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CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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THE RELATIONSHIP IN LAKE COMMUNITIES BETWEEN PRIMARY PRODUCTIVITY AND SPECIES RICHNESS

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Abstract. An understanding of the relationship between species richness and productivity is crucial to understanding biodiversity in lakes. We investigated the relationship between the primary productivity of lake ecosystems and the number of species for lacustrine phytoplankton, rotifers, cladocerans, copepods, macrophytes, and fish. Our study includes two parts: (1) a survey of 33 well-studied lakes for which data on six major taxonomic groups were available; and (2) a comparison of the effects of short- and long-term whole-lake nutrient addition on primary productivity and planktonic species richness.

In the survey, species richness of all six taxa showed a significant quadratic response to increased annual primary productivity (¹⁴C estimate, g C·m⁻²·yr⁻¹) when lake area is taken into account. However, the richness–productivity relationship for phytoplankton and fish was strongly dependent on lake area. The relationship for phytoplankton, rotifers, cladocerans, copepods, and macrophytes was significantly unimodal. Species richness generally peaked at levels of primary productivity in the range of 30–300 g C·m⁻²·yr⁻¹. For the average lake size, the highest biodiversity tended to occur in lakes with relatively low primary productivity, such as those found in the Northern Temperate Lakes Long-Term Ecological Research (LTER) site in the upper Midwest (United States) and in the Experimental Lakes Area of Ontario (Canada).

Based on short-term (3 yr) and long-term (21–24 yr) experiments, we tested whether individual lakes respond to whole-lake enrichment experiments in the manner suggested by analyses of survey data. Experimental addition of nutrients produced varied and unpredictable responses in species richness, probably due to transient dynamics and time lags. Responses to nutrient addition were taxon and lake specific.

Phytoplankton showed a variety of relationships between species richness and pelagic primary productivity (PPR), depending on the history of enrichment and recovery. No significant effect of primary productivity on rotifer richness occurred in any of the experimental lakes, whereas richness of crustacean zooplankton was negatively correlated with primary productivity in both the short- and long-term experiments.

Key words: biodiversity; cladocera; copepoda; fish; freshwater; macrophyte; phytoplankton; primary productivity; rotifer; unimodal.

INTRODUCTION

Understanding factors that control species richness (or biodiversity) in local habitats is a central concern of ecologists. The widespread threat of human-induced ecological impoverishment in virtually all ecosystems has prompted further research into developing a general

theory for understanding the determinants of biodiversity. Empirical evidence suggests that species richness often exhibits a unimodal (“hump-shaped”) pattern with increasing primary productivity (G. Mittelbach, *personal communication*).

Lakes are optimal model systems for studying the relationship between species richness and productivity. In lakes, primary productivity is routinely measured directly using standardized ¹⁴C uptake methods (Vollenweider 1974). Many lakes, particularly those with few or no inlets or outlets, provide a well-defined community with obvious borders. Finally, species com-

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position of several taxonomic groups and primary productivity have been intensively monitored in a relatively large number of lakes (Dodson 1992).

Lacustrine species richness is influenced by lake productivity. Pure water in rock pools supports few or no species (Dodson 1987) and the most productive lakes, such as sewage lagoons, also show low species richness (e.g., see Ganapati 1940). Lakes between these extremes of primary productivity generally have the highest species richness, at least for crustacean zooplankton (e.g., Dodson 1992).

Another factor that may influence aquatic species richness is lake size (Barbour and Brown 1974, Browne 1981, Dodson 1992). An increase in lake area of 10 orders of magnitude is associated with an increase in zooplankton species richness of about one order of magnitude (Dodson 1992). Over the entire range of North American lake sizes, >50% of among-lake variability in richness of crustacean zooplankton is the consequence of lake size. Typically, larger lakes have more zooplankton species, regardless of other factors including productivity.

This study examines the relationship between annual primary productivity and the species richness of each of six major lacustrine taxa; fish, aquatic macrophytes, and pelagic phytoplankton, rotifers, cladocerans, and copepods. We evaluated the effects of spatial and temporal scale on the richness-productivity relationship by using survey and experimental data. A survey of 33 well-studied lakes provided data for tests for spatial effects (particularly lake size), whereas whole-lake enrichment experiments provided insight into the temporal aspect of the relationship. In particular, we focused on five questions. (1) Is the relationship between primary productivity and species richness unimodal? (2) Is the relationship between species richness and productivity taxon specific? (3) Does lake size influence the richness-productivity relationship? (4) Do experimental manipulations of nutrient loading and resulting changes in primary productivity affect species richness, and are such responses time dependent? (5) Which mechanisms best explain the relationship between species richness and productivity in lakes?

METHODS

Lake survey

Our first goal was to understand the relationship between primary productivity and species richness for several groups of freshwater organisms. By species richness, we mean the number of species observed in a lake over a number of years. It is useful to have several years of observations because the number of species observed varies from year to year. We chose the total list of species (the asymptote of the "collector's curve") as our index of species richness. The lakes studied as part of the U.S. Long-Term Ecological Research (LTER) Program are particularly valuable be-

cause they have been studied for two decades, and complete species lists exist for many kinds of organisms in these systems. LTER lake sites occur in northern and southern Wisconsin and northern Alaska (Toolik Lake). However, because there are fewer than 15 LTER lakes (and only seven with measured rates of primary productivity), we increased sample size by including data from additional well-studied lakes of similar size, but which span a greater range of primary productivity (see Table 1). These lakes have been studied for several years, and estimates of annual primary productivity exist for each lake. Some well-studied lakes were not included, such as those which lacked much of the crucial data, or lakes that were unusually turbid or saline. For example, Lake Okeechobee (Florida, USA) is turbid and exhibits a wide range of productivity levels, depending on the part of the lake sampled, while Marion Lake (British Columbia, Canada) has a flushing rate of only a few days (W. E. Neill, *personal communication*).

Sampling design and protocol are not standardized among studies of lakes. For example, species identifications were done by different people, sampling period was quite variable, and the number of samples per lake was variable. Such heterogeneity reduces the accuracy and precision of relationships between productivity and species richness.

Primary productivity.—Pelagic primary productivity (PPR) can be measured by the ^{14}C method (Vollenweider 1974). This method gives a close approximation to gross primary productivity (GPP), but because some of the fixed carbon is respired quickly, the value obtained is less than GPP (Fee et al. 1982). Point values of PPR are then integrated by depth and area to produce estimates of whole-lake annual primary productivity per cubic meter or square meter.

Lake primary productivity is fundamentally different than productivity measured in other biomes (e.g., grasslands, forests). The ^{14}C method measures available (gross) primary productivity more than utilized (net) production, which is what is normally measured in terrestrial systems. The ^{14}C method is also a fairly direct measure of productivity, compared to the proxy methods (e.g., nutrient loading, biomass, climate, soil fertility) used in many studies.

Sampling protocols for aquatic organisms.—Sampling protocols differed among taxonomic groups and lakes (e.g., Downing and Rigler 1984). For example, phytoplankton samples are taken by capturing (at most) a few liters of lake water, either from a specific depth or with a sampler that integrates water across a range of depths. Zooplankton are usually sampled by vertical tows (i.e., raising a net through the water column). Both zooplankton and phytoplankton samples are typically taken from the center of the lake, although replicate samples at different locations may be taken from larger lakes. Planktonic organisms are much smaller than the sampling device, and hundreds to hundreds of thou-

TABLE 1. Physical parameters (location, lake area, and pelagic primary productivity) and species richness for 33 well-studied lakes.

| Lake name | Latitude | Longitude | Area (ha) | PPR (g C·m ⁻² ·yr ⁻¹) | Phytoplankton | Rotifers | Cladocerans | Copepods | Macrophytes | Fish |
|----------------------------|----------|-----------|-----------|--|---------------|----------|-------------|----------|-------------|------|
| Acton ¹ | 39°33' | 84°44' | 253.0 | 181.0 | 64 | 35 | 5 | 3 | ... | 26 |
| Biwa ² | 35°15' | 228°54' | 67 400.0 | 87.6 | 88 | 80 | 18 | 7 | 34 | 63 |
| Char ³ | 74°42' | 94°48' | 52.6 | 4.1 | 150 | 1 | 1 | 2 | ... | 1 |
| Crystal ⁴ | 46°00' | 89°42' | 36.7 | 148.9 | ... | 30 | 10 | 6 | 9 | 21 |
| Fish ⁵ | 43°10' | 89°38' | 87.4 | 292.0 | ... | ... | 11 | 6 | 20 | 20 |
| Gull ⁶ | 42°25' | 85°25' | 822.0 | 102.2 | ... | ... | 10 | 7 | ... | 50 |
| Imikpuk ⁷ | 71°18' | 156°42' | 61.0 | 8.4 | ... | 0 | 1 | 6 | 3 | 0 |
| Kasumigaura ⁸ | 36°09' | 219°40' | 16 770.0 | 608.1 | 116 | 43 | 8 | 5 | 74 | 104 |
| Kinneret ⁹ | 32°48' | 329°24' | 16 800.0 | 619.4 | 76 | 19 | 7 | 4 | ... | 19 |
| LaCaldera ¹⁰ | 37°03' | 3°18' | 2.3 | 3.4 | 45 | 12 | 2 | 2 | ... | 0 |
| Lake 239 ELA ¹¹ | 49°41' | 93°41' | 56.1 | 21.3 | 234 | 31 | 11 | 10 | 21 | 8 |
| Lanao ¹² | 08°48' | 240°48' | 35 700.0 | 620.5 | 70 | 9 | 5 | 3 | ... | 32 |
| Latnjajaure ¹³ | 68°21' | 342°24' | 73.0 | 2.7 | ... | 5 | 4 | 2 | ... | 0 |
| Lawrence ¹⁴ | 42°24' | 85°24' | 5.0 | 41.2 | 121 | ... | 9 | 5 | ... | 24 |
| Little Rock ¹⁵ | 46°00' | 89°42' | 9.8 | 91.3 | ... | 29 | 8 | 7 | 15 | 5 |
| Long ¹⁶ | 40°06' | 105°36' | 15.8 | 1.5 | ... | 3 | 2 | 2 | 2 | 2 |
| MadMetro2B ¹⁷ | 43°02' | 89°20' | 0.5 | 1300.1 | 20 | 1 | 2 | 2 | 2 | 0 |
| Mendota ¹⁸ | 43°05' | 89°25' | 3937.7 | 342.4 | 88 | ... | 13 | 7 | 20 | 36 |
| Mexcut L.1 ¹⁹ | 39°00' | 107°06' | 0.5 | 1.3 | ... | 2 | 3 | 4 | 2 | 0 |
| Micror ²⁰ | 43°54' | 71°42' | 15.0 | 47.1 | 238 | 11 | 5 | 7 | 25 | 5 |
| Monona ²¹ | 43°04' | 89°20' | 1324.0 | 343.1 | ... | ... | 13 | 7 | 11 | 27 |
| Paul ²² | 46°13' | 89°32' | 1.5 | 60.2 | 192 | 15 | 7 | 8 | ... | 1 |
| Plussee ²³ | 54°10' | 349°37' | 14.3 | 186.9 | 180 | 21 | 8 | 6 | 5 | 13 |
| Sparkling ²⁴ | 46°01' | 89°42' | 64.0 | 134.0 | ... | 34 | 11 | 7 | 8 | 24 |
| St. George ²⁵ | 44°00' | 79°24' | 10.3 | 547.5 | ... | 27 | 10 | 5 | ... | 15 |
| Suwa ²⁶ | 36°02' | 221°55' | 1445.0 | 557.0 | 126 | 38 | 13 | 5 | 39 | 25 |
| Thonotosassa ²⁷ | 28°00' | 82°06' | 345.0 | 166.4 | 47 | 23 | 5 | 5 | 18 | 23 |
| Toolik ²⁸ | 68°36' | 149°36' | 14 900.0 | 5.5 | 139 | 11 | 4 | 4 | 6 | 5 |
| Trout ²⁹ | 46°03' | 89°40' | 1607.9 | 152.9 | ... | 39 | 12 | 9 | 30 | 37 |
| Valencia ³⁰ | 10°06' | 68°06' | 35 000.0 | 821.3 | 82 | 36 | 10 | 8 | 4 | 26 |
| Washington ³¹ | 47°36' | 122°24' | 8760.0 | 96.0 | 148 | 31 | 13 | 9 | 20 | 29 |
| Wingra ³² | 43°04' | 89°25' | 139.6 | 344.9 | 110 | 12 | 9 | 6 | 21 | 14 |
| Wintergreen ³³ | 42°24' | 85°24' | 15.0 | 368.7 | 60 | 26 | 7 | 4 | ... | 15 |

Sources:

- ¹ M. J. Vanni, *personal communication*.
² Horie (1984).
³ Roff and Carter (1972), Kalff and Welch (1974), Rigler (1974), phytoplankton from Kalff et al. (1975), Hobson and Welch (1995).
⁴ North Temperate Lakes LTER data set: (<http://limnosun.limnology.wisc.edu>).
⁵ Macrophytes from Lillie (1997); zooplankton from D. Marshall at Wisconsin DNR; R. Lathrop, *personal communication*; S. Dodson, *unpublished data*.
⁶ Primary productivity, areas, and fish species from G. Mittelbach, *personal communication*.
⁷ Comita (1956), Howard and Prescott (1971), Hobbie (1980); S. Dodson, *unpublished data*.
⁸ Sakurai (1981), primary productivity from Takamura et al. (1987); fish from the Kasumigaura Information Center (www.ilec.or.jp/database/asi/dasi35.html); phytoplankton and zooplankton from T. Hanazato, *personal communication*.
⁹ Serruya (1978).
¹⁰ Martinez-Silvestre (1975), primary productivity estimated from graph in Cruz-Pizzaro (1978), Dokulil et al. (1980); rotifers, macrophytes, and fish from J. M. Conde-Porcuna, *personal communication*.
¹¹ Primary productivity from I. Shearer, *personal communication*; macrophytes from S. Kasian and D. Huebert, *personal communication*.
¹² Frey (1969), Lewis (1979), Hecky (1984); the 32 species of fish include 11 that are recently introduced (Meyers 1960, Cohen 1994).
¹³ Nauwerck (1967, 1980); macrophytes based on lists of nearby lakes.
¹⁴ Wetzel (1983), Leibold (1988); phytoplankton in Taylor and Wetzel (1988); primary productivity, areas, and fish species from G. Mittelbach, *personal communication*; A. Tessier, *personal communication*.
¹⁵ Brezonik et al. (1993), PPR estimated from Fig. 2, reference basin, in Schindler et al. (1991); fish species also from Schindler et al. 1991; T. M. Frost, *personal communication*.
¹⁶ Patalas (1964), Keefer and Pennak (1977).
¹⁷ The primary productivity data are estimates based on limnology class light-dark bottle determinations; S. Dodson, *unpublished data*.
¹⁸ Brock (1985), Nichols and Lathrop (1994); J. Padisak, *personal communication*.
¹⁹ Dodson (1982), J. Harte, *personal communication*, S. Dodson, *unpublished data*.
²⁰ Jordan and Likens (1975), Makarewicz and Likens (1979), Likens (1985), G. Likens, *personal communication*.
²¹ Nichols and Lathrop (1994); S. Dodson, *unpublished data*.
²² Zooplankton and fish from T. M. Frost, *personal communication*; phytoplankton list provided by K. L. Cottingham using *unpublished data* from S. R. Carpenter and J. F. Kitchell as counted by A. St. Amand, J. J. Elser, N. A. MacKay, and J. A. Morrice; primary productivity estimated by S. R. Carpenter, *personal communication*.

TABLE I. Continued.

²³ Overbeck and Chrost (1994).

²⁴ North Temperate Lake LTER data set; H. Boston, *unpublished data*.

²⁵ Holtby (1981), Malone and McQueen (1983), Post and McQueen (1987), McQueen et al. (1989); N. Lafontaine, *personal communication*.

²⁶ Kurasawa and Okino (1975), Kurasawa (1976), T. Hanazato, *personal communication*.

²⁷ Cowell et al. (1975), fish from T. Champeau, *personal communication*; macrophytes from J. Rogers, *personal communication*.

²⁸ Miller et al. (1986), most information from Milner and Oswood (1997); C. Luecke, *personal communication*.

²⁹ North Temperate lakes LTER data set.

³⁰ Fish from Pearse (1920), de Infante (1982), Lewis and Riehl (1982), Saunders and Lewis (1988); macrophytes from W. Lewis, *personal communication*.

³¹ Edmondson and Lehman (1981), Lehman (1988), A. Litt, *personal communication*; phytoplankton data are from S. Abella, *personal communication*; fish data are from T. Sibley, *personal communication*; macrophytes from J. Frodge, *personal communication*.

³² Bauman et al. (1973a, with rotifers from 1973b); Prentki et al. (1977), Brock (1985), Nichols and Lathrop (1994), S. Dodson, *unpublished data*; phytoplankton from J. F. Koonce, *personal communication*.

³³ Threlkeld (1979); M. Leibold and D. Hall, *personal communication*; rotifers from S. Fradkin, *personal communication*; primary productivity, areas, fish species, and phytoplankton from G. Mittelbach, *personal communication*.

sands of organisms are typically captured in a single sample. In contrast, aquatic macrophytes are sampled using quadrats and rake samples, or simply based on a walk around the lake, while fish are sampled using a variety of nets and/or electroshocking equipment.

Criteria for species lists.—Species lists for fish, macrophytes, and pelagic phytoplankton, rotifers, cladocerans, and copepods were obtained from the literature and from unpublished data. We avoided lists restricted to only dominant or common species, and thus included only lists that were exhaustive. Few lakes had species lists for all six groups of organisms. However, we included any lake that had an estimate of the average annual primary productivity and had lists for at least three taxa.

We standardized this database by developing criteria for inclusion of species in analyses. Phytoplankton lists included all prokaryotic and eukaryotic photosynthetic phytoplankton for which there were abundances of more than one organism per milliliter (a criterion also used by Lewis 1979). We included all nonsessile species caught in open water as pelagic rotifers. For the crustacean zooplankton (cladocerans and copepods), we followed the criteria of Dodson (1992). Species lists of macrophytes included all submerged, floating, or emergent species of flowering plants, including *Typha*, sedges, grasses, and duck weed. We did not include *Isoetes* or macroalgae such as *Chara* and *Nitella* as macrophytes. The fish list included all species reported from the lake, including introduced taxa. Fish species reported to occur in the watershed, but not in the lake (as in Pearse 1920) were not considered part of the lake's biota.

Statistical analyses.—We used multiple regression to evaluate the relationships between productivity, lake size, and the species richness of each of the six biotic groups. Log₁₀ transformations were applied to data for species richness, productivity, and lake size in order to normalize residuals. The transformations greatly improved the normality of the distributions.

We first determined whether there were significant colinearities between two variables (log primary productivity, P; and log lake size, A), then developed a regression model relating species richness (SR) to average annual primary productivity and lake size. The model included a quadratic term for primary productivity because we were testing for the presence of a unimodal response of species richness to this factor. The full, two-factor regression model (Eq. 1) was fit to data from each taxon separately. Backwards regression in SAS (1996) was used to produce the most parsimonious model:

$$SR = a + bP + cP^2 + dA + e(A \times P) + f(A \times P^2). \quad (1)$$

For some taxa, parameters *e* and *f* were not significantly different from zero, suggesting that there were no interactions between A and P. In those cases, we simplified by eliminating interaction terms:

$$SR = a + bP + cP^2 + dA. \quad (2)$$

If the parameter *d* was not significantly different from zero after fitting Eq. 2, we eliminated this term from the model and fit the simpler quadratic model for the effects of productivity. Significance of the quadratic model (Eq. 2 with or without parameter *d*) was assessed by determining if the parameter *c* was significantly different from zero, and whether the full model was statistically significant. We determined whether the significant quadratic models were also unimodal within the productivity range reported in these data using a procedure introduced by Mitchell-Olds and Shaw (1987). For taxa with significant unimodal quadratic relationships, we estimated the productivity level at which species richness peaked by setting the derivative of the quadratic function to zero and solving for P.

Whole-lake enrichment experiments

To explore the effects of nutrient enrichment on primary productivity and planktonic species richness at different time scales, we used data from whole-lake

experiments conducted at the University of Notre Dame Environmental Research Center (UNDERC) in Michigan and the Experimental Lakes Area (ELA) in Ontario. These experiments represent several of the dozen or so whole-lake enrichments conducted over the past 30 years, and were selected because of the ease of access to data on both plankton species richness and primary productivity.

Short-term experiment.—Paul, Peter, and Long Lakes (Gogebic County, Michigan, USA: 89°32' W, 46°13' N) are small (1.2–3.4 ha), deep (maximum depths ~10–20 m), stratified seepage lakes that were studied intensively from 1991–1995 as part of a whole-lake experiment to evaluate how contrasting food web structures may influence responses to increased nutrient loading (Carpenter et al. 1996, Christensen et al. 1996). Complete descriptions of the lakes are available elsewhere (e.g., Carpenter and Kitchell 1993). Both food web structure and nutrient loading were manipulated during the experiment (Carpenter et al. 1996, Cottingham and Carpenter 1998). The food webs of Paul and West Long Lakes remained in their pre-manipulation states (dominated by piscivorous fish and large crustaceans including *Daphnia*), whereas the food webs of East Long and Peter Lakes were manipulated to produce dominance by planktivorous fishes, small crustaceans, and rotifers (Schindler et al. 1993, 1997, Christensen et al. 1996).

In 1991 and 1992, each lake was monitored under baseline nutrient conditions (phosphorus loading rates of ~0.1–0.2 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$). Beginning in 1993, Peter, West Long, and East Long Lakes were enriched daily with liquid fertilizer containing phosphate, ammonium, and nitrate at the ambient N:P ratio of ~25:1 by atoms. Loading rates varied among years. Nutrient additions to all three lakes were ~10 \times baseline levels in 1993, and 7–8 \times baseline levels in 1994 (Carpenter et al. 1996). In 1995, additions were 5 \times baseline levels in Peter and West Long Lakes, and 11 \times baseline levels in East Long Lake (S. R. Carpenter, unpublished data).

Each lake was sampled weekly from a central station from mid-May through mid-September using procedures described in Carpenter and Kitchell (1993) and Voichick and LeBouton (1994). Profiles of light transmission through the water column were used to determine the depths of 50%, 25%, 10%, 5%, and 1% of surface irradiance; discrete water samples were then taken at the surface and at these five depths for phytoplankton and primary productivity analyses. Phytoplankton samples were pooled from the upper three sample depths (25%, 50%, and 100% of surface irradiance), preserved in glutaraldehyde, filtered, mounted in methacrylic resin, and enumerated to species (St. Amand 1990, Cottingham 1996). Only taxa that could be identified to species level were included in the estimates of richness.

Zooplankton were sampled by pooling two vertical tows through the entire water column (calibrated 80 μm mesh net); samples were then chilled, preserved

with cold sugared formalin, and enumerated and measured. In most cases, adult zooplankton were identified to species. However, there were a few taxa which were not distinguished consistently by different taxonomists (there were three taxonomists during this period); consequently, these taxa were pooled in analyses. Also, unidentifiable juveniles (e.g., copepodid and naupliar stages) were included as single, collective taxa (“copepodites,” “nauplii”).

Primary productivity was measured at monthly (1991–1992) or biweekly (1993–1995) intervals using replicated in situ ^{14}C fixation determinations (Vollenweider 1974) at each of the six depths for which discrete samples were taken (Voichick and LeBouton 1994). This resulted in estimates of carbon fixation for a given water volume per hour ($\text{mg C}\cdot\text{m}^{-3}\cdot\text{h}^{-1}$). To convert to primary productivity on an areal and annual basis ($\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), estimates were integrated over the photic zone (from 1% to 100% of surface irradiance), and multiplied by the number of hours of daylight on each sampling date. Estimates within each year ($\text{g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) were then integrated over the ice-free season, assuming no productivity under the ice. Ice-on and ice-off dates were estimated using data from the North Temperate Lakes LTER site, ~25 km south of these lakes.

Long-term experiments.—Lakes L227, L226S, L226N are located in the Experimental Lakes Area in Northwestern Ontario (93°41' W, 49°41' N). L226 is a small, double-basin lake that has been divided with a plastic curtain since May 1973. The two basins are almost equal in surface area (8.3 ha for L226N and 7.8 ha for L226S), and similar in mean depth (5.7 m for L226N and 6.3 m for L226S). Thermal stratification occurs from early May and lasts until late September. Starting in May 1973, each basin received weekly additions of fertilizer during the ice-free season (May through October) for eight years. Both basins received sodium nitrate (NaNO_3) as a nitrogen source and sucrose as a carbon source. Phosphoric acid (H_3PO_4) was added to only the north basin (L226N). Detailed methods of fertilization are available in Cruikshank (1984). Since 1981, no nutrients have been added to either basin.

L227 has a surface area of 5 ha, a maximum depth of 10 m, and a mean depth of 4.4 m. In 1969, researchers at the Experimental Lake Area (ELA) began a long-term experiment in which they added phosphoric acid to the epilimnion at an annual rate of 0.48 g/m^2 . Initially, nitrogen was added as sodium nitrate at an N:P ratio (by weight) of 13:1. In 1975, the loading rate of nitrogen was decreased to 5:1, and in 1990 addition of nitrogen ended. Throughout the experiment, phosphorus additions were constant. A more detailed description can be found in Findlay et al. (1994).

From 1973 to 1983, at ~2-wk intervals, primary productivity of phytoplankton in L227 and both basins of L226 were estimated using an incubator-numerical model (Fee 1973). Shearer et al. (1985, 1987) describe

field and laboratory methods. Total primary productivity for the ice-free season was used as an estimate of annual primary productivity.

During the course of the experiment, two phytoplankton sampling techniques were used. From 1973 to 1975, discrete 2-L samples were taken from odd meter depths to a maximum of twice the Secchi disk depth (photic zone). From 1975 to 1994, samples were taken with an integrating sampler in the epilimnion, metalimnion, and hypolimnion (Shearer 1978). Samples were taken fortnightly to monthly. Enumeration and identification have been done using the same method and by the same taxonomist throughout the course of the project (Findlay et al. 1994).

Because zooplankton sampling methods were inconsistent before 1977, which may bias estimates of species richness, we used the zooplankton database for L227 starting in 1977 (Chang and Malley 1987). In most cases, adult zooplankton were identified to species, although for some less common taxa, identifications were consistently made to genus. Unidentifiable juveniles (e.g., copepodid stages and nauplii) and littoral species were excluded from the analyses.

Statistical analysis.—Because the number of phytoplankton and zooplankton samples taken varied among years within each whole-lake experiment, we standardized sampling effort by calculating annual cumulative species richness based on a fixed number of randomly selected subsamples (n) taken from May to September. For each lake in each year, we randomly subsampled the database n times without replacement. We then counted the total number of unique species in this subsample as a measure of cumulative richness. This procedure was repeated 1000 times to estimate the mean cumulative richness for each year. Specifically, we used 15 samples for both phytoplankton and zooplankton in the short-term experiment, five samples for phytoplankton in L226, 10 samples for phytoplankton in L227, and five samples for crustacean zooplankton and rotifers in L227 (the variable number of samples reflects the total number of samples available in each year). We then explored the relationships between richness and primary productivity within each of the whole-lake experiments by fitting linear and quadratic models similar to those used for the lake survey. Because the quadratic model was significant only for one lake, we focus on the linear relationships as described by Pearson product-moment correlations in the results. Significance was assessed using $P \leq 0.05$, with marginal significance for $0.05 < P \leq 0.10$.

RESULTS

Lake survey

Relationships among factors.—A marginally significant positive relationship existed between $\log(\text{area})$ and $\log(\text{PPR})$ ($R^2 = 0.115$, $P = 0.053$; Fig. 1). The relationship between area and productivity was weak

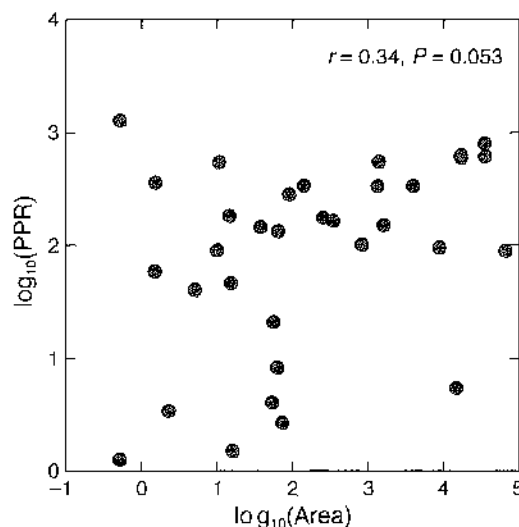


FIG. 1. Scatter plot of $\log(\text{lake area})$ and $\log(\text{PPR})$, where lake size is in hectares and primary productivity (PPR) is in grams of carbon per square meter per year.

enough, however, that the multicollinearity was unlikely to affect the multiple regressions.

There were significant positive linear relationships between $\log(\text{species richness})$ and $\log(\text{lake area})$ for rotifers, cladocerans, macrophytes, and fish, but not for phytoplankton and copepods (Fig. 2). Although the significant relationships were weak (all $R^2 < 0.33$), they presented sufficient evidence for evaluating the effect of both $\log(\text{lake area})$ and $\log(\text{PPR})$ on species richness in multiple regression models for all six taxa.

Richness-productivity relationships.—Regression analyses indicated that species richness was related significantly to primary productivity for all six groups of aquatic organisms. This is apparent both from straightforward analyses of species richness and primary productivity (Fig. 3) and from more sophisticated multiple regressions exploring the effects of lake size and productivity on species richness (Table 2).

For rotifers, cladocerans, copepods, and macrophytes, there was no significant interaction of lake size and productivity on species richness. In fact, the main effect of area was significant only for rotifers and macrophytes. However, both the linear and quadratic terms for the effect of primary productivity were significant for all four groups. The unimodality test of Mitchell-Olds and Shaw (1987) confirms that the quadratic relationship is significantly unimodal (all $P < 0.03$) in the range of PPR values included in this survey. The peaks of these unimodal (hump-shaped) curves occurred at relatively low rates of primary productivity, 67–179 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Table 2).

Significant interactions between area and primary productivity affected species richness of phytoplankton and fish (Table 2). To facilitate interpretation of these interactions, we used the parameter estimates from the

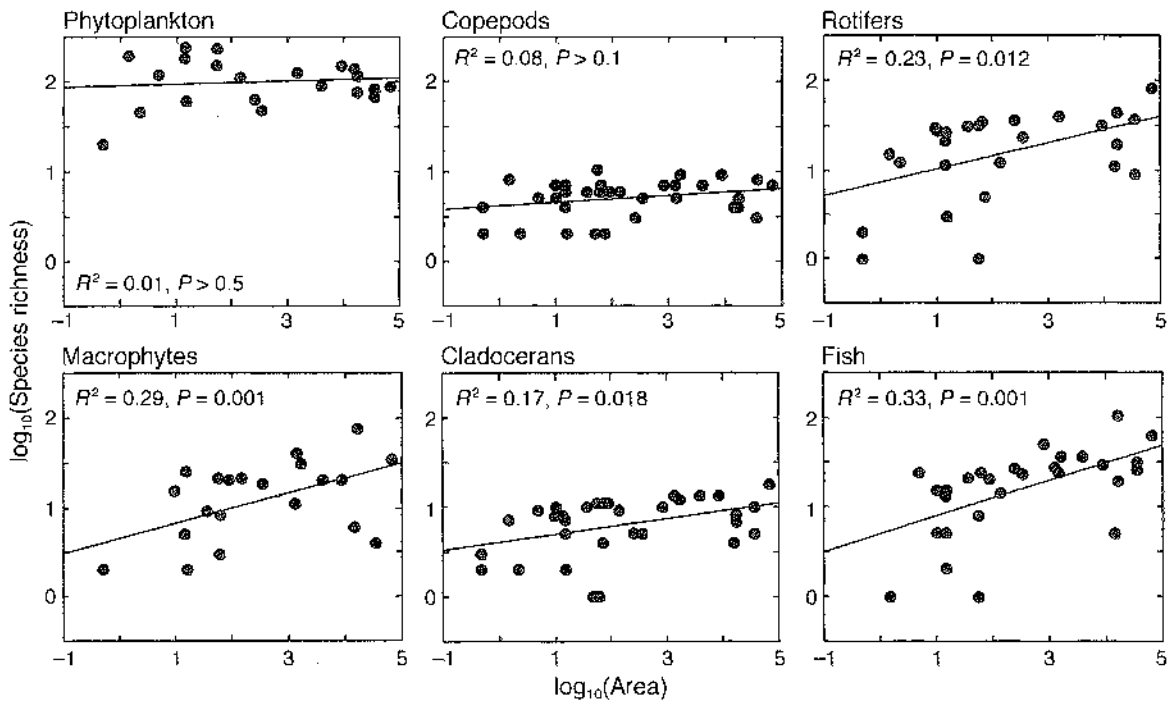


FIG. 2. A regression analysis of $\log(\text{species richness})$ as a function of $\log(\text{lake area})$, for phytoplankton, copepods, rotifers, macrophytes, cladocerans, and fish. Species richness = number of species reported.

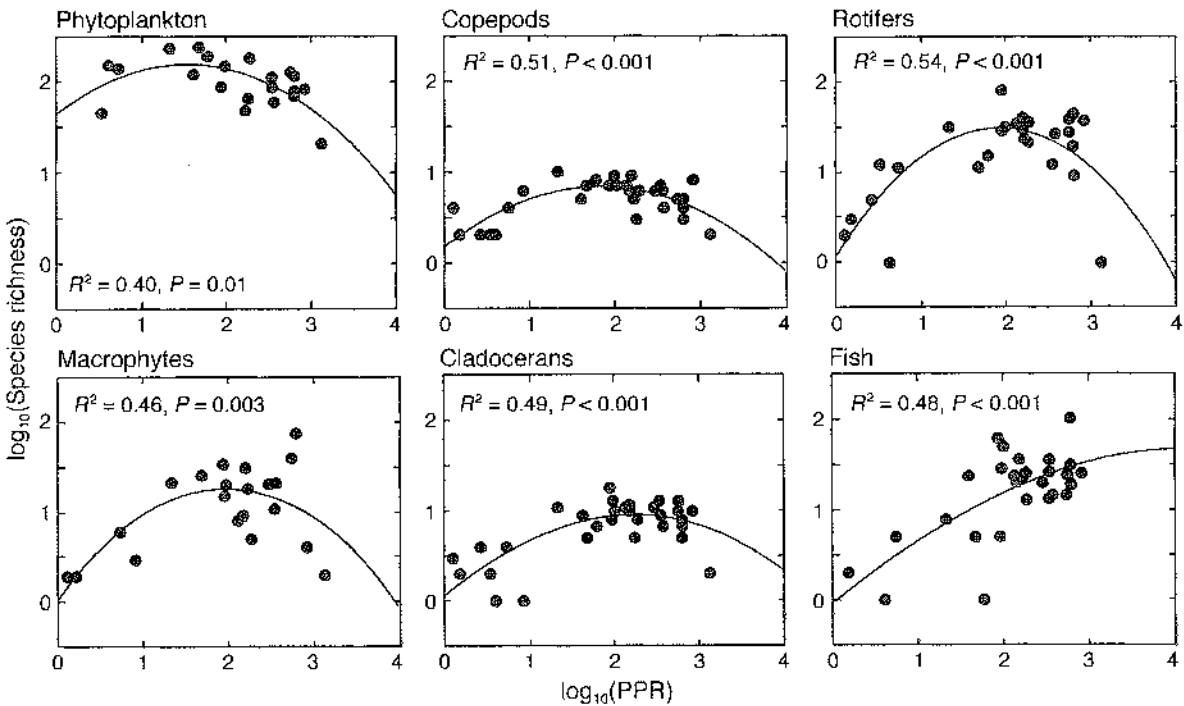


FIG. 3. A regression analysis of $\log(\text{species richness})$ as a function of $\log(\text{PPR})$, with the fitted quadratic model assuming no effect of area on the richness–productivity relationship. Panels are as in Fig. 2.

TABLE 2. Parameters for the final multiple regression model for each taxon, determined using backwards regression from the full regression model (Eq. 1): $SR = a + bP + cP^2 + dA + e(A \times P) + f(A \times P^2)$.

| Taxon | Coefficient (1 SE) | | | | | | R^2 | P ‡ | Max§ |
|---------------|--------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-------|--------|-------|
| | a † | b | c | d | e | f | | | |
| Phytoplankton | 1.08 (0.33) | 1.47 (0.39) | -0.45 (0.10) | 0.34 (0.15) | -0.44 (0.17) | 0.12 (0.04) | 0.64 | 0.005 | 30-50 |
| Rotifers | -0.03 (0.21) | 1.39 (0.29) | -0.38 (0.09) | 0.10 (0.04) | | | 0.64 | <0.001 | 67 |
| Cladocerans | 0.05 (0.15) | 0.81 (0.21) | -0.18 (0.03) | | | | 0.49 | <0.001 | 179 |
| Copepods | 0.19 (0.10) | 0.71 (0.13) | -0.20 (0.04) | | | | 0.51 | <0.001 | 60 |
| Macrophytes | -0.02 (0.25) | 1.04 (0.34) | -0.27 (0.10) | 0.11 (0.05) | | | 0.56 | 0.002 | 84 |
| Fish | 0.42 (0.52) | -0.23 (0.62) | 0.17 (0.19) | -0.32 (0.25) | 0.65 (0.27) | -0.18 (0.07) | 0.75 | <0.001 | 300 |

Notes: Terms for which SAS Type III ss had P values > 0.05 were dropped sequentially from the model.

† Intercept.

‡ P indicates the overall P value for the regression.

§ "Max." refers to the level of primary productivity at which species richness peaks for taxa with significantly unimodal quadratic relationships. Units are $g\ C\ m^{-2}\ yr^{-1}$.

|| Varies with area.

full regression model (Eq. 1) to generate response surfaces for the richness-productivity relationship as a function of lake size (Fig. 4). The response surfaces showed that although the effect of primary productivity was always quadratic, the curves switched from concave up to concave down across the gradient of lake size (Fig. 4). For phytoplankton, species richness showed the expected unimodal concave-down pattern ($P < 0.03$) with increasing productivity in lakes <1000 ha; whereas for larger lakes, the relationship tended to be concave up ($P > 0.10$). In contrast, for fish, the relationship appeared to be concave down only for large lakes (>100 ha), although none of the relationships between fish species richness and productivity were significantly unimodal ($P > 0.4$). These patterns of interaction between species richness, primary productivity, and lake size were unexpected and might bear following up with further research.

Richness-productivity relationships in the whole-lake experiments

Richness-productivity relationships in the experimental lakes provided little evidence for a unimodal relationship between richness and productivity. In all cases, except for phytoplankton in L227, the linear model provided a better fit than the quadratic model. The phytoplankton response to increased primary productivity differed among lakes (Fig. 5, Table 3). There was no significant relationship between primary productivity and phytoplankton species richness in the short-term experiments, whereas richness declined with increasing productivity in both basins of L226. In L227, the quadratic model ($SR = 0.002 + 1.7(P) - 0.39(P)^2$ ($P = 0.011$, $R^2 = 0.48$)) provided a much better fit than the linear model ($P = 0.265$, $R^2 = 0.08$). The Mitchell-Olds and Shaw (1987) unimodality test confirmed that the relationship is unimodal within the

range of primary productivity values observed in the experiment ($P < 0.01$). With the quadratic model, phytoplankton species richness peaked at $\sim 150\ g\ C\ m^{-2}\ yr^{-1}$, a level considerably higher than that predicted in the lake survey.

Zooplankton responses were more consistent among lakes (Fig. 6, Table 3). Crustacean zooplankton richness declined with increasing primary productivity in all of the experimental lakes, although the relationship was only marginally significant in the short-term enrichment experiments. There were no significant relationships between rotifer species richness and primary productivity, although rotifer richness declined with primary productivity in East Long and West Long Lakes, and increased in Peter and Paul Lakes.

DISCUSSION

Lakes provide a unique opportunity for evaluating the effects of primary productivity on species richness because of their well-defined boundaries and the direct nature of productivity estimates. We detected significant unimodal effects of productivity on species richness for all organisms examined in our lake survey except fish. The relationship between productivity and species richness was more variable in the experimental studies, probably because of complex environmental changes and transient effects.

Lake survey

Species richness responded in a significant unimodal fashion to increases in productivity for five groups of aquatic organisms (after lake size had been taken into account). The productivity at which richness peaked differed among taxa, but generally occurred at levels comparable to those of oligotrophic to slightly mesotrophic lakes (~ 30 - $300\ g\ C\ m^{-2}\ yr^{-1}$). Species richness of most taxa will likely decline as lakes become eu-

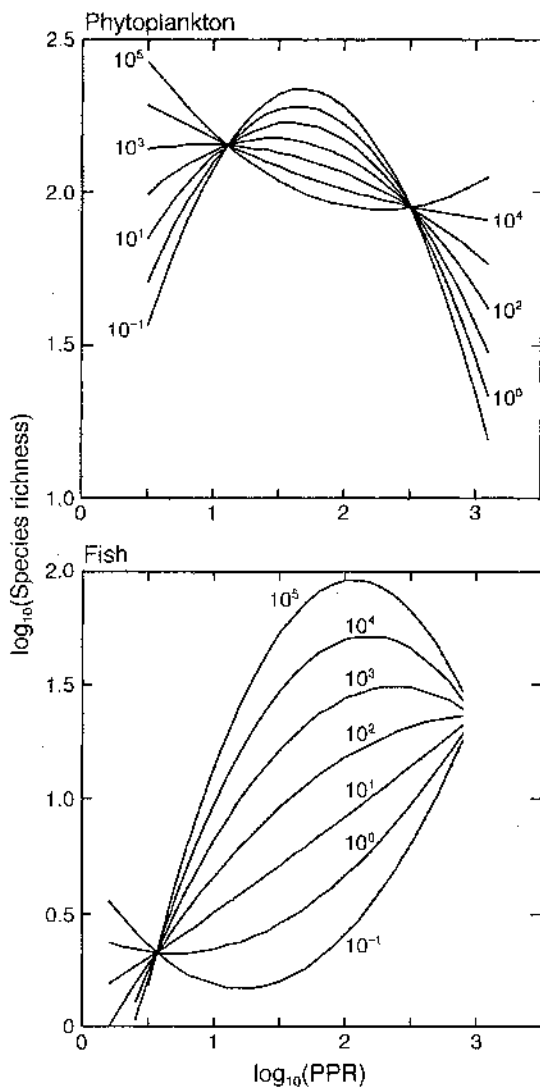


FIG. 4. Response surfaces for the interactive effects of lake area and PPR on the species richness of phytoplankton and fish. Each curve indicates the relationship between $\log(\text{species richness})$ and $\log(\text{PPR})$ for a particular lake size, in hectares. To prevent extrapolation beyond the range of available data, curves are drawn only for the region of PPR for which we actually had data on species richness.

trophic. This suggests that eutrophication, the most widespread water quality problem in lakes of the United States (National Research Council 1992), represents a potentially serious threat to lacustrine biodiversity.

For four of the six taxa, lake size significantly affected species richness. Nonetheless, this effect of lake size is weak, as compared to the situation in other surveys (e.g., Dodson 1992), possibly because of the relatively small range of lake sizes in the present survey. Our survey was designed to include well-studied lakes of about the size of the LTER and other experimental lakes, and to maximize the range of primary productivity in this restricted size range. Consequently, the

survey contains enough variation in productivity to reveal strong unimodal (quadratic) relationships between productivity and species richness, but possibly not relationships with lake size.

The relation between richness and productivity may depend on the scale of observation (G. Mittelbach, *personal communication*). In our multiple regression model for the effect of lake size and productivity on species richness, there were no significant interaction effects between lake size and productivity for rotifers, cladocerans, copepods, or macrophytes. This suggests that, in the lakes we surveyed (which span four orders of magnitude in lake size and three orders of magnitude in primary productivity), the effect of productivity on species richness was scale independent for these four taxa (across space). However, this generalization does not hold for phytoplankton and fish, for which there were significant area by productivity interactions.

When present, the interactive effects of size and productivity complicate the interpretation of the richness-productivity relationship. In particular, the response surfaces developed for phytoplankton and fish (Fig. 4) demonstrate that the particular hump-shaped curve for these taxa depends on lake size. If we fail to consider lake size, we may draw misleading conclusions regarding the relationship between species richness and primary productivity.

Whole-lake enrichment experiments

We used data from experimental whole-lake nutrient additions: (1) to test whether patterns from the lake survey applied to individual lakes, and (2) to explore how species richness responds to temporal changes in primary productivity. Responses differed with experimental manipulation and taxonomic group, and interpretation of results is complicated by transient effects, lags in response, and possible shifts to conditions that support different species. Like Mittelbach (*personal communication*), we found little evidence for unimodal patterns within sites (lakes) as compared to surveys of regional patterns.

Phytoplankton.—Overall, average annual primary productivity was a relatively poor predictor of plankton species richness in lakes with experimental manipulations of nutrient loading. Based on the survey results for lakes this size (<10 ha), we expected to see a unimodal relationship between productivity and phytoplankton richness, with maximum richness at $\sim 30\text{--}50 \text{ g-C m}^{-2}\text{-yr}^{-1}$. However, we observed a unimodal relationship in only one of the experimental lakes (L227), and its peak in species richness occurred at a productivity three times higher than predicted by the lake survey. There was no significant relationship between productivity and phytoplankton species richness in any of the short-term experimental lakes, although there was a tendency for richness to decline with increasing productivity. This tendency for a negative relationship between primary productivity and phytoplankton rich-

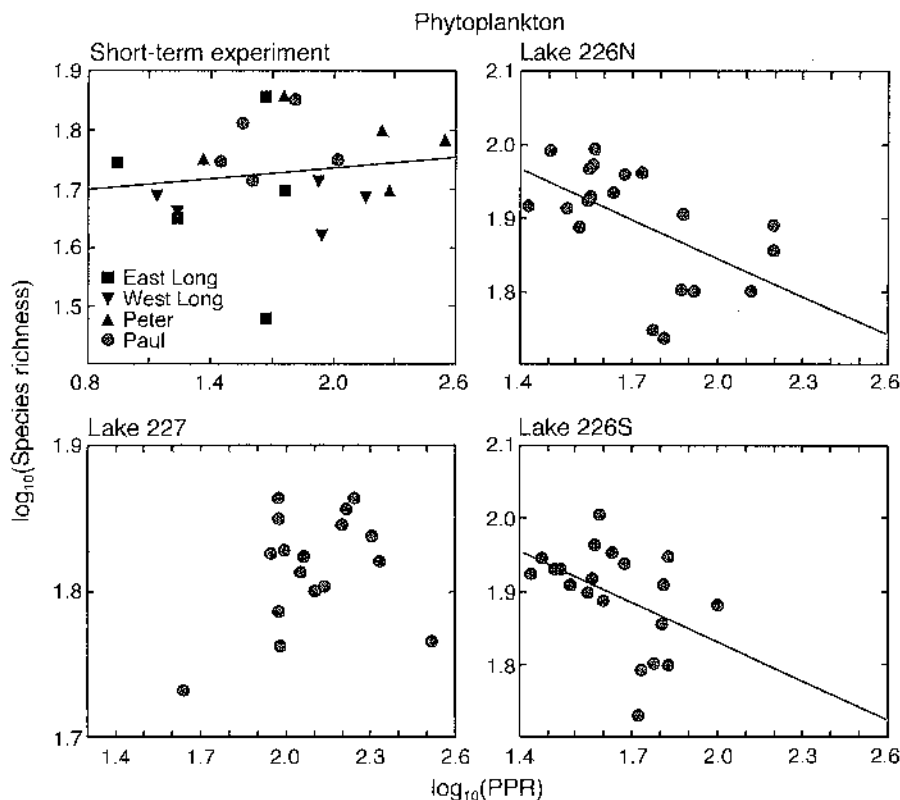


FIG. 5. Log(species richness) as a function of log(PPR) for phytoplankton in the whole-lake experiments: the four lakes of the short-term experiment, L227, L226N, and L226S.

ness was much more pronounced in both basins of L226, and is consistent with the observation of decreasing phytoplankton richness with increasing nitrogen and phosphorus concentrations in natural ponds in Michigan (Leibold 1999).

The negative relationship between primary productivity and phytoplankton richness in L226S and L226N may be the result of a delayed response to declining primary productivity. Both phytoplankton richness and productivity increased during the initial years (1973–1981) of the experiment (Fig. 7). In L226N, the positive relationship was marginally significant ($r = 0.57$; $0.10 \geq P > 0.05$) during the years when nutrients were added. In L226S, the relationship between primary pro-

ductivity and phytoplankton richness was also positive ($r = 0.55$), but not significant. From 1982 to 1994 phytoplankton richness in both basins of L226 generally remained at levels higher than those encountered during the fertilization years, even though productivity recovered to levels typical of unfertilized lakes in the region (Shearer et al. 1987). Therefore, the nutrient perturbation augmented the number of phytoplankton species in the lake, where it remained despite the termination of nutrient additions.

The response of primary productivity and phytoplankton richness to nutrient addition was different in L227 compared to other experimental lakes. Although we observed a unimodal relationship between phyto-

TABLE 3. Correlations between species richness and primary productivity in each of the lakes in the whole-lake enrichment experiments.

| Taxon | East Long | West Long | Peter | Paul | All short-term lakes | L226N | L226S | L227 |
|---------------|-----------|-----------|-------|-------|----------------------|--------|--------|---------|
| Phytoplankton | -0.14 | -0.01 | -0.15 | 0.04 | 0.14 | -0.54* | -0.42† | 0.29 |
| Crustaceans | -0.61 | -0.85† | -0.46 | -0.44 | -0.39† | ... | ... | -0.68** |
| Rotifers | -0.71 | -0.49 | 0.48 | 0.78 | 0.03 | ... | ... | 0.06 |

Notes: Ellipses (...) indicate that data are not available. For all variates in the lakes in the short-term experiment, $n = 5$ years; when the four lakes from the short-term experiment are pooled, $n = 20$ lake-years. For phytoplankton in both basins of L226, $n = 21$ years; in L227, $n = 17$ years for phytoplankton, and $n = 14$ years for zooplankton. † $P < 0.10$; * $P < 0.05$; ** $P < 0.01$.

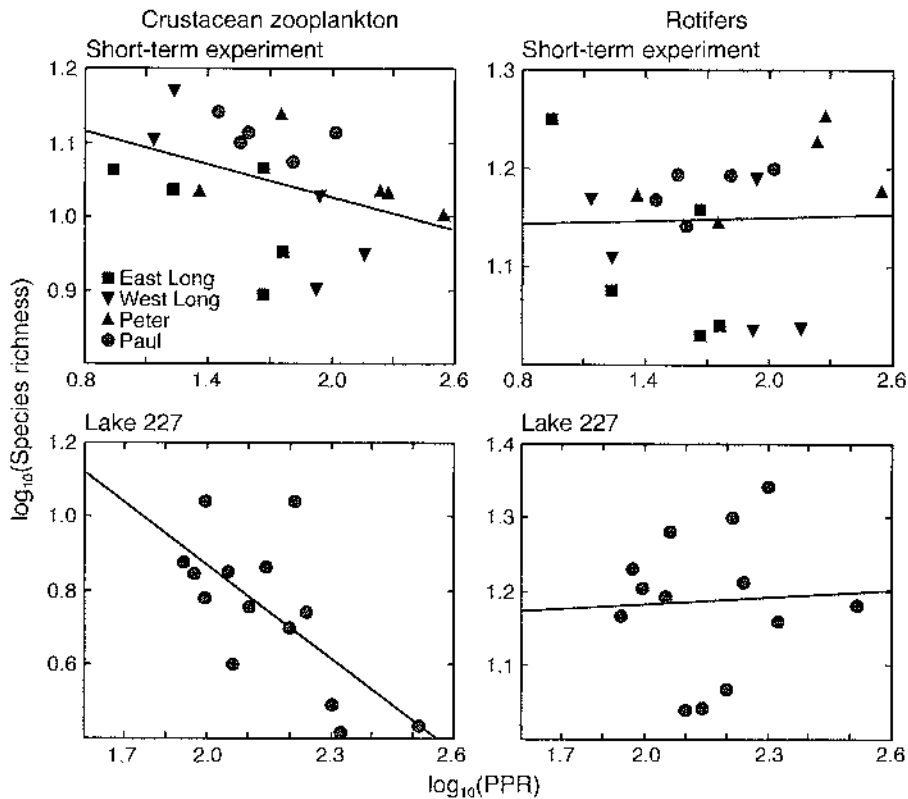


FIG. 6. Log(species richness) as a function of log(PPR) for crustacean zooplankton and rotifers in the short-term experiment and L227.

plankton richness and primary productivity, this was probably driven by a complex response of primary productivity and phytoplankton richness to nutrient loading. Nutrient limitation, changes in species dominance, and self-regulating processes likely interacted to produce transient responses in both primary productivity and community composition that were probably different from the mechanisms operating in the regional lake survey.

The response of primary productivity and phytoplankton richness to nutrient additions was variable throughout the 25-yr experiment in L227. At the onset of nutrient additions, phytoplankton biomass increased and community composition shifted from chrysophytes to co-dominance by small chlorophytes and filamentous nonheterocystous cyanobacteria (Schindler and Fee 1974, Findlay et al. 1994). This change was accompanied by a reduction in both phytoplankton richness and primary productivity, probably the result of daily occurrences of carbon limitation (Schindler and Fee 1973) (Fig. 8). When the N:P loading ratio was lowered to 5:1 in 1975, annual richness and primary productivity increased after heterocystous cyanobacteria became abundant at particular times during the summer (Findlay et al. 1994). These changes were likely due to nitrogen fixation by the heterocystous cya-

nobacteria, which relieved periods of nitrogen deficiency and increased nitrogen availability to other phytoplankton groups (Hendzel et al. 1994). From 1978 to 1983, a new nitrogen-fixing species, *Aphanizomenon schindleri*, dominated the summer phytoplankton community, coinciding with a peak in primary productivity followed by a dramatic decline (Findlay et al. 1994). After 1983, *A. schindleri* dominance waned, and primary productivity and phytoplankton richness were variable (Fig. 8). These complex shifts in primary productivity, species richness, and dominance by heterocystous cyanobacteria (such as *A. schindleri*) probably resulted from self-regulatory processes within the lake which maintained a relatively consistent TP:TN ratio despite shifts in external loading ratios (Findlay et al. 1994). Despite the apparent similarity in the richness-productivity relationship between the lake survey and L227, factors driving the relationship in L227 were complex and likely influenced by complex transient dynamics.

The contrast between the unimodal relationships between richness and productivity in the lake survey and the variable patterns in the experimental lakes underscores the importance of temporal scale in examining the relationships between species richness and primary productivity. Because colonization and extinction pro-

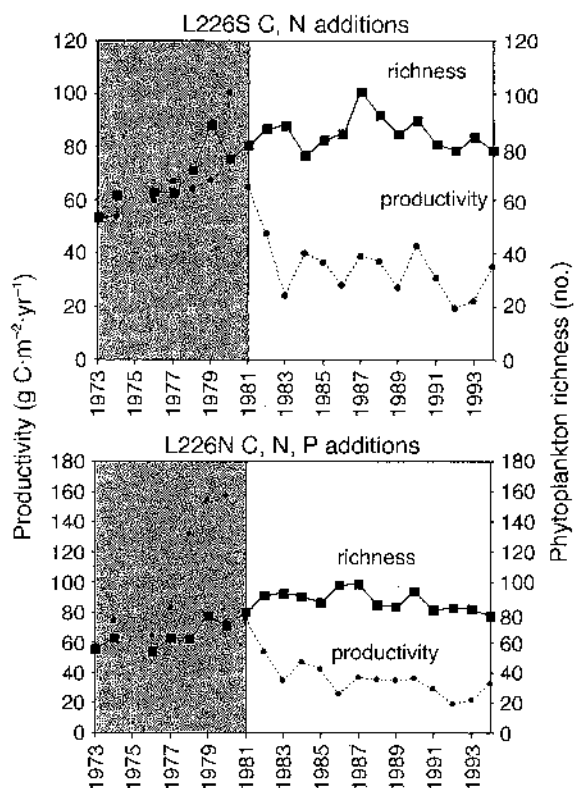


FIG. 7. Annual primary productivity and annual phytoplankton species richness across time for L226S and L226N. The shaded area indicates the years (1973–1981) when nutrients were added. The white area indicates the recovery period (1982–1994), when no nutrients were added.

cesses are probably slow relative to the changes in primary productivity, short-term relationships between primary productivity and species richness may be misleading. Leibold et al. (1997) demonstrated that discrepancies in trophic responses of lakes to nutrients between comparative and experimental studies were probably due to differences in species composition. In comparative studies, years of evolution, dispersal, and species interactions resulted in particular species assemblages associated with different nutrient levels. In experimental studies, time lags in dispersal and species interactions produced species assemblages that were more similar among treatments compared with the range observed in comparative studies (Leibold et al. 1997). This suggests that factors influencing species composition (i.e., colonization and extinction) may also be influencing the response of the system to nutrient additions. This situation is relevant to richness–productivity relationships in this study. We know that there were several extremely successful invaders into the ELA lakes following the onset of experimental enrichment (e.g., Kling et al. 1994), and that these invasions persisted through time, especially in L226. New species were also noted in Peter, West Long, and

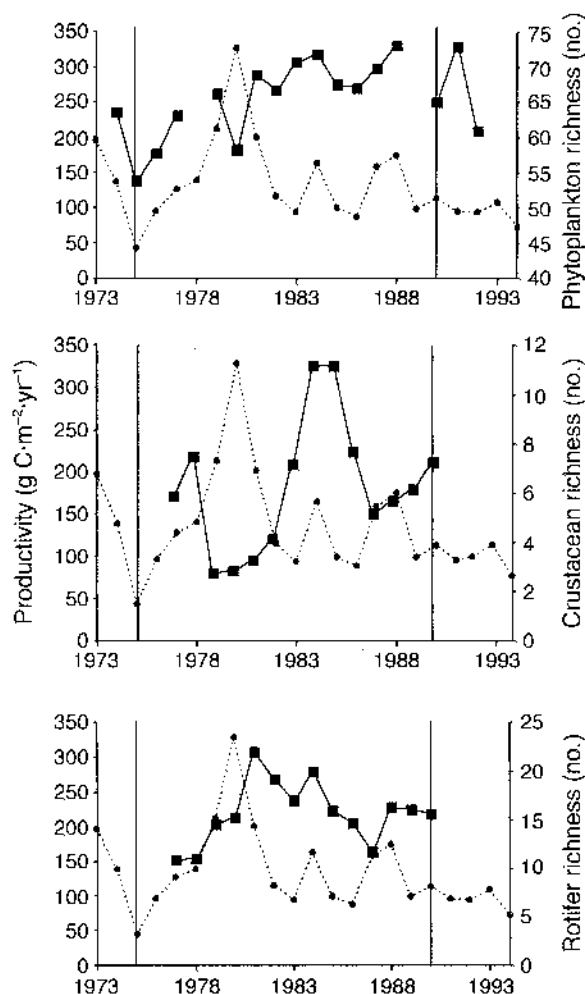


FIG. 8. Annual primary productivity and annual species richness for phytoplankton, crustacean zooplankton, and rotifers in L227. Vertical lines indicate a change in experimental additions of nitrogen. Experimental phosphorus loading was constant throughout the experiment. The circles and dotted lines show primary productivity. The squares show species richness.

East Long Lakes during the first three years of experimental enrichment (Cottingham 1996). However, it is too soon to know whether these invasions were due to transient species taking advantage of current conditions, or to persistent species that will remain in these systems for years to come. It is also too soon to know how these new species will interact with the existing community and what change in species richness will result.

Crustacean zooplankton.—The strongest and most consistent relationship between species richness and primary productivity in the experimental lakes was the decline in species richness of crustacean zooplankton with increased productivity. This contrasts with previous studies which report a positive relationship be-

tween cladoceran richness and primary productivity (Whiteside and Harmsworth 1967) and no relationship between zooplankton richness and phytoplankton chlorophyll *a* (Patalas 1971). Based on survey results and the range of productivity in the experimental lakes, we expected a unimodal relationship between productivity and zooplankton richness in the short-term experiments, and a negative relationship in the long-term experiment. Instead, we observed a decline in richness with increasing productivity in all four experimentally enriched systems for which we have data on crustacean zooplankton.

This decline could be related to several factors associated with the nutrient additions; changes in food quality, competitive exclusion due to dominance by a few taxa, or changes in water chemistry. As lakes become more eutrophic, phytoplankton size structure shifts from smaller, relatively edible species to larger, less edible species (Findlay et al. 1994, Cottingham 1999). Filamentous cyanobacteria frequently dominate eutrophic phytoplankton communities (Watson et al. 1997). As phytoplankton size increases, smaller zooplankton may have more difficulty obtaining sufficient food. In the short-term experimental lakes where zooplanktivory was low, large taxa such as *Daphnia* spp. thrived after enrichment, suggesting that they may have outcompeted smaller taxa as phytoplankton species composition changed, thus reducing richness. This was seen particularly in East and West Long Lakes (1994 and 1995), when *Daphnia* constituted 60–90% of total zooplankton biomass.

Changes in lake chemistry associated with fertilization appear to drive the negative relationship between primary productivity and crustacean species richness in L227. Malley et al. (1988) concluded that the biomass of edible phytoplankton species was not limiting to herbivorous zooplankton in L227 during 1977 to 1982 when crustacean richness and biomass were particularly low. Instead, they suggested that high pH and low oxygen concentrations in the water column due to increased primary productivity and decomposition reduced cladoceran and cyclopoid copepod populations to low numbers and in some years eliminated species. While the response of crustacean zooplankton to changes in primary productivity was similar among lakes, the mechanisms responsible for these changes appear to be lake specific and related to individual lake responses to experimental nutrient additions.

Rotifers.—Like Rublee and Bettez (1995), we found no overall relationship between rotifer species richness and productivity in either the short-term or long-term experimental studies. Based on the analyses from the lake survey, we expected a unimodal pattern of richness with productivity, such that richness initially increased with increasing primary productivity, but then declined above 67 g-C m⁻²·yr⁻¹. Although we did not observe the expected pattern, we noted some interesting rotifer responses within individual lakes of the short-term ex-

periment. Rotifer richness in Peter Lake increased with increasing productivity, whereas rotifer richness in East and West Long Lakes declined. In fact, without the three points for Peter Lake in 1993–1995, the across-lake relationship between rotifer richness and productivity is negative ($r = -0.333$), not zero (but still non-significant). Moreover, the four points for East and West Long Lakes during the second and third year of the experiment were unusually low (see lower half of Fig. 6).

Daphnia dominance in East and West Long Lakes, as compared to *Daphnia* absence in Peter Lake, may explain the different patterns in rotifer responses among lakes. As *Daphnia* abundance increased in the two basins of Long Lake as a result of low planktivory or a shift in food resources, *Daphnia* appeared to have negative effects on rotifers through competition or direct interference (Pace et al. 1998). There may be a pattern of population compensation between large cladocerans and rotifers; in the survey, peak rotifer species richness occurred at about half the productivity of peak cladoceran species richness.

Mechanisms explaining richness–productivity relationships in lakes

Many mechanisms have been proposed to produce the unimodal relationship between primary productivity and species richness, especially at the scale of local communities (G. Mittelbach, *personal communication*). Some of these explanations are only relevant to the particular conditions of organisms, such as terrestrial plants, which are sessile and sampled by quadrats. However, several of the models are more general, and can be evaluated in pelagic as well as terrestrial systems. We review some of these models and discuss their applicability to patterns observed in our study.

Unimodal relationships between species richness and productivity can be best understood by looking at the two arms of the hump. It is relatively easy to understand how an increase in productivity can increase species richness (Connell and Orians 1964, Abrams 1995, J. Moore, *personal communication*). Several factors have been suggested to explain the decline of richness at high productivities. Results from the nutrient enrichment experiments suggest that competition may be a mechanism in lakes, at least in the short term and for some taxa. In addition, predation and abiotic factors (such as reduced nocturnal oxygen concentrations) may further account for the declines in species richness above the moderate productivity levels we observed in the lake survey and in whole-lake experiments. Support for several different theories suggests that the relationship between primary productivity and species richness in lakes is driven by multiple factors.

Productivity factors that increase species richness.—J. Moore (*personal communication*) modeled thermodynamic arguments to explain an increase of species richness with productivity (Oksanen et al.

1981). The basic idea is that when there is more energy available to a system, there is the potential to support additional species and trophic levels. As energy input increases, the likelihood of adding more species and trophic levels also increases. The results from the lake survey are consistent with this model, at least in a broad sense. That is, phytoplankton (at the base of the pelagic food chain) are already diverse at the lowest known level of lake productivity ($\sim 1 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), and phytoplankton biodiversity peaks at the lowest productivity level of the six species groups, at least in small to moderately large lakes (Table 2, Fig. 4). Although herbivores are present in the lowest productivity lakes, their species richness peaks at slightly higher levels than do phytoplankton, possibly reflecting the diminution of available energy between the primary producer and the primary consumer levels. In medium to large lakes, fish species, representatives of the next trophic level, exhibit peak richness at moderate levels of productivity, generally $100\text{--}300 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$.

The thermodynamic model is also consistent with the observation that macrophyte species richness generally peaks at a higher productivity level than does phytoplankton richness. For a given level of input of sunlight, temperature, and nutrients, phytoplankton have a higher specific net primary productivity, because macrophytes have nonphotosynthetic tissue that soaks up energy fixed in photosynthesis. In a particular lake, the phytoplankton will experience a higher rate of net productivity than will macrophytes, and therefore, among lakes, the peak in macrophyte species is expected to occur at a higher productivity than the phytoplankton peak.

Productivity factors that decrease species richness.—

1. *Competition models.*—Competition for food resources can be an important determinant of zooplankton community composition (Allan 1974, Rothhaupt 1990, Lampert and Rothhaupt 1991). Zooplankton may face increasing competition for food as primary productivity increases, not because there is less food, but because the food is of lower quality (Richman and Dodson 1983, Watson et al. 1997). As total phytoplankton biomass increases with increasing productivity (Schindler et al. 1978), the amount of edible phytoplankton declines, especially in eutrophic lakes dominated by cyanobacteria (Watson et al. 1992). Peaks in richness of zooplankton occur at productivity levels $\sim 60\text{--}180 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. These peaks are just below productivity levels associated with significant amounts of unpalatable food (above $\sim 300 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$). Thus, food quality and interspecific competition may cause reductions in zooplankton richness. Species composition shifts in the short-term experiments support this theory. As productivity increased in East and West Long Lakes, the community was dominated by a large, competitively dominant zooplankton species.

Competition for light probably has little effect on

phytoplankton or plant diversity, just as competition for light in terrestrial systems does not enhance local diversity (Tilman 1988). Experimental studies in aquatic systems have documented species displacements (rather than changes in species diversity) resulting from competition for light among phytoplankton (Huisman et al. 1999). Like light, inorganic nutrients, such as phosphate and nitrate, often limit phytoplankton population dynamics. However, competition for a principal limiting nutrient such as phosphate, or for secondary limiting nutrients (such as nitrate) probably does not affect phytoplankton diversity (Leibold 1999).

2. *Predation.*—A model (Leibold 1999) predicts that generalist keystone predators can create a unimodal response in prey species richness along a productivity gradient. Predator density and, therefore predation intensity, is expected to increase along a productivity gradient (Oksanen et al. 1981, Mittelbach et al. 1988, Leibold 1999). At low productivity, superior resource competitors should dominate the prey community; whereas at high productivity, species that are not vulnerable to predation will dominate. At intermediate productivity levels, coexistence of the two species types is predicted to occur because predation keeps the superior competitors in check, thereby enabling inferior competitors to persist. The survey results show just such a unimodal pattern for phytoplankton. However, Proulx et al. (1996) found that herbivory reduced phytoplankton diversity in low-nutrient enclosures and increased diversity in high-nutrient enclosures. Thus, until further field tests of this theory are performed, it is difficult to make generalizations regarding the effects of zooplankton predation on phytoplankton biodiversity across a productivity gradient.

3. *Abiotic factors.*—As in terrestrial communities, particular aquatic species are specialized for living in a restricted range of abiotic conditions. For example, there is a regular sequence of intertaxonomic replacements of phytoplankton species groups along the productivity gradient (Reynolds 1984, Watson et al. 1997). At the upper end of the natural productivity gradient (above $\sim 1000 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), only a few phytoplankton species can tolerate extreme conditions characteristic of highly eutrophic lakes (e.g., strongly stratified light and no oxygen at night). These same extreme conditions also limit the ability of macrophytes and animals to persist. Macrophytes are light limited (shaded) in eutrophic lakes (Jones et al. 1983). In addition, few fish species can gulp enough air to live in highly eutrophic lakes that become anoxic at night. Most zooplankton species are probably sensitive to low oxygen concentrations and high pH in strongly eutrophic lakes, as evidenced in L227. Thus, extreme abiotic conditions created by high productivity may be responsible for the low species richness in these lakes.

These explanations are intrinsic to the organisms' ecology (physiological specializations or species interactions). However, an additional possibility is that

of chemical contamination related to land use (S. I. Dodson, *unpublished manuscript*). The major groups of organisms had peak species richness between 30 and 179 g C·m⁻²·yr⁻¹, except for fish, which peaked at 300 g C·m⁻²·yr⁻¹ (Table 1). Of the 15 lakes (Table 1) with more than 179 g C·m⁻²·yr⁻¹, all are in land use areas of moderate to intense agriculture. All of the 11 lakes with more than 300 g C·m⁻²·yr⁻¹ are in areas of intense agriculture, and most receive or have received sewage effluent and urban runoff from storm sewers. All of the eight lakes with less than 30 g C·m⁻²·yr⁻¹ are in remote areas with no direct agricultural, industrial, or urban land use in the watershed. The hypothesis is that the increasing (toxic) chemical contamination that accompanies increasing primary productivity reduces aquatic species richness. Because of lack of data on contamination and the extreme temporal and spatial complexity of contamination, this will be a challenging hypothesis to test.

Conclusions

Based on Mittelbach (*personal communication*), we expected to find unimodal responses of species richness to increased productivity in the lake survey (regional scale), but possibly not in the whole-lake experiments (local scale). Our results generally supported this expectation. Phytoplankton, rotifer, cladoceran, copepod, and macrophyte species richness varied in a unimodal fashion with increased productivity. Richness–productivity relationships for phytoplankton and fish were also a function of lake size.

A variety of mechanisms might account for the lack of unimodal richness–productivity relationships in the whole-lake experiments; these include transient dynamics, lagged responses, and possibly shifts to new system states. Both spatial and temporal scales need to be considered if we are to discern and then understand richness–productivity relationships in lake ecosystems.

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