EDMONDSON 1994 LAKE WASHINGTON #1

Sixty Years of Lake Washington: a Curriculum Vitae

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ABSTRACT

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The purpose of this paper is to list known disturbances of Lake Washington, to describe the effect on the lake of several of them, and to discuss results in terms of whole-lake quasi-experiments. Eutrophication with treated sewage effluent and the diversion of effluent are treated as experiments, with nutrient manipulation, which change the phytoplankton community structure. A later unexpected increase in transparency is traced through a chain of predators to flood control measures in the largest inlet. An increase in alkalinity, accompanied by changes in phytoplankton, is attributed to real estate land development. The role of paleolimnological information is illustrated.

Key Words: whole-lake quasi-experiments, land-lake interactions, eutrophication, plankton community structure, predation.

The title of this paper refers to the fact that exactly 60 years ago the first genuine limnological study of Lake Washington was made, from 14 January 1933 to 20 January 1934 (Scheffer and Robinson 1939). Rex J. Robinson was an Instructor of Analytical Chemistry at the University of Washington. He had a PhD from Wisconsin, and he liked to analyze water samples and improve methods. Victor B. Scheffer was a graduate student in the Zoology Department. Later he became a world expert on marine mammals (Scheffer 1980). Together the two made a study of Lake Washington, sampling on a regular basis as many as 13 depths at 3 stations, measuring many chemical and biological properties.

Since that time, diverse studies have been made by many people (Greenberg 1994). My associates and I have worked since 1949 with special attention to responses of the lake to disturbance. We have published papers about most of the points to be made here, and I have reviewed much of the whole story in a book (Edmondson 1991*b*, 1993*a*, 1994). Nevertheless, it might be useful to survey the situation from a different viewpoint with a different emphasis, and with some information not covered in previous accounts. I will not take much space here to convey detailed factual information that is easily available in the publications cited. My purpose is to provide a guide to results of our work and to indicate something of the motivation and way of working and thinking.

Lake Washington was formed (Fig. 1) at the end of the Pleistocene. For a short time it was connected to Puget Sound, as evidenced by the presence in sediments of diatoms characteristic of brackish water (S. E. B. Abella, pers. comm.). During its existence the lake has been subjected to many disturbances, most made by people living in its drainage area (Table 1). Each disturbance that has been studied had a measurable effect on the lake (Table 2). In 63,000 B. P. (Before Present), Lake Washington received considerable ashfall from the explosion of Mt. Mazama that formed Crater Lake. The sedimentary record shows distinct, temporary effects on planktonic and littoral diatoms (Abella 1988, see also Edmondson 1984). Evaluation of the effect on the lake community and the terrestrial community around it is complicated by a simultaneous change in climate (Abella 1988, Leopold et al. 1982). In about 1100 B. P. (= 850 A.D.), a large area of the Pacific Northwest was shaken by earthquakes. Forested hillsides slid into Lake Washington, creating sunken forests of standing trees (Karlin and Abella 1992). A by-product of this event was a widely distributed layer of silt in the sediment that serves as a clear time mark (Abella, pers. comm.). A transitory effect on the plankton is shown by a change in the proportions of diatom species. Limited activities of the small native human population probably had little effect on the lake, but that changed with the arrival of European settlers (Bagley 1916).

Some of the disturbances included in Table 1 were not accompanied by limnological studies, but probable

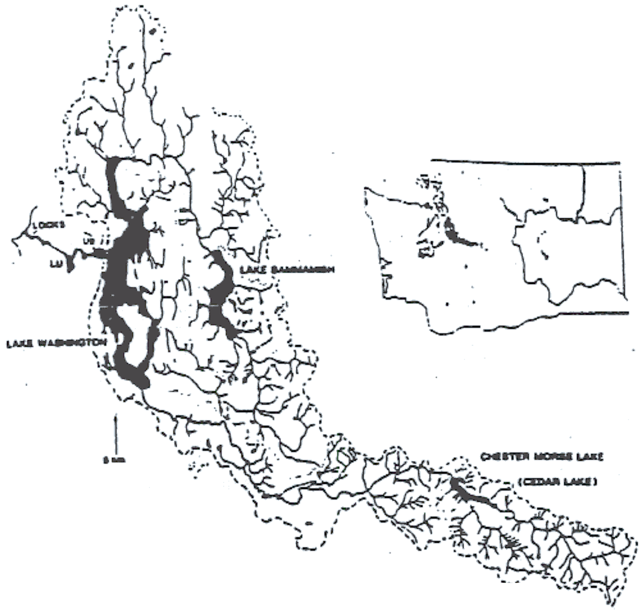

Figure 1.—Map of Lake Washington watershed, based on U.S. Geological Survey (USGS) quadrangles at scale 1:24,000, supplemented with information from USGS, Tacoma, Washington. Locations are shown for the ship canal locks, Lake Union (LU), and Union Bay (UB). For dimensions of the lake see Edmondson and Lehman 1981; for names of lakes, see Edmondson (1988); and for names of streams, see Edmondson (1991*a*). The Cedar River enters the south end.

effects can sometimes be estimated on the basis of general knowledge of limnological processes, or evaluated with paleolimnological data. For example, lowering of the lake level and introduction of the Cedar River into the south end of the lake in 1916 must have had profound effects on many features of the lake. The water input was nearly doubled with a large component of melted snow which would have affected chemical and biological conditions. About 5 km^2, or 8% of the lake bottom, was permanently exposed (Chrastowski 1983). This permitted widespread erosion and redeposition of sediment, and gave a paleolimnological time mark (Edmondson 1974, Schell et al. 1983, Schell and Barnes 1986). The abundance of chironomids seemed unaffected (Wiederholm 1979). There was a change in the proportions of diatom species at the time, but not as great as after the Mazama ashfall.

The effect of turbidity on the composition of phytoplankton was demonstrated by a flood of the Cedar River in early spring of 1972 when phytoplankton was starting its spring growth. Diatoms had started to increase as usual, but when the transparency of the lake was reduced by the turbid flood water they decreased sharply, and *Oscillatoria* grew to a density almost three times as great as the year before (Edmondson 1991*c*).

I have not found a useful contemporary published account of the condition of the lake during the episode of pollution from raw sewage that ended in 1936 with completion of trunk sewers to Puget Sound. The paleolimnological record is weak, probably being confounded by other factors. Motivation for improvement of sewage disposal at that early time seems to have been based more on issues of public health than on the publicly perceived condition of the lake. There had been a series of deaths from cholera increasing to a maximum of 564 cases in 1907, with a sharp reduction after 1911 when chlorination of the water supply from the Cedar River started (Green et al. 1944).

There were some nonlimnological effects of lowering the lake level. The present real estate value of the land exposed in 1916 is many millions of dollars; about 64% of the 115 km shoreline is occupied by residential property. Commercial and recreational boat and barge traffic between Puget Sound and Lake Washington produces considerable income to the region.

Another, more subtle, disturbance is worth mentioning because it aroused much public attention: intrusions of salt water from Puget Sound (Rattray et al. 1954). When the locks bring up a boat into the Lake Washington ship canal, some sea water is brought along with it. A siphon is supposed to drain salt water back to Puget Sound, but under some conditions salt water can flow along the bottom of the ship canal system. It occasionally has entered Lake Washington and formed a layer of slightly saline water below 50 m depth, a little warmer than the water above it. As the Puget Sound water moves toward the lake it entrains fresh water. By the time it reached the lake each fall in 1950-53 it had less than 2% of the salinity of Puget Sound, about 28 ppt. This slight increase in salinity was not enough to have a significant biological effect, but it increased the density enough to keep the warm water from floating up, and the bottom temperature was 1.6° C higher than the minimum in the hypolimnion. There was almost another intrusion in 1988. Salt water approached in the canal to the western edge of Union Bay, but was prevented from entering when the flow of water through the canal away from the lake was increased by releasing extra water from Chester Morse Lake into the Cedar River (Fig. 1). This was in response to public anxiety about the effect of salt water on the lake. With increased intrusion, the thickness of the layer on the bottom would have increased, but not its salinity. Whether a thicker layer could have stabilized the lake enough to establish meromixis is uncertain.

We have treated some of the disturbances as if they were whole-lake experiments in which the relation of the character and magnitude of the biological response to the character and magnitude of the disturbance would give information about the control mechanism of the lake community. What we did is in some ways analogous to what an experimental algal physiologist would do by assembling flasks with a variety of nutrient solutions, inoculating algae and counting them over time, and then interpreting descriptive data on the populations and chemical conditions in the flasks in terms of algal nutritional dynamics. The analogy breaks down, however, in that the physiologist has many flasks and can do multiple factorial experiments. He can develop a chain of stepwise interacting hypotheses and experiments. Nelson Hairston Sr. (1989) brought this question to attention in a book about experiments in ecology. He insisted that ecological experiments, just like laboratory experiments, must have replication and control. But there is only one Lake Washington. So either we stop doing whole-lake experiments and ignore Lake Washington or we find substitutes. I have elected to do the latter, using the idea of quasi-experimention (see Edmondson 1993*a* for an extended discussion). Appropriate statistics exist and are being developed further (Cook and Campbell 1979, Klir and Folger 1988, Matson and Carpenter 1990, McNeil and Feiberger 1993).

To organize our study I used ecosystem concepts with emphasis on plankton community structure and population dynamics. I focused on conditions in the lake that control plankton production and that give information about the activity of the community. Examples are concentrations of phosphate and oxygen which vary differently in the epilimnion and hypolimnion in response to changes in community metabolism. Everything we did was aimed at some specific question or hypothesis about causal relationships among the components of the system. Properties to be included were selected on the basis of existing information and theory. The condition of the lake was measured by a program of repeated sampling. We then evaluated the response by the patterns of

Table 1.—Events affecting the condition of Lake Washington.

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Born 13,500 years B.P. (Before Present)

6800 B.P.	Volcanic ash from Mt. Mazama
1100 B.P.	Major earthquake
1851 A.D.	Settlers arrive at site of future Seattle
1860 (ca.)	Deforestation and land development start
1900 (ca.)	All lowland timber cut Raw sewage begins to enter
1916	Ship canal system opened
1916	Lake level lowered
1916	Cedar River diverted into lake through an artificial channel
1916	Dredging starts in the artificial channel
1935	Sockeye salmon first stocked in Cedar River
1936	Diversion of raw sewage to Puget Sound completed
1940	First floating bridge across lake opens Land development on east side of lake accelerates
1941	First of 10 secondary sewage treatment plants
1947	Dredging in artificial channel reduced
1949-52	Salt water intrusions
1959-70	Revetments placed in upper Cedar River
1962	Maximum input of secondary sewage effluent
1963	Second floating bridge opens More land development on east side
1963-68	Secondary effluent diverted
1964	Sammamish River channelized (part)
1977	Annual stocking of rainbow trout begins
1994	Land development continues

Principal sources of information:

General history:	Bagley 1916, McDonald 1979, Edmondson 1991*b*
Paleolimnology:	Shapiro et al. 1971, Edmondson 1974, 1991*c*
Sewage history:	Brown and Caldwell 1958, Edmondson and Lehman 1981
6,800 B.P.	Abella 1988, Gould and Budinger 1958 (carbon dates differ slightly)
1,100 B.P.	Karlin and Abella 1992, Edmondson 1984
1860	Davis 1973
1916	Lake level from files of Army Corps of Engineers
1916	Dredging information from files of King County Public Works and King County Surface Water Management
1916	Ship Canal: Bagley 1916 (ch. 20), Purvis 1934
1935	Salmon information from Washington State Department of Fisheries
1959-70	Edmondson and Abella 1988

Table 2.—Selected list of changes observed in Lake Washington. The list includes responses to human influences except for the two earliest disturbances (Table 1). The lake has been affected by changes in the flow of the Cedar River which are partly affected by human activity in controlling release of water from Chester Morse Lake.

6800 B.P.	Temporary change in diatom community (Abella 1988)
1100 B.P.	Areas of forested land slide into lake (Karlin and Abella 1992)
1933-64 A.D.	Phosphate increases (Comita and Anderson 1959) Hypolimnetic oxygen decreases (Comita and Anderson 1959)
1949-50	Temperature anomaly (Rattray et al. 1954)
1955	*Oscillatoria* bloom (Edmondson et al. 1956)
1961 (ca.)	Salmon and smelt begin increase (Chigbu and Sibley in press *a*, *b*, Eggers et al. 1978; Fresh 1994)
1962-67	*Neomysis* decreases (Murtaugh 1981*a*)
1962-70	Alkalinity increases (Edmondson 1990, 1991*a*)
1964	Maximum input of phosphorus (Edmondson and Lehman 1981).
1976-79	Second increase of alkalinity (Edmondson 1991*a*).
1976	*Oscillatoria* disappears (Edmondson and Litt 1982). *Daphnia* becomes abundant (Edmondson and Litt 1982). Transparency increases (Edmondson and Litt 1982).
1986-89	Third increase of alkalinity (Edmondson 1990, 1991*a*).
1988	*Aphanizomenon* relatively abundant (Edmondson 1990, 1991*a*). Maximum return of spawning salmon (Fresh 1994).
1990-93	Transitory decrease in alkalinity (Edmondson 1993*b*).
1992	Reduced return of salmon (Fresh 1994).

change over time; that is, the correlations of quantities and coordination of events. We developed a potential explanation or a set of alternative explanations consistent with the observations. We made additional experiments or observations in laboratory or field to develop the most probable explanation. This way of thinking is similar to that done in a fully experimental study designed to test alternative hypotheses. In addition to the special experiments, a key is the use of literature as a substitute for replication and control. We are not starting from scratch; much generalizable information exists. How we proceeded with Lake Washington is the subject of the rest of this paper.

For fuller description I have selected four of the more conspicuous changes, and will trace them back to the disturbances that led to them. These changes are:

1). An increase in the abundance of phytoplankton during the 1940s and early 1950s, with an increase in the proportion of Cyanobacteria (Fig. 2A). The lake was not in bad condition in 1955, but a conspicuous population of *Oscillatoria rubescens* in that year was a clear signal that it was well on its way to producing nuisance conditions.

2). A decrease in phytoplankton after 1968 with increased transparency, and the disappearance of *Oscillatoria* in 1976 (Fig. 2A, B).

3). An unexpected further increase in transparency of the lake in 1976 (Fig. 2B).

4). An increase in *Aphanizomenon* in 1988 to an abundance greater, absolutely and relatively, than we had seen before (not shown).

The explanation of the first two changes is straightforward. The increase in phytoplankton accompanied increased concentrations of phosphate in the lake (Fig. 2C), which in turn closely followed the input of effluent from secondary sewage treatment plants (Fig. 2D). Earlier indications of eutrophication had been given by an increase in phosphate concentration and by a decrease in hypolimnetic oxygen (Comita and Anderson 1959, see also Lehman 1988).

There had been much experience, largely in Europe, with formerly clear lakes producing

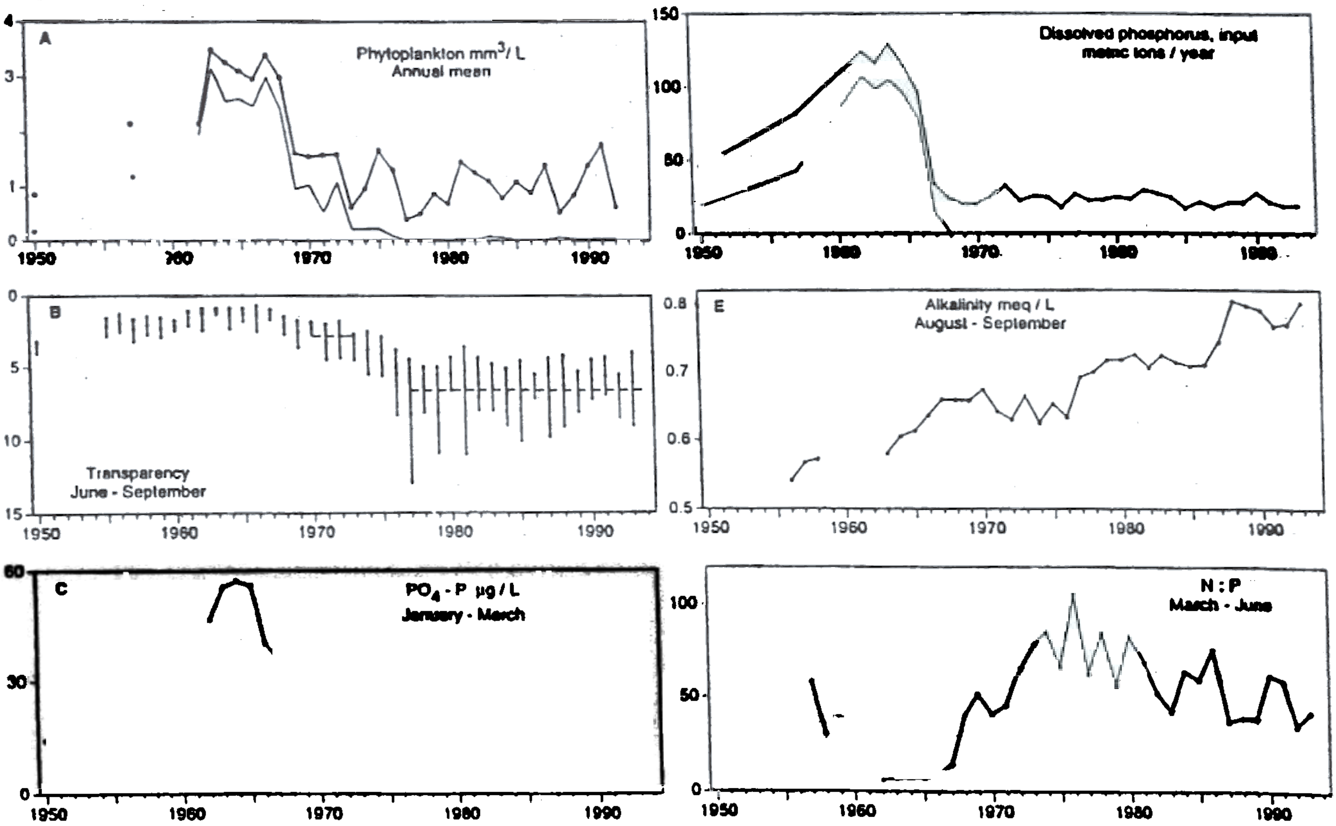

Figure 2.—Long-term graphs of properties of Lake Washington. Panels B-F show means for parts of each year selected with regard to seasonal changes. For more complete records see Edmondson 1993b. A) The thin line shows the volume of Cyanobacteria. B) Maximum, mean, and minimum Secchi disc transparency; the maximum value ever recorded was 12.9 m on 2 June 1977 (most previously published graphs in this format have been for July and August). C) Phosphate reaches its seasonal maximum during winter and usually begins to decrease in March, D) Phosphorus loading calculated as described by Edmondson and Lehman (1981); the thin line shows the amount in secondary sewage effluent. E) Alkalinity usually starts to increase in April, leveling off during August and September; previously published means were for different months. F) The mean ratio of nitrate-N to phosphate-P during late winter and the early part of the phytoplankton growing season; lowest values occurred during the period of eutrophication with phosphate-rich sewage effluent. Each year the ratio rises to a maximum during spring phytoplankton growth as phosphate is nearly exhausted, then decreases as phytoplankton decreases; note the 3 years of minimum ratio, 1987-89.

cyanobacterial blooms after enrichment with sewage. Especially striking was the number of Swiss lakes that bloomed with *Oscillatoria rubescens* early in eutrophication; we can regard them as quasi-experimental substitutes for replication of the Lake Washington bloom. The causal connection between the sewage and change of phytoplankton was provided by knowledge of algal nutrition and of the chemistry of lake water and sewage.

The diversion of effluent was responsible for the second change listed above by reducing the nutrient supply. While the effluent was being diverted from Lake Washington, a related whole-lake experiment was being done in Zürichsee, Switzerland, where phosphate was precipitated from sewage effluent with ferric chloride, successfully limiting phytoplankton (Schanz and Thomas 1981, Thomas and Wildi 1975). More recently a spectacular decrease of the phosphorus content of Lago Maggiore has been achieved by improvement of sewage disposal in the area (Calderoni et al. 1993).

There has been considerable disagreement about the role of different elements in controlling phytoplankton populations. Experimental fertilization of lakes, or parts of lakes, and bioassay have provided critical information on the effect of different elements (Schindler 1975, 1988, Elser et al. 1990).

Much detailed knowledge has come from laboratory studies specifically organized to answer questions about mechanisms of control of phytoplankton. These results validated earlier conclusions about the general relation of sewage enrichment to cyanobacterial blooms and differences in participation of phosphorus, nitrogen, and carbon. More recent work is leading to an understanding of the processes determining whether a lake becomes dominated by *Oscillatoria* or by other bluegreens—*Anabaena*, *Microcystis*, or *Aphanizomenon*. There are differences in buoyancy related to nutritional and energetic properties of nitrogen-fixers and nonfixers, and there are reactions to nutrients, mixing regimes, and gradients of light (Klemer and Konopka 1989, Reynolds 1984, Smith et al. 1987).

Anabaena and *Aphanizomenon*, but not *Oscillatoria*, were seen in 1913 (Kemmerer et al. 1924). The outburst in 1955 was not the first occurrence in the lake. A species, probably *O. agardhii*, had been reported by Scheffer and Robinson as being "rare." The maximum population of *O. agardhii* measured by Comita and Anderson in 1950 was only 2% of that at the height of eutrophication. Evidently it survived in submarginal conditions until the period of nutrient enrichment. *Oscillatoria rubescens* was seen sporadically between 1955 and 1966, sometimes in abundance. *Oscillatoria agardhii* was more consistent in occurrence and was especially abundant in 1967; it disappeared in 1976. Other species of *Oscillatoria* did not become abundant.

The decrease in abundance of phytoplankton was made possible by public concern about the lake. A public education campaign and vote led to diversion of effluent from the lake without creating the same problem elsewhere (Edmondson 1991*b*:20-38). So, the experiment was even better because we could measure the rate of recovery, a topic about which there was argument and even a wager by one of the Swiss limnologists that the lake would take many more years to recover than I had predicted. I won in 1971 when the transparency exceeded the maximum of 1950 (Edmondson 1972).

To explain the third change, an unexpected conspicuous increase in transparency, required a more complex interpretation than that of the more obvious eutrophication and recovery episodes. A sequence of steps led back eventually to flood-control measures in the Cedar River (Edmondson 1993*a*, Edmondson and Abella 1988).

The first step in understanding the increase in transparency was easy; there was a population explosion of *Daphnia*. The ability of *Daphnia* to clear the water of edible phytoplankton is well known. *Daphnia* was described as "quite common" in 1933 by Scheffer and Robinson, evidently because it was consistently present all year. However, unpublished data by Scheffer (1936) showed that it was not abundant, having a maximum of about one individual per liter. In the 1950s and 1960s *Daphnia* occurred sporadically and in small numbers. Evidently it entered the lake from time to time, but conditions did not permit development of a lasting population (Edmondson 1988). There was some advance warning of the increase. We saw no *Daphnia* in 1972. It was consistently present but not abundant in 1973-75. In 1976 it increased abruptly, exceeding 40 individuals per liter, and even more the next year. It has dominated summer zooplankton ever since.

To find a probable explanation for the increase of *Daphnia*, I simply thought of all the things known to affect *Daphnia* that might have been responsible under the conditions measured in Lake Washington; some could be eliminated easily. For instance, the idea that *Daphnia* was excluded by inadequate food could be discounted because during much of the time when *Daphnia* was scarce there was as much food as later when it became abundant (Fig. 15 in Edmondson 1993*b*). Much was already recorded in the literature of the feeding ecology of *Daphnia*. Special observations with Lake Washington material identified the species of phytoplankton that could be ingested and digested (Infante and Edmondson 1985). Laboratory experiments with various amounts of different species of algae showed how much was required for reproduction and growth (Infante and Litt 1985, A. Duncan pers. comm.). This process is similar to that used during experimental studies in which multiple falsifiable hypotheses are tested by experiments specifically designed for the purpose (see Edmondson 1979 for an earlier assessment and 1993*a* for additional discussion with documentation).

If a change in abundance of food organisms was not responsible for the success of *Daphnia*, a question still remained about the availability of food. This point was brought to mind by the presence between 1955 and 1975 of *Oscillatoria*, some species of which are known to prevent the use of edible phytoplankton by *Daphnia*, principally by mechanical interference with the feeding apparatus. Antibiosis can be involved also. Special laboratory experiments were done with organisms from Lake Washington, demonstrating a strong inhibitory effect of *Oscillatoria* against *Daphnia* (Infante and Abella 1985). *Oscillatoria* also inhibits some kinds of diatoms which are good food for *Daphnia* (Edmondson 1991c), but that fact by itself cannot explain the lack of success of *Daphnia* during the period of eutrophication.

Inhibition of feeding cannot explain the scarcity of *Daphnia* in 1933 and 1950 when *Oscillatoria* also was scarce. A second inhibitory condition must have existed then, and it is reasonable to look for a difference in predation. A substantial population of *Neomysis mercedis* lived in the lake until the early 1960s, when it decreased to about 10% of its previous abundance (fig. 1, Murtaugh 1981). Its close relative, *Mysis relicta* is well known to be a selective keystone predator on *Daphnia*. Special laboratory experiments showed that *Neomysis* too is a voracious, highly selective predator on *Daphnia* (Murtaugh 1981). Quasi-experimental replication was provided in 1965, when *Daphnia* persisted in small numbers during the summer. *Neomysis* had already started its decrease, and was only about half as abundant as earlier. Unusual weather conditions reduced the population of *Oscillatoria* (Edmondson 1988). With this temporary, partial amelioration of both predation and inhibition of feeding, small numbers of *Daphnia* did survive during the summer but did not thrive as in 1976.

Thus I concluded that before 1976 *Daphnia* had been held in check by one or both of two inhibitory conditions. It was relieved of them at different times.

Why did *Neomysis* decrease? Nothing suggested that its food had decreased. The probable answer involves another population explosion of a selective keystone predator, the longfin smelt (*Spirinchus thaleichthys*), was first observed in Lake Washington in the fall of 1960 (Edmondson and Abella 1988). The smelt is highly selective for *Neomysis*, which formed about 85% of its diet when abundant (Eggers et al. 1978). For present conditions, see Chigbu and Sibley (in press *a*, *b*).

Why did the longfin smelt increase? It spawns principally in the artificial channel of the Cedar River. Flood control measures apparently affected its success in spawning. After the channel was opened, the high discharge of the river during winter frequently caused water in it to rise, flooding farms and destroying houses. The middle part of the channel was deepened by dredging each summer to permit water to flow faster, and gravel was thrown up on the bank. Surely this would have inhibited spawning. Annual dedging was stopped in 1947 when the dredge broke down and was not replaced for lack of funds. So, this annual disturbance of spawning beds stopped, but that was not the only condition that could interfere with spawning.

Upstream parts of the Cedar River are bordered by steep banks of glacial deposit which were undercut at times of high flow causing massive landslides into the river, with consequent covering by clay of potential spawning beds downstream. This too would have interfered with spawning. To prevent such slides, revetments or riprap (piles of large rocks) were placed where slides were likely (Edmondson and Abella 1988). Evidently by the early 1960s conditions were established to permit successful spawning throughout most of the Cedar River. That is also when the sockeye salmon (*Onchorhynchus nerka*) began a promising increase in Lake Washington. Salmon had been planted in the river several times starting in 1935, but had not been conspicuous until after the revetment program (Fresh 1994). Revetments are widely regarded with disfavor by some stream fisheries biologists and flood control managers because there can be unfortunate side-effects by restriction of flow and increased scouring. I believe that in the Cedar River these were overbalanced by the favorable effects for spawning fish.

It is worth noting that there were two different flood control operations and that two species of fish were affected. As long as the artificial channel was being dredged, smelt could not develop a large population. Stopping the dredging operation had no benefit for salmon, since they spawn upstream. Ironically, both smelt and salmon feed heavily on *Daphnia* now, but evidently not as heavily as *Neomysis* did before 1962.

The fourth change is the unexpected prominence in July and August 1988 of *Aphanizomenon*, a cyanobacter that had been present, but less conspicuous, during the entire previous time (Edmondson 1990, 1991*a*). This is a relative matter, for the lake is incapable now of making prolonged nuisance blooms. Nevertheless the brief peak abundance of 1.4 $mm^3\ L^{-1}$ is not inconsiderable, being about 80% of total phytoplankton volume at the time and 15% of the maximum observed for *Oscillatoria* in 1964.

The abundance of *Aphanizomenon* was only one of several changes that made 1988 highly unusual. There were differences in several chemical and physical features known to be associated with the relative success of Cyanobacteria. The inorganic nitrogen:phosphorus (N:P) ratio and alkalinity have been emphasized (Shapiro 1990, Smith 1983). Alkalinity in Lake Washington was somewhat higher in 1987 than in 1986, then jumped by 9% in 1988 (Fig. 2E). Nitrate and phosphate concentrations decrease each year during spring phytoplankton growth, but details of the time course of concentration and the ratio differed in each year. The mean N:P ratio in spring and summer was lower in the 3 years 1987-89 than any time since the 1960s (Fig. 2F). Although ratios were similar, concentrations of both elements were higher in 1988 than in adjacent years. The usual spring diatom bloom did not develop in 1988, reaching a maximum volume of only 1.6 $mm^3 L^{-1}$ in contrast to 7.3 and 8.9 in the 2 adjacent years. Correspondingly, silicate remained high, above 1.0 mg L^{-1}, rather than decreasing to less than 0.02. Other features, not shown here, that differ to some extent among the 3 years of low N:P ratio are mixing depth, epilimnetic temperature, solar radiation, concentration of carbon dioxide, pH, and abundance of phytoplanktivorous zooplankton.

Thus, the outburst of *Aphanizomenon* was a symptom of a suite of connected chemical and physical changes. Identification of specific factors causing the behavior of phytoplankton is still under study. In addition to full use of literature results, a firm explanation will almost certainly require special laboratory experiments designed around observed environmental conditions.

Why did the alkalinity increase? In thinking about this I finally realized an obvious feature of eutrophication of lakes with sewage. Any time there is a sewage treatment plant of significant capacity, there is a city. And before there is a city, there is a major disturbance of the land. So any effect of eutrophication is likely to be preceded and accompanied by land development, and effects of the two are confounded. We had evidence of that happening to Lake Washington long before I realized what it meant. In fact, the alkalinity had been rising since the early 1960s with accelerations in 1963-70 and 1975-79 (Fig. 2E).

After the arrival of settlers in 1851, most clearing and building activity was at first confined to an area outside the Lake Washington watershed (Bagley 1916). By 1860 a few houses had been built near the lake, and clearcutting in the lowland area of the watershed was in progress. That was primarily a logging activity to produce lumber, not a real estate development. By 1900 most of the lowland area around the lake had been deforested. Some cleared land was developed as towns and some was converted to farms. Much of it was left alone, and by 1920 a large area had grown up in red alder, *Alnus rubra* (Davis 1973). By the same year there were drains taking raw sewage from about 10,000 people directly to the lake.

We are testing the hypothesis that the long-term change in alkalinity in Lake Washington was caused, at least in part, by processes of land development that altered the chemical output of the land to the streams. Since 1988, we have been analyzing samples for alkalinity, pH, major ions and nutrients from the mouths of the two main inlets and seven creeks at intervals. We also analyze samples along the streams above and below places where development has occurred or is planned. We have measured the developed part of the drainage area of several creeks in a series of aerial photographs taken at different times in the past, so far going back to 1965, 10 years before the first Landsat satellite. Earlier sets of photographs are available. We are taking our data in such a way as to be able to coordinate results with Geographical Information Systems being established with satellite data by local governmental agencies working on future developments.

Consider a forested watershed drained by a stream carrying a load of dissolved substances characteristic of the soil, vegetation, and climate. Patches within it will be developed starting at different times. Clearcutting and bulldozing will expose deep soil of different chemical content than topsoil. The chemical character of the water draining the patch will change progressively during different stages of development. The resulting condition will differ from what it was originally, the exact nature of the change being determined by soil characteristics, the amount of land cleared, depth of disturbance of the soil, the amount of building and paving, and use of the vegetated area remaining. For a given patch, change comes to an end when the area is developed as much as it ever will be, with the chemical output being permanently changed from its original condition. Output from the whole watershed will change according to the initiation of new patches.

For this hypothesis to explain the increase in alkalinity exported from developed land, deeper soil exposed by development must liberate more alkalinity to leaching than topsoil. While this condition exists in the Lake Washington watershed, it is in exaggerated form in lowland areas formerly occupied by red alder, which fixes nitrogen. Soil under a stand of red alder is highly enriched with nitrogen relative to that under native conifers. Acidification produced by nitrification leaches ions, the surface layer is acid and deeper layers are richer in base cations (Cole et al. 1990, Miegroet and Cole 1984, Johnson 1992). It would be interesting to compare the effect on stream chemistry of land development similar to that around Lake Washington with that in places with similar geology but without a history of occupation by alder.

The pronounced seasonal changes of alkalinity in the lake evidently are dominated by the changes of input to the streams rather than by in-lake processes that generate alkalinity, such as nitrate uptake by phytoplankton (Schindler 1986, Brewer and Goldman 1976).

The problem of separating causality from coincidence in quasi-experiments is illustrated by the two major increases of alkalinity in the 1960s and 1970s. The first coincided with the diversion of sewage effluent. No resulting change in the lake has been identified that could generate alkalinity. In fact, one of the major chemical effects of diversion was to reduce the input of nitrate, thus reducing the capacity of the lake to produce alkalinity. The second increase occurred during the change in abundance of *Daphnia*. No plausible mechanism has been found to connect those two changes.

Lake Washington continues to be a softwater lake. The increase of alkalinity was too small to have a significant physiological impact on animals. If it continues, there might be a change in community structure by an increase in the relative abundance of Cyanobacteria. A major increase in bluegreens would degrade zooplankton food supply and decrease the ability of the lake to support populations of desirable planktivorous fish. Further, recent evidence from bioassay tests shows that toxic phytoplankton populations occur more frequently than has been indicated by observed deaths of terrestrial animals (Hardy et al. 1994).

Our opportunity to witness a possibly significant increase in Cyanobacteria was temporarily thwarted by the largest known flood of the Cedar River, the "Thanksgiving Flood of 1990," during November 1990-February 1991. The main water supply for the Cedar is snowmelt of low alkalinity in the Cascade Mountains. Alkalinity of the lake in spring of 1991 had been diluted to 86% of its 1988 maximum. Subsequently it increased, and in May 1994 it exceeded the late summer maximum of 1988. We will carefully watch Lake Washington phytoplankton.

After more than 20 years during which several commercially valuable runs of salmon occurred, the number of salmon returning to the lake decreased over a period of about 5 years from 1988 to less than 10% of the biggest run. The reason for this change has not been determined (Fresh 1994). Surviving fish grow well during their first year of life in the lake before migrating, suggesting that their food supply is still adequate, as indicated also by our data on zooplankton. That leaves a change in predation as a possible explanation; the matter is currently under study by state agencies.

I have avoided characterizing the processes used to explain changes in plankton of Lake Washington as top-down and bottom-up control. I think that it must be widely recognized now that those terms encompass two groups of processes that operate continuously in opposition. One or the other set may dominate at times, but they do not operate separately or alternately. Neither concept adequately takes account of chemical inhibition.

Finally, one should realize that this entire study was made as basic ecological research for its own intrinsic interest; the motivation was not to improve the management of lakes. However, I am glad that an opportunity developed to use our results immediately. Every component is relevant to one or more current problems of lakes that need to be managed. I have avoided describing here the project as a monitoring operation, having already expressed myself on the concept of monitoring, and will not repeat it (Edmondson 1991*b*:282-285). In our case, each of the successive problems that came along required a program of repeated sampling to define the changing condition of the lake. Properties analyzed varied somewhat with each new phase, but we maintained a basic set with consistent methods all the way through, permitting comparability of data. We adjusted our program to take account of and contribute to developments in the field. Our results can be absorbed into the stock of generalizable knowledge needed for such topics as community structure, eutrophication, nutrient control, biomanipulation, and land-lake interactions.

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