On a Coral Reef, It's a Hard Knock Life

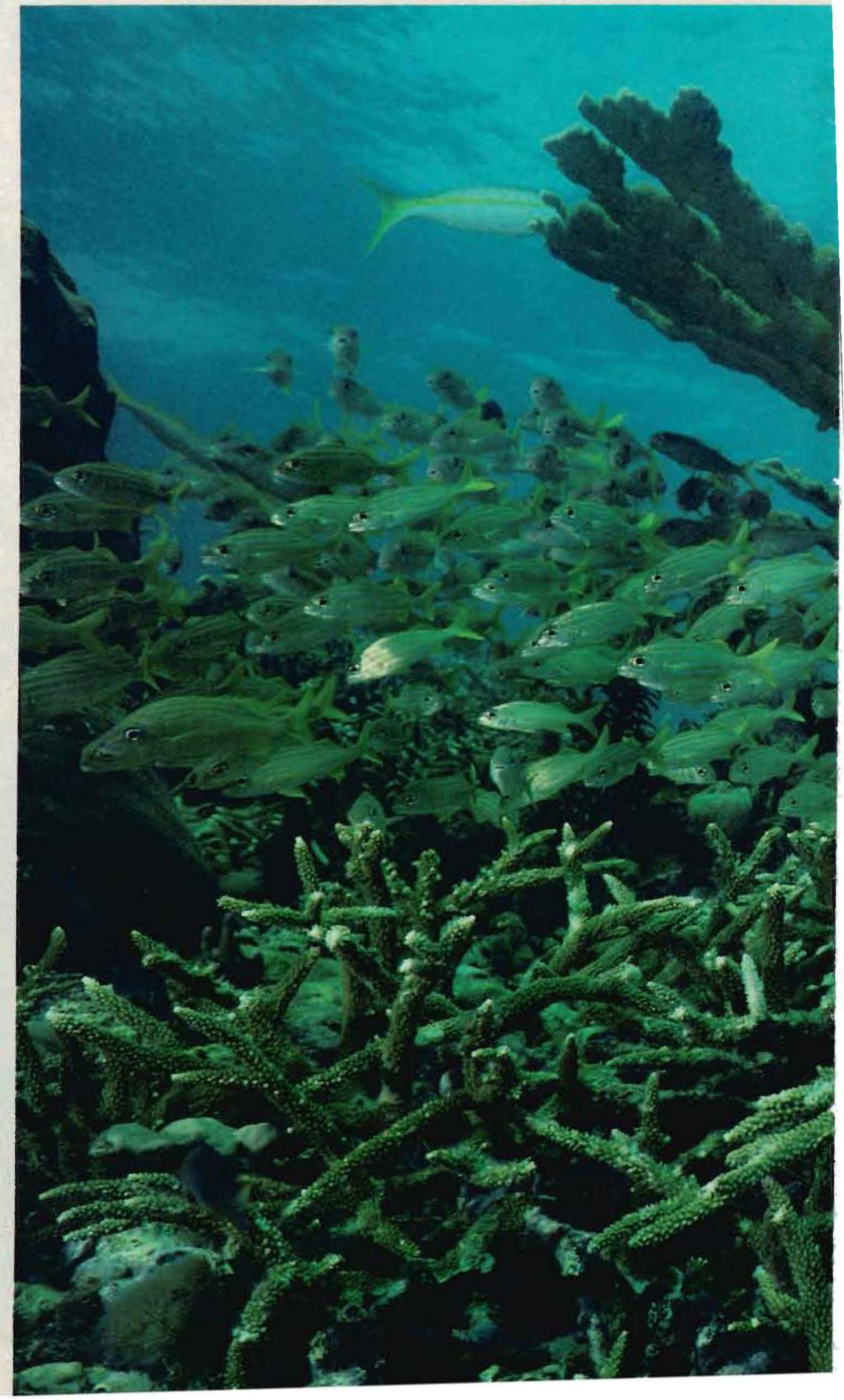
If unrelated staghorn corals don't stick together, they may all fall apart

by Joseph E. Neigel and John C. Avise

As we descend through forty feet of clear blue water over a Jamaican coral reef, we first pass through a swarm of ctenophores, jellylike animals pulsating with luminescence. We then part a school of brilliant blue chromis fish darting about in pursuit of tiny planktonic prey. Finally, we arrive at our destination: a reef zone dominated by the tangled, golden brown branches of staghorn coral. At first, there appears to be little order within this rigid meshwork of living coral, which resembles a thicket of undersea cactus; but after many dives on this reef, we have discovered a clear underlying structure. The structure is genetic, and the meshwork consists of many distinct clones—each representing the asexual descendants of a single coral larva. Shaped by the processes of birth, growth, and death within the coral population, this structure may bear the imprint of past events long after other evidence has vanished.

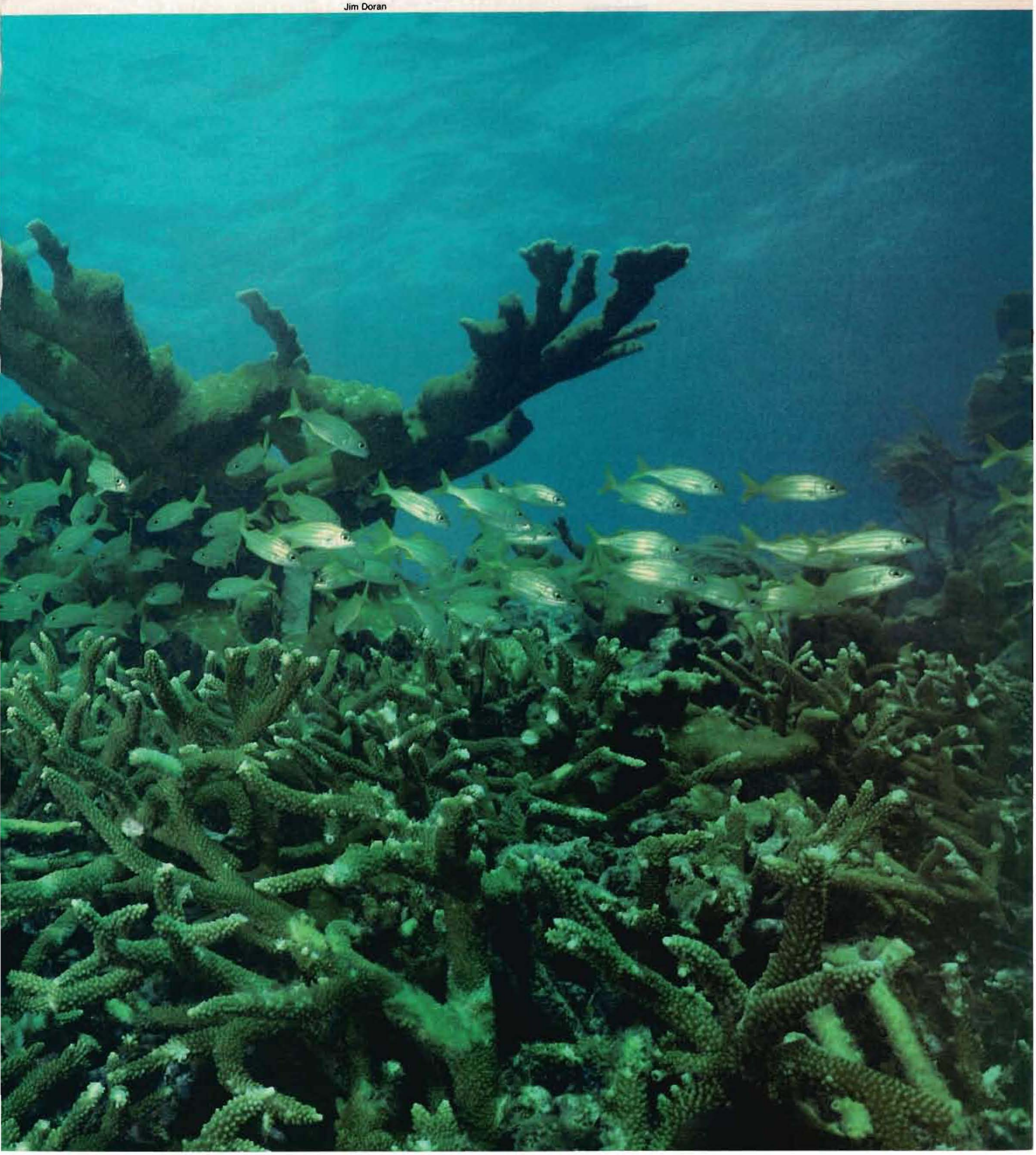
Like most corals that build reefs off tropical coasts and atolls, staghorn coral formations (*Acropora cervicornis*) are colonies of interconnected animals, the coral polyps. These polyps secrete an internal carbonate skeleton, which gives them their shape and into which they may withdraw for protection. Living within the polyp's digestive tissues are zooxanthellae, symbiotic algae from which the coral derives nutrients. In the nutrient-poor waters where coral reefs usually grow, such symbiotic relationships with algae are often the key to survival.

The form of the coral reflects its dependence on the algae. Staghorn corals, for example, grow into elaborate plantlike shapes, their branches reaching upward to expose the zooxanthellae to light. Like the shoots of a plant, these branches grow mostly at the tips. New polyps bud asexually from old ones, emerging as skeletal material is deposited beneath them. The algae residing within the polyps of staghorn coral are very productive, enabling it to grow a foot or more each year, faster than any other coral in the Caribbean. When undisturbed, staghorn coral can form impressive undersea forests with branches extending upward five feet or more. Typically, the "upper canopy" is



On a reef off the Florida keys, elkhorn coral rises above a forest of staghorn branches.

Jim Doran



about twenty feet below the surface. Brightly colored fish rely upon this habitat for cover, and delicate bottom-dwelling invertebrates find protection from currents and predators among the lower reaches of the coral's branches.

The upward growth of staghorn coral is often interrupted, however; its skeleton is fragile, and the turbulence of a storm or a shift in the rubble supporting a colony can be enough to snap a branch. Yet because the individual polyps are essentially complete animals, each fragment may survive as an independent colony. Daughter colonies produced from such fragments are genetically identical to the parent colony and are therefore members of the same clone; this sort of fragmentation is another form of asexual reproduction.

Verena Tunnicliffe, of Canada's University of Victoria, studied staghorn corals in Jamaica and concluded that they are shaped not only to capture light but also to break in such a way that the fragments are likely to survive. Typically, after a branch has grown for about a year, it divides at the growing tip into three secondary branches. Often, when such a tripod breaks off and falls to the reef, it comes to rest on its three tips; the rest of the fragment stands above the surface of the reef, exposed to light and to circulating water. Without their triple-pronged ends, staghorn fragments would fall flat and be buried by sediment, unlikely to survive.

Tunnicliffe also observed that the weakest point of a staghorn coral is usually in its older, lower portion, where it has been perforated and hollowed by the reef's multitude of tunneling organisms: a specialized group of sponges, worms, and other invertebrates. Breakage generally occurs in such weakened areas, below the newly sprouted branches.

Reproduction by fragmentation could, in theory, enable a single clone of staghorn coral to spread across an entire reef. However, corals can also reproduce sexually. Polyps shed sperm into the water, where they fertilize eggs released by other polyps. The products of this union develop into minute larvae known as planulae, which spend a period of time, perhaps a month, floating in the plankton, occasionally drifting away to colonize remote islands and atolls. A new coral colony is begun when a planula settles down on a reef, attaches itself there, and forms the first polyp, from which others bud. Because sexual reproduction provides each fertilized egg with a random mixture of parental genes, every coral colony that grows from a planula is genetically unique. Thus, many different clones may accumulate on a single reef.

The three-spot damselfish, below, lives by raising a garden of algae on exposed coral skeletons. To do so, it nips the polyps from staghorn branches, often killing the coral over a broad area. Grafting experiments, right top and bottom, can reveal genetic relationships among various coral colonies. When a fragment of staghorn coral is grafted onto a genetically unrelated colony, a natural rejection response produces a bulbous outgrowth at the point of juncture. When the corals are genetically identical, graft fusion is smooth.

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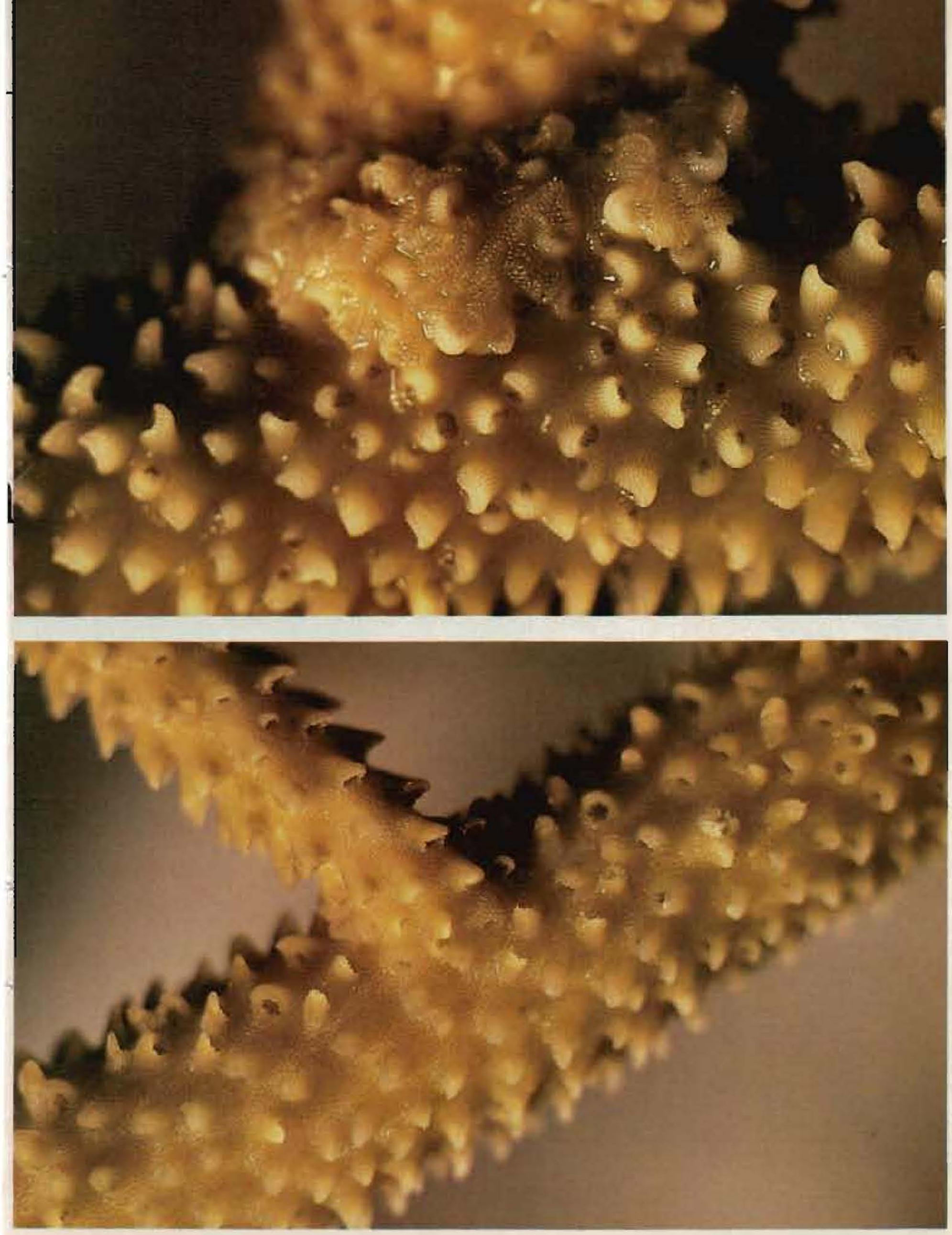
Our first job was to discover some way to tell one clone from another—a difficult task, since all staghorn corals look pretty much alike. Fortunately, there are more subtle biological characteristics that enable the corals to discriminate between members of their own clone and other, genetically different staghorns. The discovery of this self versus nonself recognition in corals came about through the work of an immunologist, William Hildemann. It was well established that the human immunological system rejects organs or tissues grafted from genetically distinct donors. One of Hildemann's contributions was to challenge the longstanding belief that only higher animals, specifically the vertebrates, possessed an immune system. Vertebrate immunity was known to depend on a complex system of organs and specialized cells, and most scientists thought it unreasonable to expect that invertebrates, lacking complex organization, could have evolved such a system. Hildemann's discovery that corals—primitive coelenterates—rejected grafts from alien colonies was therefore remarkable. Later, Hildemann demonstrated that an even more primitive group, the sponges, also shared this trait.

This finding raised the intriguing possibility that we could use a coral's immune system to identify different clones in a natural population. To investigate the feasibility of this idea we experimented with a population of staghorn coral on the fringing reef that spans the mouth of Discovery Bay in Jamaica. Named for an early visit by Columbus during his exploration of the New World, Discovery Bay has been a center of coral reef research for decades.

Several problems immediately concerned us. Hildemann had shown that grafts between corals from different atoll populations were always rejected, but we did not know if staghorn coral's self-recognition system would be sensitive enough to distinguish clones within a single population. We also needed a simple method of grafting that would allow us to make the hundreds of grafts required to discern population structure. And whatever our method of grafting, it would have to be



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performed while scuba diving on the reef, since staghorn coral, like most coral species, does not fare well in captivity.

But staghorn coral's ability to survive fragmentation worked to our benefit. We found that when we broke off small segments of a branch, only a few inches long, from one colony and tied them to others with nylon line, they survived the treatment. (Each grafting experiment took a while, however; corals showed a clear response to a graft only after about six months.) We tested the coral's ability to distinguish clone mates from nonclone mates by grafting between colonies whose relationships we already knew. For example, we could recognize "sister colonies" belonging to the same clone. These were separate, living colonies connected by the dead remains of what was once a common skeleton. We could also select colonies that we were confident did not belong to the same clone, such as those separated by a wide sandy area or other permanent natural barrier substantial enough to block the movement of living coral fragments.

Two kinds of graft response appeared in these experiments. In some instances, the calcareous skeleton and external soft tissues of the grafted branch fused to the host with a smooth, unbroken junction. This "fusion" response, representing a graft acceptance, was the outcome of every graft between known clone mates. In other instances the area of contact between the branches developed into a distinctive skeletal barrier, a bleached, swollen outgrowth that separated the living tissues of the graft from the host. This rejection response characterized every graft between staghorns we had identified as nonclone mates.

Encouraged by the consistency of our findings, we began to use graft responses to determine previously unknown clonal relationships. Prior to our study, nothing was known about the spatial pattern or extent of coral clones nor was there a ready means of determining them. It had been considered possible, for example, that an entire reef might consist of one gigantic megaclone or, alternatively, that nearly every colony had a unique genotype. Our first experiments, therefore, were designed to give us a rough idea of how large staghorn coral clones on the Jamaican reef really were. The results indicated that the clones typically consisted of small groups of colonies, spaced within a few feet of one another. In about half of the cases we examined, neighboring colonies were unrelated. The general picture was one of a diverse population, composed mostly of clones with fewer than twenty member colonies. Our next step was to set up grafting experiments that would enable us to map the invisible clonal boundaries across the reef. To obtain the necessary level of detail, we made hundreds of grafts.

A whim of nature, however, changed our plans. In August 1980, while we waited for the graft responses to develop, Hurricane Allen swept over the north coast of Jamaica, disrupting the entire reef community at Discovery Bay. Seventy-mile-per-hour winds raised thirty-five-foot waves that pounded the reef. Unlike many other coral reefs in the Caribbean, Discovery Bay has only rarely been in the direct path of a full-scale hurricane, the last one in 1917. We had grown accustomed to a reef community that changed little from year to year, but now a dramatic alteration had taken place. Coral heads several feet in diameter had been pushed across the reef like steam rollers, leaving trails of pulverized coral behind them. The once magnificent forests of elkhorn coral, a close relative of staghorn coral found in shallower water, had been leveled to rubble. Tons of sand had been scooped up and heaped in drifts upon the reef, burying corals and other animals. In areas that were once fields of waving sea fans and sea whips, drifts of sand covered all but the tips of these frag-


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ile animals, giving the impression of a stark winter snow scene. Our grafting experiments were almost completely destroyed. Only one out of every hundred colonies of staghorn coral survived the crushing impact of the waves, and many of these were badly damaged or half buried in the rubble.

Although our experiment was lost, we gained a new and important perspective on staghorn coral populations. Hurricanes and other destructive events, such as cold fronts and plagues of predators or parasites, are an essential feature of the natural history of corals. To fully understand the forces that shape the growth of staghorn coral clones, we need to take into account events that seem rare by our human sense of time but are experienced over and over again by natural populations and communities.

One way to study natural processes that take place over long periods of time is to create a model of the process in which the passage of time can be sped up and the outcome observed. Using a computer, we designed a model of a staghorn coral population in which the corals were programmed to either arrive as planulae or originate as fragments from nearby colonies. We used census data taken from our Jamaican staghorn coral population to set realistic birth and death rates. This simulated coral population showed us how clones might change through time and how, through chance alone, some clones grow in size to cover large areas, while others head into extinction. The result was a patchwork of clones, which we refer to as the "clonal structure" of the population.

After experimenting with several models, we found that two factors were of major importance. One was, as expected, that both the number and typical size of clones in a population depended to a large extent on the balance between the introduction of new clones from planula larvae and the spread of established clones through fragmentation. The other, less expected factor was the strong influence that a population's past history could exert on the size and number of clones. This historical influence implies that catastrophic events such as Hurricane Allen could affect the clonal structure of a population for more than a century, even if the population appeared to recover (in terms of the number of corals) after a few years. In a sense, the clonal structures of staghorn coral populations hold the memories of such events, and with sufficient understanding of the dynamics of clonal structure, we may be able to tap these memories.

We continued our investigations with a relatively undisturbed population of staghorn coral off Saint Croix, in the Virgin Islands. Our study area was a reef outside of Tague Bay, in water that was about thirty feet deep. As in Discovery Bay, the reefs around Tague Bay have been actively studied.

With our first exploratory dives, we became aware of several significant contrasts between the staghorn coral colonies in Saint Croix and their Jamaican counterparts (as they were before Hurricane Allen). Staghorn coral was considerably less abundant in Saint Croix, and colonies were clustered into isolated groups rather than spread as a continuous meshwork over the reef. Small juvenile staghorn corals, uncommon on the Jamaican reef, were virtually absent at Tague Bay. Although many factors could contribute to these differences, we noticed one that seemed to be of great importance: at Saint Croix, much of the reef's hard bottom was covered by a thin layer of fine sediment; by comparison, the reef bottom in Jamaica was mostly exposed.

The effects of sediment on corals can be severe. If continually buried in sediment, a coral will eventually die. Some species of coral are better equipped than others to remove sediment, by lifting it off with their tentacles or by sloughing off sheets of

Staghorn polyps, left, differ from most other corals in that they emerge from their skeletal coverings during the day as well as the night. The daytime activity may be an adaptation to gather light for the symbiotic algae that live in staghorn digestive tissue. Below: The sponge Haliclona hogarthi *is another primitive animal inhabitant of the reef. Like corals, the branches of sponges can break off and reestablish themselves as new colonies.*

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mucus in which sediment is trapped. A few species are able to live on top of loose sediments, like rafts upon a sandy sea, without the usual attachment to a solid surface and can even right themselves if capsized. The corals in our study area at Tague Bay appeared to be engaged in a constant struggle against the rain of sediment. We found many dead colonies buried beneath the sediment, and the species that were most abundant were those that were proficient at ridding themselves of sediment.

Staghorn coral, although not an excellent sediment remover, can rise above the problem by using its lower branches for supports only and growing well above the sediment-covered bottom. But this solution only works for adult colonies and large fragments of colonies. A juvenile initiated from a planula larva is less than an inch tall and can escape burial only if attached to a surface that is itself raised above the sediment. Similarly, small fragments of unsupported colonies will also perish. Sedimentation can thus explain the overall sparseness of the staghorn coral population in Saint Croix, as well as the nearly total absence of juveniles.

We are not certain why sediment rain on the Tague Bay reef is so heavy, but again we can make a reasonable conjecture. The Jamaican reef sits on a narrow shelf, less than half a mile wide, that slopes steeply into deep water. The reef at Saint Croix is on a much broader shelf, more than three miles across, and the population of staghorn coral there was far removed from deep water. Sediment carried from land into the ocean may rapidly sink into the deeper waters off the Jamaican reef, while in Saint Croix, it is trapped on the broad offshore shelf.

On the reef at Saint Croix, then, planula larvae rarely succeed in establishing new staghorn colonies. What effect does this have on the population's clonal structure? To find out, we changed our computer model of a Jamaican staghorn coral population to resemble more closely the Saint Croix population by reducing the rate at which new clones arrived in the population. The effect was a decrease in the number of clones in the population, while the area typically covered by an individual clone increased. We obtained a more direct answer from a large number of grafts between staghorn corals in the Tague Bay population. Some were used as controls, like those used in our earlier study in Jamaica, while others were used to map the extent of individual clones. As predicted by the computer model, the clones at the Saint Croix population were fewer and larger than those at the Jamaican site.

One finding surprised us. We had guessed that each isolated group of staghorn coral colonies represented the full extent of a single clone and that the edge of a cluster would mark the front of that clone's advance. We found, however, that one clone could encompass several of these clusters and that the boundaries be-

Stephan Frank; The Image Bank

A coral reef in the Caribbean is reduced to rubble after a hurricane, below. Such destructive forces may be as important as reproduction in shaping the long-term genetic history of a reef. Right: The lower reaches of a staghorn reef provide cover for many species of brightly colored fish. Here, a bigeye, a nocturnal species, hides out in coral branches during the day.

A. Kerstitch

tween clones could run through them. One interpretation of this lack of correspondence between groups of living coral colonies and clonal boundaries is that after the clones have spread outward, it is the death of colonies, rather than their propagation, that carves the population into isolated groups. Many natural agents could produce such a pattern of mortality. Localized outbreaks of predators or disease or simply an uneven distribution of sediment could kill corals in one area while sparing those nearby.

One conspicuous cause of staghorn mortality is the three-spot damselfish, a four-inch-long, gray-and-black fish that makes its living by farming a garden of algae. The damselfish begins a garden by biting at the coral polyps within its territory until it has cleared an area several feet across. The exposed coral skeleton is soon covered with a dense growth of algae, which serves both as a source of food and a nesting site for the fish. The damselfish constantly defends its garden from marauding fish and sea urchins, ferociously attacking intruders many times its size, including curious divers. Staghorn reefs—preferred sites for gardens— may support substantial communities of damselfish, whose farming activities sometimes destroy the coral over large areas of the reef and also prevent it from recovering.

Our studies have given us a deeper understanding of the many forces— predators, hurricanes, reproductive patterns—that influence the structure of staghorn coral populations. But as we make use of the ability of invertebrates to distinguish between self and nonself, we also wonder what role this ability might play in the natural lives of these simple animals. The purpose, if any, of histologic incompatibilities among individuals—whether higher animals or invertebrates—is still a matter of speculation. However, the invertebrates, more than higher animals, have given us some clues.

Among the invertebrates that have been studied in this regard are some sea anemones, close relatives of corals. Individual sea anemones resemble coral polyps without the external skeleton, and like coral polyps, many can reproduce both sexually and asexually. In a few species unrelated clones are known to engage in fights. Lisbeth Francis of Bates College studied this phenomenon in the sea anemone *Anthopleura elegantissima.* Clones of this anemone huddle together on rocky shores to hold on to reserves of water as the tide recedes. The anemones on the perimeter of the clone act as guards, equipped with tentaclelike specialized organs, or acrorhagi, which are used only in combat with other anemones. If an anemone from a different clone comes into contact with these border guards, it is recognized as a nonclone mate and violently repelled with the acrorhagi. This war between clones makes good evolutionary sense. From the standpoint of natural selection, which acts on genetic differences among individuals, each clone is a single individual. Competition between unrelated clones of the same species, with survival going to the fittest, is therefore no different from competition between genetically different individuals.

Corals also fight among themselves, but most of these fights seem to be between members of different species. Sometimes, corals fight with specialized tentacles, but more often they extend long filaments—normally used for internal digestion—out through the polyp's body wall and externally digest the victim. Judy Lang of the University of Texas at Austin has shown that each species of coral fits into a pecking order, its rank determined by the reach of its digestive filaments. These fights are probably important in dividing available living space, a precious resource on the reef.

Rejection of grafts between different clones may also represent competition for space, although we believe that this is unlikely because the effects of the rejection appear to be very mild. In our experiments, the survival rate of small pieces of staghorn coral grafted to nonclone mates was as high as the survival rate of those grafted to clone mates. Perhaps most significant is that in both graft acceptances and rejections, the skeletons become firmly cemented together. This joining provides a stronger support for both colonies and lessens their chances of a fatal collapse to the bottom of the reef. Since every colony of staghorn coral is engaged in a constant race to grow upward faster than it is consumed and eroded from below, physical support between neighboring colonies may play an important role in their survival. Evolution may have decided that under these conditions the best strategy for broken corals is, literally, to stick together. ☐