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Biodiversity and nutrient enrichment in pond plankton communities

Mathew A. Leibold*

Department of Ecology and Evolution, University of Chicago, 1101 E. 57th Street, Chicago, IL 60637, USA

ABSTRACT

There are at least four mathematically developed models that predict unimodal diversity–productivity relations in local communities. I attempt to distinguish among these theories using data from surveys of planktonic organisms in 31 fishless ponds in southern Michigan by relating plant and herbivore diversity and composition to pond nutrient levels. The density of plants (phytoplankton) was positively correlated with nutrient levels and the density of herbivores (zooplankton) was positively correlated with the density of plants. Species richness of plants and of herbivores were declining or unimodal functions of nutrient levels. The composition of each trophic level changed significantly with eutrophication as indicated by significant correlations between nutrient levels and site scores (obtained by reciprocal averaging ordination on occurrences). A concomitant lack of correlation between site scores and species richness for both trophic levels further shows that the patterns of species distributions form gradients of species replacements rather than nested subsets. Taxonomic ordination scores also showed that the algae found at low nutrient levels consisted disproportionately of small, unprotected forms (thought to be fast-growing but grazer-susceptible), whereas the algae found at high nutrient levels were larger and often sheathed or gelatinous (thought to be slow-growing but more resistant to grazers). The results of this analysis of changes in the patterns of distribution of planktonic organisms are consistent with a hypothesis of productivity-dependent 'keystone-predation' causing the unimodal relation between diversity and productivity.

Keywords: biodiversity, phytoplankton, predation, productivity, zooplankton.

INTRODUCTION

Relations between species diversity and various environmental gradients provide a unique challenge to models of community structure. Ultimately, explicit models of species interactions in communities will have to elucidate patterns of species diversity and composition in unmanipulated natural systems if they are to be considered successful. One of the more interesting such patterns is the frequent observation of unimodal (i.e. 'humped') relations between species richness and measures of ecosystem productivity (Rosenzweig and Abramsky, 1993; Tilman and Pacala, 1993). These effects of productivity on species richness are observed despite the occurrence of monotonic relations between the density or

* e-mail: mleibold@midway.uchicago.edu

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biomass of individuals and productivity, clearly implying a process quite distinct from the effects of area on diversity (Huston, 1994; Rosenzweig, 1995). These observations challenge the predictions of many models that predict that diversity should be monotonically enhanced by increasing ecosystem productivity (e.g. Connell and Orias, 1964; MacArthur and Pianka, 1966; Schoener, 1976; Abrams, 1983, 1995; Vance, 1984). These observations also suggest that species interactions are relevant to the regulation of local diversity because they cannot be easily explained by single-species demographic effects. However, reviews of the evidence for the mechanisms underlying unimodal diversity–productivity relations are inconclusive (Rosenzweig and Abramsky, 1993; Tilman and Pacala, 1993; Abrams, 1995) and stress the need for explicit links to specific theoretical models of species interactions.

Rosenzweig (1992, 1995) has also argued that the unimodal diversity–productivity curve is most applicable to relatively large-scale (i.e. 'regional') rather than small-scale (i.e. 'local') patterns that more often appear monotonic. The small-scale patterns he describes reflect largely the immediate responses of individuals to experimental manipulations rather than longer-term and spatially complex responses of entire populations that are presumed to regulate the larger-scale pattern. Thus the unimodal curve is more likely to reflect quasi-steady-state consequences of variation in productivity than the local pattern.

To date, there are at least four well-developed models that use explicit dynamical equations to predict unimodal diversity–productivity curves (for more comprehensive and critical reviews that also evaluate other hypotheses, see Rosenzweig, 1992; Abrams, 1995). The first is the 'paradox of enrichment' (Rosenzweig, 1971), where predator–prey relations are destabilized when the productivity of the environment is enhanced. In a simple food chain with a 'humped' prey isocline, an equilibrium point that is stable at low prey carrying capacity (i.e. low ecosystem productivity) can be destabilized at high prey carrying capacity. The result will be overexploitation of the prey and the subsequent crash of the dependent predator population. This result may depend on the assumption of a single homogeneous population at each trophic level (e.g. Rosenzweig and Schaffer, 1978; Leibold, 1989, 1996; Kretzschmar *et al*., 1993; see also Rosenzweig, 1992). In cases where the lower trophic levels have substantially higher dispersal abilities than higher trophic levels (as would be expected in limnetic algae–zooplankton assemblages), one might predict that this model would show stronger and steeper declines in diversity at high productivity for organisms at the higher trophic levels. This is because the prey should be able to rapidly recolonize after the extinction of the predator but predator colonizations will be unsuccessful until the prey has established itself. This model also predicts that the density of plants (as a group consisting of multiple species) increases with productivity only when the diversity of predators changes, since otherwise plant densities are entirely dependent on the death rate of the herbivores (Oksanen *et al*., 1981). In contrast with the models below, this model does not require the presence of any trade-off in the ecological traits of organisms at any trophic level to produce unimodal diversity–productivity relations.

The second model is the 'resource heterogeneity hypothesis', which emphasizes competition for spatio-temporally variable resources (for details, see Tilman, 1982; Abrams, 1988). In this model, co-existence of competitors is enhanced when there is local spatio-temporal heterogeneity in the relative supply of alternative resources (ratios in the relative rates of resource renewal via inflow and internal turnover). If there is no correlation between the amount of such local heterogeneity and the absolute supply of resources (maximum resource densities in the absence of consumption), species diversity at high productivity when supply rates are high will decline. There is also likely an increase in species diversity

with increasing resource supply in very unproductive conditions due to minimum resource requirements. Together, these two effects can result in a unimodal diversity–productivity curve (Tilman, 1982; but see Abrams, 1988, 1995; Tilman and Pacala, 1993). Much of the recent literature documenting unimodal diversity–productivity curves cites this hypothesis (e.g. Tilman, 1982; Nilsson and Wilson, 1991; Rosenzweig and Abramsky, 1993). One characteristic prediction of this model is that species lists at different levels of productivity will consist of nested subsets (*sensu* Patterson, 1987), since diversity at intermediate productivity will occur by the addition of new specialists on each of the alternate resources to a smaller pool of species common to both low and high productivity environments. These specialists become extinct as productivity becomes very high (see fig. 37 in Tilman, 1982). An important assumption of this model is that organisms at a given trophic level show a trade-off in their abilities to compete for alternative resources (i.e. minimum resource requirements for alternative resources are negatively correlated).

The third hypothesis is the 'resource-ratio hypothesis', which is very closely related to the resource heterogeneity hypothesis, but hypothesizes that an increase in ecosystem productivity is mostly affected by the supply of a single 'most limiting' resource (I will refer to this resource as the 'primary resource'). Consequently, the *relative* supply of other resources (I will refer to these as 'secondary resources') can also vary consistently as ecosystem productivity increases (see Tilman, 1982; Tilman and Pacala, 1993; Leibold, 1997) and the identity of the most strongly limiting resource changes as productivity increases. In contrast with the second hypothesis, species lists would consist of a set of species replacements that form a gradient, with species that specialize on the primary limiting resource found at low productivity, and specialists on secondary resources found at high productivity (a mixture will be found at intermediate productivities). Some patterns of compositional change in phytoplankton communities are predicted remarkably well by this model (e.g. Smith, 1983; but see Trimbee and Prepas, 1987). Previous studies have in particular emphasized the importance of nitrogen-to-phosphorus ratios as determinants of phytoplankton composition in limnetic systems, and it is commonly thought that dominance of blue-green algae in eutrophic lakes is due to an associated shift from phosphorus limitation (the primary nutrient) to nitrogen limitation (the secondary nutrient). More recently, Huisman and Weissing (1995) presented a closely related model in which a nutrient is the 'primary' resource and light acts as the 'secondary' resource. Their model would predict that the algal species assemblage at high nutrient levels is dominated by good light competitors. Like the second model, an important postulate of the resource ratio model is that organisms at a given trophic level show a trade-off in their abilities to compete for alternate resources.

Finally, the fourth model, the 'keystone-predation hypothesis', is predicated upon strong interactions among trophic levels and involves the modification of resource competition by predators (Paine, 1966; Vance, 1978; Leibold, 1989, 1996; Holt *et al*., 1994). In this hypothesis, competing species interact via two mechanisms; they compete for a common pool of resources via exploitative competition, but they also interact via 'apparent competition' (*sensu* Holt, 1977) owing to the presence of shared predators that is supported by the productivity of the lower trophic levels. The result at low productivity (when predators are absent or rare) is that vulnerable species that are good resource exploiters (with low minimum resource requirements) exclude other species that are less vulnerable to the predator but that are inferior resource exploiters. At intermediate productivity, the vulnerable species (good at resource exploitation) can co-exist with less vulnerable but poorer resource exploiters. However, at high productivity, the less vulnerable species excludes the vulnerable

species (Holt *et al*., 1994; Leibold, 1996). This hypothesis also predicts a gradient of species replacements (rather than nested subsets) along a gradient of productivity: vulnerable species at low productivity and predator-resistant species at high productivity. Leibold (1996) has examined the effects of spatio-temporal variation in this model and shown that, as in the models for resource competition (the second and third hypotheses described above), co-existence of species that compete for a single resource and share a single predator need not be limited to two species. This hypothesis, in its most general form, also predicts that the number of trophic levels and the total densities of organisms in each trophic level should increase at higher productivity.

Distinguishing among these four competing hypotheses can be difficult without conducting manipulative and potentially difficult experiments. However, an approach based on strong inference (Platt, 1964) can attempt to reject some of these hypotheses by focusing on the distinct patterns of species composition and diversity in natural unmanipulated systems predicted by each of the hypotheses (see Table 4 below). Assume a system where plants disperse rapidly relative to herbivores. If the first hypothesis is true, the decline in species richness of local communities at higher productivity should be more strongly associated with changes in the diversity of herbivores rather than plants. If the second hypothesis is true, successive species lists in communities along a productivity gradient should consist of nested subsets wherein the composition of the community at high productivity converges with the composition of communities at low productivity. If the third or fourth hypothesis is true, one should observe compositional change in terms of a gradient of species replacements as ecosystem productivity is enhanced. Distinguishing between the third and fourth hypotheses can be done by contrasting the traits of species at high productivity with those at low productivity. If the third hypothesis is true, organisms typical of more productive environments should consist of specialists on secondary resource types even if they are poorer competitors on the primary resources; if the fourth hypothesis is true, organisms typical of the more productive environments should consist of predator-resistant forms even if they are inferior at competing for resources.

I compared patterns predicted by each of the four models discussed above with those observed in open-water communities of small fishless ponds in southern Michigan by determining how plant (phytoplankton) and herbivore (zooplankton) density, diversity and composition varied with nutrient levels. Open-water limnetic habitats are convenient because almost all taxa of plants and the large majority of herbivores are comprehensively sampled by conventional methods using bottles and nets. Several previous studies have indicated that there is a unimodal relation between phytoplankton taxonomic richness and algal biomass in lakes (Ogawa and Ichimura, 1984; Agusti *et al*., 1991; but see Lambou *et al*., 1983; Eloranta, 1986) and between crustacean zooplankton species richness and average lake primary productivity (Dodson, 1992) or temperature (Rosenzweig, 1992, using data from Patalas, 1990). However, these patterns have not previously been linked to each other, nor have they been compared directly to nutrient levels or other aspects of community structure that depend on nutrient levels. Because these studies have focused on diversity, the joint analysis of diversity and compositional change that would permit discrimination among the mechanistic models as described above has not been carried out.

In the following analyses, I first document unimodal relations between species diversity and nutrient levels in both plants and herbivores. Because planktonic organisms have short generation times and because populations in different ponds are relatively independent from each other, patterns from these ponds are more likely to match the larger-scale,

'regional' pattern identified by Rosenzweig (1992, 1995) than the smaller-scale 'local' pattern. I then further evaluate the four hypotheses by considering how variation in species diversity in relation to nutrient levels is associated with distributional patterns of species and their traits.

METHODS

Thirty-one fishless ponds in southern Michigan were sampled between July and September in 1993 and 1994. The ponds were selected to represent as large a gradient in nutrient levels as possible, ranging from very oligotrophic intradunal ponds and small artificial reservoirs to extremely eutrophic abandoned dairy-waste settling ponds. All artificial ponds (4 of the 31) have been in existence and have not been disturbed in any major way for at least 8 years. Additional ponds that contained fish or that did not receive direct sunlight (i.e. forest ponds under closed canopies or those with continuous duckweed cover) were not included, since they have very distinct plant and animal communities (McPeek, 1990; D.H. Skelly and E.E. Werner, personal communication).

In each pond, a 250-ml water sample was collected for nutrient analysis using a bottle sampler. Total phosphorus was measured using an autoanalyser (in 1993) or a spectrophotometer (in 1994) after persulphate digestion (USEPA, 1987). Total Kjeldahl nitrogen was also measured on an autoanalyser after persulphate digestion (USEPA, 1987).

A 250-ml sample of water was also collected for phytoplankton analysis using a bottle sampler and was preserved in glutaraldehyde. Permanent slides of algae samples were made using a modification of methods described in Crumpton (1987; St. Amand, 1990). Algae were identified to the genus level (whenever possible) and enumerated until at least 15 fields and 300 identified cells had been counted. The slide was then comprehensively scanned for additional taxa not included in the density counts.

Zooplankton were sampled using a 63-μm mesh Wisconsin bucket zooplankton net. One to three diagonal tows through the water column (totalling 5–10 m, depending on pond size) were taken in the most open areas of each pond. Subsamples were counted in a Palmer cell until at least 200 individuals had been identified and counted. Zooplankton (except nauplii and copepodites) were identified to species including crustaceans and rotifers. All of the taxa included in the analysis are at least partially herbivorous, although some are also partially predacious (usually depending on ontogenetic stage).

Analyses of the data used linear and quadratic regression models to identify significant trends and to test for curvilinearity. All nutrient, taxonomic richness and density estimates were log-transformed (base 10) to homogenize residual variation. In addition to using species richness (number of species found per standard volume sampled), I also calculated Fisher's alpha (see Magurran, 1988) to examine diversity patterns. This metric is insensitive to the number of individuals sampled (which was variable in this study, where density varied more than 100-fold) if the population densities of species within samples follow a logarithmic series. Although some samples deviated significantly from this assumption, Fisher's alpha is somewhat robust to this assumption, especially for small samples (Boswell and Patil, 1971). No attempt was made to fit alternative non-linear models to these trends, since there are few *a priori* reasons to favour any particular model. To further test for unimodality (not just curvilinearity), I also applied a test developed by Mitchell-Olds and Shaw (1987; hereafter referred to as the MOS-test). This test estimates the variance in the location of the 'peak' of a quadratic model and tests whether the 95% confidence interval for the estimate

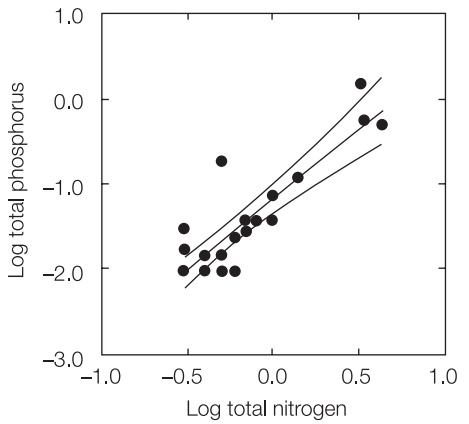

Fig. 1. Log–log plots of total phosphorus (TP in mg l^{-1}) and total nitrogen (TN in mg l^{-1}) in 31 ponds from southern Michigan. There is a significant correlation between TP and TN ($r^2 = 0.73$, $n = 30$, $P < 0.001$). The regression line is bracketed by its 95% confidence interval and has a slope of 1.47 (S.E. = 0.17). Some of the dots represent multiple data points, especially at low nutrient levels where the data are at or near the detection limits for TP.

of the peak is bounded by the range of the data. It was developed to test for stabilizing selection in evolutionary studies but provides a useful tool for testing the unimodal nature of any data set.

Compositional analyses of algae and zooplankton were done separately using reciprocal averaging (equivalent to correspondence analysis) on presence–absence data because the theoretical models described above make predictions that focus on co-existence patterns (rather than on patterns of relative or absolute abundances). Subsequent statistical analyses of composition focused exclusively on site scores for each pond obtained for the first axis in the ordination. The exclusive use of the first ordination score combined with the use of presence–absence data means that the 'horseshoe effect' that can potentially bias the interpretation of secondary ordination axes was not a problem here (Gauch, 1982). For zooplankton, I analysed site scores only. However, for phytoplankton, I analysed both site scores (which measure differences in the taxonomic composition of different ponds) and taxon scores (which measure differences in the distribution of different taxa). The analysis of taxon scores was undertaken to determine if there were correlations between the distribution of individual phytoplankton taxa and traits such as body size and surface area-to-volume ratios (data obtained from Reynolds, 1984; supplemented by data in Sutherland, 1989).

RESULTS

There was a positive correlation between total phosphorus (TP) and total nitrogen (TN) in all these ponds (Fig. 1). Both nutrients varied over more than two orders of magnitude across the set of ponds. The TN : TP ratios (ranging from about 1 to 65) were variable but indicated that both nitrogen and phosphorus might be limiting in different cases. Thus, either total nitrogen or total phosphorus provides an index of eutrophication.

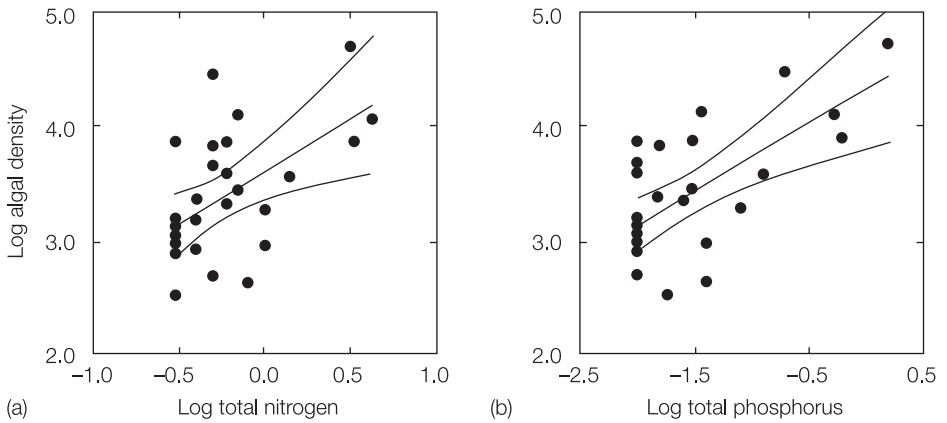

Fig. 2. Log–log correlations between algal density (units per ml) and TN (a) and TP (b). The correlation between algal density and TP is significant ($r^2 = 0.45$, $n = 31$, $P < 0.001$) and has a slope of 0.58 (S.E. = 0.12). The correlation between algal density and TN is also significant ($r^2 = 0.33$, $n = 30$, $P < 0.001$) and has a slope of 0.85 (S.E. = 0.23).

However, because minimum detection limits on total phosphorus are relatively high, the data on total phosphorus are perhaps not as informative at low nutrient levels as are the data on total nitrogen.

As might be expected from similar surveys in other types of lakes and ponds (e.g. Lambou *et al.*, 1983; Canfield *et al.*, 1985; McQueen *et al.*, 1986; Watson *et al.*, 1992), there were also significant correlations between nutrient levels and phytoplankton density (Figs 2a,b). Correlations between zooplankton density and nutrient levels, although positive, were not significant (Figs 3a,b). However, there was a significant correlation between zooplankton density and algal density (Fig. 3c). Although there was a tendency for the log density of both zooplankton and phytoplankton to increase more slowly at high nutrient levels, this deceleration was not statistically significant (quadratic terms have *P*-values between 0.05 and 0.2).

Patterns of taxonomic richness are also significantly related to nutrient levels (Fig. 4). For both phytoplankton and zooplankton richness (number of taxa per sample), there are significant quadratic terms in regressions with total nitrogen and with total phosphorus (Table 1). For phytoplankton (Figs 4a,b), the overall relationships were negative, with ponds at higher nutrient levels having lower taxonomic (genus-level) diversity. The best-fit quadratic equations had peak algal taxonomic richness at total phosphorus levels of 0.05 mg l^{-1} and total nitrogen levels of 0.56 mg l^{-1}. However, according to the MOS-test (Mitchell-Olds and Shaw, 1987; Table 1), the location of the peak is not quite significantly different from the lowest true phosphorus levels observed (0.10 mg l^{-1}). The peaks of the curves, however, occur at total nitrogen and phosphorus levels that are significantly less than the maximum observed. Thus, the diversity–productivity relation for phytoplankton can be characterized as decreasing or (more likely) humped, but not flat or monotonically increasing. For zooplankton (Figs 4c,d), the relationship is significantly unimodal (except that the peak zooplankton species richness is greater than the minimum total nitrogen level only at the $P = 0.06$ level) for both total phosphorus and total nitrogen. There are significant quadratic terms in both regressions (Table 1), and analyses of the relationships using the

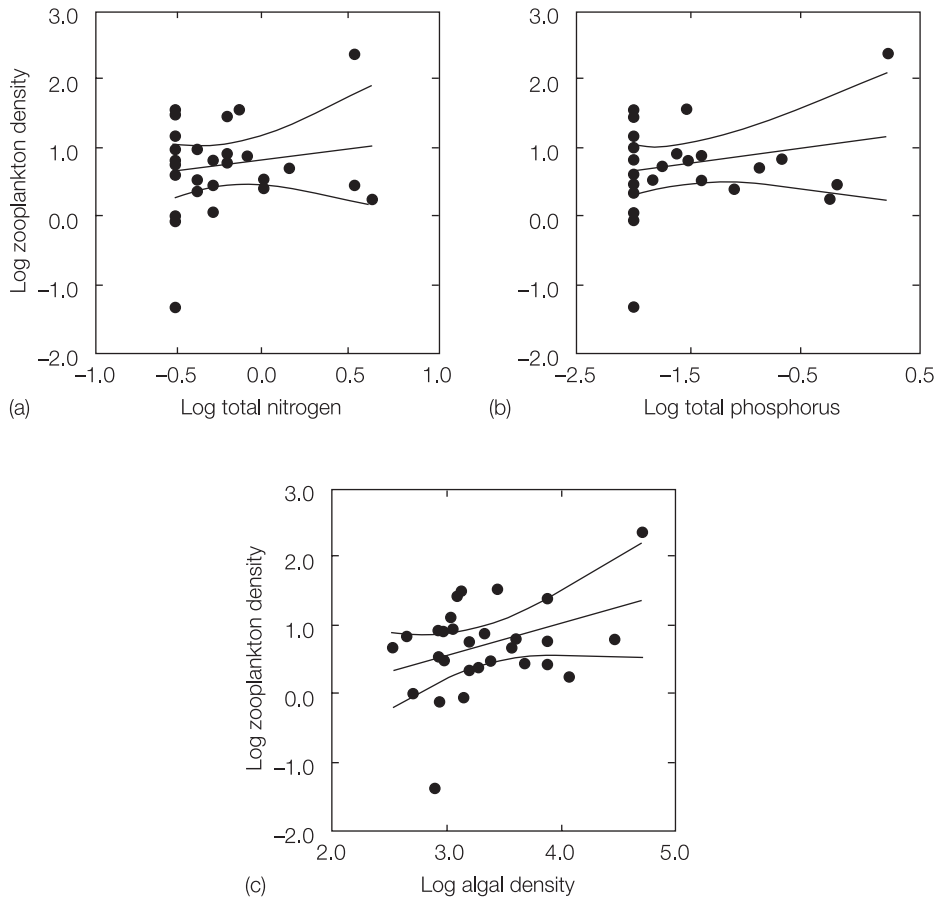

Fig. 3. Log–log correlations between zooplankton density (individuals per litre) and TN (a), TP (b) and algal density (c). Correlations with TN and TP are not significant but the correlation with algal density is significant ($r^2 = 0.13$, $n = 29$, $P = 0.05$) and has a slope of 0.46 (S.E. = 0.23).

MOS-test show that the peak in species richness occurs with the range of observed nutrient levels (Table 1).

Relationships between taxonomic diversity as measured using Fisher's alpha and nutrient levels tend to reinforce the analyses of taxonomic richness (Fig. 5). For zooplankton, the analysis of Fisher's alpha confirms the results of the analysis of species richness (Table 2); there is a significant quadratic term relating diversity to nutrient levels and the results of the MOS-test indicate that the relationship is unimodal. For phytoplankton, however, the analysis is somewhat equivocal (even more so than in the analysis of species richness described above). Although similar qualitative patterns are evident, the data are much noisier and there are no statistically significant relations between Fisher's alpha and either total nitrogen or total phosphorus (Table 2). However, in this analysis, a few samples deviated strongly from the assumption of log-series abundances assumed by Fisher's alpha. These samples are the ones that contribute most to the deviations from a unimodal curve shown in Fig. 5. The data jointly shown in Figs 4 and 5 thus lend qualified support to the

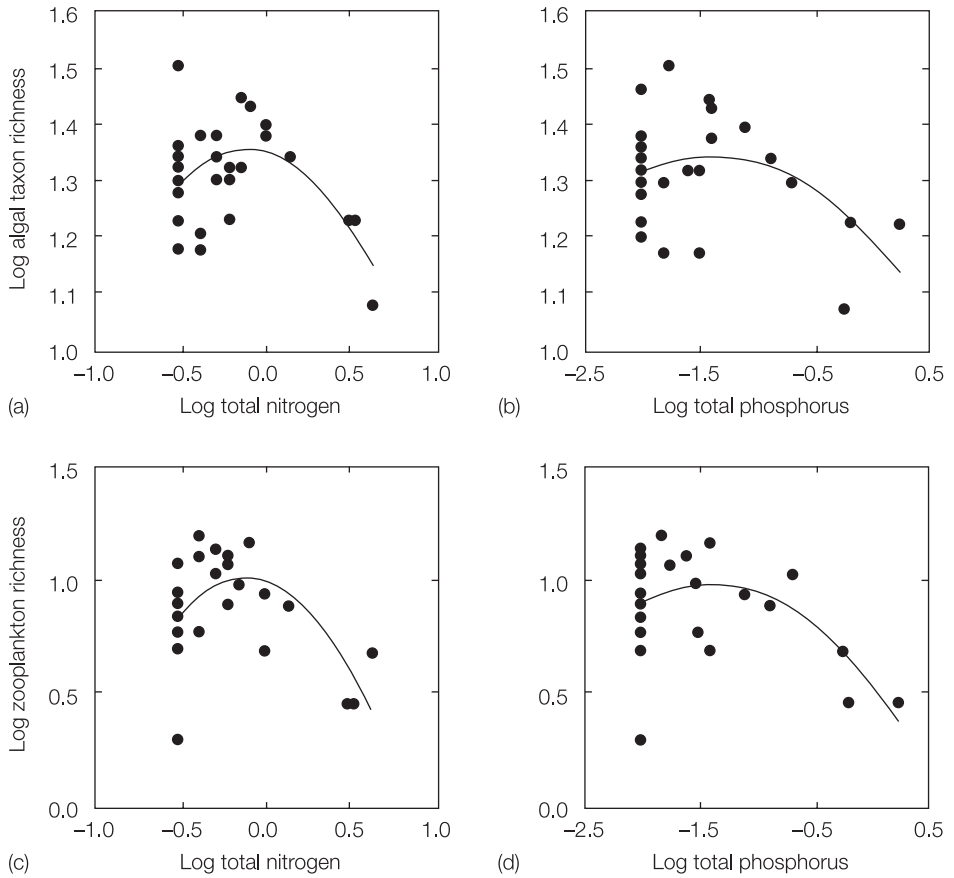

Fig. 4. Quadratic regressions of log–log relations between taxonomic richness and nutrient levels for algae and zooplankton. Analysis of variance summary tables and regression parameters are presented in Table 1. In the upper panels, algal genus richness is related to TN (a) and TP (b); in the lower panels, species richness of crustacean and rotiferan zooplankton is related to TN (c) and TP (d). Application of the MOS-test (Mitchell-Olds and Shaw, 1987) indicates that the peak of the quadratic function for both algal and zooplankton diversity is significantly lower that the maximum levels of TN, but not significantly higher than the minimum levels ($P = 0.13$ for algae and 0.06 for zooplankton). The MOS-test indicates that the peak of the function for both algal and zooplankton diversity is significantly lower than the maximum, and higher than the minimum, TP levels.

notion that taxonomic diversity of phytoplankton is unimodally related to nutrient levels in these ponds and strong support to the notion that zooplankton diversity is unimodally related to nutrient levels.

Reciprocal ordination site scores that quantify differences in composition of both algae and zooplankton in ponds are also closely related to nutrient levels (Fig. 6). In this study, site scores based on phytoplankton composition are correlated with total nitrogen levels (Fig. 6a) but the correlations with total phosphorus levels are not significant (Fig. 6b). Site scores based on zooplankton composition are significantly correlated with both total

Table 1. Analysis of variance summary tables for regression analyses of the log of algal taxonomic richness and the log of zooplankton species richness as linear and quadratic functions of total nitrogen (on the left) and total phosphorus (on the right)

	B	SE(*B*)	*t*	*P*		*B*	SE(*B*)	*t*	*P*
Algal genera									
TN	–0.10	0.04	–2.2	0.04	TP	–0.21	0.10	–2.3	0.03
TN^2	–0.20	0.08	–2.4	0.03	TP^2	–0.08	0.04	–1.9	0.07
$N^* < N_{max}$				0.02	$P^* < P_{max}$			–2.3	0.03
$N^* > N_{min}$				0.13	$P^* > P_{min}$			–2.0	0.05
Zooplankton species									
TN	–0.26	0.11	–2.4	0.03	TP	–0.63	0.23	–2.8	0.01
TN^2	–0.59	0.20	–2.9	0.01	TP^2	–0.23	0.12	–2.3	0.03
$N^* < N_{max}$			–3.1	0.01	$P^* < P_{max}$			–2.9	0.01
$N^* > N_{min}$			2.0	0.06	$P^* > P_{min}$			–2.5	0.02

Abbreviations: *B* = the regression coefficient of each term, SE(*B*) = the standard error of the coefficient, *t* = the value of the *t*-test and *P* = the probability value for each term. TN = total nitrogen, TP = total phosphorus, N = nitrogen and P = phosphorus. Also shown are *P*-values for the MOS-test of the hypothesis that the 'peak' of the function is located at nutrient levels less than the greatest observed nutrient level in the data set, and the hypothesis that the 'peak' of the function is located at nutrient levels greater than the least observed nutrient level in the data set.

nitrogen and total phosphorus (Figs 6c,d). Again, the stronger correlations observed with total nitrogen may be due to the lack of resolution in total phosphorus levels at the lower nutrient levels.

Conventional metrics used to determine deviations from random assortments of species among sites and previously used to test for nested subsets (Wright and Reeves, 1992) were significant (Table 3). These metrics indicate that the distribution of species among sites was not random. However, if compositional differences consisted of 'nested subsets' (Patterson and Atmar, 1986; Wright and Reeves, 1992), a correlation between site scores (measures of compositional similarity) and species richness would also be expected. For both phytoplankton and zooplankton, such correlations between site ordination scores and species richness were not observed (Fig. 7). Other analyses (M.A. Leibold and G.M. Mikkelson, unpublished) indicate that metrics for analysing nested subsets can be misleading when there are gradients of species replacements with an intermediate diversity peak. The lack of correlation between site scores and diversity, together with significant correlations between site scores and an environmental factor, is thus inconsistent with the notion of nested subsets. These data are more consistent with the conclusion that there are compositional replacements of taxa associated with changes in nutrient levels.

For phytoplankton, I used ordination scores for different taxa (rather than scores for different ponds) to relate the distribution of individual genera to their traits. Such correlations might reflect underlying trade-offs in their relative abilities to compete for resources and their susceptibility to grazers. Algae with large cells or colonies were more often found in eutrophic ponds than were smaller taxa (Fig. 8a). Consequently, such cells also had smaller surface area-to-volume ratios (Fig. 8b). Finally, algae with morphological traits

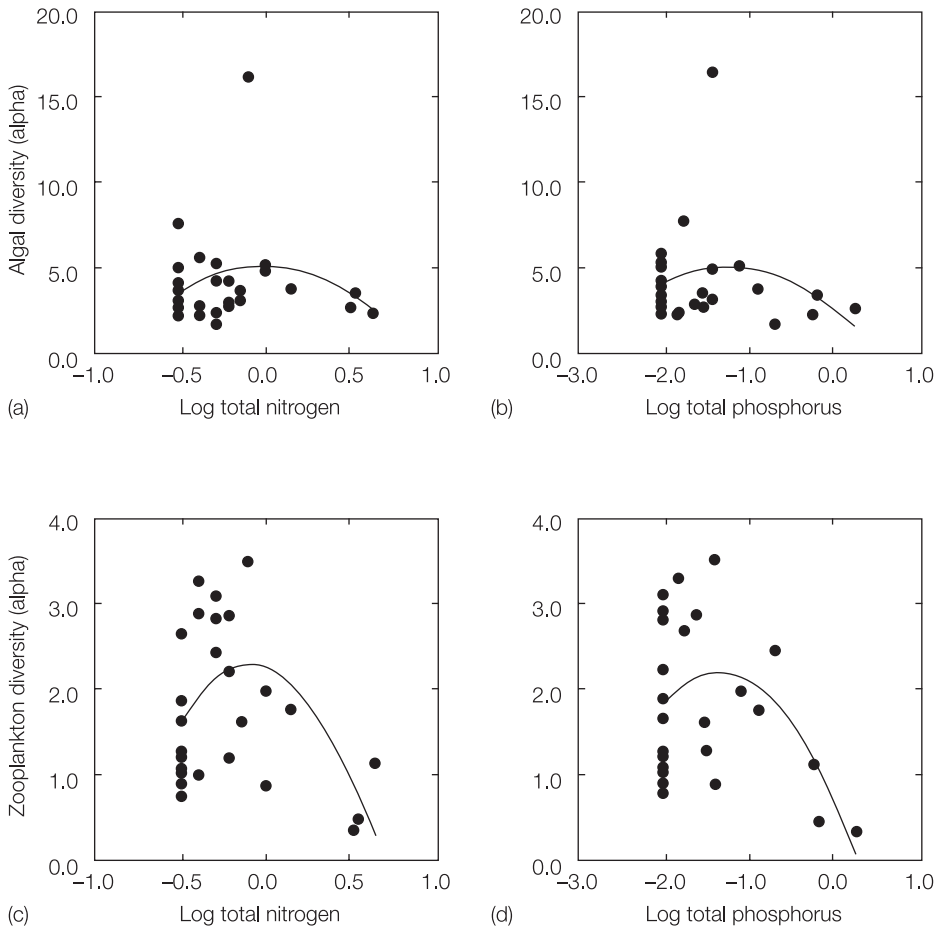

Fig. 5. As in Fig. 4 except that Fisher's alpha is used to measure diversity. For algal diversity, the quadratic curves are qualitatively similar to those obtained for taxonomic richness but none of the relations are significant (see Table 2). For zooplankton, the relationship is significantly unimodal using the MOS-test (Table 2).

thought to provide protection against grazing (e.g. gelatinous sheaths, thickened cell walls, or spines) were also more likely to be found in eutrophic ponds than algae without such morphological traits (Fig. 9). There were no significant differences in the taxon scores of algae from different phylogenetic divisions (analysis of variance: $F_6 = 1.62$, $n = 80$, $P = 0.16$).

Finally, algal diversity and composition (as described by presence–absence data) were not strongly related to nitrogen : phosphorus ratios in this study. There was no correlation between algal diversity (measured either as species richness or using Fisher's alpha) and nitrogen : phosphorus ratios (Fig. 10a). There was also no relationship between the site scores from the ordination and nitrogen : phosphorus ratios (Fig. 10b). Because other nutrients (e.g. silica, sulphate) were not measured, correlations involving the effects of other nutrient ratios could not be determined.

Table 2. Analysis of variance summary tables for regression analyses of the log of Fisher's alpha determined for algal taxonomic diversity and for zooplankton species diversity as linear and quadratic functions of total nitrogen (on the left) and total phosphorus (on the right)

	B	SE(*B*)	*t*	*P*		*B*	SE(*B*)	*t*	*P*
Algal alpha									
TN	–0.05	0.11	–0.5	0.65	TP	–0.25	0.21	–1.2	0.24
TN^2	–0.40	0.30	–1.3	0.19	TP^2	–0.09	0.09	–0.9	0.35
$N^* < N_{max}$			1.0	0.30	$P^* < P_{max}$			–1.3	0.18
$N^* > N_{min}$			0.1	0.87	$P^* > P_{min}$			–0.9	0.36
Zooplankton alpha									
TN	–0.32	0.12	–2.7	0.02	TP	–0.87	0.23	–3.8	0.01
TN^2	–1.08	0.33	–3.2	0.01	TP^2	–0.32	0.10	–3.1	0.01
$N^* < N_{max}$			2.2	0.04	$P^* < P_{max}$			–3.9	0.01
$N^* > N_{min}$			–1.8	0.08	$P^* > P_{min}$			–3.4	0.01

Abbreviations: *B* = the regression coefficient of each term, SE(*B*) = the standard error of the coefficient, *t* = the value of the *t*-test and *P* = the probability value for each term. TN = total nitrogen, TP = total phosphorus, N = nitrogen and P = phosphorus. Also shown are *P*-values for the MOS-test of the hypothesis that the 'peak' of the function is located at nutrient levels less than the greatest observed nutrient level in the data set, and the hypothesis that the 'peak' of the function is located at nutrient levels greater than the least observed nutrient level in the data set.

DISCUSSION

The keystone-predation model (in its most general formulation that allows for local spatio-temporal variability) predicts that enhanced nutrient levels will have four linked effects resulting from their consequences in enhancing the productivity of the resource base for dependent food webs (i.e. four 'bottom-up' effects; see Leibold, 1996). First, the total densities of organisms at any trophic level (summed over all the component species) will be correlated with the density of organisms at adjacent trophic levels even when there is no variation in the number of trophic levels, in contrast with many simpler models of trophic cascades in linear food chains (Figs 2 and 3). Second, the diversity of organisms at any but the top-most trophic level will be a unimodal function of nutrient levels (Figs 4 and 5). Third, the composition of organisms at any but the top-most trophic level will consist of a series of species that replace each other forming a compositional gradient associated with nutrient levels rather than nested subsets (Figs 6 and 7). Finally, these gradients will consist of vulnerable taxa with low resource requirements in oligotrophic contexts and grazer-resistant taxa with high resource requirements in eutrophic contexts (Fig. 8).

The results of this study provide solid evidence for all four of these predictions (Table 4) with two major qualifications. First, although algal taxonomic richness was a unimodal or decreasing function of nutrient levels, analysis of diversity using Fisher's alpha showed no significant pattern related to nutrient levels for phytoplankton with this index of diversity. This seemed to be in part a consequence of individual samples that did not fit the assumption that population sizes within sites follow a logarithmic series. However, the analysis of Fisher's alpha did not contradict the analysis of species richness either. The relationship was also unimodal, even if it was not statistically significant. The joint results of the two analyses therefore provide qualified support for a unimodal relationship between diversity

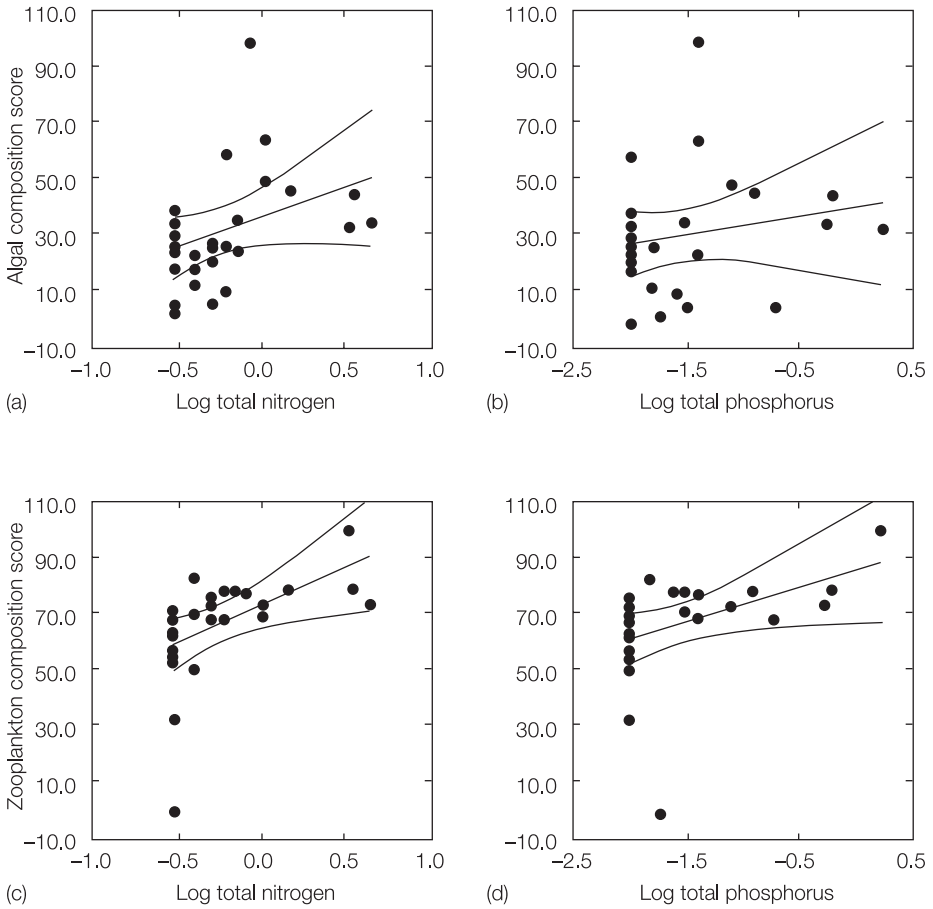

Fig. 6. Reciprocal-averaging ordination site scores from algal (a and b) and zooplankton (c and d) presence–absence data as related to the log of TN and TP nutrient levels. For algae, the correlation with TN is significant ($r^2 = 0.15$, $n = 30$, $P < 0.04$) but the correlation with TP is not ($r^2 = 0.05$, $n = 31$, $P < 0.3$). For zooplankton, the correlations with both TN ($r^2 = 0.28$, $n = 28$, $P < 0.005$) and with TP ($r^2 = 0.19$, $n = 29$, $P < 0.02$) are significant.

and nutrient levels, and certainly reject the hypothesis that algal diversity is a strictly increasing function of nutrients. In any case, zooplankton diversity showed a unimodal relation to nutrient levels in both analyses.

Second, phytoplankton patterns of composition and diversity are based on genus-level identifications, which may not necessarily reflect the same patterns that exist at the species level. However, it might be generally expected that there would be a strong correlation between generic richness and specific richness. If changes in species-to-genus ratios were to mask any of the findings described above, there would have to be a consistent change in the genus-to-species ratio in ponds correlated with different nutrient levels. For the data presented in Fig. 4, the increase in the species-to-genus ratio would have to increase two-fold from oligotrophic to eutrophic lakes to account for the observed decline in generic diversity without producing a similar decline in specific diversity at high productivity. Such an

Table 3. Nestedness metrics applied to algal and zooplankton distributions in the pond survey[a]

Variable and metric	Observed statistic	Expected statistic	Probability relative to null hypothesis
Algal genera			
N0 (Patterson and Atmar, 1986)	1064	1466	<0.01
C (Wright and Reeves, 1992)	3888	2028	<0.01
Zooplankton species			
N0 (Patterson and Atmar, 1986)	458	763	<0.01
C (Wright and Reeves, 1992)	1321	593	<0.01

[a] The statistical significance of the tests is compared with null expectations derived from Patterson and Atmar's (1986) least constrained random model (i.e. their RANDOM0 model) based on 200 iterations of the randomization algorithm. Both tests reveal significant 'nestedness' according to these metrics.

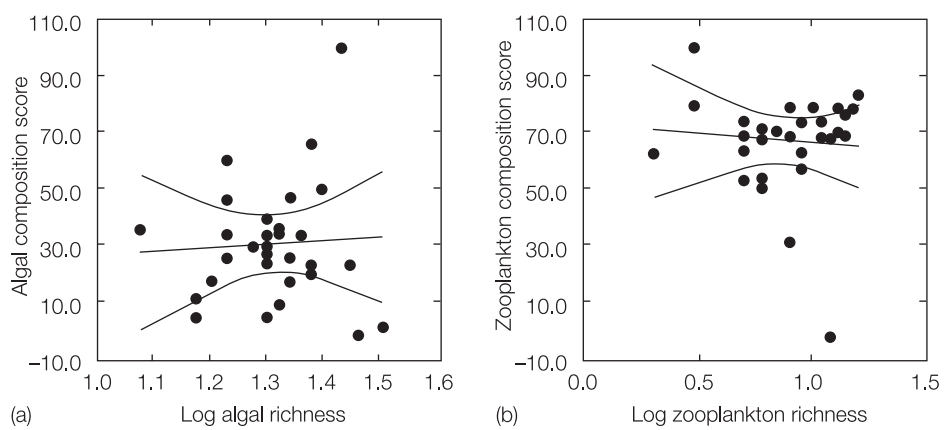

Fig. 7. Relationships between algal (a) and zooplankton (b) composition and diversity. Neither relationship is significant.

increase seems unlikely based on examinations of other studies (e.g. less than a 10% increase in the species-to-genus ratio of algae in Florida lakes over a >100-fold range of total phosphorus based on data in Taylor *et al.*, 1978).

Thus, with these caveats concerning diversity patterns in algae, the results described above indicate that biodiversity, densities and composition are all jointly associated with nutrient levels for both plants and herbivores in pond plankton communities as predicted by the keystone-predation hypothesis. A number of previous studies have documented each of these patterns but they have not previously been linked in a single analysis, nor have

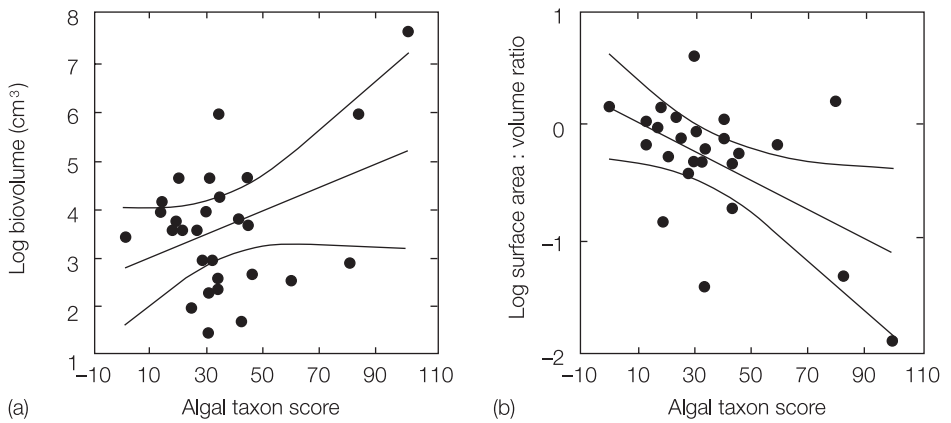

Fig. 8. Relationships between algal taxon scores from reciprocal averaging and log body size (cm^3) and surface area-to-volume ratios for algal taxa with available data (Reynolds, 1984). Relationships between the taxon scores and volume ($r^2 = 0.15$, $n = 28$, $P < 0.05$) and surface area-to-volume ratios ($r^2 = 0.28$, $n = 26$, $P < 0.01$) are both significant. The data indicate that algae with higher scores (found in more eutrophic ponds) are larger but have morphologies with lower surface area-to-volume ratios.

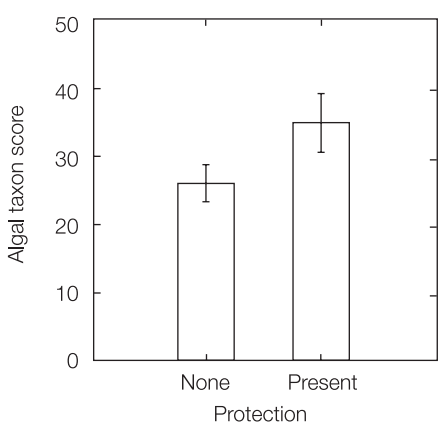

Fig. 9. Differences in algal taxon scores from reciprocal averaging and the occurrence of herbivore-resistant traits such as gelatinous sheaths, thickened cells walls, and spines. The difference is marginally significant ($t = 0.83$, $n = 80$, $P = 0.07$) and indicates that protected algae have higher scores and are found in more eutrophic lakes than unprotected algae.

comparative analyses of their relevance to community models of ecosystem enrichments often been made.

There is a large literature on responses of phytoplankton to nutrient enhancement through enhanced anthropogenic eutrophication (recently reviewed by Harper, 1992). Although many researchers have hypothesized that phytoplankton diversity declined along with the eutrophication of lakes (e.g. Hutchinson, 1967; Welch, 1980; Reynolds, 1984; Harris, 1986; Harper, 1992), the evidence has not always been particularly convincing (e.g. Lambou *et al.*, 1983; Eloranta, 1986). As argued by Rosenzweig (1992), this may be the result of the unimodal nature of the relationship as documented here and in two other

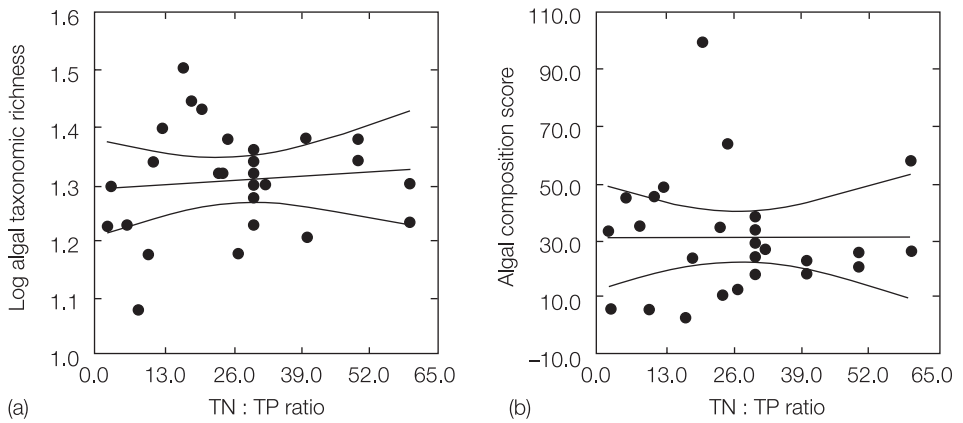

Fig. 10. Relations of log algal taxon richness (a) and algal taxonomic composition from reciprocal-averaging site scores (b) with the total nitrogen-to-phosphorus ratio of different ponds. Neither relationship is significant.

studies that related algal diversity in lakes to measures of plant biomass (e.g. Ogawa and Ichimura, 1984; Agusti *et al*., 1991). Most previous studies were conducted in larger lakes which characteristically have fish and most previous studies did not quantify relations between diversity and composition (but compare the results of Duarte *et al*., 1992, with those of Agusti *et al*., 1991). Explanations for the relation between diversity and eutrophication in lakes have mostly invoked the destabilization of predator–prey relations with zooplankton (i.e. the first model above), or the effects of nutrient supply on variability in relative resource supply ratios (the second model above), rather than the effects of grazers in allowing co-existence of competing algae.

More recently, Dodson (1992) also documented a non-linear effect of ecosystem productivity on zooplankton crustacean diversity, also in large lakes rather than the smaller fishless ponds considered here. Rotifers, which can be a significant portion of herbivore biomass and biodiversity, were not included in his survey of crustacean diversity. However, it is not clear if his findings indicate unimodal (rather than saturating) diversity curves. There are few previous conjectures about explanations for the relation between zooplankton diversity and eutrophication (Rosenzweig, 1995), although the loss of zooplankton diversity has occasionally been used as a means of evaluating the consequences of eutrophication and its effects on water quality (see Harper, 1992).

It is also fairly well documented that eutrophication is associated with parallel patterns of increased biomass in plants, herbivores and carnivores in lakes (e.g. McQueen *et al*., 1986; Mittelbach *et al*., 1988). These patterns are not easily explained by simple models of linear food chains (e.g. Oksanen *et al*., 1981). Previous explanations for these correlated patterns have often involved the role of 'inedible algae' in modifying the outcome of interactions between plants and herbivores (Walters *et al*., 1987; Leibold, 1989; Watson *et al*., 1992; reviewed by Power, 1992). However, in simple models of food web interactions in which algae are classified into edible versus inedible types, simultaneous increases in both plants and herbivores only occur under very limited conditions (Phillips, 1974; Leibold, 1989, 1996; Abrams, 1993). One possibility is that this dichotomous classification of plants may

Table 4. Summary of contrasting predictions from each of the four models and the findings of this study[a]

	Models				
Pattern	Paradox of enrichment	Resource variance	Resource ratio	Keystone-predation	Observed
PB *vs* EU	Positive	Positive	Positive	Positive	Positive*
HB *vs* EU	Positive	Not applicable	Not applicable	Positive	Positive
HB *vs* PB	Indeterminate	Not applicable	Not applicable	Positive	Positive*
PD *vs* EU	Indeterminate	Unimodal	Unimodal	Unimodal	Unimodal or declining*
HD *vs* EU	Unimodal	Not applicable	Not applicable	Unimodal	Unimodal*
PSD *vs* EU	Indeterminate	Nested	Gradient	Gradient	Gradient*
HSD *vs* EU	Indeterminate	Not applicable	Not applicable	Gradient	Gradient*
PT at low EU	Indeterminate	Generalists	Specialist on R1	Exploiters	Small, naked*
PT at high EU	Indeterminate	Generalists	Specialist on R2	Herbivore-resistant	Large, protected*
PD *vs* TN : TP	Indeterminate	Unimodal	Unimodal	Indeterminate	None
PSD *vs* TN : TP	Indeterminate	Indeterminate	Gradient	Indeterminate	None

[a] For the observed relations documented in this study, significant findings are denoted by asterisks. Most observations closely match the predictions of the keystone-predation hypothesis. *Abbreviations*: PB = plant biomass, HB = herbivore biomass, TN = total nitrogen, TP = total phosphorus, EU = degree of eutrophication (either TN or TP), PD = plant diversity, HD = herbivore diversity, PSD = pattern of plant species distribution, HSD = pattern of herbivore species distribution, PT = plant traits.

be too simple and that correlations of nutrient levels with both plant and herbivore densities may depend on the occurrence of taxonomic turnover associated with eutrophication (Leibold, 1996). This view of food web responses to eutrophication is supported by the results of this study and seems to occur for phytoplankton as well as for zooplankton (presumably as they relate to zooplanktivorous taxa not sampled in this study).

Finally, the sizes and morphologies of algal taxa found at contrasting nutrient levels indicate that large or protected taxa that are less vulnerable to grazers were found at high nutrient levels, whereas smaller unprotected algal taxa that are thought to require lower ambient nutrient and light levels were found at low nutrient levels. The shift in the size distribution in these ponds is similar to that found in many studies of larger lakes (Agusti *et al*., 1991). Larger algae (and perhaps especially those with morphological defences) are thought to have higher minimum nutrient requirements (primarily due to their low surface area-to-volume ratio), higher light requirements (due to self-shading) and higher loss rates due to sinking out of the euphotic zone (Reynolds, 1984). They also generally have lower maximum growth rates and maximum densities in cultures (Agusti *et al*., 1987; Reynolds, 1984). There are, however, two aspects of algae that might favour larger body size: increased resistance to grazers (Malone, 1980) and higher 'luxury uptake' of nutrients (uptake and storage of nutrients beyond those needed for immediate use) under temporally varying nutrient regimes (Malone, 1980; Grover, 1989). There is extensive evidence that there is higher grazing at higher nutrient levels (e.g. Sarnelle, 1992). However, evidence showing any relation between average nutrient levels and the amount of temporal variation in nutrient supply is equivocal (e.g. papers in Padisak *et al*., 1993). In this study, the shift to larger taxa and the occurrence of protected forms at higher nutrients therefore seems likely, at least in part, to relate to higher grazing as predicted by the keystone-predator hypothesis.

In many lake studies there is also a strong progression of different algal taxa, ranging from diatoms and dinoflagellates at low nutrient levels to green and then to blue-green algae at higher nutrient levels. This general progression is consistent with the notion that nutrient limitation changes from phosphorus to nitrogen (Smith, 1983; Canfield *et al*., 1985) as overall nutrient levels increase. This sequence is consistent with physiological data suggesting an underlying trade-off in minimum requirements for these two nutrients. In this study, no such associations between nutrient levels and the incidence (presence or absence) of species in major taxonomic groups were found. The role of nitrogen-to-phosphorus ratios in regulating algal diversity and composition in the context of the resource ratio model is further weakened by the lack of any correlations in composition or in diversity with TN : TP ratios measured in this study (Fig. 10). The taxonomic distributions are also inconsistent with the possibility of underlying trade-offs involving light limitation (as modelled by Huisman and Weissing, 1995), since the data indicate that larger and protected algae (thought to be poorer competitors for light due to self-shading; Malone, 1980) are more characteristic of high nutrient levels (*contra* the prediction of Huisman and Weissing, 1995). The most parsimonious conclusion from this analysis of ecological traits is that algal taxa that are typically found at high versus low nutrient levels reflect an underlying trade-off in resistance to grazers (favouring large, sheathed and colonial taxa) versus general resource competitive ability (favouring small, unprotected and motile taxa).

The results of this study are thus consistent with the keystone-predation model, but they can also be used to evaluate the other three models discussed in the Introduction (see Table 4). First, it seems that the data are clearly inconsistent with the 'resource heterogeneity

hypothesis' (the second model above), since the species distributions consist of gradient replacements rather than nested subsets. Although spatio-temporal variability is likely to enhance plankton diversity (Sommer, 1985; Grover, 1990), and although such variability is likely to be correlated with eutrophication (Padisak *et al*., 1993), any such effects seem to be less important in determining the relationship between diversity and nutrient levels in limnetic pond communities than are other mechanisms.

Second, the data provide relatively weak support for the 'paradox of enrichment' (the first model above) – at least if, after extinctions, phytoplankton are assumed to recolonize much faster than zooplankton. Under such conditions, in contrast with the prediction that nutrients should affect diversity of herbivores more than plants, the effects on zooplankton and algal diversity were very similar in relative magnitude and in their distribution along the nutrient gradient. Furthermore, in contrast with the prediction that phytoplankton density should respond less strongly to nutrient levels when zooplankton diversity is constant (i.e. near the peak of zooplankton diversity in Fig. 4), correlations between phytoplankton density and nutrient levels appeared to be largely independent of zooplankton diversity. If anything, the relationship between phytoplankton density and nutrients seemed steeper in this intermediate range in nutrient levels than at either of the extremes where zooplankton diversity was changing more strongly. These conclusions are reinforced by the observation in other studies (McCauley and Murdoch, 1987, 1990) that oscillations in algal biomass are not correlated with eutrophication.

Discriminating between the resource-ratio and keystone-predation hypotheses (the third and fourth models) using these data is more difficult. Both models make the same general predictions concerning the effects of nutrient levels on the density, diversity and species distribution patterns of plants and herbivores. However, there are two lines of evidence that distinguish these two hypotheses for algal taxa.

One way to distinguish the hypotheses comes from the traits of taxa that characterize high versus low nutrient environments. If the resource-ratio hypothesis is true, such species should contrast most strongly in their relative abilities to compete for alternative resources (e.g. minimum resource requirements for available phosphorus *vs* nitrogen). As discussed above, the evidence is much stronger in support of the keystone-predation hypothesis because there is no strong relationship between the presumed competitive abilities of major taxa for alternative nutrients or light and their distributions in oligotrophic versus eutrophic ponds as revealed by correlations between taxon scores and nutrient levels (Fig. 6).

Another way to distinguish the two hypotheses is to examine the availability of resources to phytoplankton (e.g. free available nutrient concentrations and light incidence) to see if they show any negative correlations with eutrophication. These variables were not measured in this study, but most published data sets do not show any such negative correlations among nutrient resource availabilities (Leibold, 1997). However, they do commonly show negative correlations between light availability and eutrophication. Thus, support for the resource-ratio hypothesis should be most closely related to the ability of algae to compete for nutrients versus light. However, generally positive correlations between resource availabilities and eutrophication are also to be expected under the keystone-predation hypothesis (Abrams, 1993; Leibold, 1996).

Definitive tests of these models will probably require an experimental approach. However, the data presented here provide substantial evidence against three of the models and provide support only for the keystone-predation hypothesis. They also show

that patterns of species diversity, population density and taxonomic composition of local communities in relation to eutrophication can be closely intertwined in natural (unmanipulated) ecosystems. These interrelated patterns are the raw materials available to help elucidate how natural communities that consist of complex, diverse, interacting organisms are affected by major environmental gradients. Ecological dynamics not modelled in the keystone-predation hypothesis involving alternative resources, disturbance and historical effects presumably all act to modify the distributions and diversity of organisms in ponds. Currently, the joint interactions among all these various processes have not been modelled. An important first step in such a synthesis is to identify the processes most likely to be the strongest influences on community structure. The results presented here illustrate that the keystone-predation hypothesis may be very important in elucidating how complex pond communities are affected by gradients in nutrient levels.

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