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Published in:
 Bulletin of Marine Science

DOI:
[10.5343/bms.2021.0007](https://doi.org/10.5343/bms.2021.0007)

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Document Version
 Publisher's PDF, also known as Version of record

Publication date:
 2021

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Tilstra, A., Hoeksema, B. W., & Wild, C. (2021). A presumed Lazarus coral: Outstanding regeneration capacity of a *Goniopora* coral exposed to air over several months. *Bulletin of Marine Science*, 97(3), 473-474. <https://doi.org/10.5343/bms.2021.0007>

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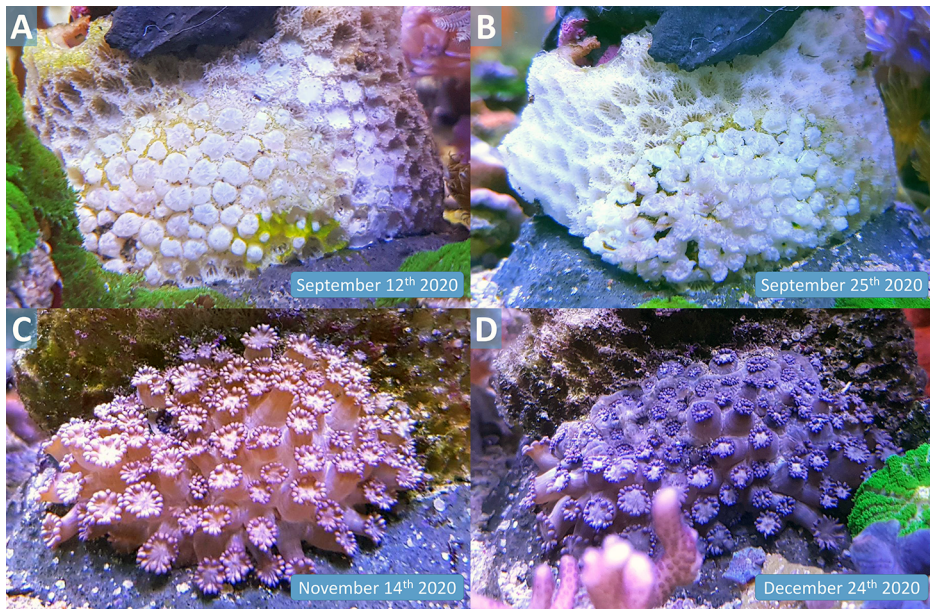
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A presumed Lazarus coral: outstanding regeneration capacity of a *Goniopora* coral exposed to air over several months

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It is a common and well-known phenomenon that reef corals harboring shallow intertidal reefs regularly get exposed to air during low tide. This can cause temporary stress, visible as tissue retraction (Brown et al. 1994), bleaching (Anthony and Kerswell 2007), and temperature shifts (visualized by thermal imagery) of air exposed colonies (Heyward and Negri 2020), with the latter two depending on factors such as coral morphology and wave exposure. In the long term, these recurrent aerial exposures are not necessarily lethal, but they can lead to significant changes in coral holobiont physiology (e.g., by shifts in the microbiome; Sweet et al. 2017). However, long-lasting aerial exposure caused by extreme low tides can be deleterious for certain coral species (Anthony and Kerswell 2007, Schoepf et al. 2015, Mejía-Rentería et al. 2020). Here we present an observation of nondeleterious prolonged exposure to air in an ex situ cultured fleshy reef-building coral.

In May 2020, a colony of the reef-building scleractinian *Goniopora* sp., which had been in stable culture for several years (salinity 33.0, temperature $26\text{ }^{\circ}\text{C}$, nitrate $\pm 2.0\text{ mg L}^{-1}$, phosphate $\pm 0.05\text{ mg L}^{-1}$, calcium 440 mg L^{-1} , magnesium 1350 mg L^{-1} , alkalinity 3.0 mEq L^{-1}), retracted its polyps after extended low light exposure caused by shading from faster growing coral colonies. As a result, the coral lost all visible tissue and was discarded from the holding tank at the beginning of June after it was presumed dead. It was subsequently left outside to face the Dutch weather in the city of Rotterdam on a pile of limestone rocks facing south. The skeleton was introduced back into the holding tank approximately 3 mo later to support the substrate for a colony of another coral. During these 3 mo outside the water, the skeleton was exposed to a mean (SD) temperature of $18.4\text{ (}3.5\text{)}\text{ }^{\circ}\text{C}$ (range = $6.2\text{--}33.8\text{ }^{\circ}\text{C}$), mean (SD) global radiation of $1801\text{ (}641\text{)}\text{ J cm}^{-2}$ (range = $517\text{--}3050\text{ J cm}^{-2}$), and precipitation ranging between 0 and 30.6 mm d^{-1} (KNMI 2021).

Within 2 wks after reintroduction, the skeleton generated tissue that was first assessed as dead tissue being slowly discarded from the skeleton (Panel A). Surprisingly, soon after this initial observation, the layer of tissue appeared to consist of living coral polyps (Panel B). In the following weeks, the coral showed a further improvement of its health by regaining its natural color (partially due to recolonization of zooxanthellae), while polyp expansion increased (Panel C). Finally, after about 4 mo, the colony fully regained its original color, while the coenosarc between all individual polyps appeared to be fully fused (Panel D).

Previous documented cases of extreme polyp regeneration from apparently dead scleractinian coral tissue did not involve such long periods of draught and concerned only a few scleractinian taxa, such as fungiid and dendrophyllid corals (e.g., Hoeksema 2004, Luz et al. 2018, Luz et al. 2021). While coral reef literature describes the effects of aerial exposure for minutes to several hours per day (e.g., Rosser and Veron 2011, Castrillón-Cifuentes et al. 2017, Sweet et al. 2017), to our knowledge, this is the longest period described in the literature of a reef coral that has survived out of water conditions. We hypothesize that this remarkable ability to regenerate may be due to the depth to which the coral retracted its polyps within the skeleton (Kitano et al. 2013), potentially linked to production of persistent mucus that efficiently protected the retracted coral tissue against desiccation (Krupp 1984), and to the regrowth of possible tissue remnants (DeFilippo et al. 2016). The remaining retracted tissue may have been in a state of quiescence (dormancy), a survival mechanism often demonstrated by temperate scleractinian corals as a response to cold water stress (Grace 2017). Our observation may lead to new ways to investigate the regenerative capacity of reef-building corals and may help coral reef conservation by identifying more resilient coral species.

ACKNOWLEDGMENTS

We thank Glenn Fong of Dutch Synthetic Reefing (DSR) for sharing this observation and providing the information and photographs. We also thank Kevin Favier for his help with photo editing.

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Date Submitted: 10 February, 2021.

Date Accepted: 3 May, 2021.

Available Online: 3 May, 2021.

