EFFECTS OF TEMPERATURE AND UV-B ON DIFFERENT COMPONENTS OF CORAL REEF COMMUNITIES FROM THE BAHAMAS

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ABSTRACT

Temperature and UV-B have been some of the most consistently implicated factors in coral bleaching episodes, and projections of current trends indicate that anthropogenic elevations of these 2 factors (if unabated) may pose environmental threats during the 21st century and beyond. We undertook a 4 week experimental evaluation of the effects of 3 different temperatures (27°, 29°, and 31°C) and 3 different intensities of UV-B flux (ambient, +10%, +20%) for coral, algae, and solitary invertebrates living in shallow reef environments at Lee Stocking Island, Bahamas. While several workers have investigated the interactive effects of temperature, UV, and in some cases salinity or other factors on corals, no research has analyzed how these factors might differentially impact different components of the community and therefore impose unforeseen long term shifts in community structure. We found that bleaching of Acropora prolifera increased with temperature and UV-B exposure; 95% of the branchlets bleached after 3 weeks in the high temperature/high UV condition. The algae we examined (Microdictyon sp.), however, grew in all of the experimental conditions, and this response was greatest at high UV/low temperature and high temperature/ambient UV conditions. The motile invertebrates tested (brittle stars, hermit crabs, urchins, bivalves) showed little mortality in any condition. If these results hold in other species of corals, fleshy algae, and solitary invertebrates, they suggest that corals will be more adversely affected than one would predict from the physical factors alone.

INTRODUCTION

Reports of mass bleaching episodes in the West Atlantic and around the world have caused considerable international concern in the last 5 years (Brown and Ogden 1993). In addition, data from monitoring studies indicate a decline in size of colonies or live coral cover for a number of reef tracts (e.g., Porter and Meier 1992, Goreau 1992). The causes of this decline in reef health usually have not been determined with certainty. Numerous West Atlantic reefs are subject to both warm and cold water intrusions, as well as marked salinity and turbidity variations (Robertson et al. 1982, Jaap 1984). A number of reef tracts suffer from natural and anthropogenic nutrient enrichment, which probably enhances disease and directly or indirectly suppresses reef growth (Hallock and Schlager 1986, Hallock et al. 1988, LaPointe and O'Connell 1988). Accelerated bioerosion also is likely to occur in corals that have been weakened by partial bleaching, disease, or environmental stress (Reaka-Kudla pers. obs.).

Bleaching episodes have been correlated most consistently (although not exclusively) with temperature deviations (Glynn 1988, 1990, 1991; Roberts 1990). Tropical organisms are known to live near their upper temperature tolerances (Jokiel and Coles 1990), and even the relatively small increases in temperature that are predicted for tropical seas during the next several hundred years due to "greenhouse" warming (IPCC 1992) are likely to exert large effects upon the vitality and growth of reef corals. When superimposed upon higher mean temperatures, intervals of warmer conditions (such as those of future El Ninos) could impose catastrophic effects upon reef communities. Even today, Glynn and deWeerdt (1991) have reported that 2 reef-building hydrocorals were largely eliminated from their ranges in the East Pacific by the elevated temperatures of the 1982-83 El Nino event.

Ambient UV-B light intensities (280-320nm) also are increasing in some parts of the world as a result of anthropogenic depletion of stratospheric ozone. Researchers using different data sets have estimated that total column ozone has decreased from 2-5%/decade in recent years (Kerr 1991). Even when cyclic solar effects and reflectivity errors in backscattered data are corrected, Herman et al. (1991) show that the global average for total column ozone declined by $2.9 \pm 1.3\%$ over an 11-year period from 1978-1989. Since the % decrease in ozone is associated with approximately double increases in UV-B penetration (Vogelmann and Ackerman 1993), these values suggest that globally averaged UV-B penetration increased by about 5.8% over this period; this in turn implies a potential increase of approximately 50% per century if the conditions of the 1980s were to persist. Although the ozone effect was at first thought to be limited largely to polar latitudes, ozone destruction has been detected

over northern mid-latitudes (Kerr 1991; Stolarski et al. 1991, 1992; Madronich 1992), and some information suggests that ozone depletion could reach the tropics (Crawford 1987). Madronich (1992) has calculated amounts of biologically active UV-B (using DNA action specra) at different latitudes; tables and graphs in this work suggest that, while the greatest increases in DNA damage are occurring at 30° N/S and above, all trends are positive even in low latitudes, and biologically active UV-B appears to increase significantly during July and August at the equator. Also, after the 1991 eruption of Mt. Pinatubo, depletions of total column ozone of 5-8% (implying 10-16% increase in UV-B) were observed above the tropics (Brasseur 1992, Vogelmann and Ackerman 1993). Even if ozone depletion in tropical regions results in a relatively small percentage increase in UV-B penetration, the absolute increase in UV intensity could be large and biologically significant because of the high intensities of radiant energy received there already.

Relatively few workers have examined the implications of changes in UV-B intensities for aquatic organisms, especially in clear tropical waters that are most likely to transmit UV. Some coral reef studies indicate that increased intensities of both UV and visible light can cause bleaching and reduced growth, photosynthesis, or calcification in corals and related organisms (Jokiel 1980; Jokiel and York 1982; Siebek 1981, 1988; Hoegh-Gulfberg and Smith 1989; Jokiel and Coles 1990; Lesser et al. 1990; Glynn et al. 1993).

Because temperature and UV have been some of the most consistently implicated (although controversial) factors in bleaching episodes and because projections of current trends indicate that anthropogenic elevations of these 2 factors pose potentially grave environmental threats for the 21st century and beyond, we undertook an experimental evaluation of the effects of 3 different temperatures (27°, 29°, 31°C, which represent approximate winter and summer ambient and above-average but encountered summer temperatures in the Exumas) and 3 different intensities of UV flux (ambient shallow water [1.5m] = 2160 joules/m²/day as quantified by Regan et al.'s (1992) summer field observations at these depths near Lee Stocking Island, and 10% and 20% above ambient, 2376 and 2592 joules/m²/day) upon a coral, an alga, and several species of solitary invertebrates. We simulated a shallow reef environment because field observations (Regan et al. 1992) suggested that shallow reef environments would be most affected by potential changes in UV-B exposure and it is here that reef organisms would be most likely to experience interactions between UV-B, visible light, and temperature. Data in the studies cited above suggest that levels of UV-B could increase to 10-20% greater than now over the next century when current decadal trends in ozone depletion, the long life of CFCs already in the atmosphere, and the effects of the Montreal Protocol all are taken into consideration.

METHODS

The organisms included in the study were collected at about 1.5m depth from a patch reef on a cay near Lee Stocking Island. The coral, *Acropora prolifera*, is a fast growing species that was flourishing on the patch reef; it also provided a comparison for a study evaluating the effects of temperature and UV-B on a West Pacific congener, *Acropora valida* (Glynn et al. 1993). Branchlets were taken from the same colony or from colonies in as close proximity to each other as possible in order to avoid genetic differences among experimental subjects. The alga, *Microdictyon* sp., is a bubble-like green alga that was observed overgrowing coral heads in shallow reef habitats near Lee Stocking Island, and the solitary invertebrates used included brittle stars (*Ophionereis reticulata*, *Ophiocoma echinata*), hermit crabs (*Calcinus tibicens*, *Paguristes* sp.), urchins (*Echinometra viridis*), and bivalves (*Arca* sp.). Clumps of algae and solitary invertebrates also were taken from as restricted an area as possible in the vicinity of the patch reef.

We used an outdoor laboratory setting covered with transparent mylar (which filters out UV-B) and a neutral density screen (black nylon netting that reduces intensity but does not alter spectral composition) so that natural visible light was maintained at intensities equivalent to those measured in these shallow water environments (1.5m) in the Exumas. To modify UV-B independently from visible light, we used solar simulators constructed of GEFS40 sunlamps surrounded by Kodacel filters (the latter screen emissions <295nm from the lamps; these wavelengths do not penetrate earth's atmosphere). These solar simulators produce wavelengths and intensities approximately equivalent to the solar spectrum (Rupert 1978, Regan and Parrish 1982, Regan 1991). Twenty-seven individual aquaria with recirculating water systems that rested in 3 separate water bath tanks were sustained at the 3 respective temperatures; the 3 UV conditions, maintained by longitudinal banks of solar simulators overhead, trisected the temperature conditions. Black plastic curtains were hung between the 3 UV conditions to prevent diffusion. UV intensities emitted by the lamps in each of the 3 conditions were confirmed during the day and night (when there was no interference from visible light) with a UV radiometer (Jagger meter calibrated against a Yellow Springs International thermopile; Jagger 1961) prior to the experiment. Temperatures, which were monitored at regular intervals throughout the day and night, were maintained at 27.15 ±0.36°(standard error), 29.03 ±0.23°, and 30.94 ±0.26°C in the 3 respective conditions. We report only major trends here because logistic constraints prevented randomization of placement of our temperature and UV conditions. A more detailed analysis, where these constraints are rectified and additional species are included, will be forthcoming. We feel that the relatively large sample sizes used, clear patterns in the data, and the simultaneous comparisons of the 3 major taxa within each experimental

condition justify the primary conclusions about how different components of the community respond to the variables tested and warrant further work on additional species.

All samples were placed into and recovered from tanks using a random number table. A 1cm mesh screen (held 2cm above the bottom by a frame) supported the branchlets of coral and the clumps of algae (tied onto the top of upright glass rods with monofilament line). The motile invertebrates were allowed to crawl about at the bottom of the aquarium. We attempted to protect the clumps of algae from any urchins that might escape from under the screen, climb the glass rods, and graze on the algae by placing small plastic shields resembling "squirrel shields" around the rod below the algae, but we observed that during the last week of the experiment several urchins emerged and outmaneuvered the shields, resulting in damage to the algae; consequently, algal weights from the last week of the experiment were discarded. For the coral, we report direct observations of bleaching (to the white condition) in branchlets that were collected and frozen for further analysis at the end of 1,2,3, or 4 weeks (other dependent variables measured will be reported elsewhere). The samples of algae were weighed individually at the beginning of the experiment and after collection of samples at either 1,2,3, or 4 weeks, at which times each set of samples was frozen for further analysis. The solitary invertebrates were observed throughout and collected and frozen at the end of the experiment.

RESULTS

The results of these experiments demonstrate negative effects of both temperature and UV-B on the coral. No coral branchlets had bleached white by the end of 1 week, but by the end of 2 weeks bleaching had begun at high temperature (10% bleached at 31°/ambient UV) and at high UV (3% bleached at 27°/+20% UV), and especially at high temperature/high UV (60% bleached). These patterns continued and intensified, culminating in the patterns seen in Table 1 at week 4. By then, the branchlets had bleached and died at high temperatures, especially 31°. Those in higher UV conditions bleached more than those at lower UV in the same temperature condition, even at 27°. An interaction between temperature and UV-B is apparent in these data, although we await data from our more stringent experimental design (above) to evaluate these trends more rigorously. The results suggest that the highest temperature (31°) exerted a more detrimental effect upon the coral than the highest UV intensity (+20%) that we tested.

In contrast, the algae grew in all conditions (Table 2). We include data only through 3 weeks because by that time the urchins had become hungry and several escaped from under the mesh frame, outmaneuvered the plastic guards, and damaged the algae. Algal growth is enhanced at high temperature (31°) at ambient levels of UV. Increased exposure to UV-B appears to enhance growth at low (27°) temperature but inhibit growth at high temperature (31°). Similar patterns in growth among conditions were seen over the first 3 weeks. Further studies will analyze these trends more stringently.

We observed minimal effects (in no particular pattern) of the levels of UV-B tested upon the solitary invertebrates (Table 3). This result may have occurred because the invertebrates could escape the UV-B by hiding under the edges of the frame (which we observed), and because the coral, algae and mesh overhead shaded them from some of the UV. The solitary invertebrates tested, like the algae, also appear to be more temperature tolerant than the corals.

Table 1. Coral bleaching at week 4. Data represent % of _Acropora prolifera_ branchlets that were bleached white (N = 40 branchlets in each condition). J = joules, d = day.

	Temperature (°C)		
	27°	29°	31°
Ambient UV (2169 J/m²/d)	0%	4%	77%
+10% UV (2376 J/m²/d)	12%	23%	78%
+20% UV (2592 J/m²/d)	32%	50%	95%

Table 2. Mean increases in algal weight through week 3. Data are % increases in weight for pieces of _Microdictyon_ sp. tied to the top of vertically oriented glass rods (N = 9 measurements in each condition).

	Temperature (°C)		
	27°	29°	31°
Ambient UV (2169 J/m²/d)	9.4%	9.1%	23.3%
+10% UV (2376 J/m²/d)	19.6%	10.5%	15.0%
+20% UV (2592 J/m²/d)	25.3%	7.5%	12.6%

Table 3. Percentage survival in solitary invertebrates. Data are derived from deaths among all taxa in each condition (1 brittle star died at ambient UV/27°, 1 urchin at ambient UV/29°, and 1 bivalve at +10% UV/29°); 21 invertebrates were placed in each condition, including 6 brittle stars (Ophionereis reticulata, Ophiocoma echinata), 6 hermit crabs (Calcinus tibicens, Paguristes sp.), 6 urchins (Echinometra viridis), and 3 bivalves (Arca sp.).

| | Temperature (°C) | | |
	27°	29°	31°
Ambient UV (2169 J/m²/d)	95.2%	100%	100%
+10% UV (2376 J/m²/d)	95.2%	100%	100%
+20% UV (2592 J/m²/d)	100%	95.2%	100%

DISCUSSION

These results, the first of their kind as far as we know, suggest that if ozone depletion causes increases in tropical UV-B intensities by as much as 10 or 20%, shallow water corals could be significantly negatively affected. This impact would occur not only because of the direct effects of UV-B upon the coral, but also because growth of algae (the corals' primary competitors for space on the reef) could be facilitated by higher levels of UV (as long as temperatures do not increase) and because solitary invertebrates (such as bioeroders) generally do not appear to be adversely affected by elevated UV-B. One other study (Dohler 1984) has reported that, in phytoplankton (diatoms), moderate doses of UV-B caused an increase in biomass production, while higher dosages of UV-B caused lower productivity and depressed protein content in the diatoms. Data in the present study also suggest that persistently warmer conditions (in the absence of elevated UV-B) could favor dominance of algae over corals, both because high temperature inflicts more damage upon corals than UV (at the levels we tested) and because high temperature did not adversely affect the algae (as long as it was not superimposed with high UV). Relationships between algae and solitary invertebrates (some of which graze algae) will be complex, depending upon the combinations of environmental temperature and UV-B that they experience. Solitary invertebrates (some of which scrape and bore coral) appear to be less affected by either UV-B or temperature than the corals, probably because most hide under structures or in crevices during the day and emerge only in crepuscular or nocturnal periods (Dominguez and Reaka 1988). The lack of an effect of temperature on solitary invertebrates in our experiments is somewhat surprising, since experiments by Glynn and D'Croz (1990) showed that survival of symbiotic crustaceans associated with corals declined at higher temperatures. However, this may have been due to the declining health of their obligate coral hosts (Glynn et al. 1985) rather than temperature alone.

Consequently, corals may suffer more than predicted by the straightforward effects of temperature and UV-B upon them, and an ensuing breakdown of the physical structure of reefs could have a devastating effect upon these high diversity systems. Our final interpretations will await more rigorous statistical analyses of these effects and studies of a number of the dependent variables that we have measured. Also, more species of corals, algae, and solitary invertebrates (particularly grazers and bioeroders) must be included before definitive conclusions about the impact of changing thermal and UV-B environments upon reef communities can be made. For example, A. prolifera is a rapidly growing species of coral and may be more prone to bleaching than some of the more slowly growing massive species of corals, and other species of algae may be more damaged by the environmental conditions imposed than was the opportunistic Microdictyon sp. We are pursuing additional comparisons, but we believe that the above patterns are provocative.

CONCLUSIONS

1. The branching coral, Acropora prolifera, is negatively impacted by exposure to increasing dosages of UV-B (to 20% above ambient) and elevated temperatures (from 27° to 31°C). These effects began at week 2 and were much amplified by the end of the 4 week experiment.

2. The opportunistic "bubble-like" alga, Microdictyon sp., survives and grows when exposed to the increased levels of UV-B and temperature tested here (growth is highest at ambient temperature/high UV and ambient UV/high temperature).

3. The solitary invertebrates tested (brittle stars, hermit crabs, urchins, and bivalves) are little affected by the environmental conditions we tested for 4 weeks.

4. If the results obtained for these species hold for other corals, algae and solitary invertebrates, this experiment suggests that altered environmental conditions potentially could induce long term changes in shallow reef communities which are unforeseen on the basis of present knowledge of the effects of temperature and UV-B on one group of organisms such as corals.

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