Potential to index climate with growth and recruitment of temperate fish

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Abstract: Those fish and communities that are measurably sensitive to episodic climate events on time scales of months to seasons may be the best candidates for examining climate change effects on longer time scales. Application of linear models to routinely collected data on age structure and scale growth allows calculation of indices of yearly recruitment and growth. Walleye (*Stizostedion vitreum vitreum*) growth indices were associated with several measures of extreme temperatures, but first-year growth was most sensitive. Changes in smallmouth bass (*Micropterus dolomieu*) growth were synchronous among six lakes near the northern limit of their range and appeared to be related to summer temperatures. Relatively short time series (<10 yr) of growth data may suffice to examine spatial scales of responses to climate events, while longer series are necessary for superposed epoch analysis of growth or recruitment.

Résumé : Les poissons et communautés dont la sensibilité aux événements climatiques épisodiques peut se mesurer sur des échelles de temps assez courtes (mois à saisons) sont peut-être les meilleurs candidats pour l'examen des effets du changement climatique sur des échelles de temps plus longues. L'application de modèles linéaires à des données recueillies systématiquement sur la structure par âge et sur la croissance des écailles permet de calculer des indices annuels de recrutement et de croissance. Les indices de croissance du doré jaune (*Stizostedion vitreum vitreum*) ont été reliés à plusieurs mesures de températures extrêmes, mais la croissance de la première année a été des plus sensible. Les changements dans la croissance de l'achigan à petite bouche (*Micropterus dolomieu*) étaient synchrones dans six lacs situés près de la limite nord de l'aire de répartition de cette espèce et semblaient liés aux températures estivales. Une série chronologique relativement courte (< 10 ans) de données sur la croissance pourrait suffire à l'examen des échelles spatiales de réactions aux événements climatiques, tandis que des séries plus longues sont nécessaires pour l'analyse par époques superposées de la croissance ou du recrutement.

Introduction

Standardized assessment of fish populations has been conducted in Minnesota lakes for approximately 40 yr (Scidmore 1970), with some lakes in the program being surveyed on a 5-yr rotation. More recently, an annual assessment program was established for Minnesota's large lakes (i.e., over 6100 ha; Wingate and Schupp 1985). Together, these survey programs provide a growing data base including samples of calcified structures and relative abundance data from key species. This sampling regime, therefore, is of potential value for establishing baseline information on growth and recruitment needed to detect significant trends arising from changes in global climate.

Temperature is one facet of climate that has important effects on the dynamics of fish populations. Regier et al. (1990) noted that many studies of the relationship of fish to climate examine indirect causal pathways involving links between climatological, hydrological, and biotic subsystems. In this paper, we do not examine causal pathways directly, but rather examine whether the effects of episodic climatological events can be detected in fisheries data providing time series of varying lengths. Those fish and communities that are measurably sensitive to episodic events occurring on a time scale of months to seasons may be the best candidates for examining climate change effects on somewhat longer time scales. Such episodic events may include years with abnormal temperatures or years during the mature phase of an El Niño event. Teleconnections from the southern hemisphere, including El Niño, influence fish stocks in the northern hemisphere (Wooster and Fluharty 1985). Teleconnections during strong El Niño events may extend to the interior of the North American continent (Ropelewski and Halpert 1986; Robertson 1989).

The best candidate lakes may be isothermal, offering little opportunity for behavioural thermoregulation. Several of Minnesota's large walleye (*Stizostedion vitreum vitreum*) lakes do not normally undergo temperature stratification during the

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summer, although walleye growth may vary between basins within these lakes (Schupp 1972). We examined walleye growth in two of these lakes (Lake Pepin and the Red Lakes) and in a large walleye lake that stratifies (Rainy Lake). Alternatively, climate change effects may be most evident for species near the limits of their distribution. Smallmouth bass (*Micropterus dolomieu*) in northern Minnesota are near the limit of their native range and may be in thermally marginal habitat (Shuter and Post 1990), especially in deep lakes. This study examines the potential of these candidate lake types and fish species for future measurement of climate change effects in Minnesota. We formally tested whether changes in recruitment or growth (at different ages) of walleye or sauger (*S. canadense*) coincide with seasonal and annual temperature changes, and we present analytical methods useful for detecting climate-induced impacts in fisheries data. Analysis of smallmouth bass growth illustrates a possible way to examine spatial scales of climatic events with relatively rapidly obtainable data.

Study Sites

Lake Pepin is part of navigational pool 4 of the Mississippi River. The lake, however, was a natural reservoir created by a delta at the confluence of the Chippewa and Mississippi Rivers. The lake is long and narrow with a fairly regular shoreline and few backwater bays. Shoal water substrates are mostly sand and gravel. Submerged aquatic vegetation is not abundant. The lake has a diverse fish community with at least 83 species recorded.

The Red Lakes (Upper and Lower) are two large, shallow oval basins in northwestern Minnesota. Shoal water substrates are mostly sand and submerged aquatic vegetation is sparse. The lakes do not stratify in the summer and are mesotrophic. The fish community is similar to that of Rainy Lake (described below). The Red Lake Band of Chippewa Indians has operated a commercial fishery since 1917. Pereira et al. (1992) explored the dynamics of this fishery.

Rainy Lake is located on the border between Minnesota and Ontario with 75% of the surface area in Ontario. Water levels in the lake have been controlled since 1909 by a dam on the outlet. The lake has a rocky, irregular shoreline and three distinct basins: the North Arm, Redgut Bay, and the South Arm. The lake is dimictic, and the South Arm is generally thermally stratified from June to September. Rainy Lake is typically ice covered from 5 to 6 mo of the year. Approximately 50 fish species occur in Rainy Lake. The most abundant species in experimental gillnet catches have been northern pike (*Esox lucius*), yellow perch (*Perca flavescens*), sauger, cisco (*Coregonus artedii*), walleye, and white sucker (*Catostomous commersoni*). Cohen et al. (1993), in analyzing patterns in the fish communities in Rainy Lake over time, found that walleye gillnet catch per unit effort (CPUE) fluctuations were more synchronized with the fish assemblage in the South Arm than in the other basins.

We also analyzed growth data for smallmouth bass from six oligotrophic lakes in northeastern Minnesota. These lakes were part of a study to evaluate interactions between lake trout (*Salvelinus namaycush*) and smallmouth bass (Eiler and Sak 1993). Physical and chemical data for all lakes included in the analysis are listed in Table 1.

Methods

All growth and CPUE data collected on walleye from Rainy Lake and walleye and sauger from Lake Pepin were derived from regular stock assessment with five-panel, variable mesh gillnets (Wingate and Schupp 1985). Most sampling was conducted during late summer. We assumed that gillnet CPUE is an index of relative abundance. Growth data for the Red

Table 1. Physical and chemical characteristics of study lakes.

Lake	Latitude	Longitude	Surface area (km^2)	Mean depth (m)	Maximum depth (m)	Total Dissolved solids (mg/L)	phosphorous (mg/L)	chlorophyll *a* (mg/L)	Alkalinity (mg/L)	pH
Walleye lakes										
Peppin	44°22'N	92°16'W	158.9	6.40	18.29	312.1	0.210	18.7	150.0	8.4
Rainy[a]	48°37'N	93°10'W	489.3	11.46	49.07	51.9	0.018	5.0	18.2	6.8
Red Lakes[b]	48°08'N	94°47'W	1168.8	4.36	10.70	190.5	0.057	16.2	112.5	7.5
Smallmouth bass lakes[c]										
Caribou	47°43'N	90°40'W	2.95	na[d]	8.2	36.5	na	na	30.5	7.9
Flour	48°03'N	90°21'W	1.35	8.4	22.9	30.7	na	na	18.3	7.6
Greenwood	48°00'N	90°07'W	8.18	9.9	30.8	14.1	na	na	6.0	7.1
Loon	48°05'N	90°38'W	3.15	20.6	61.6	22.4	na	na	12.5	7.5
Two Island	47°52'N	90°28'W	2.96	2.6	8.2	17.8	na	na	10.7	7.1
West Bearskin	48°04'N	90°24'W	2.00	10.2	23.8	26.5	na	na	17.3	7.7

[a] Data for Rainy Lake are from the South Arm.

[b] Water quality data and latitude–longitude pertains to Upper Red Lake.

[c] Total dissolved solids for smallmouth bass lakes were estimated by multiplying conductivity (micromhos·cm^{-1}) by 0.65.

[d] Not available.

Lakes were obtained from Shroyer (1991). Shroyer randomly sampled the commercial fishery in 1987 and 1988. He also used random subsamples of scales archived at the University of Minnesota that were originally collected in 1949, 1950, 1968, 1969, 1972, and 1973. Smallmouth bass were sampled by electrofishing in May and June 1988–90, using a spherical anode with the boat as a cathode. All walleye, sauger, and smallmouth bass were aged using scales.

To index recruitment, we fitted the log-linear model:

$$(1)\ \mathbf{Log_e}\ (\mathbf{Y}_{ij}) = \mu + \alpha_i + \beta_j + \varepsilon_{ij}, \qquad \varepsilon_{ij} \sim N(0,\sigma^2)$$

where Y_{ij} is CPUE (number of fish per gillnet) of year-class j caught at age i, μ is the main effect, α_i is the age effect, β_j is the year-class effect we consider to be an index of recruitment, and ε_{ij} is the error. We fit this model to field data with JMP software (SAS Institute Inc. 1989). The model is statistically similar to that presented by Kimura (1988).

Scale increments were digitized to construct growth records for walleye and smallmouth bass. We applied the linear modeling system of Weisberg (1993), because it appropriately partitions variation in scale data between age and year effects. We estimated growth series with the linear model:

$$(2)\ \mathbf{Log_e}\ (S_{ijk}) = \mu + \alpha_i + \beta_j + \gamma_{ij} + \varepsilon_{ijk}; \qquad \varepsilon_{ijk} \sim N(0, \sigma^2)$$

where S_{ijk} is a scale increment for fish k at age i in year j, μ is the main effect, α_i is the age effect; β_j is the year effect, γ_{ij} is the age-by-year interaction effect, and ε_{ijk} is the error. The vector of year effects (i.e., the β_js) represents the growth index that we subjected to further analyses with climate data. Walleye estimated to be older than 8 yr were excluded from the analyses for Rainy and Red lakes, and those greater than 500 mm were excluded for Lake Pepin because of uncertainty in ageing. For walleye, we fit the model after excluding the first increment because there was no significant correlation between growth of young-of-the-year and older fish. Subsequent analyses of walleye growth were done separately on the mean first-year log scale increments (age-0 growth) and on the year coefficients (adult growth).

To test whether key years of extreme environmental conditions had unusual fish growth or recruitment, we applied superposed epoch analysis as described by Prager and Hoenig (1989), using software by Hoenig et al. (1989). This technique compares the average response for the years just prior to, during, and after a key event and determines whether the observed differences are statistically significant using Monte Carlo randomization to formulate the null distribution. We used the *W*-statistic of Prager and Hoenig (1989) where each key-event year is compared with its own background years; this is analogous to the Student's *t*-statistic computed for paired data. Prager and Hoenig (1992) estimated the statistical power of this technique from 0.35 to 0.50 for simulated data sets with a 35-yr time series, three or five key-events, and an epoch width of 5 yr.

We explored several climate variables with air temperature data provided by the State of Minnesota Climatology Office. For all study sites with the exception of the Red Lakes, air temperatures were recorded at stations with in approximately 55 km of the lake basins. For analysis of Red Lakes data, we obtained air temperature data from the Crookston weather station, which is located approximately 105 km due west of lower Red Lake. This station is situated in a geographic area that is primarily agricultural and contains less forest cover than the area to the east around the Red Lakes. This station, therefore, has maximum and minimum daily air temperatures that are 2.5 and 1.0°C higher, respectively, than those recorded at the town of Red Lake, Minn. There are no trends through time in these differences. We used data from the Crookston station because it provided the most complete temperature data near the Red Lakes. We used cumulative degree-days above 20°C (CDD) for the entire year, mean annual air temperature, and mean July air temperature for analysis of walleye and sauger recruitment and growth. For smallmouth bass growth, we used CDD and mean temperature from June through September. The method for determining cumulative degree-days above a base temperature is

$$(3)\ \text{If MDT} > \text{BASE, then CDD} = \text{CDD} + \text{MDT} - \text{BASE} \\ \text{else CDD} = \text{CDD}$$

where MDT is mean daily temperature (i.e., mean of minimum and maximum) and BASE is the base temperature of 20°C. Our use of CDD is, therefore, similar to that used by Colby and Nepszy (1981) and McCauley and Murdoch (1987). Key-event years for temperature were those with temperatures more than one standard deviation (SD) above or below the mean. For key events related to the El Niño – Southern Oscillation (ENSO), we used years during the mature phase of strong and moderate intensity El Niños as identified by Quinn et al. (1978) and Robertson (1989). Moderate ENSO events occurred in 1966, 1977, and 1987; strong ENSO events occurred in 1973 and 1983. We defined background years as 1 yr before and 1 yr after a key event for mean temperature and CDD (epoch width = 3 yr), and 2 yr before and after an ENSO year (epoch width = 5 yr).

Results

Lake Pepin walleye and sauger

Climate and biological series analyzed from Lake Pepin are illustrated in Fig. 1. Both temperature indices indicate the warmer period beginning in the mid-1980s. Sauger and walleye recruitment appear to be closely correlated, with both species showing downward trends in recruitment. Growth of adult walleye shows a positive trend beginning in the early 1970s, which follows a possible period of relatively fast growth in the mid-1960s. Age-0 growth of walleye calculated from fish of all capture ages was variable and does not show a consistent trend, although growth appears to increase starting around 1985. There was no recent trend apparent in first-year growth when calculated only from age 1+ fish.

Superposed epoch analysis for Lake Pepin showed that walleye recruitment was positively related to high CDD events. However, sauger recruitment showed no relationship to any climate variable (Table 2). Walleye adult growth appears to be slower during cool years, as indicated by significant tests for mean annual and July temperatures. Only mean annual temperature was related to first-year growth, with growth being faster and slower during warmer and cooler years

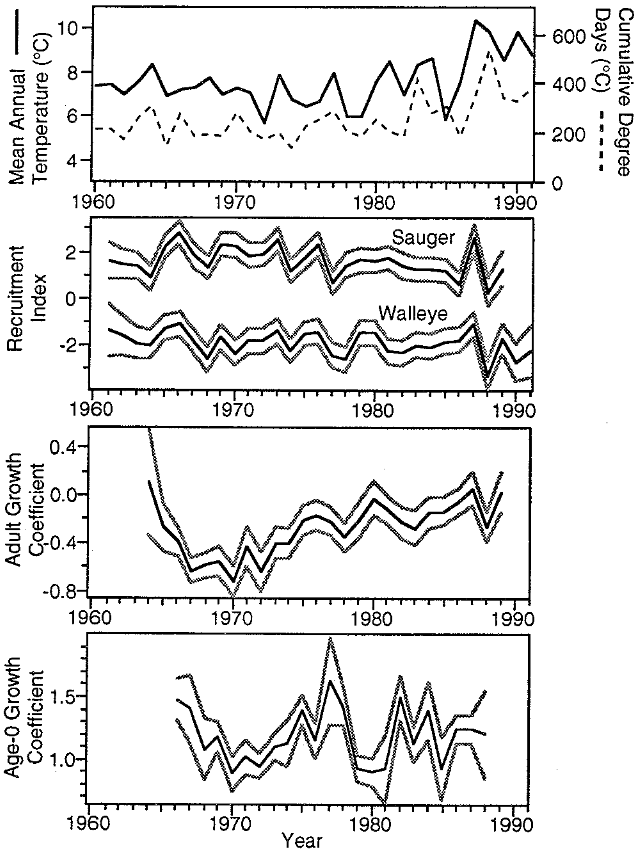

Fig. 1. Climate, recruitment, and growth series used for analysis of Lake Pepin walleye and sauger. Only recruitment data are available for sauger. Temperature data are from Winona, Minnesota. Shaded lines above and below the solid lines for recruitment and growth represent approximate 95% confidence intervals. Separate analyses were made for age-0 growth and subsequent growth of walleye. Age-0 growth was analyzed separately for fish captured at age 1+ and for fish captured at all ages. Only the data for age-0 growth estimated from fish captured at age 1+ is illustrated here. CDD is cumulative degree-days above a base temperature of 20°C.

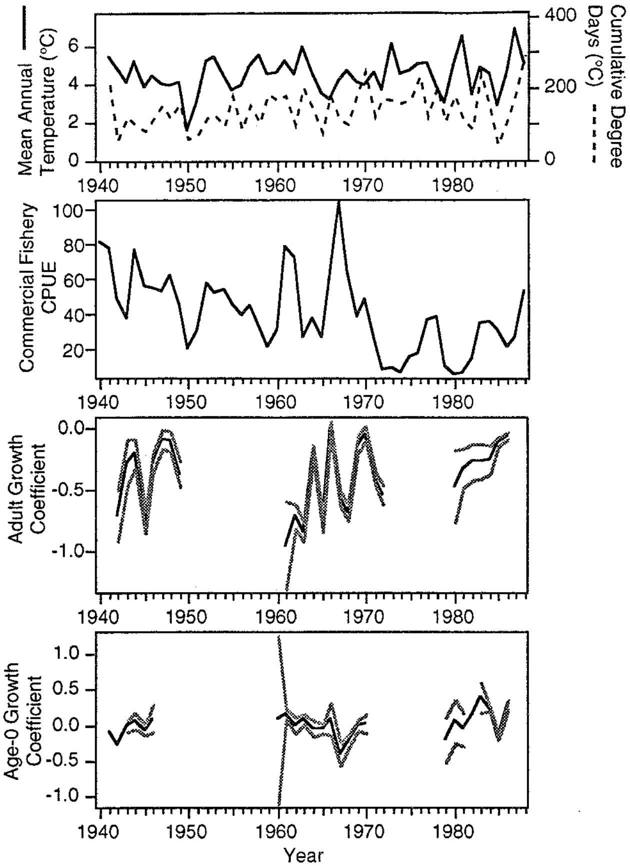

Fig. 2. Climate and growth series used for analysis of Red Lake walleye. Temperature data are from Crookston, Minnesota. CPUE data are for walleye from the Red Lakes commercial fishery, as described in Pereira et al. (1992). Growth data are from Shroyer (1991), with first-year growth coefficients estimated from fish captured at ages 2–8. Separate analyses were made for age-0 growth and for subsequent growth. CDD and approximate confidence intervals are as described in Fig. 1.

respectively. Estimates of first-year growth with fish of all capture ages showed no effect with high mean annual temperature ($P = 0.3371$), while the effect during years with low mean annual temperature was slightly significant ($P = 0.0454$). Therefore, it appears that first-year growth indexed from the scale increment of yearling fish (i.e., age 1+) is more sensitive to temperature than when estimated from fish of older ages. At the mature phase of El Niño, strong and moderate events were not related to adult growth and were only marginally related to recruitment ($P = 0.1303$) and first-year growth ($P = 0.1018$).

Red Lakes walleye

From the Red Lakes, we analyzed growth of adult and age-0 walleye (Fig. 2). The Red Lakes have supported an intensive, commercial fishery for walleye since the turn of this century (Smith 1977). Walleye dynamics are partially affected by this fishery; recruitment is currently episodic, with large year-classes following periods of 4–5 yr with little or no recruitment (Pereira et al. 1992). This pattern is illustrated in the time series of commercial CPUE (Fig. 2).

Superposed epoch analysis of Red Lakes walleye showed no significant results between adult growth and any of the climate variables (Table 3). Age-0 growth, however, was related to two temperature indices: low CDD years had slower growth, and years of high mean July temperature had higher growth.

Rainy Lake walleye

Climate, recruitment, and growth series used for analysis of Rainy Lake walleye are illustrated in Fig. 3. There were no apparent trends in recruitment, though recruitment appears to be relatively variable compared with Lake Pepin. Both growth series are relatively short, with years of good growth occurring in 1983 and 1988 for both adults and age-0 fish. Age-0 growth

Table 2. Results from epoch analysis of Lake Pepin walleye and sauger.

Population attribute	Key event (n)	*P* value	
		Walleye	Sauger
Recruitment[a]	CDD[b] ≥1 SD[c] above mean (5)	0.0139*	0.2816[d]
	CDD ≥1 SD below mean (2)	0.3075	0.3846
	Annual temp.[e] ≥1 SD above mean (4)	0.7333	0.4469[f]
	Annual temp. ≥1 SD below mean (4)	0.2752	0.6575
	July temp.[g] ≥1 SD above mean (6)	0.4380	0.7009
	July temp. ≥1 SD below mean (6)	0.0643	0.4785
	Mature phase El Niño (5)	0.1303	0.1294
Growth[h]	CDD ≥1 SD above mean (4)	0.5622	
	CDD ≥1 SD below mean (2)	0.2274	
	Annual temp. ≥1 SD above mean (3)	0.6780	
	Annual temp. ≥1 SD below mean (4)	0.0102*	
	July temp. ≥1 SD above mean (6)	0.2113	
	July temp. ≥1 SD below mean (5)	0.0192*	
	Mature phase El Niño (5)	0.4268	
Age-0 Growth[i]	CDD ≥1 SD above mean (5)	0.7646	
	CDD ≥1 SD below mean (1)	0.3922	
	Annual temp. ≥1 SD above mean (3)	0.0001*	
	Annual temp. ≥1 SD below mean (4)	0.0558*	
	July temp. ≥1 SD above mean (5)	0.7659	
	July temp. ≥1 SD below mean (4)	0.2121	
	Mature phase El Niño (5)	0.1018	

[a] Year-class main effect coefficients in Equation 1 are used for the recruitment index.
[b] CDD are cumulative degree-days throughout the year, above a base of 20°C.
[c] SD is standard deviation.
[d] This test had only four key events.
[e] Annual mean temperature (°C).
[f] This test had only two key events.
[g] July mean temperature (°C).
[h] Growth beginning in the second growing season was indexed with the year coefficients from the linear growth model using scale increments.
[i] First-year growth was indexed by the scale increment from the first growing season. Results reported in this table are from tests that included only fish captured at age 1+ (i.e., in their second growing season). Additional tests were done with this index derived from fish of all capture ages; these results are discussed further in the text.
* Significant *P* values.

was also fast in 1977. Recruitment and first-year growth had significant superposed epoch tests (Table 4). Recruitment was related to both high and low mean July temperatures. Age-0 growth was faster in years with high CDD and slower in years with low mean annual temperatures.

Walleye in Rainy Lake were the only species to have significant superposed epoch tests for the mature phase of El Niño (Table 4). The test for age-0 growth was highly significant ($P = 0.0115$). A nearly significant test for adult growth ($P = 0.0785$) suggests that the result for age-0 is not spurious.

Smallmouth bass in six northeastern lakes

Growth and climate series for smallmouth bass in six northeastern lakes are depicted in Fig. 4. Electrofishing yielded samples consisting almost entirely of fish less than 300 mm in total length. However, because growth was extremely slow, ages 1+ to 7+ were well represented. Because each of these series was quite short, we did not subject them to superposed epoch analysis. However, it is apparent that 1985 was a poor year for smallmouth bass growth in all six of these lakes. Patterns in growth also follow temperature, with 1985 and 1986 having the coolest summers for the 6 yr included in this analysis. Age distributions also indicated that there was poor recruitment of smallmouth bass in 1985, as fewer fish of the 1985 year-class were captured than of any other year-class.

Discussion

Results from superposed epoch analysis for walleye in Pepin, Red, and Rainy lakes suggest that growth of young-of-the-year may serve as a more sensitive indicator of climate events and change than growth of adult fish. Greater sensitivity of young fish is supported by evidence that the degree to which

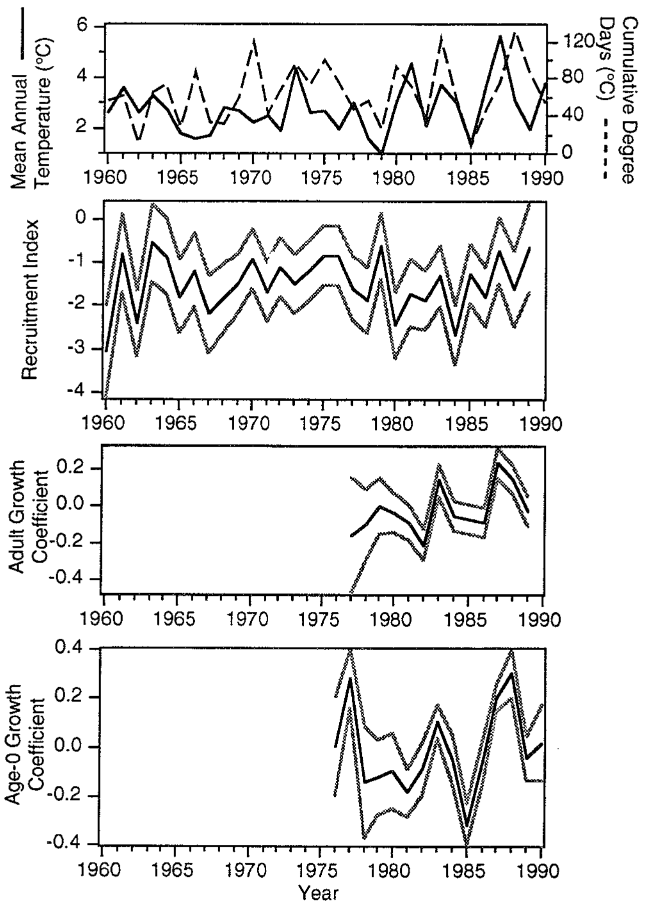

Fig. 3. Climate, recruitment, and growth series used for analysis of Rainy Lake walleye. Temperature data are from International Falls, Minnesota. Age-0 growth coefficients were estimated from fish captured at age 1+ only. CDD and approximate confidence intervals are as described in Fig. 1.

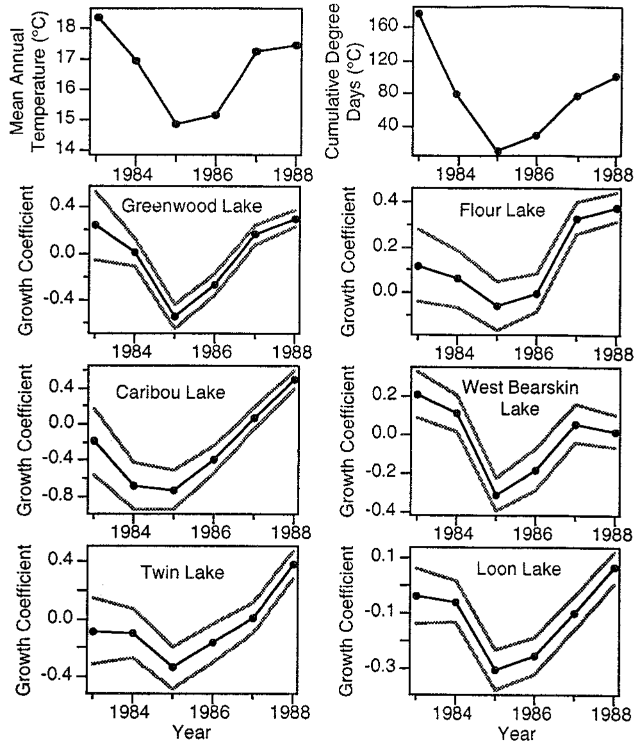

Fig. 4. Temperature and growth indices for smallmouth bass from six lakes in northeastern Minnesota. Temperature data are from the Gunflint weather station in northeastern Minnesota (latitude 48°10'N, longitude 90°53'W). CDD and approximate confidence intervals are as described in Fig. 1.

temperature affects metabolism is dependent on the size of the fish (Shuter and Post 1990). In this study, superposed epoch analysis yielded seven significant tests (of 21) for age-0 growth, while analysis of adult growth only resulted in two significant tests (both on Lake Pepin). A climate–growth link may indirectly influence the climate–recruitment relationship, as it is a common finding that walleye recruitment is positively associated with first-year growth (Forney 1976, 1980; Madenjian 1991; D. Pereira, unpublished data). Results from Pepin and Rainy lakes showed significant temperature–recruitment tests. Factors involved in the link may include prey size suitability, lipid content, or vulnerability to predation. Chevalier (1973) indicated that growth rates may influence mortality from cannibalism in Oneida Lake; that is, faster growing young-of-the-year walleye would be less vulnerable to adult predation.

Testing of temperature extremes with superposed epoch analysis may not show the form of nonlinear temperature associations with growth or recruitment. If mortality is moderated by growth rates, then year-class strength may often have a nonlinear relationship to temperature. Species have thermal optima for growth rate (Christie and Regier 1988), but additional nonlinearity may be introduced by growth-dependent predator–prey interactions. However, nonparametric superposed epoch analysis has a moderate level of statistical power to reject the null hypothesis where there are associations between extremes in environmental events and recruitment (Prager and Hoenig 1992). In addition, the selection of a temperature index may obscure associations. Colby et al. (1979) cited investigations of changes in walleye growth rates within the year as being dependent on suitable thermal conditions.

The smallmouth bass analyzed were all small and immature, and their growth fluctuations appeared synchronous in lakes in proximity. Because the fluctuations also appeared related to a climate variable, young smallmouth bass would be a good model with which to examine the spatial scale of climatic events as they drive fish production or the relative sensitivity of populations in different types of lakes.

El Niño key events had a significant relationship only with young-of-the-year growth in Rainy Lake. Ropelewski and Halpert (1986) state that teleconnections during El Niño do occur in northwestern North America as positive temperature anomalies, and Robertson (1989) reported shorter periods of ice cover for Lake Mendota in southern Wisconsin during El Niño events. Robertson also reported that effects of El Niño appear stronger in late winter, with ice breakup dates that

Table 3. Results from epoch analysis of Red Lakes walleye.

Population attribute	Key event (n)	*P* value
Growth[a]	CDD[b] ≥1 SD[c] above mean (5)	0.6162
	CDD ≥1 SD below mean (8)	0.2156
	Annual temp.[d] ≥1 SD above mean (5)	0.7757
	Annual temp. ≥1 SD below mean (6)	0.1234
	July temp.[e] ≥1 SD above mean (10)	0.2066
	July temp. ≥1 SD below mean (9)	0.2198
	Mature phase El Niño (8)	0.8169
Age-0 Growth[f]	CDD ≥1 SD above mean (6)	0.7676
	CDD ≥1 SD below mean (8)	0.0246*
	Annual temp. ≥1 SD above mean (4)	0.5604
	Annual temp. ≥1 SD below mean (6)	0.3481
	July temp. ≥1 SD above mean (10)	0.0075*
	July temp. ≥1 SD below mean (9)	0.2398
	Mature phase El Niño (7)	0.8013

[a] Growth beginning in the second growing season was indexed with the year coefficients from the linear growth model using scale increments.
[b] CDD are cumulative degree-days throughout the year, above a base of 20°C.
[c] SD is standard deviation.
[d] Annual mean temperature (°C).
[e] July mean temperature (°C).
[f] First-year growth was estimated with scale increments from fish of capture ages 2–8 (see Shroyer 1991).
* Significant *P* values.

Table 4. Results of epoch analysis of Rainy Lake walleye.

Population attribute	Key event (n)	*P* value
Recruitment[a]	CDD[b] ≥1 SD[c] above mean (5)	0.3781
	CDD ≥1 SD below mean (6)	0.4092
	Annual temp.[d] ≥1 SD above mean (3)	0.1997
	Annual temp. ≥1 SD below mean (5)	0.8711
	July temp.[e] ≥1 SD above mean (6)	0.0041*
	July temp. ≥1 SD below mean (5)	0.0287*
	Mature phase El Niño (5)	0.2546
Growth[f]	CDD ≥1 SD above mean (2)	0.1068
	CDD ≥1 SD below mean (2)	0.7764
	Annual temp. ≥1 SD above mean (3)	0.1247
	Annual temp. ≥1 SD below mean (3)	0.8287
	July temp. ≥1 SD above mean (2)	0.2781
	July temp. ≥1 SD below mean (1)	0.3028
	Mature phase El Niño (3)	0.0785
Age-0 Growth[g]	CDD ≥1 SD above mean (2)	0.0562*
	CDD ≥1 SD below mean (2)	0.1285
	Annual temp. ≥1 SD above mean (3)	0.4683
	Annual temp. ≥1 SD below mean (3)	0.0346*
	July temp. ≥1 SD above mean (2)	0.5355
	July temp. ≥1 SD below mean (1)	0.2075
	Mature phase El Niño (3)	0.0115*

[a] Year-class main effect coefficients in Equation 1 are used for the recruitment index.
[b] CDD are cumulative degree-days throughout the year, above a base of 20°C.
[c] SD is standard deviation.
[d] Annual mean temperature (°C).
[e] July mean temperature (°C).
[f] Growth beginning in the second growing season was indexed with the year coefficients from the linear growth model using scale increments.
[g] First-year growth was indexed with scale increments from fish capture at age 1+ only.
* Significant *P* values.

were 15 d earlier during El Niño events. On the basis of findings by Ropelewski and Halpert (1986), El Niño effects may be stronger when moving northwesterly from southern Wisconsin through northern Minnesota. A possible mechanism underlying the effect of El Niño on age-0 walleye growth in Rainy Lake could be a lengthening of the growing season. Madenjian (1991) showed the length of growing season and prey encounter rates determined the potential for young-of-the-year growth. Early ice breakup during El Niño events may significantly increase the length of the growing season, and therefore account for larger first-year increments.

Tests for the significance of El Niño events with Red Lakes walleye growth were not significant, which is consistent with results for freshwater drum (*Aplodinotus grunniens*) from the Red Lakes (Pereira et al. 1994). Because the Red Lakes are also located in northern Minnesota approximately 80 km south of Rainy Lake, we may expect to see results similar to those for Rainy Lake. However, the Red Lakes support an intensive fishery for walleye that is believed to induce considerable variation in recruitment and first-year dynamics of walleye (Pereira et al. 1992). Effects of other processes, such as exploitation, would hinder our ability to delineate climate signals in growth and recruitment, so analyses such as ours should be considered in light of results from other methods of stock assessment. This argument is also of concern for the analysis of Lake Pepin walleye and sauger. In that case, both species appear to have slight, downward trends in recruitment, while growth appears to increase. We suggest that trends should be explained before further analysis of climate associations is undertaken. Finally, application of these analyses to other large lakes in northern Minnesota, such as Lake of the Woods, may provide additional insight into potential teleconnections related to El Niño.

Possible synchrony in walleye year-class across wide geographical areas has been suggested (Colby et al. 1979; Serns 1982); however, year-class strengths of Rainy Lake walleye and Lake Pepin walleye were not correlated ($P > 0.05$). Böhling et al. (1991) found that patterns in the variation of year-class strength of perch were similar over large geographic areas, and attributed this to large-scale weather variations influencing water temperature. They did, however, find deviating patterns in areas exposed to environmental disturbances, such as water-level fluctuations and pollution. Water-level fluctuations in both Rainy and Pepin Lakes have been shown to influence walleye populations (Thorn 1984; Cohen and Radomski 1993). Cohen et al. (1991) found that dominant factors influencing Atlantic cod recruitment were operating on more local scales. They stated that "since recruitment is a multivariate process with different processes operating to varying degrees in different years, it is not surprising that the local scale of events is more important than the large scale." The primary factors determining year-to-year variation in fish growth include changes in stock abundance, fluctuations in the amount of available food, and climate factors such as temperature and length of growing season. With short time series such as ours, coherent variation over wide areas may be hidden by local disturbances, such as water levels and exploitation.

The methods we have applied here require the assumptions that fluctuations in predator–prey abundance are simply a source of random background variation, and that with enough data one can detect effects of climate. It appears that both walleye and smallmouth bass may serve as suitable species, with young-of-the-year providing the most sensitive life stage, and that the relative sensitivity of populations in different types of lakes may be measurable. Bioenergetic analysis (Hewitt and Johnson 1987) provides a method for separating variation in growth caused by temperature, length of growing season, and food availability. Madenjian (1991) has successfully applied similar methods to explain variation in young-of-the-year walleye growth in lakes Erie and Oneida. We propose the application of similar methods to suitable large walleye lakes in Minnesota. A review of scale increments suggests that growth of Lake Pepin age 1+ sauger during 1988 (i.e., the second growing season for the 1987 year-class) was curtailed by water temperatures exceeding 28–29°C. Bioenergetic analysis over the range of thermal conditions provided by Minnesota lakes may more clearly define temperature constraints and climate impacts on growth.

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