USING MULTIPLE TAXONOMIC GROUPS TO INDEX THE ECOLOGICAL CONDITION OF LAKES

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Abstract. Biological indicators of communities typically reflect a common environmental signal reflecting the general condition of the ecosystem, as well as individual signals by indicators differentially sensitive to particular environmental conditions. We describe here a method of integrating and interpreting such indicators from 19 New England lakes for five taxonomic groups (diatoms, benthos, zooplankton, fish, and birds). Our approach provides a systematic standardized way to integrate multiple metrics from different taxonomic groups by addressing four elements crucial to analyzing data from multiple indicators: covariate control, re-scaling of data, standardizing the sign of responses, and dimensional reduction. We evaluated the biological metrics against individual environmental stressors and against multivariate physicochemical metrics characterizing general anthropogenic stress among the lakes. The method detected a response to variation in the gross environmental condition of the lakes that was correlated across taxa and metrics. In addition, a differential response to near shore conditions was demonstrated for fish. The success of the approach in this study lends support to its general application to ecological monitoring involving complex data sets.

Keywords: benthos, birds, diatoms, ecological indicators, integrated assessment, fish, lakes, monitoring, zooplankton

1. Introduction

Increased interest in ecosystem health and integrity has created a need for new approaches in assessing ecosystem conditions. Traditional ecological indicators have focused on one of three distinct approaches (Landres *et al.*, 1988): detecting the presence and effects of environmental contaminants; tracking population trends of indicator species; and assessing physical habitat quality for species. The considerable success of contaminant monitoring programs in identifying and remedying pollution, particularly in aquatic systems, led to an early emphasis on chemical monitoring (Ellis, 1937; Hynes, 1960). An indicator species approach has been popular among biologists concerned with individual sport fisheries (e.g., Edwards *et al.*, 1990) and has also been used commonly in toxicity tests (Warren, 1971). More recently, physical habitat structure has received considerable attention (Platts *et al.*, 1983; Plafkin *et al.*, 1989; Kaufmann and Robison 1998) as water quality has improved following implementation of the Clean Water Act.

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Karr (1993) and Fausch *et al.* (1990) review two key issues involved in taking a wider view of the assessment of ecosystem integrity. First, they note that assessment intrinsically requires comparison of the observed state against an expected condition for the resource of interest. These expected conditions vary geographically, and need to be defined in terms of the multivariate nature of complex biological systems. Second, assessment of ecological condition must also incorporate evaluation of relevant biological attributes (although knowledge of physical and chemical conditions typically remain essential for diagnosing cause-and-effect (Moss *et al.*, 1996)). Such multiple requirements will not be met by any single ecological indicator. Yoder and Rankin (1998) reported that biological criteria identified impairment of aquatic life in 50% of the cases where chemical criteria did not. Given the favorable cost-effectiveness of biological monitoring (Yoder and Rankin, 1998), a suitably chosen suite of biological indicators might be the best basis on which to assess ecological condition.

Karr (1981) proposed assessing biological integrity through use of multiple metrics from fish assemblages. This approach has become popular for stream fishes (Miller *et al.*, 1988; Simon and Lyons, 1995; Hughes and Oberdorff, 1998) and has also been adapted for stream benthic macroinvertebrates (Kerans and Karr, 1994; Fore *et al.*, 1996). However, the approach is little used for lake fishes (Dionne and Karr, 1992; Minns *et al.*, 1994) and has not been used to date to integrate indicator information from multiple taxonomic groups. Although integrating several metrics has many advantages over the indicator species approach (Hunsaker and Carpenter, 1990; Landres *et al.*, 1988), Karr (1993) identified several research needs that must be addressed before this can be done effectively. Among the gaps identified, and the objectives of this paper, are development and testing of improved indices of biotic integrity, use of multiple taxonomic groups, and expansion of multimetric indices to lakes.

We address issues in the integration and interpretation of data from multiple taxonomic groups. In particular, use of a suite of multiple biological assemblages or taxonomic groups requires discriminating between two possible extreme outcomes: (1) a completely correlated response by all indicators to some generalized anthropogenic stress, or (2) completely divergent responses by individual indicators each differentially sensitive to particular stressors. We describe a systematic approach to partitioning the effects of redundancy and selectivity when an array of metrics from multiple taxonomic groups is available. The method does not prescribe which metrics and taxonomic groups belong in a final suite of indicators, except that redundancy between metrics and low responsiveness to all stressors are causes for rejection.

2. *Sources of Prototype Data*

Nineteen lakes of varied size and temperature regime were selected in the northeast USA to evaluate sampling methods for diatoms, benthos, zooplankton, fish, and birds (Larsen and Christie, 1993). The goal of this fieldwork was to develop standardized sampling methods applicable to the wide range of lake types and sizes expected in subsequent regional studies. Lakes were chosen along selected disturbance gradients to maximize the environmental range to which candidate indicators were exposed. A different person was responsible for developing metrics for each taxonomic group. The initial guidance to each taxonomic specialist was to develop candidate metrics that were of ecological importance, that would be responsive to anthropogenic disturbance, and whose sampling variances at a site would be less than the variances among sites. The metrics considered were exploratory but are suitable for demonstrating our analytical approach. Biological interpretations and conclusions about the lakes are dependent on the choice of indicators, but our goal in this paper is simply to demonstrate how data from any ecosystem might be analyzed for environmental signals.

2.1. Diatoms

The abundance and composition of diatom assemblages in lakes are strongly correlated with gradients in environmental factors, notably pH and nutrients (Dixit *et al.*, 1992, 1999). These relationships have allowed inferences of the trophic and ionic histories of lakes and about the effects of changing land use (Dixit *et al.*, 1999). We sampled sedimentary diatoms at the deepest point in the lake through use of a sediment corer (Baker *et al.*, 1997). The tops and bottoms of the cores were removed, dated, and cleared of organic matter; the remaining silicaceous diatom frustules were placed on a slide and counted. Six metrics were examined: 1) inferred chloride concentration change, 2) inferred phosphorus concentration change, 3) an index of the historical change in diatom flora over the past 150 yr, 4) change in richness over time, 5) contemporary species richness, and 6) a disturbance index (Table I). The first four metrics indexed the relative amount of change in particular lakes, richness indicated a key component of biodiversity, and the disturbance index incorporated rankings of the preceding metrics.

2.2. Benthos

Substrate conditions govern the types of benthos present and contaminants in lake sediments enter the food chain via benthic detritivores. Monitoring the benthos thus focuses on a potentially critical gateway to the integrity of the larger ecosystem. Death (1996) showed that the dominant benthic taxa changed markedly with changes in the condition of lakes. In our study, benthos were collected by petit Ponar dredge from the deepest point of the lake and by timed dip net sweeps in

TABLE I

Results of a principal components analysis of candidate biological metrics for lakes. Codes in the lefthand column are used in Figure 3.

	Biological metric	BPC1	BPC2	BPC3
	Percent variance	36.26	12.79	11.83
	Eigenvalue	10.52	3.71	3.43
	Significance (P)	0.001	0.40	0.10
Means				
M1	Mean of assemblage averages	0.976	–0.001	0.005
M2	Unweighted metric average	0.960	0.007	0.005
Benthos				
B1	Metric average	0.567	0.085	–0.018
B2	% individuals as dominant taxon	0.305	0.014	0.019
B3	Benthos biotic index	0.585	0.013	–0.002
B4	Individuals per taxon	0.168	0.087	0.015
B5	Taxa richness	0.118	0.018	–0.203
Birds				
A1	Metric average	0.768	0.073	–0.078
A2	Number of intolerant species	0.339	0.087	–0.099
A3	Bird PCA axis 1	0.778	0.000	–0.109
A4	Species richness	0.001	0.127	0.000
A5	Number of tolerant species	0.745	0.013	–0.009
Diatoms				
D1	Metric average	0.554	–0.381	0.018
D2	Inferred chloride change	0.553	–0.164	–0.007
D3	Difference in past versus present assemblages	0.320	–0.145	0.065
D4	Biotic index	0.381	–0.407	0.010
D5	Inferred total phosphorus change	0.420	–0.193	0.002
D6	Richness change	0.078	–0.434	0.148
D7	Assemblage richness	0.341	–0.299	0.050
Fish				
F1	Metric average	0.343	0.103	0.071
F2	% intolerant species	0.249	0.145	–0.220
F3	% omnivores	0.140	–0.064	–0.479
F4	% piscivores	–0.004	0.077	0.030
F5	Native species richness	0.152	0.126	0.540
F6	Total species richness	–0.000	0.024	0.647
Zooplankton				
Z1	Metric average	0.221	0.180	0.177
Z2	Size ratio	0.225	0.229	–0.000
Z3	Trophic links	0.222	0.194	0.230
Z4	Species richness	–0.004	–0.019	0.177

littoral areas (Baker *et al.*, 1997). The entire sample was processed and the organisms identified to the lowest possible taxon. Four metrics were used (Table I): the richness of the benthic assemblage, the proportional dominance of the commonest taxon, the average number of individuals per taxon, and a multimetric index of benthic integrity (modified from Plafkin *et al.*, 1989). These metrics assessed the diversity of the benthic fauna and the relative redundancy of its taxa, and provided an integrated measure of benthic integrity.

2.3. Zooplankton

Zooplankton show considerable sensitivity to environmental conditions as well as rapid response to changes in environmental quality (Stemberger and Lazorchak, 1994). Eutrophication has a marked effect on the size distribution of zooplankton assemblages (Stemberger and Miller, 1998) and zooplankton become highly contaminated by persistent pollutants (Thome *et al.*, 1993). Zooplankton were collected with a single vertical tow beginning 0.5 m from the bottom at the lake's deepest area (Baker *et al.*, 1997). Two nets were towed slowly to collect both macrozooplankton and microzooplankton; both sizes were identified to species. Just three zooplankton metrics were considered: richness, size ratio, and number of trophic links. Species richness was of interest for its own sake, the ratio of large to small zooplankton was a measure of dominance of the small forms that increased with disturbance, and the trophic links metric evaluated trophic specialization and complexity.

2.4. Fish

Karr (1981) developed his index of biotic integrity from fish data. Native lake fish have been shown to be sensitive to alien fishes, altered piscivore populations, degraded water quality and physical habitat structure, exploitation, and watershed disturbance (Smith, 1968; Minns *et al.*, 1994; Whittier *et al.*, 1997; Whittier and Hughes, 1998). In our research, fish were sampled in both the pelagic and littoral zones with a variety of gear (electrofishing, gill nets, trap nets, seines, minnow traps; Baker *et al.*, 1997). All individuals captured were identified to species. Five metrics were considered: total richness, native species richness, and the proportions of species that were respectively intolerant of general human disturbance, omnivorous, or piscivorous. Species richness was considered an important component of diversity, while intolerant species were those that generally disappeared with general anthropogenic disturbances. Omnivores and piscivores were measures of the effects of trophic changes on the fish assemblage.

2.5. Birds

Birds have been used in detecting effects of environmental contaminants (Cramp and Conder, 1961; Hickey, 1969) and broad-scale habitat changes (O'Connor and Shrubb, 1986; Croonquist and Brooks, 1991). We took bird point counts during

TABLE II

Results of a principal component analysis of selected lake habitat variables

Environmental variable	EPC1	EPC2
% Variance	38.890	16.861
Eigenvalue	6.611	2.866
Significance (P)	0.001	0.07
Chloride concentration	0.831	0.141
% of catchment urban	0.782	–0.296
Shoreline disturbance rank	0.765	0.559
% of catchment forest	–0.756	0.329
Total phosphorus concentration	0.751	–0.324
Road density rank	0.750	–0.355
Chlorophyll-a concentration	0.711	–0.503
Pollution and population rank	0.709	0.099
Riparian disturbance per site	0.689	0.603
Mean Secchi depth	–0.617	0.294
Natural fish cover per site[a]	–0.596	–0.207
% shoreline in natural riparian forest	–0.539	–0.453
Maximum depth	–0.455	0.312
% littoral macrophyte coverage	0.336	0.703
% lake area <3 m deep	0.330	–0.039
% of catchment agriculture	0.298	0.161
Shoreline complexity[b]	0.004	0.726

[a] The average number of different types (plants, overhanging vegetation, snags, boulders).
[b] Ratio of the lake perimeter to the perimeter of a circle of the same area as the lake.

the height of the breeding season along a transect 10 m from and parallel to shore (Baker *et al.*, 1997). Counts were made around small lakes every 200 m; on lakes with perimeters >4.8 km, 24 counts were spaced at least 200 m apart and were distributed in proportion to habitat types along the shore. Surveys were conducted from 30 min before sunrise to 4 h after sunrise. At each stop, all birds seen or heard within 100 m were identified to species. The bird metrics considered were total species richness, number of intolerant species, number of tolerant species, and a multivariate metric devised by Moors (1993). Richness and intolerant species were examined for reasons explained above; tolerant birds were defined as those that generally increased in disturbed areas, while the multivariate metric integrated bird foraging and migratory guilds.

2.6. Environmental variables

Moss *et al.* (1996) provide a detailed rationale for the use of multiple physical and chemical variables in characterizing the environmental quality of lakes. In addition, because lakes are products of their catchments, we collected ancillary land use and landscape information from available digital data bases (Table II). Thus in our study, environmental data included numerous water quality, nearshore physical habitat, riparian, and catchment variables (Baker *et al.* 1997). Macrophyte coverage, Secchi depth, and chlorophyll and phosphorus concentrations were measures of eutrophication. Shore line complexity, riparian forest, and fish cover provided positive estimates of physical habitat integrity while shore line and riparian disturbance offered negative estimates. Lake area and depth were used to control for size effects on species richness. At the catchment scale, the percentages of urban and of agricultural land present, road and population densities, chloride concentration and pollution sources were used to estimate disturbance while the percentage of land in forest did the opposite.

3. Index Development

Our approach was based on four components: 1) covariate control 2) re-scaling of data 3) standardizing the sign of responses, and 4) dimensional reduction.

3.1. Covariate control

Ecological indicator data reflect two sources of variation: direct or indirect effects of stressors, and effects of natural covariates essentially irrelevant to monitoring the effects of humans. Climate and habitat extent are common natural covariates; in the present study lake area offered a measure of habitat extent and temperature class distinguished cold and warm water lakes. From island biogeography theory, species richness would be expected to increase with lake size (MacArthur and Wilson, 1967). In addition, our sampling effort for birds and fish increased with lake size. We therefore used regression analysis to check all richness metrics for variation with lake size, with temperature class, and with their interaction. Species richness for fish and for zooplankton were both affected by lake area (fish richness = $2.13 * \log(\text{area})$; zooplankton richness = $16.646 + 2.771 * \log(\text{area})$). To remove purely size effects, we therefore corrected fish and zooplankton for lake area using the above equations. The remaining richness metrics showed no temperature or size effect.

3.2. Metric re-scaling

The different metrics (Table I) involved different units. In addition, many were non-normally distributed, either through skewness or outliers, making most normalizing transformations ineffective. We scaled all metrics by dividing the deviation of each datum from the metric median by the interquartile range of the metric. In addition, since some outliers led to very large values even on this transformation, we trimmed the sample values by replacing extreme outliers (transform value greater than 5) with the value 5. As a result, all metrics had a similar range of numerical values and similarly scaled response curves against environmental factors. For normally distributed or transformed data, z-scores (Zar, 1984) could have been used. A standardized rank might also have offered advantages over the scoring adopted here, but would not have discriminated lakes as clearly.

3.3. Standardizing response sign

Some metrics responded positively while others decreased in response to a given stressor. To standardize response direction we reversed the sign of all metrics that responded positively to environmental impact so that all metrics decreased with increasing impact. For metrics that did not give a monotonic response, we characterized the predominant direction.

3.4. Dimensional reduction

Given the multiplicity of assemblages and metrics, we applied multimetric and multivariate analyses to try to synthesize results into a coherent assessment. We calculated a multimetric index for each taxonomic group and computed an overall (across all taxonomic groups) lake metric by averaging the 22 individual metrics. One problem with this last measure was that different taxa were represented differentially, e.g., by six metrics for diatoms but by only three for zooplankton. We therefore also computed a second multiple group metric by averaging the averages of the five taxonomic groups, thus giving equal weight to each taxonomic group.

Many of the metrics were highly correlated and we had more biological metrics (29) than lakes (19) and nearly as many environmental metrics (17). We therefore used principal components analysis (PCA) to identify patterns of covariation and independent variation in the data. The analyses were performed on the correlation matrix and scores on each PCA axis were computed for each lake (Tables I and II). Because of the power of PCA to extract apparently meaningful patterns in data even when the source is noise (Rexstad *et al.*, 1988), we used simulation to help discriminate against noise. We conducted 10 000 simulations using random normal numbers for 19 x 17 and 19 x 29 cases x metrics, computed the correlation matrices, conducted PCA on the random matrices, and ordered them from largest to smallest. From the ordered components, we produced tables of appropriate points in the arrays that were associated with commonly used significance values (0.001, 0.01, 0.05, 0.10) and then compared these with the PCA results from the lake data. Using $P = 0.10$ as a significance cutoff and constraining subsequent components by the correlation structure of preceding components, we determined which of our biological and environmental components were significantly different from random expectations.

4. Metric Evaluation

Multivariate and multimetric biological indices are frequently proposed without careful evaluation of their responsiveness to disturbance or environmental variables. The effectiveness of our synoptic biological metrics was evaluated against the first and second environmental principal components (EPC1 and EPC2) derived from 17 environmental variables (Table II). We also computed the gross environmental index (GEI) of Larsen and Christie (1993) by ranking each lake in relation to the particular environmental conditions they used, then summing these ranks. The lake GEI incorporated ranks of shoreline disturbance, the percentages of the catchment land that were urban or agricultural, road density, point source pollution, and human population density. This GEI therefore constituted a crude synoptic index of the aggregate conditions, with higher scores signifying lower environmental integrity.

Because of the small sample size and non-random selection of lakes, this paper is intended as a demonstration of procedure and not as the outcome of a statistically designed study. Neither did the metrics considered comprise all those that should be evaluated in a monitoring program. The metrics merely provided a means of demonstrating how to resolve issues likely to arise in the development of a multiple taxonomic group approach to indicators and to ecological assessment. Similarly the biological conclusions used as examples herein are not meant to be conclusive. What is robust is the usefulness of our approach, with the validity of empirical conclusions turning on the study design and quality of the data and metrics used in future applications.

5. Results

5.1. Structure of the Multi-Taxon Indices

We examined the responsiveness of candidate metrics by plotting them against our gross environmental index (GEI) of each lake. Figure 1 shows the results for the five bird metrics. The bird PCA and the tolerant species metrics showed slower rates of change initially and a more rapid response beyond a GEI rank of 10 (Figure 1a and c). The intolerant species metric decreased rapidly in the less disturbed lakes and more slowly with increased disturbance (higher GEI; Figure 1b). Total bird species richness showed no clear pattern (Figure 1d). The average of the four individual bird metrics showed a generally negative trend and lower residuals than its component metrics (Figure 1e). Thus for birds the set of metrics tested included

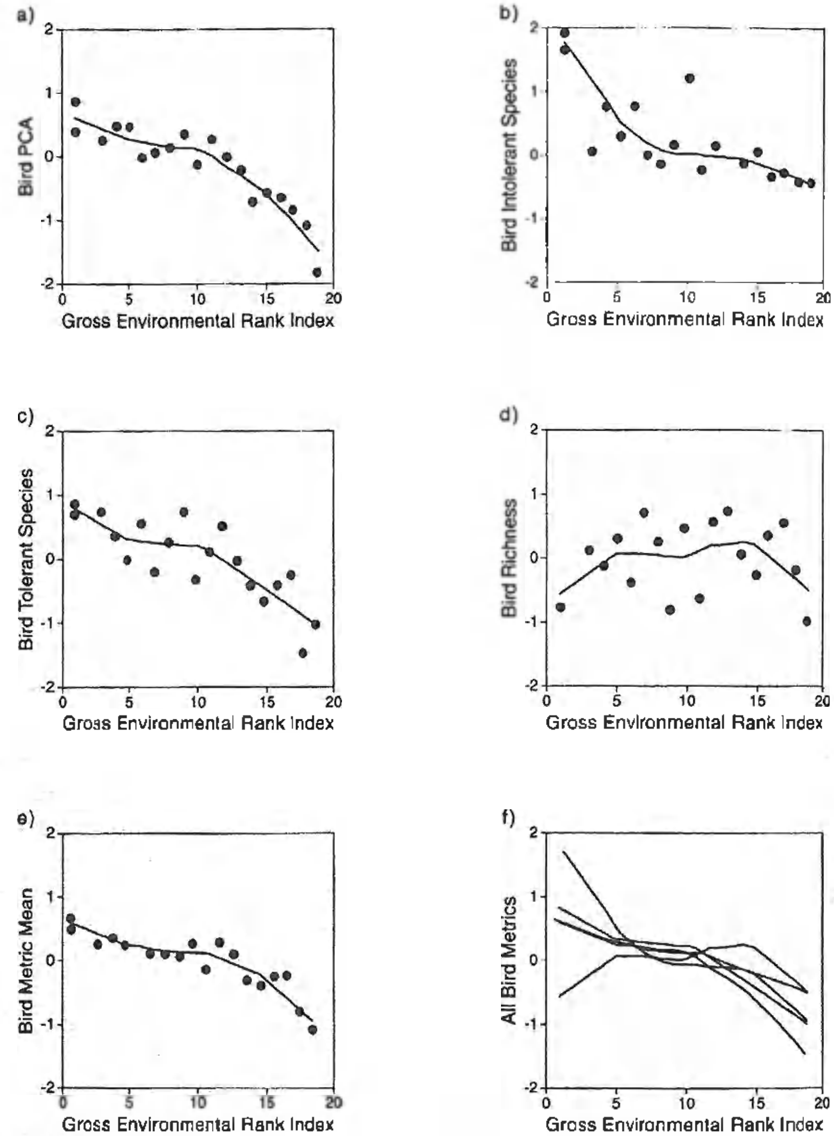

Figure 1. Bird metrics for 19 northeastern U.S. lakes in relation to the gross environmental index of Larsen and Christie (1993) for each lake. The y-axes have been standardized in terms of the interquartile ranges of each variable and for consistency in sign of response (negative) with increase in environmental stress, as described in the text. The curves are LOWESS locally weighted smooths: a) guild-based principal component axis indicator from Moors (1993), b) the number of species present that are known to be intolerant of general anthropogenic disturbance, c) the number of tolerant species present, d) the total number of species recorded at each lake, e) the average for each lake of the indicator values in a–d, and f) curves a–e overlaid on common axes.

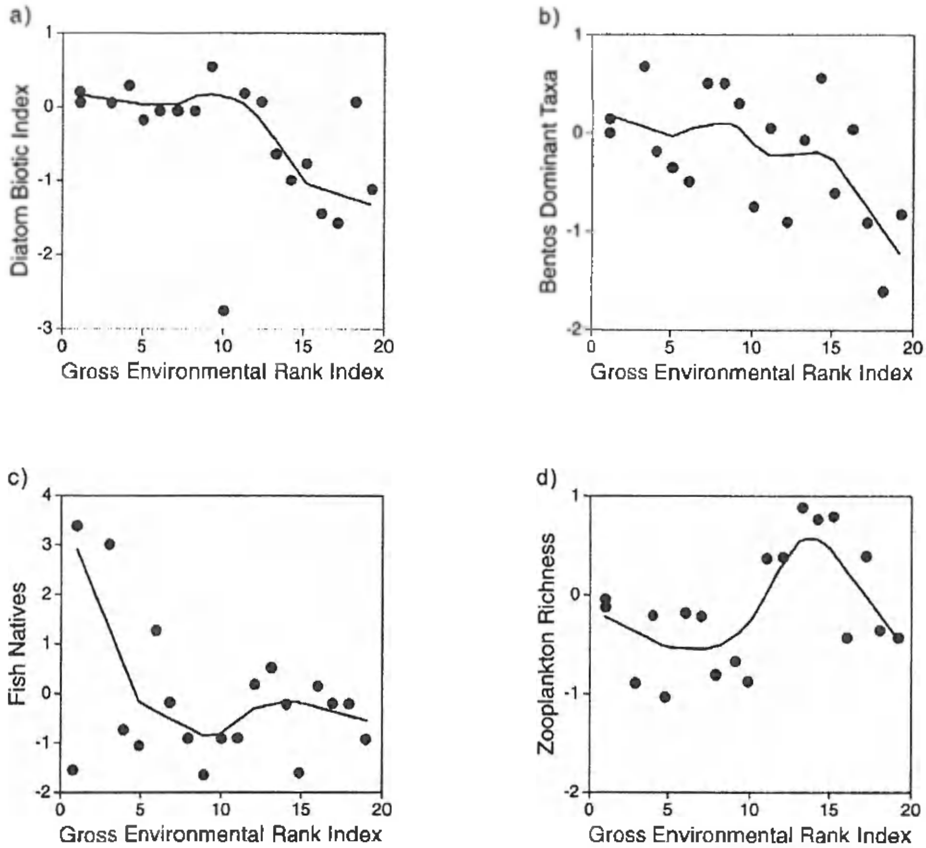

Figure 2. Selected metrics in relation to the gross environmental index (Larsen and Christie, 1993) for 19 lakes in the northeastern U.S. The y-axes and curves are standardized as in Figure 1; a) diatom biotic index, b) dominance of commonest benthos taxon, c) native fish species richness, and d) zooplankton species richness.

one that was sensitive to minimal impact, two that were most sensitive at higher levels of disturbance, and another that was moderately sensitive along the entire disturbance gradient. These are desirable features for a set of metrics regardless of taxonomic group. Bird species richness appeared to be a poor indicator of environmental disturbance, which is an undesirable feature for a metric intended for assessing ecological integrity. We also superimposed the five curves, to allow comparison of the different rates of metric responses, particularly above and below a GEI value around ten (Figure 1f).

Similar patterns were apparent in the metrics for the other four taxonomic groups, selected examples of which are shown in Figure 2. The diatom biotic index showed a generally flat response until intermediate levels of human impacts were exceeded at a GEI value around ten, after which it declined precipitously (Figure 2a). The benthos metric depicting dominance of a single taxon showed a

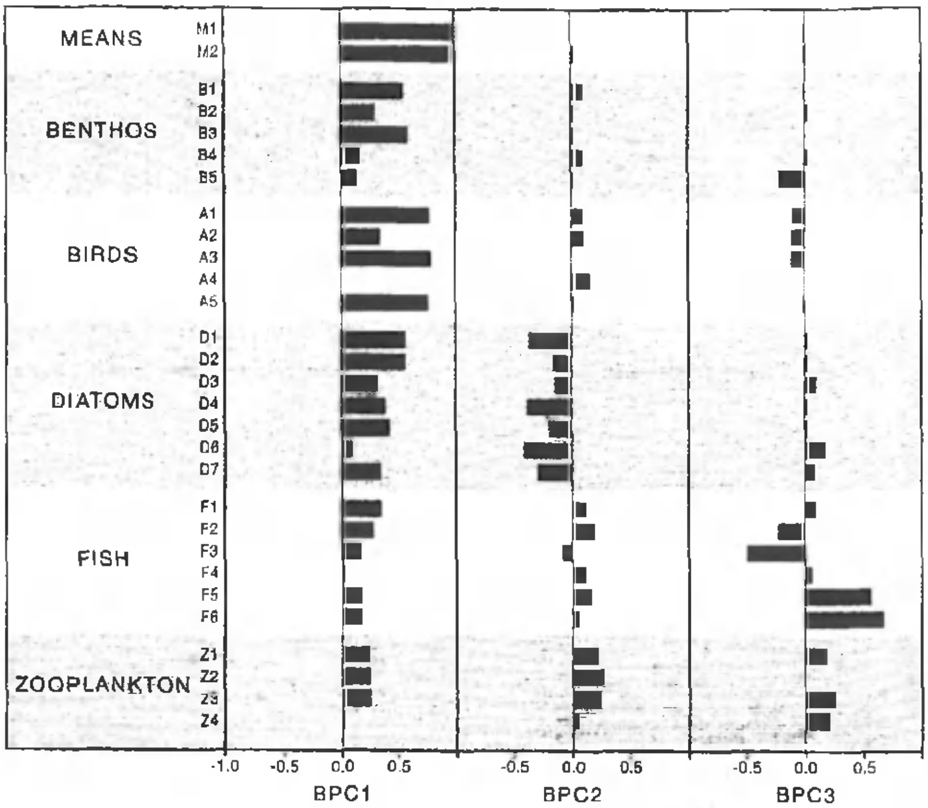

Figure 3. Loadings for the first three biological principal component axes. For a key to the variables see Table I.

slow decline until a GEI value of about 15 was reached, after which it steepened sharply (Figure 2b). In contrast, the native fish species metric decreased steeply across a GEI of 1-6 and then remained relatively constant with increased disturbance (Figure 2c). The zooplankton richness metric declined very slowly at first, then increased steeply until a value of 15, beyond which it decreased (Figure 2d). As with the bird examples, metrics for these four taxonomic groups were variable in detail, including metrics that were sensitive at low disturbance levels, at high levels, or not at all.

The 29 biological metrics were combined in a principal component analysis (Table I). The first biological PCA axis (BPC1, Figure 3) accounted for 36.3% of the variance, had a P of 0.001, and was heavily weighted on the two community means (the mean of the assemblage averages and the unweighted average of all metric values). In addition, large contributions came from the mean metric average for each taxonomic group except zooplankton, as well as from some other metrics. All loadings were positive. We believe the BPC1 score reflected the extent to which the entire biotic community of a lake responded to multiple natural and

TABLE III

Spearman rank correlations between biological (Table I) and environmental (Table II) principal component scores. The environmental axes, although computed as principal component axes, have been characterized with descriptive terms for the sake of clarity. The Gross Environment Index (GEI) is the environmental rank metric from Larsen and Christie (1993). Significant correlates are denoted by: one asterisk ($P < 0.05$) and two asterisks ($P < 0.01$)

Environmental factors	BPC1	BPC2	BPC3
Anthropogenic stress (EPC 1)	−0.788**	0.014	0.004
Riparian/Littoral condition (EPC 2)	0.005	−0.089	0.479*
Gross environmental index (GEI)	−0.856**	−0.118	0.105

anthropogenic stressors. The second component was non-significant (eigenvalue 3.71, critical value for alpha of 0.1 = 3.98) and its apparent structure – largely involving diatom metrics – could not be discriminated reliably from data noise (Table I, Figure 3). The third biological component, BPC3, had a P of 0.10 (Table I, Figure 3) and accounted for 11.8% of the variance. It was dominated by fish metrics, primarily increased omnivores (which had had a sign reversal), number of native species and overall species richness. The remaining biological components did not differ significantly from our random numbers PCAs.

5.2. Evaluation of the Multi-Taxon Indices

We considered the environmental PCA scores and GEI index to be multivariate stressor indicators that reflected multiple kinds and patterns of stressors. We therefore examined the relationships of our biological scores BPC1 (the lake biotic community) and BPC3 (the lake fish assemblage) to them. Only the first two environmental PCA axes (EPC1 and EPC2) were significantly different from random at a $P < 0.1$ (Table II). EPC1 accounted for 38.9% of the variance and reflected general human disturbance and modification of the shoreline and watershed. EPC2 accounted for 16.9% of the variance and largely reflected the riparian and littoral disturbance and fish cover of the lakes.

We found a strong negative correlation between BPC1 and EPC1 (Spearman rank correlation $r = -0.788$, $P < 0.001$; Table III) and interpreted this relationship as a generalized disturbance to which there was a generalized negative response by all five taxonomic groups sampled (Figure 4). In contrast, the BPC1 score was completely independent of the riparian and littoral condition captured for each lake in the environmental EPC2 score ($r = 0.005$, not significant; Table III). Conversely, the biological PC3 score was independent of the general environmental stress captured in the EPC1 score (0.004, not significant; Table III) but increased

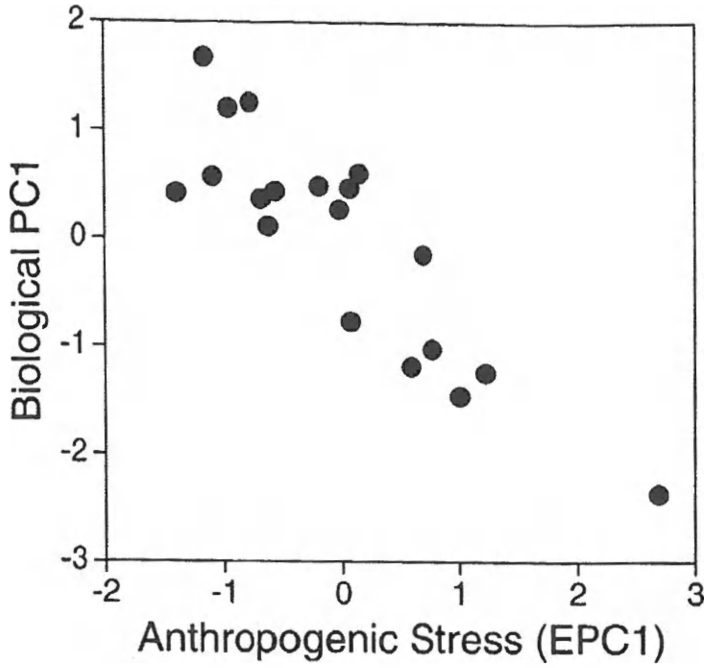

Figure 4. Scores on the first principal component axis for the biological dataset (BPC 1) – interpreted here as indexing general biological integrity in each lake – relative to an index of anthropogenic stress (EPC1) on the lake.

with EPC2 ($r = 0.479$, $P < 0.05$; Figure 5). This suggests that more fish species and more omnivorous individuals were present in lakes with complex shorelines, dense aquatic macrophyte cover, and additional riparian and shoreline disturbance (Tables I and II). This relationship, however, was considerably weaker than that between BPC1 and EPC1, as indicated by the lower correlation and greater scatter (Table III; Figure 5). None of the environmental measures proved correlated with the potentially pure noise BPC2 values (Table III).

The results for the general environmental stress measure EPC1 were paralleled by those involving the Larsen-Christie GEI index (Table III). BPC1 (the general index of biological stress) was highly correlated (-0.856, $P < 0.001$; Table III; Figure 6) with the GEI and had negligible correlation with the BPC3 value. This suggests that BPC3 (the fish indicator) was linked to fish-specific habitat structure rather than to gross or integrated stressors.

6. Discussion

A major issue in the development of ecological indicators is the extent of redundancy among metrics or taxonomic groups requiring individually distinct sampling

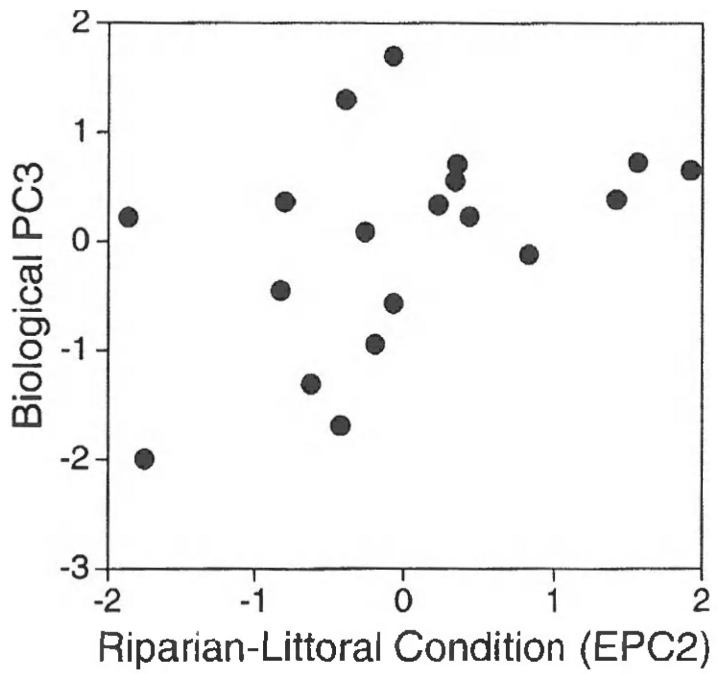

Figure 5. An index of fish integrity (score on biological principal component BPC 3) in relation to the second principal component of the environmental data EPC2, interpreted here as an index of the riparian and littoral condition of the lake (positive scores indicate complex but disturbed shorelines).

procedures (Suter, 1993; Cairns *et al.*, 1993). Although some redundancy is useful, the presence of mutually highly correlated indicators is not cost-effective (Karr *et al.*, 1986). On the other hand, an array of metrics and taxonomic groups protects against not detecting unanticipated environmental insults, especially if individual metrics and groups are differentially sensitive to different anthropogenic stressors. Our results provide some indication of how metric redundancy might be evaluated objectively.

Candidate indicators are often compared against some measure of generic stress (Larsen and Christie, 1993). In the present analysis, there was strong correlation between two general stressor indexes (EPC1, GEI) and the general response of the biotic variables (BPC1; Figures 4 and 6). The composition of this generalized biological response involved all the assemblage average responses we computed except that for zooplankton metrics (Table I). This suggests three issues are involved. First, individual metrics for particular taxonomic groups reflected differential responses that collectively averaged out to a general stress response. Second, the bird and diatom metrics appeared to be better integrators of disturbance than those of the other assemblages: the bird and diatom loadings on BPC1 were higher (Table I) and had large negative correlations with EPC1 and GEI (Table III). This ability to integrate multiple stressors is another characteristic of a useful indi-

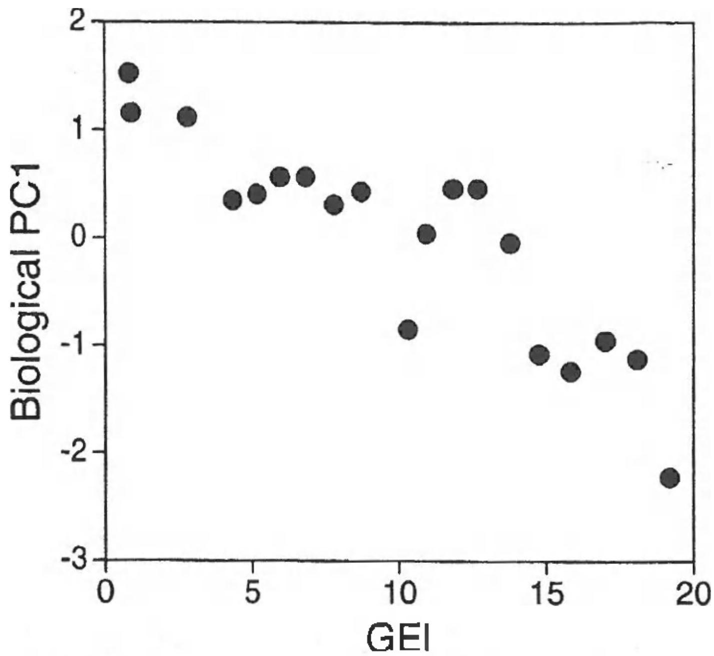

Figure 6. The biological principal component score indexing the general biological integrity of each lake (BPC1) in relation to the gross environmental index (GEI) of Larsen and Christie (1993) for the lake.

cator (Hughes *et al.*, 1998). Third, the benthos, fish, and zooplankton assemblages need the development of further metrics if these groups are to be useful in assessing biotic effects of general anthropogenic stress on lakes.

In contrast to the shared response across taxonomic groups to general stress, group-specific responses were differentially associated with particular stressors. In our data set, several biological and environmental principal components were correlated, suggesting considerable differential sensitivity among particular biotic assemblages and environmental factors. We do not discuss these here since the small sample size and large variances did not provide sufficient robustness to demonstrate significant difference from noise alone. In our study, only the fish-dominated BPC3 score was correlated strongly enough with shoreline fish cover and disturbance (EPC2) to reject the noise alternative. A larger data set and better-developed metrics are likely to produce more responsive metrics, which would be valuable for investigating causal relationships between specific environmental factors and specific biotic responses or assemblages.

A key aspect of indicator suitability for assemblage and community assessments was revealed by comparing principal component scores from lakes with those from random numbers. As noted, only four principal components (BPC1, BPC3, EPC1, and EPC2) were significantly different, at $P \leq 0.10$, from what one would expect on evaluating a random set of numbers representing the same number of sites and variables. This comparison indicated that merely having an eigenvalue > 1 and loadings >0.3, as commonly believed, is insufficient reason to assume that the principal component concerned was a useful indicator. Most of the other components could not be distinguished from noise. We therefore recommend comparing eigenvalues from PCAs run on ecological data with those obtained from using random numbers, at least for small data sets. For example, we generated eigenvalues > 1 for five components over 50% of the time from purely random numbers. Bootstrapping may be preferable with large data sets.

As Fausch *et al.* (1990) and Karr (1993) have argued, our expectations for metrics must be adjusted to account for geographical variation. For example, there are more tolerant species in the avifauna of southern New England than of northern New England, thus creating a parallel between tolerance and human population density. Consequently, impact may appear greater on southern lakes simply because of their location where the number of tolerant species is high and the number of intolerant species is low. In such a situation it is difficult to discern whether the correlation of tolerance with stressors is causal or an effect of biogeography. Such problems with indicators must be resolved before they can be applied across large regions (Allen *et al.*, in press).

Another aspect of our results reinforces this need to adjust expectations to accommodate variation in natural environmental conditions. The fish-dominated BPC3 was highly correlated with the extent of the littoral zone and with the maximum depth of the lake (EPC2) which in New England are largely measures of the natural morphology of the lakes rather than of anthropogenic effects. The natural area, depth, and fish cover of lakes govern the distribution and abundance of fish (and presumably of other assemblages): larger lakes support more species than small ones, while deeper lakes open to thermocline effects may support both warm water and cold water fish assemblages. Larger and deeper lakes therefore yield different fish assemblages than do shallower lakes with only one type of fish assemblage. In addition, the association of piscivorous fish with natural fish cover in shallow lakes is known to most serious fishermen. This linkage of biological metrics to natural lake morphology must be controlled because natural variation in the lake leads to metric variation that could be interpreted as a response to a stressor rather than as a response to a natural covariate. It is best to model the response of such metrics to lake morphology and consider only residuals about this model as the appropriate response. If natural variables such as lake size and morphology that restrict metric performance are first factored out, the effects of human stressors are likely to be more clearly detected (O'Connor *et al.*, 1996; Wickham *et al.*, 1997; Allen *et al.*, in press). This is further evidence of the need for covariate adjustment and PCA offers a quick method for detecting linear effects of such covariates.

The work described here suggests a method of integrating multiple metrics drawn from multiple taxonomic assemblages in a systematic standardized way, while at the same time accommodating a variety of measurement units and metric distributions. Four elements are crucial in this. The first is the standardization of the dispersion of each metric distribution in terms of the interquartile range, making it feasible to conduct a principal component analysis based on the correlation matrix without propagating the effects of the non-linearities of non-normal distributions into the analysis. The second element of note is the use of a sign reversal to align the expected direction of each metric to common values. Although this makes interpretation of some of the rates difficult to phrase, it facilitates detection of anomalous signals. Third, natural covariates are controlled through use of regression analysis; examination of pattern in the remaining residuals facilitates impact detection. Fourth, principal components analysis is used to clarify multivariate responses and reduce the number of variables with which one must contend in ecosystem studies. Although canonical correlation is an alternative method of analysis, the independence of the biological and environmental orthogonal axes generated in PCA clarifies the potential cause-effect relationships of metrics in each array. Additionally, patterns of variation can be detected in the principal component analysis of the biological metrics even if we have no idea what causes them, an important safeguard in environmental monitoring. Additional investigation can then determine the origins of the variations.

Our use of principal component analysis could be improved upon. We assumed that variation in our metrics reflected constrained responses to the stressors present on the lakes, and fitted these to orthogonal factor axes. In reality, some component of the variability of the metrics is due to non-stressor variation between lakes and to measurement variability. Control of covariates reduces but hardly eliminates the former, and the latter is inevitably present in any monitoring scheme. The relatively large amount of unexplained variability of individual metrics suggests the extent of the problem. While one can argue for the use of factor analysis, we preferred to retain orthogonality of axes here to emphasize the presence of independent signals from particular stressors or groups of stressors and to facilitate their interpretation. Data from a larger survey of representative lakes are necessary for exploring this issue further.

Karr (1981) suggested that a series of indicators representing an array of responses along a gradient of stress from none to extreme is desirable. Although individual metrics in our array possessed some of these properties (Figures 1 and 2), the multivariate structures elaborated here were not examined in this light. One reason for not doing so is that it is difficult to know how to array the lakes in a systematic manner when our analysis clearly indicates that there are multiple dimensions of impact at work within the lakes considered. Additionally, with only 19 lakes, chance possession of an attribute may substantially distort the pattern of variation. More lakes are needed to compute the multivariate axes described here and then to use position (e.g., along environmental PC1) to indicate generalized stress. Plotting the individual biological metrics, or aggregates thereof, against environmental PC1 might then reveal an array of sensitivity thresholds. Conversely, it should be possible to plot particular metrics against particular stressor gradients, thereby enabling us better to discuss probable causes of alterations in biotic integrity.

Using multiple taxonomic groups to assess ecological integrity at the scale of regional populations of ecosystems is a complex and rarely undertaken task, but the apparent extent and rate of ecosystem degradation calls for greater attention to this problem (Hughes and Noss, 1992). Our paper presents a multivariate, multimetric, and multi-taxon process for developing an index to assess the ecological condition of lakes. Although a much larger suite of candidate metrics and study lakes is advisable, and additional analyses of metric and index variance through space and time are needed to assess precision, we offer this approach as a method for objectively integrating key components of lake biological integrity. We cannot attach statistical significance from our results to all lakes in the northeast U.S., given both the nonrandom selection of lakes and the early stage of metric development in this study. But this will be possible by applying the method to randomly selected lakes and by using better tested metrics. Despite the stated shortcomings, we found that lake assemblages ranging from birds to diatoms may provide useful signals for lake condition, that these signals could be linked with environmental diagnostic factors, and that metrics representing the taxa themselves can be combined to produce meaningful assessments of whole lake biological integrity. We believe the approach also has potential application to other ecosystems.

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