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**Predator-prey dynamics mediate long-term production trends of Cisco
(*Coregonus artedii*) in a northern Wisconsin lake**

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Abstract: We quantified production, biomass, and P/B ratios for cisco (*Coregonus artedii*) in Trout Lake, Wisconsin USA (2001-2015). Across all years, annual production, biomass, and P/B were variable ranging $0.6\text{--}30.2\text{ kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$, $1.2\text{--}39.7\text{ kg}\cdot\text{ha}^{-1}$, and $0.4\text{--}0.9\text{ y}^{-1}$, respectively. Cisco production exhibited obvious decline. However, neither biomass nor P/B changed significantly over time. Long-term patterns of environmental conditions remained unchanged during the study, and were unrelated to cisco production. However, lake trout (*Salvelinus namaycush*) relative abundance showed a strong inverse relationship with cisco production and biomass. Intense lake trout stocking has occurred in this lake over time to conserve a genetically unique strain of the species. These management efforts may have had the unintended consequence of amplifying top-down predation on cisco. Since cisco P/B has gone largely unchanged, cisco production would be predicted to rebound quickly to adaptive reductions in lake trout stocking. Further increases in lake trout numbers could place both populations at risk of collapse. This study provides an example of a fisheries production approach for understanding and conserving cold-water fisheries, especially in lakes dominated by ciscoes.

29 **Introduction**

30 Secondary production is a classic and potentially unifying theme in fisheries
31 science (Ricker 1946; Waters 1977, 1992; Dolbeth et al. 2012; Rypel and David 2017).
32 Fisheries production is defined as the rate of elaboration of new fish biomass in a
33 population or assemblage which is indicative of a species ecological success in an
34 ecosystem (Kwak and Waters 1997; Dolbeth et al. 2012). Specifically, production rates
35 integrate critical rate functions such as mortality, growth and recruitment, and are
36 therefore extremely responsive to environmental influences (Waters 1992; Valentine-
37 Rose et al. 2007; Rypel and David 2017). This capability to reflect rate functions makes
38 production measures appealing to fish managers, since they can be used to answer a
39 variety of questions ranging from fisheries sustainability (Colvin et al. 2012; Rypel et al.
40 2015) to habitat importance (Rawson 1952; Kwak and Waters 1997; Lobón-Cerviá et al.
41 2011). Commonly, fish biologists estimate biomass as the amount of living fish tissue
42 available per unit area as an indirect measure of fish production. However, biomass is a
43 static variable, whereas production is dynamic and literally describes the flux of biomass
44 which characterizes fish productivity (Dolbeth et al. 2012; Rypel and David 2017).
45 Additionally, production to biomass (P/B) ratios measure the productive capacity of
46 populations and habitats by describing population replacement rates (Randall and
47 Minns 2000). For example, P/B ratios explicitly quantify the amount of production in a
48 population that is independent of biomass (Waters 1977), and since P/B is
49 mathematically expressed in units of inverse time, it represents a pure ecological
50 statistic (Charnov 1993).

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Cisco (*Coregonus artedii*) is an obligate cold-water species, native to glacial lakes in the upper latitudes of North America (Scott and Crossman 1973). Populations of the species are of great importance to fisheries because of their role in food web dynamics of cold-water lakes (Rudstam et al. 1993; Ebener 1995; Henderson et al. 2004). For example, lakes with robust cisco populations have a positive influence on the growth dynamics of northern pike (*Esox lucius*), lake trout (*Salvelinus namaycush*), and walleye (*Sander vitreus*) compared to lakes with other prey bases characterized by lower energy densities (Matuszek et al. 1990, Jacobson 1992, Kaufman et al. 2009). Additionally, as planktivores, cisco can effectively regulate zooplankton assemblage structure and mediate water quality via middle-out trophic cascades (Vanni et al. 1990; Rudstam et al. 1993; Lathrop et al. 2002). Cisco populations are also indicative of environmental change more generally. They are sensitive to temperature and water quality, because oxythermal conditions are narrowed in lakes during summer months (Jacobson et al. 2008; Jacobson et al. 2010; Jiang et al. 2012; Fang et al. 2012; Jacobson et al. 2012). For example, cisco are in decline across the southern edge of their range, a trend that is being driven by a combination of warming lake temperatures and land use change (Jacobson et al. 2012; Honsey et al. 2016; Rypel et al., unpublished data).

Because of the seasonally pelagic distribution of cisco in lakes, this species has been notoriously difficult to survey. Hydroacoustics and vertical gillnets have been standard assessment tools for measuring and monitoring cisco and other pelagic fish populations in glacial lakes (Rudstam et al. 1993; Milne et al. 2005, Hrabik et al. 2006). Researchers have typically limited their research to relatively simple comparisons of cisco abundance and biomass (Rudstam et al. 1993; Lathrop et al. 2002). Yet these

metrics are static in the sense that they represent ecological snapshots at a given point in time, whereas production and P/B capture dynamic rate functions and energy flux. Myers et al. (2015) recently suggested that cisco recruitment dynamics in lakes should be quantified solely based on hydroacoustics as opposed to traditional gears (e.g., gill nets or mid-water trawl); thus, the potential exists for capturing production dynamics via hydroacoustics. Briefly, mobile hydroacoustics surveys utilize active sound to measure the abundance and biomass of pelagic fish populations in large waterbodies via backscatter of the swim bladders of resident fishes. Estimation of production requires estimates of abundance, size-structure, body mass, and growth rates. Abundance and size-structure are obtainable through the use of hydroacoustics. Hence, studies of hydroacoustics and fish production are compatible. Many have utilized this information to derive fish estimates of pelagic fish biomass (Rypel and David 2017), but few have utilized hydroacoustic methods to empirically calculate production (Schulz et al. 2004).

Studies of pelagic prey bases in lakes, particularly long-term studies, are valuable for management of fisheries. For example, hydroacoustics surveys are extensively utilized in the study and management of the Laurentian Great Lakes fisheries (Fabrizio et al. 1997; Mason et al. 2005). Here, pelagic prey are monitored over time to detect and prevent over-depletion of prey resources by stocked salmonids, and to subsequently adjust harvest and stocking rates as needed to ensure fishery sustainability (Stewart et. al. 1981; Tsehay et al. 2014). However, smaller inland lake fisheries are rarely managed in this tradition, even though connected pelagic-littoral fisheries are common in lakes across the globe (Vander Zanden and Vadeboncoeur 2002; Tunney et al. 2014). Food web (e.g., Ecopath with Ecosim) and bioenergetics

modelling are two approaches that have been used to infer predator-prey interactions within lakes (e.g., Stewart et al. 1981; Cox and Kitchell 2004). However, these models are complex, and tend to rely on a host of assumptions regarding fish production, biomass, and P/B ratio values (Hansen et al. 1993; Christensen and Walters 2004; Dolbeth et al. 2012). Empirical examinations of predator-prey production dynamics could offer an additional path towards better understanding and management of lakes with pelagic food webs. First, estimation of production dynamics could allow for improved parametrization of food web models. Second, important ecological patterns may be empirically detectable, if production dynamic data are temporally explicit. Finally, empirical trends in data are sometimes more easily explained to stakeholders and managers with limited mathematical backgrounds (Dolbeth et al. 2012). Yet the data required to perform such studies are potentially rare due to the expense and difficulty associated with long-term data collection (Magnuson et al. 2006).

The goals of our study were to 1) quantify annual production, biomass and P/B for cisco in Trout Lake for all years when hydroacoustic data were available; 2) evaluate long-term trends in production, biomass and P/B of cisco in Trout Lake; and 3) examine potential ecological and food web drivers of long-term cisco production dynamics.

Methods

Study site

Trout Lake is a 1564 ha drainage lake (mean and maximum depth = 14.9 m and 35.7 m, respectively) located in Vilas County, Wisconsin. Cisco are by far the most numerous pelagic species in the lake (Ahrenstorff et al. 2013). Aside from cisco, other

common fish species include muskellunge (*Esox masquinongy*), bluegill (*Lepomis macrochirus*), yellow perch (*Perca flavescens*), largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), walleye, northern pike (*Esox lucius*), lake trout, and lake whitefish (*Coregonus clupeaformis*). The watershed is primarily forest (51%), wetland (19%) and open water (24%), and a small amount of low intensity and open space (5%) development, being primarily cottages and vacation homes. It is one of only two lakes in Wisconsin known to have historically supported naturally reproducing lake trout. A variety of studies have been conducted on Trout Lake over time because it is part of the Northern Temperate Lakes – Long Term Ecological Research (NTL-LTER) program. These studies have documented some significant ecological shifts that have occurred in the lake over the last 40 y (Magnuson et al. 2006). For example, establishment of rusty crayfish (*Orconectes rusticus*) in the lake during the early 1980s decimated littoral macrophyte communities which resulted in changes to the littoral food web (Lodge et al. 1986; Olden et al. 2006). To monitor these ecological trends, NTL-LTER continually collects numerous ecological data on an annual basis in Trout Lake, including data collect on pelagic fish assemblages from vertical gillnetting and hydroacoustic surveys. However, no studies have examined long-term dynamics of Trout Lake pelagic fishes, specifically its cisco population which dominates the pelagic assemblage (Ahrenstorff et al. 2013).

Fish and limnology datasets

Fisheries data were collected on Trout Lake and other NTL-LTER lakes annually using a consistent methodology. In 2001, the NTL-LTER established modern

standardized methods to collect and analyze hydroacoustic and vertical gillnet survey data in lakes, to effectively monitor trends on the pelagic fish communities. This dataset provided 15 years of available hydroacoustic data on cisco from Trout Lake, including fish density estimates and single acoustic target data. Hydroacoustic data collection, processing, and analyses followed methods described in Lawson et al. (2015) and the general procedures outlined in Parker-Stetter et al. (2009). Annual hydroacoustic surveys occurred during summer stratification at night and following systematic transects covering pelagic portions of the lake (i.e., water depths > 6 m). The amount of hydroacoustic data needed for collection, reflecting the amount of transects, was determined based on lake area and the spatial coverage necessary to achieve a CV = 25%, as suggested by Aglen (1983). Additional details concerning sampling design and collection settings can be accessed via pelagic prey sonar data and metadata on the NTL-LTER website (<https://lter.limnology.wisc.edu>). From 2001-2003, hydroacoustics data were collected using a Biosonics DT-6000 Echosounder with a 120kHz split beam transducer; and from 2004-2015 with a Biosonics DT-X Echosounder with a 70kHz split beam transducer. Data were collected consistently throughout the duration of the study period using the same collection settings, including a pulse width of 0.04 ms and a ping rate of 3 s^{-1} . Survey data were processed and analyzed using Echoview software (Myriax Pty Limited, Tasmania, Australia), where fish density (fish ha^{-1}) was calculated using echo integration and single echo detection using the same data processing protocol and settings as Lawson et al. (2015). Cisco densities were estimated using 200 m horizontal analysis bins. Single target data were produced by running single echo detection algorithms in Echoview which only included individual targets larger than -55

dB. Single target data were used to describe pelagic fish species composition. Further, size distribution of all targets were estimated using Love's (1977) dorsal aspect equation which allows conversion of target strength (dB) to fish total length (mm).

Each year in late summer (July-August), vertical gill nets were used to sample pelagic fish populations throughout the entire water column. A series of seven monofilament gill net panels, each being 4 m wide and 33 m long, were hung vertically from foam rollers and chained together in a gang. The gangs of net panels were arranged by graded mesh size (19, 25, 32, 38, 51, 64, and 89 mm), that were selected to consistently capture a range of fish sizes (see Rudstam and Magnuson, 1984). All nets were fished overnight for two consecutive 24 h periods (net night) at the deepest location of the lake. Catches of all fish were recorded along with total lengths (mm), depth of capture from surface (m), and a subset of fish were weighed. Catch per unit effort (CPUE) was quantified as the total number of individuals sampled in the entire gang of nets per net night (hereafter, referred to as fish net night⁻¹). Vertical gillnet CPUE was used an index of lake trout, lake whitefish and walleye relative abundance. Additionally, gill net catch composition and size structure were used to ground-truth hydroacoustics datasets (described in more detail below).

Various limnological and environmental parameters were also estimated. Sampling protocols and raw data for all these parameters can be viewed and downloaded from the NTL-LTER website (<https://lter.limnology.wisc.edu>). Parameters examined in this study in relation to cisco production statistics included winter ice duration, mean annual surface water temperature, rusty crayfish relative abundances, mean annual zooplankton biovolume, mean annual pelagic macroinvertebrates

biovolume, mean annual chlorophyll *a*, mean annual total phosphorus, and mean annual total nitrogen. We calculated a minimum summer cisco habitat width as the thickness of the oxythermal habitat between 3 mg·L⁻¹ dissolved oxygen from the bottom to the point at which water temperatures exceeded 22.8°C or the surface. Finally, we estimated maximum summer TDO3 (water temperature at a dissolved oxygen concentration of 3 mg·L⁻¹). Minimum cisco habitat width and maximum TDO3 are commonly used indices of oxythermal habitat in lakes (Jacobson et al. 2010).

Production calculations

Production estimations were made using the instantaneous growth method (Waters 1977), which summarizes production among cohorts (Dolbeth et al. 2012):

$$(1) \quad P_t = \sum G_{t,i} \bar{B}_{t,i}$$

where *P* is annual production (kg ha⁻¹ y⁻¹), *G* represents the instantaneous annual growth rate, calculated as

$$(2) \quad G_{t,i} = \ln\left(\frac{\bar{W}_{t,i+1}}{\bar{W}_{t,i}}\right)$$

$\bar{B}$ is mean standing stock biomass (kg ha⁻¹), $\bar{W}$ is mean weight (kg), *i* is age class, and *t* is the specific year corresponding to the data and estimates. For example, estimating *G* for age-1 fish in 2001 ($G_{2001,1}$), would require mean weights of age-1 fish ($\bar{W}_{2001,1}$) and age-2 fish ($\bar{W}_{2001,2}$) from 2001 to complete the calculation.

For this study, we used single target hydroacoustic data to estimate cisco size-structure data, and ultimately age-structured biomass. However, single target data do not have species assignments. Single fish target data describe where (latitude, longitude, and depth) and when a target was detected during the survey, and the size of

the target or target strength (decibels; converts to total length). Cisco population characteristics were inferred from single target data based on vertical gillnet catches. Specifically, we identified cisco targets using recursive partitioning or classification trees built with the vertical gillnet data (Yule et al. 2013; Myers et al. 2015). Thus, classification models were built for each annual gillnetting event and used to classify species in hydroacoustic datasets collected at approximately the same time. In each model, species classification was the response variable and the explanatory variables were latitude, longitude, water column depth, capture depth (from surface), and total length of fish. Because vertical gillnet efforts were focused on one location, latitude and longitude were not used as explanatory variables in the models. Classifications were built using the “rpart” package (Therneau and Atkinson 2012) in program R (R Core Team 2014, version 3.1.2). Classification trees were built using a complexity parameter ($cp = 0.0001$) and then pruned to minimize cross-validation error related to splitting. Lastly, we required a minimum of 10 fish per terminal node from pruned trees to be included in the final trees. After classification trees were constructed using the vertical gill net data, trees were applied to the single target data (including converted fish lengths) to predict pelagic fish species composition and identify cisco-sized targets. Cisco population data were then extracted from the predicted composition for production calculations as described above.

Annual population estimates were converted to age-specific population values by estimating the proportion of the population in different age classes (Rypel et al. 2015). Length-at-age estimates were based on a recent survey of the cisco population in Trout Lake by the Wisconsin Department of Natural Resources (WDNR unpublished data).

For this survey, a subset of the cisco sampled with the vertical gill nets (5 individuals per 10 mm length bin) were retained for removal of otolith sagittae and age estimation. Otolith sagittae were thin-sectioned using a low speed saw outfitted with a diamond impregnated blade. Samples were polished using a series of progressively finer sandpapers and viewed under a stereomicroscope using both transmitted and reflected light. Ages were blindly estimated by three experienced readers and consensus ages developed for any samples with disagreements between readers. A power regression was created to predict cisco age based on total length in Trout Lake. This regression was then used as a key to assign age estimates to all lengths of predicted cisco targets from the hydroacoustic surveys as described above. Population estimates were then converted to age-specific population estimates by multiplying the total population estimate by the percentage of fish estimated in each age class for the population. Mean mass-at-age was estimated for each year by applying a weight-length power regression based on the NTL-LTER data for cisco in Trout Lake for the given average length in each age class.

Annual production estimates were made using eq.1, and an example calculation can be viewed in Table 1. Biomass by age class was calculated as the mathematical product of the age-specific population estimate multiplied by the mean weight ($\bar{W}$) of individuals in that age class i . Mean standing biomass ($\bar{B}$) was then calculated as the average of the two biomass values between adjacent age-classes, which corresponds to the same age-sequence when calculating instantaneous growth (G) in eq. 2. Interval production rates were calculated between adjacent year classes following eq.1. All age-specific production estimates were then summed to gather an annual instantaneous

production estimate for all cisco in Trout Lake for each year, 2001-2015. Similarly, all age-specific biomass estimates were then summed to estimate an annual biomass for all cisco in Trout Lake for each year, 2001-2015.

Statistical analyses

We developed frequency histograms for P, B and P/B to illustrate the distribution of production statistics for cisco in Trout Lake. Shapiro-Wilks tests were used to test for normality in distributions of all three production statistics. Time series of P, B and P/B were evaluated for serial correlation using Ljung-Box tests and correlograms, and then assessed temporal trends using breakpoint regression analysis. Next, we evaluated the proportional contributions to population P and B from sub-adult (ages 0-2) and adult (ages 3-older) cisco. We further assessed P and B contributions by separately analyzing the coherence of P and B between total population and each contributing age group. We then explored potential relationships between total P, B and P/B and the 14 limnological and ecological variables described above by developing linear multiple regression models using a forward stepwise variable selection procedure. Prior to variable selection, we removed all redundant variables ($r > 0.5$) to reduce collinearity. All statistical analyses were performed in program R (R Core Team 2014, version 3.1.2). Production statistics and other variables were log₁₀-transformed prior to all statistical analyses to meet normality assumptions. Statistical significance was assessed with an $\alpha = 0.05$.

Results

Classification trees developed using annual vertical gillnet catch characteristics from 2001-2015 exhibited correct species classification rates ranging from 91-99% correct classification (Supplementary data 1). Species total length (mean variable importance = 73) followed by species capture depth (mean variable importance = 27) were the most important predictors used for species classification of the vertical gillnet catches. Once developed, trained classification trees assigned cisco to 96-99% of acoustic fish targets (total SEDs ranged from 3599-34192). Similarly, cisco tended to dominate vertical gillnet catches (mean = 84%; 34-97%) compared to other species. Data from single echo detections classified as cisco (3540-34002 targets) were then used to calculate production statistics.

Annual production statistics for cisco in Trout Lake were highly variable over time. Biomass ranged $1.2\text{-}39.4\text{ kg ha}^{-1}$ and production ranged $0.6\text{-}30.2\text{ kg ha}^{-1}\text{ y}^{-1}$, resulting in P/B ratios ranging $0.4\text{-}0.9\text{ y}^{-1}$ (Figure 1; Supplementary data 2). Production and biomass values for cisco in Trout Lake followed non-normal distributions (all Shapiro-Wilks tests P-values < 0.05), with distributions being composed mostly of low values with periodic high values; whereas P/B values followed a normal distribution (Shapiro-Wilks $P = 0.14$). Cisco production rates were largely comprised of sub-adult cisco production contributions which represented 75% (48-97%; Figure 2) of total production, whereas adult cisco only represented 25% (3-51%). Sub-adult cisco biomass represented 42% (15-85%) of total biomass and adult cisco biomass represented 58% (15-85%) to total biomass. There was strong coherence between total production and sub-adult cisco production (Pearson's $r = 0.99$, $P < 0.0001$), yet total production coherence with of adult cisco production was nearly half as strong ($r = 0.51$,

$P = 0.05$). Strong coherence occurred between both total biomass and sub-adult cisco biomass ($r = 0.88$, $P < 0.0001$) and adult biomass ($r = 0.83$, $P < 0.0001$).

Time series of cisco production statistics revealed multiple temporal patterns.

Serial correlation was detected in total production ($\chi^2 = 8.84$, $P = 0.03$) and total biomass ($\chi^2 = 6.19$, $P = 0.01$) time series, but not in P/B ($\chi^2 = 0.98$, $P = 0.32$).

Breakpoint regression analysis identified a single breakpoint in 2011 (Figure 1)

describing a step change for cisco production and biomass trends ($P < 0.01$). The step change was less strong for biomass ($R^2 = 0.46$) than for production ($R^2 = 0.54$), but was still apparent. Specifically, cisco total production exhibited a negative temporal trend (slope = -0.33, 95% CI: -0.53 to -0.12) before 2011 (SE = 1.05), followed by a period of no trend after 2011 (slope = 0.48, 95% CI: -0.09 to 1.06). For biomass, we also observed a break point in 2011 (SE = 1.46) that separated a period of decline (slope = -0.28, 95% CI: -0.42 to -0.13) from a period no trend (slope = 0.76, 95% CI: -0.08 to 1.60). No trends or apparent breakpoints were identified in the cisco P/B time series.

Using forward stepwise variable selection, only 1-2 variables were selected for use in linear multiple regression models to explain production statistics. The cisco production model selected lake trout CPUE, the cisco biomass model selected lake trout CPUE and ice duration, and the P/B model selected pelagic macroinvertebrates biovolume (Table 2). However, the only significant relationships were identified were between lake trout CPUE and cisco production ($F = 10.36$, $P = 0.01$, $R^2 = 0.40$) and biomass ($F = 6.80$, $P = 0.01$, $R^2 = 0.45$). Specifically, cisco production and biomass were negatively associated with lake trout CPUE (Table 2, Figure 3). Annual cisco P/B showed no significant relationship with any ecological variable (Table 2; $F = 2.34$, $P =$

0.15, $R^2 = 0.09$). With the exception of cisco production, few of the other ecological factors examined changed over the study period (Supplementary data 3).

Discussion

We found that production of cisco in Trout Lake exhibited considerable decline until 2011. Currently, the cisco production appears to be at its lowest state, a trend that has occurred despite no change in the quality or quantity of cisco habitat in the lake. P/B has also not changed, indicating the productive capacity of the population remains intact. Cisco biomass and production values were inversely related to annual estimates of lake trout abundance, and lake trout have only increased with time, coincident with stocking. This exogenous factor highlights a potentially important predator-prey relationship, and demonstrates how management of apex predators can significantly influence fish production rates at lower trophic levels.

Cisco production dynamics in Trout Lake

Fish production dynamics can hinge strongly on geographic location. For example, cisco populations show a positive geometric relationship between production and latitude (Rypel and David 2017). Thus, production of cisco in a range-wide context tends to be highest in northern lakes that are colder, and reduced in southern lakes that are warmer. Using the production estimates reported for 23 cisco populations in Rypel and David (2017), Trout Lake production ranked in the 36th percentile relative to the

other reported populations. Lake Winnipeg, Manitoba, Canada regularly had production estimates exceeding $100 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$, and had the highest estimated value ($1204 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$). In contrast, Mille Lacs Lake, Minnesota, USA exhibited some of the lowest cisco production estimates, with all estimates $<0.6 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$, and many years approaching $0 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$. Therefore, cisco in Trout Lake represent a relatively productive population for the southern portion of the cisco range. However, this level of production is comparatively low relative to cisco populations farther north.

Production and biomass estimates were right-skewed and log-normal in distribution, and this finding has important management implications. For example, low production years were common and high production years were rare. This finding is identical to a recent study that quantified production rates of walleye populations spatially (Rypel et al. 2017) in addition to long-term production studies of the species within a single ecosystem (Rypel et al. 2015). Furthermore, the contribution of sub-adult (ages 0-2) cisco production drives total annual production variations. Therefore, fish production might appear low or in a state of decline, but periodic high recruitment buoys the population over periods of lower production. Future research should explore the extent to which temporal heterogeneity in production differs between healthy and failing populations. More specifically, early indicators might be developed (e.g., Carpenter et al. 2011; Seekell et al. 2011) to identify fragile fisheries based on production and temporal heterogeneity in production.

The mechanisms responsible for the decline in cisco production in Trout Lake during this study period appeared to more biotic than abiotic, since decline was primarily related to increased lake trout abundance. Lake trout and cisco have very specific

oxythermal habitat constraints, particularly lake trout, which are much more sensitive to habitat perturbations than cisco (Jacobson et al. 2010). The continued persistence of sensitive lake trout in Trout Lake implies that the decline of cisco be less likely due to abiotic factors like habitat degradation. Additionally, it is much more likely that lake trout were interacting with cisco in Trout Lake, due to their specific oxythermal habitat constraints (Jacobsen et al. 2010) and habitat segregation (Kerr and Grant 2000), thus, limiting much of the predation pressures from other warm-water predator species, in Trout Lake. In Trout Lake, lake trout were observed to be mainly piscivorous and primarily selecting cisco over other prey items (Couey 1935). When available, cisco are considered to be the principle prey item for many other North American lake trout populations (Hacker 1957; Dryer et al. 1965; Martin and Oliver 1980; Matuszek et al. 1990; Kerr and Grant 2000). Based on the results of our study and work from Ahrenstorff et al. (2013), the numerically dominant species in Trout Lake were cisco and therefore, likely the best candidate for being consumed by lake trout. Numerous linkages have been identified between artificial increases in lake trout and reduced cisco populations (Kerr and Grant 2000). For instance, following the stocking and subsequent abundance increases in stocked lake trout in Lake Simcoe, Ontario, the prey community, including cisco exhibited substantial decline (Evans and Waring, 1987). Based on lake trout prey selection, the availability of cisco, and the intensive lake trout stocking history in Trout Lake, it remains most plausible that increases in lake trout have led to increasing predation on cisco.

Importantly, while cisco production and biomass responded negatively to increasing lake trout abundance, P/B ratios of the cisco population have remained

unchanged. Thus, the overall productive capacity of the cisco population remains strong, even though production and biomass were reduced. Interestingly, Rypel et al. (2015) presented a similar finding using a walleye population in a nearby lake (Escanaba Lake, Vilas County, WI USA); P/B ratios for walleye remained stable over time despite large changes in angler exploitation. Thus, although walleye production and biomass exhibited declines at high rates of exploitation, the productive capacity remained unchanged; meaning walleye biomass would take the same amount of time to develop. In our study, invariance of cisco P/B is an important finding. For example, this population is predicted to have a fast recovery potential should lake trout abundances be reduced (e.g., through reduced stocking or increased harvest of lake trout).

Fisheries managers are often geared towards single management approaches even though ecosystem-based approaches are usually beneficial (Link 2002; Pikitch et al. 2004; Walters et al. 2005). An inability to account for predator-prey dynamics can lead to fishery collapse should biomass of predators exceed the capacity of prey populations to supply energy to this trophic level (e.g., Kao et al. 2016). Stocking efforts to maintain and increase native lake trout in Trout Lake have been successful over time (Jahns and Bozek 2000), but may have unintended negative consequences for cisco. Trout Lake is only one of two known genetically-unique, naturally reproducing lake trout populations in Wisconsin (Piller et al. 2005). Based on our results, we suggest that fisheries managers evaluate and adjust lake trout stocking rates in Trout Lake, to further investigate and improve predator-prey balance and pro-actively minimize the risk of potential fishery collapse.

Secondary production estimates can be sensitive of the method of production estimation (Waters 1977). Furthermore, there are assumptions and biases in all methods of production estimation (Dolbeth et al. 2012). For the instantaneous growth method, it is worth differentiating this form of production estimation (i.e., a “snapshot” method) from other methodologies since it makes a pseudo-cohort assumption. Other methods attempt to empirically track gains and losses of biomass of particular cohorts over time (e.g., the increment summation method; Waters 1977). In the instantaneous growth method, recruitment dynamics across all age classes are integrated into the annual production estimate; thus, the annual production estimates synthesize more ecological information than what occurs during just one calendar year (Myers et al. 2017). Yet in cases where production is strongly driven by annual recruitment dynamics (i.e., age-0 abundances), the instantaneous growth method likely represents true biomass production. It is possible that production estimates could be developed for cisco and other pelagic fish populations in lakes using other (cohort) methods of production estimation. To this end, hydroacoustics data would need to be collected with a higher sampling intensity (e.g., monthly), and these topics ultimately remain beyond the scope of this research. Lastly, our empirical estimation of production statistics maybe somewhat influenced by the limited amount of age and growth information collected throughout the entire duration of the study period. Regardless, the high-resolution hydroacoustic fish density and size-structure data allowed us to identify strong patterns in age-specific fish densities, particularly for younger fish of which tends to drive total production estimates more than growth (see Rypel et al. 2015). Fortunately, we were able to compare our cisco growth data with historical growth data

from Trout Lake from Rudstam (1984) which we found to be statistically comparable to ours, so we assumed that age – specific growth (i.e., mean size at age) was relatively stable over time. Nonetheless, we acknowledged and accepted the caveat that inter-annual growth variations represented a potential source of error that we were not able to control or completely understand.

Understanding production dynamics is one of the foundational themes in fisheries science (Smith and Swingle 1938; Ricker 1946; Rawson 1952). Yet despite widespread recognition, empirical evaluations of fish production have generally declined. For some time, it was commonly thought that the effort, data and cost needed to estimate fish production was simply too high to warrant broader use. Yet in reality, all the data needed to empirically estimate fish production are already collected in many high-profile fisheries. Thus ironically, many fisheries are managed using all the component pieces of production (i.e., growth, density, size) without ever evaluating production directly. New tools like hydroacoustics may be increasing the ability and reducing the cost of making direct fish production estimates. Furthermore, the Canadian Fisheries Act was recently amended to reflect an overall goal of providing for the sustainability and ongoing productivity of commercial, recreational and Aboriginal fisheries. Thus, new tools and approaches for quantifying fisheries production should have broad appeal, especially for Canadian inland lakes, where food webs are largely based on coregonids (*Coregonus* spp.). To our knowledge, this paper provides one of the first applications of hydroacoustics for the estimation of secondary production rates in North American inland fisheries. We encourage other researchers to explore empirical production rates as a tool for understanding inland fisheries more dynamically.

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747 Figure Legends

748

749 Figure 1.- Long-term trends in production, biomass and P/B of cisco (*Coregonus artedii*)
750 from Trout Lake, Wisconsin, 2001-2015. Inset time series of log-transformed cisco
751 production statistics show where significant ($P \leq 0.05$) breakpoint regressions were
752 identified.

753

754 Figure 2.- Long-term trends in sub-adult (0-2), adult (3-older), and total production and
755 biomass of cisco (*Coregonus artedii*) from Trout Lake, Wisconsin, 2001-2015.

756

757 Figure 3.- Example relationships between lake trout (*Salvelinus namaycush*) catch-per-
758 unit-effort in vertical gill nets and cisco (*Coregonus artedii*) production and biomass.
759 Pearson correlation significance and coefficients for each comparison are noted as text
760 in the upper right corner of each panel.

- 1 Table 1. Example calculation of cisco (*Coregonus artedii*) secondary production in Trout Lake, Wisconsin USA, for one
 2 calendar year (2014). B = total annual biomass, $\bar{B}$ = mean biomass between age classes, G = instantaneous growth rate,
 3 and P = production rate.

Age	Number	Total weight (kg)	Mean Weight (kg)	B (kg·ha ⁻¹)	$\bar{B}$ (kg·ha ⁻¹)	G	P (kg·ha ⁻¹ ·y ⁻¹)
0	3682559	10137	0.003	6.48			
1	40930	1112	0.027	0.71	3.60	2.29	8.24
2	79522	2578	0.032	1.65	1.18	0.18	0.21
3	53794	2271	0.042	1.45	1.55	0.26	0.41
4	47947	2574	0.054	1.65	1.55	0.24	0.37
5	38591	2691	0.070	1.72	1.68	0.26	0.44
6	40930	3605	0.088	2.31	2.01	0.23	0.47
7	51455	5968	0.116	3.82	3.06	0.28	0.84
8	43269	6428	0.149	4.11	3.96	0.25	0.98
9	28066	5338	0.190	3.41	3.76	0.25	0.93
10	32744	8088	0.247	5.17	4.29	0.26	1.12
Totals	4139809			33.50			14.02

5 Table 2. Results of stepwise variable selection for linear multiple regression models of cisco production statistics. Model
6 output in log-10 transformation for model interpretation.

Model	Variable	Coefficient	SE	<i>P</i>	<i>F</i>	Adjusted <i>R</i> ²
Cisco production	Intercept	1.31	0.19	<0.01	10.36	0.40
	Lake trout CPUE	-0.92	0.29	0.01		
Cisco biomass	Intercept	-2.49	2.63	0.36	6.80	0.45
	Lake trout CPUE	-0.79	0.26	0.01		
	Ice duration	1.90	1.53	0.15		
Cisco P/B	Intercept	0.39	0.43	0.37	2.34	0.09
	Pelagic macroinvertebrates biovolume	-0.18	0.11	0.15		

7

Figure 1.-