Spreadsheet model descriptions

Age-structured model

Predicting maximum first year survival rates and population growth rates for invading Smallmouth Bass

Most fish have high enough fecundity (in the thousands at least) to potentially produce many age-1 recruits for each spawner under ideal conditions. But natural mortality rates of eggs, larvae, and small juveniles are almost always very high, so very few fish survive to their first birthday even under ideal conditions. A basic issue in fish population dynamics is how much that first year survival rate can increase when an unharvested population is reduced through factors like fishing, or conversely how high that survival rate can be when a fish stock is introduced at low densities into an environment. Fortunately, we have many observations of how much first year survival rate has improved in populations that have been reduced through fishing, and an elegant way to describe that improvement is with the “Goodyear compensation ratio” or just CR introduced by Phil Goodyear. CR is just the ratio of first year survival when abundance is very low (smax) to first year survival in the natural unharvested population before it is fished or after it stops growing (so), i.e. CR=smax/so.

In terms of stock-recruitment theory, we typically predict recruitment using a function of the form

R=smaxf(E) (A4 Eq. 1.1)  
where f(E) is a decreasing function of total egg deposition, e.g. 1/(1+bE) is called the Beverton-Holt function and exp(-bE) is called the Ricker function. At an unfished natural equilibrium with average recruitment Ro, unfished egg production is given by Eo=Ro\*epro, where epro is the average egg production per age 1 recruit. In an age-structured model, epro is given the sum over ages of fecundities fa times age-specific survivorships La, i.e. the Botsford incidence function for egg production, as

where survivorships L1=1 and La=La-1Sa for age a>1. (A4 Eq. 1.2).

in this equation, Sa is the annual survival rate from age a to age a+1.

An important observation about the *epro* unfished egg production per recruit is that 1/epro is the unfished recruitment per egg, i.e. so=1/epro where so is again the average unfished age 0 survival rate. What has been found in metanalysis of stock recruitment data for many fish species is that the compensation ratio CR leading to prediction of the smax=CR\*so maximum survival rate needed to predict age 0 survival rate following new introductions is relatively predictable (Hilborn and Walters 2021). When we express so and smax as instantaneous mortality rates Mo and Mmin (in the model s=exp(-M)), the difference (Mo-Mmin) is a predictable fraction, typically near 0.2, of Mo, i.e. Mmin=0.8\*Mo. The change in M, Mo-Mmin, is the natural logarithm of the compensation ratio, i.e. ln(CR)=0.2\*Mo. More simply, for an age-structured model used to predict invasions or responses to fishing using predictions of egg production and first-year survival rates from a basic stock-recruitment model of eq. (1) form, smax is given by just

smax = CR/epro (A4 Eq. 1.3).  
In this equation, epro is easily estimated given age schedules of fecundity and annual survival rates of 1+ year old fish, and CR can be predicted from meta-analysis results for many, many fish species. Using typical Smallmouth Bass survivorship and fecundity schedules from the literature and from observations in the upper basin, we estimate that CR is most likely around 6.0 but could be as high as 15 if we have underestimated maximum fecundity and if the ratio (Mo-Mmin)/Mo is as high as 0.3, the maximum seen over species by Hilborn and Walters (2021).

We developed a basic age-structured population model to predict invasion dynamics using eq. (1) to predict recruitment in conjunction with alternative assumptions about frequency of successful year-class production. The age dynamics Na,t (a=age, t=year) are given in this model by

Et= ∑faNa,t egg production year t (A4 Eq. 1.4)

N1,t=smax Et /(1-b\*Et)\*Rt Beverton-Holt recruitment (A4 Eq. 1.5)

Na,t=Na-1.t-1Sa-1,t-1 for a>1, survival of older fish over time (A4 Eq. 1.6).

Here, the scaling parameter b for maximum recruitment is set to give average recruitment near 1.0 after invasion. The Sa,t can be varied to represent effects of culling on survival rate. The annual recruitment rate multipliers Rt are set to ewt every nth year representing successful recruitment, 0 for other years, with wt being a normally distributed recruitment anomaly for successful spawning years (We used 𝛔w=0.4 to give considerable variation in recruitment for strong cohorts). For the age accounting, we assumed a maximum age of 20 years absent mortality due to harvest or mechanical removal.

We calculated fa using growth and maturity schedules assuming von Bertalanffy growth with K=0.2 and mean age at maturity 3.5. Annual survival rates Sa were assumed to vary according to a Lorenzen (Lorenzen,1996, 2022; Lorenzen et al. 2022) model for size-dependent survival rate, with survival varying as a -0.29 power of relative body weight so as to correspond with age variation in survival rates seen in Lorenzen’s metanalysis of a variety of fish species. The resulting age schedules are given in A4 Table 1.

Note that the model defined by A4 Equations 4-6 exhibits maximum population growth rate for very low numbers at age, i.e., it does not assume any questionable “Allee effects” in the invasion dynamics. By simply setting the initial numbers at age very low, e.g. 10-6, we can easily simulate the intrinsic population growth rate “r” (or annual growth rate 𝛌=er over the first 30 or so years of any simulation test, allowing simple evaluation of the effects of various parameter values on predicted invasion rates and success.

We simulated two alternative invasion patterns. For the first pattern, we simply initialized the model age structure with a low number of age-1 recruits from “upstream” sources, with no later invasion events. For the second, we assumed a low annual addition of age-1 recruits from some upstream source, like an established population in Glen Canyon. Initial sensitivity tests indicated that adding low immigrant juvenile numbers every year did not substantially affect long term population growth patterns, but did affect calculations of population growth rates *r* over the first 2-30 years after invasion.

The calculations above are implemented in a relatively simple Excel spreadsheet (available https://github.com/billpine/SMB\_Grand\_Canyon/upload). We chose this (rather than code-based methods) in order to make them as transparent and understandable as possible to model users interested in evaluating sensitivity of the predictions to various parameters and harvest culling scenarios.

Table A4.1. Assumed baseline SMB mean age-specific fecundities fa and survival rates Sa used in estimating recruitment compensation ratios and in age-structured simulations of invasion dynamics

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Age** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** |
| **fa** | 8.21 | 111 | 555 | 1572 | 2970 | 4333 | 5475 | 6394 | 7130 | 7722 | 8198 | 8578 | 8881 | 9121 | 9311 | 9460 | 9578 | 9670 | 9743 | 9799 |
| **Sa** | 0.31 | 0.49 | 0.58 | 0.63 | 0.66 | 0.68 | 0.69 | 0.7 | 0.71 | 0.71 | 0.72 | 0.72 | 0.72 | 0.72 | 0.73 | 0.73 | 0.73 | 0.73 | 0.73 | 0.73 |

Temperature and turbidity dependent growth model for Smallmouth Bass

Energetics model

We used the general bioenergetics model described in Walters and Essington (2010; see also Essington et al. 2001, van Poorten and Walters 2016) to model first year weight growth of post larval Smallmouth Bass for the 2002-2023 period, using daily water temperature and silt-clay concentration data at Bright Angel Creek, locations representative of the river reach just below the LCR where native fish impacts are first expected if Smallmouth Bass can successfully colonize that reach. The basic model growth rate equation for a fish of body weight W is

dW/dt=ft(S)fs(S)fc(T)HW2/3-fm(T)mW (A4 Eq. 2.1).  
 in this model, the annual average consumption and metabolism parameters H and m are modified for each day by three multiplicative functions of temperature T and turbidity S, as

fs(S)=exp(-S/Sh) turbidity effect on feeding (A4 Eq. 2.2)  
 fc(T)=Q10c(T-Tbar)/10  temperature effect on feeding (A4 Eq. 2.3)  
 fm(T)=Q10m(T-Tbar)/10 temperature effect on metabolism (A4 Eq. 2.4).

The parameters of this model (H,m,Sh,Q10c,Q10m, and mean temperature Tbar) were estimated from various data sources as described below with the exception of Tbar which was obtained directly from the temperature time series data recorded at Diamond Creek.

Laboratory experiments have shown that reduced prey availability due to turbidity (A4 Eq. 2.2) do not necessarily lead to reduced growth, presumably because at least small juvenile fish increase their foraging time to try to maintain growth rates needed for survival (Gregory and Northcote 1993; Sweka and Hartman 2001). We have examined the effect of such responses by including foraging time multiplier on the feeding rate term of A4 Eq. 2.1:

ft(S)=min{Tmax,1/fs(S)} (A4 Eq. 2.5).  
Here, Tmax is a maximum relative time spent foraging, and the 1/fs term inflates feeding rate in inverse proportion to reduction in reactive distance. Reasonable values of Tmax are likely to be in the range 3-5, i.e. juvenile fish are likely to be able to spend as much as 3-5 times their normal daily foraging times when apparent prey densities as impacted by turbidity are lower. Note that such increases in foraging time at low apparent prey densities are also likely to lead to increased mortality rates, and in fact one way to derive the well-known Beverton-Holt stock recruitment model is to assume that foraging times increase when competition reduces prey density, so as to maintain constant growth rates (Walters and Korman 1999).

Estimates of H and m were obtained by fitting length at age data for upper basin Smallmouth Bass in Breton et al. (2015) to the von Bertalanffy growth curve, while noting that the general structure A1 without T,S forcing is the defining relationship for the vonBertalanffy growth curve. For this curve there is a simple transformation between the H, m and the vonBertalanffy parameters K,L∞ (m=3K, H=mL∞ a1/3 where a is the intercept parameter of the length-weight equation W=aL3). The H,m estimates obtained this way are near the lower end of the set of H,m estimates reported in Fishbase for locations around North America (see “stawberry utah SMB growth.xlsx” https://github.com/billpine/SMB\_Grand\_Canyon ), i.e., Smallmouth Bass growth in the upper Colorado River basin is a bit slower than expected from Smallmouth Bass on average.

Estimates of the turbidty Sh needed to reduce feeding rate by about 2/3 (to 1/e of maximum rate) were obtained from a general relationship assembled for visual feeding salmonids by Rosenfeld and Taylor (2003).

The Q10m parameter for variation in metabolic rate with temperature can be reasonably estimated from laboratory data and is likely in the range 2.0-3.5 (Shuter et al. 1980, Tetzlaff et al. 2010, Whitledge et al. 2002; reviews of Wisconsin bioenergetics model typical parameter values). Unfortunately, the Q10c parameter is a function of feeding conditions (e.g., prey density and size) as well as basic physiology, so only a minimum value for it can be obtained from laboratory studies. Estimates for it from field growth data (references for Q10m above, also Coutant and DeAngelis 1983) imply that it is considerably higher than Q10m, most likely on order 4.0. Fortunately, simulated growth patterns using eq. A1 are quite similar for a substantial range of values of both Q10 parameters, since the annual temperature range in GC is relatively narrow and much larger effects on growth variation are predicted to occur because of turbidity variation.

The basic model structure and parameter values described above predict low but positive growth rates on order 0.1 mm/day for age 0 bass during their first winter, given Colorado River temperatures that drop to around 8°C for. Even these low growth rates may result in overestimation of spring body sizes (and hence SMB invasion risk), so the basic model is conservative in that regard. Smallmouth Bass are observed to become torpid (stop moving and feeding, seek refuge cover) at temperatures much below 14°C. So we examined this possibility by including a “torpid multiplier” that reduces both feeding and metabolic rates for every simulation day with temperature T<Ttorpid. Sensitivity tests with alternative values for Ttorpid and with multiplier values like 0, 0.5 for lower temperatures showed that including the torpid period did indeed reduce predicted spring body sizes, but did not change the basic interannual patterns of growth variation, i.e. growth is simply rescaled in ways that could be easily corrected to fit field data by increasing the H parameter.

For many fish species, juvenile length growth over the growing season is close to linear. This has led to development of so-called “biphasic growth” models (Lester et al. 2004; Quince et al. 2008) where the metabolic rate term of A4 Eq. 2.1 is replaced with the same power of weight as for the consumption term, i.e. with -fm(T)mW2/3. For this model, the exponent for both consumption and metabolism can be replaced with a higher power than ⅔, e.g., Quince et al. (2008) suggest values between 0.69 and 0.75 based on powers summarized from various studies for users of the Wisconsin bioenergetics model. We set up a version of the model with this structure and found that using single powers between 0.67 and 0.75 had only very minor effects on the predicted growth patterns, with larger powers leading to slightly larger sizes in years more favorable for growth.