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Factors Affecting the Recruitment of Lake Whitefish in Two Areas of Northern Lake Michigan

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ABSTRACT. *Stock-recruitment and integrated recruitment models incorporating biotic and abiotic factors were developed for lake whitefish populations in northern Green Bay and the North Shore areas of Lake Michigan. Abundance and recruitment indices were calculated for the 1961-1985 year classes based on lake whitefish catch and effort data from the commercial fishery in each area. Previous research indicates that spawning stock abundance, winter ice cover, and spring temperatures are important in determining the egg and larval abundance and survival of lake whitefish. Therefore, spawning stock abundance, ice cover, winter wind velocity, and spring water and air temperature variables were used as model inputs in regression modeling. The biotic/abiotic recruitment model for northern Green Bay hindcasted lake whitefish recruitment as a function of spawning stock abundance and the number of days that ice cover exceeded 40% during egg incubation. This regression model ($R^2 = 0.62$) demonstrated improved hindcasting ability of historic recruitment when compared to the Beverton-Holt ($R^2 = 0.37$) or the Ricker ($R^2 = 0.33$) stock-recruitment models for the 1961-1985 cohorts. The biotic/abiotic recruitment model for the North Shore hindcasted lake whitefish recruitment as a function of average air temperature in May after larval emergence, the number of days that ice concentration exceeded 70% during egg incubation, and spawning stock abundance. The regression model ($R^2 = 0.57$) also demonstrated improved hindcasting ability of historical recruitment when compared with Beverton-Holt ($R^2 = 0.09$) or the Ricker ($R^2 = 0.13$) stock-recruitment models. Results of this study indicate that biotic/abiotic recruitment models were more successful in hindcasting recruitment than solely biologically based stock-recruitment relationships. Consideration of significant abiotic variables will be useful in the management of lake whitefish stocks in the Great Lakes by improving forecasts of recruitment.*

INDEX WORDS: *Lake whitefish, Lake Michigan, recruitment, spawning stock, ice, weather.*

INTRODUCTION

The lake whitefish (*Coregonus clupeaformis*) is an important component of the commercial fishery of the upper Great Lakes, and currently comprises over 50% of the commercial landings in Michigan waters of Lake Michigan (Kinnunen 1991). Over the past century, there have been large fluctuations in the commercial landings and catch per unit effort of lake whitefish (Fig. 1) that have been primarily caused by variable levels of population abundance (Christie 1963, Taylor *et al.* 1987) and recruitment (Christie 1963, Lawler 1965, Patriarche 1977).

Correlative studies of lake whitefish recruitment suggest that much of the variability in the cohort strength and recruitment may be caused by variation in spawner abundance and climatic factors (Taylor *et al.* 1987). For instance, Christie (1963) reported that lake whitefish recruitment was related to winter and spring temperatures in Lake Ontario;

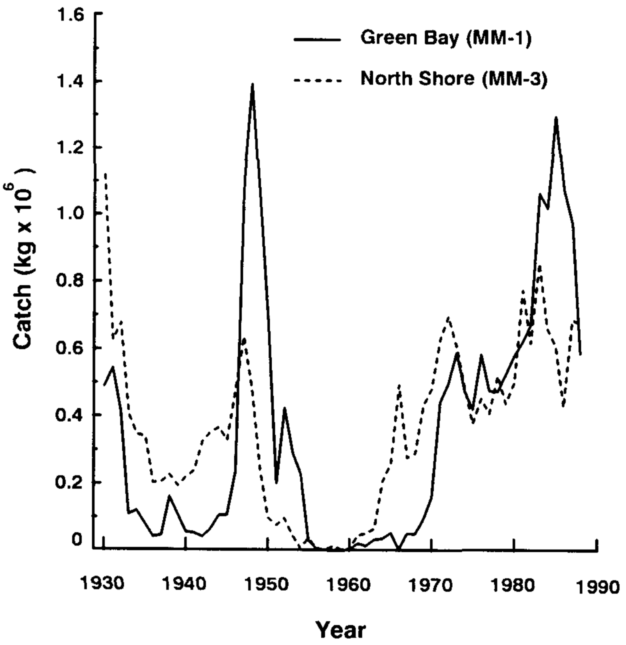

FIG. 1. Commercial fisheries landings of lake whitefish in GLFC districts MM-1 and MM-3 in Lake Michigan from 1930–1989.

whereas, strong year classes in Lake Erie were produced only during years when water temperatures were optimal for spawning, incubation, and development (Lawler 1965). Strong year classes in Lake Erie corresponded with fall temperatures less than 6.1°C prior to spawning; a steady decline in fall and winter temperatures; and gradual spring temperature increases, providing a long incubation period at optimal temperatures of 2.0 to 4.0°C. Additionally, Miller (1952) found that year class strength of lake whitefish in seven Alberta lakes was inversely related to fall and early-winter wind intensity. Freeberg *et al.* (1990) suggested that ice cover was important in reducing the effects of wind generated wave action, enhancing egg survival of lake whitefish in Grand Traverse Bay, Lake Michigan. Egg survival of lake whitefish in Grand Traverse Bay during an ice-covered winter was approximately 3.4 times greater than during an ice-free year.

Spring weather conditions may also be important in determining growth and survival of emerging lake whitefish larvae. Freeberg *et al.* (1990) found that the abundance of copepod zooplankton between 0.7 and 1.1 mm in total length significantly influenced the growth and survival of larval lake whitefish in Grand Traverse Bay, Lake Michigan. Spring weather conditions, including the timing of ice dissipation and the warming of shallow water areas, appear to influence the timing of the initiation of production of copepod zooplankton, which in turn impacts larval survival of lake whitefish (Freeberg *et al.* 1990).

Quantification of the contribution of previously identified factors to variation in cohort strength of lake whitefish would enhance the management of this fishery by enabling forecasts of lake whitefish abundance several years in advance of their recruitment to the fishery. The goal of this study was to estimate the proportion of recruitment variability caused by biotic and abiotic variables and to incorporate these variables into recruitment models for lake whitefish in two areas of northern Lake Michigan.

METHODS

Study Areas and Commercial Catch Data

Great Lakes Fishery Commission (GLFC) statistical districts MM-1 and MM-3 in northern Lake Michigan were selected for recruitment modeling because uninterrupted time series data on lake whitefish commercial catch and effort were available (Fig. 2). Tagging studies conducted by Ebener and Copes (1985) indicate that there are several discrete spawning stocks of lake whitefish in northern Green Bay. In addition, isozyme electrophoretic studies indicate that there are at least four distinct populations of lake whitefish, two west of Seul Choix Point, and two east of the point (Imhof *et al.* 1980). Because of the considerable evidence that there are distinct spawning stocks within northern Lake Michigan, we developed separate recruitment models for areas MM-1 and MM-3.

Since it is difficult to partition the effects of lamprey mortality from those of variable recruitment prior to 1958, commercial catch data from 1958 to 1989 were used to develop abundance and recruitment indices for the 1961-1985 cohorts in this study. Because of a 2 to 4 year lag between spawning and recruitment, commercial catch data prior to and after the 1961-1985 time period were used to index spawning stock abundance and recruitment. For example, commercial catch data from 1958-1960 were used to estimate the spawning stock sizes that produced the 1961-1963 year classes, whereas the 1987-1989 commercial catch data were used to estimate the year class strength of the 1983-1985 cohorts.

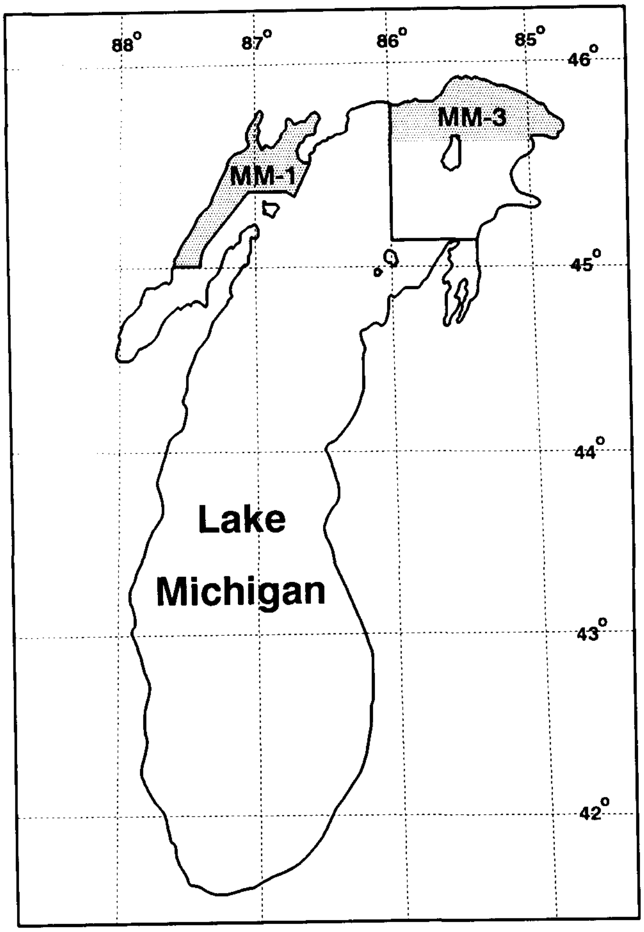

FIG. 2. Map of Lake Michigan showing the two areas for which recruitment models were developed. Recruitment models for northern Green Bay included the entire area within GLFC statistical district MM-1. Recruitment models for the North Shore included the shaded region in the northern portion of GLFC statistical district MM-3.

Commercial Fishery Gear and Effort

There was considerable variation in the gear type and effort deployed by the commercial fishery between 1958 and 1985. Up to seven types of gear have been used to fish for lake whitefish in areas MM-1 and MM-3 since 1958 including 2-inch gill nets, 4-inch gill nets, shallow water trap nets, deep water trap nets, pound nets, otter trawls, and seines (MM-3 only). Catch and effort data from 2-inch gill nets, deep water trap nets, otter trawls, and seines were not used to index abundance or recruitment because of the limited catch or time frame that these gears were fished. Catch and effort data from three principal gears, 4-inch gill nets, shallow water trap nets, and pound nets, were used to index abundance and recruitment of lake whitefish in each area. These gears accounted for 93.1% of the commercial catch of lake whitefish in area MM-1 and 94.6% of the commercial catch in area MM-3 during the period 1958-1989.

Model Construction Overview

Analysis of commercial fishery and abiotic data produced three models for each study area; two biologically based stock-recruitment models and a biotic/abiotic recruitment model. Commercial catch and effort data were used to calculate abundance and recruitment indices, which were in turn used to calculate Ricker and Beverton-Holt stock-recruitment models (Ricker 1975) for each area. Winter freezing degree day data and ice cover observations were used to construct ice-cover models for each area. Timing and duration of ice-cover, winter wind intensity data, spring temperature data, and lake whitefish stock abundance were analyzed using stepwise regression to produce a biotic/abiotic recruitment model for each area (Fig. 3).

Indices of Spawning Stock and Recruitment

Catch per unit effort was calculated for each gear during each calendar year for each area. Commercial fishing effort was standardized using measures of effort defined by the GLFC (Hile 1962). Annual indices of spawning stock abundance were calculated based on methods outlined by Hile (1962):

$$A_i = \left[\frac{\sum_{j=1}^{all\ gears} C_{ji}}{\sum_{j=1}^{all\ gears} \overline{CPUE_j} * E_{ji}} \right] * 100$$

where:

A_i = abundance index in year i (pooled for all gears);

C_{ji} = lake whitefish catch in kg by gear j in year i;

$\overline{CPUE_j}$ = mean catch per unit effort of gear j for the years 1958-1989;

E_{ji} = total effort using gear j in year i.

Several factors confounded efforts to partition abundance indices into cohorts and to estimate recruitment index values. Recruitment age was not

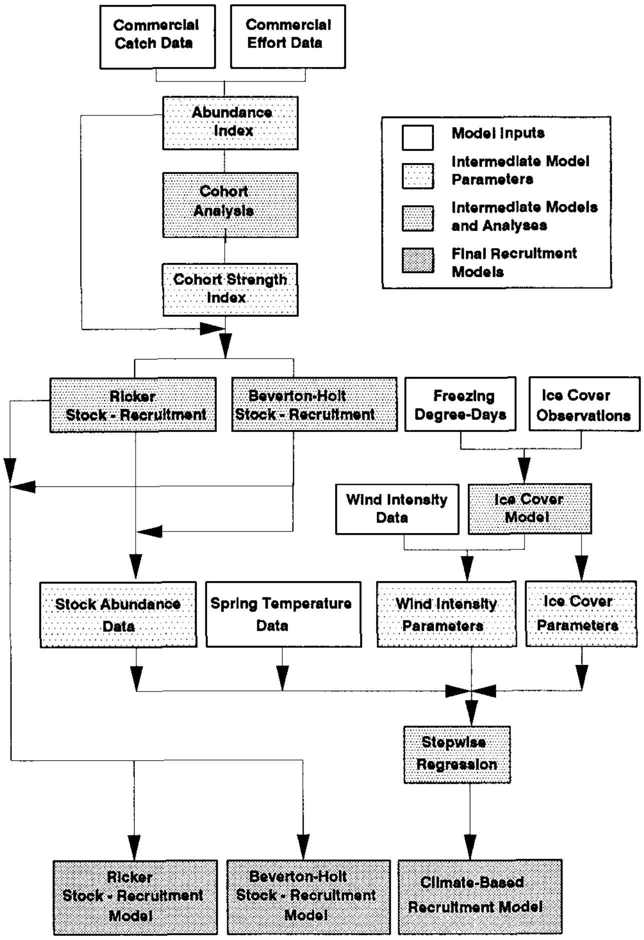

FIG. 3. Flow chart of lake whitefish biotic/abiotic recruitment modelling showing the model inputs, intermedite model parameters, intermediate models and analyses, and final recruitment models produced for each area.

constant in either stock over the time period considered in this study. As the northern Green Bay and North Shore stocks gradually recovered from extremely low levels of abundance in the early 1960s, somatic growth rates declined and the mean age of the commercial catch increased by nearly 2 years from 2.3 to 4.1 years (Smale 1988). In addition, the age at first recruitment (432 mm) was delayed in larger cohorts because of reduced somatic growth rates resulting from intraspecific competition within the cohort (Ebener and Copes 1985, Smale 1988).

To account for variable age of recruitment, cohort analysis procedures were used to partition abundance indices into recruitment index values. Age composition data were obtained for northern Green Bay (area MM-1) from Piehler (1967), NcComb (1989), and unpublished data from the Michigan Department of Natural Resources. Age composition data for the North Shore (area MM-3) were obtained from Piehler (1967), Brown (1968), Patriarche (1977), Rybicki (1980), Scheerer and Taylor (1985), and unpublished data from the Michigan Department of Natural Resources and the Chippewa-Ottawa Treaty Management Authority. Percent age composition data were usually only available for one type of gear in any given year. Because the majority of the landings from this fishery occur in the fall just prior to spawning season, there was little difference in the age composition between gears in years when age composition data was available from multiple gears. Because of relatively high commercial exploitation in both areas, the majority of the commercial landings were comprised of one to three year classes. In all years, at least 60% of the commercial catch was comprised of the two most abundant year classes, and the three most abundant year classes comprised at least 90% of the sampled commercial catch.

The abundance index value for each year was partitioned into the cohorts (pooled for all gear types) in each year based on the age composition data available in each area. The partitioned abundances were summed for all years that a cohort contributed to the commercial catch to calculate a recruitment index value for each year class. Commercial catch and age composition data were used to calculate recruitment index values for the 1961-1985 cohorts within each area. Abundance and recruitment indices were then used to calculate a Beverton-Holt (Beverton and Holt 1957) and a Ricker (Ricker 1954, 1975) stock-recruitment relationship for each area.

Ice Cover Models

Rodhe (1952, 1955), McFadden (1965), and Bilello (1964) demonstrated that time-averaged air temperature, which is an index of heat loss at the air-water interface in fall and winter, is correlated with the date of ice formation. These studies indicate that the air temperature averaging period associated with the date of ice formation increases as water depth increases. Therefore, in a area with heterogeneous bathymetry, more than one averaging period is needed to model the seasonal and spatial progression of ice cover. In this study we used 5, 10, 30, 60, 90, 120, 150, and 180 day average temperatures (from Escanaba, Michigan) to model the mean daily spatially averaged ice concentration in each study area. Ice concentration is defined as the percentage of a unit of surface area covered by ice. The general form of the ice model is given below.

$$I_t = C_o + \sum_{i=1}^{n} [C_i(\frac{1}{Del_i}) \int_{Del_i}^{t} T_t \ dt$$

where:

I_t = mean daily spatial average ice concentration;

t = any day in the ice season, t = 1 on November 1;

C_o, C_i = coefficients of regression, i= 1,2,...n ;

Del_i = $(t-t_i)$, i = 1,2,...n, $t > t_i$ (Del_i is the averaging periods);

t_i = 5, 10, 30, 60, 90, 120, 150, 180 days prior to t;

n = number of averaging periods in the summation;

T_t = daily average temperature (RC) on day t.

The model was calibrated for each lake area using spatially averaged ice cover data calculated from a 20-year computerized digital ice concentration database (Assel 1983). The ice cover data used to calibrate the models were divided into three parts, based on the winter severity classes of above normal, normal, and below normal. Seasonal maximal freezing degree-day accumulations for Escanaba, Michigan (Assel 1986) were used for the winter severity classification analysis. The number of averaging periods (Deli) for each winter classification within each lake area were determined from a computer algorithm called RSQUARE (SAS 1988) which calculated the linear combination of independent variables (averaging period temperatures) that explained the greatest variance in the dependent variable (ice concentration). The averaging periods, coefficients of multiple determination, root mean square errors (RMSE), and number of observations used in model calibration for each winter classification within each area are given in Table 1.

A cross-validation analysis was made to test the ice models over independent data. The data were partitioned into two equal parts and the ice models calibrated on one part and then applied to the second part (of the partitioned data) to calculate a RMSE value, the cross-validation RMSE.

Differences between RMSE of the models calibrated over the entire data set and the cross-validation RMSE values ranged from 4.1 to 0.1 and averaged 1.3 for the six models. These results lend credence to the RMSE values in Table 1.

Each set of models was used to produce spatially averaged mean daily ice cover concentrations for each area for the winters of 1960-1984. Because the critical level of ice cover concentration necessary to protect lake whitefish eggs was not known, the

TABLE 1. Results of ice cover modeling for areas MM-1 (northern Green Bay) and MM-3 (North Shore). Separate models were calculated based on winter severity classes of Above Normal (Maximal Freezing Degree Days (FDD) ≥ 970), Normal (670 FDD < Maximal FDD < 970 FDD), and Below Average (Maximal FDD ≤ 670 FDD). The averaging periods used to produce each model, coefficients of multiple determination, root mean square errors (RMSE) and number of observations used in model calibration for each winter classification within each area. Asterisks indicate models with significant intercept terms.

Winter Severity	Averaging Periods (Days)	R^2	RMSE	N
Northern Green Bay, Area MM-1				
Above Normal*	10, 60, 120, 150	0.62	13.9	55
Normal*	5, 30, 60, 120, 180	0.73	12.2	117
Below Normal	10, 90, 120	0.94	16.7	26
North Shore, Area MM-3				
Above Normal	10, 60, 90, 180	0.97	13.6	60
Normal	5, 60, 90, 180	0.96	13.9	163
Below Normal*	5, 10, 30, 120, 150	0.70	18.8	33

number of days with ice cover exceeding several levels were used as regression model inputs. Ice concentrations of 0, 10, 20, 30, 40, 50, 60, and 70% were chosen to produce eight ice cover variables for each area. The number of days of ice concentration exceeding each of these ice concentration levels was calculated for each area.

Winter Wind Velocity

Winter wind velocity data collected at Green Bay, Wisconsin and Sault St. Marie, Michigan were used as model inputs in areas MM-1 and MM-3, respectively. Two-day average wind velocities (m/sec) were calculated on a daily basis during November, December, and January for the years 1960-1985. Average wind velocity levels above 4.1, 5.1, and 6.2 m/sec were selected to define periods of intense wind activity. The number of days above these wind velocity levels was tabulated for each ice cover level within each area.

Ice cover data were used to define the period when intense wind events could impact survival of lake whitefish eggs. We hypothesized that intense wind events would only influence egg survival of lake whitefish prior to the formation of some critical concentration of ice cover over spawning areas. To define biologically meaningful wind variables, we only considered wind events occurring between the earliest possible spawning date and the formation of various levels of ice cover.

The starting date for tabulating intense wind events was 1 November in all cases, as this date corresponds with the earliest date of lake whitefish spawning in each area. The date when ice cover concentration first exceeded a given critical ice concentration (0, 20, 40, 60%) was used as the end date for tabulated wind events. For example, the number of days between 1 November and the date when ice cover first exceeded 20% in a given year was tabulated to create a single wind velocity variable. Using this approach, the three wind velocity levels (4.1, 5.1, and 6.2 m/sec) and the four ice cover concentration levels (0, 20, 40, 60%) were used to calculate 12 wind velocity variables for each lake area.

Spring Water and Air Temperatures

Mean monthly water temperatures for March, April, and May were available from a municipal water intake at Menominee, Michigan for the period 1961-1985. These temperature data were used to produce three monthly temperature variables as inputs in regression modelling in area MM-1. Water temperature data could not be located for area MM-3. Mean monthly spring air temperatures taken at the closest available weather station at Sault St. Marie, Michigan were used to produce three monthly temperature variables used as inputs in regression modeling in area MM-3.

Integrated Biotic/Abiotic Recruitment Model Construction

Biotic and abiotic data including spawning stock abundance, ice cover, winter wind intensity, and spring temperature were used to predict recruitment index values using a least squares multiple regression approach. Stepwise multiple regression analysis was conducted using the SAS statistical software package and the variable selection model STEPWISE (SAS 1988). Each resulting model was tested for autocorrelation using a Durbin-Watson d statistic (Durbin and Watson 1951) and for heteroscedasticity using analysis of the covariance (White 1980).

Time Detrended Recruitment Indices

Because spawning stock abundance in both areas rose continuously throughout the time period considered (1961-1985), we conducted additional analysis using detrended recruitment index values. Recruitment indices were time-detrended to examine the influence of weather variables on recruitment, independent of continuously increasing spawning stock size. Recruitment indices were time-detrended by regressing each recruitment index against time (year). Recruitment index values were time-detrended using the following generalized equation:

$$DR_i = R_i - [(a * i) + b] + \bar{R}$$

where:

DR_i = detrended recruitment index in year i;
R_i = recruitment index in year i;
a = slope of detrending regression;
b = intercept of detrending regression;
i = year;
$\bar{R}$ = mean recruitment index value for years 1961-1985.

A second stepwise regression analysis was performed using the time-detrended recruitment index as the dependent variable and ice cover, wind velocity, and temperature variables as independent variables. Because recruitment index values were time-detrended to examine the influence of weather variables on recruitment, spawning stock abundance was not included as a dependent variable in the detrended regression analysis.

RESULTS

Stock-Recruitment Relationships

We found significant biologically based stock-recruitment relationships for both areas; however, none of these relationships explained more than 37% of the observed variation in lake whitefish recruitment (Fig. 4). Both the Beverton-Holt ($R^2 = 0.373$, $P = 0.001$) and the Ricker ($R^2 = 0.330$, $P = 0.002$) models indicated a significant relationship between the abundance and recruitment indices for the northern Green Bay area (Fig. 4). In the North Shore area, only the Ricker stock-recruitment relationship indicated a significant ($R^2 = 0.126$, $P = 0.046$) relationship between abundance and recruitment indices.

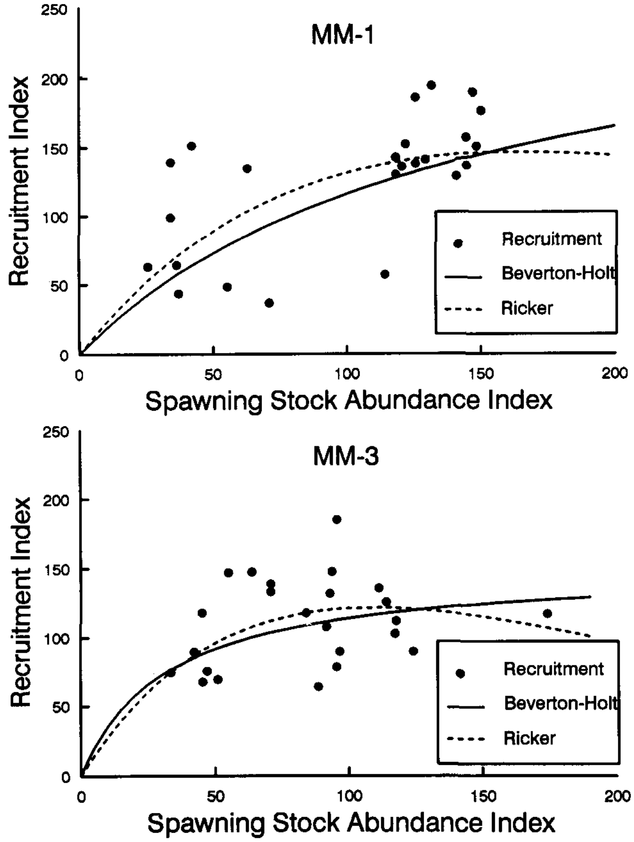

FIG. 4. Beverton-Holt and Ricker stock-recruitment models for the 1961–1985 cohorts of lake whitefish in areas MM-1 and MM-3.

Northern Green Bay Biotic/Abiotic Recruitment Model

Lake whitefish recruitment in northern Green Bay was most accurately modeled as a function of spawning stock abundance and the number of days of ice cover exceeding 40% during egg incubation (Table 2). The regression model for this area was:

$$R_i = -47.23 + 0.5681\ \mathrm{A}_{i\text{-}1} + 1.062\ I_{40\%}\ (R^2 = 0.621)$$

where:

$\mathrm{R_i}$ = recruitment index value of lake whitefish year class i;

$\mathrm{A_{i\text{-}1}}$ = abundance index value for year i-1;

$\mathrm{I_{40\%}}$ = number of days of ice cover exceeding 40% during egg incubation.

This model was used to hindcast recruitment index values for the years 1961-1985, and these values are plotted against actual recruitment index values calculated from catch, effort, and age composition data (Figure 5). Highly variable recruitment from 1961-1970 may have resulted from relatively low levels of spawning stock during these years. We noted a trend toward increasing recruitment index and model prediction index values through the time period modeled reflecting the gradual recovery of lake whitefish stocks in this area.

Residual values between the predicted and actual recruitment index values are plotted as a function of time in Figure 5. The regression model consistently overestimated recruitment for the 1962-1967 year classes when lake whitefish stock abundances were at low levels.

North Shore Biotic/Abiotic Recruitment Models

Lake whitefish recruitment in the North Shore area was modelled as a function of the average spring air temperatures in May, the number of days of ice cover exceeding 70% during egg incubation, and spawning stock abundance (Table 2). The regression model for this area was:

$$R_i = -65.78 + 0.2266\ \mathrm{A}_{i\text{-}1} + 0.6512\ I_{70\%} + 7.845\ T_{May} \quad (R^2 = 0.567)$$

where:

$\mathrm{I_{70\%}}$ = number of days of ice cover exceeding 70% during egg incubation;

$\mathrm{T_{May}}$ = mean average air temperature in May.

This model was used to hindcast recruitment index values for the years 1961-1985, and these values are plotted against actual recruitment index

TABLE 2. Model parameter coefficients, squared partial correlation coefficients, and coefficients of multiple determination for biotic/abiotic and time-detrended regression models of lake whitefish recruitment in area MM-1 and the biotic/abiotic model for area MM-3.

Area	Dependent Variable	Model Parameter	Coefficient	Squared Partial Correlation	Model R^2
MM-1	Recruitment	Abundance	0.5681	0.413	
		Ice (40%)	1.061	0.208	0.621
MM-1	Time-Detrended Recruitment	Ice (40%)	1.666	0.361	
		Ice (70%)	–0.8807	0.123	0.484
MM-3	Recruitment	Air Temp (May)	7.845	0.2771	
		Ice (70%)	0.6512	0.1808	0.567
		Abundance	0.2266	0.1090	

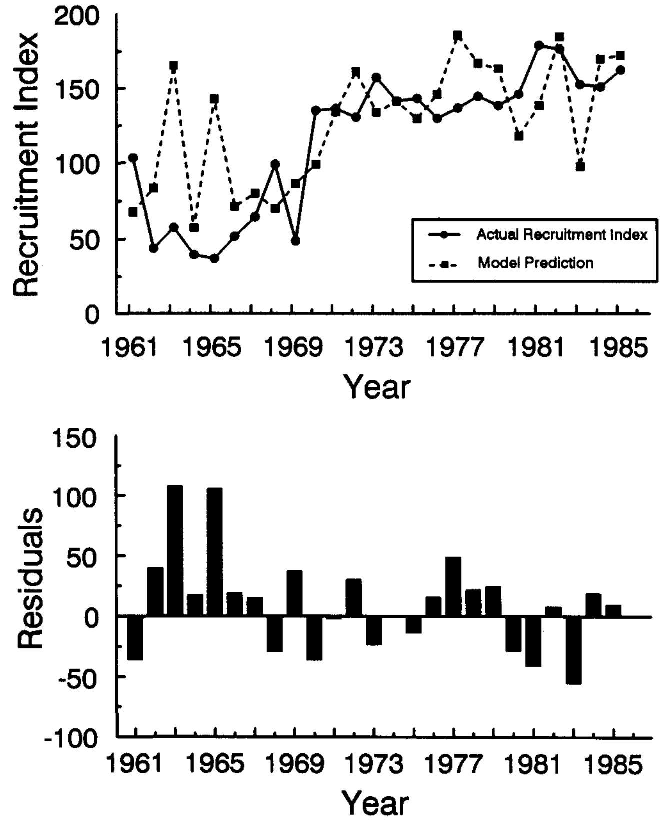

FIG. 5. (A) Biotic/abiotic regression model hindcasts, actual cohort abundance index values, and (B) model residuals for the 1961–1985 cohorts of lake whitefish in northern Green Bay, Lake Michigan.

values calculated from catch, effort, and age composition data in Figure 6. The model accurately hindcasted the largest year class during this period (1977), but was less successful in hindcasting the relatively large 1971 year class. Residual values between the predicted and actual recruitment index values showed that the regression model consistently underestimated recruitment for the 1965-1971 year classes (Fig. 6).

Time-Detrended Regression Model

Recruitment index values for northern Green Bay had a significant positive time-related trend during the period of analysis ($r^2 = 0.528$, $P < 0.001$). Recruitment index values for northern Green Bay were detrended using the following formula:

$$DR_i = R_i - [-9138.7 + (4.6960 * Year)] + 126.5$$

The results of stepwise regression analysis indicated that the number of days of ice cover exceeding 40% was the dominant weather variable related to the detrended recruitment index in northern Green Bay (Table 2). Detrending of recruitment indices and exclusion of spawning stock abundance as an independent variable had no effect on the abiotic variables selected through stepwise regression analysis (Table 2). Recruitment index values for the North Shore area did not demonstrate a significant time-related trend ($r^2 = 0.051$, $P = 0.280$); therefore, recruitment index values were not detrended.

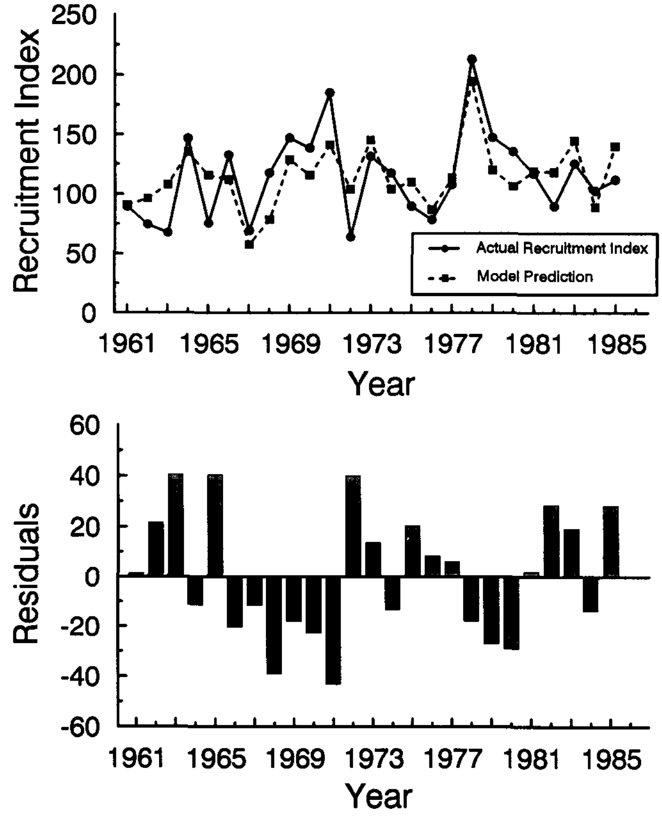

FIG. 6. (A) Biotic/abiotic regression model hindcasts, actual cohort abundance index values, and (B) model residuals for the 1961–1985 cohorts of lake whitefish along the North Shore, Lake Michigan.

DISCUSSION

Relationship between Spawning Stock and Recruitment

Based on the spawning stock and biotic/abiotic recruitment modeling results, it appears that lake whitefish recruitment in northern Green Bay is primarily dependent upon the abundance of spawning stock, and is less dependent upon abiotic influences such as ice cover, winter wind intensity, and spring temperatures over the time period examined. The stock-recruitment relationships for the northern Green Bay area explained a greater proportion of the variation in recruitment when compared to the relationships calculated for the North Shore area. Also, the partial R^2's from stepwise regression modeling indicate that spawning stock abundance made a greater contribution to the northern Green Bay model than it made to the North Shore model.

One possible cause for differences in the importance of abiotic factors between the two areas is related to variation in ice cover. Because northern Green Bay is relatively protected from wind and lake currents, there has been less variation in the timing and extent of ice cover formation (Assel *et al.* 1983). During the years in which ice cover was modeled, ice cover normally formed during or just after lake whitefish spawning (mid to late November). Because of the lack of variation in the timing of ice cover formation, there may also be less variation in the winter wind events affecting egg survival prior to ice cover formation. In contrast, ice cover and winter wind events were more variable in the North Shore area, and this variability appears to be more important than spawner biomass in determining larval production, cohort strength, and eventual recruitment of lake whitefish in this area.

A second possible reason for the stronger relationship between stock size and recruitment in northern Green Bay is related to the range of stock abundances present during the modeling time period. While abundance and recruitment indices are site-specific and not directly comparable between sites, the range of stock abundances appears to be larger for the northern Green Bay area as reflected by catch data (Fig. 1). The larger range of stock sizes may have amplified the relationship between stock abundance and recruitment in the northern Green Bay area.

Biotic/Abiotic Recruitment Modeling

Incorporation of abiotic variables increased the recruitment hindcasting ability of recruitment models in both areas. Ice cover was a significant abiotic variable in both biotic/abiotic recruitment models. Previous field research has indicated that ice cover enhances egg survival by protecting incubating eggs from wind-generated currents and waves (Freeberg *et al.* 1990).

The concentration of ice cover that was most significant in predicting recruitment was different in each area (40% in northern Green Bay vs. 70% in the North Shore area). These differences in critical ice cover concentrations may be due to differences in the lake basin morphology and prevailing storm patterns in each area. Higher concentrations of ice cover may be necessary to protect lake whitefish eggs in the North Shore area because of the prevalence of open water and westerly winter storms in this area. The northern Green Bay area normally has a lower percentage of open water area during winter (Assel *et al.* 1983), and is relatively protected from prevailing westerly storms occurring after lake whitefish spawning.

The time-detrended regression model for northern Green Bay provides evidence that selection of significant abiotic variables was not influenced by continuously increasing spawning stock and recruitment index values. After recruitment index values were detrended and spawning stock was removed as a modeling input, the number of days of ice cover exceeding 40% remained the dominate variable explaining 36% of the recruitment variation in northern Green Bay (Table 2). Although the spawning stock in the North Shore area increased from 1961-1985, there was no apparent time-related trend in the recruitment index values.

The importance of ice cover to the recruitment process of lake whitefish is dependent upon a number of factors including the quantity and quality of spawning substrates. Freeberg *et al.* (1990) found that ice cover was critical for protecting lake whitefish eggs from wind and wave action in the marginal spawning areas of Grand Traverse Bay, Lake Michigan. In areas with marginal spawning habitat (non-cobble), ice cover may be more important in protecting lake whitefish eggs from displacement and destruction by abrasion than in areas with quality spawning substrate.

Other Factors Affecting Recruitment

Several factors not included as inputs in recruitment modeling may have a significant influence on the recruitment of lake whitefish in these two areas. Variation in the production of spring zooplankton resources has been identified as a mechanism which influences the larval survival of lake whitefish (Reckahn 1970, Freeberg 1985, Freeberg *et al.* 1990). Site-specific studies are needed to identify factors, other than temperature, that are important in controlling the production of these prey resources in relationship to the abundance of larval lake whitefish.

Competition and predation may also be important factors influencing recruitment mechanisms. For instance, competition between larvae of several species including lake herring (*Coregonus artedii*), alewife (*Alosa pseudoharengus*), and rainbow smelt (*Osmerus mordax*) may be a locally significant factor influencing lake whitefish recruitment. Likewise, predation by adults of several species on lake whitefish including rainbow smelt (Loftus and Hulsman 1986) and alewife (Hoagman 1974) may be significant in some areas of the Great Lakes. Inclusion of these factors may improve performance of future recruitment models.

In summary, identification and incorporation of abiotic variables into biotically-based recruitment modeling has increased our ability to hindcast the recruitment of lake whitefish. As such, inclusion of key abiotic variables in recruitment modeling has the potential to improve our ability to produce forecasts of lake whitefish recruitment several years in advance of recruitment.

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