Resistance, resilience and regulation of north-temperate lake communities

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ABSTRACT

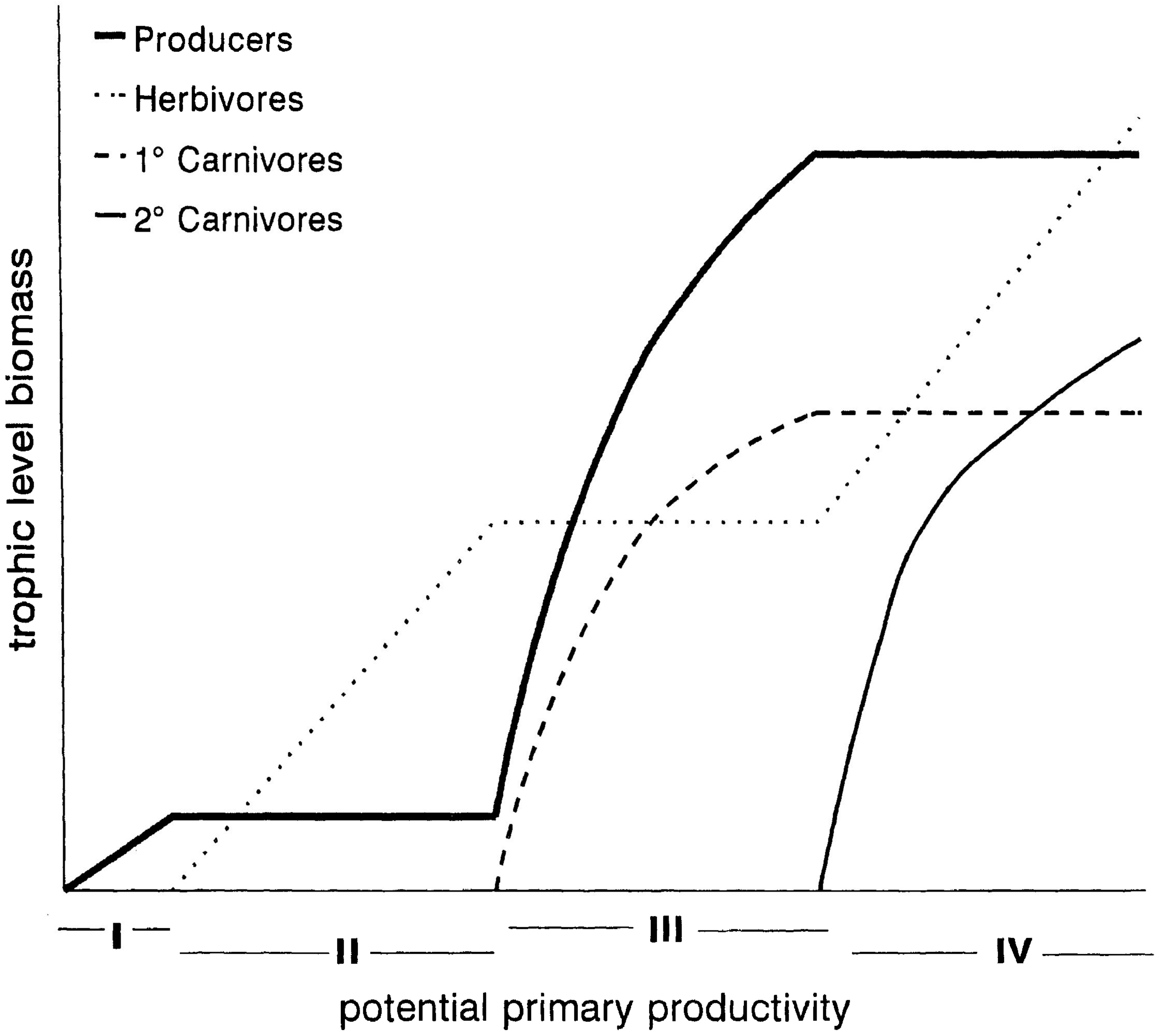
I analyzed the resistance and resilience of benthic macroinvertebrate and zooplankton communities from 36 trophically similar lakes north of Thunder Bay, Ontario to test predictions of the Oksanen et al. (OFAN) model of community regulation and the potential for alternative stable states following natural and timber-harvest disturbances. For each disturbance, only a subset of the lakes were previously affected, allowing an undisturbed control group of lakes to be used for comparison. Disturbances differed in the manner in which they "displaced" communities and every disturbance, except the impact associated with the actual area of watershed harvested, significantly altered either the zooplankton or macroinvertebrate community from the structure observed in undisturbed lakes (low overall resistance). Communities did not converge on the composition in undisturbed lakes (no resilience), suggesting a stable alternative state. These results suggest that resource managers must consider the effects of land-use disturbances, both separately and from a cumulative perspective, to evaluate the potential impacts on lake ecosystems. When potential productivity was augmented by nutrient-addition via cottage inputs, predictions of the OFAN model were rejected over the three lower trophic levels analyzed in these four trophic-level lakes. Alternative regression approaches supported predictions only at the basal trophic link, similarly rejecting the model. The OFAN model cannot account for the pervasive influence of size-structured interactions at upper trophic levels in aquatic communities.

INTRODUCTION

Ecological resistance and resilience are important descriptors of community dynamics following disturbance (Holling 1973, Webster et al. 1975, Connell and Sousa 1983, Pimm 1984, DeAngelis et al. 1989*ab*). When a disturbance increases nutrients available to the primary producers of a four trophic-level system biomass for even-numbered trophic levels should increase (Oksanen et al. 1981). The biomass in odd levels should remain constant. This alternating pattern, with top consumers always on the increase, is predicted to exist regardless of the length of the food chain. Resistance, measuring a community's ability to withstand environmental disturbance, has direct relevance to the Oksanen et al. model (abbreviated as OFAN by Oksanen 1988). Trophic levels predicted to have constant biomass should be resistant to disturbances altering productivity. When a disturbance is capable of displacing a community, one result can be the formation of alternative stable states (Lewontin 1969, Holling 1973, Sutherland 1974, Connell and Sousa 1983) that may be detected by estimating a community's resilience (how quickly the community returns to its initial state). Communities in alternative states will not be resilient.

The Oksanen et al. model considers the relationships between trophic levels along a gradient of increasing productivity (Fig. 1), assuming that each level acts as a single exploitative population whose density has no direct effect on its per capita rate of growth (Oksanen et al. 1981). Thus, if four trophic levels are present (Fig. 1), primary producers and primary carnivores will be regulated by predation and remain constant. In contrast, the biomasses of herbivores and secondary carnivores should increase, regulated solely by competition. The model is able to integrate the potential effects of both abiotic and biotic factors into one regulatory process (Persson et al.

Fig. 1. The relation of biomass of primary producers, herbivores, and primary and secondary carnivores to potential primary productivity predicted by Oksanen et al. (1981). Roman numerals along the horizontal axis refer to the numbers of interacting trophic levels within a given range of potential productivity (after Oksanen et al. 1992). The potential discontinuities associated with changes between trophic-levels (Oksanen et al. 1981) have been ignored.



Producers
Herbivores
1° Carnivores
2° Carnivores
trophic level biomass
I
II
III
IV
potential primary productivity

1988), resulting in its unique and testable predictions concerning the effect of environmental enrichment on trophic level interactions and trophic chain lengths. Persson et al. (1988, 1992) have recently found empirical support for the model's predictions, both in their review of available data from aquatic systems (Persson et al. 1988) and their comparison of 11 temperate lake ecosystems that ranged from low to intermediate productivity. These studies confirmed the OFAN model in three- and four-level systems as well as its assumption that food-chain length is limited by primary production. Oksanen et al. (1992) reviewed data on biomass patterns in plants and herbivores that also supported OFAN predictions. Alternately, Mittelbach et al. (1988), Liebold (1989) and Abrams (1993) have respectively demonstrated that ontogenic niche shifts, resource edibility (or predator diet breadth), and heterogeneity of food-web structure can alter regulation along productivity gradients thereby violating the model's assumptions and applicability to real systems.

The long term state of a community can be drastically changed by a single disturbance, and thus the current state is a function of both the biotic interactions between species as well as a community's history (Tilman 1989). This concept of alternative or multiple stable states was introduced by Lewontin (1969) and later identified by Sutherland (1974) for communities which, following a perturbation, do not return to their original structure or which persist "for some period of time in a given physical locality, in spite of forces with the potential of altering their structure". Their existence has since been documented by Sutherland (1974, 1981) and Peterson (1984) in subtidal communities (but see Connell and Sousa 1983 for problems with these and other accounts). However, Persson et al. (1993) found no evidence of alternative states following discrete disturbances of piscivores and planktivores in highly-productive temperate lakes, but suggested that certain sustained perturbations may be capable of causing shifts in the structure of lake communities.

Resistance and resilience have seldom been measured in real communities (Pimm 1991). The reasons for this likely relate, to confusion with definitions and perceptions of the resistance and resilience of communities (e.g. Holling 1973, Webster et al. 1975, Connell and Sousa 1983, Pimm 1984, Boulton et al. 1992), to the need for a consistent protocol (Steinman et al. 1992), and to the lack of long-term pre- and post-disturbance estimates of species abundance (Connell and Sousa 1983, Pimm 1991). I addressed these three concerns by estimating the resistance and resilience of northern benthic macroinvertebrate and zooplankton communities to different disturbances. In so doing, I tested OFAN predictions concerning nutrient additions and explored the potential for alternative stable communities in north-temperate lakes. I also tested the OFAN model independently in undisturbed lakes by comparing changes in biomass among benthic and pelagic trophic levels along a productivity gradient.

RESISTANCE, RESILIENCE AND DISTURBANCE

Resistance and resilience can only be defined by referring to a community's pre-disturbance "equilibrium" (Lewontin 1969, May 1974). This restriction may be unrealistic when applying these concepts to natural systems, where, at a large enough scale, a pre-disturbance trajectory or mean could serve as an approximation of equilibrial community structure (DeAngelis and Waterhouse 1987, Sutherland 1990). Resistance is the inverse of the "distance" to which a community is displaced from this state, while resilience is estimated as the rate of a community's return to its pre-disturbance equilibrium (Webster et al. 1975, DeAngelis 1989*a*). These criteria assume that disturbances are not so subtle or so insignificant that the community is totally unaffected.

Before the effect of a disturbance can be assessed, the natural variation of the community, both in time and in space, must first be known (Schindler 1987, Menge and Olson 1990, Carpenter and Leavitt 1991). Disturbance induces a change in community structure at a level above or below this background variation. A disturbance can occur either as a "pulse" of short duration or be a more or less continuous "press" (Bender et al. 1984, Yodzis 1988). The effects of pulse disturbances are likely to be of relatively short duration, whereas press disturbances can continuously alter community structure. Resistance can be quantified for both types of disturbances because each can alter the relative abundances of species. Resilience can only be realistically interpreted for pulse disturbances because press disturbances may constantly alter community composition as well as the relative abundances of species.

Disturbances associated with timber harvest have become the most prevalent anthropogenic disturbance in the northern boreal and mixed-wood forests. Only recently, however, have their effects on the structure of aquatic communities begun to be critically evaluated (Bormann and Likens 1979, Maser et al. 1988, Hicks et al. 1989, Hartman and Scrivener 1990, Rutherford et al. 1992). Disturbances associated with timber harvest span a wide range of categories (Table 1) and potential mechanisms (Krause 1982, Verry 1986, Hartman and Scrivener 1990). I include two that are only indirectly linked to timber harvest (because of the increased access associated with logging activities) - cottage development and fishing. Cottaging has been closely linked to nutrient inputs (Dillon and Rigler 1975) and fishing is most often associated with the removal of top predator biomass. We do not know whether aquatic communities are resistant to the effects of timber harvest, whether the communities are resilient enough to recover following such a disturbance and which harvest disturbances have the greatest effect on lake biota.

Table 1. Identity, type and number of disturbances, affecting macroinvertebrate and zooplankton communities in study watersheds in northwestern Ontario.

		Number of disturbed communities*	
Disturbance	Type	Macroinvertebrate	Zooplankton
Timber Harvest	Pulse	29	23
Road Construction	Pulse	31	22
Cottaging	Press	10	5
Forest Fire	Pulse	13	7
Fishing	Press	21	15

* Each community represents one of the 36 lakes sampled for macroinvertebrates and 27 lakes for zooplankton samples.

METHODS

Data and procedures for the measurement of resistance and resilience

I used biomass to estimate the relative abundances of zooplankton and benthic macroinvertebrates in order to assess the resistance and resilience of northern lake communities. For each watershed disturbance, a portion of the lakes had the potential to be affected sometime prior to sampling, while the balance were undisturbed. All lakes were sampled over the same period. This "space for time" (SFT) substitution (Pickett 1989), is not as powerful at detecting the resistance and resilience of ecological communities as replicated temporal experiments, but can, nevertheless, assess changes in community structure relative to undisturbed controls. I begin by documenting a five-phase protocol to estimate resistance and resilience using SFT sampling (Fig. 2). This protocol can be similarly applied, with minimal modification, to studies with pre- and post-disturbance data on a single community.

Phase One: Summarizing the community. - I summarized the macroinvertebrate and zooplankton communities by grouping correlated taxa along gradients of relative abundance using a principal components analysis (PCA - SPSS/PC+4.0 FACTOR analysis, Norušis 1990 - also see Appendix 1). Each disturbed or undisturbed lake community occupies a different point in a space defined by the extracted principal components (Fig. 3).

The PCA solutions included common taxa accounting for the greatest amount of variation in community data. I initially transformed ($1+\log_e x$) all biomass estimates and deleted all taxa occurring in 10% or less of the study lakes. Additional taxa were successively removed by iteratively deleting taxa with the lowest mean correlations between pairs of taxa. The analysis stopped when a maximum of 3 principal

Fig. 2. A flowchart summarizing my protocol to measure the resistance and resilience of northern lake communities.

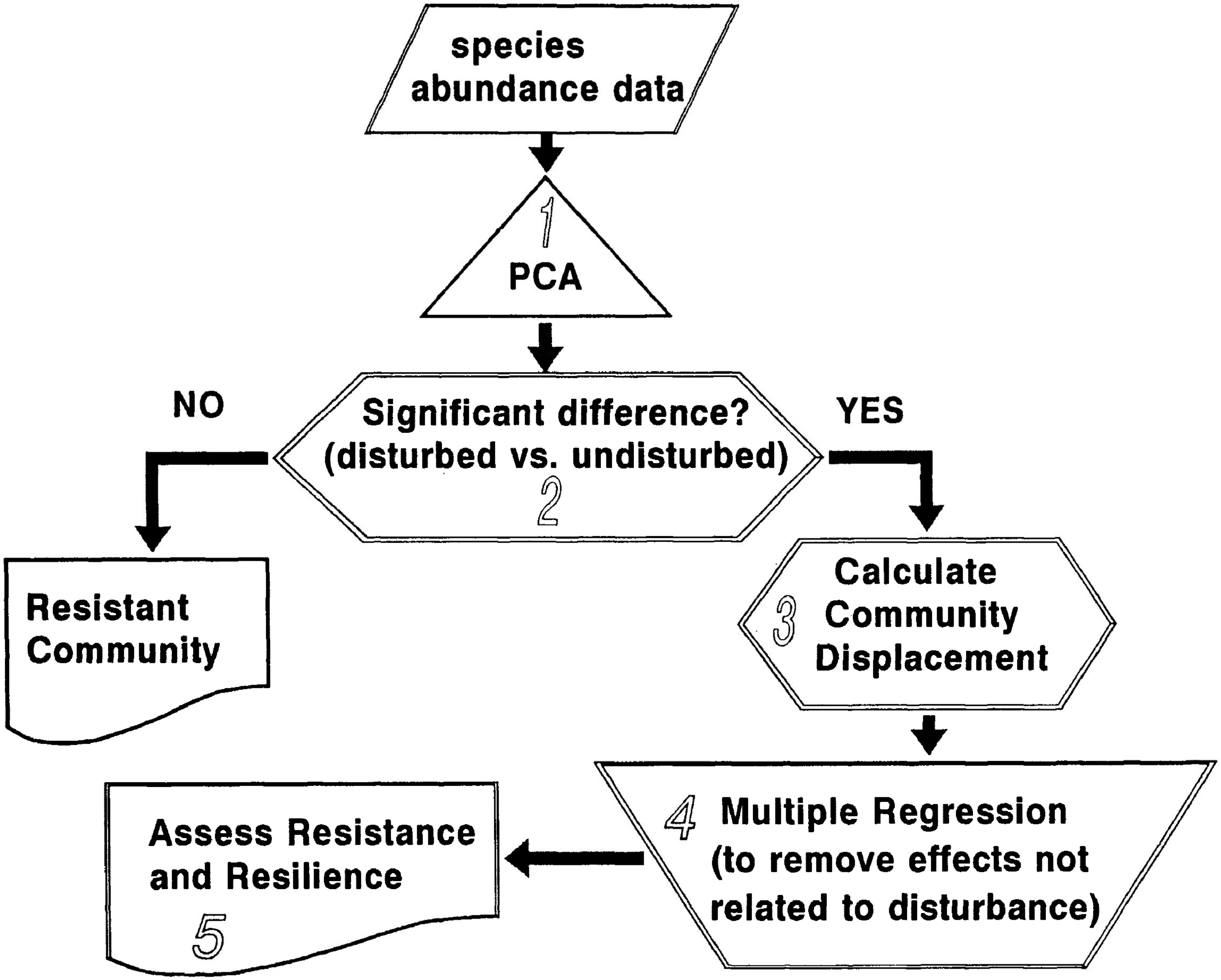
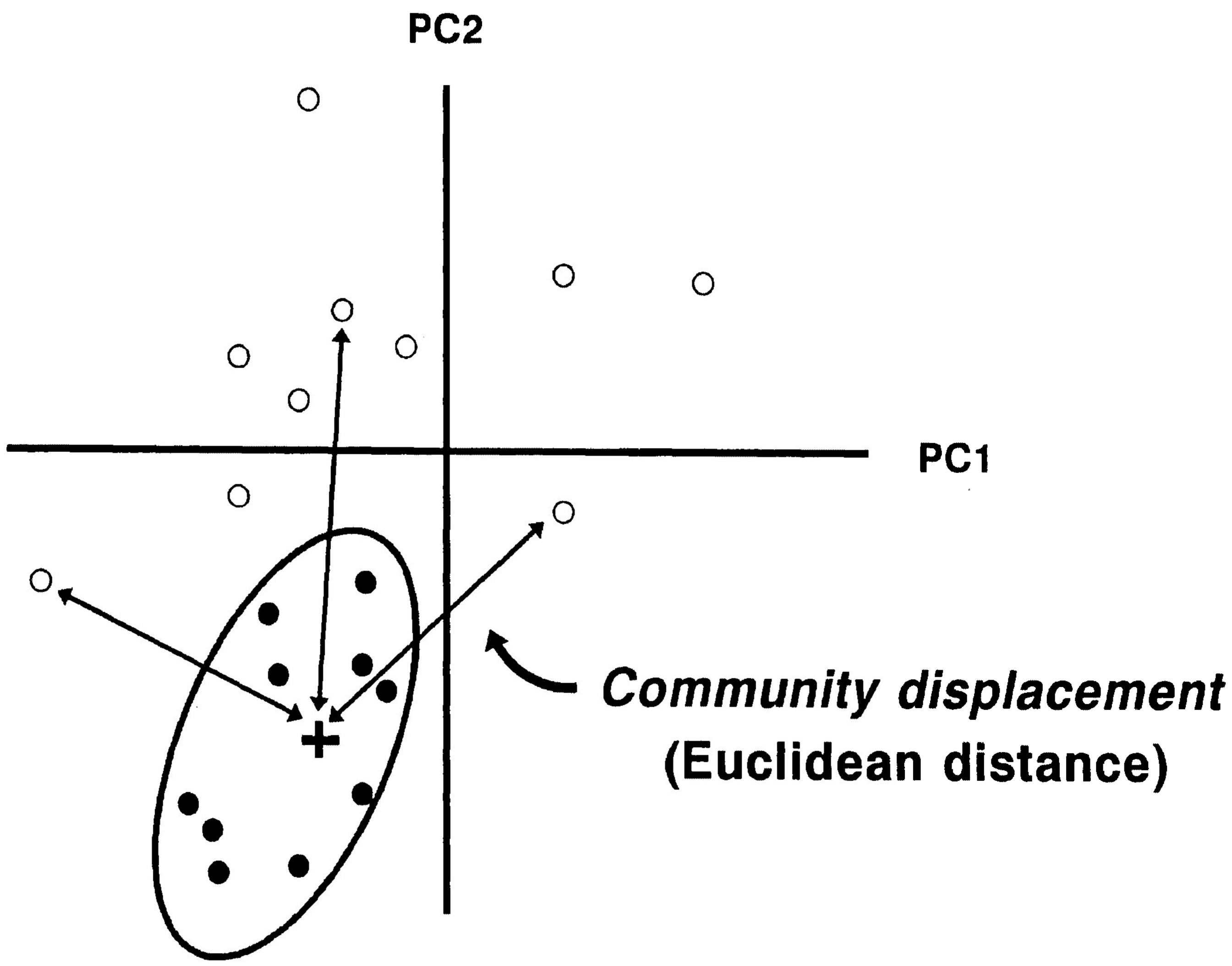

species abundance data
1
PCA
NO
Significant difference? (disturbed vs. undisturbed)
2
YES
Resistant Community
Calculate Community Displacement
3
4
Multiple Regression (to remove effects not related to disturbance)
Assess Resistance and Resilience
5

Fig. 3. An example for calculation of community displacement in two-dimensional PC space. The ellipse encloses the set of undisturbed samples (solid dots). Open circles represent a set of disturbed samples. Community displacement of each disturbed sample is calculated as the Euclidean distance to the centroid (+) of the undisturbed samples. Community displacement can be calculated for any number of PCs.


PC2
PC1
+
Community displacement
(Euclidean distance)

components explained more than 50% of the variation in the data. If the Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy was < 0.6 at this point, further taxa were deleted based on the lowest individual measures of sampling adequacy until an "acceptable" KMO value (0.6) was obtained (Norušis 1990).

Phase Two: Testing for a significant change in community structure - I tested for a difference between the PC scores of disturbed and undisturbed lakes with a multivariate "*t*-test" (SPSS/PC+4.0 DSCRIMINANT analysis - Wilk's lambda, Norušis 1990). A significant difference ($p<0.05$) indicates a change in community structure. I then used univariate *F*-ratios to test which community PC was altered most by a given disturbance.

Phase Three: Calculating community displacement - I used the PC scores to estimate the displacement of each disturbed lake community from the undisturbed control lakes. The undisturbed ellipse approximates natural variation in community structure, its centroid is the expected "equilibrium" for the undisturbed lakes. Community displacement (CD) was calculated as the Euclidean distance between the centroid of the undisturbed lakes and each disturbed lake's PC co-ordinate (Fig. 3).

Phase Four: Confounding variables - Because of inherent lake differences, I summarized two sets of $\log_e$-transformed variables (Appendix 2) describing basin morphometry and water chemistry with a PCA. Prior to the removal of any confounding variables I used a multivariate *t*-test (Wilk's lambda) to look for differences between disturbed and undisturbed lakes based on the PC scores as well as $\log_e$-chlorophyll *a* measurements for each disturbance. In a SFT analysis, an initial change in community structure may simply represent intrinsic differences among disturbed and undisturbed lakes. In most instances this bias should be detected by differences in the physical and/or chemical properties of lakes in the control and treatment groups. If a significant difference ($p<0.05$) was detected and there was a significant correlation between community displacement and any one of the summarized confounding variables, I did not analyse resistance and resilience for that disturbance.

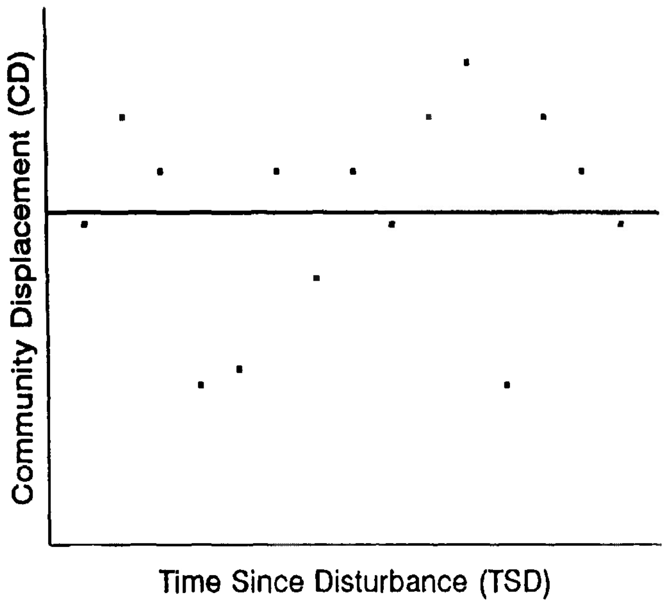
I attempted to identify any significant non-disturbance effects that might obscure my interpretation of displacement within disturbed lakes by regressing community displacement against confounding environmental variables (SPSS/PC+4.0 backward elimination multiple REGRESSION analysis, Norušis 1990). These included a diverse set of lake morphometry and chemistry variables (Appendix 2). If the fit of the regression was significant ($p<0.05$), I used the residuals in subsequent analyses. For those wishing to follow my protocol when sampling is conducted on a single community over time these confounding factors switch from environmental to autocorrelational (see Neter et al. 1989 for testing and removal).

Phase Five: Resistance and resilience - I regressed my estimates of community displacement against time since disturbance (TSD) to estimate community resistance and resilience (Fig. 4). Resilience was estimated by the slope of the regression line. Resistance was estimated as the inverse of the regression's intercept except when the phase four multiple regression was significant. In these instances, I used mean community displacement to estimate resistance and regressed residual community displacement against time since disturbance to estimate resilience.

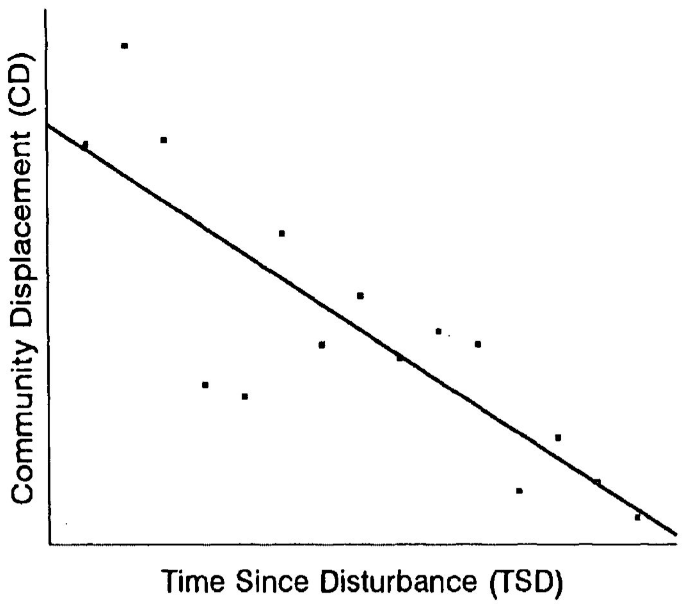
Study area and lake sampling

Community and water quality data were collected discontinuously by the Productivity Unit of the Ontario Ministry of Natural Resources (OMNR) during 1979 - 1991 on a number of lakes around Thunder Bay, Ontario. Resistance and resilience

Fig. 4. Examples of possible outcomes from the regression of community displacement versus time since disturbance. On the right the disturbed communities are converging on an undisturbed control. On the left, the disturbed communities maintain a different structure from the undisturbed control.



$CD = a$
resistance $= 1/a$
resilience $= 0$

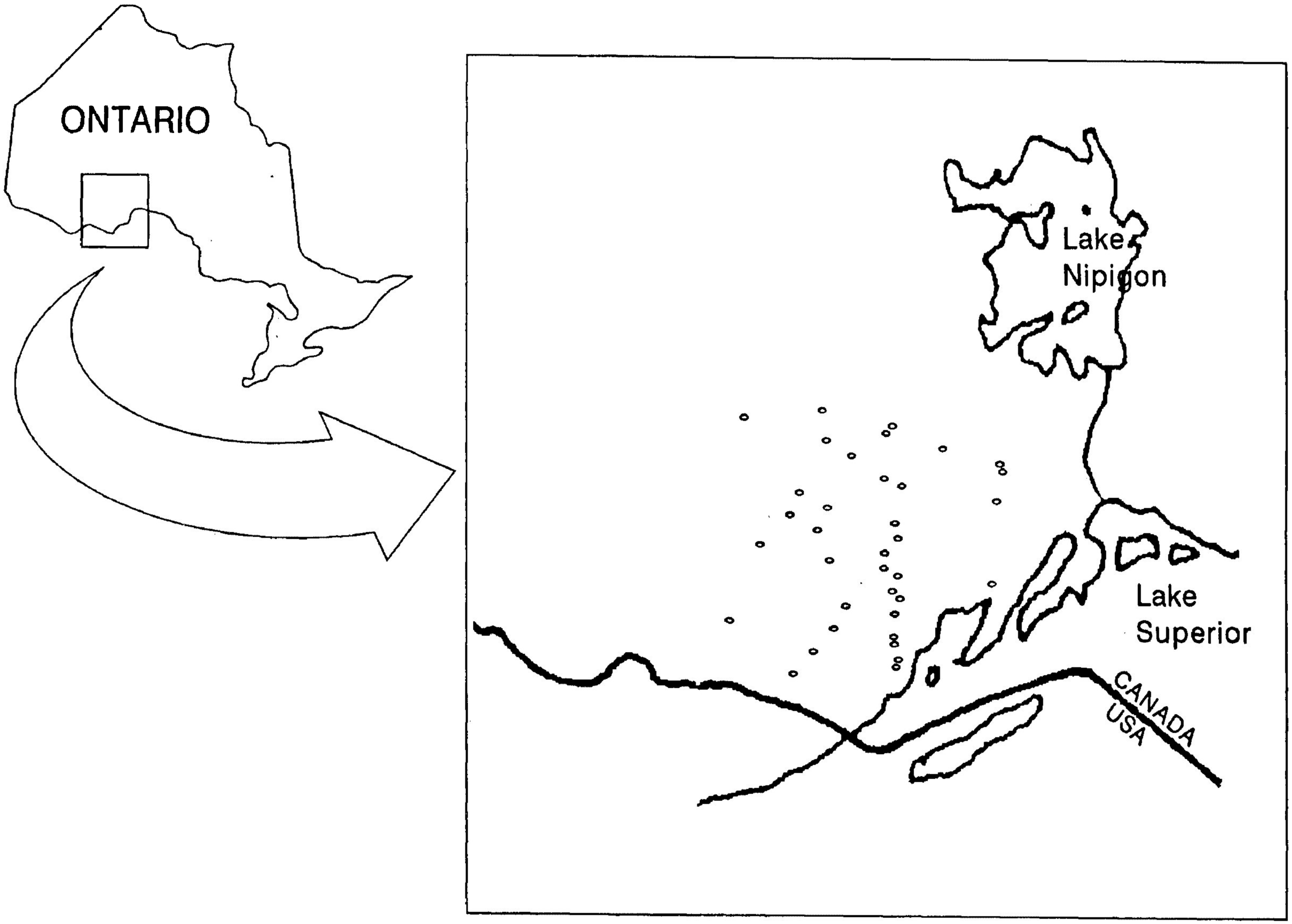


$CD = a - b\mathrm{TSD}$
resistance $= 1/a$
resilience $= b$

have been shown to vary, both theoretically and empirically, with food chain length and food-web structure (e.g. MacArthur 1955, Watt 1964, Pimm 1984, DeAngelis et al. 1989*a*, Pimm 1991). To ensure that this trophic complication did not influence my analysis of resistance and resilience, or the OFAN model, I attempted to maintain a constant food-chain length by only including lakes with northern pike *Esox lucius*, as the dominant top predator, in the analysis. I used 36 mesotrophic lakes (Fig. 5 - from 88°40'W to 91°45'W and 48°10'N to 49°20'N) in the analysis of the benthic macroinvertebrate community, and a subset of 27 lakes for "zooplankton" (includes meiobenthic cladocerans) community analysis. This difference in sample sizes exists because during early sampling, benthos was not sorted for zooplankton.

All lakes were sampled at least twice for water chemistry and chlorophyll *a* (mean values are presented in Appendix 2) following Ontario Ministry of the Environment guidelines (MOE 1989) and once for morphometry using OMNR lake survey procedures (Dodge et al. 1989). Mid-summer water chemistry and chlorophyll *a* samples were taken at maximum lake depth. Chlorophyll *a* samples were initially filtered on 1.2 µm cellulose-nitrate paper, then extracted from algal cells with 90% acetone, centrifuged, and finally measured with a scanning spectrophotometer (Beckmann DU7) to estimate biomass. Lake benthos was sampled once per lake with a ponar grab (232 cm^2) at depths of 1 metre, mid-thermocline and maximum depth along a minimum of three randomly selected transects per lake, each extending from the shore to mid-basin (Cullis 1986). Benthic samples were collected between 1979 and 1984 during the months of July and August, sorted by hand and by sugar flotation and identified, with a dissecting scope (6-40X WILD Heerbrugg M5A) to the highest taxonomic resolution possible (at least to family, with the exception of Nematoda,

Fig. 5. The locations of the 36 study lakes near Thunder Bay, Ontario.



ONTARIO
Lake Nipigon
Lake Superior
CANADA
USA

Ostracoda, Bryozoa and Porifera - Merritt and Cummins 1984, Pennak 1989, Thorp and Covich 1991 - Appendices 3 and 4). Each organism was measured for total body length and converted to biomass using measured (Erpobdellidae - mg dry mass = mm total length$^{3.46}$(0.0006), r^2=0.73, n=10) and published length-dry mass regressions and average dry mass values (e.g. Smock 1980, Meyer 1989). Biomass estimates (mg dry mass/m^2) were then weighted according to the percentage of benthic habitat in each sampled stratum to obtain estimates for the entire lake.

Pelagic zooplankton communities were sampled between 1979 and 1984 with replicate vertical hauls (maximum depth to surface) using Wisconsin and SCOR zooplankton samplers, and in lakes less than 1 m in depth, a bucket. All samples were then standardized according to gear efficiency. Subsamples of organisms were identified to functional groups (cladocerans, bosminids and chydorids, copepods, *Chaoborus*, *Mysis*, *Leptodora*, *Holopedium*, Polyphemids), measured, and biomass calculated according to published relationships (length-dry mass).

Disturbances

Disturbances to northern lakes encompassed both press and pulse and natural and anthropogenic events (Table 1). For each lake, I quantified the magnitude and timing of disturbance (Appendix 5). Timber harvest and forest fires were measured as the disturbed percentage of a lake's standardized watershed area (for headwater lakes, the topographic area upgradient from a lake, but for non-headwater lakes, only the upgradient area below major upstream lakes). Road construction was estimated by the distance, in kilometres, of roads, hydrolines, pipelines and railways within 100 metres of the shore of a lake. I measured cottaging disturbance by the number of cabins adjacent to a lake. Fishing was estimated on "uncottaged" lakes as a relative index of pressure (0, 1, or 2) determined by the number of contacts with anglers while sampling (Terry Marshall - OMNR Productivity Unit, *personal communication*) and on cottaged lakes by 1 + (number of cottages/lake area in hectares).

I standardized the area of harvest and fire by watershed area, the length of roads constructed by lake perimeter, the number of cottages by lake flushing rate, and fishing by a measure of annual fish yield ((total dissolved solids/mean depth)$^{0.45}$ * lake area(in ha)/100, Ryder 1965). These proportions were arcsine transformed prior to analysis. Time since disturbance (TSD) was estimated by the year in which the disturbance occurred. If a lake was affected more than once by a particular disturbance, TSD was calculated as the mean of the years since disturbance, weighted by the corresponding magnitude.

I assessed the independence of disturbances with separate correlations based on their pairwise scores for magnitude and timing (SPSS/PC+4.0 CORRELATION analysis, Norušis 1990). I also tested for correlations between time since disturbance and the magnitude of disturbance.

OFAN predictions

Nutrient addition - For lakes disturbed by cottaging, I evaluated the OFAN prediction of increasing herbivore biomass and constant phytoplankton and primary carnivore biomass (Fig. 1) using two independently collected sets of data, one pelagic and the other benthic. For pelagic zooplankton samples, I tested the model by comparing herbivore (cladocerans, *Holopedium*, and bosminids), primary carnivore (copepods, *Chaoborus*, *Mysis*, *Leptodora*, and *Polyphemus*), and primary producer (chlorophyll *a*) biomasses between disturbed and undisturbed lakes (SPSS/PC+4.0 T-TEST, Norušis 1990). In the benthic samples, I excluded a large number of taxa (representing omnivorous and detritivorous species) to create less ambiguous trophic levels. I compared the log-transformed biomasses of benthic herbivores (estimated by a subset of the zooplankton community - see Appendix 4) and benthic primary carnivores (estimated by a subset of the macroinvertebrate community - see Appendix 3) between disturbed and undisturbed lakes. If the OFAN model is correct, herbivore biomass should significantly increase while the biomasses of primary carnivores and producers should remain constant.

Community resistance, when communities correspond to trophic levels, can also be used to test OFAN predictions. In a nutrient-enriched four trophic-level system, primary carnivores should be resistant while herbivores should not. I examined benthic macroinvertebrate (a crude estimate of primary carnivore biomass) and benthic zooplankton (an approximate estimate of herbivore biomass) communities for resistance following the cottaging disturbance.

Productivity gradients - I tested the same prediction of biomass distribution among trophic levels by regressing primary producer and primary carnivore biomass against herbivore biomass in both the pelagic and benthic communities. As potential productivity increases with four trophic levels, no relationship should exist between either the primary producers or carnivores and the herbivores (Fig. 1). Over the range in potential productivity found in lakes undisturbed by cottaging, model II regressions of both primary producer and primary carnivore biomass on herbivore biomass should not be significant if the OFAN model is true.

RESULTS

Community summaries

Benthic macroinvertebrate community - Of the 138 benthic macroinvertebrate taxa that were identified (Appendix 3), only 40 had frequencies of occurrence greater than 10%. Of these, 21 were excluded because of their inability to summarize within-community variation (low correlations). The final PCA solution included 19 taxa in three PCs accounting for 55% of the variation in the common organisms (Table 2).

I interpreted the macroinvertebrate PCs on the basis of their trophic relationships (Merritt and Cummins 1984, Pinder 1986, Pennak 1989, Thorp and Covich 1991). PC1 varied positively with the presence of two species of amphipods (*Hyallela* and *Crangonyx*), Tanypodinae, and to lesser extent, the ostracods, indicating a trophic gradient from high to low omnivore abundance. PC2 generally described a herbivorous trophic gradient, again ranging from high to low biomass, inferred by the loadings for bryozoans and poriferans. The high loadings for the Polycentropodidae and *Sialis sp.* indicated a predatory emphasis for the PC3 trophic gradient (although the omnivorous habits of *Hexagenia sp.* contradict this interpretation). The trophic gradients also correspond to "prey"-size consumption. In general, high scores on PC2 reflected the greatest abundances of consumers of the smallest particle sizes while PC3 corresponded to the largest. High PC1 scores represented abundant predators that preyed upon intermediate-sized prey. Detritivores were found in all PCs, but with comparatively small correlations, and thus could not be reliably used to delineate trophic gradients.

Zooplankton community. - Of the 41 zooplankton taxa that were initially identified (Appendix 4), only 17 had frequencies of occurrence greater than 10% and

Table 2. Unrotated principal component loadings for the final PCA on benthic macroinvertebrate taxa in 36 northern lakes. Taxa selected for analysis, but not strongly associated with the first 3 PCs included: *Amnicola sp.*, *Chaoborus sp.*, Coenagrionidae and *Helobdella stagnalis*.

Taxon	PC1	PC2	PC3
Ostracoda	**0.731**	0.331	0.083
Hyallela azteca	**0.722**	-0.270	0.289
Caenis sp.	**0.700**	-0.285	-0.169
Crangonyx sp.	**0.672**	-0.035	0.589
Tanypodinae	**0.644**	-0.358	-0.029
Planorbidae	**0.624**	-0.117	-0.391
Porifera	0.288	**0.771**	-0.318
Bryozoa	0.468	**0.737**	-0.235
Stylaria lacustris	0.415	**0.570**	-0.186
Naididae	0.348	**0.562**	-0.271
Pristina sp.	0.401	**-0.555**	-0.369
Polycentropodidae	0.276	0.170	**0.764**
Uncinais uncinata	0.504	-0.056	**0.543**
Hexagenia sp.	-0.473	0.383	**0.516**
Sialis sp.	0.215	0.417	**0.511**
Amnicola sp.	0.375	-0.209	0.102
Chaoborus sp.	-0.442	0.032	0.206
Coenagrionidae	0.004	0.479	-0.199
Helobdella stagnalis	0.451	-0.294	-0.131

non-redundant correlations. Eight of these were excluded because of their inability to summarize within-community variation (low correlations). The final PCA contained 9 taxa that were summarized by two PCs accounting for 70% of the variation in the common organisms (Table 3).

Zooplankton gradients were best described on the basis of body-size and habitat. The first PC represented a high to low biomass gradient for comparatively small body-sized littoral benthic organisms. *Mesocyclops edax* is the only species that somewhat confuses this interpretation, but it is often found associated with the water-sediment interface during the day when sampling occurred, despite its generally planktonic existence (Pennak 1989). The second PC represented a similar gradient of low to high abundance of comparatively large body-sized planktonic organisms.

Changes in community structure

Four of the five disturbances were associated with a significant difference ($p<0.05$) in the community PCs (Table 4). However, the disturbances associated with a significant change in the benthic macroinvertebrate community were different from those associated with a displaced zooplankton community. Although macroinvertebrate communities undisturbed by forest fire were significantly different than those disturbed by forest fires, this disturbance was not considered further following the analysis of confounding variables (see below).

The univariate F-ratios from the multivariate *t*-test (Table 5) indicated how the disturbances changed the two communities. In the zooplankton community, cottaging and fishing were consistently associated with increased abundances of small littoral benthic cladocerans (PC1) more than planktonic organisms (PC2). For the macroinvertebrate community, road construction was associated with a significant

Table 3. Unrotated principal component loadings for the PCA on zooplankton taxa in 27 northern lakes. The additional taxon selected for analysis, but not associated with first 2 PCs was *Daphnia rosea*.

Taxon	PC1	PC2
Ofryoxus gracilis	**0.956**	-0.096
Acantholebris curvirostris	**0.931**	0.058
Mesocyclops edax	**0.890**	-0.100
Latona parviremis	**0.880**	-0.263
Latona setifera	**0.738**	0.015
Holopedium gibberum	0.152	**0.962**
Daphnia pulex	0.111	**0.853**
Leptodora kindtii	0.108	**0.731**
Daphnia rosea	-0.164	-0.165

Table 4. Multivariate *t*-tests (Wilk's lambda) of PC scores for undisturbed and disturbed lakes in benthic macroinvertebrate and zooplankton communities. Calculations were based on 3 PCs for the macroinvertebrate community and 2 PCs for the zooplankton community.

Community and Disturbance	Wilk's lambda	*p*	n (undisturbed/disturbed)
Macroinvertebrate			
Timber Harvest	0.968	0.788	7/29
Road Construction	0.747	0.024	5/31
Cottaging	0.970	0.802	26/10
Forest Fire	0.709	0.011°	23/13
Fishing	0.857	0.170	15/21
Zooplankton			
Timber Harvest	0.824	0.098	4/23
Road Construction	0.989	0.880	5/22
Cottaging	0.567	0.001	22/5
Forest Fire	0.899	0.278	20/7
Fishing	0.775	0.047	12/15

° Macroinvertebrate communities disturbed by forest fire existed in lakes that were subsequently shown to be significantly different in lake chemistry from undisturbed lakes (Table 6). This violates the assumptions of the SFT protocol and they will not be considered further.

Table 5. Two-tailed univariate *F*-tests between macroinvertebrate and zooplankton community PC scores for selected disturbances.

Disturbance, Community and PC	Undisturbed Mean PC (±s.d.)	Disturbed Mean PC (±s.d.)	Univariate *F*-ratio (*df*)	*p*
Cottaging				
Zooplankton				
PC1	-0.300 (±0.313)	1.321 (±1.820)	17.49 (1,25)	<0.001
PC2	-0.069 (±0.890)	0.304 (±1.482)	0.56 (1,25)	0.46
Macroinvertebrate				
PC1	0.080 (±0.970)	-0.208 (±1.099)	0.59 (1,34)	0.45
PC2	-0.058 (±1.158)	0.150 (±0.357)	0.30 (1,34)	0.59
PC3	0.040 (±1.103)	-0.104 (±0.704)	0.15 (1,34)	0.70
Fishing				
Zooplankton				
PC1	-0.390 (±0.220)	0.312 (±1.259)	3.61 (1,25)	0.07
PC2	-0.345 (±0.182)	0.276 (±1.284)	2.74 (1,25)	0.11
Macroinvertebrate				
PC1	-0.002 (±0.862)	0.001 (±1.109)	0.001 (1,34)	0.99
PC2	-0.352 (±0.594)	0.252 (±1.159)	3.42 (1,34)	0.07
PC3	0.266 (±1.305)	-0.190 (±0.683)	1.86 (1,34)	0.18
Road Construction				
Zooplankton				
PC1	-0.208 (±0.252)	0.047 (±1.101)	0.26 (1,25)	0.62
PC2	-0.042 (±0.395)	0.009 (±1.099)	0.01 (1,25)	0.92
Macroinvertebrate				
PC1	1.133 (±1.208)	-0.183 (±0.851)	9.20 (1,34)	0.005
PC2	0.299 (±2.436)	-0.048 (±0.599)	0.51 (1,34)	0.48
PC3	-0.386 (±0.868)	0.062 (±1.018)	0.86 (1,34)	0.36
Timber Harvest				
Zooplankton				
PC1	0.848 (±1.931)	-0.148 (±0.721)	3.73 (1,25)	0.065
PC2	0.506 (±2.174)	-0.088 (±0.695)	1.21 (1,25)	0.28
Macroinvertebrate				
PC1	-0.123 (±1.125)	0.030 (±0.987)	0.13 (1,34)	0.72
PC2	-0.224 (±0.748)	0.054 (±1.056)	0.43 (1,34)	0.52
PC3	-0.251 (±0.699)	0.061 (±1.061)	0.54 (1,34)	0.47

decline in omnivore abundance (PC1). No other disturbance was associated with altered macroinvertebrate community structure.

Confounding variables

Three PCs with eigenvalues greater than one were extracted for each of the two sets of potentially confounding variables (Table 6). These accounted for 75% of the variation in lake chemistry and 92% of the variation in lake morphometry. The morphometry PCs approximated gradients of lake size (PC1), lake depth and retention time (PC2), and total watershed area (PC3). Chemistry PCs summarized high-to-low gradients related to productivity (PC1), hardness (PC2) and mean temperature (PC3).

I tested the "confounding" PCs, plus the additional confounding variable of primary productivity (chlorophyll *a*), for their ability to differentiate between disturbed and undisturbed lakes. Groups of disturbed and undisturbed lakes were significantly different for the forest fire and cottaging disturbances and only for the groups of lakes used to evaluate macroinvertebrate communities (Table 7). When further examined to determine if these inherent differences influenced community response, only the benthic macroinvertebrate community displacements for lakes disturbed by forest fires were correlated with lake chemistry PCs (PC2 at p=0.023 and PC3 at p=0.040, 2-tailed tests). I did not analyze this set of macroinvertebrate communities further.

Regressions of community displacements against confounding variables (morphometric and chemical PCs and chlorophyll *a*) demonstrated that lake size (morphometry PC1) was correlated with the distance to which a community was displaced from its undisturbed mean (Table 8). Covariation of community displacement with lake morphometry could bias my estimates of resistance and resilience. I excluded its effect by calculating the residual displacement of each lake from the regression and used the standardized residuals in subsequent analyses.

Table 6. Principal component loadings for the separate unrotated PCAs on basin morphometry and water chemistry variables in 36 northern lakes. The data are listed in Appendix 2.

PCA Grouping and Lake Attribute	PC1	PC2	PC3
Basin Morphometry			
(log$_e$) Volume	**0.975**	-0.157	-0.056
(log$_e$) Shorelength	**0.953**	0.081	-0.117
(log$_e$) Area	**0.942**	0.218	-0.190
(log$_e$) Standardized Watershed Area	**0.894**	0.280	0.108
(log$_e$) Relative Depth	-0.067	**-0.791**	0.527
(log$_e$) arcsine of % Littoral Zone	-0.520	**0.734**	-0.229
Retention Time	0.372	**-0.639**	-0.590
(log$_e$) Total Watershed Area	0.574	0.330	**0.669**
Water Chemistry			
Turbidity	**0.831**	0.153	-0.360
Phosphorus	**0.821**	-0.123	-0.149
Secchi	**-0.726**	0.403	-0.397
Heat Budget	**-0.709**	-0.258	0.144
DOC	0.310	**-0.786**	0.267
(log$_e$) Conductivity	0.353	**0.642**	0.031
Mean Temperature	0.184	0.546	**0.776**

Table 7. Multivariate *t*-tests (Wilk's lambda) between physical and chemical PC scores and chlorophyll *a* for the benthic macroinvertebrate and zooplankton communities in undisturbed and disturbed lakes. Calculations were based on 3 PCs representing lake morphometry and 3 PCs for lake chemistry.

Community and Disturbance	Wilk's lambda	*p*	n (undisturbed/disturbed)
Macroinvertebrate			
Timber Harvest	0.711	0.167	7/29
Road Construction	0.754	0.283	5/31
Cottaging	0.628	0.048	31/5
Forest Fire	0.587	0.023	23/13
Fishing	0.656	0.076	15/21
Zooplankton			
Timber Harvest	0.649	0.232	4/23
Road Construction	0.703	0.371	6/21
Cottaging	0.736	0.474	22/5
Forest Fire	0.662	0.262	20/7
Fishing	0.621	0.175	12/15

Table 8. Significant multiple linear regressions of displacements (y) for benthic macroinvertebrate and zooplankton communities versus morphometry and chemistry PCs and chlorophyll *a*. The only variable remaining in the regressions following backward elimination was morphometry PC1 (x).

Community, Disturbance and ANOVA Source	Equation	Mean Square	*df*	*p*
Macroinvertebrate				
Road Construction	$y=1.91+0.29x$			
Regression		2.56	1	0.019
Residual		0.41	29	
Zooplankton				
Cottaging	$y=2.27-1.19x$			
Regression		6.33	1	0.036
Residual		0.48	3	
Fishing	$y=1.90-1.32x$			
Regression		7.81	1	0.003
Residual		0.87	11	

Resistance

I calculated macroinvertebrate and zooplankton resistance for the three disturbances associated with significant shifts in community structure (Table 9). Mean community displacements of the three disturbances were not significantly different from one another ($F_{2,48}$=2.43, p=0.099).

Resilience

The regression of residual macroinvertebrate community displacement against time since road construction was not significantly different from zero (Fig. 6). By definition, it was not possible to estimate resilience following cottaging or fishing because these represented "press" disturbances. The regression had a significant outlier, but excluding it did not result in a significant regression slope. There were no curvilinear or non-linear trends remaining in the residuals.

The time since road construction was correlated with its magnitude (r=0.492, p=0.005). This correlation, however, was influenced by a single lake (Shafton Lake). Excluding this lake still resulted in a significant correlation (r=0.374, p=0.042), describing a regression that accounted only for 14% of the variation in time since disturbance. As an extra check on the lack of resilience of the benthic macroinvertebrate community, I repeated the analysis using the residuals from the regression of timing versus magnitude. This analysis was, as before, not significant (r=0.046, p=0.804).

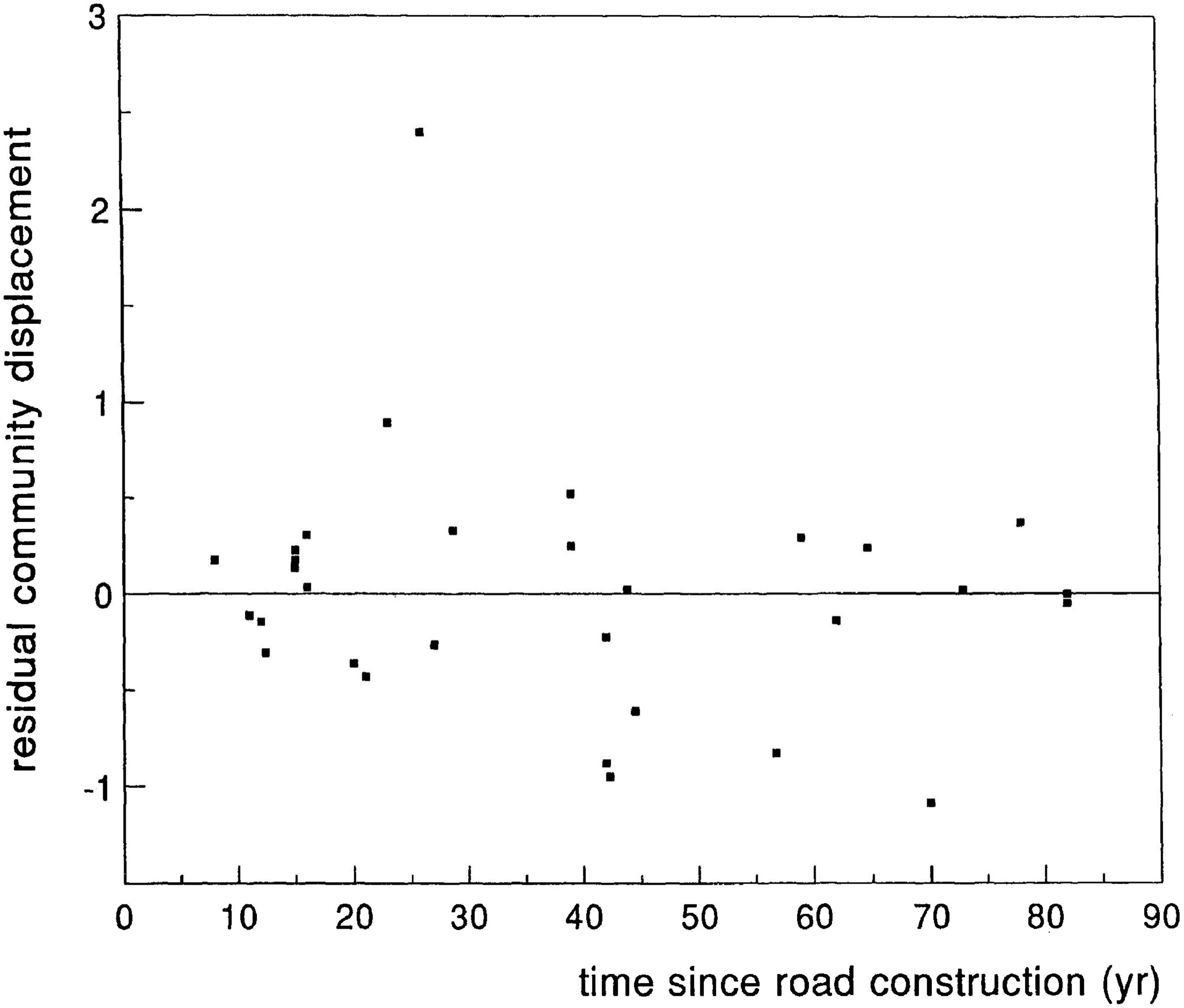
Disturbance

Independence - Significant correlations (2-tailed) existed between the standardized magnitudes of the area of watershed harvested for timber and the area of watershed burned (r=-0.672, p=0.033) for "macroinvertebrate lakes". When only the "zooplankton lakes" were analyzed, the relationship between cottaging and fishing

Table 9. Resistance and community displacement (CD) of the three significant disturbances to community structure.

Community and Disturbance	Resistance	Mean CD (±standard deviation)	n
Macroinvertebrate			
Road Construction	0.525	1.90 (±0.70)	31
Zooplankton			
Cottaging	0.422	2.37 (±1.39)	5
Fishing	0.769	1.30 (±1.54)	15

Fig. 6. Scatterplot of residual macroinvertebrate community displacement versus time since road construction to estimate resilience. The least squares regression (model I) is non-significant (r=0.176, p=0.343) and disturbed communities show no sign of converging towards the undisturbed mean. The horizontal line at zero residual community displacement represents a lack of community change, after correcting for significant environmental influences.


3
2
1
0
-1
residual community displacement
0
10
20
30
40
50
60
70
80
90
time since road construction (yr)

disturbance magnitudes was significant (*r*=0.974, *p*=0.007), as were the harvest and fire (*r*=-0.889, *p*=0.007), and road construction and cottaging (*r*=0.930, *p*=0.022) disturbances.

The timing of the harvest disturbance was correlated with the year fishing began (*r*=0.557, *p*=0.016) as well as the year of road construction (*r*=0.615, *p*<0.001) in macroinvertebrate communities. The timing of cottaging was correlated with these latter two disturbances in lakes sampled for zooplankton (*r*=0.970, *p*=0.030 and *r*=0.983, *p*=0.017 respectively). For both the macroinvertebrates and zooplankton, the timing of road construction was, by definition, strongly correlated with the onset of angling.

These correlations are partly the result of subsets of lakes undergoing more than a single disturbance (e.g. cottages occur only on lakes with road access). This effect may, in turn, be partly responsible for the lack of differences in resistance to disturbance. Yet it is important to note that the number of disturbed lakes varied dramatically with the kind of disturbance considered (Table 1). The nonsignificant differences in resistance are unlikely to be primarily caused by nonindependent data sets.

Magnitude - Regressions of community displacement versus the standardized distance of roads constructed and fishing pressure (Table 4) had neither significant slopes or y-intercepts (Figs. 7, 8). There was no apparent trend between the intensity of disturbance and subsequent community response.

OFAN

Analyses of variation in biomass for a given trophic level, following nutrient addition (cottaging), failed to support the OFAN model. Biomass comparisons between cottaged and uncottaged lakes were not significantly different for any of the trophic

Fig. 7. Scatterplot of residual macroinvertebrate community displacement versus distance of "roads" (standardized by lake perimeter). The least squares regression (model I) is non-significant (r=0.055, p=0.777). No linear relationship exists between the amount of "road" construction and the subsequent macroinvertebrate community response.

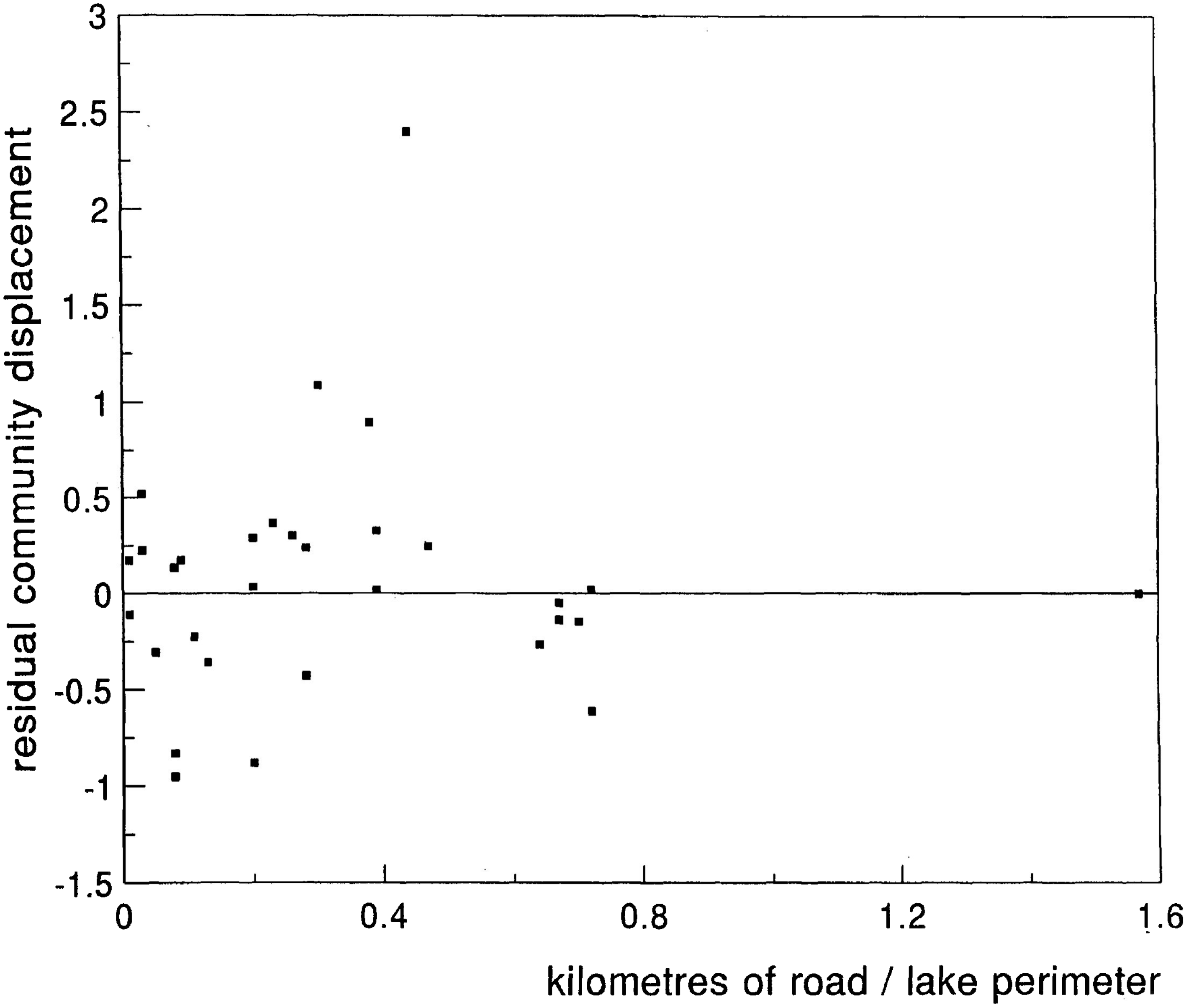
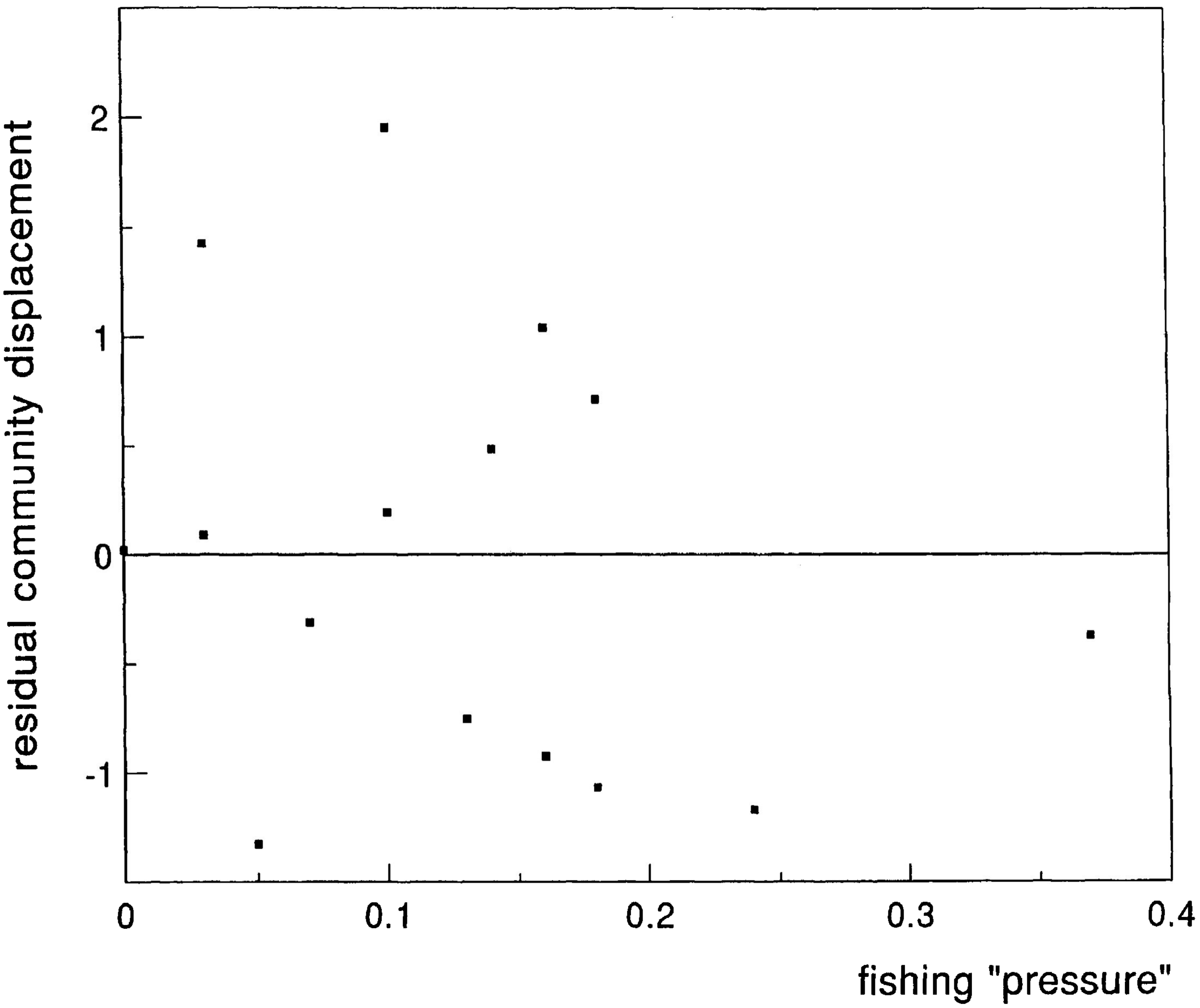

3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
residual community displacement
0
0.4
0.8
1.2
1.6
kilometres of road / lake perimeter

Fig. 8. Scatterplot of residual zooplankton community displacement versus fishing pressure (standardized by annual fish yield). The least squares regression (model I) is non-significant (r=0.257, p=0.357). No linear relationship exists between fishing "pressure" and the subsequent zooplankton community response.



residual community displacement
2
1
0
-1
0
0.1
0.2
0.3
0.4
fishing "pressure"

Table 10. Two-tailed *t*-tests for significant differences between the biomasses of phytoplankton as well as herbivores and carnivores in both the benthic and pelagic zooplankton communities of cottaged versus uncottaged lakes.

Community	Undisturbed Mean Biomass (±s.d./n)	Disturbed Mean Biomass (±s.d./n)	t-value (*df*)	*p*
Phytoplankton	1.085 (±0.51/26)	1.051	0.18 (34)	0.86
Benthos				
Herbivores	0.278 (±0.50/22)	0.098 (±0.14/5)	1.46 (23.2)	0.16
Primary carnivores	4.931 (±1.04/22)	4.909 (±0.75/5)	0.04 (25)	0.97
Pelagic Zooplankton				
Herbivores	3.554 (±1.21/22)	3.035 (±0.94/5)	0.90 (25)	0.38
Primary carnivores	3.136 (±1.21/22)	3.199 (±0.77/5)	-0.11 (25)	0.91

levels examined in the benthic or pelagic samples (Table 10). Predictions of no difference in primary producer and primary carnivore biomass were therefore met, but the predicted increase in herbivore biomass was non-existent in either the benthic or pelagic communities.

Benthic macroinvertebrate and zooplankton community resistance supported OFAN predictions at the two trophic levels analyzed. The displaced zooplankton community (herbivores) was associated with the cottaging disturbance while the macroinvertebrate community (carnivores) was resistant (Table 4). Within the zooplankton communities, the mean scores (Table 5) of both zooplankton PCs increased with the increased productivity associated with cottaged lakes (the increase for PC2 was non-significant).

The same predictions were tested along a productivity gradient in uncottaged lakes. I regressed primary carnivore and primary producer biomass against herbivore biomass in both pelagic and benthic food chains. When phytoplankton biomass was regressed against herbivore biomass, the resulting slopes were positive (Figs. 9 and 10), but only one was significant (this benthic regression, however, was heavily dependent on an influential point that corresponded to a highly productive and somewhat atypical large and shallow lake [Shillabeer]). Primary carnivore regressions showed significant, or nearly significant, increasing trends contrary to the OFAN model. These results suggest that trophic-level biomasses are positively correlated at the herbivore - primary carnivore trophic link, but not at the phytoplankton - herbivore link. Biomasses of phytoplankton and primary carnivores do not positively covary with zooplankton biomass. Thus, in lakes undisturbed by cottaging, the OFAN model of community regulation was again rejected.

Fig. 9. Relationship of the biomasses of phytoplankton and benthic primary carnivores to benthic herbivore biomass. The phytoplankton (dotted line - y=1.13+0.752x, CI_{slope}=±0.294, p=0.009) and primary carnivore (solid line - y=4.35+2.079x, CI_{slope}=±0.872, p=0.042) model II regressions were significant. Both regressions, were strongly influenced by one lake of high herbivore biomass. Removal of the atypical lake "strengthens" the carnivore regression and "weakens" the phytoplankton regression.

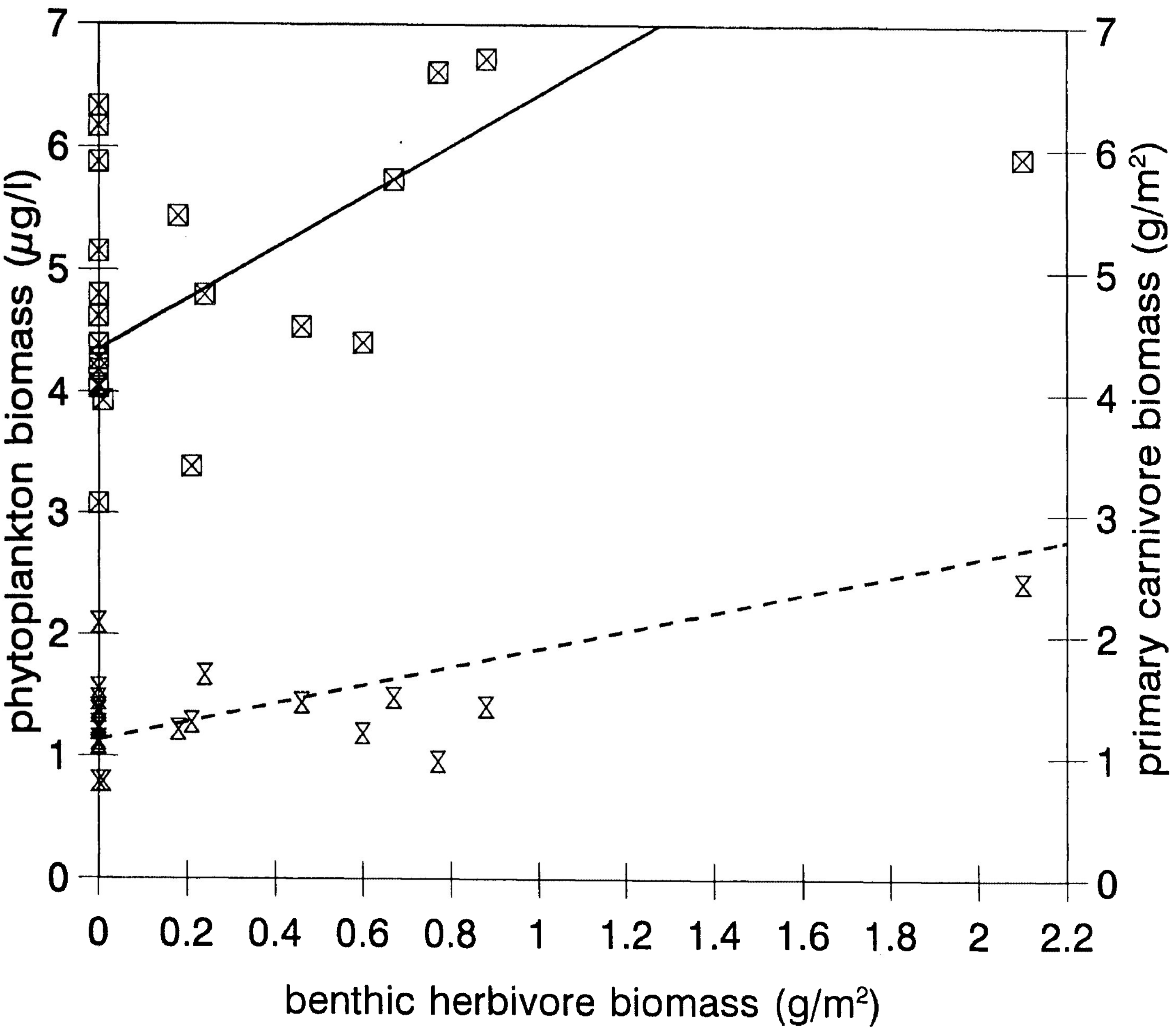
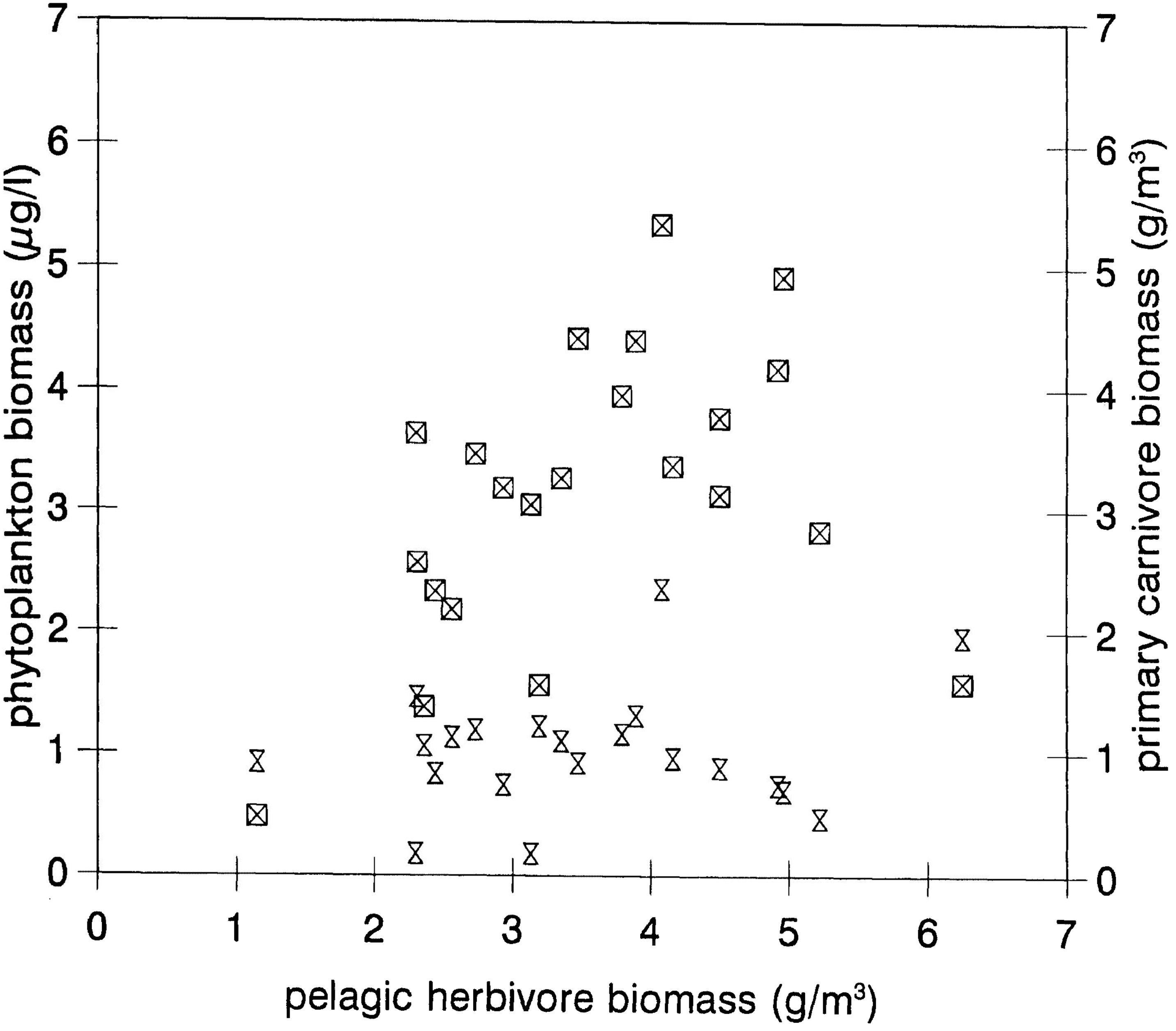

phytoplankton biomass (µg/l)
primary carnivore biomass (g/m²)
benthic herbivore biomass (g/m²)
0
1
2
3
4
5
6
7
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2

Fig. 10. Scatterplot of the biomasses of phytoplankton and pelagic primary carnivores with pelagic herbivore biomass. The phytoplankton model II regression was not significant ($y=-0.44+0.410x$, $\mathrm{CI}_{\mathrm{slope}}=\pm 0.188$, $p=0.392$). The primary carnivore model II regression was almost significant ($y=-0.44+1.007x$, $\mathrm{CI}_{\mathrm{slope}}=\pm 0.430$, $p=0.064$).


phytoplankton biomass (μg/l)
primary carnivore biomass (g/m^3)
pelagic herbivore biomass (g/m^3)
0
1
2
3
4
5
6
7

DISCUSSION

Resistance and resilience

Essentially all timber harvest disturbances were capable of displacing either zooplankton or macroinvertebrate communities. Both communities varied in their overall ability to withstand specific disturbances, but there was an unexpected lack of a significant difference in resistance, even though the modes and mechanisms of disturbance differed. This finding implies that, over the measured range of disturbances, there may be limits of resistance for a community, possibly corresponding to a resistant "core" of species. In the zooplankton this hypothesis is corroborated by the displacement of individual community components. PC2 was consistently more resistant to disturbance than PC1.

Resistance may also be spatially variable across lake habitats. This is most evident in the zooplankton community, where littoral organisms (summarized by PC1) may be buffering the typical nearshore inputs, associated with land-based disturbances, to the pelagic zone (summarized by PC2). This interpretation supports Wetzel's (1990) assertion that the production and metabolism of littoral biota frequently control the biogeochemical and energetic fluxes within lakes.

Two additional comparisons of resistance are important in understanding community-level dynamics from a theoretical perspective. The cottaging and fishing disturbances respectively represent alterations of "bottom-up" (Wetzel 1983) and "top-down" (Carpenter et al. 1985) forces in aquatic communities. These two forces, responsible for many of the dynamic properties of communities, have long been viewed as opposing theories, but more recently have been studied in an effort to determine their relative contributions (for a review see Matson and Hunter 1992). Although the OFAN model and others (e.g., McQueen et al. 1986, Mittelbach et al.

1988, Liebold 1989) attempt to integrate the effects of both resources and predators, an important question still left unanswered is when and where these regulatory forces dominate and balance within a system (*sensu* McQueen et al. 1986). Examining the cottaging and fishing disturbances can thus give insights into the relative contributions of predation and productivity in community regulation.

For both of these disturbances, the macroinvertebrate community was resistant, although the nature of this resistance differed substantially (Table 5). Fishing produced a near significant increase in the herbivorous component of the community, suggesting a potential indirect effect of the disturbance. Unfortunately, no data were available for planktivorous fish which would have been necessary to evaluate transmission of the disturbance to the zooplankton community. Within the zooplankton, the largest change observed was an increase in the littoral benthic zooplankton biomass. As a result, it appears that the top-down fishing disturbance cascades further down the food chain than the bottom-up disturbance moves up. This finding agrees with predictions, regarding the transmission of variance throughout an aquatic food chain, made by McQueen et al. (1986, 1989). They hypothesized that the trophic cascade could become uncoupled at the zooplankton - phytoplankton link in mesotrophic lakes.

Of the disturbances that I identified as pulsed, only road construction significantly displaced community structure and hence, by definition, gave the only analysis of resilience. This analysis was, however, complicated by the correlation between time since road construction and the standardized distance of roads. The resilience of the macroinvertebrate community was zero when the covariation between the timing and magnitude of road construction was removed by the analysis on residual variation.

The macroinvertebrate communities in disturbed lakes did not converge on those present in undisturbed lakes. Once displaced by road construction disturbance, macroinvertebrate species abundances are apparently not resilient. This finding is in contrast to the population and community resilience recently documented for a highly productive three trophic-level lake ecosystem (Persson et al. 1993) and the resilience of a lake phosphorus cycle in three and four-link lakes (Carpenter et al. 1992). Both studies documented very short return times (approximately two years) following piscivore or planktivore manipulations. These return times were also representative of the duration of the monitoring conducted in these systems (3-4 years). My test for resilience approximates a temporal scale an order of magnitude longer. Connell and Sousa (1983) have argued for a minimum pre- and post-disturbance record at least equal to the turnover time of the longest-lived species in a system (estimated at approximately 10 years for temperate northern pike populations) before its recovery can be assessed. The dangers inherent in ignoring this requirement have recently been empirically documented by McQueen et al. (1992). They demonstrated discrepancies between interpretations of short (2-3 years) and long-term (10-14 years) community biomass patterns resulting from experimental whole-lake manipulations of piscivore biomass.

My studies of non-resilient northern lake communities demonstrate the importance of a rigid protocol to assess community displacement. Carpenter (1992) and Persson (1993) did not assess whether communities were significantly displaced. Their estimates of resilience are therefore suspect. Secondly, my protocol includes, as a prerequisite for the measurement of resilience, that the disturbance be pulsed. Carpenter et al. (1992) apparently disregarded the problems that can arise with press disturbances. The high resilience of lake phosphorus dynamics following a piscivore addition may be confounded by an ongoing perturbation altering the post-disturbance environment. Resilience may not be the property being measured. This criticism does not apply to Persson et al. (1993) who documented high community resilience to their pulsed reductions of zooplanktivorous fish biomass.

The road construction disturbance I consider in my analysis of resilience was not pulsed in the shortest term, but should have attenuated over time. Following timber harvest, studies in British Columbia coastal forests have recorded a return to pre-disturbance levels of vegetation cover within 10 years (Hartman and Scrivener 1990) of harvest. Revegetation of abandoned logging roads and the roadsides of those that are maintained, likely proceeds at a similar rate and actual soil loss from roads (although influenced by a number of factors such as surfacing and slope) may be largely restricted to the short period before vegetation becomes well-established (in 2.5 years, 75% of the soil erosion at a stream crossing occurred in the first two months after construction - Swift 1988).

Alternative stable states?

A necessary condition for a community to occupy an alternative stable state is a constancy in the relative abundances of its components over time following a disturbance. The use of the term "stable" is unfortunate because it has a range of meanings and also because it implies a long-term unchanging condition, when in reality, the temporal dynamics described are necessarily limited by the duration of the study. Conservative criteria indicate that detection of alternative states requires similar pre and post-disturbance physical environments, termination of the external disturbance, and appropriate temporal and/or spatial scales between alternative states (Connell and Sousa 1983, Peterson 1984). The apparent lack of resilience in northern aquatic communities to a pulsed land-use disturbance may represent alternative states for macroinvertebrates following road construction.

Persson et al. (1993) were unable to demonstrate an alternative stable state in their study of a highly productive lake with three trophic levels following both planktivore manipulations and piscivore additions. They hypothesized, however, that the time scale of experiments may have affected their qualitative outcomes and hence the existence of alternative stable states. A perturbation that initially may not be capable of displacing a community to a new state may do so when sustained. This type of extended "pulse" typifies forest harvest and road construction disturbances. It thus appears that extended periods of initial disturbance can displace communities such that they have difficulty in converging on undisturbed controls.

The OFAN model

This study confirmed the OFAN prediction that primary carnivore biomass should not vary between "cottaged" and undisturbed lakes. The prediction of a significant increase in herbivore biomass depended upon whether I assessed resistance (confirmed) or herbivore biomass (rejected) as my test of the model. The discrepancy between the two analyses may be partially due to the prevalence of detritivores and omnivores in the resistant macroinvertebrate community (approximating primary carnivory). These organisms effectively decrease the number of trophic interactions between the two communities, decoupling feedback links along food chains. In addition, the detrital pool itself can have a strong buffering influence on a system's dynamics following a disturbance (DeAngelis et al. 1989*b*), and may also account for the resistance at the macroinvertebrate community level.

The comparison of chlorophyll *a* between undisturbed and disturbed lakes gave results consistent with the model's predictions of no long-term increase in primary producer biomass following nutrient addition. This test was based only on the total biomass of the pelagic phytoplankton community and thus suffered from deficiencies similar to the analysis of the entire macroinvertebrate community. The problem that might have the greatest effect on the validity of this test was modelled and tested by Liebold (1989) and concerns the relative edibility of prey organisms constituting a trophic level. Liebold found that the role of predation and productivity in determining trophic level biomass depends strongly on the diet breadth of the consumers. If the biomass of inedible prey is less than the biomass of edible prey, a positive correlation between the biomasses in adjacent trophic levels could result. I cannot assess Liebold's criticism without data on the proportion of edible and inedible algae, but nevertheless the analysis of this trophic level can be interpreted as qualified support for the OFAN model.

The regression analysis of trophic level biomasses in undisturbed communities provided yet another assessment of the OFAN model. These analyses unambiguously rejected the model's predictions of no relationship between primary carnivore and herbivore biomass while supporting the model only at the phytoplankton - herbivore link. A lack of a significant relationship between phytoplankton and zooplankton biomass has also been documented by McQueen et al. (1992) who showed that although these biomasses may covary over the short-term, the covariance disappears with longer-term studies. Even though my results for both the pelagic and benthic samples were similar, the comparison between primary producer biomass and the benthic macroinvertebrate herbivores and carnivores may be biased. Macroinvertebrate community biomass was estimated using strict trophic subsets for the benthos of the entire lake, whereas the chlorophyll *a* measurements were restricted to the pelagic zone. Since phytoplankton species composition and productivity can differ markedly between the littoral and pelagic zones (Kairesalo 1980, Barko et al.

1984), pelagic chlorophyll *a* may not be representative of the entire lake. Schallenburg and Kalff (1993) have recently reported a much closer link between macrobenthos and bacterial production in the littoral zone than in the pelagic zone, suggesting a potential decoupling between pelagic and benthic processes in lakes.

As a whole, the three tests reject the OFAN model. Some, but not all, results are consistent with an alternative prediction by Mittelbach et al. (1988), that biomasses between adjacent trophic levels should be positively correlated. Primary producers and herbivores have temporal dynamics that essentially vary together and thus may be representative of the Type I functional responses assumed in the original OFAN model. In contrast, the link between herbivore and primary carnivore biomass is confounded with numerous ontogenic niche shifts and size-structured interactions. These latter age- and size-structure influences are the primary reason that Mittelbach et al. (1988) predict the positive biomass correlations.

Disturbances

Land use and community structure - Land-use disturbances, encompassing the construction of roads and the harvest of trees, form an important subset of those disturbances associated with timber harvest since they represent the activities directly linked to logging disturbances. Road construction appears to have its greatest impact on the omnivorous component of the macroinvertebrate community (Table 5). Most species in this PC are abundant in lakes with extensive aquatic macrophyte growth. Although not significant, the timber-harvest disturbance suggested an alternate trend in the displacement of the zooplankton community, decreasing the abundance of smaller littoral organisms (characteristic of shallower lakes with some detrital accumulation). These opposing patterns appear to indicate differing pathways by which community structure is altered following land-use disturbance. Timber-harvest effects were close enough to statistical significance to suggest that land-use planners also give them serious consideration.

The cottaging disturbance was similarly correlated strongly with changes in the littoral component of the zooplankton community, while the fishing disturbance tended to impact the littoral and the pelagic zooplankton as well as the herbivorous macroinvertebrate communities. Although these relationships give little direct insight into the mechanisms of disturbance, they do at least suggest that mechanisms differ. They also demonstrate that not all components of a community are affected equally. These findings point to the need for a cumulative-effects approach to deciphering the mechanisms, and predicting the effects, of land-use and other disturbances to natural systems.

Caveats

Steinman et al. (1991) identified three important problems that resilience indices must overcome to be effective. The first is the inability to document lag time, if present, before a community is displaced following a disturbance. The second concerns the shape of the recovery curve if the relationship is curvilinear or non-linear. The third identifies the need for discrete quantifiable estimates appropriate to statistical analysis. All three concerns are accommodated in my protocol. The first two solutions can be addressed by examining the residuals from the regression of community displacement versus time since disturbance. No curvilinear or non-linear trend was apparent in my regressions.

It is surprising that I could find no relationship between community displacement and the magnitude of disturbance. This contrasts with DeMelo et al's (1992) assertion that the size of the experimental effect should reflect the degree of perturbation. One possibility is that the seasonal timing of disturbance may be especially important in structuring aquatic communities (DeAngelis et al. 1989*a*). Seasonal changes are well documented in aquatic ecosystems and may even affect the relative importance of bottom-up and top-down control by varying the rate of primary production (McQueen et al. 1986, Bartell et al. 1988, DeAngelis et al. 1989*a*). The effects of road construction (and most other monitored disturbances) should mainly be confined to a relatively short summer window of opportunity. Boulton et al. (1992) found a similar lack of a simple relationship between resistance and either disturbance magnitude or timing for a stream macroinvertebrate community subject to seasonal floods of varying magnitudes.

A criticism, by no means limited to my measurement of community resistance and resilience, concerns the arbitrary definition of communities along taxonomic lines (Oksanen 1991). Analyses focused on arbitrarily defined sub-communities limit insights into overall community processes. Although the "communities" analyzed here were somewhat arbitrarily defined, they represent benthic and pelagic habitats, and should still adequately estimate the resistance and resilience of trophic assemblages within the entire lake's biota.

Abrams (1993) has modelled the consequences of violating the primary OFAN assumption, the homogeneity of trophic levels. He found a number of theoretical food-web configurations that refute OFAN predictions, and thus argued against a reliance on ecological models that disregard heterogeneity. Even with heterogeneity incorporated, there are problems with Abrams' treatment of this problem because the nature of heterogeneity may also be important to food-web function. Experimental analyses of interaction strengths in an inter-tidal community (Paine 1992), and a terrestrial island community (Goldwasser and Roughgarden 1993), have generally shown a large dominance of "weak" food-web links that contrast with the "strong" linkages assumed by Abram's simulations. Nevertheless, models of community regulation may benefit from further consideration of temporal dynamics and size-structured interactions. Future research on patterns of resistance and resilience should strive for an experimental approach, with an emphasis on controlled disturbances that can isolate the processes involved in displacing communities.

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Appendix 1. An overview of some of the statistical tools used to estimate community resistance and resilience.

Principal Components Analysis

A PCA was used primarily as a summarization technique to reduce the dimensionality of the biological data set from a large set of correlated variables to a new (and smaller) set of uncorrelated variables (Chatfield and Collins 1980) that accounted for as much of the variation in the species abundances as possible. A secondary objective was the optimal definition of ecological gradients (Austin 1976). With these objectives, I sought to obtain a working description of overall community structure that could then be used to assess the potential effects of disturbance.

To arrive at an optimal balance between data reduction and a comprehensible and representative summary of community structure in my final PCA solution, I employed a number of rules of thumb to assist in taxa deletion following the removal of taxa occurring in less than 10% of the lakes.

1) A minimum limit of 50% of the variation in the data set had to be accounted for in the first three (or less) principal components.

2) This limit typically coincided with "larger" eigenvalues, usually greater than one, that indicate how much of the variation is contained in a specific PC.

3) The KMO score calculates an overall index of how well the PCA solution derives uncorrelated PCs by comparing the sum of partial correlation coefficients to the sum of observed (Pearson) correlation coefficients (Norušis 1990). The KMO score is close to one when this difference is small.

4) Rather than summing all the partial and observed correlation coefficients as above, measures of sampling adequacy can be similarly calculated for individual

variables. The lowest of these scores were used to remove single variables after a minimum of 50% of the variation in the data was accounted for and the KMO score was not yet "acceptable" (0.6 - Norušis 1990).

Multivariate *t*-tests

Multivariate tests of significance test the same types of hypotheses that univariate statistics do (in this case, no difference between groups of population means). The term "*t*-test" is somewhat of a misnomer because the *t*-statistic is not the test statistic in use (Wilk's lambda was chosen as the test statistic here), but this terminology has been retained because it vividly describes the objective of this test. The discriminant analysis uses Wilk's lambda as the test statistic in my test for a difference between PC scores in disturbed and undisturbed lakes.

Appendix 2. Basin morphometry (columns 1-7) and water chemistry for 36 northern pike lakes in northwestern Ontario. Asterisks denote lakes in zooplankton data set.

Lake Name	Watershed Area (km^2)	Lake Area (ha)	Volume (m^3)	Relative Depth (m)	Littoral Zone (% area)	Shore length (km)	Retention Time (yrs)	Secchi Depth (m)	Heat Budget (cal/cm^2)	Mean Temp (°C)	P (µg/l)	Turbidity (JTU)	Chl$_a$ (µg/l)	Conductivity (µmhos/cm)	DOC (mg/l)
Wartman*	4.38	34	27.8	0.52	100.0	3.58	0.2046	1.8	2235.7	6.90	14.6	1.70	5.3	23	14.1
Madalaine	67.47	99	271.5	0.37	96.8	6.65	0.1667	1.9	5669.3	7.67	17.2	2.30	3.7	38	7.4
Sunbow	54.41	563	3580.9	0.66	42.9	27.48	2.7266	2.5	10180.2	7.00	15.7	2.35	7.8	36	16.1
Un#24	5.30	23	94.4	1.79	63.2	3.22	0.7381	3.6	6424.2	6.65	15.7	0.80	3.0	40	10.4
Un#23	3.65	20	69.7	1.23	70.6	2.54	0.7911	1.8	5810.9	6.66	17.7	1.80	5.0	42	11.1
Missing	48.45	10	11.4	0.78	100.0	2.32	0.0085	2.1	2146.2	6.95	22.0	4.20	2.2	38	10.0
Paul#1	77.07	20	84.1	2.13	64.8	2.98	0.0396	3.1	5554.1	6.04	18.7	1.50	2.9	32	9.2
Un#15*	18.14	51	80.9	0.35	100.0	7.83	0.2156	2.1	3545.3	7.82	14.1	1.11	3.4	34	8.3
Pistol*	1.25	18	20.7	0.42	100.0	2.75	0.7992	2.2	2669.0	8.05	14.5	2.75	2.4	123	11.6
East Divide*	0.66	7	20.1	2.01	85.3	1.64	1.4672	3.4	6168.9	7.85	8.4	1.34	2.5	281	6.2
U. Sabrina*	26.05	122	280.5	0.44	95.9	10.14	0.5204	1.6	4943.6	7.87	17.7	2.56	3.2	38	12.5
Shafton*	5.61	120	171.9	0.22	100.0	11.75	1.4806	2.2	3058.2	7.59	17.7	3.50	7.1	107	11.8
Amp*	3.79	96	288.9	0.52	93.2	7.11	3.6849	3.2	6298.1	7.73	12.0	1.28	2.5	66	8.0
Mathe*	2.82	22	16.4	0.13	100.0	3.47	0.2813	0.0	1800.0	8.25	19.2	2.35	2.1	159	10.0
Un#13*	3.96	59	313.1	1.71	50.0	10.52	3.8230	4.6	9153.0	7.05	10.4	1.40	1.2	114	4.5
U. Clearwater*	125.55	31	77.9	1.10	81.7	3.08	0.0200	1.0	4545.9	7.02	15.8	0.36	2.1	27	23.0
Un#12*	91.50	8	10.1	2.94	100.0	1.62	0.0036	2.6	2708.4	7.62	17.7	1.23	3.1	124	13.7
Albert*	1.41	19	61.9	1.28	82.1	3.31	1.4132	2.6	6478.8	7.46	19.2	1.33	2.3	184	13.0
Handley*	16.85	114	118.8	0.16	100.0	6.80	0.2556	1.4	1472.9	5.79	16.1	4.40	2.9	72	13.6
Pesheau	6.50	28	42.4	0.18	100.0	3.78	0.2365	1.7	2387.2	6.20	16.4	4.00	3.0	78	15.0
MacCormack*	4.50	41	41.4	0.69	99.1	4.61	0.3336	2.3	2114.2	7.48	13.1	2.50	3.0	34	6.8
Howcum	4.31	10	33.4	3.17	75.0	2.04	0.2809	2.7	4572.9	5.94	11.5	0.99	2.8	29	9.4
Cummins*	4.19	26	77.7	1.49	80.8	4.54	0.5977	2.3	4422.5	6.19	17.5	1.80	2.0	43	9.7
Barnum*	9.30	73	346.7	2.57	68.0	9.71	1.2013	3.2	5595.0	5.69	9.3	0.85	1.3	30	8.4
Lottit	5.17	50	83.8	0.98	97.0	8.22	0.5224	2.7	3387.0	7.32	12.0	1.67	5.6	40	8.2
Shillabeer*	36.48	786	862.9	0.22	99.9	18.48	0.7622	1.5	1832.3	6.41	30.5	5.65	10.5	297	16.7
Wolfpup*	70.56	358	948.2	0.43	79.3	22.11	0.4330	3.0	4654.2	6.89	13.9	2.30	4.3	254	7.0
Un#05*	9.67	101	360.2	1.59	72.9	9.33	1.8001	2.9	5219.9	6.15	13.8	1.70	3.3	32	13.4
Whistle*	19.12	296	1106.0	0.41	63.0	13.39	2.0971	2.1	5651.9	6.27	17.1	2.40	3.7	49	17.8
Un#03*	2.33	26	107.3	2.27	64.7	5.35	1.4841	2.6	6422.4	6.64	12.6	1.44	2.0	34	13.3
Smiley*	167.94	383	1515.5	0.69	67.2	43.18	0.3271	1.7	6104.2	6.35	17.7	1.85	3.0	44	15.3
Scandrett*	41.12	73	437.6	1.09	40.3	8.72	0.3858	1.9	10313.8	7.29	13.7	0.90	2.4	42	16.2
Mott*	8.38	73	371.1	0.78	50.0	9.18	1.6051	1.9	9175.7	7.25	15.6	1.40	1.2	45	17.4
Keelor*	5.22	60	90.3	0.52	99.9	6.61	0.6271	1.9	3355.8	7.80	11.7	2.40	1.6	72	16.2
Edmondson*	48.17	263	2082.8	1.60	41.3	28.14	1.5674	2.2	9387.9	5.96	10.0	0.92	2.4	45	13.8
Colville*	6.17	48	368.3	1.94	38.0	6.20	2.1639	2.9	9287.5	6.02	10.9	0.45	2.6	64	15.2

Appendix 3. All individual taxa identified in the benthic macroinvertebrate community samples. Organisms included in exclusive trophic subsets are identified (primary carnivore=^{p}, herbivore=^{h}).

Haplotaxis gordioides
Aeolosoma sp
Lumbriculidae
Naididae
Stylaria lacustris
Uncinais uncinata
Pristina breviseta
Pristina sp
Pristinella sp
Tubificidae
HIRUDINEA
Erpobdellidae
Nepholopsis obscura
Glossiphonidae
Helobdella stagnalis
Hirudinidae
NEMATODA
Dugesia tigrina
HALACARIDAE
HYDRACARINA^p
Arrenurus sp^p
Forelia sp^p
Forelia floridensis^p
Huitfeldtia rectipes^p
Hydrachna sp^p
Hydrodroma sp^p
Hydryphantes sp^p
Koenikea sp^p
Lebertia sp^p
Limnesia sp^p
Mideopsis sp^p
Neumania sp^p
Piona sp^p
Unioncola sp^p
Limnochares sp^p
Sperchonopsis sp^p
Tyrellia sp^p
Hygrobates sp^p
Crangonyx gracilis^p
Hyalella azteca^p
Oronectes sp^p
Mysis relicta^p
OSTRACODA
Lutrochus sp^p
Dytiscidae^p
Dytiscus sp^p
Hydroporus sp^p
Deronectes sp^p
Elmidae^p
Narpus sp^p
Gyrinus sp^p
Haliplidae^p
Haliplus sp^p
Peltodytes sp^p
Hydrophilidae^p
Noteridae^p
Psephenidae^p
Ceratopogonidae^p
Chaoborous sp^p
Chironomidae
Chironominae
Tanypodinae^p
Culicinae
Chrysops sp^p
Tabanus sp^p
Empididae^p
Hemerodromia sp^p
Baetis sp
Callibaetis sp
Caenis sp
Ephemerellidae
Ephemerella sp
Ephemera sp
Hexagenia sp
Heptageniidae
Stenonema sp
Leptophlebidae
Choroterpes sp
Paraleptophlebia sp
Siphlonuridae
HEMIPTERA^p
Corixidae^p
Rheumatobates sp^p
Hebridae^p
Vellidae^p
LEPIDOPTERA^h
Sialis sp^p
Climacia areolaris
Anisoptera^p
Aeshnidae^p
Boyeria sp^p
Cordulegastridae^p
Corduliidae^p
Dorocordulia sp^p
Somatochlora sp^p
Gomphidae^p
Libellulidae^p
Leucorrhinia sp^p
Erythrodiplax sp^p
Pantala sp^p
Coenagrionidae^p
TRICHOPTERA
Brachycentridae^h
Calamoceratidae
Hydroptilidae^h
Oxythira sp^h
Lepidostomatidae
Lepidostoma sp
Leptoceridae
Oecetis sp
Limnephilidae
Molanna sp^h
Odontoceridae
Phryganeidae^p
Agrypnia sp^p
Polycentropodidae^p
Cyrnellus sp^p
Psychomiidae^p
GASTROPODA
Hydrobiidae
Amnicola sp
Lymnaeidae
Physa sp
Planorbidae
Gyralus sp
Helisoma sp
Pleuriceridae
Valvata bicarinata
Sphaeriidae
Unionidae
PORIFERA
BRYOZOA

Appendix 4. All individual taxa identified in the benthic zooplankton community samples. Organisms included in exclusive trophic subsets are identified (primary carnivore=^{p}, herbivore=^{h}).

Chydoridae^{h}
Alona sp^{h}
Alona guttata^{h}
Disparalona leei^{h}
Eurycerus lamellatus^{h}
Ceriodaphnia sp^{h}
Daphnia sp^{h}
Daphnia dubia^{h}
Daphnia galeata mendotae^{h}
Daphina longiremis^{h}
Daphina pulex^{h}
Daphnia rosea^{h}
Simocephalus serrulatus^{h}
Holopedium gibberum^{h}
Leptodora kindtii^{p}
Macrothricidae^{h}
Acantholeberis curvirostris^{h}
Ilyocryptus acutifrons^{h}
Ilyocryptus spinifer^{h}
Ilyocryptus sp^{h}
Ofryoxus gracilis^{h}
Polyphemus pediculus^{p}
Diaphanosoma birgei^{h}
Diaphanosoma brachyurum^{h}
Latona parviremis^{h}
Latona setifera^{h}
Sida crystallina^{h}
Diaptomidae^{h}
Epischura sp^{h}
Epischura lacustris^{h}
Cyclopidae^{p}
Eucyclops seperatus^{p}
Macrocyclops sp^{p}
Macrocyclops albidus^{p}
Mesocyclops edax^{p}
Mesocyclops leukarti^{p}
Orthocyclops modestus^{p}
Tropocyclops sp^{p}
Tropocyclops prasinus mexicanus^{p}
Harpacticoida

Appendix 5. Unstandardized disturbance data for 36 northern pike lakes in northwestern Ontario. Asterisks denote lakes in the zooplankton data set. Magnitudes of zero and dashes indicate undisturbed lakes.

Lake Name	Area of timber harvested (km^2)	Time Since Harvest (yr)		Distance of roads (km)	Time Since Construction (yr)		Number of Cottages	Time Since Cottaging (yr)	
		Benthos	*Zooplankton*		*Benthos*	*Zooplankton*		*Benthos*	*Zooplankton*
Wartman	0.00	-	-	0.20	42.00	40.00	5.00	13.00	11.00
Madalaine	0.51	0.00	-	0.08	15.00	-	7.00	16.00	-
Sunbow	1.25	6.19	-	0.03	15.00	-	0.00	-	-
Un#24	0.00	-	-	0.20	16.00	-	0.00	-	-
Un#23	0.00	-	-	0.26	16.00	-	0.00	-	-
Missing	0.02	13.00	-	0.47	39.00	-	3.00	25.33	-
Paul#1	0.50	13.00	-	0.72	44.50	-	5.00	21.80	-
Un#15*	1.35	28.69	28.69	0.00	-	-	0.00	-	-
Pistol*	0.00	-	-	0.28	64.67	64.67	0.00	-	-
East Divide*	0.03	1.00	1.00	0.67	82.00	82.00	0.00	-	-
U. Sabrina*	0.30	28.82	25.82	0.39	43.86	40.86	0.00	-	-
Shafton*	0.36	23.00	20.00	1.57	82.00	79.00	0.00	-	-
Amp*	0.00	-	-	0.38	23.00	23.00	0.00	-	-
Mathe*	0.18	16.00	16.00	0.72	72.89	72.89	0.00	-	-
Un#13*	0.04	19.00	19.00	0.39	28.71	28.71	0.00	-	-
U. Clearwater*	13.51	18.68	16.68	0.00	-	-	0.00	-	-
Un#12*	0.21	31.00	31.00	0.44	26.00	26.00	0.00	-	-
Albert*	0.92	24.68	24.68	0.64	27.00	27.00	0.00	-	-
Handley*	1.27	13.96	13.96	0.00	-	-	0.00	-	-
Pesheau	0.60	24.00	-	0.03	39.00	-	0.00	-	-
MacCormack*	0.17	29.06	26.06	0.30	69.96	66.96	2.00	30.00	27.00
Howcum	0.00	-	-	0.23	78.00	-	4.00	24.75	-
Cummins*	0.63	53.43	50.43	0.67	62.00	59.00	39.00	24.92	21.92
Barnum*	1.03	58.70	55.70	0.08	56.76	53.76	22.00	24.50	21.50
Lottit	0.67	54.82	-	0.20	59.00	-	6.00	14.50	-
Shillabeer*	10.72	33.52	33.52	0.00	-	-	0.00	-	-
Wolfpup*	21.29	27.78	24.78	0.08	42.32	39.32	0.00	-	-
Un#05*	0.23	3.43	3.43	0.09	8.00	8.00	0.00	-	-
Whistle*	8.46	11.68	11.68	0.01	15.00	15.00	0.00	-	-
Un#03*	1.37	12.00	12.00	0.70	12.00	12.00	0.00	-	-
Smiley*	15.06	8.58	8.58	0.01	11.00	11.00	0.00	-	-
Scandrett*	2.81	17.18	17.18	0.28	21.00	21.00	0.00	-	-
Mott*	1.14	12.27	9.27	0.00	-	-	0.00	-	-
Keelor*	0.00	-	-	0.11	42.00	39.00	0.00	-	-
Edmondson*	6.08	10.49	10.49	0.05	12.40	12.40	11.00	83.00	83.00
Colville*	1.72	19.08	16.08	0.13	20.00	17.00	0.00	-	-

Appendix 5 (continued). Standardized disturbance data for 36 northern pike lakes in northwestern Ontario. Asterisks denote lakes in the zooplankton data set. Magnitudes of zero and dashes indicate undisturbed lakes.

Lake Name	Area of Fire (km^2)	Time Since Fire (yr)		Index of Fishing Magnitude	Time Since Fishing (yr)	
		Macroinvertebrate	*Zooplankton*		*Macroinvertebrate*	*Zooplankton*
Wartman	0.00	-	-	1.00	21.50	19.50
Madalaine	1.13	43.00	-	2.00	7.50	-
Sunbow	8.00	43.00	-	1.00	7.50	-
Un#24	1.42	43.00	-	0.00	-	-
Un#23	0.67	43.00	-	0.00	-	-
Missing	0.00	-	-	1.00	19.50	-
Paul#1	0.19	49.00	-	1.00	39.00	-
Un#15*	0.00	-	-	0.00	-	-
Pistol*	0.00	-	-	0.00	-	-
East Divide*	0.00	-	-	0.00	-	-
U. Sabrina*	0.00	-	-	0.00	-	-
Shafton*	0.00	-	-	1.00	41.75	38.75
Amp*	0.00	-	-	0.00	-	-
Mathe*	0.00	-	-	0.00	-	-
Un#13*	0.00	-	-	0.00	-	-
U. Clearwater*	2.36	52.00	50.00	1.00	16.00	14.00
Un#12*	0.00	-	-	0.00	-	-
Albert*	0.00	-	-	0.00	-	-
Handley*	0.00	-	-	0.00	-	-
Pesheau	0.00	-	-	0.00	-	-
MacCormack*	2.05	52.00	49.00	1.00	41.25	38.25
Howcum	0.48	49.00	-	1.00	39.00	-
Cummins*	1.22	52.00	49.00	1.00	31.75	28.75
Barnum*	0.56	52.00	49.00	1.00	31.75	28.75
Lottit	0.00	-	-	1.00	29.50	-
Shillabeer*	0.00	-	-	1.00	15.50	15.50
Wolfpup*	0.00	-	-	2.00	23.25	20.25
Un#05*	4.94	47.00	47.00	0.00	-	-
Whistle*	0.00	-	-	2.00	7.50	7.50
Un#03*	0.00	-	-	0.00	-	-
Smiley*	0.00	-	-	1.00	5.50	5.50
Scandrett*	0.33	3.00	3.00	1.00	10.50	10.50
Mott*	0.00	-	-	1.00	9.25	6.25
Keelor*	0.00	-	-	1.00	21.75	18.75
Edmondson*	0.00	-	-	2.00	21.50	21.50
Colville*	0.05	2.00	0.00	1.00	10.75	7.75