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Lake Ecosystems of the Lake Washington Drainage Basin

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INTRODUCTION

Lakes are closely coupled to terrestrial systems, and the trophic state of a particular body of water reflects carbon and nutrient inputs from its entire watershed (Fisher 1970; Hutchinson et al. 1970; Fisher and Likens 1973; Likens and Davis 1975). This is particularly true in the Pacific Northwest, where the surrounding coniferous forests are among the most productive in the world, and are characterized by large accumulations of biomass and detritus (Sedell 1972; Taub et al. 1972).

One of the major objectives of the lakes program was to study these terrestrial influences in an effort to better understand their impact on lake metabolism. Four lakes in the Lake Washington drainage basin were studied. They ranged from high-altitude lakes surrounded by forests (Findley and Chester Morse lakes) to low-altitude lakes in more urban environments (Sammamish and Washington lakes). A progression from oligotrophy to mesotrophy exists in the order Findley Lake, Chester Morse Lake, Lake Sammamish, and Lake Washington (Table 11.1). More detailed physical descriptions of these lakes are provided in Chapter 1.

Here we evaluate the production and community structure of the four lakes in relation to terrestrial inputs of nutrients and carbon. The processes that control nutrient and organic matter cycling in soils and terrestrial vegetation of an ecosystem adjacent to a lake are addressed briefly to provide background. Subsequently, material pathways within the lakes are discussed. Findley Lake and Lake Sammamish are considered in terms of the behavior of primary nutrients and production of biological communities. The next section discusses the response of plankton metabolism and physiology to varying environmental conditions. Finally, the relations between forage base and fish production in Lake Washington are discussed.

Our research shows that the metabolic pathways and community structure of lakes in coniferous forests are influenced and, in certain cases, dominated by terrestrial inputs. Carbon budgets calculated for Findley Lake show that annual terrestrial inputs of particulate carbon in the lake causes the production of

TABLE 11.1 *Comparison of trophic status of four lakes in the Lake Washington drainage basin (average yearly rates, nutrient values as prebloom concentrations).*

Lake	PO_4-P ($\mu g/\ell$)	NO_3-N ($\mu g/\ell$)	Phytoplankton productivity (mg C·m⁻²·d⁻¹)	ETS (mg O_2· m⁻²·h⁻¹)	Maximum growth rate (h⁻¹)	K_t (PO_4)	Zooplankton production (mg dry wt·m⁻²·d⁻¹)	Zooplankton biomass (mg dry wt/m²)
Findley	1.3	40.0	220	9	0.011	0.17	0.4	13.3
Chester Morse	2.1	107.0	262	13	0.007	0.36	0.5	12.5
Sammamish	14.7	467.0	499	62	0.008	0.42	0.9	22.5
Washington	16.3	290.0	1070	55	0.131	2.84	2.0	—

detritivorous insects equivalent to the production of herbivorous zooplankton. Interestingly, even in Lake Washington, a large lake recently rehabilitated by sewage diversion, benthic fish communities and detrital food chains are more productive than are limnetic communities and autotrophic food chains. A comparison of the annual production and respiration for aquatic environments in different biomes further supports our hypothesis that terrestrial organic production in coniferous forests is very important in determining the patterns of metabolism in adjacent aquatic ecosystems.

Our research has also shown that primary energetic processes of lakes can be better understood through the use of physiological stress or "metabolic" indicators. These indicators include production/respiration (P/R) and carbon/adenosine triphosphate (C/ATP) ratios, and estimates of nitrate reductase activity and $^{32}PO_4$ flux. In the lakes we studied, these indicators reflect such processes as microplankton production and nutrient cycling. Changes in these parameters were due to phosphorus stress, which resulted in increased maintenance costs and a decoupling of carbon and nutrient cycles in the phytoplankton. We believe that the use of these indicators can increase our ability to assess the response of lake ecosystems to various lake restorative practices and manipulations such as fertilization for enhancement of fish production.

ELEMENTAL CYCLES IN LAKES OF THE LAKE WASHINGTON DRAINAGE BASIN

Influence of Terrestrial Ecosystems on Elemental Inputs to Lakes

The major pathways through which terrestrially-derived materials enter lake systems are leaching, weathering, erosion, and litterfall. The type of forest ecosystem surrounding the lake strongly affects the chemical characteristics of these inputs. The discussion here focuses on inputs from leaching and weathering. Litterfall is discussed specifically in a later section. Erosion is dealt with more fully in Chapters 8 and 9.

Nutrient distribution and transfer in the mature Pacific silver fir ecosystem at Findley Lake and in younger Douglas-fir ecosystems at the Thompson site in the lower drainage have been determined by Turner and Singer (1976). Inputs and losses of these nutrients below the rooting zone are shown in Table 11.2. The old-growth Pacific silver fir at Findley Lake is more conservative of nutrients than the young-growth ecosystem at the Thompson site. Also, there is relatively little loss of nitrogen (N) and phosphorus (P) from either of these ecosystems, with annual inputs almost balancing outputs. Differences in inputs and outputs of N are probably balanced by biological fixation, while losses of the other elements were assumed to be made up by weathering.

TABLE 11.2 *Anual input (I) and losses (L) from the rooting zone (kg/ha) of N, P, K, Ca, and Mg at the Thompson site[a] and Findley Lake.[b]*

Site		N	P	K	Ca	Mg
Thompson site	I	1.4	0.3	2.3	2.2	0.5
	L	3.4	0.6	13.4	12.1	3.6
Findley Lake	I	1.3	0.4	0.8	0.6	1.7
	L	2.7	0.5	2.1	7.3	1.1

[a]Turner 1975.

[b]Turner and Singer 1976.

The mechanisms involved in cation leaching below the soil rooting zone were examined at Findley Lake and the Thompson site (Chapter 7). Bicarbonate is the major anion in soil solutions at the Thompson site, while at Findley Lake organic anions dominate. However, most of the cations that reach Findley Lake probably come from bedrock weathering rather than leaching from the upper soil horizons. This phenomenon is illustrated in Table 11.3. Concentrations of cations and bicarbonate ions in talus groundwater are higher than in streams and precipitation.

Predominance of bedrock weathering in upland sites is suggested by high calcium losses, typical at both Findley Lake (Turner and Singer 1976) and the Andrews Forest (Grier et al. 1974). These upland sites have similar bedrock and soils of andesite origin whereas the Thompson site is mainly granitic and metamorphic rock. Weathering of hornblende and plagioclase feldspars in the andesite appears to be the primary source of calcium in waters at Findley Lake. The principal weathering mechanisms in the Cascade Mountains are carbonation and oxidation. These processes are controlled mainly by supplies of water and hydrogen ions from the atmosphere (Reynolds and Johnson 1972).

In summary, weathering appears as the primary source of most inorganic elements for subalpine Findley Lake. Other important terrestrial influences on the lake include interflow of water, which is coupled to soil respiration and supplies dissolved inorganic carbon, and leaching, which supplies dissolved organics. The importance of dissolved elements, particulate matter from litterfall, and surface flow in the nutrient budgets of the lakes is discussed in a later section (Elemental Transfers Within Lakes).

Elemental Contents of Lakes

Weathering, leaching, and other nutrient inputs can vary according to the relative degree of forestation or urbanization of the shoreline. The four study lakes reflect these differences in their surface water and sediment chemistry. The order of abundance of the major cations in surface waters is similar in the

TABLE 11.3 *Chemical characteristics of different waters in the Findley Lake watershed. Concentrations represent average annual values (mg/liter) except for conductivity and alkalinity.*

Water from	pH	Conductivity (μmho/cm)	HCO_3-C	Alkalinity (meq/ℓ)	Kjel-N	NO_3-N	NH_4-N	Total P	Na	K	Ca	Mg
Precipitation	5.8	21.7	—	0.095	0.37	0.438	0.163	0.016	0.80	0.11	0.30	0.06
Inlet creeks	6.0	18.2	1.38	0.137	0.17	0.012	0.020	0.015	1.27	0.02	1.80	0.22
Forest groundwater	5.3	22.3	0.71	0.055	0.23	0.012	0.053	0.017	1.30	0.27	0.75	0.21
Talus groundwater	6.5	—	3.86	—	0.20	0.112	0.076	0.169	2.13	0.40	2.42	0.51
Lake outlet	6.4	20.3	1.40	0.170	0.09	0.012	0.006	0.004	1.28	0.10	2.50	0.27

upper drainage lakes, Findley and Chester Morse, where calcium (Ca) exceeds sodium (Na) exceeds magnesium (Mg) exceeds potassium (K) (Figure 11.1; Barnes 1976). It is slightly different in Lakes Washington and Lake Sammamish (Ca $\simeq$ Na > Mg > K). There is a general increase in nutrient levels from Findley Lake to the lower, more urbanized Lake Washington and Lake Sammamish (Table 11.1).

The Ca:Mg ratio decreases from 10:1 to 20:1 in the upper lakes to about 3:1 in lowland waters. This increase in Mg relative to Ca in the lower drainage lakes is due partly to the proximity of Puget Sound to these lakes. Sea-salt aerosols are enriched in Na and Mg relative to Ca. Based on elemental ratios in seawater, however, and assuming that most of the Na increase from about 1 mg/liter to about 8 mg/liter is due to sea-salt inputs, only 0.8 to 0.9 mg/liter of the observed 3.0 mg/liter increase in Mg can be accounted for. Accordingly, we assume that most of the observed increase in Mg and other cations from the upper lakes to the lowland lakes is due to increased lithospheric contact through weathering and groundwater inputs. Levels of copper (Cu) and lead (Pb) in all four lakes were similar despite the degree of urbanization in the lower drainage basin. Zinc (Zn) showed a pattern similar to Cu and Pb.

The pattern of higher elemental concentrations in the sediments from the high- to low-elevation lakes was similar to increases observed in the water column, though total concentrations were much higher than the ionic forms in water (Figure 11.2). In general, K, manganese (Mn), and heavy metals (Zn, Cu, Pb) increased from parts-per-billion levels in water to parts-per-million values in sediments. Other elements (Ca, Na, and Mg) showed increases of similar magnitude from parts per million to parts per thousand. The largest increase for an element in the sediments relative to the water was for iron (Fe). The high concentrations of major cations, Fe and Mn, in the Chester Morse sediments reflect the large amount of inorganic material carried into the lake during periods of high runoff and increased erosion from logging activity.

The higher levels of trace metals in the sediments of the large urban lakes may be indicative of anthropogenic enrichment. Further examination of Lake Washington sediment cores for mercury (Hg), Pb, Zn, Cu, chromium (Cr), arsenic (As), and antimony (Sb) showed substantial enrichment over pre-1916 levels (Barnes 1976). The level of Pb in cores appeared to be primarily a reflection of the quantity of automobile emissions (Figure 11.3); As and Sb in sediments can be attributed directly to the Tacoma smelter, which is located upwind from the lake (Crecelius 1974).

Analyses of total C, N, and P contents of surface sediments for the four lakes suggest the importance of terrestrial matter as an energy supplement (Table 11.4). Higher C contents and C:N ratios in sediments of Findley Lake and Chester Morse Lake, compared with those in the lower drainage lakes, were attributed to relative differences in allochthonous (exogenous) and autochthonous (endogenous) C inputs. In the upper drainage lakes, most of the organic C in sediments is derived from terrestrial vegetation (Birch 1976). This
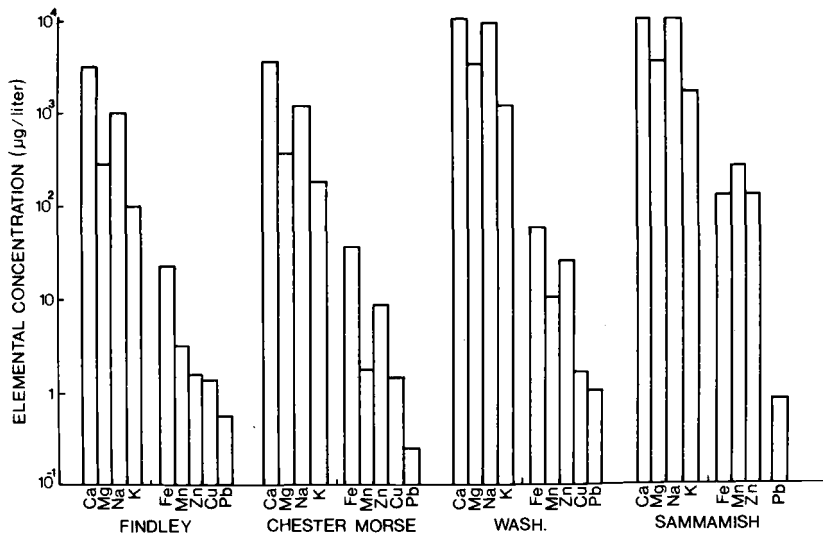
FIGURE 11.1   *Average elemental concentrations in surface waters of lakes in the Lake Washington drainage.*
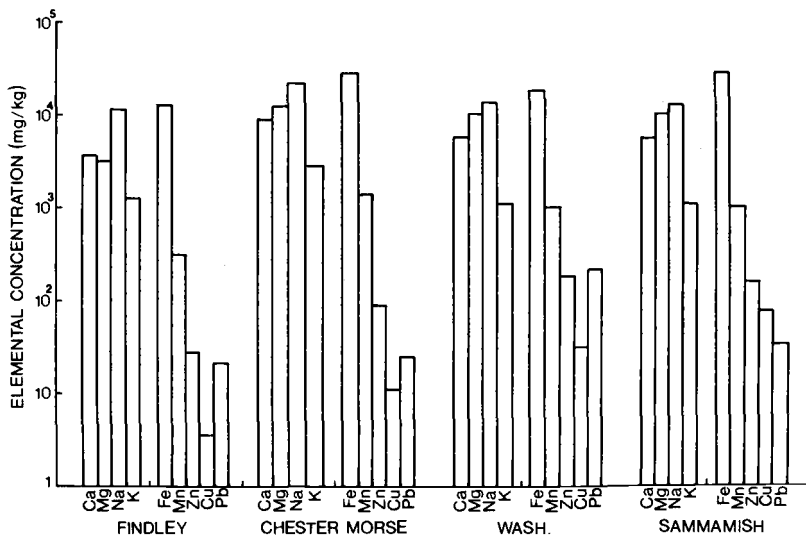

FIGURE 11.2   *Average elemental concentrations in surface sediments of lakes in the Lake Washington drainage (after Horton 1972 and R. S. Barnes pers. comm., 1976).*
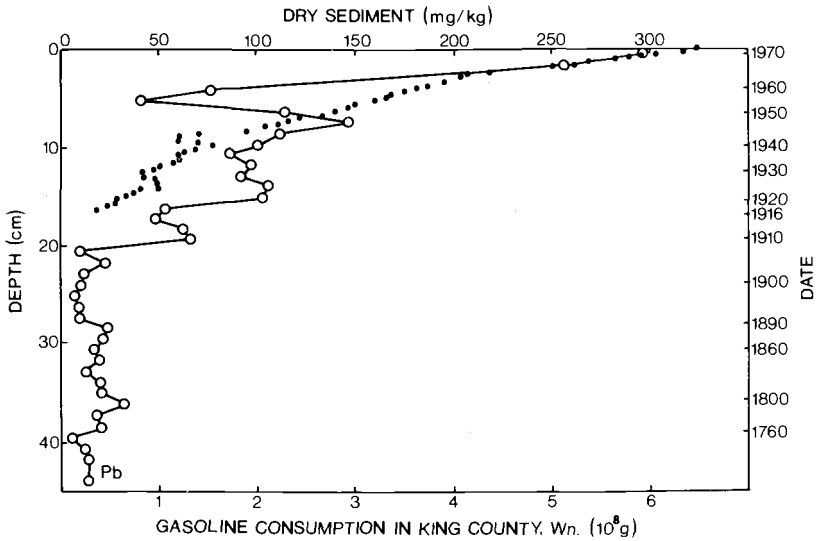
FIGURE 11.3 *Lead in Lake Washington cores (●) compared with gasoline consumption (○) (after Barnes 1976).*

TABLE 11.4 *Average C, N, and P contents of surface sediments from the Lake Washington drainage basin lakes.[a]*

Lake	C^b (%)	N (mg/kg)	P (mg/kg)	C/N ratio	N/P ratio
Findley	11.50	5.55	1.09	16.18	5.14
Chester Morse	6.08	3.71	1.56	16.41	2.37
Sammamish	4.13	4.82	1.32	10.60	3.65
Washington	4.62	3.71	2.13	11.37	1.74

Note: Values are in terms of oven-dried (104°C) sediment.
[a]Bauer 1971; Horton 1972.
[b]The sediments from all four lakes contain less than 0.1 percent $CO_3^=$ - C on an oven-dried basis.

material is relatively resistant to mineralization, partly as a result of low N content. The phenomenon is also evident in streams (Chapters 9 and 10) and some rivers in coniferous forests (Malick 1977). The high C:N ratios in the sediments of all four lakes (>10) were similar to those in the sediments of English lakes (Dean and Gorham 1976), which also receive considerable amounts of terrestrial material. In the lake sediments in the lower Lake Washington drainage, however, the importance of autochthonous sources was reflected by the higher P content in the upper lake sediments. Total P concentra-

tions for sediments in lakes suggest that P is mainly retained in the sediments in association with inorganic materials such as Fe (Figure 11.2).

ELEMENTAL TRANSFERS WITHIN LAKES

Although concentrations of nutrient elements in lake water and sediments are of interest as a reflection of inputs from the terrestrial environment, C and nutrient transfers within a lake are of greater importance in understanding total lake function. Construction of material budgets for a lake (Bormann and Likens 1967) has facilitated the examination of patterns of accumulation, distribution, and loss and development of insights into the relative importance of alternate material pathways.

We hypothesized that among the Lake Washington drainage basin lakes Findley Lake would be influenced most by terrestrial inputs because of its small size and heavily forested shoreline (Wissmar et al. 1977). In the follow-up sections this hypothesis is examined in some detail. Nutrient regimes have also been studied in Lake Washington and Lake Sammamish. Nutrient budgets of Lake Washington are not discussed in this chapter since its response to eutrophication and its subsequent recovery following sewage diversion have been documented elsewhere (Edmondson 1972, 1974, 1977). A brief description of nutrient budgets of Lake Sammamish is provided both as a contrast to Findley Lake and to examine the failure of a nutrient diversion in this lake to produce a change in trophic state similar to that of Lake Washington.

Findley Lake

The importance of terrestrial inputs to small lakes in the form of organic litter (Gasith and Hasler 1976; Rau 1976) and nutrient loading (Dillon 1975; Devol and Wissmar 1978) have been well documented. The benthic zones of these lakes serve as the principal receiving areas where decomposers and consumers process particulate allochthonous inputs (Wetzel and Rich 1973; Pieczynska 1975; Odum and Prentki 1978; Rich and Devol 1978; Wissmar and Wetzel 1978). Previous workers have linked fates of dissolved nutrients in lakes to hydrologic retention times and subsequent autotrophic production (Devol and Wissmar 1978; Johnson et al. 1978; Likens and Loucks 1978; Wetzel and Richey 1978). While there is a reasonable understanding of autotrophic C pathways in temperate lakes, little information is available on the role of detrital-C-based metabolism and mineral cycling in lakes that have high levels of terrestrial detritus inputs and rapid flushing rates. These conditions are characteristic of Findley Lake.

Research on the Findley Lake watershed was oriented toward determining

the structure, productivity, and nutrient cycles of both terrestrial and aquatic ecosystems. It included specific studies of water column processes (Taub et al. 1972; Welch and Spyridakis 1972; Hendrey 1973; Stoll 1973; Bissonnette 1974; Hendrey and Welch 1974; Pederson 1974; Rau 1974, 1976, 1978; Johnson 1975; Pederson and Litt 1976; Pederson et al. 1976; Tison et al. 1977; Richey 1979; A. H. Devol, pers. comm.); sediments (Bauer 1971; Horton 1972; Lanich 1972; Adams 1973; Wekell 1975; Barnes 1976); soils (Singer and Ugolini 1974; Johnson 1975; Ugolini et al. 1977a,b); and vegetation (del Moral 1973; Turner and Singer 1976).

Much of the information from these studies has been synthesized by considering the hypothesis that the major supply of nutrients and C, including both dissolved and particulate matter, for Findley Lake originate in the adjacent forest. Detrital inputs and outputs were measured as particulate and dissolved organic carbon (DOC) and nutrients, inorganic nitrogen (NH_4-N and NO_3-N), and soluble reactive phosphorus (SRP). Lake ecosystem budgets for these inputs and outputs included the influences of internal cycling, phytoplankton uptake, and regeneration by zooplankton.

In 1974 and 1975, allochthonous inputs to Findley Lake supplied 85 percent of the particulate P, 65 percent of the particulate C, 51 to 66 percent of the SRP, and 83 to 89 percent of the dissolved inorganic N (DIN) to the water column (Figure 11.4). Dominant pathways for particulate loss were fluvial outflow and sedimentation. Phytoplankton nutrient requirements for P were supplied by fluvial sources early in the growing season and later by zooplankton excretion. Excess DIN was present throughout the growing season. Allochthonous supplies of DOC and P apparently were not utilized in the water column.

An important feature of the budgets was that sedimentation of allochthonous particulate carbon ($\sim$4 to 8 g $C \cdot m^{-2} \cdot yr^{-1}$) indicated a major supply of energy for benthic consumers. The subsequent distribution patterns of carbon and nutrients in the sediments as well as the magnitude of insect production reflected the influence of this terrestrial input on the benthic environment. A comparison of the average C, N, and P contents of the surface sediments for Findley Lake with the other lakes of the Lake Washington drainage basin illustrates the high levels of terrestrial matter in the Findley Lake sediments (Table 11.4). The response of the benthic consumers to allochthonous inputs was shown by the detritivorous insect production (0.65 g $C \cdot m^{-2} \cdot yr^{-1}$), which was similar to that of herbivorous zooplankton (0.50 g $C \cdot m^{-2} \cdot yr^{-1}$). A more detailed discussion of Figure 11.4 can be found in Richey and Wissmar (1979).

Additional studies of plankton and inorganic carbon in Findley Lake provided dramatic evidence of the influence of terrestrial environment on a lake. Although atmospheric CO_2 is the primary source for organic C production in both terrestrial and aquatic ecosystems, a large part of the dissolved inorganic carbon (DIC) used for phytoplankton production in Findley Lake has been previously reduced and then oxidized. This carbon flux was identified by the ^{13}C-depleted character of the water column DIC and plankton C (δ ^{13}C of -44 to

−47 per mil). This ^{13}C depletion, coupled with the DIC pool, suggests that benthic metabolism and soil respiration provide important C sources for plankton production in Findley Lake and by analogy other mountain lakes in dense coniferous forests (Rau 1978).

Benthic Nitrogen Cycling

Anomalies in the nutrient budgets support the idea that elemental cycling within the benthic region is important. For example, seasonal N and P budgets did not fully account for observed losses of DIN in summer and fall and for SRP in winter and spring. Here we discuss these anomalies and offer several hypotheses to explain nutrient cycling in benthic environments of lakes such as Findley.

Levels of inorganic N in the water column begin to drop during the phytoplankton bloom and remain low through the fall (Hendrey and Welch 1974; Welch et al. 1975). Seasonal N budgets show that a significant storage, or an unknown sink, of lake N occurs in both summer and fall when total inorganic N levels in the lake are low. Phytoplankton uptake of N and subsequent loss through sedimentation appear to account for only a small portion of the N accumulation. The greatest N storage (October and November) occurs when fluvial and precipitation inputs of N to the lake increase. During this period, however, plankton production decreases and inorganic N concentrations of the water column remain low.

A possible explanation for N depletion during the latter half of the growing season may be uptake by benthic algae and N immobilization by the bacterial and fungal communities associated with allochthonous litter. Paerl (1973, 1975) has shown that microbial attachment to detrital particles occurs in Lake Tahoe and that active heterotrophic metabolism is associated with these particles. Kaushik and Hynes (1968) found that increased N content (primarily protein N) was associated with decomposition of elm leaves. These increases were related to microbial and fungal growth. Similar patterns for N increase have been observed in Oregon streams in decomposing conifer needles (Triska and Sedell 1976) and for P in decomposing leaves (Howarth and Fisher 1976).

Investigations of N accumulation by microflora on coniferous detritus in benthic regions of Findley Lake suggest that similar processes occur in this lake. Changes in N, C, ATP contents, and electron transport system (ETS) activity of decomposing detritus in the benthic environment were measured (R. C. Wissmar, pers. comm.). Results suggest that the microbial-detrital complexes immobilize N and that chemical binding (absorption and complexes) of N is also important. The importance of such binding by detrital residues has been suggested by Iverson (1973), Triska et al. (1975), F. J. Triska (pers. comm.), and Suberkropp et al. (1976).

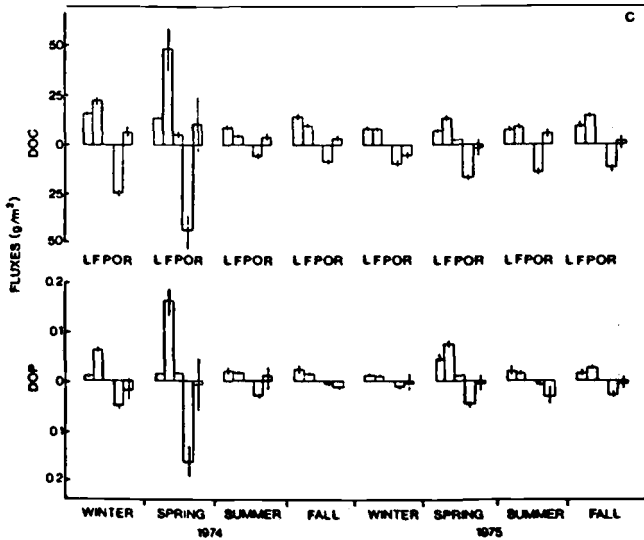Regression analyses of the above data from Findley Lake indicate that
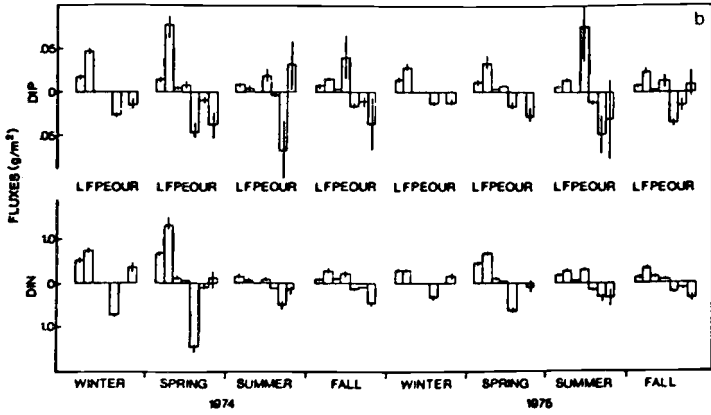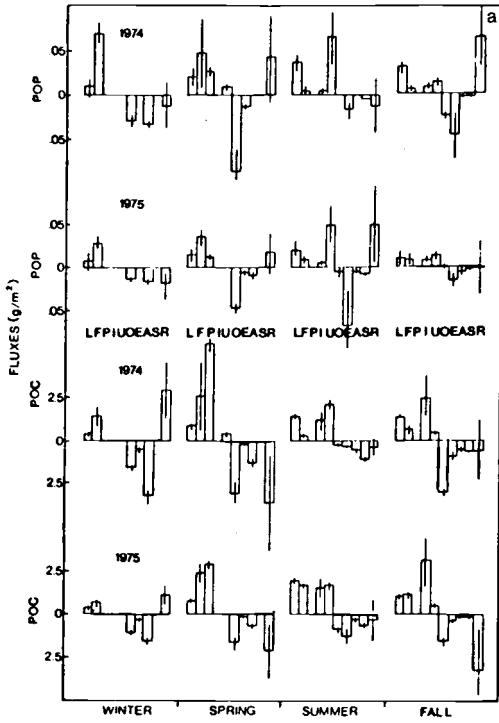
FIGURE 11.4 *Seasonal budgets (A, POC & POP; B, DIN & DIP; C, DOP & DOC) for Findley Lake, 1974–1975, with inputs above and outputs below the horizontal axis. Vertical bar indicates one σ. Key: A = allochthonous sedimentation; E = zooplankton regeneration (b), zooplankton regeneration from POP (a), and respiration from POC (a); F = fluvial inputs; L = lake concentration; O = outflow; P = snowpack plus rainfall precipitation; R = residual; S = autochthonous sedimentation; U = phytoplankton uptake.*

increases in ATP content and decreases in ETS activity of detrital microbes are significantly related to decreases in concentrations of NO_3-N and lake temperature. Microbiota associated with conifer material that has high initial C:N ratios are apparently N-limited. The organisms assimilate most of the available DIN from the surrounding water. The processes involved may be similar to those that occur in soils with high C:N ratios (Alexander 1961).

The initial accumulation of N by microflora on detritus tends to be accompanied by high C loss via mineralization. Subsequent to these primary stages of decomposition, the microbiota apparently die. The processes of autolysis and decomposition result in a release of inorganic N. Some portion of this regenerated inorganic N is assimilated by secondary microbial growth and the cycle is repeated. This process results in more C than N mineralization, thus lowering the C:N ratio of the decomposing detritus. The cycle continues, resulting in the mineralization and release into the sediments and overlying water of both C and N.

In addition to the N inputs already discussed, the other potential biological input of N to Findley Lake is N fixation; however this source is small. Nitrogen fixation (acetylene reduction) by phytoplankton was less than 1 percent of the total annual N income to the lake in 1972 (Tison et al. 1977).

Nitrogen losses other than through outflows and permanent sedimentation appear to be minimal. Denitrification is considered unlikely in these waters because of their well-oxygenated character (Goering and Dugdale 1966, A. H. Devol, pers. comm.).

The fate of N in the sediments of Findley Lake is complicated. The surface sediments have C:N ratios ranging from 12 to 19, suggesting that much of the sediment comes from outside the lake (Dean and Gorham 1976). The percentage of organic N (0.3 to 0.7 percent), E_h values of greater than $+0.200$ volts, low pH, and moisture content (60 to 90 percent) are similar to the values in a mountain lake in Virginia (Obeng-Asamoa 1976), which also receives high levels of allochthonous matter. Given these conditions, and from chemical studies by Obeng-Asamoa (1976), it can be postulated that slow rates of nitrification in surface sediments probably permit some NO_3^- to diffuse into overlying waters. Increased levels of NH_4^+ with depth in the sediment layers imply microbial activity that might be accompanied by decreases in organic N with depth. In addition, the importance of irrigation in deeper sediment layers by macroinvertebrates residing in surface sediments cannot be discounted and could influence the N cycling in the sediments (Bender et al. 1977; Grundmanis and Murray 1977; Vanderborght et al. 1977a, b).

Benthic Phosphorus Cycling

Attempts to balance water column SRP budgets in spring 1974 and winter and spring 1975 indicate that inputs exceeded losses, and suggest an unknown sink for SRP. Several possibilities might explain the result: (1) Bacterial or phytoplankton uptake and storage as polyphosphate seem unlikely, since plankton biomass and activity are extremely low at this time, and polyphosphate has not been detected in Findley Lake; (2) Dissolved inorganic P from streams enters the shallow, nearshore regions of the lake and is utilized by benthic algae and detrital microbes. Perkins (1976) demonstrated that periphyton in small streams could store phosphate as polyphosphate; (3) Some phosphate might be complexed with the iron-rich organic acids that constitute the dissolved organic pool.

During the large and sudden phytoplankton bloom in summer, inputs of SRP to the lake exceed outputs. This suggests that the phosphate required to support the bloom is not accounted for by the measured sources. There are several other possible phosphate sources. Planktonic extracellular products of DOP may be utilized through the enzyme alkaline phosphatase (Lean 1973; Richey 1977); however, Richey (1979) found only monophasic uptake kinetics

of $^{32}PO_4$ and no indication of [^{32}P] DOP in Sephadex chromatography experiments, suggesting that this source is almost negligible in Findley Lake. A more likely source of phosphate is from sediment regeneration.

The role of sediments in P cycling pathways has often been considered minimal (Mortimer 1971; Schindler et al. 1973; Richey 1974). This has been justified on the grounds that the oxidized sediments act as a P sink, in the fashion outlined by Mortimer (1941, 1942). Others have stressed the role of sediments as a buffer for P concentrations in the overlying water (Stumm and Leckie 1971). Interstitial sediment P concentrations are much higher than in overlying waters. The forms of P in the sediments and rates of exchange between these pools have been the subject of extensive experimentation. For example, different fractionation techniques have been used in attempts to separate the P species, but the kinetic and equilibrium relations between them are complex and remain poorly understood (Chang and Jackson 1957; Williams et al. 1967; Stumm and Morgan 1970; Sommers et al. 1970, 1972; Williams et al. 1971a, b; Syers et al. 1973). In view of sediment P interchange with the overlying waters, sorption and desorption mechanisms are important and have received much study (for example, Carritt and Goodgal 1954; MacPherson et al. 1958; Golterman 1967; Harter 1968; Shukla et al. 1971). These mechanisms are pH-dependent, and involve solubility relations of phosphate with Fe^{3+}, Al^{3+}, and Ca^{2+} complexes. In undisturbed sediment/water interfaces, the rate-determining step is diffusion transport through the interstitial water (Stumm and Leckie 1971); however bacteria and especially macroinvertebrate irrigation of sediments may accelerate the release processes (Neame 1975).

The mobility of sediment P is dependent on its form. Adsorbed and free inorganic phosphate is more readily available for incorporation into nutrient cycles than P tightly bound in mineral phases. The physical and biological stirring phenomena previously discussed can make the interstitital dissolved P and the loosely adsorbed phosphate available to the entire system. The direction of net P movement across the interface depends on the size of the P pools in the system. Kamp-Nielsen (1974) found that P release from the sediments occurred when the concentration in the overlying water was < 30 μg/liter, and that the subsequent rate of release in an oligotrophic lake amounted to approximately 200 μg P$\cdot$m$^{-2}\cdot$day^{-1}. Neame (1975) found phosphate release rates of 650 μg$\cdot$m$^{-2}\cdot$day^{-1} in Castle Lake, California (a lake similar to Findley Lake), in sediments having high porosity and containing large populations of benthic macroinvertebrates. Neame also suggested that the oxidized zone, normally thought to impede phosphate release from aerobic sediments, may be ineffective when these other conditions coincide. This confirmed the results of Williams and Meyer (1972). Thus it seems possible that phosphate release from the sediments could be a phosphate source for the overlying water column.

Further indirect evidence suggests that P release from the sediments may be occurring in Findley Lake. In the summer and fall growing season there is an

increase in P in epilimnetic waters. Such conditions may be due to rapid decomposition of terrestrial detritus and subsequent liberation of phosphate in shallow nearshore sediments during warm weather. Death and autolysis of algal periphyton and heterotrophs may release soluble phosphate. Once released, phosphate may be taken up rapidly by benthic microflora and phytoplankton, precluding detection of changes in ambient phosphate concentrations. In fact, peak phytoplankton biomass and production occurred within several meters of the bottom. This was previously attributed to light inhibition (Hendrey 1973), but it may also be due to proximity to nutrients from the sediments. Rate constants of $^{32}PO_4$ uptake were also generally greater close to the sediments than higher in the water column (Richey 1979).

Summary of Elemental Processing in Findley Lake

The data and discussion presented above suggest a scenario explaining the nature of elemental processing in Findley Lake. A major energy source available to the ecosystem is terrestrial detritus. Most detritus enters the lake through fluvial inputs when the snowpack melts in the spring. Other sources are summer and autumn litter and fluvial inputs. The highest inputs of inorganic P and N are from spring fluvial sources. The availability of these inorganic nutrients may enhance the growth of littoral periphyton and of microbes on detritus. Nevertheless, most nutrients pass through the lake untouched because of the high flushing rate of the lake's volume (7.8 X/yr).

The sequestering of nutrients serves to enrich the nutritional value of detritus as a forage base for benthic detritivores. Benthic detrital deposits and within-sediment accumulation of organics and nutrients suggest the potential importance of nutrient regeneration to overlying waters and to heterotrophic and autotrophic growth on surface sediments. This explanation supports the hypothesis that terrestrial inputs to sediments, and the subsequent cycling of nutrients in the sediments, have a major influence on biological activity in both benthic and water-column environments during most of the growing season. These pathways may be particularly important in years of heavy snowpack followed by rapid melting, when increased flushing rates of nutrients reduce phytoplankton production.

Lake Sammamish

The nutrient regime in Lake Sammamish is very different from that in Findley Lake. The difference is due primarily to the slower flushing rate, the larger size of Lake Sammamish, and, to a lesser extent, to anthropogenic influences. Secondary effluent from a sewage treatment plant was diverted from Lake Sammamish in the mid 1960s, with a reduction in P loading from

1.02 $g \cdot m^{-2} \cdot yr^{-1}$ to 0.67 $g \cdot m^{-2} \cdot yr^{-1}$. As yet no response in the trophic state of the lake has been observed (Welch 1977).

Lake Sammamish can be divided into distinct trophogenic (0 to 9 m) and tropholytic zones (9 to 24 m). Data from the trophogenic zone in the spring suggest that N and P recycling is fairly efficient, and that a depletion of dissolved N and P pools occurs (Figure 11.5; Birch 1976). This is the net result of a number of factors. Phytoplankton photosynthesis is fairly high during the spring diatom bloom. In early spring it is coupled with a rapid sinking rate, low solubilization rates, and relatively high sedimentation rates when the diatom bloom is at peak. In the tropholytic zone there is a decrease in concentration of particulate N, dissolved N, and particulate P, and an increase in dissolved P. The particulate P and N pools appear to be depleted, because of the combined effects of sedimentation and solubilization. Dissolved P increases due to the solubilization flux and a slight net gain from inflow. The dissolved N pool would probably increase during this period due to the same influences except for losses due to denitrification.

A somewhat different picture is presented during summer in the trophogenic zone (Figure 11.6). Solubilization is very efficient owing to the combined effect of high dissolution rates and slower sinking velocities. It appears that almost as much N and P is solubilized as is transformed into particulate form via photosynthesis. Since the sedimentation flux is rather small there is a slight increase in particulate N and P with a corresponding slight decrease in the dissolved pools. The decreases are much smaller than those observed during spring. It should be noted that there may be increases in dissolved P in the trophogenic zone in late summer as the thermocline erodes and hypolimnetic P is mixed into the epilimnion.

In the tropholytic zone, there are net increases in all the N and P pools. The measured increases in dissolved N and P can be attributed to measured fluxes to a greater extent than can increases in particulate N and P. Dissolved pools increase because of combined influxes from solubilization and sediment release. Since there is a net loss to the particulate pools due to sedimentation into the bottom sediments plus a further loss due to solubilization, the only way an increase in particulate N and P could occur is from fluxes from other pools. One possibility is heterotrophic utilization and subsequent biomass increase in particulate N and P. A second possibility is coprecipitation of P released from the sediments with Fe in contact with the more oxygenated upper hypolimnetic waters. Iron and P could also be precipitating on the surface of *Metallogenium* sp., a bacterium observed in hypolimnetic waters in late summer.

The external loading of P was reduced 30 percent after diversion. This loading of 0.62 $g \cdot m^{-2} \cdot yr^{-1}$ was about twice the internal loading from anoxic sediment release (0.3 $g \cdot m^{-2} \cdot yr^{-1}$; Birch 1976). Horton (1972) and Rock (1974) have shown, however, that since sediment P release occurs during the stratified period, most of the released P is trapped in the hypolimnion and is not available for algal nutrition until fall overturn. At that time, about 80 percent of this P is
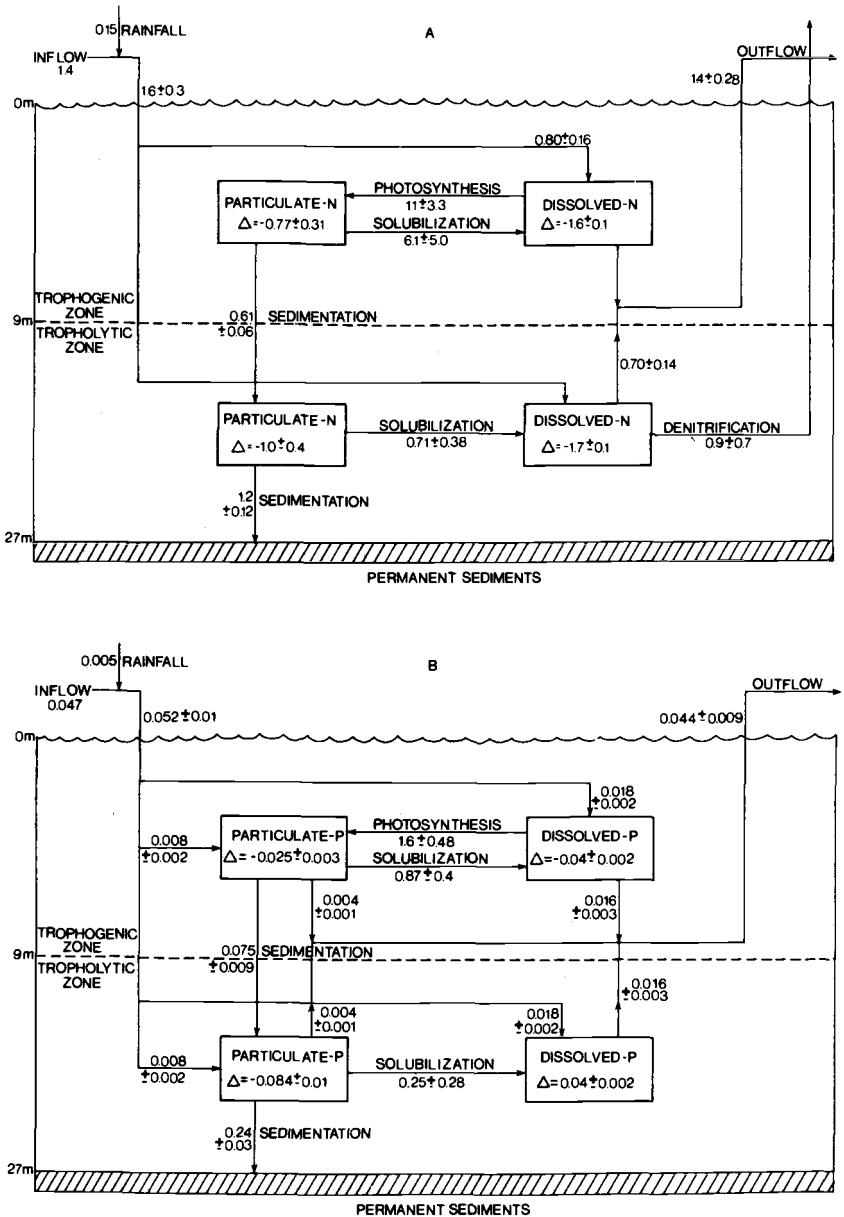
FIGURE 11.5 *Nitrogen (A) and phosphorus (B) budgets for Lake Sammamish, spring period (26 March 1975 to 21 June 1975; in grams per square meter).*
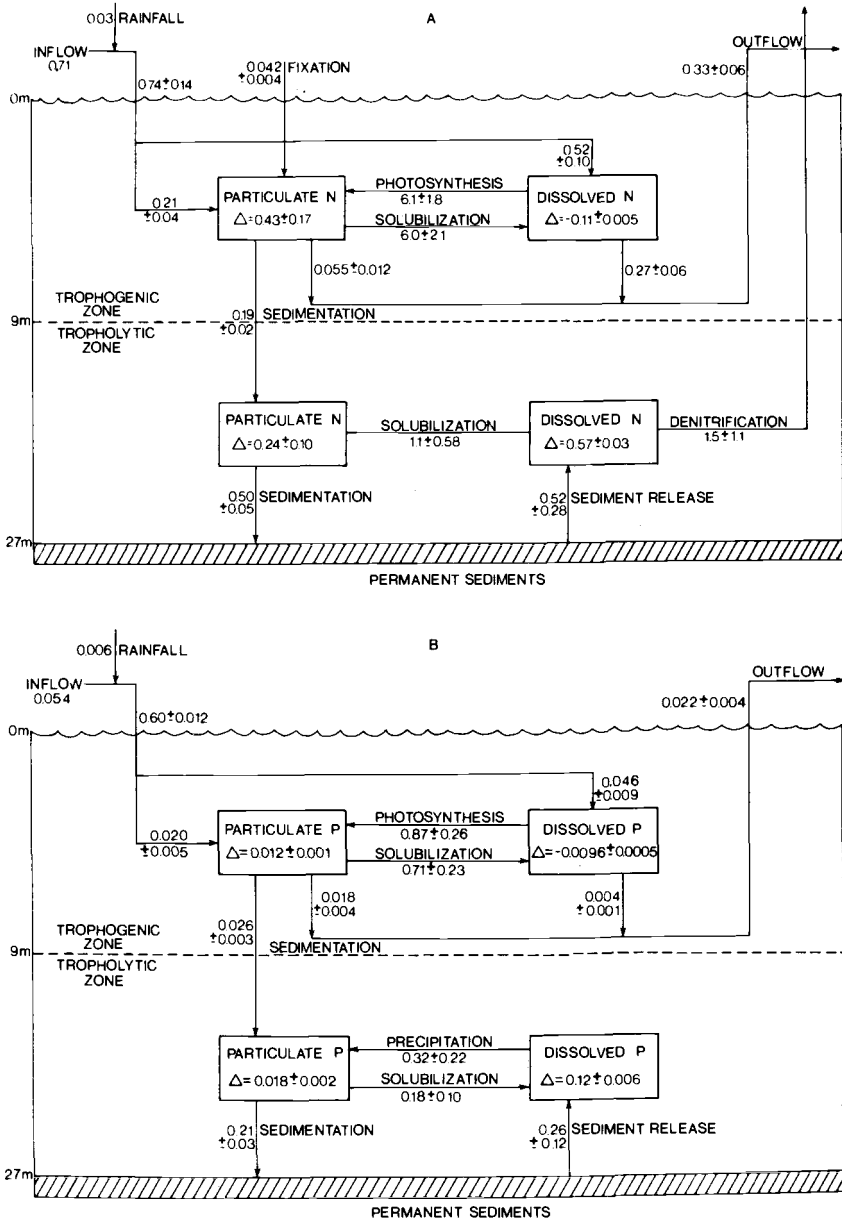
FIGURE 11.6 *Nitrogen (A) and phosphorus (B) budgets for Lake Sammamish, summer period (25 June 1974 to 1 October 1974; in grams per square meter).*

reprecipitated with Fe. Thus internal loading is of minor importance, and the lack of response is presumed due to rapid nutrient recycling during late spring and summer.

PHYTOPLANKTON PHYSIOLOGICAL RESPONSES TO CHANGING NUTRIENT REGIMES

In an attempt to further the understanding of nutrient cycling in lake ecosystems, phytoplankton were studied in some detail. Since phytoplankton metabolism is closely coupled to nutrient regimes in the water column, emphasis was placed on physiological responses of phytoplankton to varying environmental conditions.

Phytoplankton react to changes in their environment by modifications of their biochemical pathways, resulting in altered cell structure and physiology. In recent years investigators have attempted to relate changes in phytoplankton growth to physiological state through the use of biotic parameters (Sakshaug and Holm-Hansen 1977). These parameters are derived from studies of the chemical composition of phytoplankton under various types of limitations, primarily degrees of nutrient limitation. For example, it has been found that: (1) the *in vivo* fluorescence:chlorophyll-*a* ratio increases with increasing N and P limitation (Loftus and Seliger 1975); (2) the C:ATP ratio increases with increasing P deficiency (Cavari 1976; Perry 1976); and (3) the C:N and C:P ratios of phytoplankton increase under N and P limitation (Fuhs et al. 1972; Sakshaug and Holm-Hansen 1977). Other examples of relations between biotic parameters and physiological state can be found in Sakshaug and Holm-Hansen (1977) and Caperon and Meyer (1972).

The goal of such studies is to describe whether or not growth limitation is present in a given situation and, if so, to evaluate the limiting factor. The potential of this approach is indicated by the fact that in chemostat studies it has been possible to relate the chemical composition, or biotic parameters, directly to growth rate (Fuhs et al. 1972; Droop 1974; Perry 1976). At present, however, application of these investigations to field studies of aquatic ecosystems is difficult, because, in contrast to natural populations, nearly all previous studies are species-specific. Therefore they contain neither the detrital component of natural systems, which complicates the interpretation of C, N, and P measurements, nor the changing population structure characteristic of natural systems. In spite of these difficulties, it has been possible to relate biotic parameters to physiological state in some cases (Haug et al. 1973). Furthermore, as pointed out by Sakshaug and Holm-Hansen (1977), even though biotic parameters may have different ranges for field and laboratory populations, the direction of change in chemical composition is probably the same for corresponding alterations in growth conditions in both the field and in the laboratory.

Our research indicates that the biotic parameters, P:R, C:ATP, nitrate reductase activity:chlorophyll (NR:Chl), and $^{32}PO_4$ flux, undergo significant changes soon after the peak of the phytoplankton bloom. These parameters are presumed to be related to changes in the physiology of the phytoplankton community and are described as follows in relation to the chemical and physical environment in the lake.

The seasonal cycles of SRP, inorganic nitrate, temperature, carbon-14 productivity, and chlorophyll-*a* in Lake Washington during 1974 are shown in Figure 11.7. The data are presented on an areal basis integrated over the top 10 m. About 95 percent of the carbon-14 production takes place in that depth interval during all seasons (Devol and Packard 1978; Richey 1979). Furthermore, the 1975 seasonal cycle of these variables was similar to the 1974 cycle shown in Figure 11.7, with only minor changes in the timing of events and the absolute values of the parameters (Richey 1979). Lake Washington is typical of monomictic, temperate lakes with maximum nutrient concentrations and mini-
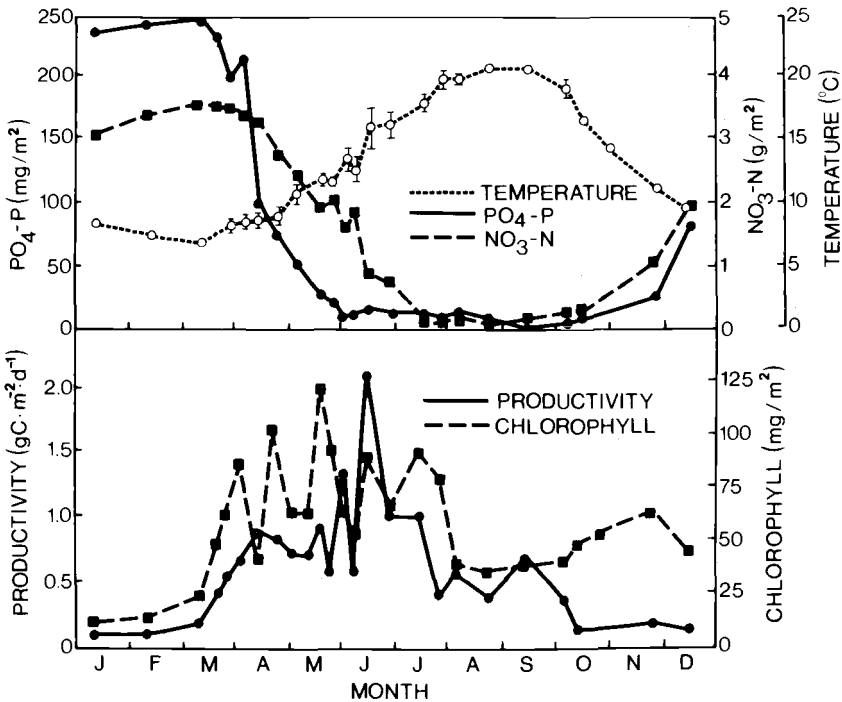

FIGURE 11.7 *The 1974 seasonal cycles of phosphate, nitrate, temperature, productivity, and chlorophyll-a in Lake Washington. All data have been integrated over the upper 10 m except temperature, for which the average and range in the upper 10 m are given (after Devol and Packard 1978).*

mum temperatures during the winter isothermal period. In 1974, surface water temperatures increased in early March, which coincided with the onset of the spring bloom as measured by productivity and chlorophyll. Nitrate and phosphate levels began to decrease as a result of biological activity. Nutrient stocks became depleted and increased temperatures resulted in thermal stratification. Low phosphate levels ($10 \, mg/m^2$) were reached in early June while low nitrate levels did not occur until mid-July. Maximum phytoplankton production occurred in mid-June and continued at reduced levels through early October. High levels of phytoplankton production and chlorophyll coincided with the period of maximum thermal stratification (deep convective overturn began in November).

The Photosynthesis:Respiration (P:R) Ratio

Steele (1965) has suggested that the P:R ratio is "the main single measure we can obtain of the physiological state of the [phytoplankton] populations." Despite its potential importance, the P:R ratio has not been well investigated. Reported values range from < 1 to 60 and vary with growth phase (Humphrey and Subba Rao 1967), depth in the water column (Yentsch 1975), light (Bunt 1965), nutrient concentration (McAllister et al. 1964), and temperature (Bunt 1965). Only a few studies of seasonal variation in the P:R ratio have been made.

Measurements of ETS activity were used in conjunction with the carbon-14 productivity data presented in Figure 11.8 to calculate two types of P:R ratios for the euphotic zone of Lake Washington (Devol and Packard 1978). The curve labeled $(P:R)_m$ in Figure 11.8 was calculated from hourly data taken at the depth of the maximum assimilation ratio (carbon-14 uptake/Chl), whereas the curve labeled $(P:R)_e$ was calculated from daily data integrated over the depth of the euphotic zone. The P:R ratio is essentially the ratio of net C production during the day to C respired at night. The values of $(P:R)_m$ range from 46 to 2.2 and are within the range reported in the literature (see Devol and Packard 1978). When calculated on a percentage basis, $(P:R)_e$ values indicate that a range of 7 to 142 percent of carbon-14 production is consumed by respiration at night.

Both $(P:R)_m$ and $(P:R)_e$ were high early in the growing season and decreased to lowest values during the thermally-stratified, low-nutrient summer period (Figure 11.8). Devol and Packard (1978) have suggested that this trend is due to increased P limitation as the summer progressed, increased respiration as the lake warmed, or a combination of both factors. Increased temperatures, however, should also result in increased production if other factors are not limiting (Eppley 1972; Goldman and Carpenter 1974). Production:respiration ratios were also calculated for Findley Lake (Figure 11.9) and for Lake Sammamish (not shown). The same trend of decreasing P:R ratios through the growing season was observed also in these lakes.
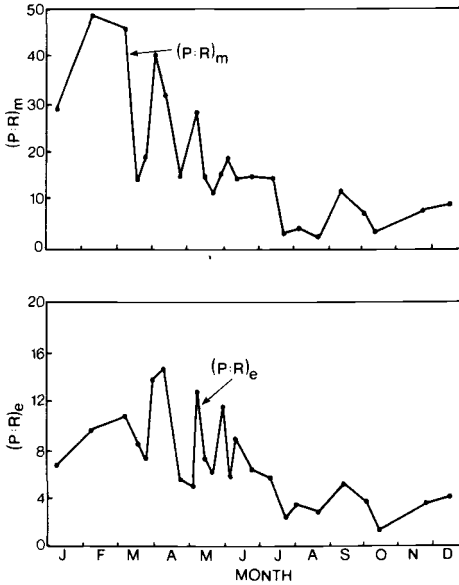
FIGURE 11.8 *Production:respiration ratios for the upper 10 m of Lake Washington during 1974. A detailed description is given in the text (after Devol and Packard 1978).*
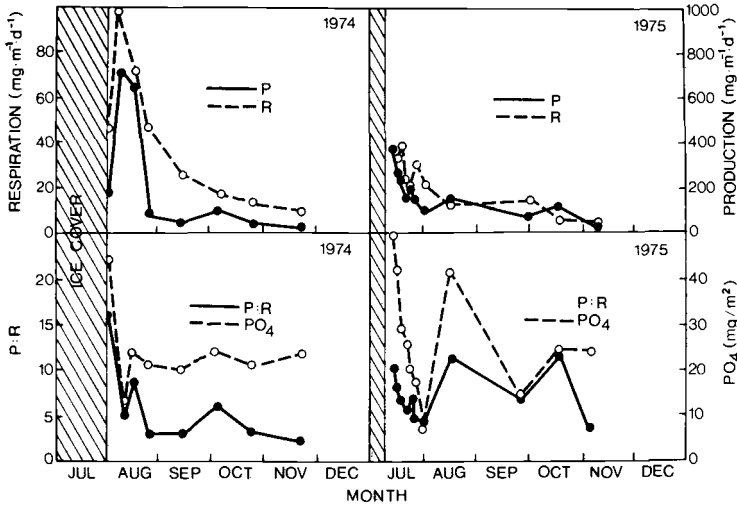

FIGURE 11.9 *Production, respiration, phosphate, and P:R ratio in Findley Lake during 1974 (left) and 1975 (right) growing seasons. All data have been integrated over the entire 25-m euphotic zone.*

Our interpretation of pooled data from Lake Washington and Lake Sammamish taken during the latter half of the spring bloom and the summer stratification period lends support to the proposed mechanism of nutrient stress. Figure 11.10 suggests that production decreases with decreasing concentrations of PO_4, and that chlorophyll-specific respiration increases with increasing temperature. In Findley Lake much of the water column productivity occurs below the thermocline (Wissmar et al. 1977). Thus fluctuations in the P:R ratio as a function of temperature can be eliminated. A regression analysis of data presented in Figure 11.10 indicates that in this region of the water column 81 percent of variation in the P:R ratio can be attributed to ambient phosphate concentration (that is, $r^2 = 0.81$).

The Carbon:Adenosine Triphosphate (C:ATP) Ratio

It is assumed generally that in viable cells ATP occurs in a constant ratio to C (C:ATP = 250:1). When C:ATP ratios were calculated for Lake Washington phytoplankton populations from algal cell volume C (using the method of Strathman 1967) and microplankton (<75 μm) ATP data, however, ratios as
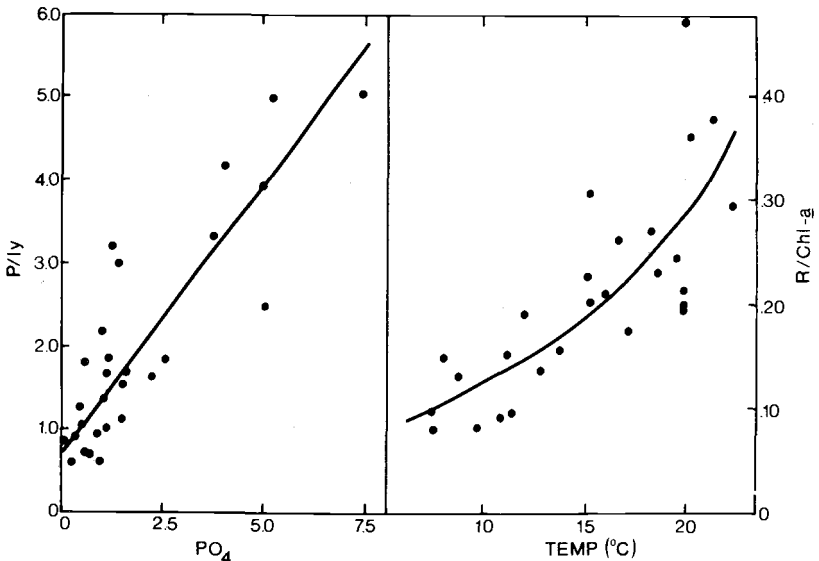
FIGURE 11.10 *Production per langley (P/ly) vs. average euphotic zone phosphate concentration (μg/liter) and respiration per unit chlorophyll-a (R/Chl-a) versus average euphotic zone temperature for plankton from lakes Washington and Sammamish. Data were collected from the latter half of the bloom and during the summer stratification. Values given for P/ly and R/Chl-a have been integrated over the depth of the euphotic zone.*

large as 750 to 1000 (Figure 11.11) were observed. There are two possible explanations for these high ratios: (1) there may have been a significant bacterial contribution to microplankton ATP; and (2) the C:ATP ratio may not have been constant. Although bacterial ATP certainly was present in all our microplankton samples, it is doubtful if it could have accounted for the observed ratios. Bacterial biomass would have had to be three times algal biomass to account for a C:ATP ratio of 1000. Estimates of bacterial biomass by the direct count and the Acridine Orange epifluorescence methods (Daly and Hobbie 1975) showed that bacterial biomass was far too low to explain the observed change.

Variations in C:ATP ratios as great as those we observed have also been reported by Holm-Hansen (1970) and Holm-Hansen and Paerl (1972). Their data indicate that cellular ATP levels decrease during periods of severe nutrient limitation to as little as 16 percent, and more commonly 30 percent, of levels found in healthy cells. This is equivalent to an increase in the C:ATP ratio from 250 to 750. Commensurate with these changes, they found changes in the
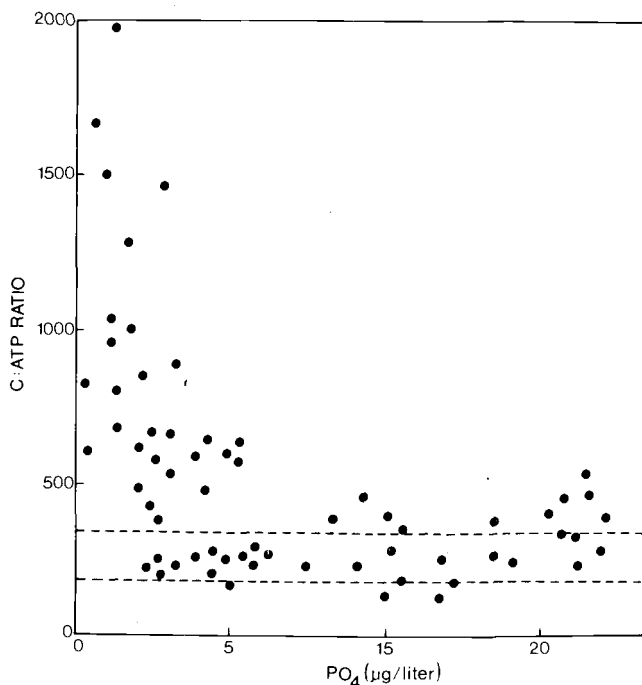

FIGURE 11.11   *Relation between C:ATP ratio of phytoplankton and concentration of inorganic PO$_4$-P in Lake Washington. The C:ATP ratios have been integrated over the top 10 m and PO$_4$-P values are averages for the same depth interval. Dashed lines indicate 30 percent confidence levels around C:ATP = 250.*

cellular C:P ratio from about 50 (w/w) for healthy cells to about 250:1 for nutrient-starved cells. The authors questioned, however, whether nutrient starvation to this extent exists in nature. Other workers have also reported high C:ATP ratios (Cavari 1976; Perry 1976; Sakshaug and Holm-Hansen 1977). These high ratios are usually attributed to nutrient limitation.

Our data for natural microplankton communities indicate that C:ATP ratios do increase with diminishing phosphate concentration (Figure 11.11), although the entire range of C:ATP ratios was observed at very low phosphate concentrations. High C:ATP ratios coincided in time with lower P:R ratios. There are several factors, both real and artificial, that could cause this shift. First, microscopic phytoplankton enumeration may include a significant number of dead algal cells; however a ratio of 1000 would require that 75 percent of the counted cells be dead. This would lead to unrealistically high assimilation rates and to phytoplankton turnover rates (production/biomass) on the order of 5/day during the summer low-nutrient period, which was not seen. Second, as cells become nutrient-limited, organic matter synthesis may shift from compounds used for active growth to storage compounds such as carbohydrates (Haug et al. 1973). Then as carbohydrates accumulate in the cell, the C:ATP ratio may increase (Fuhs et al. 1972; Khul 1974). Finally, increases in the C:ATP ratio may result from a shift in the biochemical equilibrium of the adenylate system.

Nitrate Reductase (NR) Activity

A preliminary survey of NR activity (as measured by the method of Eppley et al. 1969) was conducted on Lake Washington plankton (Figure 11.12). Although data are few, NR activity increased through the first half of the spring bloom and then decreased abruptly. When normalized to chlorophyll, NR activity remained relatively constant during the spring and then decreased to nearly zero by mid-June. The data in Figure 11.12 also show the amount of N required to support the observed carbon-14 primary production (assuming a C:N uptake ratio of 106:16, by atoms). Nitrogen requirements in February and March are almost the same as during the summer stratification, but the chlorophyll-specific NR activity is dramatically different. Although there are several potential explanations for the data (Packard et al. 1971), it is noteworthy that the decrease in NR activity takes place in the same time during which the P:R and C:ATP ratios change.

[^{32}P]Phosphate Flux

Phosphorus is the major inorganic nutrient limiting phytoplankton production in both Lake Washington and Lake Findley (Edmondson 1972; Hendrey
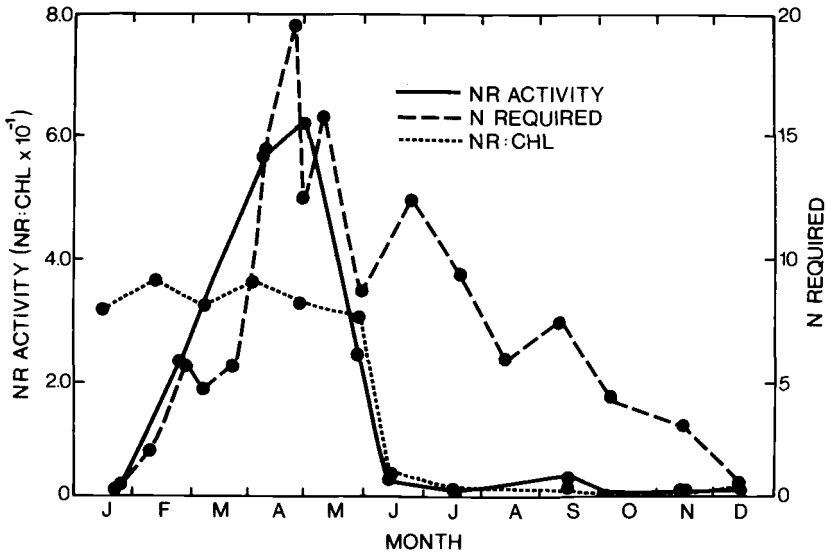
FIGURE 11.12   *Nitrate reductase activity (mmol NO_3 reduced$\cdot m^{-2} \cdot h^{-1}$) and NR:chl (mmol NO_3 reduced $\cdot mg$ $chl^{-1} \cdot h^{-1}$) as a function of season in Lake Washington. Also shown is the amount of N (mmol/m^2) required to support the observed Carbon-14 productivity as calculated from stoichiometric ratios. All data have been integrated over the depth of the euphotic zone.*

1973). Its availability appears to affect P:R and C:ATP ratios. Phosphorus dynamics were investigated in detail, using $^{32}PO_4$ tracer, organic partitioning, and nutrient addition techniques (Richey et al. 1975; Richey 1977; Richey 1979).

Phosphorus-uptake rate constants measured using $^{32}PO_4$ were compared with the theoretical rate constants required to support photosynthesis, as calculated from carbon-14 uptake and stoichiometric ratios (Richey 1979). Observed and expected rate constants matched well from overturn (November) through the peak of the spring bloom in Lake Washington (Figure 11.13). Thereafter, observed rate constants exceeded those calculated from photosynthetic demand. Through the summer the difference between observed and expected rate constants increased by up to two orders of magnitude. In Findley Lake, the measured constants were always greater than those calculated from production. Possible explanations for the consistent divergence between observed and expected rate constants include: (1) the molybdate blue method for measuring available PO_4 provided a vast overestimate at low concentration; (2) bacterial uptake of PO_4 provided the difference; and (3) the ratio of C:P uptake decreased. Although (1) and (2) undoubtedly explain some of the variance, changes in the C:P uptake are probably of greater importance (Richey 1979). Sakshaug and Holm-Hansen (1977) determined that cellular C:P ratios in-
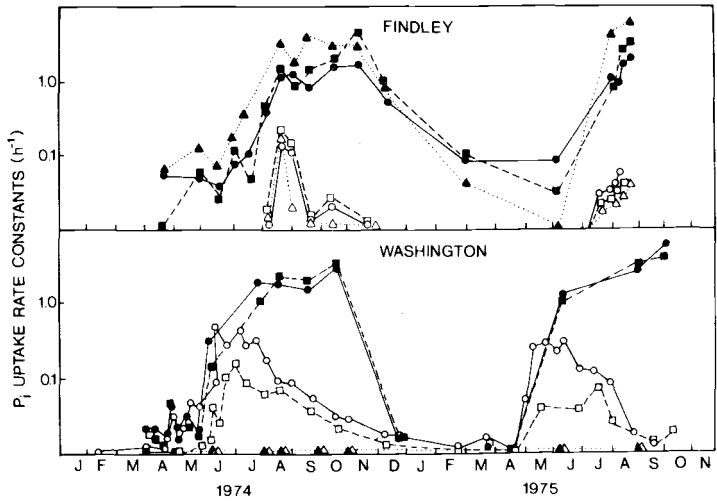
FIGURE 11.13 *Phosphorus uptake rate constants as calculated from ^{32}P uptake (solid points) and carbon-14 uptake (open points) as averages over the following depth intervals: Findley Lake 0 to 10 m (○), 10 to 20 m (□), and 20 to 25 m (△); Lake Washington 0 to 5 m (○), 5 to 10 m (□), and 10 to 58 m (△) (after Richey 1979).*
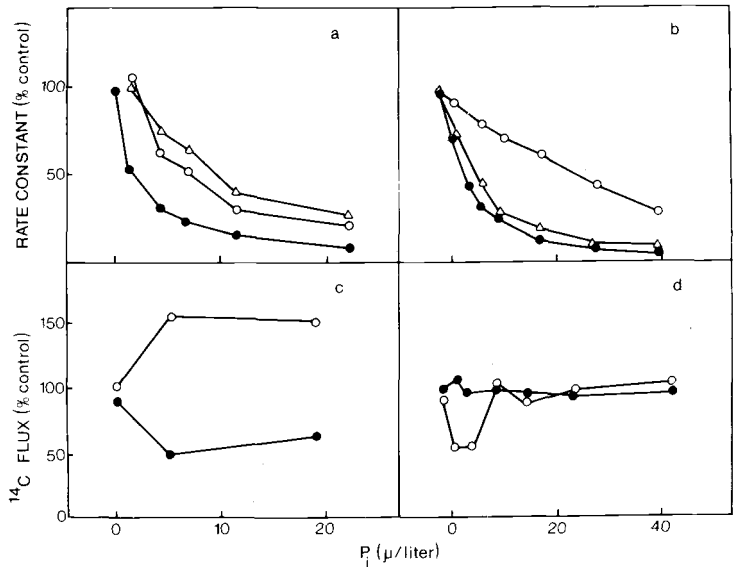
FIGURE 11.14 *Phosphorus uptake rate constants (a, May; b, August) and carbon-14 flux (c, May; d, August) as a function of phosphate addition. In (a) and (b) are shown k_{con} (●), k_i (○), and k_f (△). In (c) and (d) are shown carbon-14 incorporation (○) and extracellular release (●).*

creased by about a factor of 10 in phosphorous-deficient cultures of both *Skeleteonema* sp. and *Pavlovia* sp. Similar results have been presented by Fuhs et al. (1972) and others. Such changes in the C:P uptake ratio would drastically alter the P-uptake rate constants calculated from carbon-14-uptake rates.

Short-term bioassay experiments were conducted on Lake Washington plankton to consider the effect of PO_4 addition on P-uptake kinetics and carbon-14 flux. Results from two experiments conducted in May 1975, soon after the bloom peak, and in August 1975, during the thermally stratified, low-nutrient period, are shown in Figure 11.14. If added P does not result in increased uptake velocity, such as would occur under nutrient-sufficient conditions, then the rate constants calculated from concentrations, k_{con}, would decrease proportionately: for example, if phosphate concentration were doubled over a control, k_{con} would be 50 percent of the control. For both experiments the initial rate constants, k_i, measured immediately after P addition, increased over k_{con} by the amount predicted from the respective k_s (half saturation constant) values (Richey 1979). The final rate constant, k_f, however, remained comparable to k_i in the May experiment, but decreased to k_{con} values in the August experiment.

Patterns of carbon-14 flux also differed between the two experiments. In the May experiment incorporation was increased by 50 percent over the control after thirty hours, while extracellular release decreased by 50 percent. In August there was no response to additions with the exception of two low values for incorporation at low addition levels. These results suggest that PO_4 added in May was indeed incorporated by plankton and resulted in increased primary production, whereas in August added PO_4 was initially taken up, but could not be incorporated, and was released.

Physiological Responses: Explanations for Change

We attribute the changes observed in the biotic parameters of the lakes in the Lake Washington drainage to altered algal physiology, primarily as a response to P stress. Thus knowledge of the values of these biotic parameters and their direction of change through time could be a useful indicator of the physiological state of natural plankton populations. Possible explanations for the observed changes in these biotic parameters follow.

Production:respiration.   Decreases in the P:R ratio are the result of a decrease in production, and/or an increase in respiration per unit biomass. It is well known that phosphorus limitation decreases algal specific growth rates and therefore, presumably, carbon-14 production. On the other hand, dark respiration is required to supply energy for cell maintenance and thus, on a per-unit-biomass basis, may not decrease or increase from one production period to another. An additional or alternate explanation of decreasing P:R ratios during summer stratification is that increasing temperatures result in increased respiration rates.

Carbon:adenosine triphosphate.   The increase in the C:ATP ratio may be due to a relative increase in the synthesis of energy storage compounds during periods of P stress. This results in increased C:P and C:N ratios. An alternative explanation is that increased C:ATP ratios may be the result of a decrease in the adenylate energy charge. If the latter explanation is true the total cell adenylate concentration (A_t) would be a better estimator of viable C than ATP (that is, $C:A_t$ = constant).

Carbon:phosphorus.   The divergence between observed and expected P-uptake rate constants can be related to P stress through changes in the C:P uptake ratio. Increases in the C:P uptake ratio under P deficiency would directly decrease the rate constant calculated from carbon-14 uptake; however, it has been found that nutrient uptake and algal growth are not necessarily coupled over short time scales (Dugdale 1976). Thus the high rate constants estimated from ^{32}P during the summer stagnation may represent exchange between external PO_4 and an internal P pool (Taft et al. 1975). Since it has been proposed that the number of P uptake sites per cell increases under P stress (that is, V_{max} increases; Perry 1976), this type of exchange would inflate the values of rate constants estimated from ^{32}P-uptake experiments done during the summer stratification.

Nitrate reductase.   Sufficient data are not available to make any strong statements on the changes in NR activity. The decrease may be due to: (1) changes in the C:N ratio commensurate with changes in the C:P ratio caused by P stress; (2) changes in the biochemical pathways of NO_3 assimilation; or (3) shifts to other sources of N such as NH_3, NO_2, or nitrification.

DETERMINANTS OF CONSUMER COMMUNITY STRUCTURE AND PRODUCTION IN LAKE WASHINGTON

An understanding of lake ecosystems is far from complete without consideration of the trophic dynamics of higher consumers. The major objective of our fisheries research was to provide insight into the response of consumers to changes in lake trophic state and to identify specific determinants of fish community structure (Eggers et al. 1978). Our discussion focuses on consumer dynamics in the Lake Washington ecosystem from the dual perspective of total fish community production and the respective contributions of the fish forage bases, namely zooplankton, mysids, benthos, and fish. Lake Washington is well suited for this investigation because of its unique perturbation history of eutrophication and subsequent recovery (Edmondson 1972).

Twenty-nine species of fish are found in Lake Washington (R. S. Wydoski pers. comm.); twelve are resident species: prickly sculpin *(Cottus asper)*, juvenile sockeye salmon *(Oncorhynchus nerka)*, peamouth *(Myocheilus caurinus)*, northern squawfish *(Ptychocheilus oregonensis)*, yellow perch *(Perca flavescens)*, longfin smelt *(Spirinchus thaleichthys)*, threespine stick-

leback *(Gasterosteus aculeatus)*, largescale sucker *(Catostomus macrocheilus)*, brown bullhead *(Ictalurus nebulosus)*, black crappie *(Pomoxis nigromaculatus)*, largemouth bass *(Micropterus salmoides)*, and carp *(Cyprinus carpio)*. The first seven species mentioned are the most common and their annual production and diet are discussed below. The last four are restricted to weedy bays and undeveloped shoreline areas that constitute only a small portion of the total fish habitat of Lake Washington because of urbanization and shoreline development (Hockett 1975). Data sources for limnetic fish populations were Dryfoos (1965), Woodey (1971), Dawson (1972), Traynor (1973), Doble (1974), and Moulton (1974); and for benthic-littoral fish were Bartoo (1972), Nishimoto (1973), Olney (1975), Nelson (1977), and N. A. Rickard (pers. comm.).

Fish Production and Forage Bases

Annual fish production and dietary components were estimated to relate the Lake Washington fish community to the trophic dynamics of the lake. Annual patterns of abundance, growth, and diet for each major fish species and its respective age class were determined. Mean annual biomass and production of the limnetic species were computed for the period 1 January 1972 through 31 December 1972. The estimates included the growth of 1970 and 1971 year classes of juvenile sockeye salmon; 1971 and 1972 year classes of threespine stickleback; and 1970, 1971, and 1972 year classes of longfin smelt. Data on abundance, growth, and diet of the benthic-littoral fish species were collected from 1972 through 1975. Monthly and seasonal population abundances were essentially point estimates. Such data are considered acceptable for annual estimates since most benthic species are long-lived and show no extensive variation in year class strength. Annual production (kilograms wet weight per year) and mean annual biomass (kilograms wet weight) for each species are shown in Table 11.5. Most of the production and biomass of fish in Lake

TABLE 11.5 *Annual production and mean annual biomass of Lake Washington fishes.[a]*

Species	Annual production (kg wet wt/yr)	Percent of total production	Mean annual biomass (kg wet wt)	Percent of total biomass	Turnover rate P/B
Prickly sculpin	9.39×10^5	88.1	6.65×10^5	74.9	1.41
Juvenile sockeye salmon	4.88×10^4	4.6	4.07×10^4	4.6	1.19
Peamouth	2.65×10^4	2.5	1.98×10^4	2.2	1.34
Longfin smelt	2.68×10^4	2.5	3.07×10^4	3.5	0.87
Northern squawfish	1.55×10^4	1.3	1.16×10^5	13.1	0.13
Yellow perch	5.51×10^3	0.5	1.14×10^4	1.3	0.48
Threespine stickleback	3.42×10^3	0.3	4.53×10^3	0.5	0.75

[a]Eggers et al. 1978.

Washington is made up of prickly sculpin.

Since a tremendous number of prey items are available to Lake Washington fishes, a simple grouping system was used to describe carbon flow through both the water column and benthic communities. The prey items in the diet were grouped as zooplankton, benthos, mysids, and fish. The relative contribution of each prey group to limnetic and benthic fish production is presented in Table 11.6. Of the prey groups, benthos was the most important contributor to fish production (74.3 percent), while fish was the least important (6.4 percent).

Limnetic and Benthic Food Chains and Predator-Prey Interactions

A carbon budget was constructed to examine relations between fish and forage organisms in the Lake Washington ecosystem (Table 11.7). Details of the budget may be found in Eggers et al. (1978). The most significant feature of this budget, and of the production estimates in Tables 11.5 and 11.6, is that fish community production appears to be dominated by benthic-feeding fish. Interestingly, the magnitudes of benthos and zooplankton production are comparable. This implies that either zooplankton are not fully exploited as a food resource, or that the benthic forage production is large because an ample energy supply necessary for benthos probably exists in detritus from autochthonous and terrestrial sources. Apparently, decreases in phytoplankton primary production due to sewage (nutrient) diversion did not significantly reduce primary forage bases for consumer organisms. Also phytoplankton production may have been offset by established detrital food chains that have ample supplies of organic matter from littoral plants (periphyton and macrophytes) and terrestrial inputs. Such characteristics suggest that prey resources are not limiting the fish populations and therefore any response in fish production to eutrophication and recovery periods in Lake Washington was dampened.

The most evident change in forage-base organism availability in Lake Washington after recovery from eutrophication has been an increased abundance in *Daphnia* and a concurrent decline in *Neomysis*. Otherwise there has been no overall consistent change in abundance and species composition of the limnetic zooplankton community (copepods and cladocerans) during the post-eutrophication period (Edmondson 1972). The most probable reason for the increase in *Daphnia* is the decline in abundance of its primary predator, *Neomysis*. Evidently the nocturnal *Neomysis* population increased its residence time in the more aphotic benthic environment. This behavioral change is probably a response to the expanded photic zone caused by diversion of sewage in 1966 and subsequent lower algal densities. As a consequence the *Neomysis* population now confines its vertical migratory pattern to deep waters where it experiences large predatory losses to benthic fish. As shown in Table 11.6 *Neomysis* constitutes the major forage base of benthic sculpins.

TABLE 11.6 *Annual fish production and biomass and estimates of fish production attributable to specific forage items. Numbers in parentheses are percentage total production.*[a]

Fish feeding groups	Representative fish	Fish biomass (kg wet wt)	Fish production (kg wet wt/yr)	Fish production due to forage items			
				Zooplankton	Benthos	Mysids	Fish
Obligate planktivores	Sockeye Stickleback	45,200	52,200	47,640 (91.3)	4,110 (7.9)	450 (0.9)	0 (0)
Facultative planktivores	Smelt	30,680	26,800	9,740 (36.3)	4,200 (15.7)	12,530 (46.8)	3.30 (1.2)
Facultative benthic	Sculpin	19,610	24,460	12,000 (40.0)	11,890 (48.6)	580 (2.4)	0 (0)
Obligate benthic	Peamouth Sculpin	671,980	942,100	0 (0)	768,600 (81.5)	120,700 (13.0)	53,200 (5.5)
Facultative piscivores	Yellow perch Squawfish	127,700	19,420	0 (0)	2,790 (14.4)	2,060 (10.5)	14,570 (75.0)
Total		895,170	1,158,780	69,380 (6.5)	791,590 (74.3)	136,320 (12.8)	68,100 (6.4)

[a]Modified after Eggers et al. 1978.

TABLE 11.7 *Particulate organic carbon budget for Lake Washington (all values are given in* $g \cdot cm^{-2} \cdot yr^{-1})^a$

Water column	Value	Source	Benthic-littoral	Value	Source
INPUTS			INPUTS		
Allochthonous			*Water column*		
Fluvial	20.0	1	Sedimentation	53.0	3
Precipitation	ND				
Litter	ND				
Autochthonous			*Autochthonous*		
Phytoplankton production	157.0	2	Periphyton	ND	—
			Macrophytes	ND	—
Total inputs	177.0		*Total inputs*	53.0	
LOSSES			LOSSES		
Outflow	0.5	1	Benthic respiration	52.0	8
Sedimentation	53.0	3	Fish respiration	3.4	6
Microplankton respiration	75.0	4	Burial	35.0	9
Zooplankton respiration	48.0	5	Emergence	ND	—
Neomysis respiration	ND (2.4)	7	Macrophyte and periphyton		
Planktivorous fish respiration	0.73	6	respiration	ND	—
Piscivorous fish respiration	0.03	6			
Total losses	187.26		*Total losses*	104.9	

INTERNAL TRANSFORMATIONS

Ingestion

Material ingested by zooplankton	97.0	5
Material ingested by *Neomysis*	ND (4.70)	7
Zooplankton ingested by fish	0.33	6
Neomysis ingested by fish	0.94	6
Fish ingested by fish	0.4	6

Production

Microbial	ND	—
Zooplankton	19.0	5
Neomysis	ND (0.94)	7
Fish production supported by zooplankton	0.10	6
Fish production supported by *Neomysis*	0.19	6
Fish production supported by fish	0.01	6

INTERNAL TRANSFORMATIONS

Ingestion

Material ingested by macroinvertebrates	113.0	10
Macroinvertebrates ingested by fish	5.6	6
Fish ingested by fish	0.5	6

Production

Microbial	ND	—
Macroinvertebrates	16.9	0
Fish production supported by macroinvertebrates	1.1	6
Fish production supported by fish	0.1	6

ᵃEggers et al. 1978, sources defined therein.

As suggested above, this lack of response of fish communities in composition, abundance, and growth conditions is likely due to the buffering capacity of the tremendously diverse and productive forage bases, especially the benthic-detrital forage base. In addition, predatory/prey interactions and conditions in spawning environments have tended to regulate the various fish populations. Bryant (1976) observed that, at low planktivore abundance (primarily juvenile sockeye salmon), predaceous squawfish were predominantly benthic feeders, whereas at high planktivore abundance they consumed mainly planktivores. During the study period, however, planktivores never reached densities that would have satiated the squawfish population. Thus depensatory mortality due to squawfish predation probably prevents planktivore abundance from reaching levels that would in turn deplete zooplankton populations.

The balance of population size among the squawfish, planktivores, and zooplankton was interpreted as the result of complex feeding behavior patterns displayed by the planktivores (Eggers 1976). The planktivores engage in schooling behavior, which has the dual effect of minimizing vulnerability to squawfish predation, and of reducing its foraging efficiency for zooplankton. Predator avoidance by planktivores is also accomplished by a reduction in forage time, which also results in a limitation in feeding efficiency (Eggers 1978).

Piscivorous predation had an impact on benthic-littoral fishes in Lake Washington. Mature benthic-littoral fishes exploited prey items much larger than zooplankton; consequently, these predators were found to have larger body sizes than planktivores. This factor reduced their own losses to piscivorous predation. Larval and juvenile benthic-littoral fishes were extremely vulnerable to three predators: Northern squawfish, yellow perch, and prickly sculpin.

The influence of spawning environment on fish abundance was implied for both sockeye and stickleback populations. Sockeye abundance was related inversely to winter flow conditions in the Cedar River. Stickleback abundance appeared to be related to the improvement of spawning conditions in littoral areas that followed sewage diversion. The other principal fish species were affected only minimally by changes in spawning habitat due to consistently favorable benthic-littoral conditions.

In summary, detritus-based fish production in Lake Washington was much greater than grazer-based fish production. This observation implies that the benthic fish communities and detrital food chains are extremely important in Lake Washington. Community structure was influenced by the fact that limnetic-feeding fish populations were more vulnerable to control by piscivorous predators than were benthic-littoral-feeding fish populations. During the posteutrophication period, mysids became an increasingly important source of fish forage; hence declining mysid predation on zooplankton may have contributed to the recent increase in *Daphnia* populations in the Lake Washington zooplankton community. Given the above observations, the response of the fish

community to trophic change in Lake Washington has been slight because of the tremendously diverse and productive forage base.

COMPARISON OF AQUATIC ECOSYSTEMS IN DIFFERENT BIOMES

Knowledge of ecosystem behavior can be enhanced by comparing ecosystems in different biomes. The following comparison considers nine aquatic ecosystems and their associated terrestrial ecosystems in North America. These ecosystems can be considered as representative of four biomes: the western coniferous forest; eastern deciduous and mixed hardwood/coniferous forest; prairie or grassland; and tundra. For terrestrial ecosystems the data source is Chapter 5, and for aquatic ecosystems, the following: the watershed 10 stream, Oregon (Chapter 10), Findley Lake (Wissmar et al. 1977; Richey and Wissmar 1979), Lake Washington (Eggers et al. 1978), Marion Lake, British Columbia, Canada (Hargrave 1969), tundra ponds, Alaska (Hobbie 1972; Stanley 1972), Char Lake, Northwest Territories, Canada (Kalff and Welch 1974; Welch and Kalff 1974), Lawrence Lake, Michigan (Wetzel et al. 1972; Wetzel 1975), Lake Wingra, Wisconsin (Gasith 1974), and Mirror Lake, New Hampshire (Jordan and Likens 1975). Comparisons of Findley, Marion, Lawrence, Wingra, and Mirror lakes are given in Devol and Wissmar (1978), Odum and Prentki (1978), Rich and Devol (1978), and Wetzel and Richey (1978).

These ecosystems are compared on the basis of gross and net production. Terms for terrestrial ecosystems are defined as

$$NPP = GPP - R_A$$
$$NEP = GPP - R_E \quad (\text{where } GPP = GEP)$$
$$R_E = R_A + R_H$$

where GPP = gross primary production, NPP = net primary production, GEP = gross ecosystem production, NEP = net ecosystem production, R_E = ecosystem respiration, R_A = autotrophic respiration, and R_H = heterotrophic respiration. See Chapter 5 for further explanation.

The terminology for aquatic ecosystems is similar except that in aquatic systems GEP includes GPP plus carbon inputs from terrestrial environments. An understanding of these energetics is an integral part of assessing the productive potential of both aquatic and terrestrial ecosystems. The following discussion emphasizes ecosystem energy flux as the flow of organic C ($g \, C \cdot m^{-2} \cdot yr^{-1}$) through autotrophic respiration (R_A) and heterotrophic respiration (R_H), and through storage as net ecosystem production (NEP).

In general, in both aquatic and terrestrial ecosystems, an increase in GEP results in an equivalent increase in total ecosystem respiration R_E (Figure 11.15). The gross ecosystem productivity values compared here are greater in
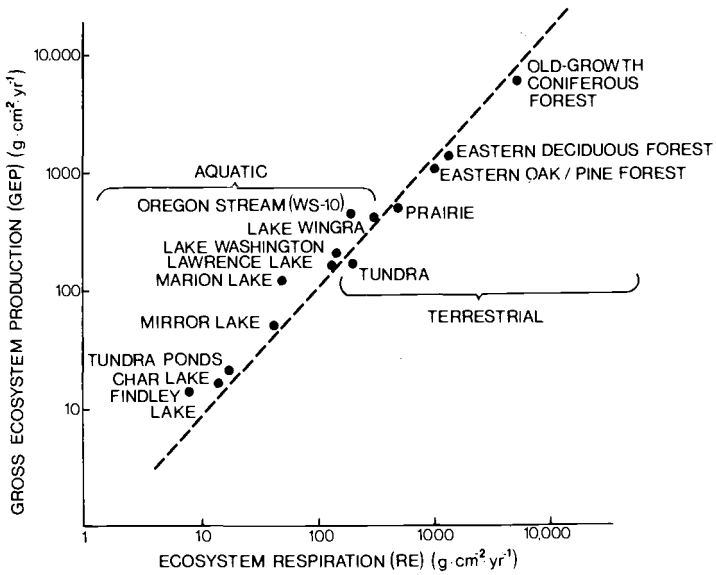
FIGURE 11.15 *Differences in gross ecosystem production for aquatic ecosystems and their associated terrestrial environments.*

the terrestrial ecosystems than in the aquatic and appear to reflect a dependence on climate. The high GEP and respiration (maintenance) levels found in coniferous forests are due mainly to the sustained growth of long-lived coniferous trees. Large evergreens are well adapted to the moisture, temperature, and nutrient regimes of the Pacific Northwest, and primary production benefits from the moist, warm, maritime climate. The vegetation is extremely conservative of its acquired nutrients. In contrast the terrestrial ecosystems of other biomes tend to have lower GEP values. This is assumed to be a function of extreme temperature conditions in which winters are colder and summers hotter than in the Pacific Northwest. Favorable interactions of wind, rain, and evaporation can constitute an energy subsidy in most temperate forests and thus enhance GEP in comparison with areas subject to harsher weather conditions— for example, the tundra.

The highest GEPs for the aquatic ecosystems considered in this comparison are found in the watershed 10 stream in H. J. Andrews Forest in Oregon and in eutrophic Lake Wingra in Wisconsin. These high values are largely the result of energy subsidies unique to their particular watershed. Specifically, watershed 10 receives large inputs of terrestrial C and Lake Wingra receives excessive nutrient loads. Such energy subsidies are especially evident in forested areas where inputs to aquatic ecosystems are related directly to the gross production of the surrounding terrestrial ecosystem. For example, the amount of terrestrial input, relative to aquatic GEP, is highest for the Oregon stream,

Findley Lake, and Marion Lake in the coniferous forest, and lowest for the tundra pond and Lake Char in the tundra (Figure 11.16). The impact of these allochthonous energy subsidies are particularly important in coniferous forest regions where aquatic primary production is usually low and energy supplements increase consumer production (Wissmar et al. 1977).

The relation between production in aquatic ecosystems and their respective terrestrial environments can be described further by the ratio NEP:GEP, termed here *effective ecosystem production*. The NEP:GEP ratios of the aquatic systems tend to be inversely related to the NEP:GEP of their respective terrestrial ecosystems (Figure 11.17). The effective ecosystem production for the aquatic ecosystems shows that relative NEP is much higher in aquatic than in terrestrial systems. Such differences in the rates of net organic matter storage (NEP) and in the rates of respiration (R_A and R_H) are indicative of energy partitioning by different aquatic and terrestrial ecosystems into components of structure, storage, and growth, and into costs of maintenance (R_A) and to consumers (R_H). In both types of ecosystems the carbohydrates synthesized by photosynthesis are utilized only partially in direct respiration processes. Portions of the carbohydrate pool serve as raw material for a variety of chemical transformations, primarily polymerization and amination. Some of the products (celluloses and lignin) become permanent structural parts of the terrestrial system while other products (for example, lipids and starch) serve as storage material in both aquatic and terrestrial systems. Ultimately, all compounds are respired (or degraded) back to CO_2 and H_2O, either during metabolic processes (R_A) or in decomposition after death, or other heterotrophic uses (R_H).

In considering the differences in NEP for aquatic and terrestrial ecosystems, terrestrial NEP is usually low, because, in contrast to aquatic plants, land plants invest a large portion of their productive energy in supportive tissue. This is necessary because the air environment has a much lower density and hence lower supporting capacity than water. In addition, the rate of metabolism of terrestrial plants, per unit of weight, is much less than that of aquatic plants. This concept can be expressed as turnover rate, the ratio of production:biomass (time^{-1}), in that aquatic plants can have turnover rates several hundred times higher than do terrestrial plants. The turnover rate is especially low in coniferous forests where NEP is very low (2 percent of GEP) and massive amounts of supportive tissue exist as wood. In coniferous forests the energetics of production and maintenance (R_A) of structural matter result in the accumulation of large forest stands (biomass) and a detrital material that consists mainly of cellulose and lignin. Although this woody material constitutes a large supply of detritus for consumers in the ecosystem, its refractory nature results in slow rates of decomposition, the principal component of R_H (Figure 11.18). In contrast, the other terrestrial ecosystems considered here tend to have higher rates of NEP (10 to 23 percent of GEP) or storage. These systems usually tie up less energy in woody structures and produce more labile organic matter (that is, leaves and grasses) that can be used readily by decomposers and other con-
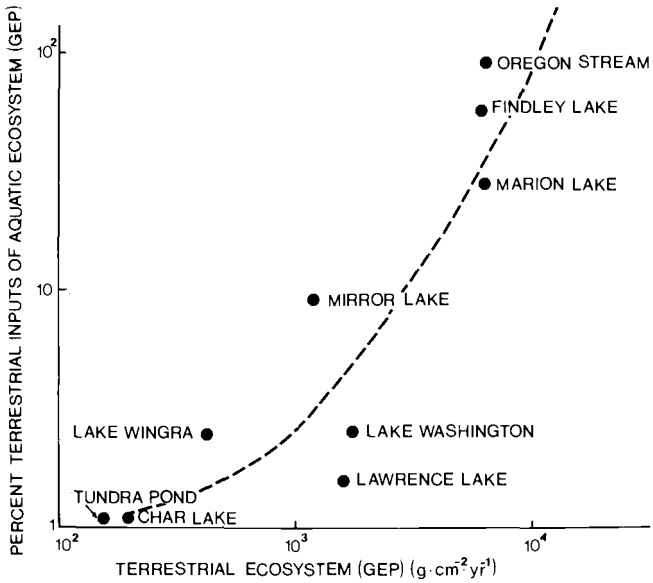
FIGURE 11.16 *Percentages of terrestrial inputs of aquatic ecosystem gross ecosystem production (GEP) in terrestrial ecosystems with varying GEP values.*
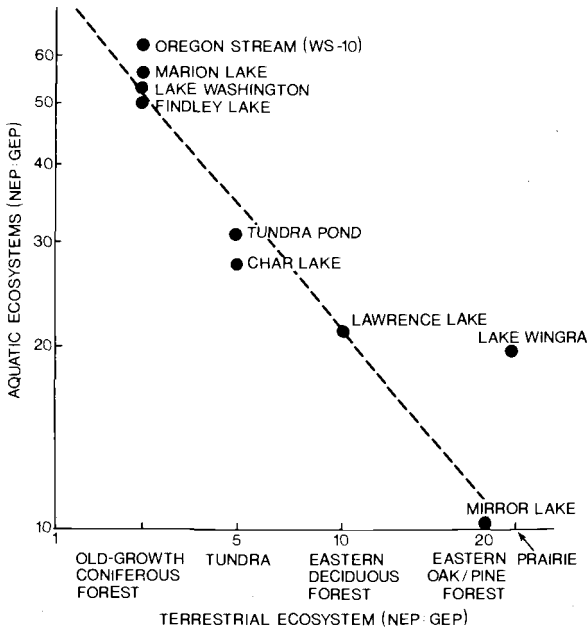

FIGURE 11.17 *Effective ecosystem production (NEP:GEP) of aquatic ecosystems and their associated terrestrial environments.*

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sumers. This phenomenon is reflected by higher heterotrophic respiration rates (R_H). An extreme example is the tundra ecosystem. This system uses almost all of its gross primary production in respiration, approximately 50 percent going to R_A and 50 percent to R_H, and thus NEP is only 5 percent of GEP.

The major difference between aquatic and terrestrial NEP is the partitioning of the respiration component. In terrestrial systems, structural maintenance requires expenditure of more energy for autotrophic respiration than for heterotrophic respiration. In contrast, most of the aquatic ecosystems show a greater percentage of respiration as heterotrophic. Thus most of the available energy is utilized by decomposers and higher consumers (Figure 11.18).

The most likely explanation for the observed higher percentage of heterotrophic respiration in aquatic systems, besides minimal structural maintenance (R_A), is that a large portion of total available energy enters the system as a subsidy from terrestrial inputs of carbon and nutrients. In the case of carbon,
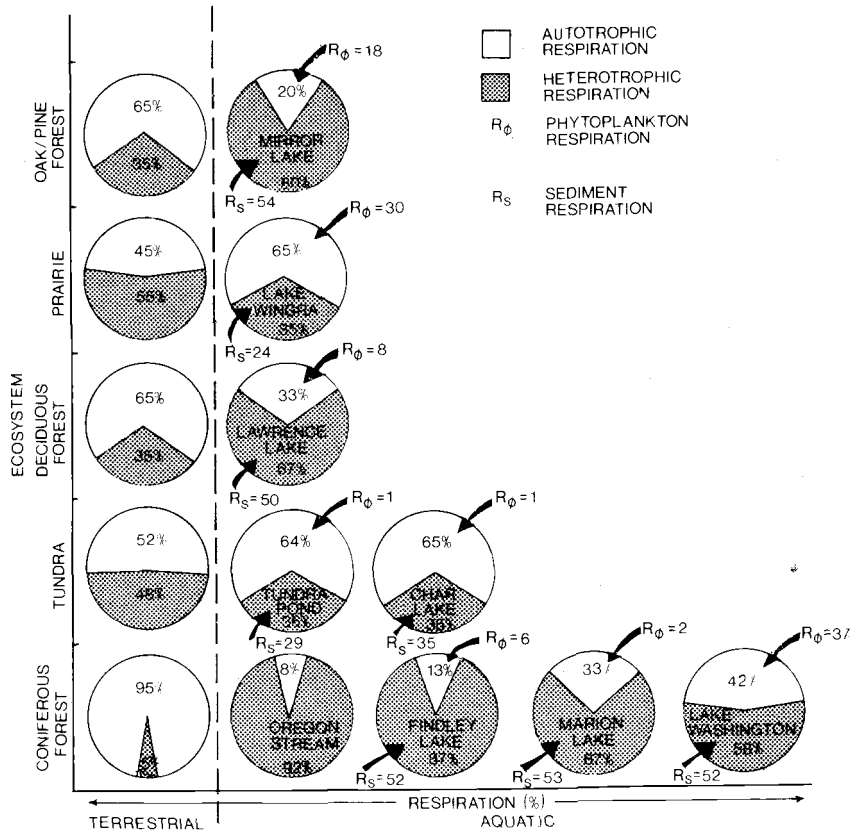

FIGURE 11.18 *Respiration components of aquatic and terrestrial ecosystems. Respiration expressed as percent of total ecosystem respiration (R_E).*

this feature is related to the occurrence of higher primary production levels in terrestrial ecosystems. For example, the terrestrial systems with the highest gross production levels (the coniferous forests, eastern deciduous, and oak/pine forests) yielded large amounts of carbon to their associated aquatic environments, which in turn showed higher percentages of heterotrophic respiration. Such relations are also evident in the fact that heterotrophic sediment respiration (R_s) in aquatic ecosystems was always greater than 50 percent of the total ecosystem respiration (R_E). Autotrophic respiration (R_A) in these aquatic systems was partitioned into three components—phytoplankton, macrophytes, and algal periphyton. Phytoplankton respiration was important only in the more productive Wingra (30 percent), Mirror (18 percent), and Washington (37 percent) lakes. In Lawrence Lake, macrophytes constituted the most important component of autotrophic respiration; macrophytes and periphyton were most important in Wingra and Marion lakes; sedges in the tundra pond; and periphyton in Char Lake. The partitioning of autotrophic respiration can be viewed as the ecosystem adaptation to constraints imposed by lake morphometry, water retention time, and light and nutrient regimes.

SUMMARY

Carbon and nutrient budgets indicate that the principal inputs of particulate carbon, phosphate, and inorganic nitrogen to Findley Lake come from terrestrial and fluvial sources. Most of the annual inputs are lost through high rates of flushing, which eliminate winter nutrient storage and minimize spring plankton blooms. The terrestrial influence on Findley Lake is reflected in the fact that the main sites of element cycling in this ecosystem are associated with benthic processing of allochthonous detritus.

Less-detailed budgets of carbon in Lake Washington and phosphorus and nitrogen in Lake Sammamish demonstrate the relative importance of exogenous and endogenous material pathways in lakes of the lower drainage basin. Element cycling in these systems appears to be dominated by endogenous processes. Phytoplankton blooms in Lake Washington and Lake Sammamish are coupled to internal winter storage of loaded nutrients. Productivity in Lake Sammamish is buffered by the anaerobic release of phosphate from sediments that are regulated by Fe-P precipitation.

The physiological state of algal populations changes with changes in environment. These alterations are primarily a response to phosphorus stress, and indicate an increase in maintenance costs and a decoupling of carbon and nutrient cycles within the cells.

The importance of detritus-based community structure was seen in the benthic regions of Findley Lake and in the fish community of Lake Washington. Detritus-based fish production in Lake Washington was much greater than grazer-based fish production. This observation implies that the benthic fish

communities and detrital food chains are extremely important in the lake eco-systems of this region. Community structure was influenced by the greater vulnerability of limnetic-feeding fish populations to control by piscivorous predators than of benthic-littoral feeding fish populations. During the study period, mysids became an increasingly important source of fish forage; hence declining mysid predation on zooplankton may have contributed to the recent increase in *Daphnia* populations in the Lake Washington zooplankton commu-nity. The response of the fish community to trophic change in Lake Washington has been slight because of the tremendously diverse and productive forage base.

Considerations of other ecosystems demonstrates the relation of terrestrial energy subsidies to lakes. This comparison also highlights the partitioning of energy within particular systems.

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