OCEAN ACIDIFICATION

Coral reefs will transition to net dissolving before end of century

Bradley D. Eyre,[1]* Tyler Cyronak,[2] Patrick Drupp,[3] Eric Heinen De Carlo,[3] Julian P. Sachs,[4] Andreas J. Andersson[2]

Ocean acidification refers to the lowering of the ocean's pH due to the uptake of anthropogenic CO_2 from the atmosphere. Coral reef calcification is expected to decrease as the oceans become more acidic. Dissolving calcium carbonate ($CaCO_3$) sands could greatly exacerbate reef loss associated with reduced calcification but is presently poorly constrained. Here we show that $CaCO_3$ dissolution in reef sediments across five globally distributed sites is negatively correlated with the aragonite saturation state (Ω_{ar}) of overlying seawater and that $CaCO_3$ sediment dissolution is 10-fold more sensitive to ocean acidification than coral calcification. Consequently, reef sediments globally will transition from net precipitation to net dissolution when seawater Ω_{ar} reaches 2.92 ± 0.16 (expected circa 2050 CE). Notably, some reefs are already experiencing net sediment dissolution.

Coral reef structures are the accumulation of calcium carbonate ($CaCO_3$) from coral aragonite skeletons, red and green calcareous macroalgae, and other calcareous organisms such as bryozoans, echinoderms, and foraminifera. This structure provides the habitat for many species, promoting rich biological diversity and an associated myriad of ecosystem services to humans such as fisheries and tourism (*1*). There are two main pools of $CaCO_3$ in coral reefs: the framework (e.g., deposited $CaCO_3$ skeletons and living coral and other organisms) and permeable sediments (e.g., broken-down framework and any infaunal production) (*2*). For net accretion to occur at the whole-reef scale, $CaCO_3$ production (plus any external sediment supply) must be greater than the loss through physical, chemical, and biological erosion and transport and dissolution as follows (*2*):

$$CaCO_3 \text{ accretion} = CaCO_3 \text{ production} - CaCO_3 \text{ dissolution} - \text{physical loss of } CaCO_3 \quad (1)$$

Net ecosystem calcification (NEC), which refers to the chemical balance of $CaCO_3$ production and $CaCO_3$ dissolution, is typically inferred from changes in total alkalinity and does not include physical loss of $CaCO_3$.

Ocean acidification (OA) refers to the lowering of the ocean's pH due to the uptake of anthropogenic CO_2 from the atmosphere. When CO_2 from the atmosphere dissolves in seawater, it decreases the pH, the CO_3^{2-} concentration, and the $CaCO_3$ saturation state ($\Omega = [Ca^{2+}][CO_3^{2-}]/K^*_{sp}$, where K^*_{sp} is the stoichiometric ion concentration product at equilibrium) (*3*). Although OA-associated changes are expected to negatively affect the accretion of coral reefs (*4*), these future predictions are mostly based on the relationship between Ω and calcification rates of individual corals or coral reef communities [e.g., (*5*, *6*); table S3] and NEC [e.g., (*7*); table S2]. However, the impact of OA on net coral reef accretion is also dependent on the poorly known effects of OA on the dissolution of permeable coral reef $CaCO_3$ sediments, which accumulate over thousands of years (*8*) and can be the major repository of $CaCO_3$ in modern coral reefs (*9*). Numerical modeling, laboratory, field, and mesocosm studies have found an increase in $CaCO_3$ sediment dissolution with decreasing Ω and pH (OA) (*10*, *11*).

Notably, a number of studies have hypothesized that $CaCO_3$ dissolution may respond more rapidly to OA than coral calcification [e.g., (*2*, *12*, *13*)]. Supporting this hypothesis, a recent in situ study found that $CaCO_3$ sediment dissolution increased by an order of magnitude more than calcification decreased, per unit decrease in Ω (*14*). However, the in situ $CaCO_3$ sediment dissolution measurements were only undertaken at one site on Heron Island, Australia, and it is unknown how applicable the findings are to coral reefs globally. For example, $CaCO_3$ sediment dissolution of different coral reefs may respond differently to OA because of differences in the present-day saturation state of the water column and differences in sediment properties such as mineralogy, porosity, permeability, grain size, organic carbon concentration, and metabolism, which in turn are controlled by factors such as light, depth, and hydrodynamics.

We measured $CaCO_3$ sediment dissolution using 57 individual in situ advective benthic chamber incubations at five reef locations in the Pacific and Atlantic Oceans (fig. S1). Incubations were undertaken over a diel light-dark cycle, and four of the reef incubations were run under control and end-of-century [high partial pressure of CO_2 (pCO_2), low pH] OA conditions. The five sites covered a range of initial water column $CaCO_3$ saturation states and sediment properties such as mineralogy, grain size, organic carbon concentration, and metabolism (table S1).

Our results show that $CaCO_3$ sediment dissolution across the five coral reefs is significantly and negatively correlated with average Ω_{ar} of the overlying seawater coefficient of determination [(r^2) = 0.49, $P < 0.0001$, $n = 57$] (fig. S2). The increase in $CaCO_3$ sediment dissolution with decreasing seawater Ω_{ar} is consistent with other recent mesocosm and in situ studies from single locations (*10*, *11*, *14*). The seawater Ω_{ar} value of ~2.92 ± 0.16 (x intercept) at which the sediments transition from net precipitating to net dissolving (Fig. 1) is well above the expected thermodynamic transition value for aragonite ($\Omega_{ar} = 1$) and saturation state of the average bulk Mg-calcite (13 to 15 mol % $MgCO_3$) found in most coral reefs (*15*). This can be explained by the interaction of

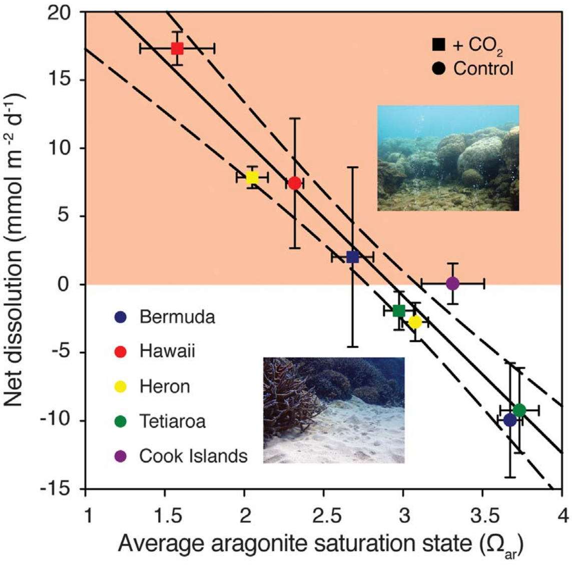

Fig. 1. Average $CaCO_3$ permeable sediment dissolution rates for each set of control (circles) and high pCO_2 (squares) treatments for each of the five reefs as a function of seawater average aragonite saturation state (Ω_{ar}) (r^2 = 0.94, $P < 0.0001$, $n = 9$; $y = -11.51x + 33.683$). No high-pCO_2 treatments were available for the Cook Islands. Error bars represent standard error. The sediments transition from net precipitating to net dissolving at a seawater Ω_{ar} value of ~2.92 ± 0.16 (±95% confidence interval). Data are in table S5. [Top photo by K. Fabricius, Australian Institute of Marine Science, and bottom photo by A. Andersson, Scripps Institution of Oceanography]

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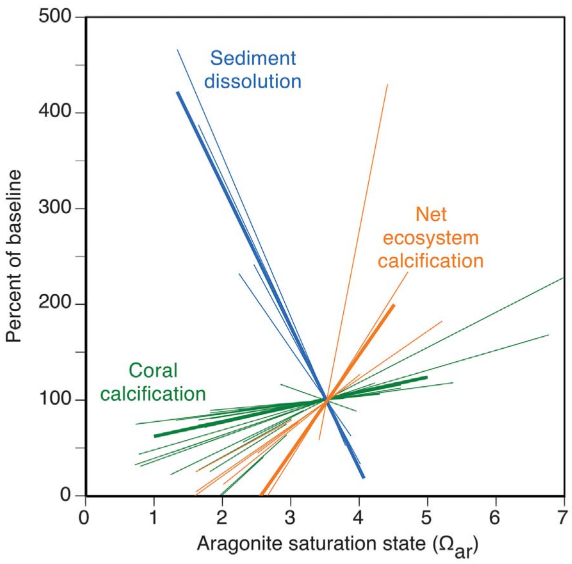

Fig. 2. Percent change in coral reef permeable sediment dissolution, coral calcification, and NEC per unit change in seawater aragonite saturation state (Ω_{ar}). The change is from a baseline Ω_{ar} of 3.5 and hence all lines intersect at Ω_{ar} = 3.5 (100%). The thin lines are the individual measurements, and the thick line is the average. The length of line is the Ω_{ar} range over which the study was done. Coral calcification data are from (*23*). NEC data are from table S2.

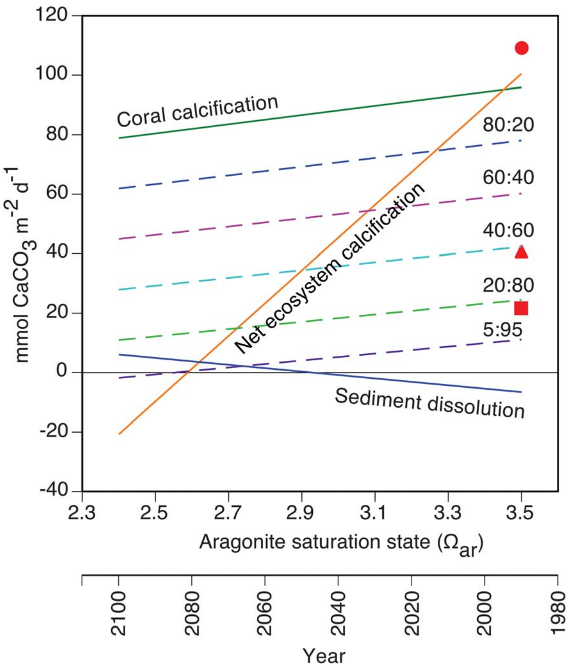

Fig. 3. Empirical model of coral reef permeable sediment dissolution, coral calcification, and NEC versus aragonite saturation state (Ω_{ar}) from reefs around the globe (solid lines). The current (2010) global average Ω_{ar} of ocean water around reefs was set at 3.3 (*37*), and the average annual change in Ω_{ar} was set at −0.01 (*18*). Theoretical reefs with coral:sand covers of 80:20, 60:40, 40:60, 20:80, and 5:95% were also modeled (dashed lines). The red symbols are global estimates of NEC for full coral reefs (109.6 mmol $CaCO_3$ m^{-2} day^{-1}) (circle), an average of coral reefs and coral reef lagoons (41.1 mmol $CaCO_3$ m^{-2} day^{-1}) (triangle), and coral reef lagoons (21.9 mmol $CaCO_3$ m^{-2} day^{-1}) (square) (*40*).

bulk seawater saturation state and porewater metabolic processes (*2*). Much lower Ω_{ar} values are typically found in sediment porewater owing to the decomposition of organic matter and associated production of dissolved inorganic carbon (*16*). It has been hypothesized that organic matter decomposition decreases porewater Ω until it becomes undersaturated with respect to the most soluble bulk carbonate mineral phase present, which then starts to dissolve at a point called the carbonate critical threshold (CCT) (*17*). Further organic matter decomposition then drives carbonate sediment dissolution. However, in shallow carbonate sediments, there is a strong diel cycle in phytosynthesis and respiration, and the daily-integrated sediment productivity/respiration ratio can drive net dissolution or precipitation (*2*, *14*). In our experiments, benthic chambers containing acidified seawater (with higher $p\mathrm{CO}_2$ and lower Ω_{ar}) (fig. S1) were placed over carbonate sands to mimic late–21st century seawater chemistry, and this seawater was advected into the permeable carbonate sands and became the starting composition of porewater (*2*). Under such conditions, less organic matter decomposition is required to reach the CCT, leaving more respiratory CO_2 available to drive dissolution (*17*). That is, for the same amount of sediment respiration, more carbonate dissolution will occur when seawater with a lower Ω_{ar} is advected into the sediments. This hypothesis is supported by results of in situ sediment chamber incubations under controlled and elevated $p\mathrm{CO}_2$ conditions (*10*) but does not unequivocally demonstrate the underlying mechanism.

Average $CaCO_3$ sediment dissolution for each set of control and high-$p\mathrm{CO}_2$ treatments at each of the five reef locations is also significantly and negatively correlated with average Ω_{ar} (r^2 = 0.94, $P < 0.001$, $n = 9$) (Fig. 1). Notably, there is no significant difference (Student's t test; $P < 0.01$) in benthic metabolism (production/respiration) between control and $p\mathrm{CO}_2$ treatments at any of the reef sites (fig. S3), with increased dissolution only driven by changes in overlying seawater chemistry (i.e., OA conditions). Carbonate sediment dissolution at each of the four reefs has the same response to lowered seawater Ω_{ar} (increased seawater $p\mathrm{CO}_2$), but the impact of OA on each reef is different owing to different starting conditions (Fig. 1). For example, carbonate sediments in Hawaii are already net dissolving and will be strongly net dissolving by the end of the century. In contrast, carbonate sediments at Tetiaroa are strongly net precipitating and will remain net precipitating at the end of the century. Carbonate sediments at Heron Island and Bermuda will both transition from net precipitating to net dissolving by the end of the century.

The transition of coral reef sands from net precipitating to net dissolving occurs when the seawater Ω_{ar} reaches 2.92 ± 0.16 (Fig. 1 and fig. S1). Hence, current reef seawater conditions control the impact that OA will have on the net carbonate accretion of coral reefs. The current seawater carbonate chemistry (e.g., pH, Ω_{ar}) of coral reefs is controlled by a combination of the open ocean source water and biogeochemical and hydrodynamic processes on the reef. There are latitudinal and regional variations in the open ocean Ω_{ar} with, for example, tropical reefs bathed in higher-Ω_{ar} water than higher-latitude reefs (*18*). The open ocean seawater composition is then modified by net ecosystem production (NEP = photosynthesis minus autotrophic and heterotrophic respiration) and NEC (*19*). Globally, it has been proposed that the average $p\mathrm{CO}_2$ of coral reefs has increased 3.5 times faster than in the open ocean over the past 20 years, most likely due to increased terrestrial nutrient and organic matter inputs (*20*). For example, in Kaneohe Bay, Hawaii, the carbonate sediments are currently net dissolving because of low reef seawater Ω_{ar} (Fig. 1) associated with low-Ω_{ar} source water (*7*) and large inputs of terrestrial nutrients and organic matter (*21*, *22*). In contrast, the carbonate sediments at Tetiaroa are strongly net precipitating because of high reef seawater Ω_{ar} (Fig. 1) associated with high-Ω_{ar} source water and most likely little to no terrestrial organic matter inputs. External inputs of organic matter are thus an important control on the dissolution and associated net accretion of coral reefs (*2*, *17*).

$CaCO_3$ sediment dissolution across the five reefs is clearly very sensitive to OA with a 170% change per unit change in seawater Ω_{ar} (Figs. 1 and 2). This is an order of magnitude greater than predicted changes in coral calcification due to OA. For example, a recent meta-analysis

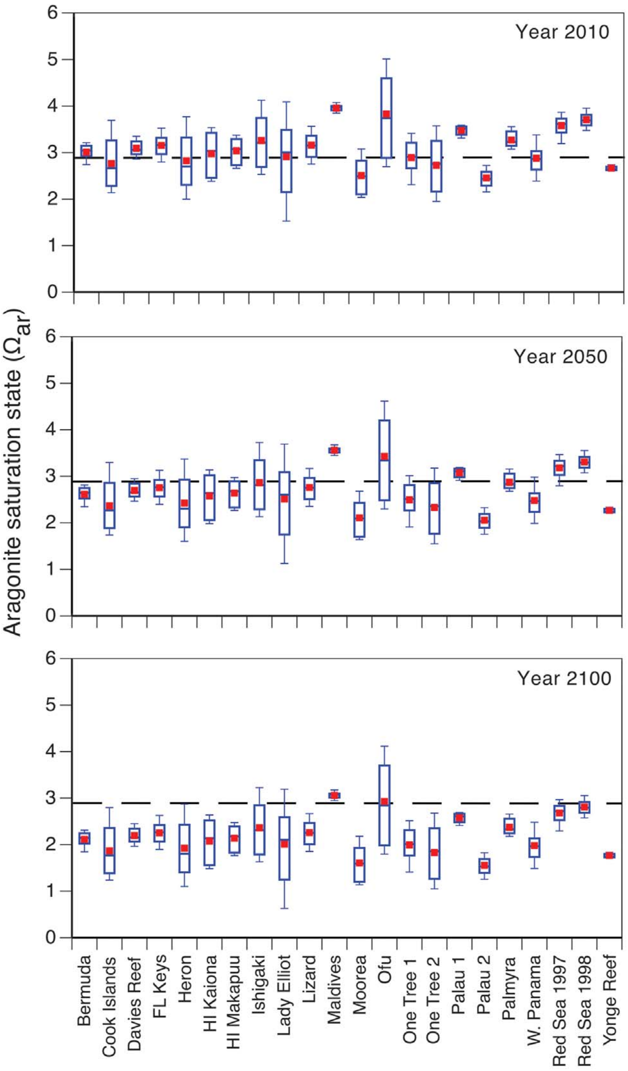

Fig. 4. Box plots of 2010, 2050, and 2100 Ω_{ar} for 22 reefs across the global oceans (details in table S4). The dashed line at Ω_{ar} 2.92 shows when the reef sediments will transition to net dissolving. The 2010, 2050, and 2100 predictions were calculated with the average annual open ocean change in Ω_{ar} of −0.01, but with average actual Ω_{ar} starting values for each reef for the year the data were collected. These calculations ignore the minor nonlinear behavior of Ω_{ar} in response to rising CO_2 over the range modeled. The box plot red square is the mean; the horizontal line in the box is the median; the upper and lower box are the 75 and 25 percentiles, respectively; and the top and bottom whiskers are the 90 and 10 percentiles, respectively.

of biologically mediated coral calcification only showed a 15% reduction per unit change in seawater Ω_{ar} (Fig. 2), or as low as a 10% reduction if only studies integrating light and dark calcification rates were considered (*23*). The change in $CaCO_3$ sediment dissolution per unit change in seawater Ω_{ar} across the individual reefs is also less variable than the response of coral calcification per unit change in seawater Ω_{ar} across the individual studies (Fig. 2). Differences in the response of carbonate sediment dissolution and coral calcification to OA most likely reflect differences in the biologically mediated process of calcification compared to the geochemically mediated process of dissolution.

Coral calcification has shown taxa-specific responses to OA (*24*) most likely due to differences in characteristics such as the percentage of skeletal tissue cover and the ability to regulate pH of calcifying fluids (*25*, *26*). Observations that both near-shore and deep-sea calcifiers can live and calcify under thermodynamically unfavorable conditions [$\Omega_{ar} < 1$; (*27*, *28*)] suggest that seawater chemistry is only part of the equation and that organisms may have mechanisms and/or strategies to deal with the predicted changes in seawater carbonate chemistry and could potentially adapt to OA (*5*, *29*). For example, given a sufficient supply of nutrition and energy, many calcifiers are less negatively affected by OA (*30*). In contrast to biologically mediated calcification, increasing $CaCO_3$ dissolution is mostly a geochemical response to changes in seawater chemistry and will increase according to thermodynamic and kinetic constraints (Fig. 3) (*31*, *32*).

Future predictions of OA effects on coral reefs are often based on the relationship between average Ω_{ar} and NEC (see table S2). On average, there is a 102% change in NEC per unit change in seawater Ω_{ar} (Fig. 2), which is more sensitive than coral calcification (10 to 15%) but less sensitive than carbonate sediment dissolution (170%). The order-of-magnitude greater response of NEC compared to coral calcification could in part be due to sediment dissolution being more sensitive to decreasing Ω_{ar} and therefore making an increasingly greater contribution to the decrease in NEC. In addition, other components of the coral reef benthic community such as crustose coralline algae and calcareous benthic macroalgae, which are also more sensitive to changes in Ω_{ar} than corals (*33*, *34*), could also contribute to the greater response of NEC. Consistent with this is the stronger response and sensitivity of whole coral reef community calcification to changes in Ω_{ar} than that observed in studies of individual organisms [e.g., (*12*, *35*, *36*)]. The highly variable response of the NEC of individual reefs to changes in Ω_{ar} probably reflects variations in composition of benthic communities, combined with the variable response of individual benthic communities (i.e., sediments, corals, crustose coralline algae).

An understanding of the absolute changes in $CaCO_3$ production and dissolution (and physical loss) as the ocean acidifies is required to be able to predict the future evolution of coral reefs (see Eq. 1). We developed a simple model based on empirical relationships between average Ω_{ar} and NEC, coral calcification, and sediment dissolution from reefs around the globe (Fig. 1 and tables S2 and S3) and predicted future changes in the open ocean Ω_{ar} (*18*) to quantify changes in the $CaCO_3$ production of coral reefs (see materials and methods for a detailed description of the model). Under present-day average tropical ocean Ω_{ar} (3.3), coral reef sediments are net precipitating and coral calcification and NEC are positive (Fig. 3). However, the model shows there has already been on average a reduction in coral reef sediment precipitation from 18.1 to 4.3 mmol m^{-2} day^{-1}, a reduction in NEC from 210.7 to 78.5 mmol m^{-2} day^{-1}, and a reduction in coral calcification of 111.4 to 92.8 mmol m^{-2} day^{-1} since pre-industrial time when the average tropical ocean Ω_{ar} was ~4.5 (*37*). When the average tropical ocean Ω_{ar} reaches ~2.92 in ~2048, coral reef sediments will become net dissolving (Fig. 3). By 2082, global average coral reef NEC will become negative (i.e., net dissolving; Fig. 3). By 2078 (Ω_{ar} = 2.62), sediment dissolution will exceed the global average coral reef NEC (Fig. 3). For coral reefs with 5% coral cover and 95% sediment cover, probably a common future scenario with increasing coral cover loss, this transition to net dissolution will also occur in 2085 (Ω_{ar} = 2.55) (Fig. 3).

The above model scenarios assumed a current average open ocean Ω_{ar} of 3.3 for coral reefs. However, an analysis of 22 coral reefs (see also table S1) shows a wide range of Ω_{ar} values, and therefore the timing of the transition to net dissolving will vary for individual reefs (Fig. 4). On average, four reefs already experience conditions that would promote net sediment dissolution, and by the end of the century, all but two reefs across the three ocean basins would on average experience sediment dissolution. The above model scenarios also assumed open ocean changes in Ω_{ar}, but the average seawater carbonate chemistry conditions of coral reefs may be appreciably different because of changes in reef biogeochemical processes and inputs of terrestrial nutrient and organic matter (*19*, *20*). One study suggests that the seawater $p\text{CO}_2$ on some reefs has increased up to 3.5 times faster than in the open ocean (*20*). Under this more rapid acidification scenario, coral reefs on average could transition to net sediment dissolution by the end of the decade (2020) (Ω_{ar} = 2.92), and NEC will become negative by 2031 (Ω_{ar} = 2.58). This study also has not included the effect of sea surface temperature increases on CaCO_3 sediment dissolution. Although initial studies show a nonadditive effect of increased temperature and lowered Ω_{ar} on CaCO_3 sediment dissolution (*38*), little is known about these combined stressors. Bleaching and coral mortality will also most likely accelerate the breakdown of coral reefs (*39*), making more sediment and organic matter available for dissolution.

A transition to net sediment dissolution will result in loss of material for building shallow reef habitats such as reef flats and lagoons and associated coral cays (*2*). However, it is unknown if the whole reef will erode once the sediments become net dissolving, as the corals will still calcify (Fig. 3), and the framework may still accrete. It is also unknown if reefs will experience catastrophic destruction once they become net eroding, or if they will slowly erode, driven by organic matter input and OA (*17*).

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SUPPLEMENTARY MATERIALS

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Materials and Methods
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Coral reefs will transition to net dissolving before end of century

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Acid reef-flux

The uptake of anthropogenic carbon dioxide from the atmosphere is reducing the pH of the oceans. Ocean acidification means that calcium carbonate––the material with which coral reefs are built––will be more difficult for organisms to generate and will dissolve more quickly. Eyre *et al.* report that some reefs are already experiencing net sediment dissolution. Worryingly, the rates of loss will increase as ocean acidification intensifies.

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