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REPORT

Ecological characterization of coral growth anomalies on *Porites compressa* in Hawai‘i

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Abstract Bulbous skeletal structures with associated aberrant corallites have been abundant on *Porites compressa* in Kāne‘ohe Bay, O‘ahu, Hawai‘i, for at least the last 19 years. These growth anomalies (GA) appear in the summer in shallow (<3 m) water on some, but not on all colonies. GA-free branches, collected from colonies with GAs, produced GAs when cultured in outdoor flow-thru aquaria. Normal branches, whose tissues were continuous with those of GAs, grew in length much more slowly than normal branches from the same colony that were not connected with a GA, suggesting that there is a translocation of materials from normal tissue to GAs. Small experimental colonies that were either exposed to, or protected from, UV radiation did not differ in their rate of GA formation. GAs had a lower probability of survival than normal branches. This characteristic, in combination with their effect on the growth of normal branches and other reported deficiencies in the tissues of growth anomalies (e.g., reduced or failed reproduction), suggests that GA-bearing colonies of this species have reduced fitness.

Keywords *Porites* · Growth anomalies · Formation · Growth · Survival

Introduction

Growth anomalies of various types or various names (neoplasia, hyperplasia, calicoblastic epitheliomas, tumors) have been reported on scleractinian corals since 1965 (Squires 1965) and are found on coral reefs around the world (Sutherland et al. 2004). In general, growth anomalies sometimes lack polyps, have abnormal or fewer polyps, display tissue necrosis (Work et al. 2008) and have reduced densities of zooxanthellae (Gateno et al. 2003). Those anomalies that do have polyps have reduced fecundity or do not reproduce (Yamashiro et al. 2001; Domart-Coulon et al. 2006), have lower energy reserves (Yamashiro et al. 2001) and reduce the growth of associated normal tissues and skeleton (Cheney 1975; Bak 1983). The skeletons of growth anomalies are less dense than those of normal branches (Gateno et al. 2003; Domart-Coulon et al. 2006) and sometimes lack or have enlarged calices.

In *Porites compressa* (Scleractinia: Poritidae), an important component of reefs around the main Hawai‘ian Islands and the most abundant coral species in Kāne‘ohe Bay, the anomalies have been termed “skeletal tissue anomalies” by Domart-Coulon et al. (2006). These appear to be what Willis et al. (2004) termed hyperplasia. In the congener, *P. lobata*, McClanahan et al. (2009) refer to apparently similar structures as growth anomalies. Growth anomalies (GAs) are the term used here. The growth anomalies on *P. compressa* have a bulbous appearance and consist of closely packed calices, some of which are large and have increased numbers of septa. The polyps of these GAs have been described as hypertrophied (Domart-Coulon et al. 2006). The tissues of these anomalies are almost the same color as the tissues of adjacent normal parts of a colony. Domart-Coulon et al. (2006) observed that the abundance of *P. compressa* GAs was higher in shallower water, specifically on the reef flat, and that GAs survive poorly and are produced in periods of high water temperature.

The etiology of growth anomalies for most coral species is currently unknown (Peters et al. 1986; Domart-Coulon

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et al. 2006). Some skeletal anomalies have been interpreted as a response to endoparasitism (Grygier and Cairns 1996; Breitbart et al. 2005). Breitbart et al. (2005) found that microbial communities on "coral tumors" of *P. compressa* grew at a faster rate than those on normal branches but could not determine whether they were the cause, or an effect, of the growth anomalies. Domart-Coulon et al. (2006) concluded that bacteria were not an infectious agent causing the *P. compressa* growth anomalies. Loya et al. (1984), Peters et al. (1986) and Coles and Seapy (1998) have hypothesized that solar UV radiation causes some growth anomalies, but this has not been confirmed. McClanahan et al. (2009) suggested that reduced calcification caused by environmental stresses allowed fungi to invade and alter calcification and produce growth anomalies.

This study examines the basic ecological characteristics of GAs on *P. compressa* in Kāneʻohe Bay, Oʻahu, Hawaiʻi in order to gain more understanding of the conditions under which they develop, and possibly the cause or causes of their formation. The characteristics studied were the distribution of GAs across reef zones, the number of GAs/unit area of *P. compressa*, their dispersion pattern, their rate of growth, their survival and the timing of their formation. The study also tested whether UV radiation induced GA formation.

Methods

Field studies

The years during which GAs became common on *Porites compressa* in Kāneʻohe Bay have been estimated using two sets of photoquadrats taken on patch reef 42 [numbering system of Roy (1970)] in the northwest sector of the Bay. The first set of photographs was taken in 1980/1981 and the second in 2007. The initial photographs were taken using a Nikonos camera mounted on a tripod attached to a 1 m × 1 m quadrat. The photographed areas occurred every 10 m along four parallel 100-m-long transects which extended across the entire width of the reef top. The patch reef is approximately 100 m in diameter, and the reef top was at a depth of approximately 2.5 m during high tide and 1.5 m during low tide. The same approximate area was re-photographed in 2007 using a digital camera on a tripod attached to a 50 × 50 cm quadrat. Photographs were taken every 2 m along three 100-m-long transect lines set in the same orientation and approximate position as the lines used in 1980/1981. Both sets of photographs had a range of % cover of *P. compressa* within each quadrat. The % cover of *P. compressa* in each quadrat was estimated, and the number of GAs occurring on *P. compressa* was counted. These values were converted into a crude estimate of GAs m^{-2} for both the 1980/1981 and the 2007 data sets. In order to statistically test whether GA occurrence was different in 1980/1981 than in 2007, the presence or absence of GAs in quadrats was examined. For the 1980/1981 data, the presence or absence of GAs in quadrats was estimated for those quadrats with at least 25% cover of *P. compressa*. For the 2007 data, the presence or absence was scored in quadrats with 100% cover of *P. compressa*. Field notes in which the presence of GAs was mentioned were also used to establish the interval when GAs first became common.

The balance of field studies of GAs, those on size distributions, density and growth rate, comes from observations on colonies of *P. compressa* on the windward (northeast) reef flat and upper slope of the fringing reef of Moku o Loʻe, Kāneʻohe Bay, Oʻahu, Hawaiʻi, 21°26.043′N, 157°47.176′W (Fig. 1). These colonies are distributed from a depth of about 7 m on the reef slope up to the reef crest (defined here as the point where the reef slope and outer reef flat meet) and from the reef crest approximately 40 m across the reef flat toward the shore. GAs occur on *P. compressa* colonies all across the reef flat and down to a depth of approximately 2 m on the slope. Field observations reported here on the abundance of GAs through time and their size distributions are generally from those occurring on scattered *P. compressa* colonies on the sandy reef flat just shoreward of the windward reef platform (Fig. 1). The windward reef platform is a zone of limestone and coral ~20 m wide occupying the outermost reef flat of Moku o Loʻe. The top of the platform and the maximum height of all colonies on the reef flat is about 30 cm above the sand level and about 10 cm higher than the level of the lowest spring tides (Fig. 1).

The GAs on *P. compressa* are recognized in the field based on the following characteristics: their bulbous or mushroom–top shape (Fig. 2a), the orientation of their growth (often at right angles to the axis of the growth of

Fig. 1 Low tide view of the windward reef flat of Moku o Loʻe facing NW. The reef platform is visible along the outer (right-hand) margin of the reef flat. The elongated lagoon to left of center and extending into the distance is a dredged moat

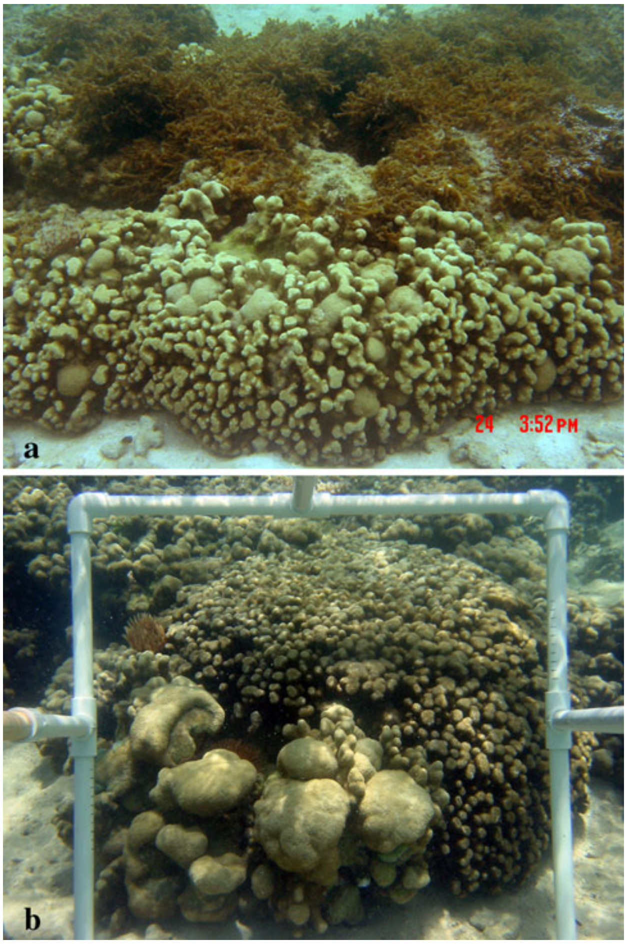

Fig. 2 **a** Portion of the perimeter of a reef flat colony of *Porites compressa* with numerous GAs. The top of the colony has been colonized by the alga *Gracilaria salicornia*. Tips of the normal branches are on the scale of 1–2 cm in diameter. **b** Two colonies of *P. compressa*, one with no visible GAs and one in the foreground, consisting almost entirely of large GAs. Frame is 50 cm wide

branches), the large size of their calices, the greater degree of the extension of their polyps and the fact that their color is often lighter than that of surrounding normal branches. GAs are more difficult to detect when small, i.e., approximately the diameter of newly developing branches (<1 cm). The relatively small number of colonies supporting numerous very large GAs (>12 cm in diameter, Fig. 2b) was not included in any of these analyses, because they seem to represent a distinct phenomenon. These colonies are characterized by the presence of large GAs, the fact that the colonies have very few normal branches, and the fact that they have only been seen on reef flats.

The density and dispersion of GAs on a given date on the reef flat were assessed by counting all GAs in a 25 × 25 cm quadrat on the side of each *P. compressa* colony, which fell under a 50-m-long transect line. The transect lines were placed approximately parallel to the reef crest in the zone at the interface of the sandy reef flat and the back of the reef platform. Most of these quadrats were on the near vertical or sloping faces of large colonies whose tops had been killed by exposure during spring low tides (Fig. 2a). Starting at the beginning of the transect line, each initial interception of the transect line and the top-most part of a coral colony dictated the placement of a quadrat on the sloping face of the coral with the left side of the quadrat touching the transect line. If the cover of *P. compressa* in the quadrat was <100%, or if the quadrat contained surfaces of two corals, the quadrat was set on the opposite side of the transect line or on the next colony intercepted by the transect line. The lower edge of the quadrat rested on the sand at the sand/coral interface. On each date that density was assessed, 30–50 quadrats (and colonies) were sampled. The greatest time span of records of density (1994–2009) is based on data collected in the fall (September, October, November), and these are used to examine the possibility of long-term trends in GA abundance. Size distributions of GAs have been collected since 1992 and are based on the maximum diameter of each GA within the quadrats.

A second transect study was performed on the windward reef slope to examine the density of GAs within three depth zones from the top of the reef slope to a depth of 4 m. The top surfaces of colonies were sampled in this analysis because it is the most common exposure in this habitat where large colonies, approximately 1 m in diameter, are densely packed. Transect lines were laid along depth contours on the slope, and each colony overlain by the line and with a near horizontal surface as large as the 25 × 25 cm quadrat was sampled by counting the number of GAs per quadrat. Each colony was sampled only once. The three depth zones were top of reef slope (0 m depth) to 0.5, 0.5–1.5 and 1.5–4 m. Colonies in each of the three depth zones were sampled on six different dates. Each sample consisted of 40–60 quadrats. The average density on each of the 18 transects was the variable used in a one-way ANOVA to test for differences in GA density among depths.

The abundance of GAs on the upper half of the total surface area of small (25–30 cm diameter) hemispherical colonies was compared with their abundance on the side half of the surface area of the same colony to examine the influence of orientation on GA development. The colonies used in this analysis occurred on the sandy reef flat near the shoreward edge of the platform. A point was located at the top center of these colonies, and the distance down from this point to each GA on the colony's surface was measured. The distance from the sand–colony interface up to the top center point of the colony and down to the opposite sand–colony interface (a semicircle) was also measured. These measurements made it possible to determine trigonometrically whether a GA was located on the top (cap) half or on the side (ring) half of a colony's hemispherical area. The densities of GAs in the two halves of each colony were compared with a paired *t*-test.

Laboratory measurements of growth rates and survival of GAs

The growth rates of GAs (solitary), normal branches (solitary), normal branches whose tissues and skeleton were continuous with a GA (fused) and GAs whose tissues and skeleton were continuous with those of a normal branch (fused) were measured on specimens that were collected on the reef flat and grown in outdoor laboratory wet tables. A specimen of each of the four types identified above was collected from each of the 31 colonies, and these 31 sets represented blocks in the analysis. Solitary GAs and solitary normal branches were removed from their source colony with no tissue or skeleton of the opposite type. Fused GAs and fused normal branches were collected as a fused pair; the tissues and skeletons of the two parts were continuous over most of their vertical extent (~1.5–2.5 cm). The surface areas of the tissues of the fused branches and fused GAs were approximately equal. The cut bases of the specimens were glued to individual plexiglass plates, and then the height and maximum width of each GA and the height of each normal branch were measured to the nearest 0.01 cm with Vernier calipers. The maximum width of normal branches was not a useful measure because branches either increase very little in width if they remain unbranched or increase rapidly in width if branch bifurcation begins during the period of the growth measurements. Initial heights were ranged from approximately 1.5 to 2.5 cm. Growth was measured as the increase in height of branches and height and greatest width of GAs.

These branches and GAs were placed in a large outdoor wet table (85 × 92 cm) in 16 cm of water (volume of 125 l). The total water flow from four outlets (16 l min^{-1}) was directed laterally at the specimens and toward drains on the opposite side of the wet table. The positions of specimens were haphazardly shuffled weekly during tank cleaning. The tank was screened with one layer of plastic mesh window screen to reduce the irradiance by 50% and compensate for the shallowness of the tank. The temperature in the tanks was ~1°C above reef flat temperatures, which ranges annually between 22 and 28°C. The growth study was run in the summer and in the winter of 2008. The sets of normal branches and GAs used in the two seasons came from different colonies. Growth data were analyzed by a randomized blocks ANOVA (treatments × blocks). Six treatments were used: vertical growth of solitary normal branches, vertical growth of solitary GAs, vertical growth of fused normal branches, vertical growth of fused GAs, lateral growth of solitary GAs and lateral growth of fused GAs. The blocks were the total of 31 colonies sampled on the two dates.

Growth rates of normal branches collected from colonies with and without anomalies were compared to determine whether these two types of colonies had different linear growth rates. Branches were collected from 34 colonies of each type in the early summer. One branch of each type was glued vertically to a plastic plate, and the initial height of each branch was measured. This set of branches was maintained in the wet table system described above for 4 months, their height was then remeasured, and their change in height was calculated.

The survival of the tissues of GAs and normal branches in the laboratory studies of growth rate was calculated at the end of the growth intervals. Tissues of GAs and branches were classified as live, dead or partly dead. Partly dead branches or GAs had lost at least 25% of their tissue by the end of the growth interval. These skeletons became covered with filamentous algae. Some of the normal branches in these studies of growth rate developed GAs during the period the branches were on the wet tables (March 2008 to March 2009). These new small GAs were measured on each occasion their supporting branches were measured.

Field measurements of growth

Twenty small GAs (2–4 cm in greatest diameter) growing on field colonies were tagged in October, and their rate of lateral growth was measured over the subsequent 2 1/2 mo. These GAs were marked by inserting a stainless steel screw into the colony 2–3 cm to the right of the GA and attaching a colored wire tie to the screw. Measurement of their diameters was taken with Vernier calipers.

Test of the effect of UV exposure on development of GAs

To test the hypothesis that UV radiation is responsible for the initiation of GA formation, normal branches, approximately 2 cm in length, were collected in February 2008 from colonies that had a high density of GAs, and then these branches were either exposed to or protected from UV radiation while cultured in outdoor laboratory tanks for the next 6 months. A pair of branches was collected from each colony, and each was attached to a 3 × 3 cm plexiglass plate. One member of each pair was placed in an outdoor tank under UV-blocking transparent plastic (Jokiel and York 1984), while the other was placed under UV-transmitting transparent plastic in the same tank. The UV-blocking plastic blocked radiation was less than

~425 nm, and the UV-transmitting plastic blocked radiation was less than ~275 nm. The outdoor tank was broad and shallow, 85 × 125 × 13 cm deep, volume 138 l and supplied with running sea water (16 l min^{-1}). The branches were placed in the experimental treatments in February, and the analysis of GA formation was made in mid September.

Results

Habitat and microhabitat differences in the distribution of GAs

GAs occur on *Porites compressa* colonies of most reefs sampled in Kāneʻohe Bay. They develop on colonies around the entire 2.5 km perimeter of the Moku o Loʻe fringing reef. GAs occur at densities of up to 60 m^{-2} of colony surface on the reef flat (Fig. 3); on the reef slope, GA densities are significantly higher (29.12 m^{-2} of colony surface) on shallow reef slope colonies (0–50 cm depth) than on deeper reef slope colonies (0.43 m^{-2} of colony surface in the depth interval 0.5–1.5 m, density of 0.06 m^{-2} in the depth interval 1.5–4 m, one-way ANOVA $F = 69.64$, $P < 0.001$) (Table 1). At a smaller scale, that of the surface of individual small hemispherical colonies of *P. compressa* on the reef flat, the GAs are four times as dense on the upper cap-like half of the surfaces of the colonies than on the more vertical side half of their surfaces (5.25 vs. 1.30 GAs m^{-2}, SE of difference = 0.96, paired *t*-test $t = 4.098$, $df = 19$, $P < 0.001$).

Initial records of GA presence

The 1980/1981 photographs of quadrats do not show readily visible GAs (>2 cm diameter) on *P. compressa* (18 m^2 of *P. compressa* examined in 43 quadrats); however, GAs are evident in this area of reef in 2007 (14.4 m^2 of *P. compressa* examined in 146, 50 × 50 cm quadrats) at a density of 8.08 GAs m^{-2} of coral tissue. The χ^2 test of independence of the two dates and the number of quadrats containing or not containing GAs was significant, $\chi^2 = 31.80$, $df = 1$, $P < 0.001$, indicating that the proportion of colonies with GAs had increased between 1980/1981 and 2007 (1980/1981, total quadrats = 40, number with GAs = 0; 2007, total quadrats = 53, number with GAs = 29). The first field note of GAs on *P. compressa* in Kāneʻohe Bay was in 1990; consequently, GAs first appeared in high densities some time after 1981 and before 1990.

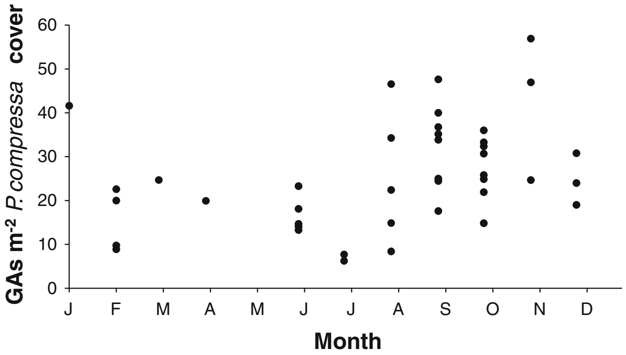

Fig. 3 Density of GAs in different months of the year on colonies of *Porites compressa* on the windward reef flat of Moku o Loʻe. Data are from surveys conducted between 1994 and 2009

Density, dispersion pattern and size structure of GAs

The average density of GAs on the reef flat is higher in the fall (Fig. 3). Fall censuses constitute the longest record of GA density available (1994–2009). The average density of GAs on the reef flat in these months over the 15-year period is 30.17 GAs m^{-2} of live *P. compressa* cover (SE = 2.35, number of surveys = 25). These fall censuses are clustered in two time intervals, 1994–2000 and 2006–2009. The average densities in these two time intervals are similar, suggesting that there has not been an increase or decrease in density over the 15-year interval (1994–2000, Average density = 30.69 m^{-2}, SE = 3.20, sample size = 7; 2006–2009, Average density = 29.97 m^{-2}, SE = 3.06, sample size = 18. Some colonies

Table 1 Comparison of densities of GAs on *Porites compressa* colonies in three depth zones on the reef slope

Depth	0–0.5 m	0.5–1.5 m	1.5–4 m	
No. of samples	6	6	6	
Average % of quadrats without GAs	56	80	94	
Average number of GAs/quadrat	1.82	0.43	0.06	
SD	0.36	0.29	0.05	
GAs/m^2	29.12	6.85	1.03	
One–way ANOVA				
Source	*df*	MS	*F*	*P*
Among depths	2	5.17	69.64	0.001
Within depths	15	0.07		
Total	17			

Densities were measured in 25 × 25 cm quadrats on the upper, approximately horizontal, surfaces of *P. compressa* colonies growing on the windward reef slope of Moku o Loʻe. Depth is measured as distance below the level of shallowest living *P. compressa* tissue on the reef slope

Least significant difference = 0.41, colonies in the 0- to 0.5-m interval have a greater density of GAs than do colonies at greater depths

Table 2 Dispersion pattern of GAs on *Porites compressa* on the reef flat of Moku o Lo‘e in two replicate samples

	Sample 1	Sample 2
Density of GAs (number m^{-2})	23.28	14.67
Index of dispersion	1.83	4.04
Number of quadrats	29	28
χ^2 value	51.4	113.04
P	<0.01	<0.01

One quadrat was sampled per coral colony. Colonies were sampled on two dates in June 2008. χ^2 value is a test of randomness of dispersion

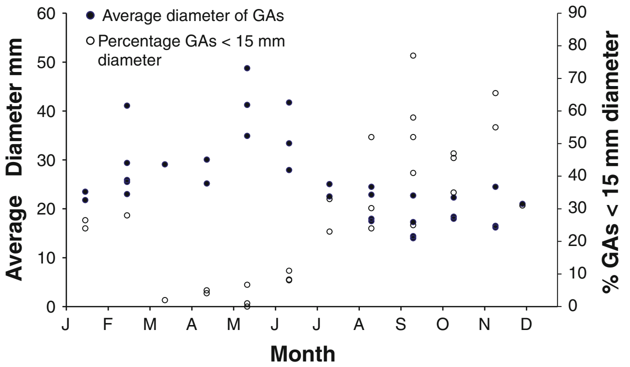

Fig. 4 Average diameter of GAs and the % of GAs < 15 mm in diameter through the year on *Porites compressa* colonies on the windward reef flat of Moku o Lo‘e. Data are derived from surveys conducted from 2002 to 2009

of *P. compressa* have high densities of GAs, while others are entirely free or virtually free of GAs, giving rise to an aggregated dispersion pattern (Table 2). The average diameter of GAs was smallest in the fall (~20 mm) and increased through the subsequent months to a high of ~35 mm in the early summer (Fig. 4). Conversely, the percentage of GAs < 15 mm in diameter was smallest in the spring and largest in the fall. These two patterns reflect the timing of the detection of new GAs in the quadrat counts and their subsequent growth. This cycle repeats each year (Fig. 5). In combination with the cyclic pattern of density through the year (Fig. 3), the cyclic patterns in average size in Figs. 4 and 5 indicate that individual GAs develop, grow and disappear from the surface of a colony in about 1–2 years.

Growth rate

When normal branches and GAs were separated from one another (solitary), the vertical growth of the normal branches was about double that of GAs in both seasons (Table 3). However, if GA tissues remained in contact with the tissues of normal branches (fused), the vertical growth of the GAs was approximately 50% greater than that of solitary GAs. Correspondingly, normal branches whose tissues remained in contact with the tissues of GAs showed about 50% less vertical growth than solitary normal branches.

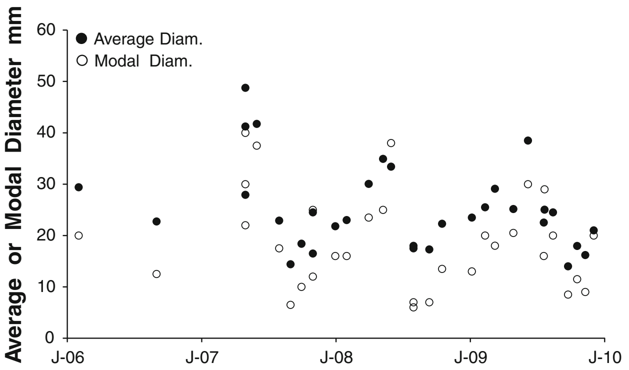

Fig. 5 Average and modal diameters of GAs over time on *Porites compressa* colonies. The letter “J” stands for January one of each year

The lateral growth rate of small GAs (<3 cm greatest diameter) that developed on normal branches housed on wet tables averaged 0.19 cm 30 day^{-1} (SD = 0.12, sample size = 19) in winter. Small GAs growing on colonies on the reef flat in winter grew in greatest diameter at a rate of 0.22 cm 30 day^{-1} (SD = 0.07, sample size = 17).

The rate of vertical extension of normal branches collected from colonies which lacked GAs (mean = 0.201 mm 30 day^{-1}, SE = 0.014, sample size = 30) or possessed GAs (mean = 0.199 mm 30 day^{-1}, SE = 0.014, sample size = 30) was not significantly different by a *t*-test.

Survivorship

The tissues of isolated normal branches survive better than do the tissues of GAs during three- to four-month culture periods in outdoor laboratory tanks (Table 4). In the field, in 23 surveys over a 2-year period the mean proportion of GAs that were dead or partly dead was 0.164 (SE = 0.032). The normal branches in proximity to a GA are almost always healthy. Measurements over a 1-year period on 10 survey dates showed that the average diameter of dead GAs is greater than that of live GAs (average difference = 8.15 mm, SE = 1.82, sample size = 10 dates, paired $t = 4.47$, $P < 0.01$), suggesting that GAs have a limited life span in the field. Disappearance of GAs was not due to a high mortality rate of GA-bearing colonies. None of seven marked GA-bearing colonies died in the period September 2007 to September 2008, and no deaths of colonies of *P. compressa* were observed in the ~200 m × ~10 m reef flat area containing hundreds of colonies, which was repeatedly monitored for GAs in 2008.

Table 3 Vertical and lateral growth rates (cm per month) of normal branches and GAs of *Porites compressa* over the periods: summer, June 13, 2008 to August 4, 2008; and winter, November 4, 2008 to December 6, 2008 in laboratory tanks

	Normal		GAs	
	Solitary	Fused	Solitary	Fused
Summer				
Vertical				
Mean	0.159	0.067	0.089	0.119
SD	0.109	0.081	0.046	0.042
Sample size	16	8	13	10
Lateral				
Mean			0.090	0.144
SD			0.052	0.055
Sample size			12	8
Winter				
Vertical				
Mean	0.208	0.112	0.074	0.137
SD	0.10	0.067	0.054	0.053
Sample size	16	15	13	13
Lateral				
Mean			0.099	0.164
SD			0.131	0.128
Sample size			12	16
Randomized blocks ANOVA				
Source	*df*	MS	*F*	*P*
Coral type	5	0.037	7.10	<0.0001
Blocks	30	0.008		
Error	110	0.005		
Total	145			

Statistical blocks represent sets of GAs and normal branches collected from individual colonies in both seasons. Lateral growth is growth in greatest diameter of a GA

Single degree of freedom tests (Duncan's multiple range test), comparisons where $P < 0.05$)

Growth in Solitary branch height > Growth in Solitary GA height

Growth in Fused GA height > Growth in Solitary GA height

Growth in Solitary branch height > Growth in Fused branch height

Growth in Solitary branch height > Growth in Fused GA height

Growth in Fused GA width > Growth in Solitary GA width

Test of UV induction of GAs

The test of the hypothesis that exposure to UV radiation induces GA formation did not indicate that UV radiation is a causative agent. Twelve of fifty-five colonies exposed to UV radiation developed at least one GA, while eighteen of forty-eight colonies not exposed to UV developed GAs (χ^2 test of independence, $\chi^2 = 3.05$, ns). Approximately 30% of all the branches developed GAs over the 6-month period of exposure on the wet table.

Discussion

While the results presented here do not make it possible to identify the causal factor(s) responsible for the development of GAs, they do help to narrow the search, and they confirm that a seasonal factor is at least partly responsible for their development (Domart-Coulon et al. 2006). The results presented here also describe the relationship between the GAs and normal tissue, showing that GAs are dependent on normal tissue and also inhibit normal tissue, and that the individual GAs are transitory, lasting for only a year or two.

Determining when high densities of GAs (~30 m^{-2}) became common, held the potential for identifying a causative agent, but the 9-year window of time is broad and does not implicate a particular environmental factor. This interval does correspond with a report by Hunter (1999) that "tumors" (apparently similar morphologically to GAs) on the congener *Porites lobata* were first seen in 1990 at a second O'ahu, Hawai'i site. Abundant anomalies on *Porites* are apparently a recent phenomenon in Hawai'i, although they were present in the Bay earlier than 1990.

The GAs of *P. compressa* in Kāne'ohe Bay are restricted to corals in less than 3 m of water (Table 1, and Domart-Coulon et al. 2006), suggesting that agents such as high levels of irradiance, high levels of UV radiation, or high water temperatures are responsible for their development. Others have also reported anomalies from shallow waters. Loya et al. (1984) reported anomalies, similar in many regards to the GAs in *Porites*, on reef flat colonies of *Platygyra* spp. McClanahan et al. (2009) reported anomalies in shallow water environments on *P. lobata* in Kenya; these anomalies were morphologically similar to those reported here for *P. compressa*. Anomalies that have a

Table 4 Comparison of the mortality of the tissues of GAs and normal branches of *Porites compressa* in lab tanks over the stated time interval

Interval	Number of GAs	% Dead or partly dead	Number of normal branches	% Dead or partly dead	χ^2	*P*
May to July 2007	14	36	32	6	6.55	<0.025
March to June 2008	20	50	20	25	3.34	<0.01
July to September 2008	31	26	26	4	5.15	<0.025

more irregular growth form and generally fail to produce calices and polyps (calicoblastic epitheliomas, Willis et al. 2004) have also been reported from shallow water or the intertidal (Peters et al. 1986; Bak 1983; Coles and Seapy 1998). Some studies have looked for and found anomalies over a greater range of depths. Work et al. (2008) found abundant "growth anomalies" (apparently calicoblastic epitheliomas) on *Acropora* at depths from 3 to 15 m at three sites in the Pacific. Hunter (1999) reported "tumors" (apparently GAs) on *Porites* spp. over a depth range of from 3 to 13 m at sites in Hawai'i, and Gateno et al. (2003) reported "tumors" (some of which are apparently GAs) to be at least as abundant at 10–13 m as they were at 3–7 m. The restriction of GAs in Kaneohe Bay to depths less than 3 m may be a result of the turbidity of the Bay waters in combination with the vertical distribution of the corals. Extinction coefficients in the Bay for UV radiation and PAR are approximately 10 and 5 times higher, respectively, in the Bay than at nearby oceanic sites (Banaszak et al. 1998), and the cover of corals remains high up into the lower intertidal in the Bay's calm waters.

In addition to their restriction to corals in shallow water, the results of this study show that new small GAs become apparent on *P. compressa* in the late summer (Fig. 3). This contributes to the development of an annual cycle in density of GAs (Fig. 3) and to an annual cycle of the size distribution (Fig. 4). The smallest discernable GAs (4, 5 and 6 mm in diameter) first appeared in August of 2007, 2008 and 2009. Given the average growth rate for small GAs on branches in the field and on laboratory-housed branches of $\sim$0.2 cm 30 day^{-1} (diameter), GAs observed in the summer with a diameter of 0.4–0.6 cm would be approximately 2–3 months old and therefore formed in May or June. Formation of GAs apparently continues into the summer based on the appearance of small GAs $\leq$ 0.6 cm in October.

Domart-Coulon et al. (2006) reported that the growth of these GAs on *P. compressa* was initiated at the time of production of high-density bands in the skeleton of *P. compressa*. High-density bands have been reported to develop in the summer in *P. compressa* in Hawai'i (Houck 1978) and in the summer in *P. lutea* at other reef sites (Highsmith 1979), or at the time of year when water temperatures are "relatively high" (Weber et al. 1975) or waters are warm (Buddemeier et al. 1974; Lough and Barnes 1989). McClanahan et al. (2009) have hypothesized that the development of anomalies is related to the occurrence of high water temperatures. The results reported here suggest that they are initiated in the late spring and early summer when UV radiation and irradiance are at or near their peaks, but earlier than the time of peak water temperatures, which occurs later in September (Stimson et al. 1996).

While water temperatures have not reached their seasonal peak when GAs are being initiated, corals on the reef flat could experience periods of high water temperatures in spring and summer during the hours of extreme low tides in the daytime at this time of the year.

These daytime low tides would also reduce the PAR- and UV-blocking effect of the water column. These conditions, the observations that GAs on *P. compressa* are commonest at the shallowest depths (Table 1; Domart-Coulon et al. 2006) and on the tops of colonies and the known damaging effects of UV, implicate UV radiation as a possible causative factor. The experimental results seem, however, to eliminate UV as a causative agent. The experiment was run during the spring and summer so that it could detect a response to either increasing UV or high UV irradiance, but neither apparently had an effect. The total amount of tissue used in this experiment was not large, and the number of GAs produced was low, so these factors probably reduced the sensitivity of the experiment. On the other hand, branches used in this study came from GA-bearing colonies in the field, a factor that potentially increased the likelihood of the development of GAs under experimental conditions, yet an effect of UV radiation was not detected. Increasing or high levels of PAR or periods of elevated water temperature during spring low tides remain the two most likely physical environmental factors contributing to GA development.

Despite their proximity to one another, *P. compressa* colonies differ in both their susceptibility to the causative agent(s) and the type of GAs produced. Some colonies of *P. compressa* on the reef flat and upper reef slope lack GAs, while other adjacent and often touching colonies can have densities of 30 GAs m^{-2} of coral tissue or more. This difference among colonies was described in this study in terms of the aggregated pattern of GAs (Table 2), and in Domart-Coulon et al. (2006) in terms of prevalence, 21.7% of colonies had GAs. Loya et al. (1984) also reported that in *Platygyra* spp., some colonies had a higher likelihood of developing anomalies than others. Among GA-bearing colonies of *P. compressa*, there is also a discreet difference in the types of GAs produced; about 1% of colonies on the reef flat consist almost entirely of a number of large $\sim$15 cm diameter GAs with very few normal branches (Fig. 2b). These large GAs are approximately double the size of the largest GAs in the colonies reported on here. These large GAs apparently survive better or grow faster than do the ones examined in this study. These differences in the responses of colonies suggest there could be a genetic basis to the susceptibility of colonies to the causative agent or agents.

As observed in this and other studies, GAs have impaired function. The tissues of GAs have reduced survival relative to tissues of normal branches from the same colony (Table 4 and Domart-Coulon et al. 2006). The GAs also showed reduced vertical growth compared with normal branches (Table 3). Others have reported that anomalies have reduced densities of zooxanthellae, e.g., Bak (1983); Peters et al. (1986); Yamashiro et al. (2000); Gateno et al. (2003); Domart-Coulon et al. (2006) and Work et al. (2008), reduced lipid content (Yamashiro et al. 2001), and that they are either less fertile than normal tissues or infertile (Hunter and Field 1997; Hunter 1999; Yamashiro et al. 2000; Domart-Coulon et al. 2006; Work et al. 2008).

These features of the individual anomalies in combination with the fact that a substantial proportion of the colony surface (5% or more, Hunter 1999; Gateno et al. 2003) can consist of anomalies means that anomaly-bearing colonies probably have reduced fitness. Evidence of reduced colony fitness can be seen in the results of Yamashiro et al. (2000) who found that the survival of colonies with anomalies was lower following episodes of high water temperature. The evidence of translocation of materials from normal tissues to GAs, the reduced growth rate of normal branches when in contact with GAs (Table 3), represents a further impairment of the fitness of the normal tissues of GA-bearing colonies. This phenomenon could be related to the translocation of materials between parts of a colony as described by Pearse and Muscatine (1971) and Rinkevich and Loya (1983). Cheney (1975) and Bak (1983) reported that neoplasia could reduce the growth rate of the branch they were on relative to branches with no neoplasia. Finally, in an intact coral colony in the field, normal branches that have no lateral contact with a GA leave the GA behind as they extend the corallum radially at the rate of $\sim$30 mm year^{-1} in *P. compressa* (Cox 1986; Grotolli 1999). Thus, the presence of GAs would be expected to reduce the overall success of a colony through their temporary displacement of the faster growing (radially) normal branches.

The aspects of fitness detailed above, growth rate, physiology, survival and reproduction, suggest that *P. compressa* colonies that develop GAs have a reduced capacity to perpetuate themselves, both asexually and sexually, and perhaps even a reduced competitive ability, thus constraining the spread of this anomaly. New GAs are formed in the spring of each year, they grow to about 8 cm but then disappear from the GA population. The study of the vertical growth of GAs and normal branches suggests they are left behind within the colony because of the faster outward growth rate of normal branches (Table 3). However, without an understanding of the cause of the development of GAs, and hence whether its effect might intensify, it is unclear what the prevalence will be in the future or what percentage of coral tissue of this species might be affected.

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