Opposing trends in survival and recruitment slow the recovery of an historically overexploited fishery

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Running head: Arctic charr demography

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# Abstract

Quantifying temporal variation in demographic rates is a central goal of population ecology, in both basic and applied settings. In this study, we analysed a multidecadal age-structured time series of arctic charr (*Salvelinus alpinus*) catch in Lake Mývatn, Iceland, to infer the time-varying demographic response of the population to reduced harvest in the wake of the fishery’s collapse. Our analysis shows that while survival probability of adults increased following the alleviation of harvesting pressure, per recruitment consistent declined over the entire study period. The countervailing demographic trends resulted in no directional change in the total population size or population growth rate. Rather, the population dynamics were dominated by large interannual variability and a shift towards a relatively older age distribution. These results are indicative of a slow recovery of the population following its collapse, despite the rising number of adults due to relaxed harvest.

*Keywords*: demography; Lake Mývatn; population dynamics; *Salvelinus alpinus*

# Introduction

Quantifying temporal variation in demographic rates is a central goal of population ecology, as this underpins efforts to characterize both exogenous and endogenous drivers of population dynamics (Twombly 1994; Zeng et al. 1998; Koons et al. 2016). However, this endeavor is challenging, as even the characterization of directional trends in demographic rates requires data spanning many years and often relies on intensive mark-recpature (and related) approaches for statistical inference (e.g., Forcada, Trathan, and Murphy 2008; Hunter et al. 2010). Both of these challenges are amplified in populations subject to large interannual variation in demographic rates, which are often the targets of both basic and applied interest (e.g., White, Bruggeman, and Garrott 2007). Consequently, there is a need for addtional studies that explict quantify temporal variation in demographic rates and the resulting population dynamics, particularly for populations that have not been the subjects of intensive mark-recpature-style campaigns.

In this study, we analysed a multidecadal age-structured time series of arctic charr (*Salvelinus alpinus*) catch in Lake Mývatn, Iceland, to infer the time-varying demographic response of the population to reduced harvest in the wake of the fishery’s collapse. Arctic charr are salmonids with a circumpolar distribution and are basis of numerous commerical fisheries (Klemetsen et al. 2003). Moreover, arctic charr have important effects in many artic and boreal freshwater foodwebs owing to their roles as top consumers (Jeppesen et al. 2001; Klemetsen et al. 2003). In Mývatn, the charr sustained a large commerical fishery throughout much of the twentieth century that was subject to exploitation rates upwards of 80%, resulting in the fishery’s collapse by the late 1980s (Gubergsson 2004). A monitoring program was instituted in 1986 to monitor the population’s response to declining harvesting pressure over the next few decades, including catch restrictions imposed in the early 2000s.

Using these monitoring data, we parameterized an age-structured demographic model with time-varying recruitment and survival to charactreize the dynamics of the population. We modeled temporal variation in the demgoraphic rates as random walks, an approach that had previously been applied to infer population growth rates from non-structured abundance (Zeng et al. 1998) and for age-specific mortality rates inferred from fisheries stock assessments (Nielsen and Berg 2014). This method takes advantage of the entire time series for estimating the parameters while allowing them to vary smoothly through time. Furthermore, the model is able to characterize a range of dynamics including those arising from negative density-dependence and environmental perturbations. The latter may be particularly important in the case of the Mývatn’s charr, as the lake is subject to large fluctuations in primary and secondary production that may cascade up to the charr population (Á. Einarsson et al. 2004; Á. Einarsson and Örnólfsdóttir 2004; Gardarsson et al. 2004). Accordingly, the purpose of our analysis is to (a) characterize interannual variability in survival recruitment in Mývatn’s charr population and (b) determine whether directional trends in these demographic rates have resulted in the recovery of the population in the wake of its collapse.

# Methods

## *Study system*

Mývatn is located in northeastern Iceland (65°40’N 17°00’W) and has a tundra-subarctic climate. The lake spans , divided into north () and south () basins connected by a narrow channel (Á. Einarsson et al. 2004). Mývatn is shallow (south basin mean depth = 2.3m) and fed by nurient rich springs that sustain high benthic primary and secondary production. The latter comprises large but temporally variable populations of benthic invertebrates such as midges and cladocerans (Á. Einarsson and Örnólfsdóttir 2004; Gardarsson et al. 2004). The benthic invertebrates are in turn an important food source for Mývatn’s vertebrate populations, including Arctic charr, threespine stickleback (*Gasterosteus aculeatus*), brown trout (*Salmo trutta*), and waterfowl (Á. Einarsson et al. 2004).

While some arctic charr populations are anadromous, Mývatn’s population to resides strictly within the lake, despite a major outflow that connects the lake to the Greenland Sea (Gubergsson 2004). Spawning occurs in the fall among individuals aged 4 years and older. There are two charr morphs within Mývatn: “regular” (size at maturation of 35–50cm) and “dwarf” (20–25cm). However, the dwarf morph is restricted to a small and relatively isolated part of the south basin; therefore, the “regular” morph is the focus of this study. Gut content data reveal a diverse diet, including midges, snails, clams, zooplankton, benthic crustaceans, and sticklebacks. The large-bodied cladoceran Eurycercus is thought to be a particularly important prey item (Gubergsson 2004). While some charr populations are cannibalistic (Klemetsen et al. 2003), especially in the absence of other large-bodied prey (e.g., fish), the charr in Mývatn appear to lack cannibalism.

## Data

Systematic surveys of Mývatn’s Arctic charr have been conducted with gill nets every year from 1986-2017 by a single researcher (G. Gubergsson) using a consistent methodology. The surveys largely took place after the period of most dramatic population decline (Gubergsson 2004) and were intended to monitor the recovery of the population following its collapse. Twelve survey stations were sampled from around the lake, most of which were located in the south basin. Captured individuals were aged either by otoliths directly or with an estimate based on length. The surveys were conducted in fall (late August through September) of every year (just before spawning) and in June in a subset of years. For this analysis we used only the September data. Therefore, in our age classifications an individual of age “x” is an individual that survived to that age (e.g., an “age 1” individual was born in the previous fall). The oldest individuals in the data set were 12 years old, although observations of individuals older than 6 years are sparse (Figure [S1](#fig:p_cohort)). In Mývatn, charr reach maturity between 4 and 5 years of age, and therefore we grouped the older individuals into a single reproductive age class denoted “age 4+”.

## *Statistical analysis*

We characterized the demography of the charr population using an age-structured model (Caswell 2001) with time-varying demographic rates (Zeng et al. 1998; Nielsen and Berg 2014). The model projected the dynamics from one time step to the next as

where is a demographic projection matrix, and is an age-structured vector of scaled population densities (see description of scaling below) at time . The projection matrix was defined as

where is per capita recruitment and is the survival probability of age class . The model assumes that only age 4+ is and that individuals surviving beyond age 4 return to the age 4+ class.

Temporal variation in recruitment was modeled as a random walk on a log scale to ensure that the values remained positive:

where is the random walk step at time . The steps of the random walk followed a Gaussian distribution with mean of 0 and standard deviation (SD) of . Temporal variation in survival probability for age class was modeled analogously on a logit-scale:

with the same random walk SD used for all age classes to reduce the number of parameters fit by the model. Note that the “random walks” used to characterize the demographic parameters do not necessarily possess the statistical properties of true random walks (e.g., non-stationarity) as they are constrained by the data during model fitting. Rather, they provided a convenient means of allowing the parameters to vary smoothly through time. The random walk SDs for recruitment and survival characterized the degree of temporal variation in the respective processes.

We fit the model in a Bayesian framework, with likelihood

where is the annual catch for station and age class , is the age-specific catch rate (constrained between 0 and 1), and is a scaling factor introduced to improve computationally efficiency by preventing exessively large values of (such that itself is the population density scaled by ). The likelihood implies that the station-level abundance follows a Poisson distribution with a rate parameter equal to the lake-wide mean population density scaled by the catch rate for the corresponding age class. We assumed that the lake-wide population was well mixed across years, and while we did not attempt to account for systematic differences between stations; no such differences were apparent from visual inspection of the data (Figure [S2](#fig:p_sites); see discussion of potential overdispersion below). Estimating a separate catch rate for each age class allowed the model to account for systematic differences in catch rates as a function of age. Such differences are quite apparent in the data, as far too few first-year individuals were captured to account for the abundance subsequent ages, assuming a closed population. We used exponential priors with rate 1/50 for the initial scaled population densities for each age class, Gaussian priors with mean 0 and SD of either 5 or 1 for initial log-recruitment or logit-survival (repsectively), Gamma priors with shape and scale both of 1.5 for the random walk SDs, and Beta priors with shape parameters both of 2 for the catch rate. Priors were selected to be weakly informative regarding overall scale, while not acting strongly against the likelihood in the posterior fit.

To assess temporal trends in the demographic rates, we used generalized least squares (GLS) to fit lag-1 autoregressive models with linear year effects. Recruitment and survival probabilities were fit on their corresponding link scales (either log or logit), and survival probabilities were fit for each age class separately. We used a similar approach to estimate trends in the asymptotic population growth rate (log scale), caclulated as the leading eigenvalue of projection matrix . We performed this analysis on the asymptotic (as opposed to realized) growth rate as we were principally interersted in the effects of the underlying demographic rates per se; the realized growth rate would also have included transient fluctuations due to non-equilibrium age structure. For all GLS models, the response variables and year were z-scored (subtracted mean and divided by SD) so that coefficients could be interpreted as effects sizes; fitted values were then back-scaled for the figures.

The demographic model was fit using the statistical language Stan (Carpenter et al. 2017), with 4 chains, 3000 iterations, maximumum tree depth set to 13, and adapt delta set to 0.95. Convergence and quality of MCMC sampling were assessed using the diagnostics provided by Stan, incuding Rhat, the number of divergences, and the effective sample size. We used posterior medians as point esitmates and the bounds of 68% posterior quantiles as uncertainty intervals (hereafter ), matching the nominal coverage of standard errors. To gauge the degree to which the data were overdispersed relative the the model expectations, we simulated 90% prediction intervals from equation [[eq: likelihood]](#eq:likelihood) and compared the coverage of these intervals to the data. To assess the extent to which the data contained statistically meaningful information regarding temporal variation in the demographic rates, we compared the fit of the full model to a reduced model with the demographic rates fixed through time. We implemented the Stan model fitting with the rstan package (Stan Development Team 2020), performed GLS with the gls function from the nlme package (Pinheiro et al. 2020), and calculated the asymptotic growth rate with the demogR package (Jones 2007). All analysis were conducted in R 4.0.3 (R Core Team 2020).

# Results

The full model provided a good visual fit to the station-level catch data (Figure [1](#fig:p_catch)), with most of the temporal variation in lake-wide catch being captured by the model. The 90% prediction intervals provided reasonable coverage relative to the observed data, although the observations were zero-inflated in some years. While in principle it would be possible to account for such zero inflation in the model, it is unlikely that this would substantively alter the model inference. In contrast to the full model, the reduced model provided a poor fit to the data (Figure [S3](#fig:p_catch_reduced)), displaying damped oscillations that did not reflect the observed dynamics (Figure [S4)](#fig:p_dens_reduced). This was corroborated the median posterior log-likelihood calculated from equation (5), which was much higher for the full model (-4826) than for the reduced (-7314). According to the full model, the catch rates increased with age; the catch rate for age 1 individuals was around two orders of magnitude lower than for the other age classes (Table [1](#tab:param)). This is consistent with the expectation that age 1 individuals are generally too small to be captured by the gill nets used in the surveys.

Mývatn’s arctic charr population fluctuated substantially over the 3-decade time series (Figure [2](#fig:p_dens)), with the asymptotic population growth rate varying across an order of magnitude (Figure [3](#fig:p_lam)). This variation was underpinned by substantial variation in survival (Figure [4](#fig:p_surv)) and recruitment (Figure [5](#fig:p_rec)), both of which had random walk SDs with posterior densities concentrated away from zero (Table [1](#tab:param)). The SD for survival as larger than for recruitment, especially when the SDs were judged against the scales of their corresponding demographic processes. This indicates that survival was generally more variable than recruitment, a fact that was visually apparent from their respective time series (Figures [4](#fig:p_surv) and [5](#fig:p_rec)), especially for age 1 and age 3 survival.

The survival probabilities for all age classes increased through time, although only the trend for age 4+ was statistically unambiguous (Figure [4](#fig:p_surv); Table [2](#tab:gls)). Elevated age 4+ survival was associated with a steady increase in the catch of age 4+ individuals from 2005 onward (Figure [1](#fig:p_catch)). In contrast, per capita recruitment declined through time, consistent with declining age 1 catch, and this trend was stronger than for survival of any age class (Figure [5](#fig:p_rec); Table [2](#tab:gls)). Therefore, the positive effect of increased survival was potentially negated by the decline in recruitment. Indeed, the geometric mean of the population growth rate across years was very close to one (0.99 [0.970, 1.02]), indicating no long-term population change. Furthermore, there was no clear trend in the population growth rate itself, despite its large interannual fluctuations (Figure [3](#fig:p_lam); Table [2](#tab:gls)). The AR coefficients were moderately positive for most of the demographic parameters, except for age 2 survival and the population growth rate for which the AR coefficients were slightly negative. These negative coefficients potentially indicate overcompensatory dynamics, although this inference is quite tentative given their low magnitudes and absence of uncertainty estimates. Overall, the GLS results show that while the arctic charr population was very dynamic over the study period, it did not undergo meaningful directional change.

# Discussion

In this study, we used data from a multidecadal survey of arctic charr in Lake Mývatn to quantify the population’s demography and potential recovery following its collapse due to heavy exploitation (Gubergsson 2004). The survival probability of all age classes fluctuated substantially among years, with only adults showing an unambiguous positive trend over the course of the study period. In contrast, per capita recruitment clearly declined and experienced comparatively little variation around this trend. The countervailing changes in per capita recruitment and adult survival resulted in no directional change in the total population size or population growth rate, despite the rising number of adults. Rather, the dynamics of Mývatn’s charr population were dominated by large interannual variability and a shift towards a relatively older age distribution. In and of itself, the increase in adult survival is a positive signal for the population’s recovery, and it has been taken as such by the local stakeholders who have called for relaxing harvest restrictions in recent years. However, persistently low recruitment provides a cautionary note that should be taken into consideration in formulating a management strategy.

A crucial step for projecting the future dynamics of Mývatn’s charr population is identifying the underlying causes for the decline in per capita recruitment. Food web interactions have been identified as an important source of fluctuations in other charr populations (Snorrason et al. 1992; Amundsen 1994; Jonsson and Setzer 2015). Mývatn is characterized by dramatic fluctuations in the abundance of primary food sources for juvenile charr, particularly benthic crustaceans and midges (Á. Einarsson and Örnólfsdóttir 2004; Gardarsson et al. 2004; Gubergsson 2004). Furthermore, there is substantial spatial heterogeneity in the abundance of these aquatic invertebrates (Bartrons et al. 2015) which might disproportionately inhibit young juveniles that have more restricted mobility than the larger age classes. The large fluctuations in aquatic invertebrates are associated various consumer species in addition to charr, including sticklebacks and brown trout that could serve as competitors for young charr, and piscivorous waterfowl that could serve as predators (Á. Einarsson et al. 2004). In addition to biotic factors, temperature has received much attention as a driver of charr populations (Winfield, Fletcher, and James 2008; Elliott and Elliott 2010; Jonsson and Setzer 2015), given their distribution restricted to arctic and cold-temperature lakes (Klemetsen et al. 2003) and the ubiquity anthropogenic climate change. While climate warming has not yet become an obvious ecological driver at Mývatn, it is nonetheless possible that temperature changes have adversely affected recruitment in Mývatn’s charr population as has been seen in other Icelandic lakes (Malmquist et al. 2009).

This study provides a demographic assessment of a population of arctic charr in a single lake, but it reinforces themes that have broad and increasing interest in applied ecology. Harvest-induced shifts in age structure have been documented in other fisheries, typically resulting in “truncation” of the oldest age classes that are typically the targets of harvest efforts (Hsieh et al. 2010). Suppression of adult abundance is expected to have deleterious effects on populations, with the corollary that relaxation of harvest should allow populations to recover following overexploitation. However, this will only be true if juvenile recruitment is sufficient to sustaining the population’s recovery. Recruitment in fish populations has long been recognized as highly variable and difficult to predict owing to the interplay of numerous biotic and abiotic factors (Dixon, Milicich, and Sugihara 1999; Houde 2008; Ludsin, DeVanna, and Smith 2014). This poses a particular challenge for management efforts, as complex suites of ecological factors are both difficult to understand and difficult to regulate, particularly in comparison to a direct anthropogenic driver such as harvest (Beamish and Mahnken 1999; Link 2002). The extent to which this is true for Mývatn’s arctic charr is currently unknown. Nonetheless, the countervailing trends in survival and recruitment in the wake of alleviated of harvesting pressure underscore the potential for heterogeneous demographic responses to management efforts due to the complex ecological context in which such efforts take place.

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**Table 1.** Posterior summaries of the parameters from the demographic model. Catch rates are dimensionless and constrained between 0 and 1, while the random walk SD are on the scale of either logit-survival or log-recruitment and constrained to be >0. Uncertainty intervals are based on 68% quantiles, matching the nominal coverage of standard errors.

|  |  |  |
| --- | --- | --- |
| Model parameter |  | Posterior median [UI68%] |
| catch rate | age 1 | 0.001 [0.0006, 0.002] |
|  | age 2 | 0.08 [0.05, 0.13] |
|  | age 3 | 0.48 [0.32, 0.67] |
|  | age 4+ | 0.66 [0.48, 0.83] |
| random walk SD | survival probability | 2.03 [1.79, 2.30] |
|  | recruitment capita^-1 | 1.45 [1.25, 1.70] |

**Table 2.** Coefficients and standard errors (SE) from the GLS models quantifying linear trends in the demographic rates through time. The models were fit on either a log (recruitment; population growth rate) or logit (survival probability) scale, and all response and predictor variables were z-scored prior to model fitting. Therefore, the coefficients can be compared as effect sizes across all of the response variables. The autoregressive (AR) coefficients were included to account for temporal autocorrelation when estimating the year trends; 0 indicates no autocorrelation, while |1| indicates strong (positive or negative) autocorrelation and statistical non-stationarity.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Response variable |  | Intercept (± SE ) | Year slope (± SE ) | AR coefficient |
| survival probability | age 1 | 0.01 ± 0.23 | 0.26 ± 0.23 | 0.26 |
|  | age 2 | 0.00 ± 0.15 | 0.13 ± 0.15 | -0.18 |
|  | age 3 | 0.04 ± 0.54 | 0.25 ± 0.44 | 0.80 |
|  | age 4+ | -0.02 ± 0.26 | 0.55 ± 0.25 | 0.53 |
| recruitment capita^-1 |  | -0.06 ± 0.29 | -0.71 ± 0.27 | 0.56 |
| population growth rate |  | 0.00 ± 0.15 | 0.08 ± 0.15 | -0.21 |

[fig:p_catch] Station-level catch (points) and 90% posterior prediction intervals (shading) from the demographic model. The prediction intervals include stochasticity arising from the Poisson sampling process, and therefore represent the predicted distribution of catch according to the model. The solid lines are medians of the the prediction distributions and quantify the expected catch; note that this is not the same quantity as the estimated population density, shown in Figure 2. The y-axis is log+1 transformed to accommodate zeros. 

**Figure 1.** Station-level catch (points) and 90% posterior prediction intervals (shading) from the demographic model. The prediction intervals include stochasticity arising from the Poisson sampling process, and therefore represent the predicted distribution of catch according to the model. The solid lines are medians of the the prediction distributions and quantify the expected catch; note that this is not the same quantity as the estimated population density, shown in Figure [2](#fig:p_dens). The y-axis is log+1 transformed to accommodate zeros.

[fig:p_dens] Average population density across stations (solid line) inferred from the demographic model. Shading depicts 68% uncertainty intervals, matching the nominal coverage of standard errors. The y-axis is log transformed. 

**Figure 2.** Average population density across stations (solid line) inferred from the demographic model. Shading depicts 68% uncertainty intervals, matching the nominal coverage of standard errors. The y-axis is log transformed.

[fig:p_lam] Asymptotic population growth rate (solid blue line) inferred from the demographic model. Shading depicts 68% uncertainty intervals, matching the nominal coverage of standard errors. The dashed horizontal line indiates a growth rate of 1, which corresponds to no change in the population size from one time step to the next. The solid black line represents the fitted values from the GLS model fit on a log-scale and then back-transformed to match the scale of the population growth rate. Note however, that the y-axis of the figure is log-transformed, thereby preserving the linearity of the data and model fit. 

**Figure 3.** Asymptotic population growth rate (solid blue line) inferred from the demographic model. Shading depicts 68% uncertainty intervals, matching the nominal coverage of standard errors. The dashed horizontal line indiates a growth rate of 1, which corresponds to no change in the population size from one time step to the next. The solid black line represents the fitted values from the GLS model fit on a log-scale and then back-transformed to match the scale of the population growth rate. Note however, that the y-axis of the figure is log-transformed, thereby preserving the linearity of the data and model fit.

[fig:p_surv] Logit-survival probability (solid colored lines) inferred from the demographic model. Shading depicts 68% uncertainty intervals, matching the nominal coverage of standard errors. The solid black line represents the fitted values from the GLS models fit separately for each age class. Note that logit-survival probability ranging from -5 to 5 corresponds to actual survival probability ranging from 0.007 to 0.993. 

**Figure 4.** Logit-survival probability (solid colored lines) inferred from the demographic model. Shading depicts 68% uncertainty intervals, matching the nominal coverage of standard errors. The solid black line represents the fitted values from the GLS models fit separately for each age class. Note that logit-survival probability ranging from -5 to 5 corresponds to actual survival probability ranging from 0.007 to 0.993.

[fig:p_rec] Log-recruitment \text{capita}^{-1} (solid blue line) inferred from the demographic model. Shading depicts 68% uncertainty intervals, matching the nominal coverage of standard errors. The solid black line represents the fitted values from the GLS models. Note that log-recruitment \text{capita}^{-1} ranging from -1 to 8 corresponds to actual log-recruitment \text{capita}^{-1} ranging from 0.4 to 3000. 

**Figure 5.**  Log-recruitment (solid blue line) inferred from the demographic model. Shading depicts 68% uncertainty intervals, matching the nominal coverage of standard errors. The solid black line represents the fitted values from the GLS models. Note that log-recruitment ranging from -1 to 8 corresponds to actual log-recruitment ranging from 0.4 to 3000.

[fig:p_cohort] Survey catch as a function of age, with each line corresponding to a unique cohort. 

**Figure S1.** Survey catch as a function of age, with each line corresponding to a unique cohort.

[fig:p_sites] Station-level catch through time, with stations shown in different colors. 

**Figure S2.** Station-level catch through time, with stations shown in different colors.

[fig:p_catch_reduced] Station-level catch (points) and 90% posterior prediction intervals (shading) from the reduced version of the demographic model with survival and recruitment fixed through time. The prediction intervals include stochasticity arising from the Poisson sampling process, and therefore represent the predicted distribution of catch according to the model. The solid lines are medians of the the prediction distributions and quantify the expected catch; note that this is not the same quantity as the estimated population density, shown in Figure 9. The y-axis is log+1 transformed to accommodate zeros. 

**Figure S3.** Station-level catch (points) and 90% posterior prediction intervals (shading) from the reduced version of the demographic model with survival and recruitment fixed through time. The prediction intervals include stochasticity arising from the Poisson sampling process, and therefore represent the predicted distribution of catch according to the model. The solid lines are medians of the the prediction distributions and quantify the expected catch; note that this is not the same quantity as the estimated population density, shown in Figure [9](#fig:p_dens_reduced). The y-axis is log+1 transformed to accommodate zeros.

[fig:p_dens_reduced] Average population density across stations (solid line) inferred from the reduced version of the demographic model with survival and recruitment fixed through time. Shading depicts 68% uncertainty intervals, matching the nominal coverage of standard errors. The y-axis is log transformed. 

**Figure S4.** Average population density across stations (solid line) inferred from the reduced version of the demographic model with survival and recruitment fixed through time. Shading depicts 68% uncertainty intervals, matching the nominal coverage of standard errors. The y-axis is log transformed.