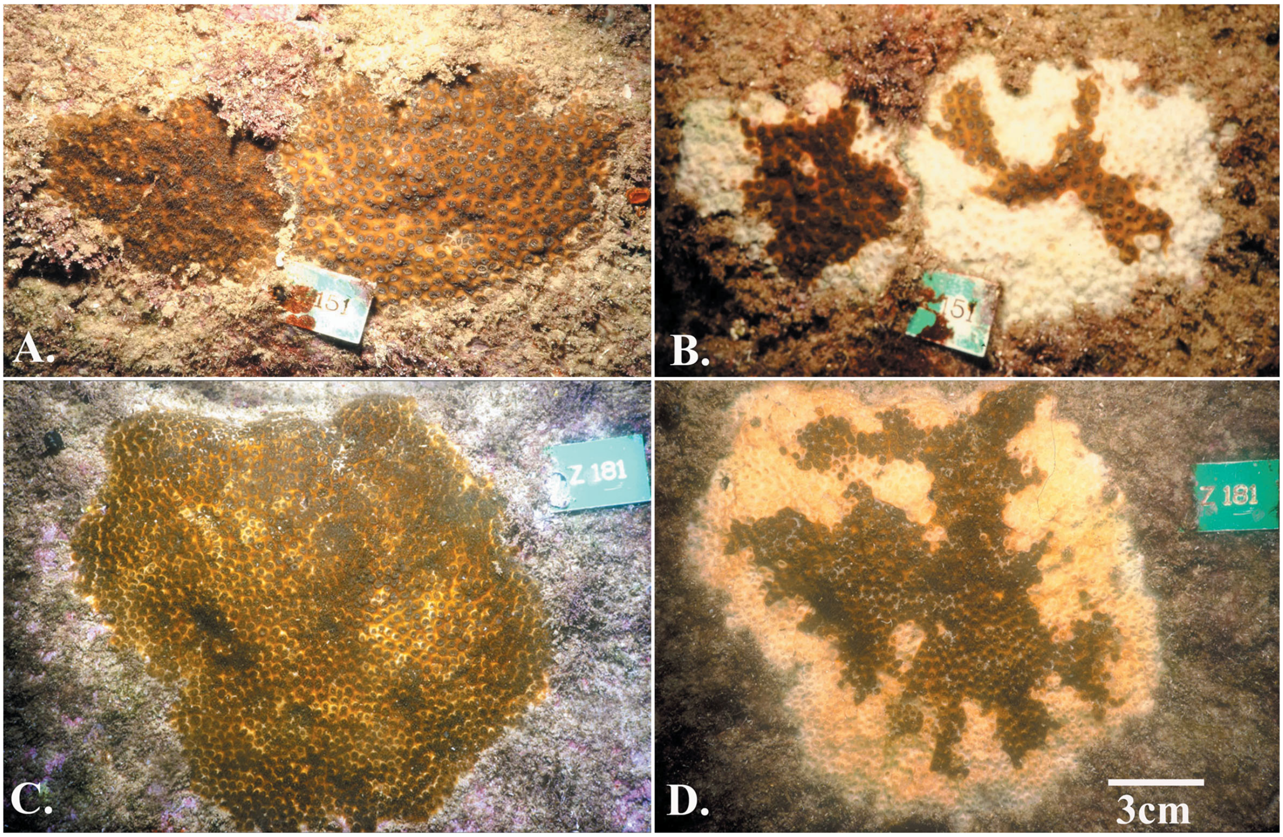

Fig. 2. *Oculina patagonica.* Bleaching progression from colony perimeter toward colony center. (A,B) Two neighboring colonies (1 of which is no. 151) in May and June 2002. (C,D) Colony no. 181 in June and July 2001

27 % of the colony live surface area, causing colonies belonging to the large size group (as measured by maximal live surface area) to be shifted to a smaller size group within the monitored population. During the bleaching season no growth was recorded in any of the tagged colonies. Concomitant with the decrease in water temperatures, the living surface area of the colonies increased, until the water temperature increased again (Fig. 3).

During the research period 25 % of the 62 tagged colonies died. Although all dead colonies had undergone bleaching at some point during the study, no significant difference was found in bleaching percentage between the group of colonies that died and those that survived (repeated-measures ANOVA, transformed data, $p > 0.05$). Of the corals that died, over half died during July (2001: $n = 6$; 2002: $n = 4$), when most of the colonies were bleached.

Both colonies that died and colonies with partial mortality in their perimeter region were significantly larger (ANOVA, followed by Fisher's LSD, $p < 0.05$) compared to the rest of the tagged colonies (Fig. 4). Together the 'dead colonies' group and the corals of the 'coral perimeter mortality' group had an average live surface area of 65 ± 42 cm^2 versus a live surface area of 40 ± 31 cm^2 for the 'intact group' (Fig. 4).

During the peak bleaching season, in August, when seawater temperature reached 30°C, we could still observe colonies that did not bleach. Surveys revealed that the colonies that did not bleach were significantly smaller (*t*-test, $p < 0.0001$), with an average colony diameter of 4.62 ± 2.3 cm ($n = 243$), than colonies that underwent bleaching (average colony diameter 7.75 ± 4.5 cm, $n = 407$, Fig. 5).

In addition, although a significant regression was found between colony diameter and the proportion of colonies that underwent bleaching (Spearman linear regression, $r^2 = 0.96$, $p < 0.05$, Fig. 6), no significant correlation ($r^2 = 0.066$, $p > 0.05$) was found between colony size and amount of within-colony bleaching (i.e. percent bleached tissue).

DISCUSSION

In the present study, we examined differential susceptibility to bleaching and survival following a bleaching event of a tagged population of *Oculina patago-*

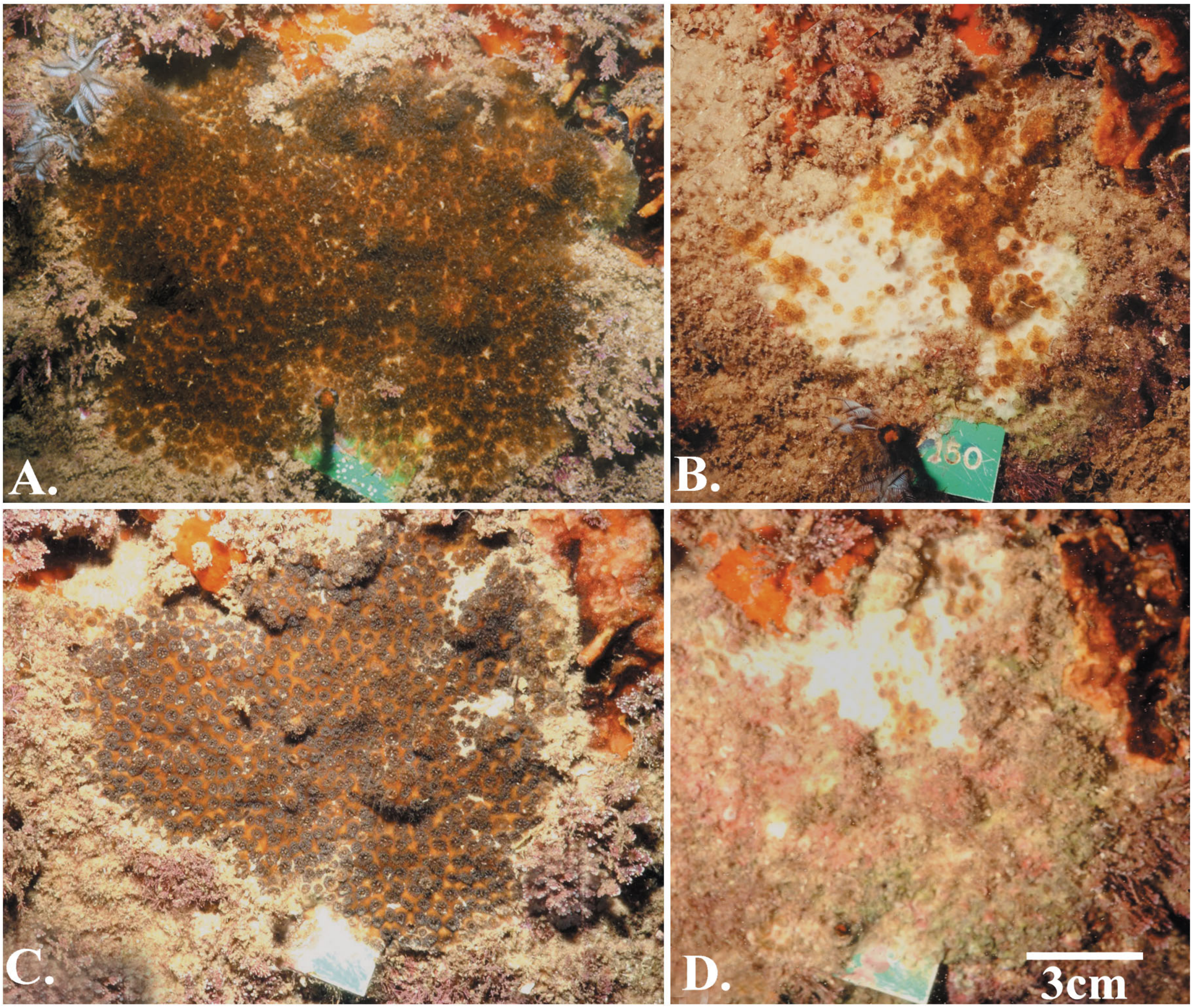

Fig. 3. *Oculina patagonica.* An example of partial mortality at the perimeter (colony no. 150) in: (A) May 2001 when the live surface area was 133 cm^2, (B) following a bleaching event when the live surface area decreased to 57 cm^2 in August 2001, (C) as the water temperature dropped the live surface area reached 125 cm^2 in May 2002. (D) As the water temperature rose again the live surface area decreased to 20 cm^2 in August 2002

nica. Some colonies within that population are apparently more susceptible to bleaching than others, and some survive bleaching better than others. We examined both inter-colony bleaching variations and intra-colonial bleaching patterns. Kushmaro et al. (1998) showed a significant correlation between seawater temperature and the percentage of bleached colonies in a population of *O. patagonica* (a colony was considered 'bleached' even if it showed a low percentage of bleaching). In the present study we also showed a significant correlation between water temperature and the within-colony bleaching percentage (Fig. 1). In June, when water temperature reaches 26°C, the first bleaching spots appear. Monthly monitoring revealed that bleaching first appears at the perimeter of the colony and progresses toward the center of the colony (Fig. 2). As no differences in zooxanthella density, or their chlorophyll content, were found between the perimeter and center of non-bleached colonies, the early onset of bleaching in distal areas of the colony is intriguing. It is possible that the bacterial agent, *Vibrio shiloi*, infects the colony from the substrate near the coral colony and not from the water column. Supporting this hypothesis are the descriptions of other coral diseases, e.g. white-band and white plague, in which the diseases frequently started at the base of the colony, the point of contact with the substrate (Gladfelter 1982, Nugues 2002).

Partial mortality is a well-known phenomenon in colonial stony corals (Bythell et al. 1993, Meesters et al.

Fig. 4. *Oculina patagonica.* Comparison of mean maximal live surface area (±SD), measured during the research period, of the colonies that died (dead colonies, n = 16), the colonies that underwent partial mortality of the perimeter region (perimeter mortality, n = 14), and the rest of the colonies (intact colonies, n = 29; 3 colonies were discarded due to technical problems)

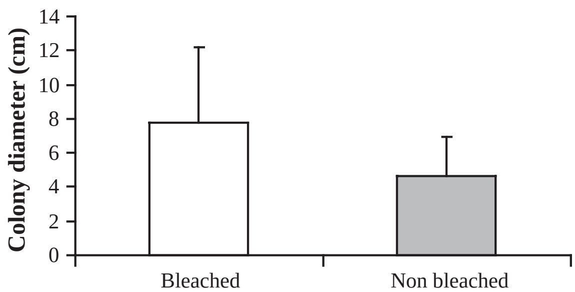

Fig. 5. *Oculina patagonica.* Comparison of mean colony diameter (±SD) between colonies that underwent bleaching (n = 407) and colonies that did not bleach (n = 243)

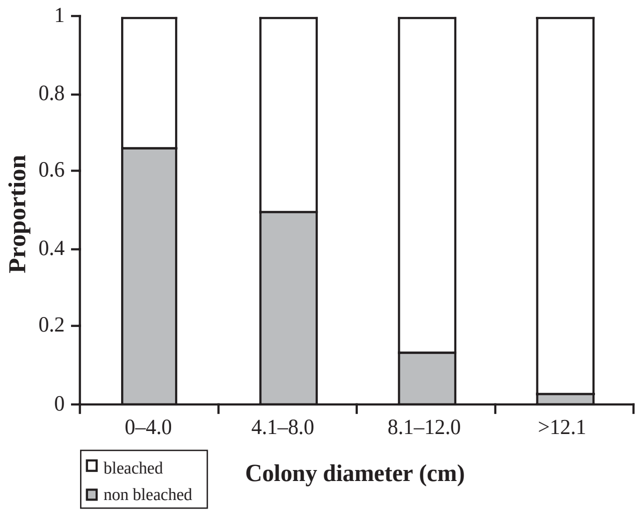

Fig. 6. *Oculina patagonica.* Proportion of bleached colonies (white) and healthy colonies (gray) according to different size groups (n = 650)

1996, 1997, Bak & Meesters 1998), causing large colonies to shrink into smaller sizes (Bak & Meesters 1999). Partial mortality occurs frequently after bleaching events (Fong & Glynn 2000, Feingold 2001, Baird & Marshall 2002). Interestingly, in colonies of *Oculina patagonica* that undergo partial mortality, the lesion progression follows a very similar pattern to that of bleaching, i.e. the perimeter dies first and the lesion progresses towards the center of the colony (Fig. 3); 22% of the tagged colonies demonstrated partial mortality of the perimeter, resulting in an average decline of 46% in the average colony size, and a shift to a smaller size group. This may be explained by a longer stress (bleaching) period experienced by polyps in the perimeter as compared with polyps at the colony center, leading to their death. Fine et al. (2002) reported termination of intra-colonial resource translocation toward bleached parts of *O. patagonica* colonies. It is possible that during bleaching there is a controlled 'blockage' of the unbleached colony section (colony center) from the bleached section (perimeter region). The breakdown of resource flow toward the perimeter polyps may explain their inability to survive during a bleaching event. Thus *O. patagonica* exhibits seasonal size plasticity, i.e. colony 'shrinkage' during summer, followed by re-growth during winter. Consequently, in *O. patagonica*, colony size cannot always serve as an indication of age, as suggested for *Stylophora pistillata* (Loya 1976) and *Fungia granulosa* (Chadwick-Furman et al. 2000), since small colonies might actually be 'old' colonies, exhibiting partial mortality following a bleaching event.

Despite the high recovery rate described for *Oculina patagonica* in previous studies (Kushmaro et al. 1996), during the present research period, 25% of the tagged colonies died. Surprisingly, the colonies that died were the large colonies (Fig. 4), which usually have a higher survivorship probability than smaller colonies under different stressors (Hughes & Jackson 1980, Johnson et al. 1995). Moreover, colonies in which partial mortality of the perimeter region took place were significantly larger than the rest of the tagged colonies (Fig. 4). Periodical surveys showed that during the peak bleaching season, when water temperature reaches 31°C, the healthy colonies were small colonies, averaging 4.62 ± 2.3 cm in diameter (Fig. 5). This may be a result of a higher probability of the large colonies to be infected by *Vibrio shiloi*, the causative agent of bleaching in *O. patagonica* (Kushmaro et al. 1996). Similar results were described by Nugues (2002) after an outbreak of the 'plague' coral disease in the Caribbean, in which small coral colonies were more likely to escape infections then large colonies. Loya et al. (2001) suggested that the higher survivorship of small *Acropora* colonies following a bleaching event may be linked to their juvenile morphology. Their hypothesis is based on Patterson's (1992) theoretical work suggesting that under a unit-flow regime flat colonies should have a higher mass transfer than branched colonies. Therefore, small *Acropora* colonies, which often remain relatively flat up to 1–1.5 yr of age, should have a higher mass transfer than large, branching colonies. Since bleaching conditions (high SSTs, high solar radiation) cause the accumulation of superoxides and other oxygen radicals in coral colonies (Lesser 1997, Jones et al. 1998), the efficient reduction or removal of these by-products will be essential to ensure colony survival. Indeed, recent studies have shown how stronger water flow, which increases mass transfer, has a positive effect on bleached corals (Nakamura & Van Woesik 2001, Nakamura et al. 2003). In addition, Nakamura & Van Woesik (2001) showed that based on Newton's law of viscosity and Reynolds number, which relates to the dimensional characteristics of the organism, the mass transfer or rates of diffusion within a given surface area to and from small organisms is more rapid than to and from large organisms. According to this theory, small *O. patagonica* colonies will have an advantage over large colonies, since they can eliminate toxins more efficiently through diffusion. Metabolic toxins, super oxides, other free radicals (Lesser 1997, Jones et al. 1998, Downs et al. 2002), and bacterial toxins (Banin et al. 2001) may cause damage to the symbiotic algae and eventually lead to colony mortality, as occurred in the large *O. patagonica* colonies following a bleaching event.

Bak & Meesters (1999) claim that global change will have an impact on recruits and the smallest size classes, causing an increase in mean colony size and a shift in the coral size–frequency distribution toward the larger size classes. In the case of bleaching of *Oculina patagonica*, however, the opposite trend exists. The current results of high mortality of large colonies, the decline in colony size due to partial mortality, and the high survivorship of the small colonies all suggest that small colony size is advantageous. This leads to the prediction that in a population that undergoes repeated bleaching events, the colony size distribution is expected to be skewed toward a smaller size, with an average colony size smaller than in an undisturbed population. Furthermore, since in this species colonies as small as 2 cm in diameter are reproductive (Fine et al. 2001), bleaching may have a less significant effect on the reproductive fitness of the small size groups in the population.

Recent field evidence from coral reefs around the world indicates that, following bleaching events, there is a higher survivorship and resilience of small colonies and recruits (Mumby 1999, Normile 2000, Loya et al. 2001, Bena & Van Woesik 2004). This may indicate that coral reefs might be more resilient than previously thought. However, considering the predicted increase in frequency and severity of bleaching events (Hoegh-Guldberg 1999), the ability of corals to mature, recover, and reproduce is still uncertain. Further research is essential in order to clarify the relationship between colony size and bleaching, as well as the ability of small colonies to thrive over time following reoccurring bleaching events.

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