Review Paper

The Lake as a System of Differential Equations – A Paradigm for the Aquatic Ecologist of the 21st Century?

key words: community dynamics, ecosystem dynamics, food web model, paradigm shift, population dynamics

Abstract

In the course of the 20th century limnology and oceanography have been transformed from purely descriptive disciplines to sciences that champion quantitative approaches and aim to reveal mechanistic relationships. In particular, the increasing use of mathematical formulations and models to understand lakes, streams and oceans as dynamical systems can be viewed as a paradigm shift. The mathematical-dynamical approach is irreversibly integrated into this field and has revolutionized aquatic ecology, although its gradual and on-going adoption is best characterized as an evolutionary process and, therefore, does not meet the criteria of the KUHNIAN concept of a paradigm shift. I here show how this new approach historically emerged from the understanding of lakes and oceans as complex yet decomposable systems and describe the development of the new paradigm into the 21st century. I explain methods of validation and give examples of successful applications of the mathematical-dynamical approach. I end with an outlook on some current, promising research directions that may influence the future path of this “ever-evolving paradigm shift.”

Seltsam ist Propheten Lied, doppelt seltsam, was geschieht
J. W. VON GOETHE, Weissagungen des Bakis

1. Mathematical Dynamic Models in Aquatic Ecology – an Incomplete Paradigm Shift

The face of aquatic ecology has changed significantly over the course of the 20th century. Limnology and oceanography have shifted from largely descriptive disciplines to sciences that embrace a dynamical ecosystem concept and attempt to understand the processes that generate the observed patterns. In particular, the use of mathematical formulations and models has emerged as a means to better describe, understand and predict the dynamical properties in lakes, streams and oceans. This new approach, bolstered by the microelectronic revolution and rapid increase in computing power, has drastically changed the way aquatic ecologists do their science; it could therefore be perceived as a paradigm shift as described by KUHN (1962). In this article, I have chosen to describe the integration of mathematical modelling approaches as an influential and promising development in aquatic ecology. However, it will become clear that the establishment of this new view does not fit particularly

1 Loose translation from German: “Strange is the prophet’s song, twice as strange is what really happens”.

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The notion that a system of differential or difference equations might be an appropriate representation of the dynamic nature of the biotic and abiotic components of a lake (or any other ecosystem) was not enthusiastically adopted by all aquatic ecologists. There was (and still is today) substantial scepticism whether mathematical equations, models and simulations are a useful tool for understanding the dynamics of aquatic ecosystems in general and for solving concrete conservation- and management-related problems. On the other hand, the new approach has gradually become an integral part of ecological science and is getting increasingly popular among aquatic scientists as revealed by the nearly exponentially increasing use of topical terms in the scientific literature since the 1960s and 1970s reveals (Fig. 1).

Why was the new paradigm so slowly accepted and why is the paradigm “shift” incomplete, i.e., it is still in progress? What are the reasons for the persistent scepticism toward mathematical-dynamical approaches in aquatic ecology? I believe there are two major explanations. First, in the early 20th century there was no tradition in limnology and oceanography of understanding the ecology and evolution of the system of study as a result of the dynamic change and the interaction of the systems’ constituent components. Although a detailed knowledge about the natural history of organisms and water bodies existed, it was not framed into a conceptual, let alone, mathematical theory of how the parts function as a system. Second, it is not obvious how a mathematical method that requires one equation per variable can be appropriately used to describe the system of sometimes hundreds of populations and resources that vary and interact in largely unknown ways with one another in aquatic ecosystems. I believe it is this persisting problem that prevents the mathematical-dynamical approach to aquatic ecology from becoming fully established as a paradigm. While there is general agreement that it would be useful to describe the dynamics of a lake or the ocean based on the first principles of population growth and material and energy

Figure 1. Increasing use of mathematical models in aquatic ecology since the 1960s. The graph shows the almost exponential increase of relevant terms appearing in the topic of research papers. Search 1: “mathematical” AND “model” AND (“lake” OR “ocean”); Search 2: “dynamic*” AND (“differential equation” OR “difference equation”) AND (“lake” OR “ocean”). Publication counts were generated with Thomson ISI Web of Science®, December 2007. Three publications prior to 1960 were omitted.
transfer, the appropriate methodology and the degree of allowable reductionism are currently still contentiously debated and the subject of theoretical and empirical research.

Reflecting on “dynamical mathematical approaches in aquatic ecology” as an incomplete paradigm shift I will give a brief overview over the historical development of the paradigm, explain how the approach can be validated, and highlight two influential examples that have more recently adopted this approach. I will conclude with an appreciation of current progress and ideas on the topic and speculate about the contribution of the new approach to the aquatic sciences of the 21st century.

2. Detecting the Dynamic Dimension of Aquatic Systems

STEPHEN FORBES’ (1887) influential paper “The Lake as a Microcosm” was a forerunner of several familiar concepts in ecology. First, FORBES informs us in his paper about the ecological community dynamics that occur in a lake and how they might arise from the interaction among species. Second, he considers the interdependence of lake organisms with their abiotic environment, thereby describing a rough concept of the lake as an ecosystem (a term introduced almost fifty years later by TANSLEY). Third, he recognizes the lake as a “microcosm”, i.e., a relatively isolated and simple system that can be studied with the intent of gaining insight into how natural systems function in general. Although neither being a manifesto of ecosystem dynamics nor advocating any quantitative approaches, FORBES’ paper set the stage for the ecological direction that limnology took early in the 20th century. The editorial “Prospectus” of the first issue of the “International Review of Hydrobiology” is a testimony to this spirit. The agenda that the editors set for the new journal sound quite up-to-date, even a hundred years later: they recognize “the necessity of a synthesis of our biological and hydrographic-geological knowledge of the waters” as well as that “the biology of the waters has now passed from the description of what is found therein to inquire into the causes and origins of the animal and plant life”. In line with the not yet formalized ecosystem concept they identify as a problem of special importance “The biological economy of the waters as a self-contained whole: the cycle of organic materials from the phytoplankton through the zooplankton to bottom mud and to the nitrogenous compounds of the surface waters” (all citations from HELLAND-HANSEN et al., 1908).

In his groundbreaking lake ecosystem study “The trophic-dynamic aspect of ecology” RAYMOND LINDEMAN (1942) achieved these goals at an unprecedented level of rigor and conceptual insight. LINDEMAN not only explicitly studied the dynamic aspects of organismal succession in a lake but also provided a quantitative treatment of several modern ecological concepts that have influenced ecological research until today: the ecosystem approach, i.e., LINDEMAN’s “food cycle” which includes trophic food web interactions as well as decomposition and recycling of material; an emphasis on the transfer of energy across trophic levels and, related to this, the notion of biological efficiency that determines levels of productivity in the food chain. In the second half of the 20th century, LINDEMAN’s paper stimulated an important and influential school of ecological thinking that advocated a systems approach to ecology and was most prominently represented by H. T. ODUM and his work on the dynamics of energy flow in the Silver Springs ecosystem (ODUM, 1957). ODUM (1971) also introduced a computer-based symbolic modelling language technique for simulating the flow of energy through ecosystems.

Already in the 1920s, however, LOTKA (1925) and VOLterra (1926) had developed a mathematical approach to describing “ecosystem” dynamics that was based on formulating the dynamics of interacting populations as coupled differential equations. The famous original Lotka-Volterra equations of predation and competition are derived from physical analogs and describe the dynamics of two populations whose individuals interact like the molecules of ideal gases. Interestingly, VOLterra’s inspiration to devise the new mathematical method
originated from the phenomenon of waxing and waning fish populations in the Adriatic Sea and the notorious Lotka-Volterra oscillations were, at least, qualitatively in agreement with these observations. The Lotka-Volterra equations are, of course, extreme simplifications and a long way from representing the structural, behavioural or spatial complexities of natural ecosystems. Nevertheless, these equations – subject to further refinement and generalization (e.g., Nicholson and Bailey, 1935; Rosenzweig and MacArthur, 1963; May, 1973) – are the mathematical tool used in the vast majority of theoretical food web and ecosystem studies up to the present time. In the 1960s, two eminent ecologists, G. Evelyn Hutchinson and Robert MacArthur, began to formally apply the mathematical method based on ordinary differential equations (ODEs) to a series of more general ecological problems, such as the coexistence of species whose niches overlap (“limiting similarity”, MacArthur and Levins, 1967) or the coexistence of a large number of species on a limited set of mineral resources (“paradox of the plankton”, Hutchinson, 1971).

Hutchinson was an ecologist but he was also a limnologist. Yet, I know of no serious attempts by him or his contemporaries to simulate the community dynamics observed in a concrete lake ecosystem with the predictions of population-based models. This is most certainly due to the limited computational capabilities that existed in the 1960s. The analytical tools and, particularly, the microprocessor-based computational power that are at our disposal today have made possible the quick assessment of large, even non-linear systems of equations which was beyond imagination a few decades ago. Advances in the process that Lotka and Volterra started in the 1920s were therefore linked to progress in other disciplines (mathematics, computer science), which explains the intermittent character of the paradigm shift. Notwithstanding, one of the persistent questions remains whether the dynamics of a system as complex as a lake or ocean can ever be realistically simulated by decomposing and re-assembling it from the dynamic behaviour of its supposedly smallest units of (inter)action, populations and nutrients. It comes down to the questions “Is the whole system more than the sum of its parts?” and “Can we identify the right parts and their attributes that are essential for the functioning of the whole?”

3. Microcosm Studies as a Link between Mathematical Models and Real Ecosystems

Experimental microcosm studies can be useful tools for answering these questions because the dynamics of sparse, well-defined communities can be investigated under constant environmental conditions and in replicated trials. Today’s aquatic experimental microcosms differ from Forbes’ notion of a microcosm in that – rather than whole communities or ecosystems – downscaled, understandable versions of them are studied in the laboratory. Some ecologists are highly critical of this approach (Carpenter, 1996). I feel this is because they wrongly assume that laboratory microcosms are meant to be perfect analogs of real systems. As Jessup et al., (2004) put it very aptly “the purpose of laboratory model systems is to simplify nature so that it can be more easily understood” and “If we cannot accurately predict the behavior of a simplified laboratory system, it is unlikely we understand enough to make predictions of field systems.” The predator-prey cycles that the models of Lotka and Volterra (and modernized versions) produce as well as the predictions about coexistence and exclusion of competing populations have stimulated a great number of laboratory tests of these theories (e.g., Gause, 1934; Halbach, 1970; Rothhaupt, 1988; Grover, 1997). A common problem in the interpretation of many of these tests is that the observed dynamics are potentially due to a multitude of mechanisms that are difficult to control even in the laboratory. Oscillatory population dynamics, for instance, can arise in mathematical models due to predator-prey interactions, delayed density-dependence, population structure
etc. I participated in a series of more recent studies investigating the community dynamics of an algal-rotifer predator-prey system in experimental (and mathematically tractable) flow-through systems. We found that a relatively simple ODE model captured the qualitative dynamical behaviour of the system quite well, including equilibria and population cycles (Fussmann et al., 2000). However, we also detected that the algal populations underwent cyclical evolution during the population oscillations. This surprising biological complexity needed to be accounted for in our model to achieve a quantitatively satisfying fit to the observed microcosm dynamics (Yoshida et al., 2003). In the light of these findings coming from a supposedly simple, heavily controlled two-species system it appears highly unlikely that a deterministic model that accurately predicts the dynamics of a natural system as complex as a lake ecosystem could ever be generated. Does that mean there is no role for population-based models as a predictive ecological tool? Not necessarily. We just need to be clear about their role. We will never be able to predict the exact future state of the components of an ecosystem to the degree we can do this for the planets in our solar system. Recent evidence for chaotic dynamics in natural ecosystems (Beninca et al., 2008) makes this an even more unlikely proposition. However, dynamical models may still be able inform us about the general dynamic consequences of certain ecosystem properties or interventions such as the removal of species, the number of trophic levels, the degree of connectivity of the community or the importance of nutrient recycling. Before I expand on these points I will give two examples of how theoretical ecologists have used mathematical models of different complexity to address concrete problems in an applied context.

4. Mathematical Models Applied to Aquatic Conservation and Fisheries: Two Examples

All sea turtle species are listed as either endangered or threatened species. They spend most of their lives at sea but return to land to lay their eggs on beaches. Eggs and hatchlings are subject to predation and human disturbance and, traditionally, most conservation efforts focused on protecting these life stages (Caswell, 2001). Crouse et al., (1987) developed a stage-structured matrix model to predict the population growth rate of the loggerhead sea turtle (Caretta caretta) in the southeastern United States and used this model to identify potentially more effective conservation strategies. The model considers only one species (Caretta) but keeps track of several life stages and the transition probabilities between these stages. In a simplified version with five life stages (Crowder et al., 1994) the stage class matrix population matrix takes the form:

\[
A = \begin{pmatrix}
P_1 & F_2 & F_3 & F_4 & F_5 \\
G_1 & P_2 & 0 & 0 & 0 \\
0 & G_2 & P_3 & 0 & 0 \\
0 & 0 & G_3 & P_4 & 0 \\
0 & 0 & 0 & G_4 & P_5
\end{pmatrix}
\]

where the indices 1 to 5 refer to the five life stages eggs/hatchlings, small juveniles, large juveniles, subadults, adults and \( F_i \) is the stage specific fertility, \( P_i \) the probability of surviving and remaining in the current stage and \( G_i \) the probability of surviving and remaining and growing into the next stage. After parameterization the matrix can be multiplied with a population vector resulting in an estimate of population size for a discrete time step in the future: \( An_t = n_{t+1} \). Iteration of this operation leads to a stable rate of population growth;
alternatively, the eigenvalue of the matrix can be computed (Caswell, 2001). Not surprisingly, the procedure yielded a negative growth rate for the turtle population, reflecting the need for protection. By selectively changing fertility entries and survival probabilities in the matrix Crouse et al., (1987) simulated different conservation strategies and their differential effect on turtle growth rates. They found that the most promising protection measures should be aimed at increasing survival probability rather than fertility and that increasing survival of life stages out at sea would be much more effective than protecting eggs, nests and hatchlings.

The results of these simple model simulations have since led to the implementation of changes in sea turtle management, notably the introduction of fishing nets with turtle excluder devices that reduce the risk of death of sea turtles as bycatch. Turtle excluder devices significantly reduced strandings of sea turtles relative to the estimated effects of shrimp trawls without these devices (Crowder et al., 1995). Because loggerhead sea turtles are long-lived it is too early to pass a final judgment about the success of this model-guided management program but the model analysis suggests that the reduction in mortality should be sufficient to return the population to positive growth rates (Crowder et al., 1994).

The second example is concerned with the concrete case of the Benguela oceanic food web. Hake (Merluccius spp.) is a commercially important fish in this ecosystem that is harvested by humans but also preyed upon by natural predators, in particular by Cape fur seals (Arctocephalus pusillus). This suggests that the – contentious – culling of fur seals could potentially have a positive effect on the hake fishery. Yodzis (1998, 2000) evaluated whether this reasoning based on the simple trophic module human-hake-seal would hold up in the complex context of the full Benguela food web. Yodzis analyzed a (still simplifying) 29-taxa dynamical model of the food web based on coupled nonlinear ODEs and was able to extract the quantitative response of hake and several other commercially valuable fishes to a seal cull. Because it is impossible to fully parameterize such a complex system some of the parameters were assumed to be randomly varying and potential gains in fish yield were computed as probability distributions. The surprising, concrete result of these analyses was that, although a cull of seals may benefit particular fish species it is more likely to be detrimental to total fish yields than it is to be beneficial (Yodzis, 1998). The more general lesson that can be learned from this multi-species food web modelling approach is that indirect, diffuse effects may modify or even reverse direct effects in food webs and that “a modular view of the system, in which only a small subset of species in the system is taken into account, is not a sensible approximation […]” (Yodzis, 2000).

5. Dynamic Modelling Approaches for Aquatic Ecosystem Complexity: the 21st Century

The two examples in the previous section have demonstrated the important role that models can play in aquatic ecology. Mathematical models can make predictive “suggestions” about the dynamic behaviour of a complex ecosystem for some period of time into the future and describe how this system is likely to react when perturbed. This is an invaluable resource of information, particularly when experimental approaches are impossible because the ecosystem in question is unique and irreplaceable or characterized by reaction times that are long compared to the human life span. The value of this information depends, of course, critically on its quality, i.e., the accuracy of the predictions. Even with the enormous increase in computing power that we will undoubtedly see in the 21st century dynamic models will always remain simplifications of nature, not least because ecologists lack sufficient knowledge about their natural history to parameterize ever more complex versions. The key challenge is to decide which level of sophistication and detail is needed for a model to
generate predictions that are useful for the problem at hand and how much simplification is permissible. This question is probably as old as the modelling approach itself but finding satisfying answers to it may occupy theoretical ecologists for quite a while longer. Continuing development of mathematical models for aquatic ecology as an “evolving paradigm” may also require some thinking outside the box of the traditional systems of differential and difference equations. In recent years, ecologists have presented some promising alternative approaches. There is not the space here to explain these ideas in great detail but I will present some of them as an outlook on how this field might develop.

One important task is to identify the appropriate lowest unit that acts and interacts in the aquatic ecosystem. In the classical approach, resources and populations of organisms constitute these units, which implies that all members of a population are assumed to be identical. The first example in the previous section showed, however, that considering the structure that exists within populations is often crucial for understanding dynamics of populations. Theoretical and experimental aquatic ecologists have identified many more cases that require explicit consideration of population structure to adequately describe the system dynamics (Persson et al., 2003; Nelson et al., 2005). Keeping track of structure in a community or ecosystem context is a mathematically challenging task but theoreticians have made great progress in developing advanced techniques (De Roos et al., 1992). A similar challenge is the non-deterministic element in the behaviour of all natural systems. Stochastic difference and differential equations are one method to allow for the additional random noise that accompanies and interacts with the deterministic dynamics. Aquatic modellers can benefit from the development in other disciplines (e.g., infectious disease dynamics) where these techniques are already frequently used (Stollenwerk et al., 2004).

A different, more radical modelling approach abandons the one-population-one-equation concept altogether and aims to understand the emergence of system-level properties based on individual organisms as agents. A set of rules determine the actions of each individual and the interactions with its environment and the system dynamics can be observed through computer simulations. This type of model is particularly promising when agents make individual decisions about their behaviour and a unifying methodology is being developed to build structurally realistic models within this framework (Grimm et al., 2005).

A special, but for natural systems extremely relevant aspect is the genetic structure of populations. We are only beginning to unravel how biodiversity among species and genetic diversity within species both contribute to the dynamics and community composition in aquatic ecosystems (e.g., Reusch et al., 2005; De Meester et al., 2007). Considering genetic (and the resulting phenotypic) differences in aquatic populations is not only ecologically important, it also opens the door for evolutionary change as an important component in aquatic systems. There is recent evidence that ecological and rapid evolutionary mechanisms may frequently codetermine the dynamics of aquatic populations and communities (Fussmann et al., 2003; Yoshida et al., 2003) and it is a field of active research how these two processes are best combined in a modelling framework (Hairston et al., 2005; Fussmann et al., 2007).

The list of challenges for the dynamical modeller of aquatic systems is long and includes the appropriate accommodation of the spatial organization of aquatic ecosystems (Holyoak et al., 2005), of their hydrology and fluid mechanics (Huisman et al., 2006), the role of nutrient recycling (Loreau, 1996) and the question how aquatic ecosystems will respond when facing global environmental change. We will continue to answer these questions by formulating extended and refined versions of population-based equation systems. At the same time, we need to be open to novel approaches that challenge these traditions; for instance, Ginzburg and Colyvan’s (2004) idea to model populations as second order differential equations to allow for transgenerational, maternal effects or the suggestion of McGill et al., (2006) that a more general understanding of community dynamics can be achieved by a niche-based approach that emphasizes the functional traits of species in the context of environmental gradients.
Mathematical modelling has certainly revolutionized aquatic science, even though its adoption was an evolutionary process. I am convinced that, in the future, mathematical models will play an even greater role for the analysis of aquatic systems than they have during the eighty years since LOTKA’s and VOLterra’s groundbreaking contributions. I believe this will be a useful and necessary development that will help ecologists master the environmental challenges of the 21st century and their impact on aquatic systems. I also do believe in the diversity of approaches that currently exist in aquatic ecology. It would be undesirable and counterproductive for the progress of our science if paradigm shifts could only be KUHNIAN and needed to replace all competing views and ways how aquatic science is done.

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7. References


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