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Causes and Consequences of Spatial Heterogeneity in Lakes

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Abstract

Lakes, far from being the homogeneous environments we might expect, offer a rich and dynamic heterogeneity at multiple spatial and temporal scales that we are just beginning to understand. At the within-lake scale, a complex set of phenomena such as internal waves and stream intrusions leads to both horizontal and vertical heterogeneity. Developing an understanding of whether and how this heterogeneity affects ecosystem processes is in its early stages, but nutrient movement both horizontally and vertically may be more structured than previously conceptualized and will depend on interactions among nutrient loading, stratification, surface meteorology, and basin morphometry. Within a landscape, lakes often differ from each other both in their average characteristics and in their among-year dynamics. Much of this heterogeneity has been linked to how water flows across the landscape. In landscapes dominated by groundwater flow, there is often more heterogeneity in lake characteristics and response to climatic events than in landscapes where exposed bedrock leads to rapid horizontal transport of water. Humans can affect heterogeneity across lakes by causing changes in land use and cover and within lakes by simplifying the physical structure of the littoral zone.

Introduction

Lakes exhibit spatial heterogeneity at many different spatial scales. From the parallel Langmuir streaks (Langmuir 1938) commonly seen by airline passengers, to among-lake differences in chemical and biological properties (Juday and Birge 1933), to regional differences in origin and setting (Soranno et al. 1999), lakes are not uniform across space (Richerson et al. 1978). Understanding the causes of spatial heterogeneity within and among lakes has been a long-standing goal of limnologists.

For the casual observer, lakes appear as discrete units delineated by their shoreline and defined by surface phenomena. This perspective implies a disconnection from external forces and internal processes. Instead, we know that lake ecosystems are shaped by abiotic and biotic forces resulting in substantial heterogeneity both within and among lakes. At broad spatial scales, geomorphic setting constrains the expression of lake features (Magnuson and Kratz 2000; Riera et al. 2000). The geology and landforms of a region dictate hydrologic flowpaths and the biogeochemical transformations that occur as water flows from the terrestrial to aquatic system (Winter 2001). Landforms characterized by steep slopes, high elevation, or hydrologic isolation can set barriers to dispersal of organisms. Climate influences seasonality of hydrologic flows, affecting the delivery of water and solutes to lakes, and sets temperature regimes that physiologically constrain species distributions. Taken together, these factors set limits on the physical properties, biogeochemistry, and biotic assemblages of lakes within a region.

Within a region, the seeming uniformity of lakes observed from the air is belied by significant among-lake variation. Lakes are hydrologically connected to their catchments, and thus their chemistry reflects inputs of nutrients and other solutes in runoff. Adjoining wetlands supply humic material, influencing lake-dissolved organic carbon and water color (Gergel et al. 1999) and, subsequently, the attenuation of light energy through the water column (Snucins and Gunn 2000). Lake size has a fundamental influence on a range of ecosystem properties of lakes including the relationship between lake depth and nutrient cycling and between lake area and productivity (Fee et al. 1992), thermal regimes, and species richness (Magnuson et al. 1998).

Within individual lakes, substantial heterogeneity exists in both near-shore (littoral) and deeper open-water (pelagic) zones. Since the late 1800s, limnologists have recognized the vertical thermal stratification characterizing many north temperate lakes during the summer (Kalff 2002). Warming of surface waters sets up density gradients that eventually separate the warm upper layer from denser and colder bottom waters. This seasonal stratification cycle generates considerable spatial and temporal heterogeneity in the open water zone of lakes in temperature, dissolved oxygen and other gases, nutrient cycling, and distributions of fish, invertebrates, and algae. The littoral zone exhibits patchy structural complexity as slope and wave action affect sediment composition, macrophyte community composition, and woody structure (Kalff 2002). Changing physics and chemistry induce a dynamic template for biological interactions such as competition and predation, as well as cycling of energy and nutrients throughout food webs. All these factors shape biological communities and ecosystem processes.

Here we examine heterogeneity in lakes, its causes, and its effects on ecosystem processes at two spatial scales that have been a focus of intense research over the past decade. First, we focus on within-lake heterogeneity related to physical processes operating at fine spatial and temporal scales. We address variation in hydrodynamics within lakes related to basin size