Habitat availability and ontogenetic shifts alter bottlenecks in size-structured fish populations

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Abstract. For species that utilize different habitats throughout their life cycle, the habitat limitation at a given stage can act as a bottleneck on population abundance, impacting density-dependent processes such as individual growth and survival. We explore the influence of habitat limitation on population dynamics by developing a multi-stage population model based on lake-dwelling rainbow trout (Oncorhynchus mykiss) populations where adults occupy the lake habitat but use tributaries for spawning and juvenile rearing. The model details density-dependent ecological processes and ontogenetic habitat shifts, harvest mortality, and the impact of climate on growth. We ran model simulations using a range of early life stage habitat availabilities and climatic conditions representative of the native range of rainbow trout in Canada and compared the results to empirical data. The results suggest that (1) increases in early life stage habitat leads to increases in population abundance but, due to density-dependent processes, also results in slower growing stunted populations; (2) population bottlenecks can occur at any life stage, even at the adult stage if spawning and rearing habitats are abundant; (3) when the level of competition for early life stages is increased, inter-cohort competition can lead to population cycles. The model’s conclusions are further reinforced by empirical data showing a similar trend in the relationship between fish density and maximum size and providing evidence that limited early life stage habitat leads to lower fish densities and larger fish size. We provide a model that links environmental conditions to population dynamics and is useful for fisheries management and habitat conservation decisions.

Key words: density dependence; habitat limitation; habitat use; multi-stage population model; Oncorhynchus mykiss; ontogenetic niche shifts; population bottlenecks; population dynamics; rearing habitat; size-structured populations; spawning habitat.

INTRODUCTION

Population dynamics are dictated by patterns of individual growth and survival. For many organisms, survival is highly size dependent (Sauer and Slade 1987, Sogard 1997, Mangel and Stamps 2001). Harvest for commercial or recreational purposes can be an important source of mortality that is almost always nonrandom as harvest selects based on large size (Fenberg and Roy 2008). In addition, larger individuals within populations are often less susceptible to predation where mortality from gape-limited predators decreases with increases in individual size (Tonn and Paszkowski 1986). Individual size is the result of growth rate, which can be associated with environmental variables such as climate, for example temperature has been linked to different physiological processes that control growth in ectotherms leading to faster growth in warmer climates (Atkinson 1994). Compensatory individual growth can also result from reductions in population density, due to reduced competition for food resources. Populations of the same species exposed to environmental variation (e.g. climate, habitat availability, harvest pressure) can express plasticity in individual growth leading to contrasting dynamical outcomes among populations due to the interplay between growth and survival (Werner 1988, Ebenman 1992).

Many indeterminate growing species experience growth of multiple orders of magnitude throughout their life cycle resulting in a size-structured population. This ontogenetic size variation also leads to changes in ecological niche that present themselves as shifts in diet or habitat motivated by habitat segregation resulting from competitive interactions, predator avoidance, or resource seeking behavior (Werner and Gilliam 1984, Werner 1988, de Roos and Persson 2003, 2013). Growth rate variation can influence the transition of organisms from one life stage to another modifying the timing of ontogenetic habitat shifts and impacting inter and intraspecific interactions (Werner and Gilliam 1984). For example, slow growth could prolong the time a cohort spends in a high predation risk habitat, impacting its survival. It can also influence the time spent in a habitat that overlaps with another competing life stage, which can further decrease growth rate and increase mortality. Density-dependent processes, such as growth, are impacted by habitat or resource availability and quality, which can vary throughout a species life as different stages experience ontogenetic niche shifts in resource and habitat use.

Competitive and predatory interactions between and within size classes, and the availability of the different habitats used by a species throughout its life cycle can influence growth and survival of a specific stage resulting in a population bottleneck that limits the size and/or maximum number of individuals in that stage and has repercussion on the overall population (de Roos and Persson 2013). Harvest can also be an important external source of mortality that limits a life stage and impacts population abundance. Bottlenecks can happen at any stage of a life cycle and can occur at different stages among populations of the same species.
depending on their environment. Since abundance is the result of survival through multiple stages, the carrying capacity of the system is not necessarily determined by the reproductive potential of the adult stage, but by the most limiting stage. Changes in growth impacting size structure can also impact carrying capacity as individuals of different size will differ in their per biomass metabolic requirements, meaning that a habitat with a set amount of resources can support more or less fish depending on their individual size and associated energetic requirements. Therefore, limiting the study of a population to a single life stage can lead to an incomplete understanding of the processes controlling population regulation (Halpern 2004). Hence, determining the right spatial and temporal scope of study is fundamental in the investigation of population dynamics.

Fish are a suitable organism to study the link between ontogenetic habitat shift and population dynamics as they typically experience size increase over several orders of magnitude and present a succession of life stages among which there is sufficient niche overlap, which leads to intercohort competition (Werner and Gilliam 1984, Ebenman 1988). Several studies have linked variability in physical habitat to population dynamics, particularly in salmonids (Milner et al. 2003, Lobón-Cerviá and Rincón 2004, Ayllón et al. 2010). Early life stages, where the two main causes of mortality are starvation and predation, are especially important in determining population recruitment (Houde 1989, Cowan et al. 2000). Therefore, models that aim to describe fish population dynamics should explicitly account for the processes driving growth and survival of young fish. Species like lake-dwelling rainbow trout (Oncorhynchus mykiss) are ideal to examine fish population dynamics as they do not perform large scale migrations like their anadromous counterparts, but use distinct habitats at the adult (lake) and juvenile stages (spawning and rearing in the lake tributaries). Population dynamics have been extensively studied among salmonids (Grant and Kramer 1990, Elliott 1994, Cattanéo et al. 2002, Milner et al. 2003, Grant and Imre 2005, Lobón-Cerviá 2007), including rainbow trout in lakes (Northcote 1962, Post et al. 1999, Cox and Walters 2002, Parkinson et al. 2004) and in streams (Keeley and Slaney 1996, Keeley and McPhail 1998, Imre et al. 2004, Wood et al. 2012). The large body of literature in this area provides a strong base on which to develop a cohesive multi-habitat model aimed at understanding bottlenecks to population growth.

The objective of this study is to assess the qualitative and quantitative outcomes of variation of habitat availability, density dependence, climate, and harvest on population bottlenecks and dynamics in spatially and size-structured fish populations. This will be done using populations simulated with an age-structured population model and by comparing the simulation outcomes to empirical data.

**Methods**

**Model development**

We used an age-structured population model detailing processes in both the adult habitat (lake) and the early life stage habitat (stream) to follow rainbow trout through their life cycle and represent the impact of spawning and rearing habitat availability to fish population dynamics. The model was parameterized using, when possible, data from field and laboratory studies on rainbow trout or steelhead populations. When such data were not available, we used data from related salmonids.

The model time step is a year and results are presented as a snapshot of the population at the end of the growing season in autumn. In general, lake-dwelling adult rainbow trout migrate to streams in the spring to spawn and then return to the lake (Scott and Crossman 1973, McPhail 2007). The eggs hatch in the stream early in the summer and the juvenile fish spend a few weeks to two years in the stream before moving to the lake, where they grow and mature (Northcote 1962, Scott and Crossman 1973, Rosenau 1991). Natural survival is stage dependent in the stream, but accompanied by density mediated migration behavior (Slaney and Northcote 1974, Elliott 1994, Keeley and McPhail 1998). While, in the lake, survival is density- and size-dependent (Post et al. 2008) and mature fish experience spawning mortality and harvest mortality resulting from recreational harvest (Parkinson et al. 2004). Growth rate varies with climate and density (Ward et al. 2017). Annual egg production varies with number of mature fish and their size. The egg production of year $t$ becomes the number of eggs deposited in year $t+1$. The general framework of the model is presented in Fig. 1 and Table 1 contains the full parameters set.

**Stream habitat**

The stream can be considered as being divided into three habitats, characterized by their environmental condition (Raleigh et al. 1984, Bjornn and Reiser 1991, Keeley and Slaney 1996), and occupied by particular life stages: (1) spawning habitat used by adult fish to construct redds in well-oxygenated gravel substrate where eggs are deposited and fertilized; (2) fry-rearing habitat characterized by more cover (cobble, boulder, aquatic vegetation, woody debris) and shallow pools, particularly located in streamside for age-0 fish; and (3) juvenile rearing habitat for immature fish older than age 1, similar to (2) but with deeper pools with more instream cover. In the model, spawning habitat varies in abundance but is always present, while rearing habitat can vary in abundance or be absent. In the wild, a situation where spawning habitat is available but rearing is not could occur if a stream does not present any fish cover, or if stream flow is highly seasonal and sufficient only for spawning in the spring but dries up later in the summer.

Fish density in the stream is presented as simple density of age class $i$ fish in their specific habitat ($D_i$) and as percent habitat saturation (PHS). The PHS metric describes how much of a habitat is used based on fish density and individual territory size (Grant and Kramer 1990):

$$\text{PHS} = 100 \times \frac{\sum_{i=1}^{n} D_i / D_{i,\text{max}}}{D_{i,\text{max}}}$$

(1)

where $D_{i,\text{max}}$ is the maximum density defined as

$$D_{i,\text{max}} = A_{\text{stream}} \times P_i / T_i$$

(2)
where $A_{\text{stream}}$ is the total stream area, $P_i$ is the proportion of stream area that is covered by habitat suitable to age class $i$ and $T_i$ is the territory area (in m$^2$) for age class $i$. The size of territory defended by salmonids is a power function of fish size (Grant and Kramer 1990, Imre et al. 2004). Territory size has also been shown to vary with food abundance and population density through the effect of intruder pressure (Slaney and Northcote 1974, Dill et al. 1981, McNicol and Noakes 1984, Keeley and McPhail 1998, Keeley 2000, Wood et al. 2012). In our model, food abundance is assumed to be constant over a given area, thus as density increases food availability to individuals decreases. Territory size increases with fish size and shrinks with increases in density. The parameters used to calculate territory size are from an experiment conducted on juvenile steelhead trout by Imre et al. (2004)

$$
\log T_i = -2.296 - 0.365 \times \log D_i + 2.027 \times \log L_i \quad (3)
$$

where $L_i$ is the fork length-at-age $i$ assuming that all fish of a same cohort in the same habitat follow the same growth curve. Territory size at low densities is limited by the area of habitat available. At high fish densities, minimum territory size is the minimum foraging area necessary for fish to meet their energy needs and results in territoriality playing an important role in limiting population density (Grant and Kramer 1990). The relationship between minimum territory size area ($A_{\text{min terr}}$) and fish size ($L_i$) is

$$
A_{\text{min terr}} = a_{\text{min terr}} \times L_i^{b_{\text{min terr}}} \quad (4)
$$

where $a_{\text{min terr}}$ and $b_{\text{min terr}}$ are parameters obtained by calculating territory size using Eq. 3 for high fish densities that corresponded to a PHS of 150% (based on the salmonid interspecific fixed territory size equation developed by Grant and Kramer [1990]).

Lake habitat

The lake is treated in the model as a single homogenous habitat. Lake fish density is calculated using effective density (ED), a metric developed to represent competition between individuals of different size through their consumption rate. Effective density has been shown, using bioenergetics and empirical models, to better represent variation in density-dependent fish growth within size-structured populations than is numeric or biomass density (Walters and Post 1993, Post et al. 1999)

$$
ED = \frac{\sum_{i=1} L_i^2}{A_{\text{lake}}} \quad (5)
$$

where $L$ is individual fish length (mm) and $A_{\text{lake}}$ is lake area (ha). In the model, fish length is calculated for each age class (see Growth) for individuals from each possible migration schedule (see Migration schedule).

Migration schedule

The timing of migration of young rainbow out of their rearing streams and into lakes is highly variable, from as soon as a few days after emergence to one or two growing seasons after hatching (Northcote 1962, Scott and Crossman 1973, Rosenau 1991). The timing of migration can be highly stream specific as variation in migration age between fry emerging from tributaries of a same lake has been observed in New Zealand lake rainbow trout populations (Rosenau 1991, Hayes 1995). In the model, the possibility of growing and overwintering in the stream depends on the availability of rearing habitat. The model captured the range in timing of migration observed in nature by simulating four scenarios of habitat availability and resulting migration schedule to the lake (see Fig. 2 for a diagrammatic description): (1) no rearing habitat...
Table 1. Parameters used in the model and their source.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Description/Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Physical habitat and density</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stream</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$A_{\text{stream}}$</td>
<td>0.5–500</td>
<td>stream total area (m²)</td>
</tr>
<tr>
<td>$f_{\text{spawn}}$</td>
<td>0.01–0.45</td>
<td>proportion of the $A_{\text{stream}}$ that is spawning habitat</td>
</tr>
<tr>
<td>$f_{\text{fry}}$</td>
<td>0.25–1</td>
<td>proportion of the $A_{\text{stream}}$ that is fry rearing habitat</td>
</tr>
<tr>
<td>$f_{\text{juv}}$</td>
<td>0.25–0.75</td>
<td>proportion of the $A_{\text{stream}}$ that is juvenile rearing habitat</td>
</tr>
<tr>
<td>PHS</td>
<td></td>
<td>percent habitat saturation (Grant and Kramer 1990)</td>
</tr>
<tr>
<td>$D_{\text{L,max}}$</td>
<td>Eq. 2</td>
<td>maximum fish density, varies with territory size</td>
</tr>
<tr>
<td>$T_i$</td>
<td>Eq. 3</td>
<td>individual fish territory size (m²), varies with $L_i$ and density (parameter values from Imre et al. [2004])</td>
</tr>
<tr>
<td>$A_{\text{minter}}$</td>
<td>Eq. 4</td>
<td>individual fish minimum territory size (m²), vary with $L_i$</td>
</tr>
<tr>
<td>$a_{\text{minter}}$</td>
<td>0.0002</td>
<td>parameters defining how minimum territory size varies with $L_i$ (calculated based on $A_{\text{ter}}$ at high densities of PHS 150%)</td>
</tr>
<tr>
<td>$b_{\text{minter}}$</td>
<td>3.1921</td>
<td></td>
</tr>
<tr>
<td>Lake</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$A_{\text{lake}}$</td>
<td>25</td>
<td>lake area (ha)</td>
</tr>
<tr>
<td>ED</td>
<td></td>
<td>effective density (cm²/ha)</td>
</tr>
<tr>
<td><strong>Natural survival</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stream</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$D_{\text{fry}}$</td>
<td>Eq. 6</td>
<td>density of fry that have survived from egg to emergence stage</td>
</tr>
<tr>
<td>$a_{\text{BH}}$</td>
<td>1.982</td>
<td>Beverton-Holt recruitment a parameter (eggs/m²), Eq. 7</td>
</tr>
<tr>
<td>$b_{\text{BH}}$</td>
<td>3.303</td>
<td>Beverton-Holt recruitment b parameter, Eq. 9</td>
</tr>
<tr>
<td>$A_{\text{reid}}$</td>
<td>0.3</td>
<td>average redd size (m²) from Ottaway et al. (1981)</td>
</tr>
<tr>
<td>$D_{\text{reid, max}}$</td>
<td>3.33</td>
<td>maximum redd density (redds/m²), Eq. 8</td>
</tr>
<tr>
<td>$N_{\text{egg}}/N_{\text{fem}}$</td>
<td>595</td>
<td>average egg produced per female (based on Eq. 22 assuming average female size is 35 cm)</td>
</tr>
<tr>
<td>$S_{\text{emerg, max}}$</td>
<td>0.3</td>
<td>maximum egg to emergence survival (Ward and Slaney 1993)</td>
</tr>
<tr>
<td>$S_{0,\text{max}}$</td>
<td>0.8</td>
<td>maximum survival rate during first year of life in the stream</td>
</tr>
<tr>
<td>$S_{1,\text{max}}$</td>
<td>0.9</td>
<td>maximum survival rate during second year of life in the stream</td>
</tr>
<tr>
<td>Lake</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$S_i$</td>
<td>Eq. 10</td>
<td>survival rate in the lake, varies with fish length and ED (Parkinson et al. 2004)</td>
</tr>
<tr>
<td>$S_{\text{L,max}}$</td>
<td>Eq. 11</td>
<td>maximum survival rate, varies with $L_i$ (Parkinson et al. 2004)</td>
</tr>
<tr>
<td>$m_i$</td>
<td>Eq. 12</td>
<td>exponent of the relationship between ED and $S_i$ varies with $L_i$ (Parkinson et al. 2004)</td>
</tr>
<tr>
<td><strong>Harvest</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$E$</td>
<td>0–5,000</td>
<td>fishing effort (angler-days-ha⁻¹-year⁻¹)</td>
</tr>
<tr>
<td>Agevuln</td>
<td>3</td>
<td>vulnerability to harvest is knife-edge and age determined</td>
</tr>
<tr>
<td>$q$</td>
<td>1.61</td>
<td>instantaneous turnover rate between pool of available and unavailable fish (year⁻¹) from Cox and Walters (2002)</td>
</tr>
<tr>
<td>$f$</td>
<td>0.09</td>
<td>catchability coefficient (ha/angler-days) from Cox and Walters (2002)</td>
</tr>
<tr>
<td>$U$</td>
<td>Eq. 13</td>
<td>instantaneous harvest mortality rate (Cox and Walters 2002)</td>
</tr>
<tr>
<td></td>
<td>Eq. 14</td>
<td>annual harvest rate for fully vulnerable fish (Cox and Walters 2002)</td>
</tr>
<tr>
<td><strong>Growth</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$L_i$</td>
<td>Eq. 15</td>
<td>length (cm) of fish at age $i$</td>
</tr>
<tr>
<td>$L_{\text{emerg}}$</td>
<td>2</td>
<td>length (cm) of fish at emergence (Murray 1980)</td>
</tr>
<tr>
<td>Climate effect (stream and lake)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$K$</td>
<td>Eq. 16</td>
<td>Von Bertalanffy $K$, metabolic constant, varies with climate (GDD)</td>
</tr>
<tr>
<td>GDD</td>
<td>1,000–2,000</td>
<td>growing degree days &gt;5°C</td>
</tr>
<tr>
<td>$a_{\text{clim}}$</td>
<td>0.0002</td>
<td>slope (a) and intercept (b) of the relationship between $K$ and GDD (based on $K$ values from Cox 2000 and GDD obtained for lakes for the appropriate year from ClimateBC 5.30 [Wang et al. 2012])</td>
</tr>
<tr>
<td>$b_{\text{clim}}$</td>
<td>0.0122</td>
<td></td>
</tr>
<tr>
<td>$b_W$</td>
<td>0.66–0.97</td>
<td>Walford slope varies with climate, Eq. 21</td>
</tr>
<tr>
<td><strong>Density effect</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$L_{\text{ao}}$</td>
<td>Eqs. 17 and 18</td>
<td>Von Bertalanffy $L_{ao}$, asymptotic length, varies with fish density</td>
</tr>
<tr>
<td><strong>Stream</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$a_{\text{W,stream}}$</td>
<td>4–12</td>
<td>Walford plot intercept, varies with PHS following a negative power curve (Imre et al. 2005), Eq. 20</td>
</tr>
<tr>
<td>$a_{\text{stream}}$</td>
<td>20</td>
<td>parameters of the decline (negative power curve) of $a_{\text{W,stream}}$ with increase in PHS</td>
</tr>
<tr>
<td>$b_{\text{stream}}$</td>
<td>-0.3</td>
<td></td>
</tr>
</tbody>
</table>
available, fish migrate to the lake immediately after emergence as would be observed in intermittent stream that dry up early in the summer for example (Erman and Leidy 1975); (2) only fry rearing habitat available, fish migrate to the lake after having spent one growing season in the stream; (3) both fry and juvenile rearing habitat available, but the habitats do not overlap, fish migrate to the lake after two growing season but fry and juvenile do not compete in the stream, limited intercohort competition would occur in highly heterogeneous stream habitat, for example where deep pools would be available for older fish to use (Ayllón et al. 2010); and (4) same habitat availability as in (3) but the different rearing stages compete for a shared portion of the homogeneous stream habitat, for example where deep pools would be available for older fish to use (Ayllón et al. 2010); and (4) same habitat availability as in (3) but the different rearing stages compete for a shared portion of the homogeneous stream habitat. Here the high niche overlap leads to intercohort competition as observed in salmonids like brown trout (Crisp 1993, Nordwall et al. 2001, Kvingedal and Einum 2011), if juvenile fish are saturating their habitat (PHS ≥ 100%) they obtain all the shared habitat, if fry are saturating their habitat and juvenile are not, then fry get the shared habitat, and, finally, if both life stages present a PHS below 100% each life stage obtains half of the shared habitat.

Once rearing habitat is saturated (PHS ≥ 100%), fish that are not able to secure a territory will be displaced (Grant and Kramer 1990) and complete an early migration to the lake, and lake conditions will determine their survival and growth for that year. Therefore, a single cohort can have individuals in both the stream and lake habitats.

Natural mortality

Egg to emergence survival is a function of egg density ($D_{egg}$) and follows a Beverton-Holt recruitment type curve where the number of fry that emerge ($D_{fry}$) reaches an asymptote once the carrying capacity of the habitat is reached

$$D_{fry} = \frac{a_{BH} \times D_{egg}}{b_{BH} + D_{egg}}$$

where $a_{BH}$ is the asymptote or the maximum fish density determined by density-dependent mortality related to redd superimposition. Once the spawning habitat is saturated with reds newly arriving females will superimpose reds on top of others, destroying previously deposited eggs (Hayes 1987, Essington et al. 1998). Therefore, only the eggs deposited by the latest females should survive. This asymptote is calculated as

$$a_{BH} = \frac{D_{redd\_max}}{N_{fem}}$$

where $D_{redd\_max}$ is the maximum density of reds that can be dug and $N_{egg}/N_{fem}$ is the average number of eggs per female.
while the numerator of Eq. 8 is the spawning habitat area and \( \text{A}_{\text{rred}} \) is the average redd area.

The second parameter in Eq. 6, \( b_{BH} \), is the egg density at 50% of the asymptote

\[
b_{BH} = \frac{a_{BH}}{2 \times S_{\text{emerg}, \text{max}}}
\]  

where \( S_{\text{emerg, max}} \) is the maximum survival rate from egg to emergence, which is the result of density-independent processes such as scouring and dewatering, its value corresponds to the highest survival rate observed in a steelhead emergence study by Ward and Slaney (1993).

In both lake and stream habitats, natural mortality is modeled as an annual event that occurs between two growing seasons. Fry and juveniles that remain in the stream will survive at a fixed rate determined by their age (\( S_{0, \text{max}} \) and \( S_{1, \text{max}} \)). In the lake, natural survival (\( S_i \)) for all life stages varies with length and effective density (ED) and is modeled using the method and parameters presented by Post et al. (1999) and Parkinson et al. (2004)

\[
S_i = S_{\text{max}} e^{-m_i ED}
\]

\[
S_{\text{max}} = 0.49 \left[ \frac{L_i - 1.81}{1 + 0.49(L_i - 1.81)} \right]
\]

\[
m_i = -3.27 \times 10^{-6} \ln(L_i) + 1.21 \times 10^{-5}
\]

where \( S_{\text{max}} \) is the maximum survival for age class \( i \) that varies with length (\( L_i \)) and \( m_i \) is an exponent also related to size (see Fig. 3a). Maximum age was set at age 7, following that last year of life, natural survival was set to 0.

Maturity is modeled as age-determined and knife-edge. The age at maturity is fixed at three years old, maturation is usually later for female than male rainbow trout and most female reach maturity by age three (Cox 2000, Ward et al. 2017). We make the assumption that maturation is age determined as, for rainbow trout, size at maturity tend to be more variable than age at maturity. This is an important assumption and we assess the influence of this parameter on the model in a sensitivity analysis described further in this section. Mature fish are assumed to spawn every year and experience post-spawning mortality due to the energy required to migrate to the stream, prepare redds, spawn and defend redds. Post-spawning survival is fixed at 0.5 to represent the high spawning mortality experienced by rainbow trout, this value was chosen arbitrarily and its impact is evaluated in the sensitivity analysis.

**Harvest mortality**

Harvest is modeled by presenting recreational fishing mortality. Vulnerability to harvest is age-determined, knife-edge, and fixed at three years old meaning that fish aged three and older have the same vulnerability. Harvest mortality is based on Cox and Walters (2002) limited vulnerability (LV) model developed for rainbow trout recreational fishery in the province of British Columbia (BC) where most of the native range of rainbow trout in Canada is located. The LV model is driven by annual angling effort (\( E \)). In this model, fish reactivity and angler and fish spatial distributions change rapidly leading to fish alternating between available and unavailable states. Fishing mortality rate (\( f \)) is defined as

\[
f = \frac{qvE}{2v + qE}
\]

where \( q \) is a catchability coefficient of 0.09 ha/angler-days and \( v \) is the instantaneous turnover rate (per year) between pools of available and unavailable fish, the harvest parameters are based on data collected in rainbow trout populations of small lakes in BC (Cox 2000, Cox and Walters 2002).

**Figure 3**

(a) Survival rate in the lake varies with effective density and size (line thickness represents fish size) (b) Growth in both the stream and the lake follows a von Bertalanffy growth curve, which varies with fish density (percent habitat saturation in the stream and effective density in the lake) and growing degree days (GDD), density impacts the asymptotic size (\( L_\infty \)) while GDD impacts growth rate (\( K \)). The blue lines represent low density populations where juveniles migrate to the lake right after egg emergence while the orange lines represent high density populations where juveniles spend two growing seasons in the stream (from egg emergence to age 1), their growth trajectory is modified once they enter the lake. The solid lines represent high GDD while the dashed lines are low GDD.
and assumes that all fish caught are harvested. This instantaneous mortality rate can then be used to obtain an annual harvest mortality rate (U)

\[ U = 1 - e^{-f} \]  

**Growth**

Size at emergence from the gravel is fixed at 2 cm (Murray 1980), based on the assumption that the size of females does not impact the size and survival of eggs, and that hatch timing is consistent across populations. Following emergence, fish growth rate is determined by climatic conditions and density of fish in their habitat following annual spawning, natural and harvest mortality (Fig. 3b). The measure of density used is PHS in the stream for each age’s habitat and total effective density in the lake.

Growth in both the stream and lake is modeled using a von Bertalanffy growth function (VBGF)

\[ L_i = L_{\infty} \left[ 1 - e^{-K t_i} \right] \]  

where \( L_i \) is length at age \( i \), \( L_{\infty} \) is the asymptotic length (cm) and \( K \) (yr\(^{-1}\)) is a metabolic constant. In this model, growth is influenced by both climate and density. Climate’s influence on growth was modeled as a positive linear relationship between growing degree days above 5°C (GDD) and \( K \), as presented above.

\[ K_{\text{clim}} = a_{\text{clim}} \times \text{GDD}_j + b_{\text{clim}} \]  

where GDD\(_j\) is the GDD value for lake \( j \) during a specific year, \( a_{\text{clim}} \) is the slope and \( b_{\text{clim}} \) is the intercept of a linear regression between the VBGF parameter \( K \) calculated for six rainbow trout lakes by Cox (2000) and annual growing degree days calculated for the appropriate year using ClimateBC 5.30 (Wang et al. 2012). Annual GDD corresponds to the difference in degrees Celsius between the mean temperature and the chosen base of 5°C. Climate and density have both been linked to growth variation for rainbow trout in BC (Ward et al. 2017).

Density (PHS in the stream, effective density in the lake) affects growth through its impact on asymptotic length (\( L_{\infty} \)). In the stream, \( L_{\infty} \) decreases with increases in saturation (PHS) following a negative power curve as described by Grant and Imre (2005) who compiled data on six species of stream-dwelling salmonids and concluded that density-dependent growth was stronger at low density rather than large density

\[ L_{\infty \text{stream}} = 64.96 \times \text{PHS}^{-0.3} \]  

In the lake, \( L_{\infty} \) decreases linearly with increases in effective density following the parameters used by Parkinson et al. (2004) based on data by Post et al. (1999)

\[ L_{\infty \text{lake}} = 64.83 - 9.6 \times 10^{-5} \times \text{ED} \]  

where ED is the effective density (cm\(^2\)/ha) in the lake.

The correlation between growth rate and maximum size is not explicitly modeled but is an emergent property of the density-dependent processes presented. By using measures of density (PHS and effective density) that include the impact of fish size, an increase in growth rate leads to higher density and decrease of maximum size.

The VBGF parameters obtained for a specific climate and density were used to build Walford plots that represent size at age based on size at the previous age

\[ L_{i+1} = a_W + b_W L_i \]  

\[ a_W = L_{\infty}(1 - b_W) \]  

\[ b_W = e^{-K} \]  

where \( L_i \) is the length at age \( i \), \( a_W \) is the Walford intercept, and \( b_W \) is the Walford slope. The Walford plot parameters are then used in the model to calculate growth for each cohort from one age class to the other. Table 1 presents the values of the parameters used to model the impact of density on the Walford plot intercept (\( a_W \) and \( b_W \)) directly instead of the relationship with \( L_{\infty} \) presented above.

**Fecundity**

Fecundity is calculated based on fish size. Parkinson et al. (2004) used data collected by local BC fish hatcheries to estimate the number of eggs produced per female (\( N_{\text{eggs,fem}} \)) depending on female size (\( L \))

\[ N_{\text{eggs,fem}} = 2.49 \times 10^{-5} \times L^{2.9} \]  

The total number of eggs (\( N_{\text{eggs}} \)) produced by the population for a year is

\[ N_{\text{eggs}} = \sum_{i=1}^{n} (N_i \times P_{\text{fem}} \times N_{\text{eggs,fem}}) \times P_{\text{eggs, via}} \]  

where \( N_i \) is the total number of fish in age class \( i \), \( P_{\text{fem}} \) is the proportion of females in that age class, and \( P_{\text{eggs, via}} \) is the proportion of eggs that are fertilized and viable (Van Winkle et al. 1998). Eggs produced during a year are then deposited in the stream in the following spring.

**Simulations**

To simulate the impact of stream habitat area on the fish population, we ran the model using different values of stream area and proportion of stream used for spawning, fry rearing, and juvenile rearing. For simplicity, the lake area was fixed at 1 ha for all simulations. The stream area varied from 0.5 to 500 m\(^2\), which, in relation to a 1-ha lake, is similar to stream to lake area ratios observed within the native range of rainbow trout in BC. Values ranging from 1% to 45% of total stream area were used for the proportion of stream used for spawning. The range of values used for rearing are presented in Table 1 and correspond to the migration scenarios explained above. GDD values ranging from 1,000 to 2,000 were used to simulate the climatic conditions.
across the native rainbow trout distribution in BC (range of 1,036–1,954 GDD observed by Ward et al. [2017]). Finally, harvest mortality rate ranging from 0 to 0.8 (corresponding to fishing effort 0 to 5,000 angler-days·ha⁻¹·yr⁻¹) were simulated, harvest rate is usually lower on most rainbow trout lakes in BC (mean of -0.6 following Eq. 14, Post et al. 2008), but extreme values were used to assess how high harvest mortality affects population dynamics. The variables used for the simulations are summarized in Table 1. A total of 6,720 factorial combinations were simulated (7 stream areas × 6 spawning habitat proportions × 4 migration scenarios/rearing habitat proportions × 5 climatic conditions × 8 harvest levels). Each simulation ran over 200 yr to ensure an equilibrium was reached.

Analysis

Simulation results were first compared based on the status of the resulting population. After 200 yr of simulations, we examined whether the population collapsed, and if so, whether it occurred as a result of overharvest or stream habitat limitations. We also assessed whether the population reached an equilibrium and, if so, whether the equilibrium was a fixed point, where abundance reached a unique value, or a bounded oscillation cycle, where abundance oscillates but repeats a cycling pattern. Abundance, which is the same as density of fish per hectare since lake size was fixed, and mean size at maturity (fixed at age 3 in the model) were used to describe the resulting population characteristics.

To assess the impact of various processes on population characteristics, alternative processes were contrasted to a baseline model. The baseline model corresponds to intermediate values of stream habitat and climatic conditions under which the model consistently reached a fixed-point equilibrium (50 m² stream area, 25% proportion spawning habitat, migration from streams after one growing season, 1,500 GDD) under no harvest and harvest mortality rate of 0.7. The harvest values used represent a situation with no harvest and what is considered high harvest in the BC rainbow trout recreational fishery (corresponding to a fishing effort of 100 angler-days·ha⁻¹·yr⁻¹; Post et al. 2008). The processes assessed in this way are presented in Table 2.

A sensitivity analysis was conducted to assess the sensitivity of key parameters (detailed in Appendix S2: Table S1) by varying them (±5%, ±10%, ±25%), and contrasting to the population characteristics from the baseline model. The following population characteristics were examined to test the sensitivity of the model parameters: population status (collapsed, fixed-point equilibrium, or stable cycle), total abundance of fish in the 1 ha lake and mean size at maturity in the lake.

Comparison to empirical data

The simulation results are compared to empirical data from 33 lake-dwelling rainbow trout populations located in the BC interior collected between 2013 and 2016 (lake information detailed in Appendix S1: Table S1). The fish population data collected consist of autumn gillnet samples that follow BC’s provincial guidelines (Ward et al. 2012), gillnet catch (number of fish per two net set) is used as a proxy for fish density in the lake and the asymptotic length (L∞) is estimated by fitting the VBGF (Eq. 15) to the size at age data obtained from gillnet fork length measurements and otolith aging. L∞ is used to compare the size of fish between populations. Environmental data (lake characteristics such as location, size, and depth) was acquired from provincial databases (British Columbia Ministry of Forests, Lands and Natural Resource Operations; Freshwater Fisheries Society of British Columbia), and field measurements of stream habitat availability and fishing effort using trail cameras (van Poorten et al. 2015). Spawning and rearing habitat availability were summarized by calculating a habitat index, the index consisted of the sum of the standardized estimated areas identified as stream-spawning, age-0-rearing, age-1-rearing, and lake-rearing (littoral) habitats. Simulations and field results were compared on the base of the trends of population density and maximum size associated with early life stage habitat availability. The population status (collapse, cycle, or fixed-point equilibrium) could not be compared since the gillnet sampling were only done for one year, which would not allow to detect population cycles, and sampling was only conducted in established rainbow trout populations, therefore no collapsed population would be observed in the field.

RESULTS

The influence of increased stream habitat availability on population dynamics, abundance, and size structure are assessed under no harvest and high harvest scenarios (Fig. 4). For those combinations of parameters that resulted in fixed-point equilibria, Fig. 5a presents the fish abundance and associated maximum size combinations and the regions of combinations covered by cycling populations. Higher GDD leads to larger size for the same abundance, unless abundance is high (Fig. 5b). In general, as stream habitat quantity (area) and quality (availability of spawning and rearing habitat) increase, fish density increases and fish size decreases (see Fig. 5c).

Population dynamics: Collapse

A small number of the simulated populations (<1%) collapsed while there was no harvest. Those were characterized by limited habitat where stream area was 0.5 m², of which 1% was spawning habitat and no stream rearing habitat was available. As such, the collapse occurred because the habitat limitation in the early life stage habitat (stream) results in individuals migrating to the lake immediately after emergence and experiencing high mortality in the lake. In these conditions, no matter the productivity of the system (GDD), modeled fish populations could not sustain themselves. In 1.3% of simulations, collapses occurred due to a combination of medium-high harvest rate (≥0.6) and low early life stage habitat availability (total stream area ≤2 m², spawning area ≤5% of total stream area and no stream rearing habitat available). As stream habitat and system productivity (GDD) increased, higher harvest was required to produce a collapse. No overharvest induced collapse were observed in simulations where streams were larger than 2 m² for the 1-ha lake area used for all simulations.
In most simulations (81% of the populations simulated), the populations reached a fixed-point equilibrium where population abundance and size-structure is constant. Population abundance increased as stream habitat quantity and quality improved, while size at age decreased. Increases in GDD led to large increases in lake fish size when stream habitat was improved.

Table 2: Results of the modification of processes from those used in the baseline population (50 m² stream area, 25% of stream habitat is spawning habitat, migration after one growing season, 1,500 GDD) under no harvest (abundance of 2,072 fish and size at age 3 of 17.97 cm) and harvest mortality rate of 0.7 (abundance of 1,690 fish and size at age 3 of 21.90 cm).

<table>
<thead>
<tr>
<th>Process change from the baseline models and harvest mortality rate</th>
<th>Population dynamics</th>
<th>Change (%)</th>
<th>Lake abundance</th>
<th>Size at age 3 (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Egg survival follows a Ricker recruitment function</td>
<td>cycle</td>
<td>−3†</td>
<td>−1†</td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td>FPE</td>
<td>−2</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>(2) Egg survival is constant (density independent)</td>
<td>cycle</td>
<td>−8†</td>
<td>5†</td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td>FPE</td>
<td>−17</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>(3) Territory size is density independent (size-dependent only)</td>
<td>FPE</td>
<td>0</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td>FPE</td>
<td>7</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>(4) Early migrants from stream to lake die; in stream, fish without a territory die instead of migrating to the lake</td>
<td>FPE</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td>FPE</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>(5) Stream growth is density independent (climate-dependent only)</td>
<td>FPE</td>
<td>6</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td>FPE</td>
<td>9</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>(6) Stream growth follows a linear decrease with density</td>
<td>cycle</td>
<td>−22†</td>
<td>−5†</td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td>FPE</td>
<td>−14</td>
<td>−2</td>
<td></td>
</tr>
<tr>
<td>(7) Stream migration behavior is density independent (juveniles stay in the stream even if no territories are available and survive following age-specific survival rate)</td>
<td>FPE</td>
<td>14</td>
<td>−15</td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td>FPE</td>
<td>16</td>
<td>−13</td>
<td></td>
</tr>
<tr>
<td>(8) Stream growth and migration behavior are density independent, (5) and (7) together</td>
<td>cycle</td>
<td>−15†</td>
<td>−19†</td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td>FPE</td>
<td>1</td>
<td>−16</td>
<td></td>
</tr>
<tr>
<td>(9) Lake growth is density independent (climate-dependent only)</td>
<td>FPE</td>
<td>−6</td>
<td>25</td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td>FPE</td>
<td>3</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>(10) Lake survival is density independent (size-dependent only)</td>
<td>FPE</td>
<td>1,104</td>
<td>−39</td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td>FPE</td>
<td>256</td>
<td>−40</td>
<td></td>
</tr>
<tr>
<td>(11) Lake growth and survival are density independent, (9) and (10) together</td>
<td>FPE</td>
<td>1,800</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td>FPE</td>
<td>1,254</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>(12) Stream and lake growth is density independent, (5) and (9) together</td>
<td>FPE</td>
<td>0</td>
<td>23</td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td>FPE</td>
<td>7</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>(13) Stream migration behavior and lake survival are density independent, (7) and (10) together</td>
<td>FPE</td>
<td>635</td>
<td>−49</td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td>FPE</td>
<td>268</td>
<td>−38</td>
<td></td>
</tr>
<tr>
<td>(14) Adult fish are fully vulnerable to harvest</td>
<td>FPE</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td>collapse</td>
<td>−100</td>
<td>NA</td>
<td></td>
</tr>
</tbody>
</table>

Notes: Simulations summarized using the resulting population status (collapse, fixed-point-equilibrium [FPE], cycle), percentage change from the baseline in abundance of fish in the lake and mean size at age 3 (cm). The entries in boldface type represent a change in qualitative dynamics for the population status or a change in quantitative predictions greater than 25%. Size at age 3 is not available (NA) in case of a population collapse. †Population cycle the abundance and size used are the mean values obtained over 10 yr.

Population dynamics: Fixed-point equilibria

In most simulations (81% of the populations simulated), the populations reached a fixed-point equilibrium where population abundance and size-structure is constant. Population abundance increased as stream habitat quantity and quality improved, while size at age decreased. Increases in GDD led to large increases in lake fish size when stream habitat was improved.
habitat was limiting, but when stream habitat was abundant, the difference in fish size was minimal and fish abundance decreased (Fig. 5b).

Population dynamics: Cycles

For 17% of the simulations, the population did not reach a stable fixed-point equilibrium but a stable cycle emerged. The cycles are characterized by the presence of a strong cohort that dominates for a period of time. We observed two types of cycles (Fig. 5a). The first type, low-density cycles, results from populations with intermediate size streams, no rearing habitat and high GDD resulting in low fish abundance and large fish size (Fig. 6a). This cyclic pattern is more prevalent under high harvest where older age classes have high harvest mortality. Young fish recruiting into the lake have higher survival due to the low density of older conspecifics (i.e., low intercohort competition). In larger streams, lower GDD and lower harvest are necessary to transition from fixed-point equilibria to cycling.

The second type of cyclic outcomes, high-density cycles, resulted from large streams with at least some age-0 rearing habitat available, leading to high abundance of small fish surviving their first year of life and migrating into the lake (Fig. 6b). In this case, high harvest tends to switch cyclic behavior to fixed-point equilibria. Abundant stream habitat provides a refuge for juveniles for 1–2 yr from the intense competition in the lake, producing a lag between egg production and impact of these young fish on density-dependent processes in the lake. This results in a strong cohort that survives better to the adult stage where it produces more eggs, which feeds the cycle observed and produces a new strong cohort. The down part of the cycle occurs due to the intercohort competition between the adult strong cohort and the young fish entering the lake, resulting in low survival of the young fish to the adult stage, lessening competition at lake entry for the next strong cohort. With larger stream habitat and more spawning and rearing habitat, and higher GDD, more harvest mortality is required to drive the cycle to a fixed point and, for streams larger than 50 m², cycles were observed even with the highest level of harvest (mortality rate of 0.8) when the proportion of stream used for spawning and rearing habitat was high.

Assessing the importance of ecological processes

The functional forms of biological processes represented here led to quantitative and qualitative changes in dynamics and demographic characteristics of the resultant fish populations (Table 2). The baseline population used led to a fixed-point equilibrium under both low and high harvest pressure. The modification of four processes led to stable
cycles, but only when there was no harvest. In all cases, harvest returned the population to a fixed-point similar to what was observed in the high density cycles described in the previous section where increased harvest mortality rate has a stabilizing effect. Modifying egg survival from an asymptotic relationship to a humped-shaped Ricker type curve (Process 1, Table 2) or to a fixed survival (Process 2) led to increased emergence survival in the stream. Similarly, when fish growth in streams followed a linear decrease with density instead of a negative exponential function (Process 6) or both stream growth and survival were density independent (Process 8), more fish survived in the stream leading to the development of strong cohorts causing cycles. By making all adult fish vulnerable to harvest (Process 14) a high harvest mortality rate was enough to deplete a population, producing the only collapse as a result of a change in an important biological process.

An increase of over 25% in size at age 3 (maturity) was observed when lake growth was density independent (Process 9) while a decrease of over 25% was observed when lake survival and stream and lake survival were density-independent (Processes 10 and 13). This decrease in size was accompanied by an increase in abundance. Density-independent lake growth and survival also lead to an increase in abundance (Process 11).

**Parameter sensitivity analysis**

The majority of the parameter perturbations of ±5%, ±10%, and ±25% did not alter either the qualitative dynamic outcomes or the quantitative outcomes greater than the magnitude of the perturbations (Appendix S2: Table S1). In a few situations, the fixed-point equilibria of the baseline simulation was changed to cycles. With harvest, when age at maturity (Age_m) is lowered or age at vulnerability to harvest (Age_v) is increased, stable cycles were observed. Cycling also occurred when egg emergence survival is increased by increasing the asymptote of the Beverton-Holt recruitment function ($a_{BH}$) by 25%. Increased stream growth rate, either through 25% increase in parameters determining how growth rate decrease with density in the stream ($a_{stream}$ and $b_{stream}$) or through a modification of how growth is impacted by climate ($b_{clim}$), also led to cycles. Finally, a decrease of spawning survival ($S_{spawn}$) also led to cycles.

Quantitatively, lake abundance increased greater than the parameter perturbation while size at age 3 decreased when (1) age at maturity decreased, (2) age at vulnerability to harvest increased, or (3) lake natural survival increased through a decrease in $m$, the exponent of the relationship between density and survival that varies with fish size, the resulting abundance and size varied more than the change in the parameter for all levels of parameter perturbation (5%, 10%, and 25%) when there was no harvest but only at 25% with harvest mortality. Conversely, lake abundance decreased and size at age 3 increased with increased age at maturity and decreased age at vulnerability.

**Comparison to field data**

Similar to the simulation results, the populations sampled in the field present smaller fish associated with high gillnet catch and larger fish associated with lower catch, none of the populations presented a high gillnet catch of large fish (Fig. 7). Most of the populations that had limited early life stage habitat are in the lower right quadrant of the plot presenting low densities and large size. Populations from intermediate habitat availabilities present a range of densities and size, while populations where high amounts of habitat is available mostly present small fish size. Because the site sampled presented negligible fishing effort, harvest mortality was not considered or presented for the empirical data.

**Discussion**

The model developed uses density-dependent ecological processes and spatial ontogeny to describe population
bottlenecks resulting from variation in availability of habitat used for reproduction and juvenile growth. The addition of simple harvest dynamics makes this model relevant to management of species that experience commercial or recreational harvest. The simulation results illustrate how populations occupying similar adult habitat can differ in abundance and size structure when early life stage conditions differ. When early life stage (spawning and rearing) habitat is limited, populations are more sensitive to increases in mortality (presented as increases in harvest mortality in this model). The simulations also showed that a minimum quantity of spawning habitat is required to support a viable population, a threshold value has to be reached even in the absence of stochastic events. Population abundance increases as the early life habitat quantity and quality increases but, due to the effect of density dependence in growth in the adult habitat, size at age tends to decrease leading to stunted populations. When large amounts of quality spawning and rearing habitat are available, the population bottleneck moves to the habitat of older stages.

The simulation results present a narrow range of combinations of population abundances and maximum individual sizes with size decreasing at high population abundances as growth is modelled as a density-dependent compensatory process. A similar trend is also observed in the empirical data where populations with larger asymptotic length present lower density. Fish grow larger at low density, and growth is slowed at high density (Rose et al. 2001). The results are consistent with observations of density-dependent growth resulting from exploitative competition in lake-dwelling rainbow trout (Post et al. 1999).

The use of a multi-stage habitat model demonstrates the nature of the population bottlenecks impacting and shaping a population by linking limiting processes at different stages of the life cycle to the resulting population dynamics. Salmon recruitment limitation has mainly been linked to bottlenecks occurring at the spawning (Knapp et al. 1998) or juvenile stages (Elliott 1985, Crisp 1993, Bond et al. 2008). Limitation at the adult stage is observed in many species (de Roos and Persson 2013), but could the lack of studies presenting limitations of the adult stage be an artifact of the complexity of salmonid life cycles? As presented by Milner et al. (2003), in anadromous fish, it is often difficult to study the processes occurring at sea and impacting the adult life stages. Also, by its nature, the marine environment presents large available habitat that is less likely to present space limitation, but could freshwater salmonids be more likely to be limited at the adult stage? For example, Elliott (1985, 1994) has shown that the main source of regulation for anadromous brown trout of Black Brows Beck was at the very early life stage, but did not find any evidence of early life stage...
regulation in the resident brown trout population of Wilfin Beck and claimed that in that case the bottleneck was instead placed on the adult stage (Elliott and Hurley 1998). We argue that, given the range of habitat combinations presented in the simulations, population regulation of lake-dwelling rainbow trout could come from all three presented stages (egg, juvenile, adult) and impact a population’s persistence, abundance, and individual growth.

Population collapses were observed when spawning habitat availability was strongly limited, in this deterministic model, this is the result of high natural mortality and insufficient compensation at low density, but it also corresponds to what would be expected based on stochastic dynamics alone in nature. At low spawning habitat availability, a bottleneck led to low egg to emergence survival resulting in low overall population densities as observed in stream-dwelling golden trout where the lack of appropriate substrate limits redd density (Knapp et al. 1998). The empirical data supports this model prediction as the largest fish were observed in systems with low fish density and limiting spawning and rearing habitat.

Limiting the available stream juvenile rearing habitat led to early lake migration, forcing young fish into less optimal lake habitat where they were in competition with older/larger fish, resulting in lower survival of the younger age classes. Here, the stream functions as a nursery habitat where juvenile fish can find shelter from predation and competition (Beck et al. 2001). The lack of appropriate nursery habitat can impact whole population and communities by controlling the juvenile stage through habitat limitation as seen in marine fishes and invertebrates (Wahle and Steneck 1991, Beck 1995, Mumbry et al. 2004, Sundblad et al. 2014). Nursery habitat’s positive impact on a population can also be the result of an increase in individual growth as in steelhead trout (anadromous rainbow trout) where access to estuarine nursery habitat has been linked to enhanced juvenile growth leading to a larger size at ocean entry that increases ocean survival (Bond et al. 2008).

When lake habitat is limiting (in this simulation framework where lake size is constant, this is seen when stream habitats are abundant) the population bottleneck is in the adult stage. In the empirical data presented, this occurs when lakes have large or many perennial tributaries offering abundant cover to young fish. The abundant stream habitat leads to high early age growth and survival, but once the juveniles migrate in the lake the high density in that habitat leads to lower growth rate resulting in slow growing stunted fish populations. Ylikarjula et al. (1999) explained that stunted populations are ultimately the result of resource limitations that can arise through increases in juvenile and/or adult survival or increases in intra-specific competition. In the simulations, stunting is indeed observed when adult survival is increased at low harvest, and when large rearing habitat is available, providing shelter to juvenile and increasing their survival.

In the first type of cycle, spawning habitat is limiting, stream rearing habitat is absent, but productivity (GDD) is high. The bottleneck on the early life stages (spawning and juveniles) leads to low stream and lake abundances, which intensifies individual growth and is further enhanced by the higher GDD. Similar to what has been observed by Borgström et al. (1993) in brown trout, the early immigration to the lake leads to high intercohort competition between juvenile age classes where one cohort becomes dominant. In the present model, this type of cycle was observed under high harvest, which increased spawner mortality and periodically removed the older age classes so that only one or two age classes of spawner were present. A simulated 25% decrease in spawning survival caused a decrease in the number of spawners and the loss of older age classes, resulting in cycling in a previously stable population. The high spawner mortality limits egg input and following year’s age-0 cohort while also decreasing the competitive pressure on the juvenile fish present in the lake, the following year that same advantaged juvenile cohort has less competition from both the age-0 coming from the stream (deposited by previous year’s spawners) and from the fished adult population. Once that advantaged cohort becomes mature, they are subjected to harvest but their higher abundance and large size allow them to produce more eggs than the previous cohort producing another strong cohort and perpetuating the cycle. Older age classes have the potential to dampen the cycles through their competitive interaction with early migrants, similar to the pressure applied by cannibalism, which usually has a stabilizing effect (Claessens et al. 2000). Once the adults experience higher mortality, however, cycles arise.

Cycles of larger amplitude and longer period were observed in situations where abundant spawning and rearing habitat were available, these populations were characterized by high abundance in both the stream and the lake, with a small size at age in the lake. Here, the stabilizing force of early life stage mortality is absent since that habitat was not limiting. Hence, high growth and survival in the stream led to high intercohort competition once these abundant and large-bodied young fish enter the lake at age-1, creating a strong cohort. Parameter sensitivity analysis results support this explanation, cycling occurred when stream growth and survival were increased through changes in the functional form, density dependence, and parameters of the stream processes. The time spent by the young fish in the stream shelters them, for up to two years, from competition with larger/older fish in the lake. This additional delay occurring between reproduction and lake entry of the young fish adds to the complexity of the life cycle and further destabilizes the population. This type of cohort cycle resulting from intercohort competition is similar to what has been observed in vendace (Coregonus albula; Hamrin and Persson 1986, Helminen and Sarvala 1994), roach (Rutilus rutilus; Persson et al. 1998), and Eurasian perch (Perca fluviatilis; Persson et al. 1998, de Roos et al. 2002).

The presence of cycles is contrary to what was observed in an experiment on lake-dwelling rainbow trout by Post et al. (1999) who did not encounter situations where younger age classes out-competed adults and speculated that rainbow trout populations should be stable rather than oscillate. This difference might come from the experimental systems used by Post et al., which only had two age classes present (age 0 and 1) and did not experimentally simulate the full age-structure of a natural population. Additionally, the input of young fish in their experiment was through stocking. They used a 10-fold variation in stocking density across treatments, which
might not have resulted in sufficient density variation as generated by the different habitat combinations simulated here.

Variation in age at maturity and age at vulnerability to harvest, both fixed at three years old in the baseline simulations, impacted the model simulation results. The interaction between those two parameters is important. If maturity occurred before individuals become vulnerable to harvest there are now adults that are not subject to harvest mortality and have higher survival. In the sensitivity analysis this situation led to population cycles due to the higher population fecundity. Life-history theory suggests that earlier maturity could occur if early growth is accelerated (Ylikarjula et al. 1999, Roff 2002), population bottlenecks leading to lower juvenile densities and higher growth rates could then lead to earlier maturation. For example, situations where fecundity is reduced due to high adult mortality and ample rearing habitat is available or where early life stage mortality is high due to limited spawning habitat, but abundant habitat is available to older life stages. In contrast, if individuals become vulnerable to harvest before reaching maturity, adult density will decrease as fewer adults survive to older age, additionally decreasing population fecundity. Delayed maturation could also occur through slow growth, if adult survival is increased through a decrease in harvest mortality for example (Ylikarjula et al. 1999). In this model, age at maturity and age at vulnerability were both fixed to age 3 to simplify the model and its interpretation. Allowing age at maturity and age at vulnerability to vary with size would likely impact population dynamics.

This multi-habitat age-structured population model links environmental conditions and habitat availability at different stages of a species life cycle to population dynamics outcomes. This information has direct applications in species management and habitat conservation. Our study species, rainbow trout, is exploited by recreational fisheries around the world meaning that our findings could provide insight to managers for this type of system but also for the management and conservation of other organisms that experience ontogenetic habitat shifts leading to population bottlenecks. Managers often oversee extensive areas composed of numerous systems that they cannot sample regularly. Information on the relative availability of habitats throughout ontogenesis could assist in identifying likely bottlenecks in production and to identify systems at risk of being impacted by habitat loss or overharvest, which would help managers orient their sampling strategy and allocation of resources. Knowledge of the importance of life-history-specific habitat requirements for recruitment, abundance, and dynamics can also help prioritize initiatives of conservation and restoration of key habitats.

Acknowledgments

This study was funded by Discovery and Collaborative Research and Development Grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Freshwater Fisheries Society of British Columbia (FFSBC) to John R. Post. Ariane Cantin was supported by a NSERC Post-Graduate Scholarship and a University of Calgary Silver Anniversary Graduate Fellowship. Valuable comments on previous drafts of this paper were given by Stephanie Mogensen and Nilo Sinnatambry. We thank Pär Byström and an anonymous reviewer for their comments that substantially improved this manuscript.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2371/suppinfo