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Oligotrophy: the forgotten end of an ecological spectrum

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Most studies that consider the relationship of diatoms and water quality have focused their attention on the questions and practicalities of water pollution or perturbations in some form or another. Many models and studies have demonstrated the environmental tolerances or changes in structure of diatom communities related to environmental challenges. This focus on the impacted end of the water quality spectrum has led, of necessity, to issues ultimately related to habitat restoration. We contend that a concentrated effort to develop more fully the theory and there is a need for practice related to oligotrophy, the other, ignored end of the water quality spectrum. We explore the historical usages of the term oligotrophy, as well as the challenges and promise of autecological and community approaches to understanding oligotrophy, and the possibility of focusing more on conservation rather than restoration in water quality issues.

Keywords: Diatom, water quality, oligotrophy, conservation

Some background

Oligotrophy refers to »poor food«, a situation where nutrients are in low quantity. The term has been used to describe a wide range of environments, including soils and other terrestrial environments (RAVEN et al. 2005), as well as almost all aquatic ecosystems; marine, estuarine and freshwater (HUTCHINSON 1967).

The meaning of low quantities of nutrients (including in some cases salts and other minerals) has become synonymous with early, primitive and natural conditions of freshwater. An exception is when oligotrophic conditions are culturally derived (»Cultural Oligotrophication« STOCKNER et al. 2000).

The concept of oligotrophy has been compared to eutrophy (»good food«), where systems have large quantities of nutrients (usually nitrogen and phosphorus). In the development of these concepts in limnology in particular, they were seen as a continuum from

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oligotrophy through an intermediate phase (mesotrophy) to eutrophy. Extremes of the ends of this spectrum (»ultra-oligotrophic« and »hyptereutrophic«) have also been recognized and discussed.

In addition to these concepts representing a continuum of conditions, they were also thought to represent an ontogenetic trajectory, with natural systems being oligotrophic and through development over time, naturally becoming eutrophic. This concept of lake trophy was applied widely to lakes (NAUMANN 1931; JÄRNFELDT 1952, 1953; RHODE 1969; HUTCHINSON 1969, 1973), and the ontogenetic sequence initially to bogs (e.g. NAUMANN 1931), but then more generally (e.g. RHODE 1969; HUTCHINSON 1969). The concept was conceived initially by NAUMANN (1919, 1929) and popularized by THIENEMANN (e.g. 1926) (MOSS et al. 1994). HASLER (1947) adapted the term eutrophication to include »cultural eutrophication«, the notion being that addition of nutrients by human agencies accelerated a natural process. This implied the process could be reversed by controlling nutrient loadings (HASLER 1969). In many cases the original terms have been expanded to the point where the word oligotrophic is used to describe any desirable condition and eutrophic to describe any undesirable condition.

Determining the trophic status of freshwater ecosystems

Within the conceptual framework of trophic status, it soon became of interest to be able to develop vital signs or indicators of trophic condition. Soon, a wide range of parameters was being developed to help classify aquatic systems relative to trophic status.

While the chemical parameters focused on the »food« (i.e. concentrations of nitrogen, phosphorus and other constituents) in the ecosystems, the physical and biological measures focused on the implications of nutrient levels (water clarity, numbers of kinds of primary producers).

At the time of this growing interest in the trophic status of aquatic ecosystems, the 1960s and 1970s, ecological disasters where being uncovered and described. Hence, much of the attention was focused on the »eutrophic« end of the spectrum – those indicators of pollution.

In biological terms, some investigators confined use of the terms to total abundance and biomass. These measures include chlorophyll a, cells/ml and other quantifiable approaches without consideration of the taxa present (CARLSON 1977, 1979, 1981). These »black box« approaches claim to be closer to the original trophy concepts. But beyond these approaches, early investigators of the concepts of oligotrophy and eutrophy did examine both autecological and synecological points of view. NAUMANN (1919) discussed phytoplankton associations, relating different communities of phytoplankton with trophic condition. PEARSALL (1921, 1932), RUTTNER (1952) and JÄRNFELDT (1956) all discussed the types of plankton found across a wide range of lake types and geography. For individual species, the focus was to identify those species that were indicators of eutrophy (e.g. PALMER 1969) – species that had preferences for or tolerances of a wide range of ecological perturbations (nutrients, but also temperature, salts, metals, pH to name a few). From a community approach, a wide range of indices and metrics were developed to help identify degraded systems and the types and levels of degradation (i.e. THUNMARK 1945, NYGAARD 1949, RAWSON 1956, STOCKNER and BENSON 1967).

Oligotrophy and diatoms

From a biological point of view, those working on diatom communities were in the forefront of the development of many of the models and of conduct of the »on the ground« research to identify and distinguish impacted and polluted ecosystems. Due to the large number of separate taxa, and large population sizes, diatom communities lent themselves to descriptive and experimental approaches to determining relative impacts on aquatic ecosystems. Ruth PATRICK (PATRICK et al. 1954) helped to develop conceptual foundations for the application of diatom communities, including her famous saying, »Diversity is the hallmark of a clean environment.«Large, nation-wide projects to assess the status and trends of U.S. freshwaters were undertaken at this time in rivers (WILLIAMS 1964, 1972), lakes (TAYLOR et al. 1978), but the coarseness of the taxonomy of the day (most workers used HUSTEDT 1930 as their taxonomic guide) render these studies difficult to interpret according to present taxonomic understanding. The large number of floristic and ecologic works that ensued allows compilations and syntheses of the ecological distributions and tolerances of diatoms (LOWE 1974; a tradition that continues today, e.g. VAN DAM et al. 1994). More recently, national scale programs to assess the »health« of U.S. freshwaters using diatoms, (Environmental Monitoring and Assessment Program »EMAP« for lentic systems, National Water Quality Assessment Program »NAWQA« for lotic systems) have continued to focus more on recognizing impacted or polluted sites than recognizing oligotrophic conditions. The two programs are sponsored and managed by two different Federal Agencies, which leads to some inconsistencies in philosophy, emphasis, and implementation.

There is important past focus on the degradation of freshwater, protocols, procedures and development of indices and metrics that allow time-efficient and cost-effective identification of impacted systems. Thus, instead of counts of several thousand to ten(s) of thousands of valves, as performed during the 1950s and 1960s, most protocols call for only 500 to 600 valves, in which dominant species swamp out the identification of rare species in counts (POTAPOVA and CHARLES 2004). It may be that it is the rare species that are indicators of oligotrophic conditions. From the diatom floras produced during this period (e.g. PATRICK and REIMER 1966, 1975) it is remarkable that almost no species that were characterized as being associated with oligotrophic conditions were identified or described. The refined taxonomy that has been developed over the last 30 years begins to make past characterizations of taxa dated (e.g. the oligotrophic »*Cyclotella*« group of HUTCHINSON 1967). More recently, high diversity in the phytoplankton has been attributed to intermediate disturbances versus system stability (e.g. PADISÁK et al. 1993).

A remarkable floristic work on what was thought to be a well-known (the best known?) freshwater diatom flora, that of central Europe, has sparked a renewed interest in oligotrophic diatoms. In this work by LANGE-BERTALOT and METZELTIN (1996), based on modest samples from three oligotrophic, or nearly oligotrophic lakes, one each in Finland, Austria and Germany, over 800 taxa were identified (the entire flora of central Europe was thought to be comprised of 1600 taxa; KRAMMER and LANGE-BERTALOT 1986, 1988, 1991a, b). Over 100 taxa were either described as new or could not be attributed to any previously described species. The remarkable species richness and the uniqueness of the taxa were thought to be the hallmark of these oligotrophic lakes.

A further innovation of LANGE-BERTALOT (1996) as applied to diatoms was the creation of a »red list« of diatom species that are rare and indicative of clean (oligotrophic) conditions. Like the higher plant and animal lists on which it is based, species on this red list are indicators of habitats worth protecting.

Oligotrophy, diatoms and a new research paradigm

Conservation of habitats

While the past decades have focused on identifying and stopping the environmental insults inflicted upon freshwater ecosystems around the world, there is a great opportunity to attempt to identify and protect those that are left. An old adage goes that »An ounce of prevention is worth a pound of cure« and thus, as freshwater issues around the world become more important, being able to identify places that are pristine and in need of protection will be more important. How will we identify these systems – by physical and chemical parameters alone? STEVENSON (1998) has suggested that diatoms are better indicators of water quality than water chemistry. How will information about diatoms to help us preserve fragile freshwater ecosystems?

The ecology of the 21st century will be one of restoration ecology

Once abatement of pollution is accomplished, a next critical step is to restore habitats, to bring them back from the brink of irreversible change. But what will we restore them to? How will we know what that condition is? And why shouldn't we strive to achieve an oligotrophic endpoint? Again, how is that determined? By the suite of species present and/or the structure of their communities?

Paleontology

A role that paleontology might play in this regard is to help us understand the natural course of a lake's ontogeny, from oligotrophic to eutrophic, without the intervention of the human species. Excellent exposures of freshwater diatomites, and core from Holocene systems may hold clues to this evolution of communities. It is too bad that the discipline of fossil freshwater diatoms is perhaps the least populated in terms of taxonomic expertise in the world of diatom science.

Documenting biodiversity

As the work of LANGE-BERTALOT and METZELTIN (1996) illustrates well, we still have a lot to do in terms of describing the diversity of diatoms from freshwater ecosystems. In many large-scale programs, from the count data of 600 valves, many species appear to be new to science. In the NAWQA datasets, nearly 25% of the taxa are undescribed. And rare species have not been sought in these samples.

Further development of the concept of oligotrophy

We believe there is a strong case to be made for a focused investigation into the concept of oligotrophy. It may be necessary to develop new terminology adequately to describe the range of conditions and causalities present in the modern world. Multivariate statistical approaches allow estimation of departures from ecosystem baselines and assignment of causality for known and well-measured parameters. Whether this approach is applicable across systems types, across different time scales and across geographic space is uncertain. Additional work is needed to understand the theoretical and practical aspects of identifying pristine places, and restoring degraded systems to their original physical, chemical, biological and functional conditions. There may also be historical perspectives that need to be taken into account. For example, what might be considered »clean« or »oligotrophic« in continental Europe might be deemed mesotrophic in areas of North America. As new measures to assess the condition of waters are developed (e.g. Index of Biological Integrity), understanding of the baseline condition(s) is imperative. As STEVENSON (1998) points out, the currently popular concept of »Reference« site does not necessarily imply »Oligotrophy«, but understanding those differences is essential as we weigh the costs/benefits (and losses) to achieving one or the other. It is time for ecologists, taxonomists, systematists, restoration biologists and aquatic scientists of many interests and specializations to take up this challenge.

It may also prove to be advantageous to consider other aspects of diatom biology to best determine trophic status. For example, the robust appearance of diatoms that grew in some habitats least affected by human interventions has been noted historically (e. g. LEWIS 1865) and in paleolimnological studies (STOERMER et al. 1985). In some cases it is possible to trace morphological changes in a species beginning before appreciable human impact until its eventual local extinction (STOERMER et al. 1989). To fully assess status of an aquatic environment it may also be advantageous to pay greater attention to the cytology and morphology of diatom species present. There are numerous examples in the literature of apparent morphological effects of various environmental perturbations and, in our opinion, this approach deserves further attention.

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