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Diet of cisco (*Coregonus* spp.) in Algonquin Park region lakes: variation among forms

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Abstract

Efforts to conserve cisco (*Coregonus* spp.) diversity in Canadian lakes have been impeded by the unresolved taxonomy of North American ciscoes. When a strictly taxonomic-based approach is not possible, conservation units of infraspecific diversity can be identified using biological, morphological, ecological, and genetic evidence. Distinct cisco forms have been reported from deep oligotrophic lakes within boundaries of the historical outflow of glacial Lake Algonquin. In this study, we described the diet of three cisco forms netted from eight lakes located in or adjacent to Algonquin Provincial Park, Ontario. Opossum Shrimp (*Mysis diluviana*) was the dominant prey of benthic, low gill raker count forms in Trout and White Partridge Lakes, and of a large-bodied, high gill raker count form in Hogan Lake. Zooplankton was the most important prey item of small-bodied, pelagic forms in White Partridge Lake, and Cisco (*Coregonus artedi*) collected from five other Algonquin Park lakes. The diet of Trout Lake Cisco was a broader mix of prey items, including chironomid pupae, Opossum Shrimp, phantom midges (Chaboridae spp.), and zooplankton. Our study provides strong dietary evidence of the special ecological context occupied by cisco forms in White Partridge Lake, and moderate evidence for Trout Lake. Past reports of Shortjaw Cisco (*Coregonus zenithicus*) in six of the study lakes were not supported by our sampling, because low gill raker count forms were not captured.

Key words: Cisco; diet; Opossum Shrimp; zooplankton; shortjaw; blackfin

Introduction

Ciscoes (*Coregonus* spp.) are among the most phenotypically variable group of fishes in North America and sympatric forms have been described over their entire range (Clarke 1973; Scott and Crossman 1998). Ecological and morphological diversity were historically well developed in the Laurentian Great Lakes (Koelz 1929; Smith and Todd 1984) and have also been described in deep, oligotrophic inland lakes located within the extent of former proglacial lakes (Clarke 1973). Across these habitats, cisco diversity has been in decline attributable to over-harvesting, invasive species (e.g., Rainbow Smelt [*Osmerus mordax*]), hybridization among closely related species, and changes to competitive and predation interactions among ciscoes after declines in Lake Trout (*Salvelinus namaycush*; Bronte *et al.* 2010). Efforts to conserve and restore remnant diversity have been impeded by uncertainty surrounding the taxonomy of North American ciscoes (DFO 2013). For inland Canadian lakes, this uncertainty is largely whether potential Shortjaw Cisco (*Coregonus zenithicus*) and Blackfin Cisco (*Coregonus nigripinnis*) populations have a shared phylogenetic history with Laurentian Great Lakes species, or individually represent examples of ecological speciation derived from ancestral Cisco (*Coregonus artedi*).

As shown for the Lake Whitefish (*Coregonus* spp.) species complex, a flexible, evidence-based approach can be used to identify cisco populations that are important representations of Canadian biodiversity when a strictly taxonomic based approach is not possible (Mee *et al.* 2015). In Canada, the designatable unit (DU) approach is used to identify conservation units of infraspecific diversity based on evidence of discreteness and evolutionary significance (COSEWIC 2020). For ciscoes of conservation concern, a DU identification approach focussed on individual lakes and informed by biological, morphological, ecological, habitat, and genetic evidence has been recommended (DFO 2013). In Ontario, inland lakes with multiple cisco forms have been reported from the south-central and northwestern parts of the province (Mandrak and Crossman 1992). Recent genetic and morphology-based research has confirmed the presence of pairs of distinct cisco forms co-existing in four south-central Ontario lakes: Cedar Lake, Hogan Lake, Trout Lake, and White Partridge Lake (Turgeon *et al.* 2016; Piette-Lauzière *et al.* 2019). These deep oligotrophic lakes are found within boundaries of the historical outflow of glacial Lake Algonquin and support several glacial relict species (Dadswell 1974). In Cedar and Hogan Lakes, the two cisco forms (referred to as Cisco and Blackfin Cisco) occupy different trophic positions reflective of diet and habitat use (Ridgway *et al.* 2020).

Past examinations of stomach contents (Anderson and Smith 1971) and recent stable isotope studies (Schmidt *et al.* 2009; Ridgway *et al.* 2020) have illustrated that phenotypic differences among cisco forms in the Laurentian Great Lakes and some inland lakes reflect diet. Specifically, variation in jaw morphology and the number (spacing) and length of gill rakers among ciscoes have been attributed to partitioning of food resources (Smith and Todd 1984). To satisfy the criteria of evolutionary significance, ecological evidence supporting such a linkage between form and function is needed to substantiate proposed cisco DUs (DFO 2013). In this study, we describe and compare the diet of three cisco forms netted from eight lakes located within or adjacent to Algonquin Provincial Park. Based on morphological characteristics, we refer to these forms as blackfin, cisco, and shortjaw (as per Turgeon *et al.* 2016; Ridgway *et al.* 2020). Cisco diet information from these lakes provides important ecological information needed for the identification of conservation units in Ontario lakes.

Study Area

Our research was conducted in eight lakes in the Nipissing District of south-central Ontario. Seven of the lakes are located in Algonquin Provincial Park (Biggar Lake, Grand Lake, Hogan Lake, Kioshkokwi Lake, Manitou Lake, Three Mile Lake, and White Partridge Lake), and the other lake (Trout Lake) is located slightly north, adjoining the city of North Bay (Figure 1). All lakes are inside the boundary of one of the outlets of glacial Lake Algonquin (Dadswell 1974). Study lakes range from 373.3 to 1673 ha in size, with maximum water depths between 32.9 and 69 m (Table 1). In 2009, we attempted to collect ciscoes from North Tea Lake in Algonquin Park (45.9421°N, 79.0376°W). As only two individuals were netted, the lake was not included in the diet study.

Historically, Shortjaw Cisco was reported from these seven Algonquin Provincial Park lakes (Martin and Chapman 1965) and Trout Lake (Clarke 1973). Multiple cisco forms, differing in gill raker counts and jaw morphology, have been described from three of these lakes: Hogan, Trout, and White Partridge (DFO 2013; Turgeon *et al.* 2016; Bell *et al.* 2019; Piette-Lauzière *et al.* 2019; Table 2). The availability of deepwater crustaceans as prey has been hypothesized to have a role in the diversification of cisco forms in deep, oligotrophic, inland lakes (Bell *et al.* 2019). Opossum Shrimp (*Mysis diluviana*, formerly *Mysis relicta*) has been recorded in all eight study lakes and the freshwater amphipod (*Diporeia* spp.) has been recorded in all the lakes except Hogan and Grand (Dadswell 1974; Bell *et al.* 2019).

Methods

Cisco sampling and processing

We collected ciscoes from late spring to early fall in 2007, 2008, 2009, and 2010. Lakes were sampled using multi-mesh, monofilament experimental gill nets (Sandstrom *et al.* 2013) set over a range of water depths (Table 1) below the thermocline. Nets were either suspended in the water column (pelagic) or on the lakebed (benthic). Pelagic nets were 6 m deep and 27.5 m long, with panels of mesh sizes between 6.25 and 55 mm. Benthic nets were 2.4 m deep and 45.6 m long, with panels of mesh sizes between 13 and 64 mm. Nets were set for either two to three hours during the day or left overnight to sample.

We froze ciscoes until processing in the laboratory. Stomach contents were removed from thawed specimens and preserved in 70% ethanol. Under magnification, we identified prey items to the lowest taxonomic level possible (typically order or family) using Lehmkuhl *et al.* (1979), Merritt and Cummins (1996), and Smith (2001) and estimated the volume of each prey item with a gridded (1 cm × 1 cm) petri dish (Gillespie and Fox 2003).

In the laboratory, we classified ciscoes based on jaw morphology, gill raker characteristics, fin colour, and conformance to Great Lakes taxonomic definitions (Koelz 1929; Hubbs and Lagler 2007). Gill raker number and jaw morphology are primary identification characters, which are interpreted to reflect differences in occupied niches among species (Todd and Smith 1992; Zimmerman and Krueger 2009). For example, Shortjaw Cisco has fewer gill rakers (typically <40) than Cisco, an included lower jaw and angled snout, and is associated with deep, benthic habitats (Scott and Crossman 1998; Murray and Reist 2003). White Partridge Lake ciscoes were also grouped based on body size differences of mature individuals (small or normal; Figure 2) and location of capture (pelagic or deep benthic habitats). Classification of forms is supported by the population genetic structure of ciscoes in Hogan, Trout, and

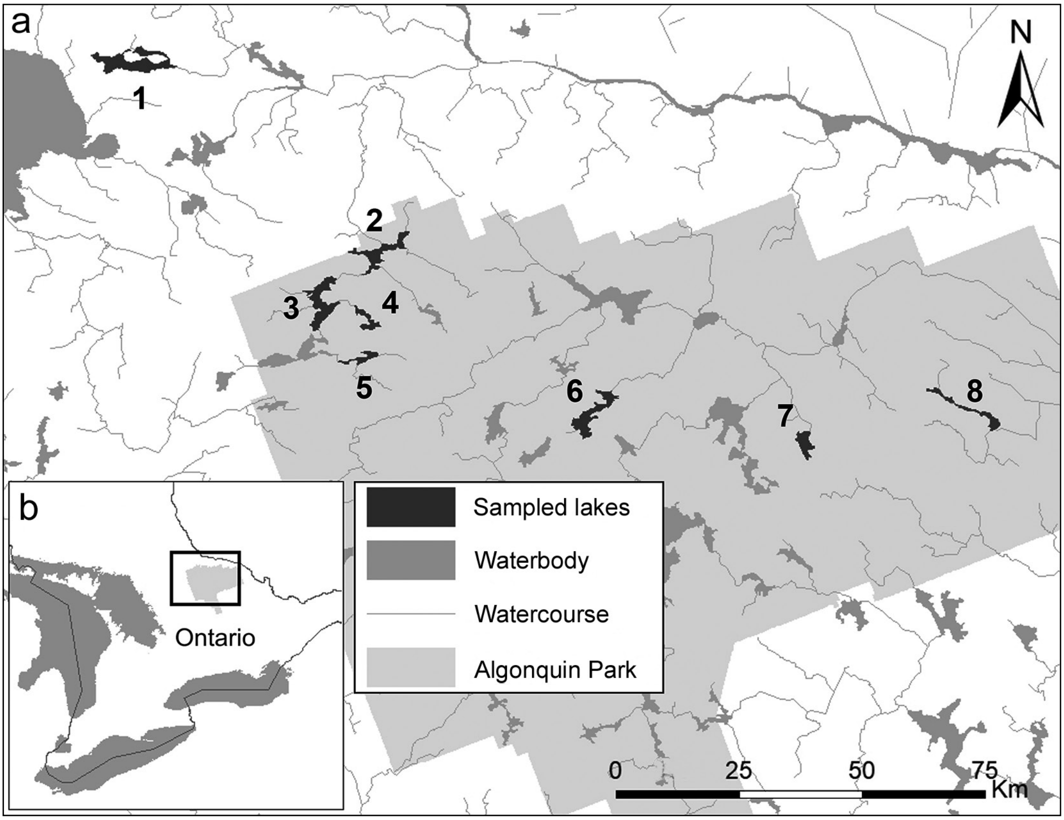

Figure 1. a. Locations of eight study lakes in Algonquin Park region, Nipissing District, Ontario (1 = Trout Lake, 2 = Kioshkiokwi Lake, 3 = Manitou Lake, 4 = Three Mile Lake, 5 = Biggar Lake, 6 = Hogan Lake, 7 = White Partridge Lake, 8 = Grand Lake). Inset map b. provides location of study area within St. Lawrence River–Great Lakes basin.

Table 1. Characteristics of lakes and multi-mesh gill net sampling details for cisco (*Coregonus* spp.) diet study in the Algonquin Park region, 2007–2010.

Lake	Mean lake depth (m)	Maximum lake depth (m)	Area (ha)	Years sampled	Net set depths (m)	Cisco collected (*n*)
Biggar	10.5	32.9	373.6	2008	18–28*	214
Grand	8.6	42.5	752.5	2008	21–35*	79
Hogan	7.4	38.4	1283.5	2009, 2010	13–30*	152
Kioshkokwi	13.8	47.5	1073.7	2008, 2009	14–45*	88
Manitou	13.5	38.6	1381.9	2009	19–37*	100
Three Mile	11.2	41.6	415.0	2008	2–40*	96
Trout	16.8	69.0	1673.0	2010	25–47†	213
White Partridge	16.9	49.3	584.4	2007 to 2009	18–48‡	429

*Pelagic nets were set at depths of 6 to 12 m.
†No pelagic nets were used.
‡Pelagic nets were set at depths of 15 to 35 m.

White Partridge Lakes (Turgeon *et al.* 2016; Piette-Lauzière *et al.* 2019) and growth-trajectory differences between forms in Trout and White Partridge Lakes (DFO 2013).

Data analyses

We described diets using: (i) the frequency of occurrence and volumetric contributions of each prey item, and (ii) the number and diversity of prey items

TABLE 2. Details and summary of stomach content information for ciscoes (*Coregonus* spp.) collected from Algonquin Park region study lakes. Median values and ranges are presented for gill raker counts (LGR = low gill raker; HGR = high gill raker) and length measurements.

Lake	Form	Sample size (*n*)	Gill raker count	Standard length (mm)	Useable stomachs (%)	Prey types (*n*)	Rare diet items (*n*)
Biggar	Cisco	214	44 (39–50)	116.0 (78–143)	61	7	5
Grand	Cisco	79	45 (37–51)	155.5 (123–177)	96	9	4
Hogan	Cisco	53	44 (41–48)	132.5 (114–278)	30	3	0
	HGR*	99	54 (50–61)	253.0 (154–312)	58	7	5
Kioshkokwi	Cisco	88	45 (41–50)	144.0 (86–193)	73	12	12
Manitou	Cisco	100	46 (41–61)	172.0 (150–203)	19	9	0
Three Mile	Cisco	96	45 (41–50)	168.0 (134–195)	59	6	1
Trout	Cisco	142	46 (42–51)	165.0 (85–173)	12	8	0
	LGR†	71	35 (29–39)	180.5 (91–274)	24	7	4
White Partridge	Benthic LGR†	182	31 (26–38)	165.0 (92–234)	68	15	7
	Pelagic LGR	118	35 (28–39)	98.0 (68–147)	43	8	1
	Pelagic HGR	129	41 (40–48)	100.5 (70–121)	40	8	4

Provisional identifications:*blackfin; †shortjaw.

FIGURE 2. a. South end of White Partridge Lake, Algonquin Provincial Park, Ontario. b. Pelagic (upper) and benthic (lower) cisco forms collected with multi-mesh gill nets in 2007. Photo a: Jason Barnucz. Photo b: Scott Reid.

in each stomach. Differences in the prey consumed between cisco forms within and among lakes were tested using an index of niche overlap and multivariate ordination methods.

We calculated prey item diversity for each cisco form using the Shannon-Wiener Diversity Index H′ (Gkenas *et al.* 2019):

$$\mathrm{H}' = -\sum_{i}^{s} p_i \ln p_i$$

where p is the proportion of stomach contents of a form made up by prey item type i, and s is the total number prey item types identified in that form.

We calculated the degree of dietary niche overlap between forms in Hogan, Trout, and White Partridge Lakes using Horn's Index of Overlap $\hat{R}o$ (Krebs 1999):

$$\hat{R}o = \frac{\Sigma\,(\hat{p}_{ij} + \hat{p}_{ik})\log(\hat{p}_{ij} + \hat{p}_{ik}) - \Sigma\hat{p}_{ij}\log\hat{p}_{ij} - \Sigma\hat{p}_{ik}\log\hat{p}_{ik}}{2\,log\,2}$$

Where j and k are two distinct forms from the same lake, $\hat{p}_{ij}$ = the proportion of the total stomach contents of form j made up by prey type i, and $\hat{p}_{ik}$ = the proportion of the total stomach contents of form k made up by prey type i.

We used ordination methods to visualize diet differences between each form in Hogan, Trout, and White Partridge Lakes, and among ciscoes from all sampled lakes (Gkenas *et al.* 2019). Non-metric dimensional scaling (NMDS) of diet data was done using the Bray-Curtis dissimilarity measure (Oksanen *et al.* 2020). Ordinations used volumetric percent composition data of each prey type. To reduce the influence of both abundant and rare prey items, we square root transformed data and grouped rare prey items (found in <5% of stomachs) with unidentifiable diet items to create an "other" prey item category. Stress values were calculated to evaluate goodness of fit of the NMDS, where values <0.2 indicate a fair fit (Clarke *et al.* 2014).

We used analysis of similarity (ANOSIM) to test if multivariate diet differences between Hogan, Trout, and White Partridge Lake forms were significant (Gandini *et al.* 2014; Gkenas *et al.* 2019). Analysis of similarity results were based on 9999 permutations, and we interpreted P values <0.05 to indicate a significant difference between forms. Values of the ANOSIM statistic R close to 1 represent strong dissimilarities between the diets of different cisco morphs, values close to 0 indicate a similar diet, and values below 0 suggest greater dissimilarity among cisco of the same form than between different forms (Buttigieg and Ramette 2014). We used similarity percentages breakdowns (SIMPER) to identify diet items with the greatest contribution to dissimilarity between forms (Gandini *et al.* 2014; Gkenas *et al.* 2019).

All analyses were conducted using R v. 4.0.0 software (R Development Core Team 2020). Bootstrap-based 95% CI were generated using the R "boot" package with 999 permutations (Canty and Ripley 2020). Non-metric dimensional scaling, ANOSIM, and SIMPER were run using the R "vegan" package (Oksanen *et al.* 2020).

Results

A total of 1371 ciscoes were collected from the eight study lakes (Table 1). Multiple forms were identified from samples netted from Hogan, Trout, and White Partridge Lakes; only Cisco was collected from the other lakes (Table 2). Ciscoes from White Partridge Lake were grouped into three forms: a benthic low gill raker count (LGR) form, a small-bodied pelagic LGR form, and a small-bodied pelagic high gill raker count (HGR) form. Trout Lake ciscoes were grouped into a normal form (≥40 gill rakers) and a LGR form. Hogan Lake ciscoes were grouped into a normal form and a HGR form. Gill raker counts across forms/individuals ranged from 26 to 61, with the highest median gill raker count associated with the Hogan Lake HGR form and the lowest with the White Partridge Lake benthic cisco form (Table 2).

Size varied between forms in lakes, and among all lakes, with standard lengths ranging from 68 mm to 312 mm. Small-bodied forms (i.e., dwarf cisco; Shields and Underhill 1993) were netted from both Biggar and White Partridge Lakes. The largest ciscoes were collected from Hogan Lake (Table 2). Low gill raker count forms were provisionally identified as shortjaw and the Hogan Lake HGR form as blackfin. The White Partridge Lake pelagic HGR form and the Hogan and Trout lakes normal forms were provisionally identified as Cisco.

Approximately 54% of ciscoes (n = 746) had useable stomach contents (Table 2). A total of 23 prey item categories were identified from cisco stomachs. Opossum Shrimp and Water Flea (*Daphnia* spp.) were the most frequently occurring prey items, with Opossum Shrimp being the only prey item consumed by all cisco forms across all lakes sampled (Appendix 1).

White Partridge Lake

Approximately 70% of the benthic form and almost half of the two pelagic forms collected had identifiable stomach contents (Table 2). Nearly twice as many prey items were identified from benthic form stomachs than both pelagic forms (Table 2). Despite these differences across White Partridge forms, niche widths were similar: benthic LGR H′ = 1.47 (95% CI 0.39–1.74), pelagic LGR H′ = 1.4 (0.8–2.1), and pelagic HGR H′ = 1.53 (0.88–2.1).

Opossum Shrimp was the dominant prey item of the benthic form but comprised <8% of pelagic cisco stomach contents (Figure 3). Occurring in three-quarters of benthic form stomachs, Opossum Shrimp was also the most frequently identified prey item, over five times more frequently than in pelagic ciscoes (Appendix 1). Bivalves, chironomids (i.e., non-biting midges) larvae, and amphipods were also common benthic form prey items; although each made up <5% of the volume of stomach contents (Figure 3).

Based on frequency of occurrence and volumetric composition, zooplankton (bosminids, *Daphnia* sp., copepods, and unidentified zooplankton taxa) was the dominant pelagic cisco prey item (Figure 3, Appendix 1). Zooplankton represented <1% of benthic LGR form stomach contents. The prevalence and volumetric contribution of different zooplankton taxa were similar between the two pelagic forms. Of identifiable zooplankton taxa, the order of dominance was bosminids, copepods, and *Daphnia* sp. Chironomid pupae were also identified from 10% of pelagic cisco stomachs and comprised 2–6% of stomach content volume (Figure 3, Appendix 1).

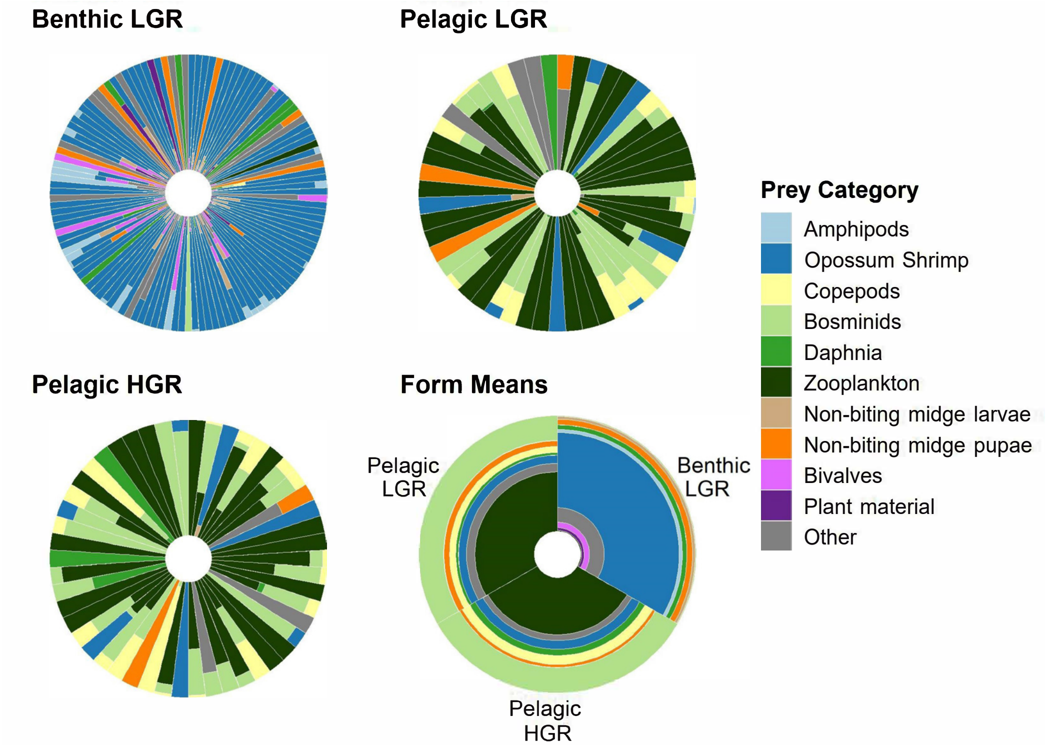

FIGURE 3. Comparison of White Partridge Lake cisco stomach contents based on the relative abundance of prey types for each individual, and on average for each form (LGR = low gill raker; HGR = high gill raker). Cisco forms were identified based on habitat of capture, body size, and gill raker counts.

Ordination of stomach content data clearly illustrated a strong difference between the diets of the benthic and pelagic forms, and substantial overlap between the pelagic forms (Figure 4). Analysis of similarity results indicate that stomach contents for the three morphs were moderately dissimilar (R = 0.43, *P* = 0.001). Subsequent SIMPER analyses identified that prey items with strong contributions to the dissimilarity were Opossum Shrimp and zooplankton (bosminid, copepods, and unidentifiable zooplankton). Similarly, the degree of dietary niche overlap was lowest between the benthic form and either pelagic form ($\hat{Ro} = 0.39$) and greatest between pelagic forms ($\hat{Ro} = 0.97$).

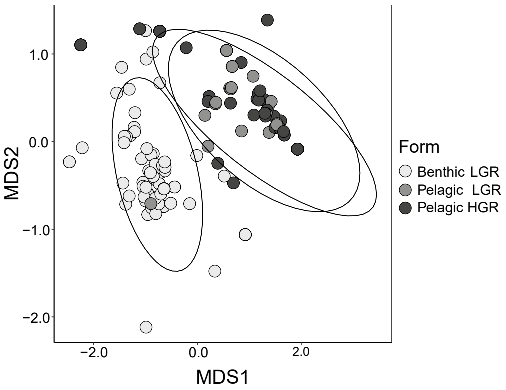

FIGURE 4. Bi-plot of the non-metric multidimensional scaling (NMDS) ordination scores representing the dissimilarity (Bray-Curtis) between stomach contents of White Partridge Lake cisco forms (LGR = low gill raker; HGR = high gill raker). Contour circles outline the spread of the ordination points for each form.

Trout Lake

More than 75% of ciscoes collected had empty stomachs, with only 12% of Cisco and 24% of the LGR form having identifiable stomach contents (Table 2). A similar total number of prey types were identified from stomachs of each form, although rare items were more prevalent in LGR form stomachs (Table 2). Conversely, the niche width of the Trout Lake LGR form (H′ = 0.74, 95% CI 0.00–1.23) was significantly lower than Cisco (H′ = 1.75, 95% CI 1.29–2.49).

The diet of the LGR form was dominated by Opossum Shrimp ($\bar{x}$ = 81% of stomach volume). Compared to Cisco stomach contents, Opossum Shrimp was four times more abundant in the LGR form (Figure 5). Opossum Shrimp occurred in almost all LGR form stomachs, but less than a quarter of Cisco stomachs (Appendix 1). Bivalves were consumed by a third of LGR form cisco (Appendix 1), but on average comprised <10% of stomach content volume (Figure 5). Unlike LGR cisco, the volumetric composition of Cisco stomachs was more evenly comprised of pelagic and benthic prey (*Daphnia* sp., chironomid pupae [none-biting midges], and Opossum Shrimp; Figure 5). Other notable, but less abundant prey included bosminids, copepods, and phantom midges (Chaoborid; Appendix I).

Ordination of stomach content data (bi-plot not shown) and subsequent ANOSIM analysis (R = −0.12, $P = 0.94$) indicated a large degree of diet similarity between cisco forms in Trout Lake. Alternatively, dietary niche overlap values indicate moderate dissimilarity between the forms ($\hat{Ro} = 0.58$).

Hogan Lake

Approximately 30% of Cisco and 60% of HGR form collected had useable stomach contents (Table 2). More than twice as many prey item types were identified in HGR form stomachs than in Cisco stomachs (Table 2). Most prey items in HGR form stomachs were rarely encountered, whereas all Cisco prey items occurred in more than 5% of stomachs (Table 2). Niche widths of the two Hogan Lake forms were similar: Cisco H′ = 1.02 (95% CI 0.27–2.03); HGR H′ = 0.86 (95% CI 0.00–1.34).

For both Hogan Lake forms, Opossum Shrimp was the most frequently occurring prey item and comprised (on average) the majority of stomach content volume. However, Opossum Shrimp was a more important prey item for the HGR form than Cisco. Zooplankton (*Daphnia* sp. and copepods) was present in more than 40% of Cisco stomachs but was rarely found in HGR form stomachs (Appendix 1).

Ordination of Hogan Lake stomach contents (bi-plot not shown), ANOSIM analysis (R = −0.03, $P = 0.58$) and the index of dietary niche overlap ($\hat{Ro} = 0.87$) all indicated a high degree of diet similarity between the two forms.

Other lakes

Cisco diets in Biggar, Kioshkokwi, Manitou, and Three Mile Lakes were dominated by zooplankton, primarily *Daphnia* sp. and, to a lesser degree, copepods (Appendix 1). Opossum Shrimp was an important prey item of Grand and Three Mile Lake Cisco and was found in two thirds of Grand Lake stomachs and almost 40% of Three Mile Lake stomachs. Other notable prey items were chironomid larvae (Manitou and Kioshkokwi Lakes), amphipods (Manitou and Three Mile Lakes), and phantom midges (Kioshkokwi and Manitou Lakes).

Ordination of stomach content diet from all study

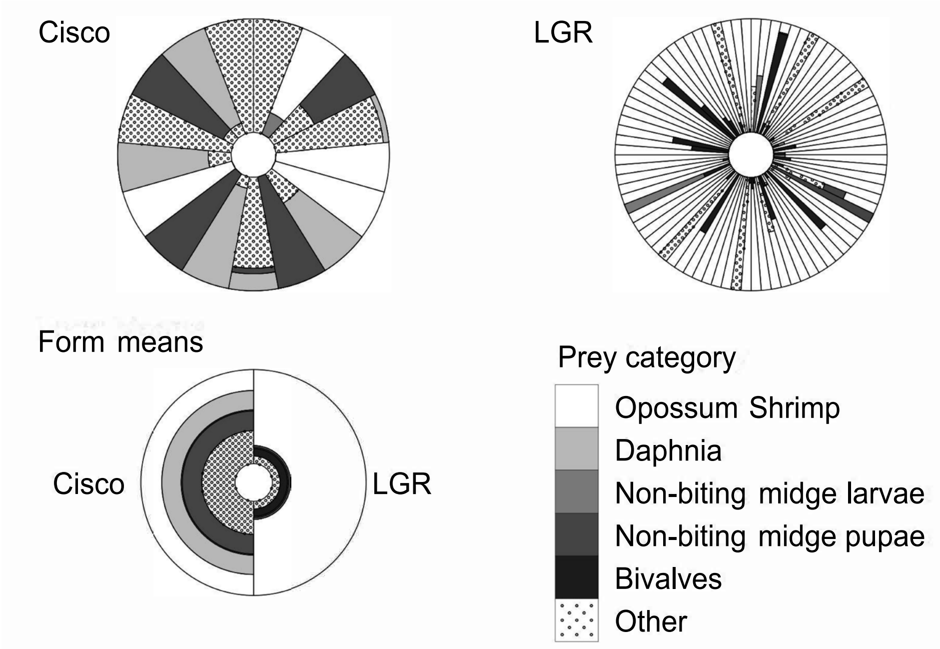

Figure 5. Comparison of Trout Lake cisco stomach contents based on the relative abundance of prey types for each individual, and on average for each form (LGR = low gill raker). Cisco forms were identified based on jaw morphology and gill raker counts.

lakes (Figure 6) illustrated the following patterns: (i) a high degree of diet similarity between White Partridge Lake pelagic forms, (ii) a high degree of diet similarity between LGR forms in Trout and White Partridge Lakes, (iii) diets of Grand and Hogan Lake Cisco were similar to LGR forms, and (iv) diets from other Algonquin Park lakes were generally dissimilar from lakes with multiple cisco forms. Variation along the first MDS axis largely reflects differences in the relative importance of Opossum Shrimp and zooplankton to cisco diets, and variation along the second MDS axis reflects the relative importance of different zooplankton taxa.

Discussion

We found large differences in prey consumed by White Partridge Lake cisco forms and moderate differences between Trout Lake forms, while the diet of the two Hogan Lake forms was similar. The diet of the White Partridge Lake benthic form and the Trout Lake LGR form were mostly Opossum Shrimp (a vertically migrating species associated with deep offshore habitats). The diet of the pelagic or HGR forms was comprised largely of smaller prey (zooplankton), which is comparable to Cisco collected from other Algonquin Park lakes (Carl and McGuiness 2006). Such differences have been reported for other lakes with multiple forms of ciscoes or whitefishes. The typical pattern is for HGR count individuals that occupy the pelagic zone to feed on smaller, pelagic prey, and LGR benthic forms to feed on larger, benthic prey (Amundsen *et al.* 2004; Howland *et al.* 2013; Leclaire 2016). Our results provide strong dietary evidence of a special ecological context occupied by cisco forms in White Partridge Lake, and moderate evidence for Trout Lake ciscoes.

In White Partridge Lake, the range of gill raker counts across both pelagic forms is broader than expected for inland lake Cisco populations. While gill raker counts are useful for classifying ciscoes, differences between benthic and pelagic LGR form diets may better correspond to variation in gill raker spacing and jaw morphology. Densely packed gill-rakers are hypothesized to increase retention capability after capture of zooplankton by increasing the filtering efficacy of the gill apparatus (Roesch *et al.* 2013). Compared to the benthic LGR form, the pelagic LGR form was much smaller and therefore expected to have a correspondingly shorter gill arch, resulting in narrower spaces between gill rakers and enhanced feeding of smaller, pelagic prey. Coregonid diets also reflect jaw orientation; a more ventrally place mouth is associated with benthic feeding and a more dorsally placed mouth is associated with pelagic feeding (Etheridge *et al.* 2012). The lower jaw was included within the upper jaw of 98% of benthic LGR individuals, while jaws of most (>90%) of the two pelagic forms were classified as either having a terminal profile or the lower jaw extended beyond the upper jaw (S.M.R. unpubl. data).

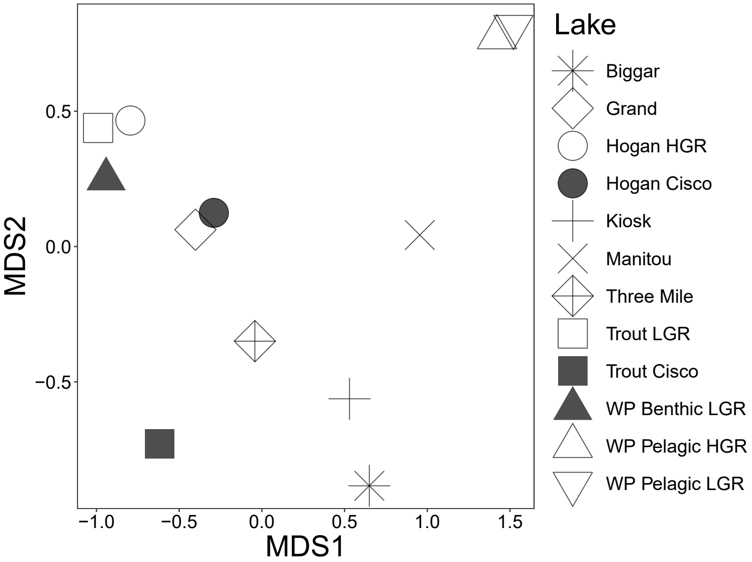

Figure 6. Bi-plot of mean non-metric multidimensional scaling (NMDS) scores for all cisco forms (LGR = low gill raker; HGR = high gill raker) and study lakes, representing the dissimilarity (Bray-Curtis) between stomach contents. For the lakes with multiple forms (White Partridge Lake [WP], Hogan Lake, Trout Lake) mean ordinations are presented for each.

Although strong dietary differences have been described among ciscoes collected from the Laurentian Great Lakes (Anderson and Smith 1971) and very large inland lakes (Turgeon *et al.* 1999; Leclaire 2016), such differences are not always apparent in smaller inland lakes. Wain (1993) reported spring and summertime diets of Cisco and Shortjaw Cisco collected from Sandybeach Lake (northwestern Ontario) to be both dominated (>98%) by zooplankton taxa. Alternatively, Steinhilber (2000) found Opossum Shrimp to be the dominant diet (96%) of Cisco and Shortjaw Cisco collected from Barrow Lake (northern Alberta). In both studies, there was also a high degree of spatial overlap in habitat use, which may explain the similarities in prey choice. In our study, stomach content differences between Hogan Lake forms were not substantial. Opossum Shrimp was the dominant prey item for both blackfin and Cisco, although zooplankton was a common prey item of Cisco. Compared to this result, Ridgway *et al.* (2020) present stronger evidence of diet differentiation using stable isotopes, with the trophic position of Hogan Lake blackfin being significantly greater than that of co-occurring Cisco. Interestingly, the contribution of Opossum Shrimp as a prey item was not identified by Carl and McGuiness (2006) who studied Hogan Lake Cisco in the early 1990s, before the recent discovery of co-occurring forms (Bell *et al.* 2019).

Stomach content data provide a "snapshot" of what individuals ate near the time of capture. However, previous diet studies have shown that the prey consumed by ciscoes and whitefishes varies with season and prey availability (Scharf *et al.* 2008; Isaac *et al.* 2012). A restricted sampling window limits the breadth of our description of variation in trophic position among ciscoes in study lakes. As well, in some lakes, a relatively high proportion of stomach items were too digested for visual identification. Stable isotope analysis of tissue samples can provide longer-term information on the dietary habitats of ciscoes (Schmidt *et al.* 2009; Ridgway *et al.* 2020) and is not affected by the condition of stomach contents. DNA barcoding (another more modern approach) of undigested and digested prey items can also improve the accuracy of diet studies (DeSousa *et al.* 2019). Stomach sample sizes from Hogan and Trout Lakes were small, as many individuals caught from these lakes had empty stomachs. Small sample sizes likely resulted in an under-representation of some prey types, and a less accurate and powerful multivariate analysis (Forcino *et al.* 2015). Overall, a more robust characterization of diet and trophic position differences among cisco forms in our study area could be achieved through the collection of a large number of seasonal diet samples (for visual and genetic-based identification), and tissue samples for stable isotope analysis.

Our understanding of cisco diversity in White Partridge Lake has evolved over the past 60 years. Based on gill raker counts from the first gill arch of six specimens provided to the Royal Ontario Museum (ROM) in 1961, Dr. Bev Scott (Department of Ichthyology and Herpetology, ROM) interpreted Shortjaw Cisco to be present. Later examination of 147 specimens provided to the ROM in 1991 revealed a bimodality in the number of gill rakers from small-bodied (dwarf) individuals that was consistent with descriptions of Cisco and Shortjaw Cisco (ROM 1992). Subsequent cisco collections from 2007 to 2009 have revealed at least two genetically distinct cisco forms are present in White Partridge Lake (Turgeon *et al.* 2016), which can be discriminated based on size, morphology, habitat, and diet (this study). Such differences among forms satisfy criteria for identifying conservation units of coregonid diversity (DFO 2013; Mee *et al.* 2015), and are interpreted to result from competition for food resources in lakes (Todd and Smith 1992) and divergent selection on morphological characters (Turgeon *et al.* 2016). Additionally, Opossum Shrimp was the dominant prey item diet of the White Partridge Lake benthic form, providing another example of the association (and potential role) of *Mysis*-based food webs with the post-glacial diversification of ciscoes in inland lakes (Ridgway *et al.* 2020).

Based on the occurrence of similar dwarf ciscoes in Lake Trout stomachs and the presence of other glacial relict species, Martin and Chapman (1965) identified Shortjaw Cisco to be present in six other Algonquin Provincial Park lakes. A secondary goal of our study was to evaluate these historical (1960s) but unconfirmed reports. Based on gill raker counts (all >40), jaw morphology (either extended lower jaws or terminal profiles), and a diet generally dominated by zooplankton, ciscoes captured from Biggar, Grand, Kioshkokwi, Manitou, North Tea, and Three Mile Lakes are classified as Cisco. The previous identification of additional Shortjaw Cisco populations was not supported by our sampling efforts.

In summary, we compared the stomach contents of cisco forms collected from Algonquin Provincial Park area lakes. Differences among forms and lakes largely reflected the varying importance of Opossum Shrimp and zooplankton as food items. In Trout Lake and White Partridge Lake, diet differences between forms support the inference that heritable phenotypic differences are adaptive, and that forms represent potential DUs. However, we are unable to assess whether these forms could be locally reconstituted if lost, a new criterion adopted by COSEWIC to assess whether potential DUs are evolutionary significant (COSEWIC 2020).

Author Contributions

Writing – Original Draft: A.D. and S.M.R.; Writing – Review and Editing: A.D. and S.M.R.; Conceptualization: S.M.R.; Investigation: S.M.R.; Methodology: S.M.R.; Formal Analysis: A.D. and S.M.R.; Visualization: A.D.; Funding Acquisition: S.M.R; Project Management: S.M.R.

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Appendix 1. Frequency of occurrence of prey items identified in stomachs of ciscoes (*Coregonus* spp.) collected from the eight Algonquin Park region lakes. Frequency was calculated as the percent of non-empty cisco stomachs with the prey item. For lakes with multiple forms (Hogan, Trout, and White Partridge [WP]) frequencies are presented for each with LGR = low gill raker and HGR = high gill raker.

Prey item	Biggar	Grand	Kiosk	Manitou	Three Mile	Trout (Cisco)	Trout (LGR)	WP (Benthic LGR)	WP (Pelagic LGR)	WP (Pelagic HGR)	Mean
Amphipod	0.0	5.3	4.7	10.5	12.3	0.0	0.0	16.9	2.0	0.0	4.3
Bivalve	0.0	0.0	0.0	5.3	0.0	0.0	33.3	23.4	0.0	0.0	5.2
Bosminid	0.0	0.0	7.8	5.3	0.0	11.8	1.2	1.6	41.2	54.9	10.3
Chaoborid	4.6	7.9	25.0	10.5	7.0	11.8	0.0	2.4	0.0	0.0	5.9
Chirnomidae larvae	0.8	9.2	20.3	21.1	7.0	5.9	7.1	18.6	2.0	2.0	8.1
Chirnomidae pupae	0.8	0.0	0.0	0.0	0.0	29.4	2.4	9.7	7.8	3.9	4.5
Chirnomidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.9	0.0	0.0	0.7
Cladocerae	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Coleoptera	0.0	0.0	0.0	0.0	1.8	0.0	0.0	0.0	0.0	0.0	0.1
Copepods	8.5	1.3	42.2	57.9	0.0	11.8	0.0	0.8	29.4	35.3	16.9
Culicidae	0.0	1.3	3.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Daphnia sp.	92.3	34.2	84.4	36.8	61.4	35.3	0.0	8.1	11.8	9.8	34.1
Diptera	0.0	0.0	0.0	0.0	0.0	5.9	1.2	0.0	0.0	0.0	0.6
Eggs (*Daphnia* sp.)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.1
Ephemeroptera	0.0	1.3	1.6	0.0	0.0	0.0	0.0	4.0	0.0	3.9	1.0
Fish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7
Formicidae	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Gastropoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.1
Hydrachnidia	0.0	1.3	4.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5
Opossum Shrimp	0.8	65.8	15.6	5.3	38.6	23.5	91.7	75.0	13.7	13.7	40.7
Ostracoda	0.0	0.0	1.6	21.1	0.0	0.0	0.0	0.0	0.0	0.0	1.9
Plant material	0.0	0.0	0.0	0.0	0.0	0.0	1.2	9.7	0.0	0.0	0.9
Unknown	70.8	52.6	48.4	63.2	52.6	41.2	9.5	8.1	9.8	3.9	33.0
Zooplankton	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	58.8	62.8	10.2