

Assessing the Interdependence of Assemblages from Rainy Lake Fisheries Data

Yosef Cohen

Department of Fisheries and Wildlife, University of Minnesota, St. Paul, MN 55108, USA

Paul Radomski

Minnesota Department of Natural Resources, Section of Fisheries, Route 8, Box 8, International Falls, MN 56649, USA

and Ron Moen

Department of Fisheries and Wildlife, University of Minnesota, St. Paul, MN 55108, USA

Cohen, Y., P. Radomski, and R. Moen. 1993. Assessing the interdependence of assemblages from Rainy Lake fisheries data. *Can. J. Fish. Aquat. Sci.* 50: 402–409.

We applied ad hoc methods to quantify differences among fish communities in four different locations in Rainy Lake using data from index netting from long-term studies. Our analysis addressed problems of inconsistencies in data collection. We established the amount of differences and similarities among the communities by analyzing species diversity over time, utilizing matrices of partial correlations and discriminant function analysis. We also identified role reversal, i.e. synchronization in fluctuations of relative catch-per-unit-effort (CUE) between pairs of species in these communities. In the less disturbed communities, walleye (*Stizostedion vitreum*) contributed most to the synchronization in the fluctuations of the yearly relative CUE among six common species. In the more disturbed locations, this contribution was primarily due to yellow perch (*Perca flavescens*) and sauger (*Stizostedion canadense*). The disturbed community in one location (the North Arm) exhibited marked decrease in species diversity. Recent restrictions on the fisheries in the North Arm resulted in an increase in species diversity. Fish communities, particularly in large lakes, may differ in the detail of species interactions and population fluctuations among locations within the lake. These differences must be taken into account in analysis and management of fisheries.

Nous avons appliqué des méthodes *ad hoc* pour clarifier les différences observées entre des communautés de poissons à quatre endroits différents du lac Rainy à l'aide de données de prises au filet provenant d'études à long terme. Notre analyse portait sur des problèmes d'incohérence dans la cueillette des données. Nous avons déterminé l'importance des différences et des ressemblances entre les communautés en analysant la diversité des espèces en fonction du temps, à l'aide de matrices de corrélation partielle et de l'analyse discriminante. Nous avons également identifié des renversements de rôle, p. ex. la synchronisation des fluctuations de la prise par unité d'effort (PUE) relative entre des paires d'espèces de ces communautés. Parmi les communautés les moins dérangées, c'est le doré (*Stizostedion vitreum*) qui a contribué le plus à la synchronisation des fluctuations de la PUE relative annuelle pour six espèces communes. Dans les secteurs plus perturbés, cette contribution venait principalement de la perchaude (*Perca flavescens*) et du doré noir (*Stizostedion canadense*). La communauté perturbée à un emplacement (le Bras nord) présentait une diminution marquée de la diversité des espèces. Les restrictions récentes pour les pêches dans le Bras nord ont entraîné une augmentation de la diversité des espèces. Les communautés de poissons, et plus particulièrement celles des Grands Lacs, peuvent présenter des différences au niveau du détail des interactions des espèces et des fluctuations, d'un lieu à l'autre dans le même lac. Il faut prendre en considération ces différences lors de l'analyse et de la gestion des pêches.

Received October 17, 1991

Accepted August 18, 1992

(JB269)

Reçu le 17 octobre 1991

Accepté le 18 août 1992

Rainy Lake and the Namakan Reservoir are located on the border between Minnesota and Ontario, Canada (Fig. 1). The history of the development of fisheries in this lake and the lake's complex geography have complicated the analysis of fisheries data and frustrated attempts to sustain the stock of walleye (*Stizostedion vitreum*).

Commercial fishing in Rainy Lake began in 1885 with a pound net fishery for lake sturgeon (*Acipenser fulvescens*). Gillnetting for lake whitefish (*Coregonus clupeaformis*) began in 1904. Since the 1920s, walleye, northern pike (*Esox lucius*) and lake whitefish have been the most important species, economically. Bonde et al. (1965) compiled data on commercial

harvests for all species before 1951. Starting in the early 1970s, management gradually reduced the commercial harvest of walleye by increasing the minimum gillnet mesh size and limiting the number of nets per license.

In response to declining walleye harvest, the Minnesota Department of Natural Resources (MDNR) established creel surveys in the 1950s. Bonde et al. (1961, 1965), Johnson et al. (1966), and Johnson (1967) documented the decline in walleye abundance from 1956 to 1967. Both reported drastic declines in commercial catch in the North Arm. To restore the walleye fishery, they recommended both specific water levels at specific dates and installation of spawning reefs (Newburg 1975).

Johnson et al. (1966) recommended restrictions on the walleye fishery: both commercial and sport. The MDNR tried to increase walleye abundance; they intermittently stocked fry and fingerlings in the Minnesota portion of the South Arm annually beginning in 1933. The Ontario Ministry of Natural Resources (OMNR) has stocked walleye eggs and fry intermittently since 1932. Artificial spawning reefs, extending over approximately 8360 m², were constructed in Rainy Lake. From 1971, management delayed the opening of the walleye fishing season by 2 wk in Black Bay, a major walleye spawning area. The OMNR has established nine fish sanctuaries throughout the lake. No fishing is permitted for any species from April 1 to June 14 in these areas. In 1990, the MDNR reduced the possession limit of walleye in Rainy Lake to six. The OMNR reduced the commercial fishing in Rainy Lake by an active buy-out program. However, recreational use of the lake is on the rise. The MDNR collected creel information through surveys during the summers of 1977–78 and 1983–89 (Ernst and Osborn 1980; Kingsley 1989). The OMNR collected creel data intermittently from 1956 to 1986 (McLeod 1988).

Fisheries managers recognize the decline of stocks, particularly in the North Arm. They are also concerned with lack of recruitment of walleye (and other species). Both the MDNR and the OMNR assess fish populations in the lake. They use experimental gill nets. The MDNR implements experimental netting as part of the Minnesota large-lake sampling program (Wingate and Schupp 1985).

Analysis of fisheries data is complicated, not only by the varying management schemes which have been employed historically but also by the complex geography of the lake. There are three basins, making up four distinct fisheries areas in the lake: the South Arm, with separate Minnesota and Ontario fisheries, Redgut Bay, and the North Arm (Fig. 1). For the sake of parsimony, we denote these by SAM, SAO, RGB, and NA, respectively. Because most of the data were collected from these areas, we restrict our analysis to these locations.

To analyze the lake's fisheries at the population level, we have had to distinguish between species assemblages and communities. When analyzing all of the species, we use the term community; when analyzing a subset of the species, we use the term assemblage.

The objectives of our analysis were to develop ad hoc methods to (i) address problems of inconsistencies in data collection, management, and locations, (ii) use these methods to interpret specific statistical relationships among species' relative catch-per-unit-effort (CUE) in the fish communities in the four locations, (iii) determine whether both the communities and species assemblages are heterogeneous in these locations and by how much, (iv) identify interspecific interactions at the population (as opposed to individual) level, and (v) relate our findings to the perceived amount of disturbance to the fish communities in the four locations.

Methods and Procedures

CUE for a species by year and location is our fundamental unit of data. Some authors believe that CUE represents density (Peterman and Steer 1981; Bannerot and Austin 1983; Gulland 1983). Others (Hamley 1975; Hubert 1983; Shephard 1988; Borgstrom 1989) suggest that it does not. Currently, fisheries scientists believe that the usefulness of fisheries data depends on catch ability coefficients, environmental conditions, fish behavior, and other factors (Gulland and Boerema 1973; Sutcliffe et al. 1977; Beddington and Cooke 1982; Gulland

1983; Roff 1983; Schnute 1985). We use CUE mostly as an index for comparisons among locations over the years for which data exist and do not mean to imply density but rather an index of proportional density, identifying changes in relative quantities over time and across locations. Proportional density is the proportion of the total CUE (at a particular year) for a species. Temporal changes (in the relative CUE) are defined as the dynamics of the community (or assemblage). Ours is a retrospective study, aimed primarily at analyzing patterns in the fish communities over time.

Study Area

Rainy Lake and the Namakan Reservoir are part of the headwaters of the Hudson Bay basin. They drain an area of 38 000 km². The surface area of Rainy Lake is approximately 92 383 ha, 75% of it in Ontario. A dam on the Rainy River constructed in 1909 at the site of the former Koochiching Falls (Fig. 1), controls water levels. The water is soft and submerged vegetation is not abundant. Bedrock comprises most of the Lake's littoral zone. The lake has a rocky and irregular shoreline and the three distinct basins previously mentioned. The shoreline along with the lake's 1600 islands is forested. Voyageur's National Park (established in 1975) contains most of the U.S. part of the lake.

Data Collection

Moyle and Burrows (1954), Scidmore (1970), and Wingate and Schupp (1985) documented the procedures for gillnet sampling for the MDNR. Data were collected from the SAM using gillnets 76.20 m long and 1.83 m deep consisting of five panels 12.24 m long with 38-, 51-, 64-, 76-, and 102-mm stretch meshes each. Each net was left in the water for 24 h. In each sampling year, 15–65 sets were used: 65 in 1959, 44 in 1965, 15 in 1967, 25 during 1970–81, and 20 since 1983. Nets were located uniformly across the SAM. In the 1970s, sets were placed in the same location every year, and deep waters were avoided. The CUE units for the MDNR experiments are kilograms fish caught per experimental gill net per 24 h. Until 1981, and from 1983 to 1987, data were collected during the first 2 wk of August and September, respectively. In 1988, the MDNR established that CUE for most species was not significantly different between August and September. Currently, data are collected in September. The experimental netting is implemented as part of the Minnesota large-lake sampling program.

In Ontario, data were collected from the NA, SAO, and RGB (Fig. 1). Merritt and McLeod (1989) described the sampling procedures. The OMNR used four different gillnet types over the years. From 1959 to 1962 the nets were 183 m long and 1.4–1.8 m deep. Each net consisted of six 30-m-long panels consisting of 51-, 64-, 76-, 89-, 102-, and 127-mm stretch mesh. The panels were arranged in order of mesh size and were attached only at the top and bottom of the net (this left a substantial gap between each panel). In 1963 and 1964, nets 107 m long and 1.4–1.8 m deep were used. They consisted of seven 15-m sections. The panels' meshes were 38, 51, 64, 76, 89, 102, and 127 mm. Mesh panels were arranged in order of mesh size, and panels were sewn together. From 1965 to 1969, the nets were 120 m long and 1.4–1.8 m deep. Each net had eight sections, each 15 m long. Their stretch meshes were 38, 51, 64, 76, 89, 102, 114, and 127 mm. Beginning in 1970, standard nets have been used. These are 1.5 m deep. They consist of eight panels, each 15 m long. However, the panels are

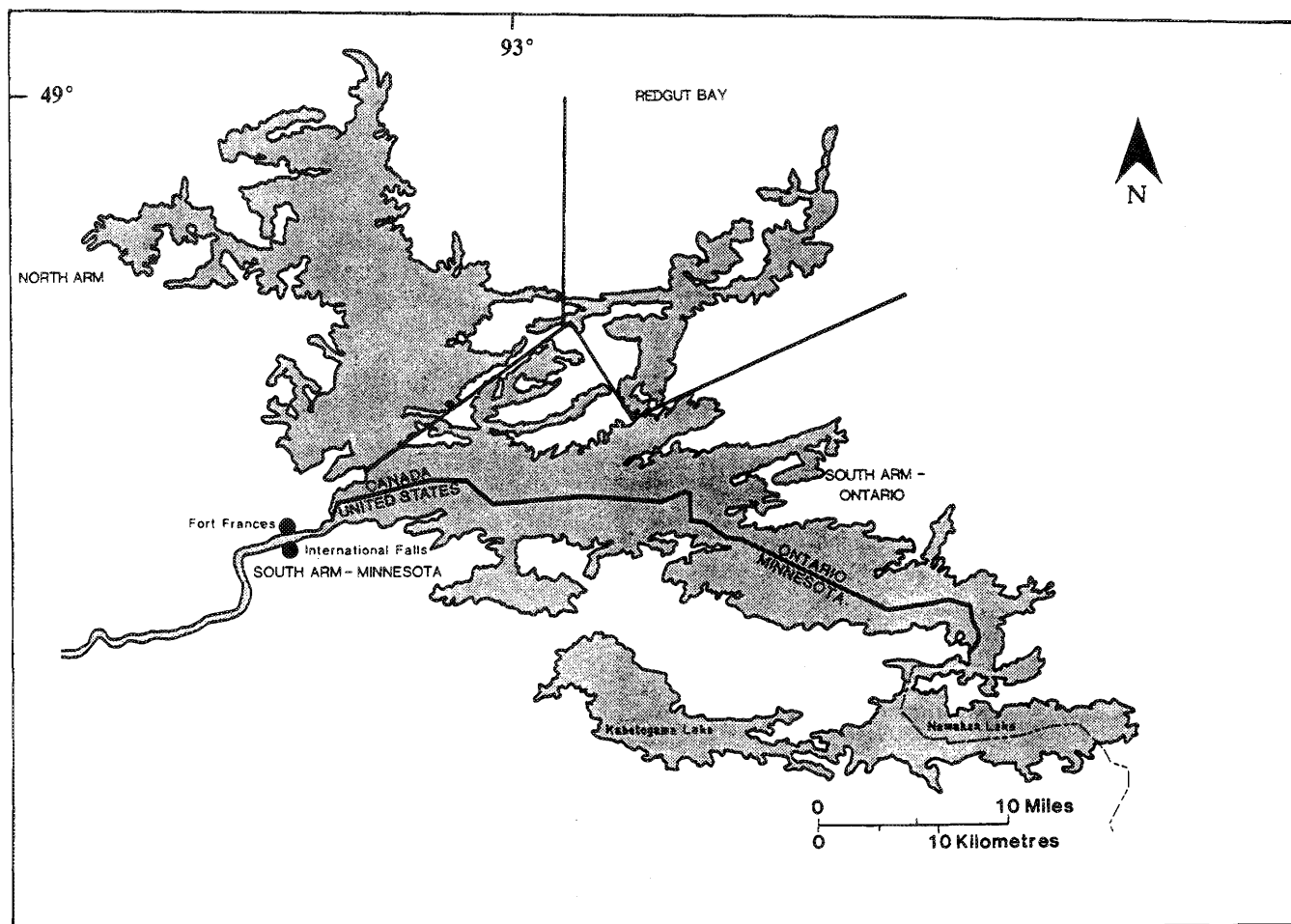


FIG. 1. Rainy Lake showing three major basins and four fisheries areas (solid lines).

arranged randomly. The stretch mesh sizes are 38, 51, 64, 76, 89, 102, 114, and 127 mm.

Prior to 1970, the OMNR sampled a variable number of sites. Since then, they have used identical sites. They employed 15, 25, and 10 sampling stations in the NA, SAO, and RGB, respectively. In most years, they placed the nets during August and September. Depths at the sampling stations ranged from 1.5 to 18 m. They fished overnight for an average of 20 h. CUE was calculated as kilograms per unit effort. A unit of effort consisted of a single net left for 20 h. Note that CUE units changed over the years. Within years, however, they were consistent. Because (i) all of our comparisons rely on within-year CUE and (ii) we mostly analyze relative CUE, we were not concerned with consistency of CUE units over years or locations. We used consistent CUE units within a year for each location.

Diversity Analysis

There are three variables of interest in the data: species, location, and year. To compare changes in the species communities over the years by locations, we calculated a yearly diversity index for each location (data available upon request) using the Shannon information index

$$(1) D = \sum_j p_j \ln p_j$$

where D is the diversity index, p_j is the relative CUE of species

j , and \ln denotes the natural logarithm (Pielou 1977). For each year and for each location, we calculated a single diversity value.

To detect changes in the communities, we compared the diversity time series among the four locations by calculating the R^2 matrix between all possible pairs of time series for the four locations.

CUE Fluctuations and Discriminant Analysis

Because the methods of data collection differed among years and sites (they were consistent within years and sites), the data were standardized by calculating the relative CUE of species each year before subjecting these transformed data to further analyses. These analyses consisted of selecting a subset of six species for each location whose combined relative CUE consistently accounted for over 90% of the catch of the 28 most abundant species. The six species were northern pike, sauger (*Stizostedion canadense*), cisco (*Coregonus artedii*), walleye, white sucker (*Catostomus commersoni*), and yellow perch (*Perca flavescens*). These six species were selected for the following reasons: (i) many species with small catches could bias further statistical analysis, (ii) although not the only species, the six most common species are of major interest to fisheries managers, and (iii) the species comprising this set were consistent across locations and thus allowed comparisons among locations.

For each location, we calculated a matrix of partial correlations among the time series of relative CUE for the six species in order to interpret how closely species' relative CUE fluctuated over time. Partial correlations quantify the association between pairs of species (changes in relative abundance) and remove the potential association among pairs of species due to their common associations with the other four species. The absolute values of the columns in the matrices of partial correlations were summed. These sums allow comparisons among locations and among the magnitude of the simultaneous fluctuations in species' relative CUE. These values indicate the degree of total association of a species with the rest of the species in the assemblage.

The number of years for which samples were available differed among locations (10, 14, 15, and 24 for the NA, RGB, SAO, and SAM, respectively). Also, because we used the relative CUE for calculation of partial correlations, we expected these correlations to be slightly negative. To test both effects on the magnitude of the partial correlations, we constructed null data sets. For a matrix of data with rows representing years for which data exist (e.g. 18 yr and 25 species in SAM) and columns representing the six species, the null data set and quantities of interest were calculated as follows: (i) shuffle the data in column j (independent of other columns), for $j = 2, \dots, 18$, (ii) sum all the values for each row i , $i = 2, \dots, 25$, (iii) divide each element j ($j = 2, \dots, 18$) in row i ($i = 2, \dots, 25$) by the sum of row i , (iv) use the standardized data (step iii) to calculate the matrix of partial correlations among the six species of interest, (v) sum the absolute values of the elements of the matrix of partial correlations (step iv) for each column j ($j = 1, \dots, 6$) (these column sums give the partial correlations of each species with the rest of the assemblage), and (vi) repeat steps i–v 100 times and calculate the 95% confidence intervals for the mean of the partial correlations of each species with the rest of the assemblage. Steps i–vi were applied (with the appropriate number of j and i) to each of the four locations in the lake.

The null data imply the following: (i) for each species, in each location, the set of CUE over the years (where the number of years represent the sample size) did not change (the sequence of CUE did) and (ii) there were no temporal interactions among the species. These simulations allowed us to test how different were each species' interactions (with the remaining species in the assemblage) under the hypotheses that (i) there were no interactions among the species, (ii) differences in sample sizes were accounted for in the calculations, and (iii) species CUE values were similar to those that had occurred in the past (but at a different sequence). The simulations also permit examination of the effect of using relative CUE on the magnitude and sign of the partial correlations.

The analysis of both the dynamics of diversity in the four fish communities and the partial correlation focuses on paired comparisons. In that sense, it is not multivariate. Thus, we used discriminant function analysis (DFA). This analysis answers the question of how unique were the combinations of relative CUE for the six species over the years, for each location. To address the data from a multivariate perspective, we view each year as a single point in a six-dimensional space. Each axis of this space represents some linear combination of the six species' relative CUE. The location of a point in this multidimensional space is determined by the set of relative CUE for a particular year. Given a set of points for each location (each point corresponds to a single year), we wish to discriminate among locations by the combination of relative CUE over the

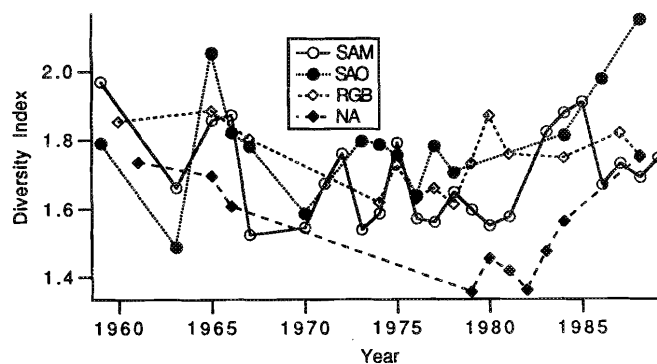


FIG. 2. Time series of the Shannon diversity index by location.

entire period of the data collection. Thus, we were able to interpret the whole data set as a combination of the relative CUE of the six species over the years.

Various multivariate methods are available; we chose DFA. Based on some optimal linear combination of the relative CUE for each year (this combination is computed by DFA), we classified each year's relative CUE to one of four locations and examined the extent to which the classification was correct, e.g. if data for a particular year came from the NA, and were classified as belonging to the NA, then the classification was correct. The fewer misclassifications, the more distinct the fish assemblage is, for a particular location. This distinction is taken from the perspective of all six species' relative CUE in a particular year.

Results and Discussion

Diversity

Changes in the diversity index over the years represent fluctuations in the relative abundance of the various species. The diversity index is based on the amount of information in the sample. Thus, high index values indicate a decrease in the predictability of the proportion of a species' CUE with respect to the sum of CUEs. The data for diversity (Fig. 2) were calculated from the data for all species for each location. The range of fluctuations of diversity of the fish community in the SAO was larger than of any of the other communities. In that respect, the SAO community was unique (Fig. 2). The diversity of the community in the NA was generally lower than of the other locations and followed a trend of decrease up to the early 1980s. This decrease coincided with managers' concern over the fishery in the NA. Only after the fishing for walleye was curbed in the NA (in 1983) did the diversity rebound. Often, fisheries managers treat a whole lake as a single management unit. For large lakes, it is important to examine data from different locations. When these data differ with respect to some measure of the community, it may reflect differences in species interactions and community dynamics. Such differences should then be taken into account in management plans.

How much does one community differ from another? To address this question, we calculated the matrix of R^2 between pairs of the diversity time series for the four locations. These correlations summarize the extent to which diversity fluctuated simultaneously in different locations. Except for the correlation between the NA and the SAO (Table 1), none of the time series of diversity index was significantly correlated. Thus, we conclude that none of the diversity time series among locations

TABLE 1. R^2 for the diversity index among four locations in Rainy Lake. Numbers indicate the value of R^2 , level of significance, and sample size (i.e. the number of years for which pairs of data exist), respectively.

	SAM	SAO	RGB
SAO	0.1, 0.26, 15		
RGB	0.09, 0.33, 13	0.42, 0.06, 9	
NA	0.31, 0.15, 8	0.96, 0.02, 4	0.06, 0.65, 6

was correlated significantly, and therefore the communities in the different basins differed (but not within the SA basin).

One may argue that much of the difference we see in the time series for diversity (across locations) is due to differing fishing pressures (which may mold a community structure) and differences in sampling, rather than changes in species interactions, and thereby community structure. Such effects are extremely difficult to partition. Yet, although the data were collected consistently (within a year) across locations in Ontario, and different data collection procedures were used in the SAM, diversity fluctuations differed among basins. Furthermore, different sampling and management methods did not destroy the assemblage relationship which exists because of geography within the SA basin. One can argue that the differences arise because of the different physiography of the three basins. For example, sampling at a particular depth in one location may yield results different from sampling at the same depth elsewhere. If this indeed is the case, then findings such as ours require further analysis to address geographical differences among locations and basins.

It is not clear that high fishing pressure invariably results in decrease in community diversity. The relationships between the magnitude of disturbance and diversity are probably not linear. For example, when the magnitude of disturbance to terrestrial plant communities was measured through the intensity of herbivory, these relationships were nonlinear: diversity was depressed at high and low intensities of disturbance (Harper 1977). In the NA, where fishing pressure prior to 1983 was high, diversity had been depressed (Fig. 2). Thus, the use of time series of a diversity index can indicate the magnitude of disturbance to a fish community. One must recognize, however, that perturbations can be relative and local, e.g. equal harvest from communities in different places can result in different disruptions of the communities, where disruptions are measured via changes in diversity. We do not claim that high diversity is inherently desirable. It is possible that a particular variance in the time series of diversity should be preserved.

Fluctuations in Species Relative CUE

Fluctuations in diversity index indicate how a community, as a whole, changes (in terms of relative abundance of species). The details of paired species interactions (that were identified by the data) and how they differ with time (across locations) were examined. If the dynamics (i.e. changes over time) of fish assemblages throughout the lake were uniform, then we expect fluctuations in the relative CUE of the various species, in different locations, to be similar. In such a case, we can conclude that although there may be differences in the absolute CUE, species interactions and the effects of environmental inputs on the communities were similar across locations. In such a case, aside from differences in, say, local absolute quotas, the lake can be managed as a single unit. Note that in interpreting the partial correlation matrices (below), we compare assemblages across locations. Thus, we can ignore potential delays in inter-

TABLE 2. Simulation-based 95% confidence intervals for species interactions with the remaining five species in a null assemblage. Species codes are listed in Fig. 3. The intervals were identical among the null assemblages for all locations in Rainy Lake.

Species	95% confidence interval	
	Lower	Upper
NOP	0.15	0.20
SAR	0.16	0.25
TLC	0.13	0.21
WAE	0.19	0.28
WTS	0.16	0.23
YEP	0.12	0.18

specific interactions. Such delays within communities can be addressed with time series analysis, or spectral analysis (Cohen and Stone 1987; Cohen et al. 1987; Stone and Cohen 1990; Cohen and Pastor 1991; Pereira et al. 1992).

We compared changes in fluctuations (in species' relative CUE from different locations). Our hypothesis was that if community dynamics were uniform throughout the lake, then temporal changes in relative CUE (of the assemblage of the six most common species) in various locations should be similar. These changes would be reflected in the magnitude of partial correlations. There is a subtle point here: we are addressing changes in the relative CUE of members of the assemblage, not in the absolute CUE. The absolute CUE may differ in two locations, yet changes in the relative CUE may not. Trends of change in relative CUE, when synchronized among species, translate to high partial correlations. Such trends are affected by both intrinsic (e.g. species interactions) and extrinsic (e.g. weather, water levels, fishing pressure) factors. Changes in relative CUE reflect the dynamics of the fish assemblage.

The simulation results were used to compare how different the empirical species assemblages are from null assemblages. Although sample sizes and the set of CUE across locations differed in our simulations, the simulation (of the species' sum of absolute values of a species' partial correlations with the rest of the assemblage) results for all locations were statistically identical. Thus, for a partial correlation matrix, which is based on (i) relative CUE of six species where (ii) these CUE values are drawn from a set of empirical CUE, (iii) there are no species interactions, and (iv) sample sizes range from 10 to 24, we expect partial correlations with confidence intervals as given in Table 2. The confidence intervals (Table 2) are for the means of the sum of the absolute partial correlations of each species with the remaining five species. These intervals are based on 100 repetitions.

The data-based partial correlation matrices for the respective locations (Table 3–6) have 13, 13, 14, and 10 negative partial correlations out of 15 unique values. Negative partial correlations do not necessarily imply competitive interactions among species. Negative partial correlations may reflect effects such as inverse reaction to environmental and habitat changes and harvest preferences. The fact that we calculated the partial correlations from the relative CUE also contributed to the number of negative partial correlations.

Recall that we interpret the column sum of the absolute values of the partial correlations as the amount of synchronization

TABLE 3. Partial correlations among the relative CUE for 1959–89 ($n = 24$) from experimental gill nets. Data are from the SAM. Species codes are listed in Fig. 3. Total = sums of the absolute partial correlations along columns. Asterisks indicate that these sums are significant when compared with the 95% confidence intervals for a null assemblage (Table 2).

	NOP	SAR	TLC	WAE	WTS	YEP	
NOP		-0.15	-0.82	-0.81	-0.71	-0.02	
SAR	-0.15		-0.11	-0.24	-0.30	-0.29	
TLC	-0.82	-0.11		-0.87	-0.83	0.16	
WAE	-0.81	-0.24	-0.87		-0.79	0.03	
WTS	-0.71	-0.30	-0.83	-0.79		-0.06	
YEP	-0.02	-0.29	0.16	0.03	-0.06		
Total	2.51*	1.09*	2.79*	2.74*	2.69*	0.56*	12.38

TABLE 4. Partial correlations among the relative CUE for 1965–88 ($n = 15$) from experimental gill nets. Data are from the SAO. Species codes are listed in Fig. 3. Total = sums of the absolute partial correlations along columns. Asterisks indicate that these sums are significant when compared with the 95% confidence intervals for a null assemblage (Table 2).

	NOP	SAR	TLC	WAE	WTS	YEP	
NOP		-0.35	-0.57	-0.45	-0.33	-0.15	
SAR	-0.35		-0.18	-0.09	0.08	0.20	
TLC	-0.57	-0.18		-0.81	-0.66	-0.29	
WAE	-0.45	-0.09	-0.81		-0.67	-0.25	
WTS	-0.33	0.08	-0.66	-0.67		-0.30	
YEP	-0.15	0.20	-0.29	-0.25	-0.30		
Total	1.85*	0.90*	2.51*	2.27*	2.04*	1.19*	10.76

in the fluctuations of the relative CUE of one species with the remaining five. The sum of species interactions (with the remaining member of the assemblage) reflects the total amount of synchrony in the fluctuations of species CUE for the assemblage. For the SAM, we found it to equal 12.38 (Table 3). Analysis of the species assemblage in the SAO (Table 4) resulted in a total partial correlation = 10.76. For the RGB and NA, we calculated total partial correlations of 16.62 and 20.78 (Tables 5 and 6).

The total sum of the absolute values of the partial correlations is a useful measure for comparisons among fish assemblages. It indicates how closely species' relative CUE fluctuated over the years. The sources of the synchronies in species fluctuations in relative CUE may be several: biological (species interactions, species habitat), environmental (weather, changes in water column temperatures), and anthropogenic (fishing pressure, pollution). Without specific, and incredibly multifactorial, population-manipulation experiments, one can never tell. The data indicate that relative CUE fluctuations for the six species of interest were most synchronized in the NA, followed by the RGB and both parts of the SA.

In highly disturbed ecosystems (such as the NA), one may expect synchronies to be higher compared with less disturbed ecosystems. This is true when the disturbance affects several species at the same time. As a hypothetical example, consider long-term fluctuations in a pollutant. These fluctuations can cause death of larvae of many species and will be likely to produce well-synchronized fluctuations in species densities.

Next, we identified those species whose fluctuations with the remaining species were synchronized identically across locations (Fig. 3). Yellow perch is considered a generalist in its food habits. It is preyed upon by almost all of the piscivore species in Rainy Lake, and in particular by the top predators walleye and northern pike. In both of the locations with high synchronization in relative CUE fluctuations (the NA and RGB), its fluctuations were synchronized with the fish assemblage more than any other species except cisco and white sucker in the RGB and SAM. Exactly the opposite occurred in the two assemblages in the SA where it was the least synchronized (Fig. 3). Colby et al. (1987) proposed a model of yellow perch dynamics which suggested that declines in piscivores allow yellow perch to increase competition with walleye. Walleye fluctu-

TABLE 5. Partial correlations among the relative CUE for 1965–88 ($n = 14$) from experimental gill nets. Data are from the RGB. Species codes are listed in Fig. 3. Total = sums of the absolute partial correlations along columns. Asterisks indicate that these sums are significant when compared with the 95% confidence intervals for a null assemblage (Table 2).

	NOP	SAR	TLC	WAE	WTS	YEP	
NOP		-0.83	-0.47	-0.73	-0.38	-0.92	
SAR	-0.83		-0.38	-0.79	-0.22	-0.90	
TLC	-0.47	-0.38		-0.49	0.28	-0.54	
WAE	-0.73	-0.79	-0.49		-0.26	-0.83	
WTS	-0.38	-0.22	0.28	-0.26		-0.29	
YEP	-0.92	-0.90	-0.54	-0.83	-0.29		
Total	3.33*	3.12*	2.16*	3.10*	1.43*	3.48*	16.62

TABLE 6. Partial correlations among the relative CUE for 1961–88 ($n = 10$) from experimental gill nets. Data are from the NA, Rainy Lake, Ontario. Species codes are listed in Fig. 3. Total = sums of the absolute partial correlations along columns. Asterisks indicate that these sums are significant when compared with the 95% confidence intervals for a null assemblage (Table 2).

	NOP	SAR	TLC	WAE	WTS	YEP	
NOP		0.35	-0.72	-0.83	-0.92	-0.95	
SAR	0.35		0.76	0.21	0.58	0.53	
TLC	-0.72	0.76		-0.48	-0.87	-0.75	
WAE	-0.83	0.21	-0.48		-0.67	-0.84	
WTS	-0.92	0.58	-0.87	-0.67		-0.93	
YEP	-0.95	0.53	-0.75	-0.84	-0.93		
Total	3.77*	2.43*	3.58*	3.03*	3.97*	4.00*	20.78

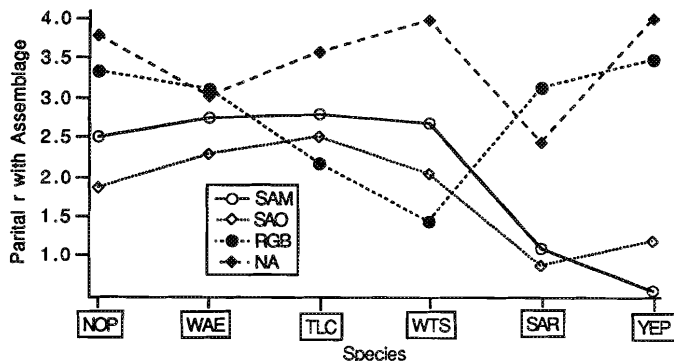


FIG. 3. Partial correlations of species with the rest of the assemblage by location. NOP, northern pike; WAE, walleye; TLC, cisco; WTS, white sucker; SAR, sauger; YEP, yellow perch.

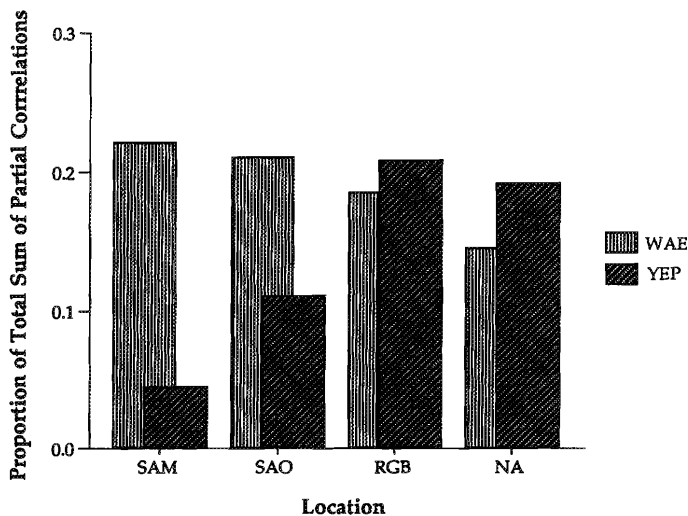


FIG. 4. Proportion of partial correlations of walleye (WAE) and yellow perch (YEP) with the rest of the assemblage paired by locations.

tuations were more synchronized with the fish assemblages in the locations with low synchronization in relative CUE fluctuations (the SAM and SAO). The inverse contribution of walleye and yellow perch to the communities with low and high amount of synchronization is clearly shown in Fig. 4. These results indicate that synchronization in fluctuations of relative CUE may reflect population-level predator-prey relationships within these assemblages. Thus, management that targets the predatory (and usually preferred) species only does not address the problem of their food source. For example, on the one hand, walleye stocking may be ineffective if fluctuations in walleye

TABLE 7. Frequency of correct classification to a location of the data based on DFA. Number of observations (years for which data were available) shown in parentheses.

Location collected	Location predicted (%)			
	NA (10)	RGB (14)	SAM (24)	SAO (15)
NA	90	0	0	67
RGB	0	86	0	13
SAM	0	0	92	13
SAO	10	14	8	67

populations and its food source (e.g. yellow perch and sauger) are not synchronized. On the other hand, stocking of yellow perch and sauger may result in higher densities of walleye.

The results in Fig. 3 (an assemblage property) and Fig. 2 (a community property) indicate that the dynamics (i.e. changes over time) of the fish assemblages and communities in the SA were more similar than those in the RGB and NA. This occurred even though data collection and management in the SAM differed from the SAO, RGB, and NA more than among the three Ontario locations. Figure 3 also indicates the distinct identity of species' fluctuations (with respect to the fish assemblage) among the three basins.

Results of Discriminant Analysis

The analysis of partial correlations has focused on paired comparisons and on the light they shed on the dynamics of species assemblages. Here, we address the data from a multivariate perspective with DFA. We wish to discriminate among locations by the combination of relative CUE over the entire period of the data collection. The interpretation of such results sheds light on the trajectories of the time series as a combination of the relative CUE of the six species. Thus, as opposed to the paired comparisons, we now look at the assemblage as a whole (a single point every year) and examine how these differed among locations. For each year, we classified the combination of relative CUE for six species to one of four locations (Table 7). Most yearly relative CUEs were correctly classified with respect to their location of collection (Table 7). For example, 92% of the observations from SAM were classified correctly whereas only 67% of the observations from the SAO were correctly classified; 15% of the misclassifications were assigned to RGB, 10% to the NA, and 8% to the SAM. This means that given a "blind" CUE sample from a particular year, one is likely to correctly identify its origin 92% of the time if the data suggest that it came from the SAM. The largest number of misclassifications (in the SAO) corresponds to the largest range in fluctuations in the diversity index in the SAO (Fig. 2).

The results from DFA differ from those derived from the partial correlation analysis. There, we surmised that of all locations, the dynamics of the species assemblage in the NA was the most unique, and both locations in the SA were similar (Fig. 3). We also used those results to interpret species interactions at a population level. When the data on relative CUE for each year are considered simultaneously (in a multi-dimensional space), the classifications (Table 7) indicate that the SAO was the least unique (classed with most errors) of all locations. The partial correlation analysis gives a picture of the dynamics of the assemblages in different locations. The DFA gives a static picture: changes in relative CUE over the years are no longer considered. A picture of the data, as a whole, emerges: the combinations of CUE over the years were unique for each location, with the assemblage in the SAO least unique.

Conclusions

We emphasize that this was a retrospective study and that other conclusions may be reached with different methods of analysis. We made no attempt here to consider the effects of delays among species' fluctuations in CUE which would require the use of time series and spectral methods (e.g. Cohen et al. 1991). Nonetheless, our analysis shows that in large lakes, it may be necessary to identify local fish communities and address management problems locally. In Rainy Lake, this has been done by developing different regulations at different locations. Other management actions, however (e.g. control of water level), cannot be location specific.

Acknowledgments

We thank Peter Colby and an anonymous referee for their constructive comments. They improved the manuscript tremendously. This study was supported by the Section of Fisheries, Minnesota Department of Natural Resources, Ontario Ministry of Natural Resources, and The University of Minnesota Agricultural Experiment Station. Ron Payer's and William Darby's help is deeply appreciated.

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