

# **ARTICLE**

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

Joseph S. Phillips, Guðni Guðbergsson, and Anthony R. Ives

Abstract: Quantifying temporal variation in demographic rates is a central goal of population ecology. In this study, we analyzed a multidecadal age-structured time series of Arctic char (Salvelinus alpinus) abundance 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 capita recruitment consistently declined over most of the study period, until the final three years when it began to increase. The countervailing demographic trends resulted in only limited directional change in the total population size and population growth rate. Rather, the population dynamics were dominated by large interannual variability and a shift towards an older age distribution. Our results are indicative of a slow recovery of the population after its collapse, despite the rising number of adults following relaxed harvest. This underscores the potential for heterogeneous demographic responses to management efforts due to the complex ecological context in which such efforts take place.

Résumé: La quantification des variations temporelles de taux démographiques est un des objectifs centraux de l'écologie des populations. Nous avons analysé une série chronologique multidécennale de l'abondance des ombles chevaliers (Salvelinus alpinus) dans le lac Mývatn (Islande) afin d'inférer la réaction démographique de la population en fonction du temps à la réduction des prises dans la foulée de l'effondrement de la ressource. Notre analyse démontre que, alors que la probabilité de survie des adultes augmente suivant la diminution de la pression de pêche, le recrutement par individu a connu une baisse soutenue durant presque toute la période à l'étude, jusqu'aux trois dernières années, où le début d'une augmentation est observé. Les tendances démographiques compensatoires ne se sont traduites qu'en des changements directionnels limités de la taille totale de la population et de son taux de croissance. La dynamique de la population est plutôt dominée par une importante variabilité interannuelle et une transition vers des âges plus grands. Nos résultats indiquent un lent rétablissement de la population après son effondrement, malgré l'augmentation du nombre d'adultes qui a suivi la diminution des prises. Cela fait ressortir la possible hétérogénéité des réactions démographiques aux efforts de gestion en raison du contexte écologique complexe dans lequel ces efforts s'insèrent. [Traduit par la Rédaction]

# Introduction

Quantifying temporal variation in demographic rates is a central goal of population ecology, because 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 the characterization of directional trends in demographic rates requires data spanning many years and often relies on intensive mark-recapture (and related) approaches for statistical inference (e.g., Forcada et al. 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 et al. 2007). Consequently, there is a need for additional studies that explicitly quantify temporal variation in demographic rates and the resulting population dynamics, particularly for populations that have not been the subjects of intensive mark-recapturestyle campaigns.

In this study, we analyzed a multidecadal age-structured time series of Arctic char (*Salvelinus alpinus*) abundance 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 char are salmonids with a circumpolar distribution and are the targets of numerous commercial fisheries (Klemetsen et al. 2003). Moreover, Arctic char have important effects in many Arctic and boreal freshwater food webs owing to their roles as top consumers (Jeppesen et al. 2001; Klemetsen et al. 2003). In Mývatn, the char sustained a large commercial fishery throughout much of the twentieth century that was subject to annual exploitation rates upwards of 80%, preceding the fishery's collapse by the late 1980s (Guðbergsson 2004). This collapse led to catch restrictions imposed in the early 2000s. A portion of the lake was also dredged during this period, which may have indirectly contributed to the decline of the fishery through depressed prey availability (Einarsson et al. 2004). A monitoring program was instituted in 1986 to track the population's dynamics in the wake of these ecological perturbations. This monitoring was conducted by one of the authors (GG) using the same methods and sampling locations within the lake for the entire time series, providing a valuable opportunity to quantify long-term demographic changes in the population.

Using these monitoring data, we parameterized an age-structured demographic model with time-varying recruitment and survival to

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J.S. Phillips. Department of Aquaculture and Fish Biology, Hólar University, Skagafjörður, Iceland; Department of Integrative Biology, University of Wisconsin, Madison, Wisconsin, USA.

G. Guðbergsson. Marine and Freshwater Research Institute, Hafnarfjörður, Iceland.

A.R. Ives. Department of Integrative Biology, University of Wisconsin, Madison, Wisconsin, USA.

Corresponding author: Joseph S. Phillips (email: joseph@holar.is).

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characterize the dynamics of the population. We modeled temporal variation in the demographic rates as random walks, an approach that had previously been applied to infer population growth rates from nonstructured abundance (Zeng et al. 1998; Ives and Dakos 2012) 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 (Ives and Dakos 2012). The latter may be particularly important in the case of the Mývatn's char, because the lake is subject to large fluctuations in primary (Phillips 2020; McCormick et al. 2021) and secondary (Einarsson and Örnólfsdóttir 2004; Gardarsson et al. 2004) production that may cascade up to the char population. Accordingly, the purpose of our analysis is to (i) characterize interannual variability in survival and recruitment and (ii) determine whether directional trends in these demographic rates have resulted in the recovery of the population in the wake of its collapse.

#### Materials and methods

# Study system and data

Mývatn is located in northeastern Iceland (65°40'N, 17°00'W) and has a tundra-subarctic climate (Björnsson and Jónsson 2004; Einarsson et al. 2004). The lake spans 37 km<sup>2</sup>, divided into north (Ytrifloi: 8 km²) and south (Syðrifloi: 29 km²) basins connected by a narrow channel (Einarsson et al. 2004). Mývatn is shallow (south basin mean depth = 2.3 m) and fed by nutrient-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 (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 char, threespine stickleback (Gasterosteus aculeatus), brown trout (Salmo trutta), and waterfowl (Einarsson et al. 2004). The north basin was historically dredged (1967–2003), which likely affected many populations in the lake, although such effects are poorly understood (Einarsson et al. 2004).

While some Arctic char populations are anadromous, Mývatn's population appears to reside strictly within the lake; there is a major outflow that connects the lake to the Greenland Sea, but natural barriers prevent individuals from entering the lake from downriver (Guðbergsson 2004). There are two char morphs within Mývatn: pelagic (size at maturation of 35-50 cm) and small benthic (20–25 cm). However, the small benthic morph is restricted to a small and relatively isolated part of the south basin fed by cold springs (Guðbergsson 2004); therefore, the pelagic morph is the focus of this study. Gut content data reveal a diverse diet, including midges, snails, clams, zooplankton, benthic crustaceans, and sticklebacks as the main prey species. The large cladoceran Eurycercus lamellatus is thought to be a particularly important prey item (Guðbergsson 2004). Some char populations are cannibalistic (Klemetsen et al. 2003), especially in the absence of other large prey (e.g., fish). However, the char in Mývatn appear to lack cannibalism based on gut content data (Guðbergsson 2004).

Systematic surveys of Mývatn's Arctic char have been conducted with monofilament gill nets every year from 1986–2020 by a single researcher (GG) using a consistent methodology. A series of mesh sizes (16.5, 18.5, 21.5, 25, 30, 35, 40, 46, and 50 mm) was used to capture individuals over a large size range; smaller nets to target young-of-the-year were not used to avoid stickleback by-catch. Fish were collected under a permit from the Icelandic Directorate of Fisheries; Icelandic law does not require animal care review for collection of fish specimens from the wild. The surveys largely took

place after the period of most dramatic population decline (Guðbergsson 2004) and were intended to monitor the recovery of the population following its collapse. Twelve survey stations were sampled from around the lake, ten of which were in the south basin; two of the south basin stations were aggregated for the purpose this analysis due to their close proximity to each other. Captured individuals were aged either by otoliths directly (78%; Jonsson 1976) or by length using the length distribution of otolith-aged individuals (22%). Guðbergsson (2004) found very limited overlap in length distributions for individuals aged from 1 to 6 based on otoliths. While age estimates based on otoliths or length have some uncertainty (Campana 1990), they should be sufficiently accurate to provide a gross categorization of the number of individuals in different age classes. The surveys were conducted in fall (late August through September) of every year before spawning and also in June in a subset of years. For this analysis we used only the August-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 hatched in the previous fall). The oldest individuals in the data set were 12 years old, although observations of individuals older than 4 years are sparse relative to the younger age classes (Supporting Information: Fig. S1<sup>1</sup>). Furthermore, char in Mývatn reach maturity at 4–5 years of age and typically spawn multiple times after maturity. Therefore, we grouped the older individuals into a single reproductive age class denoted "age 4+".

#### Demographic model

We characterized the demography of the char population using an age-structured model (Caswell 2001) with time-varying demographic rates (Zeng et al. 1998; Ives and Dakos 2012; Nielsen and Berg 2014). The model projected the dynamics from one time step to the next as

$$\mathbf{x}_t = \mathbf{P}_{t-1} \mathbf{x}_{t-1}$$

where  $\mathbf{P}_t$  is a demographic projection matrix, and  $\mathbf{x}_t$  is an agestructured vector of population densities at time t (Caswell 2001). The projection matrix was defined as

$$\mathbf{P}_{t} = \begin{bmatrix} 0 & 0 & 0 & \rho_{t} \\ \phi_{1,t} & 0 & 0 & 0 \\ 0 & \phi_{2,t} & 0 & 0 \\ 0 & 0 & \phi_{3,t} & \phi_{4,t} \end{bmatrix}$$

where  $\rho_t$  is per capita recruitment, and  $\phi_{i,t}$  is the survival probability of age class i. The model includes only four age classes, and individuals surviving beyond age 4 return to the age 4+ class. While reproductive output likely varies with age or biomass beyond sexual maturity, per capita recruitment can be interpreted as the average reproductive output for all individuals in the reproductive class. Modeling interannual variation in per capita recruitment (as described in the following paragraph) allows the model to capture variation due to a wide variety of sources, including the age- or size-structure of the reproductive class.

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

$$\begin{array}{ll} \rho_t = \exp(\chi_t) \\ \chi_t = \chi_{t-1} + \epsilon_{\rho,t} \\ \epsilon_{\rho,t} \sim \operatorname{Gaussian}(0,\sigma_\rho) \end{array}$$

where  $\epsilon_{\rho,t}$  is the random walk step at time t. The steps of the random walk followed a Gaussian distribution with mean of 0 and standard deviation (SD) of  $\sigma_{\rho}$ . Temporal variation in survival

<sup>&</sup>lt;sup>1</sup>Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2021-0161.

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probability for age class i was modeled analogously on a logit scale:

$$\begin{aligned} \phi_{i,t} &= \text{logit}^{-1}(\gamma_{i,t}) \\ \gamma_{i,t} &= \gamma_{i,t-1} + \epsilon_{\phi,i,t} \\ \epsilon_{\phi,i,t} &\sim \text{Gaussian}(0,\sigma_{\phi,i}) \end{aligned}$$

Note that the "random walks" were constrained by the data during model fitting, providing a convenient means of allowing the parameters to vary smoothly through time in accordance with the data (Zeng et al. 1998; Ives and Dakos 2012). The random walk SDs for recruitment and survival characterize the degree of temporal variation in the respective processes.

We fit the model in a Bayesian framework with a zero-inflated Poisson likelihood:

(5) 
$$\mathcal{L} = \prod_{s,i,t} \begin{cases} \theta + (1-\theta) \times Poisson(0|\kappa_i \times x_{i,t}) & \text{if } y_{s,i,t} = 0\\ (1-\theta) \times Poisson(y_{s,i,t}|\kappa_i \times x_{i,t}) & \text{if } y_{s,i,t} > 0 \end{cases}$$

where  $y_{s,i,t}$  is the annual survey catch for station s and age class i,  $\kappa_i$  is the relative sampling efficiency for different age classes (constrained between 0 and 1), and  $\theta$  is the probability of zero catch from a Bernoulli sampling processes (zero-inflation rate). The likelihood implies that the station-level abundance follows a zero-inflated Poisson distribution with a rate parameter equal to the lake-wide mean population density scaled by the relative sampling efficiency for the corresponding age class. We assumed that the lake-wide population was well-mixed across years, which is supported by a mark-recapture study showing that individuals tagged at spawning grounds were recovered in all parts of the lake (Guðbergsson 1991; technical report of the Icelandic Institute of Freshwater Fisheries). Moreover, while we did not attempt to account for systematic differences between stations, no such differences were consistently apparent from visual inspection of the data (Supporting Information: Fig. S2<sup>1</sup>). Estimating a separate sampling efficiency for each age class allowed the model to account for systematic differences in relative sampling efficiency as a function of age. Such differences were visually apparent in the data, as far too few first-year individuals were captured to account for the abundance of subsequent ages assuming a closed population (Supporting Information: Fig. S1<sup>1</sup>). Note that zero-inflation is independent of age-specific variation in relative sampling efficiency and is best understood as the consequence of processes unrelated to age- or size-specific sampling efficiency.

During model fitting, we divided  $x_{i,t}$  by 100 to improve computational efficiency by avoiding excessively large values; we then back-scaled the estimates for  $x_{i,t}$  in reporting the results. 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 (respectively), Gamma priors with shape and scale both set to 1.5 for the random walk SDs, and Beta priors with shape parameters both set to 2 for the relative sampling efficiency and zero-inflation rate. The overall scales of these priors were weakly informative relative to the scales of the corresponding parameters. The Gamma priors were unimodal, concave-down near zero, and had zero density at zero, allowing the resulting posteriors to be arbitrarily close to zero while not being drawn towards zero by the prior. The Beta priors were unimodal and concave-down, with a mode at 0.5.

The demographic model was fit using the statistical language Stan (Carpenter et al. 2017), with 4 chains, 2000 iterations, maximum tree depth set to 14, and adapt delta set to 0.95. Convergence and quality of MCMC sampling were assessed using the diagnostics provided by Stan, including the potential scale reduction factor  $(\hat{R})$ , the number of divergences, and the effective sample size. We initially attempted to fit the model with separate SDs for the survival random-walk  $(\sigma_{\phi,i})$  for each age class. However, this resulted in

inefficient MCMC sampling of  $\sigma_{\phi,i}$  as judged by the effective sample size and  $\hat{R}$ . Therefore, we refit the model with a single SD (i.e.,  $\sigma_{\phi}$ ) for all age classes. This resulted in a minor difference in the posterior log-likelihood calculated from eq. 5 between the model with age-specific  $\sigma_{\phi,i}$  (–4063) versus a single  $\sigma_{\phi}$  (–4065). Hereinafter, we only present results from the latter.

We used posterior medians as point estimates and the bounds of 68% posterior quantiles as uncertainty intervals (hereinafter  $\rm UI_{68\%}$ ), matching the nominal coverage of standard errors. To gauge the degree to which the data were overdispersed relative to the model expectations, we simulated 90% prediction intervals from eq. 5 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 model with time-varying rates to a reduced model with the demographic rates fixed through time.

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), calculated as the leading eigenvalue  $\lambda_t$  of projection matrix  $P_t$  (Caswell 2001). We performed this analysis on the asymptotic (as opposed to realized) growth rate because we were primarily interested 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 (Caswell 2001). For all GLS models, the response variables and year were z-transformed (subtracted mean and divided by SD) so that coefficients could be interpreted as effect sizes; fitted values were then back-transformed for the figures.

Our model was formulated to allow the demographic rates to vary flexibly through time due to unspecified drivers for the sake of characterizing general demographic trends. However, variation in demographic rates as a function of population density itself (e.g., through intraspecific competition) is of particular interest because density dependence can lead to an array of complex population dynamics (Turchin 2003). In the context of fisheries, it is common to characterize density dependence in the form of stock–recruitment curves, which relate total recruitment to either the total population size or the size of the spawning stock (Ricker 1954). To assess the density dependence of recruitment in Mývatn's char population, we fit a stock–recruitment curve to characterize total annual recruitment as a function of population density as inferred from our demographic model. We used the classic Ricker model, which has the following form on a log-scale:

6) 
$$\log(\text{recruitment}) = \alpha + \log(\text{population density})$$
 
$$-\frac{1}{\beta} \times \text{ population density}$$

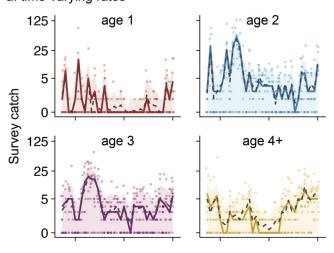
where  $\alpha$  is the rate of increase in recruitment with population density when density is near zero, and  $\beta$  is the population density at which recruitment is maximized; lower values of  $\beta$  indicate stronger intraspecific competition. We calculated overall recruitment by multiplying per capita recruitment by the density of the adult age class for each year. To characterize the stock, we used the total population density of all age classes, rather than just the reproductive class, to capture potential competition between new recruits and other immature individuals.

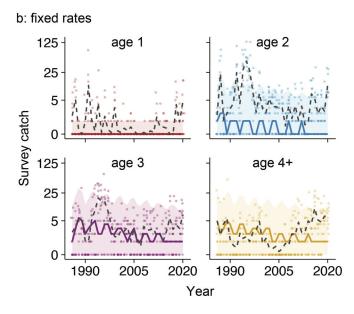
All analyses were conducted in R 4.0.3 (R Core Team 2020). We used Stan via the rstan package (Stan Development Team 2020) to fit the demographic model. The asymptotic growth rate was calculated with the demogR package (Jones 2007). We performed GLS with the gls function from the nlme package (Pinheiro et al. 2020).

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Fig. 1. Observed survey data and posterior predictive distributions from (a) the model including temporal variation in survival and recruitment and (b) the reduced model with survival and recruitment fixed through time. Points indicate observed station-level catch, and the dashed lines indicate mean catch across stations. The prediction intervals (shading) have nominal coverage of 90% and include stochasticity arising from the zero-inflated Poisson sampling process. The solid lines are medians of the posterior predictive distributions and quantify the expected catch across sites; note that this is not the same quantity as the estimated population density shown in Fig. 2 and Supporting Information (Fig. S3¹) for the time-varying and fixed rates models, respectively. The y axis is on a log + 1 scale to accommodate zeros. [Colour online.]

## a: time-varying rates





Finally, we used the nls function from the native stats package to fit the stock–recruitment curve.

### Results

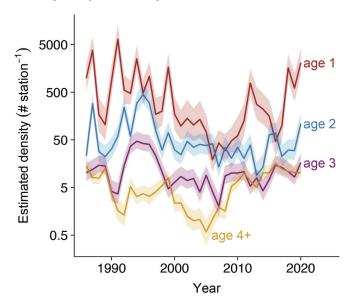
The full model provided a good visual fit to the station-level catch data (Fig. 1a), with most of the temporal variation in lakewide catch being well characterized by the model. Moreover, the 90% prediction intervals provided reasonable coverage relative to the observed data. In contrast to the model with time-varying

**Table 1.** Posterior summaries of the parameters from the demographic model.

Model parameter		Posterior median [UI <sub>68%</sub> ]
Relative sampling efficiency	Age 1	0.003 [0.001, 0.005]
	Age 2	0.13 [0.08, 0.19]
	Age 3	0.47 [0.30, 0.66]
	Age 4+	0.66 [0.46, 0.83]
Zero-inflation rate		0.34 [0.32, 0.35]
Random walk SD	Survival probability	1.94 [1.71, 2.23]
	Recruitment per capita	1.45 [1.25, 1.68]

**Note:** Catch rates are dimensionless and constrained between 0 and 1, while the random walk SDs are on the scale of either logit-survival or log-recruitment and constrained to be positive. Uncertainty intervals (UIs) are based on 68% quantiles, matching the nominal coverage of standard errors. Initial values for the random walks and age-specific population density are not shown in this table but can be seen in the corresponding figures.

**Fig. 2.** Average population density across stations (solid lines) inferred from the demographic model. Shading depicts 68% uncertainty intervals, matching the nominal coverage of standard errors. The *y* axis is on a log scale. [Colour online.]

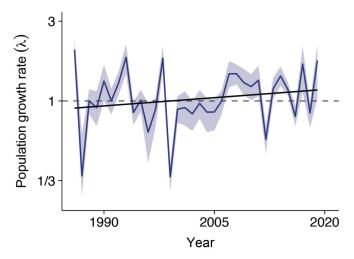


rates, the reduced model without time-varying parameters provided a poor fit to the data (Fig. 1b), displaying damped oscillations that did not reflect the observed dynamics (Supporting Information: Fig. S3¹). This was corroborated by the median posterior log-likelihood calculated from eq. 5, which was much higher for the time-varying model (–4065) than for the fixed-rates model (–6075). According to the time-varying model, the relative sampling efficiencies increased with age; the sampling efficiency for age 1 individuals was around two orders of magnitude lower than for the other age classes (Table 1). 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.

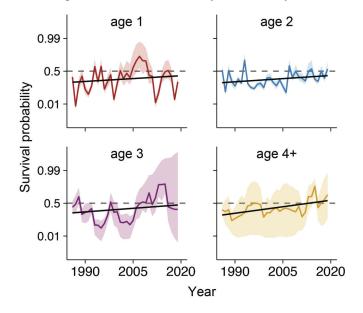
Mývatn's Arctic char population fluctuated substantially over the 3-decade time series (Fig. 2), with the asymptotic population growth rate varying across nearly an order of magnitude (Fig. 3). This variation was underpinned by substantial variation in survival (Fig. 4; Supporting Information: Fig. S4¹) and recruitment (Fig. 5), both of which had random walk SDs with posterior densities concentrated away from zero (Table 1). The survival probabilities for all age classes increased through time, although only the trend for age 4+ was statistically unambiguous (Fig. 4; Table 2).

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**Fig. 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 indicates 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 generalized least squares (GLS) model fit on a log scale and then back-transformed to the natural scale. Note, however, that the *y* axis is on a log scale, thereby preserving the linearity of the data and model fit. [Colour online.]

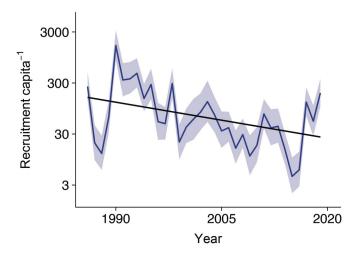


**Fig. 4.** Survival probability (solid coloured lines) inferred from the demographic model. Shading depicts 68% uncertainty intervals, matching the nominal coverage of standard errors. The solid black line represents the fitted values from the GLS models fit on a logit scale for each age class separately and then back-transformed to the natural scale. Note, however, that the *y* axis is on a logit scale, thereby preserving the linearity of the data and model fit. See Supporting Information (Fig. S4<sup>1</sup>) for the survival probability estimates plotted on the natural scale. [Colour online.]

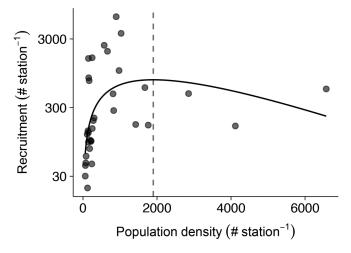


Elevated age 4+ survival was associated with a steady increase in the survey catch of age 4+ individuals from 2005 onward (Fig. 1). In contrast, per capita recruitment declined over most of the time series, consistent with declining age 1 survey catch (Fig. 5; Table 2).

**Fig. 5.** Recruitment per capita (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 model fit on a log scale and then back-transformed to the natural scale. Note, however, that the *y* axis is on a log scale, thereby preserving the linearity of the data and model fit. [Colour online.]



**Fig. 6.** Stock–recruitment relationship, with recruitment and population density inferred from the demographic model (points). The solid line shows the fit of the Ricker model, and the dashed vertical line indicates the population density at which recruitment is maximized ( $\beta$  = 1899). The y axis is on a log scale.



However, per capita recruitment increased in the most recent three years, again corresponding with the age 1 survey catch. The positive effect of increased survival was largely negated by the decline in recruitment. Indeed, the geometric mean of the population growth rate across years was very close to one (posterior median [UI<sub>683</sub>] = 1.021 [0.997, 1.046]), indicating no long-term population change. Furthermore, the trend in the population growth rate itself was only slightly positive and statistically ambiguous, especially when judged against its large interannual fluctuations (Fig. 3; Table 2). Overall, these results show that while the size of the Arctic char population was variable over the study period, it did not undergo meaningful directional change.

The AR coefficients estimated from the GLS fits were moderately positive for most of the demographic parameters, except

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**Table 2.** Coefficients and standard errors (SE) from the GLS models quantifying linear trends in the demographic rates through time.

Response variable		Intercept (±SE)	Year slope (±SE)	AR coefficient
logit survival probability	Age 1	$0.00 \pm 0.27$	$0.15 \pm 0.26$	0.41
	Age 2	-0.01 $\pm$ 0.15	$0.27\pm0.16$	-0.10
	Age 3	$0.01\pm0.53$	$0.19 \pm 0.43$	0.80
	Age 4+	$0.04\pm0.25$	$0.57\pm0.24$	0.49
log recruitment per capita		$0.05\pm0.26$	$-0.39 \pm 0.25$	0.45
log population growth rate		$-0.02 \pm 0.13$	$0.18 \pm 0.13$	-0.27

Note: 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-transformed prior to model fitting. Therefore, the coefficients can be compared as effect sizes across all of the response variables. Note that the "intercepts" give the predicted mean value of the response, which should be essentially zero due to the z-transform. Therefore, these intercepts are not of interest per se and are reported only for completeness. 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 nonstationarity.

for the population growth rate (and to a lesser extent age 2 survival) for which the AR coefficient was moderately negative. The latter implies overcompensatory dynamics, in which high values in one year predict low values in the next. This is consistent with the dynamics implied by the stock–recruitment curve, which generally follows the classic Ricker form ( $\alpha=0.087$  and  $\beta=1899$ ) and indicates negative density dependence in recruitment (Fig. 6). However, there is much variation in total recruitment not accounted for by the stock–recruitment curve, which underscores the importance of other sources of variability.

#### **Discussion**

In this study, we used data from a multidecadal survey of Arctic char in Lake Mývatn to quantify the demographic changes and potential recovery of the population following its collapse (Guðbergsson 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 declined substantially and experienced comparatively little variation around this trend until an increase over the most recent three years. The countervailing changes in per capita recruitment and adult survival resulted in essentially no directional change in overall population size and only a very limited increase in the population growth rate, despite the rising number of adults. Rather, the dynamics of Mývatn's char population were dominated by large interannual variability and a shift towards a relatively older age distribution. The somewhat elevated recruitment in recent years, alongside relatively high adult survival, does suggest that the population may in fact be recovering. However, any such recovery appears to be in its early stages and has taken several decades to manifest. Therefore, recent calls from local stakeholders to relax harvest restrictions in response to increased adult survival should be tempered by caution until the population's recovery has been more clearly established.

A crucial step for projecting the future dynamics of Mývatn's char population is identifying the underlying causes for the decline in per capita recruitment. The stock–recruitment relationship indicates that negative density dependence has inhibited the recovery of recruitment, although there is substantial unexplained variation. Food-web interactions have been identified as an important source of fluctuations in other char 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 char, particularly benthic crustaceans and midges (Einarsson and Örnólfsdóttir 2004; Gardarsson et al. 2004; Guðbergsson 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 larger individuals. The fluctuations in aquatic invertebrates are associated with fluctuations in populations of other consumer species in addition to char, including threespine stickleback and brown trout that could serve as competitors with young char and piscivorous waterfowl that could serve as predators (Einarsson et al. 2004). In addition to biotic factors, temperature has received much attention as a driver of char populations (Winfield et al. 2008; Elliott and Elliott 2010; Gerdeaux 2011; Jonsson and Setzer 2015), given their distribution restricted to Arctic and cold-temperature lakes (Klemetsen et al. 2003) and the ubiquity of 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 char population as has been seen in other lakes in Iceland and Scandinavia (Malmquist et al. 2009; Svenning et al. 2022).

This study provides a demographic assessment of a population of Arctic char 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 sustain 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 et al. 1999; Houde 2008; Ludsin et al. 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 char is currently unknown. Nonetheless, the countervailing trends in survival and recruitment in the wake of alleviated harvesting pressure underscore the potential for heterogeneous demographic responses to management efforts due to the complex ecological context in which such efforts take place.

#### Contributors' statement

GG conducted the surveys of Mývatn's Arctic char population, with contributions from staff of the Marine and Freshwater Research Institute. JSP conducted the analyses, with input from ARI. JSP wrote the first draft of the paper, with substantial contributions from all authors to subsequent drafts.

### Data and code availability statement

Data and code are available on FigShare at https://doi.org/10.6084/m9.figshare.19525609.v1.

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