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The goal of understanding in limnology

Part of the charm of science is its unpredictability
 R. MacArthur

Limnology has enjoyed a long tradition of progress based on thoughtful interpretation of empirical findings. New understanding has grown in part from refining the details of known relationships but more often from uncovering interactions and processes that were previously unknown. The field is divided at present into camps which pursue the study of integral properties like biomass, productivity, and nutrient fluxes, and those which study the biological entities at the level of populations or communities. The conceptual dichotomy is a split between primary attention to the laws of thermodynamics or to the law of evolution by natural selection. Current challenges require steps to bridge this unfortunate gap and to broaden the conceptual bases of all ecological studies.

In recent years ecologists have been presenting introspective examinations of their discipline at an alarming rate, as though practicing scientists need philosophical guidance (Platt 1964; Rigler 1975, 1982; May 1981; Paine 1981; Simberloff 1983; Andrewartha 1984). Readers are variously charged to follow prescribed methods of problem solving, to heed the apparently strong dichotomy between holism and reductionism, and sometimes to seek "predictive power" rather than causality and derivation. The issues have reached prominent proportions in ecology within the past decade, but limnology was never immune from the debate. Evidently G. E. Hutchinson unknowingly was stung by it during his tenure review when C. Juday argued that his theories about lake processes lacked the weight of real data tonnage (Hutchinson 1979, p. 246–247). In the later years of their collaboration, Juday and E. A. Birge had developed an approach based on graphical correlation and rigid empiricism. They and their colleagues surveyed hundreds of lakes

for properties like transparency, organic matter, and phosphorus. They then plotted them, either as frequency distributions or mean trend lines (e.g. Juday and Birge 1931, 1932; Juday et al. 1935) and *voilà*—*ex data venit veritas*. The approach persists for practical reasons and it continues to be the most sensible way to categorize masses of data.

What apparently got Hutchinson into hot water with some of the midwestern limnologists was his propensity to speculate and generalize beyond the data at hand. Years later the drive to comprehend empirical results in a broad conceptual context prompted one of his students to write "Scientists are perennially aware that it is best not to trust theory until it is confirmed by evidence. It is equally true . . . that it is best not to put too much faith in facts until they have been confirmed by theory" (MacArthur 1972, p. 253). Data and empirical correlations carry more force with inquisitive minds when explanations or derivations put them in a logical context. Perhaps that is why when the works of Birge and Juday are inspected in hindsight, the men are regarded less for their massive surveys than for their struggles with defined problems (Mortimer 1956, p. 206). Their scientific biographer nonetheless remarks (p. 198) "if the aim of limnology is the better understanding of the environmental control of living processes, it is a debatable point whether, for a given effort, more knowledge is to be gained by concentrating on a problem selected for one lake or organism, or by the wider survey." The data collected by those pioneer limnologists may yet achieve highest value in the hands of intellectual descendants who use them for temporal comparisons and investigations of environmental processes.

Adherence to rigid empiricism in limnology continues today, but the technical sophistication of the approach has advanced measurably. Today the trend lines

have been replaced with regression-based equations, and the visual impression of scatter is sharpened with statistical descriptions of estimation errors. Ever since Piontelli and Tonolli (1964) proposed a relationship between P-loading and retention of P in lake basins and Vollenweider (1969) modified the formula, there has been a succession of such equations. Inevitably as more and more data are produced, slopes, intercepts, or other parameters of the fitted model equations may change from the ones originally reported. Some of the changes may even be significant in a purely statistical sense. There remains a strong consensus in some quarters that these changes deserve broad dissemination because they mean that predictive capabilities have advanced. Often the improvement involves some model adjustments caused by addition of new data or by nonlinear transformations of the old ones, but the key virtue is that "residual uncertainty," in a statistical sense, is diminished. These iterations contrast instructively with the debates earlier in the century about the supposed heritability of IQ (Dorfman 1978). Cyril Burt was able to print many "improved" versions of the same correlation plot and each improvement attracted wide attention. What seems likely is that each new version of the data was greeted with anticipation not because the slope had one particular value or another, but because the *concept* was contentious and intriguing. Readers wished to learn if the notion of heritable intellectual capacity would be upheld or eroded by the new data.

The IQ results had consequences for social policy, and there are some parallels today in the application of limnological principles. I am often reminded by authors that "lake managers need to know" about an improved model fit, in order to predict the relation between P-loading and chlorophyll, for the public good. Often this is accompanied by plain or shielded hype that "predictive strength," in a statistical sense, is the goal of science and that terms like "understanding," "knowledge," and "insight" are merely tautologies of prediction. The claims help to draw a distinction between sources of ecological *knowledge* and avenues of ecological *understanding*. Many

aquatic scientists of this generation are justifiably drawn to practical issues like pollution, water supply, and fisheries harvests. This audience is the proposed target beneficiary of empirical prescriptions and improved formulas. If these masses could be furnished with equations that forecast all biomass categories in lakes from one measurement of total P alone, the argument goes, that would be service indeed. Too often these recipients are caricatured with an appetite for empirical knowledge and with a willingness to forego understanding. It seems fairly obvious, however, that if we do not know *why* a particular relationship conforms to the data, we cannot guess when it will fail or if the failure would be catastrophic. It is not unreasonable to suspect that the noble goals of applied ecology will be best served by continued basic inquiries into process and mechanism. The practice of fitting data with novel equations persists in the arsenal of ecologists because sometimes it opens paths of creative thought. Those thoughts and the understanding that may grow from them are what lead beyond the sterile exercise of numerical analysis to the substance that eventually fills the texts and review articles of the discipline.

There are no prescriptions for progress in limnology or ecology, although progress can be stifled by restricting the limits of creative thought. Those who embrace constraints crafted by others in the form of Popperian or hypothetico-deductive straightjackets may have divined a means to restrict their imagination, but there is no evidence in my view that those constraints encourage breakthroughs in biological sciences. Even though Darwin presented his efforts as the product of one who had carefully marshalled the evidence, laid out all the possibilities, and eliminated competing hypotheses, his notes and correspondences reveal considerable reliance on induction and intuition (Gruber and Barrett 1974; May 1981; Bartholomew 1982). Biological systems are characterized by nuances and complexities that trace to properties of organisms. Presence or absence of single species can make a difference to the organization of entire communities (Darwin 1859, Ch. 3; Paine 1966). Sometimes even well

planned perturbations of biological systems produce astonishing results.

The application of empirical equations to lake processes like eutrophication provides a good illustration of limitations in even this advanced and well respected endeavor. The model formulations do a good job of (statistically) fitting the overall variability in data sets that include lakes all over the north temperate zone. This is supposed to be of great applied value. It seems to me that in most applications the supposed users of the models are interested in the response of a particular lake, rather than the average response of world lakes. When Southern Indian Lake in northern Manitoba was manipulated for a hydro development project, for instance, good scientists armed with empirical models predicted the future phosphorus concentration by established procedures (Hecky et al. 1984) and the predictions were probably very accurate, even though it will take years to find out. The actual ecosystem alterations involved fishery collapse, unacceptable mercury contamination, and excessive shoreline erosion (Newbury et al. 1984). These things were not predicted because the possibilities were not a part of the model. The only thing a statistical or mathematical model can do is make evident the full range of possibilities presented in a set of formal assumptions. We are not talking now about a single response variable that deviates from expectation, but rather about system properties that were never regarded as "response variables" in the first place. A statistical model gives no clue where to look for the *unexpected* result; yet it is from such results that understanding grows most rapidly in ecological sciences.

Much of the growth in general ecological understanding comes from analog studies like the Southern Indian Lake example (National Research Council 1986). Before that work there were no comparable examples of responses by lake ecosystems to impoundment in permafrost regions of glaciolacustrine deposits. Perhaps some of the results seem obvious in retrospect, but that in itself is a sure sign of improved understanding. It is safe to assume that slight, albeit statistically significant, model adjust-

ments could improve predictions of the long term steady state levels of chlorophyll in Southern Indian Lake in proportion to altered nutrient income, but these improvements are intellectually trivial compared to the other lessons learned from the project. In short, limnology is progressing not by improved "fits" to established relationships, but by the fits and starts of uncovering new processes and previously unknown relations. That is the work of intellectual pioneers, and judging from our history, pioneers instinctively shun restrictions imposed by others.

What about the great body of "lake users" and "lake managers" who "need to know" the latest, best prescription for total P to biomass ratios or perhaps the best correlate for the square root of chlorophyll? The pursuit of such empirical relationships causes no evident harm, and it is one of many good first steps in organization and thought. Many of the pursuits, however, are bound to be intellectual deadends. During World War II, I am told, the army wanted a way to predict whether a recruit could succeed in flight school. After sundry questionnaires and correlation studies, they concluded the best predictor was the recruit's response to "Do you like Jello?" That sounds like the work of desperate men in desperate times, and maybe some lakes need the same heroics. Ad hoc constructs can serve a purpose, but they provide little foundation for understanding. In a scientific discipline where publication is treated not as a reward for work accomplished, but as a stimulus for new thoughts, such constructs are doomed to eventual obscurity.

What eventually replaces ad hoc empiricism are the results of work on general principles and discoveries of new ecosystem processes. Each natural or man-caused perturbation to a lake is to some degree a novel experiment because no two lakes are identical nor are weather and climate invariant. This is in part why individual lakes respond differently to changes in nutrient loading than one might guess from a regression assembled from many lakes (Smith and Shapiro 1981). Thankfully there are discernible trends in composite variables like total P concentration, chlorophyll, and Secchi

transparency, so that we may say "the average lake will have more than 10 mg m^{-3} Chl at this loading rate 60% of the time." Composite variables are the fodder of regression-based comparative models. By dealing with total particulate P rather than plankton species abundances, an investigator has the chance to rely on established principles of mass balance, conservation laws, and even the law of large numbers. For instance, even though individual species may differ in their cellular ratios of C:N:P, if you add enough of them together, the mean must converge on some number. Perhaps that is why these investigators favor strict adherence to Baconian dogma, logical positivism, or null model worship. The more closely a field situation can be crafted to mimic controlled, replicable laboratory conditions, the more likely a defined set of possible outcomes can be enumerated and tested. In the world of the ecologist and limnologist, however, as G. E. Hutchinson has noted, an investigator "may spend his whole life falsifying hypotheses and in the end discover he has learned nothing whatsoever about how the world actually works" ("Thoughts on Lake Benthos," February 1985, Ann Arbor).

Biological systems depend on evolution by natural selection, and the outcomes of that process are not always logically predictable in advance. It is hard to argue that most lake manipulations really promote evolution (to quote a creationist theme: "Sure, the plankton may migrate now, after the introduction of fish, but they are still just *Daphnia*; they didn't change into anything better!"), but manipulations can certainly lead to alternate communities constructed from a larger potential species pool. Processes operating at these population levels can confound the predictions of composite-based models. For instance, the rise of *Daphnia* in Lake Washington (Edmondson and Litt 1982) and Lake Michigan (Scavia et al. 1986) caused major changes in water transparency and chlorophyll levels, despite negligible changes in nutrient load. It may be comforting to "lake managers" to learn that the changes are still embraced by the broad confidence limits of existing trophic regression models, but that just

underlines an earlier point. Models can't predict anything that wasn't built into them from the start. Even the oft-cited "counter-intuitive result" is just the unrecognized consequence of the assumptions.

An apparent companion to the growing fascination and success with composite variables is the use of cell size or particle size as a scaling property in trophic models (Steele and Frost 1977; Carpenter and Kitchell 1984). Because various features of cell metabolism vary empirically with size, there is some sense that size structure can be introduced into models in meaningful ways. After all, size is an observable property of living organisms. It seems a simple extension of existing approaches to take total biomass or total particulate P and to apportion it among size classes. Then the dynamics of the size categories are estimated from sets of allometric relations. For instance, small particles are presumed to be grazed at faster rates than large ones, because there is a wider array of grazers available at small sizes, but small cells are also presumed to have higher maximum rates of growth. In short, an array of properties can be constructed that mimics the empirical observations that different size categories of the plankton wax and wane with time. There is even a tendency to generalize and say that large cells behave one way and small cells behave another. Often what is called a large cell is actually a colony or filament of small cells, but that doesn't matter if size is the property of interest.

The byproduct of this effort is the spawning of a horde of sleuths armed with log-log equations in search of parameters that describe all aspects of physiology and demography. The general trends in respiration, motility, and homeostatic costs with size are patently obvious and their elaboration fuels the quest. What lies ahead as a goal presumably is a characterization of lake communities by size frequency distributions and further predictions of composite variables like productivity or fishery yield. This work, like the study of total P or chlorophyll is far enough removed from the genetical properties of the biota to make it a plausible vehicle for engineering-type approaches. Perhaps empirical trends rely more on the

law of large numbers than on any laws of the living world. In a world where natural selection governs success, the game may include fewer allometric rules than it includes risks, tricks, and tradeoffs. The extent to which an individual species conforms to empirical, size-based models in its life history and growth strategies probably would not warrant applying these models at all. Biotic diversity represents the multiple results of novel solutions to both old and new challenges. It takes more effort to interrogate the real solutions crafted by real species, but the intellectual rewards of doing so are what have always drawn biologists to biology.

Enough writers have argued the inadequacies of physical science analogs in the context of biological problem solving (e.g. Bartholomew 1982 and references therein) that reiteration is unnecessary. Biological systems are characterized by sets of several solutions to a problem, rather than by a single, general solution. Recognition of this fact, more than any other, stands in the way of using composite variables alone as adequate abstractions of biological properties. The variables are nonetheless vital for studies of chemical properties and mass balance, so the cautionary note is in no way an indictment of their use. Sometimes, however, the draw of the physical sciences as a conceptual model for scientific thought is so strong that proponents explicitly ignore biological processes or pretend that they are intractable (e.g. Rigler 1982).

The growing recognition of individual physiological attributes of algae and their relation to ecological success represents a viable alternative to models based only on cell size, chlorophyll, or total phosphorus. Lakes supplied liberally with P and less with N eventually foster N₂-fixing cyanobacteria, not because of cell size, but because of cell physiology and metabolic pathways. Similarly, when Si is plentiful, P limitation is evident from abundant proportions of *Synedra* or, if light is limiting and turbulence is great, by *Melosira*. Application of size-structure models has more potential among zooplankton than phytoplankton. Demographic events like mortality caused by visual-orienting planktivores, or by gape-

limited invertebrate predators, are a demonstrable force in zooplankton communities. Among algae, however, it often seems that particular species prosper or decline not because they are large or small, but because they have some physiological attribute like obligate dependence on silicon, potential for N₂ fixation, or extraordinary ability to exploit a single resource. It is also evident that conceptual refinements in this field are in a vigorous state of growth (Reynolds 1984; Sommer 1985) and that it is becoming possible to characterize whole communities by attention to the properties of the organisms.

What, then, is the role of *understanding vis-à-vis prediction* in ecological science? Predictions seem to fall into two major classes. The first is based on direct experience. For instance, the phases of the moon can be predicted from the repetition of countless observations and from our innate conviction that past continua will endure. We don't regard it a major intellectual achievement to predict the night of a full moon or the date of a spring tide. Predictions that are restatements of observable, repeatable facts are the common stuff of everyday life. When we produce a bivariate plot of chlorophyll vs. total P based on extensive surveys, for instance, and then expect a new data point to fall somewhere within the existing scatter, we are engaging in this sort of prediction.

A different class of predictions arises from efforts to forecast the effects of manipulations. A well known maxim of field ecologists is "you have to perturb the system to understand it." Perhaps the perturbation involves nutrient addition, changes in hydrology, or alteration of a food web. It may be purposeful or unintended; in ecological systems it is common for more than one factor to be manipulated simultaneously. Experience plays a role here, too, because often a prediction is assembled by reference to related or analog studies in which other systems were subjected to the same type of manipulation. Regardless of the reasoning path, and regardless of what system properties are of interest, an investigator must ask if the forecasted results make sense in the context at hand. That question is vital,

because it is the ultimate criterion of quality assurance that the investigator can use. Measurements can be biased, important variables overlooked or ignored, and correlations can arise for spurious or accidental reasons, so if results arise without conceivable mechanism it is wise to evaluate both data and theory. Above all, such predictions force us to regard the world as a set of experiments in progress—on a variety of scales and degrees of manipulation. As ecologists we get to discover the nature of the experiment designs and measure the outcomes. This requires a view of the systems as dynamic entities, not as static ones. Static descriptions don't lend themselves to predictions about perturbations, or to the understanding that they provide.

Limnological understanding has grown remarkably since the time when Birge et al. (1927) fit "heat waves" to lake sediment temperatures and when Birge and Juday (1934) noted that the hydrologic renewal time of a lake "may have a more or less marked effect upon its productivity" (p. 446). Part of the understanding grew from interrogating the empirical results and finding their cause, much as Mortimer (1965) interrogated empirical temperature variabilities in Lake Michigan and sorted out the dominant modes of oscillation. But just as much understanding has grown from recognitions like those of Hrbáček et al. (1961) and Brooks and Dodson (1965) that species interactions mold communities in predictable ways or that the appearance of *Oscillatoria rubescens* signals deteriorating water quality in many north temperate lakes (Edmondson et al. 1956).

The challenge ahead seems to be in finding a way to align the dominant approaches of two schools of thought in limnology and oceanography. One group has focused on the thermodynamic constraints of mass balance, conversion efficiencies, and so forth. This is a school that measures composite variables like productivity, biomass, and turnover rates. Another school bases its studies on genetical properties of organisms, with attention to birth rates, death rates, and individual adaptations. Too often these schools find each other's efforts obtuse, uninteresting, or irrelevant. Both groups of sci-

entists, however, are pursuing excellence by their own definitions of the term. Presumably the goals and standards of excellence will merge only if tools and concepts of one approach engender a sense of new understanding across the discipline. Models based on composite variables are at a disadvantage in biological contexts because they can never address the fundamentally unique property of living entities, that of genetic integrity, so that the paradigms drawn from those models are intrinsically abiotic. New approaches based on integrating biological properties with community or food web dynamics have barely been exploited, but they hold excellent prospects for launching a new round of growth in ecological understanding. One present challenge is to produce biologically based representations which can satisfy the desires of some workers to predict composite variables like size classes of particles.

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