Predictors of fitness informal discussion

*Mixed Model Selection*

Choosing the random effects structure of the mixed model has a large effect on the significant fixed predictors retained after model selection and therefore the biological interpretation of the model. I chose a model selection procedure advocated by Ben Bolker in Zuur *et al* in several texts. I decided on this approach in advance of fitting the data and ultimately stuck to that to avoid cherry picking the model I wanted, but exploring alternative random effects structures revealed some interesting patterns that I describe at the end of this section.

For this project, we have fixed effects that are calculated entirely within the levels of the random effects. For example, release group sex ratio is the same for all individuals within a release group. But release group is also fit with a random intercept. This creates a potential problem: we are reducing our power to find significant predictors by including random effects because the fixed and random effects structures are competing for the same information. For example should we include release group fixed effects such as density, release group as a random effect, or both? The same goes for year (e.g. annual sex ratio fixed effect and year random effect).

I examined different random effect structures using AIC, with a full random effects structure turning out as best, but ultimately, the “best” random effects structure is a question about the inferences we'd like to make and AIC is only one piece of information to help us understand the relationship between parsimony and model fit. In other words, the extra degrees of freedom used to fit the random effects are worth it, but doesn’t help us decide which inferences we’d like to draw from the model, that’s up to us.

Since we are primarily interested in evaluating the significance of predictors, my preference was to be conservative and include them as random effects AND to include the fixed effects that are estimated within each level of the random effects. Of the three options this seems best. The first alternative (fixed effects at the level of release group and year, but no fixed effects) is not ideal: failing to include year and release group as random effects would imply that we are uninterested in the correlation within groups. Inferentially, a model with no random effects for year or release group implies that the fixed effects at the level of release group or year (release group: sex ratio, density and year: n and sex ratio) are the only effects that might lead to correlation within the levels of the random effects, and we are free to pool across all levels of release group or year and attribute all variation to fixed effects. This seems far too anti-conservative for our report, because there are certainly unmeasured variables that affect fitness nested within each level of the random effects producing correlation in fitness among individuals from the same year or release group. The second alternative, fitting only random effects, doesn’t allow us to ask about differences between the levels of variables calculated at the level of release group or year. For example we would be able to discuss the variance and standard deviation of fitness across release group blocks (which is interesting), but not whether a particular stocking density is better than another (which is MORE interesting). So the compromise decision (include both) is a bit conservative because shrinkage of extreme release group or year towards the grand mean by inclusion of random effect might reduce the power to find fixed effects, but is statistically sound and still allows us to draw the inferences we’d like to make.

Even with fitting year as a random effect, the annual sex ratio was a strongly significant predictor that we retained in the final model. The same was not true for release group level fixed effects. Perhaps not surprisingly (given the annual GLMs) when we do not include the random effect of release group, many release group level variables become significant in model selection (e.g. release group density). To me this suggests that the overall variance other, unmeasured variables that effect fitness at the level of release group have a large effect on fitness and we can’t parse these from the fixed effects of density and release group sex ratio.

**Putting this all together, model selection in the mixed model suggests that we only have enough information to infer that annual sex ratio and it’s interaction with sex is important. We did not find any strong evidence that other predictors of fitness are important**.

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*Multiple Comparisons and Collinearity Reduce Confidence in Annual GLMs*

We have five separate model selection procedures, and a lot of individual predictors being evaluated across all 5 years. This leads to a bit of a multiple comparison problem for the annual GLMs. Given that we only rarely have an effect with very low p-values, it is possible some spuriously significant effects are included in final models because of multiple comparisons. Also location nearly always produced multicollinearity in the model fits when used with all other predictors. Usually the multicollinearity could be eliminated by removing either release day or location, but not always. I always removed location for consistency, but the choice is arbitrary.

Taken together, significant effects in individual years should be considered with caution. Some trends are interesting though, especially considered with the mixed model results (below).

*Density*

Release group density has a significant effect (Wald test p < 0.05) and/or improves the fit the data (LRT p < 0.05) in 4 of the 5 annual GLMs. The effect does not initially appear to be consistent, until you consider the range of densities used in each year. When averaged across both males and females, density appears to improve TLF up to an optimum value somewhere above 75, then it declines. However, females and males demonstrate different fitness relationships with density.

When we combine all years into a single mixed model, we find the same pattern (see figure below), but it probably cannot considered significant. Density effects are not retained by either backward model selection by Wald Tests or by likelihood ratio tests. When fitting a saturated model with all possible effects, however, an interaction with density is marginally significant (sex \* density2 Wald test p-value 0.044). Some folks might include this as a significant effect, I’m not so sure. My inclination is to highlight that density might have an effect on TLF in the discussion, but ultimately we do not have high confidence. In any case, the effect size is pretty small.

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Figure: Estimated effect of release group density and sex from the saturated (initial) mixed model containing all possible effects (Wald test p-value of sex \* density2 = 0.044). Effect is conditioned on the “typical” value of all other variables in the model.

*Release Day*

A later release day is associated with increased TLF in 3 of the 5 annual GLMs. However the consistent confounding of release day and location precludes us from drawing any strong conclusions here. Depending on which model selection / predictor evaluation approach is applied to the data, release day may be considered a significant predictor by some workers. Our approach excluded release day from the final model, but in the initial, saturated model the Wald p-value was less than 0.05 and the estimated effect was positive (later releases have greater fitness).

*Release Group Sex Ratio*

Extreme release group sex ratios are associated with lower fitness in 2 of the 5 annual GLMs. However, similar to the situation with density, our ability to detect an effect of sex ratio from year to year is affected by the range of release group densities used in each. We do not detect a significant effect in 2011, 2012 and 2014. In 2011 and 2012 there is limited variation in release group sex ratio. In 2014 there is some variation to work with, but the significance of release group sex ratio was just beyond our p-value cutoff. Here we are better off evaluating after the benefit of combining information across years. When we do this in the mixed model, the effect is not significant, and this appears to be due to the shrinkage of extreme release group sex ratios means towards the grand mean by inclusion of release group random effect – fitting the full mixed model without a release group random effect finds a significant effect of release group sex ratio.

*Annual Sex ratios*

Many results point to an effect of sex ratios on TLF among salmon outplanted or reintroduced above Detroit Dam. Overall cohort replacement rates are often well below the sex specific CRRs, and this is strongest in years where the sex ratio is particularly skewed. Mean TLF is also strongly correlated with the strength of the departure from a balanced sex ratio and sex specific differences in mean TLF are inversely correlated with the direction of the sex bias. We subjected this relationship to hypothesis testing in the GLMM. The GLMM estimates that the effect of annual sex ratio is strong and significant. The strongest bias in sex ratio among salmon outplanted or reintroduced above the dam was in 2014. There were 1.95 fold more males than females. This level of male bias in sex ratio is estimated by the GLMM to reduce TLF to 31% and 19% of the TLF at a balanced sex ratio for females and males, respectively.

*Corroborating evidence of Annual Sex Ratio*

Interestingly, while the GLMM was fit using data from only salmon outplanted or reintroduced above Detroit Dam, the effect of annual sex ratio can also be observed among salmon reintroduced below the dam (see effect plot of GLM for TLF of salmon below Big Cliff below, likelihood ratio test for annual sex ratio p-value = 1.7 e-5).

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Even stronger corroborating evidence comes from a second source, the 2016 outplants.

When adding these individuals to the GLMM and fitting again, the parameter estimates change only a small amount, despite the new data coming from a year with a sex ratio outside of the range used to build the model (about 2x more females than males).

More formally, we can also attempt to predict the fitness of the 2016 fish from their sex and sex ratio. We only have a year 3 and year 4 offspring to fit on, so the expectation is that the model (which predicts TLF) should underpredict fitness based on only year 3 and 4 offspring by about ~20%. The model prediction for females is ﻿2.74 +- 1.2 and the model prediction for males is ﻿3.9 +- 1.8. The actual mean fitness for 2016 was 1.3 and 2.41. These empirical values are well within the confidence intervals once they are adjusted to make up for the missing year 5 offspring. (1.7 TLF female and 3.0 TLF male).