Final Remarks at the Eilat Symposium on Marine Symbioses

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The most remarkable feature of the Symposium was the diversity of subject matter and approaches, all of which were quite legitimately subsumed under the rubric of marine symbioses. Clearly, there is no one uniquely interesting problem which attracts all, or even most, of the workers in this field. In fact, the field of marine symbiosis, like ecology itself, is intractable, in a very distinct sense. Intractable sciences are defined by a concern with a class of empirical subject matter. Tractable sciences, by contrast, focus on a technological or intellectual methodology. Electron microscopy, gene cloning, and computing focus on technology, and mathematics and theoretical physics focus on intellectually bounded subject matter. All tractable sciences can define, within limits, the class of problems which they will accept and relegate other problems to some other discipline. Physicists, for example, relegated turbulent flow to hydrology until modern fractal analysis smoothed the problem sufficiently to have it readmitted to physics.

Students of symbiosis use tools derived from a broad array of disciplines, but have no way of deciding that some particular kind or aspect of symbiosis is really not their problem.

Some sciences have a single central theory and, therefore, a discrete research focus, in the sense that protein structure, enzymes, membranes, and gene transcription have each, at different times, been the focus of cell biology. We have had the pleasure of seeing symbiosis examined at every level from that of molecular genetics to natural history.

During the symposium, there were several attempts to find a single focus for symbiosis research. I do not believe that a single focus is desirable. The reason for this will be apparent after a brief overview of all symbioses.

It seems superficially reasonable that any symbiosis involves exchanges of something between the participants, and that we understand that symbiosis when we explicitly describe the budget of these exchanges. This is valid in a limited sense, but we know that the budgets are not simple ones. In particular, the apparently reasonable procedure of choosing some convenient unit for the budget is filled with peril, and the same units cannot, in principle be used for both parties.

It is by no means obvious that the unit which we assign is of basic importance to either symbiotic partner. Perhaps the energy-rich compounds known to pass from algae to coelenterate hosts are of importance in many cases, but it would not be surprising if, for some hosts, the algae are primarily significant as a carbon dioxide sink, rather than an energy source. The exchanges between symbionts and hosts are assymetric in three senses. First, benefits need not be equal to the two partners in the symbiosis. For example, where there is anatomical evidence for symbiotically luminescent fishes that the bacterial symbionts are of major importance, it is by no means clear whether it would matter very much to the total population of the bacteria if the fish were eliminated completely. Similar remarks apply to the relation between corals and zooxanthellae and to most symbioses in which one partner can survive without the other. For example, aposymbiotic hydra never occur in nature while free-living chlorella are common. Second, not only is there an assymetry in the importance of the symbiosis, but there is also an asymmetry in the kind of costs and benefits that accrue to the two partners. Corals may derive energy-rich compounds from algae and provide shelter, mineral nutrients or other things in return. It is quite obvious that energy is not all that is being traded between the partners.

Third, the spatial and temporal scale at which the symbiosis is significant may vary between the partners. There may be an advantage to zooxanthellae or chlorella to have some tiny fraction of their total population safely tucked away in coelenterate hosts and available to reestablish the main population after unusual disasters. This benefit would only be visible on a long time scale. On short time scales, there might not exist any advantage at all to the algae. Note that inability to find any short-term advantage to one member of a symbiosis does not necessarily imply that there need exist any long-term advantage! The only necessary conclusion is that neither partner is so badly

damaged by the symbiosis as to provide a selective force that would end the relationship.

To "analyze a symbiosis" consists of determining the costs and benefits to each partner, separately, and also determining how the two partners interact. Analysis, may, as we have seen, occur on any level from that of molecular chemistry through to that of evolution and economics. In symbiosis between people and chickens, the chickens gain, among other things, protection from the evolutionary extinction which threatens their asymbiotic relatives, the Malayan Jungle Fowl, and the people gain an item of commerce as well as a source of meat and cholesterol.

The conclusion from this analysis is that the study of symbiosis had best continue to follow many paths, rather than focusing on any single paradigm. The rewards will come as new and exciting intellectual insights of the sort we have been given during this symposium, which come from letting nature lead us rather than trying to drag nature onto our own favorite pathways. In short, the study of symbioses should remain elegant natural history, combined with the full spectrum of modern biology at all levels.