Chapter 9

Ecological Expertise

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I. WHO SPEAKS FOR THE ANIMALS?

I remember a scene from a science fiction movie in which a solemn council was deliberating the declaration of war on a neighboring planet. This film, by now, is quite dated—all the men around the table sported Smith Brothers beards and Flash Gordon dentist smocks. But in one respect the scene still might be an eye-opener, for the council was an absolute model of pluralism. Listening to the representatives vote in turn, one could not help but be impressed when, for example, a man intoned, "The animals say war."

Provided we believed them, it surely would be nice to have nature's representatives speaking with such authority on environmental decisions. Instead, we get ecologists.

A "pluralist" justification for having nature and her creatures represented in our decisions, on the grounds that their wishes have some right to a proper hearing, is difficult to propound in such a manner as to be persuasive in our culture. To begin with, the notion of rights attaching to other than human beings strikes most of us as something of an incongruity. The nearest we generally come to admitting such a possibility is when we manifest an aversion to excessive physical cruelty toward those among the higher vertebrates with which we occasionally empathize. Even these creatures are not generally thought to have such minimal rights as a right to life, as individuals, except that their death, especially if intentional, ought to be painless. Admittedly, it is humanly possible to believe otherwise.

We are constantly told, for example, of the contrary sentiments of the American Indian; but, by and large, such sentiments do not speak to the spirit of our times.

A second difficulty is that nature's representative at our councils would be a human, raising problems of conflict of interest, at the very least. How does he know what nature wants? And why should we believe him? King Solomon's ring would be very handy at this juncture. Our best scientists could very well ask a bee where that morning's supply of nectar and pollen came from, and get an answer; but that is about the limit to the subtlety of our present ability to communicate directly with fellow species. This seems rather distant from such grave matters as interplanetary war, or even damming a small river.

If we abandon dialogue in favor of evolutionary exegesis, we may ask Darwin's successors just what it is that nature's minions want. The reply is terrible and uncompromising: "... to multiply and inherit the earth, each and every one of them." The reply is also unhelpful, for we know, just as Malthus knew, and Darwin after him, that they can't *all* inherit the earth; even if the last human were gone, they couldn't. Whether it makes any moral difference that we interfere (for totally selfish reasons, at that), rather than let them bloody tooth and claw on their own, is not at all clear.

We will move closer to a form of argument consonant with political thinking distinctive of the last few centuries by adopting a trick of Rousseau's. Let us try to imagine a situation that, if it had existed, would account figuratively for some reciprocity of obligation between ourselves and nature, an ecological contract if you will. Mankind's part of the agreement, evidently, would be to restrain its innate rapacity, and forbear unlimited exploitation of nature. In return, nature would promise continued sustenance, and some level of security from those plagues she has in ample store. If we overstep the bounds of the contract, the deal is off and we reap the whirlwind—very good reason for admitting nature's representative to our council.

Exactly which activities exceed our rightful "claims" on nature are not determined by our little parable. This question we must settle among ourselves, probably on a case-by-case basis, with constant reference to our best understanding of the underlying reality which gives substance to the contract metaphor. Holy men or poets will not satisfy us that they can provide this understanding, for we think it a technical, scientific matter. And so it is that, when the question "Who speaks for the animals?" is asked, one answer is, "The ecological expert."

Ecology and Environment

At this point it will be useful to try to differentiate *ecological* from *environmental.* Recent use of the terms, "the environment," "environmentalist," "environmental hazard," etc., allows *environmental* to describe a wide range of issues, including issues that fall in the older domains of conservation and the esthetics of nature, as well as public health matters involving pollution and crowding, global bookkeeping in matters such as weather, food, and population, and an amalgam of natural resource management and civil engineering that bears on the prerequisites for, and consequences of, various styles of civilization. I will follow this broad usage.

The term ecological, as used in such phrases as ecological issue, will refer to that subset of environmental matters that may reasonably be construed as falling under the purview of specialists trained in the field of academic ecology. This would mainly involve interactions of living things among themselves and with aspects of their surroundings. Thus a concern such as whether air pollution will lead to another ice age is an environmental issue that, according to this usage, is not strictly ecological, since the real question is whether this climatic change will result: we all know that, if it does, it will be bad for peregrine falcons, and redwoods, and people. On the other hand, a concern over air pollution's reducing the growth rates of plants is ecological, in the sense I propose. This distinction will help narrow the focus of my discussion of "ecological expertise."[a]

II. WHAT DID THE EXPERTS KNOW?

If we consider only the ecological expertise that has been brought to bear on the Tocks controversy, and ask, "What have the experts shown that they know?" or more particularly, "What have they shown that they know about the *scientific* questions that were put to them?" the most honest short answer would have to be, "Not much."

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[a] The matter is blurred somewhat by real people and events. For example, Paul Ehrlich is recognized as a first-rate academic ecologist, yet the "population bomb" popularizations for which he is famous seem to me environmental rather than ecological. Conversely, some of the ecologists who are involved in such activities as preparing Environmental Impact Statements have become perturbed at the ease with which engineers, promoters, and possibly even charlatans can label themselves ecologists; and so the Ecological Society of America's journal, *Ecology*, and quarterly *Bulletin* have become, of late, forums for editorials, letters, and articles debating the merits of a professional code of ethics and a certification program for ecologists, even though the Society is academically based and its journal is one of the principal vehicles for publication in "pure" academic ecology.

The major environmental issues in the Tocks controversy have been the loss of a "natural system," interference with the shad migration, damage to the oyster industry in the Delaware estuary, and eutrophication of the reservoir. It is not certain that the "natural system" issue is strictly a scientific question. This matter will be explored later. Here we will concern ourselves with the three other issues, as these seem to have a clear factual basis.

The shad fishery may indeed be jeopardized by the project, as both the dam and the still water of the 37-mile-long lake will pose obstacles to the fishes' reproductive migration. Spokesmen for interested parties have variously claimed that the shad will or will not survive the project and that remedial measures such as fish ladders will or will not solve the problem. It is the recent experience of the Bureau of Sport Fisheries and Wildlife that adult shad will successfully negotiate certain kinds of fish ladders on their spawning run,[1] and as of 1971 there was a joint commitment of the Fish and Wildlife Service and the Corps of Engineers to build such facilities. (Earlier, the Corps was reluctant to incur such expenses for the benefit of fish.) There was talk of providing temporary fish passage facilities for the eight-year construction period, but no specific plan was ever adopted. The present life cycle of the Delaware shad is so short that a complete blockage for a few years could virtually exterminate the upstream spawning population.

Similarly, plans for screening various intakes to protect migrating fish from entrainment in the primary hydroelectric or possible pumped-storage flows were never made definite. The Bureau agreed that something of the sort would be needed, but this matter wasn't even mentioned in the Corps of Engineers' 1971 Environmental Impact Statement for Tocks Island Lake or in the New Jersey Electric Utilities' environmental statement to the DRBC. The Corps' "Comprehensive Evaluation of Environmental Quality" claimed that fish could pass through appropriately designed turbines without excessive injury.[2] The Corps cited a study of fish protective devices at the Muddy Run Pumped-Storage Project on the Susquehanna River, where it was concluded that "there is no need to provide protective facilities for the resident fisheries or other organisms now present at the site."[3] This study, however, did not concern migratory fish, so actually it is irrelevant to the shad question at Tocks. In fact, the report specifically states that if a migratory fish, such as the shad, were to be established in the waters in question, it would be a whole new ball game. Fisheries biologists at the Bureau of Sport Fisheries and Wildlife estimate that at the peak of the spawning run, 45,000 adult shad will pass Tocks Island in one day. The report of a Bureau hydraulic engineer points out that the diurnal cycle of a pumped-storage operation will cause migrating fish to be entrained a number of times before they are past it, with multiple opportunities both for injury and for confusion of migratory behavior.[4]

No one had an evidentiary basis for predicting that adult shad, once past the dam, would continue their upstream migration through the reservoir, or that young shad, which seem to drift with currents, would successfully pass through the reservoir in their downstream migration.[5] So the root question of whether the shad will survive the project in significant numbers never was answered authoritatively.

The question of possible damage to the oyster beds in the Delaware estuary is in a similar state. Some opponents of the dam worried that reduced springtime flow will cause the salinity in the estuary to increase, allowing the oyster drill, which normally is barred by its lower tolerance for fresh water, to migrate upstream, greatly increasing its depredation on the oysters. The Corps has indicated that the release schedule of the dam could be adjusted to keep the flow rate high enough during the critical spring period to keep the oyster drill damage to a minimum. Indeed, in its "Comprehensive Evaluation of Environmental Quality" the Corps went so far as to suggest that the release schedule might even be arranged for higher than normal spring flows so that the oyster fishery would be improved by the project.

Sooner or later the water managers will find their water sorely overcommitted. Temperature, oxygen tension, and flow rate of the release water will be important to upstream migrating adult shad in the spring, and downstream migrating juvenile shad in the fall; flow rates will affect the severity of the summer oxygen depletion in the pollution block at Philadelphia.[b] There is brave talk of using reservoir drawdowns as a fisheries "management" technique.[7] The depths from which water is withdrawn or returned to the reservoir, and the rates, will affect water condition in the reservoir with implications for management of eutrophication[c] and lake fisheries;[d] selective

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[b] The present Delaware River shad fishery represents just a fraction of 1 percent of the annual catch at the turn of the century. The primary cause of the decline of this population has been the stretch of badly polluted water, near Philadelphia, which the migrating fish must pass. This pollution barrier is essentially impassable for much of the summer, due to an insufficiency of dissolved oxygen, exacting a heavy toll on returning adults and downstream migrating juveniles. These matters are discussed in a well documented report.[6] Conceivably, appropriate water releases from the reservoir during periods of low flow could mitigate the Philadelphia pollution block.

[c] Computer modeling of the relation between water conditions and the mode of release at the dam was undertaken by a consulting firm, Water Resources Engineering.

[d] For example, the "two-story" fishery touted by the Corps in its impact statement, and described in some of the Fish and Wildlife memos (e.g., Jenkins[7]), require that the lower levels of the lake be cold but well oxygenated.

withdrawal will similarly determine the nature of river fisheries directly downstream of the dam. The Delaware conservation department was worried that a higher flow rate would simply move the Philadelphia pollution block downstream into Delaware waters, and possibly further pollute the oyster beds![8] Clearly, the systems engineers will have their hands full long after the biological facts are secured.

The Fish and Wildlife Service claims to have data indicating the correlation between salinities over the oyster beds and flow rates in the Delaware River, and they seem confident that salinity is the determining factor in controlling the oyster drill. However, nothing much seems to be known about a protozoan infection that has been making severe inroads in the Delaware oyster beds since the mid 1950s, so there is no telling whether the oyster fishery will improve or decline with or without the dam.[e]

These two issues, the shad and the oysters, were handled very casually. With the exception of the Fish and Wildlife Service's involvement in the design of a fish ladder, there was no concerted application of expertise to answer the factual questions raised in these controversies. Instead, the major parties in the debate simply asserted that one outcome or another would or would not occur, or they off-handedly quoted someone to such effect. We might easily believe that appropriate ecological expertise was underemployed in these issues. This seems all the more likely when we consider that the shad and oyster issues in themselves were not politically significant in the debate—they were mostly used as symbols, and the symbols did not excite much response.

The eutrophication issue, on the other hand, has been politically significant. It certainly has delayed project approval, and in time it may decide the matter. The eutrophication issue has proved more important than the shad and oysters, in part because people were more ready to accept that "eutrophication" is evidence of environmental deterioration of some sort. Perhaps this acceptance was conditioned by familiarity with eutrophication as an issue in other, not necessarily local, controversies—phosphate detergents, sewage

[e] The oyster catch in recent years has been about one-tenth that of the previous few decades, and even less than earlier in the century. While some upstream migration of the oyster drill has been noted, the primary cause for the recent decline of the oyster fishery seems to be the protozoan disease, which may or may not have some connection with salinites or pollution. Various bits and pieces of information on the biology of the oyster problem are summarized in the Bureau of Sport Fisheries and Wildlife memorandum by Massman.[6]

treatment, agricultural fertilizers, etc.—and by the fact that the feared outcome has a high visibility.[f]

Almost everyone will agree that a reservoir suffering algal blooms looks weird and smells bad. Because of this, the project promoters and the politicians responsible for making a decision on the project are sensitive to the possibility of eutrophication: if the lake goes sour, it will stand as a public monument to a seamy side of their decision.

The dollar cost of eutrophication is not quite so clear. If the lake becomes outrageously foul, the recreation value of the project will diminish significantly. However, many recreation activities are compatible with at least some level of eutrophication; and I don't suppose that terribly objectionable conditions will persist year round. That is, if there were no special commitment to preventing or remedying anticipatable eutrophication, the dollar cost of its occurrence would not loom large in a conventional benefit-cost analysis. Given a commitment to prevent eutrophication in the lake, the costs of appropriate effluent control programs (necessary in the entire upriver drainage basin, as well as in the immediate Tocks area) can be awesome.[10]

It is one of the ironies of the Tocks controversy that in the matter of "eutrophication"—the only environmental issue that clearly has been perceived as more than an irritant at the decision maker's level—it is quite evident that ecological expertise, as employed, was not effective in resolving the question, "Will the lake become eutrophic?" The Weston study[10] included a rough phosphorus budget of the Delaware and concluded that "the reservoir will be threatened with an increased rate of eutrophication." McCormick Associates

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[f] Part of the Bureau of Sport Fisheries and Wildlife's interest in the fish ladder to mitigate blockage of the shad migration at the dam seems to be motivated by recognition of the "visibility" of this impact. In their memo we find:

> It is inconceivable in this enlightened environmental age that hundreds of thousands of adult shad can be blocked at the dam without provision for their upstream passage, and we are certain this situation will not occur. . . ."
>
> We believe it prudent to provide a fishway to assure preservation of gene pool of the upstream races against future habitat losses downstream. It is also realistic, since the public would not likely countenance blockage at the dam if it resulted in obvious fish kills.[9]

It is tempting to conclude from this that the question of loss of shad, as adults or young, *in* the reservoir is of lower priority simply because the outcome is of lower visibility—the fish would simply disappear.

found the data base insufficient, but concluded that eutrophication seemed probable.[11] A transparently absurd computer model used by Water Resources Engineering predicted that the reservoir would not eutrophy if the present level of nutrient input were maintained.[12]

The question, "Will the lake be eutrophic?" actually encompasses several quite different possible questions, depending on the intended meaning of eutrophic. The ambiguity of the term has, of course, added to the confusion of the public debates, for project opponents use "eutrophic" to designate a truly abominable stagnation, while apologists speak of "eutrophication" as a slight enrichment which may even be somewhat beneficial to the fisheries.[g]

The Environmental Protection Agency never was satisfied with the treatment of the eutrophication problem in the documents it received,[h] and the Council on Environmental Quality refused to commit itself to a prediction on eutrophication at Tocks, given the uncertainty of the data and the calculations. All in all, the most

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[g] Compare, for example:

> Among the environmental dangers, perhaps the most serious is that, if the waters are impounded in a reservoir, as presently planned, "eutrophic conditions would develop rather rapidly." The oxygen would be virtually exhausted and the lake would be dead. . . Eutrophication of the reservoir would rule out its use for recreational purposes. Fish would not live in it and its stench would be intolerable. . . (letter from Senator Case [R-NJ] to CEQ, January 14, 1972).

And:

> Blooms of algae can be expected to occur on the reservoir, but these will not pose problems to fish production or fishing (Slater, et al., Bureau of Sport Fisheries and Wildlife memo, *op. cit.*).

Or:

> Eutrophication is the process of aging experienced by all lakes in which plant growth—algae—occurs. Such growth is accelerated when abundant nutrients, especially phosphates, are available (DRBC statement in "The Keystone Project, Tocks Island Revisited," *Delaware Basin Bulletin,* 10, Sept/Oct 1971).

[h] The Environmental Protection Agency, in its review of the Corps' 1971 Impact Statement (this was the third draft received by EPA), wrote:

> Our principal concern is the still unresolved issue of water quality in the reservoir, particularly the risk of rapid eutrophication. . . .
>
> There is a division of opinion among EPA offices which have reviewed the statement as to whether the risk of eutrophication is controllable by careful management plans or whether probable waste loads will be too great to permit maintenance of high water quality in the reservoir by management at the site. We do not have enough information to resolve this question at the present time (letter appended to the Impact Statement).

The EPA response to the revised Impact Statement, which was accompanied by the "Comprehensive Evaluation of Water Quality" and a consultants' study persuasive argument that has been brought to bear on this question is the homely observation that a nearby reservoir, which in many ways is similar to the one planned for Tocks, has in fact become disagreeably eutrophic. Thus, where ecological experts were systematically employed in the Tocks Island Dam controversy, they were ineffectual.

The failure of ecological experts to deliver the goods when asked to make a practical and specific prediction is not a peculiarity restricted to the Tocks case. Many environmental controversies involving seemingly straightforward factual questions go unresolved. Why this should be so is explored next.

III. WHAT MIGHT THE EXPERTS KNOW?

We have gained the impression that ecology is not, at present, very effective as a predictive science. This is not necessarily a dishonor, for it is quite conceivable that the phenomena that comprise the domain of "macrobiology" are refractory to the sorts of simplifying insights that have made physics and chemistry, as we know them, possible. In other words, there might be some peculiarities of the biological world that, when considered at the level of whole organisms, populations, communities, and ecosystems, make the scientific questions we want to ask of the ecological experts extraordinarily difficult—so difficult that it is too much to hope that the answers be anywhere near as reliable as the answers that could be expected of, for example, a competent chemical engineer operating within the scope of his expertise. I will argue that this is the case.

Six distinguishable features of the biological world mitigate against a predictive ecology. Three of these are simply observed facts: that there are many species; that organisms exhibit "homeostasis" in their internal milieu; and that many (perhaps most) of the species populations found living at a particular site seem to affect one another. The other three features are not direct observations but, instead, are abstract principles inferred by evolutionary logic from a few observations: that each species is in some functionally important way different from every other; that organisms do not respond in simple, generalizable ways to the factors that are important to their survival; and that whatever balance does exist in a natural system is in part a

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of the eutrophication problem, was more definite: "EPA's conclusion is that a eutrophication hazard exists for the proposed Tocks Island Lake under existing waste treatment conditions in the Upper Delaware Basin. We should point out that the eutrophication problem is a result of the impoundment. . ." This letter to the Corps then requested more specific plans for waste treatment.

consequence of its history. These facts and principles will be discussed in alternating order.

A. The Multitude of Species

One of the most striking aspects of the biological world is the vast numbers of different kinds of organisms. One attempt at compilation of the numbers of described species of various groups of animals[13] is reproduced in Table 9–1. We must add another 200,000 or so species of plants. For some of these groups the listing probably is near complete. For example, this is thought to be true for birds, on account of several kinds of evidence: it is felt that the world's bird fauna have been well researched, most of the places that birds could inhabit have been visited by naturalists, birds are readily visible to the naked eye and are not especially secretive in their habits, and, finally, the rate at which new bird species are being described is quite low. By comparison, we can see that these kinds of reasons do not apply so obviously to groups such as insects, and indeed it is thought that there may be at least as many undescribed insect species as are now known. One estimate, based on observations regarding the relative commonness and rarity of insect species, sets the total number at three million.[14]

Not only are there very many species in the world, there often are very many species in lesser geographic areas. As examples of the numbers of species that may be found in a given region or sample, one might find the following instructive: 1,395 bird species are known from Colombia;[15] about 2,500 species of flowering plants are known from Florida;[16] 134 species of ants have been found on the island of Trinidad;[17] over 300 species of shrimplike creatures of the genus *Gammarus* have been described from Lake Baikal;[18] about 300 species of the fruit fly (*Drosophila*) found in the Hawaiian Islands are found nowhere else;[19] a series of quarter acre sample plots in deciduous cove forest in the Great Smoky Mountains each encompassed 46 to 68 species of vascular plants;[20] a single block of soil eight inches square and one inch deep yielded 25 species of nonpredaceous mites;[21] and a single light trap operating in Maine for four years caught 349 species of moths.[22]

The Park Service prepared a checklist of biota of the Tocks Island Recreation Area, which is summarized in Table 9–2.[23] We note that the numbers are impressive, even though entire phyla have been omitted.

B. Every Species Is Different

It has long been recognized that organisms have a capacity for geometric increase. Only because of high mortality does this increase

Table 9-1. Estimated Number of Known Species of Recent Animals

Protozoa	30,000	Linguatula	70
Mesozoa	50	Chelicerata	35,000
Porifera	4,500	Crustacea	25,000
Coelenterata	9,000	Other arthropods (excl. insects)	13,000
Ctenophora	90	Insecta	850,000
Platyhelminthes	6,000	Mollusca	80,000
Acanthocephala	300	Pogonophora	1
Rotifera	1,500	Bryozoa	3,300
Gastrotricha	175	Brachiopoda	250
Kinorhyncha	100	Echinodermata	4,000
Nematomorpha	100	Phoronidea	4
Nematoda	10,000	Chaetognatha	30
Priapulida	5	Hemichordata	80
Nemertina	750	Tunicata	1,600
Entoprocta	60	Fishes	20,000
Annelida	7,000	Reptiles and amphibians	6,000
Echiuroida	60	Birds	8,590
Sipunculoidea	250	Mammals	3,200
Tardigrada	180		
Onychophora	65	Total	1,120,510

E. Mayr, E.G. Linsley, and R.L. Usinger, Methods and principles of systematic zoology 1953. (New York: McGraw-Hill, 1953)

Table 9-2. Numbers of Species in Tocks Island Region

Numbers of species of various groups expected in the Tocks Island region on the basis of collections, sightings, or overlap with known range:

Vascular Plants	1,129
Fish	46
Reptiles and Amphibians	52
Birds	250
Mammals	53

NOTE: No attempt was made at exhaustive listing of algae, fungi, mosses or invertebrate animals.

National Park Service, "A Natural History Survey of the Proposed Tocks Island Reservoir National Recreation Area", unpublished.

fail to materialize. In Darwin's words, ". . . as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life."[24] If the world is such a harshly competitive place, the continued existence of so many species raises unsettling questions: How can so many species, locked in bitter struggle, directly or indirectly, avoid exterminating one another? Why is not the world's biota reduced to the few most "competitive" species? Evidently, every species must have some ability, figuratively, to stay out of the way of most other species; and among those species that are in more or less direct competition, each must in some essential way be *different*, so that there is some season and some place where each species is more effective than its rivals in the struggle for existence. That each species is best at something different—something that is its "business" in life—is at the core of the ecological concept of a species' niche. There have been many attempts at giving formal mathematical expression to these ideas. Some of the more promising models have implied that for species to coexist, each, when very abundant, must be deterred from further increase by a different limiting factor.[25] These models are in accord with the naturalist's intuitions, but they are not directly applicable as scientific "laws," because simplifying assumptions upon which the proofs rest are too restrictive.

C. "Homeostasis"

Organisms do not behave as simple physicochemical systems, although as far as we know they *do* obey the laws of physics and chemistry. The difference lies in the remarkable degree of integration and regulation of the physical and chemical processes within the organism. Much of the regulation of internal processes seems directed at the maintenance of some constancy of the internal milieu. Such regulation is called "homeostasis." A simple nonbiological example might be a buffered solution, which maintains a fairly constant pH despite the addition of moderate amounts of acid or base. In the metabolism of living things, this kind of behavior is the rule rather than the exception.

Osmoregulation is one class of well documented examples of biological homeostasis: it consists in the maintenance of fairly constant concentrations of many organic and inorganic solutes inside the cell—and in some of the body fluids of multicellular organisms—despite considerable variation in the concentrations of these solutes in the surrounding medium.[26] A second, commonly observed class of examples is temperature acclimation. The rates of individual biochemical reactions are related to temperature according to the usual Arrhenius equation of physical chemistry.[i] Gross metabolic rates, such as oxygen uptake, indices of the combined activities of many individual biochemical reactions, exhibit the same kind of dependence on temperature in the short run. Thus we can predict the change in the rate of oxygen uptake as temperature changes by a simple analogy from physical chemistry. However, after a period of acclimation to the new temperature, lasting a few hours to a few days, the organism's rate of oxygen uptake generally readjusts to a rate that is closer to its original rate. This homeostatic regulation of the rate of a biological process clearly is not predicted by application of the Arrhenius equation. Warm-blooded animals, of course, maintain a constant internal temperature despite considerable variations in the temperatures of their surroundings; and many cold-blooded animals do a fair job of reducing fluctuations of their internal temperature by moving in and out of the shade and orienting themselves appropriately relative to the wind and sun, as the ambient temperature changes.

To be sure, not everything about an organism will remain constant (or more or less constant), for *some* processes must work at exceedingly variable rates in order to achieve the homeostasis we observe in other processes. For example, considerable variation in energy expenditure will at times be required for some kinds of compensation for environmental fluctuation.

We see from this that a prediction of biological responses to

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[i] The logarithm of the rate constant is equal to a constant minus a term that is proportional to inverse of the absolute temperature, approximately implying that the logarithm of the rate of the reaction will be linearly related to the centigrade temperature for small temperature changes. This phenomenon, and acclimation, are explained in Prosser and Brown.[26]

environmental conditions that rests on physicochemical analogy is very likely to be incorrect and will consistently underestimate a very fundamental complexity of the system under study.

D. Nongeneralizable Adaptations

If living things had only to contend with the problems of physical and chemical degradation, they could all adopt much the same strategy for survival—a tuning of their biochemical machinery to best advantage against the second law of thermodynamics. In fact, at a very basic subcellular level—the metabolic pathways—the basic chemical machinery of almost all organisms is very similar. At this level of chemical building blocks, organisms are using the same strategy.

Whole organisms, however, have another level of problem to contend with, rooted in the fact of competition. Above the level of chemical building blocks, organisms have to contend with *each other* in the struggle for existence. Since all the combatants in this arena are evolving, there will be a complementarity, or reciprocal evolution, to all generalizable strategies: as the prey become more fleet, so do the predators; as the hunted becomes more elusive, the hunter becomes more meticulous; as armor becomes thicker, the weapons of assault become more penetrating; as chemical defenses become more potent, the mechanisms of detoxification become more effective, and so forth. Every new evolutionary development that gives one species a temporary advantage becomes itself the source of a selection pressure, driving this species' opponents to evolve means of nullifying that advantage—move and countermove.[27]

We may assume, therefore, that all the generalizable strategies were adopted, and their reciprocal effects cancelled, very early in the history of any biotic interaction. The subsequent history, then, may be viewed as a search for nongeneralizable *tactics*; and each species, as a consequence, has become a bag of tricks rather than an easily predictable strategist.[28] In fact, the whole point of the evolutionary game is to find tactics so outlandish that the probabilities of their respective countertactics are minimal, and to deploy these capabilities as deceptively as possible.[29] The more discontinuity that an organism can display in this kind of adaptive behavior, the harder it is for his opponents to track him, and the less opportunity they have to evolve the neutralizing response.

In our recent experiences with some antibiotics and pesticides, we can see a nutshell lesson in this kind of strategy. Used intermittently, the "wonder drugs" and chemical weapons in the war against insects were devastating. Used continuously, the target species developed resistance, until the new-found arsenal, in some instances, proved all but useless. The optimal strategy, it seems, would be to use these tricks only in times of greatest need. An adaptive trick should be played often enough to derive some benefit, but seldom enough so that one's opponents do not catch on. A trick that no longer appears improbable will not fool anyone. So, not only are species different in their responses to critical factors; the *ways* in which they are different involve improbable and discontinuous behavior.

Of course, we are aware of highly visible examples of such behavior: sea turtles live in the water, but breed on land, toads live on land, but breed in water; salmon live in the sea, but breed and die in fresh water; caterpillars become butterflies; some parasitic flatworms have three successive obligate hosts. We see huge annual migrations of some large herbivores, massive irregular population eruptions of locusts, and exquisitely regular synchronization of life cycles more than a decade long in cicadas. Water fleas go through cycles of generations with altered morphology during the course of one season; rotifers may reproduce parthenogenetically or sexually, depending on environmental conditions. Tardigrades can form a drought resistant cyst that remains dormant until it is moistened; slime molds can live as single-celled, amoebalike creatures or can temporarily aggregate into a motile syncytium, and so forth.

These dramatic, visible examples are the stuff of Disney's nature movies, perhaps trivial-looking biological curialia, but this is only the tip of a very important iceberg—the obvious, unmistakable tricks some organisms play for survival just give us a hint at the diversity of tactics that might not so catch our attention but that nevertheless may be critical components of biological interaction.

E. Everything Is Connected

If, in some sense, all organisms are jostling for a slice of the same pie, it stands to reason that any change in one species population will affect other species populations. After all, one species may be host to several parasites, prey to several predators, a predator on other prey, and rival for food and space with several competitors; and these in turn, interact with their parasites, predators, prey, and competitors, till one cannot pick a flower but "trouble a star." This does not tell us, though, how much the star was troubled.

From what was said in the prior sections concerning complexity, we can guess that the intensity of effects propagated through a biological community, after perturbation, will not be predictable, a priori. Some disturbances will damp out after affecting a few populations; others will be amplified in transmission, with the effect increasing as it is passed from population to population, as in food-chain concentration of some pollutants.[30]

The eco-crisis literature is by now replete with cautionary tales of snowballing side effects, such as the story of DDT being sprayed on an Asian village in an attempt to control malaria, with the result that there was a rat epidemic and a housing disaster! According to the story, the DDT was absorbed by insects, and then concentrated by some insect-eating lizards that lived in and around the thatched huts of the village. The village cats ate the DDT-contaminated lizards and were poisoned, thus letting the rat population explode. The lizards, it seems, had been instrumental in controlling some caterpillars that specialized in eating the local roofing thatch. With the demise of the lizards, a plague of caterpillars riddled the roofs to the point of collapse.[31]

F. The Importance of History

The genetic composition of a population, relative to its initial composition, is in large part a consequence of the past selection pressures to which the population was exposed. In other words, the present adaptations represent a compendium of past successes fixed by the "memory" of natural selection.[32] This implies that whatever degree of stability may be found in an ecological interaction is a reflection of a history of past interaction. Present stability, therefore, gives no assurance of future stability under altered interactions or novel conditions. Unprecedented types of perturbation of a community seem almost certain to elicit reactions that will be qualitatively different from the stabilizing behavior that is a result of mutual adjustment in evolutionary time. This sort of theorizing does not lead to a clear picture of what the detailed reaction will be, but it does provide a strong suggestion that the reaction will be undesirable, if only by analogy with haphazard tinkering in a finely tuned mechanism.

Taken together, these six features of biology cast a pall over the prospects for a predictive science of ecology. It is as if chemistry found itself faced with a periodic chart of *millions* of elements, thousands of which may be present in any reaction, all of which are bizarrely different from one another, all of which are badly behaved from a statistical standpoint, and all of whose properties may change with history. This is an extraordinarily difficult situation for a developing science.

What little we do know of evolutionary macrobiology that stands comparison with the "hard" sciences is the legacy of men who not only were brilliant scientists but must also be ranked among history's most creative applied mathematicians. So it is not as if first rate scientists have not been trying to develop this aspect of biology: they have tried and are trying, and have achieved some limited success, but it must be understood that the inherent difficulties of a predictive biology are far greater than those that had to be resolved in order to get physics and chemistry started in their modern direction. In moments of self-pity, the biologist may feel sure that the living world evolved expressly in order to defy analysis; and from our discussion of the peculiarities of this living world, we see that in a way it has.

In the absence of predictive theory, and in the presence of fundamental obstacles to predictive theory, it is not possible to draw upon the capital of scientific expertise in the usual manner. The scientific *method* still applies, so it is worthwhile employing competent ecologists for empirical resolution of relevant questions; and the experience of the trained naturalist will be invaluable in properly phrasing the questions that are put to empirical test. But it seems exceedingly unlikely that we could profitably employ armchair expertise. We should not at present hope to find an ecological expert who can pull half a dozen key equations out of a college text, refer to the CRC handbook for the values of critical coefficients, look at the blueprints for a proposed project, and then make reliable predictions of ecological consequences.

IV. WHAT DOES THE COMPUTER KNOW?

We shall next consider what happens in this realm of complex phenomena, for which there is no adequate analytical theory, when the rococo temptations of computer modeling are present. The conventional wisdom of the day—"garbage in, garbage out"—has it that the computer can't know any more than the experts. In ecology this can be taken to mean that computer models at present generally are not much help as predictive devices. The one major ecological model employed in the Tocks case was the attempt by Water Resources Engineering at predicting eutrophication.[33] The hydrological nuts and bolts of this model are treated in the preceding essay. Here we will try to assess the biological side of the model.

The developers of this model state in the conclusions of their report that under present nutrient loads, the proposed reservoir "would not experience either algal blooms or anaerobic conditions," nor would it under the projected load for the year 2000, given "advanced" waste water treatment. Less advanced, "secondary" treatment of the projected load, it is claimed, would result in "nuisance algal conditions," but still would not create "anaerobic conditions."[34] Now the ecological question that prompted this model concerned "eutrophication." Thus, our first worry has nothing to do with the model, per se, but merely asks about the vocabulary of the questions that motivated it.[35] This is a complicated worry, for the word eutrophication is ambiguous. In general and scientific usage, we find four different but interrelated meanings of eutrophication. It may designate:

1. An *index* to the nutrient level, or nutrient load, of a body of water, most often specified in terms of phosphorous, nitrogen, carbon, or silicon, in some combination, but other elements sometimes are included.
2. An *index* to the level of organic productivity in a body of water, usually expressed as a rate, in mass or energy units, of photosynthesis per unit area or volume, but other kinds of production such as fish, may be cited.
3. A *process* in the successive chronological development of a lake, as both a biological and a physical unit, usually referred to, metaphorically, as "aging".
4. A *state* of ecological degradation of a body of water, characterized by one or more symptoms such as marked algal blooms, unpleasant odors or unpleasant flavors of algal or bacterial origin, and fish kills caused by oxygen depletion or, possibly, algal toxins.

According to usage 1, a eutrophic lake is one with a relatively high nutrient load or nutrient concentration, while according to usage 2, it would be a lake with a relatively high rate of biological production. Inasmuch as nutrients are necessary for biological production, and some are often in short supply (limiting), it is almost inevitable that the two indices, 1 and 2, will be positively correlated; but they are not identical.

The undesirable properties of a eutrophic lake in sense 4 are consequences of extreme rates of growth of certain algae or bacteria, relative to the lake's capacity for reaeration, mixing and flushing, so that incidence of this state will be related to both the indices 1 and 2.

As a lake fills in with sediment, the relationships among some of the lake parameters (depth, area, volume, inflow) change so as to increase nutrient load per unit volume and (neglecting turbidity) the average light exposure, leading to increased productivity, which may in turn cause reducing conditions in the lower water strata, permitting regeneration of nutrients from the sediments, leading to further increase in the nutrient load, etc. So the aging process of the lake corresponds to a progressive increase in the "eutrophication" indices 1 and 2, and the increase, in time, may possibly exceed the threshold for the eutrophication state, 4. In the meantime, the increased production causes an increase in the rate of sedimentation, thereby accelerating one of the initiating factors in the aging. Thus it is possible to speak of the artificial fertilization of a lake as accelerating its rate of aging. This, in recent years, has culminated in loose talk about "killing" lakes through nutrient pollution; but, as the rate of total biological production in a lake usually increases with age, the metaphor is inappropriately mixed. The virtual "death" through aging of a lake occurs only when the lake has finally been completely filled in. Admittedly the changes in species composition that accompany trophic age may not suit our tastes, but that constitutes the "death" of some favored species—hardly the "death" of the lake.

Usage 4, the description of a noxious state, is the only one that invariably implies a lessening of the lake's utility for human purposes. The other usages refer to indices and processes that only correlate with the undesirable state, and only for extreme values at that. Thus, perception of eutrophication as a problem should explicitly invoke meaning 4. In this regard, the words "algal bloom" and "nuisance algal conditions" in the model report look appropriate, but examination of the model's actual output shows that what was modeled was aggregate algal mass, without reference to the type of algae, and with no special criterion for blooms.

The modelers used the number, one milligram of algae per liter of water, as the threshold criterion for a "nuisance condition."[36] This probably represents their guess at a visibility threshold. When we consider that only certain species of algae are responsible for the objectionable tastes, odors and toxins of the eutrophic state (4), and for that matter that only certain species of algae are present in large numbers in massive algae eruptions (owing to their tolerance of certain environmental conditions and their unpalatibility to the animals that usually graze on algae), the model's output (biomass) does not speak exactly to the problem of eutrophication. The oxygen balance output, if correct, is more to the point.

Our second worry is about the workings of the model. Whatever the output does represent, is it a reliable prediction, and how can we tell? There are two quite different approaches to predictive modeling. A model may be a probabilistic assessment of purely empirical observations, largely divorced from causal interpretation; or it may be an analytical model, a coupled system of mathematized relations which individually are descriptions of causal mechanisms

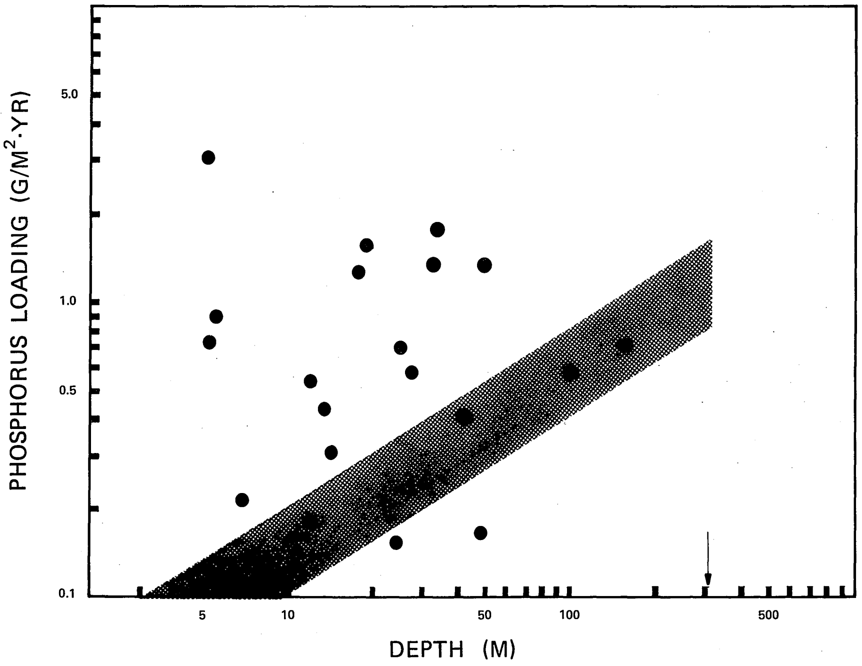

Figure 9-1. Phosphorus Input vs. Mean Depth for a Number of Lakes

Lakes above the shaded band were eutrophic, lakes below the band were not. Lakes in the band showed signs of incipient eutrophication. Lake Tahoe fell off scale in the direction indicated by the arrow. (Redrawn from Vollenweider.[37])

grounded in scientific law. Of course, models do not necessarily exist as pure types. For example, some parameters in a model incorporating causal representations may require empirical determination. The important difference between the two types is that they are justified in different ways. The information that legitimates an empirical model is strictly in the data; while the information that legitimates a causal model is derived from general scientific laws.

We might best understand empirical modeling by examination of a bare-bones model of this sort, which is so simple it does not require either a computer or explicit mathematics. Figure 9–1, redrawn from work by Vollenweider,[37] shows a two-dimensional space, a coordinate system in which each body of water is assigned a point on the basis of its average depth and its phosphorus input. When Vollenweider did this for a number of lakes, he observed that the lakes he knew to be eutrophic and those he knew not to be eutrophic fell in different parts of the "space." Moreover, when logarithmic scales were employed for the two axes, the boundary between the eutrophic and noneutrophic "phases" in the space gave the appearance of a straight band. On either side of the band trophic state seemed determinate. Lakes falling in the bank were "threatened" with eutrophication. With a healthy dose of optimism, we might use this diagram for predictions—to find out whether a lake with a given mean depth and phosphorus input will be eutrophic, locate the corresponding point in the diagram, and see which phase it falls in. (We could carry out an equivalent exercise algebraically without recourse to graphs.)

Ignoring the question of experimental error (i.e., the reliability of the empirical determinations of depth, phosphorus load, and eutrophy), how reliable are the predictions of this sort of model? If the data on which Figure 9–1 was based were exhaustive—every lake in the world being included as preliminary data—we should feel very confident about it indeed, but of course, except for newly created lakes, the model, then, would not be a predictive device at all, but rather a mnemonic device, conveniently storing certain facts for later use. Vollenweider actually used data from nineteen lakes, so we don't feel nearly so confident about the diagram as we might. On the basis of a few scattered points, how can we tell that the shape of the border is straight, and how can we tell that the two "pure" phase regions really are pure? We can't. We don't know that the twentieth lake would not alter the shape or the position of the border, or appear as a eutrophic "island" inside the noneutrophic region, or vice versa. And after the twentieth lake we would not know about the twenty-first.

What we do know is that the same model with more data surely would be more persuasive. If, say, two hundred lakes were plotted, and we found that they fit the pattern, then we might start feeling comfortable with use of this model in prediction. Also, the more thoroughly the data covered a particular region of the diagram, the more confident we would feel about predictions concerning lakes whose depth and phosphorus load corresponded to points in that region. Thus, if a dozen known lakes fell appropriately near both sides of the phase border in the lower left part of the diagram, but none was plotted near the phase border in the upper right, we should think the former part of the border reasonably justified, but we would have to admit that the latter part was guesswork.

An empirical model of this sort treats the *processes* that generate the outcomes under study as if they occurred in a "black box." All that is considered explicitly is the observed association between variables. The object of the modeling is to find patterns in the data. There are many different ways of looking for a statistical pattern: regressions may be linear, exponential, quadratic; one may try to fit the data with Fourier series or polynomials; the data may be rescaled; key factors may be sought among the data variables or among various functions of various combinations of the data variables; ad infinitum. The only way to know how well the modeled description conforms to the actual pattern, and which descriptions conform better than others, is to get lots of data and see.

The more complex the relationships, or the more numerous the variables, or the greater the range of values for the variables, the more data are required for a given level of confidence. Owing to the problematical features of the living world, described in the previous sections, large scale empirical modeling of ecological systems requires unimaginable (and unavailable) masses of data to be of any generality. To date, demonstrated success in ecological modeling has been achieved only by studying specific, restricted systems. For example, Wiegert and his co-workers, in order to develop a model predicting the time course of populations of the very few species inhabiting certain hot springs in Yellowstone National Park, have spent many field seasons gathering data on those species in those springs.[38]

An analytical model replaces the "black box" with a system of causal mechanisms. Each of the causal mechanisms that are thought important is represented by a formula (or law), and the computer just does the bookkeeping. The application of this kind of model to broad ecological problems may at first look appealing, for if these were to be modeled empirically, more data would be required than anyone can get. However, the reliability of any analytical model depends on the security of the scientific foundations of the formulas used to describe the component processes, and in ecology secure laws would require knowledge which no one has.

The water quality model developed by WRE makes some pretense of being an analytical model. Two "theoretical bases" are claimed: the "Law of Conservation of Mass" and the "Kinetic Principle."[39] Both claims are unimpressive when examined closely.

The "law" of conservation of mass turns out to be the catechism that matter can neither be created nor destroyed (under conditions prevailing over most of the earth's surface). This special knowledge is corollary to the response a sleight-of-hand coin trick will evoke from a child of normal intelligence: if something is not where you saw it last, you look for it somewhere else. I am not complaining that the "law" is false; only that I can see room for doubt as to whether it will tell us anything we don't already know.

The "kinetic principle" turns out to be an assertion of the applicability to ecological interaction of the physical-chemical law of mass action. Roughly speaking, this gives rise to equations in which the rate of an interaction between two constituents is proportional to the amounts present. That this should hold true, even approximately, in biological interactions is an assumption, not a "law."

It is true that equations embodying such an assumption are frequently *used* in ecology; they can be found in any introductory text. Equations of this sort—associated with the names Gauss, Volterra, Lotka, and Verhulst—have been employed in developing the theories of competition and predator-prey interactions. However, these theories are essentially speculative, asking merely such questions as, "If such and such a simple equation describes, say, competition between two species, then for what starting conditions and values of parameters will there be a stable equilibrium, or perhaps a cyclic solution?" This kind of speculation is good fun, and some of the results have been genuinely enlightening, but it is altogether something different to claim that these equations describe any real situation except some single-celled organisms in rigorously controlled laboratory environments. The equations found necessary to describe even such simple systems as flour beetles living in tanks of flour at constant temperature and humidity are vastly different, and vastly more complicated.[40] Descriptions of, say, predation under field conditions are more complicated yet.[41,42]

However shaky the grounds for its choice, the "kinetic principle" dictates the general form of the equations used in the model to represent interractions between living constituents. There were only six constituents so treated, each an idealized caricature of a broad category of organisms, namely: algae, microscopic animals that feed on algae, bottom dwelling animals that feed on organic debris, and three fish groups classified according to their respective diets and temperature preferences. The spatial structure of the lake appeared in the model as a series of horizontal "slices", each slice corresponding to a given depth range. Vertical movement of materials and organisms from one slice to the next was modeled in a common sense way, but no provision was made for there being any local differences or movement within a slice. That is to say, the lateral dimensions of the lake were ignored.

Three features then, attract our attention in an assessment of the credibility of the WRE model: the dubious form of the equations, the aggregation of diverse species into a small number of functional categories, and the compression of spatial differences into the vertical dimension alone.

Some details of the equations representing biological interactions are presented in Box 1. In brief, there is no easy way to justify the general forms of the equations used to represent biological interactions in the WRE model, for on the face of it, their reality does not seem very likely. One particular property of the equations, the consequences of which can be understood in advance, is that the model does not include any mechanism to represent drastic mortality under severe environmental conditions. This seems an inappropriate omission from a model that was intended to predict the possible occurrence of ecosystem dysfunction.

The model is totally unsuited to lumping species together in functional groups, such as "Algae." Undesirable water conditions such as massive algal blooms and eutrophication induced fish kills are associated only with certain kinds of algae, which otherwise are rare or absent. The presence of these algae in water of poor quality and their general absence from water of better quality are manifestations of individual species differences, including relative palatability of the algae to organisms that normally graze them, phosphorus requirements and tolerances, silica requirements, pH tolerances, responses to various algal and bacterial toxins, and the capacity for such tricks as rapid absorption of phosphorus (which is then *stored* for later use).[47]

Not only do various species of algae respond differently to critical environmental variables, they in turn affect these variables differently, both in direct ways, such as the production of specific toxins, and as side effects of metabolic activity, which can alter pH, turbidity,

BOX 1. MODELING OF SPECIES BEHAVIOR IN LAKECO

Let us see precisely how biological interactions were represented in the core equations of the WRE model. The rate of change of biomass of species 1, where species 2 feeds upon it is given as

$$\frac{dA_1}{dt} = (\mu_1 - R_1 - S_1 - M_1)\,A_1 - \mu_2 A_2 F_{2,1} - P_1 \qquad (9\text{–}1)$$

Here A_1 and A_2 are the biomass of species 1 and 2 respectively; μ_1 and μ_2 are their specific gross growth rates; R_1, S_1, and M_1 describe the depletion of the biomass of species 1 by respiration, settling, and intrinsic mortality, respectively; $F_{2,1}$ is the "biomass conversion factor" for the consumption of species 1 by species 2, and P_1 is a compound term describing physical transport processes (advection, diffusion, inflow, and outflow).

The coefficients S_1, M_1 and $F_{2,1}$ are constants in the model. The settling loss, S, applied only to algae and thus suffered no other form of intrinsic mortality. It certainly is not the case that what M and F portray —per capita mortality rates, and what ecologists call trophic efficiency— are established constants. Biological literature provides individual measurements of these parameters for some species under some conditions and they are by no means constant; nor would we on first principles expect them to be.[43] For example, we surely would expect mortality rates to increase as conditions deteriorate.

The temperature dependence of the specific reaction rates μ_1, μ_2, and R was represented by a familiar rule of thumb from physiology:

$$\mu_T = \mu_{20}\,\Theta^{T-20} \qquad (9\text{–}2)$$

where μ_T is the temperature corrected coefficient, μ_{20} is the value of the coefficient at the reference temperature (20°C), T is the temperature in degrees centigrade, and Θ is the temperature coefficient. A value of 1.047 was used for all Θ, meaning that reaction rates double at 15°C intervals. It seems reasonable that gross growth and respiration might be corrected in this manner (at least for single-species equations), though the exact choice of a value for Θ is not certain, and one wonders why other biological functions, such as the death rates, were not also corrected for temperature.

Specific gross growth rates, μ_1 and μ_2, were also adjusted for the abundance of resources in the manner of Monod kinetics; the general form of the adjustment being:

$$\mu_a = \mu\left(\frac{x}{K_x + x}\right) \qquad (9\text{–}3)$$

where μ_a is the adjusted coefficient, μ is the value of the growth rate in the presence of a superabundance of resources (i.e., the value of μ_a at saturation), x is the concentration of the resource, and K_x is the concentration of resource at which μ_a is one-half μ (called the "half-saturation constant"). Saturation factors of the form (x/K_x+x) were strung together in various combinations, depending on the number of resources that the modelers wanted to take into account for each biological constituent. In the Tocks simulation, the biological constituents were: "Algae, Zooplankton, Fish 1, Fish 2, Fish 3, and Benthos."

The *algae* were represented as responding to light intensity (L), and concentrations of carbon dioxide (C), nitrate (N), and phosphate (P), as resources. Thus the full equation for the gross growth rate of the algae was:

$$\mu_A = \mu_{A,20}\Theta^{T-20}\left(\frac{L}{K_L+L}\right)\left(\frac{C}{K_C+C}\right)\left(\frac{N}{K_N+N}\right)\left(\frac{P}{K_P+P}\right) \qquad (9\text{–}4)$$

The zooplankton were modeled as responding to the concentration of algae (A):

$$\mu_z = \mu_{z,20}\,\Theta^{T-20}\left(\frac{A}{K_A+A}\right)$$

The growth rate of *fish 1* was modeled as responding to the concentration of zooplankton; *fish 2*, responding to zooplankton; *fish 3*, responding to benthos; and *benthos*, responding to sediment. Some ecological detail was added for the fish group in that their growth was stopped whenever conditions were outside that group's range for temperature or oxygen tolerance.

There is a nonnegligible literature in agreement with the claim that Monod kinetics of the form of equation (3) are adequate descriptions of the growth of phytoplankton when limited by a single factor, but the claim that the saturation effects of several factors are multiplicative, as in equation (4), is unsubstantiated.[44] Moreover, while many simple equations for population growth do a tolerable job of modeling both the initial rapid growth of an uncrowded population and the slower growth that accompanies crowding,[45] these equations are opaque with respect to the crashes, oscillations, or equilibria that in real populations follow the phase of sigmoid population growth.[46]

In the model of equation (3), gross growth saturates at a constant positive rate in the presence of an excess of nutrients (or other potentially limiting factors), and declines to zero as the critical factor is exhausted. No level or combination of critical factors in the Monod terms can make a *negative* contribution to population growth (i.e., can cause population decline) nor can the stoppage of growth described for the fish. The population can diminish under the influence of the same sources of attrition that were operating during the period of population growth (the constant per capita mortality and the removals due to predation), but the model makes no provision for any group's really getting clobbered by environmental deterioration.

So we find no a priori justification for the equations except as very rough—and questionable—guesses.

oxygen content, and assorted nutrient concentrations. The interactions may be quite complicated, as in phosphorus metabolism: all algae can absorb and release phosphate, and, in addition, at least some algae can excrete organic phosphorus compounds which can combine with other compounds in the water to create a colloidal phosphorus component.[48] There are interconversions between particulate and dissolved organic and inorganic phosphorus in water, mediated in part by free enzymes released by some organism(s).[49] Even what we commonly suppose to be strictly physical phenomena, such as diffusion of certain gases at the water surface, may be affected by compounds of biological origin.[50] In short, the dramatic change of character in a body of water undergoing eutrophication is a process in which dramatic species differences play a critical role. An analytical model of lake eutrophication that does not include the effects of these differences is immediately suspect.

There remains the matter of spatial representation. Treating the lake as a series of horizontal slices, where lateral differences within a slice can be ignored, is equivalent to assuming instantaneous and perfect mixing within each slice. This assumes, for example, that any nutrient input from a point source is immediately diluted over the entire length and breadth of the lake.

Let us remind ourselves that the intended reservoir will be 37 miles long and about two-thirds of a mile wide; that there will be a major backwater where the present valley has a Y-shaped configuration; and that the preponderance of the nutrient input will enter the lake from the upstream inlet and a small number of local sources, such as sewage treatment plant outfalls or streams draining areas with a heavy nutrient burden.

The rates of biological uptake of nutrients are very fast—particularly for phosphorus, which is likely to be the key nutrient in determining water quality.[51] For example, a stand of the plant Callitriche can reduce the phosphorus concentration in the water from 2.05 to .01 mg/1 in one hour.[52] A good portion of the phosphorus absorbed by phytoplankton gets sequestered in the lake sediments in a short time.[53] The only common circumstances under which phosphorus is released from sediments in significant amounts is when the lower water layers are so depleted of oxygen as to present a chemically reducing environment. In shallow bodies of water, this would tend to occur as a consequence of the rapid deposition of organic detritus associated with high rates of algal production, so in this manner eutrophication can be an interestingly self-aggravating condition. These properties of phosphorus mobilization in lake systems, combined with the expected geometry of phosphorus input, make it certain that quite severe local manifestations of eutrophication would appear long before the lake as a whole were so afflicted.[j] More bothersome from the modeling point of view is the likelihood that these local problems could erupt under a total nutrient budget that would result in perfectly acceptable water conditions if the input were evenly distributed over the lake. This kind of eutrophication would be undetectable by the present sort of one-dimensional model.

By now the reader may be wondering why the WRE model, if it is as improbable a conglomeration of wishful thinking and misrepresentation as I have made it out to be, did not generate projections that were immediately recognizable as nonsense. Answering this question will illuminate the manner in which the coefficients (i.e. the various constants in the equations) were actually arrived at.

The modelers had at their disposal two main sources of data: published accounts of the course of eutrophication and recovery in Lake Washington, near Seattle; and the results of some experiments carried out previously (for quite different purposes) in four two-acre ponds near the proposed dam site.[54] The biological component of the model involved a full 57 coefficients. Justification of the form of the model, and establishment of appropriate values for the coefficients, clearly could not be accomplished on the basis of casual experiments in little ponds. So, to keep the model from behaving outrageously, the limited data were used *twice*.

First, the data were used to make some heroic assumptions about the initial values for the coefficients—as if the model, indeed, were of the analytic sort. Next, during the course of a series of trial runs of the model, the coefficients were subjected to ad hoc readjustments to make the output look more plausible. The contemporary euphe-

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[j] On a larger scale, this phenomenon is known to occur in Lake Erie, where the western basin is considerably more eutrophic than the eastern basin, and in some portions of Lake Michigan, such as off Green Bay.

misms for this kind of tinkering are "model calibration" or "tuning." What this actually accomplishes is the removal of a potentially useful means of checking the soundness of the model. If, on the basis of independently arrived at coefficients, a model generates crazy predictions, this should alert a circumspect modeler to the possibility that the basic form of the model is incorrect.[k] If instead the modelers juggle coefficients until the output looks right, the model loses its analytical character.

It is no great surprise that the output *can* be made to look right. With so great a number of coefficients decoupled from independent verification, the "model" becomes nothing more than a clumsy curve-fitting device—it could just as well be fitted to the record of the last eleven months' Dow Jones averages or the incidence of miscarriages in China. Thus the fact of a decent fit between model output and the data used to "calibrate" it in no way validates the model as a predictive device. Worse yet, the fact of such tampering with the coefficients makes it impossible to use the test cases in attaching objective confidence limits to the model's predictions: the test cases get swallowed up in adjusting the coefficients. The irony of this is that the model becomes such a tangle that even if it were producing correct predictions we would have no way of knowing it.

Let us, for the moment, forget the model's obvious failings as an analytical model, forget mechanisms, and forget the silly game of attaching ecological names to the mathematical components in the model. It is quite possible, for all the complexity of the underlying biology, that cultural eutrophication, in most cases, is driven by a few simple environmental variables. In fact, we already have every reason to believe that phosphorus load is the major determinant in a lake such as Tocks.[55] Vollenweider's simple empirical model, as described earlier, capitalizes on just this. What if the WRE enterprise blundered into an unnecessarily complicated way of representing a "black box" relationship between phosphorus and eutrophication? If Vollenweider could do it with a sheet of log-log graph paper, a team

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[k] The computer's ability to keep track of many simultaneously interacting components of a model permit an application that is probably of greater present importance than ecological prediction; namely, theory testing. One may treat the model itself as a hypothesis, and the test of that hypothesis is the fit of the model's predictions to observed results. If the fit is poor, one then knows that something is wrong with the model: perhaps there are more causal processes importantly involved that were taken into account, perhaps one or more of the formulas representing a causal relation is incorrect, or perhaps the scheme for integrating the effects of the component processes is mistaken. Each of these possibilities can lead to hypotheses which themselves are subject to test, so that with care, much may be learned.

of consulting engineers might well be able to do it with a computer and a lot of money. Only now the "kinetic principle" and "algae" and "coefficients" just appear as decorative flourishes and our appraisal of the reliability of this model, as of Vollenweider's model, rests entirely on how well the output of the model as a whole has conformed to the relevant facts.

Vollenweider's collection of facts from nineteen lakes did not seem the sort of thing we would really want to bet on. The WRE collection of facts from one lake and a few ponds is even less convincing, though the model's predictions might still be correct more often than not—and then again they might not be. Whether they are or not can only be settled by the model's eventual record of successes and failures after a substantial number of independent trials at predicting data that had not already been absorbed in calibration. In the meantime, the computer does not know very much.

V. HOW NATURAL IS NATURAL?

All sides of the Tocks Island Dam controversy claim to be sensitive to what is "natural." This should not surprise us. Since the Enlightenment, there has existed a fairly continuous Western tradition of identifying the "natural" course as preferable where alternatives exist, though of course there is equal continuity to the notion that life in the state of nature is "nasty, brutish and short."

The unofficial National Park Service plan for a Delaware Water Gap National Recreation Area, *without a dam*, presented in a twelve-page illustrated brochure, uses the words "natural," "naturalness," or "naturalistic" seven times; the title itself reads: "A Natural System Plan for Delaware Water Gap National Recreation Area." The fifteen-page illustrated brochure prepared by the architecture firm, Clarke and Rapuano, and commissioned by the Corps of Engineers, "Tocks Island Dam: A Plan for Its Architecture and Development," uses these words nine times. These words have no special technical meanings: scientists use them no differently from laymen. But the Park Service and the architects do not mean quite the same thing, and other partners to the controversy use still other meanings.

There may be a constituency of hard core conservationists who really think that a "natural" landscape is one that is literally virgin. One consultant's description of the Tocks Island regional setting evokes this meaning (we don't know if it was intended): " . . . the reservoir site, recreation area, and surrounding study area encompass beautiful and unspoiled lands which appear to have been overlooked by development that has occurred around them, and which remain virtually in their natural state."[56]

Of course, the area is far from untouched. In all probability, the area was commercially logged in the early seventeenth century and has been very much under the hand of man ever since. In addition to continued timber operations and replanting with coniferous trees after the hardwoods were removed (or died of disease), there have been coal mines, iron mines, and extensive clearing of land for farms, which were later abandoned. The National Park Service's survey of the area, in fact, lamented past mismanagement of the forests and its effect on the present-day second growth.[57] Nor have human influences been confined to the exploitation of resources. The National Park Service identified a grand total of 32 "historically significant" structures that it planned to remove from the area that would be inundated by the dam.[58] These were to be relocated to sites within the recreation area including "a restored village, an early farm complex, a community grouping and an interpretive motor trail."

So, generally, if the meaning of the "natural system" argument refers to preservation of virgin territory, it has no basis in fact in the Tocks case. But that doesn't necessarily stop such usage. For example, the language of the decision of the DRBC, in 1968, to include "the preservation of Sunfish Pond in its natural state" among the "environmental standards" of its comprehensive plan suggests a token gesture of appeasement to a demand that portions of the landscape be held inviolate.

The primary concern of the Park Service in the Tocks area is recreation, rather than preservation of "wilderness." The Park Service regards fishing, hiking, and sightseeing as appropriate to the area, and these are consistent with treating the landscape as a renewable resource. The Park Service espouses an implicit recreation ideology in which the most worthy activities are those that are "natural" in the setting where they take place. Thus activities and setting are planned jointly.

The Park Service's original 1966 Master Plan for the recreation area designated 42 percent of the acreage as "natural environment," which would receive "little development." The predilection to *manage* the landscape is evident even in the Natural History Survey, where it is noted that the deer and beaver populations will have to be "controlled" in the Tocks area, while the present scarcity of biting insects is taken as an omen that these will not require control. The preservationist leanings in this report surface in the discussion of the abundant rattle snakes and copperheads:

> The presence of these snakes in the area should cause no alarm. The incidence of snake bite in the area is very low and death from snake bite almost zero. However, it would be wise to locate as many of the dens in the area as possible. The purpose of this would not be for possible extermination of the species. They fit in their own ecological niches and are very interesting animals that are favorite animals for study by a considerable group of naturalists. It would be wise, however, to locate children's camps, hiking trails, and bridle paths at some distance from known den areas. . . .[59]

The implication that the annoyance of numerous biting insects would justify control programs, while literally poisonous snakes are to be left alone because some people like to look at them, illustrates that the Park Service is not committed to preservation per se, but perceives itself as serving a variety of constituencies. Even in the Park Service's "Natural System Plan" for a recreation area without a dam, there are plans for *modifying* the river:

> To increase the usefulness of the Delaware River for water sports without unduly sacrificing its naturalness, three low level weirs are proposed to increase water depth within the existing inner banks yet not preclude the use of the riverway for long-distance boating or disturb the fine riffles to which fishermen and canoeists are attracted. . . .[60]

In the language of the Park Service the "natural" may be "enhanced" or "restored" as well as "preserved," and the decisions to enhance, restore, or preserve depend upon judgments of "highest and best uses."[61]

The architects' usage of "natural" by contrast seems defensive and a bit cynical. In places, one senses that they are more concerned that their product be natural-looking than that it be "natural." In essence they are trying to argue that the dam will not be an eyesore. For example:

> In the proposed plan for its architecture and development, Tocks Island Dam will serve as a transition buffer between the two landscapes, the intent being to make the dam an intrinsic element of the new natural scene, just as the farmhouse, barn, silo and other works of man became a part of the valley's agricultural scene. This intent will be realized in a naturalistic park and through architectural designs that de-emphasize the

> purely mechanical functions of the dam structures, bringing them into scale and harmony with the natural setting.[62]

Their plan shows credit-worthy cosmetic intent: transmission lines are placed underground, and stone excavated from the dam site is used to face the powerhouse and visitor center (to "establish a continuity between the structures and the environment").[63] However, that the dam itself will be an "intrinsic element of the natural scene" is a strange claim for a rockpile whose exposed portion, about 80 feet wide and 45 feet high, will stretch straight as an arrow the full 3,000-foot width of the valley floor, with a fenced-in walkway or roadway across the top.

The extreme manifestations of the "natural-looking" as a palliative in the absence of the "natural" are the likes of "wood grain" formica table tops, which fool no one. Perhaps people have a psychological need to see "nature forms," and this need can be satisfied by artificial mimics as well, or almost as well, as by the original objects. Or perhaps the mimics do not really satisfy the basic need, but they serve as soothing reminders of some past pleasures which have been displaced by "progress"; in this sense the mimics may pander to sentimentality. The distinction between the natural and the natural-looking is evident in the way the body of water behind the dam is described by the two camps: those in favor of the Tocks Island Dam speak of a "lake" or even "mountain lake," while the environmentalist groups steadfastly use the word "reservoir."

The insistence on this language is related to a deep moral issue. The despair and fury of the hard core environmentalists is caused by their sensing that people probably *will* enjoy the artificial lake—and artificial grass, and artificial trees, and artificial anything else. The environmental critique of western civilization is not directed simply at cleaning up the litter and making sure there will be fish for the fishermen. In fact, it is a moral indictment of an entire way of life. From this perspective, environmental problems are evidence of moral failures—failures of self-discipline, failures of humility, failures of respect for nature—symptoms of a system that is considered heedlessly exploitative of both men and nature.

In this view then, token "real" parks or artificial surrogates, and patchwork ameliorative programs to clean up one sort of "pollution"[l] or another, are all fraudulent attempts to disguise the fundamental

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[l] The more archaic usage of the word pollution in reference to moral defilement is a reminder that the remedies to pollution are not necessarily technical.

problem, and are accomplices to the problem to the extent that they divert energy away from basic social change. Consider, for example, Marcuse's assessment:

> . . . The issue is not to beautify the ugliness, to conceal the poverty, to deodorize the stench, to deck the prisons, banks and factories with flowers. . . . When people are no longer capable of distinguishing between beauty and ugliness, between serenity and cacophony, they no longer understand the essential quality of freedom, of happiness. Insofar as it has become the territory of capital rather than of man, nature serves to strengthen human servitude.[64]

Another clue to the normative, quasi-religious aspect of the "natural system" issue is the way the word "integrity" is used. The stated objective of the Federal Clean Water Act of 1972[65] was to "restore and maintain the chemical, physical and biological integrity of the nation's waters." In the Tocks debate, one of the documents from the United States Department of the Interior Bureau of Sport Fisheries and Wildlife listed ten "recommendations for environmental integrity."[66] Although the document does not define *integrity* explicitly, it is clear that the word is doing double duty, meaning both functional completeness and genuineness or trustworthiness. The functional interpretation is remarkably clear in the language of the House Public Works Committee analysis of the Federal Water Pollution Control Act amendments of 1972, where it is noted that "natural systems" have self-regenerative and self-regulating capacities that may not survive some kinds of disruption. In this sense, the integrity of a natural system is preserved so long as these homeostatic functions persist.

The broader normative sense of environmental integrity, a sense of "oneness" and "wholeness" about nature that reflects mystical attitudes, appears in the Code of Ethics proposed by the Ethics Committee of the Ecological Society of America. (The association is not accidental, as it is a fact of ecology that everything is connected to everything else in a way that is often important to scientific understanding.) The code exhorts the Society to use professional expertise "to find ways to harmonize man's needs, demands, and actions with the maintenance and enhancement of natural and managed systems."[67] How easily a consequentialist concern shades into a value position, without benefit of even a change in vocabulary!

People have tried to calculate the worth of a given natural system in terms of services it can perform, such as the cycling of critical elements, tertiary waste treatment, water retention, timber production, and provision of recreational resources.[68] The ideas behind this sort of accounting are straightforward, but actual analyses, as a rule, do not stand up to close examination. First of all, the basic numbers available (for example, rates of nitrogen fixation per acre of swamp) are not reliable. Second, utility functions are generally arrived at by estimating the cost of performing the same service (such as reducing the same quantity of nitrogen by industrial means) without regard for how much of the natural service really is of any utility, or whether the service might be obtained at lower cost by returning some *developed* plot of land to a functionally natural state. Both these problems, however difficult, are amenable to scientific inquiry.

Of less certain scientific status are the ecological domino theories —claims that apparently minor initial disturbances will propagate themselves through an ecosystem to emerge as literal catastrophes. Things like this do happen: food chain amplification of the effects of some biologically concentrated toxins are a good example. The trouble is that such phenomena, while more or less explicable once they have taken place, are not predictable in advance.[m] No one knows *which* new pollutants or new industrial or agricultural developments will instigate dramatic second and third order effects, and which will have ecological effects limited essentially to the primary perturbation. All we know is that such things have happened, and that they were unwelcome surprises at the time. These kinds of worries are consequential in that they refer to outcomes that are fairly unambiguous in their desirability or undesirability. But as they deal in hypothetical outcomes that are not very predictable, they give rise to decision making problems that hinge not on scientific issues but on risk taking attitudes, so they will become incorporated in arguments for or against preservation of the "natural" that reflect hopes and fears whose origins are in other matters.

We can easily see that a pessimistic view of the unpredictable consequences of ecological intervention, combined with a susceptibility to the mystic unity of ecology, would engender ineffable religious feelings about the value of the natural and the horror at destroying it. In this usage, the meaning of "natural" becomes imbued with a very personal vision of what the world should be like, and purely utilitarian discussion becomes unacceptable.

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[m] Actually, ecological processes are so complicated that after the fact explanations may also be confounded. Even phenomena that are known to be recurrent may defy precise explanation—the population cycle of the lemming is a classic example.

VI. CAN WE SAVE OURSELVES FROM THE EXPERTS?

The present functioning of ecological expertise is an embarrassment to professional ecologists; but this is merely an irritating contradiction in a self-image shared by a very small interest group. The serious societal issue is whether ecological expertise, as it is currently employed, leads to better or worse decisions, and, more broadly, whether it leaves society better or worse off.

From the standpoint of the truly disinterested decision maker, with no particular scientific background of his own, the effect of ecological expertise on the outcome of the decision process may well appear to be nil. As long as spokesmen who can pass as ecological experts of superficially equivalent credibility are to be found on both sides of nearly any environmental controversy, they cancel. In individual cases, technical expertise of this sort is simply a political resource whose utility to the interested parties depends on the wisdom of the strategy determining its deployment. If all sides have more or less equal access to this resource, and exploit it with about equal intelligence, perhaps no major harm will accrue.

Unfortunately, the ideal of equal access does not often obtain, for technical expertise, like legal expertise, is expensive; and usually, if one party in a political controversy resorts to technical experts, then the other parties must do likewise, for tactical reasons. Where some groups are less able to afford this expenditure, a round of obligatory expertise can have antidemocratic consequences. In the Tocks Island Dam controversy, one can see how the minimal cost of effective participation has been steadily raised. When it was just a matter of one expert's "expert" opinion against anothers, the pro bono efforts of college professors, on the witness stand and in the media, could often equalize things. When concrete analyses began to be issued, a complete counteranalysis was required, entailing tens, perhaps hundreds of highly specialized man-hours, and attendant hardware, supply, and overhead expenses.

This is an especially acute problem with proprietary computer models, for these are so easily shrouded in highly idiosyncratic mummery that any group wishing to "cross-examine" a model's output will need an expert programmer and considerable amounts of machine time just to find out what the model is—assuming they can get their hands on a complete deck or listing. Then they will need recourse to scientists with state of the art status (or at least reputations) to find out in what ways the model does or does not make sense. This is well beyond the capacity of most citizen groups, and it represents more time and money than can routinely be expected as a donation from individuals or private institutions. So the group that can afford the first really messy computer model supporting its position in a given controversy has an edge. Generally, the advantage will lie with project promoters.

What can be done about this? The cheap tactical response is simply to debunk all expertise from a position of nonexpertise in the hopes of neutralizing the expert testimony without incurring a like expense. The danger is that overuse of this tactic, if successful, will ultimately contribute to a political atmosphere hostile to all rational analysis. On the other hand, moderate "pedagogic" employment of the debunking tactic could result in a mood of healthy skepticism among decision makers and the public, but it is difficult to know in advance where the fail-safe point lies.

A more cautious approach would be to build the skepticism into the decision making process. Our legal system embodies one archetype of institutionalized skepticism. Perhaps the rules surrounding the use of expert witnesses in court could be adapted for broader forms of decision making.[n] A reasonably simple checklist of questions could go a long way in helping decision makers, analysts, and interested parties demystify spurious models.

As regards the delay attendent upon the use of technical expertise in an environmental controversy, this is not unmitigated waste, for during this period significant political processes will be underway. This is the time when allies are gained or lost and political momentum maintained or dissipated, as the interested parties persevere in repeating and refining their respective inputs to the various loci of power that effect public decision. This is probably a healthy process.

We recall in this respect now some of the peculiarities of the Tocks controversy, especially as described in the first essay in this volume. We gained the impression that there was a deep level of poorly articulated concerns that involve pervasive value differences, and that this was linked to a tendency for the ostensible objects of debate to function as symbols of the actual tacit concerns. Conceivably, the underlying value positions, which now seem so badly served, are in fact so hazily perceived, even by the individual, that it would be a grave mistake to try to act politically on their promptings in other than an indirect, incremental fashion.

Imagine, for example, holding a national plebiscite on the

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[n] A discussion of the traditions relating to the use of expert witnesses is presented by Sive,[69] who incidentally, argues in favor of greater flexibility in the use of expert witnesses in environmental controversy, whereas I am arguing for more strictness. (Politics, bedfellows, and all that.)

question of "economic growth." At the moment, the prevailing level of political consciousness on this issue simply is not prepared for such a confrontation. Not only is there no effective consensus, there are hardly any sensible ideologies—just disjunct attitudes toward the likes of progress, pollution, and wilderness, which, however intensely felt, are not integrated into a meaningfully complete vision of the life styles and types of social organization actually required to satisfy one set of preferences or another. All we find are collections of half-believed slogans—the old ones clearly out of tune with the times and the new ones insecurely held for lack of a palpable tradition within which they could make sense.

When the political alternatives are so unsettlingly nebulous, delaying the decision with the reassuringly familiar public ritual of college professors and engineers contradicting one another provides a salubrious grace period within which support can crystallize around more coherently developed political positions, or within which conventional political forces can reassert themselves. Thus society may benefit even from the employment of ineffectual expertise.

It is tempting, of course, to look for ways to improve the expertise itself. To some extent this will occur inevitably, at a rate commensurate with the progress of the relevant sciences, though with a persistent lag in content. As for talk of quality control within the professions, it is hard to imagine how that can affect the existing incentives for shabby work, or prevent the appearance of official-looking "professional societies" whose functions are purely defensive, while giving a misleading appearance of legitimacy and regulation in exclusive areas of lucrative pseudoscience.

VII. EPILOGUE

Even though environmental issues figured prominently in the pageantry of visible debate in the Tocks controversy, ecological expertise was not instrumental in the decision process. In the one instance of a technical environmental issue that did seem to matter—the likelihood of the eutrophication of a lake—the ecolocical experts simply did not deliver the goods. It seemed that the readily available expertise "on tap," as they say, was not capable of providing a convincing prediction.

The specific matters that are, or might be, effectively attended to by competent ecological experts are necessarily questions of fact that may be far removed from what is really bothering people who participate in the controversy. The underlying concerns of participants are often questions of taste or value, and a conflict over these cannot be resolved simply on the basis of what is true. At best, these will be resolved on the basis of what is fair, and at worst, on the basis of what the decision makers can get away with.

People are worried over the style of life that building or not building the dam portends for themselves; the style of world it will leave for their grandchildren; and the style of decision it implies that "they," as a society, made, compared with the style of decision they prefer to think of themselves as making. Behind all the quasi-scientific frills of environmental debate there are basic questions of what is a good society and what is a good life. Actors in the drama are motivated by usually unexpressed hopes and fears: dreams of a technological city of Oz as opposed to Arcadian longings, desires for a more rational social order versus Orwellian nightmares, entire covert Utopias built around preferred visions of growth or stasis, progress or conservation.

An application of ecological expertise to specific and circumscribed projects will contribute little to the resolution of these fundamentally social questions, beyond perhaps clarifying some of the rhetoric. When global scenarios, rather than specific projects, are the *explicit* focus, expert analysis, at least in principle, again comes into its own. Thus the recent Club of Rome efforts may be understood as attempts to confront questions of the technical feasibility of various visions of the future. The sort of question at issue in the Tocks debate was not, for example, whether the shad will continue to migrate up the Delaware; and it certainly was not whether we could design a scientifically managed shad stocking program. Given some possible threat to the shad, decision foundered on the questions of how much we care, and why, and how many of us do and how many of us don't. Before we expect too much from the ecological experts we should try to be certain which questions we want answered.

NOTES

1. Appropriate design specifications are discussed by P.J. Dalley, "Reevaluation of fish passage facilities related to Tocks Island Dam and Reservoir," report of the U.S. Department of the Interior, Bureau of Sport Fisheries and Wildlife, June 1971 (memo).

2. Corps of Engineers, *Tocks Island Lake Development: A Comprehensive Evaluation of Environmental Quality. Delaware River Basin, Tocks Island Lake, Pennsylvania, New Jersey and New York; Delaware Water Gap National Recreation Area, DWGNRA, U.S. Department of the Interior, National Park Service; Kittatinny Mountain Project, Sponsor: New Jersey Electric Utilities, Assoc. Agencies FPC and DRBC* (*Department of the Army*, 1971).

3. T. W. Robbins, M. S. Topping, and E. C. Raney, "Studies of fishes in the Muddy Run pumped storage reservoir and connecting waters, a summary," 1970. Ichthyological Associates, Miscellaneous Report No. 4.

4. Dalley, *op. cit.*

5. Both the Corps and the Fish and Wildlife Service acknowledged the uncertainty, but both were optimistic about the prospects; e.g., Dalley's (*op. cit.*) "Summary and Conclusions" read simply "It is concluded to be feasible to pass American shad and other migratory fish over the Tocks Island Dam and through the reservoir . . ." Conservationists, including some biologists among them, took a dimmer view; e.g., the letter from E.E. MacNamara appended to the Sierra Club response to the Corps' 1971 *Environmental Impact Statement* (published with that statement).

6. W.H. Massman, *Analysis of the River Fisheries*, Bureau of Sport Fisheries and Wildlife, June 1971 (memo).

7. R.M. Jenkins, *Tocks Island Reservoir Fishery Analysis*, Bureau of Sport Fisheries and Wildlife, June 1971 (memo).

8. State of Delaware, Department of Natural Resources and Environmental Control, letter (June 4, 1971) in response to the Corps' 1971 Impact Statement, appended to that Statement.

9. D.W. Slater, W.T. Olds, Jr., W.H. Massman, R.M. Jenkins, P.J. Dalley, G.G. Taylor, *Fish and Wildlife Aspects of Tocks Island Reservoir and Related Developments*, June 1971 (memo).

10. Roy F. Weston, Environmental Scientists and Engineers, *Tocks Island Region Environmental Study*, W.O. 256-03 (April 1970).

11. "An appraisal of the potential for cultural eutrophication of Tocks Island Lake" Jack McCormick and Associates, Devon, Pa, Sept., 1971.

12. "Ecologic Simulation, Tocks Island Lake" D.J. Glanz, G.T. Orlob, and G.K. Young, Water Resources Engineers, Springfield, Virginia, February, 1973.

13. E. Mayr, E.G. Linsley, and R.L. Usinger, *Methods and Principles of Systematic Zoology*, (New York: McGraw-Hill, 1953).

14. C.B. Williams, "The range and pattern of insect abundance." *American Nature* 94: 137–151.

15. A.G. Fischer, "Latitudinal variations in organic diversity," *Evolution* 14:64–81.

16. G.L. Clark, *Elements of Ecology* (New York: John Wiley, 1954).

17. Fischer, *op. cit.*

18. M. Kozhov, "Lake Baikal and Its Life," Dr. W. Junk, The Hague, 1963.

19. H.L. Carson, D.E. Hardy, H.T. Spieth, and W.S. Stone, "The Evolutionary Biology of the Hawaiian Drosophilidae," in *Essays in Evolution and Genetics, in honor of Theodosius Dobzhansky*, M.K. Hecht and W.C. Steere (eds.) (New York: Appleton-Century-Crofts, 1970).

20. R.H. Whittaker, *Communities and Ecosystems* (New York: Macmillan, 1970).

21. N.G. Hairston, "On the Relative Abundance of Species." *Ecology* 50: 1091–1094.

22. C.O. Dirks, "Biological Studies of Maine Moths by Light Trap Methods," *Maine Ag. Exp. Sta. Bull.* (1937): 389.

23. "A Natural History Survey of the Proposed Tocks Island Reservoir

National Recreation Area," National Park Service document (apparently unpublished).

24. C.R. Darwin, *Origin of Species* (London: Murray, 1859).

25. A.J. Nicholson, "The Balance of Animal Populations," *J. Anim. Ecol.* 2(suppl.): 132–178: R.H. MacArthur, "Population Ecology of Some Warblers of Northeastern Coniferous Forests," *Ecology* 39: 599–619; S.A. Levin, "Community Equilibria and Stability, and an Extension of the Competitive Exclusion Principle", *Amer. Natur.* 104:413–423.

26. C.L. Prosser, and F.A. Brown, Jr., *Comparative Animal Physiology* (Philadelphia: Saunders, 1961).

27. For an intriguing example, see B.J. Rathcke, and R.W. Poole, "Coevolutionary Race Continues: Butterfly Larval Adaptation to Plant Trichomes," *Science* 187: 175–176.

28. The implications of this kind of process have been treated by L.B. Slobodkin in several articles: L.B. Slobodkin, "The Strategy of Evolution," *Amer. Natur.* 52: 342–357, and "On the Present Incompleteness of Mathematical Ecology," *Am. Sci.* 53: 347–357.

29. For an introduction to the use of "game" ideas in understanding evolution, see R.C. Lewontin, "Evolution and the Theory of Games," *J. Theoret. Biol.* 1: 382–403.

30. Notorious examples are chlorinated hydrocarbon insecticides and some radioactive fallout constituents. See J.J. Hickey, J.A. Keith, and F.B. Coon, "An Exploration of Pesticides in a Lake Michigan Ecosystem," *J. Appl. Ecol.* 3(suppl.): 141–154; W.C. Hanson, H.E. Plamer, and B.I. Griffin, "Radioactivity in Northern Alaska Eskimos and Their Foods," and D.C. Watson, W.C. Hanson, J.J. Davis, and W.H. Rickard, "Radionuclides in Terrestrial and Freshwater Biota," both in N.J. Wilimovsky and J.N. Wolfe (eds.), *Environment of the Cape Thompson Region, Alaska.* (Oak Ridge, Tenn.: U.S.A.E.C., 1966).

31. This particular account appeared in the *New York Times*, May 10, 1973, p. 63, "The use of DDT upsets nature's balance" and has, in a similar form, been popular on the conference circuit. I have not been able to find first-hand documentation of the entire story. Parts of it concur with the reports reviewed by G.R. Conway, "Ecological Aspects of Pest Control in Malaysia," in M.T. Farvar and J.P. Milton (eds.), *The Careless Technology; Ecology and International Development*, (Garden City, N.Y.: Natural History Press, 1972), a volume which, incidentally, is an excellent compendium of case histories of unintended, and sometimes surprising, results of various technological adventures.

32. M. Kimura, "Natural Selection as the Process of Accumulating Genetic Information in Adaptive Evolution," *Genetical Research* 2: 127–140; R. Levins, "Genetic Consequences of Natural Selection," in T.H. Waterman and H.J. Morowitz (eds.), *Theoretical and Mathematical Biology*, (New York: Blaisdell, 1965).

33. See note 12.

34. Glanz, Orlob, and Young, *op. cit.*, pp. 6–7.

35. Actually, this worry may have more to do with modeling, per se, than we at first suspected, if it turns out that all the filmflam of graphs, equations, and pages of numbers provides a ready camouflage for systematic deception with words.

36. "Report to the Delaware River Basin Commission on Sewage Treatment

Plant Effect on Eutrophication in Tocks Island Reservoir," *Water Resources Engineering*, (November 1, 1972).

37. R.A. Vollenweider, "Scientific Fundamentals of the Eutrophication of Lakes and Flowing Waters, with Particular Reference to Nitrogen and Phosphorus as Factors in Eutrophication," O.E.C.D. document, 1968.

38. R.G. Wiegert, "Simulation Modelling of the Algal-Fly Component of a Thermal Ecosystem: Effects of Spatial Heterogeneity, Time Delays, and Model Coordination," in B.C. Patten (ed.), *Systems Analysis and Simulation in Ecology*, vol. 3 (N.Y.: Academic Press, 1975).

39. Glanz, Orlob, and Young, *op. cit.*, pp. 8–9.

40. D.B. Mertz, "The *Tribolium* Model and the Mathematics of Population Growth," *Ann. Rev. Ecol. Syst.* 3:51–78.

41. C.S. Holling, "The Components of Predation as Revealed by a Study of Small Mammal Predation of the European Pine Sawfly," *Canad. Entomol.* 91: 293–320.

42. ———, "The Functional Response of Invertebrate Predators to Prey Density," *Mem. Entomol. Soc. Can.* 48: 1–85.

43. F.B. Turner, "The Ecological Efficiency of Consumer Populations." *Ecology* 51: 741–742;

J.T. Tanner, "Effects of Population Density on Growth Rates of Animal Populations," *Ecology* 47:733–745;

G. Caughley, "Mortality Patterns in Mammals," *Ecology* 47:906–918;

T. Park, D.B. Mertz, W. Grodzinski, and T. Prus, "Cannibalistic Predation in Populations of Flour Beetles," *Physiol. Zool.* 38:289–321;

P.W. Frank, C.D. Boll, and R.W. Kelly, "Vital Statistics of Laboratory Cultures of *Daphnia pulex* DeGeer as Related to Density." *Physiol. Zool.* 30:287–305.

44. E.D.S. Cormer and A.G. Davies, "Plankton as a Factor in the Nitrogen Phosphorous Cycles in the Sea," *Adv. Mar. Biol.* 9:101–204;

J. Caperon, "Population Growth Response of *Isochrysis Galbana* to Nitrate Variation at Limiting Concentrations," *Ecology* 49:866–872;

J.J. MacIsaac and R.C. Dugdale, *Deep-Sea Res.* 16:415—422;

R.W. Eppley, J.N. Rogers, J.F. McCarthy, "Half-Saturation Constants for Uptake of Nitrate and Ammonium by Marine Phytoplankton," *Limnol. and Oceanogr.* 14:912–920.

45. In fact, there are "too many" equations that will provide a fair fit in these circumstances, and it is seldom that any biological insight is gained from analysing which provides a better fit. See W. Feller, "On the Logistic Law of Growth and Its Empirical Verifications in Biology," *Acta Biotheor.* (A) 5:51–66.

46. A recent exchange concerning the effects of limiting factors on algae illustrates the confusion in inferring levels from rates. See W.J. O'Brien, "Limiting Factors in Phytoplankton Algae: Their Meaning and Measurement," *Science* 178:616–617; and M.G. Kelley, and G.M. Hornberger, "Phytoplankton Algae: Nutrient Concentrations and Growth," *Science* 180:1298–1299.

Attempts to apply analytical mathematics to population models usable beyond the sigmoid phase have largely proved a valley of no return. See P.J.

Wangersky and W.J. Cunningham, "Time Lag in Population Models," *Cold Spring Harbor Symp. Quant. Biol.* 22:329–338; and R.M. May, "Biological Populations with Nonoverlapping Generations: Stable Points, Stable Cycles, and Chaos," *Science* 186:645–647.

It is possible to construct reasonably accurate computer models for this sort of population projection, but the models are complex and their data requirements are monumental. See P.W. Frank, "Prediction of Population Growth Form in *Daphnia pulex* Cultures," *Am. Nat.* 94:358–372.

47. J. Shapiro, "Blue-Green Algae: Why They Become Dominant," *Science* 179:382–384;

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