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Reprinted from
Canadian Journal of Fisheries and Aquatic Sciences

Réimpression du
Journal canadien des sciences halieutiques et aquatiques

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Volume 57 • Number 4 • April 2000

Pages 775–788

Canada

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Abstract: We examined annual changes in relative abundance of Lake Michigan fishes using linear models with correlated errors in space and time. Abundance of bloater (*Coregonus hoyi*), deepwater sculpin (*Myoxocephalus thompsoni*), slimy sculpin (*Cottus cognatus*), alewife (*Alosa pseudoharengus*), and rainbow smelt (*Osmerus mordax*) was monitored with bottom trawls at 10 discrete depths (between 18 and 110 m) off eight fixed ports from 1973 to 1992. The model describing abundance included fixed effects of year, port, depth, and interaction terms as well as quadratic and cubic effects of year and depth because changes in abundance were not strictly linear. Observed temporal trends in abundance varied with species and depth. Additionally, trends in alewife and slimy sculpin abundances depended on port. Cubic trends in the abundance of bloater and quadratic trends in deepwater sculpin and rainbow smelt abundances were similar among ports, permitting lakewide inferences for these species. Mean bloater abundance was low throughout the 1970s, increased during the 1980s, and reached high levels by 1990. Mean abundances of deepwater sculpin and rainbow smelt increased from 1973 to the mid-1980s and declined thereafter. The linear model with correlated errors can be readily applied to repeated-measures data from other fixed-station fishery surveys and is appropriate for data exhibiting spatial and temporal autocorrelations.

Résumé : Nous avons examiné les changements annuels dans l'abondance relative des poissons du lac Michigan en utilisant des modèles linéaires avec erreurs corrélées dans l'espace et dans le temps. Nous avons surveillé l'abondance du cisco de fumage, du chabot de profondeur, du chabot visqueux, du gaspareau et de l'éperlan arc-en-ciel, à l'aide de chaluts de fond opérant à 10 profondeurs discrètes (entre 18 et 110 m) à partir de 8 ports fixes, de 1973 à 1992. Le modèle décrivant l'abondance couvrait les effets fixes de l'année, du port, de la profondeur et des interactions, ainsi que les effets quadratiques et cubiques de l'année et de la profondeur, du fait que les changements dans l'abondance n'étaient pas strictement linéaires. Les tendances temporelles observées de l'abondance variaient avec l'espèce et la profondeur. De plus, les tendances de l'abondance du gaspareau et du chabot visqueux dépendaient du port. Les tendances cubiques de l'abondance du cisco de fumage et les tendances quadratiques de l'abondance du chabot de profondeur et de l'éperlan arc-en-ciel étaient semblables d'un port à l'autre, ce qui a permis de formuler pour ces espèces des inférences à l'échelle panlacustre. L'abondance moyenne du cisco de fumage était faible tout au long des années 70, a augmenté dans les années 80 et a atteint un niveau élevé en 1990. L'abondance moyenne du chabot de profondeur et de l'éperlan arc-en-ciel a augmenté de 1973 au milieu des années 80, pour baisser ensuite. Le modèle linéaire avec erreurs corrélées peut s'appliquer facilement à des données de mesures répétées tirées d'autres relevés de pêches à station fixe, et convient bien aux données montrant des autocorrélations spatiales et temporelles.

[Traduit par la Rédaction]

Introduction

The composition and productivity of the Lake Michigan fish community have been influenced by natural disturbances, such as invasion and colonization of exotic species and human interventions that resulted in overfishing and habitat destruction (Wells and McLain 1972). Major changes in the Lake Michigan fish community include the extirpation of five species of ciscoes (deepwater cisco (*Coregonus johannae*), kiyi (*Coregonus kiyi*), blackfin cisco (*Coregonus nigripinnis*), shortnose (*Coregonus reighardi*), and shortjaw cisco (*Coregonus zenithicus*)) (Todd and Smith 1992), the loss of discrete stocks of lake trout (*Salvelinus namaycush*) (Brown et al. 1981) and lake whitefish (*Coregonus*

Received October 13, 1999. Accepted January 19, 2000.
J15398

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clupeaformis) (Smith 1972), and notable declines in lake whitefish abundance (Wells and McLain 1972). The rapid change in species composition that began in the 1940s culminated in the 1960s with Lake Michigan fish stocks in a "state of extreme instability" (Smith 1968). For example, the alewife (*Alosa pseudoharengus*), an exotic planktivore, had become part of the Lake Michigan fish community in the 1950s (Wells and McLain 1972). Alewife abundance increased rapidly in the 1960s and occasionally reached nuisance levels such that massive, lakewide die-offs resulted in economic losses and aesthetic concerns in affected lakeshore towns and cities (Brown 1972). In Lake Michigan, alewife continue to be a subject of much interest because they are important forage for top predators such as lake trout, brown trout (*Salmo trutta*), chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), and rainbow trout (*Oncorhynchus mykiss*) (Jude et al. 1987) and because high abundance of alewife has been associated with population declines of some native fishes (Brown et al. 1999).

Many of the dramatic changes in the Lake Michigan fish community were documented by examining catch records from commercial fisheries (e.g., Smith 1972). Other studies used data from restricted areas of Lake Michigan to infer general lakewide changes in inshore (<10 m) fish populations (Jude and Tesar 1985). Although the Great Lakes Science Center (Ann Arbor, Mich.) monitors the relative abundance of Lake Michigan fishes using bottom trawl surveys, only a few studies of long-term changes in abundance have been published to date, and for the most part, these studies concerned single species (e.g., Brown 1972; Hatch et al. 1981). In addition to providing critical information to management agencies in the Lake Michigan basin (Brown et al. 1999), bottom trawl survey data may be used to infer trends in species abundance.

One of the difficulties in analyzing survey data from Lake Michigan concerns the design of the survey: fixed stations are sampled annually without replication, resulting in a complex repeated-measures design. Maceina et al. (1994) recommended using a repeated-measures analysis of variance (ANOVA) to analyze fish survey data and to accommodate the temporal autocorrelation among observations. However, this approach can be used for analysis of survey data if three conditions hold: (*i*) the repeated-measures study consists of fixed effects only, (*ii*) the data are balanced, and (*iii*) a restrictive form of the correlation structure is appropriate (Neter et al. 1996). When the data are unbalanced (missing), a typical situation for many fish surveys, tests based on the expected mean square statistic are not appropriate and alternative methods must be used (Neter et al. 1996). In addition to accommodating unbalanced data, we wished to model serial correlations across time and among stations (spatial correlations). We introduce a relatively new approach — linear models with correlated errors — to address both types of correlation and to describe trends and geographic relationships in abundances of fish species measured from the bottom trawl survey. In this paper, we show how the linear model with correlated errors is applied to data from the Lake Michigan survey, but the statistical approach is appropriate for other fixed-station fishery surveys consisting of repeated measures.

The objectives of this study were to describe changes in abundance of Lake Michigan fishes from 1973 to 1992 and to introduce the application of a versatile statistical model for analyzing fishery survey data. During this 20-year period, we captured 24 species of fish (excluding salmonids). In this paper, we examine the abundance of bloater (*Coregonus hoyi*), deepwater sculpin (*Myoxocephalus thompsoni*), slimy sculpin (*Cottus cognatus*), alewife, and rainbow smelt (*Osmerus mordax*). Together, these five species composed at least 90% of the total biomass of fish captured in any given year. A secondary purpose of this study was to determine if a lakewide abundance index is valid for the five principal species or if changes in abundance are unique to geographic areas. Currently, trawl catches for these five species are summarized on a lakewide basis and used to estimate total forage biomass available to salmonid predators stocked in Lake Michigan (Brown et al. 1999).

Materials and methods

Bottom trawl survey

Fish abundance was monitored annually in Lake Michigan between 1973 and 1992 at eight ports distributed in a systematic pattern around the lake in Wisconsin, Illinois, and Michigan waters (Fig. 1). A semiballoon bottom trawl was deployed in October and early November during daylight hours when fish are associated with the bottom and most vulnerable to the gear. The trawl, which had a 12-m headrope, 15.5-m footrope, and 13-mm mesh (nominal size) in the cod end, was towed for 10 min and fished an area of about 0.5 ha (Hatch et al. 1981). A description of the gear and development of the survey design for Lake Michigan are discussed in Brown et al. (1999).

At each port, tows were taken sequentially at 10 discrete bottom depths: 18, 27, 37, 46, 55, 64, 73, 82, 91, and 110 m (Hatch et al. 1981). For every tow, we recorded latitude and longitude coordinates and collected bottom temperature data using a bathythermograph. A total of 1514 tows were taken between 1973 and 1992. A few depths were not surveyed at some ports in some years, and no surveys were conducted at Port Washington in 1976 and Benton Harbor in 1982 because of weather or gear problems. Additionally, bottom trawling at Benton Harbor was terminated after the 1989 field season. These omissions represent about 5.4% of the total number of possible tows in the time series of data. In addition to being a fixed-site survey (ports and depths were fixed), the survey lacked replication, so a sampling unit in this study was one tow taken at one depth off one port in one year.

In our analysis, we considered bottom temperature and survey sampling date because these factors may affect variation in fish abundance. Although all sampling occurred in the fall, northern ports (Manistique, Sturgeon Bay, and Frankfort) were generally sampled earlier in the season. Additionally, we noted that surveys began earlier in the calendar year during the last half of the time series (average starting date of the survey: October 15 in 1973–1977, October 12 in 1978–1982, October 6 in 1983–1987, and September 25 in 1988–1992).

Relative abundance index

Catch was weighed to the nearest gram for each species (Hatch et al. 1981), and relative abundance was expressed as the catch (in grams) per minute of tow. The abundance index or catch per unit of effort (CPUE) reflects relative fish density (abundance per unit area) in areas sampled by the trawl (Gulland 1983); we do not attempt to extend inferences on abundance estimates to untrawlable areas of Lake Michigan, as densities in these areas may differ (Fabrizio et al. 1997). We excluded catch data for young-of-the-year fish because they contributed little to the total weight of the

Fig. 1. Sampling sites (×) of the Lake Michigan bottom trawl survey in Wisconsin (Sturgeon Bay and Port Washington), Illinois (Waukegan), and Michigan (Benton Harbor, Saugatuck, Ludington, Frankfort, and Manistique) waters. Tows were obtained annually in the fall in waters ranging from 18 to 110 m.

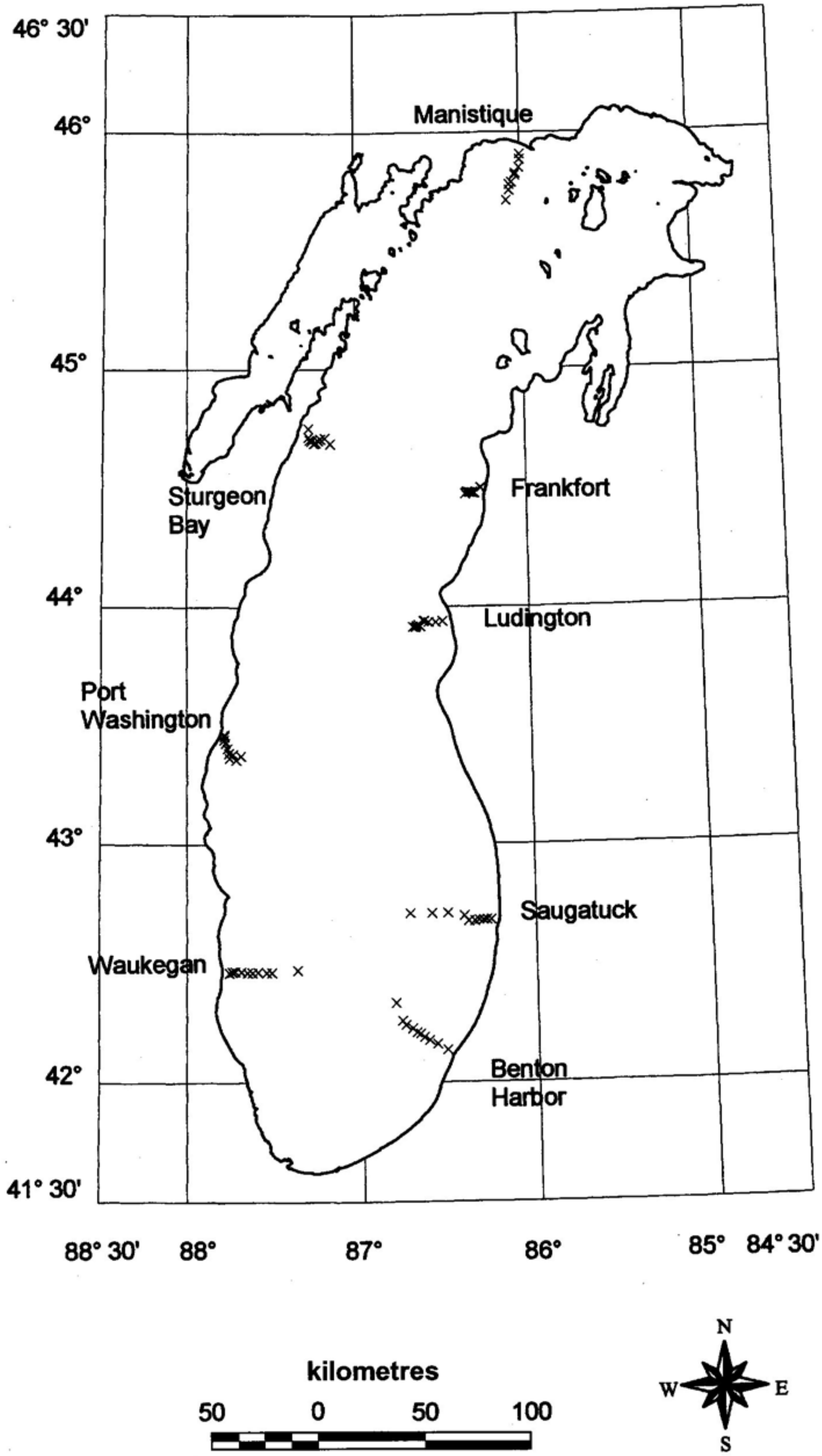


Table 1. Restricted maximum likelihood estimates of temporal correlations among errors one unit apart (95% confidence intervals are given in parentheses).

	Bloater	Deepwater sculpin	Slimy sculpin	Alewife	Rainbow smelt
Frankfort	0.263*	0.403*	0.383*	–0.016	0.014
	(0.127–0.399)	(0.271–0.535)	(0.252–0.515)	(–0.153–0.120)	(–0.123–0.151)
Ludington	0.085	0.449*	0.337*	0.017	0.176*
	(–0.051–0.222)	(0.321–0.577)	(0.205–0.470)	(–0.118–0.153)	(0.040–0.312)
Saugatuck	0.060	0.307*	0.477*	0.063	0.031
	(–0.075–0.196)	(0.173–0.440)	(0.351–0.603)	(–0.072–0.199)	(–0.104–0.166)
Benton Harbor	0.303*	0.353*	0.040	0.146	0.047
	(0.146–0.460)	(0.198–0.507)	(–0.121–0.201)	(–0.015–0.308)	(–0.114–0.209)
Waukegan	0.316*	0.428*	0.085	0.068	–0.006
	(0.183–0.450)	(0.299–0.558)	(–0.051–0.222)	(–0.068–0.204)	(–0.142–0.129)
Port Washington	–0.024	0.413*	0.316*	0.118	0.136
	(–0.165–0.117)	(0.280–0.547)	(0.177–0.454)	(–0.025–0.261)	(–0.007–0.279)
Sturgeon Bay	0.475*	0.555*	0.060	0.132	0.233*
	(0.349–0.601)	(0.436–0.675)	(–0.076–0.196)	(–0.005–0.270)	(0.097–0.369)
Manistique	0.451*	0.223*	0.302	–0.007	0.119
	(0.323–0.579)	(0.086–0.360)	(0.167–0.436)	(–0.143–0.129)	(–0.018–0.257)

Note: Units were defined by latitude–longitude coordinates or by MDS coordinates (see text for explanation). Asterisks denote significance at $\alpha \leq 0.05$.

catch and because these small fish are typically pelagic (Fabrizio et al. 1997). Because zero catches and occasional high catches contributed to skewness in the data, all abundance indices were square root transformed before further analysis to improve homogeneity of variances and to better approximate a normal distribution.

Statistical analysis

Autocorrelations and covariance structure

Data from the bottom trawl survey in Lake Michigan occur as repeated measures in four dimensions represented in our study by year, depth, and the two-dimensional location of each port. In addition, observations from the same year are likely to be correlated, as are those from the same port. Such data cannot be analyzed using standard ANOVA or regression approaches which require the user to assume that there are no correlations among tows from all ports and depths (the independent errors assumption). Also, a repeated-measures ANOVA does not permit modeling of the apparent spatial relationships in our data. Thus, the appropriate model is the linear model with correlated errors, which permits modeling and evaluation of a number of covariance structures. Evaluation of the covariance structure is a necessary step in the model fitting process to ensure valid inferences about means (Littell et al. 1996).

To identify the underlying covariance structure in the data, we fit regression models of year, port, and depth to the abundance indices for each species. This approach assumes that all observations are independent, which we knew was not the case. By examining residuals from these models, however, we could identify sources of dependency in the data. In particular, we used scatterplot matrices for each species (one for the eight ports and another for the 10 depths) to identify strong relationships in residuals from adjacent depths and weaker relationships among nearby ports. Thus, we concluded that spatial correlations existed among depths at a given port and geographically among ports.

For all species, correlations among observations from adjacent depths were higher than those among observations two or more depth units apart. This implied that the covariance structure associated with depths could be modeled approximately by the covariance structure of a first-order autoregressive process (Littell et al. 1996). Under this covariance structure, the estimated correlation between observations w depth units apart is given by ρ^w. For example, ρ is the estimated correlation between observations one unit apart, ρ^2 is the estimate for observations two units apart, and so forth. Thus, estimated correlations decrease exponentially with increasing distance between observations.

We allowed correlations to vary among pairs of ports by using an unstructured (or arbitrary) covariance model. We selected this approach because correlations among geographically proximal ports were complex and followed no consistent pattern with increasing distance. However, flexible, unstructured covariances cannot be specified in existing software when random errors exhibit correlations in more than two dimensions (e.g., depth, port, and time). Thus, in the presence of temporally autocorrelated errors (see below), we modeled correlations among ports using an alternative approach that relied on the spatial information either in the latitude and longitude data for each port or in port-to-port distances. We summarized distance data using multidimensional scaling (MDS), a method to estimate a coordinate system that parsimoniously represents the distances (Mardia et al. 1979). In our case, distances between pairs of ports were scaled to a two-dimensional coordinate system that described most of the information in the distance measures.

We found evidence for temporal correlations in the abundance data for bloater, deepwater sculpin, and slimy sculpin. Temporal correlations were examined at each port separately for each species by allowing the random errors to be correlated temporally and across depths. We used an autoregressive model to describe the correlations for both time and depth. Temporal correlations were significant at all eight ports for deepwater sculpin, five ports for bloater, and four ports for slimy sculpin (Table 1).

Linear model with correlated errors

We fit the linear model with correlated errors to our data using the Mixed procedure in SAS (SAS Institute Inc. 1996), specifying two types of covariance structures depending on the evidence for temporally correlated errors. Based on our investigation of temporal correlations, we assumed that years were uncorrelated for alewife and rainbow smelt only. For these two species, the sequence of random errors at all depths (all years) was modeled as a first-order autoregressive process (SAS option, type = AR(1)), and correlations among ports (within years) were allowed to vary arbitrarily (SAS option, type = UN). We modeled correlated errors across time, depth, and ports for bloater, deepwater sculpin, and

Table 2. Linear model with correlated errors fit to abundance indices for bloater, deepwater sculpin, slimy sculpin, alewife, and rainbow smelt from Lake Michigan.

$\text{Sqrt(CPUE)}_{sdpt} = \mu$	+	Port + year + year^2 + year^3	+	Depth + depth^2 + depth^3	+
Port × year	+	Port × year^2	+	Port × year^3	+
Port × depth	+	Port × depth^2	+	Port × depth^3	+
Year × depth	+	Year × depth^2	+	Year × depth^3	+
Year^2 × depth	+	Year^2 × depth^2	+	Year^2 × depth^3	+
Year^3 × depth	+	Year^3 × depth^2	+	Year^3 × depth^3	+
Port × year × depth	+	Port × year × depth^2	+	Port × year × depth^3	+
Port × year^2 × depth	+	Port × year^2 × depth^2	+	Port × year^2 × depth^3	+
Port × year^3 × depth	+	Port × year^3 × depth^2	+	Port × year^3 × depth^3	+
Day	+	Temperature	+	ε_{sdpt}	

Note: Sqrt(CPUE) is the square root of the abundance index, day refers to the calendar day of the year (e.g., October 17 is the 290th day in a nonleap year), temperature is water temperature (°C) along the bottom, and ε_{sdpt} is a random error term for species s (s = bloater, deepwater sculpin, slimy sculpin, alewife, and rainbow smelt) taken at depth d (d = 18, 27, 36,...,) from port p (see Table 1 for ports) in year t (t = 1973, 1974,..., 1992).

slimy sculpin abundances using a spatial power structure. The corresponding SAS option, type = SP(POWA), allows for decreasing correlations with increasing Euclidean distance between observations (SAS Institute Inc. 1996). In the special case of one dimension and equally spaced points, the spatial power structure reduces to the covariance structure of a first-order autoregressive process. For the spatial power covariance structure, ports were defined by scaled latitude and longitude coordinates (deepwater sculpin) or by MDS coordinates (bloater and slimy sculpin). Covariance parameters for all models were calculated using restricted maximum likelihood (Littell et al. 1996), and tests were conducted at the α = 0.05 level of significance.

The general form of the linear model in matrix notation is $\mathbf{y} = \mathbf{X}\beta + \mathbf{e}$, where $\mathbf{y}$ is a vector of observations, $\mathbf{X}$ is a matrix of fixed-effects values, β is a vector of fixed-effects coefficients, and $\mathbf{e}$ is a vector of possibly correlated random errors with covariance matrix $\mathbf{R}$ (Littell et al. 1996). The difference between this linear model and the general linear model is that in the general linear model, $\mathbf{e}$ is a vector of independent random variables, whereas in linear models with correlated errors, the elements of $\mathbf{e}$ are not required to be independent (SAS Institute Inc. 1996). Thus, in the linear model with correlated errors, the mean, variance, and covariance of $\mathbf{y}$ are modeled (in a standard linear model, only the mean and a single variance of $\mathbf{y}$ are modeled). In addition, linear models with correlated errors allow for missing values and in this regard offer an advantage over the repeated-measures ANOVA.

We computed the elements of the error covariance matrix $\mathbf{R}$ using restricted maximum likelihood estimators. The Mixed procedure substitutes these estimates for the true elements of $\mathbf{R}$ to compute estimates of β and the variance of the estimator of β (Littell et al. 1996).

The linear, quadratic, cubic, and interaction terms included in the model (Table 2) were considered fixed effects because inferences will be made on the set of eight ports and for the period of interest, 1973–1992, not for time in general (Sokal and Rohlf 1981; Bennington and Thayne 1994). Interaction terms in the model account for local (spatial and temporal) effects contributing to the variation in species abundance. For example, the interaction of port and year represents annual changes at a given port around a mean value for that port or around the trend for that port. Below, we report our results based on approximate F tests and approximate P values because exact F tests do not exist for these models.

Results

We detected significant two- and three-way interactions when we fit the linear model with correlated errors to abundance data for bloater, deepwater sculpin, slimy sculpin, alewife, and rainbow smelt (Table 3). Because of significant interaction terms, statements concerning main effects should be made with respect to a specific depth, port, or year. However, some general patterns emerged. Here, we focus on temporal trends in abundance and examine port- and depth-specific changes when interactions are present.

Bloater

Bloater abundance increased throughout Lake Michigan during the 20-year period of study. Bloater, which were captured at all ports, occurred in greatest densities between 46 and 64 m. Linear changes in bloater abundance over time varied with port and depth (significant year × port and year × depth^2 interaction, Table 3). For example, at Ludington, bloater abundance from 1973 to 1992 was fairly constant at 18 m but increased steadily at 64 m (Fig. 2*a*), whereas at Waukegan, bloater abundance increased at both the 18- and 64-m stations (Fig. 2*b*). In general, bloater abundance began to increase by the early 1980s at all ports at 64 m and by the mid-1980s at 110 m. At 18 m, increasing abundance of bloater was evident by the early 1980s only at Waukegan. Bloater abundance at 18 m for all other ports remained near zero throughout the period of study.

We found significant cubic trends in mean bloater abundance throughout Lake Michigan and at all depths, as evidenced by the lack of significant interactions of port or depth with year^3 (Table 3). Mean lakewide abundance of bloater (across depths and ports) was low during the 1970s and began to increase during the early 1980s. By the late 1980s, mean abundance in Lake Michigan began to level off (Fig. 2*c*).

In addition to temporal trends, the significant depth × port interaction (Table 3) suggested that patterns of change in bloater abundance from shallow to deep waters varied among ports. Neither water temperature nor survey date (calendar day) had a significant effect on bloater abundance (Table 3).

The estimated parameter of the first-order autoregressive model for the error variation in bloater abundance among depths was 0.354. This implies that after accounting for port, depth, and time effects, and the effects of the polynomial and interaction terms, the estimated correlation between observations w depth units apart (where one depth unit is 9 m)

Table 3. Tests of effects using the linear model with correlated errors to describe relative abundance of five fish species in Lake Michigan.

Effect	df[a]	Bloater	Deepwater sculpin	Slimy sculpin	df[b]	Alewife	Rainbow smelt
Year	1,1380	174.92*	1.53	27.91*	1,16	12.71*	4.33
Year^2	1,1380	0.21	10.55*	0.01	1,16	12.11*	7.04*
Year^3	1,1380	22.71*	0.13	8.97*	1,16	0.08	4.29
Depth	1,1380	7.50*	224.27*	10.84*	1,1364	32.15*	38.43*
Depth^2	1,1380	137.52*	51.71*	13.78*	1,1364	9.87*	102.84*
Depth^3	1,1380	14.34*	55.22*	3.44	1,1364	7.97*	24.75*
Port	7,1380	1.15	2.67*	11.79*	7,1364	1.47	13.87*
Depth × port	7,1380	2.40*	5.40*	2.48*	7,1364	3.31*	5.68*
Depth^2 × port	7,1380	0.53	1.07	7.20*	7,1364	0.15	5.61*
Depth^3 × port	7,1380	1.63	5.62*	2.01	7,1364	2.04*	3.33*
Year × port	7,1380	2.27*	1.07	4.54*	7,1364	2.78*	2.88*
Year^2 × port	7,1380	1.70	0.42	5.56*	7,1364	3.82*	0.65
Year^3 × port	7,1380	1.24	0.64	2.89*	7,1364	4.73*	2.20*
Year × depth	1,1380	0.19	2.64	6.24*	1,1364	11.24*	3.71
Year × depth^2	1,1380	32.34*	0.07	1.66	1,1364	1.19	6.53*
Year × depth^3	1,1380	0.07	1.77	0.01	1,1364	0.59	1.58
Year^2 × depth	1,1380	2.23	29.86*	11.19*	1,1364	0.98	0.49
Year^2 × depth^2	1,1380	0.08	0.44	1.11	1,1364	5.46*	0.31
Year^2 × depth^3	1,1380	0.02	2.21	0.82	1,1364	0.03	0.47
Year^3 × depth	1,1380	0.25	0.14	0.77	1,1364	1.55	1.89
Year^3 × depth^2	1,1380	2.74	0.06	0.00	1,1364	0.01	1.16
Year^3 × depth^3	1,1380	0.04	3.14	0.15	1,1364	0.14	0.31
Year × depth × port	7,1380	0.99	4.33*	1.23	7,1364	0.96	0.64
Year^2 × depth × port	7,1380	0.55	0.73	1.67	7,1364	1.75	0.89
Year^3 × depth × port	7,1380	0.56	2.53*	1.08	7,1364	0.86	0.63
Year × depth^2 × port	7,1380	1.10	0.60	2.14*	7,1364	0.81	3.77*
Year^2 × depth^2 × port	7,1380	0.63	1.36	3.85*	7,1364	1.57	0.71
Year^3 × depth^2 × port	7,1380	0.31	0.29	1.54	7,1364	1.59	4.00*
Year × depth^3 × port	7,1380	0.60	2.53*	1.05	7,1364	1.15	1.67
Year^2 × depth^3 × port	7,1380	0.39	1.14	1.28	7,1364	2.53*	0.97
Year^3 × depth^3 × port	7,1380	0.38	1.42	1.07	7,1364	1.15	1.63
Temperature	1,1380	3.74	0.01	0.52	1,1364	26.03*	0.30
Calendar day	1,1380	0.02	1.29	0.68	1,1364	0.04	0.26

Note: The model was fit using the restricted maximum likelihood method in the Mixed procedure in SAS (SAS Institute Inc. 1996). Tabled values (*F* statistics) are from *F* tests based on type III sums of squares. Because exact *F* tests do not exist for the model that we used, degrees of freedom (df: numerator, denominator) and *P* values are approximate; asterisks denote $P \leq 0.05$.

[a]Degrees of freedom apply to models for bloater, deepwater sculpin, and slimy sculpin.

[b]Degrees of freedom apply to models for alewife and rainbow smelt.

was 0.354^w. For example, the estimated correlations were 0.354 between stations whose depths differed by 9 m, 0.125 (0.354^2) for stations differing by 18 m, and 0.044 (0.354^3) for stations differing by 27 m. Similarly, the estimated temporal correlation between adjacent years was 0.232.

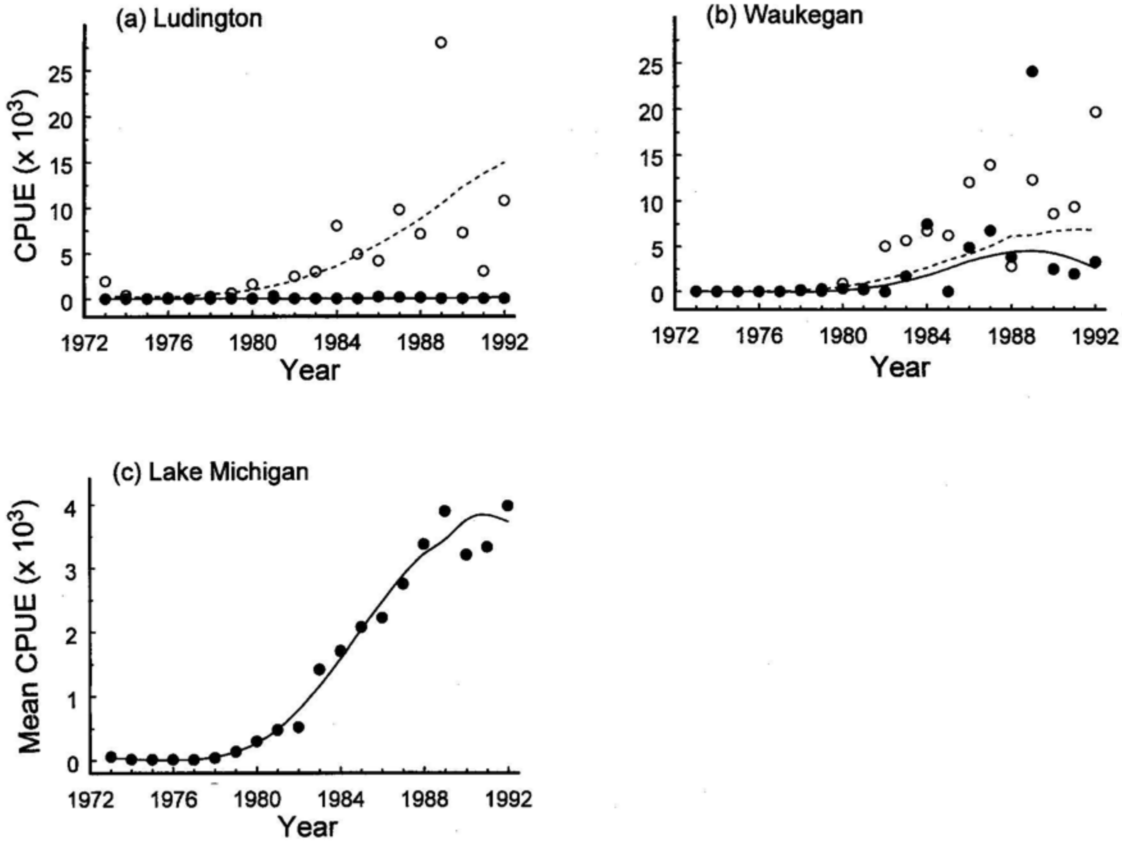
Deepwater sculpin

Deepwater sculpin abundance exhibited significant quadratic changes through time, but these changes varied with depth (Table 3). Although we encountered deepwater sculpin at all depths, most were captured in waters 64 m and deeper, and mean abundance increased with increasing water depth at all ports (Fig. 3). In general, mean lakewide abundance of deepwater sculpin at the 64-, 73-, 82-, 91-, and 110-m stations increased during the 1970s, peaked in the early to mid-1980s, and declined thereafter (Fig. 3). In contrast, mean deepwater sculpin abundance remained near zero at our 18-27-, 37-, 46-, and 55-m stations throughout the 20-year period of study. Neither water temperature nor survey date had significant effects on deepwater sculpin abundance (Table 3). The estimated parameter of the first-order autoregressive model for the error variation in deepwater sculpin abundance was 0.591 among depths and 0.372 between adjacent years.

Slimy sculpin

Slimy sculpin abundance in Lake Michigan exhibited significant linear and cubic trends between 1973 and 1992 (Table 3). Due to the significant interaction term (year × depth^2 × port), linear trends must be examined by port and depth. In general, slimy sculpin abundance decreased linearly at most ports and depths, but changes in abundance were not well described in linear terms. Cubic trends in

Fig. 2. Trends in bloater abundance (CPUE) at 18 m (solid circles) and 64 m (open circles) off two ports and mean bloater abundance in Lake Michigan. Abundance and mean abundance, calculated by averaging across 10 depths and eight ports, are expressed as $g \cdot min^{-1}$ and are represented by the solid and open circles. The fitted model is indicated by the solid (18 m or lake mean) or dashed line (64 m).



abundance varied with port only ($year^3 \times$ port, Table 3). At Frankfort, Ludington, Saugatuck, and Port Washington, mean slimy sculpin abundance decreased from a high in the mid-1970s, reached lows by the mid- to late 1980s, and increased subsequently (Fig. 4*a*). Mean abundance at Waukegan and Benton Harbor (1973–1989) decreased since 1973 and showed no increase in recent years (Fig. 4*b*). Cubic trends in slimy sculpin abundance at Sturgeon Bay and Manistique differed from trends observed at other ports (Figs. 4*c* and 4*d*): mean abundances at these two northern ports increased from the mid-1970s to the early to mid-1980s but decreased thereafter.

Slimy sculpin were most abundant at Frankfort, and most fish were found in waters 55 m and deeper. Effects of water temperature and survey date were not significant (Table 3). The estimated parameter of the first-order autoregressive model for the error variation in slimy sculpin abundance among depths was 0.322 and 0.250 between adjacent years.

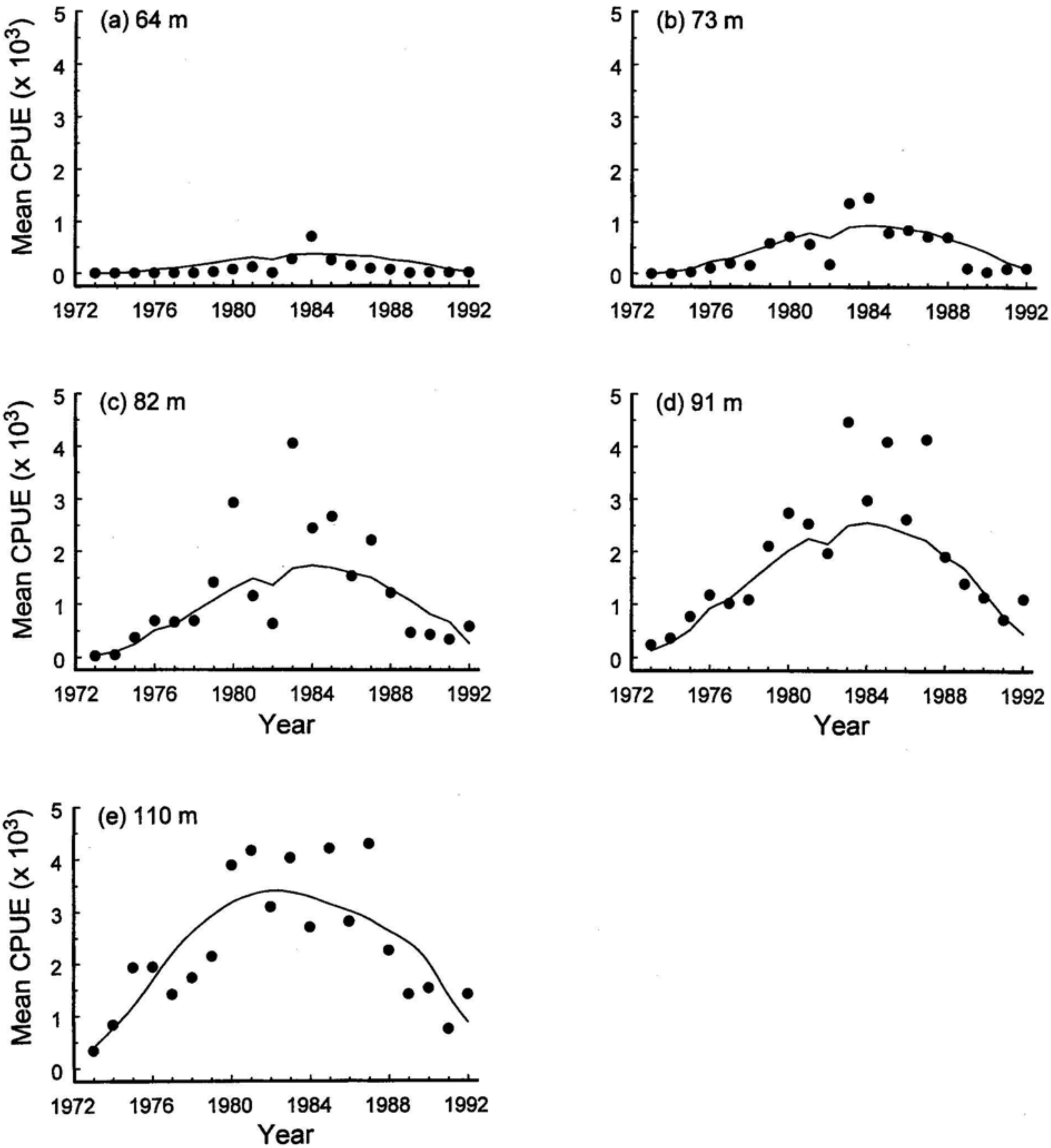
Alewife

Between 1973 and 1992, alewife abundance decreased linearly, and this trend varied with depth or port (significant year × port and year × depth interactions, Table 3). Although no declines in mean lakewide abundance were seen in waters less than 46 m (where alewife abundance was generally low), mean abundance decreased linearly in waters 46 m and deeper. Among ports, mean alewife abundance decreased linearly throughout Lake Michigan except perhaps at Sturgeon Bay (Fig. 5). The steepest declines in mean alewife abundance occurred at Frankfort, Waukegan, and Benton Harbor (Figs. 5*b*, 5*g*, and 5*h*). Peak alewife abundance at these three ports occurred at 64 or 73 m, shallower than at other ports. The relative lack of change in alewife abundance at Sturgeon Bay may be due to their distribution in deeper waters at that port. On average (across time), peak abundance of alewife at Sturgeon Bay occurred at 110 m. In 1978 and 1979, large numbers of alewife were taken in waters 55 m and deeper at Sturgeon Bay, and mean alewife catches at this port were unusually high (Fig. 5*c*). These high catches were not associated with anomalous water temperatures but may have been related to the presence of a few strong year-classes following the severe winter of 1976–1977.

Quadratic trends through time in alewife abundance varied with depth and port (significant $year^2 \times depth^3 \times$ port interaction, Table 3). For example, at the 64-m station, alewife abundance increased in recent years at Port Washington but not at Saugatuck, where abundance since the early 1980s has remained low or declined. Although not depicted here, trends in abundance at 64 m closely resembled those depicted for mean abundance averaged across depths (see Fig. 5). We also noted decreasing abundance of alewife at 46 m and deeper beginning in 1973 at Frankfort, Ludington, Saugatuck, Benton Harbor, and Waukegan (means across depths display similar trends, see Fig. 5).

Unlike results for other species, water temperature had a

Fig. 3. Trends in mean deepwater sculpin abundance (CPUE) at various depths. Mean abundance, calculated by averaging across eight ports, is expressed as g·min^{-1} and is represented by the circles. The fitted model is indicated by the line.



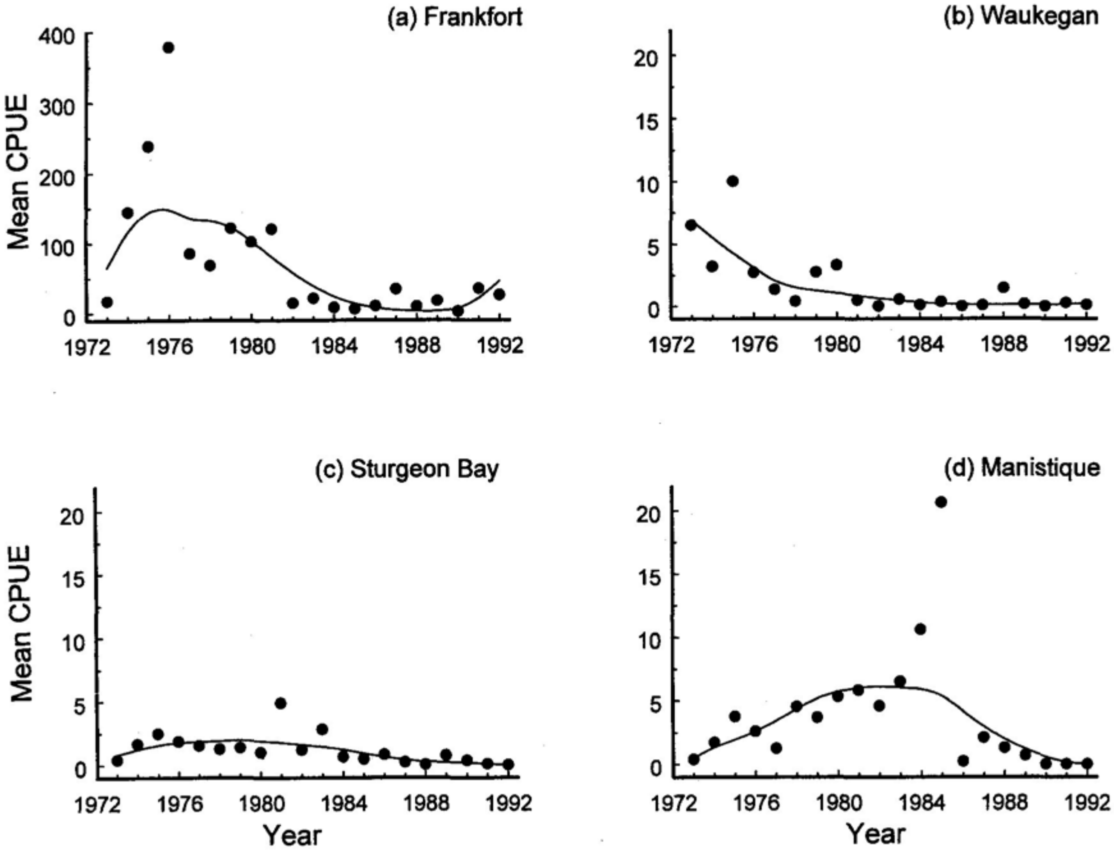
significant effect on mean alewife abundance (Table 3), such that high water temperatures resulted in slightly lower model predictions of abundance. In addition, survey date had no significant effect on alewife abundance, and port effects were significant only in interaction with time or depth (Table 3). The estimated parameter of the first-order autoregressive model for the error variation in alewife abundance among depths was 0.535.

Rainbow smelt

Rainbow smelt abundance in Lake Michigan exhibited a significant quadratic trend through time (Table 3), and this trend was consistent across all ports and depths. Lakewide mean abundance increased gradually from 1973 until the mid-1980s and decreased thereafter. Mean rainbow smelt abundances were greatest between 37 and 64 m, and abundances at the four western ports (Waukegan, Port Washington, Sturgeon Bay, and Manistique) were higher than at eastern ports (Fig. 6). Neither water temperature nor survey date had significant effects on rainbow smelt abundance (Table 3).

Linear and cubic changes in rainbow smelt abundance through time varied by depth and port (year × depth^2 × port and year^3 × depth^2 × port interactions, Table 3). Trends in abundance at western Lake Michigan ports appeared to exhibit similar patterns, and these patterns differed from those observed at eastern ports. For example, rainbow smelt abun-

Fig. 4. Trends in mean slimy sculpin abundance (CPUE) at four ports. Note the change in the ordinate of the plot for Frankfort. Mean abundance, calculated by averaging across 10 depths at each port, is expressed as g·min^{-1} and is represented by the circles. The fitted model is indicated by the line.



dance at 46 m appeared to increase in the late 1980s at western ports but not at eastern ports (Fig. 6). The estimated parameter of the first-order autoregressive model for the error variation in rainbow smelt abundance among depths was 0.427.

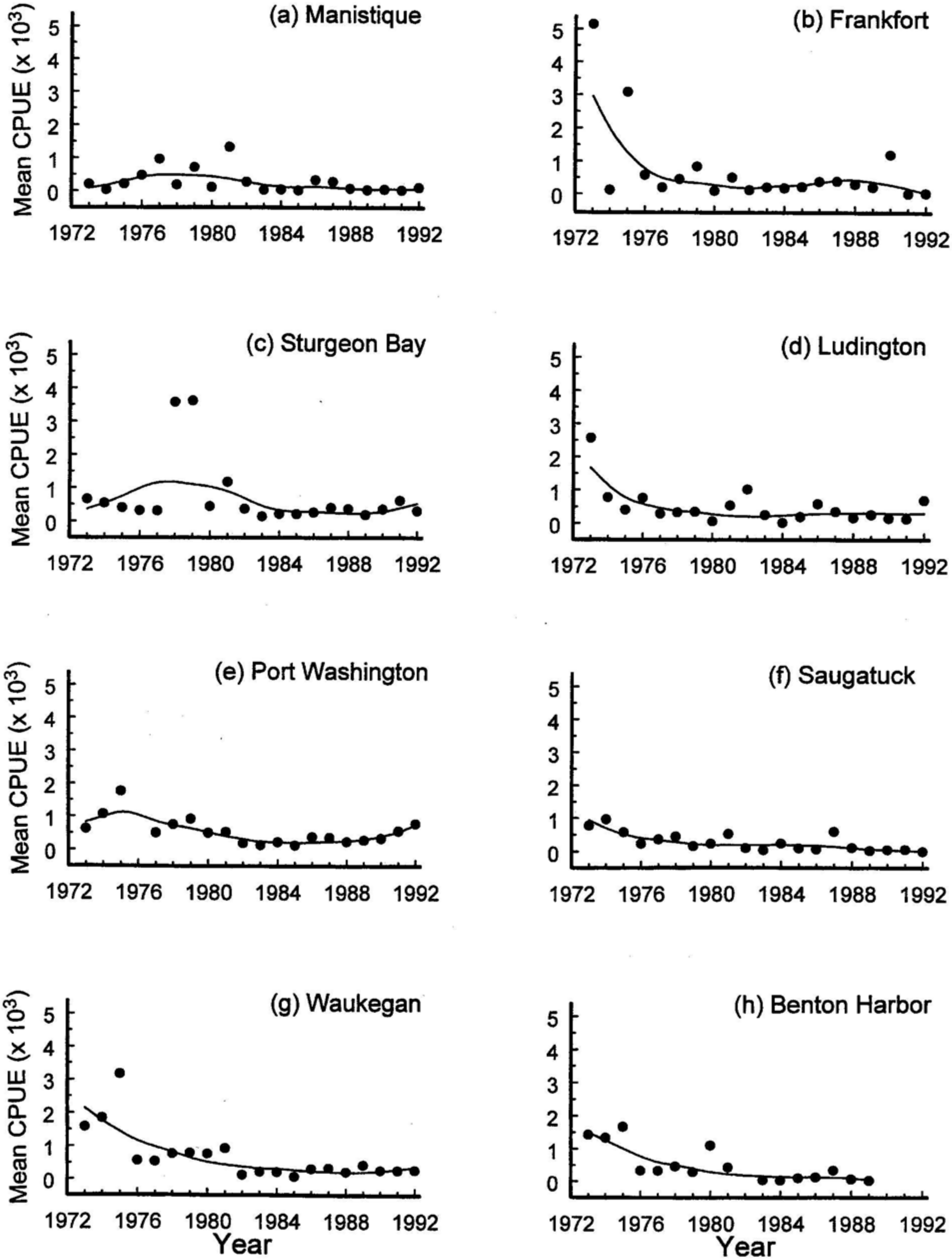
Discussion

Trends in abundance of five Lake Michigan fishes were described using linear models that included the effects of time, port, depth, and their interactions. In addition, the models allowed for correlations in time and space (ports and depths). This was accomplished by specifying the nature of correlations (i.e., autoregressive or arbitrary) in the random error term of the models. Observed temporal trends in abundance were highly variable among species, and for the most part depended on depth and port. Depth was an important influence on mean abundance of the five species studied, and, with the exception of cubic depth effects for slimy sculpin, all linear, quadratic, and cubic depth effects were significant for all species. In addition, the finding that the abundance of individual species in Lake Michigan varied with port was consistent with observations from a 1987 lakewide survey (e.g., Brandt et al. 1991). For instance, in the fall of 1992, slimy sculpin were most abundant at Frankfort, whereas rainbow smelt were more abundant in the western portion of the lake.

Of the species studied, deepwater sculpin abundance displayed the highest autocorrelations between sampling stations and slimy sculpin the least. These results may reflect the relative spatial extent of aggregations of these species in the fall, with slimy sculpin forming smaller aggregations. Although abundances of the five species in Lake Michigan were somewhat cohesive on fine spatial scales (depth differences of 9–18 m), relationships over larger scales (i.e., from port to port) varied with species and were complex. We modeled these spatial relationships in alewife and rainbow smelt abundances using arbitrary correlations and in bloater, deepwater sculpin, and slimy sculpin abundances using a spatial power structure. The more flexible arbitrary correlations could be used to describe spatial relationships only in the absence of temporal correlations among the random error terms.

The abundance of individual species followed patterns that generally conformed to water depth, but strict associations between fish abundance and depth cannot be made without regard to port or region of the lake. This is because for all species, abundance and depth relationships varied by port (significant depth × port interaction). These results supported the notion that samples from a given port and depth were not similar to samples collected at another port from the same depth. For example, mean abundance of deepwater sculpin at Benton Harbor, Waukegan, and Manistique is lower at 110 m than at 91 m, but mean abundance at the remaining five ports is highest at 110 m. Because of the de-

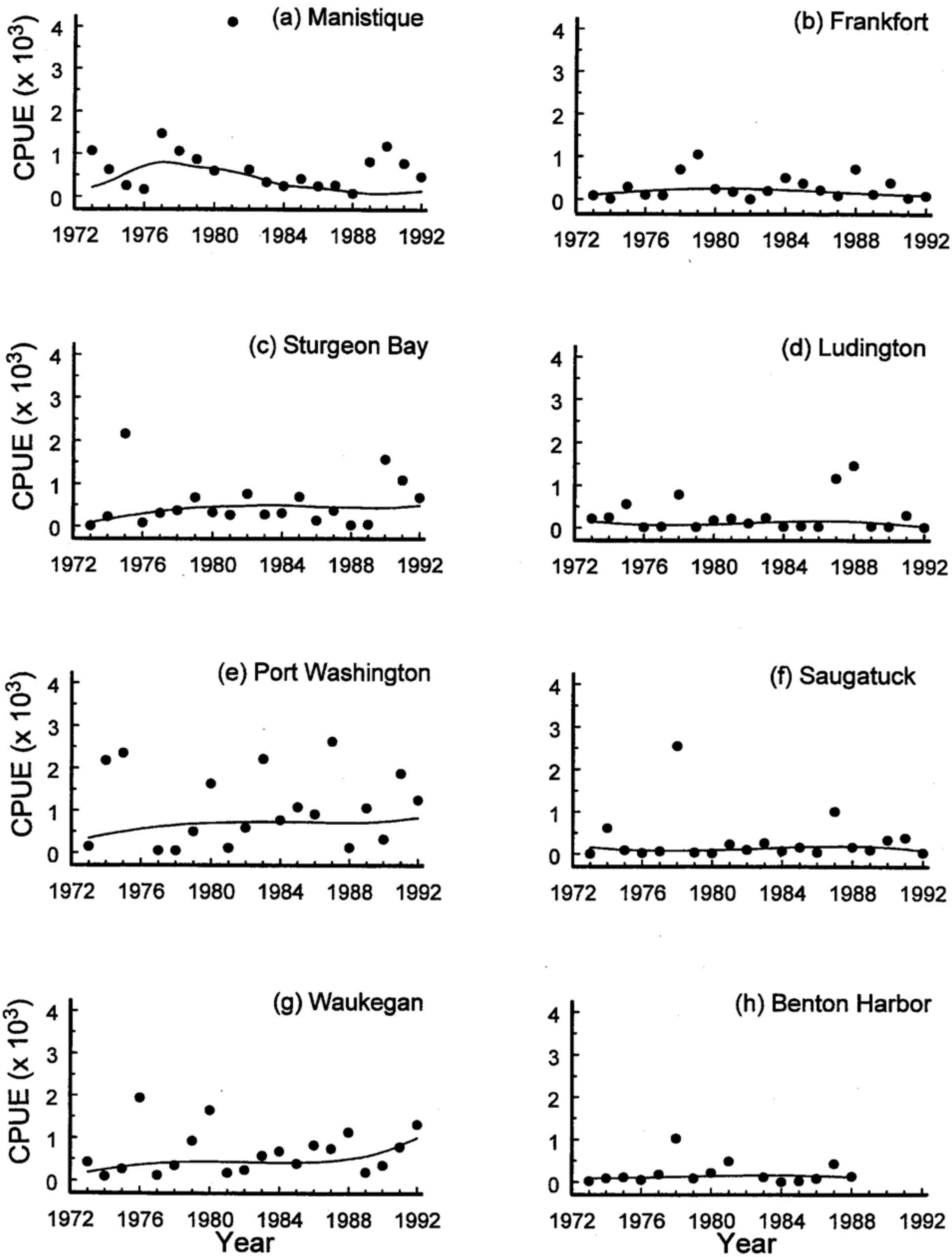
Fig. 5. Trends in mean alewife abundance (CPUE) at eight ports averaged across 10 depths. Mean abundance is expressed as g·min^{-1} and is represented by the circles. The fitted model is indicated by the line.



pendence of abundance on depth, patterns in the abundance of trawl-captured fish in Lake Michigan may be quite different when samples from a restricted set of depths are considered. For example, by excluding samples from sites deeper than 64 m, one may fail to note the steep decline in deepwater sculpin abundance since the mid-1980s (Fig. 3).

Variations in alewife abundance were partially explained by observed water temperatures. In Lake Michigan, fish re-

Fig. 6. Trends in rainbow smelt abundance (CPUE) at 46 m at eight ports. Abundance is expressed as g·min^{-1} and is represented by the circles. The fitted model is indicated by the line.



spond to changes in water temperature by altering their distribution in the water column or along shore (e.g., Wells 1968). In contrast with alewife, our analysis of lake-bottom temperatures in the fall did not provide evidence for temperature effects on the abundance of bloater, deepwater sculpin, slimy sculpin, or rainbow smelt. Distributions of these species are likely affected by additional abiotic factors operating at a local level (at a given port), such as upwelling, bottom currents, wind-driven circulation, seiches, or recent storm events. For the most part, these hydrologic conditions are expected to be strongly associated with temperature. Our inability to detect temperature-related changes in the abundance of four out of five species could simply mean that the temperature tolerances of bloater, deepwater sculpin, slimy sculpin, and rainbow smelt are broader than the observed range of temperatures in the fall. Water temperatures during the fall survey varied little relative to the overall variation in water temperature throughout the year. The variations that we observed in fish distribution and abundance in the fall may have resulted from the response (or delayed response) of fish to cues in addition to bottom water temperature such as light intensity, turbidity, and occurrence of prey or predators.

Survey date effects

Sampling date had no significant effect on the abundance of bloater, deepwater sculpin, slimy sculpin, alewife, or rainbow smelt. Our inability to detect starting-date effects was likely due to the narrow range of starting dates (days 256–293). This is an encouraging result implying that the index period for the fall survey is adequately wide and changes in starting date within this range should not induce undesirable, short-term temporal effects on measures of fish abundance. However, we note that sampling date may contribute to variability of abundance indices when date is confounded with the geographic (port) component of the sampling design (Hinch et al. 1994). For instance, if ports are sampled in the same order every year, or sampling dates decrease systematically in subsequent years, then starting date may affect abundance estimates. Confounding of sampling date and port can be eliminated by using a randomized start such that the first port sampled is randomly selected each year (Cochran 1983). Because logistics are an important consideration, survey scientists should develop a set of sampling plans that optimize trawling effort and travel time for the set of ports surveyed in Lake Michigan. For example, with a random start at Port Washington, sampling could proceed to Ludington, Frankfort, Sturgeon Bay, Manistique, Waukegan, Benton Harbor, and Saugatuck. This succession of ports minimizes ship travel between ports. Each year, a different random start is selected along with one of two or three optimized arrangements. The goal is to ensure that a single port does not have a higher probability of selection for sampling early in the field season. The recommendation to randomize port sampling in Lake Michigan to enhance the reliability of the bottom trawl data also applies to fishery surveys characterized by a fixed-station design.

Lakewide abundance estimates

Management of stocked salmonids in Lake Michigan depends on reliable estimates of the abundance of their preferred prey, and as such, bottom trawl data have been used to generate biomass estimates of available forage. Aside from the uncertainty associated with the lack of data from areas not sampled by the trawl, a lakewide estimate of abundance for an individual species can serve as a reasonable guideline in any given year. However, the value of temporal trends in lakewide abundances for an individual species depends on the consistency of the trends among ports. Among all Lake Michigan ports, we observed similar quadratic trends in abundance of deepwater sculpin and rainbow smelt and similar cubic trends for bloater abundance. If differences in temporal trends are observed among ports, as was the case for slimy sculpin and alewife, lakewide indices are not strictly appropriate. Nevertheless, by noting port-specific differences, lakewide abundance estimates may be possible for slimy sculpin and alewife. For these species, temporal trends in abundance were similar among most ports. Temporal trends in slimy sculpin and alewife abundances at Manistique or Sturgeon Bay (two northern ports) were different from trends observed throughout the remainder of the lake. Alewife abundance did not decrease at Sturgeon Bay, although abundance of this species at all other ports decreased significantly. Slimy sculpin abundance appeared to increase after a low period in the mid- to late 1980s at all ports except Sturgeon Bay and Manistique, where abundance has been decreasing since the mid-1980s. A better understanding of the limitations of lakewide estimates and conditions for their use requires additional work to understand the nature of the relationship of fish abundance among ports.

Trends in abundance of Lake Michigan fishes

Some of the changes that we observed in fish abundance may be the result of direct or indirect effects. Direct effects include habitat alterations and regulations on commercial fisheries. For example, commercial fishing for bloater was severely reduced in 1976, and the decreased exploitation of bloater populations may have contributed to the resurgence of this species (Stewart et al. 1981). However, indirect effects also may have contributed to the bloater's resurgence in Lake Michigan. Indirect effects include effects resulting from the absence or low abundance of a previously dominant species (Skud 1982). In this case, the extirpation of five species of deepwater ciscoes that occurred by 1970 (Smith 1968) may have afforded bloater an opportunity to increase in abundance. Based on our survey data, bloater were the most abundant of the 24 species caught and their abundance increased linearly since 1973. Another indirect effect — changes in community composition — may also have contributed to observed trends in fish abundance, although the mechanism (e.g., competition for resources or predation) by which changes were effected is unknown and probably varies with species. Pronounced changes in species composition occurred in Lake Michigan before the 1970s. For example, in 1964, Wells (1968) conducted an intensive bottom trawl survey between 6 and 92 m off Saugatuck and recorded the presence of shortnose cisco, longjaw cisco (*Coregonus alpenae*), kiyi, lake herring (*Coregonus artedi*), logperch (*Percina caprodes*), and quillback (*Carpiodes cyprinus*), species not captured by bottom trawling anywhere in Lake Michigan since 1973. The disappearance of these native fishes may be followed by the appearance and colonization of nonnative fishes.

Fish abundance may be affected indirectly through food web interactions when the abundance of predators is increased through aggressive stocking programs (Stewart et al. 1981). The decline in relative abundance of alewife since 1973 occurred during the period of rapid increase in salmonid predator abundance (e.g., see catch rates of Wisconsin anglers for salmonid predators in Hansen et al. 1990).

The timing of the decline in the alewife index is consistent with the hypothesis that increased predation on alewife led to the decline in abundance of this species (Stewart et al. 1981). It is less consistent with Eck and Brown's (1985) hypothesis that changes in alewife abundance were due to a series of cold winters that rendered alewife populations more susceptible to predation. The cold winter of 1983–1984, postulated by Eck and Brown (1985) as instrumental in reducing alewife abundance, occurred after general declines in alewife abundance were already evident (Fig. 5). Additionally, a severe winter was recorded in 1976–1977 (Scavia et al. 1986), but alewife abundance was already declining by that time at several ports (especially at intermediate depths at Frankfort, Ludington, and Saugatuck).

We believe that the lack of appropriate statistical methods to analyze the Lake Michigan survey data was a critical impediment to understanding the population dynamics of some species. Survey data were collected from an unconventional survey design, contained many zeroes along with continuous positive values, and also exhibited spatial and temporal correlations. The model that we developed and applied in this paper permits analyses of changes in abundance for several species individually in the presence of spatial and temporal autocorrelations. However, we could not fit the model to abundance data of species captured only seldomly or rarely. Changes in species composition may be investigated with metrics that summarize information at the community level such as species richness, diversity, or similarity (Solow 1994; Philippi et al. 1998). When working with community-level indices, care should be exercised to ensure effective sampling of all species. Bottom trawling may not be effective in capturing some species and thus may not reliably indicate abundance changes of rare, nonvulnerable, or partially vulnerable species. For example, because the spoonhead sculpin (*Cottus ricei*) is a rare species in Lake Michigan, the accurate assessment of its distribution and abundance is difficult. In addition, the vulnerability of a particular species to capture by the trawl varies with time of day (e.g., Brandt 1986). In Lake Michigan, spoonhead sculpin may be more vulnerable to bottom trawls at night (Potter and Fleischer 1992). In spite of the limitations associated with bottom trawling, this method provides a relatively good measure of trends in abundance of the more ubiquitous and abundant species. Alternatively, analyses of trends in abundance of individual species that are less frequently captured could be pursued after further methodological work towards statistical model building. Such models would need to accommodate fish abundance data characterized by a large number of zeroes in addition to spatial or temporal autocorrelations.

Acknowledgements

Edward H. Brown, Jr., Gary W. Eck, and Charles O. Hatcher (all retired, U.S. Geological Survey, Great Lakes Science Center (GLSC), Ann Arbor, Mich.) provided data from fall cruises in Lake Michigan. LaRue Wells (retired, GLSC) enabled completion of databases for some of the early cruises, and Scott R. Nelson (GLSC) assisted with data management. Gregory Kennedy (GLSC) provided the figure of Lake Michigan and calculated distance measures for our sites. We thank M. Anthony Schork and Leslie Lange (Department of Biostatistics, University of Michigan, Ann Arbor, Mich.) for many helpful discussions of the data. The critical reviews of Nicholas C. Collins (University of Toronto, Mississauga, Ont.), Jacqueline F. Savino (GLSC), and an anonymous referee improved our presentation. This paper is Contribution 1100 of the U.S. Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI 48105, U.S.A.

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