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Nonlinear dynamics, resilience, and regime shifts in aquatic communities and ecosystems: an overview

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This Special Issue contains 31 papers that collectively advance understanding of nonlinear dynamics, resilience, and regime shifts in aquatic communities and ecosystems. These papers make two basic contributions:

1. They further advance the study of resilience and regime shifts from theoretical to empirical science.
2. They expand the systems and characteristics that we can understand through the lenses of nonlinear dynamics, resilience, and regime shifts, demonstrating that these concepts are broadly applicable throughout the aquatic environment.

Within this context, several themes emerge, including processes of disturbance and recovery, changing trends, contingent and historical attributes, extreme events, compensation, and synchronization. These topics are not the result of any design by us as editors but rather reflect the diverse topical interests of the field resulting from the open submission of papers to the Special Issue. Collectively, these themes represent many of the important ideas driving modern study of aquatic systems, especially in response to large-scale environmental change.

The transition from theoretical to empirical science

A central concept in the Special Issue is resilience—the persistence of relationships in a way that absorbs changes and maintains function. Many authors consider processes that promote resilience, for example, in the oligotrophic ocean (Martiny et al. 2022) and in seagrasses (de Smit et al. 2022). Stability is a feature of resilience reflecting the ability to recover from temporary perturbations. Models of Southern Ocean plankton point to the importance of feedbacks among phytoplankton, their chemical cues (dimethyl sulfide), and grazers, in maintaining stability (Ward et al. 2022). Experiments with macroalgae removal quantify the ability of species to recover relative to the size of perturbations, and the long-term study of a set of manipulations uncovered features that stabilize alternative states (Dudgeon and Petraitis 2022). Carpenter et al. (2022) present a statistical approach to quantifying resilience by determining the average time between crossings of a critical threshold between ecosystem states. These studies are not alone in their concern for resilience, which is mentioned in nearly all papers of this Special Issue. What we see in these studies are attempts to operationalize and apply resilience, moving from a conceptual to an empirical framework.

The future of aquatic ecosystems is contingent on past and present conditions, which makes empirical analysis challenging due to the short-term nature of most research programs. Several contributions consider historical attributes using paleo-analyses to characterize changes in communities of diatoms in Ecuadorian lakes (Benito et al. 2022), and chironomids in both Chinese (Zheng et al. 2022) and Alaskan (Mayfield et al. 2022) lakes. While chironomid shifts show the strong impact of human disturbances, diatom communities demonstrate remarkable resilience over the past two centuries. These three studies illustrate the value of long-term records, which is further emphasized in a study of community composition of plants in boreal lakes. Specifically, García-Girón et al. (2022) conduct a metacommunity analysis that uncovers the importance of priority effects (meaning order of species establishment) and reinforces the conclusions of the three paleo-studies: history shapes community composition and responses to human drivers.

In time series analysis, stationarity—a constant mean and variance—is a desired property. The world, however, is nonstationary with the expectation that the future is likely to be even more so as climate and environmental changes push ecosystems away from equilibrium states. Aquatic scientists wish to describe, understand, and even forecast changing trends, and several papers take up this challenge of finding ways to analyze change. Deeds et al. (2022) use multiple types of

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reference lakes and the method of divergent trend analysis to document changes in clarity of Maine (USA) lakes due, in part, to precipitation. Their results lead to the inference that increases in precipitation predicted by climate models may reduce lake water clarity in the future, independent of other effects such as eutrophication or its reversal. A well-established trend for inland waters is the shorter duration of seasonal ice cover, raising questions about how changes in winter ice affect seasonal phenology. Modeling this process along a latitudinal gradient for an exemplar lake reveals a change-point between the date of ice breakup and the variability of the spring mixing period, with effects extending to summer stratification (Pilla and Williamson 2022). In this study, climate and latitudinal seasonality interact to produce differential impacts foreshadowing the types of complex effects that will result from warming.

The changes in trends exhibited in the studies of clarity in Maine lakes and lake ice-cover phenology may indicate simple linear or curvilinear shifts in trajectories or tipping points where a system moves abruptly and sometimes irreversibly in a new direction. Carrier-Belleau et al. (2022) review tipping point studies and find that while the number of such studies is increasing, few quantify thresholds or consider how and whether multiple stressors alter tipping points. A clear challenge for future research is to identify and analyze the location of thresholds and consequences of changes to threshold values, especially in relation to multiple stressor impacts.

Extreme events cause nonlinear change that can be temporary or permanent. Expectations for increased frequency and intensity of heatwaves, floods, and storms are motivating research to investigate the consequences of these events for aquatic ecosystems. Aho et al. (2022) measured nitrous oxide evasion from streams and observed large shifts associated with an intense storm and subsequent wet period. Changes in evasion were persistent, which reflects alterations to nitrogen cycling caused by the storm. Recovery occurs after most storms, and Thayne et al. (2022) analyze recovery along with resistance to disturbance of a lake after 25 extreme wind events. The type of repeated analyses of disturbances conducted by Thayne et al. (2022) indicates the possibility of analyzing resilience of aquatic systems through time and how this property might either be relatively stable or degrade. The examples of extreme studies in this volume demonstrate their importance for forecasting future change and should motivate new studies of the impacts of extreme weather over time both within and among aquatic ecosystems.

Many aquatic processes are nonlinear such as Michalis-Menten nutrient uptake and first-order decomposition. However, documenting nonlinear relations in aquatic systems is typically difficult because of stochasticity, limited data, and similarity of fit among alternative models (e.g., linear vs. curvilinear functions). Studies in this volume provide both examples of, and approaches to, documenting nonlinear patterns using comparative data as well as modeling. Holgerson et al. (2022) use a large compilation of data from lakes to document nonlinear patterns between two drivers—nutrients and dissolved organic matter—and three processes—gross primary production, ecosystem respiration, and consumer allochthony. Another comparative study indicates the joint and complex impacts of nutrient enrichment and fish predation on zooplankton community diversity and network structure (Li et al. 2022). Wasserman et al. (2022) implement a nonlinear forecasting method (i.e., empirical dynamic modeling) to analyze abiotic and biotic factors affecting two fish species, one of which is endangered. A long-term whole-lake nutrient fertilization experiment illustrates another approach to documenting nonlinearity and reveals a variety of ensuing responses (Budy et al. 2022). Trophic groups—phytoplankton, zooplankton, and fish—did not always increase with fertilization, nor were changes uniform across groups but instead reflected apparently subtle and indirect effects.

Compensatory replacement of species can sometimes maintain processes in the face of change. In tropical streams, Barnum et al. (2022) find that loss of tadpoles due to disease leads to an incomplete replacement of one of their functional roles—grazing on benthic diatoms. Tadpole grazing effects were not completely replaceable by compensatory responses from insects, and shifts in grazing effects were not uniform across habitats. This study also points to a topic considered in several other papers about changes in biodiversity and its consequences (e.g., Benito et al. 2022; Li et al. 2022; Rii et al. 2022). Resilience is often tied to biodiversity, and the rapid loss of species from aquatic systems, particularly lakes and rivers, suggests widespread loss of resilience.

Application to diverse systems

Loss of resilience may lead to transformation to an alternative state. Many papers in this volume document state changes and processes associated with these shifts in diverse systems and regions. In the Loire River (France), a shift from phytoplankton to macrophyte dominance resulted in modest declines in gross primary production and ecosystem respiration, illustrating partial conservation of function (Diamond et al. 2022). Long-term observations of the Baltic Sea indicate the existence of a series of regimes that establish and wane through the interactive and time-varying effects of eutrophication, climate, hydrography, and fishing (Tomczak et al. 2022). Sangil and Hernandez (2022) document mass mortality of sea urchins in the Canary Islands (Spain) that results in establishment of stable states of non-crustose macroalgae. These researchers document the threshold density of sea urchins at which shifts occur and the long-term permanence of the algal state after urchin die-off. Benthic communities in Moorea (French Polynesia) are dominated either by coral or macroalgae, with the latter establishing more readily when herbivory drops below thresholds (Schmitt et al. 2022). Intriguingly, the fate of fish herbivores on the reefs of Moorea is tied to fisher behavior that selects for low macroalgal sites (Rassweiler et al. 2022). Thus, ecological and socio-ecological dynamics influence the algae–coral regimes.

Some of the oldest and most convincing examples of regime shifts come from the study of shallow lakes. In this volume, long-term studies of larger and deeper lakes reveal regimes of water clarity and phytoplankton related to food web shifts in a north temperate lake (Trout Lake, Wisconsin, USA) (Martin et al. 2022) and to climate-driven changes in the inputs of colored dissolved organic carbon in a subtropical lake (Lake Annie, Florida, USA) (Sullivan et al. 2022). Collectively these studies of regime shifts, as well as others presented in this volume (e.g., Benito et al. 2022), indicate that ecosystems under the influence of changing internal and external forces can move quickly to a different and long-lasting state, affecting ecosystem services. The studies expand our understanding of the causes of resilience, the places where regime shifts occur, and highlight the value of long-term data.

Disturbances and subsequent recovery of marine and inland water populations, communities, and ecosystems are illustrated in studies of tidal salt marsh creeks subjected to erosion (Wu et al. 2022), oceanic food webs affected by a major oil spill (Lewis et al. 2022), picoplankton communities disturbed by episodic physical forcings in the upper ocean (Rii et al. 2022), and small pelagic fish populations in relation to changing fisheries management (Dias et al. 2022). While disturbances are often obvious, these studies document the recovery process through the use of numerous metrics. Interesting approaches, including network models and multivariate statistical analysis, are applied to complex patterns of recovery from real-world disturbances with consequences for conservation and resource populations. Such approaches should have wide potential use and demonstrate the maturation of the ecosystem properties for which we can measure resilience and recovery processes. In the context of this Special Issue, these observations illustrate how the application of new methods often goes hand-in-hand with the investigation of new systems.

Synchronization of the dynamics of separated populations has long been interpreted as reflecting controls by underlying environmental factors varying in common across space—the so-called Moran effect. Buttay et al. (2022) identify a different type of synchronization where diatom populations within the same system—the Canary Current upwelling—shift from asynchrony to synchrony when upwelling intensifies. Using a model, they attribute change in competition from multiple nutrients to a single resource (silica) as the cause. This study of synchrony represents a topic of growing interest, especially as high-frequency and long-term time series for variables ranging from population abundance to chemical concentrations become increasingly available. Such analyses can reveal clues about the drivers across the different temporal scales that structure aquatic systems.

Concluding remarks

In closing, we thank the authors for this rich collection of contributions. We encourage readers to consider the many themes collectively represented and to read beyond their salinity of interest with the hopeful benefit of seeing new ideas and new approaches.

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Conflict of interest

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