

Evaluating recreational fisheries for an endangered species: a case study of taimen, *Hucho taimen*, in Mongolia

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Abstract: Understanding the tradeoff between exploitation and conservation is difficult in data-poor situations, which are typical for most recreational fisheries, even in developed countries. In a developing country where the target species is endangered, the stakes are higher and the management resources are fewer. We combined a mark–recapture experiment, life history invariants, and meta-analysis to parameterize a delay-difference model for a population of the endangered giant Eurasian trout (taimen, *Hucho taimen*) in northern Mongolia. The model allowed us to evaluate the impacts of a recreational fishery for taimen based on a suite of population characteristics including equilibrium abundance, biomass, and mean weight. The Bayesian framework and Monte Carlo simulations combine disparate sources of information while keeping track of uncertainty as it propagates through the model. In the case of taimen in the Eg–Uur watershed, the existing catch–release recreational fishery has likely reduced taimen abundance, biomass, and mean weight by less than 10% compared with levels predicted in the absence of recreational fishing. In comparison, if all taimen caught in this fishery were retained (as they are elsewhere in Mongolia), there is a 57% chance that such harvest levels, if maintained, would lead to the eventual extirpation of the population.

Résumé : Il est difficile de comprendre le compromis entre l'exploitation et la conservation dans les pêches sportives lorsqu'il y a peu de données, ce qui est très souvent le cas, même dans les pays développés. Dans un pays en voie de développement lorsque l'espèce cible est menacée, les enjeux sont plus importants et les ressources de gestion moindres. Nous combinons une expérience de marquage–recapture, des invariants du cycle biologique et une méta-analyse afin de paramétrer un modèle de différence avec délais pour une population du huchon géant d'Eurasie (le taimen, *Hucho taimen*), une espèce menacée, dans le nord de la Mongolie. Le modèle nous permet d'évaluer l'impact d'une pêche sportive du taimen à partir d'une série de caractéristiques démographiques, dont l'abondance à l'équilibre, la biomasse et la masse moyenne. Le cadre bayésien et la méthode de Monte Carlo combinent des sources disparates de renseignements, tout en tenant compte de l'incertitude à mesure qu'elle se propage dans le modèle. Dans le cas du taimen de l'Eg–Uur, la pêche sportive actuelle avec remise à l'eau des prises a vraisemblablement réduit l'abondance, la biomasse et la masse moyenne du taimen par moins de 10 %, par comparaison aux valeurs prédites en l'absence de pêche sportive. D'un autre côté, si tous les taimens capturés dans cette pêche étaient gardés (comme ils le sont ailleurs en Mongolie), il y a une probabilité de 57 % qu'une telle intensité de capture, si elle devait se maintenir, aboutirait à une extirpation éventuelle de la population.

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Introduction

There is a growing realization that recreational fisheries have the capacity to severely reduce the abundance of fished species (Post et al. 2002; Coleman et al. 2004; Cooke and Cowx 2004). Yet recreational fisheries often produce large economic benefits (Haab et al. 2001; Cowx 2002; Kelch et

al. 2006), particularly in rural areas where alternative economic activities are limited. They also provide an economic incentive for protecting the ecosystems on which target species depend. Size limits and catch–release policies can limit the negative impacts of recreational fishing, but even mandatory catch–release may be insufficient to protect long-

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lived, low productivity species when fishing effort is high and postrelease survival is low (Coggins et al. 2007). The general lack of stock assessments for recreational fisheries, even in developed countries (Post et al. 2002), results in management that is often focused on restoring degraded fisheries. Such a retroactive focus is extremely risky for target species that are globally threatened.

Newly developing fisheries present serious stock assessment challenges, as well as a unique opportunity to gather information about fish population dynamics from relatively unexploited populations. Good management advice at the start of a fishery's development can be critical; yet without time series data, the available analytical tools are quite limited. There is a need for models of population dynamics that can combine prior information from life history invariants (Beverton and Holt 1959; Charnov 1993) and meta-analysis of other species or other populations of the same species (Myers et al. 1999) with data from limited surveys or mark-recapture experiments. These models must also be able to accurately portray uncertainty in parameters, processes, and model output. Although uncertainty in these early models is likely to be high, the relevant management questions for recreational fisheries are often quite basic (e.g., can fishing effort safely be doubled or is current effort already too high?). An early but approximate answer to such questions is more valuable than a precise postmortem. New life-history-based approaches to estimating maximum sustainable yield (MSY) and F_{MSY} have recently been developed (Beddington and Kirkwood 2005), but analogous tools applicable to recreational fisheries are lacking.

In Mongolia, recreational fisheries targeting taimen, *Hucho taimen*, are developing rapidly (Vander Zanden et al. 2007). Taimen are the world's largest salmonid, reaching a maximum size of 2 m in length and 100 kg in mass (Holčík et al. 1988). Taimen have declined in abundance throughout their range in the large rivers of the Volga/Caspian, Arctic, and Pacific drainages of northern Eurasia (Holčík et al. 1988; Matveyev et al. 1998) and are listed as endangered on the Mongolian, Russian, and Chinese red lists (Holčík 1995; Ocock et al. 2006). Healthy populations still exist, however, in the relatively unexploited and undeveloped rivers of northern Mongolia. There is little cultural tradition of fishing or fish consumption in Mongolia, though Russians and Chinese immigrants living in Mongolia have imported these practices, and both fishing and fish consumption are becoming increasingly common (Chandra et al. 2005). Private tourist companies have expanded since the end of the Soviet occupation in 1990, and many offer guided taimen fishing. Some, but not all, of these outfitters encourage or require catch-release for taimen (Ocock et al. 2006). Commercial harvest of taimen is officially illegal; however, there is little enforcement and taimen are openly sold or bartered in small numbers. Recreational fisheries represent a potentially important source of income in the undeveloped regions of northern Mongolia. Fishing offers an alternative economic activity to mining, which has caused significant habitat damage in some watersheds (Stubblefield et al. 2005). Management of recreational taimen fisheries in Mongolia consists of a license requirement and seasonal closures, though enforcement is minimal.

Management of taimen throughout their remaining range

is hampered by a general lack of knowledge about the life history and population dynamics of this species. Assessments of recreational taimen fisheries in Mongolia are urgently needed for three reasons. (i) Taimen are a globally threatened species. Their long life span and relatively high age at maturity (at least 30 years and approximately 3–8 years, respectively; Holčík et al. 1988) suggest that they are vulnerable to overfishing. (ii) High-value catch-release fisheries for trophy-sized taimen may not be sustainable if fishing pressure leads to substantially reduced abundance or average size of taimen. Taimen require at least 10 years to grow to a length of 1 m (Holčík et al. 1988; Matveyev et al. 1998), and individuals this age have disappeared in less than 20 years from exploited rivers in which they were formerly abundant (Matveyev et al. 1998). (iii) Unexploited systems provide a unique opportunity to estimate unfished abundance, a critical unknown in stock assessments (Hilborn and Walters 1992). In many fisheries, time series data are only available after the onset of heavy exploitation. Consequently, baseline abundance may be significantly lower than unfished abundance, and the expectations of scientists and fishermen underestimate the population's true potential. This "shifting baseline syndrome" (Pauly 1995) can be avoided by studying populations early in the development of a fishery.

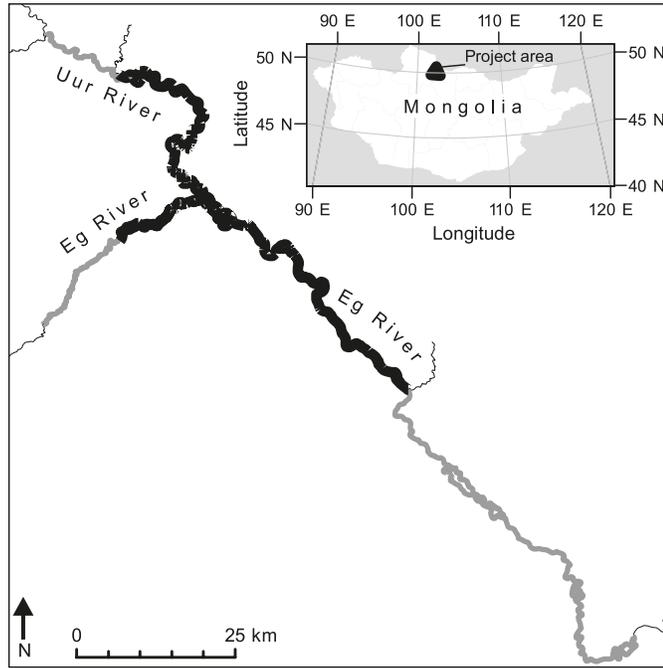
We began an assessment of a developing taimen recreational fishery in Mongolia in 2004. Although length-frequency and growth information exist for taimen populations in Russia (Holčík et al. 1988; Matveyev et al. 1998), there are no reliable time series of abundance, catch, or effort; estimates of natural or fishing mortality rates; or data on stock-recruitment relationships. Our objectives were (i) to estimate growth, unfished abundance and biomass, and recreational postrelease mortality and (ii) to develop a population model that will allow policy-makers to anticipate the population level consequences of maintaining or expanding an existing recreational catch-release fishery. Such a model must make efficient use of all available data, while accurately representing the effects of parameter uncertainty on model output.

Materials and methods

Study site and field methods

We sampled taimen populations in the Eg and Uur rivers near their confluence in northern Mongolia (Fig. 1) from May 2004 through October 2007. The Eg is the main outlet of one of Mongolia's largest lakes, Lake Hovsgol. After joining with the Uur, the Eg flows into the Selenge River, a tributary of Lake Baikal. Near their confluence, the Eg and the Uur have typical discharges of 40 and 75 m³·s⁻¹, respectively, during the spring and fall (mid-May and mid-October) and higher discharges, >54 and 370 m³·s⁻¹, respectively, during July and August (D.J. Gilroy, unpublished data). The climate of the region is temperate, with average water temperatures of 9 °C in May and 14 °C in August in the Eg and 12 °C in May and 17 °C in August in the Uur. The Eg and Uur typically freeze in late November and thaw in early May (Gilroy 2007). Fish communities include a small number of cold-water species, predominantly lenok (*Brachymystax lenok*), Arctic grayling (*Thymallus arcticus arc-*

Fig. 1. Study area in the Eg–Uur watershed of northern Mongolia. River sections in bold represent the extent of the mark–recapture study. Shaded sections represent the extent of the extended telemetry surveys.



ticus), Eurasian minnow (*Phoxinus phoxinus*), and Arctic cisco (*Coregonus autumnalis*), with taimen as the top predator. The field season was divided into spring (early May to late June or early July) and fall (late August to mid-October) sampling periods. The study region is remote and is fished almost exclusively by clients of a single fly-fishing guide service, which practices strict catch–release fishing using single barbless hooks.

Fish were sampled by angling with barbless hooks. Other methods proved to be ineffective or impractical (e.g., backpack or boat electrofishing and beach seining) or would likely have resulted in unacceptable mortality (e.g., gill nets). Captured fish were checked for tags and marks, measured to the nearest millimetre (total length), and weighed to the nearest 100 g in a net with a hanging scale. Untagged fish were tagged with individually numbered plastic t-bar anchor tags (Hallprint model TBA) as part of a multiple-season mark–recapture study ($n = 612$ over nine seasons). The posterior third of the anal fin was clipped on 124 of the t-bar tagged individuals during the spring and fall 2007 sampling seasons to estimate the tag shedding rate.

Radio (Lotek MCFT series, $n = 27$) and acoustic (Vemco V16, $n = 17$) tags were surgically implanted in a subset of captured fish to study movements (Gilroy 2007) and to estimate postrelease mortality. Two additional individuals were tagged with both types of tags for a separate detection efficiency study. All radio- and acoustic-tagged fish were anesthetized with MS-222 (tricaine methanesulfonate) prior to surgery, irrigated during surgery, and held in instream enclosures until they were swimming strongly (average of 30 min). Mobile radio and acoustic tracking surveys were conducted by boat once every 15–30 days during the ice-free season and, on average, once every two months during

the winter over a 60 km stretch of river (Gilroy 2007) within the 120 km mark–recapture study area fished by Sweetwater Travel. Six telemetry surveys were conducted over a larger area (200–250 km) that encompassed the entire mark–recapture study area.

Length at age was determined for 11 individual taimen based on sectioned saggitae otoliths. Otoliths were collected from those fish that were either found dead ($n = 6$) or died during capture ($n = 4$) or tag implantation surgery ($n = 1$). Epoxy-mounted otoliths were sectioned in the transverse plane through the origin using a low-speed saw (Casselman 1983). Annuli interpretations and counts were made directly from polished sections by an experienced salmonid otolith reader. Aging using scales was found to be ineffective due to abrasion of outer growth rings, a common problem with salmonid scales (Sharp and Bernard 1988).

Population model

We used a delay-difference population model (Deriso 1980; Schnute 1985, 1987) to simulate changes through time (t) in abundance (N_t), biomass (B_t), and mean weight (\bar{w}_t) of taimen recruited to the fishery (i.e., large enough to be vulnerable to fishing gear used to target adult taimen) within the Eg–Uur study region. The delay-difference model represents a compromise between surplus production models, in which recruitment, mortality, and individual growth are condensed into a single intrinsic rate of growth, and fully age-structured models, which track individual cohorts. Production models are unable to predict changes in size, a crucial model output for recreational fisheries, whereas fully age-structured models require age-specific information on vulnerability to fishing, natural mortality, and fecundity. The delay-difference model incorporates two separate equations for numbers and biomass in year $t + 1$ (modified from Walters and Martell 2004):

$$(1) \quad B_{t+1} = S_t(cN_t + \rho B_t) + w_k R_{t+1}$$

$$(2) \quad N_{t+1} = S_t N_t + R_{t+1}$$

The parameter w_k is the weight at age k , the age at recruitment. For taimen in the Eg–Uur study area, the age at recruitment to the fishery is ~ 4 years and is similar to the age at sexual maturity (3–8 years for males and 4–8 years for females; Holčík et al. 1988). The annual total survival rate, S_t , is a function of the instantaneous natural mortality rate (M) and the annual exploitation rate (h), i.e., the fraction of the population removed due to harvest or postrelease mortality:

$$(3) \quad S_t = e^{-M}(1 - h)$$

The parameters c and ρ are the intercept and slope, respectively, of the Ford–Brody body weight equation for predicting weight at age $a + 1$:

$$(4) \quad w_{a+1} = c + \rho w_a$$

Recruitment in year $t + 1$ (R_{t+1}) is frequently modeled as a function of biomass in the previous year (B_t), unfished recruitment (R_0), a steepness parameter (z) (Mace and Doonan 1988) representing the proportion of R_0 produced by 20% of the unfished biomass (B_0), and ϕ_0 , the spawning biomass per

recruit at unfished equilibrium (B_0/R_0). Of all the possible stock–recruit functions, the Beverton and Holt

$$(5) \quad R_{t+1} = \frac{0.8R_0zB_t}{0.2\varphi_0(1-z) + (z-0.2)B_t}$$

is the most commonly observed in empirical analyses of stock–recruit data (Myers and Barrowman 1996; Myers et al. 1999; Walters et al. 2006) and has a strong theoretical basis related to risk-sensitive foraging behavior (Walters and Korman 1999).

Although the stock–recruit functions are typically parameterized based on unfished equilibrium biomass and recruitment (B_0 and R_0), they can also be parameterized based on an arbitrary point (B^* , R^*) on the stock–recruit curve (Kimura 1988). In that case, steepness (z^*) does not have the same meaning. However, for higher values of steepness and B^* not much less than B_0 , z^* is nearly the same as z . For example, for $z = 0.8$ and $B^* = 0.8B_0$, the ratio of $z^*:z$ is 0.96 (Appendix A).

Data analysis and parameter estimation

We used lengths, ages, and weights from individuals captured in the Eg–Uur study area, taimen lengths and ages from published literature, an empirical relationship between growth and natural mortality (Pauly 1980; Jensen 1996), and data from the mark–recapture experiment to estimate c , ρ , M , B_1 , and N_1 (the time subscript 1 is used to indicate the current state, which was not assumed to be the same as the unfished state). The annual total survival rate, S_b , was estimated from its components (M and h) as described in the next section. All of these data sources were combined in an integrated analysis in which posterior distributions of model parameters were estimated by Markov chain Monte Carlo (MCMC) sampling using AD Model Builder software (ADMB, Otter Research Ltd., Sidney, British Columbia).

A von Bertalanffy (VB) growth model of length at age (L_a)

$$(6) \quad L_a = L_\infty(1 - e^{-K[a-a_0]})$$

was fit to age and length data from 31 taimen stocks (303 age–length combinations; Holčík et al. 1988; Matveyev et al. 1998) using a nonlinear mixed effects model (R, nlme package) where asymptotic length (L_∞) was allowed to vary among stocks. The maximum likelihood estimates (MLEs) of L_∞ , age at length zero (t_0), and the VB growth rate parameter (K), and their standard deviations (random effect standard deviation for L_∞) were used to set priors on these three parameters for a second round of fitting to the ages and lengths from the 11 aged individuals from the Eg–Uur study area. Embedded in this second round of fitting were four separate growth and mortality submodels: (i) a regression, $M = gK$ (Jensen 1996), using the 175 stocks from Pauly (1980), (ii) an application of this formula to predict M for taimen using the estimated regression coefficient, g , and the estimated VB K parameter, (iii) a length–weight regression, $W = \alpha L^\beta$, based on the lengths and weights of 56 individuals sampled from the Eg–Uur study area, and (iv) a Ford–Brody body weight regression (eq. 4) using simulated data for ages 1 to 30 from the VB growth model and the length–weight regression. Simulated data were used in this

last growth submodel because the relationship between w_{a+1} and w_a is slightly nonlinear when weights at age are estimated from the VB length growth model and a length–weight regression, thus there is no analytical solution for the Ford–Brody weight relationship as there is for the L_{a+1} vs. L_a relationship (Hilborn and Walters 1992). There is little weight at age information in the published literature on taimen, making it difficult to estimate the Ford–Brody weight parameters directly.

A Jolly–Seber (JS) mark–recapture model (Jolly 1965; Seber 1965) including tag shedding was used to estimate the average abundance of taimen over the study period. In the m_{ij} -array form of the JS model, the probability of the observed number of recaptures in period j of individuals marked in period i (m_{ij}) is estimated conditional on the number of releases of marked fish in period i (R_i). The predicted number of recaptures, \hat{m}_{ij} , is

$$(7) \quad \hat{m}_{ij} = \frac{R_i \cdot D \cdot C_j \cdot A^{(j-i)/2}}{N_0}$$

where D is the tag retention rate (assuming that all tag shedding occurs between the time of tagging and the following sampling period), C_j is the total number of individuals (both tagged and untagged) captured in period j , and $A^{(j-i)/2}$ is the apparent survival between the tagging period (i) and the recapture period (j). Mortality and emigration are confounded in the apparent survival parameter, A , making it difficult to estimate the natural mortality rate (M) directly from the mark–recapture experiment. We assumed a constant apparent survival rate and population size. Short-term fluctuations in the number of fully recruited individuals for this long-lived species are likely to be small in the absence of large and recent anthropogenic mortality sources, and a single population size can be estimated with greater precision than could sampling period-specific population sizes.

Assuming that the m_{ij} are independent samples from Poisson distributions with means given by eq. 7 and ignoring likelihood terms involving only the data, the log-likelihood kernel (log L), for all of the m_{ij} given the parameters (θ) is

$$(8) \quad \log L(m|\theta) = \sum_{j>i=1}^k \left(-\hat{m}_{ij} + m_{ij} \log(\hat{m}_{ij}) \right)$$

(Coggins et al. 2006). If the same fish is recaptured multiple times, then the m_{ij} are not independent (Coggins et al. 2006); however, in this study, the number of recaptures was relatively low (total = 40, not counting individuals recaptured in the same sampling period, which are not used in the JS model), and only two of these individuals were recaptured more than once. Although excellent software is available for analysis of mark–recapture experiments, the most widely used program (MARK; White and Burnham 1999) does not allow for the inclusion of a tag loss rate and has limited options for estimating population size. Our abundance estimate was within 10% of an estimate obtained by analyzing our data with another widely used program designed to estimate abundance from mark–recapture experiments (JOLLY; Pollock et al. 1990).

The double-marking (tag and anal fin clip) experiment provided an estimate of the tag retention rate (Guy et al.

1996). Fifteen of the double-marked individuals were recaptured, of which 14 had retained their tags. If no other prior information on tag retention is available and these 15 observations are considered as independent binomial trials, then the distribution of the tag retention rate is a beta distribution, $Beta(16, 2)$, with a mode at 0.94. We used this distribution as a prior on the tag retention rate. Because the mark-recapture data contain little information about tag retention, the prior and posterior distributions are very similar; however, the posterior distributions of A and abundance reflect this uncertainty in tag retention.

The stock–recruit model steepness parameter, z , could not be estimated from any of the data that we collected in our field study. The parameters of stock–recruit models are typically estimated by fitting a model to time series of spawning stock size and recruitment. Myers et al. (1999) estimated values of z from more than 700 such time series to get empirical probability distributions of z for many different fish species and stocks. To develop a prior for z , which can range between 0.2 and 1, for any particular species, Myers et al. (2002) recommend using the distribution of z for either taxonomically or ecologically related species or estimating a distribution of z using life history and environmental covariates. Similar distributions of z resulted from the taxonomic and ecological approaches. There are two species of non-anadromous salmonids for which z was estimated by Myers et al. (1999), five populations of brook trout (*Salvelinus fontinalis*; median $z = 0.87$) and one population of lake trout (*Salvelinus namaycush*; $z = 0.86$). Myers et al.'s (2002) “domain 3” group of species (older age at maturity, low natural mortality rate, and high fecundity) was the closest ecologically similar group to taimen. The probability distribution of z estimated for this group is centered on 0.84 and is closely approximated by $Beta(28.5, 6.2)$. We drew random samples of z from this distribution for the Monte Carlo simulations described below. The other stock–recruit parameter, $\varphi_1 = B_1/R_1$, was calculated from the estimated current biomass B_1 and current recruitment assuming the population is at equilibrium, $R_1 = (1 - S_1)N_1$.

We used the radio- and acoustic-tagged individuals to estimate an upper bound on the release mortality rate. Individuals relocated at more than one location more than 7 days after release were considered to have survived. Of 52 radio- and acoustic-tagged individuals, 47 survived according to this definition. We consider $1 - (47/52) = 0.096$ to be an upper bound on the release mortality rate as these individuals experienced greater trauma (tag implantation surgery) than fish released by the fishing guides, and there is some probability that an individual may not be relocated due to tag malfunction or emigration beyond the surveyed area.

Five of 122 fish landed in the recreational fishery in fall 2007 and examined for signs of injury were observed to be bleeding heavily from the gill area. We used this fraction (0.04) as a lower bound on postrelease mortality as these individuals were likely to die and some of the other individuals released alive without obvious injuries may have subsequently died from unseen injuries or stress sustained during the capture and release process. Between 2005 and 2007 (years for which complete catch records were available), the recreational catch in the Eg–Uur study area averaged 240 fish per year. Given this catch and the range of

release mortality rates, deaths due to recreational fishing within the study area ranged between 10 and 23 fish per year, on average.

Although the study area is remote, some subsistence or artisanal harvest and (or) poaching does occur. We refer to such harvest generically as “subsistence harvest”, as the disposition of the catch (consumed by fishermen or sold) and the legality of the fishing activity are generally unknown and irrelevant to the population model. This harvest is essentially unregulated and entirely undocumented. When we observed the disappearance of telemetry-tagged fish from locations within the core tracking area where they had previously been found, we attempted to ascertain through interviews with fishing guides (who traverse the core tracking area on a daily basis) and local residents whether any fishing activity had been observed in the area. On three occasions, these interviews led to confirmation that the telemetry-tagged fish had been harvested. The telemetry study resulted in a total of 1304 tag months of effort. Based on the three confirmed fish harvested, the monthly harvest rate is then 2.3×10^{-3} , which is equivalent to an annual harvest rate of 0.027. We used this rate as an estimate of the current subsistence harvest rate with the recognition that this measure is imprecise and potentially an underestimate of the true subsistence harvest rate.

Monte Carlo simulations

We estimated the probability distributions of unfished equilibrium biomass, population size, and mean weight using the maximum and minimum estimates of postrelease survival and the estimated subsistence harvest rate combined with random samples from the distributions of the model parameters. Current abundance and biomass, as estimated from the mark–recapture model, were assumed to be the equilibrium values achieved by the population under the current recreational and subsistence fishing mortality rate. The fishing mortality components of the annual total survival rate, S_i , were removed and the delay-difference model (eqs. 1 and 2) was run to approximate equilibrium (200 years). This procedure was repeated using 10 000 MCMC samples of the joint posterior distribution of the delay-difference model parameters. These MCMC samples represent every 500th trial from a 6 000 000 trial chain, where the first 1 000 000 trials were discarded as a burn-in period.

For each of these 10 000 parameter combinations, we also calculated the biomass, population size, survival to age 10, and mean weight at equilibrium for absolute harvest rates (number of fish killed per year) ranging from 0 to 500 fish per year. This range of harvest rates is equivalent to management scenarios ranging from stopping the recreational and subsistence fisheries to allowing the recreational fishery to approximately double its annual catch and switch to a 100% retention policy. At some level of constant harvest, the population is reduced to the point at which the harvest level exceeds the projected population size, i.e., a continued harvest at that level would lead to eventual extirpation of the population. For each harvest rate, we calculated the probability of extirpation as the fraction of the 10 000 simulations for which the harvest rate would exceed the population size within 200 years.

Results

Length at age for taimen in the Eg-Uur study area was similar to values observed in other locations (Fig. 2). The posteriors obtained using uniform priors on the von Bertalanffy growth parameters were broad (Fig. 3), indicating that much of the information on growth rate came from the prior distributions derived from meta-analysis of published lengths at age. The posterior modes and 95% Bayesian credible intervals of the parameters of the von Bertalanffy growth model were as follows: $K = 0.09\text{-year}^{-1}$ (0.08–0.10), $L_{\infty} = 147\text{ cm}$ (136–160), and $a_0 = -0.16\text{ years}$ (–0.41–0.10) (Table 1).

Annual natural survival estimated from the growth rate using the Jensen (1996) method was 0.86 (0.84–0.88). Estimated abundance of recruited taimen (>age 4) in the study area averaged over the 4-year study period was 2320 individuals (1363–4517), yielding a density over the 120 km study area of 19 individuals·km⁻¹ (11–38).

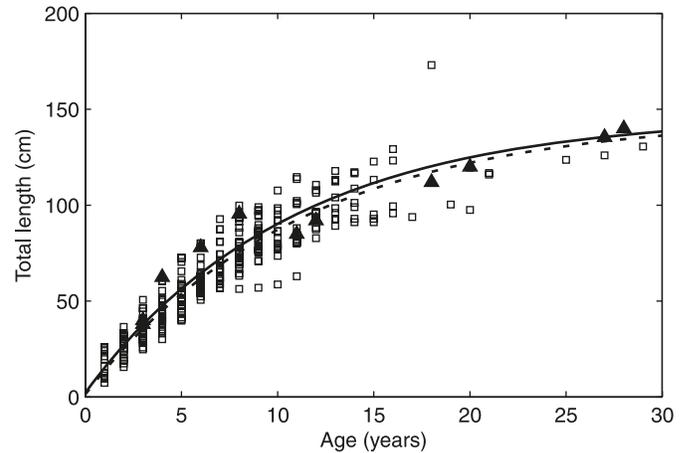
The population model results suggest that at the current size of the fishery, the effects of catch–release mortality on abundance, biomass, mean weight, and survival from recruitment to age 10 are minimal, even when the higher release mortality estimate was used. Equilibrium biomass was more sensitive than the other three indicators (abundance, mean weight, and survival to age 10) and was estimated to have been reduced to 90% (82%–94%) of levels expected in the absence of recreational fishing under the higher release mortality rate. The effects of the recreational fishery on other population characteristics were smaller (Fig. 4; Table 2). An annual harvest rate of 24 individuals, equivalent to the number of fish killed by the recreational fishery under the higher release mortality rate, resulted in zero risk of extirpation due to harvest (Fig. 5; Table 2).

In contrast, without catch–release, the effects of a recreational fishery of this size could be severe. An annual harvest of 130 individuals (approximately equivalent to a 50% release rate assuming the higher release mortality) would likely result in a reduction in equilibrium population size to 69% (0%–84%), biomass to 50% (0%–72%), mean weight to 73% (0%–90%), and survival to age 10 to 68% (0%–84%) of levels expected in the absence of a recreational fishery (Fig. 4). Note that a value of zero in the confidence limits indicates extirpation. The probability of extirpation if this level of harvest were maintained indefinitely is 4% (Fig. 5). Above this level of recreational harvest, extirpation risk rises rapidly. For example, a switch to 100% retention in the current recreational fishery (annual harvest of 240 individuals) would result in a probability of extirpation due to fishing of 57%. The effects of the estimated level of subsistence harvest appear to be greater than the effects of the recreational catch–release fishery; however, uncertainty in the subsistence harvest rate is high and cannot be quantified.

Discussion

The growth and natural mortality estimates and the population model results all suggest that taimen populations are likely to be very sensitive to fishing mortality. Holčík et al. (1988) found that in most taimen populations, sexual maturity is attained at a weight of ~1 kg for males and ~2 kg for

Fig. 2. Length and age data from the published literature (open squares; Holčík et al. 1988; Matveyev et al. 1998) and from individuals collected in the Eg-Uur study area (solid triangles). von Bertalanffy growth models fit to the literature data (broken line) and to the Eg-Uur data using the parameter estimates from a mixed-effects model based on the literature data as priors (solid line).



females. In the Eg-Uur population, this is equivalent to an age of 4 years for males and 5 years for females. The relatively slow growth, low natural mortality, late maturation, and low fecundity (10 000 – 30 000 eggs per female; Holčík et al. 1988) of taimen place them with many other salmonids between the “periodic” and “equilibrium” life history strategies (Winemiller and Rose 1992). The natural mortality rate and growth rate that we estimated for taimen are both low relative to those of other salmonids but similar to some cold-water populations of lake trout, brook trout, and lake whitefish (*Coregonus clupeaformis*; Froese and Pauly 2008). Many other species with slow growth and high longevity have proven to be especially vulnerable to overexploitation (Musick 1999).

Our modeling approach makes use of correlations among life history characteristics (Pauly 1980; Jensen 1996) and meta-analysis of stock–recruitment relationships (Myers et al. 1999, 2002) to reduce uncertainty in the survival rate and the stock–recruitment steepness parameter. Such approaches are frequently used to develop informative priors for stock assessments based on time series data (e.g., McAllister et al. 2001). When time series data are not yet available, life history correlates and meta-analysis can also be used (as we have shown here) to parameterize models that provide general predictions about the likely impacts of different levels of fishing. These initial models can later be combined with time series data in a fully integrated assessment framework advocated by Maunder (2004).

The Bayesian modeling approach linked to Monte Carlo simulation allowed us to keep track of uncertainty as it propagated through the model. For example, uncertainty in survival rate derives from both uncertainty in the growth rate (K) and variability in the natural mortality (M) vs. K relationship. Other approaches to quantifying this uncertainty exist. Gunderson et al. (2003), for example, used the delta method to estimate the standard error of M based on the Jensen (1996) method. However, by combining the

Fig. 3. Gaussian kernel densities of marginal posterior distributions (solid lines), prior distributions (shaded lines), and posterior distributions resulting from a uniform prior (broken lines) for the von Bertalanffy growth parameters (a) asymptotic length, (b) growth rate, and (c) the intercept; (d) the length–weight coefficient and (e) exponent; (f) the annual natural survival rate estimated using the Jensen (1996) method; (g) population density; (h) apparent survival; and (i) tag retention rate. Posterior densities are based on 10 000 systematic samples from a Markov chain Monte Carlo (MCMC) chain of length 6 000 000, where the first 1 000 000 were discarded to allow for convergence. Uniform priors are not shown.

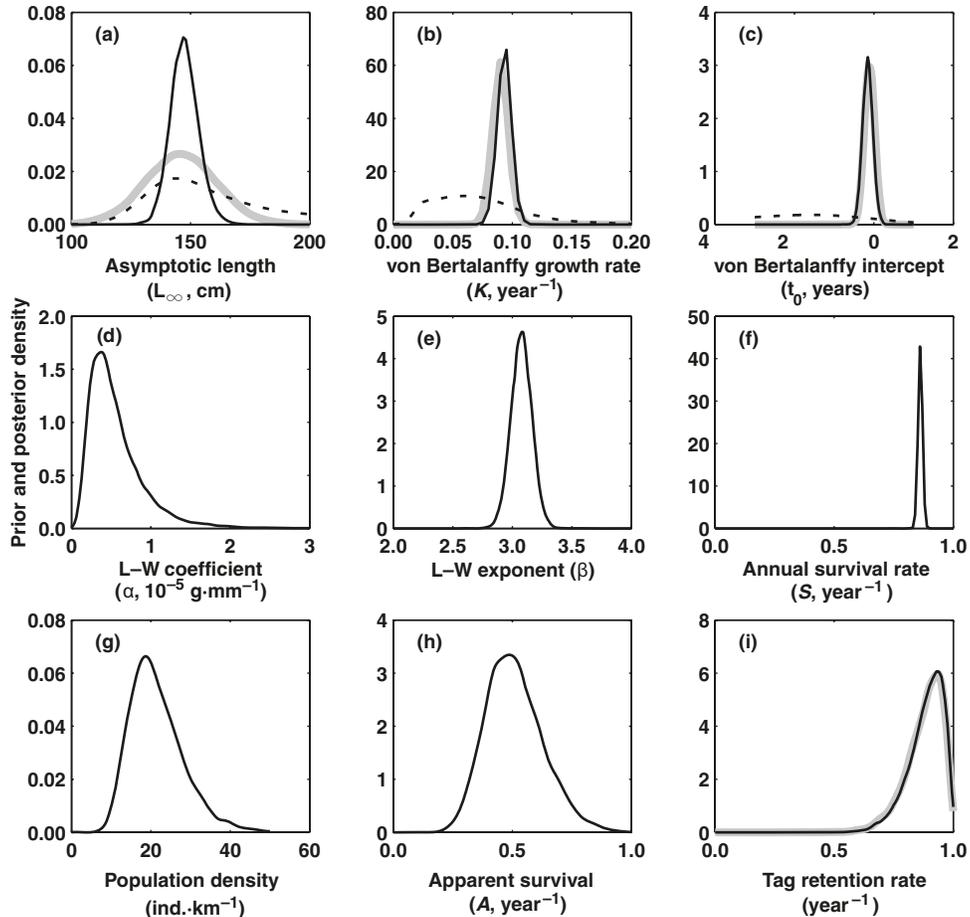


Table 1. Median values of parameters used in the delay difference model.

Parameter	Value	Unit	Method and (or) source
Growth parameters			
von Bertalanffy growth rate (K)	0.09 (0.08–0.10)	year ⁻¹	Fit to length and age
von Bertalanffy asymptotic length (L_{∞})	147 (136–160)	cm	Fit to length and age
von Bertalanffy age intercept (a_0)	-0.16 (-0.41–0.10)	years	Fit to length and age
Length–weight coefficient (α)	$4.7 (1.5–15.0) \times 10^{-6}$	g·mm ⁻¹	Fit to length and weight
Length–weight exponent (β)	3.1 (2.9–3.2)	—	Fit to length and weight
Population dynamics parameters			
Current abundance (N_1)	2320 (1363–4517)	individuals	Mark–recapture model
Current mean weight (\bar{w}_1)	5810 (4920–6700)	grams	Mean of weighed individuals
Annual natural survival rate (S_0)	0.86 (0.84–0.88)	year ⁻¹	Jensen (1996) method
Steepness (z)	0.83 (0.70–0.92)	—	Myers et al. (2002)

Note: The 95% Bayesian credible interval (95% confidence interval for mean weight) is given in parentheses.

analysis of growth with the estimation of natural mortality in a Bayesian framework, we were also able to preserve correlation between growth and survival. The Monte Carlo simulations draw from the joint posterior of S_0 and K . Thus, relatively unlikely combinations such as high growth

rate and high survival are appropriately more rare than if these parameters were drawn from two independent distributions.

Survival rate and steepness, together with population size, are the most important parameters in the delay-difference

Fig. 4. (a) Equilibrium abundance, (b) biomass, (c) mean weight, and (d) survival to age 10 relative to unfished conditions plotted against absolute harvest rate (individuals per year). Medians (solid lines) and upper and lower 95% confidence intervals (broken lines) are based on 10 000 simulations. Vertical shaded lines indicate the range of harvest rates equivalent to the mortality resulting from the existing catch–release fishery. The equivalent relative annual harvest rate is shown on the top x axis.

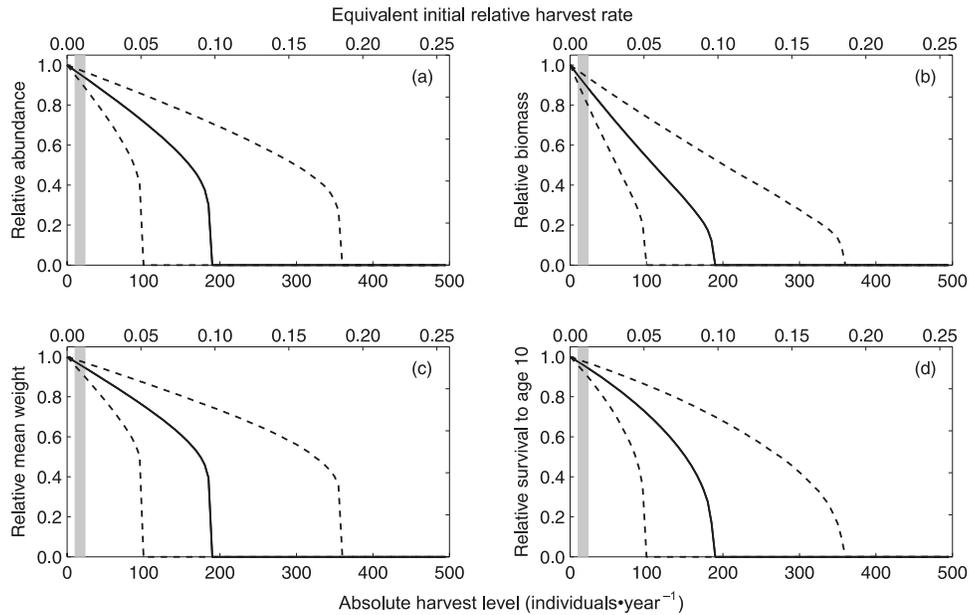


Table 2. Equilibrium abundance (N), biomass (B), mean weight (\bar{w}), survival to age 10 (S_{10}), and probability of extirpation ($p(E)$) for several exploitation scenarios (SH, current subsistence harvest levels; 2SH, double current subsistence harvest levels; CR low, CR high, and 2CR high, catch–release based on the low and high estimates of release mortality and a doubling of the recreational catch; RH, 100% retention (i.e., no catch–release) of fish caught in the recreational fishery).

Scenario	N	B	\bar{w}	S_{10}	$p(E)$
CR low (10)	0.98 (0.96–0.99)	0.96 (0.93–0.98)	0.98 (0.96–0.99)	0.98 (0.96–0.99)	0.00
CR high (23)	0.94 (0.90–0.97)	0.90 (0.82–0.94)	0.95 (0.91–0.97)	0.95 (0.91–0.97)	0.00
2CR high (46)	0.90 (0.81–0.94)	0.82 (0.68–0.90)	0.91 (0.83–0.95)	0.91 (0.82–0.95)	0.00
SH+CR low (73)	0.83 (0.68–0.91)	0.70 (0.49–0.83)	0.85 (0.72–0.92)	0.83 (0.68–0.91)	0.00
SH+CR high (86)	0.80 (0.63–0.89)	0.66 (0.42–0.81)	0.83 (0.67–0.91)	0.81 (0.62–0.90)	0.00
SH (63)	0.85 (0.73–0.92)	0.74 (0.55–0.85)	0.87 (0.76–0.93)	0.86 (0.73–0.93)	0.00
RH (240)	0.00 (0.00–0.69)	0.00 (0.00–0.50)	0.00 (0.00–0.73)	0.00 (0.00–0.67)	0.57
2SH+CR high (149)	0.63 (0.00–0.80)	0.43 (0.00–0.67)	0.68 (0.00–0.83)	0.61 (0.00–0.81)	0.09

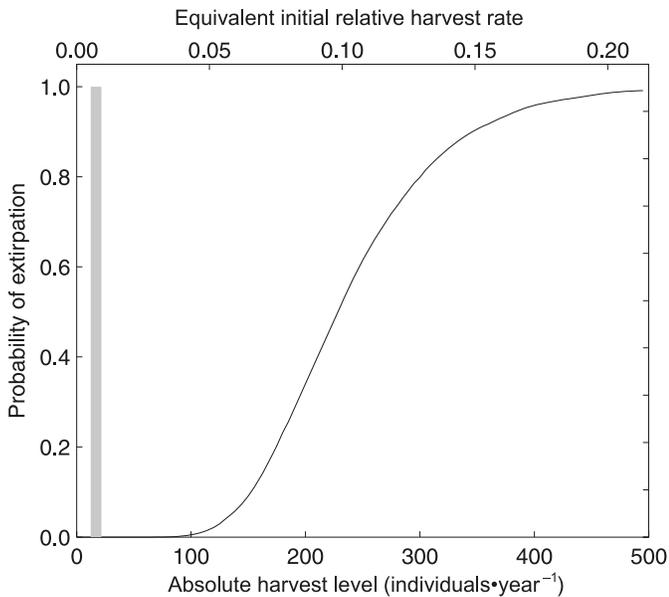
Note: All scenarios are based on an assumption of constant harvest at the level indicated in parentheses next to the scenario. All values except $p(E)$ are expressed relative to the unfished state and represent medians from the Monte Carlo simulations. The 95% confidence interval is given in parentheses. Note that a value of zero indicates extirpation. No confidence interval can be calculated for $p(E)$.

model for predicting the relative impact of different harvest rates. Although there remains substantial uncertainty in all of these parameters, the data requirements of this approach are minimal and the results are sufficiently precise to provide useful answers to the key motivating question: is the existing catch–release fishery having a substantial adverse impact on this population of taimen? Based on our analysis, the answer is clearly no. A fishery of this size, however, has the potential to seriously endanger this population if fish are retained or if postrelease mortality rates are higher (e.g., due to more harmful fishing gear such as live bait or lures with multiple-barbed hooks). Proper management of any more intense exploitation of this population would require better estimates of all parameters and adequate monitoring of

exploitation rates. Our model is clearly not sufficient for management that aims to maintain a harvest fishery near some optimal exploitation rate (e.g., F_{MSY}).

We chose to express our harvest scenarios in terms of an absolute harvest rate (individuals·year⁻¹) rather than a relative harvest rate (fraction of the population·year⁻¹), as is more commonly done when displaying the results of fisheries population models. Using a relative harvest rate would reduce the uncertainty in model output that derives from uncertainty in the population size. An absolute harvest rate is, however, more readily interpretable by managers of developing fisheries who may know the absolute harvest from a population (how many fish were caught) but are unlikely to know the exploitation rate (what fraction of the population

Fig. 5. Probability of extirpation vs. absolute harvest rate (individuals per year). The vertical shaded line indicates the range of harvest rates equivalent to the mortality resulting from the existing catch–release fishery. The equivalent relative annual harvest rate at the beginning of each simulation is shown on the top x axis.



was caught). Of course, model results expressed in terms of an absolute harvest rate are not directly transferable to other populations that differ in size.

Several other rivers in Mongolia support recreational fisheries for taimen, and the potential exists to develop such fisheries elsewhere. Our results suggest that these fisheries can have minimal impact if fishermen practice strict catch–release and if fishing effort does not grow too large. Intense recreational catch–release effort and (or) harvest fisheries, however, have the potential to threaten the continued persistence of this species in one of its last strongholds. Harvest fisheries may also threaten the economic viability of valuable catch–release fisheries if they contribute to a decline in catch rates and abundance of large fish. Fishery management and enforcement capabilities are poorly developed in Mongolia, making top-down management approaches unlikely to succeed. If fisheries for taimen are to be both sustainable and profitable, the economic incentives must be aligned in such a way that conservation is encouraged (Ostrom et al. 1999; Hilborn et al. 2005; Grafton et al. 2006).

One possible approach is to develop a system of concessions, i.e., sections of river within which one recreational fishing company has exclusive access. The value of a concession would depend on maintaining high abundance of large taimen. Strict catch–release may not be appropriate for all concessions, as some anglers value the experience of landing and keeping a fish (Holland and Ditton 1992; Arlinghaus et al. 2007). Yet limits on harvest may be necessary, and some river sections could be set aside as reserves to ensure that overharvest within one or more concessions did not threaten the viability of the entire population. Such concession systems have a long history in Europe, where

many freshwater recreational fisheries are privately owned and managed (Arlinghaus 2006). Without a concession system or effective law enforcement, there is less incentive to protect taimen populations as recreational fishing companies that deplete local populations can simply move to other locations. Such serial depletion of recreational fisheries is apparent in other locations where management has been lax (Post et al. 2002; Carpenter and Brock 2004).

In our experience in the Eg–Uur study area, the presence of a recreational fishing company operating in this area is, by itself, a deterrent to harvest, even though the fishing company has no official law enforcement authority. The fishing company hires local guides, camp cooks, and assistants, thus creating an economic incentive for the community to maintain a viable recreational fishery. Local residents working for the fishing company discourage others from fishing. In the absence of nearby markets for taimen or access to refrigeration, such social pressure appears to be effective in limiting illegal harvest. Anglers in this fishery are primarily wealthy individuals from North America, Western Europe, and Japan, with many alternative fishing options. If recreational fishing intensity or illegal harvest increased to the point that catch rates of large taimen seriously declined, the commercial viability of this fishery would be threatened. Our experience suggests that a collapse of this recreational fishery would likely lead to increased fishing mortality rates due to the loss of the deterrent effect.

In considering the impact of the recreational fishery on taimen in the Eg–Uur study area, we ignored secondary effects on the local ecosystem, which can be serious (Cowx 2002). Examples of such effects could include the impact of recreational fishing gear on habitat (e.g., Asoh et al. 2004) or the impact of jet boats on riverbank erosion (McConchie and Toleman 2003) or, potentially, on taimen survival (although a study of effects of boat traffic on Chinook salmon (Reid 2007) found little effect).

We also did not consider immigration and emigration in our population dynamics simulations. Immigration and emigration were incorporated in the analysis of the mark–recapture data through the use of an open population model. On the one hand, movement of taimen into the study area could potentially offset some of the decline in abundance predicted at higher harvest levels. On the other hand, declining abundance within the study area could lead to declines beyond its boundaries through a reduction in net emigration. The overall effect of movement is to reduce the local impact of harvest, while spreading it over a wider area.

Little is known about the scales of population connectivity in taimen. The telemetry study (Gilroy 2007), which tracked taimen for over 2.5 years, found a mean home range size (maximum distance between relocations) of 16.8 km, with 90% of telemetry-tagged individuals showing home ranges smaller than 53 km. Yet some individuals tagged within the study area were found outside it during the extended telemetry surveys. The difference between apparent survival from the mark–recapture analysis and survival estimated from growth rate also suggests that movement could be important. Population genetics studies are needed to determine the optimum scale of analysis for modeling population dynamics of taimen.

The existing recreational fishery for taimen provides economic benefits with little risk to the long-term persistence of the local taimen population. However, this fishery represents an extreme: low fishing effort, spread over a large area, with 100% release and minimum-impact fishing techniques. Our results indicate that a fishery of similar intensity managed as a 100% harvest fishery would seriously threaten the persistence of this population of the endangered taimen. Although recreational fisheries clearly have the potential to adversely impact target species, well-managed catch–release fisheries are not necessarily incompatible with conservation of an endangered species.

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References

- Arlinghaus, R. 2006. Overcoming human obstacles to conservation of recreational fishery resources, with emphasis on central Europe. *Environ. Conserv.* **33**(1): 46–59. doi:10.1017/S0376892906002700.
- Arlinghaus, R., Cooke, S.J., Lyman, J., Policansky, D., Schwab, A., Suski, C., Sutton, S.G., and Thorstad, E.B. 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. *Rev. Fish. Sci.* **15**(1–2): 75–167. doi:10.1080/10641260601149432.
- Asoh, K., Yoshikawa, T., Kosaki, R., and Marschall, E.A. 2004. Damage to cauliflower coral by monofilament fishing lines in Hawaii. *Conserv. Biol.* **18**(6): 1645–1650. doi:10.1111/j.1523-1739.2004.00122.x.
- Beddington, J.R., and Kirkwood, G.P. 2005. The estimation of potential yield and stock status using life-history parameters. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **360**(1453): 163–170. doi:10.1098/rstb.2004.1582. PMID:15713595.
- Beverton, R.J.H., and Holt, S.J. 1959. A review of the lifespans and mortality rates of fish in nature and the relation to growth and other physiological characteristics. *In* Ciba Foundation Colloquium on Ageing. Vol. 5. The lifespan of animals. Little, Brown and Co., Boston, Mass. pp. 142–177.
- Carpenter, S.R., and Brock, W.A. 2004. Spatial complexity, resilience, and policy diversity: fishing on lake-rich landscapes. *Ecol. Soc.* **9**(1): 8.
- Casselman, J.M. 1983. Age and growth assessment of fish from their calcified structures — techniques and tools. NOAA (Natl. Ocean. Atmos. Adm.) Tech. Rep. NMFS (Natl. Mar. Fish. Serv.), **8**: 1–17.
- Chandra, S., Gilroy, D., Purevdorj, S., and Erdenebat, M. 2005. The feeding behaviour of fish from the upper Lake Baikal watershed of the Eroo River in Mongolia. *Mongolian J. Biol. Sci.* **3**(1): 39–45.
- Charnov, E. 1993. Life history invariants. Oxford University Press, New York.
- Coggins, L.G., Pine, W.E., Walters, C.J., and Martell, S.J.D. 2006. Age-structured mark–recapture analysis: a virtual-population-analysis-based model for analyzing age-structured capture–recapture data. *N. Am. J. Fish. Manage.* **26**(1): 201–205. doi:10.1577/M05-133.1.
- Coggins, L.G., Catalano, M.J., Allen, M.S., Pine, W.E., and Walters, C.J. 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. *Fish. Fish.* **8**: 196–210.
- Coleman, F.C., Figueira, W.F., Ueland, J.S., and Crowder, L.B. 2004. The impact of United States recreational fisheries on marine fish populations. *Science* (Washington, D.C.), **305**(5692): 1958–1960. doi:10.1126/science.1100397. PMID:15331771.
- Cooke, S.J., and Cowx, I.G. 2004. The role of recreational fishing in global fish crises. *Bioscience*, **54**(9): 857–859. doi:10.1641/0006-3568(2004)054[0857:TRORFI]2.0.CO;2.
- Cowx, I.G. 2002. Recreational fisheries. *In* Handbook of fish biology and fisheries. Vol. II. Edited by P.B.J. Hart and J.D. Reynolds. Blackwell Science, Oxford, UK. pp. 367–390.
- Deriso, R.B. 1980. Harvesting strategies and parameter estimation for an age-structured model. *Can. J. Fish. Aquat. Sci.* **37**(2): 268–282. doi:10.1139/f80-034.
- Froese, R., and Pauly, D. 2008. FishBase [online]. Available at www.fishbase.org [accessed 7 December 2008].
- Gilroy, D. 2007. Home range and seasonal movements of taimen, *Hucho taimen*, in the Eg and Uur rivers, Mongolia. M.S. thesis, Limnology and Marine Science, University of Wisconsin – Madison, Madison, Wis.
- Grafton, R.Q., Arnason, R., Bjørndal, T., Campbell, D., Campbell, H.F., Clark, C.W., Connor, R., Dupont, D.P., Hannesson, R., Hilborn, R., Kirkley, J.E., Kompas, T., Lane, D.E., Munro, G.R., Pascoe, S., Squires, D., Steinshamn, S.I., Turriss, B.R., and Wenginger, Q. 2006. Incentive-based approaches to sustainable fisheries. *Can. J. Fish. Aquat. Sci.* **63**(3): 699–710. doi:10.1139/f05-247.
- Gunderson, D.R., Zimmerman, M., Nichol, D.G., and Pearson, K. 2003. Indirect estimates of natural mortality rate for arrowtooth flounder (*Atheresthes stomias*) and darkblotched rockfish (*Sebastes crameri*). *Fish. Bull.* **101**: 175–182.
- Guy, C.S., Blankenship, H.L., and Nielsen, L.A. 1996. Tagging and marking. *In* Fisheries techniques. Edited by B.R. Murphy and D.W. Willis. American Fisheries Society, Bethesda, Md. pp. 353–379.
- Haab, T., Whitehead, J.C., and McConnell, T. 2001. The economic value of marine recreational fishing in the southeast United States: 1997 southeast economic data analysis. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, NOAA Technical Memorandum NMFS-SEFSC-446.
- Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment. Chapman & Hall, London, UK.
- Hilborn, R., Orensanz, J.M., and Parma, A.M. 2005. Institutions, incentives and the future of fisheries. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **360**(1453): 47–57. doi:10.1098/rstb.2004.1569. PMID:15744918.
- Holčík, J. 1995. Threatened fishes of the world — *Hucho hucho* (Linnaeus, 1758) (Salmonidae). *Environ. Biol. Fishes*, **43**(1): 105–106. doi:10.1007/BF00001822.
- Holčík, J., Hensel, K., Nieslanik, J., and Skacel, L. 1988. The Eurasian huchen, *Hucho hucho*, largest salmon of the world. Kluwer Academic Publishers, Boston, Mass.
- Holland, S.M., and Ditton, R.B. 1992. Fishing trip satisfaction: a typology of anglers. *N. Am. J. Fish. Manage.* **12**(1): 28–33. doi:10.1577/1548-8675(1992)012<0028:FTSATO>2.3.CO;2.
- Jensen, A.L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Can. J. Fish. Aquat. Sci.* **53**(4): 820–822. doi:10.1139/cjfas-53-4-820.

- Jolly, G.M. 1965. Explicit estimates from capture–recapture data with both death and immigration-stochastic model. *Biometrika*, **52**: 225–247. PMID:14341276.
- Kelch, D., Lichtkoppler, F., Sohngen, B., and Daigneault, A. 2006. The value of steelhead (*Onchorhynchus mykiss*) angling in Lake Erie tributaries. *J. Gt. Lakes Res.* **32**(3): 424–433. doi:10.3394/0380-1330(2006)32[424:TVOSOM]2.0.CO;2.
- Kimura, D. 1988. Stock–recruitment curves as used in the stock-reduction analysis model. *J. Cons. Int. Explor. Mer.* **44**: 253–258.
- Mace, P.M., and Doonan, I.J. 1988. A generalized bioeconomic simulation model for fish dynamics. Fisheries Research Center, P.O. Box 297, Wellington, New Zealand.
- Matveyev, A.N., Pronin, N.M., Samusenok, V.P., and Bronte, C.R. 1998. Ecology of Siberian taimen *Hucho taimen* in the Lake Baikal Basin. *J. Gt. Lakes Res.* **24**(4): 905–916.
- Maunder, M.N. 2004. Population viability analysis based on combining Bayesian, integrated, and hierarchical analyses. *Acta Oecol.* **26**(2): 85–94. doi:10.1016/j.actao.2003.11.008.
- McAllister, M.K., Pikitch, E.K., and Babcock, E.A. 2001. Using demographic methods to construct Bayesian priors for the intrinsic rate of increase in the Schaefer model and implications for stock rebuilding. *Can. J. Fish. Aquat. Sci.* **58**(9): 1871–1890. doi:10.1139/cjfas-58-9-1871.
- McConchie, J.A., and Toleman, I.E.J. 2003. Boat wakes as a cause of riverbank erosion: a case study from the Waikato River, New Zealand. *J. Hydrol. (Amst.)*, **42**: 163–179.
- Musick, J. 1999. Life in the slow lane: ecology and conservation of long-lived marine animals. American Fisheries Society, Bethesda, Md.
- Myers, R.A., and Barrowman, N.J. 1996. Is fish recruitment related to spawner abundance. *Fish. Bull.*, **94**: 707–724.
- Myers, R.A., Bowen, K.G., and Barrowman, N.J. 1999. Maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.* **56**(12): 2404–2419. doi:10.1139/cjfas-56-12-2404.
- Myers, R.A., Barrowman, N.J., Hilborn, R., and Kehler, D.G. 2002. Inferring Bayesian priors with limited direct data: applications to risk analysis. *N. Am. J. Fish. Manage.* **22**(1): 351–364. doi:10.1577/1548-8675(2002)022<0351:IBPWLD>2.0.CO;2.
- Ocock, J., Baasanjav, G., Baillie, G., Erdenebat, M., Kotellat, M., Mendsaikhan, B., and Smith, K. 2006. Summary conservation action plans for Mongolian fishes. Zoological Society of London, London, UK.
- Ostrom, E., Burger, J., Field, C.B., Norgaard, R.B., and Policansky, D. 1999. Revisiting the commons: local lessons, global challenges. *Science (Washington, D.C.)*, **284**(5412): 278–282. doi:10.1126/science.284.5412.278. PMID:10195886.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. Int. Explor. Mer.* **39**: 175–192.
- Pauly, D. 1995. Anecdotes and the shifting base-line syndrome of fisheries. *Trends Ecol. Evol.* **10**(10): 430. doi:10.1016/S0169-5347(00)89171-5.
- Pollock, K.H., Nichols, J.D., Brownie, C., and Hines, J.E. 1990. Statistical inference for capture–recapture experiments. *Wildlife Monographs No. 107*.
- Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J., Jackson, L., and Shuter, B.J. 2002. Canada's recreational fisheries: the invisible collapse? *Fisheries*, **27**(1): 6–17. doi:10.1577/1548-8446(2002)027<0006:CRF>2.0.CO;2.
- Reid, I.S. 2007. Influence of motorboat use on thermal refuges and implications to salmonid physiology in the lower Rogue River, Oregon. *N. Am. J. Fish. Manage.* **27**(4): 1162–1173. doi:10.1577/M06-061.1.
- Schnute, J.T. 1985. A general theory for analysis of catch and effort data. *Can. J. Fish. Aquat. Sci.* **42**(3): 414–429. doi:10.1139/f85-057.
- Schnute, J.T. 1987. A general fishery model for a size-structured fish population. *Can. J. Fish. Aquat. Sci.* **44**(5): 924–940. doi:10.1139/f87-111.
- Seber, G.A.F. 1965. A note on multiple-recapture census. *Biometrika*, **52**: 249–259. PMID:14341277.
- Sharp, D., and Bernard, D.R. 1988. Precision of estimated ages of lake trout from five calcified structures. *N. Am. J. Fish. Manage.* **8**(3): 367–372. doi:10.1577/1548-8675(1988)008<0367:POEAOL>2.3.CO;2.
- Stubblefield, A., Chandra, S., Eagan, S., Tuvshinjargal, D., Davaadorz, G., Gilroy, D., Sampson, J., Thorne, J., Allen, B.C., and Hogan, Z. 2005. Impacts of gold mining and land use alterations on the water quality of central Mongolian rivers. *Integr. Environ. Assess. Manag.* **1**(4): 365–373. doi:10.1897/1551-3793(2005)1[365:IOGMAL]2.0.CO;2. PMID:16639903.
- Vander Zanden, M.J., Joppa, L.N., Allen, B.C., Chandra, S., Gilroy, D., Hogan, Z., Maxted, J.T., and Zhu, J. 2007. Modeling spawning dates of *Hucho taimen* in Mongolia to establish fishery management zones. *Ecol. Appl.* **17**(8): 2281–2289. doi:10.1890/06-1781.1. PMID:18213968.
- Walters, C.J., and Korman, J. 1999. Linking recruitment to trophic factors: revisiting the Beverton–Holt recruitment model from a life history and multispecies perspective. *Rev. Fish Biol. Fish.* **9**(2): 187–202. doi:10.1023/A:1008991021305.
- Walters, C.J., and Martell, S.J.D. 2004. Fisheries ecology and management. Princeton University Press, Princeton, N.J.
- Walters, C.J., Martell, S.J.D., and Korman, J. 2006. A stochastic approach to stock reduction analysis. *Can. J. Fish. Aquat. Sci.* **63**(1): 212–223. doi:10.1139/f05-213.
- White, G.C., and Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**(Suppl.): 120–139. doi:10.1080/00063659909477239.
- Winemiller, K.O., and Rose, K.A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Can. J. Fish. Aquat. Sci.* **49**(10): 2196–2218. doi:10.1139/f92-242.

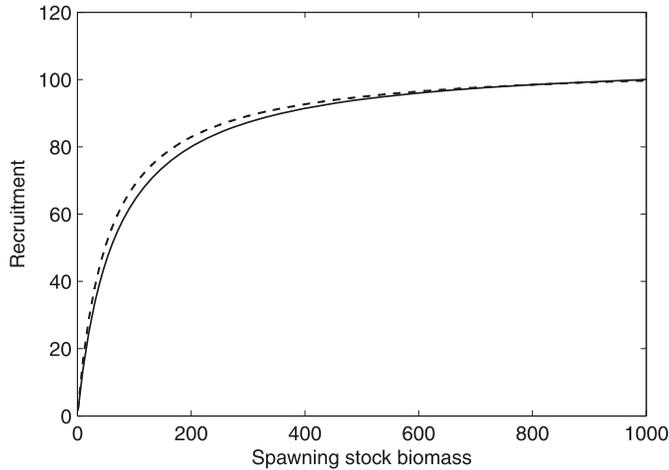
Appendix A

Beverton–Holt stock–recruit functions are frequently parameterized based on one known point on the curve (B^* , R^*) and a steepness parameter (z), defined as the proportion of unfished recruitment (R_0) produced by 20% of the unfished biomass (B_0) (Mace and Doonan 1988). B^* and R^* can be any arbitrary point on the stock–recruit curve (Kimura 1988). However, when B^* and R^* are not equal to B_0 and R_0 , the proportion of R^* produced by 20% of B^* (z^*) is not necessarily the same as z . In many cases, B_0 and R_0 are unknown, but current biomass can be estimated from surveys or mark–recapture experiments, and current equilibrium recruitment can be estimated as the product of current abundance and the annual mortality rate. When current biomass is not substantially lower than B_0 , there may be little harm in using z instead of z^* . We investigated this possibility by calculating z^* for different values of z and B^*/B_0 (Table A1). For modestly depleted populations with relatively high steepness, the effect on the stock–recruitment curve of using B^* , R^* , and z instead of z^* is minor (Fig. A1).

Table A1. The ratio of steepness defined relative to current biomass and recruitment (z^*) to steepness defined relative to unfished biomass and recruitment (z).

Steepness (z)	Current biomass (B^*) / unfished biomass (B_0)										
	0.50	0.55	0.60	0.65	0.70	0.75	0.80	0.85	0.90	0.95	0.99
0.50	0.77	0.80	0.82	0.85	0.87	0.90	0.92	0.94	0.96	0.98	1.00
0.55	0.77	0.80	0.83	0.85	0.88	0.90	0.92	0.94	0.96	0.98	1.00
0.60	0.78	0.81	0.83	0.86	0.88	0.90	0.93	0.95	0.96	0.98	1.00
0.65	0.79	0.82	0.84	0.87	0.89	0.91	0.93	0.95	0.97	0.98	1.00
0.70	0.81	0.83	0.86	0.88	0.90	0.92	0.94	0.96	0.97	0.99	1.00
0.75	0.83	0.85	0.87	0.89	0.91	0.93	0.95	0.96	0.98	0.99	1.00
0.80	0.85	0.87	0.89	0.91	0.93	0.94	0.96	0.97	0.98	0.99	1.00
0.85	0.88	0.90	0.92	0.93	0.94	0.96	0.97	0.98	0.98	0.99	1.00
0.90	0.91	0.93	0.94	0.95	0.96	0.97	0.98	0.98	0.99	0.99	1.00
0.95	0.95	0.96	0.97	0.97	0.98	0.98	0.99	0.99	0.99	1.00	1.00
0.99	0.99	0.99	0.99	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Fig. A1. A true Beverton–Holt stock–recruitment curve (solid line) defined using unfished biomass (B_0), unfished recruitment (R_0), and steepness (z) defined relative to B_0 (1000) and R_0 (100) and an estimated stock–recruit curve (broken line) defined using the points B^* (800), R^* (98.5), and z , where $z = 0.8$ and $B^* = 0.8 B_0$. Units are arbitrary.



References

Kimura, D. 1988. Stock–recruitment curves as used in the stock–reduction analysis model. *J. Cons. Int. Explor. Mer.* **44**: 253–258.
 Mace, P.M., and Doonan, I.J. 1988. A generalized bioeconomic simulation model for fish dynamics. Fisheries Research Center, P.O. Box 297, Wellington, New Zealand.