A Meta-Analysis of Fish Kinematics
- An Update on Fish Swimming -

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Abstract

A meta-analysis of data on the kinematics for steady swimming fish was done by Videler (1993). From this he could draw several general conclusions, but not many have been added up to now. In the meantime many studies on the modelling of swimming fish have been published that are based on these conclusions. To see whether we can add to the insights for live fish we present an update of the meta-analysis.

The data for the analysis of the kinematics of undulatory Body-and-Caudal-Fin steady swimming were collected from the literature. This data set comprises more than 25 species, both anguilliform and (sub)carangiform swimmers, and includes even larvae and axolotls. The size range was 0.34-69.5 cm, and the speeds 1.3-380.8 cm/s, or 0.16-55.3 in total fish lengths. The kinematic variables that could be collected are the causal variables Total length (TL), tailbeat frequency (f) and -amplitude (2A), propulsive wave length (λ) and -speed (V), and the effects as measured in swimming speed (U), Reynolds number (Re), slip, stride length and Strouhal number (St).

Several methodological problems had to be dealt with: what units of measurements were used, how the length of the individual or the tail beat amplitude were described, the temperature dependency of Reynolds numbers, and how to deal with the extremes (in speed or size). The results are presented in both units, and for the Total group and the Selection without extremes, and with swimming speed as the main dependet variable.

In the evaluation we find that propulsive wave length is the most species-specific variable and that the correlation between swimming speed and propulsive wave speed is strong and species-independent. The conclusion from Re, St and slip is that the influence of viscosity is noticeable up to a Re of about 3000. For the Selection the speed is increased mostly by frequency but also by amplitude of the tail beat, and the results on stride length show that the force of the tail beat therefore does increase when swimming faster, one tail beat has more effect. Anguilliform swimming is discriminated from carangiform by the amount of the body used in the sideways movement: this could not be tested, but body depth could. Divided according to body depth the narrow-bodied fish have the same tbf, shorter wave length, therefore wave speed is lower and swimming slower: because they are less stiff, or because the water speed was slower?

The strong species-independent correlation between propulsive wave speed and swimming speed makes this a nice test for the life-likeness of models and simulations.

Introduction

Interest

"How fish swim", the kinematics, the study of the motions, is of interest to people working to elucidate aspects in many fields: finding out how the movements are executed in morphology and neurology, what their function is in an evolutionary sense, and what their function is in the daily life of the fish (ecology and migration), but also in building models of these movements, in simulations and in underwater robotics. A good and extensive description of aspects of kinematics in a watery environment is given in the book by J.J.Videler (1993): “Fish swimming”, and the book by S.Vogel (1994) “Life in moving fluids”.

Reason for review

Most experiments that collect kinematic data study a single species, or maybe a few in a comparison. To find more general laws one needs to look at a greater variety of species. This has previously been done by Videler (1993). Among other things he collected kinematic data on several fish species and presented general trends between the kinematic variables of tail-beat frequency and speed.

The quantification of the kinematics have become more feasible with the development of computer programs to aid the labour-intensive analysis of the data collected by high-speed video, so in the time after the publication of this book many other studies have been published. Our aim is to integrate their results with those of Videler and attempt to both check whether the described trends hold, and to find new relations that may help elucidate the precise mechanics of fish swimming.

An overview of data of the many published studies of fish swimming could provide general insights. We focus purely on the effect of different swimming kinematics. Species-specific kinematics are not the issue here, though they determine how the species fit their ecological niche. Besides improving the general understanding of fish swimming, any general insights we find can be used in model building: both simulations and fish robotics.

Background

Kinematics of Swimming

Swimming fish can use several types/modes of movements that depend on what they are doing: steady swimming when migrating or searching for prey (cruising), fast-start when they suddenly spring into movement, burst-and-coast when moving in jumps, and manoeuvring/braking (Webb, 1984). The focus here is on steady swimming (Videler 1985, Sfakiotakis e.a. 1999).

Another factor is the swimming style. Fish may greatly differ in body shapes, and this affects the way they swim. These different styles of swimming may be divided according to the type of movement and the fins used. For straight-on swimming mostly the body-and-tail are used (Body and Caudal Fin). Manoeuvering and braking requires body fins (Median and/or Paired Fin). These are also used sometimes for propulsion. We here focus on Body-and-Caudal-Fin swimming.

Within this **undulatory Body-and-Caudal-Fin** style the swimming modes may vary in how much of the body is moved, ranging from the eel, undulating a large part of the body, to the tuna, which only undulates its tail and keeps the rest of its body rigid.

Swimming fish have to overcome the resistance of the environment. Vertically, gravity is countered by their natural buoyancy, and the hydrodynamic lift (if the fish is moving in respect to its environment). We try to minimize the vertical aspect by only selecting fish species with a homocercal (vertically symmetric) tail.

The forces in the horizontal plane are more relevant to the kinematics of steady swimming: here the resistance caused by the environment working on the body has to be overcome by the thrust of the fish.

This resistance, called drag, is caused by three factors: the resistance caused when the body pushes away the water (pressure, or form drag), the friction between the skin and the surrounding water (viscous drag), and the energy lost in the vortices of the wake during the movement of the body (induced drag). When a fish is moving at a constant speed as in steady swimming, the thrust is equal to the drag.

The focus of this overview is on how the propulsive forces are exerted during steady swimming, not the way in which the movements themselves are generated: data on muscle morphology and physiology will not be collected.

Variables considered

Environmental parameters like the temperature at which measurements have taken place and whether it concerned salt or fresh water were noted and corrected for in the calculations of the Reynolds number. The description of the species concerned was gathered from the papers and from FishBase (2010).

Several variables collected on properties of fish are causal variables that influence the swimming movement, and other variables represent the consequences of these movements.

Causal properties are:

the length of the fish studied	Length (in cm)	TL
tail beat frequency and –amplitude: the tail movement, expressed in a tail beat frequency and a maximum tail beat amplitude. (how often is the tail moved from one side to the other and how large is the lateral distance, as measured laterally from the midline of the fish)	Tail-beat frequency	f
	Tail-beat amplitude - normalized - absolute	 $2A_{TL}$ $2A_{cm}$
the length and speed of the body- or propulsive wave, the 'wave of curvature passing along the body from head to tail' (Videler 1993)	Propulsive wave length - normalized - absolute	 λ_{TL} λ_{cm}
	Propulsive wave speed - normalized - absolute	 V_{TL} V_{cm}

And consequences are:

the speed at which the fish swims	Swimming speed - normalized - absolute	 U_{TL} U_{cm}
stride length: the distance travelled in one tail beat	Stride length - normalized - absolute	 d_{TL} d_{cm}
slip: the percentage of the backwards body wave which gets converted into forward motion	Slip	Slip
Strouhal number, describing frequency of the vortices in the wake at a certain speed of the water	Strouhal number	St
Reynolds number: a non-dimensional number of inertial versus viscous forces	Reynolds number	Re

This set will be the set of variables used for statistics and the presentation of the results. Measurements are presented as normalized for Length of the fish, or in centimetres (where this is relevant).

Two other aspects will be considered separately: Body depth (as percentage of the length of the fish) and Swimming type, how much of the body is used in the swimming movement. They are considered as causal variables in the light of this enumeration.

General questions that we can try to answer with this data set are for instance:

length:	- is it always correct to express kinematic variables normalized for fish-lengths (or should this be limited to certain variables or within certain limits)?
speed :	- which kinematic variable is the best general predictor for swimming speed independent of species?
tail-beat frequency:	- does the positive relation between tailbeat frequency and speed hold over a large collection of different species and sizes?
tail-beat amplitude:	- what happens to amplitude when speed is increased by higher tail beat frequency?
Reynolds number :	- what influence does the viscosity regime have on kinematics?
slip and effort	- do small fish have lower slip and does this mean that they have to exert themselves more?
stride length	- what does stride length tell us about the tail beats?
body depth	- what influence does body depth have on the kinematics?
swimming style	- are body shape /swimming style essential elements in kinematic relations?

Papers, Species

Papers

A literature search or meta-analysis has its own methods, to wit: how papers are selected, which data points are extracted from the paper, and how the measurements are converted to common units.

The starting point was the data of table 6 in the book of Videler (1993). Additional papers were on first approach selected by searching for terms like "steady swimming" and "kinematics", and checking citations of several initial papers (see Videler, 1993, and Webb, 1984).

The results were varied. Inspection revealed that kinematic variables are described in various settings; sometimes the kinematics themselves are the main interest in the article, sometimes it is only a starting point. The catch contained reviews, papers on morphology and physiology, on energy costs, on different modes of swimming like C-starts, on the ecology of fishes, on vortex- and force studies, on modelling and artificial fish, and even on evolution and ichthyosaurs.

In this study only papers are used which present data on steady swimming and which present a certain minimum number of variables (see section on variables). This meant that only reports were selected with sufficiently detailed measurements, which meant laboratory studies that used high-speed film or video to record the fish. The species and length of the individual has to be clearly mentioned. Measurements in the wild of some kinematic variables are possible (tail-beat frequency by echosounder, Handegard et.al, 2009), but these measurements do not yet include body wave specifics and thus were not included.

In some articles the fish were treated in some way, for instance a change in the skin of the fish in the paper by Long et al. (1996), so from this paper only the untreated control was taken.

Species, size and speed

The range of species that exhibit steady swimming in the data that were found is wide, varying from fish larvae to cod, from 0.35 cm to 70 cm - the largest is about 200 times the size of the smallest. And this range is not limited to fish species, axolotls also swim by steady undulation (Table 1).

The largest of the larvae measures 2 cm, the size range of the other individuals is 3-70 cm. The speeds mostly fall within the range of 0.25 to 5 times their lengths per second, with the extremes in speed swimming 8-12 lengths (which in absolute terms is over 200 cm/s or 7.2 km/h).

Due to this extreme range in both size and speed, we analysed the data as 2 different groups according to the in- or exclusion criteria described in the next paragraph.

In- and exclusion: ‘Total’ and ‘Selection’

The reason for in- and exclusion criteria was the wide range and variety of species and speeds. Larvae have a very high tail beat frequency, and bigger and extremely fast-swimming fish have a very high Reynolds number, so both groups often lie far outside the main body of data. Axolotls too are exceptional, being amphibians, even if they swim with their legs pressed to the body and therefore exhibit the same undulatory swimming style.

Definition:

The ‘**Total**’ group, meaning the full dataset, will be defined as including the extremes (larvae, axolotls and the fast swimming fish with speeds > 200cm/s), and the ‘**Selection**’ will be the dataset in which the extremes are excluded. (Table 1).

The effect of this selection is clear in for instance a plot of tail beat frequency (tbf) and speed U_{cm}. Here it is very clear that the red dots (larvae, N=17) and the grey dots (fast, as defined as a speed of >200cm/s, reached by 5 fish) lie outside the main group. A plot for the ‘Selection’ dataset, which is represented in the lower left corner of the previous plot, gives a rather different impression.

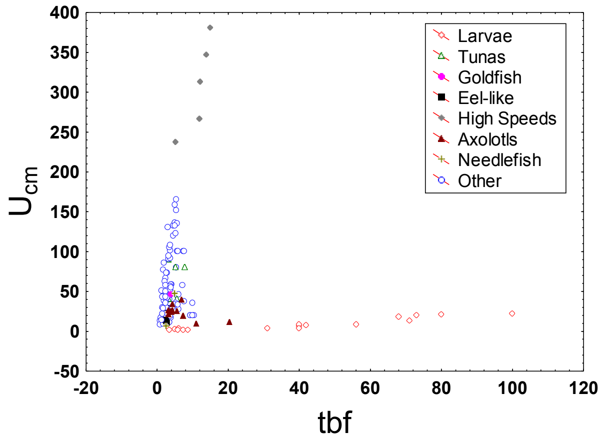


Figure 1a. Total group: TBF against Speed (in cm)

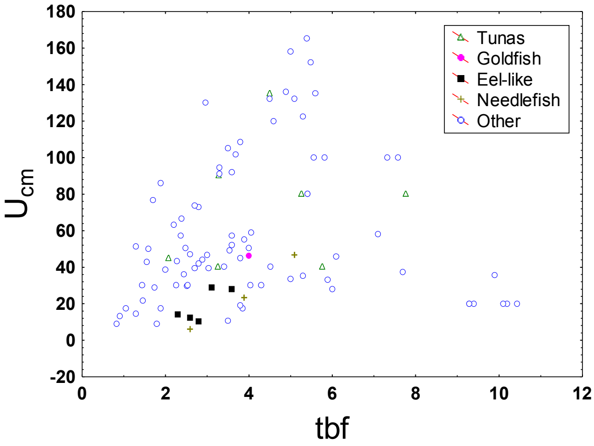


Figure 1b. Selection : TBF against Speed (in cm)

In our dataset the number of observations is: Total: N=138, and when the exclusion criteria are applied N=98. The size of sets in which we omit samples which lack data in any variable are respectively for the Total group: N=124 and in the Selection without extremes: N=88.

One data point in this dataset results may represent several things, depending on which study the data is taken from: it may represent one individual, an average, or it may have been deduced from a given regression function (Table 1).

Table 1. Species and numbers used as data points in the graphs.

Species	Nr of data points		Nr of Individ per data point and total nr.	Videler 1993	Authors
	Total	Selection			
Abramis brama	1	1	1	x	Videler (1993) citing Bainbridge (1963)
Ambystoma mexicanum	8	-	1, total 8		D'Aout, Aerts (1997)
Ambystoma mexicanum (juv)	3	-	3, total 9		D'Aout, Aerts (1999)
Ammodytes marinus	4	4	1, total 3	x	Videler (1993)
Anguilla anguilla	1	1	1	x	Videler (1993) citing Hess (1983)
Anguilla anguilla	3	3	1, total 3		Muller, Smit, Stamhuis, Videler (2001)
Anguilla rostrata	1	1	means of 3		Tytell, Lauder (2004)
Carassius auratus	1	1	1	x	Videler (1993) citing Bainbridge (1963)
Chelon labrosus risso	1	1	1		Muller, Stamhuis, Videler (2002)
Chelon labrosus risso	1	1	1		Muller,vdHeuvel, Stamhuis, Videler (1997)
Clupea Harengus (larva)	6	-	means of 10		Fuiman, Batty (1997)
Danio rerio (larva)	2	-	1, total 2		Muller, vdBogaart, vLeeuwen (2008)
Danio rerio (larva)	9	-	1, total 9		Muller, vanLeeuwen (2004)
Esox (hybrid)	1	1	1	x	Webb (1988)
Euthynnus affinis	4	4	extrapol. of 10		Donley, Dickson (2000)
Gadus morhua	4	4	1, total 2	x	Videler, Wardle (1984)
Gadus morhua	2	2	means of 9		Webb (2002)
Gambusia affinis	6	6	means of 6		Langerhans (2009)
Hyperoplus lanceolata	5	5	2	x	Videler (1993)
Lepisosteus osseus	7	7	means of 3		Long, Hale, McHenry, Westneat (1996)
Leuciscus leuciscus	1	1	1	x	Videler (1993) citing Bainbridge (1963)
Liza ramada	1	1	1	x	Videler (1993)
Micropterus salmoides	5	5	1, total 1		Jayne, Lauder (1995)
Oncorhynchus mykiss	5	-	extrapol. of 1		Jayne, Lauder (1995) citing Webb (1984)
Oncorhynchus mykiss	4	4	1, total 4	x	Webb, Kostecki, Stevens (1984)
Oncorhynchus mykiss (as Salmo gaidneri)	1	1	1	x	Webb (1988)
Pleuronect platessa	1	1	means of 10		Webb (2002)
Pollachius virens	9	9	2	x	Videler, Hess (1984)
Salmo salar	3	2	1	x	Videler (1993)
Sarda chiliensis chiliensis	2	2	means of 8		Dowis, Sepulveda, Graham, Dickson (2003)
Scomber japonicus	8	8	extrapol. of 12		Dickson, Donley, Sepulveda,Bhoopat (2002
Scomber japonicus	4	4	extrapol. of 8		Donley, Dickson (2000)
Scomber scombrus	9	5	1, total 4	x	Videler, Hess (1985)
Strongylura marina	3	3	means of 4		Liao (2002)
Total number of data points	**126**	**88**		**45**	
Extra, not in all plots:			**Missing:**		
Gadus morhua	5	5	λ,V,Slip		Syme, Gollock, Freeman, Gamperl (2008)
Lepomis macrochirus	1	1	λ,V,Slip		Flammang,Lauder (2008)
Protopterus annectens	1	1	λ,V,Slip		Horner, Jayne (2008)
Thunnus albacares	3	3	2A,λ,V		Shadwick, Syme (2008)
	136	**98**			

Focus of analysis

Before the start of the analysis of the collected data I discovered that there were two aspects that were inconsistent in the literature. Firstly, whether the variable "swimming speed" was seen as an independent or as a dependent variable, secondly, in what units the measures were reported, as absolute (cm) or as normalized (fish lengths). On these two aspects a decision was needed before this large dataset could sensibly be analysed. The decisions are described in the next paragraphs.

Speed as dependent factor

Speed, from the fish perspective, is the dependent factor, even though often a flow tank is used where the swimming speed is imposed by the flow speed of the water. The speed of the water in that case is independently regulated, but the swimming speed is something that is achieved by the fish changing its own causal kinematic variables. Therefore we decided, in evaluating the numbers found in the literature, to consider speed as a dependent factor, not as a fixed factor.

This emphasis on speed as a resultant gives some insights in the interdependence of the kinematic factors. A factor can be both related to length and to speed, but this does not always result in a linear dependency of speed on both these factors. To illustrate the effect of the choice of dependent variable in a multivariate analysis: when the three variables Tail beat amplitude, Length and Speed are considered, it matters which of these is chosen as the dependent variable. An example, applied to the Selection without extremes (normalized measures), is presented in the following Table 2.

Table 2: Effect of choice of dependent and independent variables

Dependent	Intercept	First independent	Second independent	Explained variance R^2
Length	$p<0.001$	Speed $p<0.001$	TBA $p = 0.769$	$R^2 = 0.259$
TBA	$p<0.001$	Length $p = 0.769$	Speed $p<0.001$	$R^2 = 0.277$
Speed	$p = 0.112$	TBA $p<0.001$	Length $p<0.001$	$R^2 = 0.430$

The significance for correlation between pairs is the same in all situations, but the explained variance (for the dependent variable) is not the same. This makes the decision which variable will be dependent a non-trivial point. Of course in studies of swimming the Length of the fish is never used as dependent variable, but Speed (swimming speed, not flow tank water speed) and Tail beat amplitude are. The conclusion of the second row in Table 2 would be: "Tail beat amplitude depends mostly on Speed, hardly on Length, and has an intercept" and of the third row: "Speed is dependent on both Length and Tail beat amplitude, without significant intercept". It also shows that with tail beat amplitude as the dependent variable, the regression explains less of its variance than when speed is the dependent variable.

Absolute and Normalized measures

The length of a fish is an important issue when reporting its measurements. Often the measurements given are normalized by the lengths of the fish, to get rid of effects of absolute size. This may be valid when a species characteristic is considered (for instance a morphological descriptor like the distance of nose to fin) and individuals are not of the same size, but some variables scale with the surface of the fish (length unit squared) or even volume (length unit cubed). But, as noted by Dickson et al. (2002), when an effect of length is found even after normalization, apparently normalization does not have the expected effect.

For biological aspects normalizing make sense, for physics however, this may not be correct, as for instance when properties that are included in the Reynolds number are exerting their influence.

On this point no decision was made, or rather, the decision was made to show both cases (absolute and normalised by length), so that different patterns might show up.

Definition:

'Normalized' will mean a measurement divided by Total Length of the individual - indicated by the subscript $_{TL}$, **'absolute'** will mean a measurement in centimetres - indicated by the subscript $_{cm}$.

Background on variables

Reynolds number (Re)

The Reynolds number is an old (1883) formula in fluid mechanics, relating inertial force to viscous properties:

$Re = U * L / \nu$

It is a dimensionless ratio. For fish the inertial term can be represented by L, the length of the moving object and U, the mean fluid velocity; the viscous force ν is the kinematic viscosity of the medium.The kinematic viscosity ν is the ratio of the dynamic viscosity μ and the density of the fluid ρ :

$\nu = \mu / \rho$

In the words of Vogel 1994, p.87: “inertial forces reflect the *individuality* of bits of fluid while viscous forces reflect their *groupiness*”. At very low Reynolds numbers ($Re < 1$), inertial forces can be neglected compared to viscous forces, but in this study the Reynolds numbers are above 100, and thus inertia is important.

Because the viscosity of water changes with the temperature, temperature has a strong effect on the Reynolds number: the Reynolds number of a fish of 10cm swimming at a speed of 10cm/s at 10 °C is 77% of the Reynolds number at 20 °C; going from 15 °C to 20 °C there is more than 10% difference in Re. The type of water (fresh or salt) has a smaller influence: Re in fresh water at 15 °C is 4% higher than the Re in salt water. Both effects will be properly applied in the calculations of the Reynolds number.

Strouhal number (St)

The Strouhal number is also a dimensionless ratio, representing the relation between the movement of the tail and the swimming speed due to this movement :

$St = 2 * f * A / U$

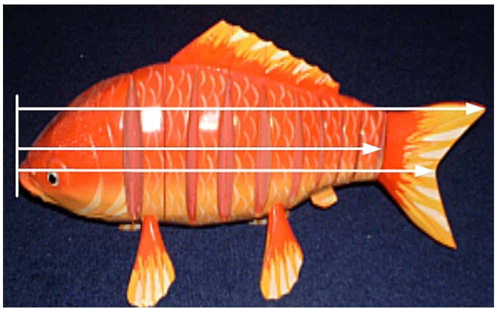
Strouhal number is frequency (f) times width of the wake (2A) divided by swimming velocity: “how often and how hard do you flap your tail to attain one unit of speed”. It describes the structure of the wake as characterised by the distance between the vortices in the forward and the lateral direction.

Length (TL or L)

All measurements in the papers that we considered are taken in the laboratory, in tanks with flowing water or standing water.

Unfortunately, in the literature multiple measurements are used for the size of the fish:

- Total length (TL, the length from tip-of-nose to end-of-tail),
- Body length (= Standard length, BL or SL, from tip-of-nose to start-of-tailfin)
- Fork length (FL, from tip-of-nose to the fork of the tailfin/ vertical midpoint of the tail fin).



← **TL Total Length**
← **SL Standard = BL body Length**
← **FL Fork Length**

In this report the different measurements are rescaled to Total Length to get common units. The fixed recalculation factors are taken from the description of the fish species in Fishbase (2010), where the measurements of different morphological properties are given as a percentage of Total Length.

Swimming speed (U)
Swimming speed is usually equal to the flow speed in a flow tank with an induced current, or is measured from video in the case of tanks without flow. In flow tanks, the swimming speed is therefore a controlled factor: the researchers impose the speed on the fish. In a kinematic sense however it is a resulting factor: the kinematics of the fish cause it to swim at this certain speed.

Tail-beat frequency (tbf or f)
The definition is “how often the tail beats back and forth”, unit is Hz (s^{-1}). Tail-beat frequency is measured from video, timing the period (T) of the edge of the tail moving from one extreme in lateral excursion via the other side to the next extreme on the same side. The reciprocal of this duration gives the tail beat frequency (f) per second. It is often used to select the period to analyze for steady swimming, by only selecting the recordings where several tail beats were executed very regularly. Abbrevations in the literature are tbf or f.

Tail-beat amplitude (tba or 2A)
This indicates the distance of the maximum lateral excursion of the tail, often measured from the midline, but also reported as the maximum lateral tail excursion from side to side. This is the cause of errors, because it is not always clear which version is reported, the amplitude or the double amplitude. Abbreviations used in the literature to describe this property are A, Z and H. In this report numbers are standardized on the double amplitude.

Propulsive wave length (lambda or λ)
This is the length of the kinematic wave of lateral bending from the leading end towards the trailing end of the animal (D'Aout, Aerts (1999). Looking from the outside, the earthbound frame of reference, the wave seen is called propulsive wavelength λ_s. "every point on the body follows a wave track in space (the stride) in the swimming direction at an average speed lower than the speed of the body wave" (Videler, 1993). Often only half of the wave can be measured, when the wave is as long as the body itself and the anterior part of the body hardly moves. The reciprocal is the wave number, the number of waves that fits on the body. It can be derived from data on propulsive wave speed V and tail beat frequency f by using the formula

$$\lambda = V / f$$

Propulsive wave speed (V)
The wave speed V of the propulsive wave λ is the speed at which the crest of the wave travels. Usually it is calculated as the length of the body wave λ times the frequency f per second:

$$V = \lambda * f,$$

or, if Slip (U/V, see below) is given: $V = U / Slip$, where U is the swimming speed.

The propulsive wave speed is also called ‘c’ in the literature.

Stride length (U/f or d)
The stride length represents the effectiveness of one tail beat: it is the distance travelled in one tail beat,

$$U / f$$

Stride length is reported as a normalized speed-variable when the reasoning is that a difference in swimming speeds is resulting mostly from an increase in tail beat frequency. Indicated in the literature with d, l or S. Also described as propulsive wavelength λ_s, as seen from an earthbound frame of reference (Videler, 1993).

Slip (U/V or slip)
“Slip” stems from the discussions on the boundary conditions, what exactly happens between a moving solid object and the fluid around it (see Goldman, 1969). The boundary layer is a thin layer around a body moving in relation to its environment: at one border, against the skin, the medium moves with the speed of the body,

and at the other border with the speed of the environment, the theoretical velocity. The ratio between speed at the outermost edge (U) and that at the innermost edge (V) is the Slip: the ratio between swimming speed and speed of the body wave:

U / V

Slip is sometimes taken as an indication of efficiency of the generation of speed, an indication of the swimming efficiency or propeller efficiency (the amount of mechanical energy lost (D'Aout and Aerts, 1997); it can also be seen as a measure for effort. It is a ratio, therefore it is not affected by the units in which the speeds involved are reported, in fish lengths or cm. If the speed U of the surrounding water and the speed V of the body wave are equal (U/V = 1) movement is solely due to the inertial mass. If the ratio is less than 1 the force exerted is sideways and backward, with a resultant force in forward direction; if the ratio is more than 1 the resultant force is backward: the fish is braking or swimming backwards.

Body Depth

Dorso-ventral cross-sectional size of the fish, taken from the descriptions in FishBase (2010), or calculated from pictures, as percentage of total length of the fish. Reason for inclusion of this aspect: the depth of the body may have an influence on the effect of the sideways motion of the body wave on speed.

Swimming type

Swimming type is the classification of fish into groups according to how much of their body they use in the swimming movement. The "classical" division is: eel-like (anguilliform), using more than half of their body, subcarangiform (using the last half of their body), carangiform (the last third) and thunniform (only tail and verly last part of the body). (Figure 2). Because the swimming types use a different percentage of the body it may influence the effect of the body wave has in generaing speed.

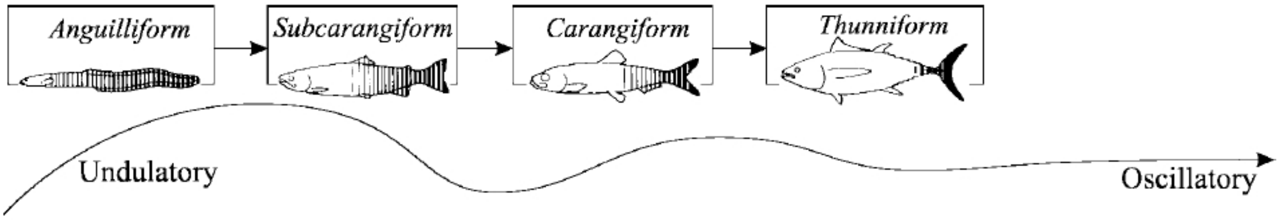


Figure 2: From Sfakiotakis et. al 1999 adapted from Lindsey (1978, not referenced).

Results

Matrixplots and correlation matrices

See the Appendix for the Matrixplots of all variables for the Total group (Figure A-1) and for the Selection which does not include extremes (Figure A-2); the correlations between all pairs are given in Table A-1.

In all 2D scatterplots in this report subgroups have been indicated by colored markers: larvae by red markers, the fish swimming at a speed of > 8 TL/s by gray markers, eels by black markers, the lone goldfish as magenta, and tunas with green triangles.

The reason for presenting the data together in these matrix plots and tables is that one correlation between a pair of variables immediately sets one to wondering how something else correlates: the interdependency is very strong, which also leads to the problems mentioned in the following section on Multiple Regression.

Numbers, ranges and other descriptive statistics are given in Table 3, again for Total group and Selection.

Table 3. Descriptive statistics of the variables.

	Total Group					**Selection without extremes**				
	N	Mean	Std.Dev.	Min	Max	N	Mean	Std.Dev.	Min	Max
Length	136	24.9	17.7	0.34	69.5	98	29.6	16.5	3.59	69.5
U$_{TL}$	136	4.7	8.8	0.16	55.3	98	2.4	1.6	0.16	6.5
U$_{cm}$	136	56.5	63.0	1.28	380.8	98	56.7	39.1	5.83	165.0
tbf	136	9.0	16.1	0.83	100.0	98	4.1	2.2	0.83	10.5
2tba$_{TL}$	128	0.2	0.1	0.05	0.6	90	0.2	0.0	0.05	0.3
2tba$_{cm}$	128	3.7	2.7	0.10	12.0	90	4.3	2.6	0.48	12.0
Lambda$_{TL}$	124	0.8	0.2	0.43	1.2	88	0.9	0.2	0.43	1.2
Lambda$_{cm}$	124	20.1	15.5	0.34	68.8	88	24.0	14.6	2.12	68.8
V$_{TL}$	126	9.2	18.1	0.76	109.0	88	3.7	1.9	0.76	9.6
V$_{cm}$	126	82.9	80.9	4.06	477.0	88	84.0	46.2	15.00	192.7
stride-l $_{TL}$	136	0.5	0.2	0.10	1.0	98	0.5	0.2	0.10	1.0
stride-l $_{cm}$	136	13.6	11.0	0.08	45.6	98	16.1	10.3	1.91	44.8
Slip	126	0.6	0.2	0.21	1.0	88	0.7	0.1	0.21	1.0
Strouhal	128	0.5	0.4	0.13	2.0	90	0.3	0.1	0.16	0.9
Reynolds	136	160260	220826	88.67	1501000	98	164803	148943	8398.7	707533

Multiple (linear) regression

Multiple linear regressions were performed with speed as the dependent variable and the causal variables length, tail-beat frequency, amplitude, and the propulsive wave characteristics as independent variables, but the multicollinearity was too strong (the variables are too interdependent). Some results of an alternative method, Partial Least Squares analysis, will be presented in the discussion.

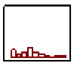
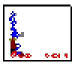
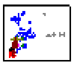
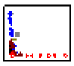
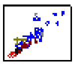
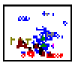
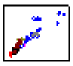
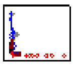
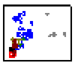
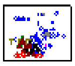
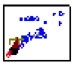
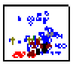
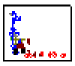
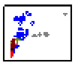
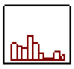
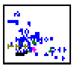
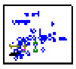
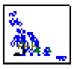
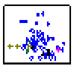
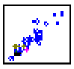
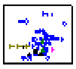
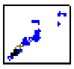
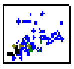
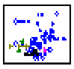
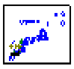
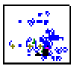
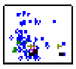
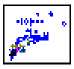
Results on Length, and normalization for Length

Often kinematic variables are corrected for variation between differently sized individuals by dividing by the body length. It is interesting to check whether this normalization has the power to really remove the influence of the size of the animal. If the influence of Length would be removed, normalized variables plotted against Length should show a random scatter.

In the matrix plot (Figure A-1 of the appendix) this influence can be viewed in the first row of plots (where Length is plotted on the Y-axis), or in the first column of plots (where Length is drawn on the X-axis).

The correlations of Length with other variables are presented separately here; the plots added (with Length on the Y-axis) are not for the purpose of showing all the details, but to give an overall impression. The correlation significances given in Table 4 are the same as those presented in Table A-1 in the appendix. The *gray+cursive* numbers are not significant ($p > 0.05$), normal format indicates a correlation with $p \leq 0.05$, and the **bold** print indicates a correlation of > 0.80 (with $p \leq 0.0001$), which means the level of explained variance (R^2) is 0.64 or higher.

Table 4. Linear correlations of Total Length against the other variables. (Length on the Y-axis)

Length against	SPEED		TBF	TBA		LAMBDA		V		STRIDE		SLIP	Strou	RE
	U_{TL}	U_{cm}	f	$2A_{TL}$	$2A_{cm}$	λ_{TL}	λ_{cm}	V_{TL}	V_{cm}	d_{TL}	d_{cm}		St	Re
Total	-0.39	0.39	-0.46	-0.57	**0.89**	*0.06*	**0.94**	-0.43	0.47	0.22	**0.84**	0.27	-0.51	0.61
TL Tot 														
Select	-0.54	0.29	-0.68	-0.24	**0.87**	*0.08*	**0.91**	-0.59	0.43	*0.01*	0.77	*-0.13*	*-0.03*	0.66
TL Sel 														

For the Total group: in a linear correlation between length and the dimensional kinematic variables, nearly all correlations are significant ($p \leq 0.05$). Normalizing for length changes the strong correlations of Length with the absolute measurements of tail-beat amplitude ($2A_{cm}$), propulsive wave length (λ_{cm}), wave speed (V_{cm}) and stride length (d_{cm}) and results in weaker correlations ($2A_{TL}$, λ_{TL}, V_{TL}, d_{TL}), but only for propulsive body wave length (λ_{TL}) does the correlation becomes non-significant, showing that it is length-independent.

For the Selection without extremes: the normalization for length reveals stride length (d_{TL}) as a second length-independent factor, and the normalized tail-beat amplitude ($2A_{TL}$) is only weakly correlated with length.

Apparently normalization works well in removing length-dependency within the selection for some variables (λ_{TL}, d_{TL}, Slip and Strouhal number), but not for the total group comprising a broad range of species and sizes. Normalized Speed, TBF, and Propulsive wave speed remain length-related.

Only the normalized propulsive body wave length never has any significant correlation with length, neither in the Total group nor in the Selection. This could imply that over the whole breadth of species this is the only really species- or shape-dependent variable. Donley and Dickson (2000) and Dickson et al. (2002) observed that in their results for the two species tested (Scomber japonicus and Euthynnus affinis) specifically these variables, lambda and stride length, were length-dependent: larger fish had proportionally longer wave lengths. If this was an species-independent property this positive correlation should also appear in these meta-data, but it does not. In an absolute sense bigger fish have larger wavelengths, but not when normalized. – *bigger is stiffer, but this does not mean that bigger species are stiffer.* Dickson et al. (2002) also found an effect of the mass of the fish, but this could not be tested in this data set.

Length and propulsive body wave speed always have a significant correlation: negative for V_{TL} and positive for V_{cm} , and together with the result on tail-beat amplitude, this implies that Length (or some factor correlated with length, like Reynolds number) should not be ignored when other correlations to wave speed and amplitude are evaluated.

Length and tail-beat frequency are negatively correlated, both in the total group and in the selection, so this is not only due to the much faster tail beat of larvae, but holds for the whole range of sizes. Checking whether the larger fish were not forced to swim at a higher relative speed in the flow tanks: the correlation of length and speed shows an inverse relation for the Total group **$U_{TL} = (9.60 \pm 1.21) - (0.20 \pm 0.04) * TL$** , $R^2 = 0.15$, and **$U_{TL} = (3.99 \pm 0.29) - (0.05 \pm 0.01) * TL$**, $R^2 = 0.13$ for the Selection. This of course is the imposed situation, fish of a certain length were “asked” to swim at a certain speed: the relation is negative, so it was the small fish that were swimming faster proportionally in these experimental settings. (see section on tail beat frequency).

For the non-dimensional variables Slip and Strouhal number no linear correlation is found in the Selection, but with the larvae included there was a weak positive correlation between Length and Slip and a negative one for Strouhal number.

Answering the question of the Length issue: only propulsive wave length λ can be normalized for Length (when dealing with many species, here the species effect is averaged out), and within not too extreme situations this can also be done for stride length, slip and Strouhal number, but not for tailbeat frequency, propulsive wave speed and Reynolds number. *Conclusion: always check (if possible and relevant) whether normalization has the desired effect: the removal of the influence of the variable which is normalized for.*

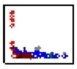
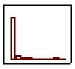
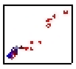
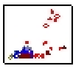
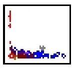
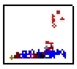
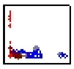
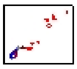
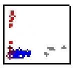
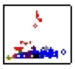
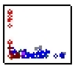
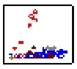
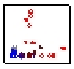
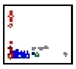
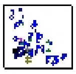
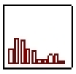
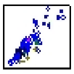
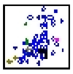
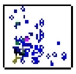
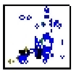
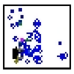
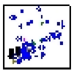
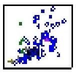
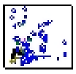
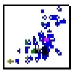
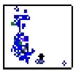
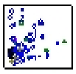
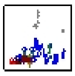
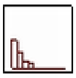
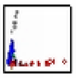
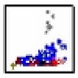
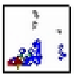
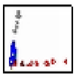
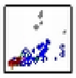
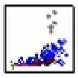
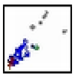
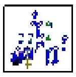
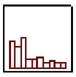
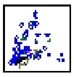
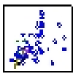
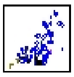
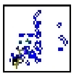
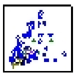
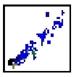
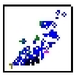
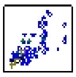
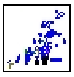
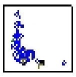
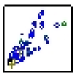
Results on speed

Speed as dependent variable

Analysing speed as a dependent variable we have as causal variables: length, tail-beat frequency, tail-beat amplitude, body wavelength and body wave speed.

Again in this table the different representations of swimming speed are on the Y-axis.

Table 5. Linear correlations of Swimming Speed against the other variables. (Speed on the Y-axis)

SPEED	**Leng**		**TBF**	**TBA**		**LAMBDA**		**V**		**STRIDE**		**SLIP**	**Strou**	**RE**
against	TL		f	$2A_{TL}$	$2A_{cm}$	λ_{TL}	λ_{cm}	V_{TL}	V_{cm}	d_{TL}	d_{cm}		St	Re
U_{TL} Tot	-0.39		**0.97**	0.65	-0.34	0.36	-0.31	**0.97**	*-0.03*	*0.13*	-0.28	*-0.12*	0.24	*-0.08*
U_{TL} Sel	-0.54		**0.90**	0.53	-0.26	0.25	-0.33	**0.94**	0.27	0.52	*-0.12*	0.61	-0.35	*0.05*
U_{TL} Tot														
U_{TL} Sel														
U_{cm} Tot	0.39		*-0.11*	*-0.16*	0.57	0.38	0.54	*-0.11*	**0.99**	0.60	0.64	0.49	-0.40	**0.89**
U_{cm} Sel	0.29		*0.13*	0.37	0.57	0.61	0.54	0.30	**0.95**	0.72	0.72	0.48	-0.53	0.66
U_{cm} Tot														
U_{cm} Sel														

Noticeable is the strong correlation of tail-beat frequency with the normalized swimming speed which does not appear for the absolute speed (see below).

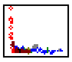
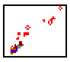
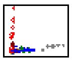
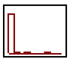
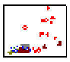
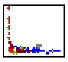
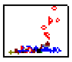
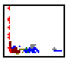
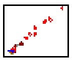
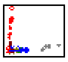
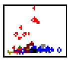
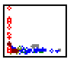
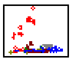
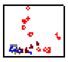
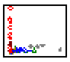
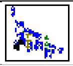
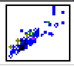
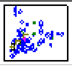
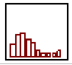
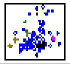
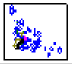
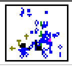
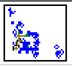
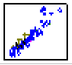
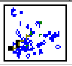
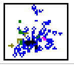
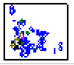
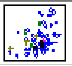
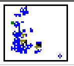
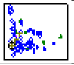
Even more noticeable is the strong linear correlation of the propulsive wave speed with swimming speed, which exists for both the normalized numbers and for the absolute numbers. Propulsive wave speed is often calculated as a multiplication of (propulsive wave length λ * tail-beat frequency f), but the propulsive wave length itself does not show a very strong correlation with swimming speed. In the normalized case the positive relation of speed with tail-beat frequency seems a large part of the explanation, but for the absolute case this is not sufficient. Apparently it is the propulsive wave speed that most strongly explains the swimming speed reached. Whether a species or individual achieves this wave speed by adapting the tail-beat frequency or by subtly changing the propulsive body wavelength is open, but the result is a very strong correlation with swimming speed.

The main conclusion here is that *the strongest predictor for swimming speed is the propulsive wave speed* (see later). This makes sense when considered from a land-bound perspective: if we imagine the rearwards-moving body wave as the legs going rearwards, this is the most important cause of the body moving forwards.

Tail-beat frequency

The relation of tail-beat frequency to swimming speed is the most reported one in literature: Videler (1993), Shadwick and Syme (2008) (normalized, linear), Syme et al. (2008) (normalized, linear), Muller and van Leeuwen (2004) (absolute, quadratic), Webb (1988) (absolute, linear), Long et al. (1996) (normalized, linear), Liao (2002) (normalized, linear), Dowis et al. (2003) (absolute, linear).

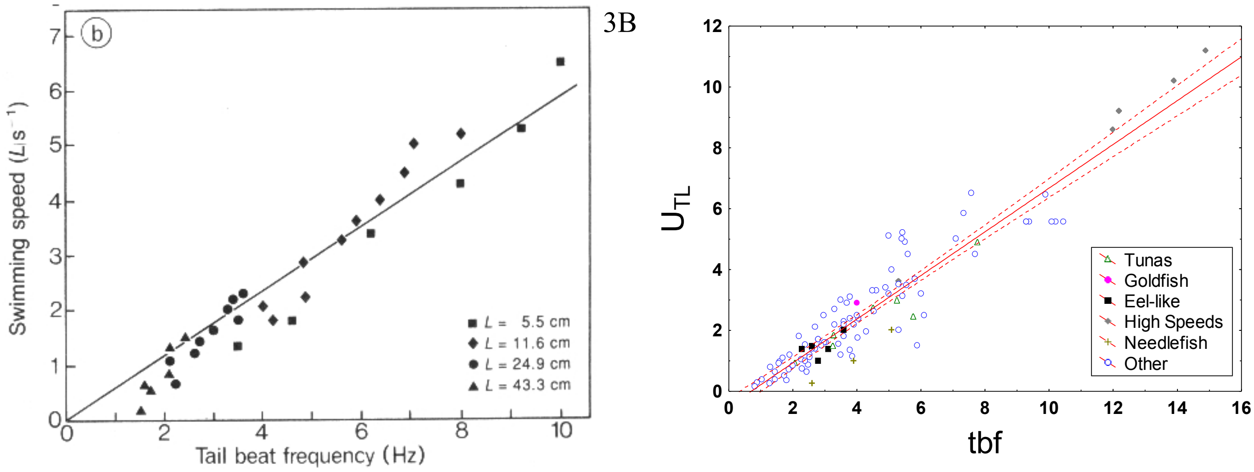
Table 6. Linear correlations of Tail Beat Frequency against the other variables. (TBF on the Y-axis)

TBF against	**Leng**	**SPEED**			**TBA**		**LAMBDA**		**V**		**STRIDE**		**SLIP**	**Strou**	**RE**
		U_{TL}	U_{cm}		$2A_{TL}$	$2A_{cm}$	λ_{TL}	λ_{cm}	V_{TL}	V_{cm}	d_{TL}	d_{cm}		St	Re
Total	-0.46	**0.97**	*-0.11*		0.70	-0.43	0.31	-0.39	**0.99**	*-0.13*	*-0.00*	-0.37	-0.27	0.39	*-0.17*
tbf **Tot**															
Select	-0.68	**0.90**	*0.13*		0.28	-0.54	*-0.03*	-0.56	**0.93**	*-0.00*	*0.22*	-0.41	*0.37*	*-0.19*	*-0.18*
tbf Sel															

The correlation given in Videler (1993) is linear: $\mathbf{U = 0.71 * f}$; $R^2 = 0.59$ (Figure 3A). Because of the inclusion of the fast fish in this graph we made a comparable selection: a selection with the fast fish, but without larvae or axolotls, to get a selection that is most similar to the data set used by Videler.

The correlation found for this adapted selection: $\mathbf{U_{TL} = -0.50 + 0.72 * f}$; $R^2 = 0.89$ (Figure 3B).

When both Length and tail-beat frequency are used as independent variables with speed as dependent: the plane is: $\mathbf{U_{TL} = -1.24 + 0.77 * f + 0.017 * TL}$, with a $R^2 = 0.90$ (Figure 3C). Length seems not to be needed here.



3C

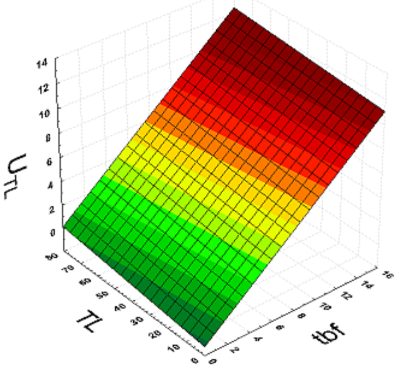
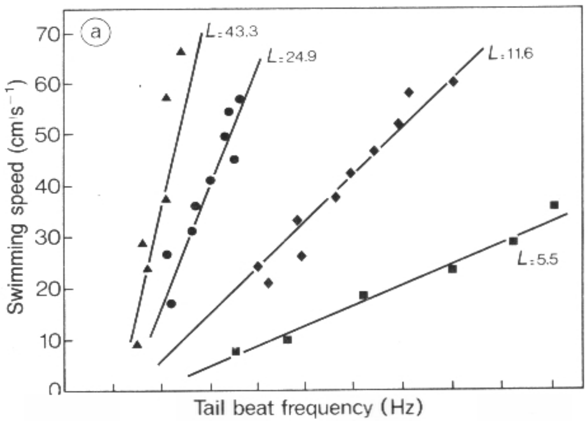


Figure 3:
3A: figure 6.1a from Videler 1993 (pg.119).
3B: TBF against normalized Speeds (with high speeds, but without larvae or axolotls),
$\mathbf{U_{TL} = (-0.504 \pm 0.135) + (0.718 \pm 0.256) * f}$ $R^2 = 0.89$
3C: Speed dependent on both TBF and Total Length.
$\mathbf{U_{TL} = (-1.241 \pm 0.237) + (0.767 \pm 0.027) * f + (0.017 \pm 0.005) * TL}$
$R^2 = 0.90$

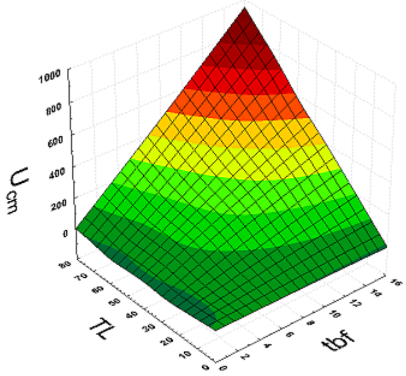
For the absolute measurements Videler (1993, figure 6.1b, citing Webb et al. 1984) shows the same correlation of tail beat frequency to Speed, separately for different lengths (Figure 4A). The 3D-graphic (distance weighed least squares, Figure 4B) corresponds very nicely to Videler's graph: the relation of U_{cm} to f is not the same at different Lengths. For *bigger fish the slope is steeper (more effect of a single tail-beat),* see the section on stride length.

The relation in a linear multiple regression is: $\mathbf{Speed_{cm} = (-107.6\pm13.6) + (21.05\pm1.58) * tbf + (2.75\pm0.27) * Length}$; $R^2 = 0.66$, showing that less of the variance is explained by this linear model compared to the 2D linear correlation of figure 3B where R^2 was 0.89. The scatterplot of tbf-U_{cm}, (figure 4C), still for the adapted selection, with fast swimmers without larvae or axolotls, also shows that something else is needed for explaining variance: without Length the $R^2 = 0.02$ (very similar to the number in Table 6 with r = 0.13 and R^2 therefore also 0.02)

4A



4B



4C

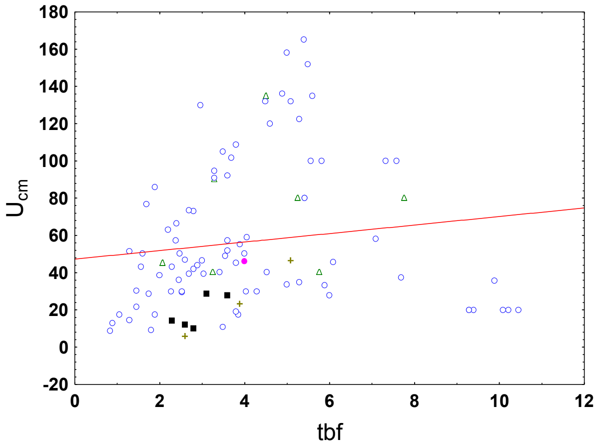


Figure 4:
4A: figure 6.1b from Videler 1993 (pg.119).
4B: Speed dependent on both TBF and Total Length.
4C: TBF against normalized Speeds $R^2 = 0.02$, showing that without Length as a factor TBF is not a good explanation for Speed
(4B, 4C:with high speeds, but without larvae or axolotls)

Our conclusion is*: tbf and speed$_{TL}$ are strongly correlated like in all papers mentioned, and when using absolute measurements, tbf and speed$_{cm}$ are correlated within length classes, as shown by Videler (1993).*

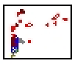
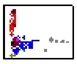
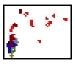
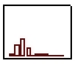
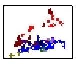
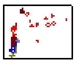
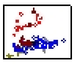
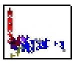
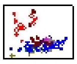
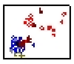
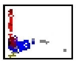
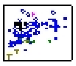
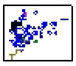
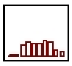
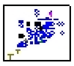
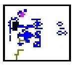
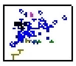
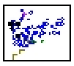
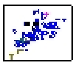
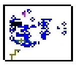
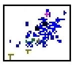
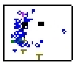
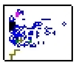
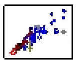
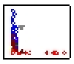
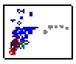
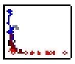
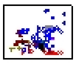
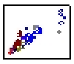
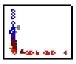
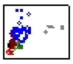
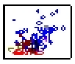
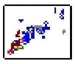
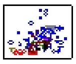
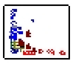
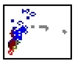
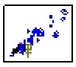
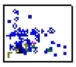
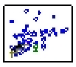
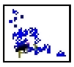
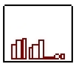
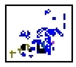
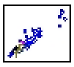
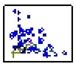
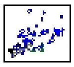
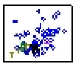
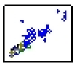
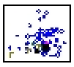
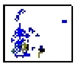
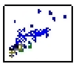
Tail-beat amplitude

When speed is increased by a higher tail-beat frequency, what does the tail-beat amplitude do?

It depends on which selection is made: In a multiple regression for the Total group for the normalized measurements only frequency is significant as a factor for speed ($R^2 = 0.94$), but for the absolute measurements only the amplitude is significant ($R^2 = 0.33$). *So with the extremes of frequency from the larvae included this factor is much more important, where in the absolute measurements for all frequencies the speed increases with an absolute larger amplitude.*

For the Selection without extremes in both representations frequency+amplitude+intercept are significant $R^2 = 0.88$ (Figure 5A) and $R^2 = 0.54$ (Figure 5B). The shape of the equation is $\mathbf{U = - a + b * f + c * 2A}$. So in the selection *the speed is increased by both the frequency and the amplitude of the tail beat.*

Table 6. Linear correlations of Tail Beat Amplitude against the other variables. (2A on the Y-axis)

TBA against	**Leng**	**Speed**		**TBF**		**LAMBDA**		**V**		**Stride**		**Slip**	**Strou**	**RE**
	TL	U_{TL}	U_{cm}	f		λ_{TL}	λ_{cm}	V_{TL}	V_{cm}	d_{TL}	d_{cm}		St	Re
$2A_{TL}$ Tot	-0.57	0.65	*-0.16*	0.70		0.30	-0.47	0.70	-0.20	*-0.01*	-0.39	-0.31	0.74	-0.22
$2A_{TL}$ Sel	-0.24	0.53	0.37	0.28		0.51	*-0.03*	0.45	0.23	0.65	*0.18*	0.55	*0.02*	*0.14*
$2A_{TL}$ **Tot**														
$2A_{TL}$ **Sel**														
$2A_{cm}$ Tot	**0.89**	-0.34	0.57	-0.43		0.26	**0.93**	-0.40	0.60	0.48	0.91	0.43	-0.48	0.66
$2A_{cm}$ Sel	**0.87**	-0.26	0.57	-0.54		0.42	**0.95**	-0.36	0.64	0.41	**0.91**	*0.13*	*-0.08*	**0.83**
$2A_{cm}$ **Tot**														
$2A_{cm}$ **Sel**														

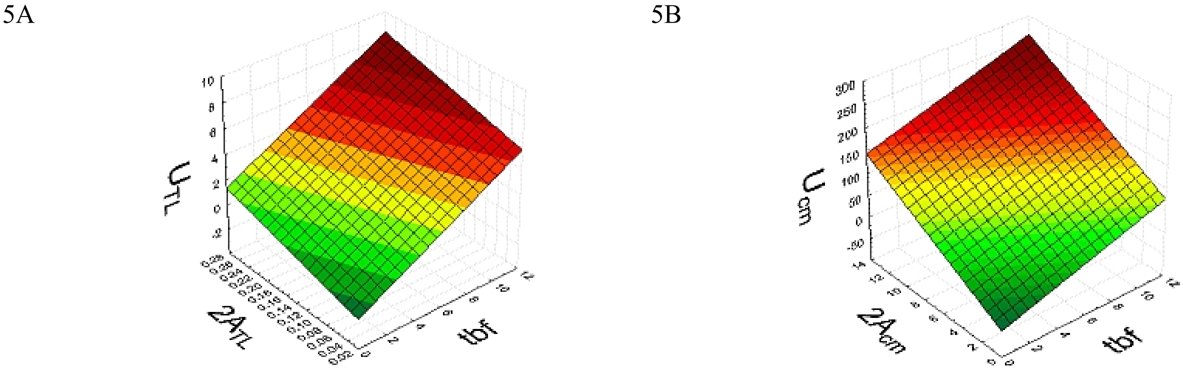


Figure 5. Selection*:*
5A: Normalized Speed dependent on TBF and normalized tail-beat amplitude, $R^2 = 0.88$.
$U_{TL} = (-1.87 \pm 0.25) + (0.59 \pm 0.03) * f + (11.39 \pm 1.50) * 2A_{TL}$
5B: Absolute Speed dependent on TBF and absolute tail-beat amplitude, $R^2 = 0.54$.
$U_{cm} = (-41.43 \pm 10.95) + (9.72 \pm 1.50) * f + (13.19 \pm 1.30) * 2A_{cm}$

When considering both length and speed: the speed as dependent on both tail-beat amplitude and length has the shape **a + b* tba – c* TL** : the speed goes up when the amplitude goes up, but in larger fish the intercept is smaller: the relation of U to TL remains the same as the one found earlier when the amplitude was not considered (the larger fish did not swim as fast proportionally). Figure 6A gives the 3D-linear model for U_{TL} dependent on $2A_{TL}$ and TL (**$U = 1.02 + 16.33 * 2A_{TL} - 0.04 * TL$**), the same regression as shown in Table 2, row 3.

(Total: normalised $R^2 = 0.42$, absolute: $R^2 = 0.36$; Selection: normalized: $R^2 = 0.43$, absolute: $R^2 = 0.44$)

The tail-beat amplitude is assumed to have a plateau (Hertel 1966, Liao 2002), as throwing the tail even wider would start meeting too much resistance and start slowing down. But in our data this plateau is not evident, which may be because the speeds at which the fish swim are not their maximum swimming speeds. In the Total group the maximum 2A is above 50, so maximum amplitude is above 25%.

In Figure 6B the correlation of speed and tail beat amplitude is depicted - here with U_{TL} as independent, to better show the (lack of) a real plateau. The linear fit is drawn, because other fits remain nearly linear, and do not explain more of the variance.

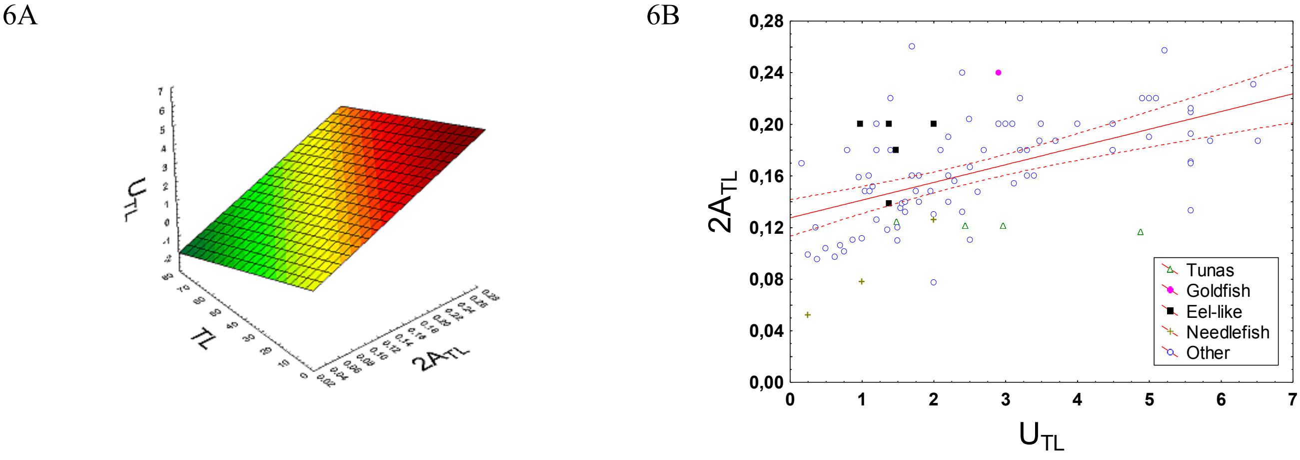


Figure 6

6A Total Length also considered (Selection): $U_{TL} = (1.02 \pm 0.63) + (16.33 \pm 3.19) * 2A_{TL} - (0.04 \pm 0.01) * TL$ $R^2 = 0.43$

6B Selection: Correlation between normalized Speed U_{TL} and Tail-beat amplitude $2A_{TL}$, $R^2 = 0.28$

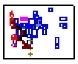
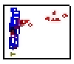
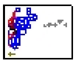
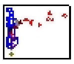
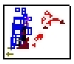
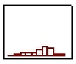
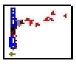
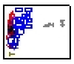
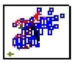
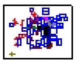
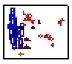
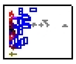
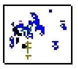
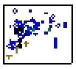
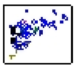
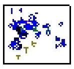
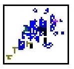
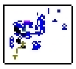
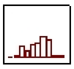
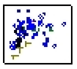
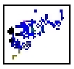
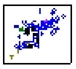
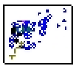
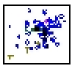
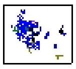
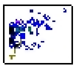
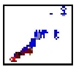
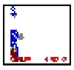
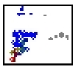
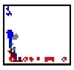
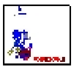
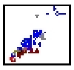
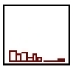
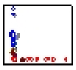
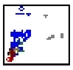
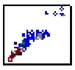
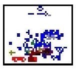
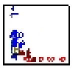
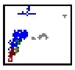
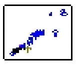
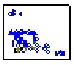
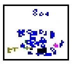
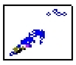
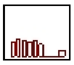
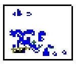
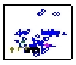
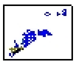
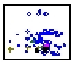
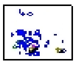
Body wave length, lambda

In the section about swimming speed the very strong correlation of speed with the propulsive wave speed was reported; in the normalized representation the tail-beat frequency plays a large role (see above). As body wave speed is a multiplication of wave frequency and wave length, the separate influence of the propulsive wave length is also interesting: does wave length change with speed or is it static?

We find that the wave is longer at higher speeds (Figure 7). The shape of the correlation is **$U = a + b * \lambda - c * TL$**, both for the different selections and for way of expression, showing that *speed is higher with a longer body wave length (normalized), but in larger fish at the same proportional wavelength the speed is lower.* But this is not a very strong effect; the amount of variance explained is less than one-third ($R^2 = 0.28$).

Looking for the Selection at the normalized linear correlations of length ($R^2=0.54^2=0.29$) or lambda ($R^{2=}0.25^2=0.06$) with swimming speed: they are in the same direction as in the 3D-multiple regression, but the explained variance of length is also near one-third and for lambda it is much smaller. For swimming speed therefore it seems that propulsive wave length is less important than length when only these two factors are considered, which is in line with the idea that lambda is species-specific and (in this data set) not correlated to length.

Table 7. Linear correlations of Propulsive wave length against the other variables. (l on the Y-axis)

<u>Lambda</u>	Leng	Speed		TBF	TBA			V		Stride		Slip	Strou	RE
Y-axis	TL	U_{TL}	U_{cm}	f	$2A_{TL}$	$2A_{cm}$		V_{TL}	V_{cm}	d_{TL}	d_{cm}		St	Re
λ_{TL} Tot	*0.06*	0.36	0.38	0.31	0.30	0.26		0.35	0.39	0.59	0.40	*0.17*	*-0.14*	0.30
λ_{TL} Sel	*0.08*	0.25	0.61	*-0.03*	0.51	0.42		0.29	0.65	0.59	0.52	0.22	-0.41	0.44
λ_{TL} Tot														
λ_{TL} Sel														
λ_{cm} Tot	**0.94**	-0.31	0.54	-0.39	-0.47	0.93		-0.36	0.57	0.47	**0.95**	0.31	-0.54	0.71
λ_{cm} Sel	**0.91**	-0.33	0.54	-0.56	*-0.03*	**0.95**		-0.41	0.62	0.34	**0.93**	*-0.02*	-0.33	**0.85**
λ_{cm} Tot														
λ_{cm} Sel														

As was concluded earlier in the section on Length, the positive relation between length and lambda reported for separate species and lengths disappears when the many lines per species are gathered in the same plot.

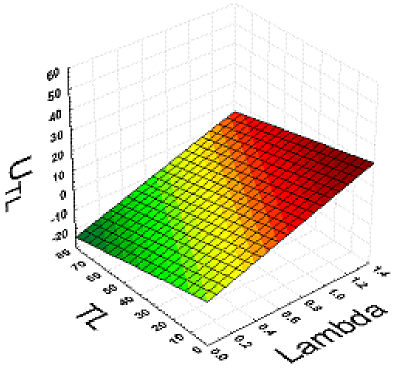


Figure 7

$$U_{TL} = (1.43 \pm 0.81) + (3.04 \pm 0.91) * \lambda_{TL} - (0.05 \pm 0.01) * TL$$

$R^2 = 0.28$

The data of Horner and Jayne (2008) with Protopterus annectens (lungfish) swimming in fluids with different viscosities show that with higher viscosity the wave length goes down and the frequency goes up while speed does not go down. (Only the control condition is present in our dataset). The parallel of the same efffects in smaller fish is interesting: *smaller fish = higher relative viscous force*. This leads us to the multiplier of these two factors: propulsive wave speed.

Body wave speed

This factor gives the strongest correlation with swimming speed, both for the Total group and for the Selection without extremes, and both for the normalized and the absolute measures. For the normalized measures the relation can quickly be seen as explained by the freqency component, but this does not hold for the absolute measurements; here it is the Reynolds number that has the next-highest correlation (see Table 8).

The equations have the shape $U = -a + b * V$; it has an Y-intercept, which has an effect on the slip (see later).

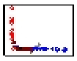
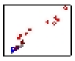
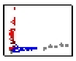
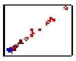
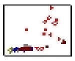
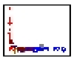
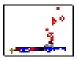
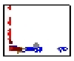
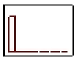
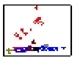
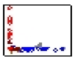
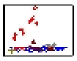
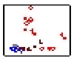
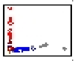
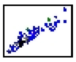
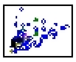
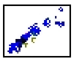
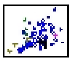
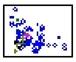
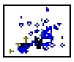
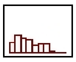
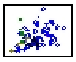
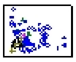
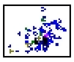
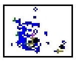
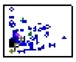
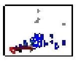
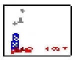
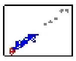
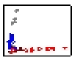
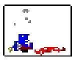
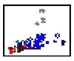
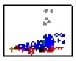
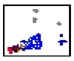
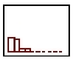
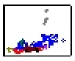
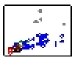
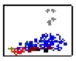
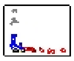
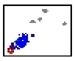
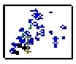
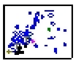
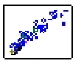
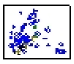
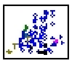
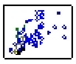
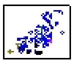
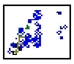
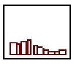
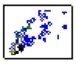
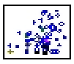
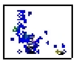
Keeping in mind that the swimming speeds are selected on the regularity of the tail-beats together with some insight that it was a speed that could be maintained for a longer period, the correlation is of course expected (since it is this wave that exerts the driving force). What was not expected was that all the measurements, whether Total group or Selection, and whether absolute or normalized, would lie along one narrow band. Of course small fish can not achieve the extremely high absolute speeds, but both very small and very large fish, and even the axolotls with their legs, all end up in the same band in the relation of swimming speed with body wave speed.

The skin, width of body, body depth, height of the tailfin, and swimming type (how much of the body is actually used in propulsion generation), vary between the different species considered. They make achieving a certain body wave length and tail-beat frequency possible, but clearly (since $R^2 = 89\%$ or higher) hardly modify the effect of the product of these two factors. This means that *morphological factors do not modify the effect (effectiveness) of the body wave speed on the swimming speed, but determine what tail-beat frequency and/or body wave length is reached.*

Under the assumption that swimming speed is determined by V (= $\lambda * f$) agile fish with a short body wave length must have a higher tail-beat frequency to swim at the same speed as a stiffer fish. The result might be that the actual speed that can be reached will be less. What it costs to achieve this is another story.

In Figure 8 columns of graphs for tail beat frequency, propulsive wave length and the result of their multiplication, propulsive wave speed, are given, just to show that the shape of the graphs resulting from this multiplication is not obvious from the original graphs.

Table 8. Linear correlations of Propulsive wave speed against the other variables. (l on the Y-axis)

V against	**Leng**	**Speed**		**TBF**	**TBA**		**LAMBDA**			**Stride**		**Slip**	**Strou**	**RE**
	TL	U_{TL}	U_{cm}	f	$2A_{TL}$	$2A_{cm}$	λ_{TL}	λ_{cm}		d_{TL}	d_{cm}		St	Re
V_{TL} Tot	-0.43	**0.97**	*-0.11*	**0.99**	0.70	-0.40	0.35	-0.36		*0.01*	-0.34	-0.27	0.37	*-0.16*
V_{TL} Sel	-0.59	**0.94**	0.30	**0.93**	0.45	-0.36	0.29	-0.41		0.34	-0.24	0.40	-0.26	*-0.09*
V_{TL} **Tot**														
V_{TL} **Sel**														
V_{cm} Tot	0.47	*-0.03*	**0.99**	*-0.13*	-0.20	0.60	0.39	0.57		0.52	0.65	0.41	-0.41	**0.90**
V_{cm} Sel	0.43	0.27	**0.95**	*0.00*	0.23	0.64	0.65	0.62		0.56	0.74	0.26	-0.54	**0.84**
V_{cm} **Tot**														
V_{cm} **Sel**														

Equations for the regression V - U:

Total normalized $U_{TL} = (0.523 \pm 0.232) + (0.490 \pm 0.011) * V_{TL}$ $R^2 = 0.93$

Selection normalized $U_{TL} = (-0.391 \pm 0.128) + (0.798 \pm 0.031) * V_{TL}$ $R^2 = 0.89$

Total absolute $U_{cm} = (-7.862 \pm 1.407) + (0.787 \pm 1.407) * V_{cm}$ $R^2 = 0.97$

Selection absolute $U_{cm} = (-9.328 \pm 2.810) + (0.801 \pm 0.029) * V_{cm}$ $R^2 = 0.90$

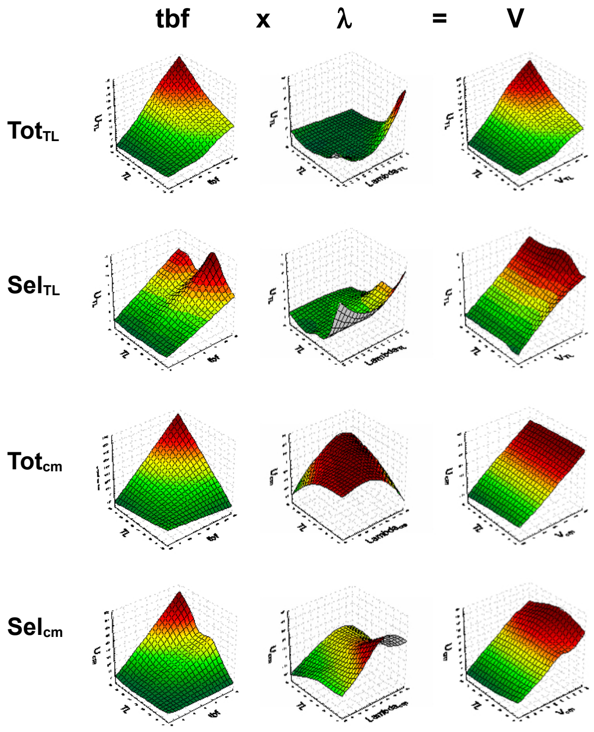


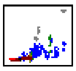
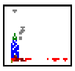
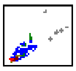
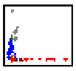
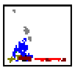
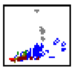
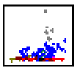
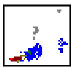
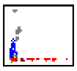
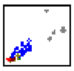
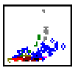
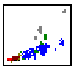
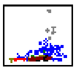
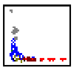
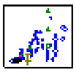
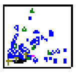
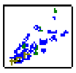
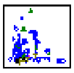
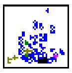
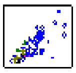
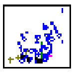
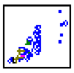
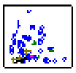
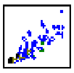
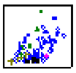
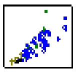
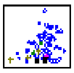
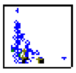
Figure 8: Constituent elements of wave speed and resultant
(fits are distance weighted least squares)
Columns: 1) tailbeat frequency and length against speed
2) wave length and length against speed
3) wave speed and length against speed
Rows: 1) Total group, normalized measurements
2) Selection, normalized measurements
3) Total group, absolute measurements
4) Seection, absolute measurements

Results on other aspects

Reynolds number

Linear correlation coefficients are presented again in red for significant correlations (p-level of 0.05), and bold for correlations stronger that r = 0.80. In the little plots the vertical axis representing Re is linear. For a view of Re on the X-axis see the column in the matrix plots in the appendix (Figure A-1 and A-2)

Table 9. Linear correlations of Reynolds number against the other variables. (Re on the Y-axis)

Re against	Leng	SPEED		TBF	TBA		LAMBDA		V		STRIDE		Slip	Strou
	TL	U_{TL}	U_{cm}	f	$2A_{TL}$	$2A_{cm}$	λ_{TL}	λ_{cm}	V_{TL}	V_{cm}	d_{TL}	d_{cm}		St
Total	0.61	*-0.08*	**0.89**	*-0.17*	-0.22	0.66	0.30	0.71	*-0.16*	**0.90**	0.49	0.78	0.39	-0.37
Total														
Select	0.66	*0.05*	**0.83**	*-0.18*	*0.14*	***0.83***	0.44	**0.85**	*-0.09*	**0.84**	0.50	**0.88**	0.28	-0.43
Select														

The Reynolds number (U * L / ν) is dimensionless, but the constituents Length and Speed are in centimetres, meaning Re scales with absolute units, so maybe it would make more sense only to present the absolute aspects of the other kinematic variables.

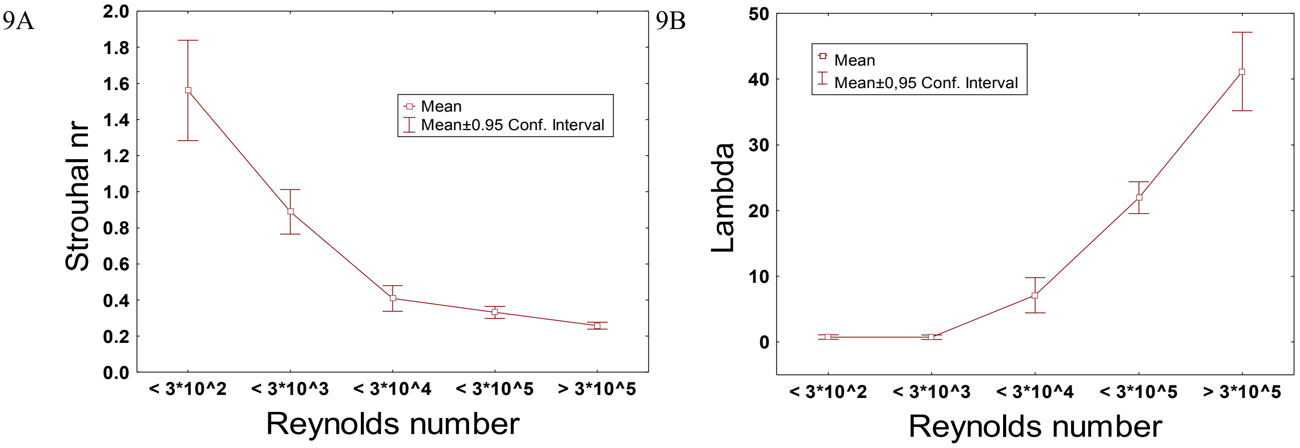
For a better view on the effects of a certain Reynolds number they were classified as 10-fold multiples of 300: Re<3 * 10^2, <3 * 10^3, <3 * 10^4, <3 * 10^5, and >3 * 10^5. The minimum value was Re = 89 for a herring larva swimming at 1.34 cm/s (Fuiman and Batty, 1997) and Re = 1501000 for the biggest salmon swimming at 237 cm/s (Videler, 1993) The number of data points in these categories can be found in Table 10.

This categorization makes plotting possible logarithmic relations between Reynolds numbers and other variables in Means-and-error plots easier. When these logarithmic scales are used Re and length, tail-beat amplitude, wave length, wave speed and stride length have positive linear correlations (Figure 9B), whereas tail-beat frequency (table 9) and, especially, Strouhal number are negatively correlated (Figure 9A).

Table 10. Reynolds categories with number of data points, with statistics for the Strouhal number

Re categories	N	Strouhal - Means	Strouhal - Std.Dev.
1: <3 * 10^2	8	1.561	0.332
2: ≥3* 10^2, <3 * 10^3	11	0.889	0.184
3: ≥3* 10^3, <3 * 10^4	18	0.408	0.143
4: ≥3* 10^4, <3 * 10^5	70	0.331	0.138
5: ≥3 * 10^5	21	0.258	0.042
total	**128**	**0.455**	**0.361**

Figure 9: Means-and-error plots for Strouhal number and Wave length (in cm) per Reynolds number categories

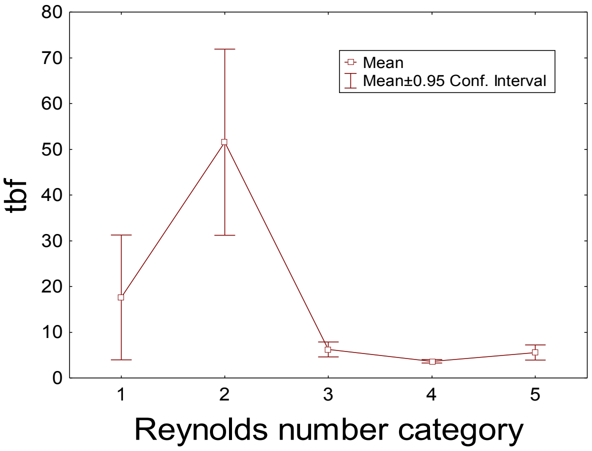


The Strouhal number (St = 2 f A / U) is inversely correlated to Reynolds numbers, and only category 3 and 4 do not differ significantly. The translation is that *at low Reynolds number you have to flap your tail a lot more to reach the same speed than at high Reynolds number*, as was mentioned earlier (lambda).

The plots for $2A_{cm}$, λ_{cm}, V_{cm}, and d_{cm} have the same general shape as the plot relating the category for Reynolds number to Length

For the Selection the mean tail-beat frequency for Re category 2 (between 3 000 and 30 000) is higher than for the Re > 30 000 (Figure 10). On first sight this looked anomalous, but since for tail-beat frequency the picture is similar to the picture for normalized speed and normalized propulsive wave speed (figures not given), and the test speeds showed the same pattern, this anomaly was due to the experimental circumstances.

Figure 10: Means-and-error plots for tail beat frequency per Reynolds number categories for the Total group

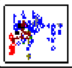
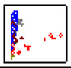
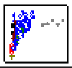
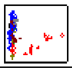
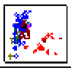
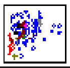
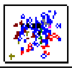
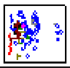
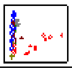
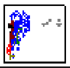
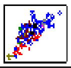
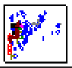
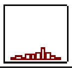
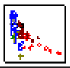
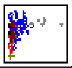
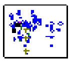
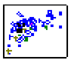
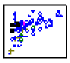
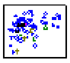
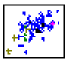
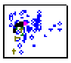
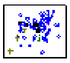
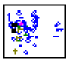
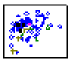
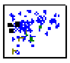
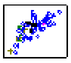
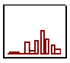
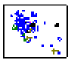
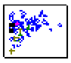


Slip

Slip is the ratio between U and V. When the regression formula derived earlier for U_{cm} depending on V_{cm} (for the Selection) is taken: $U_{cm} = -9.33+0.80*V_{cm}$, and Slip (U/V) is plotted as a ratio curve with again V as independent variable ($U/V = -9.33/V+0.80$), one gets a curve that stabilizes on a constant in the higher regions, but at the slowest body wave speeds or swimming speeds there is a lower slip, which is (mathematically) caused by the intercept.

This fits with the idea that the smallest fish are more affected by the viscosity and have to overcome this by other means than the inertia of their mass.

Table 11. Linear correlations of Slip against the other variables. (Slip on the Y-axis)

Slip against	**TL**	**SPEED**		**TBF**	**TBA**		**LAMBDA**		**V**		**STRIDE**			**Strou**	**RE**
		U_{TL}	U_{cm}	f	$2A_{TL}$	$2A_{cm}$	λ_{TL}	λ_{cm}	V_{TL}	V_{cm}	d_{TL}	d_{cm}		St	Re
Total	0.27	*-0.12*	0.49	-0.27	-0.31	0.43	*0.17*	0.31	-0.27	0.41	0.75	0.50	-	-0.67	0.39
Select	*-0.13*	0.61	0.48	0.37	0.55	*0.13*	0.22	*-0.02*	-0.40	0.26	0.73	0.28	-	-0.53	0.28
Total															
Select															

This also shows in the shape of the correlation with Reynolds number (figure 11): a low slip only occurs when the Reynolds number is low. One has to keep in mind that the water is not disturbed and therefore in these cases the water velocity can be equalled to the swimming velocity. Slip as an expression for effort is only very limited here, in the sense that when body wave velocity goes up the speed goes up too; apart from the start where the intercept term plays a role, this ratio is constant. At lower Reynolds number the slip is lower and the relation between U and V has an intercept. This could be connected to the statement that a lower slip means higher effort: as the conversion of V into U is lower, a lower slip could be considered as less propellor efficiency or more effort.

But nothing is implied here about the energy this costs. The low slip values occur in small fish, but is small fish also the surface area is smaller than that of larger fish; one would need to know how effort scales with surface area, and the effort may not be bigger at all. This last point makes the words "effort" or "propulsive efficiency" imprecise; the only thing left is *that low slip only occurs at low Reynolds number, and that for bigger or faster fish the slip is constant (meaning the ratio U/V is constant)*(figure 11).

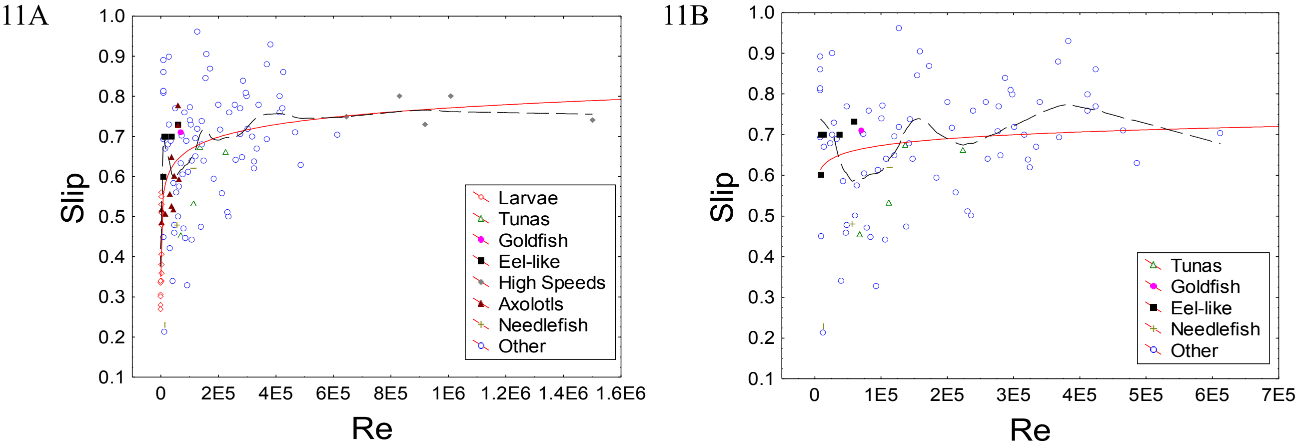
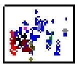
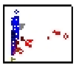
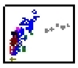
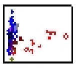
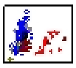
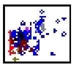
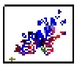
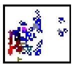
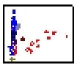
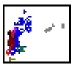
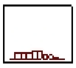
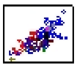
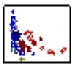
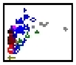
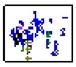
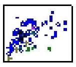
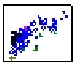
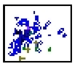
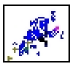
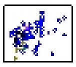
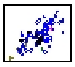
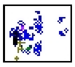
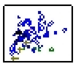
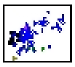
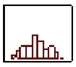
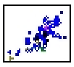
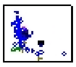
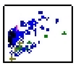
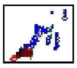
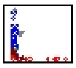
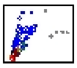
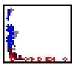
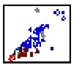
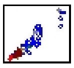
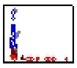
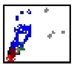
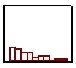
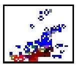
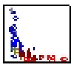
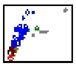
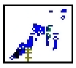
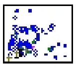
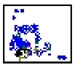
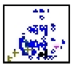
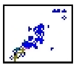
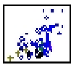
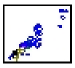
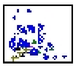
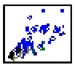
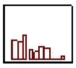
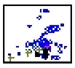
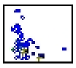
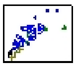


Figure 11: Slip per Reynolds number for the Total group (10A) and for the Selection (10B) with lowest Re = 8399, with logarithmic fit (red), and with a Lowess fit (black).

Stride length

Stride length as defined by U/f: this represents a speed measure normalized to tail beat. It is associated with ideas of the efficiency of the tail beat: a larger distance travelled in one beat is called more efficient.

Table 12. Linear correlations of Stride length against the other variables. (d on the Y-axis)

Stride	**Leng**	**Speed**		**TBF**	**TBA**		**LAMBDA**		**V**			**Slip**	**Strou**	**RE**
against	TL	U_{TL}	U_{cm}	f	$2A_{TL}$	$2A_{cm}$	λ_{TL}	λ_{cm}	V_{TL}	V_{cm}			St	Re
d_{TL} Total	0.22	*0.13*	0.60	*-0.00*	*-0.01*	0.48	0.59	0.47	*0.01*	0.52		0.75	-0.51	0.49
d_{TL} Sel	*0.01*	0.52	0.72	0.22	0.65	0.41	0.59	0.34	0.34	0.56		0.73	-0.53	0.50
d_{TL} Tot														
d_{TL} Sel														
d_{cm} Total	**0.84**	-0.28	0.64	-0.37	-0.39	**0.91**	0.40	**0.95**	-0.34	0.65		0.50	-0.55	0.78
d_{cm} Sel	0.77	*-0.12*	0.72	-0.41	*0.18*	**0.91**	0.52	**0.93**	-0.24	0.74		0.28	-0.42	0.88
d_{cm}Tot														
d_{cm} Sel														

The absolute is rather predictable: for the Total group the strongest relation is with Length, $2A_{cm}$, and λ_{cm}, and in the Selection with $2A_{cm}$, and λ_{cm} This tells that bigger fish have a larger wave length and larger amplitude and get farther with one tail beat.

Representing this measure in a normalized way (in Lengths): this property seems more interesting, because it is <u>not</u> correlated with U_{TL}, f, $2A_{TL}$ and V_{TL}, only with λ_{TL} and TL. Stride length and body wave length are positively correlated, which can be reformulated as: a longer wavelength therefore a longer stride length: *with a longer lever more force can be exerted in one stroke*.

If the force of a tail beat would not vary with speed one would expect the stride length to stay constant and the frequency to increase. In the Total group it is hard to see whether this reasoning holds because of the high frequency of tail beats in small fish. In the Selection higher tailbeat frequency and longer stride length are both associated with a higher speed (both absolute and normalized). *The force of the tail beat therefore does increase when swimming faster, one tail beat has more effect.*

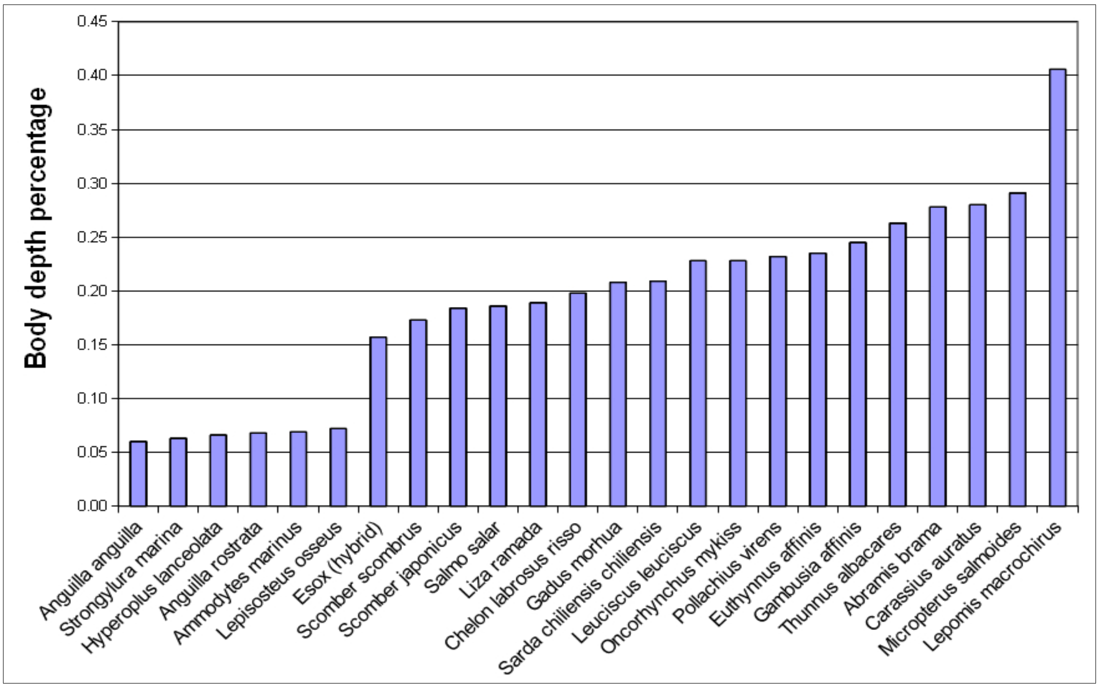
The most important aspect of stride length seems to be the connection to speed: it is often used to deduce the swimming speed. Stride length, together with Strouhal number, is used for a description of the wake of the fish, describing the distance between the vortices in the wake (Müller et al., 1997).

That Stride length and Strouhal number are related shows in the correlation: Stride length (U / f) is negatively correlated with the Strouhal number (St = (2A * f) / U), which is mathematically unavoidable, since the Strouhal number is defined as the inverse of the stride length, times the width of the sideways motion. Amplitude does not change the shape of the relation: it has a significant positive correlation with speed.

Stride length and slip have a positive correlation both in the Total group as in the Selection, stronger for the normalized stride length.

Body Depth

Dividing the fish according to their body depth: this is a bimodal distribution, with the narrow species of fish having a body depth of less than 8% of their total length, and nearly all other above 17% up to 30%. In between these two is only the pike Esox, with a depth of 16%, and highest is the Lepomis with 40%.



A division in the largest group was made: a Body depth of 15-20%, to 22% and to 24%. A matrix plot can be found in the appendix (Figure A-3 in the appendix). It is clear from these plots that the Body Depth factor does not have a specific effect (linear or multiplicative) on the relations between the pairs of variables.

It might be that the effect is only in the bi-modality: the group with a very narrow body was compared to the others. Because of a difference in speeds this was limited to 1-3 TL/s. The narrow-bodied group does not differ in size, tail beat frequency and tail beat amplitude (both absolute and normalized), slip and Reynolds number from the 17-30% group, but does differ on speed, propulsive body wave length and -speed and Strouhal number (t-test). (Table 13*)*

It appears that the eel-types do not swim as fast or are not made to swim as fast as the others: this distinction can not be made in this setup, so it is hard to draw firm conclusions based on the findings with this data set.

One is tempted from this data to equate a narrow body with the anguilliform swimming type, but whether this always is accurate can not be stated without checking the amplitude envelope of the propulsive wave.

Swimming type

It would have been interesting to check on this classification, but in the literature the difference between sub-carangiform and carangiform is not clear, and often not subdivided. In 16 papers profiles, amplitude envelopes, are given. These show that this classification is not clear-cut: most fish move their head somewhat (yaw), have a point of minimal movement behind the head and have an increasing amplitude towards the tail. Only the profile of the pike looks different in that the point of least sideways movement is the tip of its nose. The profiles given hardly include any of the narrow-bodied species.

Whether fish with a smaller vertical dimension used more of their body in the body wave movement can not be tested in the data set presented in this report. The eel-like fish do not stand out specifically in the different sub-plots in the matrix plot in figure A-3 in the appendix, where for the Selection the body depth percentage is marked in 5 subsets. The question "does body depth have an influence on the kinematics?" is therefore alas not answerable in this meta-analysis. The effectiveness of one tail beat in narrow-bodied or wider-bodied fish also is too dependent on speed to show other differences.

The answer therefore to the question posed in the introduction ("are body shape / swimming style essential elements in kinematic relations") can not be answered.

Table 13: Selection without extremes and additionally on swimming speeds from 1 to 3 TL:
t-test of differences between groups divided on body depth:
Group 1: narrow, BD 6-8%, Group 2: deeper, BD 17-30%

Variable	**Mean**		**t-value**	**df**	**p**	**Valid N**		**Std Dev.**	
Group	***narrow***	***deeper***				***narrow***	***deeper***	***narrow***	***deeper***
length (TL)	21.17	29.8	-1.908	41	0.063	11	32	9.32	13.9
speed in TL (U_{TL})	1.56	2.0	-2.166	41	0.036	11	32	0.27	0.6
speed in cm (Ucm)	33.47	56.7	-2.713	41	0.010	11	32	15.55	26.8
tbf (f)	3.18	3.4	-0.716	41	0.478	11	32	0.77	0.9
2tba in TL	0.17	0.2	0.747	41	0.459	11	32	0.03	0.0
2tba cm	3.46	4.7	-1.536	41	0.132	11	32	1.67	2.5
lambda in TL	0.76	0.9	-4.724	41	0.000	11	32	0.08	0.1
lambda in cm	16.06	27.6	-2.511	41	0.016	11	32	7.67	14.5
wave speed in TL	2.44	3.1	-2.431	41	0.020	11	32	0.44	0.9
wave speed in cm	51.31	86.1	-3.419	41	0.001	11	32	22.98	30.8
stride-length in TL	0.50	0.6	-1.789	41	0.081	11	32	0.07	0.2
stride-length in cm	10.64	18.6	-2.273	41	0.028	11	32	5.02	11.1
Slip U/V	0.65	0.7	-0.509	41	0.613	11	32	0.08	0.1
Strouhal= f2A/U	0.34	0.3	2.974	41	0.005	11	32	0.09	0.1
Reynolds number	80483.3	166595.3	-1.947	41	0.058	11	32	55325.2	142119.3

Discussion

It was surprisingly hard to find papers that reported enough kinematic variables for our purposes. This lack was often due to the different aim of the paper, such as finding the maximum speed of species or measuring oxygen consumption, but also because sometimes only the results of statistical tests were presented and no raw data.

Many of the papers were unclear or incorrectly confident as regards the causal direction of the correlations they measured. This is reflected in phrasing such as: "..propulsive wavelength increased significantly with temperature as a result of an increase in propulsive wave velocity." (Dickson et al. 2002) and ".. The ratio of swimming speed to wavespeed, ranges from 0.6 to 0.9, indicating that the speed of the wave rearward is always greater than the speed of the fish forward. This variable is the most likely determinant of increased stride length as velocity increases." (Rosenberger and Westneat, 1999)

In the first quote wave speed and tail beat frequency are directly related ($V=f*\lambda$), so there is no clear causal direction. As for the second quote: slip is mentioned (U/V), and stride length is U/f , so to call wave speed (or slip?) a cause for a change in stride length seems indirect.

Species-specificity of course is an aspect of this whole review that needs careful consideration. Of some species, data points only represent one individual, while others are means of several individuals. Several causes of variability are unavoidable: errors in measuring the variables, variability within a species, individual size, age, and history, and the behaviour of that individual. All these sources of variability occur and are not really controlled for. But some care was taken to get as much variation as possible, in species and in sizes. The number of species was in the end 26 (29 if individuals with some missing data were included), and the range in size and speeds was wide. In the total group no species accounts for more than 10% of the data; in the Selection without extremes (no larvae, very fast swimmers, or axolotls) the most-frequent species provided 12% of the data points.

It may be argued that in putting so many species together it would be necessary to consider species a separate factor, but these percentages show that numbers would generally become too small. Further, species-specific information is already the subject of the original papers.

Some general conclusions:

Length and speed: In absolute measures speed goes up with length, but not so much that the normalized speed stays the same; it goes down in larger fish, which most likely is the result of the experimental settings: measuring in flow tanks where the water speed is regulated by pumps the lower speeds are technically easier. The fact that not all variables lost their correlation to length after being normalized for this factor showed that the effect of normalization should always be checked, whenever possible and relevant.

Tail beat frequency and swimming speed: this is the relation most reported, and in this data set it is again confirmed: as fish beat their tail faster, their (normalized) speed increases. In absolute measurements this still holds, but only within length classes. Quoting Altringham and Ellerby (1999): "Increases in swimming speed are due primarily to increases in tailbeat frequency. This means that data obtained at different swimming speeds can often be compared by normalising them to tailbeat period (e.g. Wardle and Videler, 1993)." the strong correlation of tail beat frequency and speed is present for normalized speeds, but in the absolute numbers this correlation is dependent on the length-classes, so this may be the clearest case of apropriateness of normalization for kinematic variables.

For tail beat amplitude apparently there was no plateau (Figure 6B). This may be because the fish swam at a speed they could keep up for a longer time, and not at their maximum speed. It may be that at speeds near this maximum the plateau would have been reached.

Fish that swim faster not only beat their tail faster, but also further to the side (in the Selection, both normalized $R^2 = 0.54$ and absolute, $R^2 = 0.88$)

Propulsive wave length turns out to be the variable that is most species-dependent: if the relation of λ versus length is different for each species, one would expect our result of a graph without a significant correlation between these two factors. The lack of overall correlation could not be explained by speed (with the reasoning that the different-sized fish were swimming at different speeds): a regression of length, (normalized) speed and wave length shows that the amount of explained variance with or without the factor λ was similar (without: $R^2 = 0.29$ and with: $R^2 = 0.28$). This does not mean that wave length is not contributing to speed: speed and wave length did have a significant -positive- correlation.

Another aspect, namely whether there is variation in how much of the body is used in propulsion might have shown up in an analysis of the amplitude profiles, but this could not be executed due to a lack of data. This would be connected to the speculations on wave length and stiffness of the body. A longer wave length does not mean that a larger part of the body is involved in this movement, and it may well be a smaller part, as in figure 3 of Horner & Jayne (2008).

It would have been interesting if the mako sharks described by Donley et a. (2005) could have been included, they are larger (81-92 cm) and their propulsive wave length is relatively the longest ($\lambda_{TL} = 1.8\text{-}2.1$), but the swimming speed is described as 0.5-1.0L, which is not accurate enough.

Propulsive wave speed, in contrast to the wave length, did not show any species-specificity, not even for larvae. This variable comprises two others: tail beat frequency and propulsive wave length. However, the pattern of its behaviour is not directly obvious from the other two (Figure 8).

Quoting Gillis (1996) from his review paper "Undulatory Locomotion in Elongate Aquatic Vertebrates: Anguilliform Swimming since Sir James Gray", (referring to the influential series of articles of Gray (1933) describing kinematic variables of several species of fish): "Second, as Gray and others previous to him had described, the velocity of these traveling waves is faster than the velocity of the swimming animal. Again, however, the relative velocity of these waves **depends greatly upon swimming speed and taxon**."

The first dependency we would consider confirmed by this report although I would state it the other way round "the swimming speed depends greatly upon the relative velocity of these waves"; The second statement then reads as follows "taxons attain different relative velocities", but surprisingly, an influence of taxon upon the dependency between speed and velocity, is not found in this data set.

The strong correlation of swimming speed and propulsive wave speed with an explained variance of 89% (or higher depending on selection and the way of looking at the numbers) means that only 10% of the variance is left to be explained by factors like skin structure or the build of the fish (like width, depth, fins or appendages).

Of course, data for fish that had a slip of nearly 1 or higher were omitted: at a slip of 1 the wave speed is equal to the swimming speed and therefore no thrust is produced ("freewheeling", the fish will slow down), and at a slip above 1 the thrust is backwards. Our data set was selected on recordings of speeds that were as steady as possible from one tail beat to the next with thrust equaling drag (neither acceleration nor deceleration on average over a tail beat, only momentum), and could be kept up for a longer time, but the variation in speed still was quite large.

Statistical methods

When multiple regression can not be used there is an alternative method: Partial Least Squares (PLS). This analysis does not make assumptions about the relations between variables, but tries to find components or latent variables, that maximise the variance explained. PLS calculates 2 components, and gives a list of the independent variables that contribute to these components. This list is ordered according to importance in contribution to the variance explained.

For the absolute measurements the most important factor in the new latent variables is V. The complete ordered list is "Propulsive wave speed – Tail-beat amplitude – Propulsive wave length – Length – Tail-beat frequency", showing that propulsive wave speed is the most important explanatory variable. This is the same pattern as is shown in the strengths of the correlations with the dependent variable swimming speed. (see correlation matrix)

For the normalized measurements V together with f are the most important variables in the new latent variables and λ the least important. Here both propulsive wave speed and tail-beat frequency are most important.

These results agree with the conclusions drawn earlier from the separate correlations.

Viscosity and the dimensionless variables (Reynolds number, Strouhal number and Slip)

Three conclusions stand out on these aspects:

a) at low Reynolds number viscosity is relatively more important
b) Strouhal number is inversely correlated to Re for low Reynolds numbers
c) low Slip only occurs at low Reynolds number

Reynolds numbers are low when the length is small and/or the speed is low, and when kinematic viscosity is high. In this equation the influence of kinematic viscosity of the fluid is limited to a factor of 2 (for cold water of 3 °C compared to warm water of 30 °C), so most of the difference in Re comes from speed and size.

For low Reynolds numbers the Strouhal number is inversely correlated to Re, and at higher Re the relation is much more constant (Figure 9A). Strouhal and Reynolds numbers are both dimensionless.

What was shown in the relation of slip to Reynolds numbers (fig. 9A), was that for Reynolds numbers above about 1000 to 3000 the slip is close to constant *(meaning; the ratio U/V is constant)*. Below Re = 3000 the slip was lower (which could be already concluded from the regression equation of U and V (after Table 8), with an intercept # 0); for bigger or faster fish the slip is constant. Looking at these numbers the conclusion might be that the viscous forces are of diminishing importance up to a Reynolds number of 3000, where they become negligible.

The pattern for Strouhal and Slip is very similar, and it seems that a larger influence of viscosity is sufficient to explain the intercept in the relation of swimming speed to propulsive wave speed, and therefore the effects seen at low speeds and or lengths. Also for fish in a higher-viscosity medium the same effects (faster tail beat frequency and shorter wave length) were seen as for narrow-bodied fish or small fish.

The reason for a lower slip therefore could primarily be the influence of viscosity.

Body depth and swimming type

In the following section we test several examples of general statements made about the swimming of fish against our data.

At a similar tail beat frequency narrow-bodied fish have a somewhat shorter wave length and (therefore) a lower wave speed and (therefore) a slower swimming speed. The relation of wave speed to swimming speed itself seems not/hardly to be affected by this body depth. So to be stiffer increases the speed you swim at for all fish.

The idea that lives in the literature about swimming type is that in anguilliform swimming amplitude towards the tail increases linearly. This pattern is not found in the research of Gillis (1999) or Lauder (mentioned in the review papers of Lauder and Madden 2006, or Fish and Lauder 2006), – rather they find an exponential increase towards the tail.

Swimming types include anguilliform and (sub-)carangiform. Because of the problems of discriminating between sub-carangiform and carangiform - not all authors distinguish these two - there is one characteristic that can be used to at least distinguish between anguilliform and carangiform: body depth. This classification idea has been partially tested in this data set by inspecting what the effects of the body depth of the fish are. Body depth in this data set is indeed bimodal, but this may be a result of the choice of species for research.

The sideways movement of the tail beat of narrow-bodied fish should encounter less resistance (per cm), so this makes it possible and/or necessary to move the tail at higher frequency, but due to the concurrent shorter wavelength the resulting wave speed is the same as for deeper-bodied fish.

Lauder and Madden (2006, point 2.5) state: "Patterns of 2D body undulation are very similar among fishes": "Two-dimensional analyses of fish locomotion ....have shown that even fishes of very different body types such as eels, trout, mackerel, and tuna show extremely similar patterns of body movement when viewed in a horizontal section during steady undulatory locomotion..... All fish appear to move in a very similar undulatory manner ignoring the labels placed on them by biologists!"

We confirm their qualitative remarks with our findings on the relation of propulsive wave speed and swimming speed.

The point that Lauder and Madden made about the 3D-shape ("Fish vary greatly in 3D shape with important hydrodynamic consequences") on the other hand seems less strong, at least the kinematic consequences of shape on speed in this study of steady swimming. Care was taken to only choose papers on fish with a homocercal tail (with vertical symmetry), but even the axolotls do not become outliers in any of the plots discussed in this report.

Schrank et al. (1999): "It has been postulated that a deep body improves turning maneuvers by reducing both the angular resistance to turning (Alexander 1967) and slip (Webb 1997).... A deep body is thought to enhance yawing turning maneuverability by minimizing angular momentum and slip,"

Whereas nothing can be said about angular momentum, the remark about slip is a bit strange: lower slip, U/V, is not likely to be more efficient, even if it can be argued that it represents less effort. The narrow-bodied fish in this data set do seem to attain lower speeds with the same tail beat frequency and amplitude, and a shorter wave length and thus also a lower wave speed; the slip turns out to be similar.

So, no, I would consider this remark not to be of general applicability in steady swimming without turning.

Some remarks on the ideas of effort and efficiency

The low slip values occur in small fish, but this also means that the surface area is small, so the effort may not be larger at all. This last point makes the words "effort" or "propulsive efficiency" imprecise.

It is easy to imagine measures as approximation for swimming efficiency for efficiency, for instance stride length (distance covered in one tail beat: more distance = more efficiency *with a longer lever more force can be exerted in one stroke*), or effort (slip, ratio of U per V: lower slip = more effort). Consequences are drawn from these notions as in a quote from Syme et al. (2008) "it might be predicted that a long stride length would go hand in hand with economical swimming, high thrust power, and stable recruitment patterns"

But without extra information about size and speed of the fish, or other information about the actual metabolism these definitions remain only a description of general relations between kinematic variables.

To judge effort and efficiency one needs a criterium; this might be the maximum speed at which the individual or species can swim, or the oxygen consumption or whatever. A definition of Froude efficiency is "useful power / total power expended".

Because of the extraordinary difficulty of empirical power measurements, other ways to express this idea have been given: Webb (1984) and Videler and Hess (1984) give "eta = (U + V) / 2V" for steady swimming. This is the equation of Lighthill's (1960) elongated-body theory "µEBT = (1 + U/V) / 2". These expressions however suffer from the same lack of objective standard as the use of slip and stride length for effort/efficiency, so for this data set this has not been used.

Conclusion

- Species dependency: some relations are species-dependent, such as the relation between total body length and propulsive wave length (concluded from original papers and from the non-existent correlation in this data set).

- Species independency: some relations definitely are not species-dependent: propulsive wave speed to swimming speed. When a correlation is strong in both normalized terms and in absolute terms, then I would call it species-independent.

The strong relation between propulsive wave speed and swimming speed (within the size- and speed ranges of our data set) provides an excellent way to test whether the kinematic results of swimming-fish simulations and robotic fish models approach life-likeness.

References

Altringham, J.D. and D.J. Ellerby, Fish swimming: Patterns in muscle function. Journal of Experimental Biology, 1999. 202(23): p. 3397-3403.

D'Aout, K. and P. Aerts, Kinematics and efficiency of steady swimming in adult axolotls (Ambystoma mexicanum). Journal of Experimental Biology, 1997. 200(13): p. 1863-1871.

D'Aout, K. and P. Aerts, The kinematics of voluntary steady swimming of hatchling and adult axolotls (Ambystoma mexicanum Shaw, 1789). Belgian Journal of Zoology, 1999. 129(1): p. 305-316.

Dickson, K.A., et al., Effects of temperature on sustained swimming performance and swimming kinematics of the chub mackerel Scomber japonicus. Journal of Experimental Biology, 2002. 205(7): p. 969-980.

Donley, J.A., et al., Patterns of red muscle strain/activation and body kinematics during steady swimming in a lamnid shark, the shortfin mako (Isurus oxyrinchus). Journal of Experimental Biology, 2005. 208(12): p. 2377-2387.

Donley, J.M. and K.A. Dickson, Swimming kinematics of juvenile kawakawa tuna (Euthynnus affinis) and chub mackerel (Scomber japonicus). Journal of Experimental Biology, 2000. 203(20): p. 3103-3116.

Dowis, H.J., et al., Swimming performance studies on the eastern Pacific bonito Sarda chiliensis, a close relative of the tunas (family Scombridae) - II. Kinematics. Journal of Experimental Biology, 2003. 206(16): p. 2749-2758.

Epps, B.P., et al., Swimming performance of a biomimetic compliant fish-like robot. Experiments in Fluids, 2009. 47(6): p. 927-939.

Flammang, B.E. and G.V. Lauder, Speed-dependent intrinsic caudal fin muscle recruitment during steady swimming in bluegill sunfish, Lepomis macrochirus. Journal of Experimental Biology, 2008. 211(4): p. 587-598.

Froese, R. and D. Pauly. Editors. 2010. FishBase. World Wide Web electronic publication. www.fishbase.org

Fish, F.E. and G.V. Lauder, Passive and active flow control by swimming fishes and mammals. Annual Review of Fluid Mechanics, 2006. 38: p. 193-224.

Fuiman, L.A. and R.S. Batty, What a drag it is getting cold: Partitioning the physical and physiological effects of temperature on fish swimming. Journal of Experimental Biology, 1997. 200(12): p. 1745-1755.

Gillis, G.B., Environmental effects on undulatory locomotion in the American eel Anguilla rostrata: Kinematics in water and on land. Journal of Experimental Biology, 1998. 201(7): p. 949-961.

Gillis, G.B., Undulatory locomotion in elongate aquatic vertebrates: Anguilliform swimming since Sir James Gray. American Zoologist, 1996. 36(6): p. 656-665.

Gray, J., Studies in animal locomotion I. The movement of fish with special reference to the eel. JOURNAL OF EXPERIMENTAL BIOLOGY, 1933. 10

Handegard, N.O., G. Pedersen, and O. Brix, Estimating tail-beat frequency using split-beam echosounders. Ices Journal of Marine Science, 2009. 66(6): p. 1252-1258.Hertel, H. (1966) Structure, form, movement. New York : Reinhold

Hertel, H. (1966) Structure, form, movement. New York : Reinhold

Hess, F. and J.J. Videler, Fast Continuous Swimming of Saithe (Pollachius-Virens) - a Dynamic Analysis of Bending Moments and Muscle Power. Journal of Experimental Biology, 1984. 109(MAR): p. 229-251.

Horner, A.M. and B.C. Jayne, The effects of viscosity on the axial motor pattern and kinematics of the African lungfish (Protopterus annectens) during lateral undulatory swimming. Journal of Experimental Biology, 2008. 211(10): p. 1612-1622.

Jayne, B.C. and G.V. Lauder, Speed Effects on Midline Kinematics During Steady Undulatory Swimming of Largemouth Bass, Micropterus-Salmoides. Journal of Experimental Biology, 1995. 198(2): p. 585-602.

Langerhans, R.B. and A.M. Makowicz, Shared and unique features of morphological differentiation between predator regimes in Gambusia caymanensis. Journal of Evolutionary Biology, 2009. 22(11): p. 2231-2242.

Lauder, G.V. and P.G.A. Madden, Learning from Fish: Kinematics and ExperimentalHydrodynamics for Roboticists. International Journal of Automation and Computing, 2006. 4: p. 325-335.

Liao, J.C., Swimming in needlefish (Belonidae): anguilliform locomotion with fins. Journal of Experimental Biology, 2002. 205(18): p. 2875-2884.

Lighthill, M.J., Note on the Swimming of Slender Fish. Journal of Fluid Mechanics, 1960. 9(2): p. 305-317.Reid, D.A.P.; Hildenbrandt, H.; Padding, J.T., Hemelrijk, C.K. (2009). Flow around fishlike shapes studied using multiparticle collision dynamics Physical Review E (Statistical, Nonlinear, and Soft Matter Physics) Pages: 046313 (7 pp.)

Long, J.H. and K.S. Nipper, The importance of body stiffness in undulatory propulsion. American Zoologist, 1996. 36(6): p. 678-694.

Müller, U.K., et al., How the body contributes to the wake in undulatory fish swimming: Flow fields of a swimming eel (Anguilla anguilla). Journal of Experimental Biology, 2001. 204(16): p. 2751-2762.

Müller, U.K., E.J. Stamhuis, and J.J. Videler, Riding the waves: the role of the body wave in undulatory fish swimming. Integrative and Comparative Biology, 2002. 42(5): p. 981-987.

Müller, U.K., J.G.M. van den Boogaart, and J.L. van Leeuwen, Flow patterns of larval fish: undulatory swimming in the intermediate flow regime. Journal of Experimental Biology, 2008. 211(2): p. 196-205.

Müller, U.K. and J.L. van Leeuwen, Swimming of larval zebrafish: ontogeny of body waves and implications for locomotory development. Journal of Experimental Biology, 2004. 207(5): p. 853-868.

Müller, U.K., et al., Fish foot prints: Morphology and energetics of the wake behind a continuously swimming mullet (Chelon labrosus risso). Journal of Experimental Biology, 1997. 200(22): p. 2893-2906.

Nauen, J.C. and G.V. Lauder, Hydrodynamics of caudal fin locomotion by chub mackerel, Scomber japonicus (Scombridae). Journal of Experimental Biology, 2002. 205(12): p. 1709-1724.

Reid, D.A.P., H. Hildenbrandt, J.T. Padding and C.K. Hemelrijk, Flow around fishlike shapes studied using multiparticle collision dynamics Physical Review E (Statistical, Nonlinear, and Soft Matter Physics), 2009. Pages: 046313 (7 pp.)

Sfakiotakis, M., D.M. Lane, and J.B.C. Davies, Review of fish swimming modes for aquatic locomotion. Ieee Journal of Oceanic Engineering, 1999. 24(2): p. 237-252.

Shadwick, R.E. and D.A. Syme, Thunniform swimming: muscle dynamics and mechanical power production of aerobic fibres in yellowfin tuna (Thunnus albacares). Journal of Experimental Biology, 2008. 211(10): p. 1603-1611.

Statistica (StatSoft, Inc. (2007). STATISTICA (data analysis software system), version 8.0. www.statsoft.com .

Tytell, E.D., The hydrodynamics of eel swimming II. Effect of swimming speed. Journal of Experimental Biology, 2004. 207(19): p. 3265-3279.

Videler, J.J. and F. Hess, Fast Continuous Swimming of 2 Pelagic Predators, Saithe (Pollachius-Virens) and Mackerel (Scomber-Scombrus) - a Kinematic Analysis. Journal of Experimental Biology, 1984. 109(MAR): p. 209-228.

Videler, J.J., Fish Swimming Movements - a Study of One Element of Behavior. Netherlands Journal of Zoology., 1985. 35(1-2): p. 170-185.

Videler, J. J. (1993). Fish Swimming. London: Chapman & Hall.

Vogel, S. (1994). Life in Moving Fluids, 2nd edn. Princeton University Press, Princeton, NJ.

Webb, P. W., Form and function in fish swimming. Scientific American, 1984. 251(1): 72-82.

Webb, P.W., Body Form, Locomotion and Foraging in Aquatic Vertebrates. American Zoologist, 1984. 24(1): p. 107-120.

Webb, P.W., Steady Swimming Kinematics of Tiger Musky, an Esociform Accelerator, and Rainbow-Trout, a Generalist Cruiser. Journal of Experimental Biology, 1988. 138: p. 51-69.

Webb, P.W., Kinematics of plaice, Pleuronectes platessa, and cod, Gadus morhua, swimming near the bottom. Journal of Experimental Biology, 2002. 205(14): p. 2125-2134.

Webb, P.W., P.T. Kostecki, and E.D. Stevens, The Effect of Size and Swimming Speed on Locomotor Kinematics of Rainbow-Trout. Journal of Experimental Biology, 1984. 109(MAR): p. 77-95.

Viscosity and temperature tables in:
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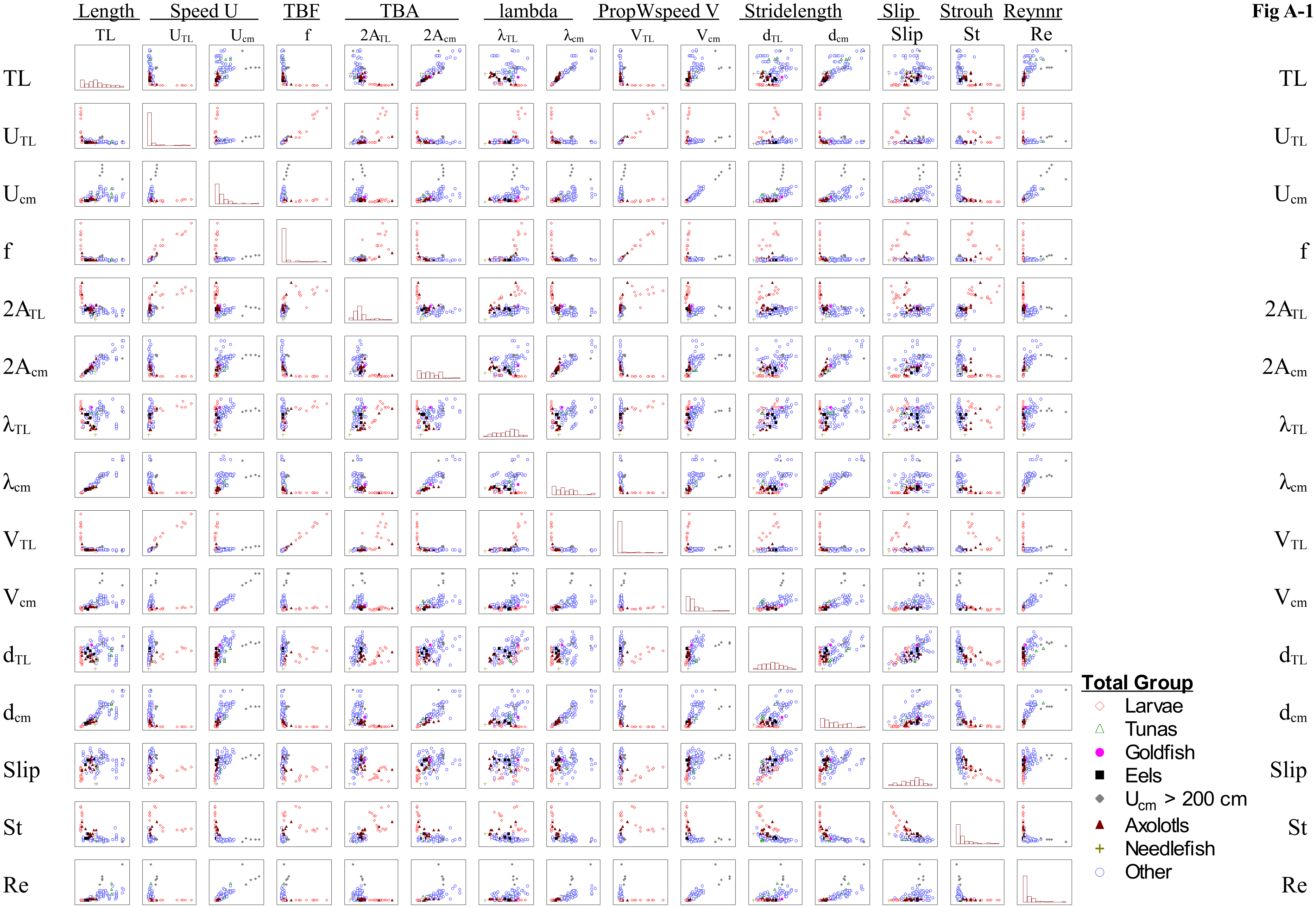
Fig A-1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+ Needlefish
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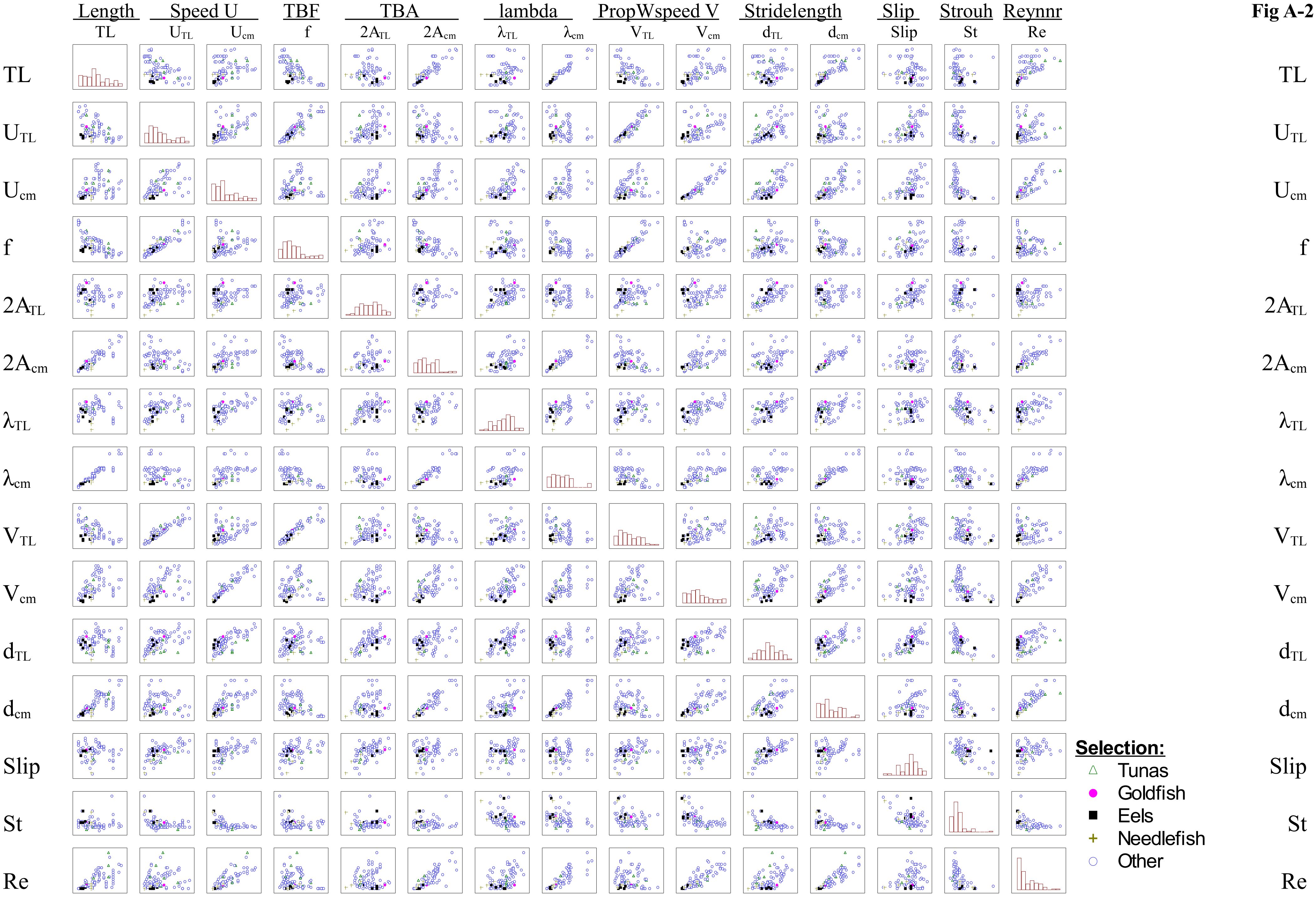
Fig A-2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● Goldfish
■ Eels
+ Needlefish
○ Other

Correlations: Red: significant at $p<0.05$, **Bold: correlation more than .80**, *Italic: not significant* **Table A-1**

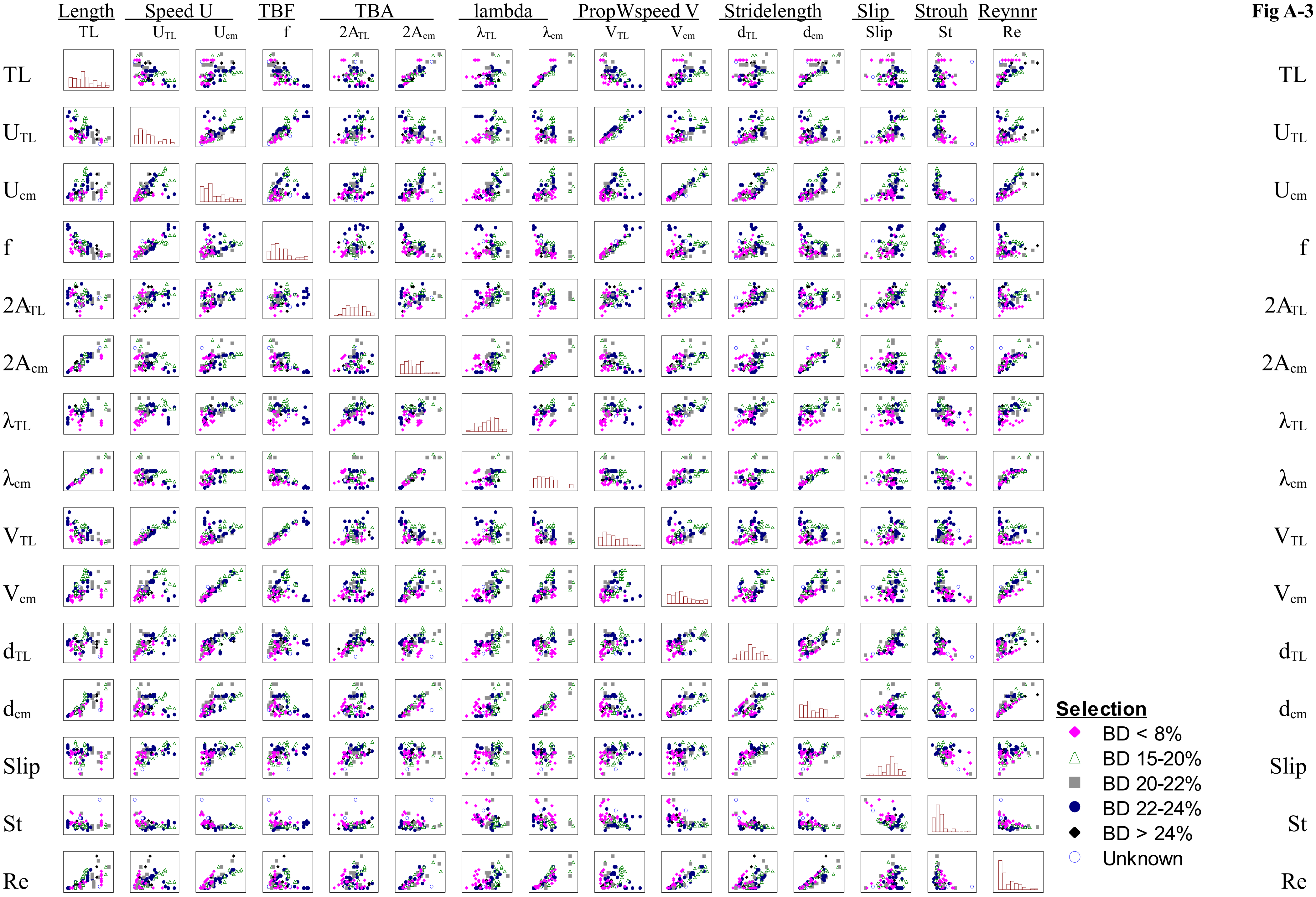
Total Group Pairwise deleted, maximum N =136, at least N=128

		Length	Speed		TBF	Tail beat ampl		Prop wave length		Prop wave speed		Stride length		Slip	Strou-hal nr	Reyn nr	BD%
		TL	U_{TL}	U_{cm}	f	$2A_{TL}$	$2A_{cm}$	λ_{TL}	λ_{cm}	V_{TL}	V_{cm}	d_{TL}	d_{cm}				
Length	**TL**	x	-0.39	0.39	-0.46	-0.57	**0.89**	*0.06*	**0.94**	-0.43	0.47	0.22	**0.84**	0.27	-0.51	0.61	*-0.10*
Speed	**U_{TL}**	-0.39	x	*-0.01*	**0.97**	0.65	-0.34	0.36	-0.31	**0.97**	*-0.03*	*0.13*	-0.28	*-0.12*	0.24	*-0.08*	*0.10*
Speed	**U_{cm}**	0.39	*-0.01*	x	*-0.11*	*-0.16*	0.57	0.38	0.54	-0.11	**0.99**	0.60	0.64	0.49	-0.40	**0.89**	*0.08*
TBF	**TBF**	-0.46	**0.97**	*-0.11*	x	0.70	-0.43	0.31	-0.39	**0.99**	*-0.13*	*-0.00*	-0.37	-0.27	0.39	*-0.17*	*0.10*
2TBA	**$2A_{TL}$**	-0.57	0.65	*-0.16*	0.70	x	-0.39	0.30	-0.47	0.70	-0.20	*-0.01*	-0.39	-0.31	0.74	-0.22	*0.11*
2TBA	**$2A_{cm}$**	**0.89**	-0.34	0.57	-0.43	-0.39	x	0.26	**0.93**	-0.40	0.60	0.48	**0.91**	0.43	-0.48	0.66	*-0.07*
Lambda	**λ_{TL}**	*0.06*	0.36	0.38	0.31	0.30	0.26	x	0.33	0.35	0.39	0.59	0.40	*0.17*	*-0.14*	0.30	0.36
Lambda	**λ_{cm}**	**0.94**	-0.31	0.54	-0.39	-0.47	**0.93**	0.33	x	-0.36	0.57	0.47	**0.95**	0.31	-0.54	0.71	*0.00*
Wave speed	**V_{TL}**	-0.43	**0.97**	*-0.11*	**0.99**	0.70	-0.40	0.35	-0.36	x	*-0.12*	*0.01*	-0.34	-0.27	0.37	*-0.16*	*0.13*
Wave speed	**V_{cm}**	0.47	*-0.03*	**0.99**	*-0.13*	-0.20	0.60	0.39	0.57	*-0.12*	x	0.52	0.65	0.41	-0.41	**0.90**	*0.07*
Stride-length	**d_{TL}**	0.22	*0.13*	0.60	*-0.00*	*-0.01*	0.48	0.59	0.47	*0.01*	0.52	x	0.63	0.75	-0.51	0.49	0.24
Stride-length	**d_{cm}**	**0.84**	-0.28	0.64	-0.37	-0.39	**0.91**	0.40	**0.95**	-0.34	0.65	0.63	x	0.50	-0.55	0.78	*0.10*
Slip	**Slip**	0.27	*-0.12*	0.49	-0.27	-0.31	0.43	*0.17*	0.31	-0.27	0.41	0.75	0.50	x	-0.67	0.39	*0.16*
Strouhal	**Strouh**	-0.51	0.24	-0.40	0.39	0.74	-0.48	*-0.14*	-0.54	0.37	-0.41	-0.51	-0.55	-0.67	x	-0.37	*-0.05*
Reynolds_nr	**Re**	0.61	*-0.08*	**0.89**	*-0.17*	-0.22	0.66	0.30	0.71	*-0.16*	**0.90**	0.49	0.78	0.39	-0.37	x	*0.03*

Selection Pairwise deleted, maximum N =98, at least N=88.

		Length	Speed		TBF	Tail beat ampl		Prop wave length		Prop wave speed		Stride length		Slip	Strou-hal nr	Reyn nr	BD%
		TL	U_{TL}	U_{cm}	f	$2A_{TL}$	$2A_{cm}$	λ_{TL}	λ_{cm}	V_{TL}	V_{cm}	d_{TL}	d_{cm}				
Length	**TL**	x	-0.54	0.29	-0.68	-0.24	**0.87**	*0.08*	**0.91**	-0.59	0.43	0.01	0.77	*-0.13*	*-0.03*	0.66	*-0.08*
Speed	**U_{TL}**	-0.54	x	0.43	**0.90**	0.53	-0.26	0.25	-0.33	**0.94**	0.27	0.52	*-0.12*	0.61	-0.35	*0.05*	0.28
Speed	**U_{cm}**	0.29	0.43	x	*0.13*	0.37	0.57	0.61	0.54	0.30	**0.95**	0.72	0.72	0.48	-0.53	**0.83**	0.23
TBF	**f**	-0.68	**0.90**	*0.13*	x	0.28	-0.54	*-0.03*	-0.56	**0.93**	*-0.00*	0.22	-0.41	0.37	*-0.19*	*-0.18*	0.24
2TBA	**$2A_{TL}$**	-0.24	0.53	0.37	0.28	x	*0.20*	0.51	*-0.03*	0.45	0.23	0.65	*0.18*	0.55	*0.02*	*0.14*	*0.12*
2TBA	**$2A_{cm}$**	**0.87**	-0.26	0.57	-0.54	*0.20*	x	0.42	**0.95**	-0.36	0.64	0.41	**0.91**	*0.13*	*-0.08*	**0.83**	*-0.02*
Lambda	**λ_{TL}**	*0.08*	0.25	0.61	*-0.03*	0.51	0.42	x	0.43	0.29	0.65	0.59	0.52	0.22	-0.41	0.44	0.38
Lambda	**λ_{cm}**	**0.91**	-0.33	0.54	-0.56	*-0.03*	**0.95**	0.43	x	-0.41	0.62	0.34	**0.93**	*-0.02*	-0.33	**0.85**	*0.06*
Wave speed	**V_{TL}**	-0.59	**0.94**	0.30	**0.93**	0.45	-0.36	0.29	-0.41	x	0.25	0.34	-0.24	0.40	-0.26	*-0.09*	0.36
Wave speed	**V_{cm}**	0.43	0.27	**0.95**	*-0.00*	0.23	0.64	0.65	0.62	0.25	x	0.56	0.74	0.26	-0.54	**0.84**	0.25
Stride-length	**d_{TL}**	*0.01*	0.52	0.72	0.22	0.65	0.41	0.59	0.34	0.34	0.56	x	0.58	0.73	-0.53	0.50	0.29
Stride-length	**d_{cm}**	0.77	*-0.12*	0.72	-0.41	*0.18*	**0.91**	0.52	**0.93**	-0.24	0.74	0.58	x	0.28	-0.42	**0.88**	*0.17*
Slip	**Slip**	*-0.13*	0.61	0.48	0.37	0.55	*0.13*	0.22	-0.02	0.40	0.26	0.73	0.28	x	-0.53	0.28	0.30
Strouhal	**Strouh**	*-0.03*	-0.35	-0.53	*-0.19*	*0.02*	*-0.08*	-0.41	-0.33	-0.26	-0.54	-0.53	-0.42	-0.53	x	-0.43	-0.40
Reynolds_nr	**Re**	0.66	*0.05*	**0.83**	*-0.18*	*0.14*	**0.83**	0.44	**0.85**	*-0.09*	**0.84**	0.50	**0.88**	0.28	-0.43	x	*0.13*

Fig A-3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