virus that the sex ratio of AIDS infections in Africa could still be 1:1.

In estimating how many will die from AIDS, investigators often assume that the more likely it is that an infected person will develop full-blown AIDS, the higher the death rate. But May and Anderson's model leads them to take issue with that assumption.

Suppose, says May, that you assume that everyone infected with the AIDS virus will die within 10 years. And then suppose you consider an alternative scenario—that 30% will die within 6 years and the rest will remain infectious for the rest of their sexually active lives, for about 30 to 40 years. "In the second case, the total number who will get infected is larger. The virus will continue to penetrate the less sexually active group of the population for 30 to 40 years. You can't say intuitively if there will be more deaths from 100% of a smaller number of people or a smaller percent of a larger number," May says. "I think this is very relevant to any long-term view in developed countries of heterosexual transmission of AIDS."

May explains that if the AIDS epidemic can take off through heterosexual transmission of the virus, it will, of course, begin among the most promiscuous heterosexuals. But, he says, "if all these people are dead within 10 years, the epidemic will likely run its course. If 70% of those infected remain infectious, there is more chance for the epidemic to spread more slowly." What will happen, he says, "depends on knowledge we don't have on how many will die and how long people remain infectious. We just don't know."

But May can use the data at hand on homosexual infections to estimate how difficult it might be to contain the AIDS epidemic in that group. The argument hinges on a parameter called R_0, which is the basic reproductive rate of an epidemic—the number of new infections each person with the virus is likely to initiate. If R_0 is less than 1, an epidemic can't take off. And the greater than 1 R_0 is, the harder it is to contain an epidemic. Since 50 to 70% of homosexual men in San Francisco are infected with the AIDS virus, R_0 must be greater than 5, according to May. "That leads to a rather depressing epidemic," he says. "The only way to halt the epidemic is to change R_0 by a factor of 5." It would mean that infected individuals must have one-fifth as many sexual partners as they had in the past or that they practice safe sex, with condoms, so as to decrease by at least a factor of 5 the chance that they will infect their partners. And, like gonorrhea, any efforts at reducing R_0 must concentrate on the core group of sexually active men who are keeping the epidemic alive. For heterosexual transmission, it is unknown whether R_0 is greater than or less than 1, according to May.

The mathematics of estimating R_0 among homosexual men also leads May and Anderson to an independent estimate of the incubation time of the virus. According to their model and the San Francisco data on infection incidences, it takes more than 5 years from infection with the virus to the disease AIDS—a time that agrees with other estimates that come from clinical data.

In the end, May and Anderson's model raises more questions than it answers. But its importance lies in its new approach to the AIDS epidemic. Says May, "Population models can give insights into the dynamics of an epidemic and can help people think about the disease more clearly." ■

GINA KOLATA

Life Thrives Under Breaking Ocean Waves

Biological productivity in intertidal communities that are constantly battered by waves greatly exceeds what is achieved by even the most fruitful tropical rain forests

"ANYONE who has felt the force of a large wave breaking on an ocean beach knows that it dissipates a large amount of energy when it crashes against the shore. Can intertidal organisms put this energy to use?"

This question was posed by Egbert Leigh, of the Smithsonian Tropical Research Institute in Panama, and his colleagues Robert Paine, James Quinn, and Thomas Suchanek. The answer, it seems, is yes. In fact, say these researchers, many intertidal communities that are subject to constant wave battering are several times more biologically productive than the world's lushest rain forests, which are usually thought of as being at the apogee of the living world. The means by which wave energy is converted into living material is, however, rather indirect: the key to the story is not so much raw energy as disturbance.

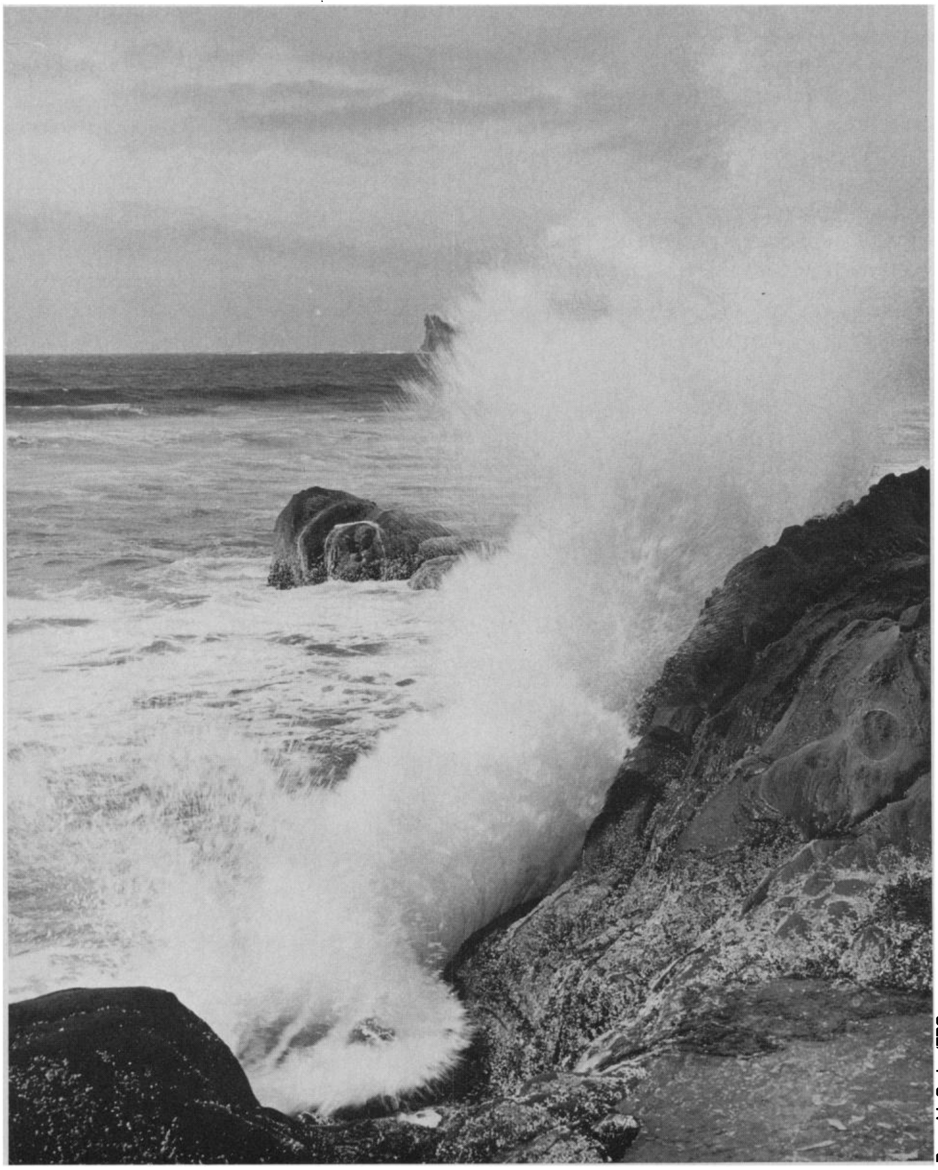
In addition to trying to unravel the network of influences that shape the composition of biological communities, ecologists are interested in what governs the use of energy within them. In other words, why is the biological productivity of one type of zone different from that of another? Availability of nutrients is clearly one important factor, as is the source and flow of usable energy. No wonder then that tropical rain forests are so very fruitful, given their propitious location on the globe.

It was something of a surprise, therefore, when Leigh first noticed that some intertidal kelp communities appeared to be even more productive than rain forests. He joined forces with Paine, Quinn, and Suchanek to analyze the energy flow in such communities in more detail. Most of their work was done on Tatoosh Island, Washington, which has long been a popular spot for ecological research by Paine and his associates.

The energy delivered to the shoreline by ocean waves in this region is enormous, and greatly exceeds that from solar radiation. On average, waves deliver 0.335 watt per square centimeter of energy to the coastline, which is about 15 times more than comes from the sun. Even during the calmest months, wave energy exceeds solar energy by more than 100%. So, the potential for enhanced productivity is great, if only the energy can be harnessed.

Leigh and his colleagues soon found that among the individual species in intertidal communities, those with the highest standing crops are restricted to the most wave-beaten areas. These species are the lower intertidal mussels, sea palms, and shrubby kelps. Now, although rain forests have enormous standing crops, much higher than in intertidal communities, a very large proportion of it is locked up in woody tissue, which is essentially dead. By contrast, a comparison of leaf (or frond) area between the two types of community gives a different perspective. For instance, the shrubby kelp in the Tatoosh intertidal zone bears around 20 square meters of frond per square meter of growing surface compared with around 8 square meters per square meter for tropical rain forests.

In terms of productivity, which is mea-



Where the waves break. *Breaking ocean waves can deliver more than ten times as much energy to intertidal communities as solar radiation delivers. The result is a biological productivity that far outstrips that of the most fruitful of rain forests.*

sured in kilograms of dry matter generated per year, shrubby kelp and sea palm are at least twice as productive—and sometimes ten times as productive—as the most fecund rain forest. For instance, sea palm communities can sometimes yield 14.6 kilograms per square meter a year as against a little less than 2 kilograms for rain forests. Even the most productive terrestrial plant so far recorded, which is a species of grass in Hawaii, only reaches 8.5 kilograms per square meter. And the humble intertidal mussel, *Mytilus californicus*, which is a consumer rather than a primary producer, matches or exceeds the productivity of most rain forests when it grows in wave-beaten zones.

So it seems indisputable that intertidal communities can harness the energy of the waves, but how do they do it? Leigh and his colleagues identify four mechanisms by which wave energy is translated into biological productivity: protection against predators, facilitation of nutrient flow, optimization of incident light, and aiding in interspecies competition.

In many intertidal communities the amount of vacant potential living space on rocks and other surfaces is typically around 50%. In the Tatoosh Island intertidal zones, however, this figure is as little as 2%. The difference appears to be the result of a greatly reduced activity of predators, such as starfish and sea urchins, which are the principal enemies of mussels and kelp respectively. Starfish and sea urchins simply cannot operate in rough sea conditions, and so, in their absence, their potential victims thrive.

Not only does moving water enhance the exchange of nutrients at the surface of fronds, but it also keeps the fronds themselves in motion, thus optimizing their use of the sun's rays. In a rain forest there is a tremendous gradient in the amount of light that can fall on leaf surfaces through the canopy, with the upper levels virtually shutting out the ones below. However, with the fronds of sea palms in constant motion in rough water, there is a much more even distribution of incident light as individual fronds repeatedly move into and out of shade thrown by other fronds. And, as photosynthesis is most efficient under these conditions of rapidly alternating light-dark exposure, marine plants in constantly moving water are optimally positioned for high productivity.

It turns out that the energy delivered to the shoreline by ocean waves . . . is enormous, and greatly exceeds that from solar radiation.

Finally, crashing waves can sometimes dislodge organisms from their living surface, which can allow other species to move into the vacated space. An example is the competition between mussels and sea palms, in which mussels usually win. Occasionally, however, mussels are ripped from their moorings and sea palms can move in. The sea palm "lets the waves compete on its behalf," say Leigh and his colleagues.

Disturbance is frequently a key factor in ecology, both in the short-term issue of influencing community structure and on the longer time scale of the evolution of new species. Its effect on productivity in intertidal communities should therefore come as no big surprise, but until Leigh and his colleagues undertook their recent analysis, no one had documented it so clearly.

The power of the waves, say Leigh and his colleagues, is like "the power that oil provides American farmers [which] increases agricultural productivity by allowing crops to be fertilized and protected from pests and competing weeds, and by permitting feed to be concentrated so that great numbers of animals can grow and reproduce in one place." ■ ROGER LEWIN

ADDITIONAL READING

E. G. Leigh, Jr., *et al.*, "Wave energy and intertidal productivity," *Proc. Natl. Acad. Sci. U.S.A.* **84**, 1314 (1987).