

Geochemical signatures of benthic foraminifera shells from a heat-polluted shallow marine environment provide field evidence for growth and calcification under extreme warmth

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Shallow marine calcifiers play an important role as marine ecosystem engineers and in the global carbon cycle. Understanding their response to warming is essential to evaluate the fate of marine ecosystems under global change scenarios. So far, most data on thermal tolerance of marine calcifiers have been obtained by manipulative laboratory experiments. Such experiments provide valuable physiological data, but it remains unclear to what degree these observations apply to natural ecosystems. A rare opportunity to test the effect of warming acting on ecosystem-relevant scales is by investigation of heat-polluted coastal areas. Here we study growth and calcification in benthic foraminifera that inhabit a thermally polluted coastal area in Israel, where they are exposed to temperature elevated by 6°C above the natural seasonal temperature range and reaching up to ~42°C in summer. Several species of benthic foraminifera have been previously shown to persist throughout the year in the heat-polluted area, allowing us to examine in natural conditions the thermal limits of growth and calcification under extreme temperatures as they are expected to prevail in the future.

Live specimens of two known heat tolerant species *Lachlanella* sp. 1 and *Pararotalia calcariformata* were collected over a period of one year from two stations, representing thermally polluted and undisturbed (control) shallow hard bottom habitats. Single-chamber element ratios of these specimens were obtained using laser ablation and the Mg/Ca of the last chambers (grown closest to the time of collection) were used to calculate calcification temperatures.

Our results provide the first direct field evidence that these foraminifera species not only persist extreme warm temperatures but continue to grow and calcify. Species-specific Mg/Ca thermometry indicates that *P. calcariformata* precipitate their shells at temperatures as high as 40°C and *Lachlanella* sp. 1 at least up to 36°C. Instead, both species showed a calcification threshold above the local winter temperatures. Calcification in *P. calcariformata* only occurred above 22°C and in *Lachlanella* sp. 1 above 15°C. Our observations from the heat-polluted area indicate that under future warming scenarios, growth and calcification in both benthic foraminifera species will not be inhibited during summer heat and the seasonal temperature window for their calcification will be expanded throughout much of the year. The observed inhibition of calcification at low temperatures indicates that the role of heat-tolerant foraminifera in carbonate production will most likely increase in future decades.