Kinematics of acceleration in swimming fishes

Running title: Swimming acceleration kinematics

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Key words:

**Summary statement**

**ABSTRACT**

**INTRODUCTION**

**MATERIALS AND METHODS**

**Animal care and maintenance**

**Swimming trials and behavior categorization**

**Measurement of kinematics and finbeat-parameters**

For each trial, the positions of the tip of the snout and the tip of the caudal fin were digitized using DLTv6 (Hedrick, 2008). For the tip of the snout, automatic tracking with the default parameters (Autotrack predictor: extended Kalman, Autotrack search area: 9, Autotrack threshold: 9) was sufficient for accurate tracking, as confirmed by manual assessment of the tracked position. In the few cases where the autotracking algorithm was inaccurate, frames were digitized manually within DLTv6. For the tail tip, autotracking was almost never sufficient, and the frames were all manually digitized. Data were saved from DLT in flat format, and all subsequent processing was done using custom written code (Supp. Materials, available in the associated git-hub repository) in Python 3 (Python Software Foundation, <http://www.python.org>).

To permit the calculation of velocity and acceleration from the slightly noisy position data, position traces were smoothed using a 2nd order Savitzky-Golay filter with a window length corresponding to 121 ms. This procedure was found to smooth the data enough for differentiation without diminishing maxima and minima more that [ x] %. For each trial, net instantaneous velocity and acceleration of the swimming fish were calculated as the first- and second-derivative of the snout position data. A second smoothing with the same parameters was used in between the velocity and the acceleration differentiation.

To determine the period and amplitude for each finbeat in every trial, we isolated the y-axis position (yaw-axis) of the caudal fin tip. These position traces were de-trended by fitting a 3rd order polynomial to the position data before using the peak-detection algorithm implemented in the open-source python package PeakUtils v.1.0.3 (L. Negri. available at <https://bitbucket.org/lucashnegri/peakutils>). Each peak was designated the start of a caudal fin beat. However, this choice is arbitrary, so all analyses were also conducted using each trough as the start of a fin beat. The y-position data were multiplied by -1, and the peak finding process repeated to find the troughs in the data. Doing the analyses with peaks-first and with troughs-first allowed us to get a sense of the effect of finbeat cycle start choice on the relationships between measured finbeat parameters and performance. There was minimal difference between the peak-first and the trough-first finbeat analyses, so for the rest of this manuscript, we refer only to the peaks-first data. Troughs-first data are presented for comparison in the supplemental materials.

Finbeat period was calculated as the time from the starting peak to the subsequent peak for each finbeat. Amplitude was calculated as the y-position distance between the starting peak, and the subsequent trough for each finbeat.

In order to associate each finbeat with some kind of performance measure, the maximum instantaneous velocity and acceleration during the duration of each finbeat was also recorded.

**Statistical analysis of kinematic parameters**

Multiple linear regression models were fit to the data to relate finbeat period and amplitude to the maximum instantaneous speed and acceleration for each fish, for a total of 3 models. The data did not match the assumptions .

**Fourier transforms and sinusoidal regression as estimate of steadiness**

**RESULTS**

**Period and amplitude variation with initial speed**

**Period and amplitude variation with maximum instantaneous speed and acceleration**

**Kinematic signatures of acceleration behaviors**

**DISCUSSION**

**Acknowledgements**

**Competing Interests**

The authors declare no competing interests.

**Author Contributions**

G.V.L. and V.D.S. collected fish swimming trial videos. K.L.F. digitized the video, designed and wrote programs for all analyses, ran all analyses, and wrote the first draft of the manuscript.

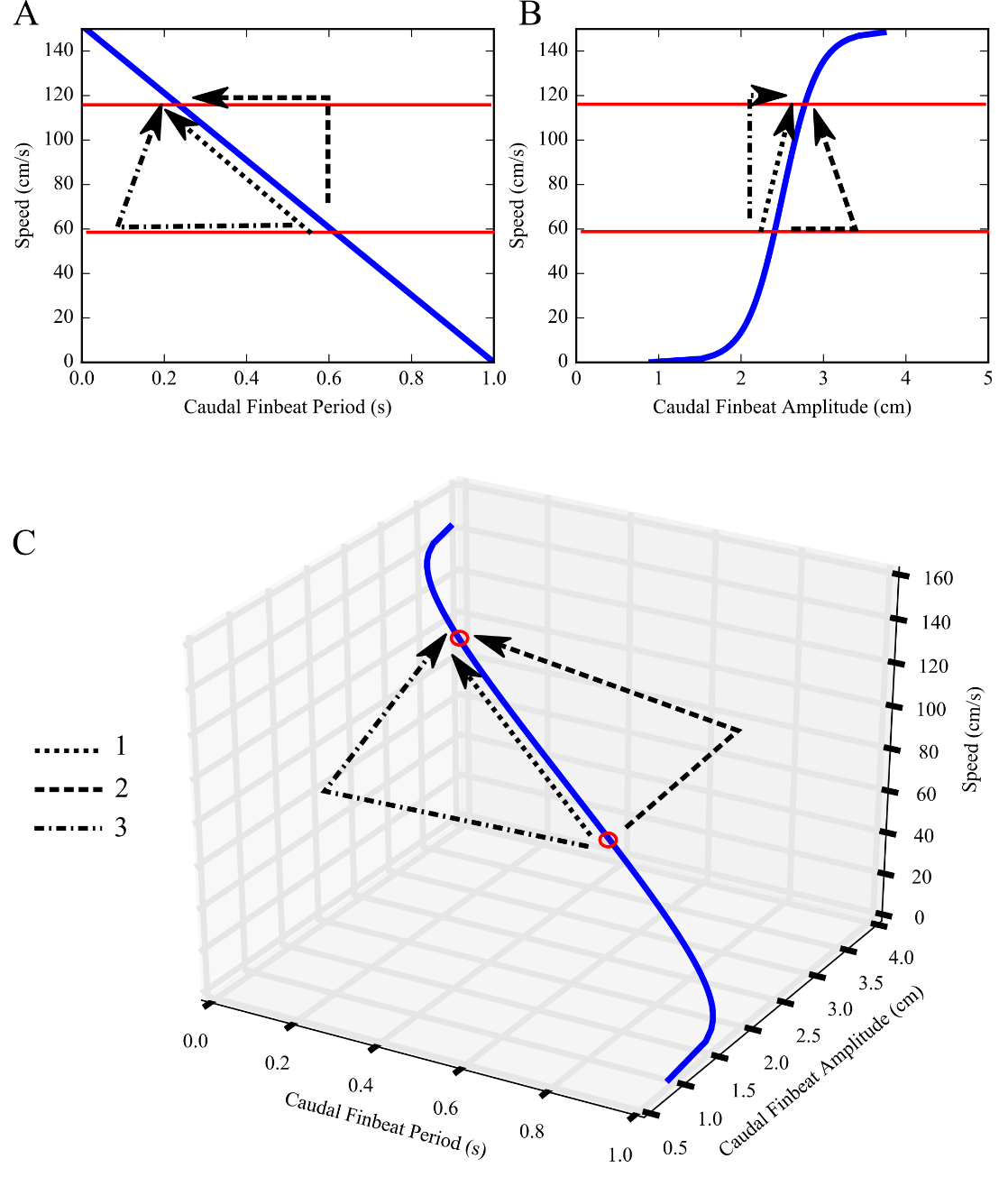
**Funding**

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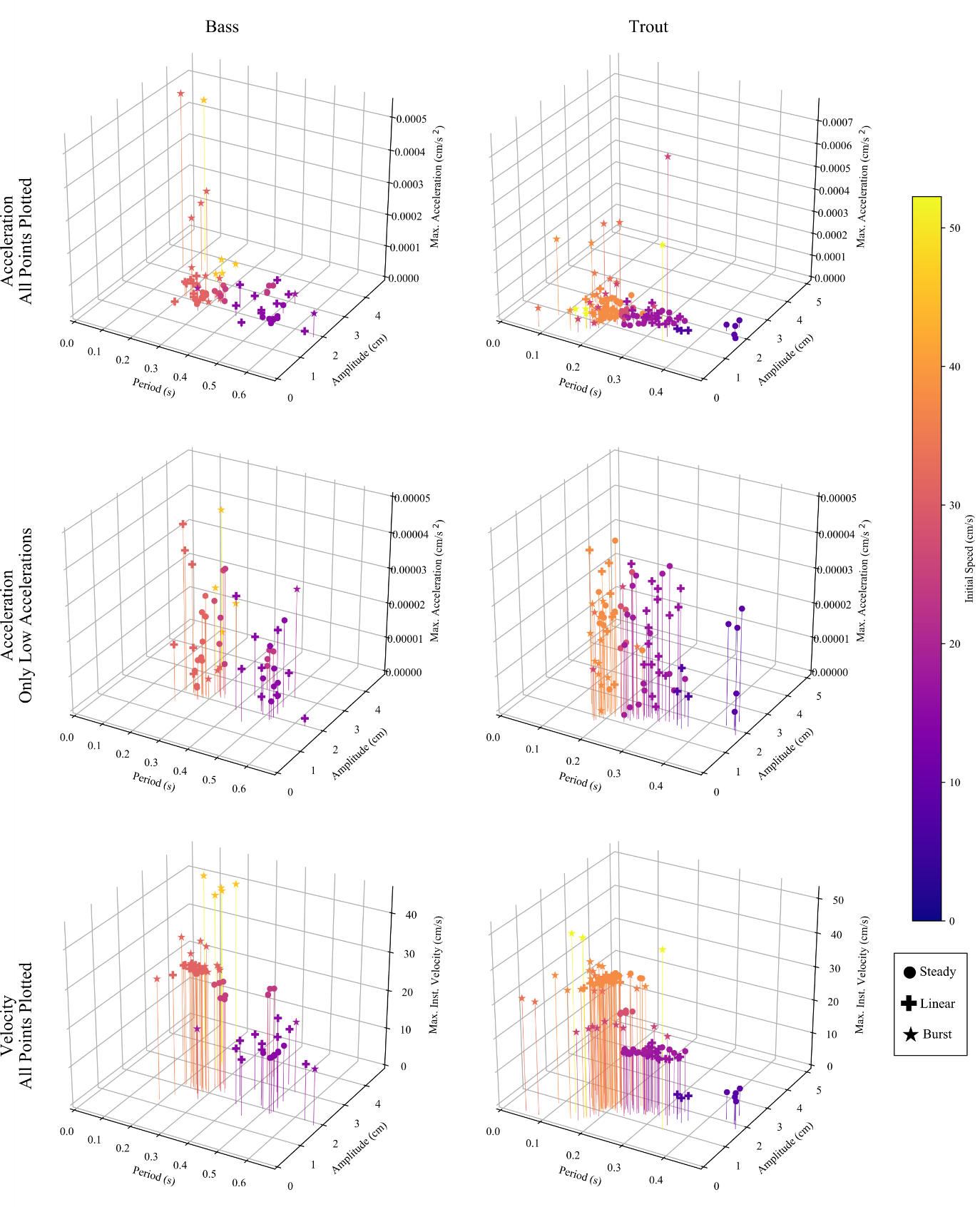
**References**

**Feilich, K. L.** (2017).

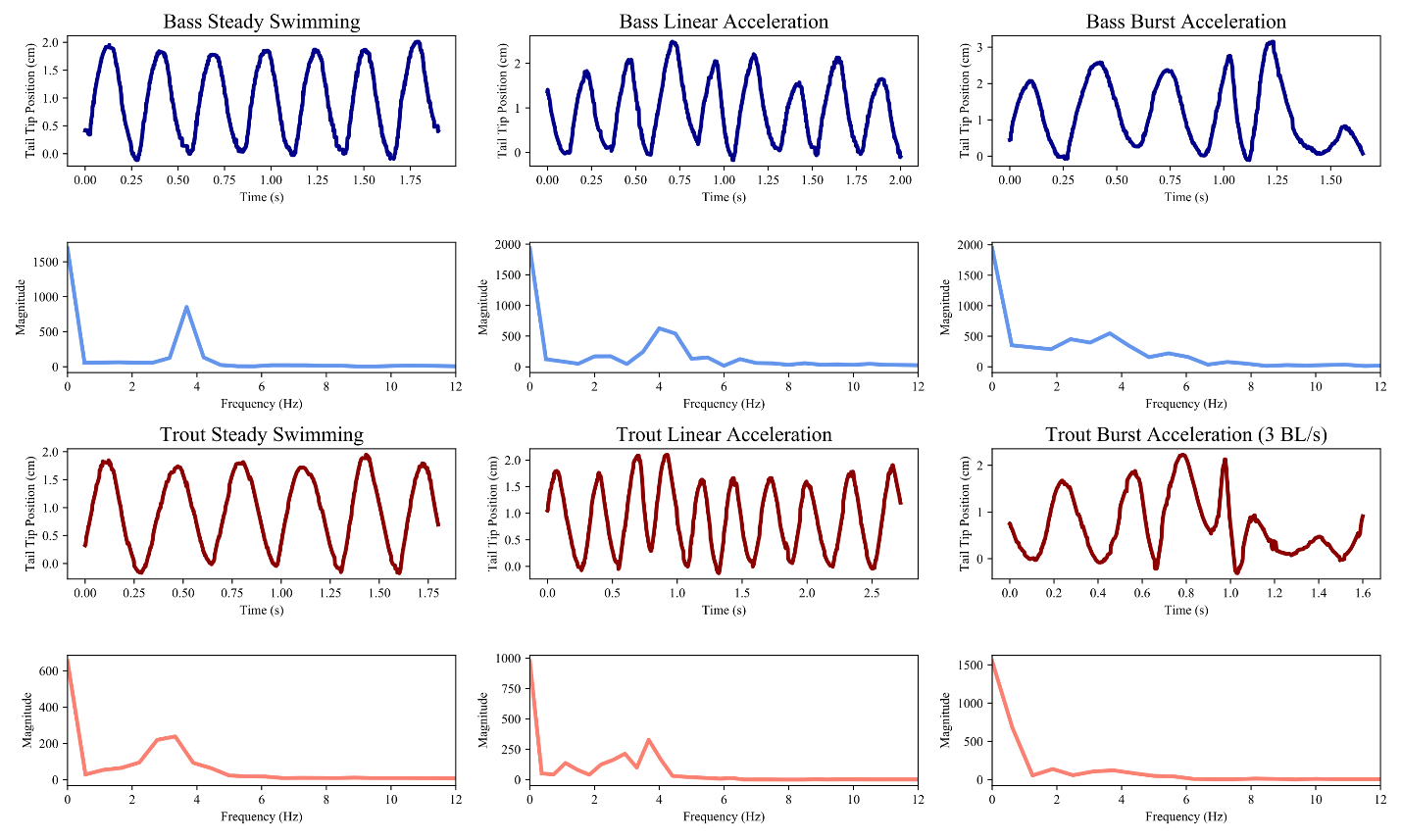
**Figures and Tables**

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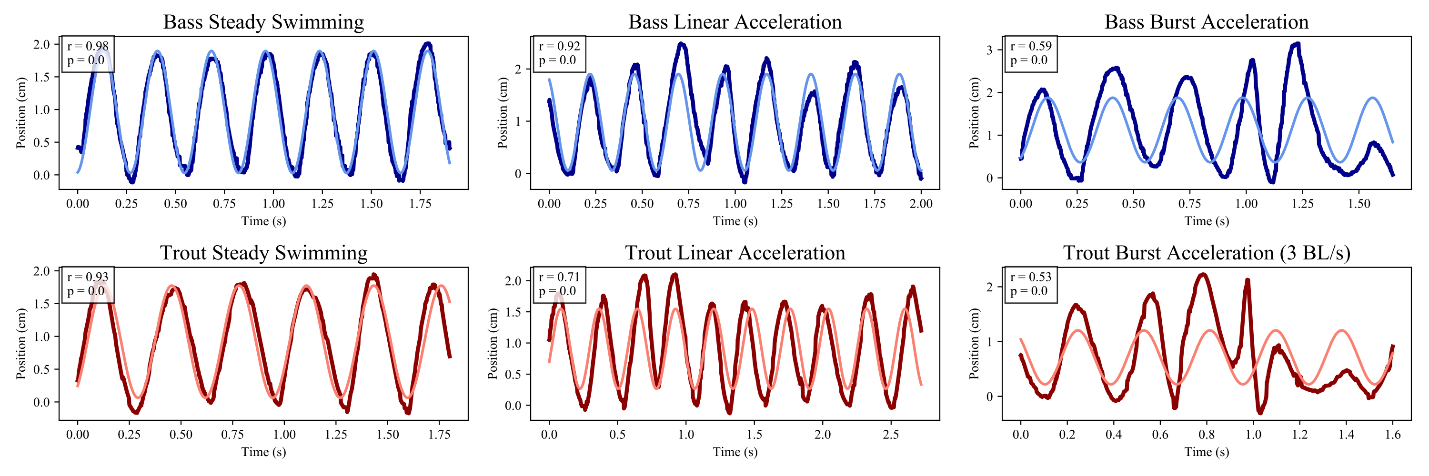
**Figure 1. Schematic diagram with simulated data showing multiple kinematic pathways to accelerate to the same final speed, assuming caudal fin propulsion only**. A. Relationship between steady swimming speed and caudal finbeat period. B. The relationship between steady swimming speed and caudal finbeat amplitude. C. A three-dimensional representation of a caudal steady swimming gait trajectory. Paths 1, 2, and 3, are a few of infinitely many different kinematic possibilities for accelerating between the two speeds highlighted in red. Path 1 represents a gradual kinematic transition where acceleration kinematics mirror the kinematics used during steady locomotion at the intermediate speeds. Path 2 represents acceleration by keeping period constant, jumping to a larger caudal fin beat amplitude to speed up, before decreasing amplitude slightly to settle in to the new steady swimming speed. Path 3 represents acceleration by keeping finbeat amplitude constant, jumping to a shorter fin beat period to accelerate, before increasing period slightly to settle into the new steady swimming speed. Data are simulated such that finbeat period has an inverse linear relationship with swimming speed, and amplitude has a sigmoidal relationship with speed. These hypothesized relationships are in keeping with the experimental observations that speed varies linearly with finbeat frequency (i.e. 1/period), and amplitude is mostly invariant with speed.



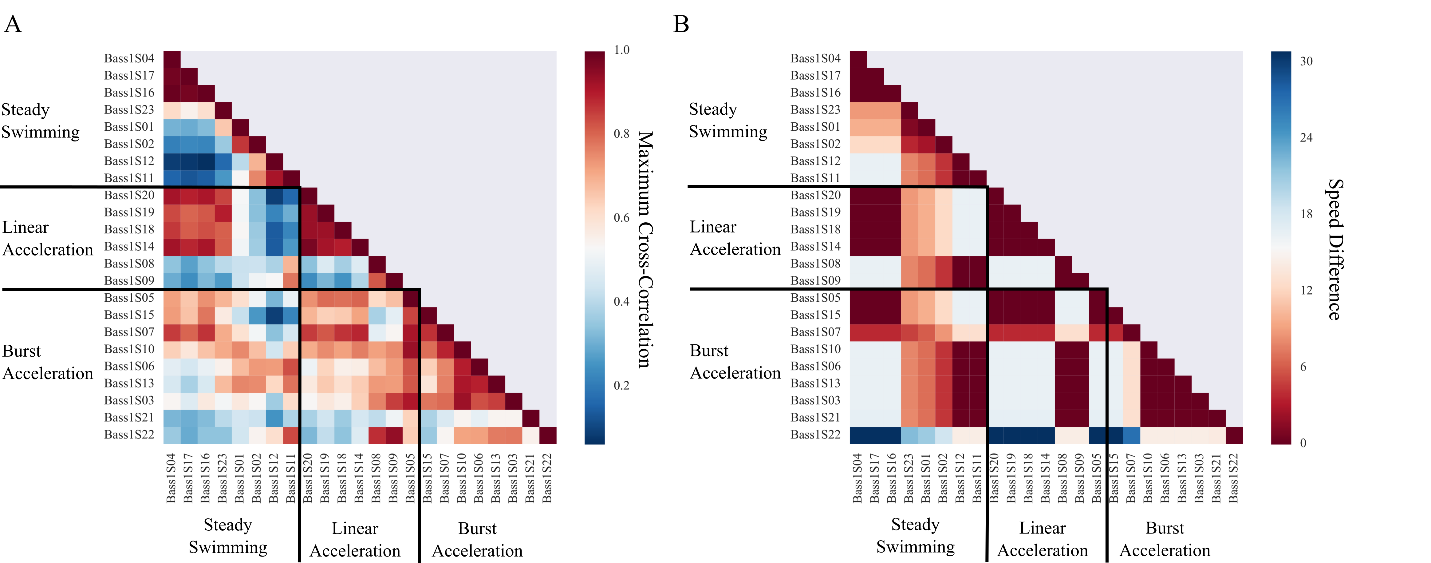
**Figure 2. Observed caudal finbeat kinematics for steady swimming, linear accelerations, and burst accelerations as encoded by the observer.** Left Column: Largemouth Bass (n=1, SL =15 cm, n\_trials = 23), Right Column: Rainbow Trout (n = 2; SL = 9 cm, 8.5 cm, 8 cm; n\_trials = 21). Top: All finbeats against maximum instantaneous acceleration. Middle: Finbeats with maximum instantaneous accelerations < 5x10-4 cm/s2, to show variation. Bottom: Finbeats against maximum instantaneous velocity. (Circles: steady swimming trials, +: linear acceleration trials, Star: burst acceleration trials. Points are colored by initial speed of trial.)



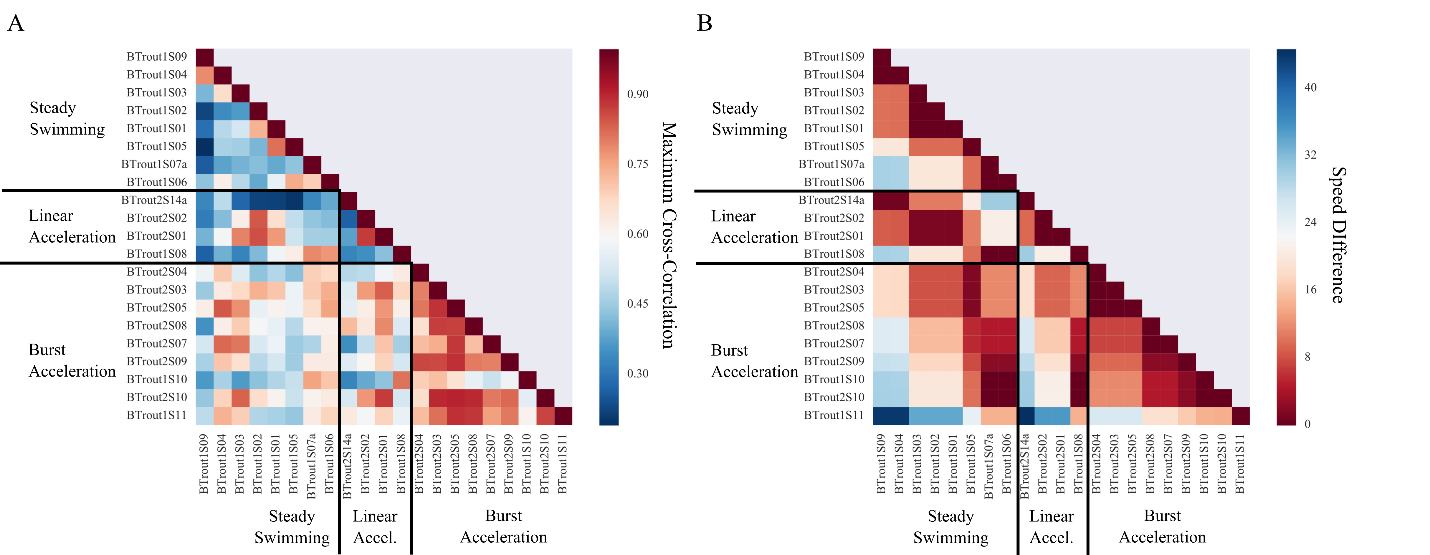
**Figure 3. Representative traces of de-trended tail tip motion during three swimming behaviors with initial speeds of 2 BL/s, and the FFTs of those traces.** Blue: Largemouth Bass (SL = 15 cm), Red: Rainbow Trout (mean SL = 8.75 cm). Top row of each species shows tail tip position in the axis perpendicular to the direction of swimming, with background trend removed. Bottom row for each species shows the FFT of the tail tip trace immediately above. The burst acceleration trace for trout is from a trial at a speed of 3 BL/s, as we were unable to elicit burst accelerations below this speed.



**Figure 4. Representative traces of de-trended tail tip motion during three swimming behaviors with initial speeds of 2 BL/s, and the best fit sine-waves for those traces.** Blue: Largemouth Bass (SL = 15 cm), Red: Rainbow Trout (mean SL = 8.75 cm). The dark curve is the detrended raw data for that trial (as in Figure 3), and the light curve is the sine wave fitted to that trial using least squares optimization. The correlation coefficient between the detrended raw position data and the best fit sine wave is shown in the top left corner of each plot, with its associated p-value. The burst acceleration trace for trout is from a trial at a speed of 3 BL/s, as we were unable to elicit burst accelerations below this speed.



**Figure 5. Heat-map showing maximum normalized pairwise cross-correlations between the Fourier transforms of detrended tailbeat motions for all bass trials, and pairwise initial speed differences between trials.** For each pairwise comparison, the detrended raw tail-tip position data (as shown in Figure 3) for the shorter length of the two trials was padded on either end with its mean value to equal the length of the longer trial before Fourier transform convolution. This made the lengths of the two Fourier transforms suitable for the purposes of cross-correlation. A: Maximum cross-correlations of FFTs. B: Pairwise speed differences between trials. The correspondence between A and B indicates that swimming speed is a major factor driving the shape of the finbeat frequency distribution.



**Figure 6. Heat-map showing maximum normalized pairwise cross-correlations between the Fourier transforms of detrended tailbeat motions for all trout trials and pairwise initial speed differences between trials.** For each pairwise comparison, the detrended raw tail-tip position data (as shown in Figure 3) for the shorter length of the two trials was padded on either end with its mean value to equal the length of the longer trial before Fourier transform convolution. This made the lengths of the two Fourier transforms suitable for the purposes of cross-correlation. A: Maximum cross-correlations of FFTs. B: Pairwise speed differences between trials. The correspondence between A and B indicates that swimming speed is a major factor driving the shape of the finbeat frequency distribution.

**Table 1. Maximum instantaneous speed related to caudal finbeat period and amplitude in a largemouth bass** Model 1: Max\_Spd ~ Period \* Amplitude; F = 63.62; p = 0.002; df = 3, 65; n=69; bootstraps: 2000

Model 2: Max\_Spd ~ Period + Amplitude; F = 91.81; p = 0.000; df = 2, 66; n=69; bootstraps: 2000

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Model 2** | **Correlations** | | **β**  **(boot 95% CI)** | **SEB** | **t** | **p**  **(boot)** |
| **Variable** | Period | Amplitude |
| Intercept | - | - | (34.8, 46.4) | 2.949 | 13.74 | 0.000 |
| Period | - | -0.10 | (-68.3, -50.3) | 4.579 | -12.93 | 0.000 |
| Amplitude | -0.10 | - | (0.9, 4.9) | 1.029 | 2.813 | 0.004 |
|  |  |  |  |  |  |  |
| **Mean** | 0.34 | 2.22 |  |  |  |  |
| **SD** | 0.12 | 0.55 |  |  | **Adj. R2** | 0.728 |

**Table 2. Maximum instantaneous speed related to caudal finbeat period and amplitude rainbow trout 1** Model 1: Max\_Spd ~ Period \* Amplitude; F = 44.56; p\_boot = 0.004; df = 3, 76; n=80; bootstraps: 2000

Model 2: Max\_Spd ~ Period + Amplitude; F = 67.48; p\_boot = 0.003; df = 2. 77; n=80; bootstraps : 2000

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Model 2** | **Correlations** | | **β**  **(boot 95% CI)** | **SEB** | **t** | **p**  **(boot)** |
| **Variable** | Period | Amplitude |
| Intercept | - | - | (57.1, 67.3) | 2.73 | 22.74 | 0.000 |
| Period | - | 0.75 | (-125.7, -63.4) | 15.69 | -6.00 | 0.000 |
| Amplitude | 0.75 | - | (-37.8, 12.7) | 3.10 | -2.15 | 0.035 |
|  |  |  |  |  |  |  |
| **Mean** | 0.24 | 2.22 |  |  |  |  |
| **SD** | 0.12 | 0.55 |  |  | **Adj. R2** | 0.627 |

**Table 3. Maximum instantaneous speed related to caudal finbeat period and amplitude rainbow trout 2**

Model 1: Max\_Spd ~ Period \* Amplitude; F = 40.70; p = 0.009; df = 3, 46; n = 50; bootstraps: 2000

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| --- | --- | --- | --- | --- | --- | --- |
| **Model 1** | **Correlations** | | **β**  **(boot 95% CI)** | **SEB** | **t** | **p**  **(boot)** |
| **Variable** | Period | Amplitude |
| Intercept | - | - | (22.01, 41.31) | 5.10 | 6.47 | 0.000 |
| Period | - | 0.37 | (-73.72, 39.50) | 30.57 | -0.68 | 0.436 |
| Amplitude | 0.37 | - | (6.46, 21.48) | 3.98 | 3.36 | 0.002 |
| Period:Amplitude | - | - | (-108.30, -25.81) | 22.33 | -2.86 | 0.011 |
|  |  |  |  |  |  |  |
| **Mean** | 0.24 | 1.32 |  |  |  |  |
| **SD** | 0.08 | 0.46 |  |  | **Adj. R2** | 0.709 |

**Table 4. Maximum instantaneous acceleration related to caudal finbeat period and amplitude in a largemouth bass**

Model 1: Max\_Acc ~ Period \* Amplitude; F = 32.77; p =0.009; df = 3, 65; n=69; bootstraps: 2000

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Model 1** | **Correlations** | | **β**  **(boot 95% CI)** | **SEB** | **t** | **p**  **(boot)** |
| **Variable** | Period | Amplitude |
| Intercept | - | - | (-66.8, -34.3)\*10-5 | 8.4\*10-5 | -6.06 | 0.000 |
| Period | - | -0.10 | (85.4, 178.6)\*10-5 | 0.000 | 5.50 | 0.000 |
| Amplitude | -0.10 | - | (22.5, 36.5)\*10-5 | 3.6\*10-5 | 8.21 | 0.000 |
| Period:Amplitude | - | - | (-94.0, -52.6)\*10-5 | 0.000 | -6.96 | 0.000 |
|  |  |  |  |  |  |  |
| **Mean** | 0.34 | 2.22 |  |  |  |  |
| **SD** | 0.12 | 0.55 |  |  | **Adj. R2** | 0.728 |

**Table 5. Maximum instantaneous acceleration related to caudal finbeat period and amplitude rainbow trout1** Model 1: Max\_Acc ~ Period \* Amplitude; F = 5.61; p\_boot = 0.100; df = 3, 76; n=80; bootstraps: 2000

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Model 2** | **Correlations** | | **β**  **(boot 95% CI)** | **SEB** | **t** | **p**  **(boot)** |
| **Variable** | Period | Amplitude |
| Intercept | - | - | (-23.7, 4.34) \* 10-5 | 7.1\*10-5 | -1.38 | 0.178 |
| Period | - | 0.75 | (38.4, 168.8) \* 10-5 | 0.000 | 2.96 | 0.006 |
| Amplitude | 0.75 | - | (-8.1, 10.7) \* 10-5 | 4.62\*10-5 | 0.14 | 0.870 |
| Period:Amplitude | - | - | (-81.8, -7.5) \*10-5 | 0.000 | -2.25 | 0.030 |
|  |  |  |  |  |  |  |
| **Mean** | 0.24 | 2.22 |  |  |  |  |
| **SD** | 0.12 | 0.55 |  |  | **Adj. R2** | 0.149 |

**Table 6. Maximum instantaneous acceleration related to caudal finbeat period and amplitude rainbow trout2**

Model 1: Max\_Acc ~ Period \* Amplitude; F =2.329; p = 0. 0.261; df = 3, 46; n = 50; bootstraps: 2000

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Model 1** | **Correlations** | | **β**  **(boot 95% CI)** | **SEB** | **t** | **p**  **(boot)** |
| **Variable** | Period | Amplitude |
| Intercept | - | - | (-46.1, 5.7) \*10-5 | 0.000 | -1.05 | 0.198 |
| Period | - | 0.37 | (8.5, 322.1) \*10-5 | 0.001 | 1.94 | 0.059 |
| Amplitude | 0.37 | - | (5.3, 45.6) \*10-5 | 0.000 | 2.25 | 0.047 |
| Period:Amplitude | - | - | (-257.9, -34.5) \*10-5 | 0.001 | -2.41 | 0.031 |
|  |  |  |  |  |  |  |
| **Mean** | 0.24 | 1.32 |  |  |  |  |
| **SD** | 0.08 | 0.46 |  |  | **Adj. R2** | 0.075 |

**Table 7. Pearson’s correlation coefficients and associated p-values for each trial when correlated with its best fit sine wave, grouped by speed and behavior.**

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Bass** | | | | | | | | |
| **Steady Swimming** | | | **Linear Acceleration** | | | **Burst Acceleration** | | |
| **Trial** | **Initial Speed** | **r** | **Trial** | **Initial Speed** | **r** | **Trial** | **Initial Speed** | **r** |
| Bass1S04 | 14.7 | 0.91 | Bass1S19 | 14.7 | 0.94 | Bass1S05 | 14.7 | - |
| Bass1S16 | 14.7 | 0.93 | Bass1S20 | 14.7 | 0.88 | Bass1S15 | 14.7 | 0.82 |
| Bass1S17 | 14.7 | 0.98 | Bass1S14 | 14.7 | 0.85 | Bass1S07 | 18.5 | 0.60 |
| Bass1S23 | 23.5 | 0.98 | Bass1S18 | 14.7 | 0.69 | Bass1S03 | 31.4 | 0.49 |
| Bass1S01 | 24.6 | 0.96 | Bass1S08 | 31.4 | 0.92 | Bass1S06 | 31.4 | 0.70 |
| Bass1S02 | 27.1 | 0.99 | Bass1S09 | 31.4 | 0.77 | Bass1S10 | 31.4 | 0.32 |
| Bass1S11 | 31.4 | 0.98 |  |  |  | Bass1S13 | 31.4 | 0.59 |
| Bass1S12 | 31.4 | 0.99 |  |  |  | Bass1S21 | 31.5 | 0.65 |
|  |  |  |  |  |  | Bass1S22 | 45.6 | 0.74 |

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Trout** | | | | | | | | |
| **Steady Swimming** | | | **Linear Acceleration** | | | **Burst Acceleration** | | |
| **Trial** | **Initial Speed** | **r** | **Trial** | **Initial Speed** | **r** | **Trial** | **Initial Speed** | **r** |
| BTrout1S09 | 8.2 | 0.99 | BTrout2S14 | 7.5 | 0.97 | BTrout2S03 | 26.3 | 0.53 |
| BTrout1S04 | 8.37 | 0.97 | BTrout2S02 | 17.0 | 0.84 | BTrout2S04 | 26.3 | 0.33 |
| BTrout1S01 | 18.2 | 0.91 | BTrout2S01 | 17.0 | 0.71 | BTrout2S05 | 26.3 | - |
| BTrout1S02 | 18.2 | 0.97 | BTrout1S08 | 37.9 | 0.78 | BTrout2S07 | 33.5 | 0.37 |
| BTrout1S03 | 18.2 | 0.93 |  |  |  | BTrout2S08 | 33.5 | 0.49 |
| BTrout1S05 | 28.0 | 0.97 |  |  |  | BTrout2S09 | 35.7 | 0.49 |
| BTrout1S06 | 37.9 | 0.84 |  |  |  | BTrout1S10 | 37.9 | 0.80 |
| BTrout1S07 | 37.9 | 0.83 |  |  |  | BTrout2S10 | 38.0 | 0.50 |
|  |  |  |  |  |  | BTrout1S11 | 52.2 | 0.26 |