Is it possible to identify habitat for a rare species? Shortjaw Cisco (Coregonus zenithicus) in Lake Huron as a case study

Benjamin T. Naumann · Stephen S. Crawford

Received: 27 January 2009 / Accepted: 29 July 2009 © Springer Science + Business Media B.V. 2009

Abstract The Government of Canada is considering a recommendation by the Committee on the Status of Endangered Wildlife in Canada to list shortjaw cisco (Coregonus zenithicus) as "Threatened" throughout its range under the Species At Risk Act (SARA). If the listing is approved, shortjaw cisco will receive legal protection, including protection for its 'critical habitat.' This study focused on habitat characteristics associated with specimens identified as shortjaw cisco collected with targeted sampling in Lake Huron of the Laurentian Great Lakes. Competing habitat-use models were developed using available data for three physical habitat variables: Water Depth, Substrate Slope, and Cliff Distance, and the models were evaluated using binary logistic regression and ranking of Akaike information criteria. For the habitat factors examined, Water Depth was the most important variable for explaining the observed distribution of identified shortjaw cisco, although this factor alone was not sufficient to adequately represent habitat for this taxonomically uncertain and rare animal. Future habitat discrimination for this hypothesized species at risk must be based on (a) reduction of taxonomic uncertainty, (b) expansion of sampling effort, and (c) consideration of additional physical and ecological habitat factors.

Keywords Coregoninae · Cisco · Laurentian Great Lakes · Species at risk · Critical habitat · Endangered · Threatened · Model selection · Uncertainty

Introduction

In 2002, the Government of Canada passed the Species at Risk Act (SARA) "to prevent wildlife species from being extirpated or becoming extinct, to provide for the recovery of wildlife species that are extirpated, endangered or threatened as a result of human activity" (SARA 2003). For species listed under SARA as "Extirpated," "Endangered" or "Threatened," the federal government is required to prepare appropriate recovery strategies which, if deemed feasible, require the identification and legal protection of "critical habitat" (Mooers et al. 2007). "Critical habitat" is explicitly defined under SARA as "the habitat that is necessary for the survival or recovery of a listed wildlife species and that is identified as the species' critical habitat in the recovery strategy or in an action plan for the species" (SARA 2003). However, in the case of taxonomically uncertain and rare species at risk, it is not clear

B. T. Naumann · S. S. Crawford Department of Integrative Biology, University of Guelph, Guelph, ON N1G 2W1, Canada

S. S. Crawford () Chippewas of Nawash Unceded First Nation, R.R. #5, Wiarton, ON NOH 2T0, Canada e-mail: scrawfor@uoguelph.ca

Published online: 07 August 2009



whether "habitat"—much less "critical habitat" (Hall et al. 1997)—can be identified in terms that would be meaningful for a species recovery strategy.

Populations of shortjaw cisco (Coregonus zenithicus) were historically found in western and central Canada (Scott and Crossman 1973; Houston 1988; Murray and Reist 2003), including deep waters of the Laurentian Great Lakes, except in Lake Ontario (Fig. 1). Over the past century Great Lakes shortjaw cisco populations declined in distribution and abundance; these changes have been variously attributed to the effects of fishing, ecological interactions with native and exotic species, or habitat degradation (Smith 1968; Smith and Todd 1984; Todd 1985; Steinhilber et al. 2002). By the mid-1980s, shortjaw cisco had been declared extirpated from Lakes Erie, Michigan and Huron (Scott and Smith 1962; Scott and Crossman 1973; Todd 1985). In 2003, routine deepwater cisco sampling in Lake Huron waters surrounding the Saugeen (Bruce) Peninsula yielded 12 specimens that were tentatively identified as shortjaw cisco. The status of shortjaw cisco was examined by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), which submitted a 2003 recommendation to the federal government that C. zenithicus be listed under SARA as "Threatened" throughout its distribution (COSEWIC 2003). After consideration, the Minister of Fisheries & Oceans referred the issue back to COSEWIC for re-evaluation, citing: (1) lack of incorporation of Aboriginal Traditional Knowledge and (2) taxonomic uncertainty concerning the species (DFO 2004). As of May 2009, COSEWIC was considering a revised assessment report for shortjaw cisco, and deliberating on a second recommendation for the federal government to list the species under SARA, with potential requirements for protection of "critical habitat."

In 2004, the Chippewas of Nawash Unceded First Nation and Parks Canada initiated a targeted sampling program with the purpose of learning more about the

Fig. 1 Historic distribution of shortjaw cisco (Coregonus zenithicus) in North America. Stars represent presence of the species in different lakes (adapted from COSEWIC 2003)





distribution, abundance and associated habitat of hypothesized shortjaw cisco in central Lake Huron. No previous attempts had been made to quantify the abiotic or biotic habitat factors that affect the distribution of shortjaw cisco in the Great Lakes generally, or in Lake Huron specifically. The goal of this study was to determine if habitat could be effectively identified for a taxonomically uncertain and rare species, using post-hoc analysis of the Lake Huron shortjaw cisco as a case study. To achieve this goal, it was necessary to satisfy the following specific objectives:

- (1) Compile and describe the distribution of targeted shortjaw cisco samples (effort and catch) for Lake Huron;
- (2) Develop a set of habitat-use models for Water Depth, Substrate Slope, Cliff Distance that represent alternative ecological hypotheses about the influence of physical habitat variables on identified shortjaw cisco distribution in Lake Huron; and
- (3) Evaluate the degree to which observed distribution of identified shortjaw cisco can be explained quantitatively by the selected physical habitat variables.

Materials and methods

Sample effort and catch

The study area consisted of waters surrounding the Saugeen (Bruce) Peninsula, Lake Huron, Canada (Fig. 2). Waters within the study area have been characterized as oligotrophic, and were representative of the Main Basin which receives major water influences from Lakes Michigan and Superior (Sly and Munawar 1988). During the 2003-2007 period, a collaboration of Nawash, Fisheries & Oceans Canada, Parks Canada, and Ontario Ministry of Natural Resources biologists conducted targeted sampling over various seasons for deepwater cisco at 73 locations around the Saugeen Peninsula (Table 1, Fig. 2). These sampling sites had been previously identified as shortjaw cisco sampling sites by Koelz (1929), or had been previously used by local fishermen who engaged in commercial fisheries for deepwater cisco. Sampling was conducted using 1,100 m bottom-set monofilament gillnets, with 6.4-6.7 cm stretched mesh sizes, and 91.4-127.0 cm mesh panels. Gillnets were deployed for 24–72 h depending on weather conditions, but were most commonly deployed for a period of 48 h. Start and finish

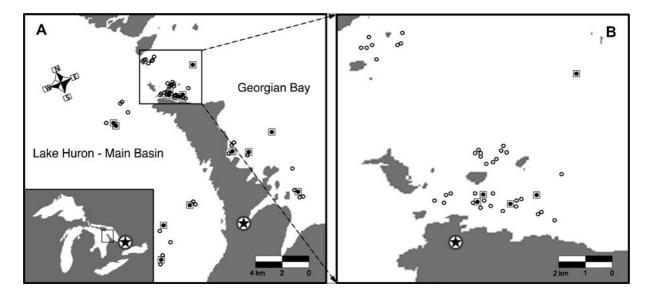


Fig. 2 Location of 73 targeted deepwater cisco samples around the Saugeen (Bruce) Peninsula in Lake Huron from 2003–2007. *Open circles* represent sample locations where no identified shortjaw cisco (*Coregonus zenithicus*) were found, while *closed circles in boxes* represent sample locations where identified

shortjaw cisco were collected. **a** map of the study area in Central Lake Huron, with a *star* representing Wiarton, Ontario (inset map of the Great Lakes basin, with a *star* representing Toronto, Ontario) **b** enlarged map of the highly sampled archipelago, with a *star* representing Tobermory, Ontario



Table 1 Seasonal summary of shortjaw cisco (*Coregonus zenithicus*) targeted sampling effort and catch from Lake Huron, based on targeted sampling (2003–2007). A total of 25 identified specimens of shortjaw cisco (SJC) were captured at 14 of 73 samples

Season	2003	2004	2005	2006	2007	Total
Winter	2	1	0	8	0	11
Spring	10	0	0	9	13	32
Summer	0	0	11	0	0	11
Fall	10	0	9	0	0	19
Subtotal	22	1	20	17	13	73
Samples with SJC	9	0	2	3	0	14
Number of SJC	12	0	4	9	0	25

coordinates for latitude/longitude of each sample event were determined using an on-board GPS.

All deepwater cisco specimens were retained for preliminary species identification by Nawash biologists using Todd (2001) as a general guide. Suspected shortjaw cisco were sent for identification by coregonid experts Nick Mandrak (Fisheries & Oceans Canada, Burlington, Ontario), Tom Pratt (Fisheries & Oceans Canada, Sault Ste. Marie, Ontario), and Tom Todd (United States Geological Survey, Ann Arbor, Michigan). Based on these expert decisions, sample locations were scored for presence/absence of identified shortjaw cisco, and identified specimens were forwarded to the Royal Ontario Museum for deposition in the ichthyology collection.

Habitat-use models

A review of the available literature on shortjaw cisco ecology revealed a set of physical habitat factors that had previously been suggested as possible determinants of shortjaw cisco distribution: Water Depth, Substrate Slope, and the distance to sharp discontinuities in topographic relief of the lake bottom hereafter referred to as Cliff Distance. Shortjaw cisco is typically considered a deepwater species, often occupying locations below the thermocline (Koelz 1929; Scott and Smith 1962; Todd and Smith 1980). Sloping substrate is a bathymetric habitat factor that may influence the distribution of shortjaw cisco in Lake Huron. In Lake Superior, the shortjaw cisco has been almost exclusively found above sloping lake bathymetry (Tom Pratt, Fisheries & Oceans Canada, personal communication). Sloping lake bottoms in the Great Lakes have been associated with high abundance of the burrowing amphipod Diporeia spp. (Evans et al. 1990). Diporeia and the freshwater shrimp (Mysis relicta) together play a major role in energy distribution between upper and lower trophic levels generally (Parker 1980; Gardner et al. 1990), and an increasingly unstable food web for deepwater fishes including shortjaw cisco specifically (Owens and Dittman 2003; Hondorp et al. 2005; Nalepa et al. 2007; Clemens and Crawford 2009). Cliff Distance is another bathymetric habitat factor that may influence the distribution of shortjaw cisco in Lake Huron. In Lake Superior, shortjaw cisco have often been found in proximity to underwater cliffs (Koelz 1929), while in Lake Huron, commercial fishermen have historically targeted deepwater cisco species in locations near underwater cliffs (Jobes 1949). Underwater cliffs can force upwelling of deep, nutrient-rich water into shallower depths, leading to high levels of primary production (Smith 1996). Taken together, this set of three physical habitat variables was selected for this study due to their potential ecological importance for shortjaw cisco, as well as availability of appropriate data from the targeted Lake Huron sampling program. The three selected habitat variables (Water Depth, Substrate Slope, Cliff Distance) were combined to form a set of seven habitat-use models representing different biological hypotheses about factors affecting shortjaw cisco distribution (Table 2). The variables were quantified for each of the 73 sample locations using a digital elevation map of Lake Huron (10× 10 m pixels) imported to ArcGIS 9.1 (Environmental Systems Research Institute, Redlands, California,

Table 2 Set of competing habitat-use models (hypotheses) proposed to explain the distribution of identified shortjaw cisco (*Coregonus zenithicus*) in Lake Huron. A total of seven models were created by combining Water Depth, Substrate Slope and Cliff Distance

Model structure
$\beta_0 + \beta_1(D)$
$\beta_0 + \beta_1(S)$
$\beta_0 + \beta_1(C)$
$\beta_0 + \beta_1(D) + \beta_2(S)$
$\beta_0 + \beta_1(D) + \beta_2(C)$
$\beta_0 + \beta_1(S) + \beta_2(C)$
$\beta_0\!+\!\beta_1(D)\!+\!\beta_2(S)\!+\!\beta_3(C)$



USA). The map was generated by Parks Canada using contour data collected by the National Oceanic and Atmospheric Administration and Canadian Hydrographic Service. Sample GPS coordinates were converted to decimal degrees, and used to identify midpoints for each sample. Circular buffers with a radius of 1,100 m were created around each sample midpoint in ArcGIS.

Water Depth was calculated by determining the average depth for all of the pixels within the sample buffer. Substrate Slope at each sample was calculated as follows: (1) a contour map layer was created from the digital map; (2) within each buffer, the maximum slope was determined by creating a line through the greatest change in elevation through the mid-point of the buffer; (3) Hawth spatial ecological GIS tools (Hawthorne 2007) were used to convert the line into points with a spacing equal to the resolution of the digital map, and the slope was taken from a linear regression of Water Depth over distance (SPSS 2006). Underwater cliffs were defined as a submerged feature with a slope of 10° or greater, and were filtered using the Spatial Analyst Extension in ArcGIS; the Extraction Values to Points function was used to determine the Euclidean distance from each sample to the nearest cliff.

Statistical analysis

To reduce redundancy in the analysis, Pearson's correlation test was used to evaluate the correlations among habitat variables. Habitat use was modeled using binary logistic regression due to the fact that shortjaw cisco occurrence was measured as presence/absence (1/0). Binary logistic regression (SPSS 2006) yielded -2 log maximum likelihood estimates as a measure of the empirical data explained by each model. Akaike's Information Criterion (AIC) was used to determine the relative strength of each model for predicting shortjaw cisco presence/absence (Burnham and Anderson 2002). Akaike's Information Criterion corrected for small sizes (AIC_c) was used to determine the rank order of fits for the set of competing models.

Results

A total of 25 specimens of shortjaw cisco were identified by experts in the catches from 14 different

sample locations distributed throughout the study area (Table 1, Fig. 2), and abundance ranged from 1–6 specimens per sample. The majority of samples with identified shortjaw cisco contained single specimens, however a combination of two samples contained a total of 10 shortjaw cisco, accounting for 40% of the total number of individuals in the study.

Water Depth for samples ranged from 24 to 155 m, while Water Depth associated with presence of short-jaw cisco ranged from 61 to 138 m (Table 3).

Table 3 Distribution of targeted samples and catch of identified shortjaw cisco (*Coregonus zenithicus*) in Lake Huron (2003–2007), based on Water Depth (m), Substrate Slope (degrees), and Cliff Distance (m)

Habitat variable	Number of Samples	Samples with SJC	Number of SJC	
Depth (m)				
1–20	0	0	0	
21–40	13	0	0	
41–60	14	0	0	
61-80	10	2	3	
81-100	15	6	6	
101-120	9	4	8	
121-140	10	2	8	
141-160	73	14	25	
Slope (degrees)				
0.001 – 0.010	39	5	11	
0.011-0.020	12	5	6	
0.021-0.030	11	1	2	
0.031-0.040	8	2	2	
0.041 - 0.050	1	0	0	
0.051 - 0.060	1	1	4	
0.061 – 0.070	1	0	0	
Cliff (m)				
0.001-1,000	27	3	6	
1,001-2,000	26	3	3	
2,001-3,000	2	1	2	
3,001-4,000	0	0	0	
4,001-5,000	4	1	1	
5,001-6,000	0	0	0	
6,001-7,000	0	0	0	
7,001-8,000	5	2	3	
8,001-9,000	1	1	6	
28,000-44,000	8	3	4	
Total for each variable	73	14	25	



Substrate Slope for the 73 samples ranged from very flat (<0.002) to moderately inclined (>0.060), with the greatest frequency of targeted samples located over very flat bathymetry (Table 3). There was no obvious relationship between Substrate Slope and shortjaw cisco presence. Cliff Distance for the targeted samples varied widely, although most of the samples were within 2.5 km of a submerged cliff (Table 3). Shortjaw cisco were found across the range of values for the Cliff Distance, from near zero to approximately 40 km.

The selected habitat variables were found to be statistically independent of each other, with Pearson's correlation coefficients reported as Water Depth \times Substrate Slope (r=0.039); Water Depth \times Cliff Distance (r=0.177); and Cliff Distance \times Substrate Slope (r=0.163). For this reason, the seven competing habitat-use models were analyzed as a single set.

The results of model selection analyses for the competing habitat-use models are summarized in Table 4. The seven models are presented in rank order associated with calculated values for: (a) corrected Akaike Information Criteria AIC_c (increasing); (b) differences in corrected Akaike Information Criteria ΔAIC_c (increasing); and (c) Akaike weight w_i (decreasing). Within the set of competing models, the univariate and bivariate models with Water Depth performed better than the others, with absolute ΔAIC_c values approximately 2.0 or less, indicating strongest model fit compared to the set of models analyzed (Burnham and Anderson 2002).

Table 4 Model fit and information criteria for the set of competing models to explain the distribution of identified shortjaw cisco (*Coregonus zenithicus*) in Lake Huron, based on targeted sampling (2003–2007). AIC_c refers to Akaike information criteria corrected for small sample sizes. Models are ranked relative to the best approximating model, based on ascending ΔAIC_c , and descending Akaike weights (w_i) which sum to 1.0

Model	AIC_c	ΔAIC_c	Akaike weight (w_i)
	- 4.00		
Depth	71.83	0.00	0.41
Depth + Cliff	72.59	0.77	0.28
Depth + Slope	73.84	2.01	0.15
Cliff	75.43	3.60	0.07
Slope	76.69	4.86	0.04
Cliff + Slope	76.89	5.06	0.03
Depth + Slope + Cliff	77.12	5.30	0.02



It is important to note that this study was based on two major assumptions concerning taxonomic uncertainty and identification uncertainty related to this hypothesized species at risk. First, it was assumed that shortjaw cisco is a valid species that indeed occurs in the waters of Lake Huron. Taxonomic uncertainty within the genus Coregonus reflects complex patterns originating from phenotypic plasticity, hybridization, and introgression—processes which may have combined to cause a merging of morphological traits and increased complexity of classifying individuals to the species level (Todd and Smith 1980; Douglas et al. 1999; Turgeon et al. 1999; Turgeon and Bernatchez 2003; Steinhilber 2004; Favé and Turgeon 2008). Considerable research has been undertaken to reduce the taxonomic uncertainty associated with deepwater cisco, however the issue is far from resolved at this time. The second major assumption for this study was, given the valid existence of shortjaw cisco in Lake Huron, that the species could be reliably discerned from other species of deepwater cisco. The plasticity of some morphological characters used to identify Coregonus species (e.g. gillrakers, snout angle, mouth shape) can lead to substantial uncertainty in final identification of an individual specimen (Todd and Steinhilber 2002). This study adopted the most commonly-used identification guide for deepwater cisco of the Great Lakes (Todd 2001), and assumed that it would lead to correct discrimination—reflected in this study by use of the phrase "identified shortjaw cisco."

Of the hypothesized habitat factors examined in this study, Water Depth was clearly the most important variable explaining the distribution of identified shortjaw cisco in the selected Lake Huron study area. Water Depth distribution for shortjaw cisco observed in the study was consistent with the literature for shortjaw cisco distribution in the upper Great Lakes (Lakes Superior, Michigan, and Huron). Shortjaw cisco have been found in water depths ranging from 18–183 m (Bajkov 1932; Van Oosten 1936), but have more commonly been reported in 55–144 m of water (Todd 2002). In Lake Superior, shortjaw cisco have been caught in Water Depths of 110–144 m in spring, 55–71 m in summer, and 73–90 m in winter (Koelz 1929; Dryer 1966).

For this study, targeted sampling effort for shortjaw cisco was deployed at various locations, based on the



practical experience of commercial fishermen and on reports of historic deepwater cisco occurrence. Therefore, the sampling effort reported in this study was non-random with respect to location and associated habitat. The reader must keep in mind that this kind of non-random, targeted sampling effort is often required to obtain specimens that are rare in distribution and/or abundance. It is possible that analysis of non-random sampled habitats has resulted in differences of presence/absence and model selection results (Type I error). In the future, this source of error can be reduced with more explicit hypotheses and quantitative predictions established prior to deployment of sampling effort.

The ultimate goal of this study was to evaluate if habitat could be effectively identified for a taxonomically uncertain and rare species. While Water Depth was identified as the most important of the selected variables in explaining the distribution of shortjaw cisco, the results also indicated that these physical and bathymetric variables alone do not allow us to reliably predict the presence/absence of shortjaw cisco in Lake Huron. We conclude that shortjaw cisco habitat in Lake Huron cannot yet be effectively defined due to (a) the rarity of identified shortjaw cisco collected, and (b) the need to investigate other important physical and biological habitat factors. One approach to addressing the challenge of small sample sizes would be to extend studies on the distribution of shortjaw cisco to systems where they are still relatively abundant. Within the Great Lakes ecosystem, Lake Nipigon/Superior is the only region still reporting a relatively high abundance of shortjaw cisco (Todd and Smith 1992; Hoff and Todd 2004); use of this ecosystem could help to ensure that more statistically adequate sample sizes could be obtained. Based on the results of this study, it would be reasonable to use the Water Depth observations of this study to establish the prior probability distribution of such a predictive model. It is likely that other physical and biological habitat factors (e.g. water temperature, predator and prey abundance) could contribute significantly to our understanding of shortjaw cisco distribution in the Great Lakes, and these should be included in future studies.

Acknowledgements Special thanks to the Chief, Council and Community of the Chippewas of Nawash Unceded First Nation for the opportunity to work with them on this research project. We are indebted to Scott Parker and Jeff Truscott (Fathom Five National Marine Park, Parks Canada) for support in project

administration, conceptual development and data management/ analysis. Bill Harford (Chippewas of Nawash Unceded First Nation) and Tom Nudds (University of Guelph) provided essential scholarly advice in all phases of research program planning and execution. Nick Mandrak, Tom Pratt (Fisheries & Oceans Canada) and Tom Todd (U.S. Geological Survey) shared their expertise with Great Lakes deepwater coregonine taxonomy, ecology and habitat requirements. Adam Bonnycastle (Geography Department, University of Guelph) provided GIS troubleshooting services, Katreena Baker provided invaluable editing assistance, and two anonymous reviewers provided helpful comments to refine an earlier draft of the manuscript. Financial support for this study was provided by the Chippewas of Nawash Unceded First Nation and Parks Canada.

References

- Bajkov A (1932) The genus Leuchichthys (ciscoes or tullibees) in Manitoban waters. Contrib Can Biol Fish 7:144–159
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York
- Clemens BJ, Crawford SS (2009) The ecology of body size and depth use by bloater (*Coregonus hoyi* Gill) in the Laurentian Great Lakes: patterns and hypotheses. Rev Fisheries Sci 17:174–188
- COSEWIC (2003) COSEWIC assessment and update on the shortjaw cisco, *Coregonus zenithicus*. Committee on the status of endangered wildlife in Canada, Ottawa, Canada, pp 19. http://dsp-psd.pwgsc.gc.ca/Collection/CW69-14-252-2003E.pdf, Accessed 27 January 2009
- DFO (2004) Response statements—Shortjaw Cisco. Minister of Fisheries & Oceans, Government of Canada., Ottawa. http://www.sararegistry.gc.ca/document/dspHTML_e.cfm? ocid=647, Accessed 27 January 2009
- Douglas MR, Brunner PC, Bernatchez L (1999) Do assemblages of *Coregonus* (Teleostei: Salmoniformes) in the central Alpine region of Europe represent species flocks? Mol Ecol 8:589–603
- Dryer WR (1966) Bathymetric distribution of fish in the Apostle Islands region, Lake Superior. Trans Am Fish Soc 95:248–259
- Evans MS, Quigley MA, Wojcik JA (1990) Comparative ecology of *Pontoporeia hoyi* populations in Southern Lake Michigan: the profundal region versus that slope and shelf regions. J Great Lakes Res 16:27–40
- Favé M-J, Turgeon J (2008) Patterns of genetic diversity in Great Lakes bloaters (*Coregonus hoyi*) with a view to future reintroduction in Lake Ontario. Conservat Genet 9:281–293
- Gardner WS, Quigley MA, Fahnenstiel GL, Scavia D, Frez WA (1990) *Pontoporeia hoyi*—a direct trophic link between spring diatoms and fish in Lake Michigan. In: Tilzer MM, Serruya C (eds) Large lakes ecological structure and function. Springer-Verlag, New York, p 224
- Hall LS, Krausman PR, Morrison ML (1997) The habitat concept and a plea for standard terminology. Wildl Soc Bull 25:173–182



- Hawthorne B (2007) Hawth's geospatial analysis tools, Spatial Ecology. http://www.spatialecology.com/htools/overview.php, Accessed 27 January 2009
- Hoff MH, Todd TN (2004) Status of the shortjaw cisco (*Coregonus zenithicus*) in Lake Superior. Ann Zool Fennici 41:147–154
- Hondorp DW, Pothoven SA, Brandt SB (2005) Influence of Diporeia density on diet composition, relative abundance, and energy density of planktivorous fishes in southeast Lake Michigan. Trans Am Fish Soc 134:588–601
- Houston JJ (1988) Status of the shortjaw cisco, *Coregonus zenithicus*, in Canada. Can Field Nat 102:97–102
- Jobes FW (1949) The age, growth, and distribution of the longjaw cisco, *Leucichthys alpenae* Koelz, in Lake Michigan. Trans Am Fish Soc 76:215–247
- Koelz W (1929) Coregonid fishes of the Great Lakes. US Government Printing Office, Washington
- Mooers AØ, Prugh LR, Festa-Bianchet M, Hutchings JA (2007) Biases in legal listings under Canadian endangered species legislation. Conservat Biol 21:572–575
- Murray L, Reist JD (2003) Status report on the shortjaw cisco (*Coregonus zenithicus*) in central and western Canada. Fisheries and Oceans Canada, Ottawa
- Nalepa TF, Fanslow DL, Pothoven SA, Foley AJ III, Lang GA (2007) Long-term trends in benthic macroinvertebrate populations in Lake Huron over the past four decades. J Great Lakes Res 33:421–436
- Owens RW, Dittman DE (2003) Shifts in the diets of slimy sculpin (*Cottus cognatus*) and lake whitefish (*Coregonus clupeaformis*) in Lake Ontario following the collapse of the burrowing amphipod *Diporeia*. Aquat Ecosys Health Manage 6:311–323
- Parker JI (1980) Predation by *Mysis relicta* on *Pontoporeia hoyi*: a food chain link of potential importance in the Great Lakes. J Great Lakes Res 6:164–166
- SARA (2003) Species at risk act, Government of Canada, Ottawa. http://laws.justice.gc.ca/en/s-15.3/text.html, Accessed 27 January 2009
- Scott EW, Crossman EJ (1973) Freshwater Fishes of Canada. Fisheries Research Board of Canada, Ottawa
- Scott WB, Smith SH (1962) The occurrence of the longjaw cisco, Leucichthys alpenae, in Lake Erie. Can J Fish Aquat Sci 19:1013–1023
- Sly PG, Munawar M (1988) Great Lake Manitoulin: Georgian Bay and the North Channel. In: Munawar M (ed)

- Limnology and fisheries of Georgian Bay/North Channel ecosystems, vol. 163. Hydrobiologia, pp 1–19
- Smith SH (1968) Species succession and fishery exploitation in the Great Lakes. J Fish Res Board Can 25:667–693
- Smith RL (1996) Ecology and field biology. Harper Collins, New York
- Smith GR, Todd TN (1984) Evolution of species flocks of fishes in north temperate lakes. In: Echelle AA, Kornfield I (eds) Evolution of fish species flocks. University of Maine Press, Orono, pp 45–68
- SPSS (2006) SPSS version 15.0. SPSS Inc, Chicago
- Steinhilber M (2004) Shortjaw cisco species at risk assessment, 2001, Alberta Sustainable Resource Development, Fish and Wildlife Division
- Steinhilber M, Nelson JS, Reist JD (2002) A morphological and genetic re-examination of sympatric shortjaw cisco (*Coregonus zenithicus*) and lake cisco (*C. artedi*) in Barrow Lake, Alberta, Canada. Archives for Hydrobiology Special Issues: Advances in Limnology 57:463–478
- Todd TN (1985) Status of Great Lakes coregonines. Great Lakes Fisheries Laboratory, Ann Arbor
- Todd TN (2001) Tom Todd's sure-fire guide to morphological characteristics of ciscoes (*Coregonus* spp.) of the Great Lakes region. United States Geological Survey, Ann Arbor
- Todd TN (2002) Status of the shortjaw cisco, *Coregonus zenithicus*. US Geological Survey, Ann Arbor
- Todd TN, Smith GR (1980) Differentiation in *Coregonus zenithicus* in Lake Superior. Can J Fish Aquat Sci 37:2228–2235
- Todd TN, Smith GR (1992) A review of differentiation in the Great Lakes ciscoes. Polskie Archiwum Hydrobiologii 39:261–267
- Todd TN, Steinhilber M (2002) Diversity in shortjaw cisco (*Coregonus zenithicus*) in North America. Arch Hydrobiol Spec Issues Advanc Limnol 57:517–525
- Turgeon J, Bernatchez L (2003) Reticulate evolution and phenotypic diversity in North American ciscoes, *Coregonus* spp. (Teleostei: Salmonidae): implications for the conservation of an evolutionary legacy. Conservat Genet 4:67–81
- Turgeon J, Estoup A, Bernatchez L (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 (1936) The age, growth and sex ratio of the Lake Superior longjaw (*Leucichthys zenithicus*). Pap Mich Acad Sci Arts Lett 22:691–711

