fluorescence due to the strong transition at intervals when weak transitions are excited allows every weak transition to be seen. In effect, the fluorescence acts like an amplifier that provides the highest possible signal-to-noise ratio. Dehmelt coined the term "shelved optical electron amplifier" to describe the operative mechanism. In 1981 David Wineland and Wayne Itano of NBS applied this idea to the measurement of an optical transition in a single ion and obtained an amplification of 10^6.

Although the argument for quantum jumps seems intuitively obvious, theorists have had to go to some effort to show that such jumps should, in fact, be observed because the quantum theory cannot predict a specific sequence of transitions; it deals with probabilities and statistics. An alternative possibility for what happens when two lasers are used to excite the strong and weak transitions is that they would drive the atom into what is called a coherent superposition of states. In this case, the bright fluorescence signal would drop in intensity as compared to that when only the strong transition is excited, but would otherwise remain constant in time. Both quantum jumps and coherent superposition of states give the same average fluorescence intensity. Several theoretical treatments that support quantum jumps have appeared or soon will appear.

The actual observation of quantum jumps, as reported last June at the International Quantum Electronics Conference in San Francisco by Warren Nagourney, Jon Sandberg, and Dehmelt of the University of Washington and by James Bergquist, Randall Hulet, Itano, and Wineland of NBS puts any doubts to rest. The Washington researchers studied a single barium ion that was confined in a trap with a potential energy well generated by a radio-frequency electric field in a special geometry. The technique of laser cooling lowered the ion's kinetic energy, so that the ion was well down in the well where it was confined to a space with a characteristic dimension of 1 micrometer. An ultrahigh vacuum of 8×10^{-11} torr greatly reduced collisions with other species that could cause transitions within the ion.

In operation, the experiment generated a fluorescence signal of constant intensity that intermittently shut off, as in a telegraph signal. Nagourney told *Science* that the blinking was clearly visible to the eye. Because of the statistical nature of the excitation processes, the on and off times were not fixed in duration. For example, the off times followed an exponentially decaying distribution. After allowing for the effects of collisions, the Washington investigators deduced from the time constant a lifetime for the shelf state of 32 ± 5 seconds. The lifetime had previously been measured by another technique to be 47 ± 16 seconds. The result has been confirmed by a group at the University of Hamburg, West Germany, consisting of Thomas Sauter, Werner Neuhauser, Rainer Blatt, and Peter Toschek.

The NBS group made a similar study of quantum jumps in a single, trapped and laser-cooled mercury ion. As compared to barium, mercury has both advantages and disadvantages. One feature that makes the experiment more difficult is that both of the relevant transitions in mercury are at ultraviolet wavelengths. The NBS researchers used nonlinear optics techniques to convert visible laser light to the appropriate wavelengths of the two transitions.

The shorter lifetime of the shelf state in mercury, about 0.1 second, also made it practical to study the quantum statistics of the fluorescence emitted when the shelf state relaxes. The quantum theory of electromagnetic radiation almost always predicts the same statistical properties as the classical theory, so it is important to verify the few instances where the two theories differ. One is a property called photon antibunching, which the NBS researchers also observed.

To understand antibunching, consider the probability for the arrival of a second photon at various intervals after the first is registered. Incoherent light exhibits bunching; that is, the probability is highest at the shortest intervals. For coherent light, such as that from an ideal laser, the probability is the same for all intervals. Antibunching refers to those instances when the probability is lowest for short intervals and is not allowed in the classical theory. One intuitively expects antibunching in the fluorescence from a single atom because, after the emission of a photon, it takes a certain time for the atom to be reexcited so that it can emit another photon. In the past, antibunching has been observed in atomic beams of sodium so dilute that only one atom at a time passed through the exciting laser beam, but a low signal-to-noise ratio made the experiment difficult. ■ **Arthur L. Robinson**

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Supply-Side Ecology

Existing models of population structure and dynamics of ecological communities have tended to ignore the effect of the influx of new members into the communities

One of the most complex issues that ecologists are attempting to address is the assembly and structure of communities. "The overall issue," says Jonathan Roughgarden of Stanford University, "is to account for the variety, abundance, and distribution of the members of the community." Availability of resources, competition, various forms of perturbation, including predation and environmental hazard, and a certain degree of stochasticity have been identified as influential factors in shaping communities. But, until recently, one factor that has been more or less overlooked in the major formulations of the problem is the supply of new individuals to the community. "Yes," says Roughgarden, "you can call the new approach 'supply-side ecology'."

You can, of course, learn a great deal about the internal dynamics of an ecological community by recording the nature and extent of biotic and abiotic influences on the individuals within it, whether this is by direct field observation or experimental manipulation. In fact, these kinds of studies are essential in the formulation and testing of general models of ecological communities, an approach that has been particularly successful for intertidal communities.

What supply-side ecology adds to this is to identify those elements of the internal dynamics whose importance depends on the abundance of new individuals entering the community.

Supply-side ecology clearly does not apply to "closed" communities, which by definition are completely self-sustaining in terms of new members. But, argue Roughgarden and his colleagues Steven Gaines and Stephen Pacala, "at some scale most ecological systems are open systems." In which case, they suggest, "the control exerted by physical transport processes on population and community dynamics matches the effect of local processes, such as predation and competition among residents of the site." Supply-side ecology can apply to larvae settling on rocks in an intertidal community, seeds entering a terrestrial habitat, and, on a grand scale, the coalescence of habitats through plate tectonic movement.

Interest in the potentially broad impact of the supply of new members to community dynamics has been developing in several parts of the academic world for at least half a dozen years, but the concept has only recently been strictly formulated, principally by Roughgarden and his colleagues and by Joseph Connell of the University of California at Santa Barbara. For historical and practical reasons, the principal focus has been on shallow-water marine habitats.

One reason why intertidal communities have been popular with ecologists interested in studying community structure is that in general they are more amenable to experimental manipulation. And, based largely on the important pioneering work of Connell and of Robert Paine of the University of Washington, the results appeared to be relatively clear cut.

For instance, from Connell's work there emerged evidence of a clear zonation in the intertidal region, in which, for instance, balanid barnacles edge their smaller chthamalid cousins from the more equable environments and toward the high-water line, where there is more desiccation and temperature stress. The zonation is the result of competition, with the balanids winning.

More dominant than the balanids, however, are mussels, which, given the opportunity, might so overgrow their lesser competitors as to form a virtual monoculture. Monocultures are rare in nature, however, largely because such communities are routinely perturbed in some way, sometimes by predators, sometimes by trauma from floating objects that smash into the rocks and dislodge the creatures living on them. As long as some form of perturbation occurs, there is an opportunity for all members of a competitive hierarchy to thrive in a locality, thus preserving a degree of biodiversity.

It was through these kinds of observations that Paine developed the notion of the keystone predator. By preying on the dominant competitor in a community, the predator maintains the structure of the community. Remove it and the community structure collapses into monoculture. Hence the term keystone predator.

From Connell's and Paine's work there developed generalizations about the dynamics of ecological communities, in which competition and biotic and abiotic perturbation loomed important. And, as Anthony Underwood of the University of Sydney, Australia, noted at a meeting on the subject in 1981, "Some of the proposed generalizations have already been widely accepted, and even raised to the status of paradigms of modern shallow-water benthic ecology."

An intertidal community on the central California coast.

The problem for Underwood was that the patterns embodied in these generalizations were absent or at best shadowy in the intertidal communities he and his colleagues studied along the eastern Australian coast. Strict zonation, competition, and physical perturbation simply did not seem to be important factors in shaping the communities he saw. "For more than a decade, Australian ecologists had failed to confirm what American ecologists had taken as dogma," observes Roughgarden.

Too much emphasis had been placed on events within the assemblies, Underwood thought, and he concluded that variation in patterns of larval settlement "has been overlooked in the design or interpretation of many experimental analyses of intertidal communities." How one might incorporate this factor into ecological models would be a major problem, he said. He referred to the supply side as "the planktonic mystery stage."

Underwood's very vocal complaints about the inadequacy of entrenched models of intertidal communities spurred Roughgarden and Connell independently to give the problem closer scrutiny. For Roughgarden it was a new problem, coming as he did as a theorist interested mainly in terrestrial ecology. For Connell it was a reexamination of an issue he thought he had settled three decades ago.

"I measured larval settlement rate in the 1950's, when I was doing my thesis work," Connell told *Science*. "And I proved to myself that variations in settlement didn't have any effect." The problem, he now realizes, was that the site he was studying, in western Scotland, had very high influxes of barnacle larvae, and so the communities were essentially saturated with newcomers: fluctuations of influx made no difference, because the community still remained saturated. Under these circumstances the principal features dominating community structure are indeed internal, such as competition, predation, and physical perturbation. It was by pure coincidence that the localities that Paine chose to study, along the Northwest coast of the United States, also had high settlement rates.

Unwittingly, therefore, Connell, Paine, and their followers assumed that the rest of the world followed these same patterns. "It is easy to get shutters over your eyes," says Connell. "I had proved to myself that variations in settlement were not important, and so I hardly considered it again. It was Tony Underwood who jogged me out of this mind-set."

As a result, Connell recently did a literature survey of data on intertidal communities and concluded that influx of larvae was indeed important. Where larval settlement was low it produced distinctly different community structure and dynamics from the picture that he and Paine had developed. "It was clear that our models were incomplete," he now says.

Roughgarden, meanwhile, was approaching the problem from a theoretical standpoint. He and his colleagues Yoh Iwasa and Charles Baxter developed a mathematical model of intertidal communities that included settlement rate, growth, and mortality. "It emerged quite quickly that the settlement rate was a key controlling parameter in the qualitative outcome of the simultaneous kinetics of the processes," says Roughgarden. "If settlement is high—say 20 to 30 larvae per square centimeter per week—then settlement is saturating and demography is determined by post-settlement processes, such as competition, predation, etc. But if settlement is low, then demography is shaped by the vagaries of settlement rate."

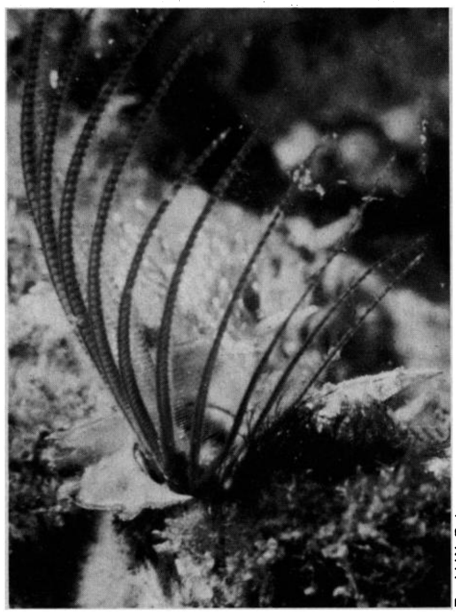
The model also predicted that populations in high settlement areas could be dominated by a nearly single cohort and might therefore oscillate in density quite substantially within each year but not vary much between years. By contrast, low settlement populations would experience substantial year-to-year variations in density, but would not swing much within years.

In addition to the theoretical work, Roughgarden embarked on an experimental study with Steven Gaines, also of Stanford University. At three intertidal localities in the Monterey Bay on the central California coast they measured influx of barnacle larvae and monitored the demographics of the resulting communities. The area is one of relatively low settlement rate, and the patterns observed conformed closely with the predictions of the model. There was no zonation and little influence from predation and physical disturbance on species diversity. Between- and within-year patterns were also as predicted.

Moreover, there was a distinct gradient of larval settlement from the offshore sites to the nearshore, with the former having higher settlement rates than the latter. "Traditionally this has been explained by saying that offshore sites are physiologically more favorable for settlement," says Roughgarden. "But we showed that growth was just as good at the nearshore as it was offshore. We suggest that the offshore rocks cast a 'settlement shadow' on localities nearer shore."

Although some species in intertidal communities produce larvae that do not stray very far, many have pelagic larvae that go way out into the water column and are carried hundreds of kilometers before finally settling on suitable rocks. In the central California coast case, such wide-ranging larvae must twice run a gauntlet of predatory fish, once as they travel from nearshore to ocean water, and again as they return. The fish inhabit the extensive kelp forests of the region, so that anything that affects the fish populations either directly or indirectly will influence the eventual larval settlement rates in the intertidal regions. And anything that moderates ocean currents, including the balance of onshore to offshore winds, will also affect settlement rates.

It so happens that in the Pacific Northwest onshore winds and ocean current predominate, whereas in the central California coast region the balance between onshore and offshore is much more even. "The implication of all this," says Roughgarden, "is that research in intertidal community ecology has got to include an oceanographic dimension. We have got to get out there and find out what is going on. This will be difficult." Underwood's "planktonic mystery stage" won't be easy to crack.



David W. Behrens

A barnacle feeds at high tide.

Both Connell and Roughgarden consider these new insights to be a major development in marine ecology. But the magnitude of the impact is difficult to quantify because there are simply not enough data to say how much of the world's coastlines are low settlement areas. "There's an understandable bias about going out and getting data where there are very few animals to study," notes Roughgarden. However, both researchers estimate that perhaps half or even more of the intertidal communities are low settlement, which indeed makes the world a more complicated place than it was before—in the realm of ecological models, that is.

Connell has recently turned his attention to terrestrial communities, with the same question in mind. He is surprised to find that the obvious system to study—the influence of seed influx into a habitat—has been virtually ignored. "It would be a lot easier to measure this sort of thing than larval settlement in marine communities, but there are very few data as yet," he notes. "Someone should look into that."

Roughgarden, meanwhile, has been reexamining populations of insectivorous lizards on the Caribbean islands. Studies on these populations have been the source of many important ideas about the influence of interspecies competition within terrestrial communities. And the precise patterns of distribution of the various species among the islands has been explained in large measure in terms of the effects of competition. It turns out, however, that just as the Connell/Paine models for intertidal communities had been "incomplete," so too have been those for the Caribbean lizards. Transport processes had again been neglected.

In the case of the lizards the transport component is large scale, both geographically and temporally. Although the Caribbean islands were once thought to have been relatively young volcanoes, each occupied by animal populations that had somehow floated in, it now seems that the region has much more ancient origins and to have been shaped more by plate tectonics than previously supposed.

According to Roughgarden and his colleagues, it remains true that in some cases of the Caribbean lizards, across-water transport accounts for the presence of certain species. And it remains true that in some cases competition has influenced the distribution and size of some of the species of lizards. But it now seems that at least some of the species distribution is to be explained as a result of the fragmentation or coalescing of communities through plate tectonic action.

These geological processes, say Roughgarden, Gaines, and Stephen Pacala, affect community ecology in the region "to an extent that matches the effect of any biological mechanisms that operate within these ecological systems."

The inclusion of large-scale processes of this sort into ecological equations has several consequences, not least of which is that the overall picture is even more complex than was previously appreciated. But there are very practical implications too. "During the last decade, small-scale species interactions have been increasingly investigated with field experiments in both marine and terrestrial environments," note Roughgarden and his colleagues. "The larger scale processes are not similarly amenable to experiments, because the enthusiasm of Welshmen for rerouting the Gulf Stream, and of Californians for provoking the San Andreas fault, is likely to be restrained."

Nevertheless, Roughgarden and his colleagues remain optimistic. "The union of ecological approaches, such as natural experiments, field perturbation experiments, theoretical models, and systematics, with methods for large-scale phenomena from earth sciences appears sufficient to solve the questions ecologists are responsible for answering." ■ ROGER LEWIN

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