

ARTICLE

Offshore Prey Densities Facilitate Similar Life History and Behavioral Patterns in Two Distinct Aquatic Apex Predators, Northern Pike and Lake Trout

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Abstract

Northern Pike *Esox lucius* are important aquatic apex predators in freshwater ecosystems across the Canadian Boreal Shield. Although Northern Pike have historically been described as nearshore ambush predators, larger individuals have been anecdotally observed foraging in offshore habitats. We used two province-wide data sets from Ontario, Canada, to investigate the degree to which Northern Pike are generalist predators by examining the influence of offshore prey fish densities on their life histories. To better understand whether the life history patterns observed were unique to Northern Pike or representative of aquatic apex predators generally, we compared Northern Pike life history and catch results to those of the Lake Trout *Salvelinus namaycush*, a well-known pelagic apex predator. We found that the asymptotic lengths of both Northern Pike and Lake Trout were positively related to Cisco *Coregonus artedii* CPUE. Furthermore, both Northern Pike and Lake Trout occupied offshore habitat more frequently in lakes with greater Cisco CPUEs. Northern Pike early growth and mortality rates were negatively related to Cisco CPUE but positively related to Yellow Perch *Perca flavescens* CPUE, suggesting that Northern Pike undergo ontogenetic shifts to foraging on Ciscos later in life. Although the growth and mortality of these predators were related to prey availability, variation in the CPUEs of Northern Pike and Lake Trout was best explained by physical lake characteristics. Our study suggests that Northern Pike and Lake Trout respond similarly to Cisco CPUE across the Canadian

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Boreal Shield, consistent with research reported for other aquatic apex predators. Results of this work collectively suggest that generalist behavior and large-bodied life history strategies of Northern Pike are facilitated by the availability of Ciscoes.

Generalist and specialist foraging strategies of animals are developed through natural selection to maximize fitness (Pyke et al. 1977). Generalists thrive in a broad range of environmental conditions, whereas specialists adapt specific ecological niches and proliferate in narrower ranges of environmental conditions. Specialization comes with the potential trade-off of being less resilient to changing environments (McKinney 1997), whereas generalists are more resilient to ecological change. One concept of generalization in aquatic apex predator communities is the use of both shallow nearshore and pelagic offshore resources in lake ecosystems. Aquatic apex predators often integrate energy across nearshore and offshore food webs (Vander Zanden and Vadeboncoeur 2002; Dolson et al. 2009), and this behavior may impact their growth and life history (Kaufman et al. 2009). As such, aquatic apex predators are expected to exhibit more generalized and opportunistic foraging strategies (Bartley et al. 2015; McMeans et al. 2016) than the historical literature suggests.

The Northern Pike *Esox lucius* is an ecologically important aquatic apex predator found throughout the Canadian Boreal Shield (Scott and Crossman 1973). Research on the Northern Pike has highlighted its adaptability as a species (Raat 1988; Craig 2008). Despite this, Northern Pike are mainly described as nearshore specialists that ambush prey from the cover of littoral vegetation or woody debris (Scott and Crossman 1973; Raat 1988). Northern Pike abundance is frequently associated with the amount of littoral vegetation that serves as their spawning and nursery habitat (Casselman and Lewis 1996; Pierce and Tomcko 2005), and stable isotope comparisons reported from 51 North American lakes indicate 60–75% nearshore reliance (Vander Zanden and Vadeboncoeur 2002). However, Northern Pike also display significant plasticity in their ecology, growth, and life history traits (Malette and Morgan 2005), and they have been observed historically to integrate offshore food webs (Makowecki 1973; Colby et al. 1987), which may influence their growth and life history strategies.

Life history strategies of organisms are under natural selection to maximize fitness; as a result, they vary across environmental gradients with respect to resource and habitat availability, competition, and mortality (Beverton 1987; Charnov 1993; Charnov et al. 2007). Many factors combine to influence the growth and life history of aquatic apex predators (Pauly 1980; Beverton 1987; Shuter et al. 1998), but the quality and quantity of food are major

determinants of these traits (Trippel and Beamish 1989; Kaufman et al. 2009). Fish exhibit indeterminate growth, with rapid growth early in life and slower growth after sexual maturation due to energy allocation to gonadal development (Stearns 1992). Thus, a surplus of energy intake over the cost of reproduction is required for post-maturation growth. Natural selection acts upon organisms to maximize their fitness by increasing the difference between energy obtained from prey and energy spent foraging (Pyke et al. 1977; Stephens and Krebs 1986). This presumably results from aquatic apex predators foraging upon larger, more energy-dense prey as they grow to larger sizes and experience increased energetic costs of foraging (Shuter et al. 2016). Since predator foraging costs increase as the ratio of predator size to prey size increases (Kerr 1971; Kerr and Ryder 1977), predators need larger prey to avoid energetic bottlenecks and stunting (Pazzia et al. 2002; Kaufman et al. 2006).

In the Canadian Boreal Shield, offshore prey such as Ciscoes *Coregonus artedi* and Lake Whitefish *Coregonus clupeaformis* often reach larger body sizes and have higher energy densities than Yellow Perch *Perca flavescens* and White Suckers *Catostomus commersonii* (Bryan et al. 1996; Pazzia et al. 2002). Yellow Perch and White Suckers are considered common nearshore prey for Northern Pike (Diana 1979; Margenau et al. 1998; Beaudoin et al. 1999). Thus, foraging on offshore prey may allow Northern Pike to attain larger body sizes and greater reproductive fitness than strictly foraging in nearshore environments. Case studies have reported that when offshore prey are available, they can be important contributors to the diet and growth of Northern Pike (Colby et al. 1987; Jacobson 1992) and other aquatic apex predators (Trippel and Beamish 1989; Kaufman et al. 2009). Thus, the availability of offshore prey is likely to have an influence on the growth and life history of Northern Pike.

The objective of this study was to evaluate evidence for a generalist foraging strategy of Northern Pike that takes advantage of large-bodied offshore prey fish when they are available. We evaluated these patterns using geographically extensive provincial fish monitoring databases from Ontario, Canada. We expected that generalist Northern Pike populations would have growth and life history traits that respond to the availability of offshore prey in a manner similar to that displayed by the Lake Trout *Salvelinus namaycush*, a generalist apex predator that is typically found offshore (Vander Zanden and Vadeboncoeur 2002;

Dolson et al. 2009). The explanatory influence of offshore prey fish abundance (i.e., Cisco and Lake Whitefish) on apex predator life histories was compared with common nearshore prey fish abundances (i.e., Yellow Perch and White Sucker), predator densities, physical lake characteristics (i.e., lake surface area and mean depth), and available environmental variables (i.e., growing degree-days [GDD]) that have been hypothesized to affect fish growth and life history (Casselman and Lewis 1996; Pierce and Tomcko 2005; Chezik et al. 2014a, 2014b). We predicted that both Northern Pike and Lake Trout would reach larger asymptotic lengths, exhibit slower early growth rates, and display lower mortality rates across a wide range of lakes characterized by greater offshore prey fish abundance (Kaufman et al. 2009). Furthermore, we predicted that Northern Pike and Lake Trout would occupy deeper offshore habitat with greater offshore prey fish abundances as evidence of greater reliance on offshore prey.

METHODS

Data Compilation

We used two Canadian province-wide gillnetting data sets to evaluate and compare variation in Northern Pike and Lake Trout life history traits with prey community composition. The Ontario Ministry of Natural Resources and Forestry's (OMNRF) Broad-scale Fish Community Monitoring (BsM) program (2008–2013) was used for Northern Pike and Lake Trout life history analyses and evaluations of the depth of occupancy for both species (Sandstrom et al. 2013). The Fall Walleye (*Sander vitreus*) Index Netting (FWIN) survey (1993–2002) was used for female and male Northern Pike life history analyses (Morgan 2002). The FWIN data set did not contain sufficient data to investigate Lake Trout life history variation, and the BsM data set did not contain sufficient data to investigate female and male Northern Pike life history traits separately. However, the use and comparison of both BsM and FWIN surveys provide a robust analysis of the patterns observed to ensure that they were not artifacts of the sampling methodology.

Fish Sampling

Fall Walleye Index Netting survey.—The FWIN sampling procedure utilized stratified random sampling that consisted of eight or more 24-h sets of multi-mesh gill nets with eight sequential mesh panels (stretched mesh sizes of 25, 38, 51, 64, 76, 102, 127, and 152 mm) set perpendicular to shore in 2–5- and 5–15-m depth strata (Morgan 2002). Sampling occurred as surface water temperatures in the fall cooled from 15°C to 10°C. All species encountered were identified and enumerated; for sport fishes, lengths

(FL and TL), round weight, sex, and maturity were recorded. Cleithra were used to estimate the age of Northern Pike. Relative abundance estimates (CPUE) were calculated as the average number of individuals per net set. Additional details are provided by Morgan (2002).

Broad-scale Fish Community Monitoring program.—The BsM procedure utilized spatially stratified sampling that distributed effort equally across eight depth strata (1–3, 3–6, 6–12, 12–20, 20–35, 35–50, 50–75, and 75+ m) over each lake. Nets were set for 16–22 h and were oriented perpendicularly to oblique contours during summer when surface water temperatures were greater than 18°C. For our life history analyses, we used data collected with North American (NA1) large-mesh gill nets (targeting fish larger than 20 cm in length; Sandstrom et al. 2013), which consist of eight nonsequential panels with stretched mesh sizes of 38, 51, 64, 76, 89, 102, 114, and 127 mm. All species captured were identified, enumerated, and measured for FL. For some species, TL, FL, round weight, sex, and gonad condition were recorded, and calcified aging structures were collected. Cleithra were used for estimating the age of Northern Pike, whereas otoliths were used for Lake Trout. All age estimation structures from the FWIN and BsM programs were examined by biologists and technicians from the provincial fisheries aging laboratory located in Dryden, Ontario. Additional details are given by Sandstrom et al. (2013).

Predictor Variables

Abiotic and biotic predictor variables (Tables A.3.1, A.3.2) were included in our analyses as potential predictors of apex predator life histories. Biotic variables included in the life history analyses were the CPUEs of Northern Pike, Lake Trout, and four putative prey species: Cisco, Lake Whitefish, Yellow Perch, and White Sucker. We calculated CPUE and benthic area in each sampled depth stratum; we then estimated the area-weighted lakewide mean CPUE. Northern Pike and Lake Trout CPUEs were included as predictor variables in their respective models to evaluate density dependence in life history response variables (Rose et al. 2001; Pierce et al. 2003). Cisco and Lake Whitefish CPUEs were used as indices of offshore prey relative abundance, whereas Yellow Perch and White Sucker CPUEs were included as indices of nearshore prey relative abundance.

Abiotic predictor variables included GDD, lake surface area, and mean depth. Growing degree-days (Terry Marshall, OMNRF, personal communication) were calculated as the cumulative number of degree-days above 5°C and were used as an indicator of annual thermal accumulation from ambient temperature (Chezik et al. 2014a, 2014b). Growing degree-days have been described to influence fish life history traits (Rennie et al. 2009; Venturelli et al. 2010). The surface area and mean depth of each lake were

compiled from the OMNRF Aquatic Habitat Inventory (Dodge et al. 1985).

Variables included in the models were evaluated for multicollinearity using Pearson's product-moment correlation coefficients among predictors and variance inflation factors (VIFs) from statistical models. We calculated VIFs for all covariates, and those with the highest VIFs were removed sequentially until all VIF values were less than 3 (Zuur et al. 2010). Percent littoral zone was the only variable to be removed from the models, as it had a high VIF and a negative relationship with $\log_{10}(\text{mean depth})$ ($r = -0.88$, $r^2 = 0.80$). Percent littoral zone was an initial variable of interest because Northern Pike depend on littoral vegetation for spawning habitat, cover from predators, and cover for ambushing prey (Casselman and Lewis 1996; Pierce and Tomcko 2005).

Response Variables

Life history traits included as response variables were asymptotic FL (L_∞), early growth rate (ω), and instantaneous total mortality rate (Z) of Northern Pike and Lake Trout populations. We included the CPUEs of Northern Pike and Lake Trout as additional response variables to investigate the connection between life history strategies and population sizes of these species. Lake Trout life histories were estimated irrespective of sex, as this species shows little evidence of sexual size dimorphism (McDermid et al. 2010). In contrast, Northern Pike exhibit considerable sexual size dimorphism wherein females mature later and reach both larger L_∞ and older maximum ages than males (Craig 1996; Malette and Morgan 2005). To address the possibility that the results of Northern Pike life history analyses would be different for data in which sexes were combined or separated, we used the FWIN data set to investigate male and female Northern Pike life history variation separately. Due to smaller sample sizes of Northern Pike in the BsM data set, male and female catch data were combined. These patterns were compared to sex-specific patterns from the FWIN data set for consistency among our life history results. The average Northern Pike sex ratio for the BsM data set was 1.62 females per male, potentially biasing results in that data set.

We estimated L_∞ of Northern Pike and Lake Trout populations from the von Bertalanffy growth model fitted to FL-at-age data (Ricker 1975),

$$L(t) = L_\infty \left[1 - e^{K(t-t_0)} \right], \quad (1)$$

where $L(t)$ is the FL (mm) at age t (years); L is the asymptotic FL; K is Brody's growth coefficient; and t_0 is the theoretical age when the fish would have been at zero length (set to 0). Early growth rates were described by the

parameter omega (ω), which corresponds to the growth rate near time zero and was calculated as the product of L (mm) and K (per year; Brody 1945; Gallucci and Quinn 1979; Charnov 2010).

We estimated Z according to the Robson–Chapman method (Robson and Chapman 1961; Ricker 1975). The Robson–Chapman method assumes that (1) all age-classes are equally vulnerable to the sampling gear, (2) survival is constant at all age-classes, and (3) all year-classes are recruited at the same abundance (Ricker 1975). Annual adult survival (S) was calculated as

$$S = T / (\Sigma N + T - 1), \quad (2)$$

where $T = N_x + 2N_{x+1} + 3N_{x+2}$; $\Sigma N = N_x + N_{x+1} + N_{x+2} + \dots$; and N_x is the number of fish for which age is equal to the modal age-class plus 1 year (Smith et al. 2012). Instantaneous total mortality rates for the populations were then calculated as

$$Z = -\log(S). \quad (3)$$

Lake Trout and Northern Pike CPUE estimates were calculated across sexes for both FWIN and BsM data sets. Life history traits were only calculated for Northern Pike and Lake Trout populations with sample sizes of at least 20 individuals per lake (and per sex for the FWIN data set). For the FWIN data set, this resulted in 155, 109, and 264 lakes with suitable sample sizes for female, male, and combined-sex Northern Pike life history analyses, respectively (Table 1; Figure 1A). For the BsM data set, this resulted in 130 and 96 lakes with suitable sample sizes for the Northern Pike and Lake Trout life history analyses, respectively (Figure 1B). Northern Pike life history traits were similar between FWIN and BsM data sets, with most BsM parameters being midway between male and female traits from the FWIN data set (Table 1). The mean and range of Lake Trout life history traits calculated from the BsM data set were comparable to those reported elsewhere (Shuter et al. 1998).

Statistical Analyses

Linear mixed models were used to investigate which predictor variables accounted for the most observed variation in life history traits of Northern Pike and Lake Trout populations. Linear mixed models were developed and analyzed in R version 3.1.2 (R Core Team 2014) using the packages "lme4" (Bates et al. 2015) and "lmerTest" (Kuznetsova et al. 2017). Significance of individual fixed effects in the models was estimated using a Satterthwaite approximation for denominator degrees of freedom (Kuznetsova et al. 2017). Random effects included in the analyses were the lake and the year in which each lake was sampled. Fixed effects included the predictor variables discussed

TABLE 1. Descriptive statistics of the response variables calculated for Northern Pike and Lake Trout populations in the Fall Walleye Index Netting (FWIN) and Broad-scale Fish Community Monitoring (BsM) data sets (Min = minimum; Max = maximum; L_{∞} = asymptotic FL, mm; ω = early growth rate, mm per year; Z = instantaneous total mortality rate; $\log_{10}[\text{CPUE}]$ = relative abundance).

Variable	<i>N</i>	Mean	Min	Max	SD	SE
FWIN						
Female Northern Pike						
L_{∞}	155	866.36	509.64	1,330.70	165.79	13.32
ω	155	220.13	119.20	417.61	51.84	4.16
Z	152	0.40	0.17	0.97	0.16	0.01
Male Northern Pike						
L_{∞}	109	646.36	480.58	911.60	86.98	8.33
ω	109	255.71	147.93	430.19	53.05	5.08
Z	108	0.52	0.25	1.39	0.22	0.02
Combined Northern Pike						
$\log_{10}(\text{CPUE})$	262	3.65	0.62	11.00	1.97	0.12
BsM						
Northern Pike						
L_{∞}	128	715.49	511.64	1,047.87	116.72	10.32
ω	130	258.14	119.92	562.59	78.22	6.86
Z	130	0.35	0.18	0.97	0.14	0.01
$\log_{10}(\text{CPUE})$	130	1.46	0.31	4.58	0.85	0.07
Lake Trout						
L_{∞}	94	600.79	355.30	910.58	98.87	10.20
ω	96	95.27	51.01	173.26	24.96	2.55
Z	96	0.16	0.06	0.45	0.09	0.01
$\log_{10}(\text{CPUE})$	96	1.11	0.24	4.43	0.73	0.07

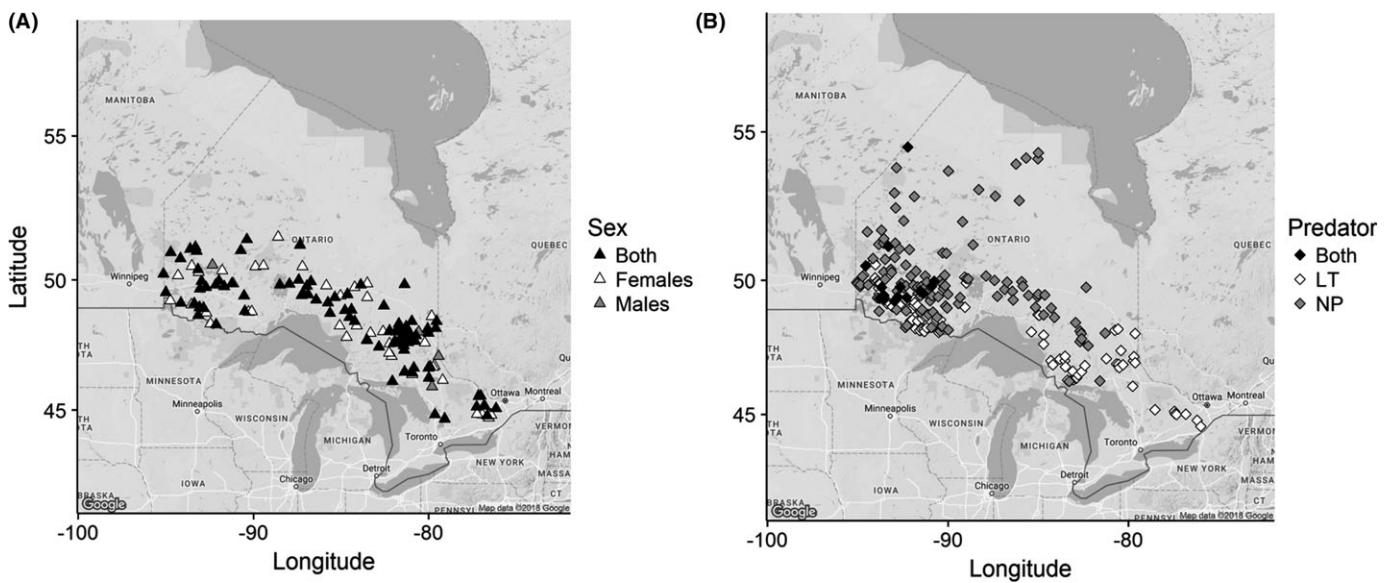


FIGURE 1. Maps of Ontario Boreal Shield lakes with suitable sample sizes for life history analyses of (A) female Northern Pike, male Northern Pike, or both (Fall Walleye Index Netting data set); and (B) Northern Pike (NP), Lake Trout (LT), or both (Broad-scale Fish Community Monitoring data set). Maps were generated using gmap (Kahle and Wickham 2013).

above, with the exception that the CPUE of each study species was removed as a fixed effect when the CPUE of that species was the response variable being tested. The CPUE data for each fish species, lake surface area, and mean depth were log-transformed ($\log_{10}[x + 1]$) to assist with data contrast and reduce the influence of outliers. Growing degree-days were scaled by subtracting the mean of all data points from each individual data point and dividing those points by the SD of all data points using the “scale ()” function so that GDD was similar in magnitude to the other predictor variables. When necessary, response variables were log transformed and outliers were removed to meet assumptions of normality.

Marginal (including only fixed effects) and conditional (including fixed and random effects) pseudo- R^2 values were estimated for the models. Pseudo- R^2 values were estimated for the linear mixed models according to methods developed by Nakagawa and Schielzeth (2013) and Johnson (2014). Marginal pseudo- R^2 values are estimated by calculating the variance explained by the fixed effects as a proportion of the sum of all variance components, whereas conditional pseudo- R^2 values are estimated by additionally including the variance explained by random effects (Johnson 2014). Finally, to estimate the relative influence of the independent predictor variables, the variables were standardized (Z -scored) similar to GDD above by using the “scale ()” function. With the predictor variables standardized to comparable ranges, larger Z -scored parameter estimates represented greater impacts on the response variables for similar changes in the standardized predictor variables (Quinn and Keough 2002).

To explicitly test the hypothesis that offshore prey CPUE affects the life history traits of aquatic apex predators, we used likelihood ratio tests to compare nested models with and without the CPUE of each offshore prey species by using the “anova ()” function (Zuur et al. 2009). A statistically significant result ($P < 0.05$) indicated a significant effect of that offshore prey species' CPUE on the life history trait being tested.

Spatial Location

Using both the small-mesh and NA1 large-mesh BsM data, we calculated two measures of habitat use to be incorporated as response variables in multiple linear regression models with the predictor variables discussed previously. First, we used the mean log depth of capture for Northern Pike and for Lake Trout in each lake, calculated as a weighted average with the weight for each depth stratum (i.e., 1–3, 3–6, 6–12, and 12–20 m) being the midpoint of the stratum (e.g., 2 m for the depth stratum of 1–3 m). Only the first four depth strata were used because small-mesh nets were only set to 20 m deep, and few Northern Pike (0.09%) and Lake Trout (27.71%) were caught in the four deepest strata. We also investigated the

presence/absence of Northern Pike in offshore habitat greater than 6 m and the presence/absence of Lake Trout in nearshore habitat less than 6 m relative to the predictor variables using binomial generalized linear models. For both spatial location measures, we used lakes with a minimum sample size of five individuals and a mean depth greater than 6 m (those lakes that have the potential to stratify and therefore provide habitat for stenothermic offshore prey like Ciscoes). This resulted in 222 and 234 lakes for Northern Pike and Lake Trout, respectively.

RESULTS

Life history traits of both Northern Pike and Lake Trout were strongly influenced by the CPUE of offshore prey (Figures 2–4; Appendix 1, Tables A.1.1–A.1.5). Though coregonine CPUE generally appeared to have strong effects on both Northern Pike and Lake Trout populations, Cisco CPUE consistently had the strongest influence on life history traits relative to Lake Whitefish CPUE (Tables A.1.1–A.1.5). Additionally, similar patterns of the influence of Cisco CPUE on Northern Pike growth and life history traits were observed separately for female, male, and combined-sex Northern Pike data (Figures 2–4A–C; Tables A.1.1–A.1.4).

Asymptotic Length

Fixed effects in the predictive models explained 11–42% of the overall variation in L_{∞} (Tables A.1.1, A.1.2, A.1.4, A.1.5). The L_{∞} values of both female (likelihood ratio test: $\chi^2 = 7.46$, $df = 1$, $P < 0.01$) and male ($\chi^2 = 9.12$, $df = 1$, $P < 0.01$) Northern Pike were positively related to Cisco CPUE (Figure 2A, B); among all of the predictor variables, Cisco CPUE had the strongest effect on female Northern Pike L_{∞} (Tables A.1.1, A.1.2). When female and male Northern Pike data were combined in the BsM data set, Cisco CPUE was similarly positively related to Northern Pike L_{∞} ($\chi^2 = 4.05$, $df = 1$, $P < 0.05$; Figure 2C). Contrary to our hypotheses, Lake Whitefish CPUE either did not have a significant effect or was negatively related to Northern Pike L_{∞} (Tables A.1.1, A.1.2, A.1.4). Neither female L_{∞} from the FWIN data set ($\chi^2 = 0.08$, $df = 1$, $P > 0.05$) nor the combined male and female Northern Pike L in the BsM data set ($\chi^2 = 0.04$, $df = 1$, $P > 0.05$) was significantly related to Lake Whitefish CPUE. However, male Northern Pike L_{∞} (FWIN data set) was negatively related to Lake Whitefish CPUE ($\chi^2 = 6.46$, $df = 1$, $P < 0.05$). Of the other predictor variables included in the L_{∞} analyses, only the CPUE of Northern Pike explained any significant variance, with male Northern Pike L_{∞} being negatively related to Northern Pike CPUE ($P < 0.05$; Table A.1.2).

Like Northern Pike, Lake Trout L_{∞} (BsM data set) was significantly positively related to Cisco CPUE

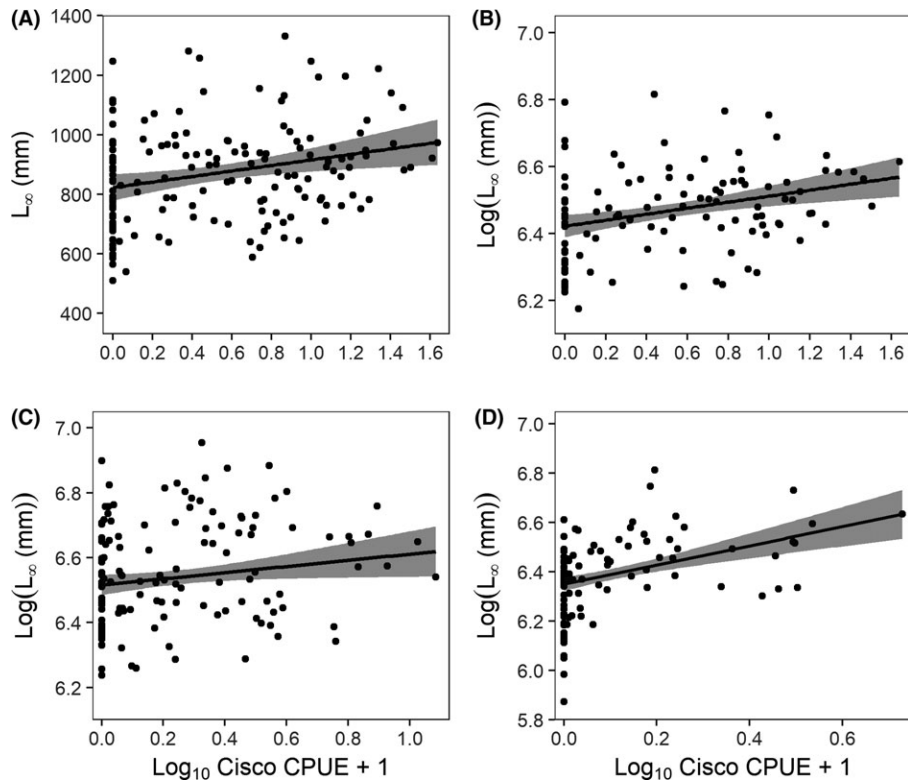


FIGURE 2. Relationships between Cisco CPUE ($\log_{10}[x + 1]$ transformed) and the asymptotic FLs (L_{∞}) of (A) female Northern Pike ($P < 0.01$); (B) male Northern Pike ($P < 0.01$); (C) combined female and male Northern Pike ($P = 0.05$); and (D) Lake Trout ($P < 0.001$) populations. The solid lines represent the relationships, and the shaded areas represent their 95% confidence intervals. Note the differences in scaling among the x- and y-axes.

(likelihood ratio test: $\chi^2 = 18.11$, $df = 1$, $P < 0.001$; Figure 2D), and Cisco CPUE had the strongest effect of all predictor variables (Table A.1.5). Lake Trout L_{∞} was not significantly related to Lake Whitefish CPUE ($\chi^2 = 1.16$, $df = 1$, $P > 0.05$). Lake Trout L_{∞} was negatively related to Lake Trout CPUE ($P = 0.01$) and positively related to lake surface area ($P = 0.02$).

Early Growth Rates

Fixed effects in the predictive models explained 13–23% of the variation in ω overall (Tables A.1.1, A.1.2, A.1.4, A.1.5). Female (likelihood ratio test: $\chi^2 = 7.42$, $df = 1$, $P < 0.01$), male ($\chi^2 = 12.31$, $df = 1$, $P < 0.001$), and combined female and male ($\chi^2 = 8.07$, $df = 1$, $P < 0.01$) Northern Pike ω values were negatively related to Cisco CPUE (Figure 3A–C). Cisco CPUE had the strongest effect of all predictor variables on female and male Northern Pike ω (Tables A.1.1, A.1.2), and Cisco CPUE had the second-strongest effect on combined-sex Northern Pike ω (Table A.1.4). Additionally, female Northern Pike ω was positively related to lake mean depth ($P = 0.05$). Analyses with both sexes combined (BsM data set) indicated that Northern Pike ω was positively related to

Yellow Perch CPUE ($P < 0.001$; Figure 3D), which had the strongest effect of all predictor variables (Table A.1.4). Combined-sex Northern Pike ω was also negatively related to lake surface area ($P = 0.01$) and GDD ($P < 0.05$). Lake Whitefish CPUE was not significantly related to Northern Pike female ($\chi^2 = 3.09$, $df = 1$, $P > 0.05$), male ($\chi^2 = 1.30$, $df = 1$, $P > 0.05$), or combined-sex ($\chi^2 = 1.11$, $df = 1$, $P > 0.05$) ω values.

In contrast to Northern Pike, Lake Trout ω was not significantly related to the CPUE of offshore prey (likelihood ratio test, Cisco: $\chi^2 = 2.38$, $df = 1$, $P > 0.05$; Lake Whitefish: $\chi^2 = 1.35$, $df = 1$, $P > 0.05$) or to any of the other predictor variables included in our models (Table A.1.5).

Instantaneous Total Mortality

Fixed effects in the predictive models explained 21–34% of the variation in Z (Tables A.1.1, A.1.2, A.1.4, A.1.5). The influence of offshore prey on Northern Pike Z varied depending on the data set being analyzed. Female (likelihood ratio test, FWIN: $\chi^2 = 11.10$, $df = 1$, $P < 0.001$; Figure 4A), male (FWIN: $\chi^2 = 6.32$, $df = 1$, $P = 0.01$; Figure 4B), and combined-sex (BsM: $\chi^2 = 4.60$, $df = 1$,

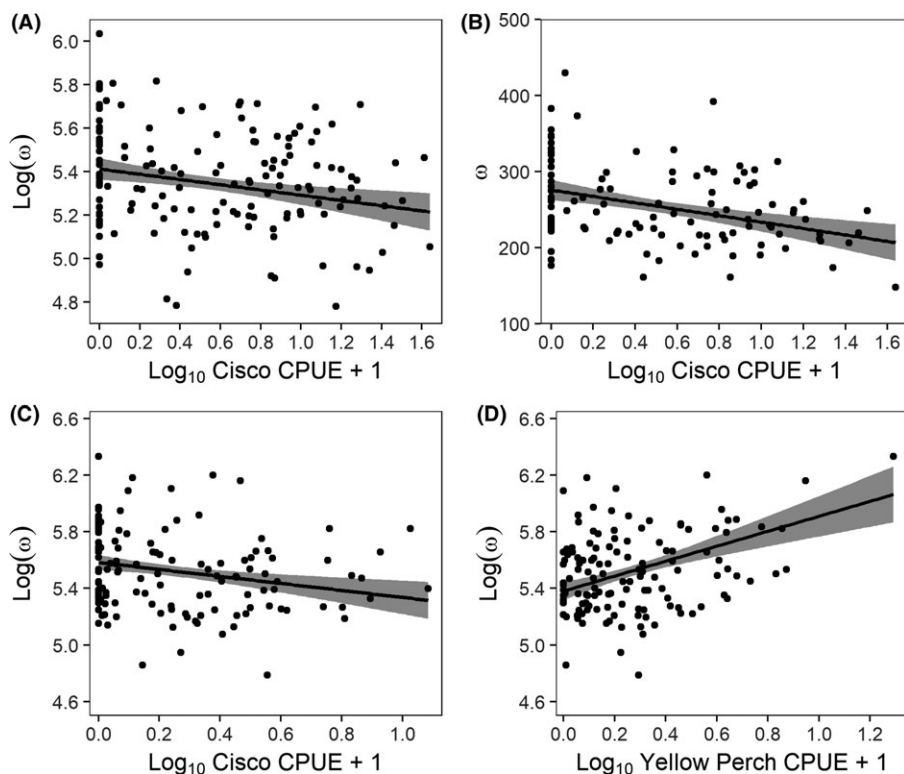


FIGURE 3. Relationships between Northern Pike early growth rates (ω) and prey CPUE ($\log_{10}[x + 1]$ transformed): (A) negative relationship between female Northern Pike ω and Cisco CPUE ($P < 0.01$); (B) negative relationship between male Northern Pike ω and Cisco CPUE ($P < 0.001$); (C) negative relationship between combined-sex Northern Pike ω and Cisco CPUE ($P < 0.01$); and (D) positive relationship between combined-sex Northern Pike ω and Yellow Perch CPUE ($P < 0.001$). The solid lines represent the relationships, and the shaded areas represent their 95% confidence intervals. Note the differences in scaling among the x- and y-axes.

$P < 0.05$; Figure 4C) Northern Pike Z -values were negatively related to Cisco CPUE (Tables A.1.1, A.1.2, A.1.4). Of all the predictor variables examined, Cisco CPUE had the strongest effect on female Northern Pike Z . By contrast, male Northern Pike Z was positively related to Lake Whitefish CPUE ($\chi^2 = 4.54$, $df = 1$, $P < 0.05$; Figure 4B), but Lake Whitefish CPUE was not significantly related to female ($\chi^2 = 0.06$, $df = 1$, $P > 0.05$) or combined-sex ($\chi^2 = 2.18$, $df = 1$, $P > 0.05$) Northern Pike Z . Combined-sex Northern Pike Z was positively related to Yellow Perch CPUE ($P < 0.001$; Figure 4D), which had the strongest effect of all predictor variables (Table A.1.4).

Physical lake characteristics and GDD appeared to be important drivers of Northern Pike Z . Female ($P = 0.01$) and male ($P < 0.001$) Northern Pike Z -values were positively related to GDD (Figure 5A, C), and combined-sex Northern Pike Z was negatively related to lake surface area ($P < 0.001$; Figure 5E; Tables A.1.1, A.1.2, A.1.4). Growing degree-days had the strongest effect of all predictor variables on male Northern Pike Z (Table A.1.2).

Lake Trout Z was not related to offshore prey CPUE (likelihood ratio test, Cisco: $\chi^2 = 0.49$, $df = 1$, $P > 0.05$;

Lake Whitefish: $\chi^2 = 0.10$, $df = 1$, $P > 0.05$). However, like Northern Pike Z , Lake Trout Z was negatively related to lake surface area ($P < 0.01$; Figure 5D) and positively related to GDD ($P < 0.01$; Figure 5B).

Relative Abundance

Fixed effects in the predictive models explained 25–46% of the variation in Northern Pike and Lake Trout CPUEs (Tables A.1.3–A.1.5). The influence of offshore prey fish CPUE on Northern Pike CPUE varied across data sets. Northern Pike CPUE in the FWIN data set was positively related to the CPUEs of both Ciscos (likelihood ratio test: $\chi^2 = 14.43$, $df = 1$, $P < 0.001$) and Lake Whitefish ($\chi^2 = 4.76$, $df = 1$, $P < 0.05$). However, Northern Pike CPUE in the BsM data set was not related to Cisco CPUE ($\chi^2 = 3.21$, $df = 1$, $P > 0.05$) or Lake Whitefish CPUE ($\chi^2 = 0.27$, $df = 1$, $P > 0.05$). Rather, Northern Pike CPUE was strongly related to physical lake characteristics. Northern Pike CPUE had significant negative relationships with lake surface area ($P < 0.001$) and mean depth ($P < 0.001$ to $P < 0.01$) in both the FWIN and BsM data sets (Figure 6A, B; Tables A.1.3, A.1.4). Additionally, Northern Pike CPUE was positively related to

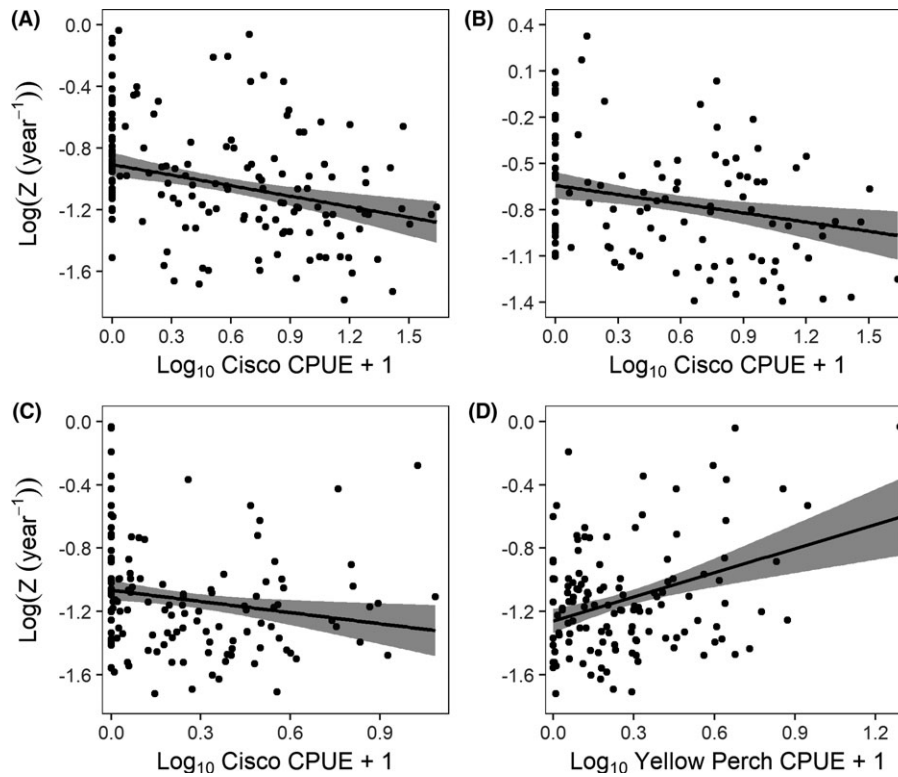


FIGURE 4. Relationships between Northern Pike instantaneous total mortality rates (Z) and prey CPUE ($\log_{10}[x + 1]$ transformed): (A) negative relationship between female Northern Pike Z and Cisco CPUE ($P < 0.01$); (B) negative relationship between male Northern Pike Z and Cisco CPUE ($P < 0.05$); (C) negative relationship between combined-sex Northern Pike Z and Cisco CPUE ($P < 0.05$); and (D) positive relationship between combined-sex Northern Pike Z and Yellow Perch CPUE ($P < 0.001$). The solid lines represent the relationships, and the shaded areas represent their 95% confidence intervals. Note the differences in scaling among the x - and y -axes.

Yellow Perch CPUE ($P < 0.01$) in the FWIN data set and White Sucker CPUE ($P = 0.01$) in the BsM data set (Tables A.1.3, A.1.4). Lake surface area had the strongest effect on Northern Pike CPUE in both data sets.

Like Northern Pike in the BsM data set, Lake Trout CPUE was not related to offshore prey CPUE (likelihood ratio test, Cisco: $\chi^2 = 1.47$, $df = 1$, $P > 0.05$; Lake Whitefish: $\chi^2 = 0.63$, $df = 1$, $P > 0.05$). Physical lake characteristics explained most of the observed variation in Lake Trout CPUE (Table A.1.5). Lake Trout CPUE was positively related to lake mean depth ($P < 0.01$; Figure 6D), whereas this relationship was negative for Northern Pike. Lake Trout CPUE was also negatively related to lake surface area ($P < 0.001$; Figure 6C) and GDD ($P < 0.01$; Table A.1.5). Like the CPUE of Northern Pike, Lake Trout CPUE was most strongly affected by physical lake characteristics (Table A.1.5).

Spatial Location

The availability of offshore prey fish had a strong influence on Northern Pike spatial location (Appendix 2, Table A.2.1). The mean log depth of captured Northern Pike was positively related to Cisco CPUE ($P < 0.001$; Figure 7A), whereas no other variables were significantly

related to the mean log depth of Northern Pike. Additionally, Northern Pike presence in offshore habitat deeper than 6 m was positively related to Cisco CPUE ($P < 0.001$; Figure 7B). Lake surface area ($P = 0.001$) and Northern Pike CPUE ($P < 0.001$) were also positively related to the presence of Northern Pike in offshore habitat, while GDD ($P = 0.01$) and White Sucker CPUE ($P = 0.01$) were negatively related to Northern Pike presence in offshore habitat.

The mean log depth of captured Lake Trout was not significantly related to offshore or nearshore prey CPUE. Instead, the mean log depth of Lake Trout was negatively related to lake surface area ($P = 0.02$) and mean depth ($P < 0.001$). However, Lake Trout presence in nearshore habitat less than 6 m was negatively related to Cisco CPUE ($P < 0.001$; Figure 7C) and positively related to Lake Trout CPUE ($P < 0.001$) and White Sucker CPUE ($P < 0.001$; Appendix 2, Table A.2.2).

DISCUSSION

Cisco CPUE had a significant influence on the life history and spatial location of Northern Pike across a large portion of the Canadian Boreal Shield. These patterns

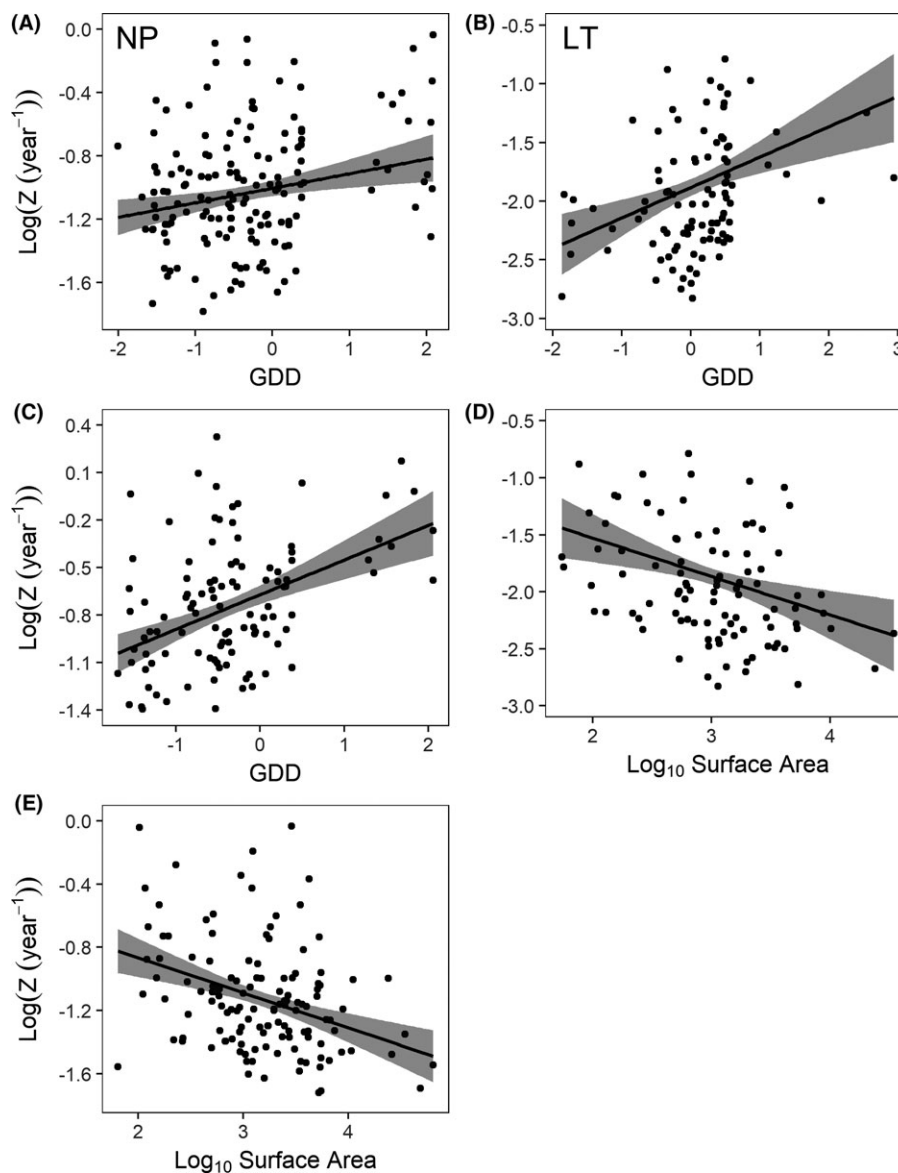


FIGURE 5. Relationships between Northern Pike (NP; left panels) and Lake Trout (LT; right panels) instantaneous total mortality rates (Z) and abiotic variables: **(A)** positive relationship between female NP Z and growing degree-days (GDD; scaled; $P = 0.01$); **(B)** positive relationship between LT Z and GDD (scaled; $P < 0.01$); **(C)** positive relationship between male NP Z and GDD (scaled; $P < 0.001$); **(D)** negative relationship between LT Z and lake surface area ($P < 0.01$); and **(E)** negative relationship between combined-sex NP Z and lake surface area ($P < 0.001$). The solid lines represent the relationships, and the shaded areas represent their 95% confidence intervals. Note the differences in scaling among the x - and y -axes.

closely resembled those of Lake Trout, which are well documented to rely on Ciscoes when present, suggesting that Northern Pike can behave as generalists and extend their foraging effort to offshore prey fish when available. These results demonstrate that Northern Pike reliance on offshore prey may be more common than previously acknowledged. Although there have been accounts of Northern Pike foraging on offshore prey fishes (Makowicki 1973; Colby et al. 1987), our study is the first to demonstrate the influence of offshore prey fish on

Northern Pike life history across a broad portion of their natural distribution. Furthermore, our work demonstrates some similarities in the importance of large offshore prey (i.e., Cisco) on apex predator life histories and is consistent with patterns observed in other aquatic apex predators (Carl 2008; Kaufman et al. 2009), suggesting that the results presented here may be a persistent pattern for freshwater apex predatory species.

Larger L_{∞} values for both Northern Pike and Lake Trout with greater Cisco CPUE occurred across a broad

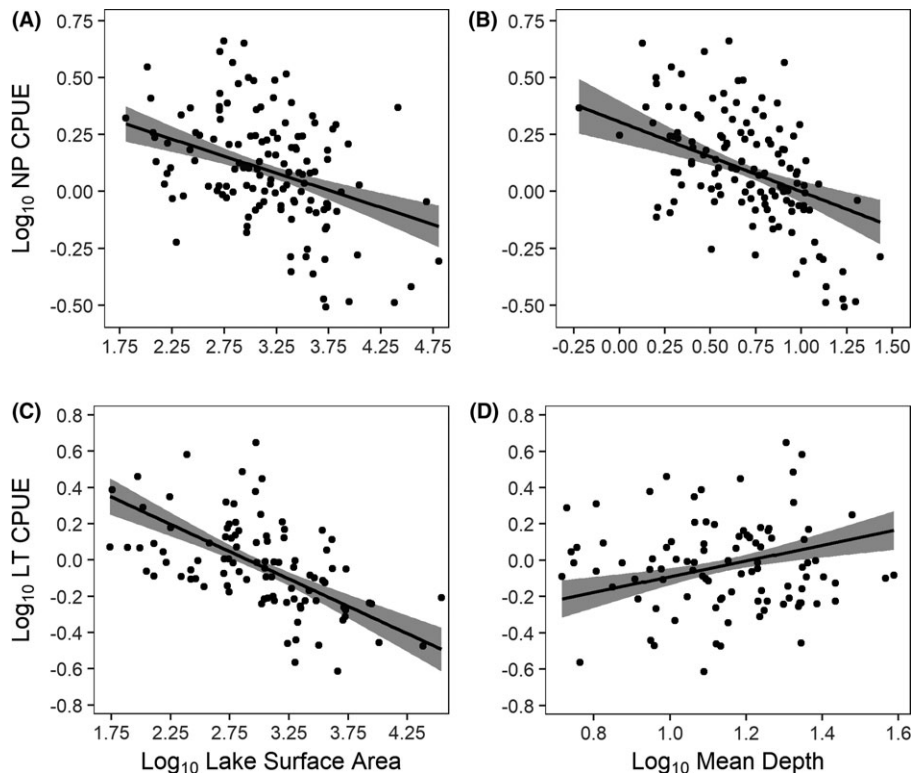


FIGURE 6. Factors influencing the CPUEs of Northern Pike (NP) and Lake Trout (LT) in Ontario Boreal Shield lakes: (A) relationship between NP CPUE (Broad-scale Fish Community Monitoring data set [BsM]) and lake surface area ($P < 0.001$); (B) relationship between NP CPUE (BsM) and the mean depth of lakes ($P < 0.001$); (C) relationship between LT CPUE and lake surface area ($P < 0.001$); and (D) relationship between LT CPUE and the mean depth of lakes ($P < 0.01$). The solid lines represent the relationships, and the shaded areas represent their 95% confidence intervals. Note the differences in scaling among the x- and y-axes.

geographic region. This result is consistent with previous studies (Trippel and Beamish 1989; Jacobson 1992; Carl 2008) and demonstrates that the presence of offshore prey plays an important role in shaping the growth trajectories of apex predators. The Cisco is a large, energy-dense, soft-rayed fusiform species, and the caloric densities of Ciscos (1,799–2,304 cal/g) are reportedly 1.5–2.7 times greater than those of the nearshore prey species we examined (Yellow Perch: ~1,000–1,300 cal/g; White Sucker: 857–884 cal/g; Bryan et al. 1996). Additionally, foraging costs are lower and growth efficiency is higher when predators forage on large, energy-dense prey (Pazzia et al. 2002; Kaufman et al. 2006; Shuter et al. 2016). The combination of size and energy density makes the Cisco an attractive prey when present relative to nearshore species. The selection gradient on Cisco predation is likely mediated through benefits for female Northern Pike, which are typically larger than males (Table 1); achieving larger L_{∞} may positively influence female clutch size and reproductive fitness (Raaf 1988; Roff 1992; Stearns 1992). Furthermore, larger body sizes mediated by foraging on Ciscos may reduce both intraspecific and interspecific predation pressure and competition; Northern Pike are cannibalistic

and compete with other apex predatory species (e.g., Walleye and Lake Trout; Scott and Crossman 1973). By contrast, Lake Whitefish may not be as commonly consumed by Northern Pike. Although previous studies have reported that large Northern Pike occasionally feed on Lake Whitefish (Makowecki 1973), the larger mean size (Rennie et al. 2010) and benthic habits (Hart 1931; Rennie et al. 2009) of Lake Whitefish may limit their exposure to predation by Northern Pike.

Our results suggest that Northern Pike foraging on Ciscos is likely ontogenetic. Cisco CPUE was positively related to Northern Pike L_{∞} but negatively related to Northern Pike ω . Instead, Northern Pike ω values were positively related to the CPUE of nearshore Yellow Perch, which agrees with previous studies reporting that Yellow Perch are important prey for juvenile Northern Pike (Heath and Roff 1996; Venturelli and Tonn 2006). Isotopic evidence from food web studies has indicated the potential for generalist foraging strategies in Northern Pike (Vander Zanden et al. 1997; Vander Zanden and Vadeboncoeur 2002). However, our results on life history patterns suggest that the degree of generalist foraging is dependent on the body size and/or life stage of prey or

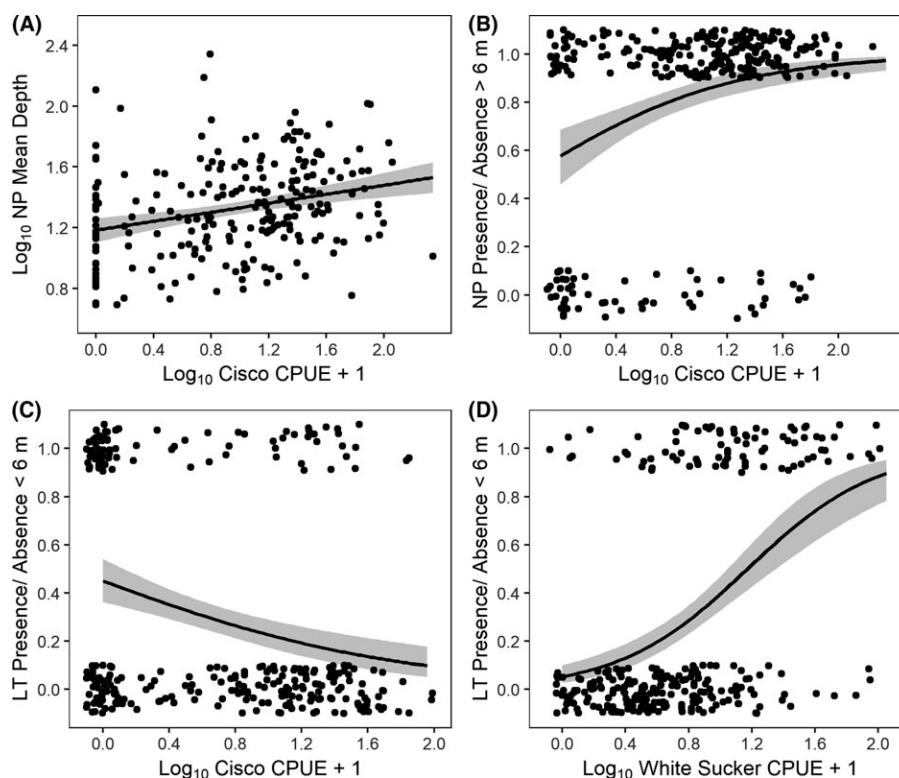


FIGURE 7. The influence of prey availability on the spatial location of Northern Pike (NP) and Lake Trout (LT) in Ontario Boreal Shield lakes: (A) relationship between NP mean depth (Broad-scale Fish Community Monitoring data set [BsM]) and Cisco CPUE ($\log_{10}[x + 1]$ transformed; $P < 0.001$); (B) relationship between NP presence/absence (1 = present; 0 = absent) in offshore habitat greater than 6 m (BsM) and Cisco CPUE ($P < 0.001$); (C) relationship between LT presence/absence in nearshore habitat less than 6 m (BsM) and Cisco CPUE ($P < 0.001$); and (D) relationship between LT presence/absence in nearshore habitat less than 6 m (BsM) and White Sucker CPUE ($\log_{10}[x + 1]$ transformed; $P < 0.001$). Panel A depicts a linear model; panels B–D represent binomial generalized linear models. Points are jittered vertically and horizontally for panels B–D. The solid lines represent the relationships, and the shaded areas represent their 95% confidence intervals. Note the differences in scaling among the y-axes.

predator. Juvenile Northern Pike spend most of their time in nearshore environments, thereby limiting their habitat overlap with Ciscoes (Casselman and Lewis 1996), and smaller Northern Pike are gape limited from foraging upon larger prey (Nilsson and Brönmark 2000). Based on our results, Northern Pike may be more reliant on nearshore species (i.e., Yellow Perch) during their early growth and development; as they grow, they may exhibit an ontogenetic shift to feeding upon Ciscoes in lakes where they are available.

In contrast to Northern Pike, Lake Trout ω values were not significantly related to any of the predictor variables included in our analysis. Lake Trout generally grow slower than Northern Pike and can rely heavily on invertebrates, such as opossum shrimp *Mysis diluviana*, during their early growth and development (Trippel and Beamish 1993). Thus, a significant effect was not detected, likely because prey at lower trophic levels were not included in our analyses. Although Carl (2008) demonstrated more rapid early growth rates for juvenile Lake Trout in lakes

with coregonines present, the observations and comparisons were based on considerably fewer lakes than were examined the current study.

Our study suggests that the quality of prey also influences the mortality rates of Northern Pike. The influence of food quality on the health and mortality rates of animals has previously been reported across both aquatic and terrestrial taxa (Sturner et al. 1993; Oedekoven and Joern 2000). We observed lower Z-values for Northern Pike populations from lakes with greater Cisco CPUEs. The availability of high-quality prey (i.e., Cisco) likely provides Northern Pike with a surplus of energy (over the costs of growth and reproduction) that could be allocated to physiological processes, such as cellular maintenance to slow down the rate of senescence (Kirkwood and Rose 1991). Additionally, it is possible that the growth and longevity of Northern Pike may be limited by lake size and shape; lake ecosystem size has been identified as positively related to food chain length (Post et al. 2000; Tunney et al. 2012), and analyses of our data sets showed positive

correlations between lake surface area and Cisco presence ($r = 0.38\text{--}0.55$). Lake shape may also impact the community structure and dynamics of lake ecosystems, as more circular Boreal Shield lakes typically have less epilimnetic benthic habitat (Dolson et al. 2009). When offshore prey are absent or are found in low abundance (a more common condition in smaller, shallower lakes), faster life history strategies (faster early growth, earlier maturity, smaller maximum size, and greater total mortality rates) may be under selection to maximize reproductive output.

The Z -values of both apex predators in our study were negatively related to lake surface area and positively related to GDD. Larger lakes that stratify typically have a greater proportion of their volume in the hypolimnion, which is supported by a positive correlation between lake surface area and mean depth in our data sets ($r = 0.28\text{--}0.46$). Additionally, warmer climates may result in greater stress for both of the cold-adapted predators in our study through limitation of optimal thermal habitat (Chu et al. 2005; Mackenzie-Grieve and Post 2006; Guzzo et al. 2017). Warmer environments result in faster metabolism for ectotherms, which can shorten life cycles (Gillooly et al. 2001; Kelly et al. 2014; Holt and Jørgensen 2015). Evidence of GDD effects on Northern Pike in the FWIN data set but not in the BsM data set may be due to the greater number of lakes at lower latitudes in the FWIN data set. Lakes at lower latitudes are closer to large urban centers, likely facilitating greater total mortality through fishing (Post and Parkinson 2012).

The availability of offshore prey also influenced Northern Pike CPUE, but results were mixed; Northern Pike CPUE was positively related to Cisco CPUE in the FWIN data set but not in the BsM data set. Larger values of L_{∞} for Northern Pike allow for greater fecundity, which may lead to increased recruitment (Raat 1988). Additionally, greater Cisco availability may allow Northern Pike to widen their ecological niche and reduce intraspecific competition. No such relationship was observed for Lake Trout. In contrast, Lake Trout recruitment has been shown to be lower in lakes with coregonines compared to those where coregonines are absent (Carl 2008), and coregonines are thought to be potential competitors of juvenile Lake Trout (Trippel and Beamish 1989).

Physical lake characteristics (lake surface area and mean depth) consistently had the strongest effects on apex predator CPUE, and they appear to describe conditions to which these species are adapted in their early life history. Although both Northern Pike CPUE and Lake Trout CPUE were negatively related to lake surface area, mean depth had contrasting effects on the two apex predators: deeper lakes supported fewer Northern Pike but more Lake Trout. Lake Trout are obligate coldwater fish (Scott and Crossman 1973; Gunn et al. 2004), whereas Northern Pike are adapted to coolwater areas and littoral vegetation

(Casselman and Lewis 1996; Pierce and Tomcko 2005). There was a strong negative correlation between mean depth and percent littoral zone in the FWIN data set ($r = -0.88$). Thus, mean depth may reflect the importance of littoral vegetation for Northern Pike prolificacy. Growing degree-days were also negatively related to Lake Trout CPUE, further highlighting the sensitivity of Lake Trout to warmer climates (Chu et al. 2005; Mackenzie-Grieve and Post 2006; Guzzo et al. 2017).

Both Northern Pike and Lake Trout appear to occupy offshore habitat more often when Ciscos are more abundant. With greater Cisco CPUE in the BsM gillnetting surveys, Northern Pike were caught in deeper water and were captured in offshore habitat more frequently. Similarly, Lake Trout were captured in nearshore habitat less often when Cisco CPUE was greater. Such habitat overlap between predators and prey is generally associated with trophic interactions (Greer and Woodson 2016). Thus, our spatial location results are consistent with our life history results, which together suggest that Northern Pike and Lake Trout forage on Ciscos when they are readily available, and this behavior may enhance their growth and survival, leading to greater fitness. These results highlight the generalist foraging strategies of these apex predators and the key role that Ciscos play in Boreal Shield lake food webs.

The overall weight of evidence in our study is consistent with patterns observed for other freshwater apex predators (Carl 2008; Kaufman et al. 2009), strongly supporting the notion that Cisco availability influences predator life histories. Despite the number of statistical tests performed (an inflated type I error rate would indicate that 7 of the 44 significant results we observed could be spurious, on average), the importance of Cisco CPUE across a range of life history traits in both species observed in two independent data sets speaks strongly to the biological significance of our results. Furthermore, these results were observed using limited environmental data to include as covariates. There are undoubtedly additional factors that influence the growth and life history of Northern Pike and Lake Trout across this range, but the effect of Cisco CPUE was consistent and widespread.

In conclusion, offshore prey fish densities had significant and consistent impacts on the growth and life history traits of Northern Pike and Lake Trout, and our results are supported by patterns observed in the literature for other apex predators (Carl 2008; Kaufman et al. 2009). Although Northern Pike and Lake Trout are adapted to different environmental conditions, their L_{∞} values were influenced similarly by Cisco CPUE. This agrees with our expectations that there are basic physiological principles driving the growth trajectories of organisms (Kerr 1971). The consistency of our results across two independent data sets highlights the reproducibility of our findings, and they

provide interesting hypotheses to be tested using dietary and behavioral analyses.

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TABLE A.1.3. Model output from relative abundance (\log_{10} [CPUE]) analysis of Northern Pike from the Fall Walleye Index Netting data set. The P -values reported are based on Satterthwaite approximations for denominator degrees of freedom. Individual variables that were significant in the model are shown in bold italics. Z -scored parameter estimates represent the relative influence of each of the predictor variables. Marginal R^2 (R_m^2) values represent the amount of variation explained by all of the fixed effects for each response variable; conditional R^2 (R_c^2) values represent the amount of variation explained by both the fixed and random effects for each response variable.

Response variable	Fixed effects	Parameter estimate	SE	t -value	P -value	Z -scored estimate	R_m^2	R_c^2
\log_{10} (CPUE)	<i>Log₁₀(Lake Whitefish CPUE)</i>	0.033	0.033	2.168	0.031	0.023		
	<i>Log₁₀(Cisco CPUE)</i>	0.024	0.024	3.799	<0.001	0.039		
	Log ₁₀ (White Sucker CPUE)	0.062	0.042	1.499	0.135	0.017		
	<i>Log₁₀(Yellow Perch CPUE)</i>	0.075	0.027	2.729	0.007	0.032		
	<i>Log₁₀(lake surface area)</i>	-0.099	0.016	-6.151	<0.001	-0.084		
	<i>Log₁₀(lake mean depth)</i>	-0.094	0.036	-2.603	0.010	-0.030		
	Growing degree-days	-0.015	0.012	-1.251	0.212	-0.015		
								0.254

TABLE A.1.4. Model outputs from life history analyses of Northern Pike from the Broad-scale Fish Community Monitoring data set. The P -values reported are based on Satterthwaite approximations for denominator degrees of freedom. Individual variables that were significant in the models are shown in bold italics. Z -scored parameter estimates represent the relative influence of each of the predictor variables. Marginal R^2 (R_m^2) values represent the amount of variation explained by all of the fixed effects for each response variable. Conditional R^2 (R_c^2) values represent the amount of variation explained by both the fixed and random effects for each response variable.

Response variable	Fixed effects	Parameter estimate	SE	t -value	P -value	Z -scored estimate	R_m^2	R_c^2
Log asymptotic length (L_∞)	Log ₁₀ (Lake Whitefish CPUE)	-0.012	0.059	-0.200	0.842	-0.427		
	<i>Log₁₀(Cisco CPUE)</i>	0.095	0.049	1.959	0.053	3.423		
	Log ₁₀ (Northern Pike CPUE)	-0.038	0.067	-0.564	0.574	-1.354		
	Log ₁₀ (White Sucker CPUE)	0.027	0.075	0.360	0.720	0.966		
	Log ₁₀ (Yellow Perch CPUE)	-0.115	0.063	-1.835	0.069	-4.131		
	Log ₁₀ (lake surface area)	0.037	0.027	1.404	0.163	1.341		
	Log ₁₀ (lake mean depth)	0.072	0.060	1.204	0.231	2.592		
	Growing degree-days	0.004	0.027	0.159	0.874	0.156		
							0.131	0.333
Log early growth rate (ω)	Log ₁₀ (Lake Whitefish CPUE)	0.112	0.109	1.025	0.308	4.035		
	<i>Log₁₀(Cisco CPUE)</i>	-0.247	0.090	-2.753	0.007	-8.891		
	Log ₁₀ (Northern Pike CPUE)	-0.042	0.123	-0.347	0.729	-1.529		
	Log ₁₀ (White Sucker CPUE)	-0.090	0.138	-0.656	0.513	-3.256		
	<i>Log₁₀(Yellow Perch CPUE)</i>	0.528	0.114	4.634	<0.001	19.025		
	<i>Log₁₀(lake surface area)</i>	-0.118	0.048	-2.486	0.014	-4.258		
	Log ₁₀ (lake mean depth)	0.127	0.111	1.149	0.253	4.571		
	<i>Growing degree-days</i>	-0.104	0.040	-2.623	0.015	-3.737		
							0.226	0.252
Log instantaneous total mortality (Z)	Log ₁₀ (Lake Whitefish CPUE)	0.200	0.136	1.464	0.146	7.192		
	<i>Log₁₀(Cisco CPUE)</i>	-0.235	0.112	-2.094	0.038	-8.467		
	Log ₁₀ (Northern Pike CPUE)	-0.198	0.152	-1.299	0.197	-7.121		
	Log ₁₀ (White Sucker CPUE)	0.049	0.172	0.285	0.776	1.768		
	<i>Log₁₀(Yellow Perch CPUE)</i>	0.508	0.141	3.607	<0.001	18.286		
	<i>Log₁₀(lake surface area)</i>	-0.222	0.058	-3.812	<0.001	-8.001		
	Log ₁₀ (lake mean depth)	-0.050	0.138	-0.359	0.720	-1.787		
	Growing degree-days	0.011	0.044	0.253	0.801	0.396		
							0.230	0.623

TABLE A.1.4. Continued.

Response variable	Fixed effects	Parameter estimate	SE	<i>t</i> -value	<i>P</i> -value	Z-scored estimate	R_m^2	R_c^2
Relative abundance (log ₁₀ [CPUE])	Log ₁₀ (Lake Whitefish CPUE)	0.043	0.080	0.532	0.595	1.543	0.459	0.706
	Log ₁₀ (Cisco CPUE)	0.109	0.065	1.666	0.098	3.925		
	Log₁₀(White Sucker CPUE)	0.251	0.099	2.531	0.013	9.026		
	Log ₁₀ (Yellow Perch CPUE)	0.064	0.084	0.766	0.445	2.314		
	Log₁₀(lake surface area)	-0.150	0.032	-4.621	<0.001	-5.403		
	Log₁₀(lake mean depth)	-0.307	0.077	-4.008	<0.001	-11.062		
	Growing degree-days	-0.010	0.030	-0.322	0.752	-0.345		

TABLE A.1.5. Model outputs from life history analyses of Lake Trout from the Broad-scale Fish Community Monitoring data set. The *P*-values reported are based on Satterthwaite approximations for denominator degrees of freedom. Individual variables that were significant in the models are shown in bold italics. Z-scored parameter estimates represent the relative influence of each of the predictor variables. Marginal R^2 (R_m^2) values represent the amount of variation explained by all of the fixed effects for each response variable; conditional R^2 (R_c^2) values represent the amount of variation explained by both the fixed and random effects for each response variable.

Response variable	Fixed effects	Parameter estimate	SE	<i>t</i> -value	<i>P</i> -value	Z-scored estimate	R_m^2	R_c^2
Log asymptotic length (L_∞)	Log ₁₀ (Lake Whitefish CPUE)	0.067	0.066	1.011	0.315	2.410	0.422	0.450
	Log₁₀(Cisco CPUE)	0.388	0.091	4.246	<0.001	13.963		
	Log₁₀(Lake Trout CPUE)	-0.183	0.071	-2.577	0.012	-6.581		
	Log ₁₀ (White Sucker CPUE)	0.040	0.089	0.449	0.655	1.433		
	Log ₁₀ (Yellow Perch CPUE)	-0.126	0.104	-1.216	0.227	-4.550		
	Log₁₀(lake surface area)	0.088	0.038	2.340	0.022	3.168		
	Log ₁₀ (lake mean depth)	-0.106	0.097	-1.093	0.278	-3.805		
	Growing degree-days	0.004	0.025	0.175	0.861	0.157		
Log early growth rate (ω)	Log ₁₀ (Lake Whitefish CPUE)	0.153	0.125	1.226	0.224	5.519	0.132	0.613
	Log ₁₀ (Cisco CPUE)	-0.261	0.174	-1.494	0.139	-9.378		
	Log ₁₀ (Lake Trout CPUE)	-0.034	0.136	-0.249	0.804	-1.214		
	Log ₁₀ (White Sucker CPUE)	0.187	0.170	1.102	0.274	6.741		
	Log ₁₀ (Yellow Perch CPUE)	0.173	0.199	0.871	0.386	6.228		
	Log ₁₀ (lake surface area)	0.067	0.070	0.952	0.345	2.404		
	Log ₁₀ (lake mean depth)	0.124	0.185	0.668	0.506	4.449		
	Growing degree-days	-0.037	0.045	-0.816	0.417	-1.330		
Log instantaneous total mortality (Z)	Log ₁₀ (Lake Whitefish CPUE)	0.059	0.198	0.298	0.766	2.122	0.308	0.442
	Log ₁₀ (Cisco CPUE)	-0.184	0.271	-0.679	0.499	-6.624		
	Log ₁₀ (Lake Trout CPUE)	-0.235	0.212	-1.109	0.271	-8.444		
	Log ₁₀ (White Sucker CPUE)	-0.415	0.265	-1.568	0.121	-14.946		
	Log ₁₀ (Yellow Perch CPUE)	-0.440	0.313	-1.406	0.163	-15.840		
	Log₁₀(lake surface area)	-0.337	0.111	-3.023	0.003	-12.132		
	Log ₁₀ (lake mean depth)	-0.555	0.290	-1.917	0.059	-19.983		
	Growing degree-days	0.259	0.079	3.274	0.002	9.337		

TABLE A.1.5. Continued.

Response variable	Fixed effects	Parameter estimate	SE	t-value	P-value	Z-scored estimate	R_m^2	R_c^2
Relative abundance (log ₁₀ [CPUE])	Log ₁₀ (Lake Whitefish CPUE)	0.081	0.098	0.824	0.412	2.914		
	Log ₁₀ (Cisco CPUE)	0.158	0.135	1.164	0.248	5.677		
	Log ₁₀ (White Sucker CPUE)	0.029	0.133	0.219	0.827	1.048		
	Log ₁₀ (Yellow Perch CPUE)	0.079	0.156	0.507	0.613	2.840		
	Log₁₀(lake surface area)	-0.302	0.045	-6.650	<0.001	-10.855		
	Log₁₀(lake mean depth)	0.432	0.138	3.145	0.002	15.568		
	Growing degree-days	-0.096	0.034	-2.784	0.007	-3.445		
							0.411	0.411

Appendix 2: Model Outputs for Northern Pike and Lake Trout Spatial Location Analyses

TABLE A.2.1. Model outputs from spatial location analyses of Northern Pike from the Broad-scale Fish Community Monitoring data set. Individual variables that were significant in the models are shown in bold italics.

Response variable	Predictor variables	Parameter estimate	SE	T/z-value	P-value	Z-scored estimate
Mean log depth of catch	Log ₁₀ (Lake Whitefish CPUE)	-0.051	0.051	-1.007	0.315	-0.023
	Log₁₀(Cisco CPUE)	0.146	0.040	3.666	<0.001	0.084
	Log ₁₀ (Northern Pike CPUE)	0.033	0.096	0.349	0.727	0.009
	Log ₁₀ (White Sucker CPUE)	-0.048	0.080	-0.599	0.550	-0.017
	Log ₁₀ (Yellow Perch CPUE)	0.001	0.041	0.030	0.976	<0.001
	Log ₁₀ (lake surface area)	0.065	0.038	1.686	0.093	0.038
	Log ₁₀ (lake mean depth)	-0.002	0.060	-0.033	0.974	<0.001
	Growing degree-days	<0.001	<0.001	-0.253	0.801	-0.007
Presence/absence in offshore habitat	Log ₁₀ (Lake Whitefish CPUE)	0.011	0.494	0.023	0.982	0.005
	Log₁₀(Cisco CPUE)	1.374	0.365	3.762	<0.001	0.819
	Log₁₀(Northern Pike CPUE)	9.100	1.548	5.877	<0.001	2.854
	Log₁₀(White Sucker CPUE)	-1.890	0.790	-2.393	0.017	-0.670
	Log ₁₀ (Yellow Perch CPUE)	0.517	0.333	1.553	0.120	0.339
	Log₁₀(lake surface area)	1.324	0.411	3.224	0.001	0.795
	Log ₁₀ (lake mean depth)	0.954	0.555	1.720	0.085	0.433
	Growing degree-days	-0.004	0.002	-2.505	0.012	-0.709

TABLE A.2.2. Model outputs from spatial location analyses of Lake Trout from the Broad-scale Fish Community Monitoring data set. Individual variables that were significant in the models are shown in bold italics.

Response variable	Predictor variables	Parameter estimate	SE	T/z-value	P-value	Z-scored estimate
Mean log depth of catch	Log ₁₀ (Lake Whitefish CPUE)	-0.154	0.082	-1.879	0.062	-0.076
	Log ₁₀ (Cisco CPUE)	0.015	0.065	0.232	0.817	0.009
	Log ₁₀ (Lake Trout CPUE)	0.269	0.141	1.910	0.057	0.077
	Log ₁₀ (White Sucker CPUE)	0.041	0.088	0.471	0.638	0.020
	Log ₁₀ (Yellow Perch CPUE)	0.014	0.049	0.289	0.773	0.012
	Log₁₀(lake surface area)	-0.178	0.075	-2.365	0.019	-0.115
	Log₁₀(lake mean depth)	-0.557	0.098	-5.702	<0.001	-0.242
	Growing degree-days	<0.001	<0.001	-0.803	0.423	-0.031
Presence/absence in nearshore habitat	Log ₁₀ (Lake Whitefish CPUE)	0.095	0.394	0.240	0.810	0.047
	Log₁₀(Cisco CPUE)	-1.174	0.342	-3.432	0.001	-0.725
	Log₁₀(Lake Trout CPUE)	3.872	0.678	5.709	<0.001	1.277
	Log₁₀(White Sucker CPUE)	1.786	0.459	3.896	<0.001	0.836
	Log ₁₀ (Yellow Perch CPUE)	0.123	0.240	0.512	0.609	0.098
	Log ₁₀ (lake surface area)	0.079	0.385	0.205	0.837	0.051
	Log ₁₀ (lake mean depth)	0.425	0.526	0.808	0.419	0.187
	Growing degree-days	-0.002	0.001	-1.724	0.085	-0.380

Appendix 3: Descriptive Statistics of Predictor Variables Included in Northern Pike and Lake Trout Life History Analyses

TABLE A.3.1. Descriptive statistics of the predictor variables included in life history analyses for female and male Northern Pike from the Fall Walleye Index Netting data set (Min = minimum; Max = maximum; GDD = growing degree-days). Variables are not transformed.

Predictor variable	<i>N</i>	Mean	Min	Max	SD	SE
Female Northern Pike						
Cisco CPUE	155	5.40	0.00	42.64	7.69	0.62
Lake Whitefish CPUE	155	1.83	0.00	14.13	2.51	0.20
White Sucker CPUE	155	3.28	0.00	20.17	2.69	0.22
Yellow Perch CPUE	155	6.55	0.08	43.62	8.87	0.71
Northern Pike CPUE	155	4.30	0.62	11.00	2.12	0.17
GDD	155	1,591.82	1,237.15	2,093.54	194.68	15.64
Lake surface area (ha)	155	10,617.89	42.90	246,718.00	32,528.13	2,612.72
Lake mean depth (m)	155	6.32	0.50	39.20	5.28	0.42
Male Northern Pike						
Cisco CPUE	109	5.00	0.00	42.64	7.22	0.69
Lake Whitefish CPUE	109	2.00	0.00	10.72	2.42	0.23
White Sucker CPUE	109	3.50	0.00	20.17	2.83	0.27
Yellow Perch CPUE	109	6.42	0.04	43.62	8.22	0.79
Northern Pike CPUE	109	4.80	1.30	11.00	2.11	0.20
GDD	109	1,582.71	1,302.77	2,087.69	172.65	16.54
Lake surface area (ha)	109	12,547.29	53.40	44,8060.00	46,379.31	4,442.33
Lake mean depth (m)	109	7.01	0.50	54.90	8.06	0.77
Combined Northern Pike						
Cisco CPUE	264	4.29	0.00	42.64	6.67	0.41
Lake Whitefish CPUE	264	1.76	0.00	14.13	2.48	0.15
White Sucker CPUE	264	3.14	0.00	20.17	2.66	0.16
Yellow Perch CPUE	264	6.00	0.00	91.88	10.07	0.62
Northern Pike CPUE	264	3.63	0.62	11.00	1.98	0.12
GDD	264	1,598.07	1,223.92	2,117.23	192.54	11.85
Lake surface area (ha)	264	40,254.35	42.90	4,165,900.00	363,050.30	22,344.20
Lake mean depth (m)	264	7.00	0.50	61.00	7.68	0.47

TABLE A.3.2. Descriptive statistics of the predictor variables included in life history analyses for Northern Pike and Lake Trout from the Broad-scale Fish Community Monitoring data set (Min = minimum; Max = maximum; GDD = growing degree-days). Variables are not transformed.

Predictor variable	<i>N</i>	Mean	Min	Max	SD	SE
Northern Pike						
Cisco CPUE	130	1.25	0.00	11.17	1.93	0.17
Lake Whitefish CPUE	130	1.08	0.00	8.33	1.33	0.12
White Sucker CPUE	130	2.10	0.03	10.31	1.65	0.14
Yellow Perch CPUE	130	1.26	0.00	18.57	2.11	0.18
Northern Pike CPUE	130	1.46	0.31	4.58	0.85	0.07
GDD	130	1,483.75	1,059.00	1,771.00	164.40	14.42
Lake surface area (ha)	130	3,681.51	64.29	63,882.82	8,052.12	706.22
Lake mean depth (m)	130	6.23	0.60	27.20	4.35	0.38
Lake Trout						
Cisco CPUE	96	0.39	0.00	4.38	0.72	0.07
Lake Whitefish CPUE	96	1.06	0.00	8.33	1.41	0.14
White Sucker CPUE	96	1.30	0.00	9.03	1.55	0.16
Yellow Perch CPUE	96	0.33	0.00	4.63	0.86	0.09
Lake Trout CPUE	96	1.11	0.24	4.43	0.73	0.07
GDD	96	1,624.24	1,225.00	2,214.00	159.05	16.23
Lake surface area (ha)	96	2,289.27	54.98	34,518.17	4,470.03	456.22
Lake mean depth (m)	96	15.30	5.20	38.70	6.67	0.68