

Plenary lecture

Global limnology: up-scaling aquatic services and processes to planet Earth

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Introduction

It is onerous to try to define the field of global limnology and encourage the world's aquatic scientists to become more engaged in a field that they already know well. I have been searching for regular patterns in rates and processes in aquatic ecosystems for some decades but was only recently encouraged to up-scale these processes to a global level. We limnologists tend to look at each of our ecosystems as a unique entity, a tradition underlain by our backgrounds as naturalists. It is therefore a special tribute to limnologists' scientific objectivity that we have already assembled one of the largest bodies of predictive theories in the environmental sciences (PETERS 1986, PACE 2001). It is this foundation of seeking patterns and performing multi-ecosystem comparative analyses that will allow limnologists to make rapid progress in our global understanding. The purposes of this paper are to define the field of global limnology, convince limnologists that it is important to pursue, provide a brief description of how to accomplish this, give some examples of global limnological analyses, and suggest areas in which global limnologists need to make rapid and concerted progress.

Key words: abundance, carbon, global, lakes, limnology, processes, scaling

Definition of global limnology

To define global limnology we can first define global ecology and then focus on the part that concerns epi-continental (MARGALEF 1994) waters. According to the journal of *Global Ecology and Biogeography*, global ecology seeks broad patterns in the ecological characteristics of organisms and ecosystems. Further, it is concerned with testing and exploring general ecological hypotheses using data of broad geographic, taxonomic, or temporal scope. The role of global ecology is therefore to docu-

ment ecological and biogeographic patterns and their causes, document global anthropogenic influences, and develop tools to study these problems. The Department of Global Ecology, Carnegie Institution, Stanford University, defines the field as understanding how interactions shape the behavior of the earth system, including responses to changes. In his book, *Inventing Global Ecology*, Michael L. Lewis concludes from these ideas that global ecology is "...a science that is held responsible, literally, for saving the world." (LEWIS 2004).

Global limnology can thus be defined as "quantifying and understanding the role of continental waters in the functioning of the biosphere." In parallel with global ecology, this includes the way this global role has been and will be influenced by human activities, the tools needed to establish the global role of continental waters, and the patterns that result, but it especially includes overall biospheric rates, quantities, and processes that result from the functioning of limnological systems.

Two good reasons to study global limnology

We need to rejuvenate limnology

Limnology has reached unique achievements in identifying global patterns in ecosystem function (PACE 2001). In spite of this, several have suggested that the relevance of limnology to ecology needs to be rejuvenated, especially concerning questions of greatest importance to science and society. Lack of involvement in these high-profile arenas is leading to decreased recognition and research funding to demonstrate the importance limnology. More important, we are leaving unsolved a key piece of the puzzle concerning global function and global change. It

is an odd conundrum that a science making the boldest progress toward recognizing, interrogating, and exploiting global patterns of ecosystem function has not translated these patterns into the global arena.

In an essay that pondered whether limnology is withering and where it should go, Peter Jumars made two observations of greatest concern (JUMARS 1990). First, “The current focus on global environmental issues appears literally and figuratively to have passed limnology by.” This is most obvious because limnology lacks global networks (compared to hydrology), lacks global initiatives (compared to oceanography), and has lagged behind several fields in developing sophisticated modeling and analytical methods. Second, he suggested that limnology is much better suited to global research than several other fields, giving us clear advantages, because (1) our systems can be manipulated, (2) we can observe and understand coupled interactions between biological, chemical, and physical components of our systems, (3) inter-annual variations in our systems are often interpretable and so not relegated as readily to “noise”, and (4) our water bodies are relatively isolated and well defined, which leads to easy analysis and comparison.

In one of the most introspective books ever written about a science, Rob Peters and Frank Rigler (RIGLER & PETERS 1995) combined their decades of experience in limnology with their strong interest in the philosophy of science and knowledge. They concluded that to make more useful contributions, limnologists need to concentrate on tractable, soluble problems. Their analyses suggested that great sciences focus on finding patterns, followed by seeking explanations for those patterns. They prescribe asking questions such as “when?”, “where?”, “how many?”, and “how much?”, then by advancing theories as needed to wonder “why?”, “how come?”, and “what for?”. They suggest a schematic view of science (Fig. 1) in which limnology is only a short distance from a state where we can predict nothing about limnological systems and their global role to a state where we could eventually predict everything. Although limnology is certainly farther along this trajectory than many sciences, they emphasize that strengthening limnology will require asking and answering tractable questions about big environmental questions. After all, scientists are supported by society, so why not answer questions that are of a scale that society needs?

Others have echoed similar themes. Colin Reynolds (REYNOLDS 1998) suggested that “...basic freshwater science is in a poor state of health...” because freshwater ecologists need to champion the relevance of their work “...for its importance in addressing pressing applications to the stewardship of the biosphere.” The

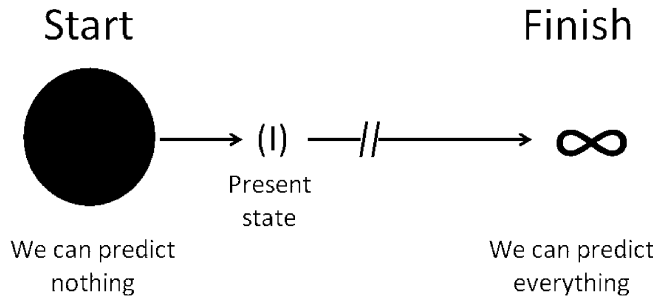


Fig. 1. Schematic depiction of the pursuit of limnological knowledge (redrawn from RIGLER & PETERS 1995).

relevance of freshwater ecosystems to large-scale environmental problem solutions must be promoted to other scientists and policy makers. We might fail as a science if we fail to promote our role. Graham Harris (HARRIS 1994, 1999) suggested that limnologists have tended to “...concentrate on short-term solutions to contracts and consultancies rather than on some of the deeper questions.” There are few sciences like limnology with major theories written into public law worldwide (e.g., phosphorus-chlorophyll-transparency relationships; e.g., DILLON & RIGLER 1975, JONES & BACHMANN 1976), so we are one of the few ecological sciences called on for such consultancies. On the other hand, new, big questions can be answered by limnologists, and Harris suggested that freshwater ecosystems may be simpler and more predictable than we think. He offered propositions for refocusing limnology toward finding more aspects of aquatic ecosystems that are predictable over broad scales of time and space.

Jon Cole and Gene Likens, then presidents of the largest limnological professional societies in the world (American Society of Limnology and Oceanography, and International Society of Limnology, respectively), undertook a mass e-mail survey of academic limnologists in 2006 because they were “...concerned about the current state and future of limnology...” Informal discussions with other scientists suggested that the number of faculty posts and courses identified with limnology were declining. They wondered whether universities and colleges were less interested in the subject matter; whether this decline was more apparent than real, resulting from dispersion of subject matter into posts and courses not labeled as “limnology”; and whether funding and support for work in limnology might be declining. They found that 27% of respondents believed that limnology (under any name) was in decline at their institution (22% had observed a drop in faculty posts), 62% believed it was in decline in their nation, and 81% and 97% believed this

was due to a lack of support and resources at the institutional and federal level, respectively. Many limnologists feel their field is declining in importance due to the lack of support, recognition, and resources made available to the field.

Ramón Margalef commented on the need for change in point of view of limnology (MARGALEF 1994). He suggested that “Traditional limnology was pleased to build research around the peaceful image of the temperate zone lake, as a small scale model of the less tractable ocean, and this was the introductory subject in most old texts of limnology.” He saw this image as changing rapidly so that it must now survive only “...as a nostalgic souvenir associated most often with calendars or posters.” More recently, WETZEL (2001) noted that “Limnology is currently experiencing a period of introspection” that will make the field “... healthy if (change is) done constructively and the causes of underlying deficiencies are recognized and addressed.” We must be in need of change if, in spite of great advances in the recognition of broad patterns in function, many eminent limnologists find the field deficient.

Summarizing the critiques and concerns about limnology:

- Limnologists concentrate on local rather than global analyses, focusing on elegant differences in detail rather than consistent, albeit messy, patterns.
- Limnologists assume complexity rather than seeking global patterns.
- Limnologists use unsuitable approaches to the large arena of biosphere-level inference.
- Limnologists should exploit the tractability of limnological systems more frequently to form research networks amenable to up-scaling to the biospheric level.
- Limnologists have wallowed in a self-fulfilling prophecy of decline by blaming our field’s decline on others’ support, not the relevance of limnology to world research priorities.

A good prescription for the rejuvenation of limnology would therefore be to:

- Concentrate on global rather than local analyses.
- Suit approaches to the large arena of biosphere-level inference.
- Seek more global patterns and be less consumed by complexity.
- Exploit the tractability of limnological systems to form research networks for up-scaling.
- Break the cycle of blame: limnology’s relevance is not due to others’ support but to world research priorities that diverge from our chosen emphases.

Limnology now seems irrelevant to global problems

A second reason to engage in global limnology is that the ecosystems we study are currently largely ignored by scientists working in a global framework. In general, continental waters are ignored as being insignificant or are thought of only as transport conduits (rivers and streams) or reservoirs where water and materials are held for a short time (lakes) before delivery to oceans. Terrestrial ecologists, climatologists, and oceanographers tend to think of continental waters as “plumbing” that delivers water and material to the sea, with little processing. Of course, we know this to be ridiculous, and the concepts of nutrient and material retention and spiraling are rudiments of lacustrine and riverine limnology.

That limnology is currently perceived as irrelevant to global problems is, however, undeniable and largely our fault. One need only look at schematic diagrams of various global material cycles to see that limnology and aquatic ecology have been left behind. Nowhere is this more obvious than in global analyses of the carbon cycle (e.g., SCHIMEL et al. 1995; Fig. 2). Continental waters are virtually ignored in these global views and processes; the carbon they store and any processing of this material they do (e.g., burial, emission) are completely omitted (Table 1).

Why are continental waters under-valued globally?

Aquatic ecosystems are ignored possibly due to a fundamental error of reasoning. Cognitive psychologists call this the “saliency error,” one of several attribution errors (KELLEY & MICHELA 1980, NISBETT & ROSS 1980, TETLOCK 1985). In short, the human mind tends to attribute causes of events or problems to the most obvious aspects of the system, or, in the case of global questions, to those largest in spatial extent. Thus, among all the biomes of Earth, we tend to look first for causes of change in the large compartments (i.e., marine, terrestrial, or atmospheric). By inference, the smallest systems are often assumed to have the least effect on any global event, cycle, or change. Even MARGALEF (1994) did not escape this cognitive bias when he wrote, “...epicontinental water systems quantitatively do not contribute very much to the total budget of matter and energy in the biosphere...(because they)...cover a relatively small extension on Earth.” Of course, experience with microscopic pathogens and many other realms of science demonstrate

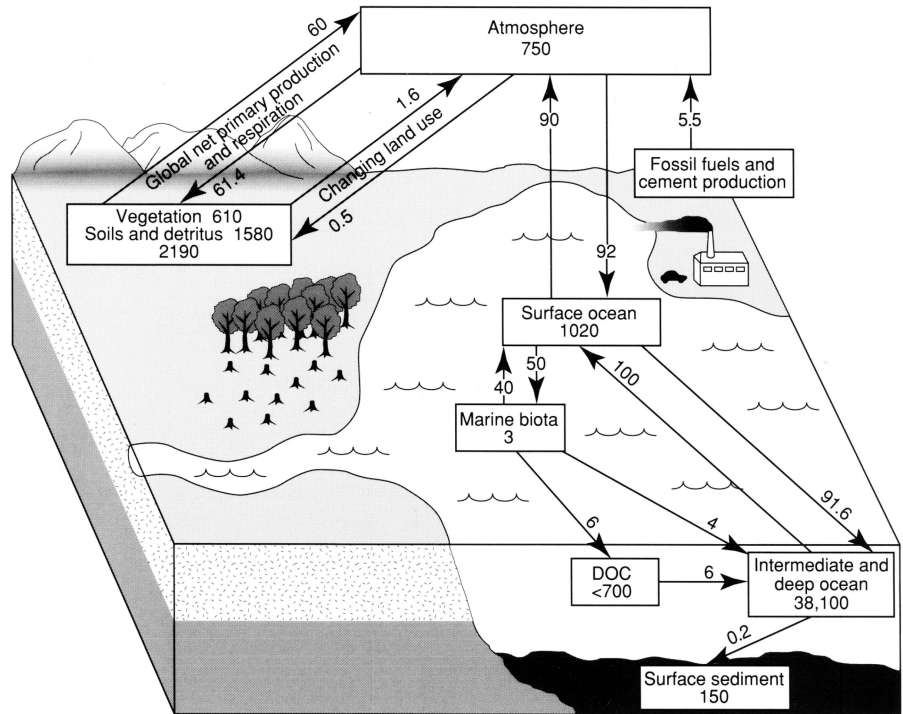


Fig. 2. Depiction of the global carbon cycle completely ignoring the active role of inland waters (from SCHIMEL et al. 1995). C flux rates are indicated in Pg/y. This is one of many examples in the published literature (Table 1). Reproduced with permission from the Cambridge University Press, Cambridge, UK.

Table 1. Examples of global cycles and budgets that ignore the role of continental waters.

Cycle or budget	Reference
Carbon	(GOODY & WALKER 1972, BOLIN 1983, SCHIMEL et al. 1995, INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE 2001, UNITED STATES CLIMATE CHANGE SCIENCE PROGRAM 2003)
Energy/Radiation	(CHRISTOPHERSON 1994, KIEHL & TRENBERTH 1997, HERMANN 2006)
Greenhouse gases	CO ₂ : (THORNELOE et al. 2002) CH ₄ : (WEISSERT 2000) N ₂ O : (SEINFELD & PANDIS 1998)
Nitrogen	(ROSSWALL 1983, CHAMEIDES & PERDUE 1997, BIN-LE et al. 2000, ROY et al. 2003, RAVEN et al. 2004)
Oxygen	(CLOUD & GIBOR 1970, GOODY & WALKER 1972, WALKER 1980, KEELING et al. 1993)
Phosphorus	(GRAHAM & DUCE 1979, RICHEY 1983, LERMAN 1988)
Silicon	(GOODY & WALKER 1972, NELSON et al. 1995, TRÉGUER et al. 1995)
Sulphur	(FRENEY et al. 1983, RAVEN et al. 2004)
Water	(CLARKE 1991, HINRICHSEN et al. 1998, WINTER et al. 1998, DEPARTMENT OF LAND AND WATER CONSERVATION 2000)

that the effect of anything is the product of its size and the rate, efficiency, or intensity of its function. The tiniest piece of plutonium can be massively deadly, as can a small exchange of DNA among bacteria cells.

It is easy to demonstrate that global limnology may be of greater importance than that implied by the spatial extent of limnological systems. For example, if lakes compose 1.8 % of the land surface as many have suggested (MEYBECK 1995, KALFF 2001, WETZEL 2001, SHIKLOMANOV & RODDA 2003), and they do things (e.g., carbon burial, methane emission; see Table 1) at the same rate or with the same efficiency as terrestrial ecosystems, then lakes represent only about 1.8 % of the global, non-

oceanic process. If rates, processes, and efficiencies are 10 times greater in lakes than in terrestrial ecosystems, then lakes contribute the same order of magnitude of effect on global processes as terrestrial ecosystems. Further, if rates, processes, and efficiencies were 100 times greater in lakes than on land, terrestrial or even marine influences could be inferior to those of lakes.

Likewise, if lakes are not 1.8 % of the continental area but 3 % or more (DOWNING et al. 2006) and have rates, processes, and efficiencies that are 100 times those of terrestrial systems, lakes represent nearly triple the terrestrial process. If one counts lakes, rivers, streams, wetlands, and impoundments that may total 12 % or more of

the global land surface, terrestrial processing may begin to appear insignificant compared to continental aquatic ecosystems. Because continental aquatic ecosystems have more water than terrestrial systems and often more nutrients than marine systems, rates and efficiencies of various processes may be 1000 to 10 000 times those observed marine and terrestrial ecosystems (PENFOUND 1956, DOWNING et al. 2008).

Because science is seeing and solving mysteries, two quotations from Sir Arthur Conan Doyle (speaking as Sherlock Holmes) are relevant (CONAN DOYLE 1920). First, from *The Boscombe Valley Mystery*, “There is nothing more deceptive than an obvious fact.” We should not be misled by the relative sizes of biomes into assuming global limnology is unimportant. Second, from *A Case of Identity*, “It has long been an axiom of mine that the little things are infinitely the most important.” We should expect the small parts of the world’s ecosystems (e.g., lakes, ponds, rivers and streams, and wetlands) to be of disproportionately great importance in world cycles and processes.

Examples of limnological efficiency: extreme carbon burial

The global importance of limnological systems is determined by the product of their abundance on Earth and the intensity or efficiency of processes compared to marine and terrestrial systems. Many processes (e.g., production; PENFOUND 1956) are more intense in inland systems than elsewhere in the biosphere. Jon Cole (Institute of Ecosystem Studies, Millbrook, NY) has given an intriguing example of how the efficiency of carbon preservation can be very high in aquatic ecosystems. He cites the “Tollund Man” (COLES & COLES 1989), a hanged Dane who was disposed of in a bog-lake during the Iron Age. The body was remarkably preserved with little deterioration, even of internal organs. The extreme preservation of carbon and structure in this environment is credited to low oxygen conditions and the preservative influence of organic acids. Archeologists frequently exploit the superb efficiency of carbon preservation in aquatic ecosystems for reconstructing regional histories (e.g., O’SULLIVAN 2007).

From an academic perspective, a more inspiring example of carbon burial efficiency is, perhaps, the case of Mabel Douglass, Dean of the New Jersey College for Women (now Douglass College, associated with Rutgers University). Dean Douglass was last seen in a rowboat on Lake Placid in 1933 when she disappeared (ORTLOFF

1985). The boat was found adrift, but an extensive search failed to locate her (ANONYMOUS 1933). Her body was found nearly perfectly preserved 30 years later at a depth of 34 m (ANONYMOUS 1963), probably through the process of saponification in which most of the carbon is conserved and structure can remain unchanged for very long periods of time.

Several other processes give rise to highly efficient preservation and burial of organic matter. For example, logs from a century or more ago have been found perfectly preserved in Lake Superior and many other lakes (SWERKSTROM 1994). These logs are in such perfect condition that they can be sawn and sold for high prices. Lake sediments are known to preserve a very broad variety of organic plant and animal remains for centuries and millennia (SMOL et al. 2001a, 2001b). This preservation of organic and inorganic remains forms the basis of the burgeoning field of paleolimnology. Most intriguingly, perhaps, is that archeologists have found that early hunters in North America were aware of the efficiency of hypolimnia in preserving organic matter. They immersed surplus mastodon meat in lakes to be consumed, safely preserved, if not a little oddly flavored, many months later (NEMECEK 2000).

Limnologists can cite a myriad of ways in which rates and processes are faster or more efficient in continental waters than in terrestrial ecosystems or the world’s oceans. Ample water, nutrients, and organic matter, combined with moderate temperatures, rapid ion transport, and divergent oxygen conditions lead to high production, fluxes, conversions, respiration, preservation, and many other biological rates and processes (KALFF 2001, WETZEL 2001). After all, the global dominance of limnological processing only requires that these processes be more than 33 times greater (on an areal basis) in lakes than in terrestrial environments and more than 115 times greater than in the world’s oceans.

Up-scaling to the biosphere

Global limnology requires that we know the role of continental waters in the biosphere, which requires calculating the aggregate roles of all lakes, streams, rivers, or wetlands in a diversity of processes of interest. In the simplest case, we might know that each ecosystem has a constant amount of something (Y) or a known average level of something (\bar{Y}). Up-scaling to a global estimate (\hat{Y}_{global}) requires only knowledge of the number of systems in the world (N). In that case:

$$\hat{Y}_{global} = \bar{Y} \cdot N \quad (1)$$

This is an extremely simple case where, for example, we might assume that each lake has a similar quantity of something, or for lack of better information, we might want to make a global estimate based on an average quantity. For example, if a series of analyses showed 10 ducks, on average, on each of a series of lakes dispersed throughout the world, one could estimate the number of lake-dwelling ducks worldwide using lakes, as in equation (1), if one knew the total number of lakes in the world.

Rates, quantities, and processes (*Y*) usually covary with one or more characteristics of ecosystems (PETERS 1986); therefore the approach illustrated above would yield a very crude estimate of any aspect of global limnology. Two things need to be considered: (1) global measurements and (2) scaling rules. Global measurements are usually characterized by global predictive relationships between an observation of interest (i.e., *Y*) and its best covariates (x_1, \dots, x_i). Scaling rules are probability density functions or distributions describing the global distribution of the covariates (Table 2). A regional probability density distribution for total phosphorus in an agricultural area of the United States can be calculated (Fig. 3); other covariates may be types, qualities, or characteristics of ecosystems.

An example would be estimating world CO₂ emission from lakes. We might realize that CO₂ evasion rates vary with the surface area of a lake (e.g., small lakes have higher rates). Therefore, up-scaling of CO₂ evasion to the global scale requires both an estimate of the covariation of CO₂ evasion with lake size and the probability density

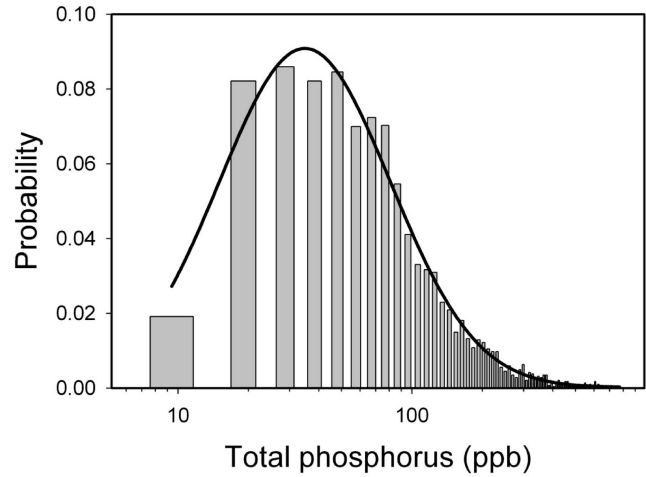


Fig. 3. Probability density distribution of total phosphorus values (as P) in lakes in an agricultural region of the United States (state of Iowa) considering all of the region’s recreational lakes. This distribution was constructed from nearly 3000 sets of observations made from 2001–2007. The solid line is a log-normal 4-parameter peaked curve, which is just one of many nonlinear functions that fit these data well.

distribution of lake size across the world (Table 2, second row). In addition, we might find that CO₂ evasion on an areal basis (i.e., per m² of surface area) is related both to lake size and depth. In this case, a global estimate of CO₂ evasion from lakes would require a function describing the covariation of CO₂ evasion with lake area and depth as well as an estimate of the joint probability density function of lake size and depth (Table 2). In practice, we

Table 2. Degrees of complexity in approaches for up-scaling processes and rates to the global scale.

The variable to up-scale (<i>Y</i>)....	Predictive relationship concerning <i>Y</i>	Scaling rule required for up-scaling	Meaning of scaling rule in words
... can be expressed as a constant or average, irrespective of ecosystem characteristics	\bar{Y}	N, V, or A	Global number (N), Volume (V), or Area (A) of ecosystems
... varies in quantity with one ecosystem characteristic (e.g., lake size, lake volume)	$\bar{Y} = f(x_1)$	$P_{x_2} = f(x_1)$	The global probability density distribution of the ecosystem characteristic that covaries with <i>Y</i>
... varies with two characteristics of the ecosystem (e.g., lake size and lake depth)	$\bar{Y} = f(x_1, x_2)$	$P_{x_2} = f(x_1, x_2)$	The global probability density distributions of the two ecosystem characteristics that covary with <i>Y</i>
... varies with many characteristics of the ecosystem (e.g., lake size, lake depth, latitude, phosphorus, etc.)	$\bar{Y} = f(x_1, x_2, x_3, x_4, \dots)$	$P_{x_2} = f(x_1, x_2, x_3, x_4, \dots)$	The global probability density distributions of the many ecosystem characteristics that covary with <i>Y</i>

integrate the product of the evasion function and the density function then multiply by the global lake area. Alternatively, we could create a series of integrals over bin ranges of size and depth from the probability density function and the global lake area and then multiply those bins by the function describing evasion as a function of lake size and depth. The process is conceptually identical for complex multiple variable relationships (Table 2), although the mathematical and statistical complexity of estimating the predictive relationships and the scaling rules is much greater. Details on the use of probability-density distributions for up-scaling can be found in recent publications (VIDONDO et al. 1997, DOWNING et al. 2006).

Five illustrations of global limnology

Halbfass, Thienemann, and the global scaling of lakes

Many aquatic and terrestrial rates and processes are expressed on a per unit area basis, and many aquatic rates and processes vary with lake size. Among ecosystem characteristics that vary with lake size are: lake chemistry (MANNIO et al. 2000); fish abundance, size structure, community composition, population dynamics, and dispersal (ALLEN et al. 2000, CLARAMUNT & WAHL 2000, RIGET et al. 2000); waterfowl abundance (EARNST & ROTHE 2004); contaminant deposition and processing (BODALY et al. 1993); phytoplankton production and composition (CYR & PETERS 1996); benthos composition (MOUSAVI 2002); littoral zone composition (HEEGAARD 2004); nutrient limitation (FEE et al. 1994); thermal regimes and responses (XENOPOULOS & SCHINDLER 2001); oxygen concentrations (CRISMAN et al. 1998); greenhouse gas emissions (MICHMERHUIZEN et al. 1996); ecosystem biodiversity (DODSON et al. 2000); invasibility (WINFIELD et al. 1998); food web structure (PASZKOWSKI & TONN 2000); resistance to perturbation (SMOKOROWSKI et al. 1999); ecosystem recovery (SMOKOROWSKI et al. 1999); gene flow (SVARDSON 1998); and human valuation and management (REED ANDERSEN et al. 2000). Therefore, one of the most fundamental needs for up-scaling limnological variables to a global scale is knowledge of the global area covered by lakes and their size distribution.

Data collection on lake area and size distribution began shortly after the beginning of the 20th century. An early inventory of the world's lakes was first published in 1914 (HALBFASS 1914), quickly augmented by August Thienemann's geographical analysis of the lakes of

Europe (THIENEMANN 1925). Thienemann suggested that "...around 2.5 million km², that is about 1.8 % of the land surface, is covered with lakes...", and that this lake area is dominated by a few very large lakes (Table 3). Despite some minor adjustments to the estimates of the surface areas of these large lakes, both due to possible real changes (HUNTINGTON 1907, KROONENBERG et al. 1997) and improved estimation methods (Table 3), this viewpoint was fundamentally unchanged for about 70 years (SCHUILING 1977, HERDENDORF 1984, MEYBECK 1995, KALFF 2001). The sole dissenting voice on this question was Robert Wetzel (WETZEL 1990), who reportedly designed the world size distribution of lakes on the back of a napkin in preparation for a presentation to SIL (WETZEL 1990), showing with remarkable accuracy how world lake area is dominated by small systems (DOWNING et al. 2006).

Later, Bernhard Lehner and Petra Döll (LEHNER & DÖLL 2004) laid the groundwork for a full inventory of world lakes by using GIS satellite imagery to count all of the world's lakes, down to those of moderate size. Their data sets included most lakes >0.1 km² and showed that the counts of different sizes of lakes follow a log-log linear relationship between lake area and the number of lakes of greater surface area. Such a relationship indicates that world lake-size follows a Pareto distribution

Table 3. Comparison of the sizes of the world's 17 largest lakes from the data of HALBFASS (1914) and HERDENDORF (1984). The "?" is from the original citation and confers a degree of uncertainty on the estimate. Herdendorf's data do not reflect recent real and large changes in size of Lake Chad and the Aral Sea.

Lake name	Area (km ²) (HALBFASS 1914)	Area (km ²) (HERDENDORF 1984)
Caspian Sea	438 000	374 000
Lake Superior	82 360	82 100
Lake Victoria	66 500	68 460
Aral Sea	63 270	64 100
Lake Huron	60 100	59 500
Lake Michigan	58 150	57 750
Lake Baikal	37 000	31 500
Lake Tanganyika	33 000	32 900
Lake Nyassa	30 800	22 490
Great Bear Lake	31 500	31 326
Great Slave Lake	30 000	28 568
Lake Erie	25 900	25 657
Lake Winnipeg	25 530	24 387
Lake Chad	20 000 (?)	16 600
Lake Ontario	18 900	19 000
Lake Balkhash	18 400	18 200
Lake Ladoga	18 150	17 700

(PARETO 1897, VIDONDO et al. 1997), which has been shown to fit lake-size distributions down to 0.001 km² (Fig. 4) as well as a complete census of the world's largest lakes (>100 km²) with very similar coefficients (DOWNING et al. 2006). This approach allows estimation of the abundance and size distribution of lakes across the entire size spectrum (Fig. 5). A similar relationship was also found to fit the abundance and size-distribution of the world's constructed lakes (Fig. 5), and analyses of regional data showed that constructed farm ponds bore a consistent relationship to agricultural land area and precipitation (DOWNING et al. 2006). Taken together, these results suggest there are 304 million natural lakes in the world that cover about 4.2 million km², nearly twice the area previously assumed. These are more strongly dominated by small water bodies than limnologists believed, although the dominance of small systems probably varies among regions and with the stage of land-form succession. In addition, constructed lakes are abundant and follow similar size distributions as do natural lakes, probably because both natural and constructed lakes depend upon regional hypsometry (DOWNING & DUARTE 2009),

which follows predictable fractal patterns (GOODCHILD 1988). Further, the number of small constructed ponds is significantly increasing, especially in agricultural areas with ample precipitation (DOWNING et al. 2006). Constructed and natural lakes probably make up >3 % of continental area. Increased accuracy of water body inventories is clearly important to a global understanding of the roles played by aquatic ecosystems. The closer we look at the aqueous portion of global "land" cover, the more we will appreciate how water dominates the contribution of landscapes to global cycles.

Horton, Strahler, and the scaling of river area

Although Luna Leopold and coworkers wrote that "...rivers are the gutters down which flow the ruins of continents..." (LEOPOLD et al. 1964), they are active sites for many global processes and thus do much more than transport materials from the land to the sea (COLE et al. 2007). The global extent of rivers is key information needed to understand their role in global processes.

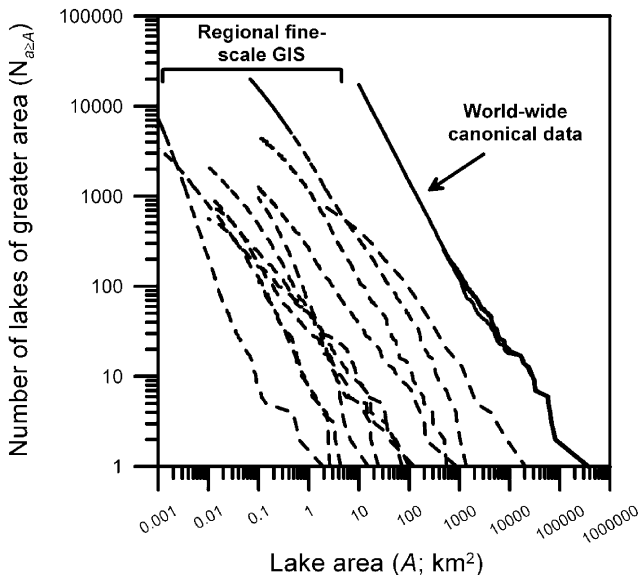


Fig. 4. Pareto lake size distribution data for specific regions and the entire earth (DOWNING et al. 2006). Data are only plotted throughout the range of lakes sizes that could be reasonably expected to exhaustively censused using the resolution of GIS coverage available. The solid black lines at right represent canonical (complete) censuses of world lakes (HERDENDORF 1984, LEHNER & DÖLL 2004) while dashed lines represent region-specific size distributions created using fine resolution GIS (DOWNING et al. 2006).

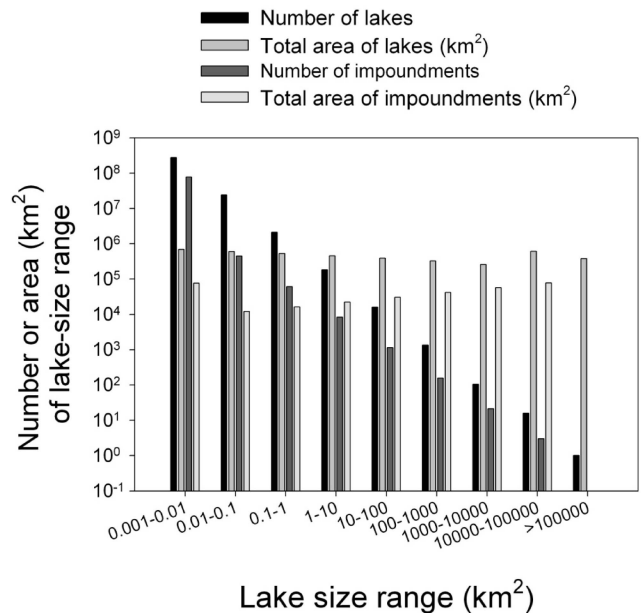


Fig. 5. Global size distributions of numbers of lakes and impoundments (darker bars) and global area covered by lakes and impoundments (lighter bars). Data are re-plotted from the original publication (DOWNING et al. 2006). The figure shows that size distribution of natural lakes and constructed lakes are similar and that global lake area is dominated by small lakes, not large ones as 20th century analyses suggested (HALBFASS 1914, THIENEMANN 1925, SCHULING 1977, HERDENDORF 1984, MEYBECK 1995).

Large rivers of the world (i.e., greater than fifth order; HORTON 1945, STRAHLER 1957) have been inventoried using coarse-scale GIS (LEHNER & DÖLL 2004) and appear to cover about 0.3 % of the surface of continents. If streams follow similar scaling rules to those of lakes (Fig. 5) then small streams and rivers may add substantially to this sum.

As with lakes, the global area covered can be determined using size-frequency distributions. Beginning in the 1930s, Horton and Strahler (HORTON 1945, STRAHLER 1957) created empirical rules based on the bifurcation frequencies of stream and river networks. They devised means of characterizing river networks that allow the approximation of the number and length of streams of different orders, applicable over wide geographical areas (LEOPOLD 1962). If coupled with relationships between stream order and breadth, one could calculate the size-distribution of stream area over large areas of the continents.

The size distribution of streams in Africa has been intensively studied as part of assessments of fisheries resources (WELCOMME 1976, 1979, 1985) and the size distribution and area of streams of order >5 has been estimated by global GIS (LEHNER & DÖLL 2004). The number and length of streams in Africa from order 1–11, were estimated through bifurcation techniques (HORTON 1945, STRAHLER 1957, LEOPOLD 1962; Table 4), along with average widths of streams of different orders estimated from a large literature review (Downing et al., in prep.). This analysis indicates there are more than 5.2 million streams in Africa with a total length of 12.9 million km, covering 124,000 km² of continental land surface area. About 41 % of the river surface area falls

below order 6 and so would not have been inventoried by global GIS analyses (e.g., LEHNER & DÖLL 2004). On a global scale, this indicates that rivers probably occupy 1.7 times the area inventoried to date; therefore, as with lakes, their importance in global cycles and processes has been significantly under-estimated.

Measuring and scaling wetlands

Wetlands are extremely valuable (MITSCH & GOSSELINK 2000), are likely to be very active in the functioning of the hydric parts of continents, and have been less well inventoried than lakes and rivers due to classification and identification difficulties (SCOTT & JONES 1995, LEHNER & DÖLL 2004). As inventories of wetlands have been created over the years (MATTHEWS & FUNG 1987, STILLWELL-SOLLER et al. 1995, LEHNER & DÖLL 2004, COGLEY 2007), estimated wetland area has grown steadily (Table 5). Growth in wetland inventories has been greatest in the tropics and in northern latitudes below about 60° (Fig. 6). Even modern surveys are likely subject to the same levels of underestimation seen in surveys of lakes because regional hypsometry influences both lake and wetland area and size distributions in similar ways (GOODCHILD 1988, DOWNING & DUARTE 2009). If wetlands have been underestimated to the average degree seen in streams and lakes, then the continents probably contain wetlands that cover about 56 % more area than the amount indicated by the most recent inventories. When the myriad of small wetlands are accurately inventoried, continents may be found to contain an average of 10–12 % wetland ecosystems.

Table 4. The number, width, length, and area covered by the Rivers of Africa. Numbers, widths, and lengths are from WELCOMME (1976, 1979, 1985) and river breadth estimates were derived from a large literature review (DOWNING et al. in prep.).

Order	Number	Mean length (km)	Total length (km)	Median breadth (m)	Area (km ²)	% of total
1	4 166 969	1.6	6 667 150	1.62	10 801	8.68 %
2	870 615	3.7	3 221 276	1.93	6217	4.99 %
3	181 900	8.5	1 546 150	5.5	8504	6.83 %
4	38 005	20	741 098	11	8152	6.55 %
5	7940	45	355 712	48	16 896	13.57 %
6	1659	103	171 375	99	16 966	13.63 %
7	347	237	82 378	164	13 510	10.85 %
8	72	547	39 391	365	14 378	11.55 %
9	15	1259	18 887	852	16 091	12.92 %
10	3	2898	8693	1125	9780	7.86 %
11	1	6669	6669	481	3208	2.58 %
Total	5 267 526		12 858 779		124 503	

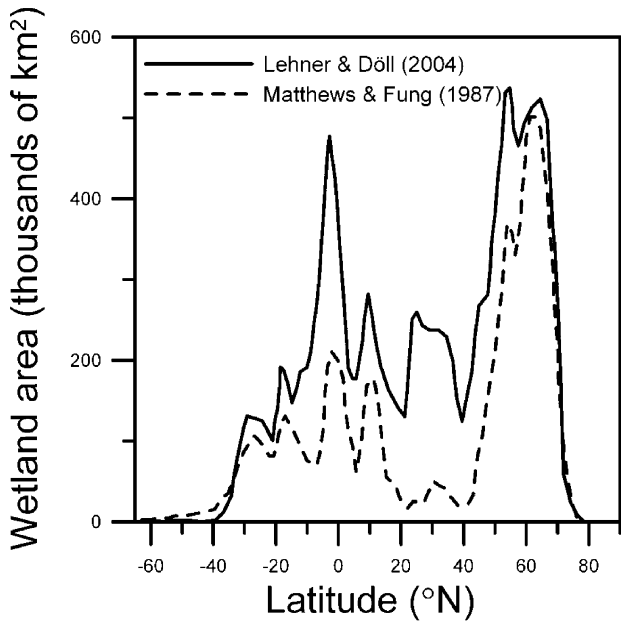


Fig. 6. Latitudinal distribution of wetlands as inventoried in the 1980s (MATTHEWS & FUNG 1987) and more recently (LEHNER & DÖLL 2004). Shows how known wetland area around the world is increasing as inventories increase resolution and detail.

Summary of lake, stream, river, and wetland inventories

All categories of aquatic ecosystems studied by limnologists have been underestimated in areal extent on a global scale (Table 6). Aquatic systems likely make up in excess of 15 % of the continents’ surfaces when all sizes of lakes, ponds, rivers, streams, and wetlands are considered. Historic assessments of natural lake and stream area have yielded underestimates because small systems have not been censused in the past. Small water bodies

make up a large proportion of the world’s lakes and streams, contrary to past belief. Constructed lakes have been accurately inventoried in the past, but small impoundments such as farm and water detention ponds have been left out and may play a substantial role in many processes. Similarly, small wetlands have been ignored in inventories and may constitute around a 50 % underestimate of the area of wetlands on continents. One way the importance of limnological systems has been underappreciated is the failure to account for the existence and function of a myriad of smaller systems that may be disproportionately important to global limnology.

Global carbon and the neutral pipe fallacy

I suggested earlier that most world models of important cycles and functions completely ignore the role played by limnological systems (Table 1; Fig. 2). Limnologists know our systems are significant in global cycles, but they have not been treated as such by global ecologists. This means that lakes, ponds, rivers, streams, and wetlands have been assumed by non-limnologists to function as simple conduits or “neutral pipes” in the transport and conversion of materials of global importance (Fig. 7). Nowhere is that more apparent than in the global carbon budget. This is serious because the accuracy of our knowledge of this budget will drive how effectively society can respond to the challenge of global climate change.

Jon Cole and coworkers, participants in a working group at the U.S. National Center for Ecological Analysis and Synthesis (NCEAS, Santa Barbara, CA, USA), integrated fragmentary knowledge on the role of inland waters into the global carbon cycle (DOWNING et al. 2006, COLE et al. 2007). They demonstrated that, far from being neutral conduits of C from lands to the sea,

Table 5. Condensed analysis (from LEHNER & DÖLL 2004) of changes in global wetlands inventories over the past decades. Data are in thousands of km².

Region	Cogley 1987–2003 (COGLEY 2007)	MATTHEWS & FUNG (1987)	STILLWELL-SOLLER et al. (1995)	LEHNER & DÖLL (2004)	Aggregate wetland inventory (LEHNER & DÖLL 2004)
North America	872	1126	1542	2866	2609
South America	578	727	1365	1594	2132
Europe	413	811	432	260	1195
Africa	368	718	265	1314	1431
Asia	2043	1688	1183	2856	3997
Australia and Oceania	67	188	8	275	342
Global total	4340	5260	4795	9167	11 711

Table 6. Area covered by aquatic ecosystems determined from GIS analyses detecting dimensions >60–100 m (LEHNER & DÖLL 2004) compared to detailed analyses considering smaller aquatic systems. If a source is not given for the global area and fraction of continents covered, the estimate was approximated by multiplying the estimate from Lehner and Döll’s work by 1.56 based on the average rate of underestimation seen for lakes, rivers, and streams in this paper.

Ecosystem	Global area (1000s of km ²) (LEHNER & DÖLL 2004)	Fraction of continental surface (LEHNER & DÖLL 2004)	Global area (1000s of km ²)	Likely fraction of continental surface
Lakes	2428	1.8 %	4200 ^a	2.8 %
Constructed lakes	251	0.2 %	335 ^a	0.22 %
Rivers and streams	360	0.3 %	508 ^b	0.42 %
Freshwater marsh, floodplain	2529	1.9 %	3945	3.0 %
Swamp forest, flooded forest	1165	0.9 %	1815	1.4 %
Coastal wetland	660	0.5 %	1030	0.8 %
Pan, brackish/saline wetlands	435	0.3 %	680	0.5 %
Bogs, fens, mires	708	0.5 %	1100	0.8 %
Intermittent wetlands & lakes	690	0.5 %	1080	0.8 %
50–100 % wetlands	882–1764	0.7–1.3 %	1380–2750	1.1–2.0 %
25–50 % wetlands	790–1580	0.6–1.2 %	1230–2460	0.9–1.9 %
Wetland complex (0–25 % wetlands)	0–228	0–0.2 %	0–360	0–0.3 %
Total lakes, rivers, and streams	3039	2.3 %	5043	3.4 %
Total wetlands	8219–10119	6.2–7.6 %	12820–15790	9.7–11.9 %

^a (DOWNING et al. 2006)

^b Assuming uninventoried rivers are about 41 % of total

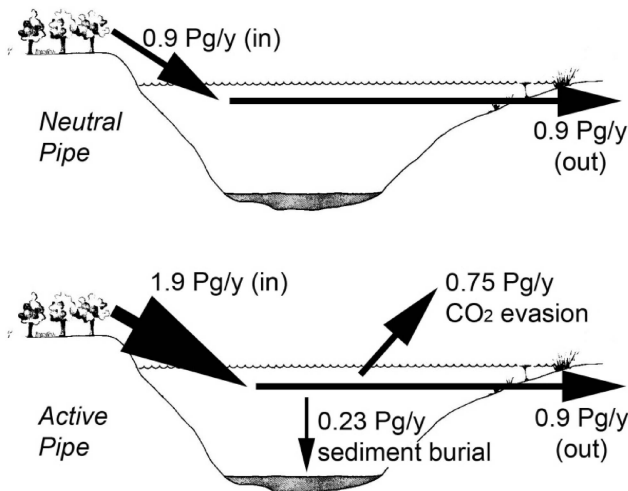


Fig. 7. Quantitative and qualitative differences between the “neutral pipe” model suggesting that inland waters transport carbon without processing it, and the “active pipe” model (COLE et al. 2007) in which preliminary estimates of the global burial of C by aquatic ecosystems and the evasion of CO₂ by aquatic ecosystems is admitted. This revision suggested that the large burial and evasion of carbon by aquatic ecosystems requires that export from land is more than 2 times greater than previously believed.

inland waters process large amounts of carbon buried in freshwater ecosystems or degassed to the atmosphere (Table 7; Fig. 7). Although their calculations used underestimates of the area covered by virtually every category of inland waters (Table 6), they demonstrated that inland waters may process about 1 Pg/y more C than was previously thought to be delivered to them. This is more than double the amount back-calculated as the landscape’s contribution to rivers and the sea through the supposedly neutral conduit of inland waters (Fig. 7). Traditional analyses have calculated the loss of C from the landscape simply as the amount delivered to the sea by rivers, but these calculations have ignored the role of inland waters in emitting and burying C.

COLE et al. (2007) calculations (Fig. 7) are being rapidly revised upward, underscoring the need for limnologists to engage in global limnology. For example, their estimate of carbon evasion and burial in lakes is an underestimate by more than 50 % because the calculations were based on historical assessments of global lake surface area and size distribution. Likewise, the role of rivers, streams, and wetlands was underestimated because these ecosystems are much more abundant on

Table 7. Summary of estimate carbon fluxes mediated within inland waters (from COLE et al. 2007). The final column indicates revisions that have been made and research needs that will lead to a more comprehensive understanding of the role of inland waters in mediating the “active pipe” (Fig. 7).

Inland water component	CO ₂ efflux to the atmosphere (evasion)	Burial in sediment (sequestration)	Revisions and research needs
Lakes	0.11 (0.07–0.15)	0.05 (0.03–0.07)	<ul style="list-style-type: none"> • All evasion and burial values underestimated by at least 50 % • Role of eutrophication and land-use change needs assessment • Small lakes may have higher rates so need to be studied
Reservoirs and impoundments	0.28	0.18 (0.16–0.20)	<ul style="list-style-type: none"> • Previous estimates of evasion ignored small, eutrophic systems and role of eutrophication • Burial greatly underestimated because estimates were based on large impoundments in areas with little agriculture
Rivers and streams	0.23 (0.15–0.30)	NA	<ul style="list-style-type: none"> • Previous estimates of evasion ignored streams <6th order so are at least 40 % underestimates • Evasion and degassing rates of small streams unknown • Burial of C through redeposition of eroded material in hydric vs oxic soils unestimated
Wetlands	NA	0.1	<ul style="list-style-type: none"> • Evasion and burial are likely very large and greatly underestimated • Wetland area may be as much as 10 % of land surface, globally • Deposition and decomposition imply high rates of burial and evasion
Groundwater	0.01 (0.003–0.03)	<0.016	<ul style="list-style-type: none"> • C pool size and residence times of groundwater not yet estimated • Exchange of terrestrial and aquatic C with groundwater unknown • Conversions, storage, and transport by groundwater poorly constrained • Role of groundwater withdrawals and hydrologic alterations unknown

continents than was determined using coarse resolution maps. Several lacunae in current knowledge (Table 7) indicate that inland water’s role in the global carbon budget is evolving upward toward an increasingly important piece of the global carbon puzzle. Inland waters are very active in this and many other global cycles. The former view that Earth’s important carbon compartments are ocean, atmosphere, and land, connected together by neutral pipes and conduits (inland waters) was convenient but inaccurate. An accurate understanding of the global C cycle requires seeing the biosphere as a network of inter-connected metabolically active sites, including inland waters and others.

The ‘Thousand Acres’ surprise – little ponds in agricultural landscapes

The global importance of an aquatic process or quantity depends, to some extent, upon the extent of the ecosystem type in the biosphere. Likewise, seemingly unimportant ecosystems, even those that cover only a small area of the land surface, can be important globally if the intensity of a process is extremely high. In Jane Smiley’s book about life on farms in Iowa, United States, *A Thousand Acres* (SMILEY 1991), water is not particularly abundant on the managed landscape (CARDEN 1997). Water is removed from wetlands by burying drain tiles causing

environmental damage (BENDER 1998). This water is drained into a myriad of small farm ponds that, in spite of their small size, play key roles because of the intensity of their importance to life on small farms. In any global or regional up-scaling, importance is the product of intensity of effect and abundance. *A priori*, it might seem that no ecosystem on Earth is less important than small constructed ponds and lakes.

Even the smallest farm ponds (1–2 ha) are very abundant on Earth, covering about 77,000 km² worldwide (DOWNING et al. 2006, DOWNING & DUARTE 2009). Agricultural ponds are increasing at rates from 0.7–60% per year in various regions as increasing pressure is put on agricultural lands to provide food for growing populations. Previous analyses of roles of constructed lakes in important global rates like organic C burial (e.g., COLE et al. 2007) have scaled-up rates of deposition and carbon content of sediments derived mostly from large water bodies and those with moderate degrees of eutrophication (DENDY & CHAMPION 1978, MULHOLLAND & ELWOOD 1982, DEAN & GORHAM 1998, STALLARD 1998). In a recent study, we used repeated bathymetric analyses and direct measures of sediment characteristics to estimate the likely rate of burial of organic C in the sediments of eutrophic lakes and impoundments (DOWNING et al. 2008).

In the 40 study lakes, we found that sediment organic carbon burial efficiencies were higher than those assumed for fertile impoundments by previous studies and were much higher than those measured in natural lakes. Organic carbon burial ranged from a high of 17 kg C/m²/y to a low of 148 g C/m²/y and was significantly greater in small impoundments than large ones (Fig. 8). The C buried in these lakes originates in both autochthonous and allochthonous production. These analyses suggest that median organic C sequestration in moderate to large impoundments may be double the rate assumed in previous analyses and exceeds rates of carbon sequestration found in any ecosystem in the world. Median areal C burial rates in these lakes were 10 times those seen in wetlands, 100 times those documented in tropical forests, and 1000 times those assessed in temperate grasslands. Extrapolation suggests that, each year, Earth's current moderately sized impoundments may bury 4 times as much C as the world's oceans. The world's farm ponds alone seem likely to bury more organic carbon each year than the oceans and 33% as much as the world's rivers deliver to the sea.

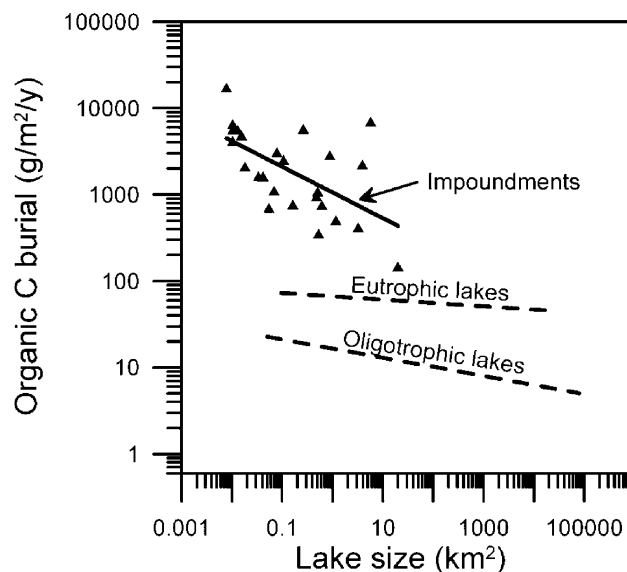


Fig. 8. The size-dependence and magnitude of organic carbon sequestration in oligotrophic and eutrophic lakes compared with measured organic carbon burial in eutrophic and hyper-eutrophic lakes (mostly constructed) in an agricultural region (DOWNING et al. 2008). The figure indicates that these eutrophic lakes have higher organic C burial rates than any ecosystem in the world.

Global limnology: objectives and research needs

Because a global understanding of the role of inland waters on processes throughout the biosphere requires inventories of aquatic ecosystems and the important rates and processes they mediate, several objectives and research needs emerge. Step one is to identify patterns in globally important quantities, rates, and processes, and understand their covariates (Table 2). Further, these quantities, rates, and process need scaling rules that allow meaningful extrapolation to the biosphere. Also, because we must create strong and reliable global science, we need to derive numerical and statistical methods to ensure that global values are accurate and well constrained (that is, have narrow enough confidence intervals). If we can accomplish these tasks, we will be on our way toward estimating human- and climate-mediated effects on the global role of continental waters.

Many variables are in need of global limnological understanding. For example, understanding the conversions of carbon in continental waters is of very high priority, to contribute substantially to discussions of global climate change. Likewise, understanding of patterns in

nutrients in continental waters, as well as fluxes and conversions of important gasses (e.g., N_2O , NH_x) and metals (e.g., Hg), will also improve global understanding of the role of inland waters in global nutrient, gas, and toxin budgets. Remarkably, inland waters have not yet been integrated into global heat and water budgets, so recognition of patterns in water and energy fluxes among aquatic systems is also important. Aquatic ecosystems are important sites for the production of food and fiber so global patterns in biological production must be understood and up-scaled. Finally, aquatic ecosystems are uniquely valuable sites for recreation and other economically important activities, so relationships between the characteristics of aquatic ecosystems and human valuation would be useful to the struggle to improve the quality and conservation of lakes, ponds, rivers, streams, and wetlands.

As we accumulate global predictive relationships (PETERS 1986, RIGLER & PETERS 1995, PACE 2001) between quantities and rates of importance and various state variables, global scaling rules need to be developed to allow up-scaling of predictive relationships to the biosphere (Table 2). Because so many characteristics of aquatic systems scale with size, global probability-density functions of area, volume, and depth are of rudimentary importance (Table 1). Some have already been developed, but refinement and improvement of these functions will lead to greatly increased accuracy and precision of global assessments. Also, because so many processes vary with trophic status (PETERS 1986) and stoichiometry (STERNER & ELSER 2002), global probability density functions of the nutrient status (e.g., P, N, Si, N:P) of aquatic ecosystems (Fig. 3) should be a high priority. Further, because temperature increases rates and processing; insolation drives primary productivity; wind promotes the mixing of nutrients as well as physical conditions; precipitation leads to nutrient and material influxes; and hydraulic characteristics of basins alter nutrient and material retention; the probability-density functions of temperature, wind, radiation, and water retention time would allow fruitful up-scaling functions. Whenever a given ecosystem characteristic is related to an important process across aquatic systems, global limnology will be served by knowledge of the probability-density distribution of that ecosystem characteristic. There is an urgent need for these scaling rules.

Most limnologists have been trained to look for precise details about particular water bodies; this detailed understanding satisfies our curiosity and serves the conservation of that particular ecosystem. In practicing global limnology, we will be forced to perform calculations on a global scale that necessarily lead us to sacrifice

some precision for generality and breadth of inference. This challenges our learned reductionism and makes us nervous that our inference on the global scale may be inaccurate or imprecise. Sir Francis Bacon wrote that "...truth will sooner come from error than from confusion..." (BACON 1620), and an essential part of scientific enquiry is making flawed inferences that improve systematically as knowledge and abilities increase over time (KUHN 1970). This means we should proceed fearlessly toward estimating the global role of aquatic systems because global environmental problems are too large to allow us the luxury of perfection.

As global limnologists, we need to quantify and understand the role of continental waters in the functioning of the biosphere. When we do so for our own special area of this pursuit, we should start by asking and answering two essential questions: (1) is the quantity or process large or small with respect to other types of ecosystems, and (2) how well constrained is our estimate of that quantity or process? In the first question, we ascertain whether the likely magnitude of a process is great enough to justify seeking a more accurate and precise answer. In the second question, we ascertain the likelihood of being wrong and the precision with which the answer to the first question is known. Therefore, much of global limnology is oriented toward making estimates of biosphere-level rates and processes attributable to inland waters, comparing these to estimates made for other types of environments, and refining and improving our estimates to yield a more accurate and precise assessment of the global role of limnological systems.

Conclusions about global limnology

Lakes, ponds, rivers, streams, and wetlands are important drivers of Earth's environment and economy but their global role has been ignored. Historically, limnologists studied aquatic ecosystems as discrete entities embedded within local environments and as biogeochemical subordinates of watersheds. Comparative and predictive limnology now exploit the discrete nature of waters to serve both science and society by creating predictive relationships that are amongst the world's most successful ecological theories. Despite these strengths and the importance of limnological resources, the global role of limnology is neglected both by limnologists and by analysts of the global environment. This is due to limnology's lack of global focus, the assumption that the relatively small area of continents covered by water indicates small importance, and the paucity of appropriate scaling rules and approaches for limnological ecosystems. The global

dominance of limnological processing only requires that these processes be more than 33-times greater (on an areal basis) in lakes than in terrestrial environments and more than 115-times greater than in the world's oceans. To encourage Earth's limnologists to take their rightful place in the global arena, I surveyed the process of global science, outlined requisite scaling rules and needs, summarized procedures for making global estimates, listed the most urgent variables in need of up-scaling, and have shown that the intensity of limnological services and processes makes them disproportionately important at the global scale.

Limnologists need to take their rightful place in the arena of global science. In the past, we have assumed that inland aquatic systems are of little global importance because of their small spatial extent. Global importance is the product of spatial extent and activity levels. We are learning that virtually all inland aquatic systems are much more prominent in landscapes than was previously appreciated. Further, intensities of activities of some of the most important processes amplify the role of aquatic ecosystems in the global environment. Although historically limnologists have not contributed as much to global ecology as some others, the abundance of aquatic ecosystems in landscapes, the central role of water in human society, and the extreme intensity of activity of aquatic systems mean that we have an important global responsibility to fulfill. The emerging field of global limnology is important to our science and our careers and, more important, to understanding the role of aquatic ecosystem in the changing biosphere.

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