

Decline of the Shortjaw Cisco in Lake Superior: the Role of Overfishing and Risk of Extinction

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Abstract.—Recent reviews have further documented the decline of the shortjaw cisco *Coregonus zenithicus* in Lake Superior. This fish was the most abundant deepwater cisco species in Lake Superior in the early 1920s but presently makes up less than 1% of all deepwater ciscoes (i.e., including shortjaw cisco, bloater *C. hoyi*, and kiyi *C. kiyi*) captured in biological surveys. Directed overfishing of deepwater cisco species during the 1930s and again during the mid-1960s and 1970s has been suggested as the cause of the shortjaw cisco's demise. In this paper, we re-examined the overfishing hypothesis by using historical and recent survey data to estimate the proportion of the historical commercial fishery landings that comprised shortjaw ciscoes. We developed time series of estimated harvest and relative abundance for all statistical districts in Michigan waters of Lake Superior during 1929–1996, for which aggregate catch and effort data were available but not previously examined. The spatial distribution of the fishery and the relationships of catch to fishing effort were examined for evidence of overfishing. Our analysis suggested that directed overfishing was probably not the cause of shortjaw cisco demise, as this species appeared to be declining in all statistical districts regardless of the intensity of the fishery. A count-based population viability analysis indicated that quasi-extinction of the shortjaw cisco is highly probable in the near future. We propose an alternative hypothesis based on the decline of Lake Superior's keystone predator, the lake trout *Salvelinus namaycush*, which resulted in an expansion of the population of its principal prey, the cisco *C. artedi*, due to release from predation pressure. Competitive or predation interactions between the cisco and shortjaw cisco may be more likely explanations for the demise of the latter species.

Historically, the Great Lakes contained a morphologically and ecologically diverse assemblage of deepwater coregonine fishes (*Coregonus* spp.), collectively known as “deepwater ciscoes” (Koelz 1929). These fish had highly variable phenotypic features that

were engendered in part by the environment and through hybridization. Many different taxonomic designations were initially proposed, but experts ultimately settled on seven species. Lakes Michigan and Huron contained the most diverse group (bloater *C. hoyi*, deepwater cisco *C. johanna*, kiyi *C. kiyi*, blackfin cisco *C. nigripinnis*, shortnose cisco *C. reighardi*, and shortjaw cisco *C. zenithicus*), while Lake Superior had bloaters, kiyis, and shortjaw ciscoes

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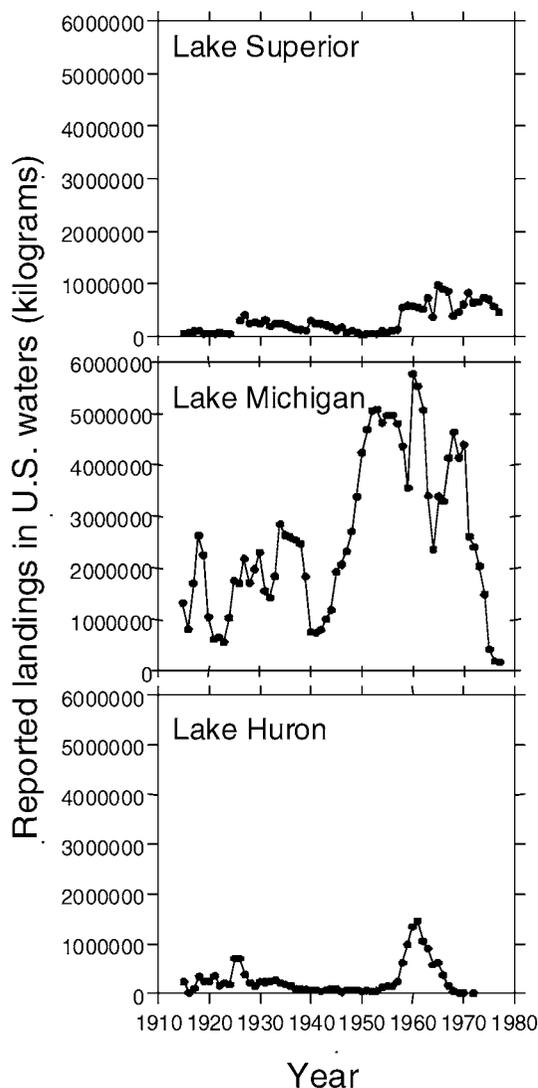


FIGURE 1.—Reported annual harvest of all deepwater cisco species from U.S. waters of Lakes Superior, Michigan, and Huron during 1915–1977. Data are from Baldwin et al. (1979).

and Lake Ontario had shortnose ciscoes, bloaters, and kiyis (Bailey and Smith 1981). Lake Erie had only the shortjaw cisco. In addition, the ubiquitous, more shallow-water cisco *C. artedi* (formerly known as lake herring) was found in all of the Great Lakes. Overfishing, introduction of exotic species that altered the fish communities, and hybridization with closely related species during the last century have been proposed to explain the extinction of most forms (Smith 1964, 1968, 1970; Berst and Spangler 1972; Christie 1972, 1974; Wells and McLain 1972; Hartman 1973; Scott and Crossman 1973; Todd and Stedman

1989; Todd 2003). Today, Lake Michigan contains only bloaters, Lake Huron has bloaters and very few shortjaw ciscoes, and Lakes Erie and Ontario have lost all of their deepwater cisco species. Lake Superior, in contrast, maintained its original deepwater cisco community, which is composed of bloaters, kiyis, and shortjaw ciscoes (hereafter, the term “deepwater ciscoes” refers to this community rather than to *C. johanna*; Lawrie and Rahrer 1972, 1973; Bronte et al. 2003). Little genetic differentiation has been found among these fishes, and species designations have been questioned (Reed et al. 1998; Turgeon et al. 1999).

The shortjaw cisco, which is the largest of the three deepwater ciscoes in Lake Superior, was once widely distributed throughout the lake and composed more than 90% of the fish landed in the commercial deepwater cisco fishery during the early 1900s (Koeltz 1929; Van Oosten 1937). From the 1920s to 2000s, shortjaw ciscoes declined in abundance lakewide and now make up less than 1% of all deepwater ciscoes (Hoff and Todd 2004; Gorman and Todd 2007). This decline has been attributed to overfishing (Lawrie and Rahrer 1972, 1973; Hoff and Todd 2004; Gorman and Todd 2007) based on trends in reported landings but without any detailed examination of the commercial catch and effort data. Landings of deepwater ciscoes (mostly shortjaw ciscoes and some bloaters) in U.S. waters of Lake Superior were small compared with those in Lake Michigan but were similar to landings in Lake Huron during 1912–1977 (Baldwin et al. 1979; Figure 1). The early Lake Superior fishery in U.S. waters averaged 395,000 kg/year during 1895–1908 (not shown in Figure 1) and then declined and remained low during 1910–1925, with a mean of 38,000 kg/year (Hoff and Todd 2004). Koeltz (1926) reported that deepwater ciscoes, especially shortjaw ciscoes, were ubiquitously abundant but were not in demand by the Chicago markets and were fished only for local consumption. From 1926 to 1957, harvest increased slightly and averaged around 163,000 kg/year in U.S. waters, but then increased to an average of 624,000 kg/year during the 1960s and 1970s (Baldwin et al. 1979), mostly from an expanded fishery in Michigan waters (Peck 1977).

Because of its depressed status in Lakes Superior and Huron and its extirpation in Lakes Michigan and Ontario, the shortjaw cisco is being considered for listing under the Endangered Species Act of 1973 in the United States and was recommended for listing as “threatened” by the Committee on the Status of Endangered Wildlife in Canada (Todd 2003), but this recommendation has not yet been acted upon. A recovery plan for the species is in preparation for Canadian waters, while no actions are being considered

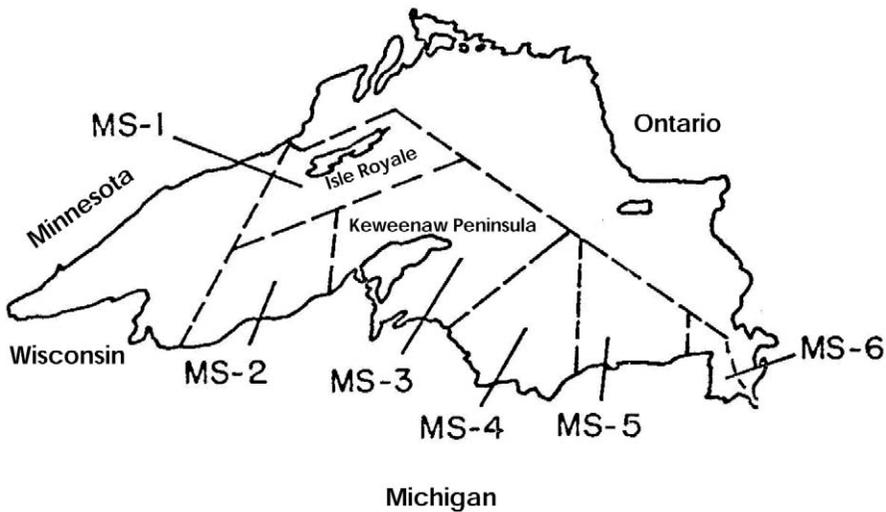


FIGURE 2.—Map of fishery statistical districts (MS-1–6) in the Michigan waters of Lake Superior (Hile 1962).

for U.S. waters pending a listing decision by the U.S. Fish and Wildlife Service (USFWS).

Pursuant to this situation, we re-examined the historical information on the 1929–1996 commercial fishery for deepwater ciscoes in the Michigan waters of Lake Superior as well as observations from Koeltz (1929) in the 1920s and fishery-independent survey data for 1953–2004 from the USFWS and U.S. Geological Survey (USGS), as previously published by Hoff and Todd (2004) and Gorman and Todd (2007). Our objectives were to (1) develop the first time series of relative abundance of shortjaw ciscoes in Michigan waters of Lake Superior from 1929 to 1998, (2) re-examine the shortjaw cisco decline relative to the “overfishing hypothesis” in light of historical catch and effort data not considered previously, and (3) provide the first estimates of the probability of extinction using the new relative abundance data from commercial catches. Furthermore, as a result of our analysis of objective 2, we developed a new hypothesis for the decline of the shortjaw cisco in Lake Superior.

Methods

Time series development.—We developed a time series of the relative abundance of shortjaw ciscoes from the commercial small-mesh gill-net fishery in the Michigan waters of Lake Superior. Commercial catch and effort statistics from mandatory monthly catch reports filed by fishers were summarized annually according to fishery statistical districts (Figure 2; Hile 1962) by the U.S. Bureau of Commercial Fisheries during 1929–1973 (Jensen and Buettner 1976) and by

the Michigan Department of Natural Resources thereafter.

Catches of the cisco (i.e., lake herring) were reported separately from deepwater cisco catches, but unfortunately the design of the report forced all deepwater cisco catches to be grouped under a single column entitled “chubs, including blackfins” (referring to the vernacular for deepwater ciscoes). Hence, we needed to partition shortjaw cisco catches from the total reported landings. Recent reviews of trends in shortjaw ciscoes from the 1920s through 2004 (Hoff and Todd 2004; Gorman and Todd 2007) provide point estimates (years where data were available) of the proportion of shortjaw ciscoes and bloaters captured in small-mesh gill-net assessments in Michigan waters of Lake Superior. These estimates were taken from assessment gill nets set at depths of 40–160 m; the assessment gill nets had 64–70-mm stretch-measure mesh (1922, 2000–2004) or 51–76-mm mesh (1953, 1958–1992). The 1922 studies by Koeltz (1929) used mesh sizes that ranged from 54 to 76 mm although meshes of 64–70 mm were most common. These mesh sizes were similar to those used in the commercial fishery, which mostly ranged from 64 to 70 mm, although smaller and larger meshes were occasionally used (Koeltz 1929; Anderson and Smith 1971). Proportional changes in the composition of shortjaw ciscoes and bloaters were not drastically different in a detailed examination of catches made in 1953 that used mesh sizes smaller than 64 mm (USGS, Ashland, Wisconsin, unpublished data). Kiyis were not considered in the catches because the fishery typically occurred in water depths less than

100 m, which is near the shallow limit of their distribution (Gorman and Todd 2007). This species has the smallest apical size of all the deepwater ciscoes; hence, kiyis were not a target of the fishery, especially in the early years.

From these data, we employed a Bayesian beta regression (Branscum et al. 2007) to model the proportion of shortjaw ciscoes in the harvest over time. Because of its flexibility in the shapes and varieties of densities that can be accommodated, the beta family is a natural choice for modeling continuous data restricted to the interval (0, 1). Because most of these historical observations of shortjaw ciscoes were from locations east of the Keweenaw Peninsula, we modeled harvest proportion as a function of year and an east–west binary covariate to capture any potential spatial differences in the proportional changes in species composition. A priori model exploration (via examination of penalized spline and polynomial regressions) suggested a model with covariates for year and year-squared (year^2) would best approximate the data. Because of the sparsity of the data, model fitting was conducted in WinBUGS software (Spiegelhalter et al. 2004) with Markov-chain Monte Carlo sampling. We used as an informative prior distribution for the shape of a second-order polynomial to initially guide model fitting (Bedrick et al. 1996). We ran three chains each for 100,000 iterations after a burn-in of 10,000 iterations, thinning by 3 to reduce within-chain correlation. We compared the model with the east–west covariate to a model without the covariate using information-theoretic methods (Burnham and Anderson 2002). We calculated the deviance information criterion (DIC) for each model; DIC is a Bayesian analog to Akaike's information criterion (Spiegelhalter et al. 2002). We differenced the model DIC values from the DIC for the best model, and we calculated model weights and model likelihoods. In addition to the fixed-covariate model described above, we also assessed mixed-effects models whereby year and area were treated as random effects. These models did not converge, probably because of the high proportion of missing information in shortjaw cisco data coupled with an expansion in the number of parameters needing to be fit. We applied the fixed-covariate models to the reported total landings of all deepwater ciscoes from 1929 to 1996 to estimate a time series for shortjaw cisco landings for each statistical district in Michigan waters of Lake Superior. Bloater landings were estimated by subtracting the estimated shortjaw cisco harvest from the total reported harvest for each year within each district.

Catch per unit effort (CPUE; kg/km of net) was calculated by using the estimated catches from our

above models and the year-specific totals of the cumulative length of small-mesh gill nets corrected for changes in relative efficiency due to the transition from linen to cotton nets and then to multifilament nylon nets during this time period (Lawrie and Rahrer 1973). We assumed that the transition in mesh material was similar to that of the cisco fishery as described by Selgeby (1982). At that time, the nets used to harvest ciscoes and deepwater ciscoes were similar in construction and mesh size (Selgeby 1982); hence, materials that increased catches, reduced gear maintenance, or both would have been incorporated by both fisheries simultaneously. Gill-net webbing was initially made of linen and then of cotton; nets of cotton were used up until the 1950s. The relative efficiency of linen and cotton nets is not known but appears to be similar based on comparisons from other locations (Scidmore and Scheftel 1958). Conversions from cotton nets to multifilament nylon nets occurred during the 1950s and increased the catch efficiency (Hile 1962); by 1960, most of the nets used were made of nylon. While there are no relative catch efficiency data for nets made of the various materials used to fish for deepwater ciscoes, we adjusted the commercial CPUE by estimating the proportion of fishing effort that was composed of nylon nets in each year using the schedule of conversion from Selgeby (1982) for the Wisconsin cisco fishery and then adopting his efficiency ratio of 2.5:1.0 (nylon : cotton) for conversion of gill-net material based on Dryer and Beil (1964). Failure to make any adjustment for net materials would inflate the relative abundance of deepwater ciscoes after 1950. Soak time was not available from the cumulative effort totals but was assumed to be similar over the time period and did not vary considerably from year to year within a statistical district to significantly affect CPUE estimates (Hile 1962).

Determination of overfishing.—To determine whether direct overfishing was a reasonable hypothesis for the demise of the shortjaw cisco, we calculated the Pearson product-moment correlation coefficients and Bonferroni probabilities for the estimated 1929–1996 catches and total fishing effort for deepwater ciscoes in sequential years in each statistical district and for all districts combined. Linear and positive relations between catch and effort suggest that catch was proportional to effort and that stocks are not likely to be significantly affected by fishing mortality (Ricker 1975). Evidence of overfishing would be a parabolic relationship between catch and increasing effort: as fishing effort increases, catches would decline in response to the population's failure to compensate for mortality increases (i.e., compensation via growth, reproduction, or both). Hile (1962) was uncomfortable

TABLE 1.—Posterior means and 95% posterior confidence intervals (CI) for the beta regression used to estimate the proportion of shortjaw ciscoes in the harvest from Michigan waters of Lake Superior during 1929–1996. Gamma (γ) is the variance of the regression.

Parameter	Variable	Mean	95% posterior CI
β_1	Intercept	5.2580	4.7260–5.8140
β_2	Year	-0.1794	-0.2082 to -0.1513
β_3	Year ²	0.0007	-0.0004 to 0.0010
β_4	East-west	0.2328	-0.0116 to 0.4752
γ		12.1200	9.2240–15.4000

with effort conversions as we described in the previous section and instead recommended among-year comparisons within periods of years where gear conversions and other changes were similar or had stabilized. To overcome any problems associated with changing gears or our methods of correction, we conducted the correlation analysis for three periods: (1) 1929–1950, when only cotton nets were used; (2) 1950–1959, a transitional period when cotton was slowly replaced by nylon; and (3) 1960–1996, when most nets were made of nylon.

Probability of extinction.—To determine risk of extirpation for the shortjaw cisco, we employed a count-based population viability analysis that has been used successfully for single populations surveyed for lengthy periods (Lande and Orzack 1988; Dennis et al. 1991; Morris and Doak 2002; Lande et al. 2003). Population viability analysis assesses the rate of population decline and risks of extinction or quasi-extinction over a defined time horizon (Gilpin and Soule 1986; Boyce 1992; Holmes 2001; Morris and Doak 2002). Extinction risk from this count-based perspective was parameterized by trend and variability in trend of the annual indices of population relative abundance from the commercial fishery CPUE during 1929–1996.

The approach we used estimates extinction risk via a diffusion approximation from data that contain both environmental noise in the year-to-year transitions in population indices (“process error”), random errors in sampling, and possible biases in sampling (these latter two sources of error are described as “nonprocess error”; Holmes 2004). A Bayesian sampling–importance–resampling algorithm was used to address uncertainty in the parameter estimates given the data. Thus, rather than developing a single function describing the probability of population extinction through time, we used uncertainty in the parameter estimates to estimate the uncertainty surrounding the probability of extinction through time. These probabilities of the extinction probability were derived from a large number of candidate vectors that were chosen at

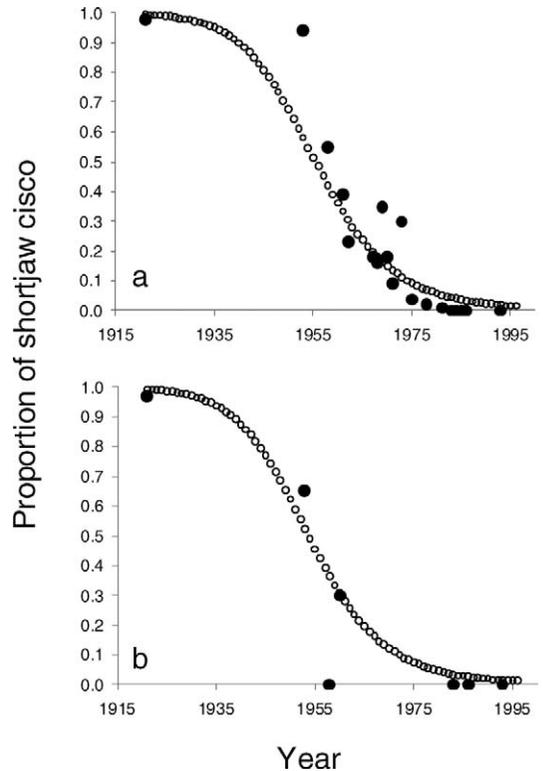


FIGURE 3.—Observations (black circles) of the proportion of all deepwater ciscoes (i.e., shortjaw cisco, bloater, and kiyi) that were shortjaw ciscoes from survey data collected in Lake Superior on the (a) east side and (b) west side of the Keweenaw Peninsula (Michigan) during 1920–2005. Also shown is the beta regression (open circles) used to predict the proportion of deepwater cisco harvest made up of shortjaw ciscoes in the commercial fishery in Michigan waters of Lake Superior during 1929–1996.

random from prior distributions and based on their importance (i.e., their contribution to the likelihood; Punt and Hilborn 1997). Samples of these vectors were drawn with replacement and in proportion to their importance to generate a sample from the posterior distribution. We used a state-space Kalman filter, which evaluated likelihoods from a running-sums method (Holmes 2004), to discriminate process error from nonprocess error.

We focused on predicting population viability at levels above which demographic stochasticity and Allee effects may become important (Lande et al. 2003; Fagan and Holmes 2006). As such, we did not measure absolute risk of extinction per se, but rather the potential for quasi-extinction: a drop in the population below a subjective but meaningful level of 0.01 kg/km of net. Both the World Conservation Union’s International Union for the Conservation of

TABLE 2.—Years of data, mean annual fishing effort (km of gill net), and mean annual estimated catch (kg) for shortjaw ciscoes by statistical district and all districts combined in Michigan waters of Lake Superior from 1929–1998. Pearson's product-moment to correlation coefficients (r) and P -values refer to the relation between the estimated landings and total effort for periods when specific net materials were used: 1929–1950 (cotton nets only), 1951–1959 (conversion from cotton to nylon nets), and 1960–1996 (nylon nets only). Missing data indicate two or fewer years of fishing during that year grouping.

Statistical district	Years of data	Mean annual effort (km)	Mean annual catch (kg)	Annual effort and catch r (and P) by year grouping		
				1929–1950	1951–1959	1960–1996
MS-1	18	192	730			0.56 (0.024)
MS-2	45	677	7,354	0.95 (<0.001)	0.95 (<0.001)	0.95 (<0.001)
MS-3	52	1,912	12,688	0.68 (0.008)	0.83 (0.022)	0.72 (<0.001)
MS-4	66	600	5,612	0.90 (<0.001)	0.99 (<0.001)	0.77 (<0.001)
MS-5	24	277	2,339		0.85 (0.067)	0.53 (0.029)
MS-6	48	309	6,297	0.89 (<0.001)	0.90 (0.001)	0.88 (<0.001)
All districts combined	67	2,860	25,860	0.91 (<0.001)	0.90 (<0.001)	0.79 (<0.001)

Nature (IUCN) risk criteria (Mace and Lande 1991) and the proposed quantitative criteria for the U.S. Endangered Species Act (DeMaster et al. 2004) rely on quasi-extinction probabilities for inference.

Results

Time Series Development

The Bayesian beta regression that describes the proportion of harvest represented by shortjaw ciscoes for each observation year indicated that the proportion declined from an estimated 99.5% of the harvest in

1929 to 1% in 1996 (Table 1; Figure 3). The proportion of shortjaw ciscoes in the harvest slightly differed for the east and west sides of the Keweenaw Peninsula, with the percentage in the east approximately 2.4% greater than that in the west. The model with this east–west covariate was compared with a model that lacked the covariate, and information-theoretic methods indicated that the model with the covariate was favored 2.6 times over the model without the covariate (model weights were 72.4% and 27.6%, respectively).

Fishing effort of small-mesh gill nets for deepwater

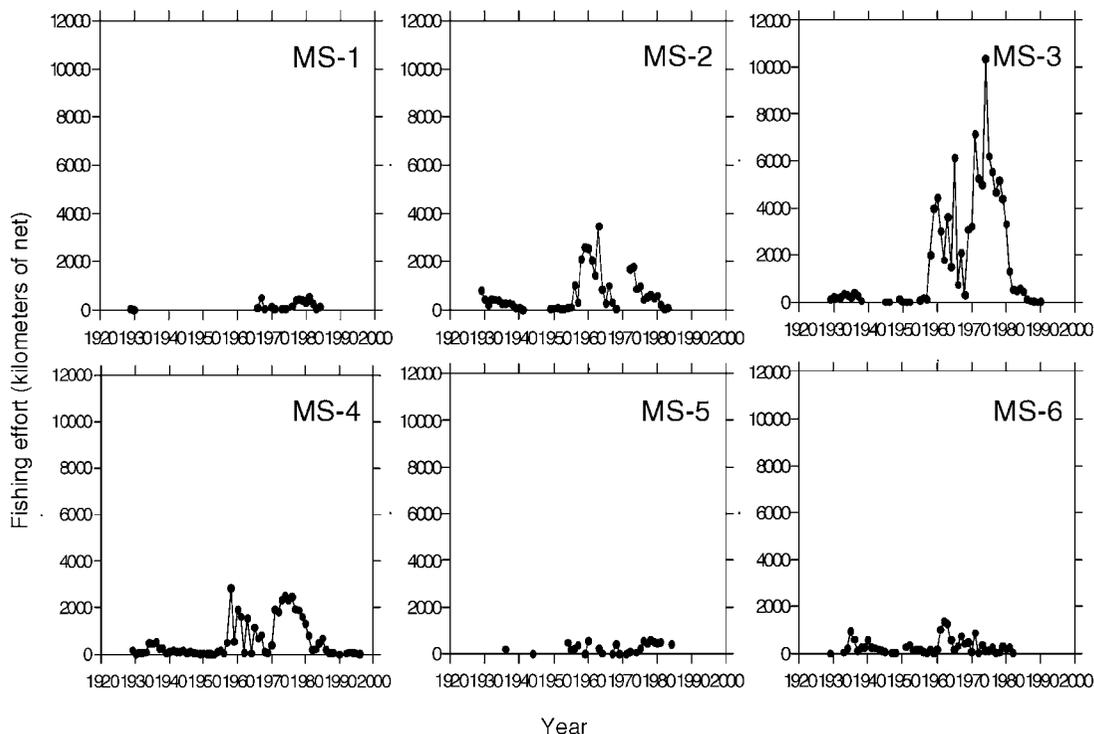


FIGURE 4.—Fishing effort (km of net) for deepwater cisco species by statistical district (Figure 2) in the Michigan waters of Lake Superior, 1929–1996.

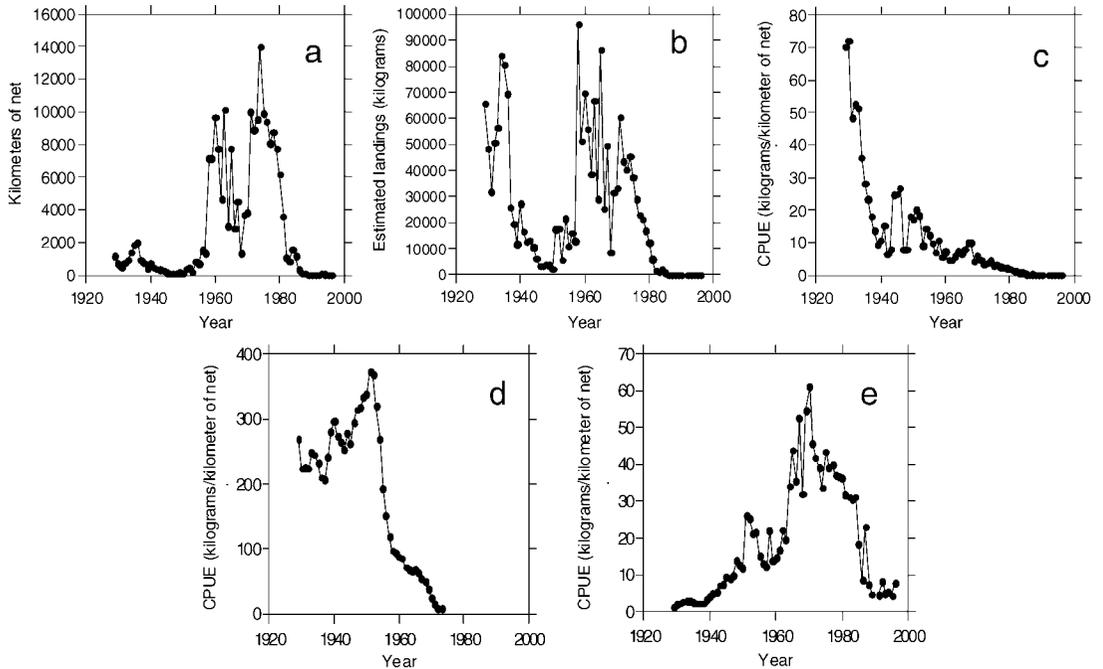


FIGURE 5.—(a) Total fishing effort (km of net) for deepwater cisco species, (b) estimated total landings (kg) of shortjaw ciscoes, (c) relative abundance (catch per unit effort [CPUE]; kg/km of net) of shortjaw ciscoes, (d) CPUE of ciscoes, and (e) CPUE of bloaters in commercial fisheries in all Michigan waters of Lake Superior, 1929–1996. All data are corrected for changes in catch efficiency due to the conversion from cotton to nylon gill nets.

ciscoes during 1929–1996 differed considerably among statistical districts and varied greatly among years within statistical districts (Table 2; Figure 4). Most of the fishery before 1940 was conducted in statistical districts MS-2, MS-3, MS-4, and MS-6 and was nearly absent from MS-1 and MS-5. Annual fishing effort during these early years was low even in statistical districts where the fishery occurred (Figure 4) and was generally less than 2,000 km of net for all Michigan waters combined (Figure 5a). During the late 1950s through the mid-1970s, effort increased greatly and the fishery operated mostly in MS-3 (Figure 4), which encompasses the east and west sides of the Keweenaw Peninsula (Figure 2); similar fishing effort was expended in all of the remaining statistical districts combined. Fishing effort for deepwater ciscoes declined significantly throughout the 1980s and 1990s and remains extremely low today (Figures 4, 5a).

Total estimated landings of shortjaw ciscoes in all Michigan waters exceeded 80,000 kg/year in the mid-1930s and then declined rapidly during the late 1930s and 1940s to less than 10,000 kg/year by the late 1940s (Figure 5b). Harvest remained relatively low until the late 1950s but then increased rapidly to approach 100,000 kg in 1958 and then varied considerably

between 50,000 and 90,000 kg/year during 1961–1974. Thereafter, the harvest declined steadily, and by 1980 the fishery collapsed and never recovered. Mean annual catches in years when the fishery was prosecuted were the highest in statistical district MS-3 and lowest in MS-1 (Table 2). As with fishing effort, most of the harvest came from MS-3 (Figure 6) but was more evenly distributed among districts MS-2, MS-3, MS-4, and MS-6 before 1940. Harvests in these districts were declining early on and were modest—generally less than 30,000 kg/year—and recovered during the late 1950s–1970s but only in MS-2, MS-3, and MS-4.

Relative abundance of shortjaw ciscoes declined steadily and simultaneously in all statistical districts (Figure 7) and throughout Michigan waters combined (Figure 5c), regardless of the trends in or distribution of fishing effort or catches. The decline was already underway during the 1930s, continued throughout the time series, and had progressed markedly before the increase in fishing effort during the 1960s and 1970s. Declines in abundance were most pronounced during the 1930s in districts MS-3 and MS-4 and were apparent also in MS-1, where little fishing occurred. The highest relative abundances (greater than 50 kg/km)

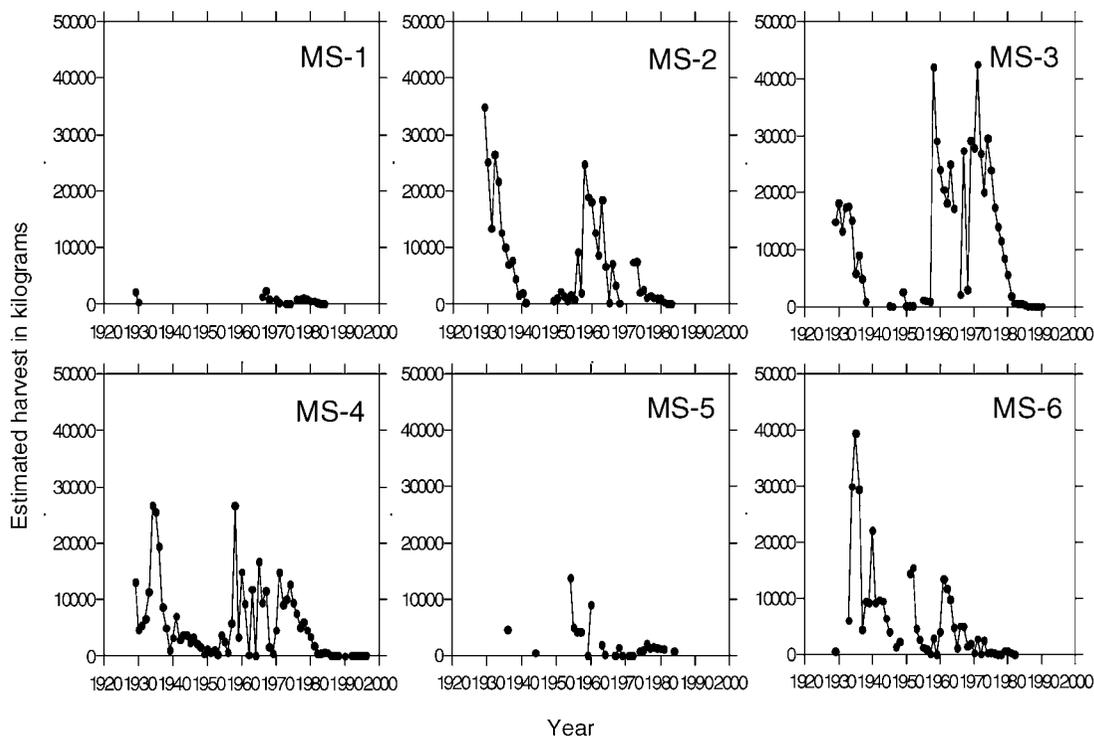


FIGURE 6.—Estimated total landings (kg) of shortjaw ciscoes by statistical district (Figure 2) in the Michigan waters of Lake Superior, 1929–1996.

that occurred in the early years were in MS-2, MS-3, MS-4, and MS-6, which are the districts that received most of the early fishing effort.

Determination of Overfishing

Estimated catches of shortjaw ciscoes were positively and significantly related to fishing effort in all statistical districts and year periods except (in MS-5) during 1951–1959 and for all districts combined (Table 2). Correlation coefficients were generally high in all districts and in all year periods, ranging between 0.53 in MS-5 (which had a modest fishery) during 1960–1996 and 0.99 in MS-4 during 1951–1959. The correlation coefficients for catch and effort for all districts combined were also high and significant (Table 2).

Probability of Extinction

At a threshold level of 0.01 kg/km of net, the likelihood of quasi-extinction was 100% (95% Bayesian credible interval = 97.7–100.0%) at 100 years (Figure 8). Our analyses suggest that the quasi-extinction risk in the 12th year (2008) past the last commercial CPUE date (1996) was 92.2% (95% Bayesian credible interval = 77.3–98.4%). The median

risk of quasi-extinction was predicted to exceed 99% by 2028 (with a lower credible interval suggesting a threshold crossing as early as 2010). Based upon IUCN criteria, the distribution of extinction probabilities at 10 years suggests that this population should be defined as critically endangered (greater than 80% decline in the population over a 10-year period).

Discussion

Our analysis of the commercial catch and effort data suggests that shortjaw ciscoes were declining in all districts of the Michigan waters of Lake Superior and that the decline was unrelated to the intensity of the fishery. Reported fishing occurred only in 18 of 67 years in statistical district MS-1 and in 24 of 67 years in MS-5, and annual catches were relatively low; hence, fishing could not explain the declines in those districts. The most active fishery was conducted in MS-3, but the annual catch there was highly correlated to fishing effort as was the case for most other districts and for all Michigan waters combined. Large significant correlations of catch with effort may suggest that fishing had not been severe enough to deplete stocks (Ricker 1975). Populations appear to have been declining since the 1930s, before the increase in fishing effort in the

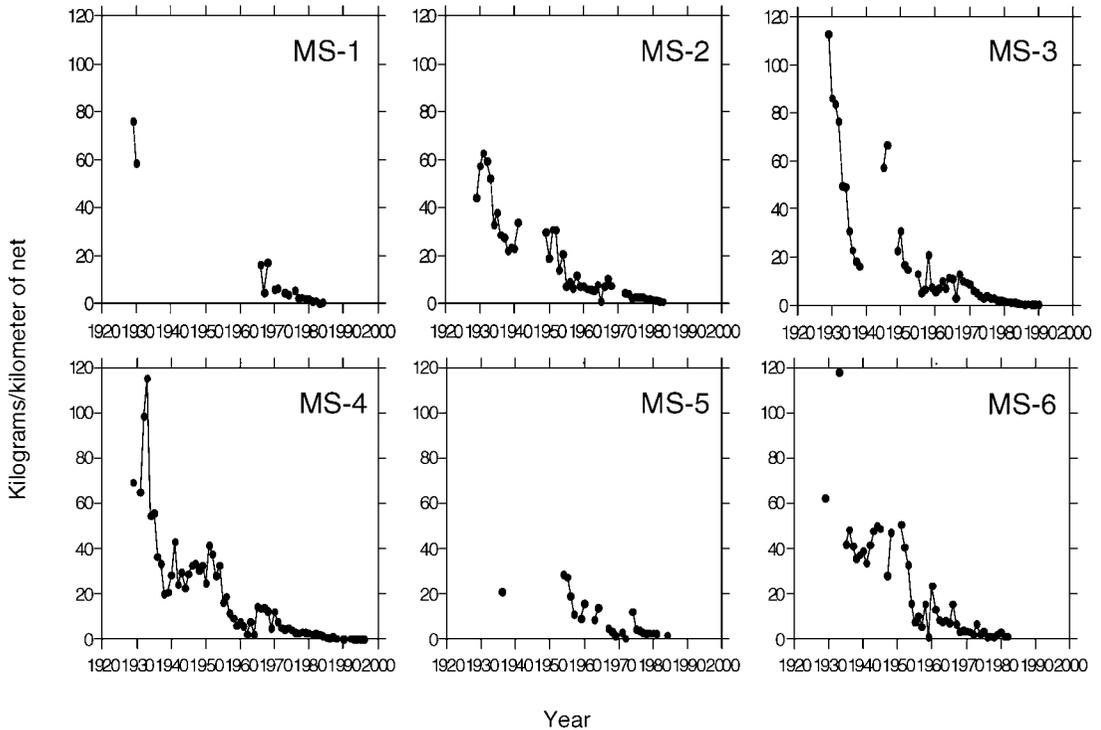


FIGURE 7.—Relative abundance (kg/km of net) of shortjaw ciscoes by statistical district (Figure 2) in the Michigan waters of Lake Superior, 1929–1996.

1960s and 1970s and well before the invasions of the sea lamprey *Petromyzon marinus* and rainbow smelt *Osmerus mordax* in the 1950s, which were previously implicated in the demise of other native species (Lawrie and Rahrer 1973). The ubiquitous decline of shortjaw ciscoes in Michigan waters and lakewide (Hoff and Todd 2004), even when fishing effort and landings were modest at best, suggests that commercial harvests were having little effect on the stocks.

Our analysis of the commercial CPUE time series also suggests that quasi-extinction of the shortjaw cisco is highly probable in the near future. Options for conservation and restoration are limited. Limiting harvest is a first consideration. Fisheries targeting deepwater ciscoes have largely disappeared due to low catch rates, nuisance bycatch of siscowet (a deepwater morphotype of lake trout *Salvelinus namaycush*), and attrition of fishers; hence, these fisheries are not likely to return. Bycatch of shortjaw ciscoes in fall spawning aggregation fisheries for the cisco may also be a problem. However, these fisheries, which historically used bottom-set gill nets, are now executed with pelagic nets set under the water surface for prespawning gravid females; therefore, encounters with shortjaw ciscoes are unlikely. Deepwater ciscoes are taken as

bycatch in bottom-set gill-net cisco fisheries in winter, but again these activities have largely disappeared. Predation pressure (Ebener 1995; Kitchell et al. 2000; Ray et al. 2007; Negus et al. 2008) on deepwater coregonines by the large standing stock of siscowet (Bronte et al. 2003) may hinder any recovery of

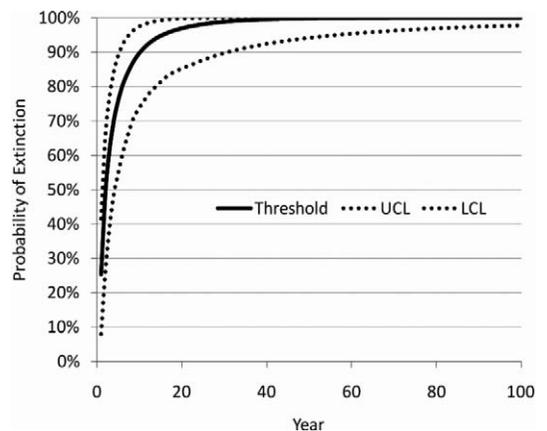


FIGURE 8.—Percent probability of shortjaw cisco extinction (with 95% prediction intervals: UCL = upper confidence limit, LCL = lower confidence limit) in Michigan waters of Lake Superior between 1997 (year 0) and 2097 (year 100).

shortjaw ciscoes, although the effect may be dampened by the low probabilities of shortjaw cisco encounter by siscowet (i.e., because so few shortjaw ciscoes are present compared with other prey). Trawl surveys by the USGS continue to index the relative abundance of shortjaw ciscoes lakewide and have noted a slight increase in their relative abundance, especially in eastern Lake Superior, but catches are extremely low (USGS, Ashland, Wisconsin, unpublished data).

The question remains that if directed fishing on shortjaw ciscoes cannot be implicated for the population collapse, what could have affected stocks lakewide? Other factors, such as negative interactions with exotic sea lampreys and rainbow smelt and hybridization with closely related species, may explain the demise of the shortjaw cisco. We dismiss the "exotic species hypothesis" because, as previously mentioned, the decline of the shortjaw cisco was already apparent in the 1930s, well before the sea lamprey and rainbow smelt became established as significant components of the fish community (Lawrie and Rahrer 1973). Beyond the timing issue, and even though recent stable isotope analysis of sea lampreys in Lake Superior indicate some predation on coregonines (Harvey et al. 2008), this is not a convincing argument for an effect on shortjaw ciscoes. It is likely that larger, more numerous ciscoes and lake whitefish *C. clupeaformis* would have been the targets of size-selective (Schneider et al. 1996) sea lamprey predation rather than the smaller shortjaw cisco, which was already declining in the 1950s when sea lamprey abundance was increasing. While rainbow smelt predation on larvae has been again suggested for the demise of ciscoes (Myers et al. 2009), similar interactions may have been possible for the species' decline, but again the occurrence of the rainbow smelt expansion in the 1950s (Anderson and Smith 1971) was far later than the shortjaw cisco declines suggested by our analysis. Competitive interactions with rainbow smelt were unlikely since it has been only recently (after the 1970s) that rainbow smelt and deepwater ciscoes have occupied similar trophic space (Schmidt et al. 2009). We do not believe that introgressive hybridization has played a significant role in the decline and recovery of ciscoes in Lake Superior. Densities of cisco species, bloaters, and kiyis in Lake Superior did not decline to levels as low as those observed in Lake Michigan (Smith 1964), where introgressive hybridization has been suggested as a cause for the declines. The effect that these other species would have had on shortjaw ciscoes would have been genetic swamping as populations of shortjaw ciscoes declined to very low levels relative to other deepwater ciscoes. Despite prolonged periods of low densities for more than 40 years, most adult shortjaw

ciscoes captured since 1999 do not appear to be hybrids but are similar morphologically to those described by Koeltz (1929).

We suggest an alternative hypothesis that may explain the decline of the shortjaw cisco, once one of the most abundant deepwater ciscoes. Historically, the cisco—and to some extent deepwater ciscoes—constituted the forage for the lake trout (Dryer et al. 1965), which was, and still is, the principal keystone predator in Lake Superior. Large-scale commercial fisheries for lake trout date back to the 1830s but expanded and modernized with European settlement in the 1880s (Lawrie and Rahrer 1973). Lakewide harvest of lake trout averaged around 2 million kg/year from the late 1880s to the 1950s, after which stocks collapsed due to overfishing and sea lamprey invasion (Hile et al. 1951; Lawrie and Rahrer 1973; Hansen et al. 1995). The increases in fishing intensity, which sustained high harvests, masked declines in relative abundance of lake trout. Stocks of both the nearshore lean morphotype of lake trout (Hile et al. 1951; Pycha and King 1975; Hansen et al. 1995; Wilberg et al. 2003) and the offshore siscowet (Bronte and Sitar 2008) were declining throughout 1929–1960. Commercial fisheries before the 1930s were minimally regulated and enforced (Regier and Applegate 1972); therefore, overfishing and stock declines probably began much earlier than the late 1920s, when commercial catch and effort reporting became mandatory. We suggest that the continual decline of the keystone predator, lake trout, from directed overfishing during 1850–1950 resulted in a release of predation pressure on ciscoes, the principal prey of lake trout. Lake trout declined almost simultaneously everywhere after 1929 in Michigan waters (Wilberg et al. 2003; Bronte and Sitar 2008) and elsewhere (Hansen et al. 1995). Thus, the decline was so widespread that it could explain the lakewide increase in cisco abundance that we hypothesize led to the decline of the shortjaw cisco.

The decline in lake trout-induced predation mortality allowed cisco populations to increase during 1930–1950 as evidenced by commercial CPUE data for some areas in Wisconsin waters of Lake Superior (Selgeby 1982). This decline was more pronounced for Michigan waters of Lake Superior (Figure 5d), where cisco CPUE (corrected for net material changes) increased over 50% from the 1930s to a peak in the early 1950s. In Minnesota waters, cisco CPUE was increasing steadily from 1949 (the earliest year reported) to the mid- and late 1950s before fishing effort peaked during 1959–1961 (Wright 1973). The increase of ciscoes in Michigan waters was simultaneous with the declines in shortjaw cisco abundance (Figure 5c, d), which probably began before 1930 (i.e., before any records

of relative abundance). Of the four cisco species of Lake Superior (cisco, shortjaw cisco, bloater, and kiyi), the shortjaw cisco and bloater have similar bathymetric distributions, although shortjaw ciscoes are found at greater depths than are bloaters (Gorman and Todd 2007). The cisco is more abundant in shallower waters and the kiyi is found at greater depths than is the shortjaw cisco. Dietary specialization provides further segregation; the principal food items of ciscoes are calanoid copepods, whereas shortjaw ciscoes and kiyis consume primarily shrimp *Mysis* spp., and bloaters have a more varied diet (Anderson and Smith 1971). Thus, the potential for resource competition among adult ciscoes and deepwater ciscoes appears limited due to niche segregation. However, there is potential for resource competition among age-0 coregonines given their common need for warm, productive habitats to achieve sufficient growth to survive their first winter. Laboratory studies have demonstrated that sufficient growth in the first summer of life requires temperatures of 15–20°C (Edsall and Frank 1997; Edsall 1999) and sufficient food (Pangle et al. 2004). Warm, productive nursery habitats represent a limited resource for juvenile coregonines in Lake Superior, which is cold and oligotrophic. Hoff (2004) modeled cisco recruitment dynamics and concluded that adults preyed on their own larvae; hence, adult ciscoes may also prey on shortjaw cisco larvae. However, it is unlikely that shortjaw ciscoes would suffer from disproportionate mortality caused by adult ciscoes. On the contrary, synchronization of recruitment events among cisco species (Bronte et al. 2003; Gorman and Hoff 2009) would probably serve to buffer the effects of mortality of juveniles of rarer cisco species. Although the actual mechanisms responsible may never be known, we suggest that there is a distinct possibility that an interaction detrimental to the shortjaw cisco existed. Recent stable isotope analysis of the historical Lake Superior food web indicates that the cisco was sharing the same trophic resources as the deepwater ciscoes during 1934–1966 (Schmidt et al. 2009) and may have had a greater effect on the shortjaw cisco than the distinct ecologies of these species would suggest.

Cisco relative abundance declined greatly during the 1960s; thus, in the absence of shortjaw ciscoes and with low levels of siscowet in deep water (>80 m; Bronte et al. 2008), the abundance of bloaters increased markedly because they were the only coregonine left to occupy this bathymetric niche. Bloater CPUE (corrected for net material changes) increased during the 1960s and 1970s (Figure 5e) and accounted for most of the harvest of deepwater ciscoes in Michigan waters during these years (Peck 1977). The subsequent decline of

bloaters after the peak in harvest during 1980–1995 may have been the result of recruitment overfishing coupled with predation from an increase in siscowet biomass, which was occurring during this time period (Bronte et al. 2003). Large bycatches of small siscowet were increasing during the 1990s (Bronte et al. 2003), and smaller catches of deepwater ciscoes led to the end of the fishery in the late 1990s. The lack of shortjaw cisco recovery after cisco and siscowet populations declined may have been because their abundance was too low for a rapid population recovery. From what we know of the cisco recovery in Lake Superior, these processes may take years if the intermittent recruitment patterns seen in the cisco (Bronte et al. 2003; Stockwell et al. 2009) are shared by the shortjaw cisco.

The decline of the shortjaw cisco and its high risk of extinction in Lake Superior represent a potential a threat to the ecological integrity of the most pristine native fish community in the Great Lakes (Bronte et al. 2003). Only the paddlefish *Polyodon spathula* and Arctic grayling *Thymallus arcticus*, both glacial relicts, have been extirpated from Lake Superior (Bailey and Smith 1981), but these species were probably of minor ecological importance compared with the predominant deepwater species (*Coregonus* spp., lake trout, deepwater sculpin *Myoxocephalus thompsonii*) that make up or prey upon most of the biomass in Lake Superior (USGS, Ashland, Wisconsin, unpublished data). Several other species of Great Lakes ciscoes have become extinct or have been extirpated in major portions of their ranges (Fleischer 1992). This fauna was unique and endemically derived with specific adaptations to various aspects of the aquatic environment of the Great Lakes (Todd and Smith 1992). The great fluctuations that have been observed in the population dynamics of the surviving species, such as the cisco (Bronte et al. 2003) and bloater (Madenjian et al. 2002), may be the result of ecological destabilization based on this lost diversity. In Lake Superior, the loss of deepwater cisco diversity highlights the importance of the keystone predator, the lake trout (both lean and siscowet morphotypes; see Paine 1966). Lake trout, through predation, may have maintained community diversity and stability (of all cisco species) by preventing overt competition in the trophic level below by feeding on the most abundant species, the cisco. The reduction in lake trout predation allowed cisco populations to expand, which resulted in a decline of the shortjaw cisco. Although the cisco and all three deepwater ciscoes remain in Lake Superior, total biomass in deep water has shifted toward the kiyi and bloater, whereas the previously abundant shortjaw cisco is on the brink of extirpation. Continued surveys by USGS have captured more shortjaw ciscoes in recent years, and

this may represent some level of population recovery or may simply be an artifact of more rigorous classification rules compared with previous years. If the former is true, then this could represent a return to conditions that are more favorable for shortjaw cisco recruitment in the presence of restored populations of the keystone predators (the lean lake trout and siscowet) and a further recovery of Lake Superior's fish community.

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References

- Anderson, E. D., and L. L. Smith. 1971. Factors affecting the abundance of lake herring (*Coregonus artedii* LeSueur) in western Lake Superior. *Transactions of the American Fisheries Society* 100:691–707.
- Bailey, R. M., and G. R. Smith. 1981. Origin and geography of fish fauna of the Laurentian Great Lakes basin. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1539–1561.
- Baldwin, N. S., R. W. Saalfeld, M. A. Roos, and H. J. Buettner. 1979. Commercial fish production in the Great Lakes, 1867–1977. Great Lakes Fishery Commission Technical Report 3.
- Bedrick, E. J., R. Christensen, and W. O. Johnson. 1996. A new perspective on priors for generalized linear models. *Journal of the American Statistical Association* 91:1450–1460.
- Berst, A. H., and G. R. Spangler. 1972. Lake Huron: effects of exploitation, introductions, and eutrophication on the salmonid community. *Journal of the Fisheries Research Board of Canada* 29:877–887.
- Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23:481–506.
- Branscum, A. J., W. O. Johnson, and M. C. Thurmond. 2007. Bayesian beta regression: applications to household expenditure and genetic distance between foot-and-mouth disease viruses. *Australian and New Zealand Journal of Statistics* 49:287–301.
- Bronte, C. R., M. P. Ebener, D. R. Schreiner, D. S. DeVault, M. M. Petzold, D. A. Jensen, C. Richards, and S. J. Lozano. 2003. Fish community change in Lake Superior, 1970–2000. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1552–1574.
- Bronte, C. R., and S. P. Sitar. 2008. Harvest and relative abundance of siscowet lake trout in Michigan waters of Lake Superior, 1929–1961. *Transactions of the American Fisheries Society* 137:916–926.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.
- Christie, W. J. 1972. Lake Ontario: effects of exploitation, introductions, and eutrophication on the salmonid community. *Journal of the Fisheries Research Board of Canada* 25:913–929.
- Christie, W. J. 1974. Changes in the fish species composition of the Great Lakes. *Journal of the Fisheries Research Board of Canada* 31:827–854.
- DeMaster, D., R. Angliss, J. Cochran, P. Mace, R. Merrick, M. Miller, S. Rumsey, B. Taylor, G. Thompson, and R. Waples. 2004. Recommendations to NOAA Fisheries: ESA listing criteria by the Quantitative Working Group, 10 June 2004. NOAA Technical Memorandum NMFSF/SPO-67.
- Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. *Ecological Monographs* 64:205–224.
- Dryer, W. R., and J. Beil. 1964. Life history of lake herring in Lake Superior. *Fishery Bulletin* 63:493–529.
- Dryer, W. R., L. F. Erkkila, and C. L. Tetzloff. 1965. Food of the lake trout in Lake Superior. *Transactions of the American Fisheries Society* 94:169–176.
- Ebener, M. P. 1995. Bioenergetics of predatory fish in western U.S. waters of Lake Superior. Report prepared for the Red Cliff Band of Lake Superior Chippewas, Red Cliff Fisheries Department, Bayfield, Wisconsin.
- Edsall, T. A. 1999. The growth–temperature relation of juvenile lake whitefish. *Transactions of the American Fisheries Society* 128:962–964.
- Edsall, T. A., and A. M. Frank. 1997. The effect of temperature on growth of juvenile bloater. *Journal of Great Lakes Research* 23:468–471.
- Fagan, W. F., and E. E. Holmes. 2006. Quantifying the extinction vortex. *Ecology Letters* 9:51–60.
- Fleischer, G. W. 1992. Status of coregonines fishes in the Laurentian Great Lakes. *Polskie Archiwum Hydrobiologii* 39:247–259.
- Gilpin, M. E., and M. E. Soule. 1986. Minimum viable populations of species extinction. Pages 19–34 in M. E. Soule, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer, Sunderland, Massachusetts.
- Gorman, O. T., and M. H. Hoff. 2009. Changes in the Lake Superior fish community during 1978–2003: chronicling the recovery of a native fauna. Pages 493–532 in M. Munawar and I. F. Munawar, editors. *State of Lake Superior*. Ecovision World Monograph Series, Aquatic Ecosystem Health and Management Society, Burlington, Ontario.
- Gorman, O. T., and T. N. Todd. 2007. History of the shortjaw cisco (*Coregonus zenithicus*) in Lake Superior, 1895–2003. *Advances in Limnology* 60:433–458.
- Hansen, M. J., J. W. Peck, R. G. Schorffhaar, J. H. Selgeby, D. R. Schreiner, S. T. Schram, B. L. Swanson, W. R. MacCallum, M. K. Burnham-Curtis, G. L. Curtis, J. W.

- Heinrich, and R. J. Young. 1995. Lake trout (*Salvelinus namaycush*) populations in Lake Superior and their restoration in 1959–1993. *Journal of Great Lakes Research* 21(Supplement 1):152–175.
- Hartman, W. L. 1973. Effects of exploitation, environmental changes, and new species on the habitats and resources of Lake Erie. Great Lakes Fishery Commission Technical Report 22.
- Harvey, C. J., M. P. Ebener, and C. K. White. 2008. Spatial and ontogenetic variability of sea lamprey diets in Lake Superior. *Journal of Great Lakes Research* 34:434–449.
- Hile, R. 1962. Collection and analysis of commercial fishery statistics in the Great Lakes. Great Lakes Fishery Commission Technical Report 5.
- Hile, R. J., P. H. Eschmeyer, and G. F. Lunger. 1951. Status of the lake trout fishery in Lake Superior. *Transactions of the American Fisheries Society* 80:278–312.
- Hoff, M. H. 2004. Biotic and abiotic factors related to lake herring recruitment in the Wisconsin waters of Lake Superior, 1984–1998. *Journal of Great Lakes Research* 30(Supplement 1):423–433.
- Hoff, M. H., and T. N. Todd. 2004. Status of the shortjaw cisco (*Coregonus zenithicus*) in Lake Superior. *Annales Zoologici Fennici* 41:147–154.
- Holmes, E. E. 2001. Estimating risks in declining populations with poor data. *Proceedings of the National Academy of Sciences of the United States of America* 98:5072–5077.
- Holmes, E. E. 2004. Beyond theory to application and evaluation: diffusion approximations for population viability analysis. *Ecological Applications* 14:1272–1292.
- Jensen, A. L., and H. J. Buettner. 1976. Lake trout, whitefish, chubs, and lake herring yield and effort data for state of Michigan waters of the upper Great Lakes: 1929–1973. Michigan Sea Grant Program, Technical Report Number 52, Ann Arbor.
- Kitchell, J. F., S. P. Cox, C. J. Harvey, T. B. Johnson, D. M. Mason, K. K. Schoen, K. Aydin, C. Bronte, M. Ebener, M. Hanson, M. Hoff, S. Schram, D. Schreiner, and C. J. Walters. 2000. Sustainability of the Lake Superior fish community: interactions in a food web. *Ecosystems* 3:545–560.
- Koeltz, W. 1926. Fishing industry of the Great Lakes. Pages 553–617 in Appendix XI to the Report of the U.S. Commissioner of Fisheries for 1925. Department of Commerce, Bureau of Fisheries, Document 1001, Washington, D.C.
- Koeltz, W. 1929. Coregonid fishes of the Great Lakes. U.S. Bureau of Fisheries Bulletin 43:297–643.
- Lande, R., S. Engen, and B. Sæther. 2003. Stochastic population dynamics in ecology and conservation. Oxford University, Oxford, UK.
- Lande, R., and S. H. Orzack. 1988. Extinction dynamics of age-structured populations in a fluctuating environment. *Proceedings of the National Academy of Science of the United States of America* 85:7418–7421.
- Lawrie, A. H., and J. F. Rahrer. 1972. Lake Superior: effects of exploitation and introductions on the salmonid community. *Journal Fisheries Research Board of Canada* 29:765–776.
- Lawrie, A. H., and J. F. Rahrer. 1973. Lake Superior: a case history of the lake and its fisheries. Great Lakes Fishery Commission Technical Report 19.
- Mace, G. M., and R. Lande. 1991. Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. *Conservation Biology* 5:148–157.
- Madenjian, C. P., G. L. Fahnenstiel, T. H. Johengen, T. F. Nalepa, H. A. Vanderploeg, G. W. Fleischer, P. J. Schneeberger, D. M. Benjamin, E. B. Smith, J. R. Bence, E. S. Rutherford, D. S. Lavis, D. M. Robertson, D. J. Jude, and M. P. Ebener. 2002. Dynamics of the Lake Michigan food web, 1970–2000. *Canadian Journal of Fisheries and Aquatic Sciences* 59:736–753.
- Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts.
- Myers, J. T., M. L. Jones, J. D. Stockwell, and D. L. Yule. 2009. Reassessment of the predatory effects of rainbow smelt on ciscoes in Lake Superior. *Transactions of the American Fisheries Society* 138:1352–1368.
- Negus, M. T., D. R. Schreiner, T. N. Helpem, S. T. Schram, M. J. Sider, and D. M. Pratt. 2008. Bioenergetics evaluation of the fish community in the western arm of Lake Superior in 2004. *North American Journal of Fisheries Management* 28:1649–1667.
- Paine, R. M. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- Pangle, K. L., T. M. Sutton, R. E. Kinnunen, and M. H. Hoff. 2004. Overwinter survival of juvenile lake herring in relation to body size, physiological condition, energy stores, and food ration. *Transactions of the American Fisheries Society* 133:1235–1246.
- Peck, J. W. 1977. Species composition of deep-water ciscoes (chubs) in commercial catches from Michigan waters of Lake Superior. Michigan Department of Natural Resources, Fisheries Division, Fisheries Research Report 1849, Lansing.
- Punt, A., and R. Hilborn. 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. *Reviews in Fish Biology and Fisheries* 7:35–63.
- Pycha, R. L., and G. R. King. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950–1970. Great Lakes Fishery Commission Technical Report 28.
- Ray, B. A., T. R. Hrabik, M. P. Ebener, O. T. Gorman, D. R. Schreiner, S. T. Schram, S. P. Sitar, W. P. Mattes, and C. R. Bronte. 2007. Diet and prey selection by Lake Superior lake trout during spring, 1986–2001. *Journal of Great Lakes Research* 33:104–113.
- Reed, K. M., M. O. Dorschner, T. N. Todd, and R. B. Phillips. 1998. Sequence analysis of the mitochondrial DNA control region of ciscoes (genus *Coregonus*): taxonomic implications for the Great Lakes species flock. *Molecular Ecology* 7:1091–1096.
- Regier, H. A., and V. C. Applegate. 1972. Historical review of the management approach to exploitation and introduction in SCOL lakes. *Journal of the Fisheries Research Board of Canada* 29:683–692.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* 191.
- Schmidt, S. N., M. J. Vander Zanden, and J. F. Kitchell. 2009. Long-term food web change in Lake Superior. *Canadian*

- Journal of Fisheries and Aquatic Sciences. 66:2118–2129.
- Schneider, C. P., R. W. Owens, R. A. Bergstedt, and R. O’Gorman. 1996. Predation by sea lamprey (*Petromyzon marinus*) on lake trout (*Salvelinus namaycush*) in southern Lake Ontario, 1982–1992. Canadian Journal of Fisheries and Aquatic Sciences 53:1921–1932.
- Scidmore, W. J., and Z. Scheftel. 1958. Relative efficiency and selectivity of experimental nets of linen and nylon. Minnesota Fish and Game Investigations, Fisheries Service 1:46–53.
- Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184.
- Selgeby, J. H. 1982. Decline of the lake herring (*Coregonus artedii*) in Lake Superior: an analysis of the Wisconsin herring fishery, 1936–1978. Canadian Journal of Fisheries Aquatic Science 39:554–563.
- Smith, S. H. 1964. Status of the deepwater cisco population of Lake Michigan. Transaction of the American Fisheries Society 93:155–163.
- Smith, S. H. 1968. Species succession and fishery exploitation in the Great Lakes. Journal of the Fisheries Research Board of Canada 25:667–693.
- Smith, S. H. 1970. Species interactions of the alewife in the Great Lakes. Transactions American Fisheries Society 99:754–765.
- Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. Van der Linde. 2002. Bayesian measures of model complexity and fit (with discussion). Journal of the Royal Statistical Society, Series B 64:583–616.
- Spiegelhalter, D., A. Thomas, and N. Best. 2004. User manual, WinBUGS: Bayesian inference using Gibbs sampling, version 1.4. MRC Biostatistics Unit, Cambridge, UK. Available: mrc-bsu.cam.ac.uk/bugs/winbugs/contents.shtml. (February 2009).
- Stockwell, J. D., M. P. Ebener, J. A. Black, O. T. Gonnar, T. R. Harbik, R. E. Kinnunen, W. P. Mattes, J. K. Oyadomari, S. T. Schram, D. R. Schreiner, M. J. Seider, S. P. Sitar, and D. L. Yule. 2009. A synthesis of cisco recovery in Lake Superior: implications for native fish rehabilitation in the Laurentian Great Lakes. North American Journal of Fisheries Management 29:626–652.
- Todd, T. N. 2003. Status of the shortjaw cisco, *Coregonus zenithicus* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.
- Todd, T. N., and G. R. Smith. 1992. A review of differentiation in Great Lakes ciscoes. Polskie Archiwum Hydrobiologii 39:261–267.
- Todd, T. N., and R. M. Stedman. 1989. Hybridization of ciscoes (*Coregonus* spp.) in Lake Huron. Canadian Journal of Zoology 67:1679–1685.
- Turgeon, J., A. Estoup, and L. Bernatchez. 1999. Species flock in the North American Great Lakes: molecular ecology of Lake Nipigon ciscoes (Teleostei: Coregonidae: *Coregonus*). Evolution 53:1857–1871.
- Van Oosten, J. 1937. The age, growth, and sex ratio of the Lake Superior longjaw, *Leucichthys zenithicus* (Jordan and Evermann). Papers of the Michigan Academy of Science, Arts, and Letters 22:691–711.
- Wells, L., and A. L. McLain. 1972. Lake Michigan: effects of exploitation, introductions, and eutrophication on the salmonid community. Journal of the Fisheries Research Board of Canada 29:889–898.
- Wilberg, M. J., M. J. Hansen, and C. R. Bronte. 2003. Historic and modern abundance of wild lean lake trout in Michigan waters of Lake Superior: implications for restoration goals. North American Journal of Fisheries Management 23:100–108.
- Wright, A. T., editor. 1973. A summary finding report on Lake Superior cisco (*Coregonus artedii*) populations. Prepared for the Lake Superior Cisco Subcommittee of the Lake Superior Committee of the Great Lakes Fishery Commission, Ann Arbor, Michigan.