tects the presence of a quorum-sensing molecule—a chemical produced by cells that corresponds with population density and controls the expression of specific genes. In this circuit, when the quorum-sensing molecule reaches sufficiently high concentrations, the cells are programmed to burst open, releasing their contents as a proposed means of drug delivery. This population-dependent lysis yields a stable oscillation in culture density, and because it relies on a diffusible signal to trigger lysis, any newly added cells carrying the same gene circuit are quickly synchronized to the established population, maintaining oscillations of cell density with similar periodicity.

Given the inherent fitness cost of the lysis circuit, growing these bacteria quickly results in the evolution of mutants, and the communities typically stop lysing after 2 days. By pairing this costly pathway with their RPS system, the authors were able to remove any potential mutants and reset the genetic integrity of continuous cultures through addition of the next strain in the RPS sequence, considerably elongating the longevity of their density-dependent lysis. Of note, this kind of RPS approach should be a generalizable means of continually rebooting communal gene pools of engineered microbiomes, which, if combined with previously established approaches, could considerably extend the lifetime of synthetic probiotics and other in vivo therapies.

The growing understanding of the connected nature of life underscores the impact ecological systems have on human health and that of the environment. The collective genetic network of the microbiome, for example, is now implicated in a number of diseases (*14*). As synthetic biology continues to build more complex devices, echoing these distributed genetic networks could unlock higher-order functions for the next generation of engineered microbes. ■

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CORALS

Coral spawning, unsynchronized

A breakdown in the coral spawning synchrony may threaten coral reef recovery

By **Nicole D. Fogarty**[1] *and* **Kristen L. Marhaver**[2]

During annual mass spawning events, hundreds of corals release millions of egg–sperm bundles in a coordinated manner. Underwater, the reef appears awash in a blizzard of pink snowflakes, but instead of falling, they rise to the surface, resulting in a slick of eggs that has even been seen from space. Mass spawning helps to overcome the dilution that is an ever-present challenge to fertilization for free-spawning marine species. It provides high gamete densities to ensure fertilization (*1*) while swamping gamete predators (*2*). However, the reproductive coordination of corals may be breaking down. On page 1002 of this issue, Shlesinger and Loya (*3*) compared four recent years of coral spawning observations to data collected from the same reef in the Red Sea 30 years before. They show that three of five species exhibited spawning asynchrony in recent years relative to earlier observations at the same site.

As Shlesinger and Loya report, not only did coral species at their study site spawn in different months from year to year, but colonies also spawned asynchronously over a broad range of days within each month. The authors further examined the potential consequences of spawning asynchrony on population demographics, finding a paucity of coral recruits and juveniles in the species with disrupted spawning. Even well-synchronized corals, such as Caribbean *Orbicella* spp. (*1*), can suffer recruitment failure (*4*) if mortality occurs after fertilization or during larval development, dispersal, and recruitment. However, Shlesinger and Loya demonstrate that the two Red Sea species that maintained spawning synchrony also maintained high recruitment, leading them to hypothesize that asynchronous spawning was a major contributor to recruitment failure in the other three species.

Spawning corals rely on a hierarchy of environmental cues to coordinate the months-long gametogenesis cycles that lead up to a narrow, minutes-long mass spawning window; therefore, they are particularly sensitive to changes in the environment (*2*). Resulting mistiming of coral spawning can be detrimental at multiple levels. Individual corals that deviate from the population's peak spawning time by even a few minutes can suffer reduced fertilization; individuals that miss the peak spawning time by hours or days often fail to achieve fertilization at all (*1*). Below a threshold density of spawning individuals, populations may fail to reproduce as a result of sperm limitation. Although fertilization failure is the main concern, low sperm densities and spawning discordance can also cause fertilization mistakes if the breakdown of temporal reproductive isolation between closely related species contributes to accidental hybridization (*1*).

Shlesinger and Loya warn that coral populations around the globe might appear healthy while suffering silently from these reproductive struggles. They posit that climate change, thermal stress, light pollution, and endocrine disruption are among the likely culprits. Yet now more than ever, the world's coral reefs need the genetic diversity generated by sexual reproduction to create new, stress-tolerant genotypes to adapt to global change.

How could human pressure cause so

How coral synchronize mass spawning

Reproductive stage and spawning times are correlated to a hierarchy of factors over multiple temporal scales.

TIME	FACTORS CORRELATED WITH CORAL SPAWNING	CORAL REPRODUCTIVE STAGE
Month	Solar irradiance, sea surface temperature, rainfall, wind, tides	Late-stage gametogenesis
Night	Lunar cycle	Gamete bundle formation
Hour	Sunset	Setting of gamete bundles
Minutes	Pheromones and coral genotype	Release of gamete bundles

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Corals employ synchronized mass spawning to overcome gamete dilution and swamp gamete predators.

much discordance in one of nature's most precisely coordinated processes? Coral spawning synchronization is regulated on four temporal scales: month, day, hour, and minute (see the table) (*1*, *2*). Researchers long assumed that mean sea surface temperature (SST) was the main cue coordinating the month of spawning, but recent evidence suggests a far stronger role for rapid increases in SST (*5*), rates of change in solar irradiance (*6*), periods of limited rainfall (*7*), tidal cycles and atmospheric pressure (*8*), and regional wind patterns (*9*). Climate change can easily and effectively scramble these environmental signals.

To synchronize the day and hour of spawning, corals are thought to detect lunar cycles and the onset of darkness using circadian and light-sensing proteins (*10*–*12*). Additionally, recent evidence suggests that corals coordinate even finer synchrony, on the scale of minutes, by detecting shifts in twilight color and intensity (*13*), by detecting pheromones released from nearby spawning colonies, and through regulating genes at the individual level (*1*). Light pollution and endocrine disruption could easily derail such finely tuned systems. The challenge of decoding the relative importance of each coral spawning cue is made more difficult by correlated environmental cues, hundreds of spawning species, differing circadian (*13*) and sexual systems (*2*), and local stressors that may alter spawning behavior.

Fragile animals with complex behaviors make for a challenging study system, but experiments in captivity are now revealing factors that regulate coral spawning while creating new opportunities for research and restoration. Aquarium control systems can now can accurately reproduce location-specific temperature fluctuations and solar and lunar cycles over the entire reproductive period from gametogenesis to spawning (*14*). Thus, for a growing list of species, researchers can induce spawning in daytime instead of nighttime, and in different subsets of a captive population at different times during the year. This accelerates research by allowing multiple spawning events per year while providing a new source of gametes for restoration, complementing collections in the wild. It was once nearly impossible to repopulate reefs using spawned eggs, but recent advances in large-scale gamete collection, in vitro fertilization, and larval propagation have created the potential to reintroduce coral juveniles by the thousands (*15*, *16*).

The report by Shlesinger and Loya highlights the importance of long-term datasets and the need for observations that span large geographic areas to determine whether spawning asynchrony is a localized anomaly or a global trend. These findings add to the growing concern about the effects of climate change and pollution on coral resilience and recovery. New thermally tolerant coral genotypes can only be created through sexual reproduction, but coral reproductive success is potentially undermined by spawning asynchrony. Recent advances in technology, husbandry, and natural history have rapidly improved researchers' ability to propagate broadcast-spawning corals for restoration, giving conservationists a powerful tool to bolster coral population numbers and add genetic diversity. Yet the fact remains that unless anthropogenic stressors on coral reefs in the wild are reduced, the best place for future generations to experience the awe of a well-synchronized pink blizzard of coral spawning might just be in an aquarium. ■

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