



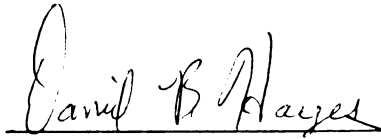
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SAMPLING VARIABILITY OF TEN FISH SPECIES AND POPULATION  
DYNAMICS OF ALEWIFE (*Alosa pseudoharengus*) AND BLOATER (*Coregonus  
 hoyi*) IN LAKE MICHIGAN

By

Ann Elizabeth Krause

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## ABSTRACT

### SAMPLING VARIABILITY OF TEN FISH SPECIES AND POPULATION DYNAMICS OF ALEWIFE (*Alosa pseudoharengus*) AND BLOATER (*Coregonus hoyi*) IN LAKE MICHIGAN

By

Ann Elizabeth Krause

Since 1962, the USGS-BRD Great Lakes Science Center has assessed the fish community of Lake Michigan using a bottom trawl survey. In this study, I analyzed a subset of the survey data by applying two different statistical approaches. First, I evaluated the measurement variability of ten fish species using a measurement error regression model to replicate trawl data. I found that the measurement error estimates ranged from 0.19 (deepwater sculpin) to 0.68 (alewife) on a log scale (coefficient of variation = 46-99%). The ranking of the fish species by their measurement variability appeared to be related to behaviors such as orientation in the water column and schooling. For two of the ten species, alewife and bloater, I estimated yearly indices of abundance at age from 1962-95 using a mixed model approach. The mixed model included a year effect, location effect, depth function and covariance matrix where correlations decrease as the distance between observations increased. In general, alewife numbers at age have decreased over time and may have been influenced by predation, fishing, and food availability. Bloater numbers showed strong year class specific patterns that could be followed as a cohort aged and clearly played an important role in determining bloater population size.

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Dedicated to my husband

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## **Chapter 1**

### **MEASUREMENT VARIABILITY IN TEN LAKE MICHIGAN FISH SPECIES**

#### **Introduction**

Fish stock assessment is an important step in the fishery management process. Good management practices are based on the information gained from stock assessments; such information includes abundance trends, mortality rates, and recruitment (Hilborn and Walters 1992). This information helps managers make decisions by indicating the current status of the fish population, portraying the past response of the population to the fishery, and allowing predictions of the impact certain decisions may have on fish stocks (e.g., Ricker 1975, Hilborn and Walters 1992, Hilborn et al. 1993). For example, a manager may change the size limits for a sport fishery based on an analysis of the current population status and a projection of how the population would respond with a different size and age at harvest. Even with stock assessments, we are unable to exactly predict how fish stocks will change in the future because of the uncertainty (and variability) present in fishery data. Interpretation and use of a stock assessment should include an understanding of the associated uncertainty (Ludwig and Walters 1981, Walters and Ludwig 1981, Hilborn and Walters 1992, Hilborn et al. 1993). By taking uncertainty into account, fishery managers can increase their understanding of the potential outcomes of their management decisions.

Measurement variability is part of the contribution to the uncertainty associated with stock assessments (Ludwig and Walters 1981, Walters and Ludwig 1981, Hilborn and Walters 1992). I define measurement variability as how precise (repeatable) an observation is when a fish stock is surveyed. In Lake Michigan, the measurement variability related to stock assessments has not been taken explicitly into account when interpreting fish population dynamics, building models, or making management decisions (e.g., Eck and Wells 1987, Brandt et al. 1991, Stewart and Ibarra 1991).

One of the largest, long-term stock assessment databases for Lake Michigan is located at the Great Lakes Science Center (GLSC-Biological Research Division, United States Geological Survey). The GLSC has surveyed the Lake Michigan prey fish community annually since 1962. The primary information they obtain from this bottom trawl survey is species composition, biomass, and relative abundance. The information obtained from these surveys has been widely used in both research and management settings. For example, they have been used to determine species population trends over time (e.g., Eck and Wells 1987), test competition hypotheses (e.g., Crowder 1986), and construct salmonid consumption models (e.g., Stewart and Ibarra 1991). The stock assessments can be used by Lake Michigan managers to make decisions; for example, how many lake trout (*Salvelinus namaycush*) should be stocked in the lake (e.g., Eck and Brown 1985). The information on the uncertainty for these stock assessments has not been published on or used to date. In this study, I quantified the measurement variability for ten species in Lake Michigan sampled in a long-term bottom trawl survey using a measurement error regression model (Fuller 1987).

## Methods

### Fish Collections

Every fall since 1962, the GLSC has conducted bottom trawl surveys to assess fish stocks. The trawls are conducted during the daylight hours in the fall between September and November. Start date and duration varies from year to year. The ten fish species evaluated in this study were alewife (*Alosa pseudoharengus*), bloater (*Coregonus hoyi*), deepwater sculpin (*Myoxocephalus thompsoni*), johnny darter (*Etheostoma nigrum*), ninespine stickleback (*Pungitius pungitius*), rainbow smelt (*Osmerus mordax*), slimy sculpin (*Cottus cognatus*), spottail shiner (*Notropis hudsonius*), trout-perch (*Percopsis omnicomaycus*), and yellow perch (*Perca flavescens*). Other species caught in the trawls were not used in this study either because not enough fish were caught to support the analysis (e.g., lake trout) or the fish were not identified to species (e.g., unidentified chubs).

To estimate measurement variability, I used a subset of the survey data where trawls had been repeated within a few days at the same location. Since the trawls at a location were conducted within a few days of each other, I would expect differences between replicate trawls to be due to random factors such as fish movement rather than changes in the species abundance over broad regions. The variability associated with the replicate trawls is a measure of how precisely the site-specific relative abundance is measured.

From 1962-72, 201 pairs of replicate trawls were made using a semi-balloon bottom trawl. The bottom trawl had a 11.9 m headrope, 15.5 m footrope, and a 13mm stretched mesh in the cod end (Hatch et al. 1981). The replicate trawls were taken along

depth contours at four locations in Lake Michigan--off the coasts of Saugatuck, Benton Harbor and Ludington, MI and Waukegan, IL (Figure 1). At each location, one to fourteen depth contours were replicated within one to six days; an exception was one replicate trawl pair conducted sixteen days apart. The depth contours were based on a standard series of depths: 6, 7, 13, 18, 22, 27, 31, 37, 46, 55, 64, 73, 82, and 91 meters (Wells 1968). Two vessels were used to collect the data, the R/V Cisco and the R/V Kaho but the same vessel collected a replicate pair. Trawl times ranged from five minutes to ten minutes; I standardized all catches to catch per ten-minutes.

After each trawl, the fish were separated into species and lifestage (young of the year, adult, or unknown). The catch of each species was then counted and weighed. For trawls when few fish were caught, total catch was separated into species, counted, and weighed. For very large catches, when separation by species was impractical, a random subsample of fish was analyzed, and then expanded based on the total weight of the catch.

## **Analytical Methods**

All life stages were summed for species for which life stage was determined (alewife, bloater, rainbow smelt) in order to maximize sample size. My preliminary analysis did not show an appreciable difference between models for each lifestage. Catches on the arithmetic scale showed increasing variability with increasing catch per unit effort (cpe), and showed a skewed lognormal-like distribution. I transformed the cpes by taking natural logarithm in order to approximate a normal distribution and stabilized variance. Without the transformation, variability increased as the cpe increased.



Figure 1 - The locations of the replicate bottom trawl surveys

For each species, I pooled all paired trawl observations where a zero catch was recorded for one or both trawls. By pooling these observations, I did not have to add a constant to the catches before log transforming them. In order to determine the influence of adding a constant to the catch data, I conducted an analysis using a range of constants from 0.000001 to 10. In my preliminary analysis, the variability estimates varied with the size of the constant, indicating that the results are dependent on the arbitrary constant chosen. By eliminating the need for a constant, I was able to minimize this potential bias. A second advantage to pooling was to minimize the bias of paired trawls where no individuals of a species were caught in either trawl. Some species were not caught in multiple replicate pairs. The zero catch pairs would have artificially lowered the measurement variability estimate because the variance for the pairs would be zeros. By pooling zero catches, I gave less weight to those pairs of trawls without losing the measurement error information altogether. Because the zero catch data pairs were pooled, the number of paired trawls used in the regression analysis for each fish species was less as the number of zero-catch pairs increased.

I used a measurement error model to quantify measurement variability (Fuller 1987). The measurement error model I selected was based on the assumption that the ratio of measurement variances is known. I assumed that both of my replicate trawls had equal measurement variances, and therefore the ratio between the two variances would be equal to one. The measurement error regression model looks similar to a simple linear regression:

$$\begin{aligned} y_t &= \beta_0 + \beta_1 x_t, \\ (Y_t, X_t) &= (y_t, x_t) + (e_t, u_t), \end{aligned} \tag{1}$$



where  $y_t$  is the true value of the log (cpe) of the second trawl in time,  $x_t$  is the true value of the log (cpe) of the first trawl in time,  $(e_t, u_t)$  is the vector of measurement errors on individual trawls, and  $(Y_t, X_t)$  are the corresponding observed log (cpes). Note that, unlike a simple linear regression, there are two vectors of measurement errors, one associated with the y-variable ( $e_t$ ) and one associated with x-variable ( $u_t$ ). As such, the x variable cannot be defined as the “independent” variable because it also has a measurement error related to it. In a simple linear regression, I would have to assume that either the first or second trawl taken in time measured the species population perfectly. I know that this is not the case for either of the replicate trawls. The measurement error model allows me to assign measurement error to both replicate trawls. The covariance between the two measurement errors,  $\sigma_{eu}$ , was assumed to equal zero. As the variance of the x and y variables are taken into account in the measurement error regression, the least squares fit model is developed by minimizing both the horizontal and the vertical distance of a point. This translates to the 45° angle distance (or Euclidean) to the predicted regression line.

All calculations were programmed using SAS proc iml, a matrix language routine, following methods presented in Fuller (1987). The results of the analysis consisted of predicted points along a regression line, an intercept, a slope, a variance associated with the first trawl, and a variance associated with the second trawl. I expected a one to one relationship between the replicate trawl cpes, and tested for significant differences from 1 using a t-test ( $\alpha = 0.05$ ). In the results, I averaged the measurement variability for each species. Assuming a lognormal distribution, I

converted the average variance in the log scale into a coefficient of variation (C. V.) using the conversion equation:

$$C. V. = (e^{\sigma^2} - 1)^{1/2} \quad (3)$$

The coefficient of variation gave me a measure of standard deviation for differences between replicate trawls on an arithmetic scale, expressed as a proportion of the mean or expected cpe.

## Results

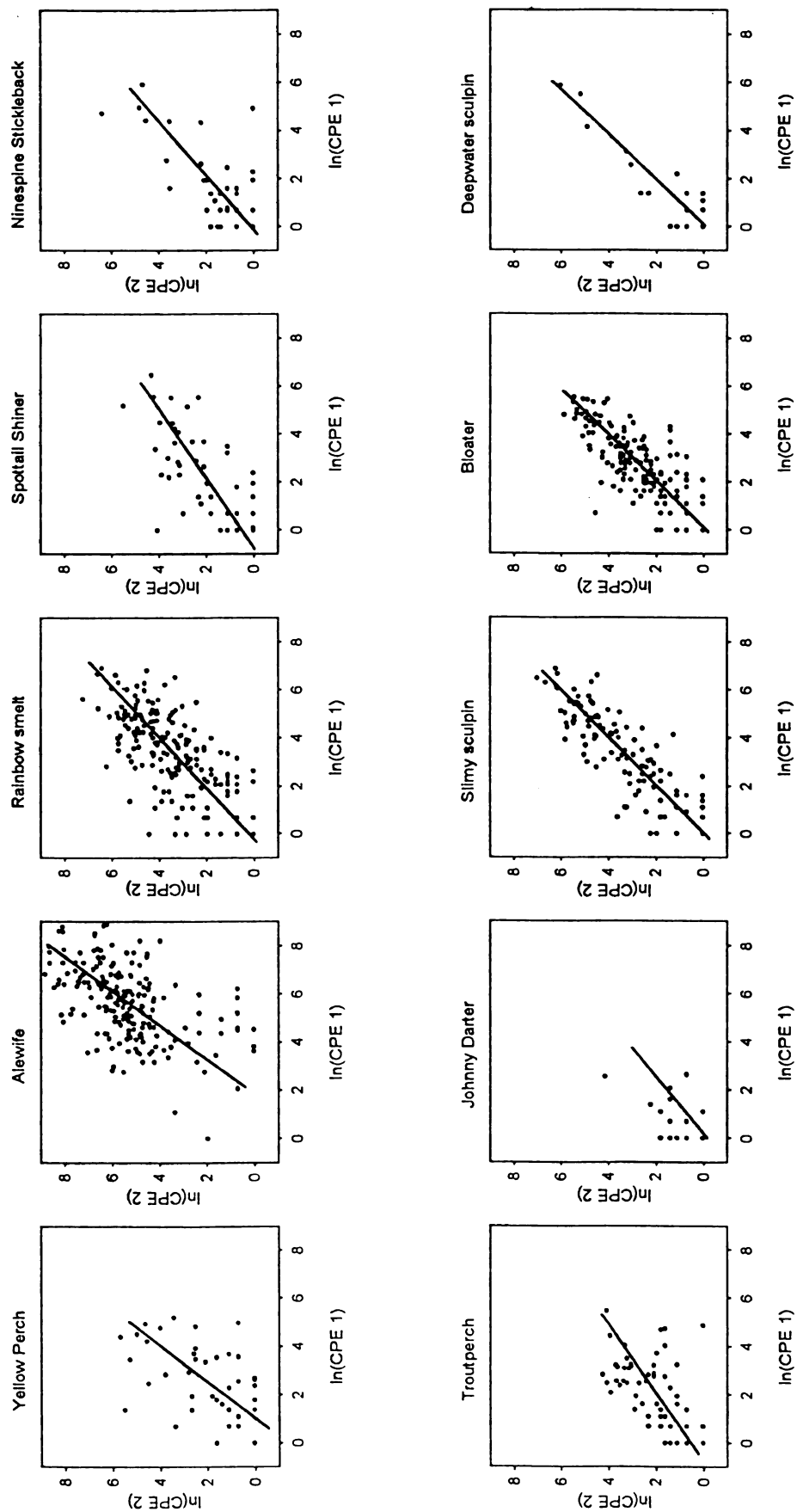
Because of pooled zero cpe pairs, the number of data points used in the regression analysis ranged from 200 (alewife) to 14 (johnny darter, Table 1). The alewife was the species with the fewest zero catches whereas the johnny darter had the most. The slopes ranged from 1.40 (alewife) to 0.69 (spottail shiner, Table 1, Figure 2). Alewife and spottail shiner were the only species whose slopes were significantly different from 1 ( $p < 0.05$ ), with the slope for alewife greater than 1 and the slope for spottail shiner less than one. Slimy sculpin was the species with a slope closest to 1. Average log variances ranged from 0.68 (yellow perch) to 0.19 (deepwater sculpin) with a corresponding coefficient of variation range of 99% to 46%.

The slope and the variability estimates did not appear to be associated with the number of zero catches. As the number of zero catches increased, the slopes and variability estimates did not increase or decrease. The high cpe values did not appear to affect the overall patterns of slope or variability estimates. However, there appeared to be

TABLE 1 - Measurement error regression results for ten Lake Michigan fish species

<b>Species</b>	<b>Number of pairs</b>	<b>Slope</b>	<b>Average Variance (ln)</b>	<b>Coefficient of Variation %</b>
Yellow Perch	42	1.33	0.68	99
Alewife	200	1.40**	0.64	95
Rainbow Smelt	172	0.94	0.47	77
Spottail Shiner	46	0.69**	0.46	76
Nine-spine Stickleback	43	0.88	0.41	71
Troutperch	62	0.71	0.40	70
Johnny Darter	14	0.85	0.30	59
Slimy Sculpin	113	1.01	0.26	55
Bloater	139	1.04	0.26	55
Deepwater Sculpin	18	1.07	0.19	46

\*\* Slope significantly different from 1 ( $p > 0.95$ )



**Figure 2 - Measurement Error Regressions of the ten fish species in Lake Michigan**

a pattern between slopes and variability estimates. Those species with high variability ( $>0.6$ ) had slopes that were greater than 1 by a larger amount than the other species with low variability. Those fish species with intermediate variability ( $0.3 - 0.5$ ) had slopes that were less than 1. Low variability ( $< 0.3$ ) species had slopes slightly greater than 1.

Whether there is a true relationship between these two parameters would be difficult to prove with the small amount of data available. When, in a preliminary analysis, the first trawl and second trawl were incorrectly identified by time of day rather than the date of the survey, the results did not show a relationship between slope and variability even though the species pattern in variability was similar to the final analysis.

### **Discussion**

The Great Lakes Science Center's goal for the fall forage assessment is to follow trends in prey species population abundance through time (Passino-Reader et al. 1996) in order to help manage these stocks. This assessment is one of the few long-term programs that samples multiple locations around Lake Michigan. I can apply my estimates of measurement variability to quantify part of the uncertainty associated with such assessments and to interpret species abundance trends. Although replicate trawl data were collected for only a portion of the complete GLSC database series, the measurement variability estimates are applicable to the entire database as the bottom trawl methodology has not changed dramatically over the period of the complete time series.

Because the measurement error regression model allowed variability to be associated with both the x and y variable, and because it was reasonable to assume that

the variability of the variables was equal, it was preferable to a simple linear regression. Another important difference between the two regression models is that, in a simple linear regression, the  $x$  variable is used in the model to predict the  $y$  variable. In the measurement error regression, the predicted value for the first trawl ( $x_i$ ) and the predicted value of the second trawl ( $y_i$ ) depend on the observed value of its replicate partner. The estimates of measurement variability are very important when the cpe is used as a predictive variable. When data are used in this way, and the variance is ignored, the slope of the relationship will be underestimated (slope attenuation). The simple linear regression is an example of when the slope would be underestimated (Hilborn and Walters 1992).

For all ten species, there was a substantial amount of measurement variability (Figure 2, Table 1). One source of variability that affects all species is when subsamples are taken from very large catches. When subsamples are taken from a large catch, researchers thoroughly mix up the fish before taking their subsample. Although the subsample is selected as randomly as possible, it will still have potential measurement error because only the weight of all the fish disposed of is taken. These subsamples add measurement uncertainty. If the seas are rough, the weight estimates can also add to the measurement uncertainty. It is difficult to obtain a steady reading on a scale when the boat has any motion. The sharper the motion, the more difficult it is to take an accurate reading. If the weights are off on the subsamples and the discarded catch, then the extrapolated total catch numbers will be uncertain for all species equally. This is only one example of why there is common measurement variability for all species.

In addition to variability shared across all species, there are species-specific factors that influence measurement uncertainty. I believe that there are three different behavioral mechanisms that explain some of the differences among species. First, the group dynamics of the fish species is likely to be important. Fish species that are known to aggregate tend to have the higher estimates of measurement variability in my analysis (Figure 2). Alewife, rainbow smelt, and spottail shiner are known to be true schooling species (Scott and Crossman 1972, Bigelow and Schroeder 1953). If the first replicate trawl catches a school of fish and the second replicate trawl catches a different sized school or misses a school, the difference between the replicate trawls has the potential to be large even though they are measuring the same underlying population. For example, in the rainbow smelt data set, there was a replicate pair where one hundred fish were caught in the first trawl and only one fish in the second trawl. It is reasonable to speculate that this results from their schooling behavior. Yellow perch in Lake Michigan are not thought to have a true schooling behavior but they are known to aggregate and are even noted to aggregate by age (Thorpe 1977). This has the same potential effect on the measurement variability as true schooling.

Another behavioral mechanism that could increase measurement variability is a species location preference in the water column (Brandt et al. 1991). Benthic species are more likely to occur near or on the bottom consistently. As such, catches would be expected to also be relatively consistent. Slimy sculpin and deepwater sculpin are benthic species and have low measurement variability (Wells 1968). In contrast, species that are more pelagically oriented may not occur near the bottom in the same density each day

because of possible changes in vertical distribution. Yellow perch, alewife, and spottail shiner are more pelagic species and have high measurement variability.

A third behavior, temperature orientation, may interact with water column preference and schooling behavior. Species with higher measurement variability have been shown to also have wider temperature ranges in the lake. Wells (1968) reported temperature ranges for most of the species: yellow perch, 11 to at least 22; alewife, 8 to 22; spottail shiner, 13 to at least 22; rainbow smelt, 6 to 14; trout-perch, 10 to 16; bloater 6 to 10; slimy sculpin, 4 to 6; and deepwater sculpin (fourhorn sculpin) 4 to 4.5. Species with the wider temperature ranges and the higher maximum temperature tend to have higher measurement variability. Low thermal ranges and low minimum temperatures correspond with lower measurement variability. As the assessments were collected during the fall, it is possible that some of the replicate trawls were collected when large thermal structure changes were occurring. In the same paper, Wells (1968) discussed how temperature could affect the observations of the GLSC survey data. He noted that detectable redistribution of fish could occur within a few hours and major redistribution within a few days. He also pointed out how bloater and sculpin were least affected because the temperatures at their depth ranges (i.e. the hypolimnion) remained unchanged. In his study, alewife showed little movement, however, he made this observation based on August trawls conducted specifically for the study. His paper also stated that alewife were likely to be in water greater than 8°C. During the fall, the temperature changes may be more drastic, thereby increasing the movement of alewife. Brandt et al. (1980) found that thermal habitat can be very dynamic in the fall in Lake Michigan. They documented substantial day to day thermal habitat changes at bottom



depths. These day to day changes could result in large range population movements for species with higher maximum temperatures or wider temperature ranges. This would add to the measurement variability. Both studies were unable to support good estimates of thermal regimes for ninespine stickleback and johnny darter.

In my study, relating temperature changes with the estimated differences in observed replicate trawls to their predicted abundance (residuals) has proven to be difficult. For many of the trawls, temperature data has yet to be added to the overall database. Bathythermograph casts were conducted before each trawl, therefore the information is potentially available. Ideally, to test a measurement error vs. temperature relationship, the full temperature profile must be accessible. Although it would be useful to fully understand how measurement variability relates to temperature, this is not needed to use measurement variability in future studies.

The measurement variability estimates can be used when interpreting population changes through time, estimating population parameters, and constructing simulation models using GLSC Lake Michigan forage fish assessment data. As the forage fish stock assessments are used to show trends over time, knowledge about the measurement variability can help in interpreting trends. For example, Eck and Wells (1987) concluded from their results that there was obviously no correlation between alewife and rainbow smelt abundance in the early 1980s. However, from this analysis, I know that both of these species have high measurement variability estimates. This can affect the precision of the yearly estimates of abundance, which will impact trend lines. Therefore, it is possible a real relationship existed between the populations of these two species even though they did not detect one. If the population estimates are imprecise because of

measurement variability, it follows that population parameter estimates will also be imprecise. Brown (1972) estimated mortality rates and stock-recruitment relationships for alewife. His analysis used the replicate trawl data by averaging the replicate catches. The mortality rates and stock-recruitment relationship showed high variability. Although Brown discusses possible reasons for the variability, I can conclude that alewife's high measurement variability is a contributing factor to his results. Lake Michigan fishery researchers who build bioenergetic models have used these fish assessments to either estimate parameters for their models or interpret their results (Stewart et al. 1981, Eck and Brown 1985, Stewart and Ibarra 1991, Eby et al. 1995). They need to understand the implication of measurement variability has on their use of the information from the fish assessments. Measurement variability affects the precision of the forage fish stock assessments, which in turn affects the model's ability to predict how many salmonids the lake can support or predation rates. The uncertainty of the measurement associated with these important Lake Michigan fish stocks should be taken into account when the GLSC survey information is used for Lake Michigan fishery management.

Although these estimates of measurement variability can only be used in association with GLSC bottom trawl data, the implications of this study are not restricted to the ten species stock assessments. Part of the variability associated with any fish stock assessment can be attributed to measurement variability (Walters and Ludwig 1981). The measurement variability of a given fish species' stock assessment is dependent on the sampling process, fish behavior, and the interaction of the two factors. The link postulated in this study between measurement variability and fish behavior may help in the interpretation of other similar fish assessments. Whenever possible, a measurement

error analysis should be a part of all stock assessments. Knowing the degree of our uncertainty about fish stocks can help us to manage our important fishery resources for future returns.

## Chapter 2

### POPULATION DYNAMICS OF LAKE MICHIGAN ALEWIFE AND BLOATER

#### Introduction

The Lake Michigan fish community has changed dramatically in the past century from its historic species composition (Smith 1972, Wells and McLain 1973, Christie 1974, Stewart et al. 1981, Eck and Wells 1987). Three primary human perturbations have been implicated in directing the change in species composition and abundance. Overfishing, habitat alteration (including nutrient loading), and exotic species introduction have changed the lake's fish community composition from a historic structure dominated by lake trout (*Salvelinus namaychus*), lake sturgeon (*Acipenser fulvescens*), burbot (*Lota lota*), and eight species of coregonids to the current structure dominated by exotic salmonids, alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*) and one species of coregonid, the bloater (*Coregonus hoyi*). In the last half of the century, numerous species are thought to have been extirpated from the system including lake trout and five species of deepwater coregonids (Smith 1970).

Historically, six species of deepwater coregonids (*Coregonus nigrapinnis*, *C. johanne*, *C. zenithicus*, *C. reighardi*, *C. kiyi*, *C. hoyi*) were important components of the Lake Michigan fish community (Smith 1970, Christie 1974, Brown et al. 1987). The

chub fishery was comprised of these species in aggregate and was regarded to be the second most valuable fishery in Lake Michigan before the fishery collapsed in the sixties (Wells and McLain 1973). The only deepwater cisco in Lake Michigan to have survived the intensive fishery was the bloater (Brown and Eck 1992). The bloater is included in the group of five deepwater coregonids endemic to the Great Lakes ecosystem (Scott and Crossman 1973). As the deepwater coregonid species were closely related to each other (Koelz 1929), bloater has become the remaining species to help understand this unique collection.

The bloater has been the sole species supporting the deepwater chub fishery. Bloater recruitment became depressed at the time of rapid increase in alewife abundance during the 1960's (Wells and McLain 1973). Subsequent to the bloater population decline in the early 1970's, a ban on commercial fishing was put into effect from 1976 to 1980 (Brown et al. 1987). During the late seventies, bloater recruitment rebounded, and they became the predominant prey species in Lake Michigan in terms of biomass (Eck and Wells 1987). In the late eighties, bloater recruitment declined once more, a possible result of colder temperatures, alewife abundance (Rice et al. 1987), or density dependence (Brown and Eck 1992). The consequences of the current population decline on the fish community are uncertain, but if past events repeat themselves, the chub fishery is likely to be in danger once again. Despite having once supported a large fishery, extirpated native coregonids (e.g., lake herring (*Coregonus artedii*), short-jaw cisco (*C. zenithicus*)) have not been restocked into the lake.

Alewife play a pivotal role in the Lake Michigan fish community by reducing native species populations and supporting the exotic salmonid population as an important

prey item (Eck and Wells 1987). Originally a marine species, the alewife is thought to have invaded Lake Michigan in the late forties through the Erie or Welland Canal from Lake Ontario (Smith 1970). Alewife existed in the lake at low numbers until the population greatly expanded in the early 1960s. The loss of the large predators in the lake has been the predominant explanation for the population explosion (Smith 1970, Eck and Wells 1987). By the mid to late sixties, alewife comprised most of the estimated fish biomass in the lake. The reduction of bloater, emerald shiner, and yellow perch populations (Wells and McLain 1973, Eck and Wells 1987) are thought to be directly linked to the alewife population explosion of that time. It has been hypothesized that this exotic preys on the eggs and fry of other fish species and has out-competed native species for food resources (Smith 1970, Crowder and Crawford 1984, Brown et al. 1987). Another undesirable effect of the alewife has been the periodic, massive population die-offs that littered the lake's shoreline with dead fish (Brown 1968). Part of the justification behind the exotic salmonid stocking program was to reduce the population of alewife (Smith 1970, Eshenroder et al. 1995). Ironically, it is thought that a decline in alewife number led to the large reduction in chinook populations observed in the late 1980's (Stewart and Ibarra 1991). Current fishery stocking practices are working towards a balance between the alewife populations and the exotic salmonids (Eshenroder et al. 1995). The exotic alewife has become a part of the Lake Michigan ecosystem and is a key species in influencing recent changes in the fish community.

To aid in the understanding of the Lake Michigan fish community and management of the fishery, I estimated age-specific abundance indices, associated variability, and survival indices for alewife and bloater from 1962-95. The time range

covers the important recent changes in these populations from the rise in alewife abundance to the current decline in bloater recruitment. Similar reports have not included this time frame in its entirety nor estimated trends in abundance at age (e.g., Eck and Wells 1987, Brown et al. 1987). The associated variability is an important part of this study as it helps to quantify how uncertain these variables are. Hilborn and Walters (1992) maintain that understanding the uncertainty associated with stock assessments is as relevant to fishery management as understanding the population dynamics. Only one alewife study (Hatch et al. 1981) and no bloater studies that I am aware of in the peer-reviewed literature calculate the variability of their population estimates or parameters. My goal is to gain greater insight into the species' population dynamics and the fish community through good estimates of age-specific abundance indices, associated variances, and relative survival estimates. My specific objectives were to:

- 1) To select a statistical modeling method that fits the survey design.
- 2) To apply the method to each age of alewife and bloater and select the best model to obtain indices of abundance for each year together with their variance estimates.

## **Methods**

### **Data Collection**

I used information collected on alewife and bloater during a fall bottom trawl survey of fishes in Lake Michigan conducted annually since 1962 by the Great Lakes Science Center (United States Geological Survey - Biological Resources Division). The fish were sampled during daylight hours between September and November when Lake

Michigan is typically destratified. The isothermal lake conditions should minimize the thermal habitat preferences of fish species therefore allowing fish to be more evenly dispersed (Hatch et al. 1979).

The survey design is a fixed station design, but some changes in the stations sampled have occurred over time (Table 2, Figure 3). Only one station has been sampled continuously since 1962 - off the coast of Saugatuck, MI. From 1962 to 1966, this was the only station sampled. In 1967, three stations were added, one station each off the coasts of Benton Harbor and Ludington, MI and Waukegan, IL. Another expansion was made in 1973 when four stations were added. A station was established off the coasts of Port Washington and Sturgeon Bay, WI and Manistique and Frankfort, MI. There have been four occasions where, for numerous reasons (usually weather related (Hatch et al. 1981)), trawls were not taken at these eight ports since they were established. Port Washington was not sampled in 1976; Benton Harbor was not sampled in 1982; and Manistique was not sampled in 1995. Beginning in 1990, sampling at Benton Harbor was discontinued. In recent years, two stations were added briefly and then dropped. One was off the coast of Two Rivers, WI and the other was off the coast of Little Traverse Bay. Because of the small number of years sampled relative to the larger database, I did not include these two stations in my analyses.

A semi-balloon bottom trawl was used to collect the samples. The trawl had a 11.9m headrope, 15.5m footrope, and a 13mm stretched mesh in the cod end (Hatch et al. 1981). Three vessels have been used over the years: the R/V Cisco, the R/V Grayling, and the R/V Kaho. The R/V Cisco has been used most consistently. The two other



TABLE 2 - Ports sampled by year in the fall bottom trawl survey conducted by GLSC

PORT* YEAR	L Tr Bay	Fran	Ludg	Saug	Bent Harb	Wauk	Port Wash	Two River	Sturg Bay	Mans
1962	---	---	---	X	---	---	---	---	---	---
1963	---	---	---	X	---	---	---	---	---	---
1964	---	---	---	X	---	---	---	---	---	---
1965	---	---	---	X	---	---	---	---	---	---
1966	---	---	---	X	---	---	---	---	---	---
1967	---	---	X	X	X	X	---	---	---	---
1968	---	---	X	X	X	X	---	---	---	---
1969	---	---	X	X	X	X	---	---	---	---
1970	---	---	X	X	X	X	---	---	---	---
1971	---	---	X	X	X	X	---	---	---	---
1972	---	---	X	X	X	X	---	---	---	---
1973	---	X	X	X	X	X	X	---	X	X
1974	---	X	X	X	X	X	X	---	X	X
1975	---	X	X	X	X	X	X	---	X	X
1976	---	X	X	X	X	X	---	---	X	X
1977	---	X	X	X	X	X	X	---	X	X
1978	---	X	X	X	X	X	X	---	X	X
1979	---	X	X	X	X	X	X	---	X	X
1980	---	X	X	X	X	X	X	---	X	X
1981	---	X	X	X	X	X	X	---	X	X
1982	---	X	X	X	---	X	X	---	X	X
1983	---	X	X	X	X	X	X	---	X	X
1984	---	X	X	X	X	X	X	---	X	X
1985	---	X	X	X	X	X	X	---	X	X
1986	---	X	X	X	X	X	X	---	X	X
1987	---	X	X	X	X	X	X	---	X	X
1988	X	X	X	X	X	X	X	---	X	X
1989	X	X	X	X	X	X	X	---	X	X
1990	X	X	X	X	---	X	X	X	X	X
1991	X	X	X	X	---	X	X	X	X	X
1992	X	X	X	X	---	X	X	X	X	X
1993	X	X	X	X	---	X	X	X	X	X
1994	---	X	X	X	---	X	X	---	X	X
1995	---	X	X	X	---	X	X	---	X	---

\* Port abbreviations are: L Tr Bay = Little Traverse Bay, Fran = Frankfort, Ludg = Ludington, Saug = Saugatuck, Bent Harb = Benton Harbor, Wauk = Waukegon, Port Wash = Port Washington, Sturg Bay = Sturgeon Bay, Mans = Manistique



Figure 3 - The eight locations of the bottom trawl surveys referenced in this study

vessels had been used to help with replicate tow collections made prior to the 1973 expansion and to help with the northern station collections.

At each station, bottom trawls are towed along a series of depth contours. The boat tows the trawl along a transect where the depth is constant. Tow times have ranged from five minutes to ten minutes, with a ten minute tow used as a standard. The depth contours sampled have varied over the years. Generally, trawl tows have been taken at 6,7,13,18,22,27,31, 37, 46, 55, 64, 73, 82, 91, 110, and 128 meters. Only one trawl was taken at three depth contours (5, 33 and 113m) for the whole data series. These three depths were dropped from the analyses. The 6 and 31m contours have not been sampled since 1977 and the 13 and 22m contours have not been sampled since 1981. Sampling at the 128m contour started in 1973 and continued at various ports until 1982. Since 1982, it was sampled only once at Port Washington in 1988. Some depths are not sampled at specific stations (Appendix, Table 1). If the substrate was unsuitable for bottom trawling, shallow depths were not sampled (6, 9, 13m). Often, if the shallow depths could not be sampled, an extra depth was added in the deeper waters (128m). Occasionally, depths were not sampled at ports.

From these tows, the most comprehensive biological information on prey fish was collected from alewife and bloater. From each tow, the total catch was weighed in aggregate and then fish were separated into species. The fish were counted and weighed by species. For some of the species, the catch was first divided up by lifestage (young of the year, adult) before counts and weights were conducted. If a lifestage could not be determined then it was recorded as unknown. When a tow was too large for all individual fish to be counted, a random subsample was counted and weighed. The subsample values

were expanded to total numbers and weight per species based on the weight of the total catch.

Over the time series, alewife and bloater were divided into lifestages fairly consistently. Until 1989, alewife under 120mm in length were recorded as young of the year. In 1989, young of the year were considered to be less than 100mm. After this time, the lifestage of the fish was determined based on an approximate cutoff of 120mm. For bloater, the length cutoff between young of the year and adult changed over time. The length cutoff was set at 140mm from 1967-80, 120mm from 1981-85, 110mm in 1986, and 100mm from 1987 to present.

Fish lengths were recorded to document the length frequency characteristics of the alewife and bloater catch. If the sample was too large or time was constrained, a random subsample of the catch was measured. Due to time constraints, length frequency data was not collected for some catches.

Aging structures were collected from alewife and bloater. The length, weight and maturity were recorded for the fish where age structures were collected. The aging data began in 1965 and aging structures have been collected to the present with the exception of 1966, for both species, and 1992, for alewife only (Table 3 and 4). Aging structures had not been fully processed by the GLSC for 1994-97 at the time of the analysis. From 1965 to 1981, the alewife aging structure collected was scales. Since 1981, alewife otoliths have been collected for aging data as it was determined to be a more reliable aging structure for older fish (O’Gorman et al. 1987). For bloater, scales have been consistently used as the aging structure. Aging structures were taken from the fish used in the length frequency sample (1962-82). If the length frequency sample was large, a

TABLE 3 - Alewife aging data availability at ports by year

PORT YEAR	Fran	Ludg	Saug	Bent Harb	Wauk	Port Wash	Sturg Bay	Mans
1962	---	---	---	---	---	---	---	---
1963	---	---	---	---	---	---	---	---
1964	---	---	---	---	---	---	---	---
1965	---	---	X	---	---	---	---	---
1966	---	---	---	---	---	---	---	---
1967	---	X	X	X	X	---	---	---
1968	---	X	X	X	X	---	---	---
1969	---	X	X	X	X	---	---	---
1970	---	X	X	X	X	---	---	---
1971	---	X	X	X	X	---	---	---
1972	---	X	X	X	X	---	---	---
1973	X	X	X	X	X	X	X	X
1974	X	X	X	X	X	X	X	X
1975	X	X	X	X	X	X	X	X
1976	X	X	X	X	X	---	X	X
1977	X	X	X	X	X	X	X	X
1978	X	X	X	X	X	X	X	X
1979	X	X	X	X	X	X	X	X
1980	X	X	X	X	X	X	X	X
1981	X	X	---	X	X	X	---	X
1982	X	X	X	---	X	X	X	X
1983	X	X	X	---	X	---	X	---
1984	---	X	X	---	X	---	X	---
1985	X	X	X	X	X	---	X	---
1986	---	X	X	---	X	---	X	---
1987	---	X	X	---	X	---	X	---
1988	---	X	X	---	X	---	X	---
1989	---	X	X	---	X	---	X	---
1990	---	X	X	---	X	---	X	---
1991	---	X	X	---	X	---	X	---
1992	---	---	---	---	---	---	---	---
1993	---	X	X	---	X	X	X	X
1994	---	---	---	---	---	---	---	---
1995	---	---	---	---	---	---	---	---

TABLE 4 - Bloater aging data availability at ports by year

PORT YEAR	Fran	Ludg	Saug	Bent Harb	Wauk	Port Wash	Sturg Bay	Mans
1962	---	---	---	---	---	---	---	---
1963	---	---	---	---	---	---	---	---
1964	---	---	---	---	---	---	---	---
1965	---	---	X	---	---	---	---	---
1966	---	---	---	---	---	---	---	---
1967	---	X	X	X	X	---	---	---
1968	---	X	X	X	X	---	---	---
1969	---	X	X	X	X	---	---	---
1970	---	X	X	X	X	---	---	---
1971	---	X	X	X	X	---	---	---
1972	---	X	X	X	X	---	---	---
1973	X	X	X	X	X	X	X	X
1974	X	X	X	X	X	X	X	X
1975	X	X	X	X	X	X	X	X
1976	X	X	X	X	X	---	X	X
1977	---	X	X	X	X	X	X	X
1978	X	X	X	X	X	X	---	X
1979	X	X	X	X	X	X	X	X
1980	X	X	X	X	X	X	X	X
1981	X	X	X	X	X	X	X	X
1982	X	X	X	---	X	X	X	X
1983	X	---	X	---	X	---	---	X
1984	X	---	X	---	X	---	---	X
1985	X	---	X	---	X	---	---	X
1986	X	---	X	---	X	---	---	X
1987	X	---	X	---	X	---	---	X
1988	X	---	X	---	X	---	---	X
1989	X	---	X	---	X	---	---	X
1990	X	---	X	---	X	---	---	X
1991	X	---	X	---	X	---	---	X
1992	X	---	X	---	X	---	---	X
1993	X	---	X	---	X	---	---	X
1994	---	---	---	---	---	---	---	---
1995	---	---	---	---	---	---	---	---

random subsample was taken. In later years (1983-present), aging structures were collected from a stratified sample by length bin. Alewife length bins were set to 5mm intervals and bloater length bins were set to 10mm intervals. Aging structures were collected from each port sampled until 1980. Since then, aging structures for alewife have only been collected at the Ludington, Saugatuck, Waukegan and Sturgeon Bay stations. Starting in 1980, bloater aging structures were collected from Frankfort, Saugatuck, Waukegan, and Manistique.

## **Data Manipulation**

### **Age-length keys**

The age-length key was the first step to estimating catch per unit effort's (cpe) at age. To start, I grouped the aged fish into length bins following the guide set by GLSC—5mm intervals for alewife and 10mm intervals for bloater. Then, I pooled the age information together by year into port groupings. Ideally, I would have set up an age-length key for each port for each year. However, the length frequency bins at every port did not always have age structures associated with them. Also, I had to find a way to develop age-length keys for those ports where age structures were not collected after 1982. In order to pool ports with similar lengths at age together, I tested for differences in the age vs. length bin relationship between ports to see how growth varied around the lake. Using an ANCOVA, I ran a model where year (1973-93) and port were class effects and length bin (60-235mm for alewife & 70-400mm for bloater) was a continuous variable to predict age. Since age samples were not collected from all the ports in later years, I did a separate analysis on the subset of data where all ports had aging structures

collected (1973-1982) to see if the missing ports had an effect on the port groupings.

Based on the results, I judged how the ports should be grouped to develop combined age-length keys by year.

Once I had pooled ports together for the age-length keys, the next step was to fill any remaining areas in the pooled age-length keys where a length frequency bin was not associated with aging data in the age-length keys. I estimated the proportion at each age for the length bins without age data based on the age proportions of adjacent length bins and/or adjacent years. There were years where aging structures were not collected or processed (1962-4, 1966, 1992 (alewife only), 1994-5) or too few were collected (1965) to construct an age-length key. For the missing years in the 1960's, I used the average of the age-length keys for the years 1967-72 as a replacement age-length key. The average of 1989-91 and 1993 was used as the replacement age-length key for the missing 1990 years. I took an average of four to six years to reduce any influence a large cohort could potentially have on an age-length key for a year. After all the missing data had been replaced, I calculated the probability at age for each length bin.

### **Length frequency**

The method I chose to divide up the catches into ages was to use the age-length keys to divide the length frequency data into ages and then calculate probability at age for each lifestage catch. This meant that each lifestage catch had to have a length frequency associated to it. Before I could use the age-length key to divide up the length frequency, I had to correct for two different types of missing data in the length frequency database. One type was the absence of a lifestage value associated with a few length frequency



samples. I assigned a lifestage to them using the same criteria as the sampling protocol. For example, alewife length bins less than 120mm were labeled young of the year and all others were label adult. The second type of missing data was when fish were caught but a length frequency sample was not collected.

More effort was required to fill in information on length frequencies when none were collected. I used a three-step hierarchy. First, if there was a replicate trawl taken at that site during the same year, I used the length frequency from the replicate to fill in the missing data. If there wasn't a replicate trawl available, I used the average length frequency structure at the same depth over all ports. I based my decision to use depth averages on an ANOVA analysis (Appendix, Table 2). In the analysis, I tested to see if ports or depths were better at describing the mean and variance of the length at lifestage. Alewife and bloater length frequencies at lifestage were unimodal distributions. If neither a replicate trawl or a depth length frequency sample at another port was available, then I averaged the length frequency of the adjacent depths to the missing depth. Using these three methods, I was able to fill in all of the missing length frequency data.

### **Catches**

I multiplied the number of fish caught in each length bin by the age probabilities associated with its bin. This gave be the number of fish at each age for that length bin. I summed the number of fish at each age for each depth, port, and year combination to calculate the age probability for each catch. The catch for each trawl was divided into ages using the age probabilities. I standardized the catch per effort (cpe) to numbers caught per minute. If alewife or bloater were not caught in a trawl, a zero was recorded

for all age classes. There was an estimate of the number of fish caught per minute per trawl for every age class.

## **Analytical Methods**

Most fishery data contain a large proportion of zero catches and have a skewed distribution and a multiplicative error structure (Pennington 1995). These characteristics were evident in the bloater and alewife catch at age data. The skewed distribution was due in part to a high frequency of zero catches (Appendix, Table 3). I transformed the cpe at age to the log base  $e$ , a common transformation in fisheries (Pennington 1995). I added a constant of 1 to the zero catches also following traditional fishery statistical practices (Gunderson 1993). It is thought that the constant of one is sufficiently small enough to not add a bias to the analysis. It works on the assumption that when fish are caught, the minimum catch other than zero is one fish. However, after I set the effort to number per minute, the minimum catch for a 10 minute trawl turned into 0.1 fish. This 0.1 fish could have been further divided if its length had more than one age associated with it. A substituted length frequency based on more numbers of fish caught would have further divided this fish into a small fraction at each age. I found that a constant of one was not ideal when I ran some preliminary analyses. A plot of residuals against predicted  $\ln(\text{cpe} + 1)$  was skewed (Appendix, Figure 1). Tukey (1977), cited in Stewart-Oaten (1986), suggested  $1/6$  the minimum non-zero cpe as an alternative constant to 1. The basis for this suggestion is unclear (Stewart-Oaten 1986). In any case, this alternative constant also had a skewed plot of residuals against the predicted. Therefore, Dr. James Bence (Department of Fisheries and Wildlife) suggested a constant =

$\exp(x) * (\text{minimum non-zero cpe})$  where  $x$  is derived through some criteria. My criterion for choosing  $x$  was to iteratively find a value where approximately 5% of the non-zero observations were equal to or less than the calculated constant. Generally, most analyses used the same constant. The nature of this methodology produced a different constant for each species and age. Therefore, I decided to select the same  $x$  for each species whose ages produced similar results for  $x$  to provide some consistency. One case where I varied from the constant equation was for the older aged fish. The minimum non-zero cpes for age 9 alewife and age 9 and 10 bloater were larger than the other ages. These large values were primarily due to the small number of observations that were non-zero. A large constant had the potential to skew the analysis, therefore I assigned the age 8 minimum to these aged fish. I used these criteria for calculating a constant and added it to all the cpes. From there, I could log-transform the observations and approximately meet the parametric assumption of normality.

For my analysis, I chose to use a mixed model approach. A basic description of a mixed model is a general linear model that can contain continuous or class variables with fixed parameters and random parameters (Littell et al. 1996). For the deterministic part of the models, I chose to use a continuous function to relate cpe at age to depth, and treated year and port as fixed class variables. A fixed class effect was appropriate for years (because it measured population changes over time) and ports (because it measured a persistent influence of the site on the observations). When I estimated an overall mean at depth for each age, not accounting for any other factors, distinct patterns emerged. Wells' (1968) results also indicated that there was a pattern in the distribution of alewife and bloater at depth. The patterns suggested linear, quadratic or cubic functions, therefore

I tested each of these functions for every analysis. I also tested fixed interaction terms between the continuous depth parameters and either year or port. From these interaction terms, I would gain important information about how these functions may have shifted through time or by location. A fixed year by port interaction was not appropriate because if such an interaction existed, it was more likely due to a random event about the day(s) of collection rather than a tractable reason.

I compared four different modeling treatments of the year by port interaction: (1) no year by port interaction, (2) random year by port interaction, (3) autoregressive covariance structure by depth for every year and port, and (4) spatial-power covariance structure by depth for every year and port. The second approach used the assumption that at each port for every year, there was a common random component that influenced each of the trawls at a station. The third and fourth approaches were similar in that they assumed that the depths at a port were repeated measures of the same fish population for a given year. The model used two different types of covariance matrices to model the correlation of residual errors within year by port combinations (the observational unit).

Both the third and fourth approaches assumed that the residuals at adjacent depths were more closely correlated than other depths and that the correlation was weakened the farther apart the depths were. The autoregressive approach modeled the correlation of

residuals for every year by port combination through the variance-covariance matrix:

	Depth	9	13	18	22	27	...
$\sigma^2 *$	9	1	$\rho$	$\rho^2$	$\rho^3$	$\rho^4$	...
	13	$\rho$	1	$\rho$	$\rho^2$	$\rho^3$	...
	18	$\rho^2$	$\rho$	1	$\rho$	$\rho^2$	...
	22	$\rho^3$	$\rho^2$	$\rho$	1	$\rho$	...
	27	$\rho^4$	$\rho^3$	$\rho^2$	$\rho$	1	...
	.	.	.	.	.	.	...
	.	.	.	.	.	.	
	.	.	.	.	.	.	

where  $\rho$  is the correlation coefficient and  $\sigma^2$  is the residual error or variance. It describes the correlated nature of the residuals. The autoregressive approach assumed that the correlation coefficient is raised to a power equal to the number of intervals that separates depth categories of the observations.

Similarly, the spatial power approach also raised the correlation coefficient to a power value. However, the power value was difference in depth between two sampling locations ( $d_{ij}$ ), leading to the variance covariance matrix for the residuals of:

	Depth i	9	13	18	22	27	...
	j						
$\sigma^2 *$	9	1	$\rho^{d_{13,9}}$	$\rho^{d_{18,9}}$	$\rho^{d_{22,9}}$	$\rho^{d_{27,9}}$	...
	13	$\rho^{d_{9,13}}$	1	$\rho^{d_{18,13}}$	$\rho^{d_{22,13}}$	$\rho^{d_{27,13}}$	...
	18	$\rho^{d_{9,18}}$	$\rho^{d_{13,18}}$	1	$\rho^{d_{22,18}}$	$\rho^{d_{27,18}}$	...
	22	$\rho^{d_{9,22}}$	$\rho^{d_{13,22}}$	$\rho^{d_{18,22}}$	1	$\rho^{d_{27,22}}$	...
	27	$\rho^{d_{9,27}}$	$\rho^{d_{13,27}}$	$\rho^{d_{18,27}}$	$\rho^{d_{22,27}}$	1	...
	.	.	.	.	.	.	...
	.	.	.	.	.	.	
	.	.	.	.	.	.	

For example, the correlation coefficient would be raised to the power of 4 to estimate the correlation between the residual error of the observation taken at 9 m and residual error of the observation taken at 13 m.

The second, third and fourth approaches are similar in that they all assume that after adjusting for fixed effects the remaining variation within a year and port observational unit is correlated. In the second approach, the random year by port interaction leads to this correlation, which is equal among all observations within an year x port unit. Hence we could equivalently drop the random year by port effect from the model and instead describe the residual variation by a compound symmetric variance covariance matrix:

	Depth	9	13	18	22	27	...
	9	1	$\rho$	$\rho$	$\rho$	$\rho$	...
	13	$\rho$	1	$\rho$	$\rho$	$\rho$	...
$\sigma^2 *$	18	$\rho$	$\rho$	1	$\rho$	$\rho$	...
	22	$\rho$	$\rho$	$\rho$	1	$\rho$	...
	27	$\rho$	$\rho$	$\rho$	$\rho$	1	...
	.	.	.	.	.	.	...
	.	.	.	.	.	.	
	.	.	.	.	.	.	

This emphasizes the relationship between the second approach and the third and forth approaches.

The model building proceeded by comparing the results of 72 different models (Appendix, Table 4). There were eighteen basic models that started with a simple model with only a year effect and built up to a full model with year, port, and depth effects with interaction terms with a total of 171 parameters. The basic set of models were repeated for each of the four approaches to the year by port interaction.

To select a model, I used the Akaike's Information Criterion (AIC) which is based on the calculated maximum likelihood adjusted for the number of parameters in the model (Littell et al. 1996). In most cases, I selected the model with the highest AIC. A

few times, there was only a small difference between the AIC of a model with the lowest AIC (full model) and AIC of a model with fewer parameters (reduced model). In these cases, I tested to see if the additional parameters explained the variation significantly better than a model without those additional parameters using a chi-square test ( $\alpha = 0.005$ , Littell et al. 1996).

I conducted a preliminary analysis of survival trends through time. In the analysis, I calculated relative survival where (Hilborn and Walters 1992):

$$S_{a,i} = e^{-Z} \quad (1)$$

$$Z = -(\hat{Y}_{a+1,i+1} - \hat{Y}_{a,i}) \quad (2)$$

where  $S_{a,i}$  is relative survival at age  $a$  for year  $i$ ,  $Z$  is the mortality rate,  $\hat{Y}_{a,i}$  is the predicted year effect at age  $a$  for year  $i$  (used as an index of abundance, see explanation in results section), and  $\hat{Y}_{a+1,i+1}$  is the predicted year effect at age  $a + 1$  for year  $i + 1$ . The survival estimates are relative changes because I used the year effect at age rather than an estimate of the true abundance. I did not back-transform estimates of log cpe; I did not correct for gear selectivity; and I did not expand the values to lake area estimates (Hilborn and Walters 1992). Therefore the survival of a cohort at age 1 can be compared to the other cohorts at age 1 but not to the survival of that cohort at age 2. However, when interpreting apparent trends in the survival estimates by age, I made the assumption that selectivity did not change through time for a specific age class. This assumption may be flawed, particularly for bloater, where size at age has changed over time.

Strong year influences could be seen across indices of abundance at age, particularly for alewife, indicating that there was a year effect in the fish collections. A

year effect for all age classes would not be corrected for in the previous modeling exercise because ages were analyzed separately, and therefore they were assumed to be independent. The consequences of this assumption are not so important when deriving abundance indices as it is when using the abundance indices to calculate survival. The year bias was more apparent in alewife than bloater. To account for such an effect, I pooled relative survival into three year bins. I then analyzed these data using a general linear model with a pooled year effect, an age effect, and an interaction term between the two effects. The pooled year effect allowed for an interaction term because there were more than one observation in a category. The results from this analysis were smoothed relative survival for each species across ages and time.

## **Results**

### **Age-length keys**

For the ANCOVA where 1973-93 data were analyzed, the maximum difference in mean age at length between ports was similar for both species (alewife = 0.208; bloater = 0.200, Table 5). For alewife, the ports could be separated into three groups based on the estimates of port effects. These groups were: Saugatuck, Benton Harbor, Waukegan, and Manistique as group A; Ludington and Port Washington as group B; and Frankfort and Sturgeon Bay as group C. The bloater results indicated two groups based on the port parameter results. Saugatuck, Benton Harbor, and Waukegan were group A and Ludington, Frankfort, Port Washington, Sturgeon Bay and Manistique were group B.

When the data were selected to include only 1973-82, there were different port parameter pattern for alewife but not bloater. For alewife, a important result was that



TABLE 5 - Age-length key port groupings according to ANCOVA results

<b>ALEWIFE</b>					
	<b>Parameter Estimate</b>	<b>Probab. same as Manistique</b>		<b>Parameter Estimate</b>	<b>Probab. same as Manistique</b>
<b>PORT</b>	<b>Years 1973-93</b>	<b>Years 1973-93</b>	<b>GROUP</b>	<b>Years 1973-82</b>	<b>Years 1973-82</b>
Port Washington	-0.082	0.0048	B	-0.081	0.0036
Ludington	-0.071	0.0093	B	-0.048	0.0831
Waukegan	-0.056	0.0370	A	-0.054	0.0458
Saugatuck	-0.042	0.1180	A	0.002	0.9327
Benton Harbor	-0.029	0.3271	A	-0.025	0.3729
Manistique	0.000	.	A	0.000	.
Sturgeon Bay	0.097	0.0003	C	0.057	0.0393
Frankfort	0.126	0.0001	C	0.132	0.0001

<b>BLOATER</b>					
	<b>Parameter Estimate</b>	<b>Probab. same as Manistique</b>		<b>Parameter Estimate</b>	<b>Probab. same as Manistique</b>
<b>PORT</b>	<b>Years 1973-93</b>	<b>Years 1973-93</b>	<b>GROUP</b>	<b>Years 1973-82</b>	<b>Years 1 973-82</b>
Waukegan	-0.125	0.0001	A	-0.300	0.0001
Benton Harbor	-0.087	0.0001	A	-0.351	0.0001
Saugatuck	-0.067	0.0008	A	-0.374	0.0001
Frankfort	-0.009	0.6360	B	-0.130	0.0001
Manistique	0.000	.	B	0.000	.
Ludington	0.018	0.5233	B	-0.169	0.0001
Port Washington	0.052	0.1000	B	-0.192	0.0001
Sturgeon Bay	0.075	0.0499	B	-0.118	0.0010

Ludington was moved from group B to group A, leaving Port Washington alone in B. Unfortunately, Port Washington was one of the ports not sampled for ages in later years, and therefore needed associated ports. As groupings were not tightly linked to geographic proximity, I decided to group all the ports together to create an age-length key by year for alewife.

Unlike alewife, using the restricted set of years in the two bloater analyses resulted in no changes in port groupings. In fact, the differences between the port groups was larger in the subset year analysis (maximum difference between two ports = 0.374). This result indicated that separate age-length key groups may be more important in earlier years. Also, the two groups for bloater were logically grouped by area—the southern basin and the northern basin. Therefore, I used the two groups to develop separate age-length keys by year for bloater.

### **Constant**

For both species of fish, the results of the best constant analysis were similar for most ages (Table 6). The analysis resulted in an  $x$  value used to calculate the constant added to each cpe. For alewife, the calculated  $x$  for all of the ages, ranged from 3.1 to 4.1 except for ages 0 ( $x = 5.1$ ) and 9 ( $x = 0.1$ ). The calculated  $x$  for all ages of bloater ranged from 2.3 to 3.8 with the exception of age three ( $x = 4.7$ ) and age 10 ( $x = 0.1$ ). I rounded the calculated  $x$  to  $x = 3.5$  for all ages of alewife, except for age 0, where I rounded the calculated  $x$  to  $x = 5$ . For bloater, I used  $x = 3.0$ , except for age 4 where I used  $x = 4.5$ . The rounded  $x$  values resulted in a constant where the constant was greater than no more than 5.4% of the cpes for both species.

TABLE 6 - Constant and associated variables used in log-transformation of cpes

	AGE	X	MINIMUM CPE	CONSTANT = $\exp(X) \cdot \text{minimum cpe}$
<b>ALEWIFE</b>	0	5	0.00010	0.01484
	1	3.5	0.00012	0.00397
	2	3.5	0.00042	0.01391
	3	3.5	0.00078	0.02583
	4	3.5	0.00076	0.02517
	5	3.5	0.00028	0.00927
	6	3.5	0.00012	0.00397
	7	3.5	0.00003	0.00099
	8	3.5	0.00002	0.00066
<b>BLOATER</b>	0	3	0.00057	0.01145
	1	3	0.00030	0.00603
	2	3	0.00091	0.01828
	3	4.5	0.00010	0.00900
	4	3	0.00072	0.01446
	5	3	0.00028	0.00562
	6	3	0.00013	0.00261
	7	3	0.00004	0.00080
	8	3	0.00011	0.00221

## Model Selection

In the following results, I have not reported age 9 alewife or age 9 and 10 bloater because of the high percentage of zero counts (> 93% of the total number of observations). It is difficult for the model to fit non-zero points when there is a large ratio of zero observations to non-zero observations and the results can be biased. As so few of these ages are observed, a biased prediction of these ages does not contribute much to the overall analysis or interpretation.

The four lowest AIC value models for each age and species can be found in Table 7. All of these selected models contained one of the covariance error structures and most of them contained a depth parameter. If an interaction term was present, most often it was the port by first order depth interaction. The lowest AIC model was selected as the best model for all ages and species except for alewife ages 0 to 2 and bloater age 5. For these three exceptions, the additional parameters of the full model (lowest AIC model) failed to lead to a significantly better fit when it was compared to the reduced model (second lowest AIC model,  $\alpha = 0.005$ ). For the three exceptions, the second lowest AIC model was selected as the best model.

The selected “best-fit” models did not have the same depth function, error structure, or number of parameters across ages (Table 8). The depth functions for alewife shifted as they aged from linear (age 0) to quadratic (ages 1-3) to cubic (ages 4-7) and back to linear (age 8). Accordingly, the number of parameters increased with age until age 8. The error structure for most alewife ages was the autoregressive correlation, but changed for the older aged fish (7 & 8), where the spatial power structure had a better fit.

TABLE 7 - Lowest four Akaike's criterion and their associated models by age

**ALEWIFE**

<b>AGE</b>	<b>AKAIKE'S</b>	<b>ERROR STRUCTURE</b>	<b>MODEL PARAMETERS*</b>
0	-4813.7	ar(1)	$Y + P + D + D^2 + D^3$
0	-4814.7	ar(1)	$Y + P + D$
0	-4822.1	ar(1)	$Y + P + D + D^2$
0	-4830.7	ar(1)	$Y + P + D + P \cdot D$
1	-4672.9	ar(1)	$Y + P + D + D^2 + D^3$
1	-4673.3	ar(1)	$Y + P + D + D^2$
1	-4677.9	ar(1)	$Y + P + D + D^2 + P \cdot D$
1	-4678.1	ar(1)	$Y + P + D + D^2 + D^3 + P \cdot D$
2	-3976.0	ar(1)	$Y + P + D + D^2 + P \cdot D$
2	-3978.7	ar(1)	$Y + P + D + D^2$
2	-3988.1	ar(1)	$Y + P + D + D^2 + D^3 + P \cdot D$
2	-3990.9	ar(1)	$Y + P + D + D^2 + D^3$
3	-3760.7	ar(1)	$Y + P + D + D^2$
3	-3761.1	ar(1)	$Y + P + D + D^2 + D^3 + P \cdot D$
3	-3761.5	ar(1)	$Y + P + D + D^2 + P \cdot D$
3	-3761.9	ar(1)	$Y + P + D + D^2 + D^3$
4	-3567.7	ar(1)	$Y + P + D + D^2 + D^3$
4	-3570.6	ar(1)	$Y + P + D + D^2 + D^3 + P \cdot D$
4	-3578.4	ar(1)	$Y + P + D + D^2$
4	-3583.5	ar(1)	$Y + P + D + D^2 + P \cdot D$
5	-3688.9	ar(1)	$Y + P + D + D^2 + D^3$
5	-3695.5	ar(1)	$Y + P + D + D^2 + D^3 + P \cdot D$
5	-3709.1	ar(1)	$Y + P + D + D^2$
5	-3718.4	ar(1)	$Y + P + D + D^2 + P \cdot D$
6	-3677.9	ar(1)	$Y + P + D + D^2 + D^3$
6	-3689.0	ar(1)	$Y + P + D + D^2 + D^3 + P \cdot D$
6	-3691.5	sp(pow)	$Y + P + D + D^2 + D^3$
6	-3703.0	sp(pow)	$Y + P + D + D^2 + D^3 + P \cdot D$
7	-3991.6	sp(pow)	$Y + P + D + D^2 + D^3$
7	-4002.1	ar(1)	$Y + P + D + D^2 + D^3$
7	-4010.7	sp(pow)	$Y + P + D + D^2 + D^3 + P \cdot D$
7	-4012.4	sp(pow)	$Y + P + D + D^2$
8	-3363.8	sp(pow)	$Y + P + D$
8	-3368.5	sp(pow)	$Y + P + D + D^2 + D^3$
8	-3371.3	sp(pow)	$Y + P + D + D^2$
8	-3391.9	sp(pow)	$Y + P + D + P \cdot D$

\* Y= year class variable, P = port class variable, D = depth continuous variable

TABLE 7 (cont'd)

**BLOATER**

AGE	AKAIKE'S	ERROR STRUCTURE	MODEL PARAMETERS*
0	-3857.7	ar(1)	$Y + P + D + D^2 + D^3$
0	-3879.0	ar(1)	$Y + P + D + D^2 + D^3 + P \cdot D$
0	-3888.6	ar(1)	$Y + P + D + D^2 + D^3 + Y \cdot D$
0	-3899.3	sp(pow)	$Y + P + D + D^2 + D^3$
1	-4135.0	ar(1)	$Y + P + D + D^2 + D^3 + P \cdot D$
1	-4155.8	ar(1)	$Y + P + D + D^2 + D^3$
1	-4167.1	sp(pow)	$Y + P + D + D^2 + D^3 + P \cdot D$
1	-4191.9	sp(pow)	$Y + P + D + D^2 + D^3$
2	-3761.7	sp(pow)	$Y + P + D + D^2 + D^3 + P \cdot D$
2	-3772.6	sp(pow)	$Y + P + D + D^2 + P \cdot D$
2	-3779.1	ar(1)	$Y + P + D + D^2 + D^3 + P \cdot D$
2	-3795.2	sp(pow)	$Y + P + D + D^2 + D^3$
3	-3932.0	sp(pow)	$Y + P + D + D^2 + P \cdot D$
3	-3940.7	sp(pow)	$Y + P + D + D^2 + D^3 + P \cdot D$
3	-3951.9	sp(pow)	$Y + P + D + D^2$
3	-3960.1	sp(pow)	$Y + P + D + D^2 + D^3$
4	-3652.2	sp(pow)	$Y + P + D + D^2 + P \cdot D$
4	-3661.3	sp(pow)	$Y + P + D + D^2$
4	-3665.0	sp(pow)	$Y + P + D + D^2 + D^3 + P \cdot D$
4	-3674.1	sp(pow)	$Y + P + D + D^2 + D^3$
5	-3851.9	sp(pow)	$Y + P + D + D^2 + P \cdot D$
5	-3852.5	sp(pow)	$Y + P + D + D^2$
5	-3863.6	sp(pow)	$Y + P + D + D^2 + D^3 + P \cdot D$
5	-3864.6	sp(pow)	$Y + P + D + D^2 + D^3$
6	-3877.2	sp(pow)	$Y + P + D + D^2$
6	-3882.6	sp(pow)	$Y + P + D + D^2 + P \cdot D$
6	-3887.7	sp(pow)	$Y + P + D + D^2 + D^3$
6	-3892.2	sp(pow)	$Y + P + D + D^2 + D^3 + P \cdot D$
7	-4134.8	sp(pow)	$Y + P + D + D^2$
7	-4145.3	sp(pow)	$Y + P + D + D^2 + D^3$
7	-4147.1	sp(pow)	$Y + P + D + D^2 + P \cdot D$
7	-4156.8	sp(pow)	$Y + P + D + D^2 + D^3 + P \cdot D$
8	-3124.8	sp(pow)	$Y + P + D + D^2$
8	-3135.8	sp(pow)	$Y + P + D + D^2 + D^3$
8	-3143.6	sp(pow)	$Y + P + D$
8	-3147.9	sp(pow)	$Y + P$

\* Y= year class variable, P = port class variable, D = depth continuous variable

TABLE 8 - Summary of the best models for each age of both species

	AGE	DEPTH FUNCTION	CORRELATION STRUCTURE	# of PARAMETERS
<b>ALEWIFE</b>	0	Linear	Auto-Regressive	46
	1	Quadratic	Auto-Regressive	48
	2	Quadratic	Auto-Regressive	48
	3	Quadratic	Auto-Regressive	48
	4	Cubic	Auto-Regressive	50
	5	Cubic	Auto-Regressive	50
	6	Cubic	Auto-Regressive	50
	7	Cubic	Spatial Power	50
	8	Linear	Spatial Power	46
<b>BLOATER</b>	0	Cubic	Auto-Regressive	50
	1	Cubic w/ Port*Depth	Auto-Regressive	58
	2	Cubic w/ Port*Depth	Spatial Power	58
	3	Quadratic w/ Port*Depth	Spatial Power	56
	4	Quadratic w/ Port*Depth	Spatial Power	56
	5	Quadratic	Spatial Power	48
	6	Quadratic	Spatial Power	48
	7	Quadratic	Spatial Power	48
	8	Quadratic	Spatial Power	48

Although the depth function also shifted with bloater age, the shift was from a cubic (ages 0-3) down to a quadratic (ages 4-8). The depth function varied among ports for young bloaters (ages 1-4) with significant port by first order depth interaction effects.

Therefore, the number of parameters increased from age 0 to age 1 and then decreased as the fish aged. For the first two ages (0 & 1), the autoregressive correlation was better at describing the error structure but for all other ages, the spatial power correlation was better.

## **Model Results**

In the following paragraphs, I have covered the results for all parameters of the model in the order of the model structure. Specific information on parameter significance is in Appendix, Table 5.

The year effects were used as an index of abundance at age. I was able to use these because no parameter had a fixed interaction term with year. That is, all the other parameters were fixed through time, therefore they would scale all the year effects by a constant amount for each age. As I was only interested in an index, not an absolute amount, the year effect served the purpose well. For alewife, the index of abundance showed a general decline over time for older aged fish (age 2-7) although it was by no means a smooth decline (Table 9, Figure 4). The other ages had more year to year variation with no apparent trend. A stronger trend was observed in the bloater abundance indices at age (Table 10, Figure 5). An apparent increase in abundance started in 1979 for age 0 and continued until the mid-eighties. After that time, there was a steady decrease in age 0 bloater. This trend could be followed through each age for the



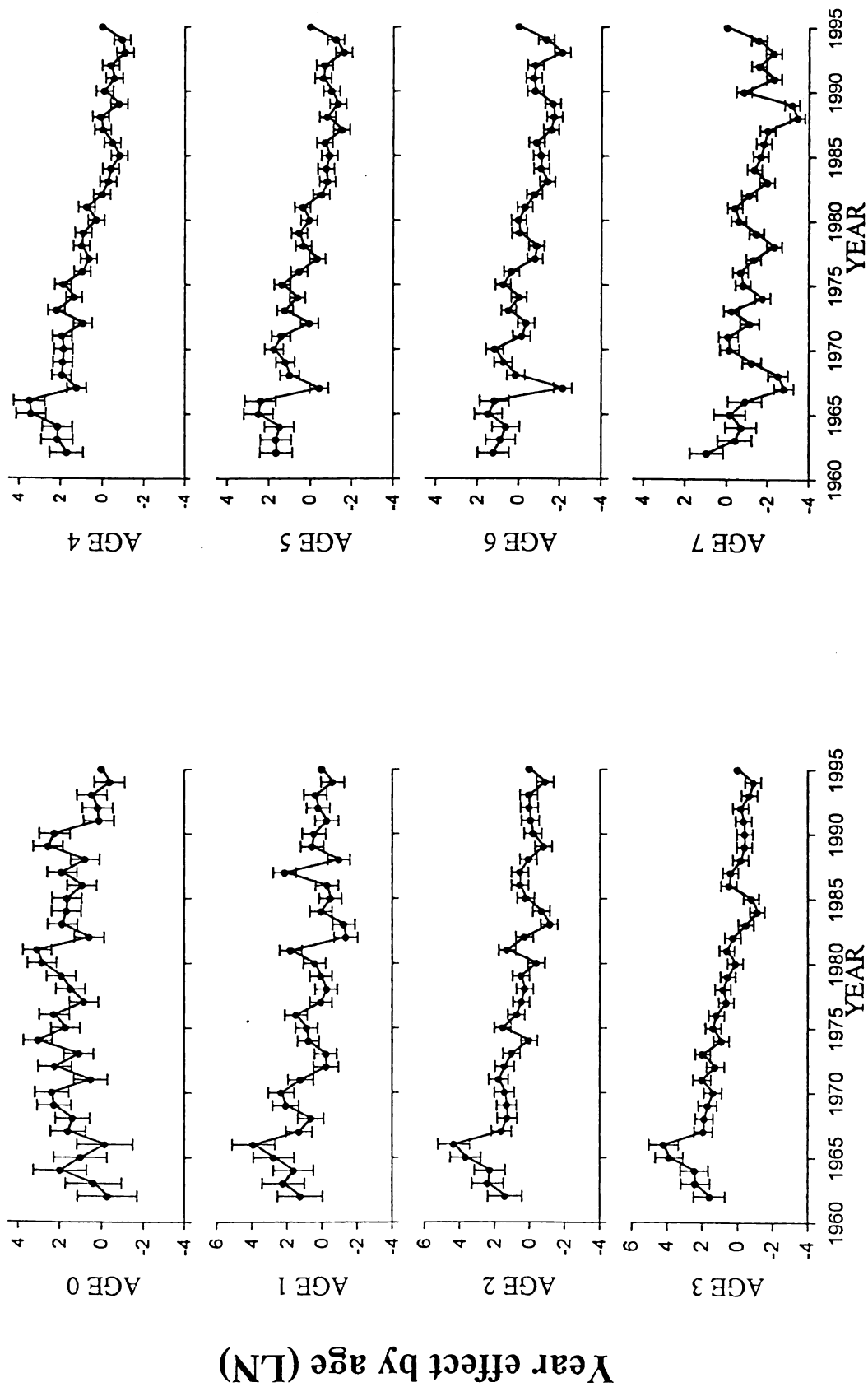
TABLE 9 - Alewife year effects by age and standard error

**YEAR EFFECTS**

<b>AGE YEAR</b>	<b>0</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>6</b>	<b>7</b>	<b>8</b>
1962	-0.279	1.252	1.406	1.598	1.718	1.653	1.222	0.960	-1.796
1963	0.386	2.217	2.385	2.395	2.167	1.680	0.868	-0.400	-2.474
1964	1.989	1.643	2.266	2.445	2.149	1.495	0.618	-0.689	-2.360
1965	1.003	2.758	3.659	3.879	3.420	2.508	1.460	-0.153	-2.576
1966	-0.154	3.909	4.331	4.200	3.503	2.411	1.160	-0.888	-3.265
1967	1.603	1.321	1.602	1.944	1.232	-0.427	-2.141	-2.773	-3.486
1968	1.389	0.646	1.282	1.895	1.943	1.002	0.126	-2.493	-3.515
1969	2.281	2.075	1.317	1.696	1.901	1.219	0.731	-1.223	-3.515
1970	2.377	2.337	1.433	1.405	1.864	1.766	1.155	-0.141	-2.005
1971	0.526	1.213	1.772	2.015	1.930	1.421	-0.159	-0.076	-3.550
1972	2.232	-0.227	1.419	1.265	0.936	0.042	-0.367	-1.115	-3.620
1973	1.092	-0.223	1.024	1.970	2.204	1.243	0.474	-0.225	-3.719
1974	3.054	0.780	0.025	0.925	1.357	0.631	-0.031	-1.743	-2.373
1975	1.719	0.874	1.526	1.376	1.884	1.366	0.741	-0.798	-3.811
1976	2.262	1.487	0.742	1.205	0.958	0.558	0.329	-0.663	-3.776
1977	0.846	0.069	0.470	0.630	0.657	-0.331	-0.788	-1.304	-2.905
1978	1.488	-0.249	0.276	0.829	0.994	0.330	-0.876	-2.315	-3.848
1979	1.920	0.060	0.482	0.547	0.916	0.542	-0.052	-1.456	-3.860
1980	2.848	0.422	-0.388	0.125	0.293	0.056	-0.012	-0.579	-2.341
1981	3.084	1.803	1.269	0.608	0.751	0.371	-0.307	-0.387	-2.332
1982	0.585	-1.359	0.276	0.267	0.016	-0.542	-0.770	-1.078	-2.139
1983	1.874	-1.240	-1.134	-0.465	-0.273	-0.830	-1.383	-1.948	-2.768
1984	1.681	0.063	-0.683	-1.119	-0.412	-0.760	-1.094	-1.348	-2.766
1985	1.655	-0.473	0.209	-0.781	-0.819	-0.931	-1.090	-1.654	-3.576
1986	0.929	-0.285	0.546	0.493	-0.484	-0.706	-0.874	-1.811	-3.778
1987	1.898	2.132	0.554	0.409	-0.014	-1.513	-1.563	-1.985	-3.778
1988	0.795	-0.970	0.067	-0.179	0.087	-0.824	-1.710	-3.419	-3.782
1989	2.561	0.571	-0.796	-0.378	-0.806	-1.327	-1.649	-3.159	-3.554
1990	2.252	0.471	-0.200	-0.393	-0.104	-1.028	-0.800	-0.821	-2.523
1991	0.138	-0.260	-0.059	-0.324	-0.575	-0.616	-0.717	-2.293	-0.901
1992	0.194	0.224	0.023	-0.172	-0.401	-0.696	-0.809	-1.563	-1.290
1993	0.465	0.379	0.030	-0.669	-1.082	-1.610	-2.091	-2.274	-3.768
1994	-0.378	-0.599	-0.882	-0.890	-0.943	-1.222	-1.329	-1.552	-1.709
1995	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

TABLE 9 (cont'd)

<b>STANDARD ERROR</b>									
<b>AGE YEAR</b>	0	1	2	3	4	5	6	7	8
1962	1.425	1.293	0.977	0.882	0.809	0.790	0.757	0.799	0.746
1963	1.342	1.217	0.920	0.830	0.762	0.742	0.711	0.817	0.764
1964	1.274	1.155	0.873	0.788	0.724	0.704	0.674	0.756	0.711
1965	1.274	1.155	0.873	0.788	0.724	0.704	0.674	0.756	0.711
1966	1.342	1.217	0.920	0.830	0.762	0.742	0.711	0.817	0.764
1967	0.829	0.752	0.568	0.513	0.471	0.459	0.440	0.479	0.447
1968	0.817	0.741	0.560	0.505	0.464	0.452	0.433	0.471	0.440
1969	0.817	0.741	0.560	0.505	0.464	0.452	0.433	0.471	0.440
1970	0.813	0.737	0.557	0.503	0.462	0.450	0.431	0.467	0.437
1971	0.809	0.734	0.555	0.501	0.460	0.448	0.429	0.464	0.434
1972	0.796	0.722	0.546	0.492	0.452	0.440	0.422	0.452	0.423
1973	0.698	0.633	0.478	0.432	0.396	0.387	0.370	0.373	0.347
1974	0.693	0.629	0.475	0.429	0.394	0.384	0.368	0.369	0.345
1975	0.694	0.630	0.476	0.430	0.394	0.385	0.369	0.369	0.344
1976	0.710	0.645	0.487	0.440	0.403	0.393	0.377	0.380	0.354
1977	0.699	0.635	0.479	0.433	0.397	0.388	0.371	0.364	0.340
1978	0.696	0.631	0.477	0.430	0.395	0.385	0.369	0.365	0.340
1979	0.698	0.634	0.478	0.432	0.396	0.387	0.371	0.365	0.341
1980	0.700	0.636	0.480	0.433	0.398	0.388	0.372	0.368	0.343
1981	0.698	0.633	0.478	0.432	0.396	0.387	0.371	0.366	0.341
1982	0.725	0.658	0.497	0.449	0.412	0.402	0.385	0.377	0.352
1983	0.707	0.641	0.484	0.437	0.401	0.392	0.375	0.369	0.344
1984	0.707	0.641	0.484	0.437	0.401	0.392	0.375	0.369	0.344
1985	0.707	0.641	0.484	0.437	0.401	0.392	0.375	0.369	0.344
1986	0.707	0.641	0.484	0.437	0.401	0.392	0.375	0.369	0.344
1987	0.707	0.641	0.484	0.437	0.401	0.392	0.375	0.369	0.344
1988	0.707	0.641	0.484	0.437	0.401	0.392	0.375	0.369	0.344
1989	0.716	0.650	0.491	0.443	0.407	0.397	0.381	0.373	0.347
1990	0.730	0.663	0.500	0.452	0.415	0.405	0.388	0.383	0.357
1991	0.727	0.660	0.498	0.450	0.413	0.403	0.386	0.380	0.354
1992	0.728	0.661	0.499	0.451	0.414	0.404	0.387	0.380	0.355
1993	0.727	0.660	0.498	0.450	0.413	0.403	0.386	0.380	0.354
1994	0.727	0.660	0.498	0.450	0.413	0.403	0.386	0.380	0.354
1995									



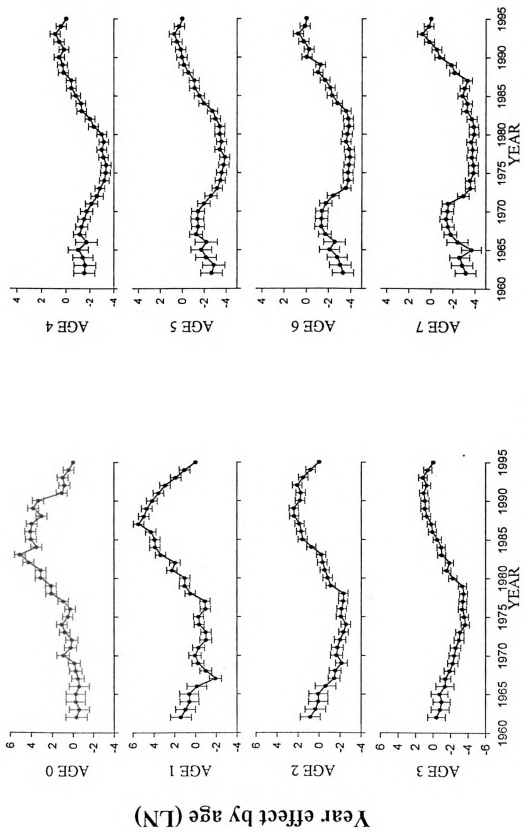
**Figure 4 - Alewife indices of abundance at age  $\pm 1$  standard error**

TABLE 10 - Bloater year effects by age and standard error

<b>YEAR EFFECTS</b>									
<b>AGE YEAR</b>	<b>0</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>6</b>	<b>7</b>	<b>8</b>
1962	-0.309	1.414	0.843	-0.374	-1.540	-2.678	-3.304	-3.154	-2.150
1963	-0.587	0.963	0.348	-0.790	-1.582	-2.877	-3.052	-2.829	-1.923
1964	-0.238	0.598	0.085	-0.965	-1.397	-2.159	-2.795	-2.604	-2.065
1965	-0.238	0.615	0.064	-0.731	-1.023	-1.727	-2.103	-3.683	-2.135
1966	-0.587	-0.136	-0.602	-1.342	-1.708	-2.174	-2.555	-2.411	-1.953
1967	-0.459	-1.917	-1.430	-1.406	-1.138	-1.259	-1.686	-1.772	-2.099
1968	-0.239	-0.972	-1.519	-1.869	-1.304	-1.439	-1.338	-1.539	-1.958
1969	-0.095	-0.218	-2.127	-2.247	-1.506	-1.365	-1.366	-1.378	-1.478
1970	0.978	0.059	-1.656	-2.392	-1.719	-1.432	-1.422	-1.498	-1.761
1971	0.270	-0.284	-1.729	-2.555	-2.133	-1.959	-1.763	-1.560	-1.247
1972	0.137	-0.991	-2.000	-2.943	-2.594	-2.614	-2.417	-2.932	-2.145
1973	0.829	-0.988	-2.321	-3.054	-2.829	-3.193	-3.569	-3.575	-2.359
1974	1.105	-0.347	-2.538	-3.659	-3.195	-3.466	-3.758	-3.556	-2.443
1975	0.544	-0.286	-2.056	-3.545	-3.303	-3.576	-3.735	-3.857	-2.458
1976	0.315	-0.934	-2.144	-3.334	-3.344	-3.781	-3.843	-3.854	-2.494
1977	0.987	-0.905	-2.290	-3.381	-3.123	-3.873	-3.916	-3.708	-2.508
1978	2.126	0.514	-2.317	-3.468	-2.979	-3.416	-3.852	-3.786	-2.368
1979	2.161	1.058	-1.091	-3.337	-3.148	-3.575	-3.562	-3.669	-2.527
1980	3.139	1.039	-0.808	-2.238	-2.982	-3.416	-3.681	-3.915	-2.538
1981	3.128	2.272	-0.521	-1.548	-2.297	-3.423	-3.817	-3.898	-2.441
1982	4.295	1.976	-0.303	-1.851	-2.004	-3.028	-3.768	-3.724	-2.514
1983	5.111	3.363	-0.194	-0.971	-1.299	-2.756	-3.565	-3.226	-2.479
1984	3.545	3.903	0.754	-0.913	-1.234	-1.955	-2.798	-3.315	-2.399
1985	4.067	3.921	1.583	-0.463	-0.804	-1.547	-2.305	-2.863	-2.548
1986	4.115	4.300	1.721	0.109	-0.435	-1.108	-2.143	-3.060	-2.548
1987	3.983	5.470	1.884	0.224	-0.415	-1.080	-1.666	-3.312	-2.548
1988	3.065	4.966	2.398	0.767	0.230	-0.534	-1.052	-2.129	-1.778
1989	3.857	4.682	2.424	0.971	0.311	-0.153	-1.259	-1.844	-2.253
1990	3.371	4.184	1.819	0.964	0.572	0.043	-0.038	-0.767	-1.337
1991	1.116	3.571	1.774	1.095	0.185	0.145	-0.223	-0.517	1.736
1992	0.869	2.912	2.114	0.774	0.584	0.509	0.248	0.160	-0.293
1993	1.033	1.903	1.519	1.191	0.906	0.737	0.747	0.818	-0.333
1994	0.453	1.054	0.840	0.630	0.412	0.278	0.140	0.209	0.517
1995	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

TABLE 10 (cont'd)

<b>STANDARD ERROR</b>									
<b>AGE YEAR</b>	<b>0</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>6</b>	<b>7</b>	<b>8</b>
1962	1.058	1.013	0.961	1.014	0.890	1.000	0.956	0.952	0.714
1963	1.000	0.955	0.984	1.039	0.911	1.023	0.979	0.974	0.730
1964	0.952	0.905	0.917	0.968	0.849	0.954	0.912	0.904	0.681
1965	0.952	0.905	0.917	0.968	0.849	0.954	0.912	0.904	0.681
1966	1.000	0.955	0.984	1.039	0.911	1.023	0.979	0.974	0.730
1967	0.616	0.589	0.575	0.607	0.533	0.598	0.572	0.570	0.427
1968	0.608	0.581	0.566	0.598	0.524	0.589	0.564	0.561	0.421
1969	0.608	0.581	0.566	0.598	0.524	0.589	0.564	0.561	0.421
1970	0.605	0.578	0.563	0.594	0.521	0.585	0.560	0.557	0.418
1971	0.602	0.575	0.559	0.590	0.517	0.581	0.556	0.553	0.415
1972	0.593	0.566	0.546	0.576	0.505	0.568	0.543	0.539	0.405
1973	0.518	0.496	0.447	0.472	0.414	0.465	0.445	0.443	0.332
1974	0.515	0.492	0.444	0.469	0.411	0.462	0.442	0.439	0.330
1975	0.516	0.493	0.443	0.467	0.410	0.461	0.441	0.439	0.329
1976	0.528	0.505	0.457	0.482	0.423	0.475	0.454	0.452	0.339
1977	0.519	0.497	0.438	0.462	0.405	0.455	0.435	0.433	0.325
1978	0.517	0.494	0.438	0.462	0.405	0.456	0.436	0.433	0.325
1979	0.518	0.496	0.439	0.463	0.406	0.457	0.437	0.435	0.326
1980	0.520	0.498	0.443	0.467	0.410	0.460	0.440	0.438	0.329
1981	0.518	0.496	0.439	0.463	0.407	0.457	0.437	0.435	0.326
1982	0.538	0.515	0.454	0.478	0.420	0.472	0.451	0.449	0.337
1983	0.524	0.502	0.443	0.468	0.410	0.462	0.441	0.439	0.329
1984	0.524	0.502	0.443	0.468	0.410	0.462	0.441	0.439	0.329
1985	0.524	0.502	0.443	0.468	0.410	0.462	0.441	0.439	0.329
1986	0.524	0.502	0.443	0.468	0.410	0.462	0.441	0.439	0.329
1987	0.524	0.502	0.443	0.468	0.410	0.462	0.441	0.439	0.329
1988	0.524	0.502	0.443	0.468	0.410	0.461	0.441	0.439	0.329
1989	0.531	0.509	0.447	0.471	0.414	0.465	0.445	0.443	0.332
1990	0.542	0.519	0.460	0.485	0.426	0.479	0.458	0.456	0.342
1991	0.539	0.516	0.456	0.481	0.422	0.475	0.454	0.452	0.339
1992	0.540	0.517	0.457	0.482	0.423	0.476	0.455	0.453	0.340
1993	0.539	0.516	0.456	0.481	0.422	0.475	0.454	0.452	0.339
1994	0.539	0.516	0.456	0.481	0.422	0.475	0.454	0.452	0.339
1995									



**Figure 5 - Bloater indices of abundance at age by year  $\pm$  1 standard error**

corresponding consecutive years. In later years and ages, the trend is more difficult to track in this way, but it is still present. For the early years (1962-1973) and the all ages except for age 0, a similar but smaller traceable trend of an abundance increase and decrease was observed.

Port effects did not have the same pattern across ages, across species, or by age between species (Table 11). There were a few notable insights from the alewife and bloater port effects by age. Port Washington had the largest effect for alewife age 0 fish (2.1). In general, more fish were found there than at other ports. The effects for the locations on the western side of the basin (Waukegan, Port Washington, Sturgeon Bay) were larger than the eastern locations (including Manistique) for alewife age 1 to 5. By comparing the smallest effect in the western basin to the largest effect in the eastern basin, I found that the effects were 1.1X (age 5) to 2X (age 2) larger in the western basin location than the eastern basin location (on an arithmetic scale). For age 1 to 4 bloater, the differences between ports occurred between southern ports and northern ports. The port effects of Saugatuck, Benton Harbor and Waukegan were larger than Manistique, Sturgeon Bay, Frankfort, and Ludington. The Port Washington effect was larger than the northern ports for ages 1 and 2 but not for ages 3 and 4.

The parameters for the continuous depth variables can be found in Table 12. In the fall, older alewife are generally found at deeper depths. Most of the alewife age 0 fish were found in shallower depths (Figure 6). The depth distribution changed with fish age. For age 1, the peak abundance hit between 64 and 73m and declined fairly rapidly from there. Age 2 fish peaked in abundance at 82m and declined at deeper depths. From

TABLE 11 - Port effects of alewife and bloater

ALEWIFE		AGE								
PORT		0	1	2	3	4	5	6	7	8
Frankfort		-0.029	-0.203	0.098	0.169	0.375	0.443	0.483	0.612	0.124
Ludington		0.158	-0.874	-0.144	0.096	0.276	0.421	0.563	0.615	0.201
Saugatuck		0.149	-1.116	-0.324	-0.034	0.070	0.125	0.171	0.237	-0.023
Benton Harbor		-0.899	-1.099	-0.004	0.341	0.416	0.514	0.515	0.608	0.268
Waukegan		-0.089	0.726	1.065	1.028	0.907	0.892	0.788	0.540	0.328
Port Washington		2.100	0.861	0.791	0.700	0.703	0.716	0.747	0.686	0.244
Sturgeon Bay		0.369	0.447	0.980	0.850	0.797	0.749	0.748	0.605	0.268
Manistique		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

BLOATER		AGE								
PORT		0	1	2	3	4	5	6	7	8
Frankfort		1.563	0.625	-1.052	-1.688	-1.677	-0.103	-0.121	-0.148	-0.048
Ludington		1.186	1.200	-0.151	-0.777	-0.847	-0.097	-0.173	-0.255	-0.120
Saugatuck		0.883	1.863	0.706	0.467	0.129	-0.142	-0.414	-0.453	-0.599
Benton Harbor		0.583	2.291	1.241	1.148	0.665	0.143	0.114	-0.031	-0.220
Waukegan		0.404	4.391	2.707	1.914	1.031	0.042	-0.265	-0.395	-0.612
Port Washington		0.911	2.087	0.472	-0.182	-0.412	0.030	-0.127	-0.227	0.026
Sturgeon Bay		0.610	0.029	-2.040	-2.344	-1.982	-0.515	-0.484	-0.443	-0.225
Manistique		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000



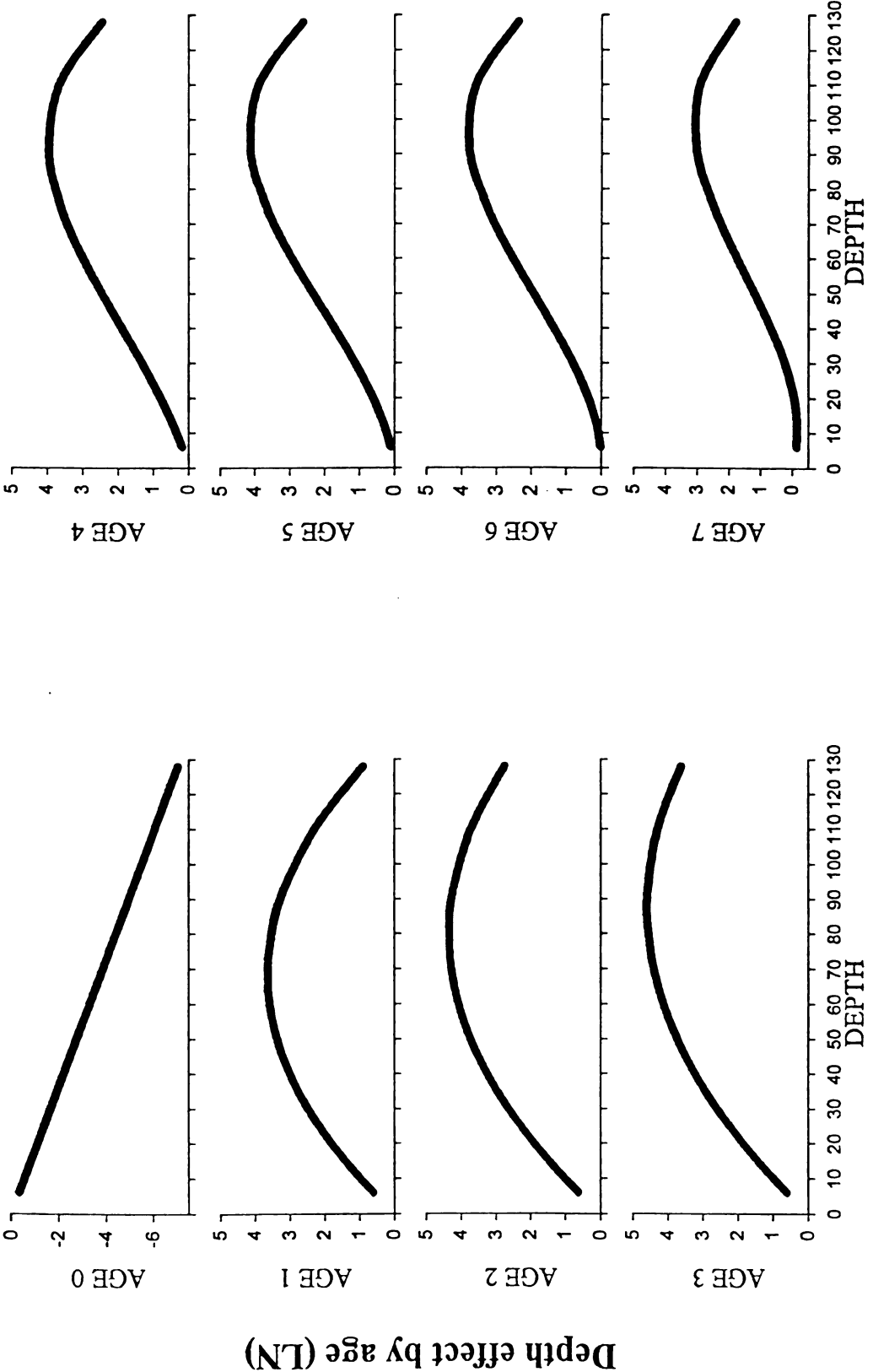
TABLE 12 - The continuous depth effects by age for each species

**ALEWIFE**

AGE	0	1	2	3	4	5	6	7	8
D	-0.055	0.106	0.109	0.105	0.026	0.011	-0.005	-0.031	0.015
D <sup>2</sup>	0	-0.00077	-0.00068	-0.00060	0.00079	0.00112	0.00131	0.00157	0
D <sup>3</sup>	0	0	0	0	-0.0000066	-0.0000082	-0.0000088	-0.0000095	0

**BLOATER**

AGE	0	1	2	3	4	5	6	7	8
D	0.138	0.336	0.230	0.171	0.136	0.125	0.103	0.082	0.034
D <sup>2</sup>	-0.00297	-0.00496	-0.00269	-0.00130	-0.00102	-0.00084	-0.00068	-0.00053	-0.00023
D <sup>3</sup>	0.0000142	0.0000198	0.0000078	0	0	0	0	0	0

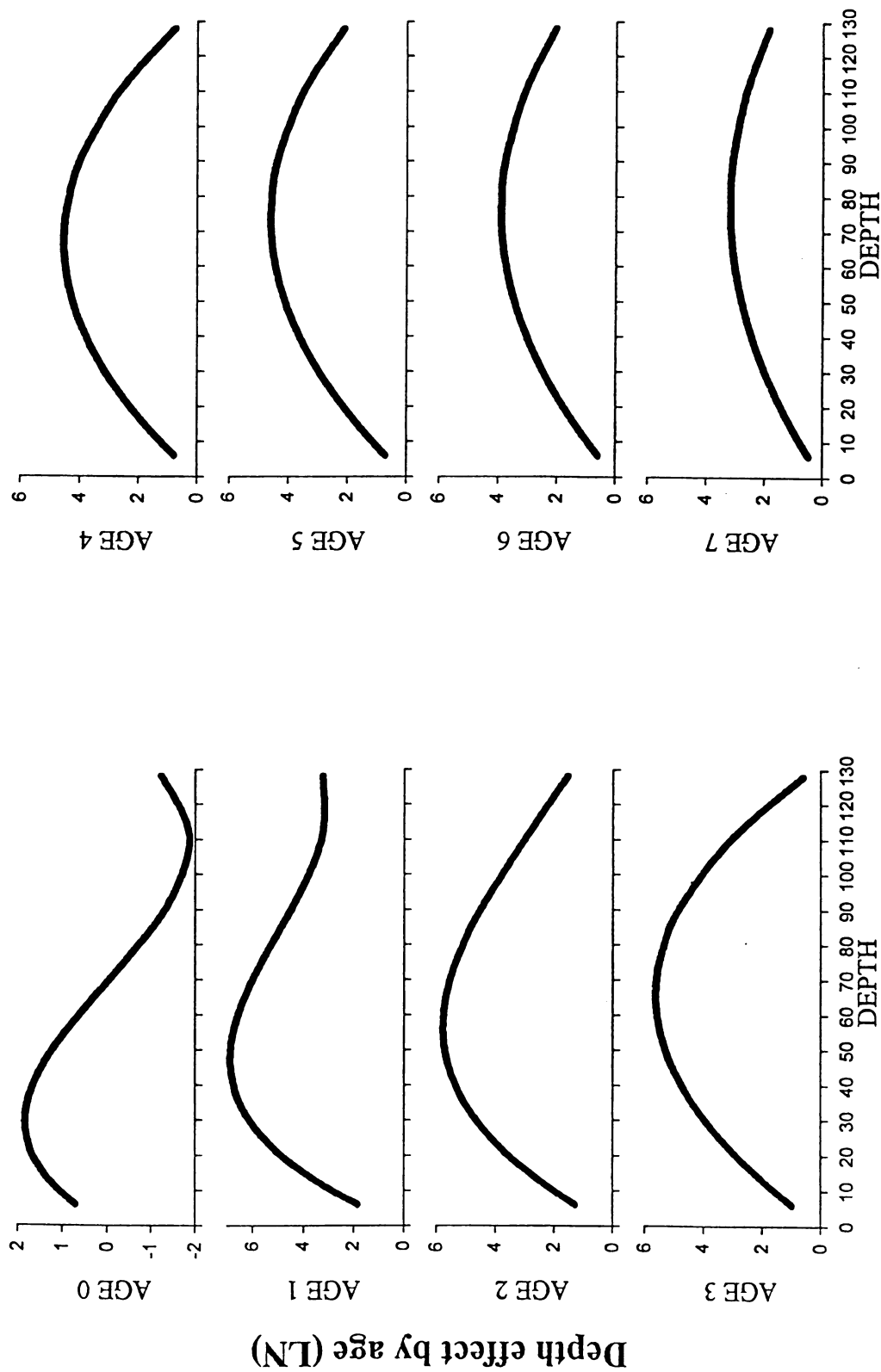


**Figure 6 - Alewife depth functions by age**

age 3 and on, the peak abundance could be found at the 91m trawl. However, the relative number of fish found at shallower depths decreased as the age increased.

For bloater, the overall pattern of depth at age was similar to alewife; older fish were out deeper in the fall (Figure 7). The relative number of age 0 bloater did not reach its peak until 31m but, at greater depths, decreased more rapidly than any other age of bloater. The age 1 bloater reached its peak relative abundance at a depth of 46m, age 2 at 55m, age 3 and 4 at 64m, age 5 and 6 at 73m, and age 7 at 82m. All peak relative abundance depths for age 1 and greater bloater were shallower than those of the alewife. Since none of the models selected for alewife had a year by depth interaction term, their estimated depth distributions have been constant over time. Except for four bloater ages (1-4), the estimated depth distributions were also constant across ports. Any deviations from the predicted depth structure for a year by port combination were accounted for in the variance-covariance matrix structure.

Based on the significant port by first order depth by port interaction for bloater ages 1 to 4, there appears to be differences in depth distribution among ports for these age classes. The differences between ports in their depth distribution did not have the same pattern for each age (Figure 8). The only similarity across ages was that Waukegan had shallower peak abundance than the other ports. For age 1, all of the ports had the same peak depth of 46 m, like the overall depth distribution for age 1, except for Waukegan, where relative abundance peaked earlier, at 37m. Frankfort and Ludington appeared to have more fish out deeper than the other ports despite having similar relative numbers at shallower depths. Age 2 fish were out deeper at Frankfort, Ludington, and Sturgeon Bay



**Figure 7 - Bloater depth functions by age**

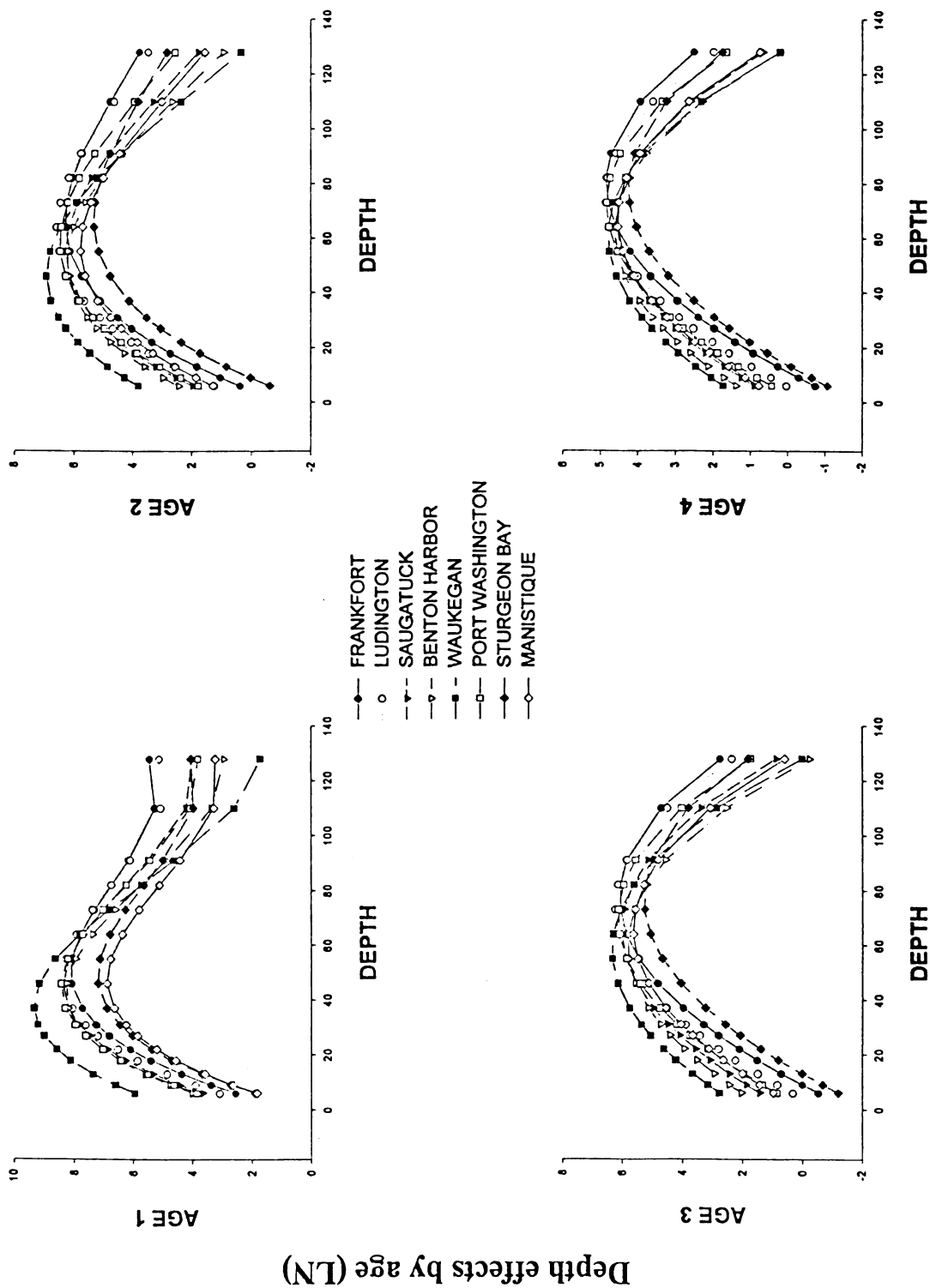


Figure 8 - Bloater depth functions by port for ages 1-4

(peak = 64 m) than the other sites. A comparison of the other locations' age 2 peak relative abundance showed that Waukegan was the only deviant from a 55 m peak, peaking at 46 m, the shallowest depth for age 2. Age 3 fish had a similar depth distribution as age 2 fish, where their peak was the deepest (73 m), with the addition of Port Washington. All other locations had a peak at 64 m, except for Waukegan. Again, this port's peak was shallower than all other ports at 55 m. For age 4, the ports with deeper peak relative abundance were separated into two groups, Frankfort and Sturgeon Bay with 82 m and Ludington and Port Washington with 73 m. All of the other locations had the same peak of 64 m, including Waukegan.

The residual error (or variance,  $\sigma^2$ ) is the variability that was not explained by any of the above parameters. Overall, the residual error estimates (on a log scale) and the corresponding coefficients of variation (C.V., transformed to the arithmetic scale) were large. The alewife residual error at age ranged from 5.9 (age 0) to 1.6 (age 8, C.V. range = 1878% to 200%) whereas the bloater residual error ranged from 3.0 (age 1) to 1.4 (age 8, C.V. range = 441% to 171%, Table 13). For ages 3-7, the bloater residual error was larger than that of the corresponding alewife residual errors. It is the residual error, the correlation coefficient, and the variance-covariance matrix that is used to calculate the standard error estimates on the year effects. These standard error estimates are the quantification of the uncertainty associated with the index of abundance (Tables 9 & 10). The interpretation of the trends should include this uncertainty.

Autoregressive and spatial power were the error structures associated with all the selected best fit models (Table 13). These types of error structures indicated that the

TABLE 13 - Correlated error (covariance) and residual error estimates and standard error

**Alewife**

<b>Age</b>	<b>Correlation Structure*</b>	<b>Correlation Coefficient <math>\rho^{**}</math></b>	<b>Standard Error of <math>\rho</math></b>	<b>Residual Error <math>\sigma^{2**}</math></b>	<b>Standard Error of <math>\sigma^2</math></b>	<b>Coefficient of Variation</b>
0	AR(1)	0.5705	0.0181	5.8689	0.2451	1878%
1	AR(1)	0.5542	0.0181	5.0028	0.2036	1216%
2	AR(1)	0.5705	0.0179	2.7558	0.1145	384%
3	AR(1)	0.5680	0.0182	2.2583	0.0941	293%
4	AR(1)	0.5714	0.0182	1.8891	0.0792	237%
5	AR(1)	0.5274	0.0189	1.9708	0.0786	249%
6	AR(1)	0.5052	0.0192	1.8942	0.0737	238%
7	SP(POW)	0.9078	0.0051	2.3614	0.0865	310%
8	SP(POW)	0.9353	0.0036	1.6081	0.0664	200%

**Bloater**

<b>Age</b>	<b>Correlation Structure*</b>	<b>Correlation Coefficient <math>\rho^{**}</math></b>	<b>Standard Error of <math>\rho</math></b>	<b>Residual Error <math>\sigma^{2**}</math></b>	<b>Standard Error of <math>\sigma^2</math></b>	<b>Coefficient of Variation</b>
0	AR(1)	0.6404	0.0170	2.7777	0.1279	388%
1	AR(1)	0.5614	0.0193	3.0182	0.1286	441%
2	SP(POW)	0.9447	0.0032	2.3915	0.1054	315%
3	SP(POW)	0.9421	0.0032	2.7473	0.1175	382%
4	SP(POW)	0.9416	0.0032	2.1267	0.0901	272%
5	SP(POW)	0.9431	0.0031	2.6442	0.1117	362%
6	SP(POW)	0.9376	0.0033	2.5742	0.1048	348%
7	SP(POW)	0.9236	0.0039	2.9357	0.1110	422%
8	SP(POW)	0.9420	0.0031	1.3647	0.0568	171%

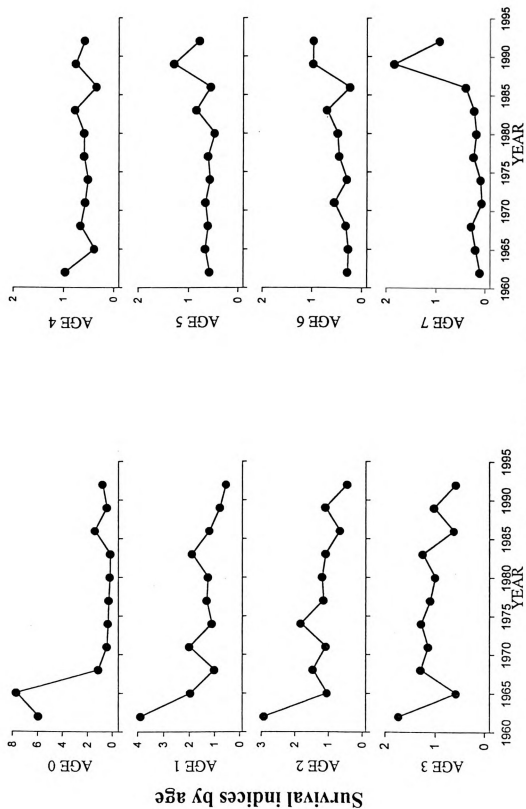
\* AR(1) = autoregressive, SP(POW) = spatial power

\*\* All estimates are significantly different than 0 ( $p < 0.0001$ )

residuals of observations within a year and port observational unit were not independent of each other and that the distance between observations [both figuratively (autoregressive) and actual (spatial power)] was an important descriptor of these residuals in the model. Although the spatial power (most ages of bloater) and the autoregressive (most ages of alewife) models describe correlation among residuals differently, the resulting estimated correlations among residuals were similar (Appendix, Table 6). All of the correlation coefficient estimates were significantly different from zero (Z-test,  $p < 0.0001$ ). Bloater autoregressive correlation coefficient estimates between nearby depths ( $\rho$ ), raised to the first power (smallest interval between nearby depths), ranged from 0.64 (age 0) to 0.56 (age 1). The range of the alewife autoregressive correlation coefficient estimates ( $\rho$ ), raised to the first power, was from 0.57 (ages 0 & 4) to 0.50 (age 6). The spatial power correlation estimates ( $\rho$ ) for both species were in the range of 0.95-0.90. When the correlation coefficient was raised to the power of the shortest distance between two nearby depths (power coefficient =  $d_{ij} = 6-9\text{m} = 3\text{m}$ ), the transformed range was 0.84 (age 2) to 0.78 (age 7) for bloater and 0.82 (age 8) to 0.75 (age 7) for alewife. The range of the correlation coefficient raised to the longest distance between nearby depths ( $d_{ij} = 73-82\text{ m} = 9\text{m}$ ) was 0.60 to 0.49 for bloater and 0.55 to 0.42 for alewife. The corresponding covariance between nearby depths (for depths where  $d_{ij} = 9\text{ m}$ ) ranges, combining covariance structures, were 1.78 (age 0) to 0.80 (age 8) for bloater and 3.35 (age 0) to 0.88 (age 8) for alewife.

General decreases in survival were seen in ages 1-3 alewife from the early 1960's to the present (Figure 9). Age 4 alewife showed little change in survival over time.





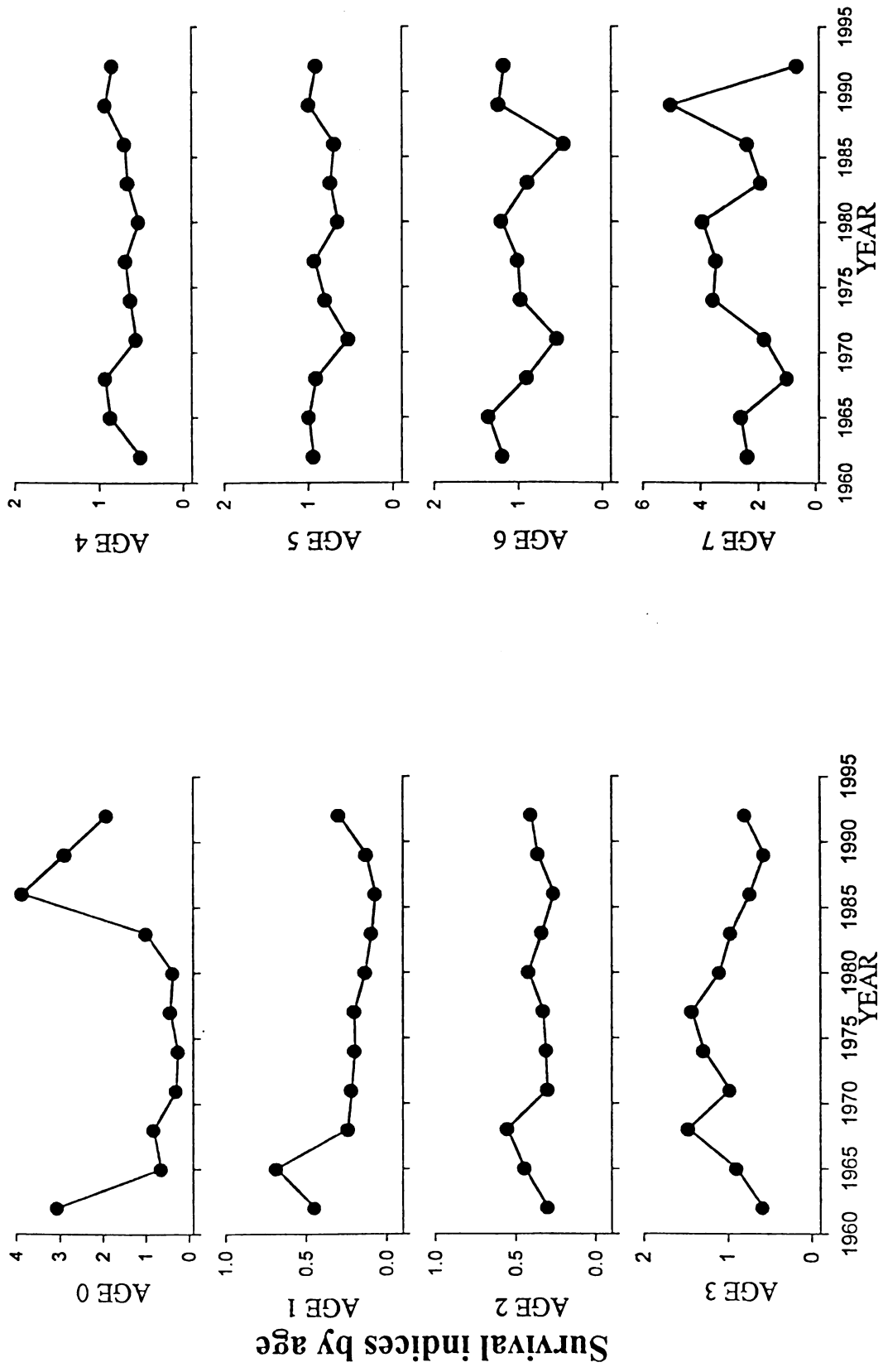
**Figure 9 - Alewife indices of survival at age**

Alewife ages 5-7 survival was relatively constant from the early 1960's to the mid 1980's but increased from 1989-1994. Lower survival was observed for alewife ages 2-6 in the 1986-88 period of time (the estimate for the pooled three years). With the exception of age 0 and 7 bloater, there was no obvious survival trend over time for most ages (Figure 10). Estimated bloater age 0 survival widely fluctuated from a high level in the early sixties to low levels until 1983 when levels increased. Age 7 bloater survival shows wide fluctuations in survival without any discernible trend; it is most likely due to aging error and to the relatively low numbers of individuals observed at these older ages.

## **Discussion**

### **Statistical Choices**

No published studies of alewife and bloater fish population trends in Lake Michigan have used the same statistical techniques reported here. Previous studies have treated the sampling design in various ways. The most sophisticated statistical analysis of this survey design was presented by Hatch et al. (1981). In their study, they increased the accuracy of the statistical analysis of the sampling design by separating the collection sites into 5 different strata through the use of ANOVA techniques based on a factorial model. A stratum included a group of depths and could include only a subset of the ports. They argued that treating the survey as a random sample was inaccurate, particularly in regards to the associated variance. A simple random sample would assume all of the samples were independent of each other across ports and depth (e.g., Eck and Wells 1987). The Hatch et al. study assumed that the depths and ports were dependent on each other within a stratum. Due to the statistical construction, there was the possibility that



**Figure 10 - Bloater indices of survival at age**

nearby depths within a port were assumed to be independent. In this study, the depth functions and the high correlation between depths within a port shows that the assumption of independent nearby depths is invalid for this survey design.

The survey design is a statistical challenge. The survey sampling design was structured according to the logistical constraints of the equipment and the ease of implementation of the researchers rather than by a statistical sampling design theory. Depths did not exceed 124 m because the bottom trawl gear performance was below what was considered acceptable (Gary Curtis, personal communication). Ports were added as the importance of fish population trends based on lakewide sampling increased. Surveys have been collected at the same location for consecutive years because of the convenience of knowing both the nearest safe dockage and the smoothness of the substrate (Ralph Stedman, personal communication).

The unbalanced data collection and the fixed stations were two important elements in the survey design that are difficult to compensate for in statistical analyses. The use of fixed stations is not unusual in fisheries sampling design, but the fixed station sampling design has yet to be dealt with in a satisfactory statistical manner (Gunderson 1993). It violates the primary assumption of most statistical tests, that of a random selection of observations. The justification for a fixed sampling design has been that fish populations are randomly distributed in the lake so that even if the same site is visited, the fish population will not be the same population as the last year (Hatch et al. 1981). An added complexity to this fixed station design was that the depths within a port (repeated samples) were collected close together in space. A sampling design that was based on

statistical sampling theory would not only have randomized ports but also the depths sampled (Gunderson 1993).

The mixed model approach was a good statistical technique to partially accommodate these characteristics of the sampling design. The fixed port effects and depth functions described systematic spatial variation that was constant over time. Therefore, the fixed parameters adjusted for the unbalanced data by estimating what would have been observed had the sampling design stayed constant over time. The residual error accounts for events that affect only one depth observation along a transect, such as the net filling with rocks instead of fish (personal observation aboard the 1997 assessment). The repeated measures covariance structure accounts for events affecting nearby depths in a similar way, such as changes in temperature due to fall turnover (Brandt et al 1980).

The mixed model approach could accommodate missing data to model repeated measures at a year by port combination. If the GLM procedure in SAS would complete a multivariate analysis with each depth observation as a dependent variable. This procedure does not allow for any missing depth observations (Littell et al. 1996). Because the ports I used in the analysis were sampled for at least 21 of the 36 years, I assumed that the model could adequately assess a fixed class parameter for each port based on the years that were sampled. A few of the previous studies of this survey have excluded data collected before 1973 when only one to four ports were sampled (e.g., Eck and Wells 1987, Brown and Eck 1992). My assumption allowed me to use the survey data to the fullest extent.

The same consistency in design did not hold true for the depths sampled. A few depths have been sampled at every port for the entire time series but many of the depth locations have been sampled at select ports (e.g., 6 m depth is only sampled at three ports) and for select years (e.g., 128 m depth was only sampled for 11 years). This restricts the number of data points that can be used to estimate fixed, class parameters for depth locations. A fixed, class parameter for a depth location has the potential to be biased towards the ports and years the depth location was sampled. As the estimated parameter would be used in the model to estimate abundance and variability at age over the entire time series, the predicted values would also be biased. Although for most ages the class depth effect models had higher AIC values than any of the continuous depth effect models, I did not consider them a possibility in model selection. A continuous depth function was advantageous because it could accommodate the case where the depth sampled changed from port to port and year to year. An additional advantage was that the continuous depth function could be modified to allow the depth distribution vary by year or port. This flexibility was found to be important for bloater ages 1-4. The missing depths may have biased the fit of the function because there was no information both shallower and deeper than the missing depths, and I was forced to extrapolate the patterns based on sampled depths at the same location and by depth distributions at other locations and/or years. Similarly, Hatch et al.'s (1981) analytical techniques used regressions with dummy variables to circumvent the missing depth data at ports.

A minor difference between my analysis and previous studies was selecting a constant. Other than the constant of one used by most studies, Hatch et al. (1981) used a different method of transformation (using Taylor's power law to chose a transformation)

to normalize the distribution of fish biomass. Histograms of the untransformed and transformed catch data (numbers of fish) indicated that the log transformation was appropriate in my case. My results of the residual plots from three different constants did indicate that caution should be used when selecting a constant where the lowest non-zero observation has the potential to be substantially smaller than one.

## **Modeling Results**

The port effects lend support to two previous observations related to alewife and bloater. The first is that there are more alewife on the Wisconsin side of the basin [Benjamin, in press; Guy Fleisher, (Lake Michigan Technical Committee meeting, July 15-16, 1998, Charlevoix, MI)]. The second was observed in my analysis for the bloater age-length keys. Both the clusters for the age-length key and the port effects for ages 1-4 suggest that there is a north-south difference in bloater populations. Saugatuck, Waukegan, and Benton Harbor fell out as ports that were different than the northern ports. The bloater age-length key analysis suggested that growth was faster in the southern cluster than that of the northern ports. The faster growth was more apparent in the years when there were fewer bloater overall (1973-82). The length table for bloater (Appendix, Table 7) shows slower growth for the population as a whole when the population increased. Brown and Eck (1992) also found a reduction in bloater weight at age as the population increased. The decreased distinction between parameter estimates in the cluster age-length key analysis when additional years were included (1983-93) may be a result of increased population size. If the southern basin is good for growth when there are fewer numbers in the population, then the large distinction between the northern

and southern ports would be expected. However, conditions promoting rapid growth may also lead to high recruitment of bloater (Brown and Eck 1992). When recruitment increased basin wide, the port effects suggest that there would have been greater numbers in the south than the north. This may have caused a larger reduction in bloater growth in the south than the north, thereby decreasing the distinction in the cluster age-length key analysis. The patterns in port effects for both species are in keeping with our expectations.

The depth functions followed a logical progression through the ages for both species. Not only were peak depths deeper as each species aged but the functions themselves made smooth transitions through the ages. Because both of these characteristics occurred, even though each age was analyzed independently, the use of these depth functions as a statistical tool is supported. The fall depth patterns reported by Wells (1968) for these two species displayed a migration towards deeper depths as the fall turnover occurred. His relative catch was higher for alewife at 9 m and from 18 to 46m and for bloater at 55 to 91 m than his other observed catches. The **peak** in relative alewife numbers at shallower depths might reflect a larger relative abundance of younger fish, if the depth functions generally hold true for this time. Because he found few to no bloater in the shallower depths ( $\leq 22$  m), this may reflect the relatively low numbers of young fish in the lake that year (1964). In addition, there is the possibility that the young fish were less vulnerable to the trawls in the 1960's because they were higher in the water column (Wells 1968, Crowder and Crawford 1984). Wells documented the migration of these fish to deeper depths in the fall but my results suggest that the migration is not age independent. Wells did note that the young-of-the-year alewife congregated in shallow



water for much of the fall, despite the migration of the older fish. His results also showed a larger proportion of fish in shallower depths (6 m to 27 m) during the summer than the winter, when he observed a larger proportion of the fish at much deeper depths (46 m to 91 m). In the fall, the fish are dispersed across all depths, suggesting that alewife migrate in the fall to the deeper water they occupy in the winter. My results indicate that it is the older fish that migrate to the deeper depths first whereas the younger fish appear to stay in shallower water longer. Wells (1968) commented that the larger alewife led the spring migration to shallower depths, indicating that again, the older ages are the first to move. The port by depth interactions revealed that generally younger fish were distributed out to deeper depths at the northern ports. This could support the hypothesis that the younger fish stay in warmer water longer as the cooling of the water and fall turnover should start in the north earlier than the south. However, this could also be a reflection of available bottom area as the more southern ports have a larger percentage of shallow bottom depths than the more northern sites (Holcombe et al. 1997). A restriction of this habitat may have an effect on young bloater distribution, particularly when fish densities increase. Or it could be an artifact of the depth range difference between some of the northern ports and the southern ports, if the range truly has an effect on fitting the function in the model.

Although the general patterns of older aged fish distributed deeper than younger fish and logical depth function progression were similar between the two species, the patterns were different when the results were compared between species at the same age. Overall, the depth patterns show that alewife are in general distributed at deeper depths than same age bloater, with the exception of age 0. It appears that age 1 to 3 alewife have

an overlapping depth distribution with bloater older than age 2 during the fall migration. It would be insightful to explore the patterns during rest of the year. It would also be worth investigating how age and overlapping depth distribution might impact the populations of these two species (Crowder and Crawford 1984). Unfortunately, the existing fall survey data do not allow me to further explore potential interactions of age classes as a result of depth overlap.

One limitation to the interpretation of these depth distributions is that the dynamic nature of the lake's thermal structure in the fall (Brandt et al. 1980) adds to the variability. The fish react to the fall turnover temperature changes in the lake by moving to deeper depths where temperatures are more stable (Wells 1968). The stage of lake turnover varies through time and location adding variation to a specific port and year. The dynamic nature of fall turnover would tend to mask any changes through time in the overall depth distribution of fish at a specific port. For example, the alewife depth distributions may have changed when there was an increase in the bloater population. Although summer populations are thought to be more stable in their depth distribution, they are also located too nearshore for adequate bottom trawl sampling (Wells 1968). These depth distributions are most certainly influence by fall temperature dynamics (Wells 1968, Brandt et al. 1980). Temperature may even be a better prediction of relative abundance than depth, but I was unable to test this hypothesis because current temperature data collected during these surveys is not in the GLSC database.

In addition to the use of temperature as a potentially useful variable for extracting variation and modeling year to year changes in depth distributions, it may be important to survey a different season in the lake or multiple seasons in the lake, similar to the Wells

study. The feasibility of changes in sampling should be explored from this aspect. Any changes in depth distribution through time could help discern any potential ecological interactions or behavioral changes such as displacement of alewife from optimal habitat when bloater became more abundant. Displacement of alewife to marginal habitat may be reflected in abundance changes at age. The marginal habitat may allow them to be more vulnerable to predation or lethal temperature changes. When alewife were abundant, bloater may also have been displaced as well (Crowder and Crawford 1984). I can not assess these hypotheses with the present results.

It was surprising that the residual error estimates and correlation coefficients for bloater were generally as high as or higher than the comparable alewife estimates. Because of the bloater's lower measurement variability estimated in the measurement error analysis (see Chapter 1), I expected lower residual error estimates and higher correlation coefficients for bloater. However, it may be difficult to relate the variability results of these two analyses to each other because of the space and time differences in the collection of the observations. The covariance matrix modeled the variability of observations taken at larger distances apart than the measurement error model. The shortest distance between two observations was 3m in this analysis whereas the paired observations in the measurement error model were taken at the same location. Another confounding factor may be the difference in the time of collection between the two observations in each analysis. The covariance matrix related observations that were often taken in the same day whereas the paired observations in the measurement error model were always collected 1-6 days apart.

As for the pattern in the correlation matrix type, there appears to be very little difference in the estimate of the calculated correlation coefficient between depths. The shallower depths for the spatial power correlation matrix are more highly correlated than those for the autoregressive matrix. However, I am unsure why older aged bloater abundance was better modeled using the spatial power correlation matrix. The older aged fish of both species were found at deeper depths so it does not make intuitive sense why the bloater would have higher correlation in the shallower depths than the alewife. It may be that older bloater display a behavior where they will occasionally move to shallower depths during the fall creating a patchy distribution different than the predicted depth distribution.

There are several components in sampling that add to the residual variability. One component would be sampling young of the year alewife and yearlings with a bottom trawl in the fall. Both ages are still pelagic during the fall (Wells 1968) and the descent of some to the bottom is probably not a consistent proportion of the population. I doubt the results presented here are reliable indicators of their true population dynamics from year to year for these ages, especially when their large residual errors are taken into account. This may also be true of the older aged alewife (Brandt et al. 1991) though not to the same degree as the youngest ages. The use of scales as an aging structure is another component that may add variation to older aged fish through underestimating their true age (O’Gorman et al. 1987). A final component may be net avoidance of the older aged bloater (Brown and Eck 1992). These factors added to the variance seen in the abundance indices. Therefore the results should be interpreted cautiously.

## **Abundance Trends**

The results of this analysis lend further insight into the patterns of abundance through time and how those patterns relate to the surrounding environment. There are many ways in which the results presented can be interpreted. They may even lend support to previously published theories such as competition (Crowder and Crawford 1984) and salmonid predation (Stewart and Ibbara 1991) through additional analysis. For now, I will concentrate on what I believe to be the most important influences for each species abundance at age trends.

Since the early eighties, a number of papers have been published using the GLSC alewife and bloater data to portray the population dynamics of these two species (e.g., Eck and Wells 1987, Brown and Eck 1992). Because of the potential influence of alewife on many native biota populations, their population dynamics have been of great concern in fishery management (Wells and McLain 1973). There have been two contradictory management view points on this species. One was that alewife populations were to be depressed so that die-off events did not pollute the Lake Michigan shoreline and native populations could recover (Wells and McLain 1973). Perhaps the largest die-off event was in the winter of 1966-67 and was well documented (Brown 1968). The die-off event is a strong signal in the abundance trends reported here. After the chinook salmon was established during the 1960's and 1970's and went through dramatic declines in the late 1980's and early 1990's, another management view point emerged. Alewife abundance should be maintained to support the salmonid (in particular, chinook) fishery (Stewart and Ibbara 1991). For either goal to be achieved, the influencing factors of alewife population dynamics need to be explored.

In the literature, three influencing factors have been hypothesized to be the most important; 1) Temperature (Eck and Wells 1987; Eck and Brown 1985), 2) Predation by salmonids (Stewart et al 1981), or 3) Competition with bloater (Crowder and Crawford 1984, Crowder et al.1987). All three hypotheses have merit but have not been rigorously tested in the literature. Most likely, all three have contributed to the general declining trend in older aged alewife. Eck and Wells (1987) argued that the alewife population declines were due to a series of cold winters. I doubt that cold winters could have caused a decline over a 25+ time span such as the one seen in my results. Although they were using the same data set as this study, my analysis allowed a more careful look at the data through the partitioning at age and variability. Colder temperatures or slower springs could have had a negative influence on the population during certain years and caused more intense die-off events (Colby 1973, Flath and Diana 1985). Higher mortality rates would indicate a high die-off event for a given year. I would not venture to guess which years may have had such an influence on my results without pertinent temperature data and further analysis. Most likely, predation had the largest influence on the general declines. Adult alewives have been shown to be a preferred food item of chinook salmon (Jude et al. 1987). Stocking numbers during the seventies and eighties had been increased in a step-wise fashion. Therefore, the somewhat unstable decline in alewife could have been due to these increases.

After the chinook salmon decline, the older alewife population trends did not show an appreciable increase as would be expected if chinook predation were the influencing factor on alewife populations. In fact, the indices continued at low relative values indicating that there were other factors that were influential to the alewife

population dynamics. Two additional predation factors may be burbot and commercial harvest of alewife. Burbot numbers declined in the same time frame as the other native species (1950's and 1960's, Wells and McLain 1973) but have recently rebounded in the mid to late eighties (Passino-Reader et al. 1995). In diet studies, they have been shown to prey on alewife (Ralph Stedman, personal communication) particularly when they have a strong year class. This may have helped to depress the alewife population.

Commercial harvest may have been a substantial contributor to the reduction of adult alewife, particularly prior to the 1980's. I compared the estimated weight of commercial harvest of alewife in 1978 (the second largest recorded alewife harvest, Baldwin et al. 1979; Commercial harvest database on the Great Lakes Fishery Commission website) to the estimated total salmonine consumption of adult alewife from the Stewart and Iberra (1991) bioenergetics model for the same year. The commercial harvest was about 20,000 metric tons (Brown 1995) and the salmonine consumption estimated to be approximately same. I would assume that during the 1966-77 time period, commercial harvest of alewife was similar to or exceeded the salmonine consumption. Commercial harvest ranged from approximately 12,000 metric tonnes to 22,000 metric tonnes. Although Stewart and Iberra's estimates did not cover this time period, their approximate population numbers of salmonids during that time show that total salmonid numbers were well below their 1978 estimate. Yet during this time, the alewife numbers at most adult ages were declining. The scale of alewife commercial harvest was also considerably higher than the chub, lake trout, lake whitefish, and lake herring fisheries where the highest harvest of a single species reached a maximum of 6,500 metric tonnes per year (Brown 1995). From 1979 to 1989, the percentage of

commercial harvest in the overall total alewife consumed (commercial harvest + estimated salmonid consumption) did not exceed 50% and was as low as 28%. Still, it was never below a quarter of the overall amount of alewife removed. Stewart and Iberra (1991) did not include the increased mortality in chinook salmon populations during the late 1980's in their estimates which suggests that their estimates of chinook consumption of alewife may be overinflated during that period of time. The alewife commercial fishery was closed in 1990 (Jim Francis, Lake Michigan Committee Meeting, March 20-21, 1996, Duluth, MN). Relative abundance indices did not reflect an appreciable gain after this time either. However, the alewife relative survival for ages 5,6, and 7 did show an increase in the 1990 to 1995 period of time. The close of the fishery could have been a larger factor than the reduced chinook populations in increasing the survival of these older ages, particularly because the 1986-1989 alewife survival was low despite a potential reduction in chinook salmon predation.

The third influencing factor reported in the literature has been competition between alewife and bloater for food resources (Crowder and Binkowski 1983, Crowder and Crawford 1984, Crowder et al. 1987). Competition with the increased bloater population may have helped in maintaining low alewife abundance. In support of this hypothesis, the noticeable reduction in alewife age 2-7 survival in the 1986 to 1988 period was possibly a result of competition between adult alewife and young of the year and age 1 bloater. During that time period, Makarewicz et al. (1995) observed low relative abundance of Cladocera (August sample). They hypothesized the decline was a result of fish predation and/or *Bythotrephes* but were unable to prove either case. As alewife numbers were low and their survival declined during that period of time, it is



doubtful that they were the cause of the Cladocera decline. Age 0 and 1 bloaters, however, were at their peak during this period of time. Cladocera have been shown to comprise up to 62% of the diet for adult alewives, 97% of the diet of young of the year bloater, and 18% of the diet of yearling bloater during late summer and early fall, a period of time when most of the alewife consumption occurs (Rand et al.1995). The competition during this time may have reduced the survival of alewife.

The overall patterns in alewife relative survival show that ages 0-2 survival had declined since the early sixties whereas ages 5-7 survival had been steady until the early eighties when survival trends became more erratic. Age 3 survival was variable in the sixties and eighties but was fairly stable through the seventies. Age 4 survival had similar but weaker signals as age 3. Alewife age 1 relative survival has declined from 1986 to 1994. As I did not calculate the true variability of survival (i.e., I did not use the variability of the abundance indices), it may be that the error is large enough that the survival estimates are not that different from each other. Relative survival of age 2 and 3 was also comparatively lower from 1991-1994. This may be a result of using an approximate age-length key for 1992, 1994, and 1995. If the survival trends were true, the result indicates that the first years of life are crucial in influencing the adult population. The reasons why these trends may be occurring could be a result of cold spring temperatures, predation, competition, a combination of all three, or something yet to be identified. Survival trends are a useful indicator to understand how influencing factors are shaping the alewife dynamics. These survival estimates should be refined using better modeling methods and more up-to-date survey information so that a more in

depth analysis of influencing factors can be conducted. The stronger analysis should explicitly account for correlations among ages in residual errors.

For bloater population dynamics, the first year of life has been identified as crucial in setting bloater abundance trends and the results presented here strongly support previous observations (Brown et al. 1987, Rice 1987, Brown and Eck 1992). The thorough age analysis revealed two time periods where bloater recruitment increased then subsequently declined. Although the first time period is not apparent in the young of the year abundance trends, I assume that it did occur as it is traceable in the consecutive ages. In the catch records, lifestage was assigned as unknown for these early years. It may be that the small young of the year were not recorded at that time in the length frequency records, therefore it would show as no young of the year caught in the trawls. It could also be because the age 0 bloater were higher in the water column at that time or were less vulnerable to the trawl when alewife relative abundance was high. The second time period can also be traced through cohorts, resulting in relatively flat survival trends. The additional years of data in my study continue the trend presented in Brown and Eck (1992), whose results ended with 1989. The results show a continued decline in the bloater recruitment (age 0 and 1) and increase in older bloaters. The influencing factors in bloater recruitment have been suggested as adult alewife abundance, spring temperatures, and density dependence.

High alewife abundance has been implicated in reducing bloater population dynamics through predation on fish larvae (Smith 1970, Wells and McLain 1973, Crowder 1980) and reducing large zooplankton (Wells 1970, Evans and Jude 1986, Crowder et al. 1987, Evans 1990). Declining alewife abundance in the late seventies and

early eighties may have contributed to the resurgence in bloater recruitment (Rice et al. 1987, Crowder et al. 1987). However, it is clear that alewife population abundance has not been the only factor in shaping bloater recruitment for two reasons. First, the relative abundance of age 1 bloater has steadily declined since its peak in 1987. This was at a time when adult alewife relative abundance was relatively lower than in the late seventies when bloater recruitment started to increase. Second, the abundance indices at age reflect two relatively smooth population increases and decreases that can be traced through the ages. If alewife were a strong influence, the bloater trends should reflect some of the larger fluctuations in the adult alewife population dynamics. The argument also argues against spring temperatures as a strong influencing factor in larval survival (Rice et al. 1987).

The smoothness and the apparent repetitive pattern suggests that a large part of the bloater population dynamics is probably controlled by intraspecific factors. Bloaters have been shown to have a lower growth rate, a lower lipid content, and a female-predominant sex ratio when the adult biomass is large (Brown et al. 1987, Brown and Eck 1992). Lower growth and lipids may be due to lower food resources as intra-competition increases. Brown and Eck (1992) summarized a study that found bloater lipid content had decreased by 49% from 1980 to 1986. A rough comparison of lengths at age (Appendix, Table 7) for that time period revealed an average reduction of 14%. These factors may reduce the number and quality of fertilized eggs produced. This argument would help to explain relative abundance reductions of age 0 and 1 bloater as adult relative abundance increased. The female predominance would also lower the number of fertilized eggs assuming that there were insufficient males. The percentage of females

increased to a high of 97% in the 1960's when adult populations were relatively larger compared to the 1970's when females were closer to 50% of the population (Brown et al. 1987). These density dependent phenomena may have been regulated through competition and predation when there were other deepwater chubs occupying the lake (Brown and Eck 1992).

Bloater population dynamics are more tractable than alewife. Large, repeated fluctuations in bloater populations permit better evaluation of the potential influencing mechanisms than alewife despite the similar estimates of variability. In modeling exercises, there is a good chance that the behavior of bloater populations can be precisely captured. The same thing cannot be said about alewife. As both species are important to understand the fish community as a whole, it is unfortunate that the alewife dynamics are so imprecisely defined. Further analysis may help to refine knowledge of mechanisms influencing dynamics to aid in model building.

### **Conclusions and Implications for Lake Michigan fisheries management**

In this discussion, I have only briefly touched on the major results. Many other questions were raised by the results reported here that have yet to be explored. There are many possibilities for influencing factors in alewife and bloater dynamics. Although this study did not provide conclusive evidence for any influencing factor, it does provide a detailed analysis of relative abundance at age with the associated variability for these two species. Isolating the major influencing factors of these populations could be attainable through further study with these results and would be extremely useful in the future Great Lakes management.

There are many possibilities for the use of the results in further interpretation of Lake Michigan fish community dynamics and research for better fisheries management. So far, there are plans to use the results to aid in the analysis of relative abundance trends for other species collected during the same survey, to construct an ecological understanding of the fish community structure and function, and to construct a salmonid stocking model similar to the SIMPLE model (Jones et al. 1993). Because the alewife and bloater have been pivotal species in the recent history of Lake Michigan, any new insights are relevant to fishery management procedures despite their relative unimportance as commercial or sport species. The results of this analysis will hopefully inspire other researchers to use them to aid in our understanding of the Lake Michigan ecosystem.

## APPENDIX

TABLE 1 - Depths sampled at each port

Port* Depth	Frankfort	Ludington	Saugatuck	Benton Harbor	Waukegan	Port Washington	Sturgeon Bay	Manistique
6	---	---	X	X	X	---	---	---
9	---	X	X	X	X	---	---	X
13	---	X	X	X	X	---	---	X
18	X	X	X	X	X	X	X	X
22	---	X	X	X	X	---	---	---
27	X	X	X	X	X	X	X	X
31	---	X	X	X	X	---	---	---
37	X	X	X	X	X	X	X	X
46	X	X	X	X	X	X	X	X
55	X	X	X	X	X	X	X	X
64	X	X	X	X	X	X	X	X
73	X	X	X	X	X	X	X	X
82	X	X	X	X	X	X	X	X
91	X	X	X	X	X	X	X	X
110	X	X	X	X	X	X	X	X
128	X	---	---	---	---	X	X	---

\* Note: The depths assigned to ports in this table does not indicate that the depths were sampled for the entire series of that port

TABLE 2 - ANOVA results used to fill in missing length frequency data

**ALEWIFE**

<b>SSR</b>	63733
<b>SSE</b>	240
<b>Probability</b>	0.0001
<b>R<sup>2</sup></b>	0.895

<b>FIXED EFFECT</b>	<b>MSE</b>	<b>PROB.</b>
	<b>TYPE III</b>	
PORT	2319	0.0001
DEPTH	12863	0.0001
LIFESTAGE	2589772	0.0001
PORT*DEPTH	223	0.6666

**BLOATER**

<b>SSR</b>	12904
<b>SSE</b>	387
<b>Probability</b>	0.0001
<b>R<sup>2</sup></b>	0.903

<b>FIXED EFFECT</b>	<b>MSE</b>	<b>PROB.</b>
	<b>TYPE III</b>	
YEAR	43124	0.0001
PORT	15741	0.0001
DEPTH	130204	0.0001
LIFESTAGE	1549572	0.0001
PORT*DEPTH	413	0.3259
YEAR*PORT	930	0.0001
YEAR*DEPTH	700	0.0001



TABLE 3 - Number of zero catches in the entire trawl series for each species' age

**ALEWIFE**

Age	# of zero catches (out of 2277)
0	636
1	545
2	466
3	471
4	514
5	576
6	713
7	1126
8	1811
9	2133

**BLOATER**

Age	# of zero catches (out of 2277)
0	1197
1	765
2	724
3	766
4	849
5	1012
6	1230
7	1527
8	1869
9	2219
10	2275

TABLE 4 - Example of model comparison used to select the best model

ALEWIFE Age 0		Akaike's			
Model*	Error structure	None	Y*P Random	AR(1) D by Y*P	SP(POW) D by Y*P
Y		-5762	-5711	-5013	-5092
P		-5864	-5766	-5053	-5132
Y + P		-5720	-5692	-5004	-5082
Y + P + D		-5200	-5105	-4815	-4879
Y + P + D + Y*D		-5260	-5154	-4897	-4962
Y + P + D + P*D		-5198	-5099	-4831	-4896
Y + P + D + Y*D + P*D		-5268	-5160	-4917	-4982
Y + P + D + D <sup>2</sup>		-5202	-5106	-4822	-4887
Y + P + D + D <sup>2</sup> + Y*D		-5267	-5160	-4906	-4971
Y + P + D + D <sup>2</sup> + P*D		-5204	-5106	-4839	-4904
Y + P + D + D <sup>2</sup> + Y*D + P*D		-5276	-5168	-4926	-4991
Y + P + D + D <sup>2</sup> + Y*D + P*D + Y*D <sup>2</sup> + P*D <sup>2</sup>		-5484	-5361	-5161	-5222
Y + P + D + D <sup>2</sup> + D <sup>3</sup>		-5193	-5091	-4814	-4880
Y + P + D + D <sup>2</sup> + D <sup>3</sup> + Y*D		-5256	-5143	-4897	-4963
Y + P + D + D <sup>2</sup> + D <sup>3</sup> + P*D		-5194	-5089	-4831	-4897
Y + P + D + D <sup>2</sup> + D <sup>3</sup> + Y*D + P*D		-5266	-5151	-4917	-4983
Y + P + D + D <sup>2</sup> + D <sup>3</sup> + Y*D + P*D + Y*D <sup>2</sup> + P*D <sup>2</sup>		-5463	-5330	-5146	-5208
Y + P + D + D <sup>2</sup> + D <sup>3</sup> + Y*D + P*D + Y*D <sup>2</sup> + P*D <sup>2</sup> + Y*D <sup>3</sup> + P*D <sup>3</sup>		-5821	-5678	-5513	-5573

\* Y = year class variable, P = port class variable, D = depth continuous variable

TABLE 5 - Variable significance in all best mixed models

<b>Alewife</b>					
<b>Age</b>	<b>Variable</b>	<b>Numerator DF</b>	<b>Denominator DF</b>	<b>F</b>	<b>Probability</b>
0	Y	33	163	3.46	0.0001
	P	7	163	9.31	0.0001
	FZ	1	2072	550.70	0.0001
1	Y	33	163	4.50	0.0001
	P	7	163	12.43	0.0001
	FZ	1	2071	220.29	0.0001
	FZ2	1	2071	196.72	0.0001
2	Y	33	163	5.76	0.0001
	P	7	163	10.66	0.0001
	FZ	1	2071	422.90	0.0001
	FZ2	1	2071	280.37	0.0001
3	Y	33	163	8.94	0.0001
	P	7	163	7.48	0.0001
	FZ	1	2071	476.23	0.0001
	FZ2	1	2071	260.49	0.0001
4	Y	33	163	11.82	0.0001
	P	7	163	5.67	0.0001
	FZ	1	2070	6.03	0.0141
	FZ2	1	2070	17.29	0.0001
	FZ3	1	2070	47.75	0.0001
5	Y	33	163	11.29	0.0001
	P	7	163	5.02	0.0001
	FZ	1	2070	1.03	0.3096
	FZ2	1	2070	32.28	0.0001
	FZ3	1	2070	67.44	0.0001
6	Y	33	163	9.62	0.0001
	P	7	163	4.52	0.0001
	FZ	1	2070	0.19	0.6631
	FZ2	1	2070	45.88	0.0001
	FZ3	1	2070	80.91	0.0001
7	Y	33	163	10.49	0.0001
	P	7	163	2.95	0.0061
	FZ	1	2070	6.15	0.0132
	FZ2	1	2070	49.72	0.0001
	FZ3	1	2070	68.71	0.0001
8	Y	33	163	14.49	0.0001
	P	7	163	1.09	0.3732
	FZ	1	2072	151.96	0.0001

TABLE 5 - (cont'd)

<b>Bloater</b>					
<b>Age</b>	<b>Variable</b>	<b>Numerator DF</b>	<b>Denominator DF</b>	<b>F</b>	<b>Probability</b>
0	Y	33	163	18.24	0.0001
	P	7	163	6.13	0.0001
	FZ	1	2070	118.37	0.0001
	FZ2	1	2070	180.03	0.0001
	FZ3	1	2070	164.27	0.0001
1	Y	33	163	33.70	0.0001
	P	7	163	21.22	0.0001
	FZ	1	2063	566.01	0.0001
	FZ2	1	2063	422.49	0.0001
	FZ3	1	2063	264.11	0.0001
2	FZ*P	7	2063	15.65	0.0001
	Y	33	163	26.75	0.0001
	P	7	163	21.33	0.0001
	FZ	1	2063	369.42	0.0001
	FZ2	1	2063	155.56	0.0001
3	FZ3	1	2063	48.38	0.0001
	FZ*P	7	2063	20.10	0.0001
	Y	33	163	23.82	0.0001
	P	7	163	17.62	0.0001
	FZ	1	2064	930.26	0.0001
4	FZ2	1	2064	823.13	0.0001
	FZ*P	7	2064	15.58	0.0001
	Y	33	163	21.91	0.0001
	P	7	163	12.76	0.0001
	FZ	1	2064	773.68	0.0001
5	FZ2	1	2064	648.05	0.0001
	FZ*P	7	2064	12.40	0.0001
	Y	33	163	19.59	0.0001
	P	7	163	1.24	0.2834
	FZ	1	2071	525.41	0.0001
6	FZ2	1	2071	399.01	0.0001
	Y	33	163	21.57	0.0001
	P	7	163	1.41	0.2055
	FZ	1	2071	370.04	0.0001
	FZ2	1	2071	266.72	0.0001
7	Y	33	163	19.97	0.0001
	P	7	163	1.15	0.3336
	FZ	1	2071	208.25	0.0001
	FZ2	1	2071	142.37	0.0001
8	Y	33	163	19.40	0.0001
	P	7	163	4.39	0.0002
	FZ	1	2071	74.80	0.0001
	FZ2	1	2071	58.03	0.0001

TABLE 6 - Correlation structures for year 1962 at Saugatuck representing the sp(pow) rho range

**Alewife Age 7**

DEPTH	9	13	18	27	37	46	55	64	73	82
9	1	0.6792044	0.4187947	0.175389	0.0666812	0.0279257	0.0116952	0.0048979	0.0020512	0.000859
13		1	0.6165959	0.2582271	0.0981755	0.0411154	0.0172189	0.0072112	0.00302	0.0012648
18			1	0.4187947	0.1592218	0.0666812	0.0279257	0.0116952	0.0048979	0.0020512
27				1	0.3801905	0.1592218	0.0666812	0.0279257	0.0116952	0.0048979
37					1	0.4187947	0.175389	0.073452	0.0307613	0.0128827
46						1	0.4187947	0.175389	0.073452	0.0307613
55							1	0.4187947	0.175389	0.073452
64								1	0.4187947	0.175389
73									1	0.4187947
82										1

**Bloater Age 2**

DEPTH	9	13	18	27	37	46	55	64	73	82
9	1	0.7964712	0.5992839	0.3591412	0.2033248	0.1218493	0.0730223	0.0437611	0.0262253	0.0157164
13		1	0.7524239	0.4509155	0.2552821	0.1529865	0.0916823	0.0549437	0.0329269	0.0197326
18			1	0.5992839	0.3392796	0.2033248	0.1218493	0.0730223	0.0437611	0.0262253
27				1	0.5661417	0.3392796	0.2033248	0.1218493	0.0730223	0.0437611
37					1	0.5992839	0.3591412	0.2152276	0.1289824	0.0772971
46						1	0.5992839	0.3591412	0.2152276	0.1289824
55							1	0.5992839	0.3591412	0.2152276
64								1	0.5992839	0.3591412
73									1	0.5992839
82										1

TABLE 7 - Bloater unweighted mean lengths at age for all available years

AGE	0	1	2	3	4	5	6	7 +								
LENGTH*																
	MEAN	STD	MEAN	STD	MEAN	STD	MEAN	STD								
YEAR																
1965	-	-	198	7.9	206	6.9	221	10.3	240	11.5	263	11.3	274	21.3	-	
1967	-	-	-	-	211	10.6	228	11.1	246	11.7	261	9.9	275	9.4	286	18.5
1968	-	-	195	11.5	215	10.7	231	11.1	246	10.5	262	10.4	275	16.4	295	11.6
1969	-	-	165	19.5	209	15.9	231	10.3	250	10.3	264	13.3	283	16.4	293	14.3
1970	128	20.8	176	19.0	213	18.2	237	11.5	251	10.7	265	9.4	279	11.7	294	15.3
1971	151	3.5	171	17.4	215	19.5	238	18.0	255	11.8	266	10.1	278	16.0	301	20.4
1972	179	-	167	16.4	215	16.4	240	13.1	255	16.5	272	11.2	280	23.2	305	21.1
1973	-	-	180	16.5	215	13.1	244	15.0	262	14.7	275	13.3	291	13.9	311	13.9
1974	144	4.3	167	17.1	204	16.2	246	17.7	261	14.9	279	19.2	294	16.1	301	19.8
1975	118	23.3	164	18.4	211	19.9	241	17.4	258	16.8	279	18.1	279	16.1	328	28.5
1976	-	-	182	22.4	225	17.0	249	20.0	266	17.8	268	35.8	309	30.2	287	-
1977	-	-	173	26.7	223	21.1	255	16.7	269	23.7	293	17.6	289	15.6	314	40.3
1978	127	25.4	157	14.6	209	18.0	250	15.8	270	19.1	281	19.7	293	17.6	322	29.5
1979	126	6.3	158	14.4	204	17.6	230	22.5	269	19.2	295	23.4	293	23.2	344	37.3
1980	132	8.5	154	14.9	207	17.3	237	17.5	259	17.7	296	32.6	321	16.1	322	9.2
1981	129	8.3	154	15.9	199	16.8	235	16.4	255	17.2	283	28.3	333	57.6	325	23.8
1982	129	7.2	151	17.3	191	19.7	230	19.0	252	17.1	262	10.4	272	27.6	318	18.8
1983	130	11.5	149	16.0	186	17.4	223	21.2	252	24.5	264	13.0	279	6.4	266	37.5
1984	110	8.8	140	16.2	175	18.5	209	20.2	238	18.5	256	15.9	267	8.3	283	12.2
1985	117	6.1	137	13.9	170	17.7	206	19.4	232	18.8	255	17.3	267	13.1	257	-
1986	117	9.3	133	14.3	171	18.3	206	19.0	236	19.4	253	16.0	272	11.8	284	16.4
1987	-	-	135	15.5	172	17.8	206	18.8	234	18.1	252	16.4	263	13.9	292	39.3
1988	108	7.5	135	16.7	167	18.7	200	20.2	227	19.8	244	17.9	258	16.1	267	9.0
1989	106	5.9	138	16.5	170	18.9	202	21.1	234	22.1	249	20.4	266	15.6	274	16.8
1990	136	40.3	133	14.5	165	16.4	191	22.9	216	20.7	244	20.1	247	20.2	261	18.3
1991	97	6.2	127	13.4	164	13.9	193	19.1	221	18.4	237	13.9	252	22.3	269	11.6
1992	112	-	135	11.8	167	16.4	194	16.1	217	23.0	237	17.6	249	18.7	264	15.4
1993	-	-	134	12.4	165	18.9	192	19.4	210	24.4	233	21.7	250	17.5	264	22.5

\* STD is the standard deviation of length at age

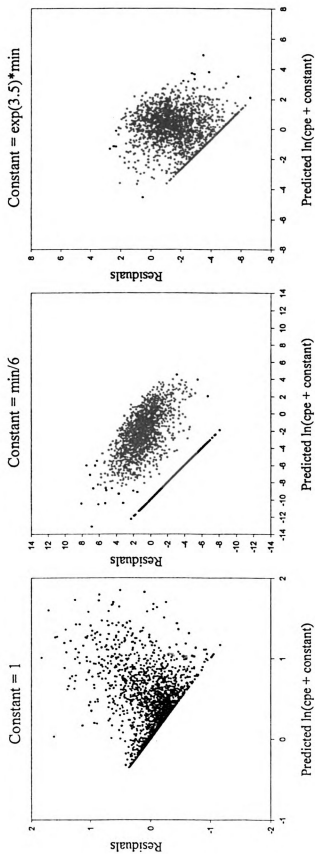


Figure 1 - Residual plots of age 5 alewife to show the effect of different constants

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