

Long-term perspectives in aquatic research

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Abstract

Long-term research provides a unique perspective on environmental processes, dynamics of populations and communities of organisms, and emergent properties of ecosystems. Many key ecological relationships can be obscured in short term studies by common features such as time lags, natural variability, nonlinear relationships, interactive drivers, or relatively slow processes. Aquatic ecosystems have yielded major scientific discoveries through long-term research, through both observational and experimental studies. These research results have ranged from the detection of multi-decadal climate oscillation effects on ecosystems to finer-scale understanding of the trophic and biogeochemical pathways through which nutrient pollution affects water quality. In this special issue of *Limnology and Oceanography*, the contributing authors demonstrate that—whether designed for the monitoring of managed natural resources, to answer fundamental scientific questions, or both—long-term research enables researchers to move far beyond their initial questions as unexpected dynamics are revealed over time. With the widespread maturation of long-term data sets and rapid emergence of new technologies that enhance research capabilities, opportunities for synthesizing knowledge are now creating unprecedented opportunity for scientific discovery that builds on this legacy of long-term aquatic research.

There is no perfect substitute for time in ecological studies. Ecosystems are constructed of complex biogeochemical and trophic pathways, and populated with organisms with varying capacity for flexibility, such that cause and effect can be separated by time lags of unknown duration (Magnuson 1990). For example, low resource availability in one summer may cause low fecundity for organisms at maturation over several subsequent years. Evolution has armed organisms with a variety of mechanisms to handle stressors—such as reallocations of resources, metabolic alterations, changes in behavior—all of which can temporally distance the consequence from the original stressor. Long-term studies can capture ecosystem responses to environmental “surprises” such as hurricanes and other natural disasters, and reveal nonlinear dynamics that would be otherwise obscured over shorter time spans (Dodds et al. 2012). The fact that many seminal ecological studies are based on long-term data collections is testimony to the widespread recognition of

the importance of time in the scientific community (Callahan 1984).

A brief history of scientific advances from long-term research

The scientific advances that have arisen from long-term environmental research on aquatic ecosystems may, in part, be explained by several fundamental characteristics of these systems. First, in aquatic ecosystems major processes occur rapidly, compared to the terrestrial environment. Both the primary and secondary producers—such as algae and invertebrate grazers—grow and die quickly (frequently hours to months), in contrast to annual or perennial plants in terrestrial systems. Second, aquatic ecosystems can provide integrative measures of regional activity—they lie at low points in the landscape, collecting material from the watershed and airshed (Moss 2012; Chezik et al. 2017). Third, aquatic studies have historically been integrative—data on abiotic parameters, animals, and primary producers are often collected at the same time, unlike terrestrial ecology which has historically divided animal and plant ecology (Moss 2012). Fourth, even among aquatic ecosystems, lakes have a special advantage—the boundaries of lakes are easy to see, creating a relatively

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constrained system in which all the cogs and wheels of energy flow can be studied (Moss 2012). Since Forbes' (1887) famous treatise on "The Lake as a Microcosm," the scientific community has gained much greater awareness of the permeability of lake boundaries, but even so, lake boundaries provide useful compartmentalization of ecosystem processes. Finally, marine and freshwater systems are important to human societies in providing readily available water, nutritious food, transportation routes, recreational opportunities, and aspects of cultural identity. Many long-term aquatic studies are based on the need to monitor these natural resources for management and protection of these ecosystem services. Beyond these intrinsic properties of ecosystems is a shared characteristic of almost all successful long-term studies—tenacious individuals who manage to create long-term funding with short-term grants, impassioned by the scientific mysteries unfolding, the societal importance of the issues at hand, and frequently by the majesty of the ecosystem itself.

It is increasingly clear that following the ecosystem responses of management actions over long time periods is necessary. Lake Washington is a famous story of lake restoration following sewage pollution and diversion, a case study on which many subsequent sewage diversion plans have been based (Edmondson 1991). Underlying the long-term data collection that documented both the problem and the management action's success is a story of piecemeal funding. Recognizing a sudden shift in the algal community, suggestive of nutrient pollution, W. T. Edmondson and colleagues pursued successive grants to document algal and nutrient relationships, ultimately pointing to phosphorus as a driver. The team provided input on the public process that led to the sewage diversion, and then pursued subsequent grants to document the results of the management action—a reduction in nuisance algae and a return to prior levels of water clarity (Edmondson 1970). By 1972, those questions might have been considered resolved; but further, puzzling increases in water clarity drew the researchers' attention to trophic interactions that had taken several decades to play out and became evident in the growing time series at hand (Edmondson 1991; Hampton et al. 2006). Years after these findings, the relative effectiveness of controlling nitrogen and phosphorus pollution to manage eutrophication in lakes continues to be debated, in part because of the possibility of nitrogen fixers compensating for reductions in nitrogen inputs. With 37 yr of data including a 20 yr period with substantial reductions in nitrogen and phosphorus loading, Shatwell and Köhler (this issue) demonstrated that decreasing nitrogen inputs controlled summer cyanobacteria, that nitrogen fixers did not compensate, and that reducing only phosphorus would not have been sufficient. Swarbrick et al. (this issue) have demonstrated that the form of nitrogen introduced and the taxonomic identity of primary producers are both important, with both suppression and stimulation of algal growth occurring in ammonium addition bioassays conducted each summer over

15 yr with natural assemblages of lake phytoplankton. Analysis of 20 yr of data from the Oria River (Spain) revealed that ecosystem response to wastewater treatment has been successful in allowing invertebrates and fish to recolonize the river, and in reducing stream metabolism; yet these results were so gradual that they could not have been captured in short-term monitoring (Arroita et al. this issue). In one of the most heavily modified estuaries in North America, California's San Francisco Bay and Sacramento-San Joaquin Delta Estuary, managers rely on a number of species-environment relationships for developing recovery plans for at-risk species. Tamburillo et al. (this issue) re-examined nine of those relationships using an additional 9–40 yr of data since they were established, and found that not only did prediction error generally increase over time, but it did so very quickly in some cases, indicative of rapid regime shifts. Long-term data also inform the implementation of water quality management at watershed scales; relationships of watershed management approaches and in-stream water quality in the Baltimore Ecosystem Study LTER (Reisinger et al. this issue) show that both "gray" and "green" infrastructure have been instrumental in controlling in-stream pollutants.

While many long-term freshwater programs have been motivated by water quality concerns, long-term studies in marine ecosystems have largely (although not exclusively) evolved from two complementary objectives: (1) Documenting time-dependent changes in important fisheries and describing links between climate-forcing and the ecology that underpins variability in these fisheries; and (2) Quantifying temporal variability in biogeochemical properties and processes that influence the ocean as a sink or source of carbon dioxide (CO₂) to/from the atmosphere. The collapse of the Pacific sardine fishery that began in the 1940s motivated a partnership between state and federal government agencies and the Scripps Institution of Oceanography, which ultimately led to formation of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program in 1949. In the early years of the program, CalCOFI focused on spatiotemporal surveys of net plankton biomass in the coastal waters off California, extending from north of San Diego to near Point Conception. Transitioning into the U.S. Long-Term Ecological Research network in 2004, the program has expanded its focus to include assessment of the linkages between plankton biomass and productivity and basin-scale climate variability. Among the notable findings, ocean-atmospheric feedbacks, such as those attributable to El Niño-La Niña fluctuations, appear to be key drivers of temporal oscillations in population dynamics of sardine and anchovy fisheries in this region (Chavez et al. 2003; Lindegren et al. 2013).

Oceanic time series focused on quantifying biogeochemical variability resulted from recognition that the ocean plays a globally significant role in planetary carbon cycling. In particular, based on the successes of Keeling's work at the Moana Loa observatory, documenting progressive increases in

atmospheric CO₂ (Keeling et al. 1976), ocean scientists began securing funding to establish time series sites that would enable quantification of the sink/source dynamics of CO₂ in the oceans. Recognition of the important role of biology in regulating the pathways and magnitudes of carbon flux through the sea led to formation of ship-based biogeochemical sampling programs. Among the most notable examples were the formation of the Hawaii Ocean Time-series (HOT) program and the Bermuda Atlantic Time-series Study (BATS) in 1988 with funding from the US National Science Foundation (NSF) via the Joint Global Flux Study (JGOFS). Among key findings, these programs continue to document the role of ocean-climate variability in regulating biological processes that feedback on nutrient cycling and stoichiometry (Karl and Church 2017). Similarly, Bode et al. (this issue) explore time-varying connectivity between rates of upper ocean primary production, concentrations chlorophyll *a* (Chl *a*), and climate-driven changes in the intensity of upwelling in the eastern boundary ecosystem off the coast of NW Spain. At regional scales, such long-term changes in nutrient supply, including those attributable to anthropogenic sources, can result in important modifications to both inorganic and organic nutrient inventories (Kubo et al. this issue). In addition, programs such as HOT and BATS now provide some of the most robust observations documenting progressive changes in seawater chemistry attributable to ocean uptake of CO₂ (Dore et al. 2009; Bates et al. 2014). Such changes directly influence the physiology and ecology of marine plankton, notably calcifying organisms that include phytoplankton (i.e., coccolithophores) and zooplankton (i.e., pteropods). Assessment of how long-term changes in ocean chemistry impact the physiology and distribution of such organisms is key to improving predictive understanding of how such organisms may respond to future ocean change (Thibodeau et al. this issue).

Long-term research generates data points numerous enough, and over long enough time periods, to not only discern trends and relationships in highly variable systems but also frequently to attribute “noise” to longer term background cycles such as climate oscillations. The body of seminal work that is linked to the long-term research in England’s Lake District ranges from lake physics to trophic cascades and phenological changes subtle enough to have been missed had these programs been shorter or less detailed (Maberly and Elliott 2012). A key contribution of the Lake District long-term research illustrates the importance of such programs; the research did not originate with the objective of understanding climate teleconnections acting on local lake variables, yet it was among the first to do so (George and Harris 1985). These teleconnections and climate cycles, in turn, became the subject of new research using long-term data (e.g., Katz et al. 2011). Now, many long-term aquatic data sets have articulated the emergence of trend from variability that could not have been observed on short time scales. In the Chesapeake Bay, Rose et al. (this issue) applied a semi-analytical model of

attenuation in ultraviolet and photosynthetically active portions of the solar spectrum from 1986 to 2014, detailing substantial variability that occurs in water transparency over time and space and across the solar spectrum. Similarly, Cloern (this issue) demonstrates that 10 water quality variables in the San Francisco Bay estuary fluctuate at multiple time scales from months to decades, largely in concert with freshwater inflow and anthropogenic disturbances such as dams, water diversions, wastewater discharge, and species introductions. As societal pressures on water have grown, the application of long-term data to questions of socioeconomic importance have grown accordingly.

The Experimental Lakes Area (ELA) has had a large impact on science and society, perhaps most famous for the capability to do sustained whole-lake experimentation such as that leading to the demonstration that phosphorus pollution promotes nuisance algal blooms (Schindler 1974). The ELA has continued to examine the impacts of pollutants and other anthropogenic stressors of immediate policy relevance (e.g., Schindler 1988; Kidd et al. 2007), and the long-term studies have become a resource for answering some of the most fundamental questions in ecology such as those of species diversity and coexistence (Dodson et al. 2000; Fox et al. 2010). Hall et al. (this issue), working in the ELA, used 40 yr of data to show that carbon sequestration in sediments was a larger sink than evasion to the atmosphere or outflow, and suggest that droughts may increase carbon sequestration. Mass balances of carbon in lakes integrate inputs and losses via hydrological and biogeochemical processes and reflect changes in environmental conditions (Tranvik et al. 2009), yet very few such studies are long-term. For years to come researchers will be reaping the benefits of the data that have amassed from large-scale experimentation and carefully designed long-term data collection.

All of these programs, in addition to the questions that they were established to address, have created the opportunity to ask and answer questions that were not conceived at the time of their creation. Effects of invasive species, climate change, and land use change were not part of the inception of many of the long-term monitoring programs, and yet now have been demonstrated across many independent ecosystems. For example, Strayer et al. (this issue) used 24 yr of data from the Hudson River to evaluate the support for several alternatives to Parker et al.’s (1999) classical model of an invader’s impact. In contrast to that classical linear model, they discovered that *Dreissena* spp. tended to have nonlinear effects on lower trophic levels. In the 1990s, an invasion into a Norwegian lake by a highly specialized planktivorous fish, *Coregonus albula*, subsequently depleted zooplankton and caused sharp declines in the planktivorous morph of native *Coregonus lavaretus* (Amundsen et al. this issue). Tachibana et al. (this issue) used monthly data from a sampling program initiated in 1981 to investigate how the phenology of marine copepods has shifted in Tokyo Bay due to climate warming.

Peaks in abundance for *Acartia omorii* now occur 1–2 months later, which could negatively affect upper trophic levels through a trophic mismatch. An aspect of climate warming now receiving greater attention has been effects of melting permafrost on aquatic systems. Drake et al. (this issue) use an exceptionally long record spanning 43 yr in three lakes located in the Russian tundra to document significant increases during the late summer ice-free period of epilimnetic temperature, alkalinity and primary, and bacterial productivity. As the permafrost has thawed, the lakes have increased in size and carbon is being metabolized and released as carbon dioxide.

Another recent example of a topic not foreseen at the inception of most aquatic sampling programs has been the rise of winter limnology. Limnological programs typically collect few samples during winter, particularly for those lakes with seasonal ice cover, possibly because the winter was previously thought to be primarily a time of decay and slow metabolism, unlikely to offer exciting insights (Hampton et al. 2015). However, the retreat of ice (e.g., Magnuson et al. 2000; Sharma and Magnuson 2014; Sharma et al. 2016) has turned attention toward winter, to better understand processes being altered by these widespread changes (Bertilsson et al. 2013; Hampton et al. 2015). A recent synthesis of existing under-ice data (Hampton et al. 2017a) shows that while each individual long-term program may have few winter samples, synthesis of these data sets asserts the large role winter plays in whole-lake productivity, and longer time series additionally demonstrate clear connectivity between winter and summer. New analyses and syntheses of winter data are now emerging, including rich demonstrations of oxygen, nutrient, and carbon dynamics that have not only within-lake effects (e.g., Powers et al. 2017) but also implications for greenhouse gas emissions (e.g., Denfeld et al. 2018). While potent arguments have been advanced that long-term environmental data collection requires purpose and careful design to be a net benefit in a world with limited science and conservation funding (McDonald-Madden et al. 2010), and the promise of serendipitous discovery alone cannot be the basis for the use of scarce resources, the preponderance of evidence tells us that long-term research will answer questions not yet considered.

Concurrent with this recognition of the value of long-term research has been the broad acknowledgement that reliance of long-term programs on the tenacity of individual investigators is a fragile model. Accordingly, in the United States, NSF began investing in the Long-Term Ecological Research (LTER) program in 1980, a national network that includes freshwater, marine, and terrestrial environments, and the Foundation has established funding opportunities for supporting independent long-term ecological studies. Importantly, renewal of these long-term grants is contingent on favorable evaluation of prior activities, including open access to data, as well as the proposal of creative new questions and tractable research plans. Coordination of activities across sites creates efficiencies

and synergies, and opportunities for comparative studies, making the network more than the sum of the parts (Franklin et al. 1990; Swanson and Sparks 1990). The U.S. LTER sites have contributed important knowledge on topics ranging from biogeochemistry and ecosystem ecology to trophic dynamics, providing the capability for not only engaging in whole-lake experiments at the sites but then following the results over subsequent decades. The 28 contemporary LTER sites include both freshwater and marine ecosystems, urban and remote environments, from the polar regions to the tropics. The duration of the Arctic stream research associated with the LTER program (Kendrick et al. this issue) has been key to identifying trends in an inherently “flashy” ecosystem, particularly as rapid warming and permafrost thaw have contributed not only to changes in flow but also increasing nutrients. Similarly, the duration of the North Temperate Lakes LTER data has allowed detection of decadal scale effects of lake level on water clarity (Lisi and Hein this issue).

Similar large-scale, long-term programs have more recently been established, taking advantage of the lessons learned from existing long-term programs and also new technologies that can provide information at both broader and finer scales than has been typical. The National Ecological Observation Network (NEON) has been established to provide continental-scale data, including a variety of lakes and streams, and the Integrated Ocean Observing System focuses on marine systems. Technological advances in the design and construction of biogeochemical sensors and platforms (e.g., floats, gliders, moorings), together with satellite-based detection of ocean dynamics, have enabled synoptic-scale observations. Such autonomous and remote sensing approaches have highlighted key scales of variability in ocean dynamics, ranging across spatial scale that span sub-mesoscale (10s of km) to basin scale (1000s of km), and time scales that range from hourly to decadal scales. Moreover, by leveraging existing shipboard time-series programs for historical context, instrument testing and deployment, and for high quality calibration purposes, such autonomous sensing based studies are providing new insights into temporal variability in ecosystem processes (Riser and Johnson 2008; Johnson et al. 2010).

Manipulative experimentation is a hallmark of many long-term research programs. As early as the 1970s, efforts were underway at the Experimental Lakes Area to understand the role of phosphorus in lake eutrophication. Lake 226 was divided with an impervious curtain and one side received carbon, nitrogen, and phosphorus while the other side received only carbon and nitrogen. During the course of the 8-yr study, only the phosphorus-enriched side experienced algal blooms (Schindler 1974). Early studies at the Hubbard Brook Experimental Forest focused on a watershed approach to understanding how forest management practices affect the biogeochemistry of terrestrial and aquatic ecosystems. Through experimental logging researchers were able to link deforestation to increases in the export of nutrients and

increased turbidity in streams (Bormann et al. 1974). Beginning in the 1980s, a series of whole-lake experiments at the University of Notre Dame Environmental Research Center (UNDERC) demonstrated how top-down predation by piscivorous fishes can control lake productivity via so-called trophic cascades (Carpenter et al. 1985). Later experiments focused on the joint role of top-down predation and bottom-up fertilization (e.g., Carpenter et al. 2001). To demonstrate reproducibility of the well-known Chl *a* response to nutrient additions, Pace et al. (this issue) used time-series data on nutrients, Chl *a* and other water chemical variables from UNDERC's Peter Lake over a 33-yr time period that included 9 yr when nutrients were added. Results were reproducible for seven of 9 yr when nutrients were added. Outliers in this case may help identify factors that modify the otherwise repeatable relationship (high water color and relatively large grazers). Studies began in Norway in the early 1980s to understand how harvest might affect fish communities in oligotrophic lakes (Amundsen et al. this issue). Through a series of massive fish removals in three different lakes, researchers drove shifts in fish diets through changes in age and size distributions of both predator and prey species. These are but a few of the many long-term studies that have yielded valuable insights through a dedication to careful data collection before, during, and after the manipulations.

Looking forward

The most exciting scientific challenges that now appear on the horizon are those of data integration and synthesis, taking advantage of technological advances to gain broader perspective through the synthesis of historical data sets with each other and with contemporary data. The Global Lake Ecological Observatory Network (GLEON) is a grassroots network of lake researchers with a common goal to build a persistent network of ecological data collection that can support collaboration leading to synthetic studies (e.g., Solomon et al. 2013) as well as shared tools for research (e.g., Winslow et al. 2018) and education (e.g., Carey et al. 2015). GLEON involves a variety of lakes around the world, some of which are using sensor data to build on historical lake sampling programs, and others that are newly established. Motivated in part by GLEON discussions, O'Reilly et al. (2015) synthesized in situ and satellite derived lake temperature data to reveal strong heterogeneity but overall positive warming trends throughout the lakes of the world, with the longer time series providing valuable insight into the strength and variability of trends.

Synthesizing historical and disparate data sets is far more challenging than the casual observer might anticipate (Hampton et al. 2013). Sociocultural issues around sharing data abound, such that incentives must be substantial to confront the technological and analytical challenges. Assuming that access to multiple data sets is possible, investigators will

then embark on a lengthy process of data-wrangling and iterative clarification with the data providers. Although some methods are common, such as the Secchi disk to measure water clarity, there is little standardization of protocols among programs. Further, the foci of programs differ depending upon the questions the program was designed to answer, such that measurements of the same process (e.g., photosynthesis) or compartment (e.g., primary producers) may be carried out in varied ways. Each program has idiosyncrasies, unrelated to the research questions, perhaps due to logistical or other constraints. When comparable data are finally aligned across data sets, suitable statistical frameworks can be applied to allow inference of patterns across systems, although such techniques are still relatively uncommon in the environmental sciences. Greater access to training in the required analytical and computational skills is needed to break new ground with these data, particularly as sensors open up many more possibilities for integration at a variety of scales (Hernandez et al. 2012; Hampton et al. 2017b).

Sensors allow investigators to be in many places at the same time, and to be in places that are logistically unfeasible to monitor (Hampton 2013). From instrumented satellites and aircraft to tiny tracking devices, sensors open up possibilities of simultaneously taking measurements at very broad spatial scales, and at very fine spatial and temporal scales, for a fraction of the time and cost otherwise expended. The fine spatial scale of in situ sensors is increasingly complemented by the capacity to use remote sensing (e.g., Pekel et al. 2016), often at coarser resolution but with vast spatial extent. The use of remote sensing products to infer nighttime "skin" temperatures, water level, and algal dynamics provide active and promising fields of research. Certainly it is exciting to contemplate the prospect of using spectral and imagery data to address global-scale questions about aquatic ecology, with this information available beginning in the 1980s. The publication of such a global-scale analysis of lake temperature sparked excitement in aquatic science some years ago (Schneider and Hook 2010), and a subsequent active dialog to resolve disagreements between long-term in situ lake temperature data with those that are inferred from satellite data (Lenters et al. 2012). Underlying causes for these disagreements could be the comparatively short duration of satellite records or variability in the correlation between nighttime skin temperature and in situ surface water temperature (Gray et al. 2018). More extensive ground-truthing and mechanistic work to refine temperature estimates and other potential remote sensing products, more collaboration among aquatic scientists and remote sensing experts, and availability of remote sensing products at finer spatial scales together will revolutionize the tractability of multi-decadal global lake studies.

While sediment cores are well suited for providing information on historical conditions, the synthesis with long-term observational data creates context for modern change. What

paleolimnological data may lack in completeness can be forgiven for the length of the records and the breadth of information that the sediments yield. Walsh et al. (this issue) use paleolimnological data to show that anthropogenic eutrophication was evident in Lake Mendota in the late 19th century, and that in recent decades quasi-seasonal phytoplankton dynamics recorded in the North Temperate Lakes LTER data appear to help reduce ambient phosphorus concentrations. Once the domain of fossil experts, paleolimnology now includes increasingly refined biogeochemical analysis of the sediments generating information about trophic interactions, such as algal pigments that indicate grazing pressure from zooplankton, and molecular techniques that can help to reconstruct population-level evolutionary change.

The emergence and refinement of statistical methods is also creating new opportunities for re-examining historical data, synthesizing information from across studies, and making forecasts of future conditions. State-space models account for both environmental stochasticity and observation errors due to non-exhaustive sampling, mistakes in identification, or changes in personnel. They also allow for the combination of different data types or changes in protocols or instrumentation. Among their strengths, state-space models can elucidate common trends or patterns in the data over time and space (Thorson et al. 2015; Ohlberger et al. 2016). For example, Barber et al. (this issue) used data from an extensive monitoring program in Puget Sound, Washington to examine the degree to which clams from adjacent beaches displayed population dynamics that were more similar than those from distant beaches.

In order for dreams of large-scale integration to be realized, investments must be made in (1) cyberinfrastructure and training that increase the capacity of aquatic scientists to use emerging technologies, and (2) mechanistic studies that help aquatic scientists to place appropriate bounds of inference on various sensor products.

Conclusion

In *The Log from the Sea of Cortez*, Steinbeck (1951) eloquently described the boredom that challenges the initially enthusiastic scientist over the course of time: “It is very easy to grow tired at collecting... At first the rocks are bright and every moving animal makes his mark on the attention. The picture is wide and colored and beautiful. But after an hour and a half the attention centers weary, the color fades, and the field is likely to narrow to an individual animal. Here one may observe his own world narrowed down until interest and, with it, observation, flicker and go out.” A vital aspect of long-term research programs is frequent returns on the investment of our attention, with programs designed to make shorter term scientific contributions even as the long-term questions are held in mind. The history of long-term research in aquatic ecosystems provides ample

demonstration of the rich rewards that can cascade from these investments.

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