Appendix 19

Excerpt on the Limnology of Flathead Lake from J. A. Stanford and B.K. Ellis. 2002. Natural and Cultural Influences on Ecosystem Processes in the Flathead River Basin

The pages that follow are excerpted from *Natural and Cultural Influences on Ecosystem Processes in the Flathead River Basin (Montana and British Columbia) In: Baron, J.S. (ed.) Rocky Mountain Futures: An Ecological Perspective. Island Press, Washington D.C.*

Limnology of Flathead Lake

Flathead Lake is one of the least culturally eutrophied (nutrient-enriched) large lakes in the Northern Hemisphere (figure 14.1). With an area of 480 km^2 (185 $mi.^2$) and volume of 23.3 cubic kilometers (km^3), or 5.6 cubic miles ($mi.^3$), seasonal heating and cooling is slow, and the lake moderates regional temperature and precipitation patterns. Surface temperatures range from freezing during midwinter in very cold years to a maximum of 22°C during late summer in hot years. Summer stratification is intense, however, and a thin layer of warm water, the epilimnion, lies above most of the volume of the lake. Below the epilimnion, water temperatures never exceed 6°C–8°C. The lake circulates to the bottom all winter in most years, with the entire water column reaching 2°C during very cold winters and briefly freezing over during calms. Stratification initiates in June, and fall turnover typically occurs in late October. The less dense water near shore circulates counterclockwise around the colder water in the main part of the lake, owing to gravitational force associated with Earth's rotation. This Coriolis current entrains the inflow from the Flathead and Swan Rivers and pulls the river water down the western shore. This is very observable during spring freshet (snowmelt), when the river is turbid and warmer than the main lake. The turbidity plume of river water overflows the denser, colder lake water and moves down the western shore, the dirty brown water appearing in strong contrast to the blue waters in the deeper parts of the lake. The Coriolis current persists all year but is less observable in fall.

Most of the year, Flathead Lake is crystal clear. Fine sediments from the Flathead River freshet reduce clarity during spring, depending on the intensity of the runoff. Nonetheless, the average depth of visibility, or Secchi disk, since 1975 has been 9 m (30 ft.), with values exceeding 20 m (66 ft.) often recorded

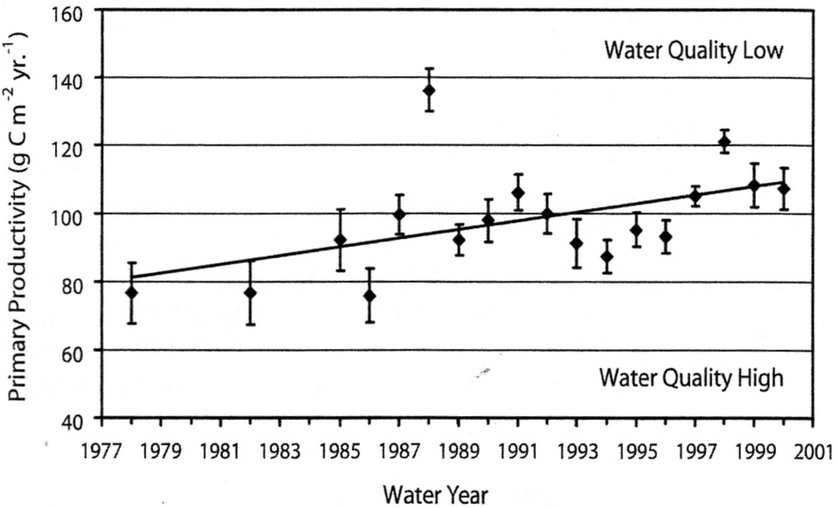

FIGURE 14.1 *Water Quality in Flathead Lake Measured as Annual Rate of Primary Production, 1977–2001.* Primary production was measured with ^{14}C uptake in 4 hr. midday incubations using methods of Pregnall 1991. Data are means (±1 standard deviation) of 12–15 measures throughout each year. The trend line is significant ($P < 0.01$): water quality is deteriorating as primary production increases.

in fall. Biomass in the lake is uniformly low (1.0 microgram [μg] of chlorophyll per liter [L] of water) year-round. Pelagic primary production is limited by paucity of nitrogen (N) and phosphorus (P) (figure 14.1; Spencer and Ellis 1990). As noted earlier, the river system does not export much of a nutrient load. Surprisingly, as much as 30% of the annual N and P load during the 1980s and 1990s was fallout from the atmosphere. This was mainly fugitive dust from local rural roads and smoke particulates from forest fires and agricultural burning inside and often far outside (usually west of) the Flathead basin. Nutrient loading from human sources upstream of Flathead Lake has steadily increased since the 1970s, and annual loading weakly correlates with increasing primary production.

Organisms smaller than 10 μm (microplankton), mostly bacteria and very small green and blue-green algae, are responsible for 90% of the total primary production (Ellis and Stanford 1982). But diatoms (more than 400 species and varieties), dinoflagellates, and other macroalgae are always very visible in plankton samples. A vernal bloom of large diatoms occurs in spring along with the microplankton in response to elevated nutrient levels, increasing day length, and warming water. By late summer, when the lake is thermally stratified, primary production and sinking of plankton to the bottom depletes nutrients in the surface waters, and productivity begins to decline.

In 1984 and 1994, lakewide blooms of macroalgae, *Anabaena flos-aquae* and *Botryococcus,* were documented prior to fall turnover. These algae had never been observed in Flathead Lake during 100 years of lake studies. The algae collected in windrows on the shoreline and clearly represented sudden and alarming declines in water quality. *Anabaena* and *Botryococcus* were common in late-summer samples in other years but did not reach bloom proportions. These outbreaks of macroalgae very likely are linked to increasing nutrient inputs from human activities. Similar patterns of lake eutrophication, of course, have been documented many times worldwide, and the federal Clean Water Act requires states to reduce nutrient loading in impaired lakes.

Efforts to reduce nutrient pollution from human sources have been initiated in the Flathead basin in response to the apparent decline in water quality associated with steadily increasing primary productivity and the observed *Anabaena* blooms (figure 14.1; Stanford et al. 1997). However, the mechanisms and interactions that cause these rare events in Flathead Lake and other large lakes are not clear. Certainly primary productivity is at or approaching a threshold in which complex interactions favor production of macroplankton over microplankton.

The highest annual rate of primary production occurred in 1988, corresponding with onset of the trophic shift caused by establishment of *Mysis relicta* in the lake (figure 14.1). Mysid numbers peaked in 1986–1987. The food web shift from pelagic (open-water) to benthic (bottom-dwelling) orientation was firmly in place for the first time in 1988. This suggests a top-down stimulus on phytoplankton production: the mysids had virtually eliminated the cladoceran grazers by 1988. This may have altered microbial nutrient cycling to favor microconsumers that cycle biomass and nutrients rapidly, thereby increasing primary production rates. On the other hand, atmospheric fallout of nutrients was very high in the summer of 1988 as a result of extensive forest fires and smoke plumes. Similar levels of smoke occurred during the fire years of 1998 and 2000, and primary production levels were again above the trend line. *Anabaena* did not bloom in 1988, 1998, or 2000.

Conclusions about the mechanisms that control productivity in Flathead Lake remain elusive in spite of the long-term record. However, the record does change the obvious conclusion that *Mysis relicta* is the strong interactor in the lake food web, influencing trophic structure at multiple levels and far beyond expectations based on its biomass alone.

Linking the Rivers and the Lake: A Conceptual Ecosystem Model

The studies described here show strong biophysical linkages between the river system and Flathead Lake (figure 14.2). The catchment delivers water and nutrients into the lake, and a wide variety of fishes pump nutrients upstream into the catchment. Temperature, precipitation, and light regime are the prime drivers that introduce natural variation in processes controlling structure. Cultural drivers, particularly invasions of non-native biota, eutrophication, and control of river flow and lake levels by Kerr and Hungry Horse Dams, moderate processes. This conceptual construct applies to the other deep lakes in the basin (plate 8) because they all are similarly oligotrophic, have large catchment basins relative to lake surface area, and are inhabited by adfluvial fishes.

The mysid-mediated immigration of lake trout from Flathead Lake is more than

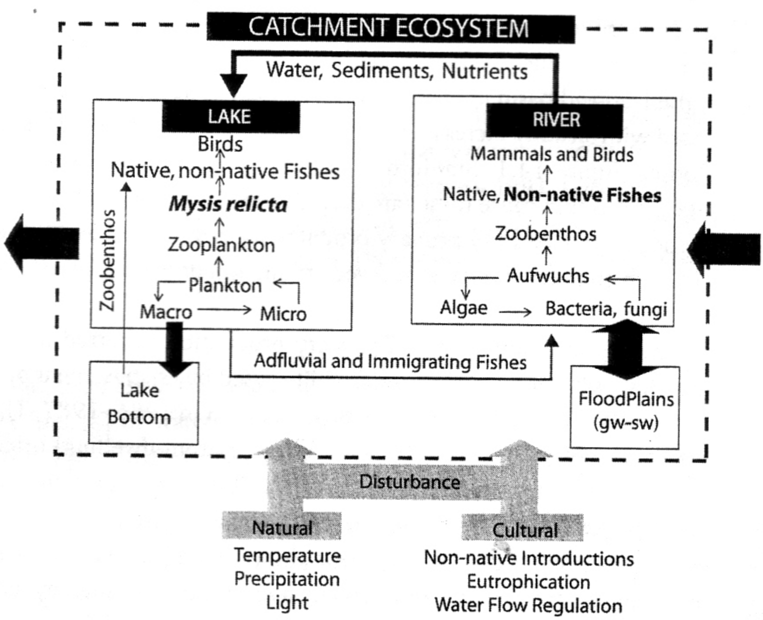

FIGURE 14.2 *Conceptual Model of Trophic Interactions and Drivers That Control Cycling of Materials and Energy in the Flathead River–Flathead Lake Ecosystem.* In this model, heavy arrows indicate materials and energy pathways. *Mysis* and non-native fish interact strongly to elicit cascading changes in trophic structure. *Aufwuchs* refers to attached (to rocks, plants) aquatic organisms; *gw-sw* is groundwater–surface water.

a nutrient pump, however, because they have invaded other large lakes in the basin, thereby changing food webs in potentially predictable ways. Indeed, lake trout establishment, coupled with the pattern of mysid introductions into the deep, oligotrophic lakes of the basin, provides an interesting array of potential trajectories and outcomes of food web change that could shed considerable new light on lake trophic ecology and cascading effects of non-native invasions (table 14.2).

The lake bottom functions as a subsystem because about 40% of the annual nutrient input into the lake is retained, tied up by a steep chemical gradient in the bottom sediments (figure 14.2). The bed sediments of Flathead Lake are dense clays deposited at a rate of about 1 millimeter (mm), or 0.04 inch (in.), per year, depending on location in the lake. Productivity in the lake and delivery of allochthonous organic matter (from the rivers and airshed) are too low to generate a significant organic load in the hypolimnion (bottom waters), where the water column remains oxygen-saturated. Hence, the mud-water interface is aerobic, and nutrients, especially phosphorus, collect on the bottom and remain insoluble (Wetzel 2001). The lake bottom is therefore a materials and energy sink. Very little organic matter actually gets to the lake bottom because of decomposition and extreme nutrient limitation within the water column: organic matter is consumed by microplankton before it settles to the bottom. Moreover, mysids consume zooplankton and organic detritus within the water column and metabolize it on the bottom. Nonetheless, the fishes that now dominate the lake are adapted to life in the deep waters, where they feed on mysids and zoobenthos, such as fingernail clams, midges, and caddis flies. These observations suggest that organic matter conversion is very rapid at the lower trophic levels and the lake remains nutrient-limited.

The river floodplains function as riverine subsystems (figure 14.2). We do not know whether they are net sinks or sources of material and energy for the rivers, but clearly, strong interactions occur. The riparian forests and wetlands provide organic inputs to the river and entrain and cycle nutrients in surface and subsurface flow paths. The river supplies sediments, nutrients, and biota to the floodplains.