Water Level Regulations and Fisheries in Rainy Lake and the Namakan Reservoir

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The difference between the yearly maximum and minimum water levels (YMXR) is an index of lake dynamics: shoals are exposed and inundated, nutrients are oxidized and reduced, and the diversity and density of the aquatic plant community are affected. Shoals and emergent macrophytes provide spawning habitat for fish. The 5-yr moving variance of YMXR fluctuates regularly with periods of about 11.2 yr (periodicity of sunspot cycles). This reflects the effects of within-year consecutive periods of storms and dry spells. Water level regulations resulted in changes in both amplitudes and frequencies of YMXR compared with natural fluctuations. We established links between fluctuations in YMXR and fluctuations in fish populations. Water level regulations, through their effects on YMXR, corresponded to changes in interspecific interactions on Rainy Lake and the Namakan Reservoir. In both, walleye's (*Stizostedion vitreum*) fluctuations were synchronized with both those of lake whitefish (*Coregonus clupeaformis*) and northern pike (*Esox lucius*) more than those of either species with the other two. On the Namakan Reservoir, YMXR fluctuations were accentuated by water level regulation; on Rainy Lake, they were dampened. Regulations should consider frequencies and amplitudes of changes in water level and their effect on fish populations.

La différence le niveau maximal et le niveau minimal annuels de l'eau (YMXR) est un indice de la dynamique d'un lac : les hauts fonds sont exposés et inondés, les nutriants sont oxydés et réduits, la diversité et la densité de la communauté aquatique végétale est affectée. Les hauts fonds et les macrophytes émergés fournissent aux poissons un habitat pour la ponte. La variance mobile sur 5 ans de YMXR fluctue régulièrement avec une période d'environ 11,2 ans (périodicité des cycles des taches solaires). Ce phénomène reflète les effets des périodes consécutives de grosse pluie et de sécheresse au cours d'une année. La régulation du niveau de l'eau a provoqué des changements dans l'amplitude et la fréquence de YMXR par rapport aux fluctuations naturelles. Nous avons établi des liens entre les fluctuations de YMXR et celles des populations de poissons. La régulation du niveau de l'eau, par ses effets sur YMXR, correspondait à des changements dans les interactions interspécifiques au lac à la Pluie et au réservoir Namakan. Dans ces deux plans d'eau, les fluctuations des populations de doré (*Stizostedion vitreum*) étaient synchronisées avec celles du grand corégone (*Coregonus clupeaformis*) et du grand brochet (*Esox lucius*) plus que celles de l'une ou l'autre espèce avec les deux autres. Dans le réservoir Namakan, les fluctuations de YMXR étaient accentuées par la régulation du niveau de l'eau; au lac à la Pluie, elles étaient amorties. Les mesures prises doivent tenir compte des fréquences et des amplitudes des changements du niveau de l'eau et de leur effet sur les populations de poissons.

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Our goal was to examine the relationships among the fish populations, the fishery, and water level regulations in Rainy Lake and the Namakan Reservoir (which we shall call Namakan Lake), which are located on the border between Minnesota, USA, and Ontario, Canada (Fig. 1). We wished to establish relationships (or lack of) in the context of time-related ecosystem processes while ignoring potential delays. We assume that fluctuations in ranges of water level are important in effecting changes in fish communities. Ecosystem processes and fish populations interact dynamically (Magnuson 1991). If one assumes that ecosystem processes (such as aquatic plant regeneration, cleansing of shoals from filamentous algae, and changes in nutrient concentration due to repeated inundation and drying of shallow areas) are influenced by the extent of periodic flooding and exposure of shallow areas around lakes, then the yearly maximum difference between high and low water levels (YMXR) should be a suitable index to examine the extent to which such processes occur. The relationships between water level and fish populations in Rainy and Namakan lakes are not clear. Traditional analyses examined the relationships between water levels in the spring and fish abundance, expressed as catch per unit effort (CUE) or catch (kilograms). For example, on Rainy Lake, Johnson and Scidmore (1965) and Johnson (1967) reported a correlation between lake water levels at the time of spawning of walleye (*Stizostedion vitreum*) and its subsequent year class strength. Chevalier (1977) concluded that spring water levels and exploitation have been important in affecting walleye abundance. Osborn et al. (1981) found no significant relation-

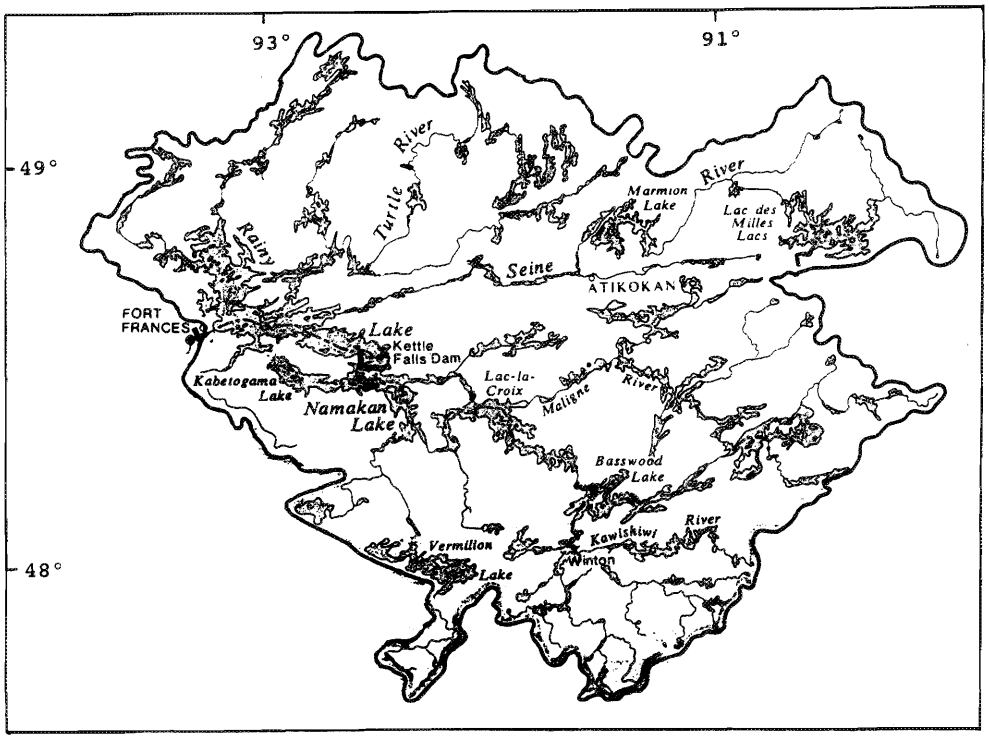

FIG. 1. Study area.

ships between spring water levels and subsequent walleye abundance 5 yr later. Kallemeyn (1967) found positive correlation between young of the year walleye abundance and lake levels 15 and 30 d after ice-out.

Rainy and Namakan lakes are part of the headwaters of the Hudson Bay basin. They drain an area of 38 000 km^2. The Namakan Reservoir (Fig. 1) includes Namakan, Kabetogama, Crane, Sand Point, and Little Vermilion lakes. Namakan Lake drains into Rainy Lake, which in turn drains into the Rainy River (Fig. 1). Water levels in Rainy and Namakan lakes are regulated by a U.S.–Canadian International Joint Commission (IJC) for hydropower production. These regulations, implemented since 1949, specify upper and lower limits of water level through the year. The regulations have used larger than natural fluctuations in lake levels on Namakan Lake to maintain less than natural fluctuations on Rainy Lake. Recently, Namakan Lake annual fluctuation has been approximately 0.9 m greater than estimated natural whereas Rainy lake's has been 0.8 m less (Flug 1986).

The Fishery on Rainy Lake

Commercial fishing on Rainy Lake began in 1885 with pound nets used to capture lake sturgeon (*Acipenser fulvescens*). Since the 1920s, gill nets have been the primary gear, with walleye, northern pike (*Esox lucius*), and lake whitefish (*Coregonus clupeaformis*) the most important components of the commercial fishery. Between 1908 and the mid-1960s, individual fishing areas were used. In 1916, there were 62 licensed commercial fishers operating in 25 designated fishing areas in the Ontario portion of Rainy Lake. Starting in the mid-1960s, there had been a gradual decline in the number of commercial fishers and fishing areas. In Minnesota waters, there had been 4–10 commercial fishers fishing in designated areas. In 1986, Ontario began a commercial fishing buy-out program. In Minnesota, all commercial fishing stopped in 1985. The commercial fishery was initially regulated by limiting the amount and size of gear. Later, location, time of fishing, and the fish size regulations were added. In 1970, the minimum gillnet mesh size was increased by Ontario. Since 1984, Ontario has implemented an individual fisher quota system where licenses no longer limited the amount of gear set. Bonde et al. (1965) compiled data on commercial harvest for all species before 1951.

In response to declining walleye harvest, the Minnesota Department of Natural Resources (MDNR) and the Ontario Ministry of Natural Resources (OMNR) 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. They reported drastic declines in commercial catch in the North Arm of Rainy Lake. 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 waters 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 m^2, were constructed in Rainy Lake. From 1971, management delayed the opening of 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. Fisheries managers recognize the decline of stocks, in particular in the North Arm.

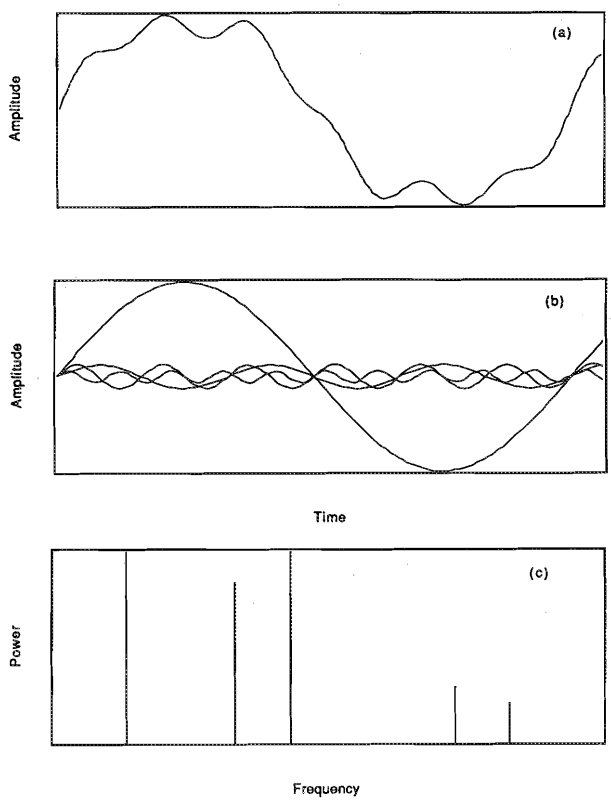

FIG. 2. Time and frequency domain representation of a time series. (a) The "data"; (b) four components; (c) the frequency representation of these components.

They are also concerned with the lack of walleye (and other species) recruitment. 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).

Recreational use of the lake is on the rise. The MDNR collected creel information through surveys during the summers of 1977–78 and 1983–90 (Ernst and Osborn 1980; Eibler 1991). The OMNR collected creel data intermittently from 1956 to 1986 (McLeod 1988).

The Fishery on Namakan Lake

Commercial fishing on the lake began in 1916. Two to four commercial fishers per year have been active on the lake. In 1946, the MDNR eliminated commercial fishing for walleye and northern pike. Since the 1950s, a small commercial fishery for lake whitefish has operated in Minnesota waters. Their average yearly catches have been about 1456 kg in the 1980s. The OMNR uses a fishery quota system, set to 2727 kg for walleye, 1220 kg for northern pike, 10 000 kg for lake whitefish, and 454 for lake sturgeon. Recently, Ontario's harvest has been near the quotas. The MDNR stocked about 23.6 million walleye fry, 115 bass fingerlings, and 1200 crappie fingerlings from 1918 to 1943. They did not stock since then.

The assemblages of fish species in the lakes of the Namakan Lake are similar to those in Rainy Lake. Fishery research on these lakes began in 1941 (Sharp 1941). Fish populations in the reservoir's lakes have been assessed with experimental gill nets since 1962. Since 1983, the MDNR has collected fishery data according to the large-lake program guidelines (Wingate and Schupp 1985). The MDNR conducted creel surveys from 1977 to 1978 (Ernst and Osborn 1980), and from 1983 to 1990 (Eibler 1991). Surveys indicated that the lake received about 23.5 angler-hours·ha·yr (Kingsley 1989). More details about the lakes and the history of fisheries are given in Cohen et al. (1991, 1993).

Methods

Study Sites

Rainy and Namakan lakes, both mesotrophic, lie within the southern range of boreal forests in North America. Rainy Lake has a surface area of approximately 92 383 ha, a mean depth of 9.9 m and a maximum depth of 49.1 m and the littoral area comprises 42% of the lake. A dam on the Rainy River, constructed in 1909 at the site of the former Koochiching Falls, controls water levels. The water is soft and submergent vegetation is never abundant. Bedrock comprises most of the lake's littoral zone. There are three basins, making up four distinct fisheries areas in the lake (Cohen et al. 1993); South Arm Minnesota, South Arm Ontario, Redgut Bay, and North Arm (Fig. 1). In this paper, all of the data from Rainy Lake pertain to the Minnesota waters of the South Arm, which we call Rainy Lake for the sake of persimony. The shoreline, along with its 1600 islands, is forested.

Namakan Lake is part of the Namakan Reservoir, which also includes Kabetogama, Sand Point, Crane, and Little Vermillion lakes. The surface area of the Namakan Reservoir is 25 973 ha. Waters are soft and infertile; 20% of Namakan lake (its area is 10 160 ha) is littoral, with a mean depth of 13.6 m and a maximum depth of 45.7 m. Until 1988, the lake was not accessible by road. Two dams, at Kettle Falls and at Squirrel Falls, have been in operation since 1914. The lake shoreline is forested and irregular. There are numerous islands. The U.S. portion of Namakan Lake lies within Voyageurs National Park. Lac LaCroix, a 13 788-ha lake, belongs to the watershed of Rainy and Namakan lakes. It drains into Namakan Lake, and water levels on it have never been regulated.

Data Collection

We transcribed the commercial catch data from the original forms and used reports from both Minnesota and Ontario. Commercial fishers submitted reports on catch and effort since the turn of the century, and there is no direct way to estimate data integrity. For Rainy Lake, we used the data from MDNR only. CUE units are expressed as kilograms of fish harvested per kilometre of 102 or 133-mm-mesh commercial gill net per day.

Daily water levels were obtained (Water Survey of Canada, Water Resources Branch, Inland Waters Directorate, Environment Canada, 513-269 Main St., Winnipeg, MB R3C 1B2, Canada) that have been collected since 1911 for Rainy Lake and 1912 for the Namakan Lake. We also used data of water levels from Lac LaCroix, a lake about 100 km southwest of Rainy Lake (Fig. 1). Water levels in Lac LaCroix have never been regulated and thus provide baseline data for comparisons with Rainy and Namakan lakes.

To explore the relationships between fish populations and water level, we constructed the following index: for each year, we calculated the difference between the maximum and minimum water levels above sea. This we call the yearly maximum range (YMXR). Because YMXR reflects periods of high or low precipitation during the year (which affect water levels), its

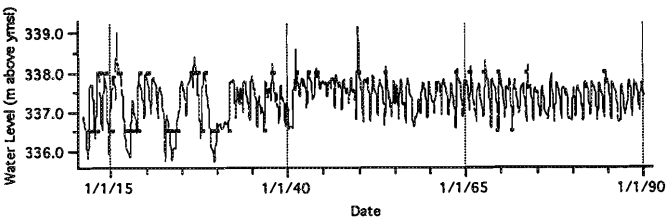

FIG. 3. Daily water levels in Rainy Lake from January 1, 1911, through December 31, 1990. Horizontal points show level-crossings at 336.5 and 380 m above yearly mean sea level. Level-crossings become further apart with time.

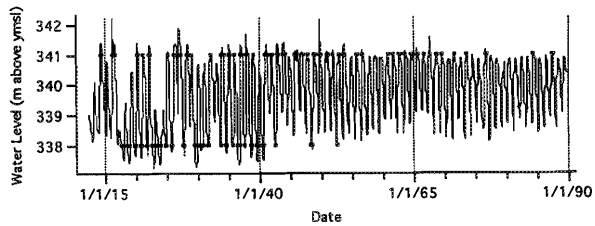

FIG. 4. Daily water levels in the Namakan Reservoir from January 1, 1911, through December 31, 1990. Horizontal points show level-crossings at 338 and 341 m above yearly mean sea level. Level-crossings become further apart with time.

multiyear variance indicates the extent of a sequence of exceptionally large storms, and exceptionally dry spells, within a year. To explore changes in such periods, we calculated the 5-yr moving variance for the YMXR data, i.e., the first variance was calculated for the first 5 yr of the available YMXR data, the second variance for the second through sixth year of data, and so on. Because the choice of the period chosen for moving variance calculation may affect the results, we calculated the moving variance repeatedly for periods of 5–12 yr.

Spectral Analysis

One can expect ecosystem processes to respond to changes in conditions, as opposed to the conditions themselves. A particularly suitable method for examining changes in ecosystem processes is spectral analysis. In such analysis, one is not interested strictly in levels of a variable, but rather in changes in these levels over time. Ecosystem-related changes may be cyclical. Such cycles can be detected by spectral analysis. Cohen and Stone (1987), Cohen et al. (1987, 1991), Stone and Cohen (1990), and Pereira et al. (1992) applied this analysis to fisheries data. A heuristic exposition of the analysis follows.

Suppose that a fish population fluctuates perfectly. There is a single cycle over a specified time interval, T. Thus, for T, there is a single frequency, f. The amplitude, A, is known (it is the peak of the cycle). This gives a point (f,A) in Cartesian coordinates. Thus, a time domain represenation of data has a corresponding frequency domain representation. Frequency is the inverse of period, and they may be used interchangeably, e.g., cycles per year versus years per cycle. Next, suppose that a population's density over time flutuates, as shown in Fig. 2a. The so-called Fourier transform (Bloomfield 1976; Priestly 1981) can be used to decompose the data to exactly four sine waves of differing amplitudes and frequencies (Fig. 2b) such that

$$(1)\quad x(t) = 4\sin(t/15) + 0.25\sin(t/15) + 0.5\sin(t/2.5) + 0.5\sin(t/5)$$

where $x(t)$ represents the original data in Fig. 2a and t represents time. The decomposed data are plotted as amplitude versus frequency. Every time series can be decomposed to a sum of sine waves that will fit the series based on some fitting criterion (e.g., least squares). Similar to polynomial fitting, time series with sharp peaks require a larger number of sine waves to fit. The set of relative amplitudes at each possible frequency in a data set constitutes the so-called power spectrum (Fig. 2c).

We used spectral analysis to examine the regularity of fluctuations of a measure of fish populations and water levels. With such analysis, we bypass problems such as changes in harvest levels, declining fish populations, delays among levels of related time series, and the absolute density of fish populations. For the analysis of all of the time series, $X(t)$, $t = 1, 2, \ldots, n$, we followed these steps: (1) $x(t) = \sqrt{X(t)}$, $t = 1, 2, \ldots, n$; (2) if required, a polynomial (of second degree at most) was fit to the series to render it stationary, i.e., $y(t) = a + bt + ct^2$; and (3) the residuals $r(t) = x(t) - y(t)$ were subjected to spectral analysis using the Daniel's window and two-pass smoothing. More technical details are given in Bloomfield (1976) and Priestly (1981). To avoid cumbersome wording, when we speak of powers of, and coherencies between, time series, we refer to the powers and coherencies of the residuals $r(t)$. We analyzed the residuals, as opposed to the original data, because we were interested in fluctuations, not in trends.

To examine the extent to which the residuals of two time series were fluctuating simultaneously (with or without delays), we used the so-called squared coherency. Much like the squared correlation coefficient, the squared coherency is bounded between 0 and 1, where 1 represents a perfect synchrony in the fluctuations of two time series. Note that coherency is a function of frequency. In some cases, we compared data from three potentially interacting time series. When performing pairwise comparisons, it is important to remove the coherency between two time series that is due to their common coherency with a third. The squared partial coherency, like the squared partial correlation, accomplishes this task. Powers, coherencies, and partial coherencies are explained in more detail in Cohen et al. (1987, 1991) and Periera et al. (1992). We used formulas and equations given in Priestly (1981).

To compare the total amount of synchrony in the fluctuations of pairs of time series for a single body of water, we summed the values of the significant squared coherencies (or squared partial coherencies) for each pair. This index reflects the total amount of synchrony among various time series from a single body of water.

Results

Water Levels

Due to water level regulations, the amplitudes of fluctuations in water levels for both Rainy and Namakan lakes have been declining steadily. Note that the frequencies of level crossings (Fig. 3 and 4) have been decreasing over the years. Although amplitudes have been decreasing, there is no evidence that the frequencies of these fluctuations have been deliberately changed.

The difference between yearly maximum high and yearly maximum low was consistently highest for Namakan Lake and

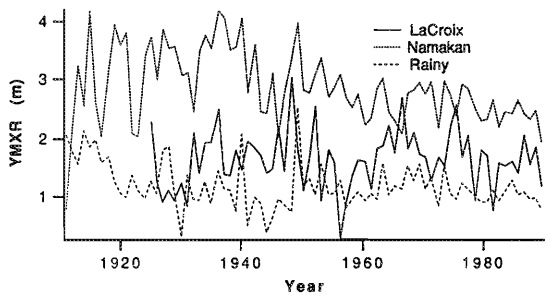

FIG. 5. Yearly difference between maximum high and maximum low (YMXR) for Lac LaCroix and Namakan and Rainy lakes from 1911 through 1990.

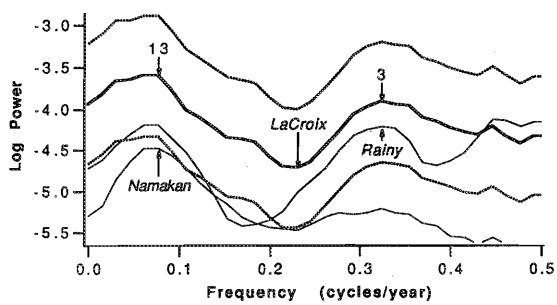

FIG. 6. Log power spectra for YMXR from Lac LaCroix, Rainy Lake, and Namakan Reservoir. Dotted lines indicate 95% confidence interval. Numbered vertical arrows indicate dominating periods (yr/cycle).

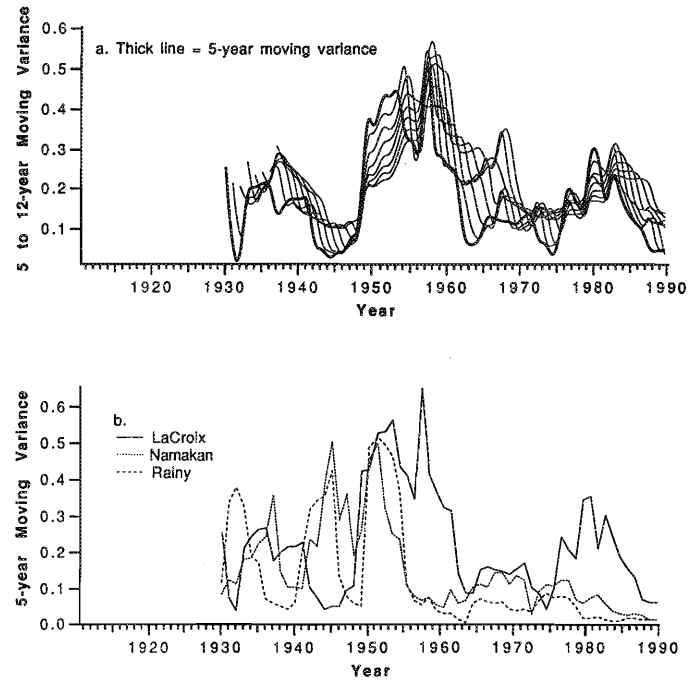

FIG. 7. (a) Five- to 12-yr moving variance for Lac LaCroix. Note the regularity of cycles for all of the chosen periods. The thick line indicates the 5-yr moving variance. (b) Five-year moving variance of YMXR. For Lac LaCroix, note the five distinct cycles (1932–44, 1944–56, 1956–63, 1963–74, 1974–88) with an average period of 11.2 yr/cycle. Also note the shorter cycles within these 12-yr cycles.

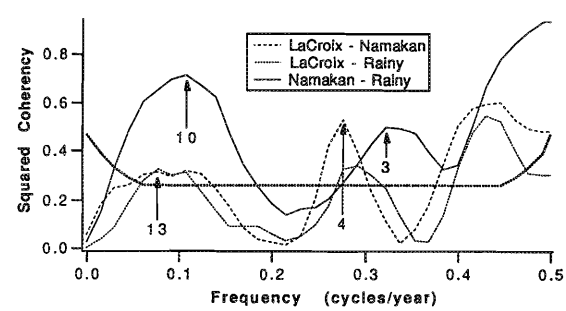

FIG. 8. Squared coherency between Rainy Lake, Namakan Reservoir, and Lac LaCroix YMXR. Values above the thick dotted line indicate significance ($p \leq 0.05$). Numbered vertical arrows indicate dominating periods (yr/cycle).

lowest for Rainy Lake, with Lac LaCroix Lake in between. Because Rainy Lake is the largest of the three, this result is expected even in the absence of water level regulations. Namakan Lake serves as a backup for water level regulations on Rainy Lake. Thus, although it is larger than Lac LaCroix, both its mean and amplitude of YMXR fluctuations were higher than those of Lac LaCroix (Fig. 5). Rainy and Namakan lakes represent opposing departures from the unregulated YMXR fluctuations of Lac LaCroix.

The power spectra of YMXR for the three lakes peak at 3 and 13 yr/cycle (Fig. 6). This means that on the average, once every 3 and 13 yr YMXR reaches a maximum, then gradually decreases, and reaches a maximum 3 or 13 yr later. These are the two frequencies at which larger than usual shallow areas around the lakes are exposed and flooded. For most frequencies, the power of Rainy Lake YMXR time series is within the 95% confidence interval of the power of Lac LaCroix. The Namakan Lake YMXR remained largely outside the 95% confidence interval of the Lac LaCroix spectrum. Thus, Rainy Lake and Lac LaCroix were more similar (in terms of dominating amplitudes of YMXR at specific periods of 3 and 13 yr/cycle) to each other than Lac LaCroix and Namakan Lake.

YMXR cycles, which were detected by spectral analysis (Fig. 6), became more apparent after we calculated the 5-yr moving variance from the data (Fig. 7). Because of the potential idiosyncrasy of choosing a specific period for calculating the moving variance, we first calculated the 5- to 12-yr moving variances for Lac LaCroix (Fig. 7a). These revealed definite cycles in the moving variance, regardless of the number of years chosen for the calculation. This definite periodicity is disrupted for the lakes where water levels have been regulated (Fig. 7b), yet periodicities are apparent even for Rainy and Namakan lakes. Because of its peculiarity, we chose to further analyze the 5-yr moving variance for Lac LaCroix.

There were five high-amplitude cycles for Lac LaCroix during 1932–44, 1944–56, 1956–63, 1963–74, and 1974–88, for an average period of 11.2 yr/cycle (Fig. 7). Note also the shorter periods with smaller amplitudes within these cycles (compare Fig. 6 and 7). This is an interesting finding; it indicates that starting at 1990 (for example) the variance in YMXR is expected to be at its minimum for the next 5 yr. This variance will slowly increase to a peak at 1996, at which time the 5-yr variance is expected to be at its maximum, and then start to decrease. The 5-yr moving variance reflects blocks of time during a year when

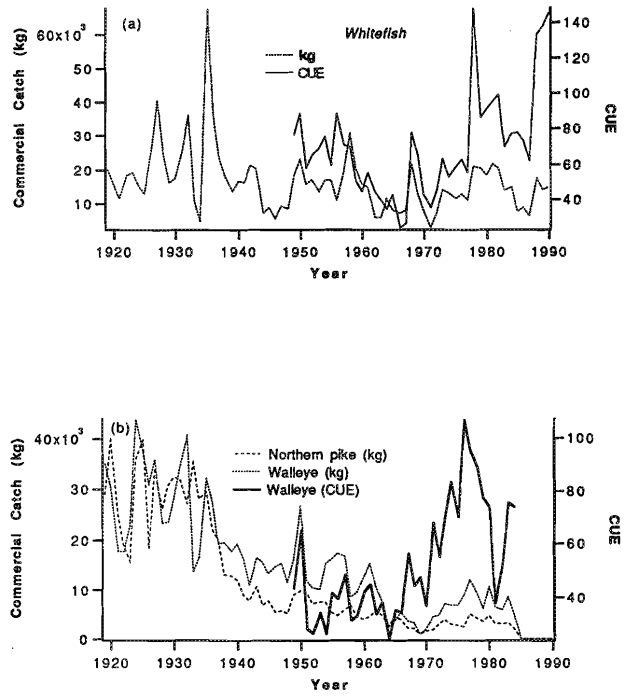

FIG. 9. Catch and (a) CUE (kg·km^{-1}·d^{-1} of 133-mm-mesh gill nets) for lake whitefish and (b) CUE (kg·km^{-1}·d^{-1} of 102-mesh gill nets) for northern pike and walleye from the South Arm of Rainy Lake.

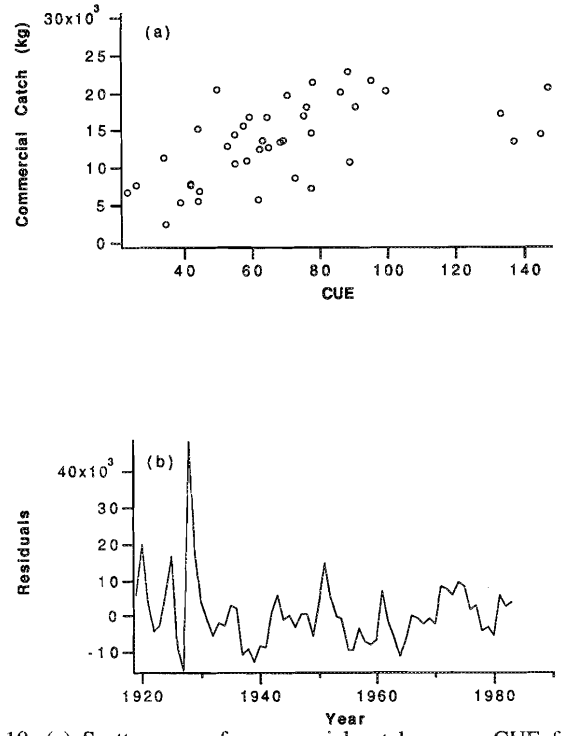

FIG. 10. (a) Scattergram of commercial catch versus CUE for lake whitefish from the South Arm of Rainy Lake and (b) residuals from fitting a second-degree polynomial to the lake whitefish commercial catch data (in Fig. 9a).

precipitation is consistently high, or consistently low. This results in high or low water levels, which in turn are reflected in YMXR. We were surprised to find that 11.2 yr is precisely the periodicity of the sunspot cycles (Bloomfield 1976).

The extent to which YMXR fluctuations are temporally synchronized is reflected in the squared coherency (Fig. 8). The synchrony at periods (years per cycle) of 4 and 13 yr was significant between both Rainy Lake and Lac LaCroix and Namakan Lake and Lac LaCroix. This is in contrast with the synchrony between Rainy and Namakan lakes, which is not significant at 3 and 10 yr. Thus, the effect of water level regulations was to shift the synchrony in YMXR fluctuations between Rainy and Namakan lakes.

The fact that (i) 3 and 13 yr/cycle were dominant for all lakes (including Lac LaCroix, where water levels have never been regulated; Fig. 6) and (ii) Rainy and Namakan lakes were synchronized at different periods than each with Lac LaCroix (i.e., 3 and 10 yr/cycle versus 4 and 13 yr/cycle) indicates that water level regulations changed the frequencies at which YMXR fluctuated. Such regulations may have also affected the amplitudes of YMXR fluctuations (Fig. 5 and 6). Summing the total amount of significant squared coherency resulted in a squared coherency between Lac LaCroix and Rainy Lake of 14.4, Rainy Lake and Namakan Lake of 14.3, and Lac LaCroix and Namakan Lake of 7.4. Thus, Namakan's YMXR fluctuations are different from natural. As opposed to Rainy Lake, it is out of synchrony with Lac LaCroix.

The YMXR power spectrum of Lac LaCroix represents natural fluctuations for lakes in the watershed. Short- and long-term fluctuations were synchronized at different periods for rainy and Namakan lakes (3 versus 4 and 13 versus 10 yr/cycle). If we can establish relationships between fish populations and YMXR, then we can conclude that fluctuations in fish populations in Namakan and (perhaps) Rainy lakes are not natural. If such fluctuations are essential for consistently fluctuating (but not necessarily high) densities of fish, then one can achieve such a consistency by emulating the natural long-term fluctuations in YMXR through water level regulations.

The fluctuations in YMXR in both the short and long term (3 and 10 yr/cycle) are well synchronized between Rainy and Namakan lakes (Fig. 8). The amplitudes at these periods, however, are not as high as those in Lac LaCroix (Fig. 6). Overall, water level regulations affected both amplitudes and frequencies of YMXR.

Comparison of CUE and Commercial Catch

Long-term data for commercial catch are available for lake whitefish, walleye, and northern pike. CUE data are available for shorter periods of time and, for Rainy Lake, for walleye and lake whitefish only (Fig. 9). To what extent CUE and catch are related, and if they are, we can use catch, as opposed to CUE, to examine the relationships between water levels and fish populations? Recall that we are not interested in examining trends in CUE (or catch). We are interested in how these changes fluctuate together with time.

Rainy Lake

No significant linear correlation between lake whitefish catch and CUE exists for Rainy Lake (Fig. 10a). Similar conclusions were drawn for walleye and for both species from other locations in Rainy Lake. Because the steps in the analysis were repeated for other species and location, we follow these in detail for this case only. The time series for catch and CUE for lake whitefish are shown in Fig. 9a. These series are not stationary. Thus, we fitted a second-degree polynomial to the series and analyzed the residuals (Fig. 10b). For all periods above 3 yr the squared coherency between the stationary CUE and commercial catch

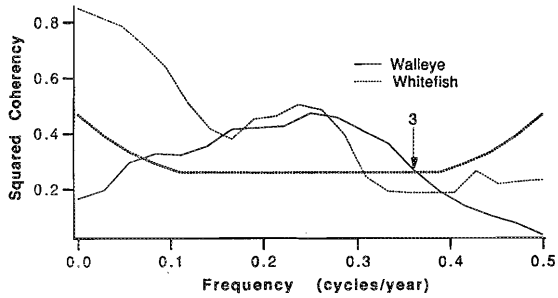

FIG. 11. Squared coherency between the residuals of the CUE and commercial catch (kg) time series for walleye and lake whitefish from the Minnesota waters of the South Arm, Rainy Lake. Values above the thick dotted line indicate significance ($p \leq 0.05$). The arrow indicates the location of the 3 yr/cycle.

series was significant (Fig. 11). Thus, although no correlation existed between CUE and catch (Fig. 10a), the frequency of fluctuations of these variables correspond tightly. To proceed, we can therefore compare fluctuations in YMXR and catch (instead of YMXR and CUE). We can also say that catch and CUE fluctuate in synchrony, reflecting (perhaps) changes in the density of fish populations.

Similar to lake whitefish, no correlation existed between walleye CUE and catch. The squared coherencies reflect tight synchrony in the fluctuations of walleye CUE and catch over a wide range of frequencies (Fig. 11). We may therefore use catch, instead of CUE, to compare walleye fluctuations with YMXR. CUE data for northern pike from Rainy Lake are not available. Thus, we cannot verify that CUE fluctuations correspond to those of the commercial catch. The squared coherencies between walleye and northern pike catches were significant for short (3 yr/cycle) and long (24 yr/cycle) frequencies.

Namakan Lake

Lake whitefish CUE and catch from Namakan Lake (Fig. 12a) were not correlated significantly (Fig. 12b). The squared coherencies (Fig. 12c) indicate that the CUE and catch series were synchronized with periods of 10 yr/cycle. This synchrony is not as tight as found for rainy Lake (Fig. 11), where the synchronies were significant for cycles with all periods between 3 and 24 yr. For lack of data, we were not able to calculate the CUE for walleye or northern pike from Namakan Lake. We will therefore apply our analysis to the catch data only (Fig. 13) and use it for comparison with Rainy Lake.

Comparison of Commercial Catch and YMXR

Rainy Lake

For lake whitefish and walleye, the log of the second-pass smoothed power spectra (including its 95% confidence intervals) of the commercial catch series from Rainy Lake indicates that there are two dominating periods: 4 and at 24 yr (Fig. 14a, 14b); the 4-yr cycles are missing from the northern pike data (Fig. 14c). Both lake whitefish and walleye catch series are synchronized with water levels in Rainy Lake at frequencies of 3–4 yr. This synchrony is missing from the series for northern pike (Fig. 15). The sum of significant squared coherencies indicates that walleye – YMXR were most tightly synchronized (4.8) followed by YMXR – whitefish (2.2). The northern pike catch series was not synchronized with YMXR at all.

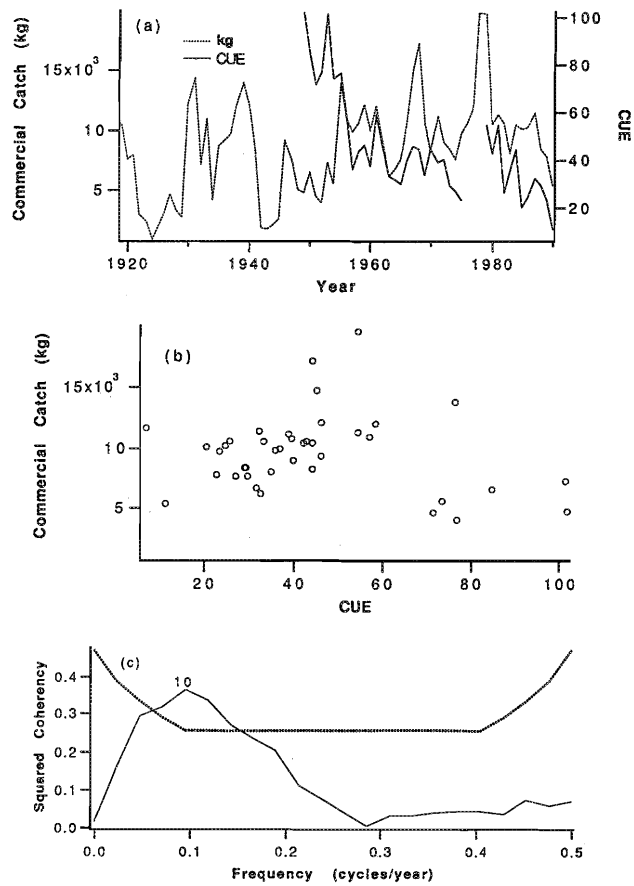

FIG. 12. (a) Lake whitefish commercial catch from Namakan Lake and its CUE ($kg \cdot km^{-1} \cdot day^{-1}$ of 133-mm-mesh gill nets). (b) Scattergram of commercial catch versus CUE. (c) Squared coherency between the residuals of the commercial catch and CUE time series; dotted line indicates $p \leq 0.05$.

Namakan Lake

The second-pass smoothed log power spectrum of lake whitefish (for data from Namakan Lake) displays periods of about 12 yr, with a minor peak at 3 yr/cycle (Fig. 14a). For walleye, we find a single dominating period at 24 yr (Fig. 14b). Northern pike shows dominating periods at 3 and 24 yr/cycle (Fig. 14c). In spite of these differences in the power spectra among species, the squared coherency indicates that (for Namakan Lake) only lake whitefish fluctuates in synchrony with YMXR at a period of 4 yr (Fig. 16) whereas for Rainy Lake, both lake whitefish and walleye fluctuate in synchrony with YMXR at periods between 3 and 4 yr (Fig. 15).

Species Comparisons

Rainy Lake

How did the catch series for the three species fluctuate with each other? The squared partial coherencies reveal that the catch series, from Rainy Lake, for lake whitefish and walleye, were synchronized at periods of 3–4 yr/cycle (Fig. 17). Lake whitefish and northern pike fluctuated at periods of 6 yr, and all three species fluctuated at periods of 24 yr (Fig. 17).

The sum of the values of significant squared partial coherencies for each species with the other two (Table 1) indicates that the catch series (in Rainy Lake) for lake whitefish and walleye (squared partial coherency = 7.5) were synchronized more than those of lake whitefish versus northern pike (2.5) or walleye

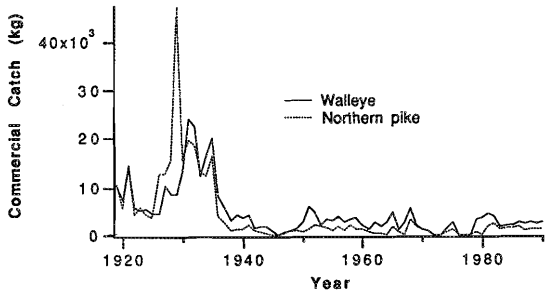

FIG. 13. Commercial catch from Namakan Lake for walleye and northern pike.

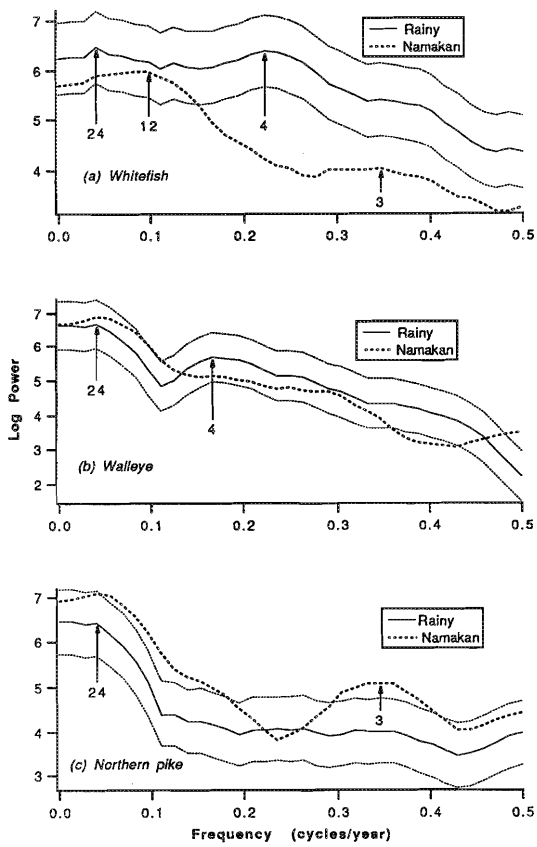

FIG. 14. Log power spectra computed from the residuals of the commercial catch series from the Minnesota waters of the South Arm, Rainy Lake, and Namakan Lake for (a) lake whitefish, (b) walleye, and (c) northern pike. Dotted lines indicate 95% confidence interval for the data from Rainy Lake. Vertical arrows indicate dominating periods (yr/cycle).

versus northern pike (5.9). Furthermore, in Rainy Lake, 42% of the total interspecific coherencies were attributed to walleye, 27% to lake whitefish, and 31% to northern pike (Table 1).

Namakan Lake

In contrast with Rainy Lake, the partial squared coherencies for the catch series for walleye and northern pike only were synchronized at 18 yr/cycle in Namakan Lake. Short-term fluctuations existed among the three species on both lakes (Fig. 17 and 18). In Namakan Lake, the catch series of walleye versus

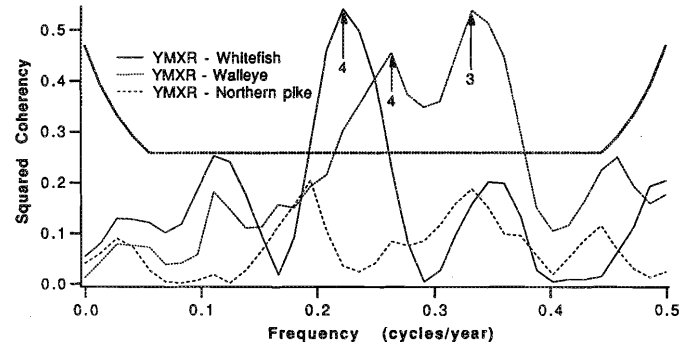

FIG. 15. Squared coherency between the residuals of the YMXR and species' series of commercial catch (kg) for the Minnesota part of the South Arm, Rainy Lake. Values above the thick dotted line indicated $p \leq 0.05$. Vertical arrows indicate dominating periods (yr/cycle).

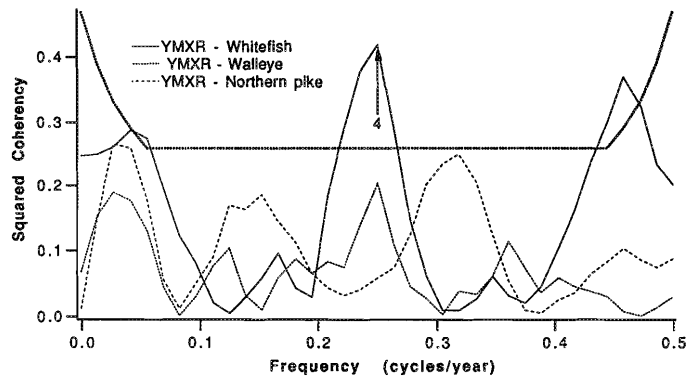

FIG. 16. Squared coherency between the residuals of the YMXR and species series of commercial catch (kg) for Namakan Lake. Values above the thick dotted line indicated $p \leq 0.05$. Vertical arrows indicate dominating periods (yr/cycle).

northern pike (sum of squared partial coherency = 11.4) were more synchronized than those of lake whitefish versus walleye (4.7) or lake whitefish versus northern pike (2.6) (Table 2). Furthermore, walleye interaction with the remaining species (where interactions are defined as the synchrony of fluctuations in commercial catch series) accounted for 43% of the total synchrony in Namakan Lake (Table 2). Compared with Rainy Lake, lake whitefish and northern pike contribution to the total synchrony was switched, i.e., northern pike's 31% in Rainy Lake became 20% in Namakan Lake (Tables 1 and 2).

Integration of Results

Most of the results are summarized and compared in Fig. 19. Although complex, it merits close scrutiny. Lac LaCroix represents natural fluctuations. These are summarized as the amount of power at various periods (Fig. 19a). All three bodies of water had similar dominating amplitudes at periods of 3 and 13 yr, yet those of Lac LaCroix were most dominant, followed by Rainy Lake and then Namakan Lake (Fig. 19a). The squared coherency between Lac LaCroix and Rainy Lake remained unchanged (and significant) at periods of 4 and 13 yr; that of Lac LaCroix and Namakan Lake was high at a period of 4 yr/cycle and low at 13 yr/cycle (Fig. 19b). The squared coherency between Namakan and Rainy lakes was higher than the other two paired

TABLE 1. Sum of significant ($p \leq 0.05$) squared partial coherencies among pairs of species for the South Arm of Rainy Lake.

	Lake whitefish walleye	Lake whitefish northern pike	Walleye northern pike	Total
Lake whitefish – walleye	–	7.5	2.5	
Lake whitefish – northern pike	7.5	–	5.9	
Walleye – northern pike	2.5	5.9	–	
Total (%)	10.0 (31%)	13.4 (42%)	8.4 (27%)	31.8

TABLE 2. Sum of significant ($p \leq 0.05$) squared partial coheriencies among pairs of species for Namakan Lake.

	Lake whitefish walleye	Lake whitefish northern pike	Walleye northern pike	Total
Lake whitefish – walleye	–	4.7	2.6	
Lake whitefish – northern pike	4.7	–	11.4	
Walleye – northern pike	2.6	11.4	–	
Total (%)	7.3 (20%)	16.1 (43%)	14.0 (37%)	37.4

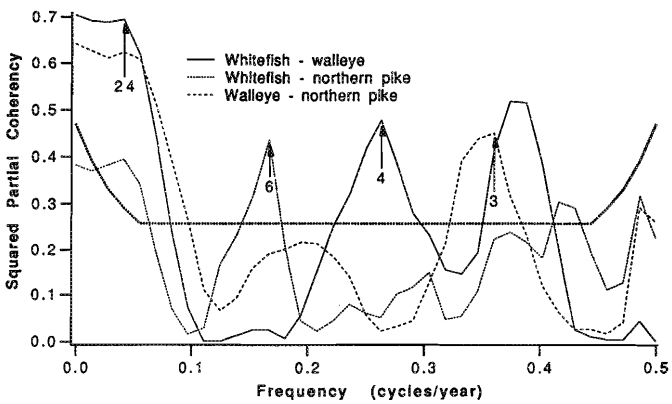

FIG. 17. Squared partial coherency between pairs of species residual series of commercial catch (kg) for the Minnesota part of the South Arm, Rainy Lake. Values above the thick dotted line indicated $p \leq 0.05$. Vertical arrows indicate dominating periods (yr/cycle).

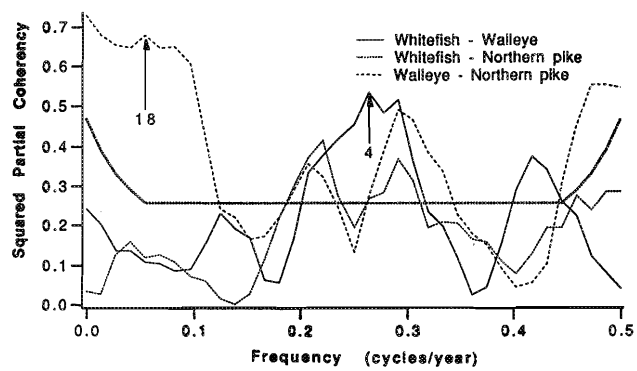

FIG. 18. Squared partial coherency between pairs of species residual series of commercial catch (kg) for Namakan Lake. Values above the thick dotted line indicate $p \leq 0.05$. Vertical arrows indicate dominating periods (yr/cycle).

coherencies at periods of 10 yr/cycle. These results indicate that (1) Lac LaCroix, Rainy, and Namakan's YMXR fluctuations may be ranked from most to least natural and (2) water level regulations increased the synchrony (in fluctuations of YMXR) between Rainy Lake and Namakan Lake and changed the periods of synchrony.

The squared coherencies between the three fish species and YMXR show that there were more significant coherencies for more species on Rainy Lake compared with Namakan Lake (Fig. 19c). The paired squared partial coherencies between species indicate that long-term coherencies (24 yr/cycle) did not exist between species on Namakan Lake. They did on Rainy Lake (Fig. 19d). Also, the sum of significant squared partial coherencies between one species and the other two indicates that the total interspecific coherency was larger in Namakan Lake (37.4) compared with Rainy Lake (31.8) (Tables 1 and 2). For both bodies of water, walleye interactions with the other two species were highest (42 and 43% for Rainy and Namakan lakes, respectively). The interaction of northern pike and lake whitefish with the remaining two species switched (in percent contribution to the total coherency) between Rainy and Namakan lakes (Tables 1 and 2).

This summary of results indicates that the fishery on Namakan Lake was more disturbed than that on Rainy Lake. These disturbances can be attributed (at least in part) to the effects of water level regulations on the frequencies and amplitudes of fluctuations in YMXR.

Discussion

The results indicate that water level regulations affected both the frequencies and amplitudes of fluctuations in YMXR compared with natural fluctuations. There is a clear link between changes in YMXR and changes in the commercial catch series. The commercial catch series do not necessarily indicate densities of fish populations, but those that were compared fluctuate in concert with the CUE series. Chevalier (1977) suggested that the walleye commercial catch in Rainy Lake was an index of abundance due to favorable economic incentives through time. Thus,

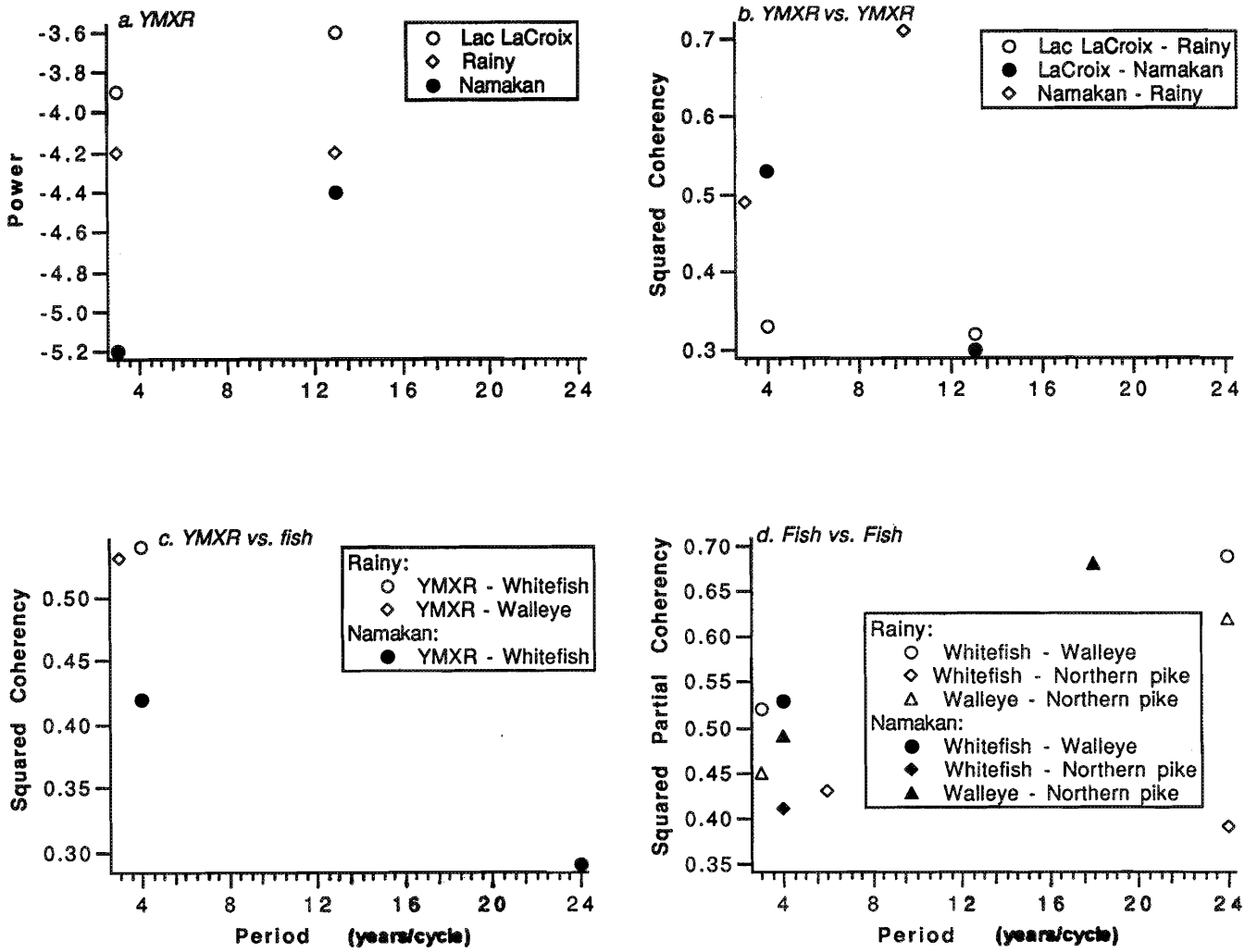

FIG. 19. (a) Power of dominant periods for the residuals of the YMXR series for Lac LaCroix, Rainy Lake, and the Namakan Reservoir. (b) Periods of significant squared coherencies among the three bodies of water. (c) Squared coherencies between lake whitefish, walleye, and northern pike (residuals of commercial catch data) on the one hand and the residuals of the YMXR on the other for both the Minnesota waters of the South Arm of Rainy Lake and Namakan Lake. (d) Squared partial coherencies between the residuals of the commercial catch series for species pairs in Namakan and Rainy lakes.

catch and CUE series reflect each other in terms of frequencies and amplitudes (but not in terms of trends), more so in Rainy Lake than in Namakan Lake. We used the catch dynamics (changes over time) to examine the dynamics of fish populations. These dynamics were examined in terms of fluctuations around a long-term (and potentially changing) moving average, which is removed by analyzing the residuals. Furthermore, the catch and YMXR dynamics compared differently between Rainy and Namakan lakes, and so did the YMXR. It is difficult to imagine reasons other than differences in YMXR fluctuations (between Rainy and Namakan lakes) that may have affected differences in the frequency content of the commercial catch data on both lakes.

Fluctuations in YMXR affect the frequency and amplitude of fish population dynamics. Why should changes in water levels affect fish populations? Small fluctuations in water levels may not change the extent of shoals along lakeshores by much. Thus, walleye spawning success might not be affected. Such fluctuations may, however, cause flooding and exposure of large areas of emergent vegetation. This stimulates growth and diversity of aquatic emergent vegetation. For example, Keddy and Reznicek (1986) found that high water levels kill some aquatic plants (e.g., *Typha* spp.). They reported that increases in water level fluctuations affect large areas of shoreline vegetation in the Great Lakes. Such fluctuations resulted in creation of large marsh areas and high aquatic vegetation diversity (due to seed exposure). These effects may increase northern pike spawning success and recruitment (Johnson 1956; Grimm 1983).

Because large fluctuations in YMXR result in large areas of sediments that are alternately inundated and exposed, they have consequences to the diversity and abundance of littoral flora (Rorslett 1984). Wilcox and Meeker (1991) compared aquatic macrophyte communities in Rainy and Namakan lakes with those in unregulated Lac LaCroix; the latter supported a more diverse (structurally and taxonomically) plant community. For Namakan Lake, the manipulated hydrological regime favored the establishment of low rosette and mat-forming plant species which provide low structural diversity. Fluctuations in YMXR also influence nutrient conditions by increasing nutrient exchanges between littoral and pelagic zones (Kennedy and Walker

1990). Fee (1979) correlated rates of primary production with the fraction of epilimnetic surface area in direct contact with bottom sediments. Fluctuations in YMXR affect, directly or indirectly, fish populations (Ploskey 1986; Prosser 1986). Thus, frequencies of YMXR changes may be expected to be coupled with frequencies of change in fish populations.

Such findings correspond to the response of northern pike to the larger fluctuations in YMXR on Namakan Lake, compared with Rainy Lake. Northern pike coherencies with other species were larger on Namakan Lake, compared with Rainy Lake. Its catch series changed from displaying only long-term fluctuations on Rainy Lake to both long- and short-term fluctuations on Namakan Lake. A fundamental message of this research is that in regulating water levels, one must be concerned with frequencies and amplitudes of water level fluctuations (i.e., in their dynamics). It is not enough to address problems of annual mean water levels only. This reemphasizes the connection between ecosystem dynamics and fish population dynamics, e.g., injection of nutrients to bodies of water because of flooding and exposure of large areas, changes in the extent of spawning habitat for shallow-water spawners (e.g., walleye and northern pike), and changes in substrate, such as cleansing of shoals, that are important for the spawning of walleye (Johnson 1961).

In Cohen et al. (1987), species whose partial coherencies with the remaining species in a community were highest were defined as keystone species. These are species whose dynamics are intertwined most with other species. Cohen et al. (1987) found that in Lake Superior, lake herring (*Coregonus artedi*) was the keystone species. Examination of the results here indicates that walleye (in both Rainy and Namakan lakes) may be the keystone species.

We maintain that in managing fish populations, it is not the population mean that needs to be considered as an index of the state of the fisheries. Rather, management should strive to maintain a certain amount of fluctuation in fish populations, with appropriate amplitudes. For assuring adequate spawning habitat, the appropriate frequencies of fluctuations in fish populations could correspond to those of YMXR. The appropriate amplitudes of YMXR fluctuations are more difficult to recommend. Analysis of the extent of shallow waters and lake topography (e.g., slopes and aspects) may help in this respect. For example, Cohen et al. (1991) used Geographic Information System to analyze the distribution of depth of shallow waters in Rainy and Namakan lakes.

The 5-yr moving variance of YMXR provided a surprising result; it fluctuated with remarkable consistency. We are unaware of similar results reported in the literature. The moving variance of YMXR is a particularly suitable index of the severity of within-year consecutive storms and dry spells because lakes act as "low-pass filters," i.e., they average over high frequency changes in weather conditions. For example, an isolated large storm is not likely to affect the maximum yearly high water because a following dry period will prevent water levels from increasing. Only a sequence of few storms, following on the heels of each other, will result in a maximum yearly high. For reasons discussed above, large variance in YMXR should affect changes in fish populations. The fact that such variances fluctuate regularly indicates that fish populations in lakes such as Rainy and Namakan may fluctuate regardless of management efforts and that these fluctuations do not necessarily indicate overfishing, but rather may be natural phenomena.

As in any correlation study, we did not prove cause (YMXR fluctuations) and effect (fluctuations in fish populations). There are other factors that may lead to cycles in fish populations. For example, Hilborn and Walters (1992) discussed the importance of the dynamics of commercial fishers (i.e., predators) in exploring catch series data and the possibility of cycles due to learning of individuals and consolidation of the industry. Also, density-dependent processes can produce complex population dynamics, from regular oscillations to chaotic dynamics (May 1976; Turchin and Taylor 1992). Bledsoe and Megry (1989), in simulating a cannibalistic population with a bioenergetic food web model, suggested that a strong environmental signal might be undetectable in time series of fish harvest data, even if the population responds to strong environmental variation because of the cannibalistic behavior (which stabilizes the population). Most of these studies are theoretical. Yet, large fluctuations in YMXR represent a major abiotic factor (Ryder 1978), and in ecosystems such as Rainy and Namakan lakes, yield is regarded to be more dependent on abiotic than biotic factors (Kerr and Ryder 1988).

Acknowledgments

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