Aim: The overarching goal of my research is to understand the role that median fins, in particular the dorsal and anal fins, play in the hydrodynamics of steady swimming in fish. We already have some idea of how fish use these fins when turning, but not how they affect straight line swimming. Fish likely want to reduce lateral forces during steady swimming to increase efficiency. I aim to understand how these fins can improve straight swimming efficiency by reducing the total lateral force that the fish experiences.

This question is complicated by the fact that any hydrodynamic benefits of the median fins in straight swimming are likely small in magnitude and would be highly behaviorally dependent. In addition to this, it is very hard to measure the energetics or force production of a single behavior in a live fish. Here I use biomimetic robots in order to create consistent motion and measure the energetics of this motion. Although any positive results wouldn't prove any effect in live fish, they would demonstrate that it is possible to gain a hydrodynamic advantage from these structures that most fish already possess.

Methods: In order to understand the role of median fins, I first created three biomimetic models/foils. The control foil lacks a dorsal or anal fin, but has a slightly larger body so that the total surface area remains the same. The other two foils have both of these fins, but in different positions (Figure 1). For each of these models, I created two copies. The first copy is cut out of a flimsier material to represent a softer bodied fish, and the second is cut out of a stiff material. Each of these six models was flapped at six frequencies (.5-3 Hz) to represent different swimming patterns that fish might perform. At this point, I have only done each model at each frequency once, but I intend to do each one 5-10 times for my final data set.

From these trials, I am measuring several variables; the self-propelled speed (SPS), phase angle between dorsal and caudal fins, the flapping amplitude of each fin, and the maximum lateral force experienced by the model while swimming. SPS is a measure of how fast the robot would swim if it were free-swimming, and is used to determine how fast the water in the flow tank should move around the foil during each trial. Phase angle and amplitudes are measured by digitizing videos of the motion. The amplitude of the dorsal fin is then divided by the amplitude of the caudal fin to get a ratio which represents the relative motion of the fins. My response variable, the lateral force, was measured by a force transducer built into the robot. The signal from the transducer is run through a Chebyshev digital signal processing filter, and maxima were extracted. I then subtracted the lateral force in the control foil from the forces in the experimental foils. This created a variable that expressed the difference from the control instead of directly representing the lateral forces experienced by the foil. Once I collected all the data, I combined it all into one data frame (see R code).

The first thing that I did after collating my real data was to create fake data to complete my data set. I generally did this by finding the measurement error of one data point, and then creating a normal distribution centered around the measured data point with the measured error. The exception to this is the lateral force where I actually had many measurements from each trial, so I was able to calculate a true measurement error. After generating all of this data, I centered my variables so that my intercepts would be easily interpretable. I first centered my frequencies to 1.5, since I think of this as my intermediate value. I then centered the rest of the predictor variables to the mean of each variable when it was run at 1.5 Hz. I didn’t center to the mean of all the data points, because they my intercept would represent a data point that doesn’t actually exist. Finally, I split my data into two groups, one with data gathered from flimsy foils and one with data gathered from stiff foils. I did this because I expect the two materials to behave very differently, and so I don’t expect the parameters to be the same between them.

Finally, I began to consider what my model should be. I first considered a variable slopes hierarchical model, grouping by frequency. This accurately reflects the nature of the data in that each set of points measured at a frequency/material combination is essentially a distribution around a specific mean for that group. However, my data doesn’t quite fit the structure of a hierarchical model because this model assumes that the intercepts for each of these groups are themselves normally distributed around a central point. In my data, the intercepts are correlated with the actual value of frequency. Alternatively, I could use a simple linear model where each variable had an interaction effect with frequency. This would have a somewhat similar effect to a hierarchical model in that it would allow the values to vary more in response to the frequency. However, it would be the slope not the intercept that would change. In order to determine if one model was better than the other, I used leave one out cross validation. This comparison revealed that the interaction effect model was much less predictive (elpd difference of -27.1, S.E.=11). As a result I decided to focus on the hierarchical model, Fy~position+SPS+phaseAng+flapAmpRatio+(1|frequency).

Before I could totally trust the results of my hierarchical model, I wanted to make sure that the relationship between the frequency and the intercept wouldn't have a detrimental effect on my models ability to fit parameters. In order to address this, I created two sets of test data. In one set, the intercepts were drawn from a single normal distribution, as the model expected. In the other set, the intercepts were drawn from 6 different distributions, each with its own mean that was dependent on the frequency (Figure 2). I believe that this more accurately reflects the data, but is different from how the model would treat the data. I then chose test coefficients for each variable based on the effect size that I expected and based on the observed range of the variable. Test data vectors for my continuous variables were drawn from normal distributions centered around an expected mean, and with arbitrary small standard deviations. Frequency and position/body shape were assigned such that there were the correct number of observations of each combination. Finally, I fit my hierarchical model to each set of response variables, and compared the coefficients (Figure 3). Apart from the intercept variance, both models accurately predicted my test coefficients. This gave me confidence that my model would allow me to accurately answer questions about my data even though it didn't quite fit the assumptions of my model.

Finally, I fit my hierarchical model to my real data using the function stan_lmer() from the RStanArm package. I fit one model for my pink data, and one model for my coral data. I checked these results using ShinyStan to generate posterior predictive check plots, and found that the discrepancies could be explained by the incorrect assumption that the model made about my intercepts. Finally, I looked at the coefficients and errors of each predictor for the model from each material.

Results: I defined my test coefficients to be: Position=50, SPS=1, Phase angle=-1, Amplitude ratio= -100. My model using the intercepts that matched the models expectations gave the coefficients: Position=48 ±1, SPS=1.1 ±<.1, Phase angle=-1 ±<.1, Amplitude ratio=-93.2 ±9. Finally, my model using the intercepts that were more similar to my real data gave the coefficients: Position=49.2 ±1, SPS=1 ±.1, Phase angle=-1 ±<.1, Amplitude ratio=-89.5 ±9.5. In summary, the two models both recovered the parameter values with fairly equal accuracy. The primary difference between the models was in the sigma of the intercept distribution. In the first test data set, this sigma was 54.7. In the second test data set, this sigma was 1221.

My posterior predictive checks revealed that the model recreated data with accurate distributions of response variables for both materials (Figure 4). The primary difference was that the real response variables were not evenly distributed since I only ran the robot at discrete frequency values. The models did not create such discrete groups, and so there were more intermediate values. Otherwise, the data looked very similar. This apparent similarity was validified by the fact that the mean and standard deviation of my response variable was consistent between the simulations and my actual data. The major inconsistency was in the maxes and mins. In the pink data, my true max was lower than simulated, and my true min was higher than simulated. I believe that this is a result of the high sigma for the intercept that the model assumes, and is not a sign that anything else in the model is wrong. The coral model had a similar pattern, except the true min was actually much lower. I am currently unable to explain this.

My final step was to examine the coefficients and see what they tell me about the effects of my different predictor variables. In the pink model, my 95% confidence interval was well below zero (-77.2 mN, S.D.=21.4), telling me that an experimental foil flapping at 1.5 hz experiences less lateral forces than the control foil without a dorsal fin. The intercepts at frequencies far from 1.5 (namely .5Hz, 2.5 Hz, and 3Hz) were different from this intercept such that the confidence intervals did not overlap. This suggests to me that the difference between experimental and control is similar in foils swimming at similar speeds. However, as the difference in speed increases, we are able to see that faster swimming foils are more different from the control foil than are slow swimming foils. I also found that the fin positioning matters (20, S.D.=6.9), so in pink foils moving the fin backwards on the body causes an average increase of 20 mN in lateral force. Finally, the ratio of amplitudes between the dorsal and caudal fin had a large effect on the lateral forces (286.5, S.D.=36.4). The magnitude of the coefficient is a bit exaggerated since the range of the data is only about .4. However, this still means that from the lowest value to the highest, the foils will experience over 100 mN more of force, a massive effect compared to all the other coefficients. The model fit to the coral data gave fairly different parameter values. While the pink model had many effects that seemed to be real, the coral model had very few. The intercept was not differentiable from zero, but there was a difference between the intercepts in some of the high and low frequencies (1Hz and 2.5 Hz). The only other coefficient that had a discernable effect was the amplitude ratio (247.2, S.D.= 63.4). Interestingly, this was almost the same effect as in the pink model.

There seemed to be many predictor variables that affected the lateral forces in the pink foils. At 1.5 Hz, the pink foil experienced less lateral force than did the control, and the magnitude of this difference varied with the frequency, position of the fin, and flapping amplitude ratio. Conversely, the coral foils were not differentiable from the control foil, and were only really affected by the flapping amplitude ratio. Since the only difference between the data going into each of these models was the stiffness of the material used to collect the data, this suggests that median fins can reduce lateral forces during steady swimming, but only in less stiff bodied fish.

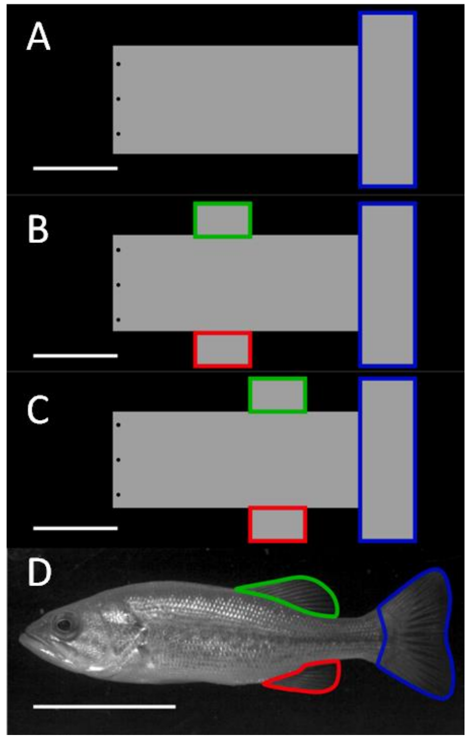

Figure 1. A) Control foil lacks a dorsal and anal fin, but makes up the loss in surface area by increasing the body width. B) The "far" experimental foil has anteriorly displaced dorsal and anal fins. C) The "near" experimental foil has posteriorly displaced dorsal and anal fins. D) A real fish (bass) has a generally similar body shape as my foils. The area of the fins relative to the body are also similar.

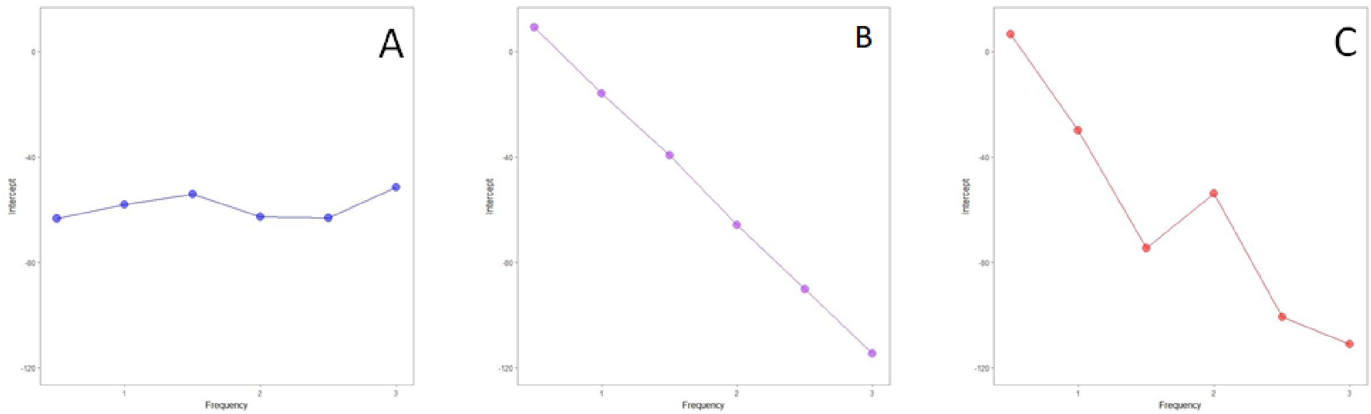

Figure 2. A) The first set of intercepts are distributed around one intermediate mean. This is similar to what a hierarchical model expects. B) The second set of intercepts is a better representation of the real data, since each individual intercept is drawn from a separate distribution. C) Average values of my real lateral force data approximate the expected real intercepts.

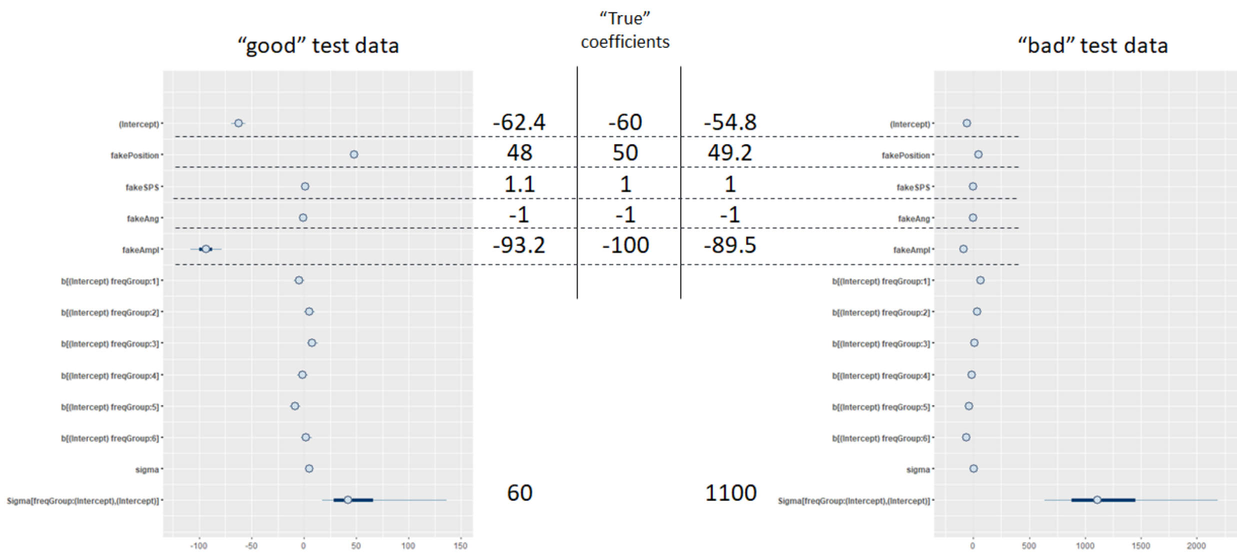

Figure 3. The coefficients for the two sets of test data using different intercepts were very similar to each other as well as being similar to the true values. The main difference between the two models is the sigma value for the distribution of intercepts (60 vs. 1100).

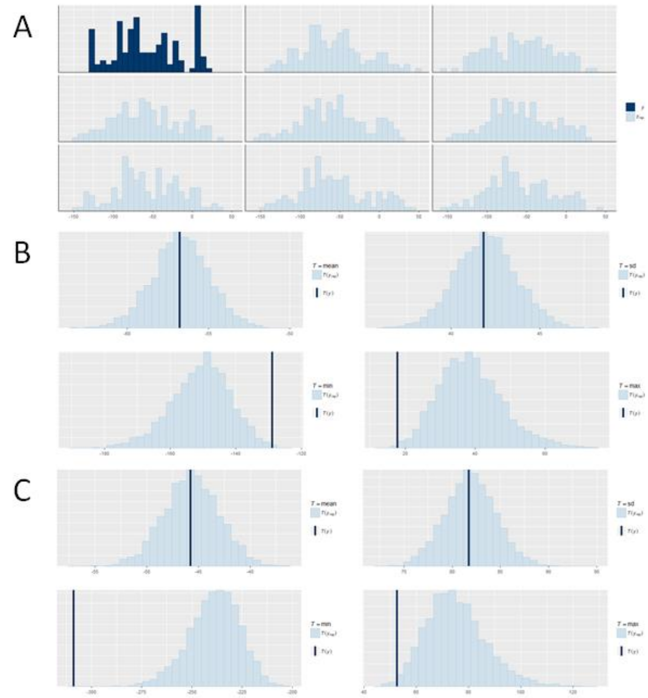

Figure 4. A) From the model fit to the flimsy foils. The distributions of the response variable show that my actual data is more punctuated than the simulated data, but the general distributions are similar. B) From the model fit to the flimsy foils. The mean and standard deviations of the real response variable closely fit the simulated response variables. The max. and min. are not as similar. B) From the model fit to the stiff foils. As before, the mean and standard deviations of the real response variable closely fit the simulated response variables. The max and min are also not similar, but this time the real min. is well below the simulated minima.