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Research Article

Integrating acoustic telemetry and demographic modeling to inform cisco (*Coregonus artedi*) restoration in Keuka Lake, New York

Alexander L. Koeberle[a], **Brad E. Hammers**[b], **Webster Pearsall**[b], **Daniel Mulhall**[b], **Adam Haley**[c], **Stephen J. Grausgruber**[d], **Marc Chalupnicki**[e], **James E. McKenna, Jr.**[e], **Evan G. Cooch**[a], **Lars G. Rudstam**[a], **and Suresh A. Sethi**[f,a]

[a]Department of Natural Resources and the Environment, Cornell University, Fernow Hall, Ithaca, NY 14853, USA; [b]New York State Department of Environmental Conservation, Division of Fish and Wildlife, Region 8 – Avon, NY 14414, USA; [c]New York State Department of Environmental Conservation, Bath Fish Hatchery, Bath, NY 14810, USA; [d]New York State Department of Environmental Conservation, Bureau of Fisheries, Albany, NY 12233, USA; [e]U.S. Geological Survey, Great Lakes Science Center, Tunison Laboratory of Aquatic Science, 3075 Gracie Road, Cortland, NY 13045, USA; [f]Aquatic Research and Environmental Assessment Center, Earth and Environmental Sciences, Brooklyn College, 123 Ingersoll Hall, Brooklyn, NY 11210, USA

Corresponding author: **Alexander L. Koeberle** (email: alk239@cornell.edu)

Abstract

Stocking is an important conservation tool to restore fish populations. Yet, assessing restoration success is often limited by a lack of field-based demographic information at low abundance, particularly for juvenile fish. Using outcomes from cisco (*Coregonus artedi*) reintroductions to Keuka Lake, New York, USA, we demonstrate a data-driven approach to assess fish stocking performance and evaluate the likelihood of achieving conservation goals. Multistage juvenile survival estimates from acoustic telemetry quantified high post-stocking mortality rates across three distinct stages. Modeled post-stocking stages include immediate release, acclimation, and long-term survival assumed to reflect natural mortality of cisco in Keuka Lake. High juvenile mortality severely limited the probability that stocked fish will reach reproductive maturity, and population viability analysis with a Leslie matrix life-stage model indicated that re-establishing a cisco population is unlikely with current stocking practices and lake conditions. By contrast, using cisco life history parameters extrapolated from other systems would have resulted in false optimism for restoration success. Our results highlight the importance of utilizing in situ demographic estimates for designing and implementing conservation stocking efforts.

Key words: acoustic telemetry, conservation and management, coregonine restoration, population ecology, survival modeling

Introduction

Conservation stocking to recover imperiled fishes is common and population assessments are needed to guide and evaluate restoration outcomes (Cochran-Biederman et al. 2015; Jachowski et al. 2016). Post-stocking evaluation has long been recognized as a crucial component of fisheries management for identifying causes of success or failure of stocking programs (see Cowx 1994). Management actions, including hatchery rearing and release practices, stocking abundance, and stocking duration are important predictors of reintroduction success and represent key controls for fishery managers to improve restoration outcomes (Cochran-Biederman et al. 2015; Fonken et al. 2023). Despite recent integration of defined success criteria into management objectives, species reintroductions frequently have high failure rates (Seddon et al. 2007; Armstrong and Seddon 2008). Adaptive management can improve long-term restoration success rates, but system-specific information on reintroduced populations is rare and difficult to obtain (Bacon et al. 2015; Jachowski et al. 2016; Lennox et al. 2021).

An important tool for designing fishery recovery programs is population viability analysis. This approach is well-suited for fish restoration efforts because it informs adaptive management by identifying risk factors and quantifying uncertainty of long-term persistence (Boyce 1992; Beissinger 2002; Ellner and Fieberg 2003). Population viability analysis features a population projection model parameterized with vital rates of the modeled species (e.g., *Leslie matrix*; Leslie 1948) whereby recovery or extinction probabilities are calculated for future population trajectories. Population growth is often sensitive to specific life history vital rates; therefore parameterizing the population projection model with accurate demographic estimates is important for generating realistic outcomes (Caswell 2001; Beissinger 2002; White et al. 2002).

This can be problematic when life history data are unavailable (Boyce 1992). For example, in fisheries restoration applications sparse empirical data may limit the capacity of managers to specify appropriate target stock, hence impeding their ability to accurately quantify restoration success.

Because in situ demographic information on reintroduced fish populations is costly and difficult to generate, population analyses often apply vital rates from comparable systems with extant populations of the species of interest or by borrowing rates from similar species (Jachowski et al. 2016). While this provides a baseline to design recovery efforts, this practice could also lead to biases if these borrowed vital rates are not reflective of conditions in the study system. In addition, when reintroduced, the species may recover slowly or persist at low densities. The population may therefore go undetected via traditional netting techniques, limiting inference to vital rates despite active monitoring efforts (Thompson 2013; Jachowski et al. 2016). Furthermore, relying on borrowed estimates from other systems to design stocking programs, without post-stocking monitoring, risks failure to meet restoration objectives if conditions are unsuitable for population establishment. Ideally, population assessments for species restoration efforts would feature reliable demographic estimates across a species' life history using system-specific data. For juvenile fishes, which are often underrepresented with traditional survey methods, this information is critical but sparse (Boyce 1992; Munzbergova and Ehrlen 2005).

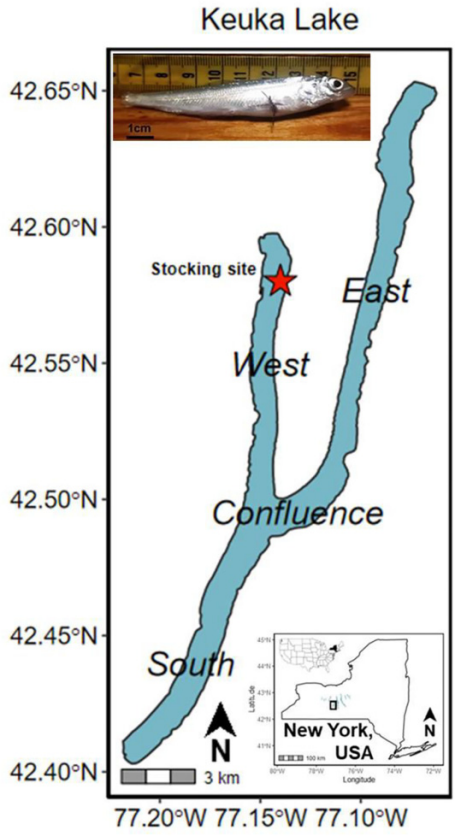
Stocked fish can provide valuable data for parameterization of population models to inform the design and adaptive implementation of species reintroductions. Novel technologies like acoustic telemetry create additional opportunities to overcome data limitations in demographic estimates like juvenile survival. Hatchery-raised juvenile fish are commonly used to recover or reintroduce populations, yet their survival after stocking is often poorly understood (Brown and Day 2002; Cochran-Biederman et al. 2015). This is because sampling different life stages requires unique fishing gears and surveying distinct habitats, complicating comparisons across age groups (Rudstam et al. 1984; Murphy and Willis 1996; Kubečka et al. 2012). Further, it is difficult to tag and monitor the movement, growth, and survival of small fish with previously available tracking technologies that are focused on larger-bodied and adult-stage fish (Mitchell et al. 2019; McKenna et al. 2021). To address this, recent advances in miniaturized transmitter technology coupled with spatially extensive telemetry arrays have provided greater understanding of survival processes of small fish (McMichael et al. 2010; Koeberle et al. 2023). In addition, spatially extensive arrays can generate time-to-event data, providing opportunities to apply multistage survival modeling to improve understanding of mortality rates associated with stocked fish (Sethi et al. 2024). This approach is useful for managers to evaluate stocking success by distinguishing post-stocking mortality of tagged fish from natural mortality of wild fish, providing in situ survival estimates missing from many population assessments.

We demonstrate a quantitative assessment of fish restoration stocking through an ongoing native cisco (*Coregonus artedi*) reintroduction to Keuka Lake, New York, USA conducted by New York State Department of Environmental Conservation (NYSDEC). Cisco are a pertinent study species within the *Coregonus* (Salmonidae: Coregoninae) species complex. Anthropogenic-driven cisco population declines have occurred from overfishing, water quality and habitat degradation, and non-native species introductions throughout its native range (Stockwell et al. 2009; Eshenroder et al. 2016; Bunnell et al. 2024). In North America, efforts to restore coregonines have intensified with hatchery augmentation throughout the Great Lakes region. These efforts have included basin-wide, international partnerships with State, Federal, and Tribal organizations to implement an adaptive management framework to increase lake ecosystem resilience (Zimmerman and Krueger 2009; Bunnell et al. 2023). Population assessments of cisco restoration are available for the Great Lakes (Fisch et al. 2019; Rook et al. 2021*a*, Rook et al. 2021*b*; Fielder and McDonnell 2024). Nevertheless, managers lack population projections for cisco reintroduced to inland lake settings, including Keuka Lake.

Keuka Lake, an inland lake in the Lake Ontario basin, is a deep, meso-oligotrophic lake with 4688 ha total surface area, 3 km maximum width, 57 m maximum depth, and three distinctive arms (West, South, and East) that meet at the Confluence region (Bloomfield 1978; Fig. 1). Cisco formed the historical prey fish base in Keuka Lake, located close to the southern extent of cisco distributions in North America (Page and Burr 2011). Their population in Keuka Lake declined from the 1970s to the early 1990s, likely from predation on larval stages by introduced forage fishes alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) (Hrabik et al. 1998; Mrnak et al. 2023). Lake managers considered cisco extirpated by the mid-1990*s*. Lake whitefish (*Coregonus clupeaformis*) were also present but were no longer observed after 1988. Since then, Keuka Lake has recently introduced piscivorous walleye (*Sander vitreous*) confirmed in 2016 and several established non-native invertebrate species including both zebra and quagga mussels (*Dreissena* spp.; zebra mussels confirmed in 1994, quagga mussels in 2008). Keuka Lake also has an abundant native mysid (*Mysis diluviana*) population, an important prey source for cisco, and wild-reproducing lake trout (*Salvelinus namaycush*) that is the base for a popular sport fishery. Improved water quality and a steep decline in rainbow smelt and alewife populations occurred from the 2000s to mid-2010s. This observed prey fish crash led managers to implement cisco reintroductions in 2018 to present and to cease non-native brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) hatchery stocking. Cisco restoration is hypothesized to stabilize Keuka Lake's mid trophic fish assemblage and to improve food web resilience to support the recreational Lake Trout fishery. Managers are considering restoration outcomes related to achieving a standing stock target abundance of adult cisco, and achieving a long-term, self-sustaining cisco population.

This study applies contemporary technology for observing released fish, in situ demographic modeling, and system-specific information to evaluate the probability of reestablishing a fish population. Specifically, we sought to answer the following questions: (1) Are current stocking efforts and

Fig. 1. Map of Keuka Lake, New York, USA and photograph of an acoustic-tagged fall fingerling cisco (*Coregonus artedi*). The map uses a latitude–longitude coordinate system with NAD83 datum. Cisco image from M. Chalupnicki, U.S. Geological Survey.



practices sufficient to restore the cisco population in Keuka Lake? (2) Will the reintroduced cisco population be self-sustaining over the long-term? (3) Is our approach useful for informing adaptive stocking practices to improve recovery?

We obtained juvenile and adult cisco mortality rates from Keuka Lake using whole-lake acoustic telemetry and multistage survival modeling for juveniles and using catch curve analysis from historical (pre-extirpation) survey data for adults. We then conducted a population viability analysis with system-specific information. We assessed the likelihood of achieving the management goals of establishing a minimum adult standing stock and establishing a self-sustained population over 50 years. We anticipate that our data-driven approach will prove useful for fisheries conservation where augmentation efforts focus on stocking juvenile fish to restore populations.

Methods

Fish reintroductions

Cisco eggs were collected from adult broodstock captured in the Great Lakes (see Table S1 for more information) annually in late November or early December (McKenna et al. 2021). Annual stocking occurs the following October at the fall fingerling juvenile stage (10 months old from hatching). From October 2018 through October 2024, over 450 000 total fall fingerlings have been stocked into Keuka Lake (see Table S1 for stocking numbers and fish sizes). Additionally, in 2019 and 2020 a smaller number ($n < 2000$) of older juvenile cisco were stocked as yearling fish cohorts (18, 19, or 22 months old from hatching). Hatchery stocking primarily releases fall fingerlings, except for the yearling cohorts noted above. Current hatchery production has capacity for annual releases of 100 000 fall fingerlings or 2000 yearlings. All cisco cohorts were stocked offshore via boat in the northwestern arm of the lake at ~50 m depths (see Fig. 1).

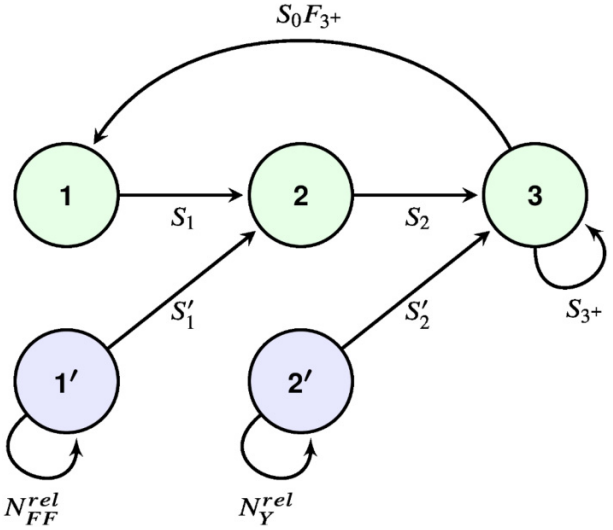
In situ demographic modeling

We leveraged a whole-lake acoustic telemetry dataset provided by NYSDEC and described in Koeberle et al. (2023) to estimate juvenile fish survival for population-level inferences of stocked fish. A subset of stocked cisco were equipped with small acoustic transmitters (hereafter, tags) and tracked across a whole-lake acoustic receiver array from years 2019 to 2021 in Keuka Lake (see S1.1 for acoustic telemetry specifications). The system is assumed to be a closed population (i.e., no immigration and emigration), validated by movement results from the acoustic telemetry experiment (Koeberle et al. 2023). Previous laboratory experiments indicated that tag burden did not increase mortality (McKenna et al. 2021), and all tagged fish were held in the hatchery to monitor their survival and tag retention two weeks prior to their release into Keuka Lake (Koeberle et al. 2023). Thus, we assumed that demographic estimates of tagged fish represented the broader population of stocked fish. All subsequent analyses were conducted in program R version 4.4.1 (R statistical programming, R Core Team 2024).

To estimate juvenile cisco survival, we applied a multistage modeling method using time-to-event data analysis procedures from Koeberle et al. (2023) and model procedures by Sethi et al. (2024). This technique provided an opportunity to estimate post-stocking mortality partitioned into three sequential stages including a "straight-to-death" mortality period immediately upon release (stage one), a period of elevated mortality during stocked fish acclimation (stage two), and finally a longer-term natural mortality regime (stage three). This is particularly useful for obtaining an estimate of wild juvenile fish survival rates which can be taken as the stage three "natural mortality" rate. We conducted multimodel selection with Deviance Information Criterion by testing covariates on stages and transition times between stages including size, age-at-release, and condition. See text S1.2 for multistage modeling specifications.

In situ estimates of adult (age-3+) mortality were calculated from a historical dataset of cisco catches provided by NYSDEC. This dataset pre-dates the cisco collapse with lake-wide gillnet surveys conducted from the 1970s to present (Table S2). We constructed netted cisco age and length distributions from each survey from 1979 to 1991 with age information estimated from scales (Figs. S1 and S2). We then applied regression-based catch curve analysis with the R package "FSA" (fishR, R Core Team 2024) to estimate adult

Fig. 2. Life-cycle graph specifying the population model structure for reintroduced cisco (*Coregonus artedi*) stocking and wild recruitment in Keuka Lake, New York, USA. Nodes 1–3 represent wild stages and nodes 1′ and 2′ represent hatchery stages. N_{rel} refers to the number of hatchery fish released into Keuka Lake as either fall fingerling (*FF*) or yearling (*Y*) stages.



instantaneous total mortality rates and annual mortality rates. Historical angler records do not indicate a cisco fishery in the lake. Therefore, we assume total mortality estimates from catch curve analysis is equivalent to natural mortality. Catch data suggest that the last year of cisco reproduction in Keuka Lake occurred in 1983 with a maximum observed age of 10 years across survey years (Fig. S1). Finally, we excluded gillnet surveys from 1971 to 1976 from catch curve analysis due to a lack of corresponding age data; however, we observed higher numbers of cisco catches during this period (Table S2). Because in situ adult mortality rates were derived from a period when cisco may have been in decline, we also obtained literature values for adult mortality rates from cisco populations in comparable lakes.

Population modeling

For this analysis, we specified a standing stock target of N = 1000 adult spawners (age-3+). We also identified a range of adult density targets based on other lake systems with extant cisco populations and considered long-term population establishment goals over a 50-year time horizon. To quantify standing stock targets and enable population viability analysis projections for the cisco population in Keuka Lake, we developed a stage-based (Lefkovitch 1965) matrix population projection model based on the life-cycle graph presented in Fig. 2. We assumed that adult cisco spawning would occur in November or December at age-3 (Fisch et al. 2019; Gatch et al. 2023). The life cycle was therefore truncated at age-3 with constant annual mortality rates (e.g., age-3+ is a terminal adult stage). Annual hatchery and wild juvenile survival rates reported here were expressed as a pre-spawning census. For example, stocked fall fingerlings released in October were treated as juvenile 1-year-old fish at release (hereafter, age-1 in our life-cycle graph) while yearlings were treated as juvenile (sub-adult) 2-year-old fish at release (hereafter, age-2) with annual survival estimates derived accordingly from the top-ranked multistage model. Discrete-time forward population projections are based on the product of the projection matrix:

$$n(t+1) = \mathbf{A} \cdot n(t)$$

where $n(t)$ is a vector of abundances of each stage at time t and $\mathbf{A}$ is the female-based projection matrix.

To account for fixed annual stocking protocols, let $\mathbf{R} = \left[\delta_1\ \delta_2\ \ldots\ \delta_k\right]^{\mathrm{T}}$, where δ_x is the number of released fish within an age class. We then defined a stocked matrix model $\mathbf{A}'$ and a vector of stocked fish $n'(t)$ such that:

$$n'(t) = \begin{bmatrix} n(t) \\ 1 \end{bmatrix}$$

The stocked system becomes

$$n'(t+1) = \mathbf{A}' \cdot n'(t)$$

where the stocked matrix is defined as

$$\mathbf{A}' = \begin{bmatrix} \mathbf{A} & \mathbf{R} \\ 0 & 1 \end{bmatrix}$$

with a constant annual rate of juvenile fish released as a single age class, $\mathbf{R}$:

$$\mathbf{R} = \begin{bmatrix} 0 \\ 0 \\ \delta \end{bmatrix}$$

such that

$$\mathbf{A}' = \begin{bmatrix} 0 & 0 & f_{3+}s_0 & 0 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & s_{3+} & \delta \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

where s_1 is wild juvenile survival from age-1 to age-2, s_2 is wild juvenile survival from age-2 to age-3, and s_{3+} is adult (age-3+) survival. Wild-reproduced age-0 survival, s_0, is the product of adult fertility rates f_{3+} (number of female eggs per fish) and s_0, where $s_0 = s_{egg} \cdot s_{fry} \cdot s_{sf}$. We specified s_{egg} as the probability of egg hatch at $t = 0$, s_{fry} as survival from $t = 0$ to 6 months, and s_{sf} (summer fingerling) as survival from six months to one year (Fielder and McDonnell 2024). A cohort of stocked fish, δ, enters the population as the product of N_{rel}, number of hatchery fish released, and S', their post-stocking annual survival rate. For stocked yearlings in Keuka Lake, the

stocked vector (column 4 in matrix $\mathbf{A}'$), $\mathbf{R}_Y$, is:

$$\mathbf{R}_Y = \begin{bmatrix} 0 \\ 0 \\ N_{rel}S'2 \\ 1 \end{bmatrix}$$

For stocked fall fingerlings, the stocked vector, $\mathbf{R}_{FF}$, can be parameterized as:

$$\mathbf{R}_{FF} = \begin{bmatrix} 0 \\ N_{rel}S'1 \\ 0 \\ 1 \end{bmatrix}$$

with hatchery fish that survive and enter the wild population as wild age-2 fish. With this formulation, fall fingerlings first enter the wild population at time $t = 1$ year (as juvenile age-2 fish) when projecting from the initial population (see text S1.3 for more information).

Population scenarios and sensitivity analyses

To evaluate the potential effectiveness of stocking on population viability, we used a combination of perturbation analysis and numerical simulation to evaluate efficacy of different stocking schemes in enhancing the viability of cisco populations. We conducted prospective perturbation analysis of our deterministic baseline matrix to identify key life cycle events that determine population growth rate, λ (see text S1.3 for details). Additionally, we derived the minimum vital rates necessary to maintain a minimum stable trajectory by solving for the characteristic polynomial for the matrix model where λ was constrained to 1.0 (representing the condition of zero population growth). We parameterized the baseline model for Keuka Lake using in situ juvenile survival estimated from the top-ranked multistage time-to-event model and adult mortality derived from the catch curve analysis. Remaining vital rates for fecundity and age-0 survival (egg hatch through year 1 survival) were derived from coregonine studies in North America and Europe (Table S3).

We also considered stochastic versions of our baseline population models in two ways, both using numerical simulation experiments. First, we simulated vital rate stochasticity by constructing sets of random matrices to reflect variation driven by environmental conditions, and projecting the populations based on a random selection of a matrix from this set at each time. Ideally, we would either (1) sample for a multivariate distribution where the covariances among parameters were specified, or (2) sample for a multivariate distribution where the parameter covariance structure is implicit in the annual matrix (Fieberg and Ellner 2001). In the absence of covariance estimates among parameters, we instead sampled parameter values from specified statistical distributions to generate a set of random matrices, over which individual matrices were sampled randomly at each time step. The statistical distributions used were specified for literature-derived fecundity and age-0 survival estimates to reflect environmentally driven variation of vital rates (Table S3). We then conducted bootstrapping from this set of matrices to evaluate the probability of obtaining a representative matrix with a positive population growth rate where $\lambda > 1.0$.

The preceding approach generated a set of random matrices that implicitly varied around a multivariate mean population growth rate, which was assumed to be stationary over the projections. To account for periodic shifts from this mean growth rate in our random matrix approach, we also simulated scenarios with episodic high recruitment events typical of pelagic schooling fishes, including cisco (Cury et al. 2000; Yule et al. 2006). In coregonines, this "boom-and-bust" recruitment dynamic (hereafter, boom recruitment) is hypothesized to be linked to cold winters with increased ice cover improving age-0 survival rates (Karjalainen et al. 2015; Myers et al. 2015; Stewart et al. 2021; Brown et al. 2022; Marjomäki et al. 2024). Boom recruitment years are observed for extant cisco populations in the Great Lakes and adjacent lakes including Lake Simcoe (Brown et al. 2024), Long Term Ecological Network inland lakes in northern Wisconsin (J. Vander Zanden pers. comm. 8 November 2024), and for vendace (*Coregonus albula*) and whitefish (*Coregonus lavaretus*) populations in northern European lakes (Marjomäki 2005; Axenrot and Degerman 2016; Sarvala et al. 2024). High abundance but infrequent year classes may improve the probability of re-establishing a population and are therefore important to model (Fielder and McDonnell 2024).

We incorporated boom recruitment scenarios by constructing a set of environmental state matrices with vital rates representative of boom (increased age-0 survival) and average (current age-0 survival estimates) recruitment years. Subsequently, population simulations randomly draw from state matrices with probabilities that represent the likelihood of boom recruitment occurrence. The periodicity of cisco recruitment cycles ranges from 4 to 7 years in the Great Lakes (Yule et al. 2006; Fisch et al. 2019; Rook et al. 2021b). Lake managers specified that Keuka Lake historically had cold winters with increased ice extent approximately every 3 years, so we specify population scenarios for both 3-year (similar recruitment frequency observed in Lake Ontario and Lake Simcoe; see Brown et al. 2024) and increased risk of longer 7-year boom cycles. Boom recruitment matrices were populated with a +600% magnitude increase in joint survival across age-0 life stages (Fielder and McDonnell 2024).

Hatchery stocking analysis

To evaluate the success of restoration stocking efforts in achieving standing stock density targets, we calculated the minimum stocking density and post-stocking survival rates necessary to accrue an adult (age-3+) population abundance of $N = 1000$ spawners. A scenario-based approach to account for uncertainty in juvenile fish survival was implemented to contrast hatchery juvenile survival rates and stocking effort under current estimates (median value of posterior distributions from the top-ranked multistage survival model) and optimistic estimates (upper 95% credible interval) for fall fingerling (S'_1 in the life-cycle graph) and yearling (S'_2) stocked fish.

We also explored standing stock target success with scenarios (Table S4) for wild juvenile survival (age-1, S_1 and age-2, S_2), specified as: (1) *Low*: current in situ estimates (median value), (2) *Medium*: upper 95% credible interval of in situ estimates, and (3) *High*: optimistic (upper 95% credible interval for S_1, equivalent survival S_2 and adult S_{3+}). The *High* scenario assumes that wild age-2 juvenile fish have exceeded a size threshold to escape predation (see length-at-age data; Fig. S2). Deterministic projections were implemented with 10 years of juvenile cisco stocking with estimates provided for both stocking numbers and equivalent lake-wide densities.

Population viability analysis

Because of high uncertainty about the fate of stocked fish and Keuka Lake ecosystem conditions, managers sought to compare both pessimistic and optimistic scenarios to inform decision making. Thus, we explored our set of *Low* (current), *Medium*, and *High* juvenile survival scenarios to quantify the likelihood of cisco re-establishment in Keuka Lake. Success of this restoration effort was specified through management objectives as: (1) a self-sustaining population characterized by $\lambda \geq 1.0$, (2) proportion $\geq 50\%$ of population trajectories over a minimum standing stock size of $N = 1000$ adults, and (3) with long-term persistence over a 50-year time horizon with projected adult fish densities reflective of comparable lakes with wild coregonine populations. Across scenarios, we tested the management effects of stocking age (fall fingerling or yearling) and stocking rate (annual number stocked and duration 10 or 20 years). We also explored the viability of the reintroduced cisco population by considering boom recruitment frequency every 3 or 7 years.

Population trajectories specific to the boom recruitment analysis were simulated with bootstrap sampling from our set of environmental state matrices and associated probabilities (e.g., 1/3 likelihood for a 3-year boom recruitment cycle or 1/7 likelihood for a 7-year boom recruitment cycle) over $n = 10\,000$ iterations. We also calculated the stochastic growth rate for each scenario. While this approach did not explicitly simulate a periodic cycle within a single trajectory, we assumed that trajectories across the simulated set are, on average, representative of the effects of an environmentally driven boom recruitment cycle on the population growth rate. We also assumed that few stocked cisco have survived to date in 2024, therefore all simulations were initialized with no cisco present in Keuka Lake. Next, we quantified the probability of extinction for each scenario, defined as the proportion of simulations with a terminal abundance of fewer than 100 adults with replicates ($n = 250$) to average out the periodic cycle of boom recruitment years. A population trajectory was considered functionally extinct if fewer than 100 adults persisted. Lastly, we compared our environmental state matrices approach to the set of random matrices approach for stochasticity by conducting sensitivity analyses to evaluate how λ responded to variation of early life history survival (age-0), our wild juvenile survival scenarios, and in situ versus literature-based adult mortality rates. Since the cisco population has been reintroduced from extirpation, we assumed that modeled populations experience density-independent growth during their recovery and are not subject to fishing mortality.

Results

In situ demographic estimates

Multistage survival models proved useful for estimating the handling and release survival of hatchery-stocked juvenile fish and distinguishing natural mortality rates representative of wild-equivalent juvenile fish (Table 1). Our top-ranked multistage model indicated that age-at-release was an important predictor of survival (Fig. 3, see Table S5 for multimodel selection results). Mortality was particularly high upon release for fall fingerlings, with only 21% of tagged fish surviving past the "straight-to-death" period after release (stage one; <1 day). Stocked yearlings had higher initial estimated survival of 78% (e.g., stage one) and annual cumulative survival of 2.4% (e.g., joint survival taken as stages one, two, and three). For fish that survived stage one, estimated stage two acclimation periods were ~25 days for fall fingerlings and ~61 days for yearlings. Finally, wild equivalent discrete annual survival rates were estimated from the multistage model as $S_1 = 0.004$ (95% credible interval < 0.001, 0.078) for fall fingerlings and $S_2 = 0.053$ (95% credible interval < 0.001, 0.18) for yearlings. The second-ranked multistage model included the covariate length with moderate support. Nonetheless, we inferred that age may be associated with a size threshold to escape predation and selected the multistage model associated with age over length.

The historical survey dataset also provided key insight into adult mortality rates prior to the cisco collapse. Our in situ catch curve analysis from historical data estimated adult (age-3+) mortality rates of 48.6% annually from years 1979 to 1991 (Fig. S3; see Table S6 for examples from extant cisco populations). This was parameterized in our population model as annual survival, $S_{3+} = 0.514$. Survey years 1971–1976, though excluded from catch curves as netted fish were not aged, indicated that cisco were distributed throughout Keuka Lake pre-extirpation (Fig. S4).

Deterministic population model and vital rate sensitivities

Our augmented matrix provided a convenient method for tracking hatchery fish contributions as they enter a wild population and for conducting sensitivity analysis. The population growth rate for the deterministic *Low* scenario (current juvenile survival) was $\lambda = 0.52$. The cisco population also showed negative population growth for *Medium* and *High* scenarios, with $\lambda = 0.61$ and $\lambda = 0.72$, respectively. Using our baseline population projection model, we solved for the stage-specific survival rates that led to a stable population (i.e., $\lambda = 1.0$) and results demonstrated that substantial reductions in juvenile mortality rates are necessary to achieve a self-sustained cisco population in Keuka Lake. Under the *High* scenario, wild age-1 juvenile survival would need to increase from $S_1 = 0.004$ (95% credible interval < 0.01, 0.078) to $S_1 = 0.44$ in average years, or to $S_1 = 0.064$ in boom recruitment years. Perturbation analysis revealed early life

Table 1. In situ stage-specific survival estimates and 95% credible intervals (CI) for juvenile cisco (*Coregonus artedi*) stocked into Keuka Lake, New York, USA.

Release age	Survival stage	Parameter	Time (days) after release	Stage survival	Daily mortality[c]	Cumulative survival	95% CI lower, upper
Fall fingerling	I. Straight-to-death	N/A	1	0.205	1.585	0.205	0.146, 0.278
Fall fingerling	II. Acclimation	N/A	25.4	0.215	0.063	0.044	0.011, 0.099
Fall fingerling	III. Long-term[a]	S'_1	365	0.006	0.015	<0.001	<0.001, 0.009
Fall fingerling	Wild annual[b]	S_1	365	N/A	N/A	0.004	<0.001, 0.078
Yearling	I. Straight-to-death	N/A	1	0.780	0.248	0.780	0.697, 0.862
Yearling	II. Acclimation	N/A	60.7	0.358	0.017	0.279	0.157, 0.487
Yearling	III. Long-term[a]	S'_2	365	0.086	0.008	0.024	<0.001, 0.117
Yearling	Wild annual[b]	S_2	365	N/A	N/A	0.053	<0.001, 0.180

Note: Survival was estimated from the top-ranked multistage model: 3-stage survival ~ release age with covariate effects on survival in each stage and on transition times.
[a]Equivalent to discrete annual post-stocking survival cumulative of stages I, II, and III.
[b]Equivalent to discrete annual survival (stage III), independent of handling and release effects of stages I and II.
[c]Daily instantaneous mortality rate for each stage.

stage (age-0) survival and adult survival were most influential in population growth rates (Table S7). For the deterministic *Low* scenario, wild survival rates were most sensitive with age-1 survival sensitivity = 0.501 and adult (age-3+) survival sensitivity = 0.992. Elasticity analysis revealed adult mortality as the most influential stage driving population growth (elasticity = 0.988), followed by fertility, $F_{3+}S_0$, rates (elasticity = 0.016). The elasticity of the adult survival parameter decreased (elasticity = 0.462) under the *High* scenario (Table S8). Finally, perturbation analysis revealed that the number of hatchery fish stocked, and their post-stocking survival, does not substantively affect λ, which was primarily driven by wild recruitment and adult mortality rates for stocked juvenile fish that survived to age-3+ and potential wild-reproduced fish (Tables S7 and S8).

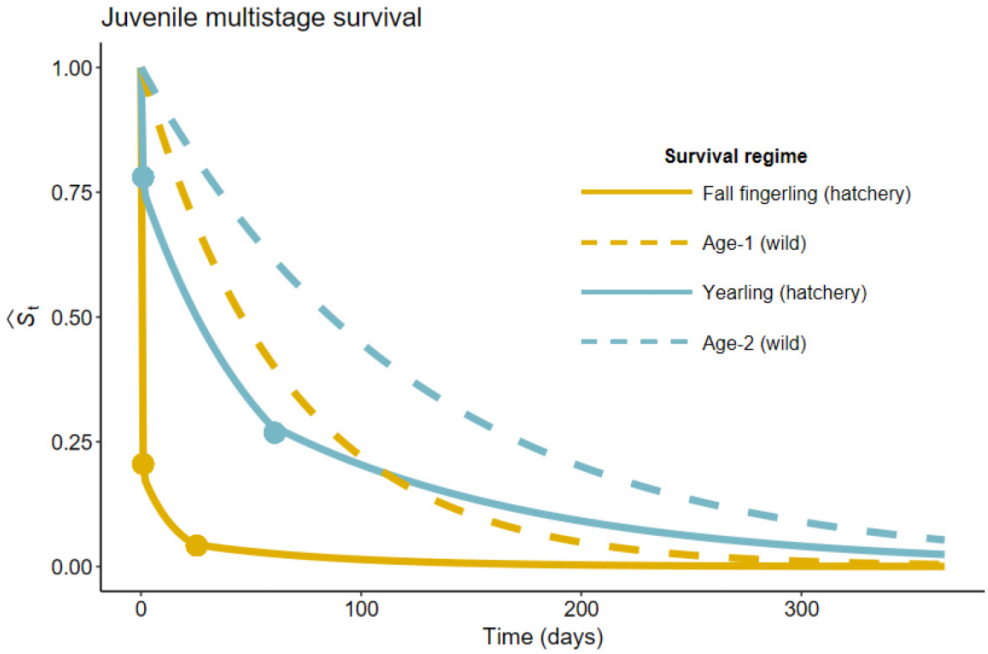
Hatchery stocking success

Our in situ demographic analysis revealed that accruing a standing stock target of $N = 1000$ adult (age-3+) spawners (lake-wide density 0.21 fish/ha) with current stocking efforts is not attainable for the given rates (Table 2). For the *Low* juvenile survival scenario, reaching this standing stock target, independent of long-term population establishment, required stocking fall fingerlings at densities >7500 fish/ha, two orders of magnitude higher than current hatchery production capabilities. Alternatively, stocking yearlings at densities ≥ 4.3 fish/ha achieved the standing stock target. For the *High* scenario, the standing stock target was achieved with fall fingerling stocking densities >19 fish/ha annually (Table 2). This result suggests fall fingerling stocking is sufficient under the *High* scenario, although this scenario represents a greater than 30× increase in the survival of these young-of-year fish (Table 3). When using hatchery costs reported by NYSDEC (see Table S9), we estimated the annual cost to accrue $N = 100$ adult spawners per year with current stocking practices is >$5 million USD for fall fingerlings, compared to $829 000 USD for yearlings. Given low survival and high costs to achieve management objectives with stocking fall fingerlings, we proceeded with population viability analyses using yearling stocking only.

Viability of the reintroduced population

Population viability analysis featuring simulations of environmental stochasticity indicated that long-term recovery of the reintroduced Keuka Lake cisco population is unlikely at the derived survival rates (Fig. 4). Across stochastic scenarios, the modeled population always fell below an extinction threshold of $N = 100$ adults and reached 100% probability of extinction by the long-term time horizon at 50 years (Fig. 4c). While boom recruitment frequency is not directly managed, periodic, strong recruitment events reflect ecological realism observed in many cisco populations and provided insights into the potential future trajectories of the reintroduced population in Keuka Lake. The 3-year boom recruitment scenario had a stochastic growth rate $\lambda_s = 0.87$. An increase in duration between boom recruitment years; however, increased the risk of population collapse ($\lambda_s = 0.78$ for the 7-year recruitment scenario). Boom recruitment scenarios increased

Fig. 3. Estimated survival curves, $\widehat{S}_t$, of stocked juvenile cisco (*Coregonus artedi*) for Keuka Lake, New York, USA. Survival estimates are derived from the top-ranked multistage model for acoustic-tagged juvenile hatchery fish which includes an age effect on stage-specific mortalities (solid lines) and transition times (solid points). This model includes a sequential straight-to-death, acclimation, and natural mortality stages, and estimated transition times between stages. Equivalent wild juvenile survival (dashed lines) is derived from the third stage mortality rate from the multistage model.



the population growth rate and projected adult fish density compared to deterministic models, though conditions were insufficient for long-term recovery.

Population viability analysis also revealed that even under the most optimistic survival and recruitment assumptions, the reintroduced cisco population was at risk of collapse soon after current stocking efforts cease (modeled yearling release of 2000 fish/year; Fig. 4). Projected populations under optimistic conditions failed to reach adult densities reflective of self-sustaining populations (see Table S10). Under the most optimistic scenario with a modeled 3-year boom recruitment cycle, the present 10-year stocking strategy yielded a median 0.24 adults/ha (Fig. 4*b*) at year 10. In addition, while 30% of simulated trajectories under the most optimistic scenario exceeded the management target of 0.21 adults/ha at year 10, no trajectories exceeded this target long-term at year 50 (Fig. 4*a*). Doubling the stocking duration to 20 years increased the probability of successfully accruing an adult standing stock, yet trajectories still showed long-term decline. Projected adult densities increased to ~1.0 adults/ha (maximum trajectory values) over a longer time horizon by year 39, which approached lower density estimates observed in extant cisco populations (Table S10). Although 53% of trajectories exceeded the standing stock target after 20 years of stocking, almost all simulated population trajectories still decreased at the cessation of stocking, with <0.01% of trajectories exceeding 0.21 adults/ha at year 50.

Our random matrix approach to simulate environmental stochasticity of age-0 vital rates provided further insight into key stages that drive population growth rates (Fig. 5). Simulations revealed that low wild juvenile survival could be ameliorated by higher adult survival. For example, lower adult mortality reflective of literature values (see Table S6) increased the probability of drawing a matrix with $\lambda > 1.0$ and increased the average population growth rate (λ geometric mean, $\bar{\lambda}_{geom}$) across the sampled set of matrices ($\bar{\lambda}_{geom} = 0.86$ for 70% literature-based survival, compared to $\bar{\lambda}_{geom} = 0.69$ for 51.4% in situ survival). Nevertheless, simulation results indicated that boom recruitment years in the study system were critical for long-term population viability, despite higher adult survival estimates. Compared to our environmental matrix approach, the only modeled *High* scenario with positive population growth occurred with a 3-year boom likelihood and a literature-based 70% adult survival rate, where $\lambda_s = 1.04$ (Table S11).

Discussion

Conservation stocking is an important management tool for fisheries restoration, yet the recovery challenges presented in this study underscore the need to use system-specific data for accurately assessing population viability. Our study of cisco reintroductions to Keuka Lake found that present fish stocking practices are unlikely to achieve management targets. Further, our results from population viability analysis using in situ juvenile and adult survival rates highlight that Keuka Lake conditions are likely prohibitive for the long-term viability of reestablishing a cisco population. By contrast, our data-driven approach was successful for informing adaptive stocking as solely relying on life history

Table 2. Hatchery stocking effort analysis to identify annual juvenile cisco (*Coregonus artedi*) stocking densities (fish/ha with 4688 ha total surface area) necessary to accrue a standing stock target of at least 1000 eligible spawners (age-3+ adults), given 10 years of stocking, juvenile survival scenarios, and in situ estimates of adult survival from catch curve analysis ($S_{3+} = 0.514$).

Release age	Model parameter	Wild scenario[a]	Hatchery scenario[b]	Stocking density target (fish/ha)	Equivalent number stocked (No. fish)
Fall fingerling	N_{rel}^{FF}	Low	Current	7536	35.3 M
Fall fingerling	N_{rel}^{FF}	Low	Optimistic	218	1.0 M
Fall fingerling	N_{rel}^{FF}	Medium	Current	2075	9.7 M
Fall fingerling	N_{rel}^{FF}	Medium	Optimistic	60	281 000
Fall fingerling	N_{rel}^{FF}	High	Current	641	3.0 M
Fall fingerling	N_{rel}^{FF}	High	Optimistic	19[c]	87 000
Yearling	N_{rel}^{Y}	Low	Current	4.3	20 300
Yearling	N_{rel}^{Y}	Low	Optimistic	0.9	4200
Yearling	N_{rel}^{Y}	Medium	Current	4.0	19 000
Yearling	N_{rel}^{Y}	Medium	Optimistic	0.8	3900
Yearling	N_{rel}^{Y}	High	Current	3.6	16 700
Yearling	N_{rel}^{Y}	High	Optimistic	0.7	3400

Note: Current hatchery capacity supports annual stocking of 100 000 fall fingerlings (≈21 fish/ha) or 2000 yearlings (≈0.4 fish/ha).
[a]Wild-equivalent juvenile survival: *Low* (in situ) ($S_1 = 0.004$, $S_2 = 0.053$, *Medium* (upper 95% credible interval) $S_1 = 0.078$, $S_2 = 0.18$, *High* (age-2 equivalent to age-3+ survival) $S_1 = 0.078$, $S_2 = S_{3+} = 0.514$.
[b]Hatchery-stocked juvenile multistage survival: *Current* (in situ) $S'_1 = 0.00026$, $S'_2 = 0.024$, and *Optimistic* (upper 95% credible interval) $S'_1 = 0.009$, $S'_2 = 0.117$.
[c]Indicates scenario with stocking density target achieved.

Table 3. Hatchery stocking effort analysis to identify management targets for annual post-release survival (target survival) of juvenile cisco (*Coregonus artedi*) released into Keuka Lake, New York, USA.

Release age	Model parameter	Stocking rate (fish/year)	Wild Scenario[a]	Target annual survival[b]	Multiplier[b]
Fall fingerling	S'_1	100 000	Low	0.092	354×
Fall fingerling	S'_1	100 000	Medium	0.026	100×
Fall fingerling	S'_1	100 000	High	0.007	31×
Yearling	S'_2	2000	Low	0.244	10×
Yearling	S'_2	2000	Medium	0.227	9.5×
Yearling	S'_2	2000	High	0.199	8.3×

Note: Target survival represents the minimum survival estimates necessary to achieve a standing stock of at least 1000 eligible spawners (age-3+ adults), given 10 years of annual stocking and in situ estimates of adult survival derived from catch curve analysis ($S_{3+} = 0.514$).
[a]Wild-equivalent juvenile survival: *Low* (in situ) ($S_1 = 0.004$, $S_2 = 0.053$, *Medium* (upper 95% credible interval) $S_1 = 0.078$, $S_2 = 0.18$, *High* (age-2 equivalent to age-3+ survival) $S_1 = 0.078$, $S_2 = S_{3+} = 0.514$.
[b]Factor for increasing post-stocking survival from current (in situ) $S'_1 = 0.00026$ or $S'_2 = 0.024$.

Fig. 4. Population viability analysis of the reintroduced cisco (*Coregonus artedi*) population in Keuka Lake, New York, USA under the most optimistic juvenile survival scenario with a 3-year boom recruitment cycle (e.g., 1/3 boom recruitment likelihood). This analysis reveals a low probability of establishing a self-sustained reintroduced cisco population over a 50-year time horizon. Here, we illustrate the (*a*) population trajectories (10 000 iterations; random subset 100 iterations shown for visualization), (*b*) average population densities, and (*c*) and the long-term probability of extinction (threshold $N = 100$ age-3+ adults) for simulated cisco reintroductions in Keuka Lake. All population trajectories are initiated with $N_0 = 0$ fish and include annual stocking rates of 2000 yearlings for 10 or 20 years. While trajectories indicate the population increases above a target spawner density of 0.21 fish/ha (dashed gray lines), all trajectories crash soon after stocking ceases and the extinction probability asymptotes to 100% by the end of the 50-year management horizon.

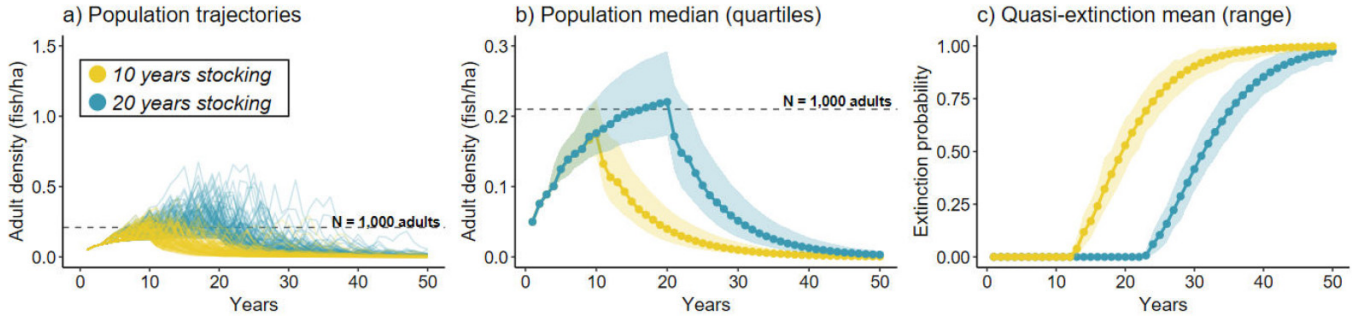
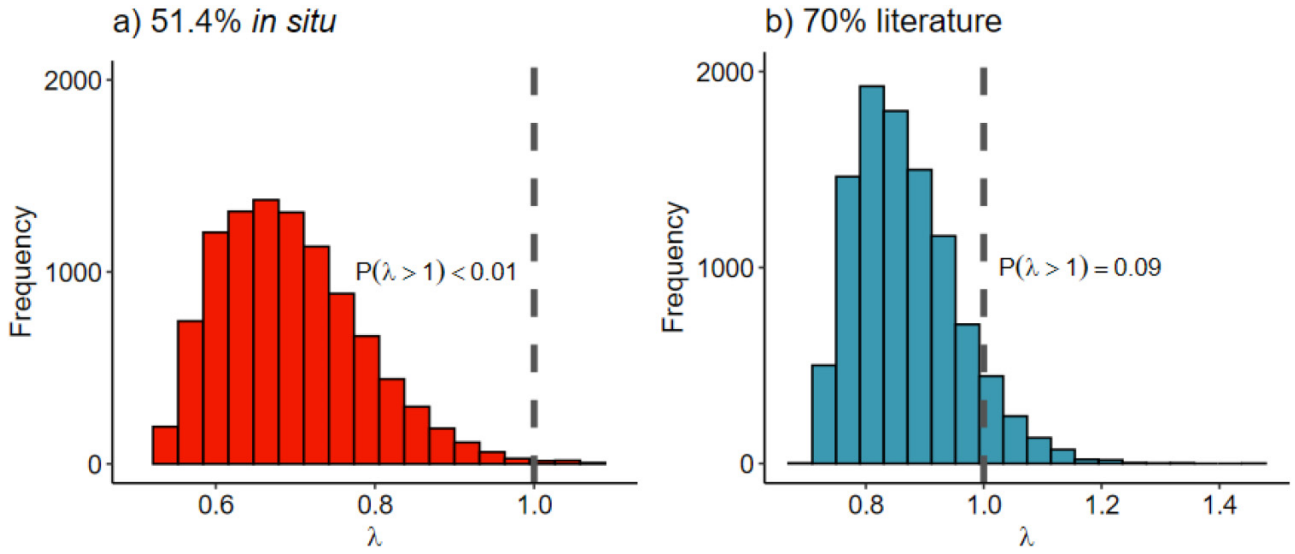


Fig. 5. Sensitivity analysis of population growth rates to adult (age-3+) cisco (*Coregonus artedi*) annual mortality rates estimated as (*a*) in situ 51.4% survival and (*b*) literature-based 70% survival. To simulate environmental stochasticity, we constructed 2500 projection matrices from random sampling of probability distributions of fecundity and early life history (age-0) survival values. We then bootstrap sampled from this set of random matrices (10 000 iterations) to calculate the expected population growth rate λ at each time step. Higher adult survival rates reflective of literature-derived estimates increase the probability of achieving positive population growth, e.g., $P(\lambda > 1.0)$, in contrast to in situ survival estimates from the study system.



parameters extrapolated from other systems would have led to false optimism for restoration success. Despite testing a range of juvenile survival estimates and a literature-derived adult mortality estimate in our population assessment, population recovery remained unlikely, even under the most optimistic scenarios.

Post-stocking survival assessments and population analyses highlight two demographic processes that are important for future cisco recovery efforts in Keuka Lake: (1) high mortality of stocked juvenile fish immediately upon release (previously difficult to estimate without acoustic telemetry technology) points to the need to implement alternative stocking practices, and (2) improved lake conditions for higher wild juvenile and adult survival rates are needed to increase the probability of establishing a self-sustaining population.

Empirical estimates from Keuka Lake indicated that current fall fingerling stocking rates fail to result in a long-term sustainable population growth rate, and thus stocking efforts focused on releasing this younger stage will not achieve spawner targets. High immediate mortality of fall fingerlings was attributed to a combination of heavy Lake Trout preda-

tion, avian predation, and physiological stress from release (Koeberle et al. 2023). While older, larger yearling cisco are also susceptible to these factors, multistage survival modeling revealed that stocking of yearlings increased long-term survival and the ability to accrue an adult standing stock. For hatchery managers, a more practical approach identified in our stocking analysis could combine increased yearling cisco production from 2000 fish/year to 3400 fish/year and modified rearing and release practices to improve their stocking-related survival ≈4*x* (upper 95% credible interval). High juvenile mortality; however, cannot be overcome by increasing the number of stocked yearlings alone due to current hatchery production constraints. These field-based insights have facilitated adaptive management of stocking. For example, in 2025 lake managers plan to hold surplus fall fingerlings through winter to explore spring yearling stocking ($n = 2000$) and potentially stock surplus adults ($n = 400$) in Keuka Lake (see Table S1). Managers are also considering modified rearing or release practices for future cohorts of stocked juvenile cisco.

System-specific adult survival rates estimated from historical (pre-extirpation) cisco catch data combined with our in situ juvenile survival estimates result in a low probability of establishing a self-sustaining population. Under optimistic (*High* juvenile survival) scenarios, we calculated adult annual survival would need to improve from in situ 51.4% to >66% (3-year boom recruitment) or >76% (7-year boom recruitment) to achieve a stable population. Such rates are within the range of adult cisco mortality estimates observed in the Great Lakes basin (see Table S6); however, their application to Keuka Lake could lead to false optimism for population restoration if current Great Lakes conditions for cisco may be better than in inland lakes. Although perturbation analysis revealed adult mortality and recruitment were important to the projected population, adult mortality cannot easily be manipulated by managers.

Post-release survival assessments revealed that stocking enough fish to achieve adult cisco density targets in Keuka Lake would require numbers beyond current hatchery capacity. This result is consistent with Rook et al. (2021*a*) who found that restoring cisco populations to historic levels in the Great Lakes required stocking fish at densities two orders of magnitude higher than present stocking rates. Increased mortality of hatchery fish compared to wild fish of equivalent age is well-documented in hatchery stocking programs for salmonids (see Brown and Day 2002; Saloniemi et al. 2004; Araki et al. 2007; Beamish et al. 2012; Kitada 2020; James et al. 2023). Extended time in the hatchery increases the risk of reduced fitness to environmental conditions (Brown and Day 2002; Jachowski et al. 2016), which in Keuka Lake may be reflected by stocked yearlings spending more time in the second acclimatization stage of the multistage model than stocked fall fingerlings. Studies demonstrate modified rearing practices can effectively reduce stress and improve fitness of hatchery fish, including in-tank structure, e.g., gravel substrate and overhead covers (Cogliati et al. 2019), periods of light and dark conditions (Maynard et al. 1995; Brown and Day 2002), and varying growth rates, diet composition, and feed particle size (Cogliati et al. 2023). Chemical or physical predator cues applied in hatcheries also improve predator avoidance behavior (Manassa and McCormick 2012; Wilson et al. 2021). While management strategies in North America primarily stock juvenile cisco, techniques such as translocations of adults or in situ placement of early life stages (e.g., eggs or larvae) have also been implemented for coregonine restoration in Europe (Maitland and Lyle 2013; Adams et al. 2014; Bunnell et al. 2024), and studies for salmonids have called for reduced times in hatcheries to minimize the lack of natural selection (Lennox et al. 2021). Studies have also found that smaller, younger fish acclimated to outdoor ponds before release survive better than older, larger fish held in hatchery facilities (Olson et al. 2000). Future coregonine research could investigate whether alternative rearing and release strategies impact the survival of stocked fish, and thus their recruitment to an adult standing stock. Such strategies could then be incorporated into perturbation analyses to evaluate their costs, benefits, and effects on model parameters in population assessments (Nichols and Hines 2002).

The Keuka Lake cisco reintroduction demonstrates that a combination of acoustic telemetry and time-to-event modeling now enables the estimation of juvenile fish life history parameters in situ, providing managers with empirical demographic information central to the evaluation of stocking efforts. Combined with multistage survival modeling, we expect these approaches will prove useful for identifying key mortality stages for stocked fish. In Keuka Lake, significant mortality at stocking and through acclimation supports testing modified release practices to increase survival through these initial stages and to reduce the influence of loading, transport, and stocking related stress. For example, net pen acclimation whereby fish are held in nets in situ for several days to weeks may prevent high initial predation, promote lake acclimatation, and improve the transition to wild defensive behaviors such as schooling (Brown and Day 2002; Rillahan et al. 2011). A study using net pens for chinook salmon (*Oncorhynchus tshawytscha*) in Lake Ontario found that smolt-to-lake harvest rates were 1.7–2.3 times higher for pen acclimated fish than those directly stocked (Connerton et al. 2022). Further, cisco exhibit predator-driven diel migration (Stockwell et al. 2009). Our findings that ≈80% of stocked fall fingerlings perished within the first several hours of daytime release into Keuka Lake support testing whether nighttime stocking could alleviate predation mortality upon stocking (Roberts et al. 2009).

Population viability analysis was important to evaluate the risks and uncertainty of restoration scenarios. The failure to achieve positive population growth across modeled scenarios indicates that present ecosystem conditions are not suitable to restore a cisco population to Keuka Lake. Positive population growth rates were not achieved, even under scenarios reflective of optimistic environmental conditions. If strong year classes for this species are linked to ice cover, which has decreased in recent decades in the Northern Hemisphere, time between strong recruitment years could increase (Sharma et al. 2019; Brown et al. 2024; Fielder and McDonnell 2024). This increased duration resulted in a higher extinction risk in our models. Population assessment outcomes are also reinforced by the absence of empirical evidence for long-term survival

and recruitment from netting surveys. Since the onset of reintroductions to date, no larval cisco have been collected in annual spring larval fish surveys. The only evidence of multi-year survival is one cisco netted in July 2022 during a lake-wide bottom gill net survey and estimated from otolith and scale analysis to be 2 years 8 months old (see Fig. S5). This age coincides with the October 2020 fall fingerling release, with $N = 6$ (95% credible interval < 1, 401) fall fingerlings estimated to have survived to this time period as age-2+ fish.

The cisco population analysis presented here poses several limitations. First, wild-derived survival estimates of juvenile cisco in Keuka Lake were estimated from tagged fish. Any tagging effect could therefore bias hatchery estimates which in turn are propagated to wild-equivalent estimates. In addition, the sample size of fish surviving to the third stage is low. Our simulations also lacked features of demographic stochasticity and the Allee effect, processes expected to increase extinction rates (Lande and Orzack 1988). While decreased predation through schooling has been observed in cisco (Milne et al. 2005; de Kerckhove and Shuter 2022), our models lacked depensatory mortality through a schooling effect, where survival increases with larger populations and schooling effectiveness decreases with smaller school size (Clark 1974; Magurran 1990). Future modeling efforts could explore how stocking density and fish behavior impact schooling effectiveness and post-release mortality of cisco in Keuka Lake and for other stocked schooling pelagic species. Additionally, although adult mortality was important in our perturbation analysis, we lack information on how much adult mortality varies annually and the in situ rates applied to population modeling were estimated from a time when the cisco population was in decline. Lastly, our analysis focused on demographic processes and did not explore lake ecosystem drivers of cisco establishment. For example, future assessments could integrate perturbation analysis with environmental covariates important for coregonine fishes such as temperature (Jacobson et al. 2010; Fang et al. 2012; Stewart et al. 2021), oxythermal habitat and nutrient availability (Jacobson et al. 2008; Jacobson et al. 2010; Magee et al. 2019), and ice cover duration and extent (Karjalainen et al. 2015; Brown et al. 2022) to further identify minimum conditions required for achieving positive population growth (Polansky et al. 2024). Understanding these conditions is important to achieve management objectives as fish reintroductions are often more successful if the mechanisms causing decline are identified and addressed (see Mrnak et al. 2025).

Species reintroduction efforts are challenging and adaptive stocking practices that apply in situ demography and population modeling could improve the probability of success. We found that an absence of in situ monitoring and over-reliance on borrowing life history information extrapolated across systems could lead to false optimism of ecosystem conditions for Keuka Lake and thus cisco restoration success. Unsuccessful restoration attempts are underrepresented in peer-reviewed literature yet offer insights into future efforts elsewhere (Schaub et al. 2009; Jachowski et al. 2016). Our modeling approach elucidated in situ juvenile survival processes previously difficult to measure for coregonine species and wild population dynamics that hinder the ability to restore a pelagic forage fish species in a temperate lake.

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Data availability

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Author information

Author ORCIDs

Alexander L. Koeberle https://orcid.org/0000-0003-0522-9202
Lars G. Rudstam https://orcid.org/0000-0002-3732-6368
Suresh A. Sethi https://orcid.org/0000-0002-0053-1827

Author contributions

Conceptualization: ALK, BEH, WP, DM, MC, JEM, EGC, LGR, SAS
Data curation: ALK, BEH, WP, DM, AH, SJG, MC, JEM
Formal analysis: ALK, EGC, LGR, SAS
Methodology: ALK, EGC, LGR, SAS
Supervision: BEH, EGC, LGR, SAS
Visualization: ALK, EGC, LGR, SAS
Writing – original draft: ALK, EGC, LGR, SAS
Writing – review & editing: ALK, BEH, WP, DM, AH, SJG, MC, JEM, EGC, LGR, SAS

Competing interests

The authors declare no competing interests.

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Supplementary material

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