NRC Research Press

ARTICLE

Changes in the condition, early growth, and trophic position of lake trout (*Salvelinus namaycush*) in response to an experimental aquaculture operation

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Abstract: We analyzed changes in the condition, early growth, and resource use of lake trout (*Salvelinus namaycush*) from a Boreal Shield lake in response to an experimental aquaculture operation. Annual small-scale commercial production of rainbow trout (*Oncorhynchus mykiss*) resulted in increased lake trout body condition during aquaculture operations, which was positively related to minnow catch per unit effort (CPUE). Incremental increases in growth led to larger lake trout following aquaculture. While the littoral energy assimilated by lake trout did not change linearly from 2002 to 2009, we observed a shift towards littoral energy use in the last year of aquaculture and for 2 years after the experiment, coincident with low densities of *Mysis diluviana*. Lake trout trophic position declined from 2002 to 2009, suggesting increased foraging on secondary versus tertiary consumers. Minnow and slimy sculpin (*Cottus cognatus*) CPUE increased by 5.2- and 5.5-fold, respectively, and *Mysis diluviana* densities decreased by 93%. Changes observed in the experimental lake were much greater than those observed in a nearby reference lake. Our results suggest that moderate nutrient enrichment from aquaculture may benefit lake trout in oligotrophic Boreal Shield lakes.

Résumé : Nous avons analysé les changements de l'embonpoint, de la croissance précoce et de l'utilisation de ressources des touladis (*Salvelinus namaycush*) d'un lac du Bouclier boréal en réaction à une exploitation aquacole expérimentale. La production commerciale annuelle à petite échelle de truites arc-en-ciel (*Oncorhynchus mykiss*) s'est traduite par une augmentation de l'embonpoint des touladis durant les activités d'aquaculture, qui était positivement reliée à la captures par unité d'effort (CPUE) de menés. Des augmentations graduelles de la croissance se sont traduites par des touladis plus gros après les activités aquacoles. Si l'énergie littorale assimilée par les touladis n'a pas changé linéairement de 2002 à 2009, nous avons observé un changement vers l'utilisation d'énergie littorale durant la dernière année d'aquaculture et pour 2 ans suivant l'expérience, qui coïncide avec de faibles densités de *Mysis diluviana*. La position trophique des touladis a baissé de 2002 à 2009, ce qui indiquerait une augmentation des consommateurs secondaires par rapport aux consommateurs tertiaires dans leur alimentation. Les CPUE de menés et de chabots visqueux (*Cottus cognatus*) ont été multipliées par 5,2 et 5,5, respectivement, et les densités de *Mysis diluviana* ont connu une baisse de 93 %. Les changements observés dans le lac expérimental étaient beaucoup plus importants que ceux observés dans un lac de référence situé à proximité. Nos résultats portent à croire qu'un enrichissement modéré en nutriments provenant de l'aquaculture peut être bénéfique pour les touladis dans des lacs oligotrophes du Bouclier boréal. [Traduit par la Rédaction]

Introduction

Aquaculture has expanded rapidly and is the world's fastest growing food-production technology (Anderson et al. 2017). Freshwater caged aquaculture is expected to be a growing contributor to fish production; however, concerns around the potential environmental impacts of nutrient deposition from these operations have slowed the growth of the industry (Podemski and Blanchfield 2006). Nutrient enrichment, often observed during aquaculture operations (Bristow et al. 2008), typically leads to increases in primary production, algal biomass, and changes in the species composition of algae and bacteria in aquatic ecosystems (Anderson et al. 2002; Schindler and Fee 1974; Sinkko et al. 2013). Bacterial decomposition of algae and fish feed can result in decreased hypolimnetic dissolved oxygen levels, which can be detrimental for stenothermic organisms, such as *Mysis diluviana* (hereinafter *Mysis*; Paterson et al. 2011) and lake trout (*Salvelinus namaycush*; Plumb and Blanchfield 2009), that require cold, well-oxygenated water. However, moderate nutrient enrichment can also stimulate the productivity of

Received 28 December 2017. Accepted 23 September 2018.

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*Michael D. Rennie currently serves as an Associate Editor; peer review and editorial decisions regarding this manuscript were handled by Yong Chen.

Can. J. Fish. Aquat. Sci. **76**: 1376–1387 (2019) dx.doi.org/10.1139/cjfas-2017-0578

freshwater ecosystems, enhancing the growth, condition, and survivorship of aquatic organisms (Ashley et al. 1997; Johnston et al. 1990), including top predators (Hyatt et al. 2004; Mills et al. 2008).

Lake trout is an aquatic apex predatory species found throughout the Boreal Shield (Scott and Crossman 1973). Lake trout thrive in deep, well-oxygenated lakes and are sensitive to the effects of eutrophication (Evans et al. 1996; Evans 2007; Gunn et al. 2004). Previous fertilization experiments revealed lake trout growth and recruitment increased following nutrient enrichment, but prolonged eutrophication-induced hypoxia may cause declines in lake trout recruitment over time (Lienesch et al. 2005). There remains considerable uncertainty around how changes in community dynamics of lake ecosystems with eutrophication influence lake trout early growth, condition, and resource use.

Lake trout display ontogenetic shifts in diet and foraging behavior (Trippel and Beamish 1993; Zimmerman et al. 2009); *Mysis* are important to the diet of immature lake trout, whereas minnows (Cyprinidae), cisco (*Coregonus artedi*), slimy sculpin (*Cottus cognatus*), and yellow perch (*Perca flavescens*) often dominate the diets of larger individuals (Konkle and Sprules 1986; Trippel and Beamish 1993). In the absence of offshore prey fishes, nearshore prey may be particularly important to lake trout diets (Guzzo et al. 2017). Furthermore, the invasion of *Mysis* into Flathead Lake, Montana, led to increased recruitment of non-native lake trout (Devlin et al. 2017).

From 2003 to 2007, an experimental aquaculture facility was operated at the International Institute for Sustainable Development (IISD) Experimental Lakes Area (IISD-ELA, previously ELA) in northwestern Ontario, Canada, to examine its effects on a whole-lake ecosystem. Aquaculture operations resulted in increases in nutrient inputs (Bristow et al. 2008), phytoplankton (Findlay et al. 2009), and abundance of prey fishes (Mills et al. 2008), as well as decreases in hypolimnetic dissolved oxygen and *Mysis* densities (Paterson et al. 2011). Measurements of lake trout in the first 2 years of aquaculture operations revealed increases in growth and condition (Mills et al. 2008). However, there remains considerable uncertainty around the long-term impacts of aquaculture operations on lake trout growth, condition, and resource use.

We used archived ageing structures, historical data, and stable isotope data to analyze changes in early growth rates (defined here as premature growth, ages 1–5; Rennie et al. 2019), condition, and resource use of lake trout before, during, and after aquaculture operations. We predicted the growth rates, condition, and trophic position of piscivorous lake trout would increase following the start of aquaculture operations corresponding to a greater dietary reliance on abundant and energy-rich littoral prey. Additionally, we predicted the decline in *Mysis* would negatively impact early growth rates and condition of nonpiscivorous juvenile lake trout. Where possible, measured parameters were compared with a nearby reference lake.

Methods

Study sites and aquaculture operation

The IISD-ELA is a remote research facility located in northwestern Ontario, Canada, and consists of 58 Precambrian shield lakes designated for whole-ecosystem experimentation and long-term monitoring (Cleugh and Hauser 1971). Experimental Lake 375 (49°44′43.61″N, 93°47′15.56″W) and the reference lake, Lake 373 (49°44′41.46″N, 93°47′55.35″W), are small (23.2 and 27.1 ha, respectively), oligotrophic, dimictic lakes with maximum depths of 26 and 20 m, respectively (reference maps in Paterson et al. 2011). An experimental aquaculture operation was initiated in Lake 375 in the spring of 2003, and 10 t of rainbow trout (*Oncorhynchus mykiss*) were raised annually for 5 years in a single 10 m × 10 m × 10 m steel frame cage placed in the north basin of Lake 375 over 15 m of water. Each spring, 10 000 fingerlings were stocked in the cage. Rainbow trout were fed pellets of Martin Mills Profishent twice daily. Caged trout were harvested in late autumn each year when they weighed about 1 kg each. Additional details can be found in Blanchfield et al. (2009), Rooney and Podemski (2009), Paterson et al. (2011), and Wellman et al. (2017).

Fish collection and processing

The native fish community of Lake 375 consists of the minnows finescale dace (*Chrosomus neogaeus*), northern redbelly dace (*Chrosomus eos*), pearl dace (*Margariscus margarita*), and fathead minnow (*Pimephales promelas*), as well as slimy sculpin, white sucker (*Catostomus commersonii*), and lake trout. The native fish community of Lake 373 consists of the same fish species except for the absence of fathead minnows. Both lakes were sampled regularly from 2001 to 2011. Fish were sampled in the spring and fall of each study year using small-mesh (7 mm) Beamish-style trap nets at fixed locations. Monitoring of lake trout populations was also conducted for Lake 375 in the fall of 2013 and 2016, while Lake 373 was sampled each year from 2013 to 2016. No sampling occurred in 2012. Two types of trap nets were used for sampling fish: those with central leads, set perpendicular to shore; and those without central leads, set parallel to the shoreline, with one wing extended and tied to shore to capture fish moving in one direction (Guzzo et al. 2014; Mills et al. 1987). Trap nets contained holding pots with volumes of 2.2–6.1 m^2 that were anchored in place and set in ~3–4 m of water (Beamish 1973; Mills et al. 1987). In the fall of each study year, short sets of small-mesh gill nets (38 mm) were used to sample lake trout on spawning shoals via mandibular entanglement (Mills et al. 2002). Captured fish were lightly anaesthetized using trimethane sulfonate, measured for their total and fork lengths (mm), weighed (g), and marked for the season by dorsal fin ray scarring. Lake trout fin rays were clipped for age estimation and stable isotope analysis (see below). Additional details can be found in Beamish (1973), Mills et al. (1987), and Mills et al. (2002). Animal care approvals were obtained through Lakehead University in 2015–2016 (1464656), University of Manitoba in 2014 (F14–007), and Fisheries and Oceans Canada prior to 2014.

Prey abundance and density

Relative abundance (catch per unit effort, CPUE) estimates of minnows and slimy sculpin were estimated as the number of fish caught per 24 h in each trap net set. Between two and three trap nets were set simultaneously at fixed locations in both lakes during the spring and fall of each year. Nets were fished for 2–5 days and were reset immediately after collections. Between three and seven sets were conducted in each time period. Yearly CPUE estimates for both taxa were calculated by averaging the CPUE estimates for each trap net set across both seasons. Percent change in the CPUE of minnows and slimy sculpin was calculated between the following time periods: before (2001–2002), during (2003–2007), and after (2008–2011) aquaculture operations. Lake-wide *Mysis* densities (number·m^{-2}) from vertical net hauls (0.75 m diameter, 500 μm mesh) were calculated as a weighted average of densities determined at different depths and the proportion of the total lake area represented by each depth interval (Paterson et al. 2011). *Mysis* were sampled from four to eight stations 1 h after sunset every 4 weeks during the open-water season (May–October). *Mysis* densities for the open-water season were averaged over all sampling sites and time periods for each year from 2002 to 2011, and percent changes were determined between the year(s) sampled before, during, and after aquaculture operations. *Mysis* were only sampled during June and (or) July in the years 2009–2011 in Lake 375, and *Mysis* data from Lake 373 only included the years 2002–2008.

Lake trout length-at-age

Archived pectoral fin rays were used to age and back-calculate changes in Lake 375 lake trout growth over time. Fin rays were mounted in epoxy, cut into 1 mm thick cross-sections using a

Beuhler Isomet low-speed saw, and mounted on slides in sequential order for ageing. Slides were aged under a Leica M125 stereo microscope using a combination of reflected and transmitted light. Ages were estimated by counting the number of annuli. Annuli were identified as the non-growth hyaline bands (dark under reflected light, translucent under transmitted light), while growth was identified as the opaque bands (light under reflected light, dark under transmitted light; DeVries and Frie 1996). Images of aged samples were captured and digitized using a Leica DFC490 digital camera and Leica Application Suite software. Images were taken of the clearest section and ray for each sample. Three distinct "shapes" of the fin ray sections were observed on individual sections (Figs. A1–A2), which corresponded to different rays on the fins collected. Relative to "shape one", "shape two" was ventrally expanded, while "shape three" was ventrally compressed (Fig. A1). Because of the possible influence of shape on back-calculation procedures, the shape was noted for each sample and included as a categorical variable for back-calculations.

Lake 375 lake trout fin ray sections were analyzed using the image processing program ImageJ to back-calculate the length-at-age of lake trout over time (Schneider et al. 2012). Anterior regions of the fin ray sections were measured for back-calculations because of their consistency among the sections, and axes of measurement were perpendicular to the annuli (Fig. A1). As there are no origin points for fin rays, origins of measurements for the back-calculations were set to the first identified annuli. Length-at-age of lake trout was back-calculated using the Fraser–Lee intercept correction procedure (Campana 1990; DeVries and Frie 1996; Pierce et al. 1996):

$$(1) \qquad L_a = d + (L_c + d)F_c^{-1}F_a$$

where L_a is the estimated fish fork length (L) at a given age (a), d is the intercept correction factor, L_c is the fork length (L) of the fish at capture (c), F_c is the size of the fin ray section (F) at capture (c), and F_a is the measured size of the fin ray section (F) at a given age (a). The intercept correction factor was calculated using the relationship between lake trout fork length (mm) and the radius of each fin ray section (pixels·mm^{-1}). Intercept correction factors were calculated and applied to the equation for each of the three fin ray shapes (Fig. A2).

Mean estimates of length at ages 1–5 for Lake 375 lake trout were calculated for the following time periods: 2001–2002, 2003–2004, 2005–2006, 2007–2008, 2009–2010, 2011–2012, and 2013–2015. Years were pooled to increase sample sizes. We combined 3 years of data from 2013 to 2015 in the recovery period due to reduced sampling frequency on the lake during this time. To ensure the changes in Lake 375 lake trout length-at-age were a result of aquaculture operations, we compared observed fork lengths of captured lake trout in the reference Lake 373 among the same time periods for ages 4–6 lake trout. Sample sizes were not sufficient for comparisons among time periods for ages 1–3 Lake 373 lake trout.

Lake trout annual growth-at-age

Annual growth rates (mm·year^{-1}) for individual Lake 375 lake trout in age classes 1–5 for each annual increment (considering years 2001–2015) were calculated by taking the difference between the back-calculated length-at-age of lake trout in year i and their back-calculated length-at-age from year i – 1. As the first annuli were used as the origins for the measurements, the annual growth at age 1 for individual lake trout was calculated by taking the difference between their back-calculated length at age 2 and their associated intercept correction factor (which represents the first annulus, as there is no origin point on fin rays; Fig. A1). Mean annual growth rates for ages 1–5 were estimated for the time periods described above for the length-at-age of lake trout.

Lake trout condition

Relative weight (W_r, %) was used as a measure of condition for Lakes 375 and 373 lake trout. W_r was estimated for captured lake trout by first calculating their standard weight (the expected weight at a given total length), using the following equation (Piccolo et al. 1993):

$$(2) \qquad \log_{10} W_s = -5.681 + 3.246\log_{10} \mathrm{TL}$$

where W_s is the weight of the lake trout (g), and TL is their total length (mm). Relative weight was then calculated using the following formula:

$$(3) \qquad W_r = 100\left(\frac{W}{W_s}\right)$$

where W_r is relative weight expressed as a percentage of W_s, W is the measured weight of the individual fish, and W_s is the length-specific standard weight (Piccolo et al. 1993). All fish included in the analyses were within the range of Piccolo et al.'s equation (280–618 mm, total length). Mean relative weights of lake trout were estimated for the following time periods: 2001–2002, 2003–2004, 2005–2006, 2007–2008, 2009–2010, 2011–2013, and 2014–16.

Stable isotope preparation and analysis

We used previously published stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope data to estimate Lakes 375 and 373 lake trout trophic position and their proportion of littoral energy assimilated from 2002 to 2009 (Kullman et al. 2009; Wellman et al. 2017). Pectoral fin ray tips from lake trout and dorsal muscle from littoral minnows were collected each fall. *Mysis* were collected monthly during the open-water season by vertical tows of a 0.75 m diameter, 500 μm mesh net at depths of at least 13 m. Isotope samples were dried, weighed, loaded into tin capsules, and measured using standard methods at the University of Waterloo or the University of New Brunswick. Isotopes analyzed at the University of Waterloo were analyzed using a Finnegan Delta EA or Micromass IsoChrom EA stable isotope ratio mass spectrometer, while isotopes were analyzed at the University of New Brunswick using a Finnegan Mat Delta Plus interfaced via continuous flow to a NC2500 elemental analyzer. To determine δ values of the samples, carbon and nitrogen isotope ratios were standardized against reference gases and corrected to the same International Atomic Energy Agency standards (Kullman et al. 2009). QA–QC for the stable isotope measurements can be found in Kullman et al. (2009) and Wellman et al. (2017).

The δ^{13}C and δ^{15}N values from lake trout pectoral fin rays were corrected to the equivalent of muscle values using the following equations (Wellman et al. 2017):

$$(4) \qquad \delta^{13}\mathrm{C}_{\mathrm{muscle}} = -8.107 + 0.728 \times \delta^{13}\mathrm{C}_{\mathrm{fin}}$$

$$(5) \qquad \delta^{15}\mathrm{N}_{\mathrm{muscle}} = 0.925 + 0.777 \times \delta^{15}\mathrm{N}_{\mathrm{fin}}$$

Lake trout δ^{13}C and δ^{15}N values were also corrected for relationships with body size by centering the residuals of the relationships with size around the mean δ^{13}C and δ^{15}N values (Wellman et al. 2017). To evaluate the necessity of lipid corrections, we mathematically lipid-corrected prey δ^{13}C values (*Mysis*) where C:N ratios exceeded 3.5 (Post et al. 2007). However, using lipid-corrected δ^{13}C values provided identical results to our non-lipid-corrected δ^{13}C values. Thus, our results are presented with non-lipid-corrected δ^{13}C values. We determined the proportion of littoral energy assimilated by lake trout using a two-source mixing model with littoral minnows and *Mysis* as the littoral and pelagic end members, respectively (Guzzo et al. 2017; Vander Zanden and Vadeboncoeur 2002; Table A5):

$$\text{(6)}\qquad \text{Proportion of littoral energy} = \frac{\delta^{13}\mathrm{C}_{\text{lake trout}} - \delta^{13}\mathrm{C}_{\mathit{Mysis}}}{\delta^{13}\mathrm{C}_{\text{minnows}} - \delta^{13}\mathrm{C}_{\mathit{Mysis}}}$$

These prey were chosen as end members, as they both have been noted as important contributors to the diets of lake trout populations in small lakes like those in the current study (France and Steedman 1996; Guzzo et al. 2017; Konkle and Sprules 1986). If δ^{13}C values for lake trout were greater than either of the prey end members in the mixing model, which would result in values >100% or <0% for proportion of littoral energy, values were set to either 100% or 0% (Vander Zanden and Vadeboncoeur 2002). The trophic position (TP) of Lakes 375 and 373 lake trout was determined using the following equation (Post 2002; Table A6):

$$\begin{aligned}\text{(7)}\qquad \text{Lake trout TP} = 3 + \Big\{&\delta^{15}\mathrm{N}_{\text{lake trout}} - \big[\delta^{15}\mathrm{N}_{\text{minnows}} \\ &\times \text{lake trout prop. littoral energy} + \delta^{15}\mathrm{N}_{\mathit{Mysis}} \\ &\times (1 - \text{lake trout prop. littoral energy})\big]\Big\}/3.4\end{aligned}$$

This was confirmed using the available data (mean minnow TP = 3.11, 2002–2009). There were 158 and 163 lake trout available for the Lakes 375 and 373 stable isotope data sets, respectively, with fork lengths ranging from 165 to 502 mm.

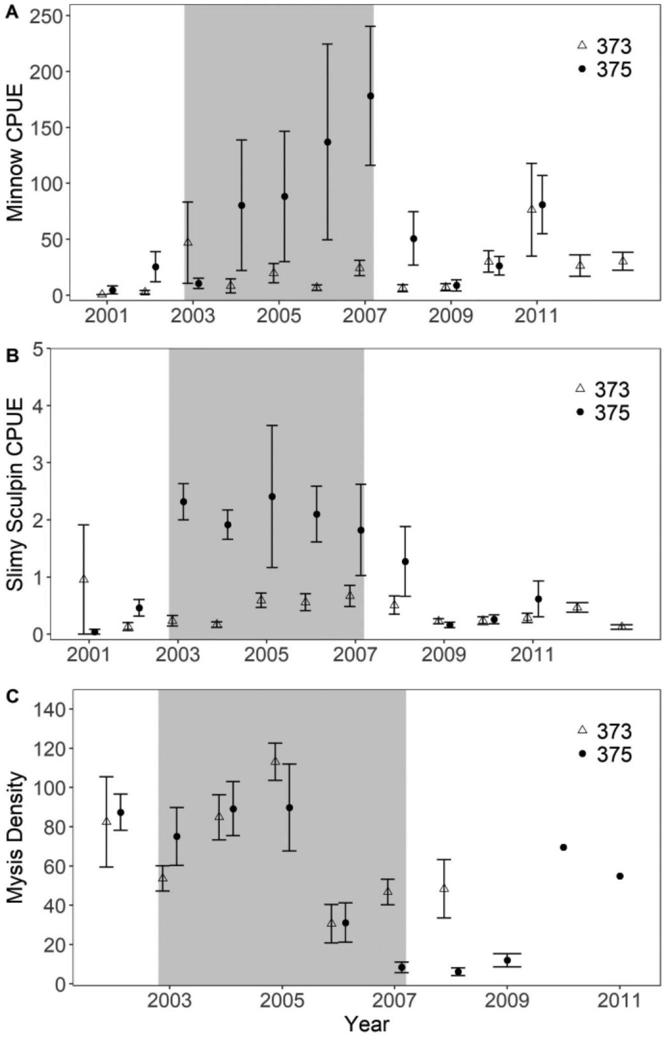
Statistical analysis

Analyses were performed in R 3.1.2 (R Core Team 2014). Assumptions of linear mixed effects models and linear regression were evaluated, and data were transformed where necessary. Mixed-effects models were run using the package "lme4" (Bates et al. 2015), and Tukey honestly significant difference (HSD) post hoc tests were run using the package "lsmeans" (Lenth 2018). Significance of interaction terms were determined using likelihood ratio tests.

We analyzed changes in length-at-age, annual growth-at-age, and condition of Lakes 375 and 373 lake trout using a mixed effects analysis of variance (ANOVA) approach, followed by Tukey HSD post hoc tests. The length-at-age and annual growth-at-age mixed effects ANOVAs for Lake 375 lake trout included the age corresponding to the length or growth of the lake trout and experiment period as fixed effects with an interaction between them, as well as individual fish ID and the year corresponding to the back-calculated length or growth as random effects. Mixed effects ANOVAs for the length-at-age of Lake 373 lake trout and the condition of Lakes 375 and 373 lake trout included experiment period as a fixed effect and the sampling year as a random effect.

Mean estimates (±standard deviation, SD) of the proportion of littoral energy assimilated by Lakes 375 and 373 lake trout were calculated for each year with available data (i.e., 2002–2009) using individual lake trout δ^{13}C values within each year. Annual estimates of growth at ages 1–5 for Lake 375 lake trout, as well as the condition of Lakes 375 and 373 lake trout, were tested for linear relationships with minnow CPUE, *Mysis* density, and the proportion of littoral energy assimilated by lake trout. To determine if the proportion of littoral energy assimilated by lake trout was driven by changes in the abundance or density of their prey, we tested annual estimates of the proportion of littoral energy assimilated by Lakes 375 and 373 lake trout for linear relationships with year, minnow CPUE, and *Mysis* density. Annual estimates of Lakes 375 and 373 lake trout trophic position were tested for linear relationships with year to determine if they changed over the course of the experiment.

Fig. 1. Change in mean (standard error shown by error bars) lake trout prey availability before, during (shaded), and after aquaculture operations in Lake 375 and in the reference Lake 373: (A) relative abundance (number of individuals caught per 24 h) of all minnow species; (B) relative abundance (number of individuals caught per 24 h) of slimy sculpin; and (C) density (number·m⁻²) of *Mysis* (data from 2002 to 2008 are reproduced from Paterson et al. 2011).



Results

Prey community changes

Mean annual CPUE of prey fish (i.e., minnows and slimy sculpin) in Lake 375 increased following the initiation of aquaculture operations (2003–2007) relative to premanipulation conditions (2001–2002), unlike those in Lake 373, which remained relatively stable (Figs. 1A–1B). Prey fish densities in Lake 375 reverted to background levels within 1–2 years following aquaculture operations (2008–2011; Figs. 1A–1B). We observed 5.2- and 5.5-fold increases in the mean annual CPUE of minnows and slimy sculpin in Lake 375, respectively, during aquaculture operations when compared with the years before aquaculture operations. Additionally, there were 70% and 75% decreases in the CPUE of minnows and slimy sculpin, respectively, from the years during aquaculture operations to the years after aquaculture operations. In our reference Lake 373, we observed 8.3- and 1.6-fold increases in the CPUE of minnows and slimy sculpin, respectively, from 2001–2002 to 2003–2007. However, the overall CPUE of minnows and slimy sculpin from 2003 to 2007 was an order of magnitude less in Lake 373 compared with Lake 375 during aquaculture (minnows: 18.7 versus 110.4 fish per net days, respectively; slimy sculpin: 0.5 versus 2.1 fish per net days, respectively). The mean CPUE of minnows in Lake 373 continued to increase from 18.7 in 2003–2007 to 27.1 in 2008–2011, a 1.45-fold increase, which was driven by greater catches in a single year (i.e., 2011). In contrast, the CPUE of slimy sculpin in Lake 373 decreased from 0.49 in 2003–2007 to 0.29 in 2008–2011, a 39.7% decrease (Figs. 1A–1B).

Mysis density decreased over the course of aquaculture operations in Lake 375 (Fig. 1C). The mean density of *Mysis* (number·m^{-2}) in Lake 375 decreased from 87.40 m^{-2} in 2002 to 6.09 m^{-2} in 2008, a 93% decrease (Fig. 1C; Paterson et al. 2011). The density of *Mysis* in Lake 373 also decreased in 2006 and 2007, but to a lesser extent than in Lake 375. The mean density of *Mysis* decreased from 82.5 m^{-2} in 2002 to 48.4 m^{-2} in 2008, a 41% decrease (Fig. 1A; Paterson et al. 2011). However, densities of *Mysis* in Lake 375 remained well below densities observed in Lake 373 in 2007 and 2008. By 2010–2011, *Mysis* densities appeared to have improved in Lake 375.

Length-at-age

The average back-calculated length of ages 2–5 lake trout in Lake 375 increased over the course of the experiment. There were no significant changes observed in the length of age 1 lake trout (Table A1). The back-calculated length of age 2 lake trout was significantly greater 4–5 years after aquaculture in 2011–2012 than in 2001–2002 (Tukey HSD, df = 49.79, $t = 5.12$, $p < 0.01$; Fig. 2A), while the length of age 3 lake trout was significantly greater in all periods from 2005–2006 to 2013–2015 (Tukey HSD, df = 61.51 to 268.40, $t = 3.99$ to 5.67, $p < 0.05$) compared with 2001–2002 (Fig. 2A). Similarly, the length of age 4 lake trout was significantly greater in 2009–2010 than in 2001–2002 (Tukey HSD, df = 239.61, $t = 4.68$, $p < 0.01$), and as well as in 2007–2008 (Tukey HSD, df = 52.76, $t = 4.29$, $p < 0.05$), 2009–2010 (Tukey HSD, df = 212.39, $t = 4.87$, $p < 0.01$), and 2013–2015 (Tukey HSD, df = 109.57, $t = 4.04$, $p < 0.05$) compared with 2003–2004 (Fig. 2A). Finally, the length of age 5 lake trout was greater in 2011–2012 than in 2001–2002 (Tukey HSD, df = 343.92, $t = 4.12$, $p < 0.05$) and 2003–2004 (Tukey HSD, df = 258.99, $t = 3.94$, $p < 0.05$; Fig. 2A).

In contrast with Lake 375, the average observed length for ages 4–6 lake trout in reference Lake 373 did not change or decreased over the study period. There were no changes in the average length of ages 4 and 5 Lake 373 lake trout (Tukey HSD, $p > 0.05$), and the average length of age 6 lake trout was significantly smaller in 2009–2010 compared with 2003–2004 (Tukey HSD, df = 8.13, $t = 4.65$, $p < 0.05$; Table A2). No other statistically significant differences were detected for the average length of age 6 Lake 373 lake trout.

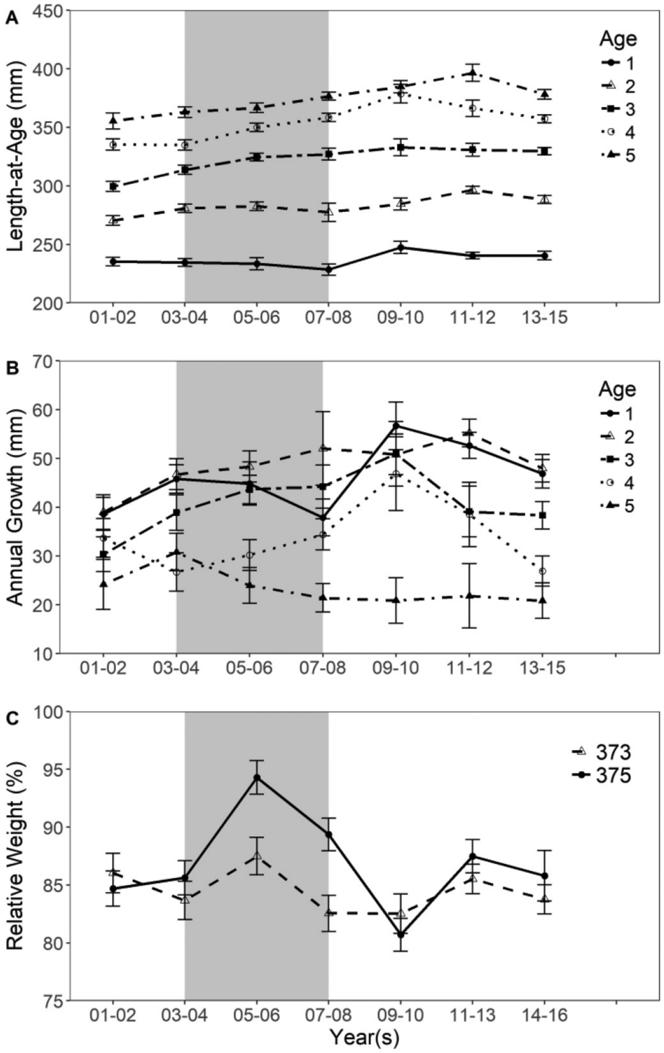
Annual growth-at-age

The average annual growth of Lake 375 lake trout appeared to increase for age classes 2–4 following the start of aquaculture operations (Fig. 2B). However, no significant differences in the average annual growth between periods were detected for any of the age classes investigated using the linear model we employed (Tukey HSD, $p > 0.05$; Table A3). The average annual growth of Lake 375 lake trout for ages 1–5 was not significantly related to minnow CPUE, *Mysis* density, or the proportion of littoral energy assimilated ($F_{[1,6-8]} = 0.04$ to 4.77, $p > 0.05$).

Condition

The body condition (W_r, %) of Lake 375 lake trout increased significantly during aquaculture operations for years 2003–2008 compared with years prior and subsequently decreased in the years following aquaculture operations (Fig. 2C; Table A4). In contrast, the condition of lake trout in the reference Lake 373 did not show any significant changes over the 15-year study period (Tukey HSD, $p > 0.05$; Fig. 2C; Table A4). The condition of Lake 375 lake trout was greater in 2005–2006 compared with that in 2001–2002, 2003–2004, and 2009–2010 (Tukey HSD, df = 5.63 to 6.40, $t = 4.18$ to 6.71, $p < 0.05$). Additionally, the condition of Lake 375 lake trout was significantly greater in 2007–2008 compared with that in 2009–2010 (Tukey HSD, df = 5.36, $t = 4.33$, $p = 0.05$). No other statistically significant differences were detected among periods for Lake 375 lake trout condition (Tukey HSD, $p > 0.05$). The condition of Lake 375 lake trout was positively related to minnow CPUE ($F_{[1,9]} = 10.85$, $p < 0.01$, $r^2 = 0.50$; Fig. 3), but was not significantly related to *Mysis* density ($F_{[1,8]} = 0.10$, $p > 0.05$) or the proportion of littoral energy assimilated by lake trout ($F_{[1,6]} = 1.91$, $p > 0.05$). The condition of lake trout in the reference Lake 373 was not significantly related to minnow CPUE (Fig. 3), *Mysis* density, or the proportion of littoral energy assimilated by lake trout ($F_{[1,5-9]} = 0.10$ to 1.14, $p > 0.05$).

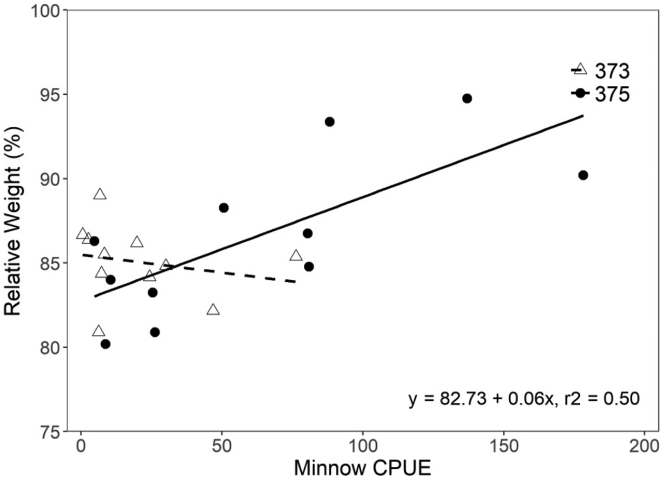
Fig. 2. Change in lake trout growth and condition before, during (shaded), and after aquaculture operations: (A) the average back-calculated length-at-age (mm) for Lake 375 lake trout at the end of ages 1–5; (B) the average annual growth (mm·$year^{-1}$) for ages 1–5 Lake 375 lake trout; and (C) the average condition (W_r, %) of Lakes 375 and 373 lake trout. Error bars represent the standard errors for each group.



Littoral energy and trophic position

The proportion of littoral energy assimilated by lake trout did not change linearly from 2002 to 2009 in Lake 375 or the reference Lake 373 ($F_{[1,6]} = 0.90$ to 1.19, $p > 0.05$). Additionally, the proportion of energy assimilated by lake trout was not linearly related to

Fig. 3. Relationship between Lakes 375 and 373 lake trout annual condition (W_r, %) and minnow catch per unit effort (CPUE) from 2001 to 2011. Solid line indicates a significant relationship ($p < 0.05$). The equation for the relationship in Lake 375 is displayed.



minnow CPUE or *Mysis* density in either lake ($F_{[1,5-6]}$ = 0.05 to 4.12, $p > 0.05$; Fig. 4). However, the greatest values for the proportion of littoral energy assimilated by Lake 375 lake trout (2007–2009) coincided with the collapse of *Mysis* in the lake (Fig. 4). Additionally, we compared the results of our simple mixing model with a more complicated model including additional end-members using the "simmR" package in R and obtained similar results regarding patterns in nearshore versus offshore use. The trophic position of Lake 375 lake trout decreased linearly from 2002 to 2009 ($F_{[1,6]}$ = 19.37, $p < 0.01$; Fig. 5). Lake 373 lake trout trophic position did not change during the study period ($F_{[1,6]}$ = 0.03, $p > 0.05$).

Discussion

Following the onset of aquaculture operations and the resulting increase in whole-lake productivity in Lake 375 (Findlay et al. 2009), we found the early growth (e.g., length-at-age) and condition of lake trout increased. Our results suggest that these increases in size and condition may have resulted from greater overall prey availability and accessibility during aquaculture. Slimy sculpin and minnow CPUE in Lake 375 increased dramatically during aquaculture operations, and these increases were accompanied by a decrease in the lake-wide mean areal density of *Mysis*. However, the relative increase of minnows was far greater than that observed for slimy sculpin during aquaculture. These changes were much greater than changes in lake trout prey populations in the reference Lake 373, suggesting that they were induced by aquaculture operations rather than variations in climate or other regional drivers.

Growth rates of fish have repeatedly been shown to increase with an increase in prey abundance (Graeb et al. 2004). Fertilization of an oligotrophic Alaskan lake resulted in elevated growth rates of lake trout in response to increased prey abundance (Lienesch et al. 2005). Additionally, a recent study on the same lake used as a reference in this study revealed that the condition of adult lake trout was greater when they had longer-term access in the spring to productive littoral habitats containing energy-rich prey fishes (Guzzo et al. 2017). Our results agree with this observation, as lake trout condition was positively related to minnow CPUE in our experimental lake.

Like our study, a previous experiment at the IISD-ELA resulted in elevated growth of lake whitefish (*Coregonus clupeaformis*) in the fertilized basin of Lake 226 during and after fertilization compared with the nonfertilized basin of the lake (Mills and Chalanchuk 1987). However, the length-at-age of lake whitefish in Lake 226 declined in the years after cessation of fertilization. By contrast, we observed the length-at-age of lake trout in Lake 375 was greatest in the years following aquaculture operations. During and after aquaculture operations, lake trout were frequently captured at sizes greater than 450 mm and 1 kg, while no fish this large were captured before aquaculture operations began. This is presumably because lake trout experienced greater early growth in the years during aquaculture operations when prey availability was elevated, resulting in steeper growth trajectories and larger size-at-age. Despite there being no **significant** increases in the annual growth increments of immature lake trout in this study, small increases in growth during aquaculture operations likely led to cumulative increases in lake trout size over time, resulting in larger body sizes in the years following aquaculture operations.

Our mixing model analyses revealed that the proportion of littoral energy assimilated by lake trout in Lake 375 varied following the start of aquaculture, and these changes did not have linear relationships with time or the density of their prey (Tables A5). The proportion of littoral energy assimilated by lake trout decreased during aquaculture operations from 2003 to 2006, suggesting a greater dietary reliance on pelagic resources during this period. However, once *Mysis* densities declined below 25 individuals·m^{-2} in 2007, the proportion of littoral energy assimilated by lake trout increased dramatically to its highest recorded value. This jump is suggestive

Fig. 4. Changes in Lakes 375 (A) and 373 (B) lake trout proportion of littoral energy assimilated with adjusted mean annual minnow catch per unit effort (CPUE) and *Mysis* density from 2002 to 2009. Minnow CPUE (number of individuals caught per 24 h) and *Mysis* density (number·m^{-2}) are relative estimates adjusted to values between 0 and 100 for display purposes. Proportion of littoral energy assimilated is displayed between 0% and 100%.

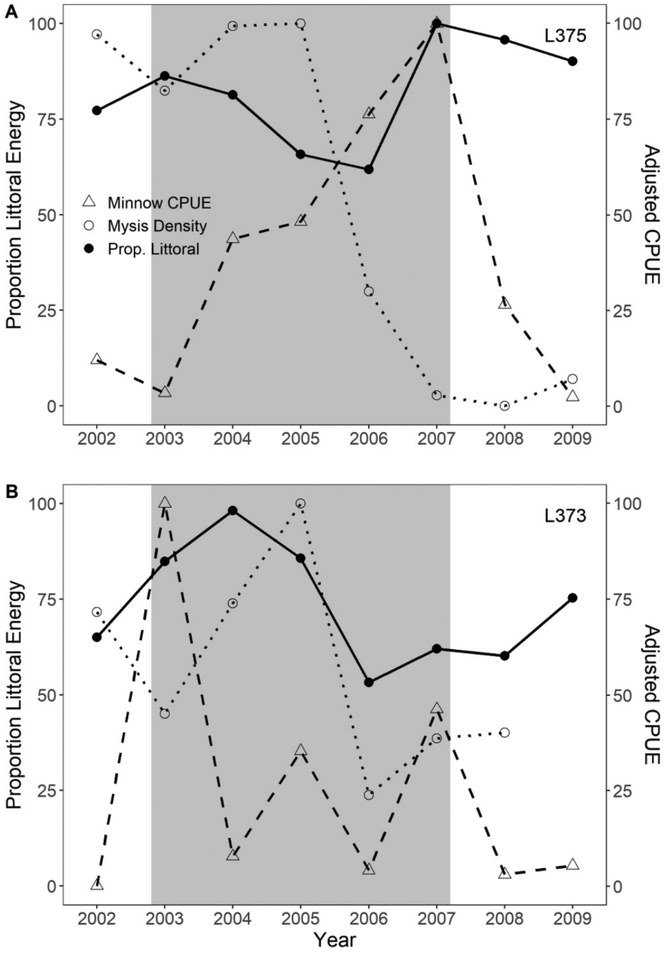
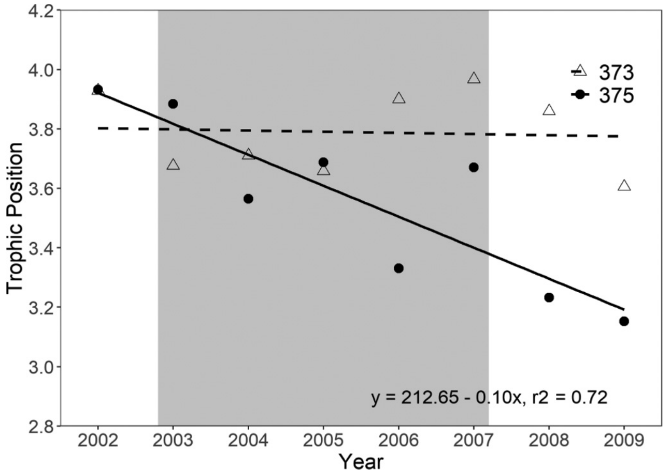


Fig. 5. Relationship between year (2002–2009) and estimates of Lakes 375 and 373 lake trout trophic position. Solid line indicates a significant linear relationship ($p < 0.05$).



of a regime shift in lake trout diets due to increased littoral resources. Further, the high proportion of littoral energy assimilated by lake trout during the period of prey fish decline suggests that lake trout predation may have directly contributed to prey fish decline following aquaculture in the absence of abundant offshore prey (e.g., *Mysis*). No similar increase in the proportion of littoral energy assimilated by lake trout was observed in the reference Lake 373 from 2007 to 2009.

Our findings combined with those reported elsewhere suggest that the observed decrease in Lake 375 *Mysis* densities may have been a result of greater predation pressure by lake trout. As hypolimnetic dissolved oxygen levels declined during aquaculture in Lake 375, available habitat for *Mysis* in Lake 375 became constricted, forcing them into an increasingly narrow depth range (Paterson et al. 2011). The distribution of lake trout would similarly be constrained by low oxygen levels, likely increasing spatial overlap with and predation upon *Mysis* as they became more concentrated (Charles et al. 2017). The decrease in the proportion of littoral energy assimilated by lake trout, despite declining densities of *Mysis*, suggests increased per-capita predation by lake trout on offshore resources, particularly from 2003 to 2006. As carbon isotopes are relatively stable between trophic levels, it is possible that offshore feeding represents predation by lake trout on slimy sculpin, which have been shown elsewhere to be similar in δ^{13}C to *Mysis* (Sierszen et al. 2006; Sierszen et al. 2014). Given the declining trend observed in lake trout trophic position, lake trout predation on slimy sculpin (higher in δ^{15}N than *Mysis* by 2‰ to 2.5‰; Sierszen et al. 2006; Sierszen et al. 2014) may have been greater at the beginning of the experiment as their densities increased, but lake trout concentrated more on *Mysis* later in the experiment due to habitat restrictions and increased overlap. However, in other lake trout diet studies, slimy sculpin are frequently found at lower proportions in lake trout diets compared with *Mysis*, particularly at smaller lake trout sizes (Trippel and Beamish 1993; Sierszen et al. 2014).

Lake trout condition in Lake 375 was positively related to minnow CPUE. However, lake trout trophic position in Lake 375 decreased throughout aquaculture operations, suggesting they switched to feeding on lower trophic-level organisms (e.g., littoral invertebrates, which had similar δ^{13}C to minnows; Wellman et al. 2017) rather than minnows. While previous studies have shown that growth rates of predatory fish are typically elevated when they have greater dietary reliance on prey fishes compared with invertebrates (Pazzia et al. 2002; Venturelli and Tonn 2006), the increased productivity in Lake 375 overall may have led to a surplus of all available prey for lake trout, not just small fishes. Fertilization experiments elsewhere in small lakes with simple fish communities have demonstrated increased growth rates of lake trout because of increased invertebrate abundance (Lienesch et al. 2005), and invertebrates, including terrestrial invertebrates, are important components of lake trout diets (Chavarie et al. 2016; Guzzo et al. 2017).

The lack of any relationship between lake trout littoral feeding and minnow CPUE in Lake 375 likely reflects (*i*) the increasing vulnerability of *Mysis* to lake trout predation, as *Mysis* became more concentrated and easier to detect in a smaller volume of water, and (*ii*) evidence that lake trout were potentially foraging on nearshore prey at a lower trophic level than minnows. Additionally, reliance on nearshore resources in Lake 375 peaked and remained high only after *Mysis* densities became depressed (while minnow densities were increasing dramatically), suggesting that *Mysis* availability remained high until 2007 due to habitat constriction, despite their decreasing lake-wide densities. The timing of lake trout sampling (fall) presents an integration of lake trout feeding habits primarily during the summer, a period where lake trout movement is restricted under the thermocline (Plumb and Blanchfield 2009; Guzzo et al. 2017). Thus, inferred lake trout diets via stable isotopes collected in fall are a priori less likely to reflect reliance on nearshore resources when there is available prey in cold water (e.g., *Mysis*). Isotopic turnover rates in fish tissues are on the order of 3 months and can accelerate during periods of rapid growth (Hesslein et al. 1993). As such, the availability of nearshore resources to lake trout as prey and the ability of stable isotopes to reflect them as components of their diet may depend greatly on the time of year in which lake trout are sampled. Despite this, the fact that we saw increased reliance on nearshore resources for fall-captured fish (when they are least likely to have access to nearshore resources) strongly suggests that lake trout suffered from food limitation in cold hypolimnetic waters and were ultimately forced to forage in thermally suboptimal habitat upon the collapse of *Mysis* densities in Lake 375.

A detailed study of lake trout ecology in Lake 373 found the condition of lake trout and their time spent in the littoral zone were positively related to spring season length and the amount of energy assimilated from littoral prey (Guzzo et al. 2017). This is consistent with phenological trends reported for other regional lake trout populations (Fry 1939; Morbey et al. 2010). While our annual densities of minnows reported here (averaged over both spring and fall) increased with aquaculture, this does not reflect potential differences in seasonal patterns that might influence minnow availability during particular times of year (Rennie et al. 2019). However, the fact that nearshore reliance increased (based on fall-caught lake trout) only after *Mysis* densities declined is a potential indicator of nearshore resource use during a time when foraging nearshore is physiologically stressful due to high water temperatures, which may ultimately prove energetically costly. Indeed, lake trout body condition declined sharply by 2009 after 3 years of elevated reliance on nearshore resources, suggesting increased physiological stress associated with a lack of sufficient offshore prey.

Based on a sum of evidence, it is unlikely that changes in lake trout population densities influenced our results. Abundance of lake trout during aquaculture was previously reported to have increased (Mills et al. 2008) and has been confirmed by more recent analyses (Rennie et al. 2019). Further, analyses of the proportion of individuals caught in different size and age classes revealed potential increases in lake trout recruitment and abundance over the course of aquaculture operations (Fig. A3). Increases in lake trout abundance (density dependence) should result in decreased growth and body size of individuals due to lower per capita resource availability (Hazlerigg et al. 2012; Rose et al. 2001). By contrast, our results revealed that lake trout had greater early growth and condition during aquaculture operations. Following aquaculture, it is additionally possible that lake trout growth remained elevated due to a decrease in lake trout recruitment and population size, decreasing competition for food among individuals (Rennie et al. 2019).

The results of this research further exemplify how increased nutrient inputs into oligotrophic lakes can affect the growth and condition of lake trout populations. As a variety of stressors have contributed to eutrophication in freshwater systems (Bristow et al. 2008; Carpenter et al. 1998; Schindler 2006), it is important to understand how these changes will impact lake trout populations across North America. Although we detected no clear negative impact of aquaculture operations on lake trout growth and condition, prolonged nutrient enrichment has the potential to negatively impact lake trout recruitment through reductions in their optimal habitat (Lienesch et al. 2005). However, our results suggest that moderate nutrient enrichment from aquaculture operations in oligotrophic lakes may positively impact the growth and productivity of lake trout, at least initially. Our hypotheses that the growth, condition, and trophic position of piscivorous lake trout would increase corresponding to greater reliance on littoral resources were partially supported. While lake trout growth, condition, and reliance on nearshore resources did increase throughout aquaculture, lake trout trophic position decreased over time. Furthermore, the decline in *Mysis* did not negatively impact lake trout growth or condition, but rather lake trout length-at-age and condition increased and seemed to mirror a greater proportion of energy derived from offshore resources initially after the start of aquaculture.

Although the altered diet, growth, and condition of lake trout in this experiment was the result of an experimental aquaculture operation, the effects on the ecosystem provided a unique opportunity to investigate how lake trout growth and condition are impacted by fluctuations in prey community dynamics. Despite detecting only positive effects of aquaculture operations on growth and condition of lake trout, further examination of changes in fish life histories in response to aquaculture operations is needed to understand the long-term sustainability of these operations. The capacity of freshwater ecosystems to withstand aquaculture operations will likely vary based on their physical, chemical, and biological states, and detailed research is needed to identify their long-term ability to sustainably support aquaculture operations.

Acknowledgements

The authors thank Ken Mills, Sandy Chalanchuk, Doug Allan, Shelly Wellman, Lee Hrenchuk, Chandra Rodgers, Matt Guzzo, and all of the past and present IISD-ELA staff for providing field support, data, and (or) early reviews for this project. Three anonymous reviews aided in improving the manuscript. Additionally, the authors thank Rick Wastle and Susan Mann for their support with the age determination portion of this study. This work was supported by grants from the NSERC Discovery and Canada Research Chair programs to MDR and KAK; the Aquaculture Collaborative Research and Development Program (Fisheries and Oceans Canada and the Northern Ontario Aquaculture Association) to PJB, KM, and CLP; the Rainy Lakes Fisheries Charity Trust to MDR; and the IISD Experimental Lakes Area to PK.

References

Anderson, D.M., Glibert, P.M., and Burkholder, J.M. 2002. Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. Estuaries, **25**(4b): 704–726. doi:10.1007/BF02804901.

Anderson, J.L., Asche, F., Garlock, T., and Chu, J. 2017. Aquaculture: its role in the future of food. *In* World agricultural resources and food security (frontiers of economics and globalization). *Edited by* A. Schmitz, P.L. Kennedy, and T.G. Schmitz. Emerald Publishing Limited. pp. 159–173.

Ashley, K., Thompson, L.C., and Lasenby, D.C. 1997. Restoration of an interior lake ecosystem: the Kootenay Lake fertilization experiment. Water Qual. Res. J. Can. **32**: 295–323.

Bates, D., Maechlerk, M., Bolker, B., and Walker, S. 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. **67**: 1–48. doi:10.18637/jss.v067.i01.

Beamish, R.J. 1973. Design of a trapnet for sampling shallow-water habitats. J. Fish. Res. Board Can. **30**(4): 587–590. doi:10.1139/f73-104.

Blanchfield, P.J., Tate, L.S., and Podemski, C.L. 2009. Survival and behaviour of rainbow trout (*Oncorhynchus mykiss*) released from an experimental aquaculture operation. Can. J. Fish. Aquat. Sci. **66**(11): 1976–1988. doi:10.1139/F09-127.

Bristow, C.E., Morin, A., Hesslein, R.H., and Podemski, C.L. 2008. Phosphorus budget and productivity of an experimental lake during the initial three years of cage aquaculture. Can. J. Fish. Aquat. Sci. **65**(11): 2485–2495. doi:10.1139/F08-155.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths? Can. J. Fish. Aquat. Sci. **47**(11): 2219–2227. doi:10.1139/f90-246.

Carpenter, S.R., Caraco, N.F., Correll, D.L., Howarth, R.W., Sharpley, A.N., and Smith, V.H. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecol. Appl. **8**(3): 559–568. doi:10.1890/1051-0761(1998)008[0559:NPOSWW]2.0.CO;2.

Charles, C., Blanchfield, P.J., and Gillis, D.M. 2017. Site fidelity of escaped Rainbow Trout to an experimental freshwater aquaculture facility and habitat overlap with native fish fauna. Aquacult. Environ. Interact. **9**: 415–428. doi:10.3354/aei00243.

Chavarie, L., Howland, K., Gallagher, C., and Tonn, W. 2016. Fatty acid signatures and stomach contents of four sympatric Lake Trout: assessment of trophic patterns among morphotypes in Great Bear Lake. Ecol. Freshw. Fish, **25**: 109–124. doi:10.1111/eff.12195.

Cleugh, T.R., and Hauser, B.W. 1971. Results of the initial survey of the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. **28**(2): 129–137. doi:10.1139/f71-027.

Devlin, S.P., Tappenbeck, S.K., Craft, J.A., Tappenbeck, T.H., Chess, D.W., Whited, D.C., and Stanford, J.A. 2017. Spatial and temporal dynamics of invasive freshwater shrimp (*Mysis diluviana*): long-term effects on ecosystem properties in a large oligotrophic lake. Ecosystems, **20**: 183–197. doi:10.1007/s10021-016-0023-x.

DeVries, D.R., and Frie, R.V. 1996. Determination of age and growth. *In* Fisheries techniques. 2nd ed. *Edited by* B.R. Murphy and D.W. Willis. American Fisheries Society, Bethesda, Maryland. pp. 483–512.

Evans, D.O. 2007. Effects of hypoxia on scope-for-activity and power capacity of Lake Trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. **64**(2): 345–361. doi:10.1139/f07-007.

Evans, D.O., Nicholls, K.H., Allen, Y.C., and McMurtry, M.J. 1996. Historical land use, phosphorus loading, and loss of fish habitat in Lake Simcoe, Canada. Can. J. Fish. Aquat. Sci. **53**(S1): 194–218. doi:10.1139/f96-012.

Findlay, D.L., Podemski, C.L., and Kasian, S.E.M. 2009. Aquaculture impacts on the algal and bacterial communities in a small boreal forest lake. Can. J. Fish. Aquat. Sci. **66**(11): 1936–1948. doi:10.1139/F09-121.

France, R., and Steedman, R. 1996. Energy provenance for juvenile Lake Trout in small Canadian Shield lakes as shown by stable isotopes. Trans. Am. Fish. Soc. **125**: 512–518. doi:10.1577/1548-8659(1996)125<0512:EPFJLT>2.3.CO;2.

Fry, F.E.J. 1939. A comparative study of Lake Trout fisheries in Algonquin Park, Ontario. Publications of the Ontario Fisheries Research Laboratory, No. 58. pp. 1–69.

Graeb, B.D.S., Dettmers, J.M., Wahl, D.H., and Cáceres, C.E. 2004. Fish size and prey availability affect growth, survival, prey selection, and foraging behavior of larval Yellow Perch. Trans. Am. Fish. Soc. **133**: 504–514. doi:10.1577/T03-050.1.

Gunn, J.M., Steedman, R.J., and Ryder, R.A. 2004. Boreal Shield watersheds: Lake Trout ecosystems in a changing environment. Lewis Publishers, CRC Press, Boca Raton, Fla.

Guzzo, M.M., Rennie, M.D., and Blanchfield, P.J. 2014. Evaluating the relationship between mean catch per unit effort and abundance for littoral cyprinids in small Boreal Shield lakes. Fish. Res. **150**: 100–108. doi:10.1016/j.fishres.2013.10.019.

Guzzo, M.M., Blanchfield, P.J., and Rennie, M.D. 2017. Behavioral responses to annual temperature variation alter the dominant energy pathway, growth, and condition of a cold-water predator. Proc. Natl. Acad. Sci. U.S.A. **114**: 9912–9917. doi:10.1073/pnas.1702584114. PMID:28808011.

Hazlerigg, C.R.E., Lorenzen, K., Thorbek, P., Wheeler, J.R., and Tyler, C.R. 2012. Density-dependent processes in the life history of fishes: evidence from laboratory populations of Zebrafish *Danio rerio*. PLoS ONE, **7**(5): e37550. doi:10.1371/journal.pone.0037550. PMID:22655056.

Hesslein, R.H., Hallard, K.A., and Ramlal, P. 1993. Replacement of sulfur, carbon, and nitrogen in tissue of growing Broad Whitefish (*Coregonus nasus*) in response to a change in diet trace by δ^{34}S, δ^{13}C, and δ^{15}N. Can. J. Fish. Aquat. Sci. **50**(10): 2071–2076. doi:10.1139/f93-230.

Hyatt, K.D., McQueen, D.J., Shortreed, K.S., and Rankin, D.P. 2004. Sockeye Salmon (*Oncorhynchus nerka*) nursery lake fertilization: review and summary of results. Environ. Rev. **12**(3): 133–162. doi:10.1139/a04-008.

Johnston, N.T., Perrin, C.J., Slaney, P.A., and Ward, B.R. 1990. Increased juvenile salmonid growth by whole-river fertilization. Can. J. Fish. Aquat. Sci. **47**(5): 862–872. doi:10.1139/f90-099.

Konkle, B.R., and Sprules, W.G. 1986. Planktivory by stunted lake trout in an Ontario lake. Trans. Am. Fish. Soc. **115**: 515–521. doi:10.1577/1548-8659(1986)115<515:PBSLTI>2.0.CO;2.

Kullman, M.A., Kidd, K.A., Podemski, C.L., Paterson, M.J., and Blanchfield, P.J. 2009. Assimilation of freshwater salmonid aquaculture waste by native aquatic biota. Can. J. Fish. Aquat. Sci. **66**(11): 1965–1975. doi:10.1139/F09-128.

Lenth, R.V. 2018. Package "lsmeans" [online]. Available from https://cran.r-project.org/web/packages/lsmeans/lsmeans.pdf.

Lienesch, P.W., McDonald, M.E., Hershey, A.E., O'Brien, W.J., and Bettez, N.D. 2005. Effects of a whole-lake, experimental fertilization on Lake Trout in a small oligotrophic arctic lake. Hydrobiologia, **548**: 51–66. doi:10.1007/s10750-005-3620-9.

Mills, K.H., and Chalanchuk, S.M. 1987. Population dynamics of Lake Whitefish (*Coregonus clupeaformis*) during and after the fertilization of Lake 226, the Experimental Lakes Area. Can. J. Fish. Aquat. Sci. **44**(S1): s55–s63. doi:10.1139/f87-280.

Mills, K.H., Chalanchuk, S.M., Mohr, L.C., and Davies, I.J. 1987. Responses of fish populations in Lake 223 to 8 years of experimental acidification. Can. J. Fish. Aquat. Sci. **44**(S1): s114–s125. doi:10.1139/f87-287.

Mills, K.H., Chalanchuk, S.M., and Allan, D.J. 2002. Abundance, annual survival, and recruitment of unexploited and exploited Lake Charr, *Salvelinus namaycush*, populations at the Experimental Lakes Area, northwestern Ontario. Environ. Biol. Fishes, **64**: 281–292. doi:10.1023/A:1016058705612.

Mills, K.H., Chalanchuk, S.M., Blanchfield, P.J., Podemski, C.L., and Allan, D.J. 2008. Enhanced growth and condition of Lake Trout in a small Ontario lake during cage aquaculture of rainbow trout. Canadian Technical Report of Fisheries and Aquatic Sciences, 2778. pp. 200–202.

Morbey, Y.E., Couture, P., Busby, P., and Shuter, B.J. 2010. Physiological correlates of seasonal growth patterns in Lake Trout *Salvelinus namaycush*. J. Fish Biol. **77**: 2298–2314. doi:10.1111/j.1095-8649.2010.02804.x. PMID:21155784.

Paterson, M.J., Podemski, C.L., Wesson, L.J., and Dupuis, A.P. 2011. The effects of an experimental freshwater cage aquaculture operation on *Mysis diluviana*. J. Plankton Res. **33**: 25–36. doi:10.1093/plankt/fbq096.

Pazzia, I., Trudel, M., Ridgway, M., and Rasmussen, J.B. 2002. Influence of food web structure on the growth and bioenergetics of Lake Trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. **59**(10): 1593–1605. doi:10.1139/f02-128.

Piccolo, J.J., Hubert, W.A., and Whaley, R.A. 1993. Standard weight equation for lake trout. N. Am. J. Fish. Manage. **13**: 401–404. doi:10.1577/1548-8675(1993)013<0401:SWEFLT>2.3.CO;2.

Pierce, C.L., Rasmussen, J.B., and Leggett, W.C. 1996. Back-calculation of fish length from scales: empirical comparison of proportional methods. Trans. Am. Fish. Soc. **125**: 889–898. doi:10.1577/1548-8659(1996)125<0889:BCOFLF>2.3.CO;2.

Plumb, J.M., and Blanchfield, P.J. 2009. Performance of temperature and dissolved oxygen criteria to predict habitat use by lake trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. **66**(11): 2011–2023. doi:10.1139/F09-129.

Podemski, C.L., and Blanchfield, P.J. 2006. A scientific review of the potential environmental effects of aquaculture in aquatic ecosystems. Vol. V. Can. Tech. Rep. Fish. Aquat. Sci. 2450. pp. 30–79.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology, **83**: 703–718. doi:10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2.

Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., and Montana, C.G. 2007. Getting to the fat of the matter: models, methods, and assumptions for dealing with lipids in stable isotope analyses. Oecologia, **152**: 179–189. doi:10.1007/s00442-006-0630-x. PMID:17225157.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rennie, M.D., Kennedy, P.J., Mills, K.H., Rodgers, C.M.C., Charles, C., Hrenchuk, L.E., Chalanchuk, S., Blanchfield, P.J., Paterson, M.J., and Podemski, C.L. 2019. Impacts of freshwater aquaculture on fish communities: a whole-ecosystem experimental approach. Freshw. Biol. [Online ahead of print.] doi:10.1111/fwb.13269.

Rooney, R.C., and Podemski, C.L. 2009. Effects of an experimental rainbow trout (*Oncorhynchus mykiss*) farm on invertebrate community composition. Can. J. Fish. Aquat. Sci. **66**(11): 1949–1964. doi:10.1139/F09-130.

Rose, K.A., Cowan, J.H., Jr., Winemiller, K.O., Myers, R.A., and Hilborn, R. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish Fish. **2**: 293–327. doi:10.1046/j.1467-2960.2001.00056.x.

Schindler, D.W. 2006. Recent advances in the understanding and management of eutrophication. Limnol. Oceanogr. **51**: 356–363. doi:10.4319/lo.2006.51.1_part_2.0356.

Schindler, D.W., and Fee, E.J. 1974. Experimental Lakes Area: whole-lake experiments in eutrophication. J. Fish. Res. Board Can. **31**(5): 937–953. doi:10.1139/f74-110.

Schneider, C.A., Rasband, W.S., and Eliceiri, K.W. 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods, **9**(7): 671–675. doi:10.1038/nmeth.2089. PMID:22930834.

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. *In* Fisheries Research Board of Canada 184, Ottawa, Ont.

Sierszen, M.E., Peterson, G.S., and Scharold, J.V. 2006. Depth-specific patterns in benthic–planktonic food web relationships in Lake Superior. Can. J. Fish. Aquat. Sci. **63**(7): 1496–1503. doi:10.1139/f06-057.

Sierszen, M.E., Hrabik, T.R., Stockwell, J.D., Cotter, A.M., Hoffman, J.C., and Yule, D.L. 2014. Depth gradients in food-web processes linking habitats in large lakes: Lake Superior as an exemplar ecosystem. Freshw. Biol. **59**: 2122–2136. doi:10.1111/fwb.12415.

Sinkko, H., Lukkari, K., Sihvonen, L.M., Sivonen, K., Leivuori, M., Rantanen, M., Paulin, L., and Lyra, C. 2013. Bacteria contribute to sediment nutrient release and reflect progressed eutrophication-driven hypoxia in an organic-rich continental sea. PLoS ONE, **8**(6): e67061. doi:10.1371/journal.pone.0067061. PMID:23825619.

Trippel, E.A., and Beamish, F.W.H. 1993. Multiple trophic level structuring in *Salvelinus*–*Coregonus* assemblages in boreal forest lakes. Can. J. Fish. Aquat. Sci. **50**(7): 1442–1455. doi:10.1139/f93-165.

Vander Zanden, M.J., and Vadeboncoeur, Y. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology, **83**(8): 2152–2161. doi:10.2307/3072047.

Venturelli, P.A., and Tonn, W.M. 2006. Diet and growth of Northern Pike in the absence of prey fishes: initial consequences for persisting in disturbance-prone lakes. Trans. Am. Fish. Soc. **135**: 1512–1522. doi:10.1577/T05-228.1.

Wellman, S., Kidd, K.A., Podemski, C.L., Blanchfield, P.J., and Paterson, M.J. 2017. Incorporation of wastes by native species during and after an experimental aquaculture operation. Freshw. Sci. **36**: 387–401. doi:10.1086/692028.

Zimmerman, M.S., Schmidt, S.N., Krueger, C.C., Vander Zanden, M.J., and Eshenroder, R.L. 2009. Ontogenetic niche shifts and resource partitioning of Lake Trout morphotypes. Can. J. Fish. Aquat. Sci. **66**(6): 1007–1018. doi:10.1139/F09-060.

Appendix A

This appendix summarizes ageing and back-calculation methodology, changes in Lakes 375 and 373 lake trout growth and condition, changes in Lakes 375 and 373 lake trout estimated proportion of littoral energy assimilated and trophic position, and shifts in Lake 375 lake trout size and age structure before, during, and after aquaculture.

Table A1. Mean (±one standard error) back-calculated fork length (mm) of ages 1–5 Lake 375 lake trout from 2001–2002 to 2013–2015.

	Age				
Year(s)	1+	2+	3+	4+	5+
2001–2002	235.29±3.79a (20)	270.45±4.02a (17)	299.44±4.27a (17)	335.32±4.84ac (13)	355.38±7.13a (7)
2003–2004	234.54±3.34a (30)	280.81±3.46ab (24)	313.71±4.03ab (16)	334.91±4.33c (13)	363.03±4.47a (14)
2005–2006	233.48±5.44a (10)	282.62±3.67ab (24)	324.59±3.34b (30)	350.01±3.47abc (24)	366.75±4.04ab (16)
2007–2008	228.47±4.80a (16)	277.40±7.91ab (3)	327.08±5.10b (10)	358.48±3.65ab (24)	376.63±3.34ab (30)
2009–2010	247.40±5.19a (8)	284.52±5.04ab (12)	332.92±7.22b (4)	378.68±7.89b (3)	384.81±5.21ab (9)
2011–2012	240.46±2.94a (45)	296.64±3.15b (38)	330.93±5.52b (7)	366.32±7.04abc (4)	396.50±7.24b (4)
2013–2015	240.45±3.72a (25)	288.32±3.38ab (27)	329.70±3.19b (27)	357.25±3.43ab (22)	378.15±3.99ab (15)

Note: Sample sizes for each group are in parentheses. Letters indicate whether or not the **means within each age class** are significantly different among year(s). Means in each age class with the same letter are not significantly different.

Table A2. Mean (±one standard error) observed length (mm) for ages 4–6 Lake 373 lake trout from 2001–2002 to 2014–2016.

	Age		
Year(s)	4	5	6
2001–2002	382.94±10.11a (9)	401.38±7.50a (7)	407.50±11.32ab (2)
2003–2004	389.18±10.70a (9)	399.03±5.67a (16)	410.44±4.20a (17)
2005–2006	359.34±12.10a (6)	390.92±6.59a (10)	403.31±4.70ab (13)
2007–2008	365.55±13.98a (4)	398.19±5.83a (15)	393.77±4.44ab (15)
2009–2010	365.75±14.75a (4)	366.60±6.58a (11)	376.49±5.96b (8)
2011–2013	382.80±10.74a (7)	401.37±5.95a (12)	396.63±5.00ab (11)
2014–2016	350.06±7.81a (16)	378.89±5.25a (16)	400.87±3.47ab (25)

Note: Sample sizes for each group are in parentheses. Letters indicate whether or not the **means within each age class** are significantly different among year(s). Means in each age class with the same letter are not significantly different.

Table A3. Mean (±one standard error) back-calculated annual growth (mm·year^{-1}) of ages 1–5 Lake 375 lake trout from 2001–2002 to 2013–2015.

	Age				
Year(s)	1	2	3	4	5
2001–2002	38.62±3.35a (20)	38.99±3.56a (17)	30.34±3.57a (17)	33.70±3.95a (13)	24.12±5.12a (7)
2003–2004	45.79±2.93a (30)	46.76±3.15a (24)	38.87±3.65a (16)	26.70±3.95a (13)	30.80±3.83a (14)
2005–2006	44.84±4.44a (10)	48.33±3.17a (24)	43.64±2.93a (30)	30.20±3.15a (24)	23.96±3.65a (16)
2007–2008	37.88±3.79a (16)	52.03±7.55a (3)	44.21±4.45a (10)	34.41±3.17a (24)	21.41±2.93a (30)
2009–2010	56.68±4.88a (8)	50.83±4.19a (12)	50.95±6.63a (4)	46.84±7.56a (3)	20.86±4.66a (9)
2011–2012	52.67±2.65a (45)	55.19±2.84a (38)	39.12±5.19a (7)	38.50±6.62a (4)	21.81±6.62a (4)
2013–2015	46.84±2.93a (25)	47.97±2.85a (27)	38.33±2.85a (27)	26.91±3.09a (22)	20.83±3.66a (15)

Note: Sample sizes for each group are in parentheses. Letters indicate whether or not the **means within each age class** are significantly different among year(s). Means in each age class with the same letter are not significantly different.

Table A4. Mean (±one standard error) condition (W_r, %) of Lakes 375 and 373 lake trout from 2001–2002 to 2014–2016.

Year(s)	Lake 375	Lake 373
2001–2002	84.69±1.52ac (125)	86.04±1.70a (79)
2003–2004	85.62±1.49ac (146)	83.67±1.65a (106)
2005–2006	94.30±1.45b (210)	87.50±1.61a (120)
2007–2008	89.38±1.41ab (333)	82.55±1.57a (144)
2009–2010	80.70±1.42c (271)	82.53±1.70a (100)
2011–2013	87.48±1.45abc (210)	85.51±1.27a (246)
2014–2016	85.80±2.18abc (52)	83.76±1.26a (269)

Note: Sample sizes for each group are in parentheses. Letters indicate whether or not the means are significantly different among year(s). Means for each lake with the same letter are not significantly different. Lake 375 was only sampled in 2016 from 2014 to 2016.

Table A5. Estimated proportion (±one standard deviation) of littoral energy assimilated by lake trout in Lakes 375 and 373.

Year	Lake 375	Lake 373
2002	0.77±0.19 (21)	0.65±0.18 (20)
2003	0.86±0.17 (22)	0.85±0.15 (21)
2004	0.81±0.21 (17)	0.98±0.16 (20)
2005	0.66±0.09 (11)	0.86±0.19 (22)
2006	0.62±0.24 (19)	0.53±0.15 (20)
2007	1.00±0.24 (27)	0.62±0.20 (20)
2008	0.96±0.18 (22)	0.60±0.24 (21)
2009	0.90±0.16 (24)	0.75±0.18 (14)

Note: Sample sizes for each year are in parentheses.

Table A6. Estimated trophic position of lake trout in Lakes 375 and 373 using stable isotopes of nitrogen.

Year	Lake 375	Lake 373
2002	3.93 (21)	3.93 (20)
2003	3.88 (22)	3.68 (21)
2004	3.56 (17)	3.71 (20)
2005	3.69 (11)	3.66 (22)
2006	3.33 (19)	3.90 (20)
2007	3.67 (27)	3.97 (20)
2008	3.23 (22)	3.86 (21)
2009	3.15 (24)	3.61 (14)

Note: Sample sizes for each year are in parentheses.

Fig. A1. Digital images of the three distinct shapes of the Lake 375 lake trout pectoral fin ray cross-sections. The red dots represent marked annuli. The red lines represent the axes of measurement for the back-calculations on the anterior portion of the fin rays. [Colour online.]

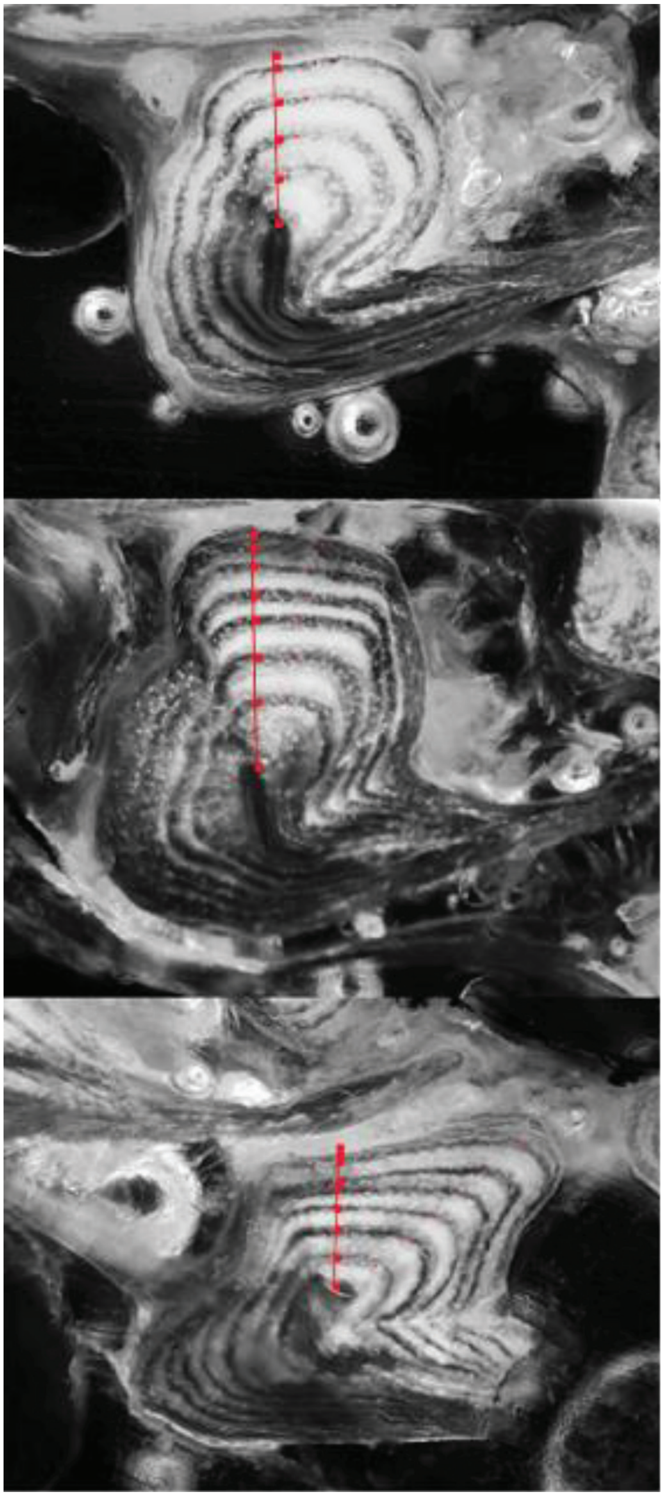


Fig. A2. Linear relationship between fork length (mm) and fin ray radius (pixels·mm⁻¹) for each shape of the Lake 375 lake trout pectoral fin ray cross-sections. Equations, r^2 values, and sample sizes (*n*) are displayed in the same colors as each fin ray shape. [Colour online.]

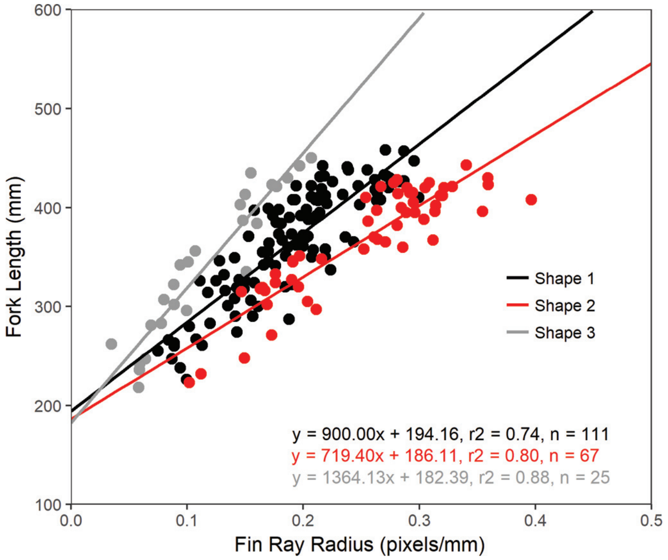


Fig. A3. Proportion of captured Lake 375 lake trout in different (A) fork length (mm), (B) weight (g), and (C) age classes (years) before (1999–2002), during (2003–2007), and after (2008–2016) aquaculture operations.