

Mechanisms of coexistence between native bull trout (*Salvelinus confluentus*) and non-native lake trout (*Salvelinus namaycush*): inferences from pattern-oriented modeling

Jake M. Ferguson, Mark L. Taper, Christopher S. Guy, and John M. Syslo

Abstract: Determining the ecological mechanisms that control population abundances is an important issue for the conservation of endangered and threatened species. We examined whether a threatened bull trout (*Salvelinus confluentus*) population could coexist at observed levels with the ecologically similar introduced species, lake trout (*Salvelinus namaycush*), using a pattern-oriented analysis of population dynamics models. We used a large suite of stage- and age-structured models to examine how both competitive and predatory interactions, combined with differing life-history strategies and species vital rates, drove salmonid coexistence patterns. In our models, an ontogenetic shift in juvenile bull trout resource use was the most important factor contributing to the two species coexistence; however, this coexistence occurred with reduced abundances in bull trout that increase the chances of extirpation for the native species. **Observed levels of competition were found to have stronger effects than predation on population abundances.** We used a pattern-oriented modeling approach to inference; this approach assumes process models that can generate patterns similar to the observed patterns are better supported than those that cannot. This methodology may find wide use on a number of data-limited fishery management and conservation problems.

Résumé : La détermination des mécanismes écologiques qui contrôlent l'abondance des populations est un problème important pour la conservation des espèces en péril et des espèces menacées. À l'aide d'une analyse basée sur les patrons des modèles de dynamique de population, nous examinons si une population menacée d'ombles à tête plate (*Salvelinus confluentus*) peut coexister aux densités observées en présence de l'espèce introduite à écologie semblable, le touladi (*Salvelinus namaycush*). Nous utilisons une importante série de modèles structurés d'après le stade et l'âge afin d'examiner comment à la fois les interactions de compétition et de prédation, combinées aux stratégies de cycle biologique et aux taux vitaux différents des espèces, expliquent les patrons de coexistence de ces salmonidés. Dans nos modèles, le changement ontogénique dans l'utilisation des ressources par les jeunes ombles à tête plate est le facteur qui contribue le plus à la coexistence des deux espèces; cependant, cette coexistence se fait à des abondances réduites chez l'omble à tête plate, ce qui augmente les chances d'extirpation de cette espèce indigène. Les niveaux observés de compétition ont des effets plus importants sur les abondances des populations que la prédation. Nous utilisons une méthodologie de modélisation centrée sur les patrons pour étudier l'interférence; cette approche présume que les modèles de processus qui peuvent produire des patrons semblables à ceux qu'on observe sont mieux appuyés que ceux qui ne le peuvent pas. Cette méthodologie pourrait s'avérer de grande utilité pour résoudre des problèmes de gestion et de conservation dans plusieurs pêches, lorsque les données sont limitées.

[Traduit par la Rédaction]

Introduction

Ontogenetic shifts occur in many taxa although their ecological functions are in many ways still not fully understood. In many species, size-based energy requirements necessitate that species change resource dependencies and interspecific interactions as they grow (Werner and Gilliam 1984). These ontogenetic shifts may provide an important mechanism for coexistence of species that occupy similar niche spaces at dif-

ferent times during their development (McCann and Yodzis 1998; Takimoto 2003). An understanding of how interacting species persist in sympatry may require knowledge of species interactions at several points in their ontogeny, because interactions between species with complex life histories can lead to biological outcomes not predicted by looking at single life-history stages (Polis and Holt 1992; Mills et al. 2004; Moll and Brown 2008). For example, three closely related maple species in Japan were shown to undergo different on-

Received 8 November 2010. Accepted 6 December 2011. Published at www.nrcresearchpress.com/cjfas on 26 March 2012. J2011-0217

Paper handled by Associate Editor William Tonn.

J.M. Ferguson, M.L. Taper, and J.M. Syslo. Department of Ecology, Montana State University, Bozeman, MT 59717, USA.

C.S. Guy. US Geological Survey, Montana Cooperative Fishery Research Unit, Montana State University, Bozeman, MT 59717, USA.

Corresponding author: Jake Ferguson (e-mail: troutinthemilk@ufl.edu).

togenetic shifts at <30 cm, promoting niche differentiation between the species and contributing to coexistence (Tanaka et al. 2008). It is well known that species interactions can change as nutritional and habitat requirements change (Werner and Gilliam 1984), but documenting and understanding their consequences can be difficult. Nevertheless, it is likely that such changes play an important role in the maintenance of species in ecological communities (Mittelbach et al. 1988; De Roos et al. 2002, 2003).

The introduction of non-native species into communities can induce negative changes in a native species through many possible pathways. Direct impacts on natives through competition or predation are well documented (Davis 2003; Kats and Ferrer 2003), as are indirect mechanisms that propagate through trophic levels or modify the behavior or abundances of predators that exploit native species (Vander Zanden et al. 1997). In this study, we examine the possible consequences of an ongoing invasion of lake trout (*Salvelinus namaycush*) into mountain lakes occupied by bull trout (*Salvelinus confluentus*) in northwestern Montana. These invasions have introduced new predatory and competitive interactions for bull trout and have repeatedly coincided with observed decreases in populations (Fredenberg 2002) and extirpation in some lakes (Donald and Alger 1993).

The ranges of lake trout and bull trout are mostly allopatric. In overlapping areas, it has been suggested that elevation historically separates the two species, though there are several examples of populations in sympatry (Donald and Alger 1993). Coexisting indigenous populations of lake trout and bull trout exist in southwest Alberta in Glacier, Clearwater, Moab, and Minnewanka lakes; unfortunately, historical population data do not exist for these lakes. In other southwestern Alberta lakes (e.g., Spray, Hector, and Bow lakes), indigenous bull trout have been extirpated with the introduction of lake trout (Donald and Alger 1993). St. Mary Lake in Montana is reported to support coexisting lake trout and bull trout populations. However, these populations may be functionally allopatric with bull trout mostly utilizing river systems while lake trout occur only in the lake (Mogen and Kaeding 2005). Because coexistence appears to be occurring in some lakes but not others, we should evaluate the role of interspecific interactions as a first step in understanding future prospects for the conservation of bull trout regionally.

The striking concordance of temporal patterns over five lakes in northwestern Montana suggests that salmonid population dynamics are driven by fundamental aspects of species' ecological differences. In this study, we seek to understand which factors allow bull trout and lake trout to coexist at observed levels, given what we know about the system. Our study uses pattern-oriented modeling (POM) with deterministic population models to identify the processes that most likely influence the persistence of bull trout at observed levels. We examined the potential of competitive and predatory interactions to match the observed coexistence patterns of empirical populations using interactive stage- and age-structured models of species' dynamics within a simplified model of the ecological community. Specifically, we examined whether lake trout and bull trout can persist at observed levels when the species compete for resources, when lake trout adults prey on bull trout subadults, or when the predation interaction is symmetric and bull trout adults

also prey on lake trout subadults. Our inferential approach allowed us to distinguish the functions that species vital rates, ontogeny, and interspecific interactions play on bull trout persistence and to determine a range of system variables consistent with observations. Because little is understood about the basic food web dynamics of these lakes and very little data are available to model food web interactions, we focused on several simple questions based on potential mechanisms of interspecific coexistence. We were interested in determining (i) what are the roles of interspecific interactions (predation and competition) on coexistence, (ii) what is the role of species ontogenetic differences in observed patterns, and (iii) do differences in species vital rates play a role in maintaining the observed relative abundances of species?

Materials and methods

Data sources

We examined gill net catches for a set of lakes in the Flathead River drainage of northwest Montana (Fig. 1). Data were available from Kintla, Bowman, and Logging lakes, as well as Lake McDonald (Meeuwig 2008; Fredenberg 2002), all located within Glacier National Park. We also analyzed data from Flathead Lake (Confederated Salish Kootenai Tribes, and Montana Fish and Wildlife Management 2006). Flathead Lake has an introduced lake trout population that appears to have achieved coexistence with the native bull trout population and is currently undergoing intensive management action (Confederated Salish Kootenai Tribes, and Montana Fish and Wildlife Management 2006). Other lakes in the system have presumably been colonized by lake trout from the original introduction in Flathead Lake (Spencer et al. 1991; Fredenberg 2002; Meeuwig 2008). All populations appear to have achieved similar equilibria, and relative abundances are currently at a ratio of approximately four lake trout for every bull trout.

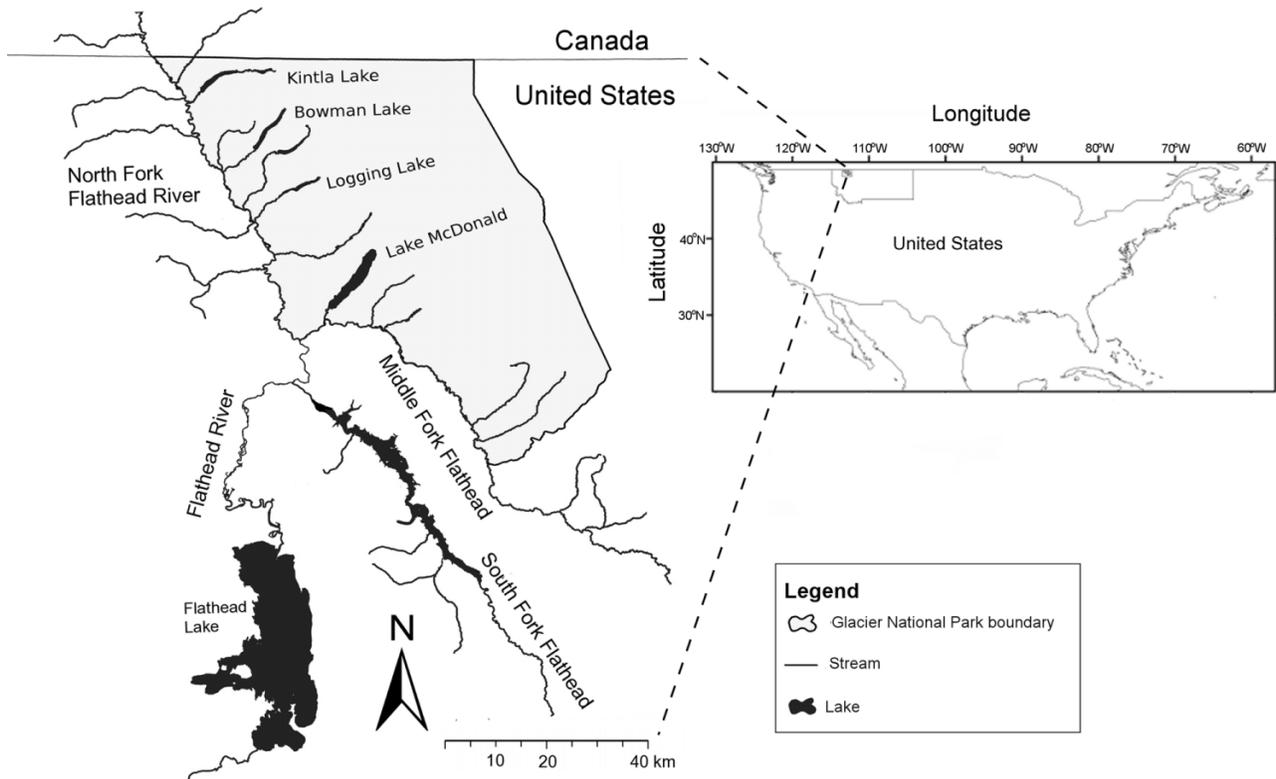
Lake trout vital rates used to parameterize our age-specific models are from a regional study (Syslo 2010). Bull trout fecundities come from Fraley and Shepard (1989). Expert opinion was used for bull trout survival rates, emergence rates, and emigration rates, for which data were unavailable (Staples 2006).

Modeling approach

We developed a suite of models to compare the contributions of species interactions (i.e., competition and predation) and biological differences (i.e., vital rates and ontogeny) with species' persistence in our study system. This allowed us to better understand the mechanisms driving empirical observations of coexistence and to differentiate between the physiological and the ecological constraints regulating bull trout populations in the presence of non-native lake trout.

We addressed our first question, the role of interspecific interactions on coexistence, by changing the type of interspecific interaction occurring between species. We examined a model with competitive interactions, a model with predatory interactions, and a null model with no interspecific interaction. The structure and strength of the interactions were based on previous empirical work and are described heuristically in the Model definitions section (see below; more detailed model definitions are given in Appendix A).

Fig. 1. Map of the upper Flathead River drainage in Montana (inset shows the location of the study region in the United States). The lakes used in the study are labeled. Study area map is adapted with permission from Fredenberg et al. (2007).

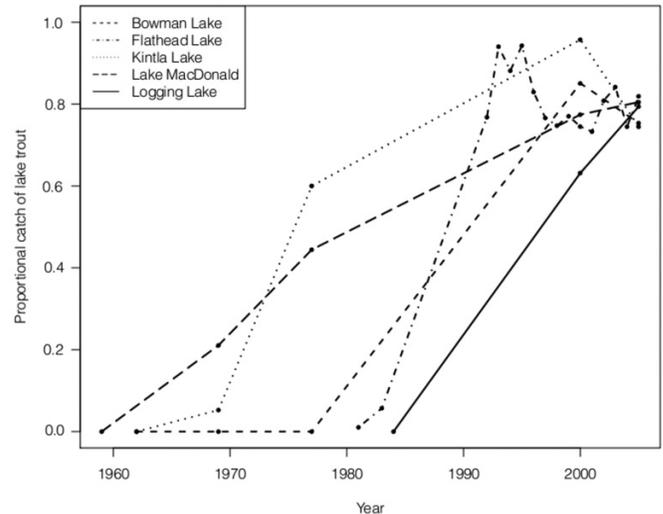


Our second question addressed the role of species' ontogenetic differences on coexistence and included the same interactions as described in the above models (competitive, predatory, and null interactions), but examined how changing species ontogeny determined persistence at the observed relative abundances. We studied hypothetical scenarios where bull trout juveniles were not spatially segregated from lake trout and either compete with lake trout juveniles or are preyed upon by lake trout adults and compared these with realistic scenarios where bull trout juveniles were spatially segregated from lake trout. These comparisons allowed us to identify the importance to coexistence of subadult bull trout rearing in streams to bull trout coexistence with lake trout.

Our third question, the importance of vital rate differences between species, was addressed by comparing species coexistence in models with species-specific vital rates with models where species have equivalent vital rates. The stage-based models parameterize both species with equivalent vital rates, while the age-based model parameterizes lake trout using data from Syslo (2010). Because age-specific vital rates have not been measured for bull trout, we were unable to build an age-structured bull trout model.

Verification of model results was difficult because only limited information was available. Therefore, we compared model predictions with general trends in the data and determined when models were consistent or inconsistent with observed patterns. This approach to model confirmation has been called pattern-based optimization or Pareto optimization (Grimm et al. 2005; Komuro et al. 2006). Models that satisfied the following conditions, termed coexistence conditions, were considered consistent with empirical observations.

Fig. 2. The proportion of lake trout in gill net samples over time in the study lakes. Proportional catch is the total number of lake trout caught divided by the sum of all lake trout and bull trout in the catch. Each closed circle represents a sample point.



There were three coexistence conditions determined from empirical patterns in the data (Fig. 2): (i) the final relative abundance of lake trout must be approximately 80% (the approximate asymptotes in Fig. 1); (ii) the time for the lake trout population to become predominant in a lake must be greater than 11 years (the minimum time at which lake trout relative abundances reach greater than 50% in Fig. 2); (iii) bull trout abundance must decrease by more than 10%.

Table 1. Our statements of the formal coexistence conditions.

Condition	Constraint	Formulation
<i>i</i>	Lake trout subadults and adults ($L_{\text{subadult+adult}}$) achieve nearly 80% the total catchable salmonids lake abundance ($L_{\text{subadult+adult}} + B_{\text{subadult+adult}}$)	$0.7 < \frac{L_{\text{subadult+adult},t=500}}{L_{\text{subadult+adult},t=500} + B_{\text{subadult+adult},t=500}} < 0.9$
<i>ii</i>	Time to lake trout predominance takes at least 11 years	$\frac{L_{\text{subadult+adult},t=11}}{L_{\text{subadult+adult},t=11} + B_{\text{subadult+adult},t=11}} \leq 0.5$
<i>iii</i>	Bull trout population in the lake ($B_{\text{subadult+adult}}$) decreases by more than 10% after 50 years	$\frac{B_{\text{subadult+adult},t=0} - B_{\text{subadult+adult},t=50}}{B_{\text{subadult+adult},t=0}} > 0.1$

Note: These conditions were used to determine whether models of bull trout and lake trout population dynamics were consistent with empirical trends.

as indicated by declining redd counts in lotic waters and reduced bull trout catches in lentic waters of the Flathead Drainage (Fredenberg 2002; Staples et al. 2005). A more formal description of these conditions is also provided (Table 1).

Model definitions

Null model

This section describes the basic life history of lake trout and bull trout. Here, stage transitions and intraspecific competition terms as well as the parameterizations of our stage- and age-structured models are defined. These basic life-history models contained no interspecific interactions; therefore, they were guaranteed a priori to fail to meet coexistence condition *iii*, which requires a drop in bull trout density after lake trout invasion. However, these models provided a useful baseline for evaluating how interactions in the lake affected the relative abundance of species and were used as a null model for comparison with the interactive models.

Bull trout express several ontogenetic shifts during their life history. Juveniles feed on invertebrates but switch to piscivory as they reach larger sizes (about 500 mm in length) (Guy et al. 2011). Bull trout also show developmental shifts in location. Juveniles rear in the stream for 2–3 years and then outmigrate to the lake (Fraley and Shepard 1989). Most bull trout populations in northwestern Montana display a lacustrine–adfluvial life history; adults live in lakes but display an ontogenetic shift when they reach maturity (age 5 or 6) and migrate upstream to tributaries to spawn in the fall.

By contrast, lake trout have a purely lacustrine life history. Lake trout spawning occurs in the fall. Age at maturity for female lake trout is variable throughout their range, likely because of variation in resource abundance and community composition leading to differences in growth rate (Martin and Olver 1980). Age at 50% maturity for female lake trout varies from 6 to 15 years old for populations in the Intermountain West (Dux 2005; Cox 2010; Syslo 2010). Juveniles feed on invertebrates and adults are primarily piscivorous, and the switch to piscivory occurs around 500 mm (Guy et al. 2011).

Our single sex null model was discrete in time and density-dependent. The stage-structured version of the model is referred to as the life-history stage model (LH-stage), and the number of life-history stages was determined through ontogenetic considerations. Because juvenile bull trout rear in headwater streams and then out-migrate to lakes as subadults, juveniles utilize different habitat and resources than subadults and adults. Bull trout subadults also use different habitat than adults. Conversely, all stages of the lake trout life history oc-

cur in the lake. Juvenile, subadult, and adult lake trout all feed in different areas of the lake and on different food sources (Beauchamp et al. 2006), thus we assumed there is no intraspecific competition among stages. We assumed density dependence affects survival in the juvenile and subadult stages for both lake trout and bull trout (known parameter values for this model are defined in Appendix C, Table C1). These values are adapted from Staples (2006) and their sources are discussed extensively therein.

Our stage-structured populations at time t for bull trout (B_t) and lake trout (L_t) are defined by the state vectors

$$B_t = \begin{bmatrix} B_{\text{juv},t} \\ B_{\text{subadult},t} \\ B_{\text{adult},t} \end{bmatrix}$$

and

$$L_t = \begin{bmatrix} L_{\text{juv},t} \\ L_{\text{subadult},t} \\ L_{\text{adult},t} \end{bmatrix}$$

where the subscript notations juv, subadult, and adult are used to keep track of the juvenile, subadult, and adult stages, respectively. Juvenile density-dependent survival in both lake trout and bull trout were modeled with the Ricker equation, consistent with analysis of juvenile bull trout by Johnston et al. (2007). Juvenile survival was modeled as

$$s_{\text{juv}}(X_{\text{juv},t}) = s_{\text{juv}} \cdot \exp\left(-\frac{X_{\text{juv},t}}{K_{X,\text{juv}}}\right)$$

where s_{juv} is the intrinsic survival rate of juveniles of species X , $X_{\text{juv},t}$ is the juvenile abundance for the species at time t , and $K_{X,\text{juv}}$ is the carrying capacity for the juvenile stage of species X , where X can be L (lake trout) or B (bull trout). We model young of the year (YOY) to have identical density-dependent effects as the juvenile class, but with a different intrinsic survival rate, s_{YOY} . YOY survival is modeled as

$$s_{\text{YOY}}(X_{\text{juv},t}) = s_{\text{YOY}} \cdot \exp\left(-\frac{X_{\text{juv},t}}{K_{X,\text{juv}}}\right)$$

We assumed that subadult bull trout and lake trout followed discrete logistic density dependence survival because we have no evidence on the form of density dependence in the subadult stage. We also assumed that the environmental lim-

itations for lake trout and bull trout subadults are the same for both species; therefore, they have the same carrying capacity, defined as K_{subadult} . Subadult survival was then given by

$$S_{\text{subadult}}(X_{\text{subadult},t}) = s_{\text{subadult}} \cdot \left(1 - \frac{X_{\text{subadult},t}}{K_{\text{subadult}}}\right)$$

where s_{subadult} is the intrinsic subadult survival rate, $X_{\text{subadult},t}$ is the subadult abundance at time t , and K_{subadult} is the total carrying capacity for both subadult species in the lake. There

$$(1) \quad \mathbf{T}_{X,t} = \begin{bmatrix} S_{\text{juv}}(X_{\text{juv},t}) \cdot (1 - m_{\text{juv}}) & 0 & p_{\text{spawn}} \cdot \frac{f_{\text{adult}}}{2} \cdot S_{\text{YOY}}(X_{\text{juv},t}) \\ S_{\text{juv}}(X_{\text{juv},t}) \cdot m_{\text{juv}} & S_{\text{subadult}}(X_{\text{subadult},t}) \cdot (1 - m_{\text{subadult}}) & 0 \\ 0 & S_{\text{subadult}}(X_{\text{subadult},t}) \cdot m_{\text{subadult}} & s_{\text{adult}} \end{bmatrix}$$

where p_{spawn} is the proportion of females that spawn in a year, and f_{adult} is the number of offspring produced per female (an equal sex ratio is assumed).

The age-structured null model for lake trout uses species-specific vital rates from lake trout in Yellowstone Lake (Systo 2010; Appendix C, Table C2). We chose to use an age-structured model because reproductive rates increase with age. Although we use a Leslie matrix to define age-specific growth and fecundity, interspecific and intraspecific interactions were determined through stages, where the sum of ages 0–2 are the juvenile stage, ages 3–5 are the subadult stage, and ages 6+ are the adult stage. Density-dependent survival for the subadults is

$$S_{\text{juv}}(X_{\text{juv},t}) = s_{\text{age}} \cdot \exp\left(-\frac{X_{\text{juv},t}}{K_{X,\text{juv}}}\right)$$

where s_{age} is the age-specific survival for ages 0–2, and $X_{\text{juv},t}$ is the total abundance for juveniles of ages 0–2. Similarly, subadult survival is given by

$$S_{\text{subadult}}(X_{\text{subadult},t}) = s_{\text{age}} \cdot \left(1 - \frac{X_{\text{subadult},t}}{K_{\text{subadult}}}\right)$$

where s_{age} is the age-specific survival for ages 3–5. Adult survival was modeled as density independent.

Predation model

Mature lake trout are known to prey on bull trout in Flathead Lake (Beauchamp et al. 2006). Our predation models used the same basic structures described in the null life-history model, but were modified to incorporate predation terms. We assumed that the number of individuals eaten by lake trout adults reduced subadult bull trout abundances proportionally. This interaction was assumed to obey a Lotka–Volterra type I functional response (Begon et al. 2005), $-\alpha_{\text{subadult}} \cdot L_{\text{adult}} \cdot B_{\text{subadult}}$, where the predation constant is α_{subadult} (proportion of the subadult bull trout population consumed per predator per year). The value of the type I response gives the total number of bull trout subadults eaten in the population. This modifies our formula for bull trout subadult survival in the LH-stage model to

are then three important unknown quantities that determine the final abundances of each species. These quantities are the bull trout juvenile carrying capacity ($K_{\text{juv},B}$), lake trout juvenile carrying capacity ($K_{\text{juv},L}$), and combined carrying capacity for both species subadults in the system (K_{subadult}). We let the transition rates for juvenile and subadult stages be defined by m_x , where x denotes the stage. The stage-structured matrix model for species X is given by $X_{t+1} = \mathbf{T}_{X,t} X_t$, where the transition matrix is given by

$$S_{\text{subadult}}(B_{\text{subadult},t}, L_{\text{subadult},t}) = s_{\text{age}} \cdot \left(1 - \frac{B_{\text{subadult},t}}{K_{\text{subadult}}}\right) - \alpha_{\text{subadult}} \cdot L_{\text{adult}}$$

The total number of subadult bull trout eaten in a year is then added to the lake trout juvenile population as an increase in fecundity with conversion efficiency $e = 0.1$ (proportional number of prey items converted to new predators per year; Rand and Stewart 1998). The alteration of these terms to eq. 1 is shown in Appendix A (eqs. A.1, A.2).

Predation by lake trout on bull trout was observed in Flathead Lake in 4 out of 497 lake trout stomachs (Beauchamp et al. 2006). To determine an α_{subadult} consistent with observations, we assumed the observed Flathead Lake populations were near equilibrium when observations were made and that bull trout are identifiable in lake trout stomachs for 1 day before being digested. The observed number of bull trout consumed in a year per lake trout adult, ϕ , was then

$$\phi = \frac{X}{L_{\text{adult}}} \cdot 365 = 2.9$$

where ϕ is the number of bull trout subadults consumed in a day by a lake trout adult. The predation coefficient, α_{subadult} , can be then be written as

$$\alpha_{\text{subadult}} = \frac{X}{L_{\text{adult}} \cdot B_{\text{subadult}}}$$

which can be rewritten $\alpha_{\text{subadult}} \cdot B_{\text{subadult}} = \phi$. We used a bisection search algorithm (Burden and Faires 2000) to find a predation coefficient that matched the observed predation rate from Flathead Lake at population equilibrium.

Predation models with the same vital rates (P-stage model) were compared with a model parameterized with species-specific vital rates (P-age model). We also compared the bull trout ontogenetic shift in habitat use (P-age model) with a model where bull trout maintain a fully lacustrine life history (a life-history strategy that is not observed in the study area). This change in ontogeny allowed predation by lake trout adults on bull trout juveniles (P-age-lac model). We used this suite of models to compare differences in predictions due to species-specific vital rates versus differences due to ontogenies. To explore behavior in the P-age-lac model, we

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by NATGEORIBF on 03/29/12 For personal use only.

simulated dynamics over a range of possible juvenile predation rates, given by α_{juv} , and introduced a Lotka–Volterra interaction term into the bull trout juvenile stage, $-\alpha_{\text{juv}} \cdot L_{\text{adult}} \cdot B_{\text{juv}}$. We also tested the impact of our assumption of no predation on lake trout subadults by bull trout adults by conducting simulations including an equal predation interaction of bull trout adults on lake trout subadults (P-age-symmetric model).

Competition models

Previous work on the diet of sympatric populations of lake trout and bull trout found substantial diet overlap between the two species (Meeuwig et al. 2011; Guy et al. 2011). Further evidence from stable isotope analysis in the Flathead drainage suggests that lake trout and bull trout occupy a similar feeding niche (Meeuwig et al. 2011); thus, resource competition between lake trout and bull trout may also be an important factor in regulating abundances.

We estimated competition coefficients between lake trout and bull trout from a previous diet analysis on allopatric populations (Donald and Alger 1993). We assumed competition occurs only between subadult fish because adult abundances are low relative to their prey base, so are not likely to be prey limited. For the stage-structured model (C-stage), the competitive interaction modifies the $S_{\text{subadult}}(X_{\text{subadult},t})$ term in eq. 1. We model this interaction using the Lotka–Volterra competitive interaction equations so that survival of subadults is given by

$$S_{\text{subadult}}(X_{\text{subadult},t}, Y_{\text{subadult},t}) = s_{\text{subadult}} \cdot \left(1 - \frac{X_{\text{subadult},t} + \beta_{X,Y} Y_{\text{subadult},t}}{K_{\text{subadult}}} \right)$$

where s_{subadult} is the intrinsic subadult survival rate for species X , which competes with species Y , and $\beta_{X,Y}$ is the competitive impact of species Y on species X . In the age-structured competition model (C-age), the competitive effect of species X on species Y is

$$S_{\text{subadult}}(X_{\text{subadult},t}, Y_{\text{subadult},t}) = s_{\text{age}} \cdot \left(1 - \frac{Y_{\text{subadult},t} + \beta_{Y,X} X_{\text{subadult},t}}{K_{\text{subadult}}} \right)$$

where s_{age} is the survival for ages 3–5, and $X_{\text{subadult},t}$ and $Y_{\text{subadult},t}$ are the subadult abundances for ages 3–5 of species X and Y , respectively. The values $\beta_{B,L} = \beta_{L,B} = 0.5$, $\beta_{B,L} = \beta_{L,B} = 0.8$, and $\beta_{B,L} = \beta_{L,B} = 1$ were all explored in our analysis.

Competition coefficients, $\beta_{j,k}$, were estimated using the niche overlap formulation from MacArthur and Levins (1967):

$$\beta_{j,k} = \frac{\sum_i p_{i,j} p_{i,k}}{\sqrt{\sum_i p_{i,j}^2}}$$

where the p_{ij} and p_{ik} terms represent the proportional use of the i th resource by species j and k , respectively. Confidence intervals on coefficients were estimated by bootstrapping diet observations. We note that diet overlap may not necessarily denote the competitive effect of one species upon another

(Lawlor 1980). For example, this measure does not take into account differences in habitat use, size differences between individuals of different species, or territorial behavior.

As in the predation model, we compared models with the same vital rates (C-stage model) with those with species-specific vital rates (C-age model) to understand how important vital rate differences are to coexistence. We also removed the lacustrine–adfluvial ontogenetic shift of bull trout by allowing interspecific competition to occur in juveniles as well as subadults (C-stage-lac and C-age-lac models). We assumed that juveniles were ecologically equivalent and therefore had competition coefficients equal to 1. This comparison between life-history strategies allowed us to determine the importance of the spatial distribution of habitat use on coexistence. Although we assume that adult salmonids do not compete for resources, it is likely that adults do compete at some level; therefore, we tested our assumption of no adult competition by including an interspecific adult interaction, but with the assumption that adult carrying capacities were the same as subadult carrying capacities (C-age-adult).

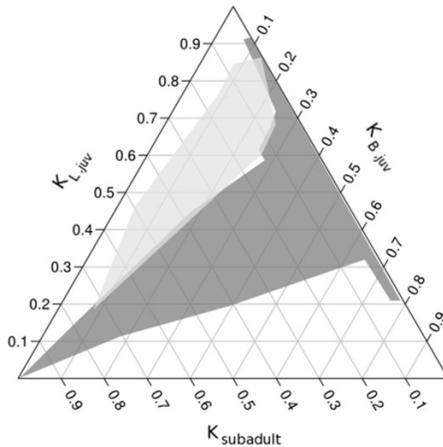
Simulation procedures

All model simulations were conducted using the R software environment (R Development Core Team 2010). Because the density dependence parameters $K_{L,\text{juv}}$, $K_{B,\text{juv}}$, and K_{subadult} were unknown for this system, we explored parameter values in $\{1 \times 10^2, \dots, 1 \times 10^6\}$, equally spaced on the log scale with 25 values for each parameter. All simulations were initialized with bull trout at equilibrium population levels for the given parameter values. For stage-based models, lake trout populations were initialized with one female adult, while for age-based models, lake trout were initialized with one age 6 adult. These low levels are consistent with genetic evidence on the size of the founding lake trout population in nearby Swan Lake (Kalinowski et al. 2010). We ran simulations out to 500 time steps (years) and evaluated the final abundances and temporal dynamics in terms of the quantities defined in Table 1.

Presentation of results

The sating of coexistence conditions for each model is presented in terms of de Finetti diagrams or triangle plots. Triangle plots provide a way to visualize three variables in a two-dimensional space when those variables are constrained to sum to a constant (Cannings and Edwards 1968). The parameters driving observed patterns are the distribution of carrying capacities at varying life stages ($K_{B,\text{juv}}$, $K_{L,\text{juv}}$, and K_{subadult}). Each coordinate point in the triangle plot space is constrained to sum to one; thus, we normalized each K variable by the sum of all three K values. Each axis is then read as a proportion of the sum of all K values. Along a triangle axis, the scale is from 0 to 1, each value representing the proportional contribution of that variable to the sum. This is a useful representation in our study system because it is not absolute values of carrying capacities that drive dynamics; it is the relative size of those carrying capacities that drive observed abundance patterns. Simulation results showing this scale independence are presented (Appendix B). These plots allowed us to explore a wide range of carrying capacity parameterizations for our system and present those that were consistent with the coexistence conditions.

Fig. 3. Results for models with no interaction between lake trout and bull trout. The darker region denotes where the LH-age model meets coexistence conditions *i* and *ii*, while the lighter region highlights where the LH-stage model meets coexistence conditions *i* and *ii*. The three axes are the three carrying capacities in the lake–stream system. $K_{L,juv}$ is the relative juvenile lake trout carrying capacity in the lakes (with levels indicated by horizontal lines), $K_{B,juv}$ is the relative juvenile bull trout carrying capacity in the stream (with levels indicated by forward leaning lines, /), and $K_{subadult}$ is the relative subadult lake trout and bull trout carrying capacity in the lake (with levels indicated by backward leaning lines, \).



Results

We found that in all models the limiting coexistence condition was condition *i*, that the final relative abundance of lake trout subadults and adults must be approximately 80%. When condition *i* was met, conditions *ii* and *iii* were always satisfied, excluding the null models where condition *iii* is not met by definition.

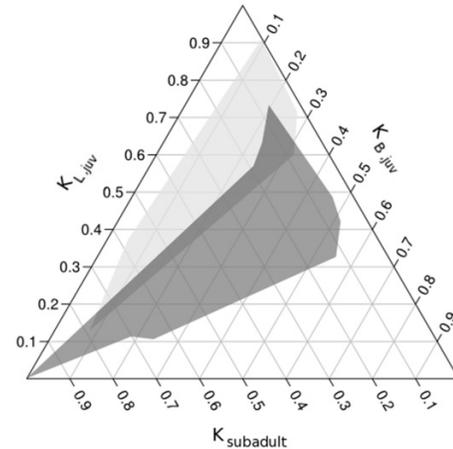
Null model

In the model without interspecific interactions, it was impossible to match the observed coexistence conditions because condition *iii* (i.e., bull trout abundance must decrease by at least 10%) cannot be met. Thus, differences in vital rates alone cannot be responsible for the observed coexistence patterns between the two species. If we ignore the third coexistence condition, there is a broad range of carrying capacities that are consistent with conditions *i* and *ii* (as presented in Fig. 3). The LH-age model had a different equilibrium state than the LH-stage model because of differences in vital rates. The equilibrium conditions were also met over a wider range of carrying capacities in the LH-age model (Fig. 3).

Predation

The inclusion of predation on bull trout subadults changed the range of predictions in the LH-stage and LH-age models from the null models, but only slightly (Figs. 3 and 4). The addition of extra offspring due to predation effects had little effect on lake trout production because they reached the juvenile carrying capacity quickly. However, predation did depress bull trout populations sufficiently so that coexistence condition *iii* could be met. The range of carrying capacity parameters over which coexistence occurs in the P-age model is

Fig. 4. Plot of the areas that meet the coexistence criterion for predation models. The darker region denotes where the P-age model meets the three observed coexistence conditions, while the lighter region highlights where the P-stage model meets the observed coexistence conditions. The three axes are the three carrying capacities in the lake–stream system. $K_{L,juv}$ is the relative juvenile lake trout carrying capacity in the lakes (with levels indicated by horizontal lines), $K_{B,juv}$ is the relative juvenile bull trout carrying capacity in the stream (with levels indicated by forward leaning lines, /), and $K_{subadult}$ is the relative subadult lake trout and bull trout carrying capacity in the lake (with levels indicated by backward leaning lines, \).



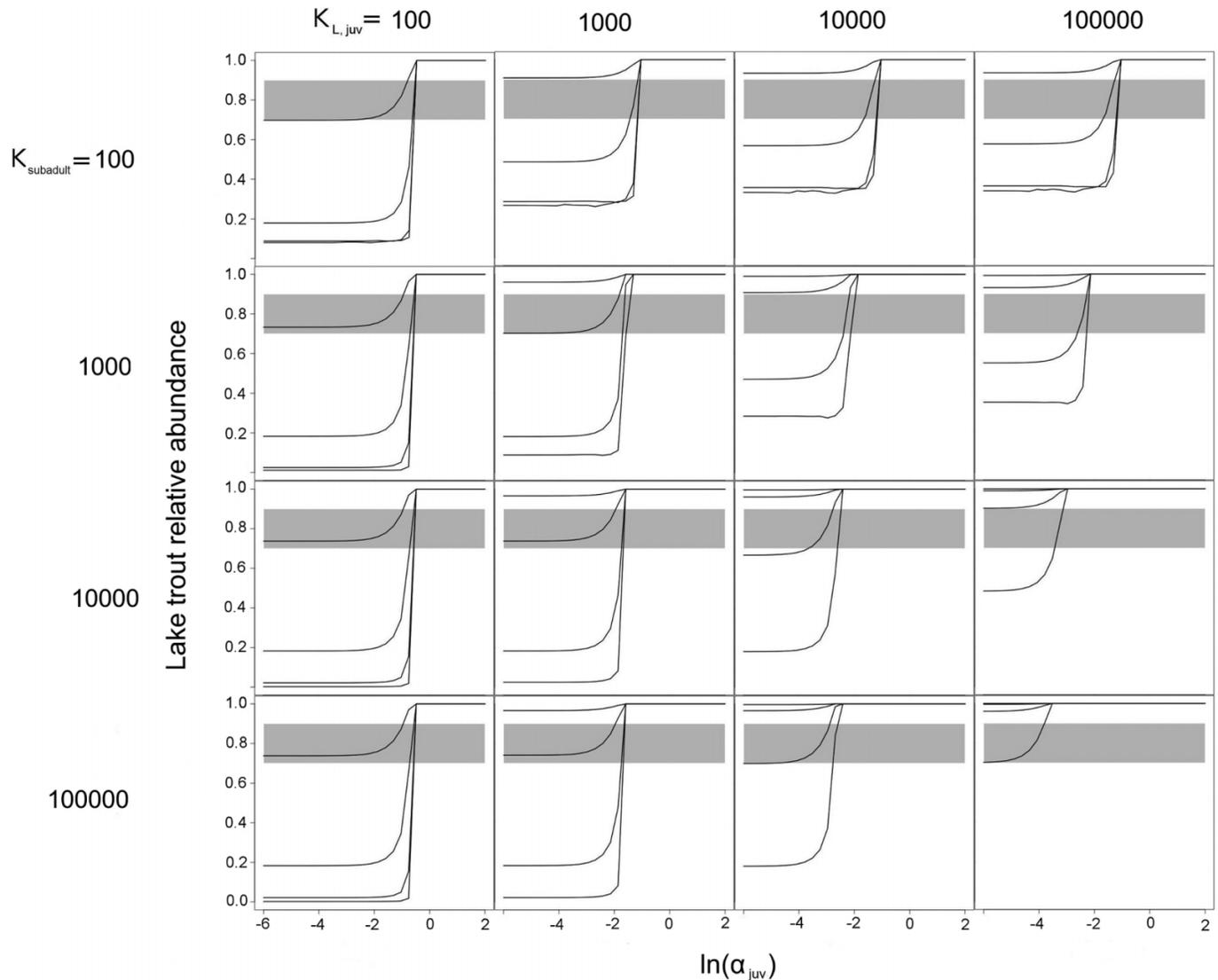
much of the range for $K_{subadult}$ (~ 0.05 – 1) and $K_{L,juv}$ (~ 0 – 0.7), but on the lower end of $K_{B,juv}$ (~ 0 – 0.5) (Fig. 4).

In the P-age-lac model, very low levels (< 0.5 individuals consumed per lake trout adult per year) of juvenile predation, in addition to empirically observed levels of subadult predation, were found to drive bull trout populations to extirpation (Fig. 5). We also tested the model assumption of no predation by bull trout adults on lake trout subadults by including a symmetric interaction with bull trout adults feeding on lake trout subadults in the P-age-symmetric model. We found that our predictions were sensitive to this interaction, and our predictions on whether the populations could coexist changed substantially at observed levels (Fig. 6), indicating that our results are sensitive to our model assumption of no bull trout predation on lake trout.

Competition

Estimated diet overlap coefficients between lake trout and bull trout for Hector Lake were estimated as $\beta_{B,L} = 0.63$ (95% confidence interval (CI), 0.25–0.98) and $\beta_{L,B} = 0.78$ (95% CI, 0.31–1.22); for Glacier Lake they were $\beta_{B,L} = 0.44$ (95% CI, 0.16–0.81) and $\beta_{L,B} = 0.48$ (95% CI, 0.12–0.95). We explored a range of subadult competition values in our simulations. When $\beta_{B,L} = \beta_{L,B} = 1$, coexistence occurred for the C-age model for $K_{B,juv}$ (~ 0.1 – 1), $K_{subadult}$ (~ 0 – 0.8), and the lower end of $K_{L,juv}$ (~ 0 – 0.2). As the competition coefficient decreased, the coexistence pattern became more similar to the LH-age models (Fig. 7), except that in the LH-age model condition *iii* was not satisfied. Allowing juvenile competition in the C-age-lac model by removing the bull trout's ontogenetic shift reduced the predicted range of coexistence considerably, to a single line, for both C-stage-lac and C-age-lac models (Fig. 8).

Fig. 5. Results from the P-age-lac model, which includes predation by lake trout adults on bull trout juveniles. Each row corresponds to the labeled K_{subadult} values, and each column corresponds to the labeled $K_{L,\text{juv}}$ values. The lines inside each plot correspond to a $K_{B,\text{juv}}$ value; from the bottom line to the top line in each plot $K_{B,\text{juv}}$ is 100, 1000, 10 000, and 100 000, respectively. The x axis varies the predation coefficient α_{juv} . Grey regions in each plot correspond to the range of coexistence criterion i . The value of α_{juv} where bull trout go extinct is independent of $K_{B,\text{juv}}$.



Discussion

We used a suite of two-species deterministic models to examine whether coexistence is possible between native bull trout and non-native lake trout and to identify mechanisms that play a role in controlling system dynamics. Our goal was not to make precise predictions for the system, but rather to understand if lake trout and bull trout can coexist at existing levels, and if so, what factors contribute to coexistence. Although this method of inference is useful, we refrain from making recommendations for management actions, which are inherently a risk assessment process, and therefore need an explicit probability framework. However, by better understanding the mechanisms limiting bull trout populations, we might also provide insight on current efforts to conserve bull trout.

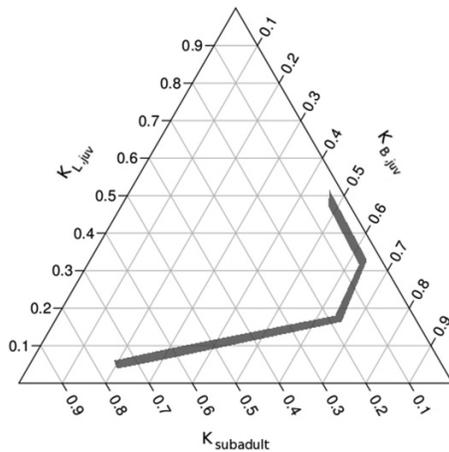
Based on empirical evidence, it is not clear that these two species will coexist over time; our analysis provides the first

evidence that persistent coexistence at current levels is a possible outcome given the information available. Our results suggest that bull trout populations are more sensitive to interspecific competitive interactions (C-age model) between subadults than to predation on subadults (P-age model), a conclusion that is conditional on our model assumptions.

Although our results appear robust when competition between adults exists (C-age-adult model), they are sensitive to our assumptions about predation. The addition of predation on juvenile bull trout by lake trout adults (P-age-lac model) and predation by bull trout adults on lake trout subadults (P-age-symmetric model) led to substantially different predictions in our P-age model, suggesting that more needs to be known on interspecific predatory interactions.

We attempted to identify the role that interspecific interactions have on species coexistence. Both predatory and competitive interactions, at levels consistent with observations,

Fig. 6. Plot of the areas that meet the coexistence criteria for the P-age-symmetric model. The three axes are the three carrying capacities in the lake–stream system. $K_{L,juv}$ is the relative juvenile lake trout carrying capacity in the lakes (with levels indicated by horizontal lines), $K_{B,juv}$ is the relative juvenile bull trout carrying capacity in the stream (with level indicated by forward leaning lines, /), and $K_{subadult}$ is the relative subadult lake trout and bull trout carrying capacity in the lake (with levels indicated by backward leaning lines, \).



allowed coexistence between species. However, predictions from the P-stage and P-age predation models were similar to the null model, while C-stage and C-age models predictions were quite different. The shift in dynamics due to competitive interactions shows that predation in these systems is not strong enough to drive changes in relative abundances. It also suggests that perturbations to current levels of competition may severely influence salmonid species relative abundances. Competition between subadults in the C-age model was shown to provide lake trout a mechanism to achieve coexistence at observed levels even when there is relatively little habitat available (i.e., lower $K_{L,juv}$).

We also attempted to identify the role of differences between species life histories as mechanisms for coexistence. In the C-age-lac and P-age-lac models, we removed resource partitioning between the juveniles of the two species, and the system dynamics were changed considerably. In the C-age-lac model, the coexistence regions collapse to single lines when juveniles compete. In the P-age-lac model, the bull trout population can only tolerate very low levels of predation on juveniles before going extinct. Our results suggest that current abundances are relatively insensitive to current levels of predation; however, introducing predation onto juvenile bull trout may have negative consequences for bull trout populations. Such an interaction does not occur in our systems, but the degradation of bull trout juvenile rearing habitat may lead juveniles to emigrate to the lake earlier, which could increase predation rates. Thus our results suggest that the bull trout ontogenetic shift is fundamentally important in determining when and where these populations can coexist.

Finally, we attempted to identify whether differences in species vital rates play a role in the observed coexistence patterns; we found that vital rates determined the relative carrying capacities where coexistence occurred. Species-specific differences (comparing a stage model with the corresponding

age model) in vital rates broadened the range of predicted carrying capacities where our observed coexistence conditions were met in both the predation and competition models; however, they did not determine whether the empirical coexistence conditions occurred.

We found that coexistence can occur over a broad range of stream and lake carrying capacities, indicating that there are still a number of critical data gaps to be filled to make more detailed predictions about coexistence. Our models use a parameterization arrived at by an expert panel of regional fisheries biologists (Staples 2006). Although useful, these parameters are not as reliable as parameters estimated from data. Information on interaction strengths is also weak and is likely to vary among lakes; further diet analyses would be useful, especially for predation rates. Furthermore, there is not enough information to understand differences between lake and stream environments, so it is difficult to estimate the relative scales of the carrying capacity parameters of the lake–stream systems that we examined.

The role of stochasticity in the system was not considered in this analysis. Stochastic dynamics will increase the probability of bull trout extinction in these systems (Iwasa and Mochizuki 1988; Stacey and Taper 1992), because populations in streams are likely to be smaller than lake populations and are therefore more at risk for demographic stochasticity. We also ignored the connectivity of the lakes in this study. Genetic analysis has shown that the connectedness of the lakes has led to linked populations (Meeuwig et al. 2010). Ignoring this metapopulation structure may lead to inflated estimates of short-term bull trout extinction probabilities (Huffaker 1958; Stacey et al. 1996).

The effects of complex ontogenetically structured interspecific and intraspecific interactions on persistence in interacting populations have been studied through simulation studies (McCann and Yodzis 1998; Moll and Brown 2008). Often, theorists describe the role of random environments on species coexistence; however, niche differentiation through ontogeny may also lead to coexistence. Here, we have shown that ontogenetic shifts in interactions serve to alleviate the effects of a competitive bottleneck when bull trout enter the lake and interact with lake trout. Because many aquatic species undergo ontogenetic shifts, they are likely to be an important component of persistence in many populations. The modeling exercise we have presented here has identified preserving this shift as a fundamental component of bull trout conservation. Our results suggest that maintaining the habitat for bull trout juveniles is crucial for long-term bull trout conservation. Perturbations to stream habitat may decrease juvenile bull trout survival or cause juveniles to migrate to the lake earlier. This would drive the system dynamics to be more similar to our C-age-lac and P-age-lac models, both of which predict further decreases in bull trout populations. Therefore, efforts to prevent anthropogenic disturbances from reducing the suitability of riverine habitat for juvenile bull trout (e.g., Hauer and Muhlfeld 2010) are important for bull trout conservation.

This exercise indicates two counter-intuitive phenomena of potentially great importance to bull trout conservation biology. First, our modeling indicates that despite previous focus on lake trout predation on bull trout (e.g., Beauchamp et al. 2007; Muhlfeld et al. 2008), species' relative abundances are more sensitive to interspecific subadult competition than to

Fig. 7. Plots of the areas that meet the coexistence criteria in the competition models with three different values of the competition coefficient. The darker regions denote where the C-age model meets the three observed coexistence conditions, while the lighter regions highlight where the C-stage model meets the observed coexistence conditions. Panels (a) to (c) correspond to competition coefficients of 0.5, 0.8, and 1.0, respectively. The three axes are the three carrying capacities in the lake–stream system. $K_{L,juv}$ is the relative juvenile lake trout carrying capacity in the lakes (with levels indicated by horizontal lines), $K_{B,juv}$ is the relative juvenile bull trout carrying capacity in the stream (with level indicated by forward leaning lines, /), and $K_{subadult}$ is the relative subadult lake trout and bull trout carrying capacity in the lake (with levels indicated by backward leaning lines, \).

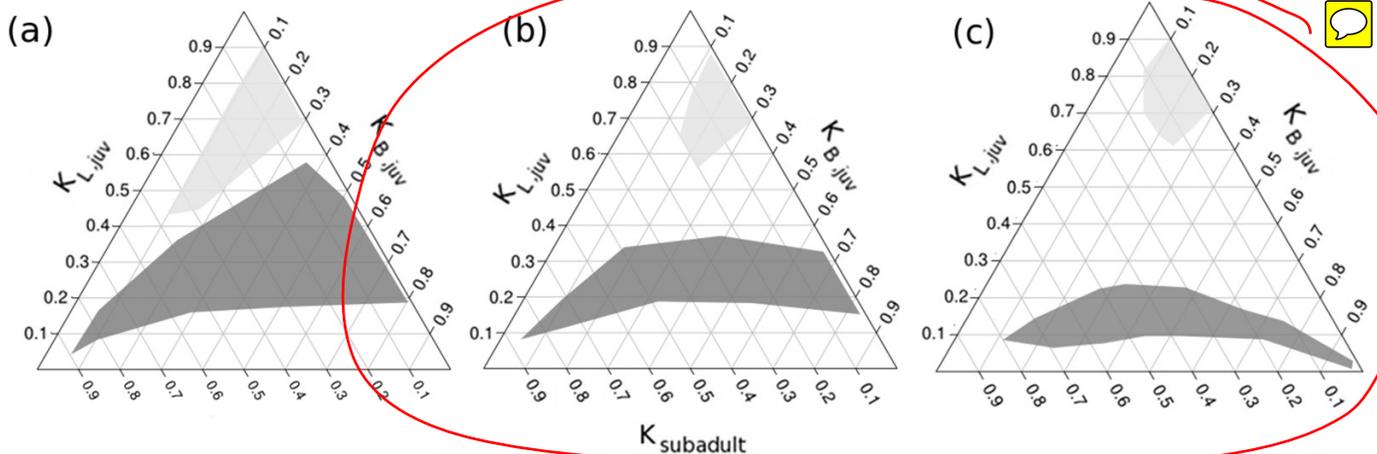
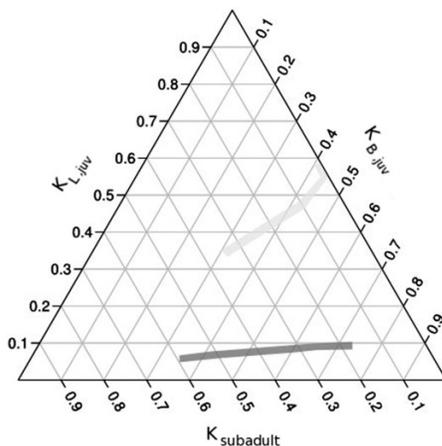


Fig. 8. Results for models that removed the bull trout lacustrine–adfluvial life history and inclusion of interspecific juvenile competition (C-age-lac model). The darker region denotes where the C-age-lac model meets the three observed coexistence conditions, while lighter region highlights where the C-stage-lac model meets the observed coexistence conditions. The three axes are the three carrying capacities in the lake–stream system. $K_{L,juv}$ is the relative juvenile lake trout carrying capacity in the lakes (with levels indicated by horizontal lines), $K_{B,juv}$ is the relative juvenile bull trout carrying capacity in the stream (with level indicated by forward leaning lines, /), and $K_{subadult}$ is the relative subadult lake trout and bull trout carrying capacity in the lake (with levels indicated by backward leaning lines, \).



adult predation. Our second surprising result is that although the threat to bull trout persistence is in the lake, protection of the bull trout by management actions in the tributaries are a necessary step for conservation, in addition to suppression of lake trout in the lake. Because of the coarse nature of our modeling and the data that supported it, it would be inadvisable to view these last two statements as predictions; rather they should be considered questions as strongly raised by

this analysis. More informative answers on the consequences of conservation actions should come in the form of fine-scaled ontogenetic modeling of the linked tributary–lake community dynamics and targeted empirical research to support such efforts.

Despite the paucity of data, the empirical patterns are striking. Our inferential methodology allowed us to formulate model objectives based on widely observed patterns while avoiding many of the assumptions that would be necessary for a likelihood-based approach to inference. Although likelihood is a more common approach in fisheries, we found that by focusing on broadscale patterns in the data that we wished to capture with our models, we were able to infer at an appropriate level of detail, given our limited data, without making unsound assumptions about the stochastic processes operating in the lake. While some claims on the inferential power of POMs have been exaggerated (e.g., Hartig et al. 2011), the fundamental core of scientific inference is the relative matching of predictions from alternative models to observations from the real world (Taper and Lele 2004). Using POMs, we have been able to address questions that would not have been possible with more traditional methods of inference. We hope that the inferential procedure outlined here will find use on other problems coping with limited data and complex ecological processes.

Acknowledgements

We thank Lora Tenant, Michael Meeuwig, and Garrett Dickman for reviewing earlier drafts of the manuscript, as well as Michael Meeuwig and Felipe Carvalho for their assistance with Fig. 1. We also thank three anonymous reviewers and Associate Editor William Tonn for their suggestions that have greatly improved the quality and scope of this manuscript. Any use of trade, product, or firm names is for description purposes only and does not imply endorsement by the US Government. MLT was partly supported by NSF grant DEB 0717456.

References

- Beauchamp, D.A., Kershner, M.W., Overman, N.C., Rhydderch, J., Lin, J., and Hauser, L. 2006. Trophic interactions of nonnative lake trout and lake whitefish in the Flathead Lake food web [online]. Technical Report to the Confederated Salish-Kootenai Tribes. Available from <http://www.flatheadtu.org/indexFiles/WebDocs/FB1.pdf> [accessed 1 September 2011].
- Beauchamp, D.A., Wahl, D., and Johnson, B.M. 2007. Predator-prey interactions. *In* Analysis and interpretation of inland fisheries data. Edited by C.S. Guy and M.J. Brown. American Fisheries Society, Bethesda, Md. pp. 765–842.
- Begon, M., Townsend, C.R., and Harper, J.L. 2005. Ecology: from individuals to ecosystems. Wiley-Blackwell, Malden, Mass.
- Burden, R.L., and Faires, D.J. 2000. Numerical analysis. Brooks/Cole, Boston, Mass.
- Cannings, C., and Edwards, A.W.F. 1968. Natural selection and the de Finetti diagram. *Ann. Hum. Genet.* **31**(4): 755–428. doi:10.1111/j.1469-1809.1968.tb00575.x. PMID:5673165.
- Confederated Salish Kootenai Tribes, and Montana Fish and Wildlife Management. 2006. Phase II of the Five Year Review of the Flathead Lake and River Fisheries Co-Management Plan Technical Synopsis and Management Recommendations Section. Technical Report. Available from FWP Region 1 Headquarters, 490 North Meridian Road, Kalispell, MT 59901, USA.
- Cox, B.S. 2010. Assessment of an invasive lake trout population in Swan Lake, Montana. M.S. thesis, Montana State University, Bozeman, Mont.
- Davis, M. 2003. Biotic globalization: does competition from introduced species threaten biodiversity? *Bioscience*, **53**(5): 481–489. doi:10.1641/0006-3568(2003)053[0481:BGDCFI]2.0.CO;2.
- De Roos, A.M., and Persson, L. 2002. Size-dependent life-history traits promote catastrophic collapses of top predators. *Proc. Natl. Acad. Sci. U.S.A.* **99**(20): 12907–12912. doi:10.1073/pnas.192174199. PMID:12237404.
- De Roos, A., Persson, L., and McCauley, E. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecol. Lett.* **6**(5): 473–487. doi:10.1046/j.1461-0248.2003.00458.x.
- Donald, D.B., and Alger, D.J. 1993. Geographic distribution, species displacement, and niche overlap for lake trout and bull trout in mountain lakes. *Can. J. Zool.* **71**(2): 238–247. doi:10.1139/z93-034.
- Dux, A. 2005. Distribution and population characteristics of lake trout in Lake McDonald, Glacier National Park: implications for suppression. M.S. thesis, Montana State University, Bozeman, Mont.
- Fraley, J.J., and Shepard, B.B. 1989. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River System, Montana. *Northwest Sci.* **63**(4): 133–143.
- Fredenberg, W. 2002. Further evidence that lake trout displace bull trout in mountain lakes. *Intermountain Journal of Sciences*, **8**(3): 143–152.
- Fredenberg, W., Meeuwig, M.H., and Guy, C. 2007. Action plan to conserve bull trout in Glacier National Park. US Fish and Wildlife Service, Kalispell, Mont.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W., Railsback, S., Thulke, H., Weiner, J., Wiegand, T., and DeAngelis, D. 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science*, **310**(5750): 987–991. doi:10.1126/science.1116681. PMID:16284171.
- Guy, C.S., McMahon, T.E., Fredenberg, W.A., Smith, C.J., Garfield, D.W., and Cox, B.S. 2011. Diet overlap of top-level predators in recent sympatry: bull trout and non-native lake trout in Swan Lake, Montana. *J. Fish Wildl. Manag.* **2**(2): 183–189. doi:10.3996/012011-JFWM-004.
- Hartig, F., Calabrese, J.M., Reineking, B., Wiegand, T., and Huth, A. 2011. Statistical inference for stochastic simulation models — theory and application. *Ecol. Lett.* **14**(8): 816–827. doi:10.1111/j.1461-0248.2011.01640.x. PMID:21679289.
- Hauer, F.R., and Muhlfeld, C.C. 2010. Compelling science saves a river valley. *Science*, **327**(5973): 1576. doi:10.1126/science.327.5973.1576-a. PMID:20339049.
- Huffaker, C.B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia*, **27**: 343–383.
- Iwasa, Y., and Mochizuki, H. 1988. Probability of population extinction accompanying a temporary decrease of population size. *Res. Popul. Ecol. (Kyoto)*, **30**(1): 145–164. doi:10.1007/BF02512609.
- Johnston, F.D., Post, J.R., Mushens, C.J., Stelfox, J.D., Paul, A.J., and Lajeunesse, B. 2007. The demography of recovery of an overexploited bull trout, *Salvelinus confluentus*, population. *Can. J. Fish. Aquat. Sci.* **64**(1): 113–126. doi:10.1139/f06-172.
- Kalinowski, S.T., Muhlfeld, C.C., Guy, G.S., and Cox, B. 2010. Founding population size of an aquatic invasive species. *Conserv. Genet.* **11**(5): 2049–2053. doi:10.1007/s10592-009-0041-8.
- Kats, L., and Ferrer, R. 2003. Alien predators and amphibian declines: review of two decades of science and the transition to conservation. *Divers. Distrib.* **9**(2): 99–110. doi:10.1046/j.1472-4642.2003.00013.x.
- Komuro, R., Ford, E.D., and Reynolds, J.H. 2006. The use of multi-criteria assessment in developing a process model. *Ecol. Model.* **197**(3–4): 320–330. doi:10.1016/j.ecolmodel.2006.03.033.
- Lawlor, L. 1980. Overlap, similarity, and competition coefficient. *Ecology*, **61**(2): 245–251. doi:10.2307/1935181.
- MacArthur, R., and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* **101**(921): 377–385. doi:10.1086/282505.
- Martin, N., and Olver, C. 1980. The lake charr, *Salvelinus namaycush*. *In* Charrs: salmonid fishes of the genus *Salvelinus*. Dr. W. Junk Publishers, The Hague, the Netherlands. pp. 205–277.
- McCann, K., and Yodzis, P. 1998. On the stabilizing role of stage structure in Piscene consumer-resource interactions. *Theor. Popul. Biol.* **54**(3): 227–242. doi:10.1006/tpbi.1997.1369. PMID:9878602.
- Meeuwig, M.H. 2008. Ecology of lacustrine-adfluvial bull trout populations in an interconnected system of natural lakes. Ph.D. thesis, Montana State University, Bozeman, Mont.
- Meeuwig, M.H., Guy, C.S., Kalinowski, S.T., and Fredenberg, W.A. 2010. Landscape influences on genetic differentiation among bull trout populations in a stream-lake network. *Mol. Ecol.* **19**(17): 3620–3633. doi:10.1111/j.1365-294X.2010.04655.x. PMID:20723065.
- Meeuwig, M., Guy, C., and Fredenberg, W. 2011. Trophic relationships between a native and a nonnative predator in a system of natural lakes. *Ecol. Freshwat. Fish*, **20**(2): 315–325. doi:10.1111/j.1600-0633.2011.00498.x.
- Mills, M., Rader, R., and Belk, M. 2004. Complex interactions between native and invasive fish: the simultaneous effects of multiple negative interactions. *Oecologia (Berl.)*, **141**(4): 713–721. doi:10.1007/s00442-004-1695-z. PMID:15322899.
- Mittelbach, G., Osenberg, C., and Leibold, M. 1988. Trophic relations and ontogenetic niche shifts in aquatic ecosystems. *In* Size-structured populations. Edited by B. Ebenman and L. Persson. Springer-Verlag, Berlin, Germany. pp. 219–235.
- Mogen, J.T., and Kaeding, L.R. 2005. Identification and characterization of migratory and nonmigratory bull trout populations in the St. Mary River drainage, Montana. *Trans. Am. Fish. Soc.* **134**(4): 841–852. doi:10.1577/T04-143.1.
- Moll, J.D., and Brown, J.S. 2008. Competition and coexistence with

- multiple life-history stages. *Am. Nat.* **171**(6): 839–843. doi:10.1086/587517. PMID:18462131.
- Muhlfeld, C.C., Bennett, D.H., Steinhilber, R.K., Marotz, B., and Boyer, M. 2008. Using bioenergetics modeling to estimate consumption of native juvenile salmonids by nonnative northern pike in the upper Flathead River System, Montana. *N. Am. J. Fish. Manage.* **28**(3): 636–648. doi:10.1577/M07-004.1.
- Polis, G., and Holt, R. 1992. Intraguild predation: the dynamics of complex trophic interactions. *Trends Ecol. Evol.* **7**(5): 151–154. doi:10.1016/0169-5347(92)90208-S. PMID:21235990.
- R Development Core Team. 2010. R: a language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org/>.
- Rand, P.S., and Stewart, D.J. 1998. Prey fish exploitation, salmonine production, and pelagic food web efficiency in Lake Ontario. *Can. J. Fish. Aquat. Sci.* **55**(2): 318–327. doi:10.1139/f97-254.
- Spencer, C.N., McClelland, B.R., and Stanford, J.A. 1991. Shrimp stocking, salmon collapse, and eagle displacement. *Bioscience*, **41**(1): 14–21. doi:10.2307/1311536.
- Stacey, P.B., and Taper, M. 1992. Environmental variation and the persistence of small populations. *Ecol. Appl.* **2**(1): 18–29. doi:10.2307/1941886.
- Stacey, P.B., Johnson, V.A., and Taper, M.L. 1996. Migration within metapopulations: the impact upon local population dynamics. *Metapopulation biology: ecology, genetics and evolution*. Academic Press, New York. pp. 267–291.
- Staples, D.F. 2006. Viable population monitoring: Risk-based population monitoring for threatened and endangered species with application to bull trout, *Salvelinus confluentus*. Ph.D. thesis, Montana State University, Bozeman, Mont.
- Staples, D.F., Taper, M.L., and Shepard, B.B. 2005. Risk-based viable population monitoring. *Conserv. Biol.* **19**(6): 1908–1916. doi:10.1111/j.1523-1739.2005.00283.x.
- Syslo, J.M. 2010. Demography of lake trout in relation to population suppression in Yellowstone Lake, Yellowstone National Park. M. S. thesis, Montana State University, Bozeman, Mont.
- Takimoto, G. 2003. Adaptive plasticity in ontogenetic niche shifts stabilizes consumer-resource dynamics. *Am. Nat.* **162**(1): 93–109. doi:10.1086/375540. PMID:12856239.
- Tanaka, H., Shibata, M., Masaki, T., Iida, S., Niiyama, K., Abe, S., Kominami, Y., and Nakashizuka, T. 2008. Comparative Demography of three coexisting *Acer* species in gaps and under closed canopy. *J. Veg. Sci.* **19**(1): 127–138. doi:10.3170/2007-8-18342.
- Taper, M.L., and Lele, S.R. (Editors). 2004. The nature of scientific evidence: A forward-looking synthesis. *In The nature of scientific evidence. Statistical, philosophical and empirical considerations*. The University of Chicago Press, Chicago, Ill. pp. 527–551.
- Vander Zanden, M.J., Lester, N., and Rasmussen, J. 1997. Stable isotope evidence for the food web consequences of species invasions in lakes. *J. Geophys. Res.* **102**: 24729–24739.
- Werner, E.E., and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst.* **15**(1): 393–425. doi:10.1146/annurev.es.15.110184.002141.

Appendices

Appendices A, B, and C appear on the following pages.

Appendix A. Model definitions

Predation models

P-stage model: This model is defined by the transitions over time, $\mathbf{B}_{t+1} = \mathbf{T}_{B,t} \mathbf{B}_t$ and $\mathbf{L}_{t+1} = \mathbf{T}_{L,t} \mathbf{L}_t$, where the transition matrices are given by

$$(A.1) \quad \mathbf{T}_{B,t} = \begin{bmatrix} s_{juv} \cdot (1 - m_{juv}) \cdot \exp\left(-\frac{B_{juv,t}}{K_{B,juv}}\right) - \alpha_{juv} \cdot L_{adult,t} & 0 & p_{spawn} \cdot s_{YOY} \cdot f \cdot \exp\left(-\frac{B_{juv,t}}{K_{B,juv}}\right) \\ s_{juv} \cdot m_{juv} \cdot \exp\left(-\frac{B_{juv,t}}{K_{B,juv}}\right) - \alpha_{juv} \cdot L_{adult,t} & s_{subadult} \cdot (1 - m_{subadult}) \cdot \left(1 - \frac{B_{subadult,t}}{K_{subadult}}\right) - \alpha_{subadult} \cdot L_{adult,t} & 0 \\ 0 & s_{subadult} \cdot m_{subadult} \cdot \left(1 - \frac{B_{subadult,t}}{K_{subadult}}\right) - \alpha_{subadult} \cdot L_{adult,t} & s_{adult} \end{bmatrix}$$

$$(A.2) \quad \mathbf{T}_{L,t} = \begin{bmatrix} s_{juv} \cdot (1 - m_{juv}) \cdot \exp\left(-\frac{L_{juv,t}}{K_{L,juv}}\right) & 0 & p_{spawn} \cdot s_{YOY} \cdot f \cdot (1 + e \cdot \alpha_{juv} \cdot B_{juv,t} \cdot L_{juv,t}) \cdot \exp\left\{-\frac{L_{juv,t}}{K_{L,juv}}\right\} \\ s_{juv} \cdot m_{juv} \cdot \exp\left(-\frac{L_{juv,t}}{K_{L,juv}}\right) & s_{subadult} \cdot (1 - m_{subadult}) \cdot \left(1 - \frac{L_{subadult,t}}{K_{subadult}}\right) & 0 \\ 0 & s_{subadult} \cdot m_{subadult} \cdot \left(1 - \frac{L_{subadult,t}}{K_{subadult}}\right) & s_{adult} \end{bmatrix}$$

For the P-stage model, the known parameters in $\mathbf{T}_{B,t}$ and $\mathbf{T}_{L,t}$ are defined in Table C1. The remaining parameters are treated as unknown ($K_{B,juv}$, $K_{L,juv}$, $K_{subadult}$) or estimated ($\alpha_{subadult}$) in the text. We note that in the P-stage model, $\alpha_{juv} = 0$.

P-age model: Bull trout are modeled using vital rates from Table C1, while lake trout stage classes were defined as follows for the purposes of applying interspecific and intraspecific interactions: $L_{juv,t} = \sum_{x=0}^3 A_x$, $L_{subadult,t} = \sum_{x=4}^6 A_x$, and $L_{adult,t} = \sum_{x=7}^{18} A_x$, where A_x is the abundance of lake trout in age class x . In eq. A.2, the total fecundity f is a function of age-specific fecundity F and the probability of spawning M , so that $f = \sum_{x=0}^{18} M_x \cdot F_x$. Population dynamics of lake trout were then simulated using the life table given in Table C2. At each time step, we aggregated individuals into stage classes based on the definitions given above to apply the interactions defined in $\mathbf{T}_{B,t}$ and $\mathbf{T}_{L,t}$.

Table A1. Definitions of model parameters.

Symbol	Definition
s_{stage}	Yearly survival for a fish in a life-history stage, where stage can be young of the year (YOY), juvenile (juv), subadult (subadult), and adult (adult)
s_{age}	Yearly survival for an age x -year-old fish
m_{stage}	Probability of emigration for a fish in a life-history stage
p_{spawn}	Probability of spawning in the current year
f_{stage}	Fecundity of a fish in a life-history stage
f_{age}	Fecundity for a fish for an age x -year-old fish
$K_{B,juv}$	Carrying capacity of bull trout juveniles
$K_{L,juv}$	Carrying capacity of lake trout juveniles
$K_{subadult}$	Carrying capacity for subadults of both species, in the lake
e	Conversion efficiency of new predators from consumed prey per year
α_{stage}	Yearly predation rate on bull trout juveniles in a life-history stage
$\beta_{Y,X}$	Competitive impact of a juvenile individual of species Y on species X
$B_{x,t}$	Abundance of bull trout in stage or age x at time t
$L_{x,t}$	Abundance of lake trout in stage or age x at time t

Note: Parameter values for the stage-based model are given in Appendix C, Table C1, and values for the age-based model are given in Appendix C, Table C2. $K_{B,juv}$, $K_{L,juv}$, $K_{subadult}$ are unknown parameters, and a range of values were explored in this analysis as described in the Materials and methods. $B_{x,t}$ and $L_{x,t}$ are the response variables in our analysis.

P-age-lac model: In this model we assumed $\alpha_{juv} \neq 0$, as described in the text.

Competition models

C-stage model: This model is defined by the transitions over time, $B_{t+1} = U_{B,t} B_t$ and $L_{t+1} = U_{L,t} L_t$, where the transition matrices are given by

$$(A.3) \quad U_{B,t} = \begin{bmatrix} s_{juv} \cdot (1 - m_{juv}) \cdot \exp\left(-\frac{B_{juv,t} + \beta_{juv} L_{juv,t}}{K_{B,juv}}\right) & 0 & p_{spawn} \cdot s_{YOY} \cdot f \cdot \exp\left(-\frac{B_{juv,t}}{K_{B,juv}}\right) \\ s_{juv} \cdot m_{juv} \cdot \exp\left(-\frac{B_{juv,t} + \beta_{juv} L_{juv,t}}{K_{B,juv}}\right) & s_{subadult} \cdot (1 - m_{subadult}) \cdot \left(1 - \frac{B_{subadult,t} + \beta_{B,L} L_{subadult,t}}{K_{subadult}}\right) & 0 \\ 0 & s_{subadult} \cdot m_{subadult} \cdot \left(1 - \frac{B_{subadult,t} + \beta_{B,L} L_{subadult,t}}{K_{adult}}\right) & s_{adult} \end{bmatrix}$$

$$(A.4) \quad U_{L,t} = \begin{bmatrix} s_{juv} \cdot (1 - m_{juv}) \cdot \exp\left(-\frac{L_{juv,t} + \beta_{juv} B_{juv,t}}{K_{L,juv}}\right) & 0 & p_{spawn} \cdot s_{YOY} \cdot f \cdot \exp\left(-\frac{L_{juv,t}}{K_{L,juv}}\right) \\ s_{juv} \cdot m_{juv} \cdot \exp\left(-\frac{L_{juv,t} + \beta_{juv} B_{juv,t}}{K_{L,juv}}\right) & s_{subadult} \cdot (1 - m_{subadult}) \cdot \left(1 - \frac{L_{subadult,t} + \beta_{L,B} B_{subadult,t}}{K_{subadult}}\right) & 0 \\ 0 & s_{subadult} \cdot m_{subadult} \cdot \left(1 - \frac{L_{subadult,t} + \beta_{L,B} B_{subadult,t}}{K_{subadult}}\right) & s_{adult} \end{bmatrix}$$

For the C-stage model, the known parameters in $U_{B,t}$ and $U_{L,t}$ are defined in Table C1. The remaining parameters are treated as unknown ($K_{B,juv}$, $K_{L,juv}$, $K_{subadult}$) or estimated ($\beta_{L,B}$) in the text. We note that in the C-stage model, $\beta_{juv} = 0$.

C-stage-lac: In this model $\beta_{juv} = 1$; all other parameters are the same as in the C-stage model.

C-age model: Lake trout are modeled using vital rates from Table C2. Bull trout are modeled using vital rates from Table C1. Lake trout stage classes were defined as follows for the purposes of applying interspecific and intraspecific interactions: $L_{juv,t} = \sum_{x=0}^3 A_x$, $L_{subadult,t} = \sum_{x=4}^6 A_x$, and

$L_{adult,t} = \sum_{x=7}^{18} A_x$, where A_x is the abundance of lake trout in age class x . In eq. A.4, $f = \sum_{x=0}^{18} M_x \cdot F_x$, where M_x and F_x are from Table C2.

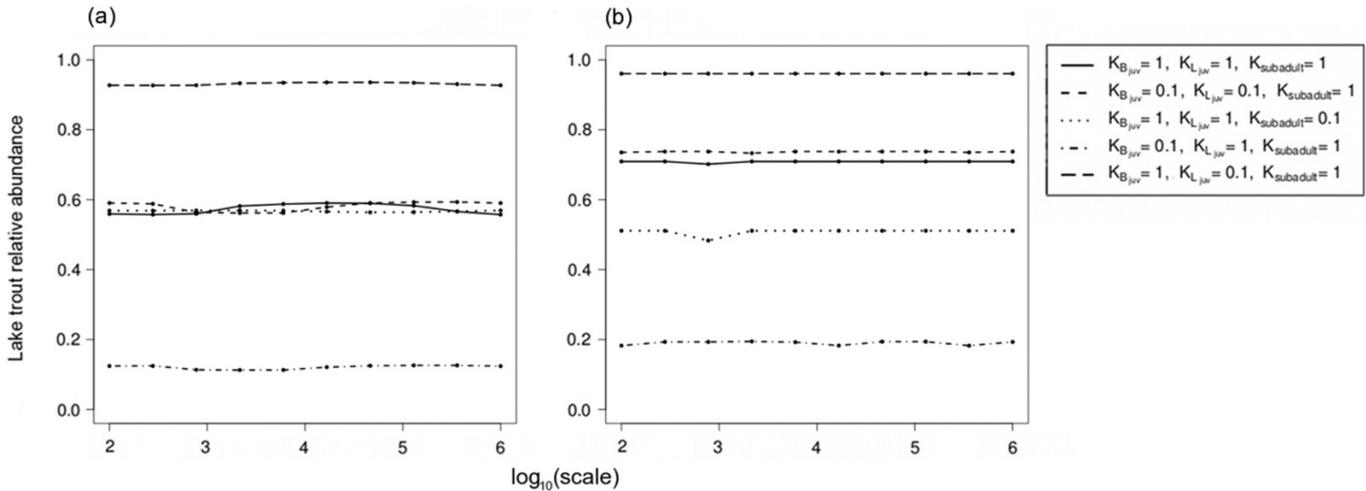
C-age-lac: In this model $\beta_{juv} = 1$; all other parameters are the same as in the C-age model.

Null models

LH-age, LH-stage: Taking either the competition model or predation model and setting all parameters to 0 arrives at the LH models. See eq. 1 in the manuscript for the LH-stage model.

Appendix B. Scale independence of models

Fig. B1. Demonstration of scale invariance in predation and competition models; each set of $K_{B,juv}$, $K_{L,juv}$, and $K_{subadult}$ values in the legend are multiplied by the scale factor on the x axis. The plotted points are the relative lake trout abundance after 500 time steps. Panel (a) shows results from the C-stage model, and panel (b) shows results from the P-age model.



Here we show how the ratio of lake trout to bull trout, in subadult and adult stage classes, is invariant to the scale of the carrying capacities ($K_{B,juv}$, $K_{L,juv}$, $K_{subadult}$) and only dependent on the relative scales for our models. This property made the presentation of our results much more straightforward than otherwise would be the case for these potentially complex models. We held constant the relative values of $K_{B,juv}$, $K_{L,juv}$, and $K_{subadult}$ and changed the scale by multiplying these carrying capacities by a constant value. This allowed us to explore how the relative abundance of lake trout sampled changed as a function of scale.

In Fig. B1 we show results from simulating from our C-age and P-age models. We found that scale does not affect the dynamics significantly and that using the normalized carrying capacities was justified. We note, however, that the scale invariance property holds only roughly for the crossing times property of the models. Despite this, we found that crossing times were always greater than 11 years in our models, so this did not generate a problem in the presentation of our results.

Appendix C. Parameter values

Table C1. Annual vital rates used for the stage-based model (values adapted from Staples 2006).

Vital rate	Value
Young-of-year survival (s_{YOY})	0.0065
Juvenile survival (s_{juv})	0.5
Probability of juvenile emigration (m_{juv})	0.13
Subadult survival ($s_{subadult}$)	0.42
Probability of subadult emigration ($m_{subadult}$)	0.3
Adult survival (s_{adult})	0.64
Probability of spawning (p_{spawn})	0.5
Fecundity (f_{adult})	4700

References

- Shuter, B.J., Jones, M.L., Korver, R.M., Lester, N.P., 1998. A general, life history based model for regional management of fish stocks: the inland lake trout (*Salvelinus namaycush*) fisheries of Ontario. *Can. J. Fish. Aquat. Sci.* **55**(9): 2161–2177. doi:10.1139/f98-055.
- Sitar, S.P., Bence, J.R., Johnson, J.E., Ebener, M.P., Taylor, W.W., 1999. Lake trout mortality and abundance in southern Lake Huron. *N. Am. J. Fish. Manage.* **19**(4): 881–900.
- Staples, D.F. 2006. Viable population monitoring: risk-based population monitoring for threatened and endangered species with application to bull trout, *Salvelinus confluentus*. Ph.D. thesis, Montana State University, Bozeman, Mont.
- Syslo, J.M. 2010. Demography of lake trout in relation to population suppression in Yellowstone Lake, Yellowstone National Park. M. S. thesis, Montana State University, Bozeman, Mont.

Table C2. Lake trout annual vital rates from Yellowstone Lake in 2007.

Age	% Mature (M_{age})	Survival (s_{age})	Fecundity (f_{age})
0	0	0.01*	0
1	0	0.45	0
2	0	0.7	0
3	0	0.9	0
4	0	0.9	0
5	0.03	0.9	0
6	0.13	0.9	1049
7	0.39	0.9	2095
8	0.7	0.9	3071
9	0.89	0.9	3999
10	0.96	0.9	4855
11	0.99	0.9	5664
12	1	0.9	6425
13	1	0.9	7162
14	1	0.9	7828
15	1	0.9	8471
16	1	0.9	9065
17	1	0.9	9636

Note: Survival estimates of adults are corrected for mortality from gill net catches (Syslo 2010). Survival of ages 0 and 1 are from Shuter et al. (1998) and Sitar et al. (1998), respectively.

*The original observed value was 0.0048 and was assumed to have been measured near carrying capacity. This corrected intrinsic survival was calculated by assuming that survival followed a Ricker density-dependent function.