Analysis of fast-start movements using accelerometry and video tracking in the Great Sculpin (Myoxocephalus polyacanthocephalus)

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Fish Swimming 2011

Summer 2011

Keywords: *Myoxocephalus polyancanthocephalus*, Behaviour, Video, Acceleration, Fourth of July Beach

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Abstract

While the use of accelerometers in the aquatic environment becomes an increasingly used tool in remotely observing animals; however, the data obtained from deploying accelerometers still needs better understanding. Observations gathered by studies using accelerometers are largely limited to the identification of simple behaviours such as resting and swimming, yet fine-scale movements such as feeding and escape responses are mostly undetected. In this experiment, we aim to establish a link between acceleration traces and fast-start movements in the Great Sculpin (M. polyacanthocephalus) by the analysis of acceleration data from accelerometers and a high-speed video camera. Feeding events, escape events and spontaneous movements were triggered and observed using a 100Hz recording accelerometer (Little Leonardo Ltd, Japan) and a high-speed video camera for n = 7 great sculpin. Kinematic comparison between acceleration obtained from accelerometers and high-speed video camera were performed using vector transformation, yet prove to be difficult due to differences in reference frames and different sources of error. To establish a link between behaviour and acceleration, statistical analysis shows that the signature of spontaneous events can be described by the variation of the magnitude of acceleration which is significantly lower in spontaneous events compared to fast-start movements. Most of this information is lost (50%) if the accelerometer sampling rate is lower than 30Hz. Furthermore, two parameters (the value of A_{max} the variation of acceleration in lateral and forward direction) allow us to differentiate between escape events and feeding events. These results are a valuable contribution to understanding acceleration data in the field and the issues associated with low sampling rates.

Introduction

Information on behaviour and locomotion of fish in their natural environment is fundamental for insights into their ecology and physiology. However, field observations in aquatic environments are challenging. Recently, the use of micro-accelerometer tags have provided an effective means of indirectly monitoring the behaviour and locomotion of fish in the field.

Observations obtained by previous studies using accelerometers have been limited to the identification of relatively simple behaviours encompassing a broad range of movements, such as resting and swimming. These were based on broad categorization of the acceleration signals, using the mean, maximum or minimum value of the acceleration intensity or frequency components of the signals (FFT and wavelet). Few studies have attempted to identify the acceleration signature of the behaviour involving fast-start locomotion, in spite of the ecological importance of the movement in terms of predator-prey interactions and activity. In addition, it is important to relate acceleration to kinematic movement of fish to find the missing link between acceleration signals and behaviour.

Video analysis based on kinematic experiments on fast-start and spontaneous movement in fish in laboratory settings have demonstrated the relationship between acceleration and swimming motion. These observations indicate the potential for accelerometers to identify more detailed locomotion and behaviour. For example, it has been shown that fast-start locomotion in fish have two distinctive movements: C-starts and S-starts (Domenici, 1997, Hale 2002, Domenici *et al.* 2004, Wöhl and Schuster, 2007), which may be attributed to escape and feeding tasks. Additionally, these two movement patterns exhibit different acceleration signature. These

conclusions were based on the analysis of acceleration resulting from tracking fast-start movements recorded by high-speed video cameras. Accordingly, we predict that if acceleration is recorded at sufficient frequencies these fast-start movement patterns should be identifiable and can possibly be related to distinct kinematic events as defined in previous studies (e.g. Stage I, Stage II, S-start, C-start).

This acceleration signature could then be used in field studies to remotely monitor more complex fish behaviour than previously possible.

There are several objectives to this study:

- 1. Validate whether fast-start locomotion can be identified by accelerometer signals compared to spontaneous movement (such as swimming, turns etc.)
- Validate whether detailed categorization of the fast-start locomotion is possible to identify escape and feeding tasks
- 3. If 1 (and/or 2) is possible, clarify how much recording frequency of the acceleration is needed to sample those fast-start movements.
- 4. Find the missing link between acceleration and fast-start movement in fish (e.g. what does a C-start look like in accelerometer-recorded acceleration?)

These research objectives were analyzed using a readily available, hardy model species; the Great sculpin *Myoxocephalus polyacanthocephalus*.

Materials and Methods

Study Animal

Great sculpin (*Myoxocephalus polyacanthocephalus* (Pallas, 1814)) were collected by beach seine in two locations on the southeast side of San Juan Island, Washington USA. Experiments were carried out at the Friday Harbor Laboratories. The fish were held in a 170cm diameter outdoor tank with flow-though seawater at 11±1°C with a water level of 1m. Fish were maintained in the tanks for at least one week prior to the experiments and tagging. The fish were not fed before the experiment to ensure responsiveness to prey during the predator-prey trials.

Accelerometer

An ORI-380D3GT microaccelerometer (Little Leonardo Ltd., Tokyo, Japan) was used to record tri-axial acceleration. The sampling rate was set to 100Hz (1 recording every 10ms) with a resolution of 12 bit and a 10h recording capacity. The tag is 12x45mm in dimension with a weight of 10g (2% or less of the overall body weight). The accelerometer recorded acceleration up to $\pm 4g$.

Experimental Protocol

Fish were tagged with Petersen Disk tags several days before the experiments using MS222 as the anaesthetic agent. The Petersen Disks are made up of two plastic disks which are attached to each side of the fish at 0.5 cm below the first dorsal fin - assumed to be the least invasive position (Fig. 1A & B). The accelerometer was attached to the Petersen disk tag 30 min before the experimental trials via a male-female Velcro system. The male part of the Velcro is permanently attached to the

surface of one of the Petersen Disks, and the corresponding Velcro is attached to the accelerometer. The attachment of the accelerometer and direction of acceleration is shown in Fig. 1A.

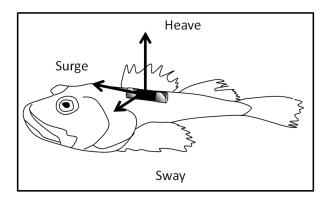




Figure 1A&B. *M. polyacanthocephalus* tagged with a Petersen Disk Tag and accelerometer (Little Leonardo Ltd.)

For the experiments individual fish were transferred to an identical (170cm diameter) flow-through experimental outdoor tank (height 1m) filled with seawater to a depth of 50cm adjacent to the holding tank (same water temperature). The transferral and tagging time ranged between 2 and 3min. In addition to the accelerometer, a piece of reflective tape was attached to the caudal peduncle to allow high-speed video tracking. Due to short tagging times, none of the animals showed signs of stress post-tagging and settled quickly in the experimental tank. Fish were kept in the experimental tank 30min prior to the start of the experiment. Escape responses were triggered by manually thrusting a 140cm long pole (2.5 cm diameter) on the bottom of the tank 10cm from the end of the caudal fin when the animal was located at least 1BL away from the tank wall - a similar method has been used in escape response studies of other fish (Harper and Blake, 1990; Domenici 2004). Escape responses were elicited in 30-min intervals, allowing for a recovery time of 30 min after initial transport. During feeding experiments, 5 live sandlance (*Ammodytes spp.* - preferred prey of Great Sculpin) (less than 15cm in size) were introduced to the

experimental tank. Fish were observed while feeding ad libitum. Feeding and escape trials were carried out over several days for each animal. For each fish a minimum of 9 escapes were elicited. Depending on the responsiveness of the fish between 10 and 22 feeding events were observed. The observations for each fish are detailed in Table 1.

The escape and feeding responses of each fish were recorded with a high-speed camera (GiGE Vision, Fastec Imaging HiSpec 2G Mono) with a 25mm COSMICAR (Japan) lens at 500 frames $\rm s^{-1}$ as well as with the animal – borne accelerometer at 100 Hz. Additionally, swimming behaviour was constantly recorded using a 30Hz standard USB webcam, Microsoft LifeCam VX-1000. The distance between the tank bottom and the high-speed and USB camera was 260cm. Fast-starts were recorded using HiSpec Control Software. Behavioural observations were recorded with a H264 Webcam 3.83 software. The resolution of the HiSpec camera is 1280×1024 pixels at 500 frames $\rm s^{-1}$.

Table 1. Summary of fish length, weight and number of observed events (E_f = feeding event, E_e = escape event, E_s = spontaneous event)

Fish	Length (FL) [cm]	Length (TL) [cm]	Weight in [g]	# E _f	# E _e	# E _s
A	29	35	560	12	15	10
В	35	40	760	10	9	11
C	33	40	940	15	10	10
D	32.5	39	701	11	12	5
E	31	36.7	570	22	15	10
F	32.5	38.5	560	12	13	10
G	30	35	590	15	9	10

Analysis

Kinematics of Feeding: Video versus Accelerometer

Acceleration recorded from the high speed camera and the accelerometer was standardised to 100 Hz. Lanczo's algorithm was used to smooth the acceleration trace over a moving window of five frames. To create a comparative acceleration trace between the video recorded acceleration and the tri-axial accelerometer, a low pass filter was used to extract the dynamic component of the \mathbf{x} and \mathbf{y} axes from the tri-axial acceleration trace. The \mathbf{x} and \mathbf{y} dynamic acceleration was then combined using the following equation to obtain the summed value of acceleration on 2 axes:

Comparison of the acceleration between video tracking and accelerometer

Acceleration obtained by the video tracking is defined in the coordinate fixed to the tank (hereafter referred to as video reference frame), while acceleration obtained by the accelerometer is defined in the coordinate fixed to the accelerometer (hereafter referred to as accelerometer reference frame). From the video reference frame, the accelerometer coordinate always changes when the accelerometer moves with the body of the fish, therefore it is necessary to transform the acceleration obtained by video tracking to the acceleration that would be sensed in the accelerometer reference frame, to be able to compare the two sources of acceleration data. To achieve that, following calculation was performed:

We assume that the acceleration coordinate is defined as the coordinate composed of two vectors, one of which is the vector (Y_A axis) connecting the two markers

attached to the both ends of the accelerometer in the longitudinal direction, the other is the vector (X_A axis) perpendicular to the Y_A axis going through the centre of the two markers. Assume M_t , M_{t+1} , and M_{t+2} to be the 2D points of the centre of the two marker obtained by the video tracking at time t, t+1, and t+2 respectively in the video coordinates. Acceleration obtained by the video tracking at time t should be defined as the acceleration measured in terms of the change of the points M_t , M_{t+1} , and M_{t+2} with the direction \overline{m} from M_t to M_{t+2} . On the other hand, acceleration obtained by the accelerometer at time t is defined as the acceleration with the two directions of the X_A axis and the Y_A axis at time t in the accelerometer reference frame. Therefore acceleration Av_t obtained by the video tracking at time t is transformed to the acceleration Ax_t and Ay_t in the accelerometer reference frame using the angle α between \overline{m} and the Y_A , following [2] and [3]

$$Ax_t = Av_t \sin \alpha$$
 [2]

$$Ay_t = Av_t \cos \alpha \tag{3}$$

Finding a signature of acceleration corresponding to behavioural events

Selection and extraction of data

Acceleration data of events were extracted with the help of examining behavioural observations recorded by the video camera. At least 10 spontaneous 1sinterval events (such as random turns or swimming) were extracted per fish. Start of feeding and escape events in the acceleration record were chosen to be the first point of change in acceleration from rest when the stimulus was applied. Feeding events were extracted in a similar matter (since sculpin are sit-and-wait predators, start of feeding events may be categorized by change in acceleration from rest). The data extraction was performed using IGOR Pro 6 (Wave Metrics Inc., Lake Oswego, OR, USA). Acceleration data will be explored as 3-dimensional acceleration as well as the magnitude thereof (MA, not corrected for gravitational acceleration) to investigate statistical parameters that are descriptive for one and only one type of event. Parameters explored stem from the frequency domain (spectral and wavelet analysis), probability domain (probability density function, population parameters such as mean, maximum, variation in acceleration) and time domain (time change points that are biologically motivated such as the end of Stage I in fast-start movements). A technique of optimization over various parameters will be employed over highest variability within events as well as lowest variability amongst individuals. The precision and accuracy of resulting parameters will be tested on n=1 fish which is excluded from finding the parameter. Statistical analyses will be carried out using the program R and IGOR Pro 6.

Results

Kinematics of Feeding: Video versus Accelerometer

Acceleration was compared from the individual \mathbf{x} , \mathbf{y} and \mathbf{z} axes of the accelerometer to that of the combined \mathbf{x} and \mathbf{y} of the video track (Fig. 2).

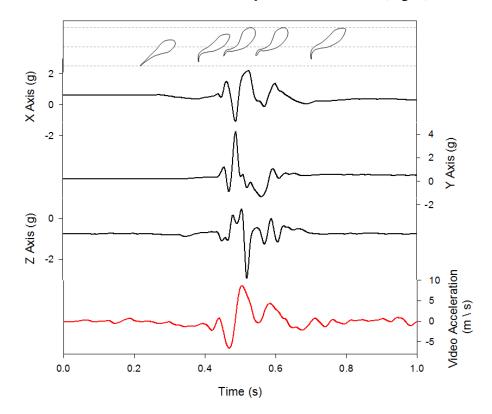


Figure 2. Acceleration recorded at 100 Hz on the **x**, **y** and **z** axis of a tri-axial accelerometer and from video-tracking (acceleration derived from the **x** and **y** vectors of movement).

Differences are evident in the acceleration from the video track and that of the accelerometer, though the timing of minimum and maximum acceleration is comparable from the x- axis of the accelerometer and the video tracking signal (Fig. 2).

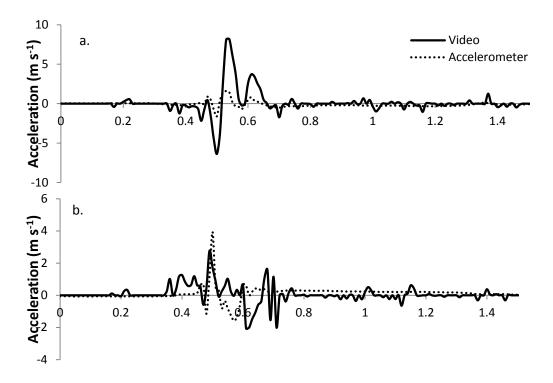


Figure 3. Transformed acceleration data from the \mathbf{x} (a.) and \mathbf{y} (b.) axes. RMSE \mathbf{x} =065. \mathbf{y} =1.26

Acceleration from the \mathbf{x} (lateral) and \mathbf{y} – axes (forward acceleration) of the high speed video was extracted and compared to that of the \mathbf{x} and \mathbf{y} trace from the tri-axial acceleration. The location of the minima and maxima in the x-axis (lateral acceleration) is consistent, yet the \mathbf{y} axis has few similarities with a much larger RMSE (Fig. 3).

Finding a signature of acceleration

The most desirable parameter for detection of behavioural events should have the following properties:

- 1. Low individual variation
- 2. Size-independent
- 3. Independent of absolute values (such as maximum acceleration in one axis)
- 4. Independent of comparison of escape vs. feeding cut off values

Properties of probability distributions of events posses most of these properties and were therefore investigated initially. Additionally, frequency properties of fast-start events were investigated using spectral analysis and wavelet analysis. However, both techniques suffer from low data density (at 100Hz an escape event that occurs over an average of 250ms will contain only 25 data points and therefore is suboptimal for spectral investigation) and were therefore dismissed.

It was impossible to find one powerful parameter that can be used to identify acceleration specific to spontaneous, escape and feeding events respectively. This lead to the development of a conceptual decision tree approach (Fig. 4) to identify behavioural movements in terms of testing a series of multiple parameters (Φ) that differentiate between spontaneous and fast-start movements and a family of parameters, $\Omega = [\Omega_1, \Omega_2, ..., \Omega_i]$ that allow to distinguish between feeding and escape events.

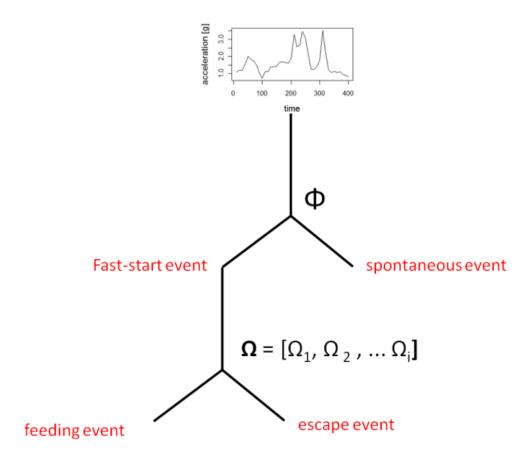


Figure 4. Conceptual approach to detecting behavioural events based on acceleration traces

Detection of spontaneous movement

The most powerful parameter (Φ) that allows differentiating between spontaneous and fast-start movement is the variation (σ^2) in combined acceleration, MA, which is the magnitude of the acceleration vector in three dimensions [1].

[1]

The standard deviation of MA, σ_{MA} is significantly lower in spontaneous activity than in fast-start events (Fig. 5, Table 2, n = 6) based on a Wilcox Rank Sign test within fish. The summary statistics for each event can be found in Table 2.

Table 2. Summary Statistics of magnitude of acceleration for spontaneous (E_s), feeding (E_f) and escape events (E_e), p-values Wilcox Rank Sign test for H_0 : $\mu_1 = \mu_2$

Fish	Sample Size	$E_s \; \mu_\sigma \!\!\pm SE \; [g]$	$E_f \mu_{\sigma}\!\!\pm SE [g]$	$E_e \; \mu_\sigma \!\! \pm SE \; [g]$	H_0 : μ_s = μ_f	H_0 : $\mu_s = \mu_e$
A	$n_s = 10, n_e = 15, n_f = 12$	0.10±0.03	0.44±0.01	0.28±0.01	< 0.001	< 0.001
В	n_s =10, n_e = 9 , n_f = 15	0.02 ± 0.00	0.61±0.01	0.90 ± 0.01	< 0.001	< 0.001
D	$n_s = 10, n_e = 11, n_f = 12$	0.02 ± 0.00	0.21 ± 0.00	0.40 ± 0.01	< 0.001	< 0.001
E	$n_s = 5$, $n_e = 12$, $n_f = 11$	0.03 ± 0.00	0.38 ± 0.02	0.62 ± 0.03	< 0.001	< 0.001
F	$n_s = 10, n_e = 9, n_f = 15$	0.02 ± 0.00	0.40 ± 0.01	0.79 ± 0.02	< 0.001	< 0.001
G	$n_s = 11, n_e = 9, n_f = 10$	0.02 ± 0.00	0.62±0.02	0.83 ± 0.05	< 0.001	< 0.001

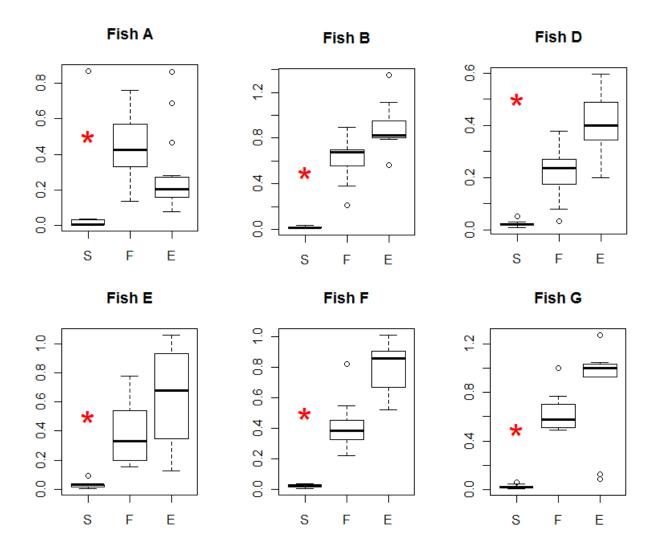


Figure 5. Variation in standard deviation of magnitude of acceleration for 6 *M. polyacanthocephalus* for spontaneous activity (S), feeding (F) and escape (E)

This parameter can now be used to detect fast-start movements in an acceleration trace (MA) that spans several hours. We designed a 1-s window that calculates standard deviation of acceleration and, given a (conservative) cut-off parameter of Φ = σ_{MA} = 0.3 identifies fast-start movements. The window-estimate was tested using a random acceleration trace (from Fish C, Fig. 5). The parameter was able to pick up 100% of the fast-start event without falsely detecting spontaneous movement (results were checked with behavioural observations from 30Hz camera).

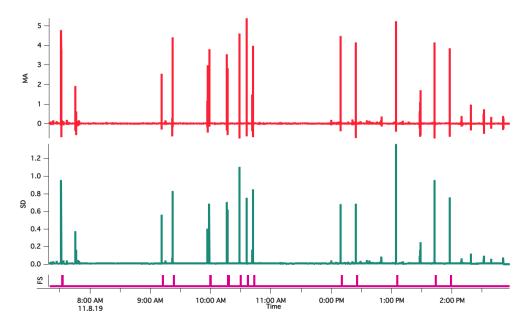


Figure 5. Identification of fast-start movements based on $\Phi = \sigma_{MA}$, MA – magnitude of acceleration, SD - standard deviation, FS – fast start detections

Assessing the power of Φ given different sampling frequencies (subsampling)

The same acceleration data (from Fish C) was subsampled with a frequency ranging from $10 \sim 90$ Hz at 10 Hz intervals, and then the fast-start movements were identified based on the same cut-off parameter of Φ as used for the data without subsampling. The detection rate of the fast-start movements decreased as the sampling frequency decreased (Fig. 6). Especially, the detection rate decreased to the rate less than 50 % when the data was subsampled with the frequency less than 30 Hz.

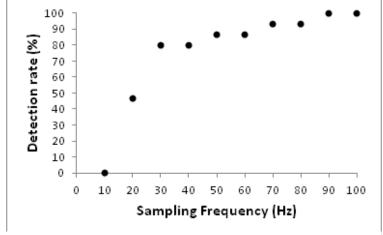


Figure 6. Detection rate of fast-start movements of the subsampled data based on $\Phi = \sigma_{MA}$

Detection of characteristic fast-start movements (escape vs. feeding)

Parameter: $\sigma_x - \sigma_y$

A parameter that was tested and resulted in significant differences in feeding and escape events is the variation in lateral acceleration compared to the variation in forward acceleration (Fig. 6)

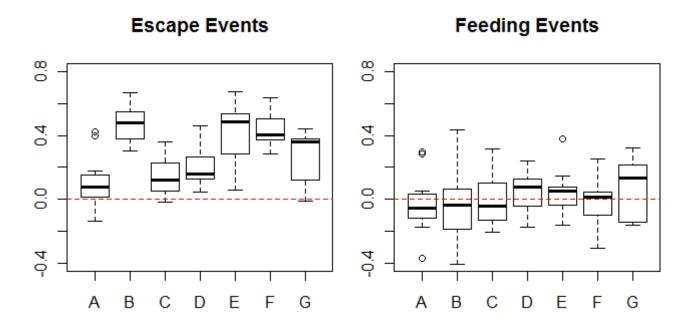


Figure 7. Difference in variation of lateral and forward acceleration in n = 7 fish (A...G) for feeding and escape events.

Table 3. Summary statistics of lateral and forward acceleration in feeding (E_f) and escape events (E_e) , p-values Wilcox Rank Sign test for H_0 : $\mu=0$, * indicates significance

Fish	Sample Size	$E_f \mu_{\!\sigma}\!\!\pm SE [g]$	$\begin{array}{c} E_e \; \mu_\sigma \!$	H_0 : $\mu_{Ef} = 0$	H_0 : $\mu_{Ee} = 0$
A	$n_e=15 \ , n_f=12$	-0.03±0.01	0.1 ± 0.01	0.38	0.01 *
В	$n_e = 9$, $n_f = 15$	-0.03 ± 0.01	0.45 ± 0.01	0.56	0.004 *
C	$n_e = 15, n_f = 22$	-0.00 ± 0.00	0.14 ± 0.00	0.57	< 0.001 *
D	$n_e = 11, n_f = 12$	0.04 ± 0.01	0.20 ± 0.01	0.30	<0.001 *
E	$n_e = 12, n_f = 11$	0.04 ± 0.01	0.42 ± 0.01	0.41	<0.001 *
F	$n_e = 9, n_f = 15$	-0.03 ± 0.00	0.43 ± 0.01	0.60	0.004 *
G	$n_e = 9$, $n_f = 10$	0.09 ± 0.01	0.27 ± 0.02	0.22	0.008 *

Summary statistics and as results from Wilcox Rank Sign test where the mean of the variation in acceleration is compared to zero are shown in Table 3. In all fish, variation in lateral acceleration does not differ significantly from variation in forward acceleration in feeding events, while in escape events, variation in lateral acceleration is always higher than variation in forward acceleration, and always significantly different from zero. Hence, $\Omega_1 = \sigma_x - \sigma_y$

Parameter: Amax, x vs. Amax, y

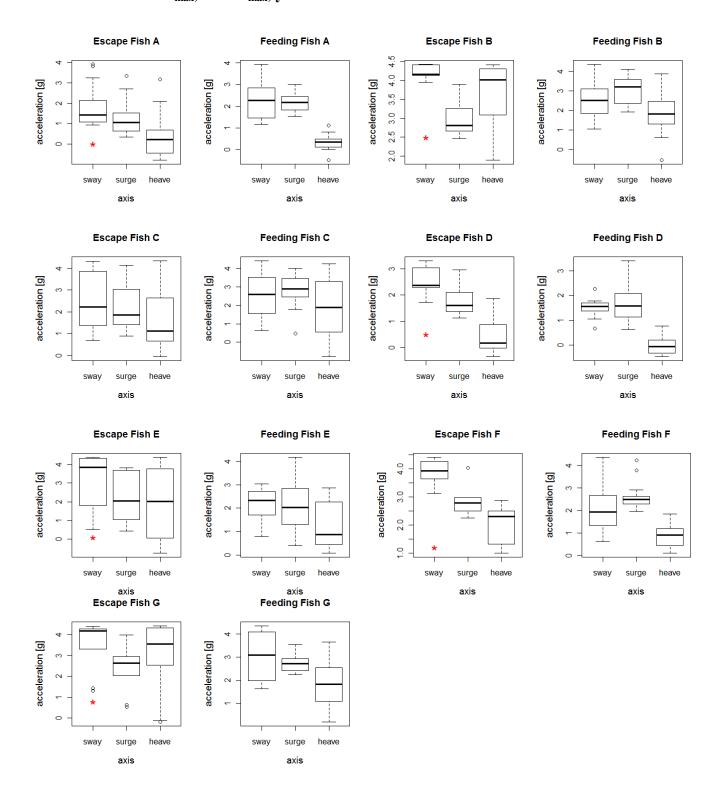


Figure 7. Maximum acceleration in sway, surge, and heave axis. Asterisk (*) indicates a significant difference in sway and surge acceleration

There is a difference between the maximum acceleration in the heave axis and the surge and sway axes in the feeding event (Fig. 7, Table 4.). Sway maximum acceleration seems to be significantly higher than surge A_{max} in the escape event. No significant differences are found in the feeding events in A_{max} for surge and sway. This is not the case for Fish C.

Table 4. Summary Statistics of Lateral and Forward maximum Acceleration in feeding (E_f) and escape events (E_e), p-values Wilcox Rank Sign test for H_0 : μ_{sway} - $\mu_{surge} = 0$

Fish	Sample Size	H_0 : $\mu_{Ef sway} = \mu_{Ef surge}$	H_0 : $\mu_{Ef sway} = \mu_{Ef surge}$
A	$n_e = 15, n_f = 12$	0.93	0.06*
В	$n_e=9, \qquad n_f=15$	0.15	< 0.001*
C	$n_e=15, n_f=22$	0.37	0.52
D	$n_e=11, n_f=12$	0.71	0.003 *
E	$n_e=12, n_f=11$	0.95	0.09 *
F	$n_e=9, \qquad n_f=15$	0.16	0.002 *
G	$n_{\rm e} = 9, \qquad n_{\rm f} = 10$	0.49	0.03 *

Hence, there is strong evidence to conclude that the this can be used as second signature parameter, i.e. $\Omega_2 = A_{max}$, forward vs. A_{max} , lateral

Discussion

Video vs. Acceleration

Two comparisons were made to assess the difference in acceleration defined by the accelerometer and the video tracking. Though there are some similarities in the timing of the maximum and minimum acceleration in the \mathbf{x} axis, signal scaling and change over time is highly variable.

Differences found between the tri-axial accelerometer and the video tracking acceleration are likely influenced by the comparison of two-dimensional video recording to three dimensional accelerometer recording:

- The angle of the accelerometer causing multiple dimensions to be recorded on any given axis. For example the **x** axis has components of **z** and **y** acceleration.
- Drifts in the timing of the acceleration on the accelerometer resulting in difficulties comparing accelerometer data with video tracking

Though video recording is a useful tool for observing fine-scale movements of untagged animals (such as small changes in fin motion), where other accelerometer tagging methods fail, two dimensional recordings loose a component of acceleration which is important for aquatic animals. Tri-axial acceleration in comparison may be useful for recording fish motion in low light conditions, though is restricted by sampling rate and the amount of time animals can be monitored.

Transformation

The shape of the transformed acceleration from the accelerometer was very different from the shape of the acceleration from the video tracking, although the timings of the peaks of the accelerations were close (Fig 3). The difference may result

from the (different) measurement noise of both the accelerometer and video tracking. In the video tracking, the acceleration was obtained by the double derivative of the digitized position, hence a slight error of the position estimate, possibly coming from image magnification, film speed, and digitization error by human, would make a large difference in the acceleration even though appropriate smoothing technique was performed (Harper and Blake 1989, Walker 1998). While the accelerometer, is considered quite accurate compared to the video tracking (Harper and Blake 1989), it still has a measurement error coming from its mechanism for discretizing the true acceleration of the fish. However, most difference between the two measurement apparatus of acceleration may be coming from the fact that accelerometer measured gravity acceleration as well as movement acceleration at the same time, and the two acceleration components cannot be accurately separated. If the movement of the fish were steady, since the change of the gravity acceleration was considered much slower than the change of movement acceleration, frequency based filtering method such as low-pass filter (e.g. Tanaka et al. 2001) and running mean technique (e.g. Wilson et al. 2006) would accurately separate the gravity acceleration from the movement acceleration. However, during unsteady movements, such as fast-start events, there is no way accurately differentiating the movement acceleration from the gravity acceleration because the fish might change its posture as quickly as the change of the movement acceleration, i.e. there is no knowledge about how much posture (hence, gravity acceleration) of the fish changed except for the accelerometer. If the posture of the fish changed, the imaginary two dimensional plane created by the \mathbf{x} and \mathbf{y} axis of the accelerometer is not parallel to the two dimensional plane of the video tracking, which requires accurate posture information to transform the force measured in the accelerometer axis to the force that would be measured in the axis of the video

tracking plane. We conclude therefore that all the error mentioned above accumulated and made the difference in the acceleration estimation. Hence, comparing video and acceleration to conclude the usefulness of either is very difficult given the intrinsic problems with the comparison.

Identification of signatures

Accelerometers are often used in settings where the sampling rate of the device depends on the technology and the size of the animal (high sampling frequencies generally mean larger battery and larger storage capability, both increasing the dimensions of the tag). They are attached to animals in the field, retrieved at some later point and analyzed. However, most of the time the researcher does not have a good idea of linking the acceleration trace to the 'observed' movement, and a lot of the analysis becomes guesswork. Simple parameters such as tail beat, 'activity' (i.e. when is the acceleration not zero) and the like are readily available, yet most of accelerometer data in the field still leaves too much to interpretation. Additionally body size constrained sampling frequencies might be too low to detect some more fine-scale movements. In this experiment we could detect one parameter that is characteristic to spontaneous movements. This parameter, $\Phi = \sigma_{MA}$, is the variation in acceleration and allows us to differentiate between fast-start movements and spontaneous movements such as feeding or escape response. The variation in the magnitude of acceleration which combines all three axes is much lower in spontaneous movements than fast-starts. This is kinematically sensible, since during escape and feeding responses great sculpin acceleration in all three dimensions while during spontaneous movements there is a change in acceleration in the lateral direction (tail beat during a e.g. a sharp turn or swimming), and a very slow (little)

change in the forward acceleration (increase of speed from rest), while there is little change in vertical acceleration. Consequently the variation of the combination of these axes is expected to be much lower than in fast-starts, where rapid changes in acceleration occur in all three dimensions. This parameter has been successfully tested and is very reliable with little false detections.

Additionally, we find that sampling acceleration at equal or less than 30Hz significantly reduces the detection of fast-start movements based on the parameter Φ . Coincidentally, <30Hz is a standard sampling frequency used in many experiments (e.g. 16Hz in Kawabe *et al.* 2003, 32, 16 or 8Hz in Tsuda *et al.* 2006, or 5Hz in Murchi *et al.*2011) and should be re-considered based on these findings. While one might argue that the focus of some of these studies is not so much the fine-scale movement but general activity, short burst acceleration such as spontaneous turns should be classified as 'activity' and are severely underestimated with a sampling frequency as low as 5Hz.

Not one single parameter may be used to differentiate between feeding and escape events. In general, feeding events are much longer and more variable than escape events (visible to the eye), yet both events exhibit variation in all three axes. We find two parameters that are characteristic to escape and feeding movements. The first parameter, $\Omega_1 = \sigma_x - \sigma_y$ shows that there is a significant difference in the variation of the forward and lateral acceleration in escape events (much higher variation in lateral acceleration), while the variation in forward and lateral acceleration is not different in feeding events. This means that there is a higher variation from mean acceleration within an escape event in the lateral direction than in the forward direction, while there is no difference in the variation from the mean

acceleration in the lateral direction compared to the forward direction within a feeding event.

The second parameter, $\Omega_1 = A_{max}$, $x - A_{max}$, y shows the relative difference in maximum acceleration of the lateral and forward direction. There is a significant difference in maximum acceleration for feeding and escape events. In escape events sway A_{max} is much is much higher than surge A_{max} , this is not the case in feeding events. This mean that during escape events the lateral maximum acceleration is higher than the forward acceleration, while in feeding events there is no difference in maximum acceleration for these two axes. This parameter is consistent with the parameter of different variation.

This difference may potentially result from the different movement of the fish for the respective tasks (i.e. feeding and escape). The fact that variation is larger in the lateral direction for escape means that on average the fish moves with larger variability from the mean in the lateral direction than in the forward direction. This may mean that the fish moves in the lateral direction with higher intensity compared to the mean (which is true given the higher values of A_{max} in the lateral direction for escape events, as described by the second parameter). While this is not possible to say, using only the standard deviation to describe the probability density function since it is not Gaussian, it is still reasonable for the prey during escape responses to show more variability in movement in the lateral direction than in the forward direction in order to establish unpredictability or to show high maneuverability for predators. Additionally, the C-bend and following unbend observed during escape responses requires more variation in acceleration in the lateral direction than in the forward direction; this is seldom the case in feeding responses. For predators, it is simple to reach and sustain a maximum speed when moving in the same direction continuously.

The same might apply to sculpin when feeding. During feeding events it may be easier to move to the same direction (forward, or in specific: towards the prey) to achieve maximum acceleration rather than turning (as during escape responses). However, sharp turning events do occur during feeding as well (depending on the position of the prey) and this may indicate the large variation in standard deviation observed in the analysis of the feeding events. This may also explain why Fish C, which has the highest variability in feeding events (and some of them seem somewhat unnatural when observed with the video camera), did not show this pattern. Our analysis did not indicate a significant difference between later and forward directional acceleration but this might just mean the fish didn't move to the lateral direction with a large acceleration enough to change its directions.

Ideally, these parameters should be tested in terms of detection probability on a new set of animals or in the field. While this was not possible, the methodology developed in this study could be used in the future to develop tags that are more fitting for the size of the animal, the research question in mind and the sampling frequency required to answer these questions. Studies in the laboratory settings are necessary to understand what acceleration means in animal-terms and to better understand the vast amounts of data that are collected in the field with accelerometers.

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