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A meta-analysis of steady undulatory swimming

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Abstract

The mechanics underlying undulatory swimming are of great general interest, both to biologists and to engineers. Over the years, more data of the kinematics of undulatory swimming have been reported. At present, an integrative analysis is needed to determine which general relations hold between kinematic variables. We here perform such an analysis by means of a meta-analysis. Using data of 27 species, we examine the relationships between the swimming speed and several kinematic variables, namely frequency and amplitude of the tail beat, length and speed of the propulsive wave, length of the body, the Reynolds number, the Strouhal number and the slip ratio U/V (between the forward swimming speed U and the rearward speed V of the propulsive wave). We present results in absolute units (cm) and in units relative to the length of the organism (total length, TL). Our data show several kinematic relations: the strongest influence on swimming speed is the speed of the propulsive wave, and the other variables (amplitude and frequency of the tail beat, length of the propulsive wave and length of the body) influence it more weakly (but significantly). In several cases, results differ when variables are expressed in different units (absolute or relative to length). Our data reveal significant differences between kinematics of swimming of shallow-bodied and deep-bodied individuals, with shallow-bodied ones swimming with a shorter propulsive wave length and a higher Strouhal number. The slip ratio U/V and the Strouhal number appear to depend on the Reynolds number in a non-linear manner.

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Introduction

Undulatory swimming is considered to be an efficient mode of aquatic locomotion, because it evolved over millions of years and is used by species that migrate over thousands of kilometres (Helfman *et al.* 1997; Videler 1993; Vogel 1994, Sfakiotakis *et al.* 1999; Tytell *et al.* 2010b). How the achieved speed is related to the specifics of undulatory propulsion is of great interest: it may help biologists to better understand the evolution of aquatic species and may help engineers to improve the design of underwater vehicles. Over the years, many studies have reported data of kinematics of single species (e.g. Videler and Wardle 1978; Jayne and Lauder 1995; Liao 2002). From these studies, a clear, general relationship has emerged, namely that a higher frequency of the tail beat results in faster swimming (Bainbridge 1958; Webb *et al.* 1984; Videler 1993; Shadwick and Syme 2008). Because only a few studies have compared data across more than a few species (Gray 1933; Bainbridge 1958; Videler 1993), and none have done so with recent data, in the present study, we apply a meta-analysis to study a large data set of many kinematic variables as measured in multiple species.

Studies on the kinematics of fish performing steady undulatory swimming show that the amplitude of the propulsive wave varies along the body, typically being lowest at a point close behind the head of the fish and maximal at the tail tip (Videler and Hess 1984; Müller *et al.* 1997; Gillis 1998; Tytell and Lauder 2004). The speed *V* with which the wave travels rearward is the product of the propulsive wave length λ and the tail beat frequency *f*. Due to the undulation, water is propelled rearwards and the fish moves forward at speed *U*. Because the transmission of speed from the propulsive wave to the water is not perfect, the forward speed *U* is usually lower than that of the propulsive wave *V*. Based on the elongated body theory, the ratio *U/V* (the so-called slip ratio) is often used as an indication of the efficiency of swimming (Lighthill 1971). It should be noted, however, that this prediction is not borne out by recent simulation work (Borazjani and Sotiropoulos 2009; Reid *et al.* 2012). Maximal efficiency is supposed to be attained at a Strouhal number St of 0.25–0.35 (Triantafyllou *et al.* 1991), but recent modelling studies contradict this (Borazjani and Sotiropoulos 2008, 2009; Reid *et al.* 2012). The Strouhal

number St relates effort of periodic motion to achieved speed: St = $2Af/U$ (with $2A$ the distance between the maximum lateral excursions of the tail tip, *f* the tail beat frequency and *U* the swimming speed). Simulation studies have shown that for carangiform swimmers, the prediction of an optimal Strouhal number of approximately 0.25 indeed holds, but for anguilliform swimmers, a Strouhal number of 0.6 appears to be optimal (Borazjani and Sotiropoulos 2008, 2009; Reid *et al.* 2012).

For single species, the relationships have been reported between swimming speed and several variables, such as the amplitude of the tail beat (Bainbridge 1958; Webb 1971; Liao 2002), the length and speed of the propulsive wave (Gray 1933; Wardle *et al.* 1995; Tytell and Lauder 2004) and the swimming style (i.e. how much of the body undulates) (Breder 1926; Müller *et al.* 2001; Blake 2004). To eliminate the effects of length on kinematic variables, several variables have often been expressed in lengths of the individual ('normalized'), for example swimming speed, tail beat amplitude, length and speed of the propulsive wave. For example, the swimming speed of an individual has been expressed as both centimetres per second and lengths per second. The reason for expressing the speed in lengths per second is that by eliminating the influence of the length of the body, the measures become comparable for individuals of different lengths. The effectiveness of this normalization technique is debated (Packard and Boardman 1999; Donley and Dickson 2000). Therefore, we here perform analyses both in absolute units (cm) and in normalized units [total lengths (TL)].

Because the speed of the animals is frequently set by the experimenter, the speed of swimming has often been considered to cause the kinematics (Webb *et al.* 1984; Long *et al.* 1996; Liao 2002; Müller and van Leeuwen 2004). In our meta-analysis, we instead consider the speed to arise as a consequence of the kinematics. We investigate the relationship between swimming speed and the kinematics, including the standard dimensionless measures, that is, the slip ratio *U/V*, the Strouhal number and the Reynolds number Re = $U^* L/v$ (with *U* the forward swimming speed, *L* the length of the fish and *v* the kinematic viscosity).

In the present study, we have used online search engines to collect data from the scientific biological literature. We confined our investigation

to data reported on animals swimming at a constant speed and collected specifically data of the swimming speed, the tail beat (its frequency and amplitude), the propulsive wave (its speed and length) and the body depth. For instance, several recent studies were not included because of missing data on the propulsive wave length λ [Flammang and Lauder 2008; Shadwick and Syme 2008; Horner and Jayne 2008; Syme *et al.* 2008). We included data only when it was clearly stated at which swimming speed a particular kinematic measurement was taken.

Methods

In our literature search, we used the online engines ISI Web of Knowledge and Google Scholar. We searched for data of kinematics of individuals that swam at a constant speed using undulatory propulsion. We included only papers that reported data on the following variables from Table 1: the length of the individual, the swimming speed, the frequency and amplitude of the tail beat and at least one of the following variables: the length or speed of the propulsive wave or the slip ratio U/V. To determine the Reynolds number, we calculated the viscosity based on the actual temperature and salinity indicated by each study (Reynolds 1883).

We analysed the data with measures of distance expressed both as a normalized value relative to an individual's TL and in absolute units (cm) (Table 1). For example, a fish swims at 2 TL s^{-1} if its TL is 23 cm and its swimming at speed U is 46 cm s^{-1}. The length of a fish has been measured in three ways, namely body length (or standard length), fork length and TL (Fig. 1). In the present study, we confine ourselves to TL.

If a study from our data set used a different measure of length, we converted the data to TLs using the ratio of the reported measure and TL given by Fishbase for the species in question (Fishbase 2009–2012). If body depth was not reported, we took its ratio to TL from Fishbase.

Another method that is supposed to eliminate the effect of length is to compare individuals within a specific length class. We classified individuals smaller than 2.5 cm into the category of smallest individuals and doubled the maximal length of each subsequent class. Because the classes with individuals of length 2.5–5 and 5–10 cm comprised insufficient data, we combined them into a single class (Table 2, Fig. 3).

Visual inspection of the data showed that there were extreme values in the speed and size of individuals. These came from individuals swimming faster than 200 cm s^{-1} and being smaller than 2 cm. Whereas the main body of our data concerned fish, it also included data on few other undulatory swimmers such as axolotls (*Ambystoma mexicanum*, Ambystomatidae) and sea snakes (*Pelamis platurus*, Hydrophiidae). In analysing the data, we studied the total data set and a set that comprised only fish, without extremes as regards size and speed.

To determine the relation between swimming speed U and the other kinematic variables, we used Pearson product–moment correlation and
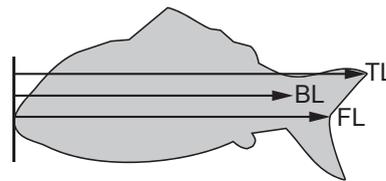
Figure 1 Different measurements of fish length: body length (BL), fork length (FL) and total length (TL). This study uses total length.

Table 1 Variables used in the analysis and their conversions.

Measure	Symbol	Units
Length	L	cm
Swimming speed	U	cm s^{-1} and TL s^{-1}
Tail beat frequency	f	Hz
Tail beat amplitude	$2A$	cm and TL
Propulsive wave length	λ	cm and TL
Propulsive wave speed	$V = \lambda * f$	cm s^{-1} and TL s^{-1}
Slip	U/V	Dimensionless
Strouhal number	$St = 2 * f * A / U$	Dimensionless
Reynolds number	$Re = U * L / v$	Dimensionless

Table 2 Length classes for analysis of the relation between tail beat frequency f and swimming speed U and the relationship between f and U. *** $P < 0.001$.

Length class	Number	Slope	R^2	P
(1) <2.5 cm	19	0.2	0.77	***
(2) 3–10 cm	12	1.2	0.16	ns
(3) 10–20 cm	24	13.0	0.63	***
(4) 20–40 cm	52	27.2	0.88	***
(5) ≥ 40 cm	21	38.0	0.77	***

simple linear regression with the ordinary least square estimator. We applied Student's t-test to determine the significance of the differences between the groups of different body depths. All tests were two-tailed and performed in Statistica 8.0 (StatSoft, Inc., 2007).

Results

We considered approximately 400 papers, of which twenty-four studies covering 27 species and 25 genera included all the required kinematic variables (Table 3, Data S1 in the Supporting Information). Remarkably, most papers that fit our criteria have been published before the year 2000. Note that unless stated otherwise, the results discussed below are for the total data set, that is, including extremes of size and speed, and axolotls and sea snakes.

We present in Table 4 the relations of the different kinematic variables with the swimming speed U as dependent variable, with size expressed both in absolute terms (cm) and in relative terms (TL). Here, we discuss these relations in descending order of influence on the swimming speed.

Propulsive wave speed V

Simple linear regression analysis shows that the variance of the swimming speed U is almost entirely explained by the speed V of the propulsive wave (Table 4, Fig. 2). This holds both when including extremes and without them and when expressed in TL and in centimetre (Table 4). In contrast, the explanatory power of the two components of the propulsive wave V appears to differ depending on the unit of measurement: the tail beat frequency explains the variance in the swimming speed U only when the speed is expressed in TL, whereas the length of the wave is significant for both measurement units, but it has more explanatory power when both it and the speed are expressed in absolute units (cm).

Tail beat frequency f, propulsive wave length λ and tail beat amplitude $2A$

Besides the propulsive wave speed V, each of the other kinematic variables (tail beat frequency f, propulsive wave length λ and tail beat amplitude $2A$) also appears to significantly influence the swimming speed in at least one unit of measurement, normalized or absolute (Table 4). Only the

frequency of the tail beat can explain the variance of the swimming speed as strongly as the speed of the propulsive wave does, but does so only when the influence of length is weakened. The influence of length can be reduced by measuring the swimming speed in TLs (Table 4) or only studying individuals of similar length as in Videler's study (1993) (Fig. 3, Table 2). A larger tail beat amplitude $2A$ appears to increase the swimming speed regardless of the unit of measurement, but less so than the speed of the propulsive wave V does. The direction of the relation between the swimming speed U and the length of the individual L appears to depend on the unit of measurement: when the length of the individual is measured in cm and when speed is measured in absolute units, larger organisms swim faster (Table 4); when it is measured in TLs, larger ones swim more slowly.

Length

The length L of the individual in centimetre does not correlate with the length of the propulsive wave in TL (explained variance $R^2 < 0.002$, $P = 0.59$). In other words, contrary to what one might expect, for the propulsive wave length, it does not appear to matter how long an animal is. The correlation (determined using a general linear model) between the swimming speed U and the speed of the propulsive wave V does not depend on the length of the fish (neither in TL nor in cm) (Table 5). This independence is unexpected, because the correlations with the swimming speed of both components of the propulsive wave speed V, that is, tail beat frequency f and wave length λ each depend on length: they become significantly steeper as the length L of the individual increases (Fig. 3, Table 5). This is the case even when attempting to eliminate the influence of length L by expressing these variables in TL. Thus, it appears that the speed of the propulsive wave eliminates the influence of an individual's length through its combination of tail beat frequency and length of the propulsive wave, even though the correlation with swimming speed U of both these components becomes significantly steeper as length increases.

Reynolds number, Slip and Strouhal number

The slip ratio and Strouhal number both appear to depend on the Reynolds number in a non-linear way (Figs 4 and 5). The slip ratio follows a

Table 3 Collected data of 27 species. Data points may be based on 1–10 individuals. References with [V] indicate that data were taken from Videler (1993).

Species	Total number of data points	Data without outliers	Study
Abramis brama (Cyprinidae)	1	1	Bainbridge (1958)
Ambystoma mexicanum (Ambystomatidae)	8	–	D'Aout and Aerts (1997)
Ambystoma mexicanum young	3	–	D'Aout and Aerts (1999)
Ammodytes marinus (Ammodytidae)	4	4	Videler (1993)[V]
Anguilla anguilla (Anguillidae)	1	1	Hess (1983)[V]
	3	3	Müller *et al.* (2001)
Anguilla rostrata (Anguillidae)	1	1	Tytell and Lauder (2004)
Carassius auratus (Cyprinidae)	1	1	Bainbridge (1958)
Chelon labrosus risso (Mugilidae)	1	1	Müller *et al.* (2002)
	1	1	Müller *et al.* (1997)
Clupea Harengus (Clupeidae)	6	–	Fuiman and Batty (1997)
Danio rerio (Cyprinidae)	9	–	Müller and van Leeuwen (2004)
	2	–	Müller *et al.* (2008)
Esox (hybrid) (Esocidae)	1	1	Webb (1988)[V]
Euthynnus affinis (Scombridae)	4	4	Donley and Dickson (2000)
Gadus morhua (Gadidae)	4	4	Videler and Wardle (1978)
	2	2	Webb (2002)
Gambusia affinis (Poeciliidae)	6	6	Langerhans (2009)
Hyperoplus lanceolata (Ammodytidae)	5	5	Videler (1993)[V]
Lepisosteus osseus (Lepisosteidae)	7	7	Long *et al.* (1996)
Leuciscus leuciscus (Cyprinidae)	1	1	Bainbridge (1958)
Liza ramada (Mugilidae)	1	1	Videler (1993)[V]
Micropterus salmoides (Centrarchidae)	5	5	Jayne and Lauder (1995)
Oncorhynchus mykiss (Salmonidae)	5	–	Jayne and Lauder (1995), from Webb *et al.* (1984)
	4	4	Webb (1988)[V]
	1	1	Webb *et al.* (1984)[V]
Pelamis platurus (Hydrophiidae)	2	–	Graham *et al.* (1987)
Pleuronectes platessa (Pleuronectidae)	1	1	Webb (2002)
Pollachius virens (Gadidae)	9	9	Videler and Hess (1984)[V]
Salmo salar (Salmonidae)	3	2	Videler (1993)[V]
Sarda chiliensis chiliensis (Scombridae)	2	2	Dowis *et al.* (2003)
Scomber japonicus (Scombridae)	8	8	Dickson *et al.* (2002)
	4	4	Donley and Dickson (2000)
Scomber scombrus (Scombridae)	9	5	Videler and Hess (1984)[V]
Strongylura marina (Belonidae)	3	3	Liao (2002)
Total number of data points	128	88	

Table 4 Relationship between several variables and swimming speed U per cell is given: s: the direction of correlation, (+ or −), R^2: the explained variance, L is given in cm and P: significance. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

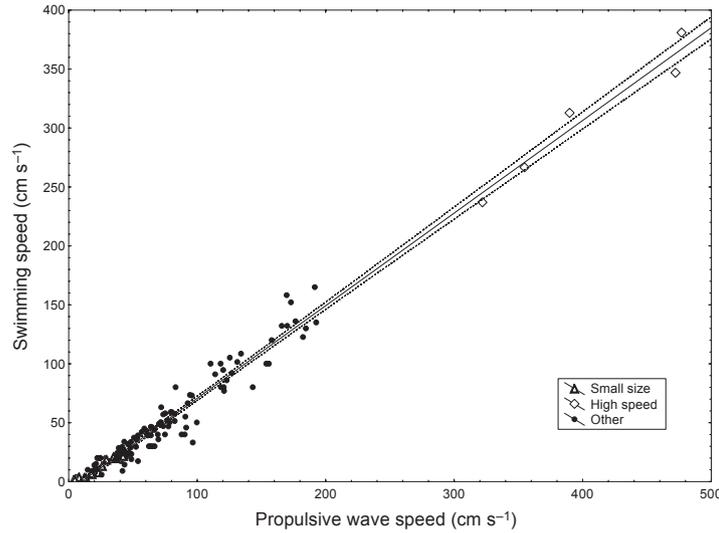| Data	Unit of measurement	Propulsive Wave Speed V s R^2 P	Tail beat frequency f s R^2 P	Tail beat amplitude 2A s R^2 P	Propulsive Wave Length λ s R^2 P	Length of individual L s R^2 P
All ($N = 128$)	Total length	(+) 0.94***	(+) 0.93***	(+) 0.41***	(+) 0.16***	(−) 0.15***
Without outliers ($N = 88$)	Total length	(+) 0.89**	(+) 0.80***	(+) 0.29***	(+) 0.06*	(−) 0.19***
All ($N = 128$)	cm	(+) 0.98***	(ns) 0.01	(+) 0.27***	(+) 0.29***	(+) 0.17***
Without outliers ($N = 88$)	cm	(+) 0.91***	(ns) 0.00	(+) 0.38***	(+) 0.30***	(+) 0.13***

Figure 2 Swimming speed vs. speed of propulsive wave, both in absolute units, for the data including extremes. Striped bands indicate the 95% confidence interval. Equations for the generalized linear model with swimming speed as the dependent variable are $U = (-7.885 \pm 1.284) + (0.7857 \pm 0.011)*V$; $R^2 = 0.9752$; $r = 0.9875$, $P < 0.0001$ (both estimates for the independent parameters highly significant).
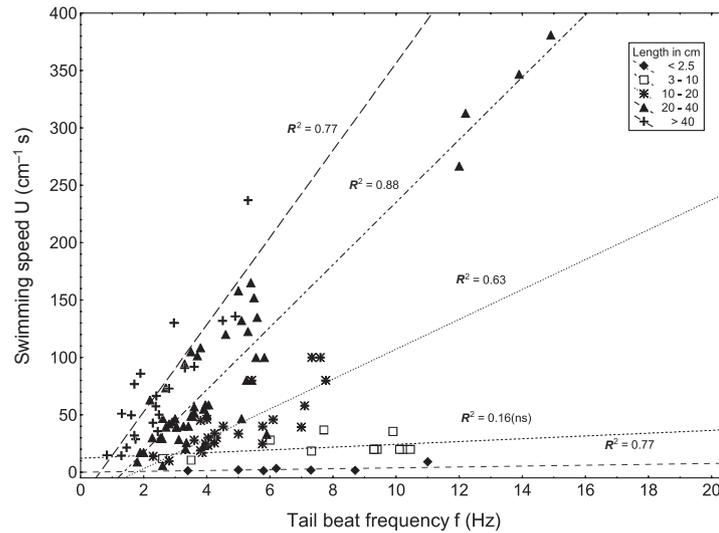

Figure 3 Swimming speed in absolute units vs. tail beat frequency (the total data set) with the data separated into different length classes (Table 2). The lines are linear fits for the relation of tail beat frequency to swimming speed. For clarity, 11 individuals <2.5 cm are omitted because their tail beat frequency was so high (>25 Hz).

positive logarithmic curve that sharply increases at low Re (below 2000) and plateaus at high Re (above 8000) at a slip ratio of approximately 0.75 (Fig. 4). The Strouhal number appears to follow a negative logarithmic curve, with much higher Strouhal numbers at lower Re and approaching the theoretical 'optimum' Strouhal number of 0.2 at high Reynolds number (over 50 000) (Fig. 5). This indicates that this Strouhal number of 0.2 is

unlikely to be optimal for lower Re. There is a clear gap in data between Reynolds numbers 2000 and 8000.

Body depth

The data of body depth are bimodally distributed in two classes with ratios of the depth to the length of 0.05–0.08 and 0.17–0.30. Dividing

Table 5 Relation between swimming speed U and the propulsive wave speed V, the tail beat frequency f and the propulsive wave length λ, with length L (in cm) as extra independent variable. General linear models of the total data set ($N = 128$). Speed and kinematic variables are expressed either TL or cm. P-values indicate per coefficient the significance of the difference from zero.

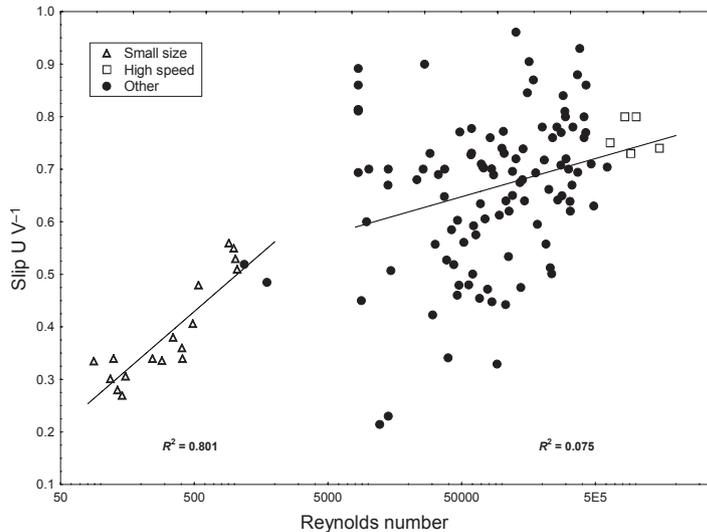| Unit	Variable X	GLM ($U = a + b*X + c*L$)	P-values of a	b	c
In TL	V	$U = +(0.007 \pm 0.422) + (0.495 \pm 0.013)*V + (0.019 \pm 0.013)*L$	0.987	<0.0001	0.155
	f	$U = -(1.009 \pm 0.432) + (0.546 \pm 0.014)*f + (0.034 \pm 0.013)*L$	0.021	<0.0001	0.010
	λ	$U = -(6.906 \pm 3.449) - (19.321 \pm 3.786)*\lambda + (0.191 \pm 0.039)*L$	0.047	<0.0001	<0.0001
In cm	V	$U = -(6.179 \pm 1.559) + (0.796 \pm 0.012)*V + (0.108 \pm 0.057)*L$	<0.001	<0.0001	0.061
	f	$U = +(13.82 \pm 11.18) + (0.335 \pm 0.354)*f + (1.684 \pm 0.335)*L$	0.218	0.345	<0.0001
	λ	$U = -(19.07 \pm 7.846) + (4.734 \pm 0.828)*\lambda - (2.388 \pm 0.737)*L$	0.017	<0.0001	0.002

Figure 4 Slip ratio U/V vs. Reynolds number, for the total data set. The lines are logarithmic fits. Up to Re 2000: Slip = $-0.166 + 0.221*\log10(x)$; $P < 0.0001$. From Re 8000: Slip = $0.306 + 0.073*\log10(x)$; $P = 0.0039$.

individuals into these two classes based on a single morphological parameter also appears to divide them according to the common broad classification of fish according to swimming styles, that is, anguilliform and carangiform (Fig. 6, Table 6). For the whole data set, deep-bodied individuals have a much greater range of lengths and swimming speeds than shallow-bodied ones. To discover purely the effect of body depth, we confine ourselves to the range of lengths and swimming speeds in which there were data of both shallow- and deep-bodied individuals. This range concerns individuals of 8.1–69.5 cm swimming at 0.5–2TLs^{-1}. The two groups appear to be similar in

all aspects except for three differences (Table 6): shallow-bodied organisms have shorter propulsive wave lengths (both in cm and in TL), slower propulsive wave speed (in cm s^{-1}) and a slightly higher Strouhal number (i.e. use a higher tail beat frequency to achieve their swimming speed) than deep-bodied ones (Table 6). As a consequence of the shorter propulsive wave length (with similar tail beat frequency), shallow-bodied individuals have a lower propulsive wave speed V. From this, we would expect that their swimming speed U would also be lower, but because we explicitly selected data where the swimming speeds were similar for both groups, this effect is masked.
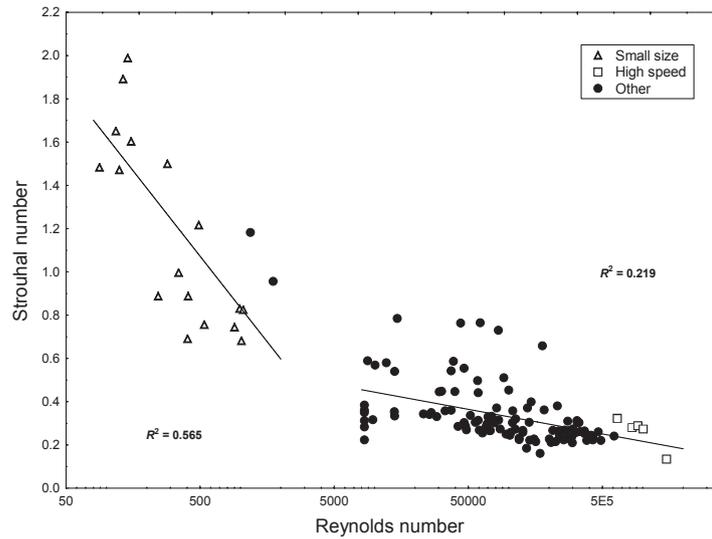
Figure 5 Strouhal number vs. Reynolds number, for the total data set. The lines are logarithmic fits. Up to Re 2000: Strouhal = 3.206−0.790*log10(Re); $P = 0.0002$. From Re 8000: Strouhal = 0.899 − 0.114*log10(Re); $P < 0.000$.

Table 6 Comparison between shallow-bodied and deep-bodied fish swimming at 0.5–2TLs^{-1}. Degrees of freedom:.35 in all cases, 17 samples represent shallow-bodied swimmers and 20 represent deep-bodied ones, (*t*-value of Student's *t*-test. *$P < 0.05$).

Variable	Mean ± SD		*t*-value	*P*-value
	Shallow-bodied (*N* = 17)	Deep-bodied (*N* = 20)		
Length *L* in cm	29.16 ± 17.93	33.38 ± 17.58	−1.908	0.475
Speed *U* in TL	1.32 ± 0.41	1.39 ± 0.38	−2.166	0.589
Speed *U* in cm	34.58 ± 15.81	43.98 ± 20.23	−2.713	0.129
Tail beat frequency *f*	3.02 ± 0.73	2.76 ± 0.88	−0.716	0.342
Tail beat amplitude 2*A* in TL	0.15 ± 0.04	0.15 ± 0.03	0.747	0.926
Tail beat amplitude 2*A* in cm	3.89 ± 1.88	5.03 ± 3.21	−1.536	0.204
Prop. wave length λ in TL	0.72 ± 0.11	0.91 ± 0.12	−4.724	0.000*
Prop. wave length λ in cm	19.87 ± 10.80	30.91 ± 18.58	−2.511	0.038*
Prop. wave speed *V* in TL	2.09 ± 0.64	2.50 ± 0.84	−2.431	0.111
Prop. wave speed *V* in cm	54.12 ± 23.22	73.83 ± 24.38	−3.419	0.017*
Slip ratio *U/V*	0.64 ± 0.08	0.63 ± 0.14	−0.509	0.797
Strouhal number St	0.35 ± 0.10	0.28 ± 0.06	2.974	0.015*
Reynolds number Re	12 6366 ± 11 2400	15 4308 ± 13 5860	−1.947	0.505

Discussion

Our analysis shows that swimming speed depends mostly on the speed of the propulsive wave more so than on any of the other variables (including the tail beat frequency). This finding confirms the early results of Gray (1933) for six species and is independent of the unit of measurement. Although in studies of the kinematics of swimming, the two components of the speed of the propulsive wave (i.e. tail beat frequency and wave length) are often analysed separately, our results show that only the combination of the two truly determines the swimming speed. A useful analogy may be walking: both the frequency with which one swings one's legs and the length of one's stride are necessary to determine the speed of walking (Zajac *et al.* 2002). Therefore, it is crucially important to
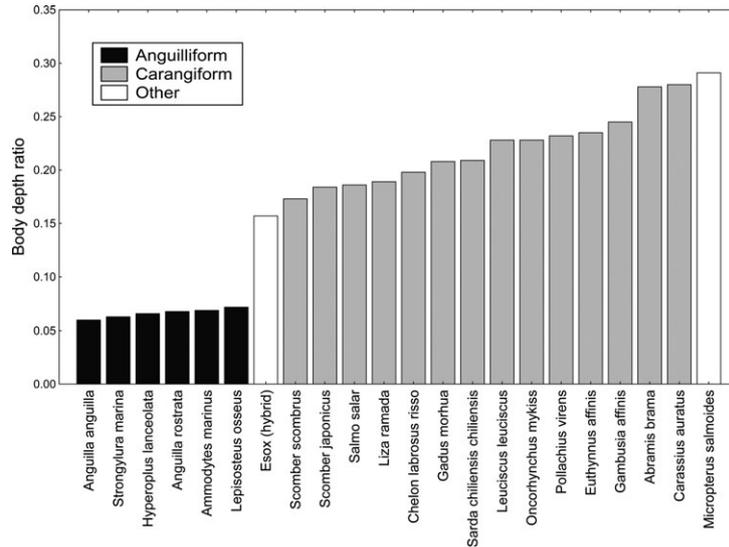
Figure 6 Average body depth for several species of fish, in terms of ratio of their total length. Bar colour indicates swimming style (Webb 1984).

report next to the tail beat frequency also the propulsive wave length in studies of undulatory swimming.

Our data concern animals that differ greatly in the length and depth of their body and their kinematics of swimming. In spite of this, the relation between the speed of the propulsive wave and that of swimming is consistent for all our data (Table 4, Fig. 2). This suggests that the speed of undulatory swimming depends on the rearward speed of the propulsive wave, regardless of differences in other morphological and kinematic factors, including body stiffness and thus propulsive wave length (Tytell *et al.* 2010a). This finding may be applied by engineers to optimize their robotic vehicles. Assuming that evolution has selected for good swimming performance, engineers may optimize their models of undulation by making them fit the relations between kinematics and swimming speed reported here, especially as regards the strong relation between swimming speed and the speed of the propulsive wave.

Strikingly, our study also shows that the unit of measurement influences the most well-known relationship between tail beat frequency and swimming speed (Table 4): swimming speed only increases with tail beat frequency when the influence of the length of the individual is reduced through either normalization or subdivision into length classes. Even when size is supposedly factored out through normalization, we find that it

still influences the relationship between tail beat frequency and swimming speed, as also noted by Donley and Dickson (2000) (Table 5, Fig. 3). This means that care should be taken to always report the unit of analysis.

The hypothesis of a single optimal Strouhal number that all undulatory swimmers attempt to attain (Triantafyllou *et al.* 1993) appears not to be borne out by our data; instead, the Strouhal number appears to be associated with their Reynolds number. This is in line with recent results of simulation studies (Borazjani and Sotiropoulos 2008, 2009, 2010; Reid *et al.* 2012). These simulations also show that the Reynolds number affects how effectively carangiform swimming converts the rearward speed of the propulsive wave into forward speed: the slip ratio of the carangiform swimmers simulated by Reid *et al.* (2012) increased with the Reynolds number. Further, in simulations of Borazjani and Sotiropoulos (2010), at Reynolds number 4000, an anguilliform swimmer achieved higher swimming speed U than a carangiform swimmer, despite having a lower propulsive wave speed V. Unfortunately, in our data, there is a gap between Re 2000 and 8000, and therefore, our data are not directly comparable to those of their simulations. However, the idea that carangiform swimming does not perform well up to Re 4000 is supported by the fact that we did not find any data of carangiform swimmers for Re lower than 8000.

The relation between Reynolds number and slip ratio U/V (Fig. 4) shows that at lower Reynolds numbers (below approximately 2000), the rearward motion of the propulsive wave is less effective at propelling an individual forward. We find the same relation in our computer simulations of hydrodynamics, based on multiparticle collision dynamics (Reid *et al.* 2009, 2012). These simulations suggest the following explanation: when their tail beat reverses, fish may slow down more at lower Reynolds numbers than at higher Reynolds numbers, because the influence of the viscosity is stronger and of inertia is lower. However, despite this decrease in effectiveness of the rearward propulsive wave at propelling the fish forward at low Re, the propulsive wave's speed V remains the strongest explanatory variable for the swimming speed at low Reynolds numbers.

Some of our data at low Reynolds numbers concern fish larvae. Although these larvae do not normally perform steady cruising, the data that we use concern larvae that maintained a steady swimming velocity over several tail beats, thus fitting our requirements (Fuiman and Batty 1997; Müller and van Leeuwen 2004; Müller *et al.* 2008). A transition between swimming styles has been shown for developing larvae when the Reynolds number becomes higher than 200 (Weihs 1980). We find a further point of transition at the location where the regression lines would intersect, which is somewhere in the range between Reynolds numbers 1200 and 2000: the slip ratio U/V largely increases with the Reynolds number until this range (Fig. 4). A lack of data makes it impossible to be more precise about the exact location of this point of transition. This transition may reflect the decreasing influence of viscosity. Because the slip ratio may relate to the swimming efficiency when viscosity becomes less important (i.e. for Reynolds numbers over 1000), this point of saturation between Re 1200 and 2000 could have biological significance. It suggests that there is an additional transition (at higher Reynolds than 200 suggested earlier). A second transition point was also found for coasting (dead) zebrafish (*Danio rerio,* Cyprinidae) (McHenry and Lauder 2005).

Two of our results differ from previous results for single species. First, in our data, the relation between tail beat amplitude and swimming speed does not reach a plateau (data not shown), as it has been shown to do for single species (Bainbridge 1963; Webb 1975). This may indicate that these plateaus are species specific, and in our data of many species, the plateaus are intermingled. Second, in our analysis, the propulsive wave length, both in absolute units and in total lengths, does not increase with the length of an individual, as it has been shown to do for single species (Donley and Dickson 2000). Therefore, we infer that the propulsive wave length is characteristic for a particular species: because organisms of different species but similar length have different propulsive wave lengths, there is no correlation between length and propulsive wave length in our cross-species comparison.

We note two things that may bias our data. First, the length of the propulsive wave may differ along the body (Webb *et al.* 1984). For example, Gillis (1998) showed that the propulsive wave length of eels was as much as 0.2 TL shorter on the front half of the body than on the rear half. Researchers normally measure the wave length either over the entire body or only over the rear half (overestimating the wave length). Thus, errors in our data are likely to be biased in the same direction. Second, one of our results may be a consequence of experimental constraints. The slower swimming (in TL per second) of larger individuals (Table 4) may be a consequence of the tank size. The limited size of the tank may have prevented the large individuals from reaching their maximum speed.

The division of our data between classes of shallow-bodied and deep-bodied individuals, which is suggested by the bimodality of body depth in our data (Fig. 6), appears to also divide individuals as regards their supposed swimming style (Table 6). In our data, shallow-bodied individuals appear to swim with kinematics as commonly ascribed to anguilliform fish, which tend to have shorter propulsive waves than carangiform and thunniform fish (Breder 1926; Webb 1984). However, an individual's kinematics of swimming at a given moment may not always be predicted by its classification as anguilliform or carangiform. The propulsive wave length of fish may vary across contexts (Long and Nipper 1996), and simulations have shown that even anguilliform fish may benefit from a carangiform swimming style when they swim at extremely high Reynolds numbers (Tytell *et al.* 2010b). Therefore, we have chosen to base our analyses purely on morphological and kinematic measurements.

Because our data set contains data of many species, it clearly shows general relations between variables (such as swimming speed and speed of the propulsive wave) that were previously reported only for single species and for sets of a few species. Our analysis shows that the effect of normalizing by the length of the body can significantly affect results (Table 4). Therefore, it is crucial to report results in both units of measurement (TL and cm). We show that body depth indicates swimming style through its strong association with the propulsive wave length. There are few kinematic data of steady undulatory swimming in the range of Reynolds numbers between 2.000 and 8.000 and above 500.000 (Fig. 5). We therefore emphasize the need for further data collection of steady swimming, reporting all the kinematic variables used in this study.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1 All data used in the paper are provided in absolute units. [1]indicates data taken from Videler [1993].