# Sculpin Community Dynamics in Lake Michigan

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**ABSTRACT.** *Two hypotheses have been proposed to explain the dynamics of sympatric populations of deepwater sculpin* (Myoxocephalus thompsonii) *and slimy sculpin* (Cottus cognatus). *The first hypothesis is that slimy sculpins negatively affect survival of deepwater sculpins, and therefore deepwater sculpins coexist with slimy sculpins only when a keystone predator, lake trout* (Salvelinus namaycush), *is abundant. According to the second hypothesis, changes in the abundances of the sculpins are driven by interactions with fishes other than sculpins. To evaluate both hypotheses, we applied regression analyses to long-term observations on abundances of both sculpin populations in Lake Michigan during 1973–2002. For slimy sculpin abundance, we considered the predation effect by lake trout and the effect of deepwater sculpins on slimy sculpins. For deepwater sculpin abundance, we considered the effect of alewife* (Alosa pseudoharengus) *on deepwater sculpins, the predation effect by burbot* (Lota lota), *and the effect of slimy sculpins on deepwater sculpins. An information criterion was used to select the best regression model explaining the temporal trends. The best model to explain trends in slimy sculpin abundance was the model that included the lake trout predation term only. The best model to explain trends in deepwater sculpin abundance was a model including the alewife and burbot predation terms. Thus, a negative effect of slimy sculpins on deepwater sculpins was not essential in capturing the sculpin community dynamics. Therefore, our results supported the second hypothesis. Further, our results supported the contention that control of the alewife population was a prerequisite for restoration of deepwater sculpin populations.*

*INDEX WORDS:   Deepwater sculpin, food web, predation, restoration, slimy sculpin, species invasions.*

## INTRODUCTION

Brandt (1986) proposed that the dynamics of deepwater sculpin (*Myoxocephalus thompsonii*) and slimy sculpin (*Cottus cognatus*) populations in the Laurentian Great Lakes were regulated by the presence of a keystone predator, lake trout (*Salvelinus namaycush*). The basic premise for his hypothesis was that slimy sculpins, through competition with or predation on juvenile deepwater sculpins, exerted a negative effect on the survival of deepwater sculpins. Therefore, deepwater sculpin and slimy sculpin populations would coexist only when the abundance of lake trout was sufficiently high.

When abundance of lake trout remained too low for a sufficient amount of time, deepwater sculpin would be extirpated. To support his hypothesis, Brandt (1986) presented data showing habitat overlap between slimy and deepwater sculpin in Lake Michigan. Citing other studies, he also documented that the diets of the two sculpin species were similar, and that slimy sculpin is the preferred food of juvenile lake trout. Finally, he argued that deepwater sculpin was extirpated from Lake Ontario during the 1950s because lake trout had been absent from the lake for too long a period of time.

Others have argued that the dynamics of deepwater and slimy sculpins in the Laurentian Great Lakes were driven by interactions with non-sculpin

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fishes (Smith 1970, Wells and McLain 1973, Madenjian *et al.* 2002). The decline in deepwater sculpin abundance in Lake Michigan in the 1960s, as well as the disappearance of deepwater sculpin from Lake Ontario, have been attributed to the alewife (*Alosa pseudoharengus*), an invader from the Atlantic Ocean, interfering with natural reproduction by feeding upon the pelagic fry of deepwater sculpin (Smith 1970, Wells and McLain 1973). Further, the recovery of the deepwater sculpin population in Lake Michigan during the 1970s coincided with a decline in alewife abundance (Eck and Wells 1987). In addition, the decline in deepwater sculpin abundance in Lake Michigan between 1983 and 1990 has been attributed to predation by burbot (*Lota lota*), which showed a remarkable population recovery during 1983–1990 (Madenjian *et al.* 2002). Burbot is a native predator, and deepwater sculpin represents a significant portion of the diet of burbot in Lake Michigan (Fratt *et al.* 1997). Finally, declines in the abundance of slimy sculpin in Lake Michigan during 1973–1984 and in Lake Ontario during 1980–1987 have been attributed to increases in predation by juvenile lake trout (Eck and Wells 1987, Owens and Bergstedt 1994); and the increase in slimy sculpin abundance in Lake Michigan during 1985–1999 has been attributed to a concomitant decrease in predation by juvenile lake trout (Madenjian *et al.* 2002).

The availability of a long-term series of observations on the fish community in Lake Michigan should prove useful in assessing the importance of various species interactions on sculpin (family Cottidae) community dynamics. Just as analyses of long-term series for alewife abundances in Lakes Ontario and Michigan have been used to identify important factors determining alewife recruitment in the Laurentian Great Lakes (O'Gorman *et al.* 2004, Madenjian *et al.* 2005), so too an analysis of the long-term series of observations of sculpin abundances in Lake Michigan should reveal important determinants of sculpin community dynamics.

The objective of this study was to determine which of these two hypotheses for sculpin community dynamics was better supported by the long-term series of observations on sculpin abundances. Our approach was to apply regression techniques to long-term series of observations on the abundances of slimy and deepwater sculpins in Lake Michigan during 1973–2002. We developed a suite of regression models, considering the factors mentioned above, for both the slimy and deepwater sculpin time series, and we chose the models which best explained the temporal trends in abundance. Additionally, management implications from the findings were also discussed. As pointed out by Eshenroder and Krueger (2002), efforts for restoring native fish populations may be hindered by not knowing the causes for extirpation. Thus, results from our regression analysis may be applicable toward restoring deepwater sculpin populations to lakes where they have been extirpated or their abundance is very low.

## METHODS

### Field Surveys

The Great Lakes Science Center (GLSC) has annually sampled the prey fish community of Lake Michigan in the fall using bottom trawls at standard locations since 1973 (Madenjian *et al.* 2003). Seven transects (Frankfort [Michigan], Ludington [Michigan], Saugatuck [Michigan], Waukegan [Illinois], Port Washington [Wisconsin], Sturgeon Bay [Wisconsin], and Manistique [Michigan]) have been regularly sampled. Tow depths ranged from 9 to 110 m, in 9-m depth increments, within a transect. A bottom trawl (12-m headrope) was dragged on contour for 10 min at each sampling depth (Hatch *et al.* 1981), and towing speed averaged 3.4 km/hr (Fleischer *et al.* 2000). Fish caught in the bottom trawl were sorted by species, counted, and weighed in aggregate. When total catch was large (exceeding about 20 kg), a random sample of roughly 10–15 kg was sorted, counted, and weighed; the remainder of the catch was weighed and composition was estimated by direct proportion. During the past 30 years, the sculpin community in Lake Michigan has been dominated by two native species: the slimy sculpin and the deepwater sculpin (Wells and McLain 1973, Kraft and Kitchell 1986, Fleischer *et al.* 2000).

### Construction of Time Series

For each year, lakewide biomass estimates of slimy sculpin, deepwater sculpin, and burbot were generated based on swept-area calculations, using the algorithm outlined in Argyle *et al.* (1998) and Fleischer *et al.* (2000). Lakewide biomass estimates were expressed in kilotonnes (kt; 1 kt = 1,000 metric tons). Because predation on deepwater sculpin fry was likely limited to adult alewives (Krueger *et al.* 1995, Mason and Brandt 1996), we used the alewife spawner time series generated by Madenjian *et al.* (2005) to model the effect of alewives on

deepwater sculpins; this series consisted of annual lakewide biomass estimates of alewives ≥ 150 mm in total length derived from the bottom trawl survey.

Due to problems with trawl deployment in 1998, data from that year were not included in our analyses. Mechanical failures aboard the research vessel during the 2000 survey limited us to sampling only three of the seven transects, so the 2000 data were also not included in our analyses.

### Data Analysis

Our approach for analysis of the lakewide biomass time series for slimy sculpin and deepwater sculpin was to apply a set of regression models to each time series. The set of models considered for each time series corresponded with the two abovementioned hypotheses for sculpin community dynamics in the Great Lakes. For slimy sculpin biomass, we considered the predation effect by juvenile lake trout (LTPRED) and the interaction effect between slimy and deepwater sculpins (SCULPIN). For deepwater sculpin biomass, we considered the effect of alewives on the deepwater sculpin population (ALEWIFE), the predation effect by burbot (BRPRED), and the interaction effect between slimy and deepwater sculpins (SCULPIN). We fitted regression models to the slimy sculpin biomass time series for all four possible combinations of the two effects LTPRED and SCULPIN. Similarly, we fitted regression models to the deepwater sculpin biomass time series for all eight possible combinations of the three effects ALEWIFE, BRPRED, and SCULPIN. For both the set of models applied to the slimy sculpin time series and the set of models applied to the deepwater sculpin time series, we selected the model with the lowest Akaike's Information Criterion (AIC), an index that balances goodness of fit with model complexity (Akaike 1969, Burnham and Anderson 2002), as the best model. In addition to comparing AIC across the suite of regression model applications, we also tested for the significance of each of the effects by determining whether its regression coefficient was significantly different from zero. To determine whether autocorrelation had an effect on our testing for significance of the regression coefficients, we applied intervention analysis and transfer function modeling techniques when necessary (Box and Tiao 1975, Box and Jenkins 1976). We set $\alpha = 0.05$ for all statistical testing.

We modeled the LTPRED effect by assuming a linear decrease in slimy sculpin biomass during 1973–1985 followed by a linear increase in slimy sculpin biomass during 1986–2002. Other studies have shown that a linear decrease in slimy sculpin abundance accompanies the stocking of lake trout (Eck and Wells 1987, Owens and Bergstedt 1994). Slimy sculpin is an important constituent of the diet of lake trout during their first 2 years of life in Lake Michigan, however the importance of slimy sculpin decreases rapidly for lake trout ages beyond 3 (Eck and Wells 1983, Stewart *et al.* 1983, Madenjian *et al.* 1998). During 1965–1985, about 2.0 million lake trout yearlings were stocked in the nearshore zone of Lake Michigan each year during 1973–1985, whereas only 0.2 million lake trout yearlings were annually stocked on offshore reefs over the same time period (GLFC 2002). In contrast, about 1.1 million yearlings were annually stocked in the nearshore zone and about 1.1 million yearlings were annually stocked on the offshore reefs during 1986–2002 (GLFC 2002). This shift in stocking policy precipitated a decrease in the nearshore abundance of juvenile (< 400 mm total length) lake trout in Lake Michigan, as measured by the GLSC bottom trawl survey, between the 1973–1985 and 1986–2002 time periods (CPM, unpublished data). It follows that we expected slimy sculpin abundance, as measured by our bottom trawls, to increase during 1986–2002 in response to the change in the lake trout stocking regime. However, a simple linear correlation of slimy sculpin biomass with juvenile lake trout biomass would not accurately depict the predator-prey dynamics between these two populations, because: (1) the practice of stocking precluded the lake trout population from responding numerically to fluctuations in prey abundance, and (2) slimy sculpin abundance appeared to respond slowly to changes in the abundance of stocked lake trout (Eck and Wells 1987, Owens *et al.* 2003). Therefore, to account for the change in lake trout stocking practices, we modeled the effect of lake trout predation on slimy sculpin abundance using change-point regression analysis (Draper and Smith 1981), assuming a linear decrease in slimy sculpin abundance during 1973–1985 and a linear increase in abundance during 1986–2002.

To model the effect of deepwater sculpin abundance on slimy sculpin abundance, we assumed a negatively linear response. In other words, if slimy sculpin and deepwater sculpins were competing for resources, an increase in the abundance of one

species should precipitate a decrease in the abundance of the other species.

The full regression model for slimy sculpin lakewide biomass was

$$SLIMY = \alpha_1 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 DEEP \quad (1)$$

where SLIMY = slimy sculpin biomass (kt), $X_1$ = year-1972 for years 1973–1985, $X_1 = 0$ for years 1986–2002, $X_2 = 0$ for years 1973–1985, $X_2 = 1$ for years 1986–2002, $X_3 = 0$ for years 1973–1985, $X_3$ = year-1985 for years 1986–2002, DEEP = deepwater sculpin biomass (kt), and $\alpha_1$, $\beta_1$, $\beta_2$, $\beta_3$, and $\beta_4$ are regression coefficients. The LTPRED effect was represented by the second, third, and fourth terms on the right-hand side of Eq. 1. The SCULPIN effect was represented by the fifth term on the right-hand side of Eq. 1.

To model the effect of alewives on deepwater sculpins, we assumed a negatively linear response. As mentioned above, alewives are suspected of preying upon the fry of deepwater sculpins, and the decline in alewife abundance in Lake Michigan began in the late 1960s and continued through the early 1980s (Madenjian *et al.* 2002, 2005). Therefore, we would expect an increase in deepwater sculpin abundance with decreasing abundance of alewife spawners. In our initial analysis, we did not consider a time lag between alewife predation on deepwater sculpin fry and a decline in deepwater sculpin biomass fished by the bottom trawl in the fall because age-0 deepwater sculpins are susceptible to the bottom trawl in the fall (Geffen and Nash 1992).

To model the effect of burbot predation on deepwater sculpin abundance, we assumed that the predation effect was zero during 1973–1986, but was at full strength during 1987–2002. Thus, the burbot predation variable was assigned a value of zero for each year during 1973–1986, and a value of one for each year during 1987–2002. According to the bottom trawl survey, burbot biomass was practically negligible during 1973–1983, but then rose rapidly between 1983 and 1987. By 1987, burbot biomass was more than 50% of the mean annual value for burbot biomass during the 1990–2002. Based on examination of burbot stomach contents during 1986–1988 and in 1994, deepwater sculpin was an important diet constituent of Lake Michigan burbot diet (Fratt *et al.* 1997, Madenjian *et al.* 2002). However, year-to-year variability in burbot diet composition and burbot growth rate has not been continuously tracked. Thus, bioenergetics modeling

could not be accurately applied to the burbot population to determine annual consumption of deepwater sculpins by burbot during 1984–2002.

To model the effect of slimy sculpins on deepwater sculpin abundance, we again assumed a negatively linear response.

The full regression model for deepwater sculpin lakewide biomass was

$$DEEP = \alpha_2 + \beta_5 ALEWIFE + \beta_6 X_6 + \beta_7 SLIMY \quad (2)$$

where DEEP = deepwater sculpin biomass (kt), ALEWIFE = alewife spawner biomass (kt), $X_6 = 0$ for years 1973–1986, $X_6 = 1$ for years 1987–2002, SLIMY = slimy sculpin biomass (kt), and $\alpha_2$, $\beta_5$, $\beta_6$, and $\beta_7$ are regression coefficients. The ALEWIFE effect was represented by the second term on the right-hand side of Eq. 2. The BRPRED and SCULPIN effects were represented by the third and fourth terms, respectively, on the right-hand side of Eq. 2.

Burbot predation on slimy sculpins was not entertained as a potential factor affecting slimy sculpin abundance because slimy sculpin abundance increased substantially during the 1990s while burbot abundance was relatively high (Madenjian *et al.* 2002). Lake trout predation on deepwater sculpins was not entertained as a potential factor affecting deepwater sculpin abundance because the deepwater sculpin population in Lake Michigan exhibited a strong recovery during 1970s, when lake trout abundance was high compared with lake trout abundance during the 1960s (Eck and Wells 1987, Madenjian *et al.* 2002).

Under the Brandt (1986) hypothesis, we would expect the following results from the regression analysis: (1) the best regression model for the slimy sculpin series includes both the LTPRED and SCULPIN effects, (2) testing for the significance of the regression coefficients corresponding to these two effects indicates that both effects exert a significantly negative influence on slimy sculpin abundance, (3) the best regression model for the deepwater sculpin series includes only the SCULPIN effect, and (4) testing for the significance of the regression coefficient corresponding to the SCULPIN effect indicates that this effect exerts a significantly negative influence on deepwater sculpin abundance. Under the hypothesis that sculpin community dynamics have been driven by interactions with non-sculpin fishes, we would expect the following results from the regression analysis: (1) the best regression model for the slimy

sculpin series includes only the LTPRED effect, (2) testing for the significance of the regression coefficients corresponding to the LTPRED effect indicates that this effect exerts a significantly negative influence on slimy sculpin abundance, (3) the best regression model for the deepwater sculpin series includes only the ALEWIFE and BRPRED effects, and (4) testing for the significance of the regression coefficient corresponding to these two effects indicates that these effects exert a significantly negative influence on deepwater sculpin abundance. We also acknowledge that other outcomes from the regression analysis are possible. For example, both significantly negative effects by non-sculpin fishes and a significantly negative interaction between sculpin species may be detected. In this case, the regression analysis results would support the hypothesis that sculpin community dynamics are influenced by both interactions with non-sculpin fishes and a negative interaction between the two sculpin species.

To determine whether the results of our analysis for trends in deepwater sculpin abundance were robust to our assumption of a zero burbot predation effect during 1973–1986 followed by a full predation effect during 1987–2002, we repeated the analysis assuming that the effect of burbot predation on deepwater sculpin abundance was directly proportional to burbot biomass. In other words, the full regression model for deepwater sculpin abundance in this new analysis was the same as that shown in Eq. 2, except that $X_6$ was no longer a 0,1 variable but instead was equal to the lakewide biomass estimate for burbot.

To determine whether the results of our analysis for trends in deepwater sculpin abundance were robust to the use of lagged responses of deepwater sculpin abundance to alewife and slimy sculpin effects, we lagged both alewife and slimy sculpin abundances 1, 2, and 3 years behind deepwater sculpin abundances, and developed regression models including these lagged effects. If deepwater sculpins are similar to other prey fishes in Lake Michigan with regard to gear vulnerability, then they should be fully recruited to the bottom trawl by age 3 (TeWinkel *et al.* 2002, Madenjian *et al.* 2005); thus, we considered lags up to 3 years. Considering the eight possible forms of regression models for deepwater sculpin lakewide biomass, but now entertaining three possibilities (one possibility for each of the three lags) for ALEWIFE and SCULPIN effects, yielded a total of 32 different regression models. We fitted all 32 regression models to the deepwater sculpin lakewide biomass time se-

ries, and then selected the best model based on AIC.

## RESULTS

Slimy sculpin biomass showed a decreasing trend during 1973–1985 and an increasing trend during 1986–2002 (Fig. 1). Deepwater sculpin biomass increased rapidly during 1973–1983 (Fig. 1), concomitant with a marked decrease in alewife spawner biomass (Fig. 2). Biomass of deepwater sculpins decreased substantially during 1983–1990 (Fig. 1), concomitant with the burbot population recovery in Lake Michigan (Fig. 2). Deepwater sculpin biomass increased slightly during 1990–1997, but then leveled off during 1997–2002 (Fig. 1). Alewife spawner biomass leveled off during 1982–2002 (Fig. 2).
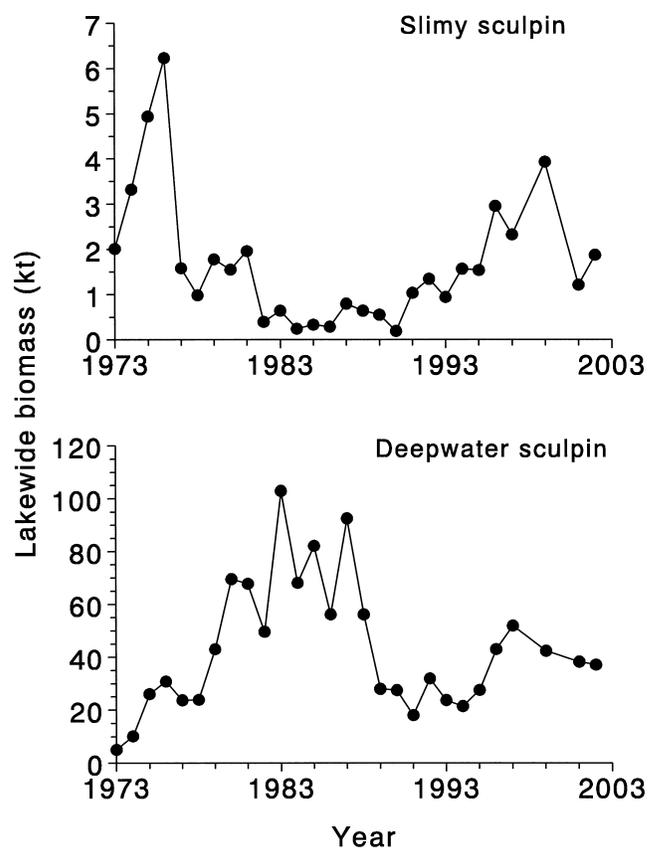


**FIG. 1.** *Estimated lakewide biomass of slimy (top graph) and deepwater (bottom graph) sculpins in Lake Michigan, 1973–2002. Estimates based on annual bottom trawl surveys conducted by the Great Lakes Science Center (GLSC) each fall. See Methods for more details.*
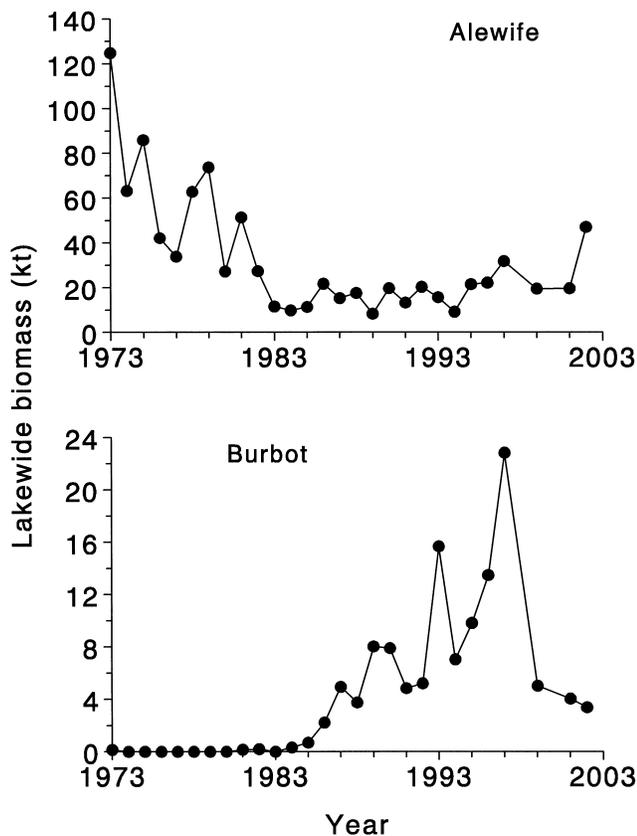
**FIG. 2.   *Estimated lakewide biomass of spawner (≥ 150 mm total length) alewife (top graph) and burbot (bottom graph) in Lake Michigan, 1973–2002. Estimates based on annual bottom trawl surveys conducted by the Great Lakes Science Center (GLSC) each fall. See Methods for more details.***

The best regression model to explain the temporal trends in slimy sculpin biomass in Lake Michigan during 1973–2002 was the model that included just the LTPRED effect (Table 1). This model explained 50% of the variation in slimy sculpin lakewide biomass. All of the regression coefficients from the best model fit were significantly different from zero ($\alpha_1$: $t = 6.63$, $df = 24$, $P < 0.0001$; $\beta_1$: $t = -3.99$, $df = 24$, $P = 0.0005$; $\beta_2$: $t = -4.72$, $df = 24$, $P < 0.0001$; $\beta_3$: $t = 2.43$, $df = 24$, $P = 0.0227$), indicating that lake trout predation had a significant effect on slimy sculpin biomass in Lake Michigan. A significant effect of deepwater sculpin abundance on slimy sculpin abundance was not apparent from our analyses (Table 1).

The best regression model to explain the temporal trends in deepwater sculpin biomass in Lake

Michigan during 1973–2002 was the model that included the ALEWIFE and BRPRED effects only (Table 2). This model accounted for 36% of the variation in deepwater sculpin lakewide biomass. All of the regression coefficients from the best model fit were significantly different from zero ($\alpha_2$: $t = 8.04$, $df = 25$, $P < 0.0001$; $\beta_5$: $t = -3.61$, $df = 25$, $P = 0.0013$; $\beta_6$: $t = -2.73$, $df = 25$, $P = 0.0115$), indicating that alewives and burbot predation were having significant effects on deepwater sculpin biomass in Lake Michigan. No significant effects of slimy sculpin abundance on deepwater sculpin abundance were detected (Table 2).

Of the 12 regression models applied to the time series, 10 of the model applications yielded residuals with significant autocorrelation. However, results from the intervention analysis and transfer function modeling revealed that this autocorrelation did not affect the outcomes of the hypothesis testing for significance of the regression coefficients. In other words, when the autocorrelation was taken into account by applying the Box-Jenkins time series techniques, the outcomes of the statistical testing for significance of the regression coefficients were identical to the outcomes reported in Tables 1 and 2, where autocorrelation was not taken into account.

Results from our alternative analysis of trends in deepwater sculpin abundance were similar to the results from the original analysis displayed in Table 2. For this alternative analysis assuming that the burbot predation effect was directly proportional to lakewide burbot biomass, the best model remained the model including the ALEWIFE and BRPRED effects only.

Lagging the effects of alewives and slimy sculpins on deepwater sculpin lakewide biomass yielded results similar to the original analysis in that both approaches led to a best model including ALEWIFE and BRPRED effects only. Of the 32 regression models applied to the deepwater sculpin biomass series, the best model was the one including ALEWIFE (with a lag of 3 years) and BRPRED effects only, according to AIC. Our original analysis, which did not consider lagged effects, indicated that deepwater sculpin lakewide biomass was best explained by ALEWIFE and BRPRED effects only (Table 2).

## DISCUSSION

Our results supported the hypothesis that sculpin community dynamics in Lake Michigan during

**TABLE 1.** **Results from fitting regression models (see Eq. 1) to assess the effects of deepwater sculpin (SCULPIN) and lake trout predation (LTPRED) on slimy sculpin lakewide biomass in Lake Michigan, 1973–2002. Results from the null model (no effects) application are included.**

| Rank | List of effects | Values of regression coefficients | | | | | Error sum of squares | AIC |
|---|---|---|---|---|---|---|---|---|
| | | $\alpha_1$ | $\beta_1$ | $\beta_2$ | $\beta_3$ | $\beta_4$ | | |
| 1 | LTPRED | 4.26* | −0.32* | −4.03* | 0.14* | | 28.67 | 103.70 |
| 2 | LTPRED, SCULPIN | 4.29* | −0.45* | −4.95* | 0.16* | 0.02 | 26.45 | 104.43 |
| 3 | SCULPIN | 2.51* | | | | −0.02 | 51.17 | 114.67 |
| 4 | | 1.69* | | | | | 57.15 | 115.43 |

*Note*: $\beta_1$, $\beta_2$, and $\beta_3$ correspond to the LTPRED effect (see Eq. 1).
  $\beta_4$ corresponds to the SCULPIN effect (see Eq. 1).
  * denotes a regression coefficient significantly differently from zero ($P < 0.05$).
  AIC = Akaike's Information Criterion.


**TABLE 2.** **Results from fitting regression models (see Eq. 2) to assess the effects of slimy sculpin (SCULPIN), alewife (ALEWIFE), and burbot (BRPRED) on deepwater sculpin lakewide biomass in Lake Michigan, 1973–2002. Results from the null model (no effects) application are included.**

| Rank | List of effects | Values of regression coefficients | | | | Error sum of squares | AIC |
|---|---|---|---|---|---|---|---|
| | | $\alpha_2$ | $\beta_5$ | $\beta_6$ | $\beta_7$ | | |
| 1 | ALEWIFE, BRPRED | 74.11* | −0.58* | −23.79* | | 10,193 | 265.42 |
| 2 | ALEWIFE, BRPRED, SCULPIN | 75.62* | −0.53* | −23.17* | −2.16 | 9,978 | 267.57 |
| 3 | ALEWIFE | 55.14* | −0.37* | | | 13,223 | 270.19 |
| 4 | ALEWIFE, SCULPIN | 57.85* | −0.30 | | −2.93 | 12,825 | 271.86 |
| 5 | SCULPIN | 51.99* | | | −5.41 | 14,342 | 272.47 |
| 6 | | 42.87* | | | | 16,017 | 273.23 |
| 7 | BRPRED, SCULPIN | 58.23* | | −10.78 | −5.92 | 13,544 | 273.38 |
| 8 | BRPRED | 47.13* | | −8.52 | | 15,509 | 274.66 |

*Note*: $\beta_5$ corresponds to the ALEWIFE effect (see Eq. 2).
  $\beta_6$ corresponds to the BRPRED effect (see Eq. 2).
  $\beta_7$ corresponds to the SCULPIN effect (see Eq. 2).
  * denotes a regression coefficient significantly different from zero ($P < 0.05$).
  AIC = Akaike's Information Criterion.


1973–2002 was driven by interactions with non-sculpin fishes. The best regression models for slimy and deepwater sculpin biomass included effects from non-sculpin fishes, including lake trout, alewife, and burbot, but did not include effects of negative interactions between sculpin species. Moreover, according to the results presented in Tables 1 and 2, the effects of non-sculpin fishes were significant in the best regression models, whereas our analyses failed to detect any significant interactions between the two sculpin populations.

We conclude that the recovery of the deepwater sculpin population in Lake Michigan was most likely due to the decline in alewife abundance during the 1970s and early 1980s. Because the buildup of salmonine biomass was primarily responsible for this decline in alewife abundance (Madenjian *et al.*

2002, 2005), recovery of the deepwater sculpin population in Lake Michigan can be viewed as a benefit of the salmonine stocking program initiated in 1965. Our results also suggested that the disappearance of deepwater sculpin from Lake Ontario during the 1950s was most likely caused by alewives interfering with deepwater sculpin reproduction. Alewives invaded Lake Ontario during the 1860s (Christie 1973), whereas alewives did not invade Lake Michigan until the 1940s (Wells and McLain 1973). Further, density of alewives has been substantially higher in Lake Ontario than in Lake Michigan (Madenjian *et al.* 2003). Wells and McLain (1973) observed a pronounced decline in deepwater sculpin abundance in southeastern Lake Michigan during the 1960s. Perhaps the duration and intensity of the occupation of Lake Ontario by

alewives was sufficiently strong to result in extirpation of deepwater sculpins from the lake, but not strong enough in Lake Michigan to cause extirpation. Alewife abundance in Lake Michigan peaked in 1966 (Brown 1972), and then declined during the 1970s and early 1980s. Recovery of the deepwater sculpin population in the 1970s and early 1980s was correlated with the decline in alewife abundance, as documented by our study.

Our study provided evidence for a predator-prey link in the dynamics of the burbot and deepwater sculpin populations of Lake Michigan. The burbot population in Lake Michigan exhibited a strong recovery during 1983–1990, the very time period that deepwater sculpin biomass declined substantially. Burbot abundance leveled off during the 1990s, as did deepwater sculpin abundance. Importance of deepwater sculpin in burbot diet increased with increasing lake depth (Van Oosten and Deason 1938, Fratt *et al.* 1997). Burbot inhabit waters of the Lake Superior at depths ranging as shallow as 5 m to as deep as 300 m (Selgeby and Hoff 1996). Deepwater sculpins have been found as deep as 250 m in Lake Michigan, but the bulk of the population is believed to occur in waters between 75 and 130 m deep (Wells 1968). During spring, summer, and fall months, deepwater sculpin is typically the most abundant prey fish available to the bottom trawl in Lake Michigan at depths greater than 80 m (Wells 1968). Based on the results of our analyses, the depth distributions of the two populations, and the diet composition data for burbot, the burbot population could be exerting top-down control of the deepwater sculpin population in Lake Michigan.

Although the degree of diet overlap between the slimy and deepwater sculpins in Lake Michigan has been documented as being very high, our analyses of the long-term time series for sculpin abundances revealed no significantly negative interactions between the two sculpin populations. Based on examination of stomach contents of slimy and deepwater sculpins from Lake Michigan during spring, summer, and fall 1994–1995, Davis *et al.* (1997) reported a diet overlap index of 73% between the two species. Both species relied heavily on the amphipod *Diporeia* in their diets, although the opossum shrimp *Mysis* was also an important diet constituent. Martin (1984) proposed that a diet overlap index exceeding 60% suggested a potential for competition between two species. Therefore, based on the Davis *et al.* (1997) study, competition for food may have been suspected of occurring between slimy and deepwater sculpins in Lake Michi-

gan. Perhaps competitive interactions are reduced by a modest degree of spatial segregation between the two populations. Although the two populations showed a substantial amount of overlap in their spatial distributions within Lake Michigan, the mean depth of capture for deepwater sculpins was about 18 m greater than the mean depth of capture for slimy sculpins (CPM, unpublished data). Additionally, diet data for sculpins from the southeastern waters of Lake Michigan during 2000–2001 has shown that, during some years, *Mysis* may be the predominant food of deepwater sculpins, while *Diporeia* remains the predominant food of slimy sculpins; the diet overlap index was only 51% during this time period (Hondorp *et al.* 2005; DWH, unpublished data). Perhaps diet overlap between the two species does not remain consistently strong over very long periods of time.

## Management Implications

Our results indicated that control of alewife abundance is a prerequisite for restoration of the deepwater sculpin population. Therefore, our study has important management implications for the proposed reintroduction of deepwater sculpin into Lake Erie and Lake Ontario. The inability to identify the causes of extirpation renders the task of restoration problematic (Eshenroder and Krueger 2002). Further, reintroduction efforts could be wasted if the same causes of extirpation are still present in the lake. Results from our study indicated that alewife abundance would have to be at a sufficiently low level for reintroduction of deepwater sculpin to be successful. If attempts to reintroduce deepwater sculpin into Lake Ontario, for example, were to continue to fail, the suspected leading cause for the failure would be too high levels of alewife abundance, in light of our study results. Alewife abundance can be lowered by increasing the lakewide biomass of salmonines (Madenjian *et al.* 2002, 2005). Thus, one management option that may prove effective in successfully re-establishing the deepwater sculpin population in Lake Ontario could be to increase the stocking rate of salmonines.

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