EXPERIMENTAL LIMNOLOGY

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Wise management of our freshwater supplies is a privileged obligation. We owe, therefore, thoughtful consideration to the growing problems associated with our aquatic resources so that future generations will not accuse us of careless damage to their heritage.

In order to utilize our lakes and streams efficiently, however, fundamental processes of aquatic environments and communities, their trends, rates, and interacting factors must be better understood. Results from studies in experimental limnology, in my opinion, will guide us toward intelligent use of lakes and streams. Moreover, these studies may give us knowledge for understanding the sea as well.

1. Experiments in lakes

I would like to summarize for you a trend in aquatic science which is designated as experimental limnology. It would be shallow indeed to attempt to review the vast modern literature in this brief essay. Instead, I have elected to abstract a selection of examples from our Wisconsin research program as illustrations.

The major emphasis of our limnological work has been away from the classical, descriptive study and toward experimental limnology which has been augmented by the development of modern apparatus and automation. In these studies, we have attempted to apply the methods of the experimental laboratory to the field as precisely as limiting circumstances permit.

In the late 1940's, interest developed in the possibility of using small lakes as experimental models for limnological studies. Cather Lake, in northwestern Wisconsin, was initially used for this study because it contained brown-stained water which prevented the full utilization of the sun's energy. Its limnological characteristics were measured from 1948 to 1949, and in 1950 commercial hydrated lime $Ca(OH)_2$ + $Mg(OH)_2$ was added in sufficient quantity to change the pH from 5.4 to 7.1 and the carbonates from 5.0 to 20 mg/L $CaCO_3$. A marked clearing of the water resulted, which enabled sufficient light to penetrate into the previously dark thermocline for photosynthesis. The lakes, so changed, could now support trout.

This before-and-after type of experiment was improved by concurrent observations on the two halves of an hourglass-shaped lake which was divided by an earthen barrier erected at the constriction (Fig. 1). To one of these lakes, Lake Peter, hydrated lime was added which raised the pH from 5.9 to 7.3. There was a 60% increase in the depth of the well lighted (euphotic zone) of the treated portion of Peter-Paul Lake, but readings taken 2 years later showed a total increase of 160%, a change from 2.7 to 7.0 m.

Subsequently, we found important differences in the plankton produced by the two lakes. We computed a turnover rate for the population of Daphnia of 2.1 weeks in the lime-treated lake and 4.6 weeks in the untreated twin, which suggested that the changed conditions were associated with a rapid increase in the size and rate of energy transfer of the population. Hence, this method of analyzing the effect was more dramatic, as well as more biologically realistic, than when the differences were measured by the conventional basis of standing crop only, an estimate which, when used, demonstrated very little influence of the treatment. There has been an increasing emphasis among contemporary limnologists on the importance of measuring rates of reproduction and less on the measurement of standing crop. The latter has little significance in the population dynamics and measure of energy flow through an animal community.

2. Cause and effect in Ecology

By adding hydrated lime to this lake, several changes were measured: (1) several ions, principally calcium and magnesium, increased in concentration, (2) the pH increased, (3) a significant amount of humic colloids were precipitated, hence the depth to which light penetrated was tripled, (4) new planktonic species of algae appeared, (5) the rate of zooplankton production more than doubled, (6) aquatic plants of the hard-water type, such as cattails, invaded and stand now in eutrophic contrast to its bog twin. In short, the changing of one factor induced a series of dynamic reactions.

The ecologist is often in a dilemma because he has been educated, in his developing years, to plan an experiment with adequate replicates, in which all factors are kept constant except one, alongside of which appropriate controls stand watch. A cleancut single-factor cause-and-effect result is the hopeful outcome. In nature, however, the interactions are too complex for a simplified one-factor deduction of cause to be assigned.

Events which occur in nature are seldom, if ever, related to or caused by a single factor but are owing rather to multiple factors which the organism or the community are able to integrate in order to produce an effect which, in turn, can be observed or measured.

When R. A. Fisher applied the methods of biometry to design of experiments on agricultural field plots, and their evaluation through multiple correlations, he performed an invaluable service to biology. In doing so, he broke with the traditions of experimentation which had been imposed by the exact sciences — namely, the manipulation, during an experimental series, of only one factor at a time.

In order to decipher cause and effect better in ecology and physiology, we need to develop new ways of dealing with the interactions of multiple factors. Often it requires special and broad preparation and also collaboration with others whose mathematical talents can serve in the solution of a problem.

While it is good policy to bring ecological problems into the laboratory for more careful analysis and under more exact controls, we are often perturbed by the variation even in these results. Biological processes possess, it seems, collateral or ancillary routes which lead to the same goal. Perhaps it is not so astonishing, after all, that we are often unable to relate cause and effect to a single factor.

Lakes Peter and Paul . . . . *Photo by Hasler*

3. Studies on ion transport

It is a well-known axiom in limnology that a lake is wasteful of the phosphorus that enters it via effluents from the surrounding drainage basin. In fact, the bottom water and mud of these lakes contain sufficient nutrients to bring them into an enriched condition, but, owing to the seasonal stratification of the water, nutrients accumulate near or on the bottom of the basin where they are unavailable to the aquatic organisms in the surface layers. Investigations have shown that most of the phosphorus, added to a lake, invariably collects at the water-mud interface where it is eventually incorporated into the mud.

Several years ago, I drew attention to the vast stores of phosphorus in Lake Mendota (1.1 million metric tons P under the 10 m contour) and re-emphasized how extravagant lakes are with the phosphorus they receive, and, in a later work, I proposed as a conservation measure that lakes might be refertilized with their own phosphorus. In an aquarium experiment, circulation of the water above phosphorus-rich mud with the aid of air bubbles showed that bubbles of compressed air would lift P^{32} from the bottom water to the surface. In practice, bottom deposits could be harrowed to produce clouds of sediment, while bubbles of compressed air could be simultaneously introduced into the hypolimnion in order to transport the phosphorus-rich particules to the trophogenic zone in a thermally stratified lake. In fact, in tests under summer conditions, we used air to transport deep (hypolimnetic) water up into the well lighted (euphotic) zone of a small experimental lake, Sawmill Lake, with a maximum depth of 7.1 m and an area of 1250 m^2. Air was delivered through small perforations spaced along the length of an air conductor which was suspended just above the lake bottom. The daily rate of flow was 101 L/m^3 of lake volume, under a pressure of 1 atm at 20C. An almost homoiothermal condition was observed after only 4½ hours of treatment. The concentrations of soluble phosphorus became isometric with depth. Prior to treatment, soluble phosphorus was found in typically high concentrations in the 2m to 3m zone. The absolute content of the total phosphorus in the upper 2m was higher in every case than the mean of the pretreatment values.

In an experiment conducted in Tub Lake (0.7 ha) in which lower daily rates of treatment (5.6 L of air/m^3 of lake volume) were used, radioactive phosphorus which had previously been placed in the hypolimnion could be brought to the surface, hence substantiating our suggestion that a lake's own phosphorus could be used to fertilize its surface waters.

Extending the use of radionuclides in experimental limnology, I proposed that lakes could be used as models of the sea in studies designed to study the physical-biological transport of nuclides in marine situations.

From preliminary studies conducted in a small, chemically stratified (meromictic) lake (Stewart's Dark Lake) in northwestern Wisconsin, we discovered that dipteran larvae transported measurable quantities of radioiodine (I^{131}) from the deep water of this lake to the surface and thence, as pupated flying insects, to the shoreline. The radioiodine was first detected in samples of adult midges collected in lighted shoreline traps 20 days after we had deposited it in the bottom water of the lake. It remains of course to be demonstrated whether vertically migrating marine organisms can do this in the sea; nevertheless, my thesis is here illustrated that a lake may serve as a miniature segment of the sea that can be subjected to experimentation.

The physical transport of nuclides within meromictic Stewart's Dark Lake was measured by using Na^{24}. The results of replicated experiments showed that radiosodium was transported horizontally in all directions from its release point deep within this small lake (of one hectare in area) at a maximum rate of about 16-18 m per day. Only slight vertical transport of the radiosodium was measured during the experimental periods.

Sodium-24 was also used to measure the physical movement in an ice-covered lake nearby Tub Lake in 1962. The results showed that the radiotracer (Na^{24}) was transported horizontally for a distance of 15-20 m during the first 24 hours of replicated experiments. These data furnish evidence that oxygen-bearing water can, at this rate of flow, supply eggs of fishes layed in the fall with the adequate metabolic requirements as they incubate on the bottom.

4. Scientific areas for manipulative or experimental research

These lakes were all on private property and were made available to us for experimentation without interference from trespassers. Our studies could hardly have been made on public lands because of legal restrictions or public interference. Their value to the experimental limnologist points up, therefore, the dire need in ecology to establish not only primitive areas but also scientific areas which are available for experimentation and manipulation.

A significant ecological advance was made in Wisconsin in 1951 when the Wisconsin Legislature created the State Board for Preservation of Scientific Areas. Botanists, zoologists, entomologists, foresters, conservationists, politicians, and nature lovers worked together to back the concept of scientific reserves under the leadership of an eminent ecologist, the late John T. Curtis. This agency was organized to foster the investigation of plant and animal communities in unique, natural areas in order to determine the factors necessary for their existence and to preserve their scientific and esthetic value.

When the Board is assured that an area of the land or water is unique as a scientific area and that it can be protected, it makes recommendations for management practices and enters the area on the official list of Scientific Areas under the jurisdiction of the University or Conservation Department. Every effort is made to find funds or legal means to acquire these areas. Some are to be made available for scientific study, experimentation, and manipulation; others are to remain untouched and to serve as baselines for future comparison and inventory.

The result of this united effort will benefit ecology for years to come. At the present time, there are over 40 scientific areas in Wisconsin — including prairies, forests, bogs, and lakes — which are available for scientific research, for teaching ecology, and for the preservation of rare or valuable plants, animals, and whole biotic communities. Recently an energized chapter of Nature Conservancy, under the leadership of Paul Olson, has been acquiring extensive ecological areas for University research. This is only a beginning. We must use our influence to establish scientific areas in all states and in other nations — especially in developing nations on other continents.

5. Plankton migration and aggregation of fishes

The zooplankters of the genus *Daphnia* comprise the bulk of the food of the white bass (*Roccus chrysops* Raf.) in Lake Mendota. We have correlated the presence of aggregations of *Daphnia* with the feeding behavior of the white bass. These pelagic fishes are attracted to aggregations of zooplankters found in foamlines, where air-locked *Daphnia* are abundant. Likewise, the pattern of feeding activity of these fish was shown to correspond with the morning and evening migration to the surface of *Daphnia*. Thus, to understand the diel periodicity of the white bass, an extensive study of the diel movements of *Daphnia* was initiated.

These studies led to the development of a new sampling method for estimating the rate of vertical movement of a planktonic population. We are now able to compare the rate of movement to various environmental factors. In most cases, a linear relationship exists between the rate of vertical movement and the rate of change in the logarithm of the light intensity. Migrating to the surface of the lake at both dusk and dawn, these *Daphnia* demonstrate precision in movement in relation to changing intensity, especially at dawn, when they reach the surface about 60 minutes following sunrise.

With the suggestion that light quality was important in the regulation of the diel movements of *Daphnia,* we have recently undertaken field experiments in order to clarify its role. Each cruise of an instrumented barge sampled, for comparison, the natural or reference population and the experimental population. Simultaneously, the experimental area was exposed to light and the plankton automatically sampled under these lights. In this manner, we have studied the effect of light, of restricted quality, on dark-adapted populations of *Daphnia*. In a similar fashion, we have observed the effect of an artificial change in the migratory behavior of Daphnia on the behavior of their predators, the white bass. By bringing the zooplankters to the surface with artificial light, the white bass respond by feeding on this artifically induced concentration of food organisms.

6. Summary

Theories evolved from surveys of large lakes and even in the ocean can be put to test by experimentation with small lakes. They can serve as models in such studies. Studies of process and the evaluation of interacting factors through surveys and inventory need to be augmented, however, by experiments with the lake itself. The manipulation of factors on a modest scale gives an insight into the dynamics of an aquatic community. Lakes where chemical composition has been changed artificially or where compressed air has been used to change the thermal stratification or where isotopes are planted for tracing are examples of the type of manipulations which produce effects that can be compared with prior studies of the same lake or preferably with similar undisturbed reference lakes.