To elucidate the mechanism responsible for coral bleaching and to project the status of coral
communities in the near future, a coral bleaching model was developed based on a reef-scale
three-dimensional hydrodynamic–biogeochemical model coupled with a polyp-scale coral bleaching
model.

The polyp-scale bleaching model was developed by incorporating the dynamics of pho
toinhibition, reactive oxygen species (ROS), and zooxanthella abundance based on a previously developed coral polyp
model by Nakamura et al. (2013). The polyp-scale model assumes that ROS are produced by
zooxanthellae and that corals expel zooxanthellae when the concentration of ROS in their tissues exceeds
tolerable levels. When temperature increases, corals release more zooxanthellae because the ROS
production rate per zooxanthella cell increases with increasing temperature. This mechanism accounts for
coral bleaching at high temperatures. The model assumes that ROS are produced from excess electrons
transferred from photosystem II (PSII) that are not used in the downstream photosynthetic process.
Photoinhibition, which is a key factor in the transfer of electrons from PSII, was included in the model, and
the temperature dependence of Rubisco activity was introduced as a blocking factor in the downstream
photosynthetic process. The ROS dynamics include detoxification of ROS by antioxidant substances, and
the zooxanthella population dynamics include reproduction, mortality, and the rate of zooxanthellae
release, which depends on the ROS damage of the coral cell. Results of simulated incubation experiments
under different temperature conditions by the bleaching model reproduced the temperature dependence
of the coral bleaching phenomenon. Moreover, recovery process after bleaching was also reproduced,
and the ability of the model to describe the recovery process is a unique feature. The model also
reproduced the phenomenon that coral bleaching is effectively reduced by light shading. A comparison
between photoinhibition and its absence revealed that photoinhibition effectively reduced electron
transport from PSII and consequently reduced the production of excess electrons that form ROS.
Photoinhibition therefore protects the photosystem and tissues from oxidative damage by ROS. A
temperature-dependent repair delay from photoinhibition also reduces ROS production and thereby
prevents coral bleaching. The delay may be strategically controlled by zooxanthellae.

The polyp-scale bleaching model was coupled with reef-scale hydrodynamic-biogeochemical model
based on the model framework by Nakamura et al. (2018). The model was applied to both the Shiraho
coral reef based on Nakamura et al. (2018), and Sekisei Lagoon based on Bernardo et al. (2017). The
results of the model simulation confirmed that the model accurately reproduced the spatiotemporal

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variations of bottom water temperatures on the reef. In particular, the temperatures during the daytime were significantly higher on the reef crest and in shallow nearshore areas than in the offshore seawater. The model confirmed that the spatial pattern of zooxanthella density coincided with the spatial pattern of water temperature on the reef. The model can use the internal condition of the corals to output the parameters that characterize coral population dynamics, such as coral growth rates and mortality rates. The coupled model therefore has the potential to simulate long-term spatiotemporal changes in coral coverage. Although the model still needs some improvement, incorporation of additional modules and improvement of the model will make it a useful tool for evaluating how corals respond to multiple environmental stresses on the reef-scale.

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