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Modelling the hydrodynamics of swimming fish, from individuals to infinite schools

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Document Version

Publisher's PDF, also known as Version of record

Publication date:

2011

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Reid, D. A. P. (2011). *Modelling the hydrodynamics of swimming fish, from individuals to infinite schools*. s.n.

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A META-ANALYSIS OF FISH SWIMMING¹

Abstract

THE PRECISE MECHANICS UNDERLYING THE SWIMMING OF FISH ARE OF GREAT GENERAL INTEREST, BOTH TO BIOLOGISTS AND TO ENGINEERS. SO FAR, ONLY ONE GENERAL PRINCIPLE HAS BEEN REPORTED, NAMELY THAT SWIMMING SPEED INCREASES WITH TAIL BEAT FREQUENCY. IN THE PRESENT PAPER, WE PERFORM A META-ANALYSIS IN ORDER TO INVESTIGATE WHETHER THERE MAY EXIST MORE OF SUCH GENERAL PRINCIPLES. USING DATA OF 26 SPECIES, WE EXAMINE THE RELATIONSHIPS BETWEEN THE SWIMMING SPEED AND SEVERAL KINEMATIC VARIABLES, NAMELY LENGTH OF THE BODY, FREQUENCY AND AMPLITUDE OF THE TAIL BEAT, AND LENGTH AND SPEED OF THE PROPULSIVE BODY WAVE, AND THE INTERRELATION OF THESE VARIABLES WITH THE HYDRODYNAMICALLY IMPORTANT DIMENSIONLESS REYNOLDS NUMBER, THE STROUHAL NUMBERS AND THE SLIP RATIO U/V (BETWEEN THE FORWARDS SWIMMING SPEED U AND THE REARWARDS SPEED V OF THE BODY WAVE). OUR DATA REVEAL SEVERAL GENERAL PRINCIPLES: SWIMMING SPEED IS MAINLY THE RESULT OF THE SPEED OF THE PROPULSIVE BODY WAVE; IT IS ALSO SIGNIFICANTLY (BUT MORE WEAKLY) AFFECTED BY FREQUENCY AND AMPLITUDE OF THE TAIL BEAT, LENGTH OF THE PROPULSIVE BODY WAVE, AND LENGTH OF THE BODY. BODY DEPTH APPEARS TO CORRELATE STRONGLY WITH SWIMMING STYLE, I.E. SHALLOW-BODIED FISH ARE ANGUILLIFORM AND DEEP-BODIED FISH ARE CARANGIFORM OR THUNNIFORM. FINALLY, CONTRARY TO COMMON EXPECTATION THE SLIP RATIO U/V AND THE STROUHAL NUMBER DEPEND ON THE REYNOLDS NUMBER.

5.1 INTRODUCTION

Undulatory swimming is supposed to be an efficient mode of aquatic locomotion, because it is the result of many millions of years of evolution of species that may migrate over thousands of kilometres (Helfman et al., 1997). The general principles governing undulatory propulsion are therefore of great interest to both biologists (for better understanding of the constraints on the evolution of aquatic species) and engineers (for the design of underwater vehicles). However, despite many experimental data of kinematics only a single general principle has been reported, namely that a higher frequency of the tail beat results in faster swimming (Bainbridge, 1958; Webb et al., 1984; Videler, 1993). To search for more principles is the aim of the present meta-analysis.

The kinematics of steady undulatory swimming are largely formulated in terms of the wave that travels rearwards through the body of the fish, with speed $V = \lambda \cdot f$, wavelength

¹ SUBMITTED TO JOURNAL OF EXPERIMENTAL BIOLOGY AS: J. F. VAN WEERDEN, D. A .P. REID, C. K. HEMELRIJK – “A META-ANALYSIS OF FISH SWIMMING”

λ and frequency f . The amplitude of this wave varies along the fish body, typically being lowest at a point close behind the head of the fish, and maximal at the tail tip (Videler and Hess, 1984). As a result of the wave, water is propelled rearwards and the fish moves forwards at speed U . Because the transmission of speed from the rearwards body wave to the water is not perfect, the forwards speed U is usually lower than that of the body wave V . The ratio U/V (the so-called slip ratio) between the two is often used as an indication of the efficiency of the swimming fish and is supposed to be approximately constant (Webb et al., 1984).

After the discovery of the relationship between tail beat frequency and swimming speed, the kinematics of a number of fish species have been investigated in many studies. However, so far the results of these studies have not been integrated. Studies have reported on the relation between swimming speed and variables such as the tail beat amplitude (Bainbridge, 1958; Webb, 1971; Liao, 2002), the length and speed of the body 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). In order to eliminate the effects of fish length on kinematic variables, the variables have often been expressed in fish lengths ('normalised'). The general effectiveness of this standardisation technique is debated, however (Packard and Boardman, 1999; Donley and Dickson, 2000). Based on the Elongated Body Theory, the swimming efficiency is commonly described by the slip ratio U/V (Lighthill, 1971). Experiments with oscillating foils suggest that fish swim most efficiently at an almost constant Strouhal number of 0.25-0.35 (Triantafyllou et al., 1991). These suppositions have so far not been verified empirically however.

In the present study we used online search engines to collect data from the scientific biological literature. We confined our investigation to steadily cruising fish, and collected specifically data of the tail beat (its frequency and amplitude), the body wave (its speed and length) and of the body depth.

We note that the swimming speed is generally incorporated in analyses as a causal variable of the kinematics of the fish (Webb et al., 1984; Long and Nipper, 1996; Liao, 2002; Müller and van Leeuwen, 2004). We assume instead that the kinematics cause the forwards speed, and investigate their relationship with the standard dimensionless measures, i.e. the Reynolds number $Re = UL/\nu$, (with U the forwards swimming speed, L the length of the fish and ν the kinematic viscosity), the slip ratio U/V and the Strouhal number $St = 2Af/U$ (with $2A$ the distance between the maximum lateral excursions of the tail tip and f the tailbeat frequency). We analyse these variables both in absolute units and in fish lengths ('normalised'). Besides, in our calculations of the Reynolds numbers we take the effect of water temperature on the viscosity into account.

5.2 METHODS

In our literature search we used the online search engines ISI web of Knowledge and Google scholar. We searched for data of kinematics of steady, undulatory swimming. We included only those papers that reported data on all of the following variables: the frequency and amplitude of the tailbeat, the length and speed of the body wave, and the length and depth of the body of the fish (Table 5.1). If morphological data were absent, we took them from

Fishbase, World Wide Web electronic publication (2011). To determine the Reynolds number we calculated the correct viscosity for the temperature reported in the paper (Reynolds, 1883).

Measure	Symbol	Units
Fish length	L	cm and TL
Body depth	H	% of TL
Swimming speed	U	cm/s and TL/s
Tailbeat frequency	f	Hz
Tailbeat amplitude	2A	cm and TL
Body wave length	λ	cm and TL
Body wave speed	$V = \lambda \cdot f$	cm/s and TL /s
Slip	(U/V)	dimensionless
Strouhal number	$2A \cdot f/U$	dimensionless
Reynolds number	$U \cdot L/\nu$	dimensionless

Table 5.1.: Measures used for analysis.

The size of a fish has commonly been measured in three ways, namely body (or standard) length, fork length and total length (Fig. 5.1). Here we use total length (TL). We analysed the data in both absolute units (cm) and in total fish lengths (TL). Our data contained outliers as regards swimming speed (≥ 200 cm/s) and size (≤ 2 cm). They comprised not only fish but also axolotls. We studied both the total data set and that with neither outliers nor axolotls.

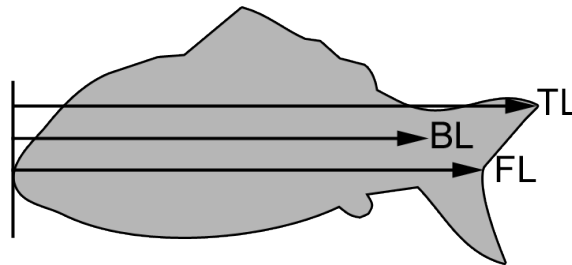


Figure 5.1.: Different ways to measure fish length: Body Length (BL), Fork Length (FL) and Total Length (TL). The present study uses Total Length.

Another method (besides normalisation) to reduce the effect of fish length is to divide the fish into size classes. Individuals of 0-2.5 cm belong to the smallest category and each larger one doubles the length. Because the categories 2.5-5 and 5-10 comprised insufficient data we combined them into one group (Table 5.2).

In most of our analyses we use correlations rather than regressions, because many of the variables are mutually dependent, rather than causal in one direction.

5.3 RESULTS

Twenty-three studies were found that included all required kinematic variables (Table 5.3). They concern 26 species of 24 genera.

Length class	N	slope	R ²	p
2: 3-10 cm	11	1.2	0.16	ns
3: 10-20 cm	18	14.4	0.74	***
4: 20-40 cm	41	24.1	0.47	***
5: ≥ 40 cm	18	29.2	0.67	***

Table 5.2.: The correlation between tailbeat frequency and swimming speed of several length classes.

The speed of the body wave V appears to be the strongest explanatory variable of the variance in the swimming speed U (Table 5.4). This holds both when expressed in body lengths and in absolute units, and both with and without outliers (Fig. 5.2). Each of the other kinematic variables also appears to significantly influence the swimming speed.

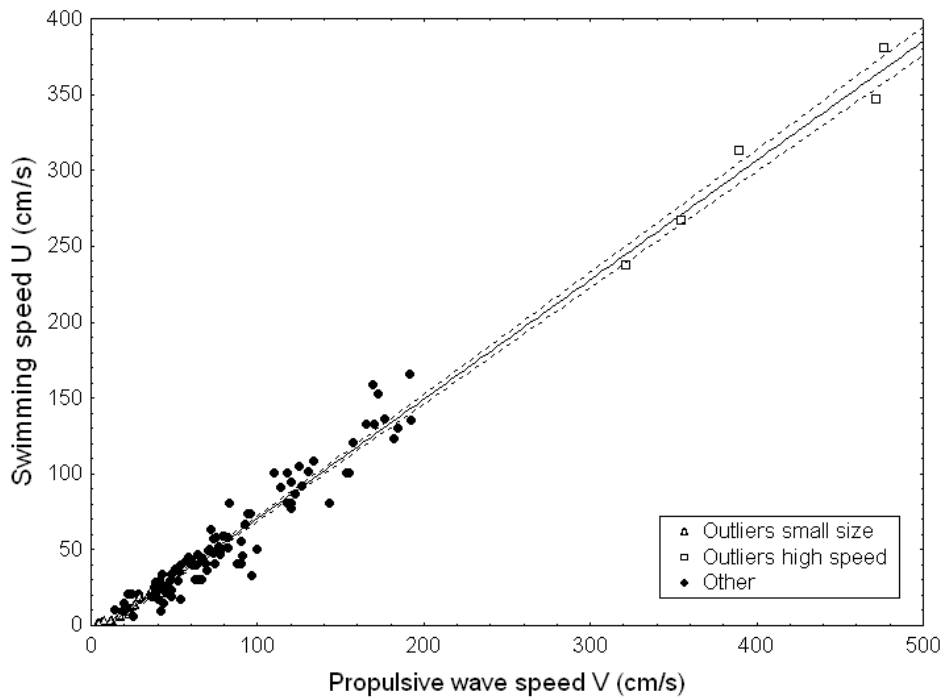


Figure 5.2.: Swimming speed as a function of body wave speed, both in absolute units, for the data including outliers.

The variance of the swimming speed is explained with similar strength by the tail beat frequency as it is by the speed of the propulsive wave, but only when the effect of fish length is reduced, either by normalisation (Table 5.4) or by studying effects per size class (Fig. 5.3).

The unit of measurement appears to influence the relation between the swimming speed U and the fish length L : in absolute units, larger fish swim faster, whereas in fish lengths smaller fish swim faster (Table 5.4).

The correlation of the swimming speed U with the speed of the propulsive wave V is independent of the length L of the fish, which is unexpected because the correlations with

Species	Total nr of data points	Data with-out extremes	Study
Abramis brama	1	1	Bainbridge (1958) ^V
Ambystoma mexicanum	8	-	D'Aout and Aerts (1997)
Ambystoma mexicanum (juv)	3	-	D'Aout and Aerts (1999)
Ammodytes marinus	4	4	Videler (1993) ^V
Anguilla anguilla	1	1	Hess (1983) ^V
Anguilla anguilla	3	3	Müller et al. (2001)
Anguilla rostrata	1	1	Tytell and Lauder (2004)
Carassius auratus	1	1	Bainbridge (1963)
Chelon labrosus risso	1	1	Müller et al. (2002)
Chelon labrosus risso	1	1	Müller et al. (1997)
Clupea Harengus (larva)	6	-	Fuiman and Batty (1997)
Danio rerio (larva)	2	-	Müller et al. (2008)
Danio rerio (larva)	9	-	Müller and van Leeuwen (2004)
Esox (hybrid)	1	1	Webb (1988) ^V
Euthynnus affinis	4	4	Donley and Dickson (2000)
Gadus morhua	4	4	Videler and Hess (1984)
Gadus morhua	2	2	Webb (2002)
Gambusia affinis	6	6	Langerhans (2009)
Hyperoplus lanceolata	5	5	Videler (1993) ^V
Lepisosteus osseus	7	7	Long and Nipper (1996)
Leuciscus leuciscus	1	1	Bainbridge (1963)
Liza ramada	1	1	Videler (1993) ^V
Micropterus salmoides	5	5	Jayne and Lauder (1995)
Oncorhynchus mykiss	5	-	Jayne and Lauder (1995), from Webb et al. (1984)
Oncorhynchus mykiss	4	4	Webb et al. (1984) ^V
Oncorhynchus mykiss (as Salmo gaidneri)	1	1	Webb (1988) ^V
Pleuronectes platessa	1	1	Webb (2002)
Pollachius virens	9	9	Videler and Hess (1984) ^V
Salmo salar	3	2	Videler (1993) ^V
Sarda chiliensis chiliensis	2	2	Dowis et al. (2003)
Scomber japonicus	8	8	Dickson et al. (2002)
Scomber japonicus	4	4	Donley and Dickson (2000)
Scomber scombrus	9	5	Videler and Hess (1984) ^V
Strongylura marina	3	3	Liao (2002)
Total number of data points	126	88	

Table 5.3.: Collected data of 26 species. Data points may be based on 1 to 10 individuals. ^V: data taken from Videler (1993).

Data	Unit	V	f	2A	λ	L
All	Fish length	(+) 0.94***	(+) 0.93***	(+) 0.42***	(+) 0.16***	(-) 0.15***
Without outliers	Fish length	(+) 0.89***	(+) 0.80***	(+) 0.29***	(+) 0.06*	(-) 0.19***
All	cm	(+) 0.98***	(ns) 0.02	(+) 0.35***	(+) 0.30***	(+) 0.25***
Without outliers	cm	(+) 0.91***	(ns) 0.00	(+) 0.38***	(+) 0.30***	(+) 0.13***

Table 5.4.: Swimming speed U and its correlation with several variables: direction, explained variance (R^2) and significance. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$. V is the speed of the propulsive body wave, f the tail beat frequency, $2A$ is the tailbeat amplitude, λ is the length of the propulsive body wave and L is the total length of the fish.

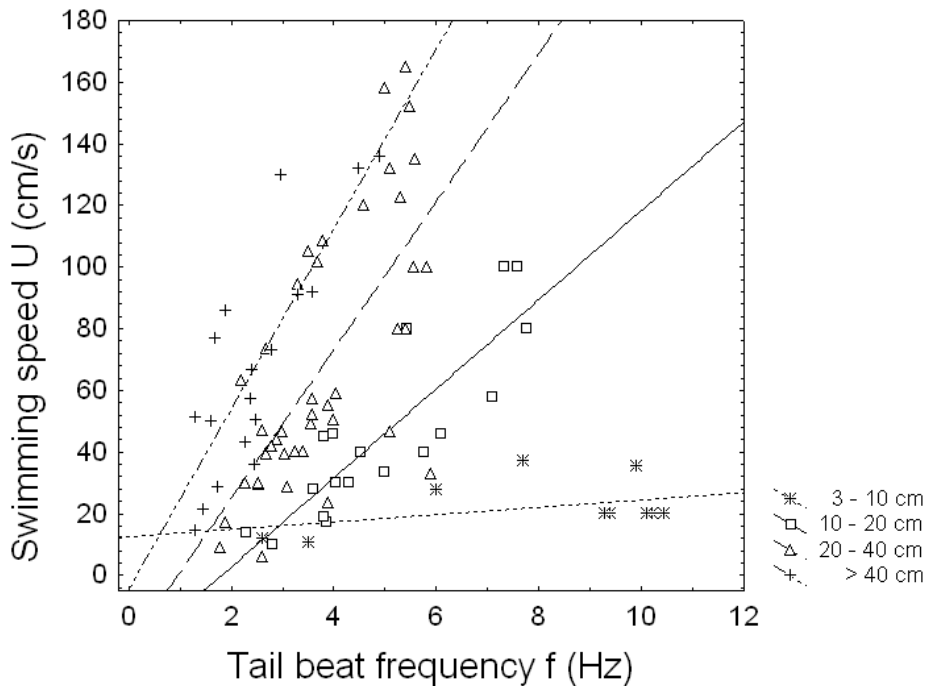


Figure 5.3.: Swimming speed in absolute units as a function of tailbeat frequency of the data without outliers, with the data separated into different length classes (Table 5.2)

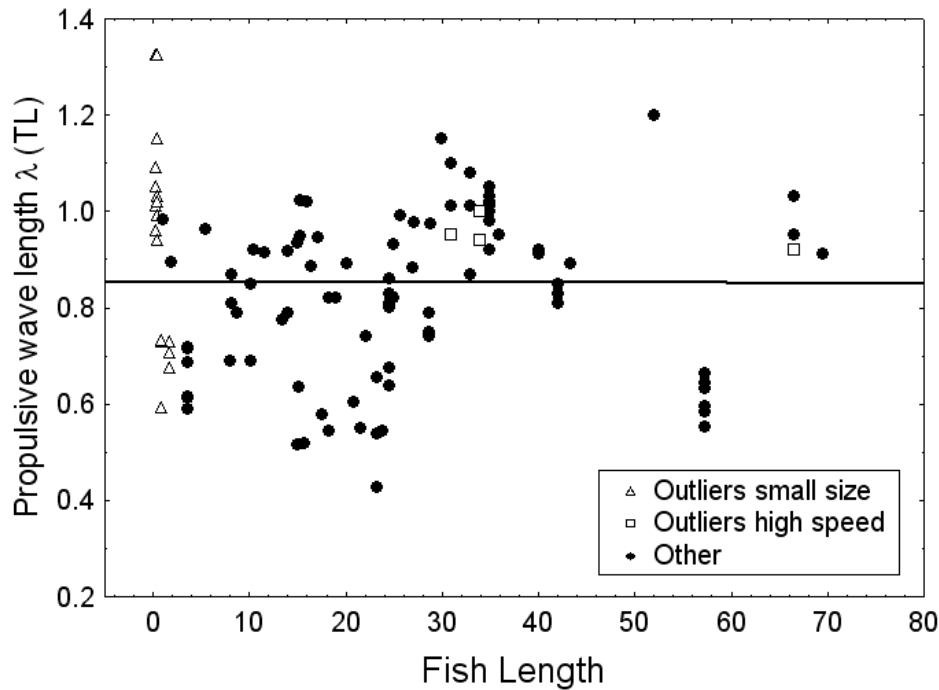


Figure 5.4.: Propulsive wave length λ , as a function of fish length, for the data including outliers.

the swimming speed of both components of V , i.e. tail beat frequency f and propulsive wavelength λ are significantly influenced by the fish length (tail beat frequency $R^2 = 0.283, p < 0.05$, propulsive wavelength: $R^2 = 0.809, p < 0.001$).

Fish length does not correlate with the length of the body wave ($R^2 < 0.001, p = 0.98$) (Fig. 5.4)

The data on body depth are bimodally distributed in two classes with depths of 5-8% and 17-30% of the fish length (Fig. 5.5). These classes appear to differ in swimming style: shallow-bodied individuals are anguilliform and deep-bodied individuals are carangiform and thunniform (Breder, 1926; Webb, 1984; *Fishbase, World Wide Web electronic publication, 2011*). To obtain an approximately equal sample size in both classes, we limit our comparison of fish of different body depths to those that swim at $1 - 3Ls^{-1}$ (Table 5.5). It appears that despite their similarity in body length and in tailbeat frequency, shallow-bodied fish swim slower and have shorter propulsive wavelengths and a slightly higher Strouhal number (i.e. use a higher tail beat frequency to achieve their swimming speed) than deep-bodied ones (Table 5.5).

The slip ratio and Strouhal number both appear to depend on the Reynolds number in a non-linear way (Figs. 5.6, 5.7).

Variable	Mean \pm StDev		t-value	p-value
	Shallow	Deep		
Length	21.2 \pm 9.32	29.8 \pm 13.9	-1.908	0.063
Speed in TL	1.56 \pm 0.27	2.0 \pm 0.6	-2.166	0.036*
Speed in cm	33.47 \pm 15.55	56.7 \pm 26.8	-2.713	0.010*
Tailbeat frequency	3.18 \pm 0.77	3.4 \pm 0.9	-0.716	0.478
Prop. wave length in TL	0.76 \pm 0.08	0.9 \pm 0.1	-4.724	0.000*
Prop. wave length in cm	16.06 \pm 7.67	27.6 \pm 14.5	-2.511	0.016*
Prop. wave speed in TL	2.44 \pm 0.44	3.1 \pm 0.9	-2.431	0.020*
Prop. wave speed in cm	51.31 \pm 22.98	86.1 \pm 30.8	-3.419	0.001*
Slip ratio U/V	0.65 \pm 0.08	0.7 \pm 0.1	-0.509	0.613
Strouhal number	0.34 \pm 0.09	0.3 \pm 0.1	2.974	0.005*
Reynolds number	80483 \pm 55325	166595 \pm 142119	-1.947	0.058

Table 5.5.: Comparison between shallow-bodied and deep-bodied fish, showing results of Student’s t-test. Degrees of freedom were 41 in all cases. There were 11 samples representing shallow-bodied fish and 32 representing deep-bodied ones. *: $p < 0.05$.

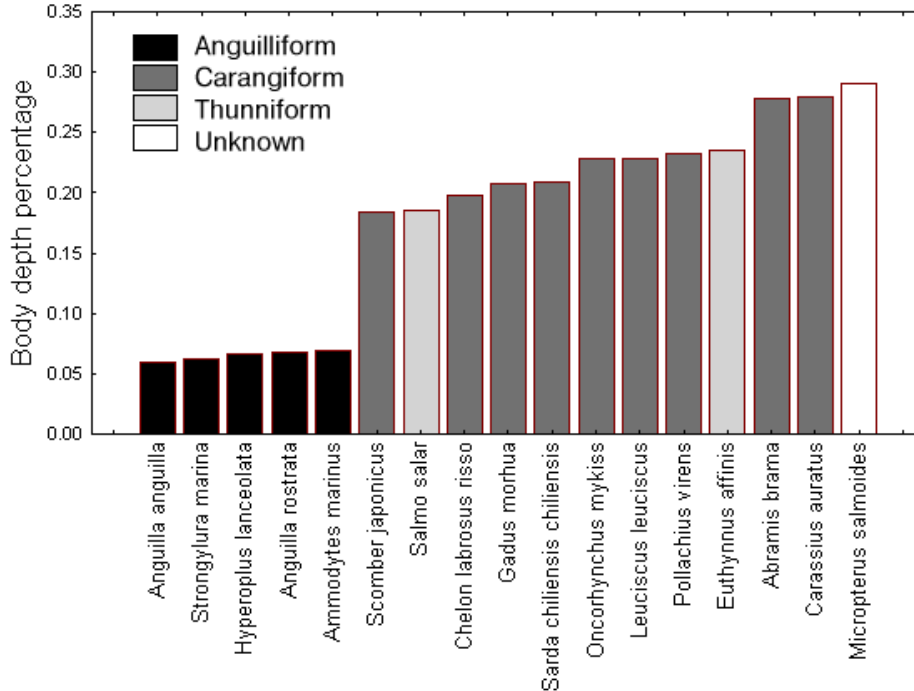


Figure 5.5.: Average body depths for several species of fish, in terms of % of their total length. Colour indicates swimming style.

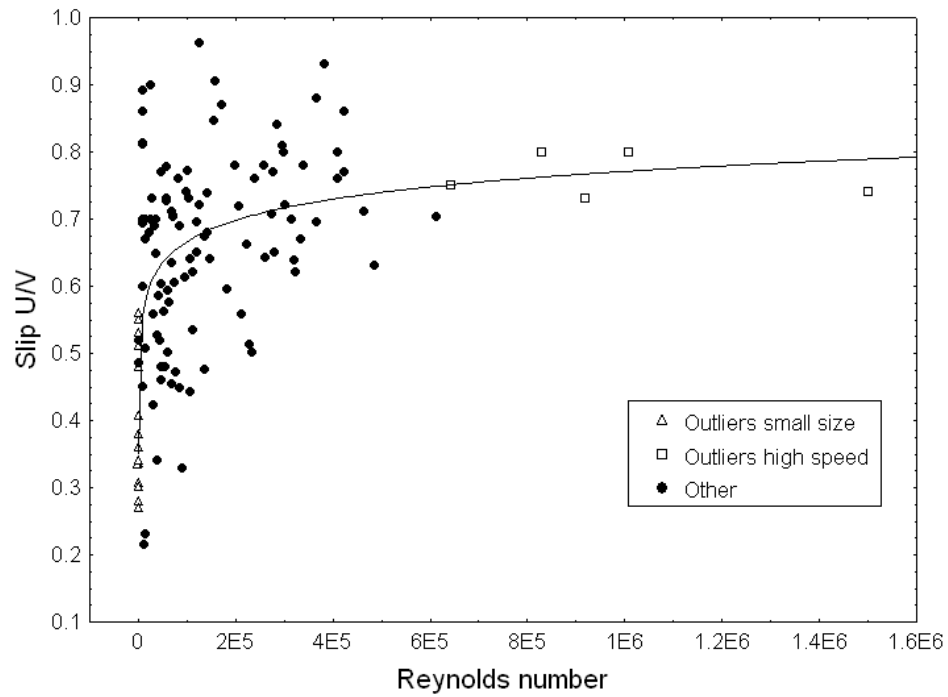


Figure 5.6.: Slip ratio U/V as a function of Reynolds number, for the data including outliers.

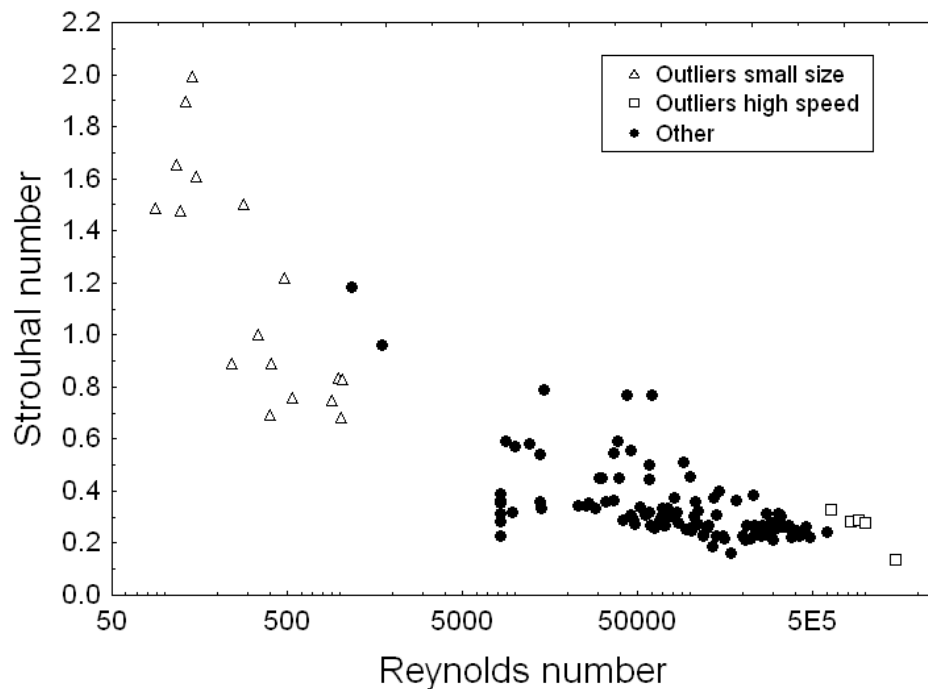


Figure 5.7.: Strouhal number as a function of Reynolds number, for the data including outliers.

5.4 DISCUSSION

Our analysis shows that swimming speed depends almost entirely on the speed of the propulsive body wave, and more so than on any of the other variables (including the tail beat frequency). This finding is independent of the unit of measurement. It confirms the early results for 6 species of Gray (1933). The two components of speed of the propulsive wave (ie. tail beat frequency and wave length) are often used separately for the analysis of swimming speed, but seldom in combination. Our results show however that only the combination of the two truly determines the swimming speed. An appropriate analogy is that of walking: the frequency with which one swings one's legs and the length of one's stride together determine the speed of walking.

Our data concern fish that differ greatly in their size, body depth and swimming style. In spite of this, the relation between the speed of the body wave and swimming speed is consistent throughout the data (Table 5.4, Fig. 5.2). This suggests that the speed of undulatory swimming depends almost entirely on the rearwards speed of the body wave, regardless of differences in other morphological and kinematic factors. This finding can be used by engineers to test whether robotic vehicles resemble swimming of real fish. Assuming that evolution has selected for swimming performance, engineers may optimise their models of undulation by making them fit the relation between swimming speed and propulsive wave speed.

Results of our large dataset differ in two cases from previous results for single species. First, the relation of tail beat amplitude and swimming speed has been shown to reach a plateau for single species (Bainbridge, 1958; Webb, 1975), but this does not happen in our data. Possible explanations for this difference are that in contrast to the other studies in our data animals were not swimming at their maximum speed, and that the maximum tail beat amplitudes differed among species. Second, within a single species the propulsive wave length, both in absolute units and in fish lengths, has been shown to increase with the total fish length (Donley and Dickson, 2000). In our analysis however, this association is absent (Fig. 5.4). Thus we conclude that the propulsive wavelength is characteristic to a particular species: because fish of different species but similar length have different body wave lengths, there is no correlation in our cross-species comparison.

Two of our results may be due to experimental constraints. First, when comparing shallow- and deep-bodied fish, shallow fish are slower than deep ones. This may be due to having their swimming speed artificially biased by the experimenter, through incidentally setting the speed of the flow tank too low because of a belief that anguilliform fish are incapable of fast swimming. Second, large fish may be prevented from swimming at their preferred cruising speed because the tank is too small, which could explain our finding that larger fish swim slower in terms of fish length. Our results thus point to the need to report details of the maximum speed of fish also.

The hypothesis of a single optimal Strouhal number that all fish attempt to attain (Triantafyllou et al., 1993) appears not to be borne out by our data: instead, the Strouhal number of fish appears to be associated with their Reynolds number.

In contrast to earlier findings (Webb et al., 1984), the slip ratio U/V is not constant, but varies with the Reynolds number (Fig. 5.6). It appears that at lower Reynolds numbers the

rearwards motion of the body wave is less effective at propelling an individual forwards. Our computer simulations of hydrodynamics, based on Multiparticle Collision Dynamics, suggest the following explanation (Reid et al., 2009, 2011): 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 inertia is lower. This implies a related effect on stride length λ_s (i.e. the distance that a fish travels forwards in a single tailbeat). At lower Reynolds numbers the stride length ($\lambda_s = \lambda U/V$) is shorter, at higher re numbers it is longer.

Further, above this point between Reynolds number 1200 and 2000, the increase of the slip ratio U/V with the Reynolds number slows down (Fig. 5.6). This may reflect the lower influence of viscosity. Due to this lower viscous influence, the swimming efficiency may be higher (Reid et al., 2011). Thus, this point of saturation may be ecologically significant. It is supplementary to the one between swimming styles at a Reynolds number of 200 for developing larvae (Weihs, 1980).

Although the unprecedented size of our data set enables us to clarify the effects of variables on speed that were previously reported only for single species, such as the propulsive wave speed and fish length, still further research would be helpful, especially at the extremely low and high Reynolds numbers where data are still sparse.

Our main conclusion is that more attention should be paid to the speed of the propulsive body wave in relation to swimming speed.

ACKNOWLEDGEMENTS

We are grateful to Jimmy Liao for constructive comments on earlier presentations of our work and to John Videler for comments on the text as well as several informative discussions.

