Depth segregation of deepwater ciscoes (*Coregonus* spp.) in Lake Michigan during 1930–1932 and range expansion of *Coregonus hoyi* into deeper waters after the 1990s

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with 5 figures and 5 tables

Abstract: The deepwater cisco (*Coregonus* spp.) assemblage in Lake Michigan was among the most diverse in the Laurentian Great Lakes. During the 1930s, seven species were identified, but by the early 1970s, six species were extirpated, primarily due to overfishing, leaving only one species (*C. hoyi*). To quantify the degree of depth segregation that occurred within this assemblage, we applied generalized additive models (GAM) to gillnet data collected in 1930–1932 from the R/V *Fulmar*. Our results generally supported findings published earlier. *C. hoyi* and *C. reighardi* typically exhibited peak catch-per-unit-effort (CPUE) in the shallowest depths (50–68 m) and *C. kiyi* and *C. nigripinnis* always exhibited peak CPUE in the deepest depths (127–150 m). The peak CPUEs for *C. alpenae* and *C. zenithicus*, species described previously as occupying waters of "intermediate" depth, occurred at intermediate depths (88–94 m) in the northern region and at shallow depths (50 m) in the southern region. The nearly complete overlap in their depth distributions was consistent with a prior hypothesis that *C. alpenae* was synonymous with *C. zenithicus*. The depth of peak CPUE of *C. johannae*, previously described as inhabiting intermediate depths, was highly variable, ranging from very shallow (50 m) to very deep (150 m), depending on region and season. We found no clear evidence that deepwater ciscoes changed depths for spawning. We found little evidence that deepwater cisco species collected in gillnets during 1930–1932 were distributed by depth as a function of fish size. *C. hoyi* collected by bottom trawl from 1974 to 2007 exhibited a positive relationship between depth and fish size. When we applied a GAM to the 1974–2007 trawl data, we found that *C. hoyi* shifted to markedly deeper waters from 1988–1991 to 2004–2007. Based on the ability of *C. hoyi* to shift to deeper depths, this species should occupy deeper waters in the lower Great Lakes (Erie, Ontario) should managers seek reintroduction of native deepwater ciscoes.

Keywords: niche partitioning, deepwater ciscoes, bloater, Lake Michigan.

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Introduction

The tremendous phenotypic diversity exhibited by ciscoes (*Coregonus* spp.) of the Laurentian Great Lakes in North America is suggestive of adaptive radiation into unique niches reminiscent of other better-known examples including the cichlids of Lake Victoria (MEYER et al. 1990) or the finches of the Galapagos Islands (GRANT & GRANT 2002). Although hybridization (i.e., reticulate evolution) and introgression (TURGEON et al. 1999; TURGEON & BERNATCHEZ 2003) in the post-glacial period (i.e., past 8,000 to 12,000 years) are currently believed to be a more likely mechanism than adaptive radiation, this phenotypic diversity is believed to have arisen independently in several North American Great Lakes from two *Coregonus artedi* progenitors (SMITH & TODD 1984; TURGEON et al. 1999; TURGEON & BERNATCHEZ 2003). Perhaps owing to this hybridization and introgression, genetic differentiation is generally not found among these named "species" (TODD & SMITH 1980; TODD 1981; REED et al. 1998; TURGEON & BERNATCHEZ 2001, 2003). Nonetheless, scientists continue to recommend that these unique and local morphotypes be managed as evolutionarily significant units in the same way that traditional phylogenetic species would be managed (TODD & SMITH 1980, 1992; PHILLIPS & EHLINGER 1995; TURGEON & BERNATCHEZ 2003). Herein we will use the term species with the caveat that geneticists have generally failed to recognize them as distinct species.

Deepwater ciscoes (*Coregonus hoyi, C. reighardi, C. alpenae, C. zenithicus, C. johannae, C. kiyi, C. nigripinnis*, see Table 1) were once present in all five of the Laurentian Great Lakes: one species in Lake Erie, three in Lake Superior, three in Lake Ontario, and at

Table 1. Summary of ecological and morphological data for seven deepwater cisco species (with common name in parentheses) from Lake Michigan. 95% confidence interval is in parentheses below the average value. Species are ordered from shallow to deepest, based on depth category.

	Relative Depth[1]	Total Length (mm)[2]	Gill raker count[3]	Spawning time[3]	Spawning Depth[3] (m)
C. hoyi (bloater)	Shallow	241.6 (240.7, 242.5)	42.6 (42.5, 42.7)	March	36–54
C. reighardi (shortnose cisco)	Shallow	274.3 (273.8, 274.8)	36.2 (36.0, 36.4)	May	<36
C. alpenae (long-jaw cisco)	Intermediate	304.2 (303.5, 305.1)	39.7 (39.4, 39.9)	November	18–46
C. zenithicus (short-jaw cisco)	Intermediate	295.4 (294.5, 296.3)	39.7 (39.4, 40.1)	November	"deeper than *C. alpenae*"
C. johannae (deepwater cisco)	Intermediate	296.1 (293.5, 298.6)	30.1 (29.7, 30.5)	Aug–Sept	110
C. kiyi (kiyi)	Deep	266.8 (265.0, 268.6)	38.5 (38.2, 38.7)	October	110
C. nigripinnis (blackfin cisco)	Deep	334.7 (328.6, 340.8)	47.6 (47.0, 48.3)	January	110

[1] MOFFETT (1957)
[2] 1930–1932 data
[3] KOELZ (1929)

least six in Lakes Michigan and Huron. One of the unique facets of the deepwater ciscoes is that they resulted from radiations into multiple morphotypes in four of these lakes, rather than the typical specialization into a pair of morphotypes (SCHLUTER 1996; TURGEON et al. 1999). As a result, a fundamental research question is how this morphological diversity was maintained. In his seminal work, KOELZ (1929) described how these species differed in gill raker count, head morphology (snout, jaw, and eye sizes), fin placement and size, and whole-body morphology (depth and length). He also noted how the species segregated into different depth strata within offshore waters (Table 1), a scheme later modified by MOFFETT (1957). Segregation by depth, at least partially, likely minimized competition, but when depth overlap occurred, diet overlap was presumably minimized through differences in gill raker number and in mouth and jaw morphology. KOELZ (1929), recognizing that maintenance of these species required reproductive isolation, described how each spawned in a unique combination of season and depth within each lake (see Table 1 for an example from Lake Michigan).

By the 1930s, the integrity of the deepwater cisco species flock in Lake Michigan was threatened because of overfishing, and the largest-sized species, *C. nigripinnis*, was rarely captured by commercial fishers (DEASON 1932). As a result, a large cooperative effort was undertaken from 1930 through 1932 by the U.S. Bureau of Fisheries and the states of Michigan and Wisconsin to determine the effect of different gillnet mesh sizes on the catch of deepwater ciscoes, collectively marketed as chubs. This study was the first to employ a dedicated research vessel (R/V *Fulmar*) on the Great Lakes, and provided scientific justification for managers to increase the minimum mesh-sizes for the gillnet fishery (VAN OOSTEN 1941). Unfortunately, the recommendations to increase mesh-sizes were largely ignored (SMITH 1964). Apart from its application to management, the fishery-independent data from this lake-wide survey provided us an opportunity to better quantify the niche separation of the ciscoes described by KOELZ (1929). The same data were used previously to summarize and describe the Lake Michigan deepwater cisco community (MOFFETT 1957; SMITH 1964), as well as to provide important species-specific synopses on their age and growth patterns and their bathymetric distributions (*C. reighardi*: JOBES 1943; *C. kiyi*: DEASON AND HILE 1947; *C. alpenae*: JOBES 1949a; *C. hoyi*: JOBES 1949b).

Unfortunately, the trajectory of reduced deepwater cisco abundance that had begun by the 1930s in Lake Michigan was not reversed. In Lake Michigan by 1969, *C. hoyi* dominated the deepwater cisco assemblage, with *C. reighardi* or *C. kiyi* being very rarely captured, and all other species extirpated (WELLS & MCLAIN 1973). Today, deepwater ciscoes have been extirpated from Lakes Erie and Ontario, and only one species (*C. hoyi*, common name "bloater") remains abundant in Lakes Michigan and Huron. The primary cause of the extirpations was overfishing, and the invasive sea lamprey (*Petromyzon marinus*) also played a secondary role (SMITH 1964). Only Lake Superior retains its full deepwater cisco assemblage. As a result of these losses, these unique species flocks can no longer be sampled to determine how niche segregation was maintained. The extraordinary 1930–1932 data set, however, can be revisited and modern statistical techniques can be employed to better quantify spatial segregation.

Our paper focuses on Lake Michigan (one of the most diverse deepwater cisco assemblages) and uses the 1930–1932 data, as well as the 1974–1977, 1988–1991, and 2004–2007 data derived from bottom trawling to address three focal research questions:

1) Does analysis of the 1930–1932 data support the hypothesis that spatial segregation by depth occurred among the deepwater cisco species in Lake Michigan? Are the species-specific relative-depth distributions described by Moffett (1957) supported by statistical analyses? Are species-specific depth distributions consistent across seasons, or if seasonal differences occurred, could they be linked to spawning? Are species-specific depth distributions consistent between the northern and southern regions of Lake Michigan? Previous authors (Todd et al. 1981; Smith and Todd 1984), using morphometric characters, suggested that *C. alpenae* was synonymous with *C. zenithicus*. Do the depth distributions of these two species support this synonymy?

2) Within each species, did larger individuals occupy deeper water than smaller individuals? Eshenroder and Burnham-Curtis (1999) reported this relationship for several planktivorous fishes (including *C. hoyi*) in Lake Michigan, based on data collected during the summer of 1987. Did this fish size versus depth relationship also occur during 1930–1932, 1974–1977, 1988–1991, or 2004–2007? Does separation of the data by sex and season (within a species) improve any fish size versus depth relationship?

3) Did *C. hoyi* in Lake Michigan, previously described as occurring in "shallow" water, shift to deeper waters following the extirpation of the other deepwater ciscoes? The answers to these questions will not only provide a better understanding of how this unique deepwater fish community was maintained, but also will provide useful information to fishery managers who recently have become interested in reintroducing deepwater ciscoes from lakes where they are extant to lakes where they were extirpated. The goal of such a reintroduction would be to re-establish native planktivorous fishes in deep waters. For example, *C. hoyi* from lakes Superior, Michigan, and Huron are being considered for reintroduction into Lake Ontario (Favé & Turgeon 2008). A finding that the *C. hoyi* population of Lake Michigan shifted to deeper water after 1930 should increase the confidence of Lake Ontario managers that reintroduced *C. hoyi* would occupy the deeper waters of Lake Ontario, where pelagic planktivorous fish are largely absent.

Methods

1930–1932 data

This data set consists of 222 gillnet sets and 41,126 records of individual deepwater ciscoes collected by the R/V *Fulmar* from around Lake Michigan. We grouped the data by port of departure, as did Ward et al. (2000) for their analysis of burbot and lake trout collected in the same gear. Unlike Ward et al. (2000), we divided the lake into northern and southern regions (Fig. 1). We chose this simpler spatial division rather than the 6-region subdivision of Ward et al. (2000) for two reasons. First, it follows a natural bathymetric division of the lake, with the northern region being considerably deeper than the southern basin. Second, two regions provided a more tractable number of interaction terms in our statistical analyses than would have occurred if we had used six regions (details below). Although the R/V *Fulmar* fished from three ports in Green Bay, we excluded these ports from our analysis because this bay is relatively shallow. The method of fishing employed by the R/V *Fulmar* was described by Deason (1932), Moffett (1957), and Ward et al. (2000) and will only be briefly summarized here. Multi-mesh (6.0, 6.4, 6.7, 7.0, 7.6 cm), linen gillnets were fished on the bottom during spring (April 15–June 30), summer (July 1–September 15), and autumn (September 16–November 30) of most years (autumn not fished in 1932). At each port, two multi-panel gillnet sets were generally completed at the same time:
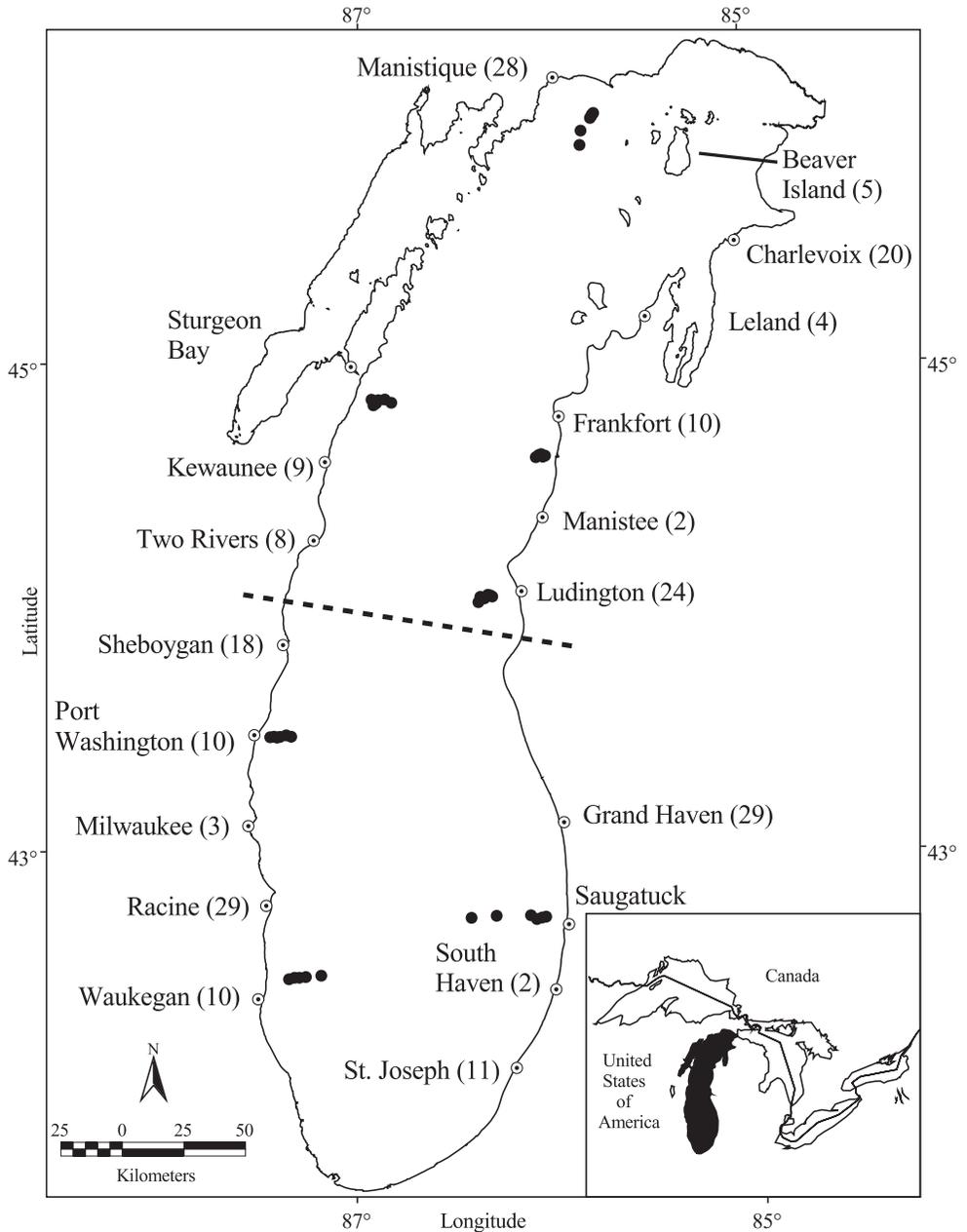
Fig. 1. Map of Lake Michigan showing the 17 ports used by the R/V *Fulmar* in their 1930–1932 gillnet survey (open circles, where number of gillnet sets follows in parentheses) and the seven ports (solid circles) used in the 1973–2007 bottom trawl survey (Manistique, Frankfort, Ludington, Saugatuck, Waukegan, Port Washington, Sturgeon Bay). The dashed line separates the northern and southern region used for these analyses.

one in "shallow" water (46–82 m) and another in "deep" water (110–183 m). We followed WARD et al. (2000) and calculated the mean depth of each gillnet set as the mean between the starting and ending depths of each set. The number of panels fished per gillnet set ranged from 3 to 22, and each panel was 155 m long and 1.5 m tall. Because the distribution of effort varied across years, we pooled all data rather than including a year effect in our model. For example, effort in 1932 was restricted to the northern basin and to spring and summer, and the 6.0- and 7.6-cm gillnet mesh sizes were not fished. The number of nights fished ranged from 5–15 nights (shorter and longer net sets were excluded because they were rare and were limited to only the summer of 1930 or the spring and summer of 1932). We calculated catch-per-unit-effort (CPUE) as the number of fish captured (for a given species) divided by the number of panels fished within that gillnet set.

1974–2007 data

We used data collected during the USGS Great Lakes Science Center annual bottom trawl survey to describe the bathymetric distribution of *C. hoyi*, the only extant deepwater cisco species in Lake Michigan. Details of this survey are described elsewhere (e.g., BUNNELL et al. 2006), but we provide a general summary below. The survey occurred in September or October at seven ports distributed around Lake Michigan (Fig. 1). As was done for the 1930–1932 data, we divided the lake into northern (4 ports) and southern (3 ports) regions. At each port, a 10-minute bottom-trawl (12 m headrope) tow was made at up to 11 different depth strata, ranging from 9 to 110 m at approximately 9 m increments. Using area swept for each tow, we calculated the annual numeric density (#/ha) of *C. hoyi* at each port and depth combination. Because smaller fish were rarely captured in the 1930–1932 gillnet survey, we restricted our density estimates to those fish >180 mm total length (TL).

Because *C. hoyi* demographics such as individual growth and condition are density dependent (BROWN et al. 1987; TEWINKEL et al. 2002; SZALAI et al. 2003), we modeled *C. hoyi* bathymetric distribution in autumn for three periods of contrasting density during 1974–2007 (see BUNNELL et al. 2006): 1974–1977 (low density), 1988–1991 (high density), and 2004–2007 (low density). The 1974–2007 data set was not ideal for making comparisons with the 1930–1932 data set because the depths sampled during 1974–2007 (9–110 m) were shallower than the mean depths of the gillnets set during 1930–1932 (45–156 m). Nonetheless, within the 9–110 m range, we made comparisons of predicted depth for *C. hoyi* during 1930–1932 with predicted depth during 1974–1977, 1988–1991, and 2004–2007.

Statistical analyses

We used a generalized additive model (GAM) approach (WOOD 2004; R DEVELOPMENT CORE TEAM 2007) to determine how CPUE of deepwater cisco species in 1930–1932 varied as a function of depth, region, the number of nights fished, and season. We used a GAM rather than a generalized linear model to accommodate the non-linear relationship between CPUE and depth. In essence, a GAM estimates smoothing parameters for non-linear relationships, in addition to traditional linear parameters, and then "adds" these separate functions (see HASTIE AND TIBSHIRANI 1990). Before fitting each model, we added 0.043 (the smallest non-zero CPUE estimated in the data set) to each CPUE estimate and then applied a natural-log transformation to attempt to normalize the distribution. We used Akaike's Information Criterion (AIC) to determine which of four candidate models best explained the variation in the data. Model 1 was the most complex; it included two interaction terms: depth × region and depth × season, given that the relationship between CPUE and depth could vary among seasons or among regions:

(1) $\ln(CPUE) = \beta_0 + s(depth) + region + season + night + s(depth) \times region + s(depth) \times season + \varepsilon$

where β_0 is the estimated overall mean, $s(depth)$ is a smoothing function of mean bottom depth (in m), *region* is a categorical variable with two levels (north, south), *season* is a categorical variable with three

levels (spring, summer, autumn), *night* is a continuous variable describing the number of nights fished, and ε is the normally distributed error with a mean of 0 and a variance of σ^2. In model 2, we included only the depth × region interaction:

(2) In$(CPUE) = \beta_0 + s(depth) + region + season + night + s(depth) \times region + \varepsilon$

Conversely, model 3 included only the depth × season interaction:

(3) In$(CPUE) = \beta_0 + s(depth) + region + season + night + s(depth) \times season + \varepsilon$

Finally, model 4 contained no interaction terms:

(4) In$(CPUE) = \beta_0 + s(depth) + region + season + night + \varepsilon$

For each species, the models that had ΔAIC <4 were considered to provide the most empirical support to the observed data (BURNHAM AND ANDERSON 2002), where ΔAIC$_i$ equaled the difference between the lowest AIC value among the candidate models and the AIC value of candidate model *i*. To make comparisons of depth distributions across species, we calculated the predicted depth distribution for each species using the model with the lowest AIC value. Because model 1, which included both interaction terms, was the top-ranked model for six of the seven named species, we estimated the predicted depth distribution for every combination of region and season. Finally, for each of these combinations, we identified the depth at which the model predicted peak (maximum) CPUE.

   We also used a GAM approach to predict the depth distribution of *C. hoyi* during autumn of each of three time periods: 1974–1977, 1988–1991, 2004–2007. We added 1.42 (the smallest non-zero CPUE estimated) to each CPUE and then performed a natural-log transformation to make the distribution more normal. Because we did not have seasonal data, we only compared two models. Model 5 included a depth × region interaction term:

(5) In$(CPUE) = \beta_0 + s(depth) + region + s(depth) \times region + \varepsilon$

Model 6 did not include this interaction term:

(6) In$(CPUE) = \beta_0 + s(depth) + region + \varepsilon$

As was done for the 1930–1932 data analysis, we used AIC to select the most parsimonious model, and then calculated the predicted depth distribution for each species in each region during autumn.

   For the 1930–1932 data, we evaluated whether fish size was correlated with water depth, both within and across species. To avoid pseudoreplication, we used the mean TL of fish captured within a gill-net set and only used gillnet sets where at least three fish (of a given species) were caught. Within a species, we calculated separate Pearson correlation coefficients (significance level $\alpha = 0.05$) for each of the three seasons (with sexes pooled) and for males and females separately within a season when sample size permitted separate analyses. We revisited the mean size versus depth correlation with the 1974–2007 data. Here, we limited the data to trawl samples when 5 or more fish were captured. We also conducted the analysis with all available data (i.e., all sizes of fish), as well as with fish >180 mm TL, a procedure used to make the trawl data more comparable to the 1930–1932 data.

Results

Did spatial segregation by depth occur among deepwater ciscoes in the 1930s?

For each of the seven species, model 1, which included both interaction terms (depth × region and depth × season), was among the top-ranked models (i.e., ΔAIC <4), and for six of the species it had the lowest AIC value (or ΔAIC = 0, Table 2). As a result, when making inter-specific comparisons of predicted CPUE as a function of depth, we had to consider every combination of region and season. For the two species (*C. hoyi, C. reighardi*) that Moffett (1957) described as occupying shallow depths, CPUE almost always was predicted to peak at the shallowest depth (50 m) and declined with increasing depth (Table 3, Fig. 2 and 3). The only exception was *C. hoyi* in the spring in the northern region, where the peak CPUE was predicted to occur at a depth of 105 m (Table 3). Overall, the generalizations about depth segregation of deepwater ciscoes put forth by Moffett (1957) held true for the "shallow" species.

For the three species (*C. alpenae*, *C. zenithicus*, *C. johannae*) that Moffett (1957) described as occupying "intermediate" depths, the depth patterns differed between regions. *C. alpenae* and *C. zenithicus* were predicted to attain peak CPUE at intermediate depths (i.e., 76–100 m) in the northern region, but at shallow depths in the southern region (Table 3). The depth distributions of *C. alpenae* and *C. zenithicus* were strikingly similar for all seasons and regions, which was consistent with the hypothesis of Todd et al. (1981) and Smith and Todd (1984) that they were the same species. *C. johannae* was predicted to attain peak CPUE at the deepest depths (i.e., 130–150 m) during spring (northern and southern regions) and summer (in the northern region only). During the other season and region combinations, *C. johannae* was predicted to attain peak CPUE at the shallowest depths (i.e., 50 m). Overall, averaging peak depth across seasons indicates that all three species occupied intermediate depths, especially in the northern region (Table 3). This oversimplification, however, ignores the observations that these intermediate species actually occupied either deep or shallow depths as a function of season or region.

The two species (*C. kiyi*, *C. nigripinnis*) that Moffett (1957) described as occupying "deep" depths consistently attained peak CPUE at the deepest depths (Table 3). *C. kiyi*

Table 2. ΔAIC values resulting from four candidate generalized additive models to explain variation in catch-per-unit-effort of deepwater cisco (*Coregonus*) species from Lake Michigan from 1930 to 1932. ΔAIC values less than 4 were considered the superior models.

	Model 1	**Model 2**	**Model 3**	**Model 4**
C. alpenae	0	6.2	12.5	19.7
C. hoyi	0	10.3	26.2	42.6
C. johannae	0	3.0	4.5	9.6
C. kiyi	3.1	0.6	2.4	0
C. nigripinnis	0	6.4	3.3	7.9
C. reighardi	0	3.7	3.3	14.6
C. zenithicus	0	0	33.9	31.4

Table 3. Depth at which maximum catch-per-unit-effort of seven deepwater cisco (*Coregonus*) species was predicted to occur in each of three seasons from generalized additive model 1 in the northern and southern regions of Lake Michigan in 1930–1932. Areas highlighted in gray represent the season of spawning for a particular species, following SMITH AND TODD (1984). *C. nigripinnis* spawns in January and *C. hoyi* spawns in February–March, months not sampled. Within each region, species are listed according to relative depth distributions by MOFFETT (1957).

	Spring (April–June)	Summer (July–Sept. 15)	Autumn (Sept 16–Nov.)	Average
Northern region				
"Shallow"				
C. hoyi	105	50	50	68
C. reighardi	50	50	87	62
"Intermediate"				
C. alpenae	87	100	76	88
C. zenithicus	95	93	93	94
C. johannae	150	150	50	117
"Deep"				
C. nigripinnis	138	122	127	127
C. kiyi	150	150	150	150
Southern region				
"Shallow"				
C. hoyi	50	50	50	50
C. reighardi	50	50	50	50
"Intermediate"				
C. alpenae	50	50	50	50
C. zenithicus	50	50	50	50
C. johannae	130	50	50	77
"Deep"				
C. nigripinnis	150	150	150	150
C. kiyi	125	150	126	134

was predicted to reach its peak CPUE at 150 m in all seasons in the northern region and at 125–150 m in the southern region. *C. nigripinnis* was predicted to reach its peak CPUE at 122–138 m in the northern region and at 150 m in the southern region. In both regions, the average depth of peak CPUE across seasons for these two species was always the greatest among the seven species (Table 3).

Spawning appeared to have a minimal effect on depth distribution for *C. alpenae*, *C. zenithicus*, *C. reighardi*, and *C. kiyi*. For these species, the depth at which peak CPUE occurred was not markedly different for spawning and non-spawning seasons (Table 3). Spawning may have had some effect on the two remaining species that spawned during the 1930–1932 sampling seasons. In the northern region, *C. johannae* attained peak CPUE in deeper water (150 m) during its spawning season, but in the southern region peak CPUE
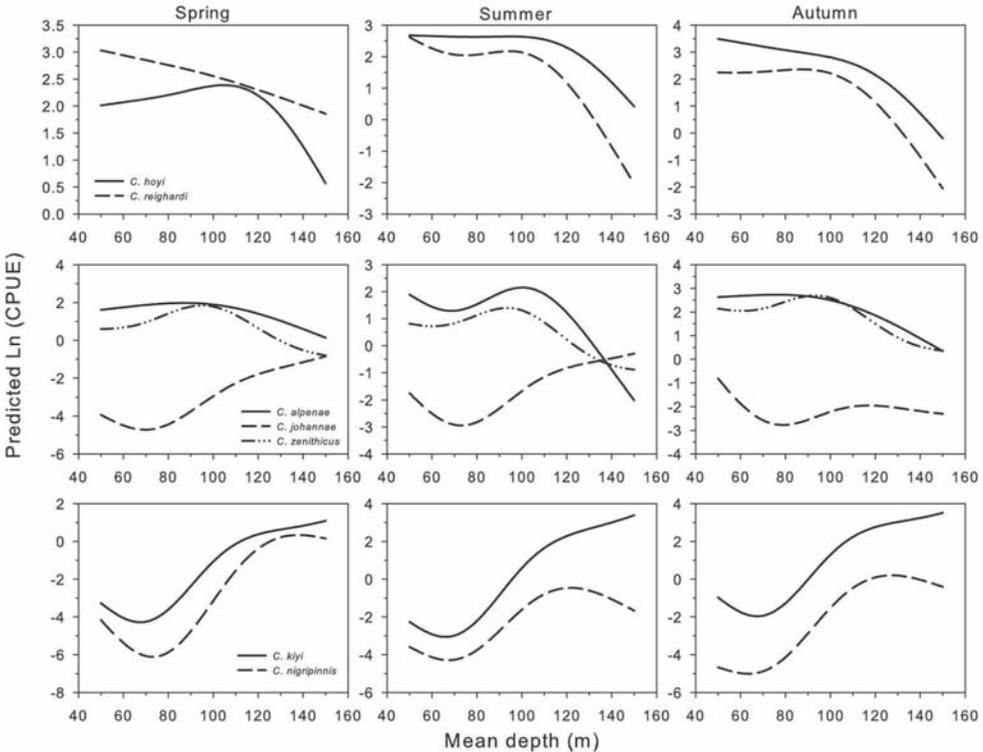
Fig. 2. Predicted CPUE (natural-log transformed) for each of three seasons as a function of depth using the top-ranked generalized additive model for deepwater ciscoes in the northern region of Lake Michigan during 1930–1932. Following MOFFETT (1957), the top row includes species whose depth was classified as "shallow," the middle row includes "intermediate," and the bottom row includes "deep."

during the spawning season occurred at only 50 m. Because *C. johannae* exhibited the most extreme seasonal variation in depth of peak CPUE among the seven species, deciding whether this variation was due to spawning is problematic. In the northern region, *C. hoyi* attained peak CPUE at an intermediate depth (105 m) during spring, just following its late winter spawning. In the southern region, however, peak CPUE occurred in shallow depths (50 m) during spring, which suggests that the intermediate-depth occupancy in the northern region was unrelated to spawning.

Did larger individuals occupy deeper water than smaller individuals?

In the 1930–1932 data, we observed no consistent relationship between depth of capture and fish size. When we pooled all species and ignored the effect of sex and season, there was no correlation ($r = 0.03$; $P = 0.75$; $n = 115$). When we grouped the data by species and season, significant negative correlations were observed in the spring for *C. alpenae*, *C. zenithicus*, and *C. reighardi*, indicating that larger fish were shallower than smaller fish (Table 4). When
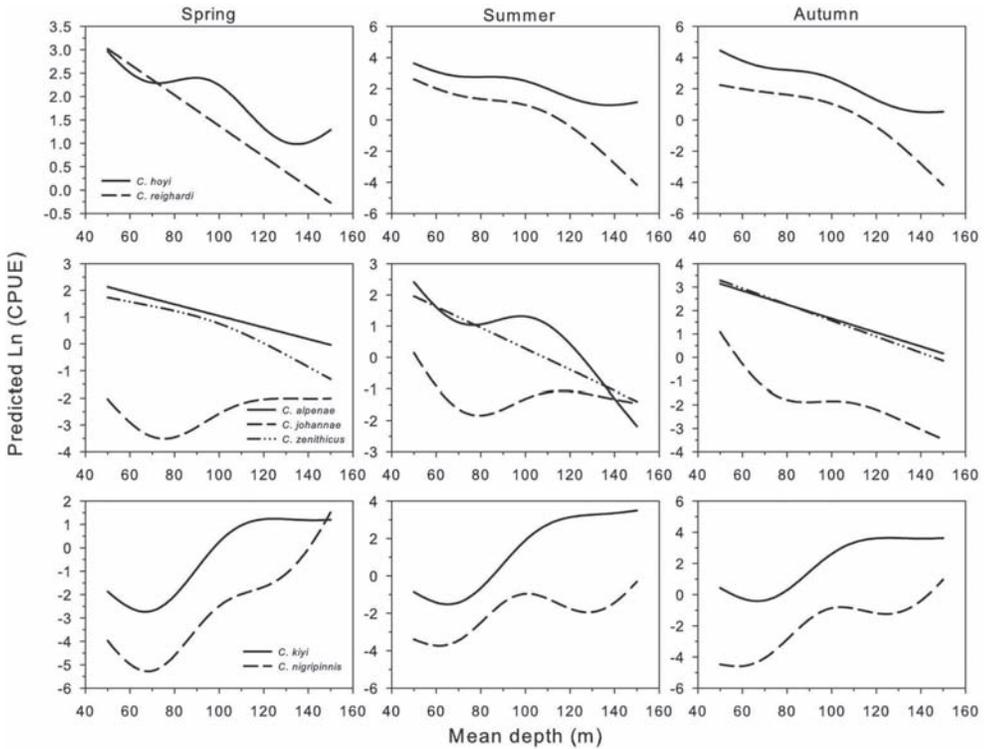
Fig. 3. Predicted CPUE (natural-log transformed) for each of three seasons as a function of depth using the top-ranked generalized additive model for deepwater ciscoes in the southern region of Lake Michigan during 1930–1932. Following MOFFETT (1957), the top row includes species whose depth was classified as "shallow," the middle row includes "intermediate," and the bottom row includes "deep."

further grouping the species data by sex, within the spring we found negative correlations for female *C. alpenae* and *C. zenithicus* and for male and female *C. reighardi* (Table 5), a spring spawner. Depth of capture and fish size were not correlated during summer (Table 4). During autumn, when sample size was lowest, we found a positive correlation only for *C. kiyi* (sample size prevented an evaluation by sex). Overall, we found limited support in the 1930–1932 data for the hypothesis that for each species larger individuals occupied deeper depths than smaller individuals, but the generalization that this occurred for all species and for all seasons was not supported.

For each of the three periods evaluated between 1974 and 2007, larger *C. hoyi* were captured at greater depths than smaller *C. hoyi*. The highest correlation was for 2004–2007 ($r = 0.82$, $P < 0.0001$, $n = 141$, Fig. 4), the next highest was for 1988–1991 ($r = 0.75$, $P < 0.0001$, $n = 290$), and the weakest correlation was for 1974–1977 ($r = 0.70$, $P < 0.0001$, $n = 162$). Even when average fish size was limited to fish >180 mm TL, positive correlations remained significant, albeit lower: 2004–2007: ($r = 0.56$, $P < 0.0001$, $n = 113$), 1988–1991: ($r = 0.55$, $P < 0.0001$, $n = 245$), 1974–1977: ($r = 0.48$, $P < 0.0001$, $n = 113$).

Table 4. Pearson correlation coefficients (with sample size below in parentheses) between mean total length (where number of fish ≥3) and mean depth of capture for seven species of deepwater ciscoes (sexes combined) gillnetted from the R/V *Fulmar* in Lake Michigan 1930–1932. Columns indicate whether all seasons were pooled (overall) or whether correlations occurred by season. Significant correlations ($P < 0.05$) are shown in bold font.

	Overall	Spring	Summer	Autumn
C. alpenae	–0.08	**–0.40**	0.05	0.03
	($n = 109$)	($n = 36$)	($n = 56$)	($n = 17$)
C. hoyi	–0.00	-0.24	0.10	0.51
	($n = 107$)	($n = 34$)	($n = 59$)	($n = 14$)
C. johannae	–0.07	0.36	–0.21	
	($n = 30$)	($n = 4$)	($n = 24$)	($n = 2$)
C. kiyi	0.11	-0.84	–0.00	**0.65**
	($n = 53$)	($n = 3$)	($n = 39$)	($n = 11$)
C. nigripinnis	–0.02		0.08	–0.56
	($n = 22$)	($n = 1$)	($n = 16$)	($n = 5$)
C. reighardi	**–0.28**	**–0.71**	0.20	0.13
	($n = 95$)	($n = 32$)	($n = 54$)	($n = 9$)
C. zenithicus	0.04	**–0.46**	0.14	0.41
	($n = 86$)	($n = 18$)	($n = 54$)	($n = 14$)

Table 5. Pearson correlation coefficients (with sample size below in parentheses) between mean total length (where number of fish ≥3) and mean depth of capture for seven species of deepwater ciscoes (for males and females separately) gillnetted from the R/V *Fulmar* in Lake Michigan 1930–1932. Columns indicate whether all seasons were pooled (overall) or whether correlations occurred by season. Significant correlations ($P < 0.05$) are shown in bold font.

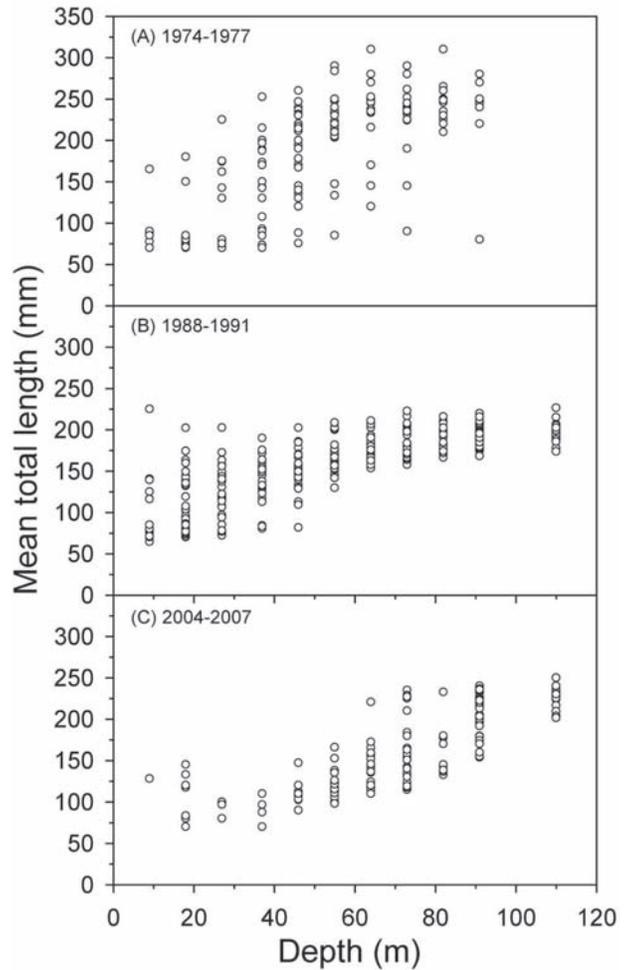|	Overall		Spring		Summer	
	Male	Female	Male	Female	Male	Female
C. alpenae	0.14	–0.10	–0.13	**–0.42**	0.12	0.05
	($n = 83$)	($n = 108$)	($n = 18$)	($n = 36$)	($n = 50$)	($n = 55$)
C. hoyi	0.10	–0.04	-0.10	-0.30	0.13	0.10
	($n = 94$)	($n = 106$)	($n = 28$)	($n = 33$)	($n = 54$)	($n = 59$)
C. johannae	0.09	–0.04		0.98	0.09	–0.28
	($n = 8$)	($n = 21$)		($n = 3$)	($n = 8$)	($n = 18$)
C. kiyi	0.20	0.10			0.11	–0.19
	($n = 30$)	($n = 50$)		($n = 2$)	($n = 20$)	($n = 37$)
C. nigripinnis	0.70	–0.19			0.76	–0.24
	($n = 7$)	($n = 18$)		($n = 1$)	($n = 3$)	($n = 14$)
C. reighardi	–0.20	**–0.28**	**–0.70**	**–0.72**	0.26	0.16
	($n = 68$)	($n = 92$)	($n = 23$)	($n = 30$)	($n = 37$)	($n = 54$)
C. zenithicus	**0.28**	–0.01	0.38	**–0.60**	0.29	0.14
	($n = 67$)	($n = 85$)	($n = 13$)	($n = 17$)	($n = 40$)	($n = 54$)

Fig. 4. Mean total length of *C. hoyi* captured in a single bottom trawl tow as a function of bottom depth for three different time periods during 1974 to 2007.

Did *C. hoyi* shift to deeper waters following extirpation of the other deepwater ciscoes?

For each of the three periods (1974–1977, 1988–1991, 2004–2007) where bottom-trawl data were analyzed, model 5, which included the depth × region interaction, was always the top ranked model to account for the variation in the CPUE of *C. hoyi* >180 mm TL (i.e., ΔAIC for model 6 ranged 23–88). In the northern region (Fig. 5a), peak CPUE occurred at 62 m during 1974–1977 (low abundance), slightly deeper at 70 m during 1988–1991 (high abundance), and then considerably deeper out to 110 m during 2004–2007 (low abundance). Depths at which peak CPUE occurred were shallower in the southern region, but the trend of increasing depths through time persisted (Fig. 5b): peak CPUE at 52 m during both 1974–1977 and 1988–1991, and then out to 85 m during 2004–2007. Comparisons to 1930–1932
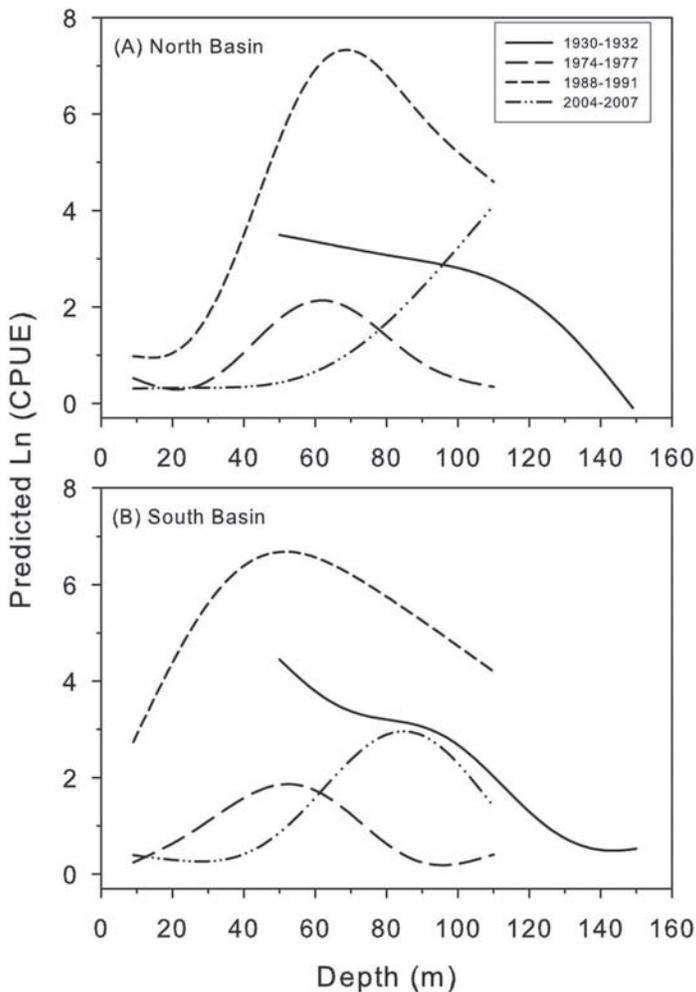
Fig. 5. Predicted CPUE (natural-log transformed) as a function of depth using the top-ranked generalized additive model for *C. hoyi* in the northern (panel A) and southern (panel B) regions of Lake Michigan during autumn for four periods. The 1930–1932 period is based on gillnet surveys that ranged from 45 to 156 m in depth, the 1974–1977, 1988–1991, and 2004–2007 periods were all based on a bottom trawl survey that ranged from 9 to 110 m in depth.

are problematic given those sampled in deeper waters than in later years. However, the depth at which peak CPUE occurred in 1930–1932 (50 m) was not markedly different from the 1974–1977 (52–62 m) or 1988–1991 (52–70 m) data. Hence, sometime after 1988–1991 but before 2004–2007, the *C. hoyi* population appears to have shifted to deeper waters. This shift appears unrelated to *C. hoyi* population density. Given that this shift occurred approximately 25 years after the extirpation of the deepwater ciscoes in the early 1970s, some other factor is likely responsible for bloaters moving into deeper waters.

Discussion

Did spatial segregation by depth occur among deepwater ciscoes in the 1930s?

KOELZ (1929) was the first to recognize that the deepwater cisco community was segregated by depth. He described *C. alpenae*, *C. zenithicus*, *C. reighardi*, and *C. hoyi* as occupying relatively "shallow" waters and *C. johannae*, *C. kiyi*, and *C. nigripinnis* as occupying relatively "deep" waters. He referred to these two habitats as "zones", wherein each species had a normal distribution with the highest density at the center and smaller densities at the extremes. As a result, KOELZ (1929) noted that although each species occupied a wide zone of habitat, the overlap among species from different zones was generally minimal. Our analysis of the 1930–1932 data generally agrees with KOELZ's (1929) observation that zone of occurrence can be wide but that high-density areas occur at specific depths. Using the 1930–1932 data, MOFFETT (1957) modified the depth categories of KOELZ (1929) by introducing an intermediate depth habitat in which *C. alpenae*, *C. zenithicus*, and *C. johannae* occurred. He maintained *C. hoyi* and *C. reighardi* as "shallow" and *C. kiyi* and *C. nigripinnis* as "deep" species. We elected to test the predictions of MOFFETT (1957), because they were more precise than those of KOELZ (1929) and found that they generally held true for six of the seven species.

The species with the greatest deviance from the categories of MOFFETT (1957) was *C. johannae*. In the northern region, peak CPUE for *C. johannae* occurred at the deepest depths during spring, but then shifted to the shallowest depths during autumn. During summer, peak CPUE occurred at 150 m in the northern region, but only at 50 m in the southern region. Therefore, we would not characterize *C. johannae* as occupying intermediate depths, but rather as occupying either shallow or deep depths, depending on the season or region. KOELZ (1929) noted that *C. johannae* could be captured in depths ranging from 55 to 165 m depending on the season, which is consistent with our results. KOELZ (1929) also stated that its spawning depth was unknown in Lake Michigan, and speculated that spawning occurred in deep waters (130–165 m). Given that spawning occurred during August–September and that peak CPUE during summer varied dramatically between regions, spawning does not appear to account for the extreme seasonal fluctuations in *C. johannae* depth distributions. Also of interest, our data suggest that its common name, deepwater cisco, is somewhat misleading.

Given that the peak CPUE of *C. johannae* occurred in such a wide range of depths depending on the season or region, how did this species reduce the potential for interspecific competition? Here we reiterate the elegant hypothesis of KOELZ (1929): that even if the species overlapped in depth distribution, differences in gill raker counts could lead to minimal competitive interactions. Given that the depth distribution of *C. johannae* could have overlapped with nearly every other deepwater cisco species within some combination of season or region, we hypothesize that *C. johannae* minimized competitive interactions mainly because of its gill raker count, which was considerably lower than that of its congeners. Fish with fewer rakers typically consume larger benthic prey items and fish with more rakers typically consume smaller planktonic prey items (LARSON 1976; BENTZEN & MCPHAIL 1984; MALMQUIST et al. 1992). Some authors (BODALY 1979; BERGSTRAND 1982; KAHILAINEN & OSTBYE 2006) have found diet results that support this assumption for coregonid assemblages, but others (e.g., SANDLUND et al. 1987; KEELEY & GRANT 1997) have found gill raker morphology to be a poor

predictor of diet. In the Lake Nipigon deepwater cisco community, for example, Turgeon et al. (1999) found that the species with the lowest and highest number of gill rakers had considerable overlap in their diet. Conversely, the two species with high overlap in gill raker counts had virtually no diet overlap. As a result, Turgeon et al. (1999) cautioned against the assumption that differences in gill raker count are related to differences in diet, and hypothesized that species with higher gill raker counts may be more omnivorous in prey selection, whereas species with low gill raker counts (and more distant spacing) may specialize on larger zoobenthos because they are unable to efficiently consume smaller zooplankters. Therefore, *C. johannae* in Lake Michigan may have specialized on large zoobenthos, but we cannot conclude that other deepwater cisco species did not consume similar prey items.

Deviations from the categories of Moffett (1957) were less dramatic for the other species. *C. hoyi* (classified as "shallow") exhibited a peak CPUE at an intermediate depth (105 m) during only spring in the northern region. We cannot explain this anomaly, but doubt that it was related to spawning. Koelz (1929) reported *C. hoyi* spawning in shallow/intermediate depths (i.e., 50–100 m) in February and March. By the time the spring sampling began in the 1930s (April 15), *C. hoyi* spawning was likely ending. Other modest deviations included *C. alpenae* and *C. zenithicus*, which were classified as "intermediate". For all seasons, we found that in the southern region their peak CPUE occurred in the shallowest depth (50 m). In the northern region, the CPUE of these two species peaked at intermediate depths, as predicted by Moffett (1957). We cannot explain this inter-region difference, but note that the peak CPUE of all species occurred at deeper depths in the north than in the south. Moreover, the greater median depth of the gillnet sets in the northern region (91 m; range: 48–156 m) than in the southern region (78 m; range: 45–154 m) provided a greater contrast within which depth effects could be documented.

Did larger individuals occupy deeper water than smaller individuals?

Eshenroder and Burnham-Curtis (1999) advanced a concept that among diel-vertically migrating (DVM) planktivorous fishes, and especially among deepwater ciscoes, the larger-sized individuals within a species would tend to occupy deeper water than smaller-sized individuals. They reasoned that DVM in deepwater ciscoes evolved in response to selection pressures related to feeding on *Mysis relicta*, which inhabits the deepest waters of the Great Lakes and undergoes extensive DVM. In theory, larger-bodied deepwater ciscoes should be more energetically efficient at DVM, and Eshenroder and Burnham-Curtis (1999) showed that this relationship held true for *C. hoyi* collected in August 1987 from Lake Michigan.

Within the 1930–1932 data, however, the depth of occurrence for each of the seven species was not consistently positively related to fish size. Of 66 correlations, only 11 were significant and nine of these were negative, rather than the predicted positive relationship. *C. reighardi* accounted for five of the negative correlations, when the larger males and females occurred closer to shore during spring. Among the deepwater ciscoes, only *C. reighardi* spawned in the spring. Perhaps the larger, mature *C. reighardi* aggregated in shallower waters for spawning. In their monograph on *C. reighardi* (based on the 1930–1932 data), Jobes (1943) noted that *C. reighardi* was captured over a wider depth range in spring than in the summer and autumn.

Sizes of *C. alpenae* and *C. zenithicus* individuals also were negatively correlated with depth in the spring, but only for females. These species spawned in autumn, so spawning did not cause this relationship. When seasons were pooled, fish size and depth were correlated only for male *C. zenithicus*. This instance was our only finding where *C. zenithicus* and *C. alpenae* depth distributions did not appear to be synonymous. When sexes were pooled, fish size and depth were correlated only for *C. kiyi* during autumn. Given that *C. kiyi* spawned in autumn, this correlation could be explained by larger individuals migrating to deeper waters for spawning, essentially the opposite from *C. reighardi*.

In contrast to the 1930–1932 data for *C. hoyi*, there was a strong positive correlation between fish size and depth of capture for the 1974–2007 *C. hoyi* data. Why this relation-ship was largely absent from the 1930–1932 data is unclear. The mesh sizes used in the 1930–1932 gillnets may have biased the results by allowing many of the smaller individuals to escape. In addition, smaller-sized individuals in the early 1930s might have inhabited shal-lower, warmer waters (see Eshenroder et al. 1998) that were not sampled by gillnets. Both of these factors would have limited the capture of smaller individuals, which in turn, could have made it more difficult to detect a weak fish size versus depth relationship.

We are reluctant to attribute the absence of a fish size versus depth relationship in the 1930s exclusively to sampling bias, given the extensive nature of the 1930s data set. Alter-natively, we offer a speculative hypothesis to explain why larger deepwater ciscoes in the early 1930s were not caught in gillnets in deeper waters when compared to smaller deep-water ciscoes, despite finding this positive size versus depth relationship for *C. hoyi* in later years. We hypothesize that *Diporeia* spp. were even more important in the diets of deepwater cisco species in the 1930s than assumed by previous authors. *Diporeia* spp. are as lipid- and energy-rich (perhaps even more so) as *Mysis relicta* (Gardner et al. 1985), yet *Diporeia* spp. do not undergo DVM, which could reduce energy expenditure by deepwater cisco predators. We speculate that *Diporeia* spp. may have been the preferred diet item in depths from 30 to 90 m, where they attain their highest densities (Nalepa 1989) and where *Mysis relicta* are less abundant than in deeper waters (Reynolds & DeGraeve 1972; Pothoven et al. 2000). Additionally, deepwater ciscoes were much more abundant in the 1930s than in later years as fishing pressure increased, and their high numbers may have reduced *Mysis* densities to the point that *Diporeia* spp. (and other prey) were targeted. Therefore, larger individuals may have been occupying both shallow (where energy-rich *Diporeia* spp. were available) and deep depths (where *Mysis relicta* would be most efficiently captured by large ciscoes) in the 1930s, effectively nullifying any fish size versus depth relationship.

Did *C. hoyi* shift to deeper waters following extirpation of the other deepwater ciscoes?

Our data spanning 1974–2007 clearly showed that the *C. hoyi* population dramatically shifted to deeper waters sometime after 1991 and before 2004, a continuation of a trend first reported by Smith (1964), but likely having a different cause. For 1930–1932 data, the peak CPUE was in water <50 m deep. Smith (1964) reported a modest shift of the *C. hoyi* population to deeper waters by 1954–1955, where it remained through at least 1960–1961. Smith (1964) attributed this response to a niche opening caused by the depletion of the other deepwater

cisco species. In 1930–1932, *C. hoyi* comprised 31% of the deepwater cisco catch, but by 1954–1955 it comprised 76% of the catch, and by 1960–1961 it comprised 94% of the catch.

The modest shift of the *C. hoyi* population to deeper water, which was evident by 1954–1955, persisted into 1974–1977. By then, the peak CPUE of *C. hoyi* was at 62 m in the northern region and 52 m in the southern region. By 1988–1991, the depth of peak CPUE had increased slightly to 70 m in northern region while remaining at 52 m in southern region, and more tellingly, the population appeared to occur beyond 110 m, the maximum depth that was trawled. By 2004–2007, however, the *C. hoyi* population was occupying markedly deeper waters, as the predicted CPUE was still increasing at 110 m in the northern region and in the southern region peaked at 85 m.

The shift of the *C. hoyi* population to markedly deeper waters after 1988–1991 does not appear to have been a continuation of the modest changes documented before this time. Instead, we propose that a severe reduction in the population of *Diporeia* spp., a burrowing amphipod and primary prey for *C. hoyi* (WELLS AND BEETON 1963; CROWDER AND CRAWFORD 1984; DAVIS et al. 2007), from the nearshore waters of Lake Michigan best explains the recent event. During 1994–1995 (and presumably earlier), *Diporeia* spp. reached peak abundance at depths of 31–90 m (NALEPA et al. 2006), depths where *C. hoyi* reached peak CPUE prior to 1991. By 2005, densities of *Diporeia* spp. had declined to only very small percentages of their 1994–1995 densities: 0.4% in the 31–50 m depth strata and 8% in the 51–90 m depth strata (NALEPA et al. 2009). By 2005, the peak density of *Diporeia* spp. occurred at depths >90 m (NALEPA et al. 2009). We hypothesize that the *C. hoyi* population shifted to deeper waters recently in response to the scarcity of *Diporeia* spp. in shallower waters. At depths beyond 90 m, *C. hoyi* is more likely to also encounter higher densities of its other primary prey, *Mysis relicta* (POTHOVEN et al. 2000).

The plasticity in *C. hoyi* depth preferences has implications for managers considering reintroduction of *C. hoyi* from extant populations, such as Lake Michigan's, into other Laurentian Great Lakes where all deepwater ciscoes have been extirpated, such as in Lake Ontario. In addition to restoring a native deepwater planktivore to Lake Ontario, managers are seeking a species that could capitalize on the high densities of *Mysis* in deep (i.e., >100 m) offshore waters (MILLS et al. 2003; JOHANNSSON et al. 2003; RUDSTAM et al. 2008), which comprise about 43% of the lake surface area. We believe that if *C. hoyi* were successfully reestablished, it would occupy the deep offshore waters. However, recent food web changes in Lake Ontario would cause *C. hoyi* to compete with other introduced (alewife *Alosa pseudoharengus*, rainbow smelt *Osmerus mordax*, round goby *Neogobius melanostomus*) and native (slimy sculpin *Cottus cognatus*, deepwater sculpin *Myoxocephalus thompsonii*) fishes, just as it currently does in Lake Michigan. With the proliferation of dreissenid mussels (*Dreissena polymorpha, D. bugensis*) in Lake Ontario, alewife and rainbow smelt populations shifted to deeper water (O'GORMAN et al. 2000), where they likely consume more *Mysis relicta* (MILLS et al. 1992; LANTRY AND STEWART 1993; WALSH et al. 2008). Round goby invaded in the late 1990s (OWENS et al. 2003) and proliferated thereafter (WALSH et al. 2007). A portion of the population overwinters in offshore waters where it consumes *Mysis* (WALSH et al. 2007). The sharp decline of *Diporeia* spp. (LOZANO et al. 2001) apparently caused slimy sculpin to rely more heavily on *Mysis relicta* for prey (OWENS AND DITTMAN 2003). Despite this existing predation pressure, it seems unlikely to us that that the reintroduction of *C. hoyi* to the lake would exert more predation pressure on the *Mysis relicta* population than what

had historically occurred when the lake's native deepwater community, consisting of three species of deepwater ciscoes (SMITH AND TODD 1984) and deepwater sculpin (CHRISTIE 1973), was intact. Therefore, we believe re-establishment of *C. hoyi* or another deepwater cisco species to Lake Ontario would not be an additional threat to the lake's *Mysis relicta* population.

In conclusion, we provided evidence of spatial segregation in the Lake Michigan deepwater cisco community that likely contributed to the maintenance of this unique species flock. We found no evidence in our analyses of the gillnet data from 1930–1932 of spatial structuring as a function of fish size when data for all species were combined. However, we did find positive relationships between size of *C. hoyi* captured in bottom trawls and depth in all three periods evaluated between 1974 and 2007. Based on our analyses of the 1930–1932 fish distributions, we concur with the hypothesis of TODD et al. (1981) and SMITH AND TODD (1984) that *C. alpenae* was likely synonymous with *C. zenithicus*. We also found that the shift of *C. hoyi* to modestly deeper waters, observed by SMITH (1964) in 1954–1955, continued into 1974–1977, and became much more pronounced by 2004–2007. We attribute this recent and dramatic shift in depth distribution to the sharp decline of its primary prey, *Diporeia* spp., in waters <90 m in depth.

Acknowledgements

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