late Holocene deglaciation, when the West Antarctic Ice Sheet retreated to roughly where Lake Whillans is today. During the deglaciation period, seawater flooded the exposed ice stream bed and seeped into the porous glacial till. As the ice sheet readvanced, the presence of thick ice cut off ocean access to the bed, and the remanent seawater was sealed as groundwater beneath the Whillans Ice Stream.

Ultimately, the impact of groundwater on ice motion hinges on its ability to exchange water with subglacial hydrology. If the groundwater reservoir can soak up a substantial amount of subglacial water, the amount of lubricating water that contributes to hard-bed sliding would be reduced. Similarly, deeper transport of water into the bed substrate may dewater shallower sediment layers, potentially reducing the amount of ice motion supported by soft-bed sliding. In addition to affecting the ice sheet sliding processes, groundwater hydrology, which resides underneath the subglacial hydrology, could also store water for an unknown period and result in time lags that affect ice sheet dynamics. The importance of Antarctica's groundwater hydrology may have been overlooked in ice flow models. To better the understanding of ice sheet groundwater hydrology, existing instrumental technologies can be combined to conduct joint analyses of radar, seismic, and EM sounding (7, 9, 13) to constrain ice sheet geology and geomorphology and to map potential locations of permeable sediments and groundwater. Other modeling developments, such as the inclusion of groundwater hydrology in subglacial drainage models (14), are underway now, and paleorecords in numerical ice sheet simulations (15) should soon be ripe for assessing the importance of groundwater hydrology in the stability of Earth's polar ice masses.

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POLLUTION

Sunscreens threaten coral survival

Oxybenzone-based sunscreens are increasing the mortality rates of stressed corals

By Colleen M. Hansel

oral reefs are among the most biologically rich and economically valuable ecosystems on the planet (1). Despite their immense environmental and socioeconomical value, coral reefs are in global decline because of an array of anthropogenic-derived stressors, including increasing seawater temperatures, coastal nutrient pollution, and overfishing (2). In recent years, chemicals in topical sunscreens have been identified as an additional threat to coral health (3). Concerns about higher concentrations of sunscreenderived chemicals and their potential toxicity to corals have led to bans of certain ultraviolet (UV) filters in sunscreens in some coastal communities. On page 644 of this issue, Vuckovic et al. (4) point to the metabolic products of oxybenzone-based sunscreen as a possible factor in increasing the mortality rate of corals, particularly those already affected by other stressors.

Oxybenzone, one of the most common UV filters in sunscreens, was among the first

sunscreen filters to be banned in Hawaii and some island nations (5). It is a broadspectrum UV filter, meaning that it absorbs and reflects both UVA radiation, which has a longer wavelength, and UVB radiation, which has a shorter wavelength. Although a consensus on the toxicological effects of sunscreens on corals (based on systematic toxicological tests) is lacking (3), some studies have found dose-related bleaching and toxicity in corals over a range of life stages (6, 7). In line with those studies, Vuckovic et al. discovered, in controlled laboratory experiments, that oxybenzone in the presence of UV light leads to a higher mortality rate in a mushroom coral (Discosoma sp.) and a sea anemone (Aiptasia sp.).

Vuckovic *et al.* show that the loss of a symbiotic partner increases oxybenzone-related mortality. Thus, corals and other cnidarians—a large phylum that contains aquatic animals, including sea anemones and jellyfishes—may receive assistance in

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The metabolic products of oxybenzone-based sunscreen threaten the survival of bleached corals, which have already lost their symbiotic algal partners that could have helped minimize the toxic effects of the chemicals.

evading the toxic effects of UV filters from microscopic partners living within their tissue. Corals do not live in isolation but instead rely on beneficial symbiotic relationships with a rich diversity of microbes residing within them (8). Without these symbionts, the host animal is more susceptible to nutrient starvation, pathogenic infection, and oxidative stress (9). The loss of these essential symbionts in corals, which results in the corals being "bleached," can be triggered by external stressors, such as increased seawater temperatures. The authors show that mortality rates are substantially lower for pigmented coral colonies that contain symbiotic algae than for colonies that are bleached and algal deficient.

Considering the increasing frequency and severity of bleaching of corals within reefs globally (10), oxybenzone-based sunscreens pose an additional and synergistic threat to the survival of corals in already compromised reefs. These findings point to the need for coral-friendly alternatives to oxybenzone sunscreens, which ultimately requires a fundamental knowledge of the mechanisms of the toxicity at play. It is to this point that Vuckovic et al. take a critical step in identifying harmful reactions induced by sunscreen degradation products as the underpinning phototoxicity process involved. A chemical is said to be phototoxic if it can react with light to create chemicals harmful to the host. When oxybenzone comes into contact with corals, it enters the coral tissue, where it has several fates. Within pigmented corals, the oxybenzone acts as a UV filter, absorbing harmful UV radiation until it is metabolized by tissuehosted microbes. Unlike oxybenzone itself, these metabolic by-products, such as oxybenzone-glucoside, have phototoxic properties and produce reactive oxygen and/or reactive halogen species that can degrade essential biomolecules within the coral. For healthy, pigmented colonies, algal symbionts sequester these phototoxic metabolites, resulting in lower mortality rates for the coral host. Therefore, the fate of corals presented with oxybenzone rests on a delicate balance between the UV light protection afforded by oxybenzone accumulation in the coral tissue and the damaging effects of phototoxic metabolites, where algal partners minimize and/or decelerate the toxic effects to the animal host.

With increasing incidences of global stressors on corals that lead to bleaching

and/or disfunction of the coral-symbiont relationship, it is imperative to minimize secondary threats such as the toxic effects imposed by sunscreen-derived UV filters. Yet despite observations of the presence of several UV filters within reef waters and sediments, reliable risk assessments and decision-making has been compromised by a lack of systematic characterization of the impact of UV filters on corals (11). Future research efforts should aim to characterize the toxicological thresholds and mechanisms of toxicity of UV filters and their degradation products under environmentally relevant conditions. These studies should incorporate various coral life stages as well as relevant sunscreen levels and the duration of exposure of the chemicals to coral and their symbiotic partners.

With an eye toward ecosystem protection more holistically, it is important to also consider the toxicity of sunscreens and their degradation products on other reef members and partners that are key to overall reef health. Coral reefs are complex ecosystems that rely on a multitude of mutualistic interactions among diverse micro- and macrofauna inhabitants within reefs, including crustose coralline algae, sea anemones, and sponges (*12*). Thus, risk and toxicology assessments should incorporate feedback of the toxic effects between reef members and work to scale from the individual to the entire ecosystem.

In the face of a changing ocean, even perceived small actions may have compounding effects within compromised ecosystems. Because ecotourism is more popular than ever, efforts should be made to minimize the inadvertent contribution of sunscreenderived toxic chemicals to the decline of reef health. The research presented by Vuckovic *et al.* provides critical insight for developing ecologically friendly sunscreens and should inform policy decisions for regulating sunscreen use within reefs and sensitive coastal ecosystems globally.

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CORONAVIRUS

Rapid response modeling of SARS-CoV-2 transmission

What can modelers learn from recent history to help prepare for the next pandemic?

By Jon Zelner^{1,2} and Marisa Eisenberg^{1,3,4}

he COVID-19 pandemic has cemented the role of mechanistic infectious disease models as drivers of the scientific, public, and policy discourse during infectious disease emergencies. On page 596 of this issue, Pulliam *et al.* (1) add to these contributions through their use of a mechanistic model to document the high rate of reinfection with the severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) Omicron variant in South Africa among people previously infected by the initial wildtype strain or the Alpha, Beta, or Delta vari-

ants. This work provides another example of how rapid-response modeling has facilitated the testing of key hypotheses and assumptions with unprecedented speed and nearimmediate public health impact.

That sophisticated mechanistic models were rapidly pressed into action reflects decades of investment in the intellectual and technological resources to do so. It also reflects lessons learned from previous crises, including the 2003 SARS-CoV-1 outbreak, 2009 H1N1 influenza pandemic, and 2014 Ebola epidemic (2). Because modeling is inherently an integrative and historical enterprise, the failures of modeling during the COVID-19 crisis also reflect lessons not learned from these previous emergencies as well as ones that were impossible to anticipate owing to the novelty of the COVID-19 pandemic.

Much of the power of transmission models comes from their ability to create "stylized

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