Aquat. Living Resour. 22, 79–91 (2009)
© EDP Sciences, IFREMER, IRD 2009
DOI: 10.1051/alr/2009008
www.alr-journal.org

Aquatic
Living
Resources

Hydrodynamic abilities of riverine fish: a functional link between morphology and velocity use

Pierre Sagnes[a] and Bernhard Statzner

UMR CNRS 5023, Ecologie des Hydrosystèmes Fluviaux, Université Lyon 1, 69622 Villeurbanne, France
Université de Lyon, 69003 Lyon, France

Received 4 July 2008; Accepted 8 January 2009

Abstract – To better understand the effects of perturbations (e.g. global change) or habitat restorations on fish population dynamics, it is crucial to improve the knowledge about strategies of habitat use (especially in terms of velocity use) by fish. Many recent studies accurately describe kinematics or energetic budgets of swimming activities, which are often species-specific and hardly transferable to other species. The main goal of the present study was to revive more general ecomorphological relationships between body shape and strategies of velocity use by highlighting a functional aspect of fish morphology: the hydrodynamic potential. For this purpose, potential relationships between minimum drag coefficients (C_{dmin}, constant at high Reynolds numbers), velocity use, fish morphology and drag in given flow conditions were investigated. To assess these relationships, dead drag values (i.e. drag values measured on dead, straight individuals) of 27 riverine species (108 individuals in total) common in France were experimentally measured under various flow conditions. These values served to estimate the C_{dmin} of fish. For pelagic species, C_{dmin} values were related to both preferred and near-maximum flow velocity used by the fish in nature. Explaining 61% of its variability, C_{dmin} was described using six morphological variables, which demonstrates the functional link between fish morphology and velocity use. For all studied species, a model explained 94% of drag variability using the Reynolds number of fish and three morphological variables. The link between morphology and drag force at given velocity conditions provides simple elements for modelling fish energetics in the context of physical habitat use. Moreover, the relationships between fish velocity use and their C_{dmin} open many applied perspectives, such as assessing the species abilities to withstand discharge modulations.

Key words: Ecomorphology / Adaptation / Drag coefficient / Habitat preferences / Fish energetics

Résumé – Aptitudes hydrodynamiques des poissons dulçaquicoles : un lien fonctionnel entre morphologie et utilisation des vitesses de courant. Améliorer la connaissance des stratégies d'utilisation de l'habitat physique (notamment des vitesses de courant) par les poissons est cruciale pour mieux comprendre et/ou estimer les effets de perturbations (e.g. changement global) ou de restaurations sur la dynamique des populations piscicoles. Des études récentes décrivent précisément des cinématiques ou des bilans énergétiques de nage, souvent spécifiques et difficilement transposables à d'autres espèces. Le but de cette étude est de revenir à des relations écomorphologiques générales entre forme du corps et utilisation des vitesses de courant, en s'intéressant à un aspect fonctionnel de la morphologie des poissons : leur potentialité hydrodynamique. Pour cela, les relations entre le coefficient de traînée minimum (C_{dmin}, constant aux forts nombres de Reynolds), l'utilisation des vitesses de courant, la morphologie des poissons et la force de traînée s'exerçant sur eux dans des conditions d'écoulement données sont étudiées ici. Afin de préciser ces relations, des valeurs de traînée passive (mesurées dans différentes conditions d'écoulement sur des individus morts) ont été prises sur 27 espèces (108 individus au total) dulçaquicoles, communes en France. Ces valeurs de traînée ont permis de déterminer le C_{dmin} des poissons. Pour les espèces de pleine eau, ce C_{dmin} a pu être mis en relation avec les vitesses de courant préférées et les vitesses maxima fréquentées en milieu naturel. Le C_{dmin} a pu être estimé (variabilité expliquée à 61 %) grâce à six variables morphologiques, ce qui a permis d'établir un lien fonctionnel entre la morphologie des poissons et leur utilisation des vitesses de courant. La traînée en pleine eau de toutes les espèces étudiées a pu être modélisée (variabilité expliquée à 94 %) grâce au nombre de Reynolds des poissons et trois variables morphologiques. Le lien entre morphologie et force de traînée dans des conditions d'écoulement données apporte des éléments simples pour estimer la dépense énergétique des poissons en milieu naturel. De plus, les relations entre l'utilisation des vitesses de courant par les poissons et leur C_{dmin} ouvrent de nombreuses perspectives appliquées, notamment en ce qui concerne l'estimation des capacités de résistance des espèces face à des modulations de débit.

---

[a] Corresponding author: `sagnes@biomserv.univ-lyon1.fr`

1 Introduction

1.1 Scientific context

Relating species traits to environmental constraints has been a major objective since the beginning of ecology as a scientific discipline (Statzner et al. 2001). Predicting communities from ecological and biological traits of species and habitats characteristics is still a key issue in modern ecology (Keddy 1992). For example, it is now well known that species trait diversity increases with the heterogeneity of the physical habitat, whereas they decrease when environmental constraints are great (Statzner et al. 2001). In running waters, flow is a major factor determining ecological processes and patterns (Statzner et al. 1988; Power et al. 1995). Consequently, lotic fish ecologists often linked biological characteristics of fish to physical habitat characteristics at various spatial scales (Reiser et al. 1989). However, at any scale, the existing predictive models of riverine fish ecology cannot be applied to species with unknown habitat preferences (Horwitz 1978; Schlosser 1982; Gore and Nestler 1988; Nestler et al. 1989; Palmer and Poff 1997). To solve this problem, models have to include general fish traits that are related to physical habitat use (Oberdorff and Hughes 1992; Persat et al. 1994). It was previously demonstrated that water flow drives predictable phenotypic variation in disparate groups of fish (Langerhans 2008). In this context, the present study relates the hydrodynamic characteristics of riverine fish to their physical habitat (i.e. velocity) use and some readily measurable morphological traits, as the latter could serve to predict habitat use of fish.

Fish morphology depends on different environmental or behavioural factors such as salinity (Holliday 1969), presence of predators (Brönmark and Pettersson 1994), food regime (Robinson and Wilson 1995), and often on flow constraints in natural habitat (Hubbs 1941; Gatz 1979; Scarnecchia 1988; Wikramanayake 1990; Pouilly 1993; McLaughlin and Grant 1994; Pakkasmaa and Piironen 2001; Brinsmead and Fox 2002; Langerhans et al. 2003). In all these studies, morphological and ecological patterns were linked using a descriptive approach (i.e. statistical correlations between fish morphology and environmental variables), whereas functional analyses of different morphotypes that quantify their "performance" under given constraints are rare (e.g., Lagergren et al. 1997). Given that "*the utility of morphological variables as ecological indicators depends upon our understanding of how the variable affects the ability of the organism to perform a particular task*" (Wainwright 1996, p. 1336), such functional analyses should provide insights into relationships between morphology and ecology (see also Ricklefs and Miles 1994). Correspondingly, variation in habitat use of *Thymallus thymallus* (the European grayling) depended on differences in the hydrodynamic potential (i.e. a performance potential) of its different life stages (Sagnes et al. 1997; Sagnes et al. 2000).

The hydrodynamic potential of fish affects their energetic budget and minimization of flow resistance should favor the use of lotic habitats. In such habitats, the energetic loss due to swimming is considerable (Boisclair and Sirois 1993) and may be partly governed by morphological characters (Boily and Magnan 2002) and/or swimming behaviour (Borazjani and Sotiropoulos 2008). The energy expenditure of swimming fish has been estimated for several freshwater fish species (Fausch 1984; Hughes and Dill 1990; Frith and Blake 1995; Hughes and Kelly 1996; Pettersson and Brönmark 1999; Rosenfeld and Boss 2001), as well as robot-fish (Barrett et al. 1999). These estimates rely upon field observations of fish swimming behaviour, respirometry experiments, numerical simulations or design and control of biomimetic swimming machines, which all may be quite costly. In addition, as the predictive models on habitat use, these estimates are not applicable to other species. Therefore, the main goal of the present study was to revive more general (and potentially transferable) ecomorphological relationships between body shape and strategies of velocity use by highlighting a functional aspect of fish morphology: the hydrodynamic potential.

1.2 Physical framework and objectives

The ability of a fish to swim towards a shelter or to resist flow depends partially on its hydrodynamic characteristics that affect the drag (i.e. the force into the direction of the relative water movement) acting on it (Vogel 1994). Drag can be calculated by:

$$D = 0.5\,\rho\,S\,U^2 C_d \tag{1}$$

where D (N) = drag, ρ (kg m^{-3}) = freshwater density, S (m^2) = a reference surface area of the body, U (m s^{-1}) = relative velocity between flow and the body, C_d (dimensionless) = drag coefficient, which depends on the body shape and the Reynolds number (Re). The latter scales the relative importance of inertial to viscous forces (Vogel 1994), through:

$$Re_L = (LU)/\nu \tag{2}$$

where Re_L (dimensionless) = Reynolds number scaled to L, L (m) = a linear dimension of the body, and ν (m^2 s^{-1}) = kinematic water viscosity, which depends on water temperature. Here, Re_{Ls}, which is the Reynolds number scaled to fish standard length (L_S), will be used. Dimensionless parameters such as Re_{Ls} are largely used in physics, engineering and ecology, as they describe energetic similitude among systems of different scales (Charnov and Berrigan 1991; Yalin 1992).

In a given flow, morphology governs the hydrodynamic potential of a fish, as body shape affects C_d in Eq. (1). For example, a spherical or a streamlined shape will minimize C_d (and subsequently drag) at low-Re_{Ls} (i.e. viscous forces predominating) or high-Re_{Ls} (i.e. pressure forces predominating) conditions, respectively (Webb 1975; Vogel 1994). As an example, in fish swimming behaviour, viscous forces effects remain important up to a Re_{Ls} of ~450 (Fuiman and Batty 1997). Moreover, C_d values of different body shapes partly depend on the relative position (along the body) of the maximum body depth (i.e. relative shoulder position) (Welch 1935; Fish et al. 2007) or the ratio of body length to its maximum depth (i.e. the fineness ratio) (Webb 1975; Blake 1983; Statzner and Holm 1989). Theoretically, a plot of C_d against Re_{Ls} should level towards a minimum value of C_d (called hereafter C_{dmin}) at high Re_{Ls} (but before the transition to fully turbulent wake, which occurs at Re values between 5×10^5 and 1×10^6 for streamlined bodies, see Vogel 1994, pp. 94, 111). At these Re_{Ls} conditions, the optimal value (i.e. minimizing C_{dmin} and subsequently drag of submerged bodies) of the fineness ratio is ~4.5 (Webb 1975; Blake 1983). The optimal value of shoulder position should be ~0.3, which is the usual value for standard NACA (i.e. National Advisory Committee for Aeronautics) streamlined bodies [considering old surveys (Welch 1935), an average value for fish is 0.36; the average value for some cetacean flukes is 0.285 (Fish et al. 2007)].

We know that drag values of swimming fish may not be comparable to those of rigid bodies under similar flow conditions (see Methods). However, 1) following the above theoretical background, we expected that fish morphology could be related to their dead drag values (or coefficients) and 2) following ecomorphological perpectives, we wanted to check whether dead drag values (or coefficients) were correlated or not to the velocity fish use in their natural habitats. In this context, the first objective of the present study was to quantify the passive hydrodynamic performance of different fish species in terms of drag forces and to determine their C_{dmin} values, as C_{dmin} can be considered as a parameter synthesizing the hydrodynamic abilities of fish at high flow conditions. The second objective was to establish relationships between fish hydrodynamics (i.e. C_{dmin} values) and velocities they use in their natural habitat. A narrower and lower range of C_{dmin} values was expected for species inhabiting high velocity habitats (see above) in comparison to species using low velocity habitats. Thus, could C_{dmin} be used as a general physical trait that indicates fish velocity use? The third objective was to determine the relevant morphological variables playing a role in fish hydrodynamics, so we checked if C_{dmin} could be estimated from fish morphology. Thus, could C_{dmin} provide a functional link between fish morphology and velocities they use in their natural habitat, so that the latter could be predicted in a simple way (using morphology) for species with unknown habitat preferences? The fourth objective was to check if drag values could be estimated from Re_{Ls} conditions and fish morphology. We expected *a priori* that Re_{Ls} would explain much of the drag variability for fish (as Re explained 77% of C_d variability among lotic invertebrate species; Statzner 1987), but wanted to quantify how fish morphology contributed to the remaining percentage of unexplained drag variability. Thus, could the energetic costs of fish for known velocity conditions be predicted using Re_{Ls} and morphological variables?

2 Materials and methods

2.1 Problems in the quantification of fish hydrodynamics

Determining the drag and thereby the C_d values of fish is a difficult task, as drag may depend on body movements (Blake 1983; Anderson et al. 2001), schooling (McCutchen 1977), changes of pressure forces along the body (Gray 1936; Lang 1966), and/or skin mucus conditions (Bernadsky et al. 1993; Sagnes et al. 2000). Addressing all these details to assess potential relationships between fish hydrodynamics and habitat use would lead to complex and species-specific models, i.e. it would be impossible to elaborate a general and synthetical tool in the context of water management applications. Therefore, the present study was simplified by determining the hydrodynamic potential of dead fish. The implications of this simplification will be discussed in detail in the discussion section.

Even if performed on dead fish, drag measurements remain complicated. Several authors quantified drag of dead fish, plotting the C_d of fish over different Re_{Ls} values (reviewed in Webb 1975; Blake 1983). These results did not allow reliable interspecific comparisons of C_d values because of the heterogeneity of the methods used (Sagnes 1998). Thus, an accurate drag measuring device (see below) was used for a consistent drag assessment of four dead individuals (juveniles and/or adults obtained in diverse field campaigns) of the 27 most common species of fish (spanning a wide range of morphology and velocity use, Table 1) occurring in French running water systems. As each individual was exposed to various flow conditions (i.e. had various Re_{Ls}), comparable drag-Re_{Ls} and C_d-Re_{Ls} relationships were obtained for 108 specimens.

2.2 Morphometric measurements

Twenty eight morphometric variables (Fig. 1) potentially important for hydrodynamic considerations were measured on each fish using a method of image analysis that minimizes errors (Sagnes 1995). Fish shape was analysed after dividing all the measurements by L_S (note that fin areas were previously transformed by taking the square root of their value). Although such ratios can change during fish development due to allometric growth and although there are other ways to circumvent size effects (Atchley et al. 1976), e.g. when studying morphological changes during ontogeny (which is not the case here), we wanted to focus on easily interpretable variables reflecting a general body shape. Moreover, we wanted to check if variables known to be theoretically important in hydrodynamics of man-made streamlined bodies (e.g. relative shoulder position and fineness ratio, both related to length, see introduction) could be of particular interest in fish hydrodynamics.

As some of these morphometric variables might be correlated with each other, the potentially redundant variables had to be eliminated from the analyses. However, the five variables known to be theoretically important in hydrodynamics (Vogel 1994) were always included, ignoring correlations among them. These variables were: (1) maximum body depth (D_{ma}) over L_S (the reciprocal value of the fineness ratio); (2) maximum body width (W_{ma}) over L_S (the reciprocal value of a lateral fineness ratio); (3) length to the maximum body depth (L_{dma}) over L_S (the relative shoulder position); (4) length to the maximum body width (L_{wma}) over L_S (a lateral relative shoulder position); and (5) the compression index (D_{ma}/W_{ma}). Pearson correlation values among these five variables were <0.50, except that D_{ma}/W_{ma} had a value of 0.79 with D_{ma}/L_S. In addition, five other variables with correlation values <0.60 among each other and with any of the previous five variables (this was an arbitrary choice to include some of the least correlated morphological variables in the analyses) were retained. These five additional variables were: (1) length to the anterior insertion of caudal fin (L_{ca}) over L_S; (2) length of caudal peduncle (L_{cp}) over L_S; (3) length to posterior edge of operculum (L_{op}) over L_S; (4) length to the anterior insertion of pelvic fins (L_{pv}) over L_S; and (5) width of caudal peduncle at the posterior insertion

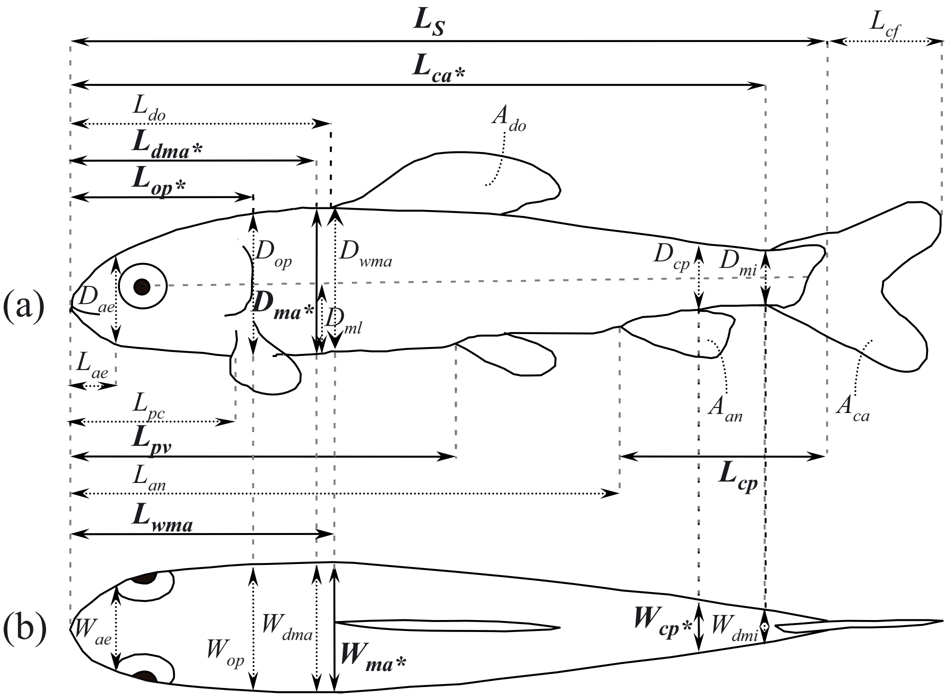

Fig. 1. Measurements (ordered alphabetically) taken on each fish: (a) lateral view, (b) dorsal view. Areas: A_{an}, A_{ca} and A_{do} = respectively anal, caudal and dorsal fin area. Depths: D_{ae} = pre-orbital depth; D_{cp} = depth of caudal peduncle at the posterior insertion of anal fin; D_{ma} = maximum body depth; D_{mi} = minimum body depth at the anterior insertion of caudal fin; D_{ml} = part of D_{ma} below the median line (which runs through the centre of the eye and the most distal vertebra); D_{op} = depth at the posterior edge of operculum; D_{wma} = depth at W_{ma}. Lengths: L_{ae} = pre-orbital length; L_{an} = length to the anterior insertion of anal fin; L_{ca} = length to the anterior insertion of caudal fin; L_{cf} = length from posterior scale to end of caudal fin; L_{cp} = length of caudal peduncle, from the anterior insertion of anal fin to the most posterior scale; L_{do} = length to the anterior insertion of dorsal fin; L_{dma} = length to D_{ma} ("shoulder" position); L_{op} = length from tip of the snout to the posterior edge of operculum; L_{pc} and L_{pv} = respectively length to the anterior insertion of pectoral and pelvic fins; L_{wma} = length to the maximum body width; L_S = standard length; Widths: W_{ae} = pre-orbital width; W_{cp} = width of caudal peduncle at D_{cp}; W_{dma} = width at D_{ma}; W_{dmi} = width at D_{mi}; W_{ma} = maximum body width; W_{op} = width at D_{op}. Variables in bold and with solid arrows were used for modelling fish hydrodynamics (see methods), those with an asterisk were significant in the models (see results).

of anal fin (W_{cp}) over L_S. Hereafter, all analyses will refer to and use these 10 "independent" (i.e. being the least correlated) morphometric variables.

2.3 Drag measuring device and assessment of the hydrodynamic potential of fish

Drag on dead fish was measured in an open laboratory flume with a hydrodynamic balance (see details in Sagnes et al. 2000), through the deformation of strain gauges. This deformation was transformed to drag values by a conditioner. To avoid body fluttering that would have increased the variability of measurements (Webb 1975; Sagnes et al. 2000), fish were straightened for two months in a 4% formaldehyde solution. Before measurements, their paired fins were glued along the body and their mouth was fixed shut (see Sagnes et al. 2000). Fish were fixed to the device via a steel rod having a diameter being proportional to fish size (i.e. 1.2 mm for small, 2.0 mm for medium and 4.0 mm for large specimens). Preparing all fish in this way enabled hydrodynamic comparisons among them. Steel rod drag was measured for each used rod diameter (no fish attached) at different current velocities. Fish drag was calculated as difference between the fish+rod drag and the rod drag alone at the same velocity (see details and rationale in Sagnes et al. 2000). The measured drag values were also corrected for fish weight, which induced a vertical component tending to underestimate drag (see Sagnes et al. 2000).

For each individual fish, drag measurements at 10 different current velocities (regularly distributed between ~0.09 and ~1.18 m s^{-1}, determined at fish snout with a mini-propeller: Streamflo Velocity Meter 400, probe No 403, NIXON, Cheltenham, Gloucestershire, England) allowed the calculation of the C_d. For this purpose, S_f (m^2) (i.e. the profile area, which is the area of the organism projected onto a plane perpendicular to the main direction of the flow) was used as the reference surface area in Eq. (1). S_f was estimated as the surface area determined by two orthogonal ellipses that had main axis corresponding to the maximum depth (D_{ma}) and the maximum width (W_{ma}) of the body respectively (see Fig. 1 for abbreviations of morphometric variables):

$$S_f = (D_{ma}/2 \times W_{dma}/2 \times \pi) + (W_{ma}/2 \times D_{wma}/2 \times \pi) - (W_{dma}/2 \times D_{wma}/2 \times \pi). \tag{3}$$

Previous unpublished data on fry and 0+ grayling showed that Eq. (3) provides good estimates of S_f [i.e. fits between measured (from image analysis of frontal fish views, see

Table 1. Species name, C_{dmin} (mean of four individuals, ±1 SE, from the present experiment), velocity class preference (*Pref*, from Lamouroux et al. 1999a and Greenberg et al. 1996) and upper velocity beyond which the preference coefficient drops below 0.2 ($U_{p<0.2}$ in m s^{-1}, from Pouilly 1994). *Pref* classes: **1** = 0 – 0.05 m s^{-1}, **2** = 0.05 – 0.2 m s^{-1}, **3** = 0.2 – 0.4 m s^{-1}, **4** = 0.4 – 0.8 m s^{-1} and **5** > 0.8 m s^{-1}. When available, *Pref* and $U_{p<0.2}$ were indicated for the length-class of fish that was used in drag measurements.

Scientific name	Common name	$C_{dmin}(\times 10^{-1})$	*Pref**	$U_{p<0.2}$*
Abramis brama (L., 1758)	Carp bream	2.73 ± 0.09	1	
Alburnoides bipunctatus (Bloch, 1782)	Spirlin	2.56 ± 0.03	2	0.90
Alburnus alburnus (L., 1758)	Bleak	2.03 ± 0.03	4	1.18
Ameiurus nebulosus (Lesueur, 1819)	Brown bullhead	3.23 ± 0.07	2	
Barbatula barbatula (L., 1758)	Stone loach	3.09 ± 0.14	4	2.40
Barbus barbus (L., 1758)	Barbel	2.58 ± 0.08	5	2.40
Blicca bjoerkna (L., 1758)	White bream	2.83 ± 0.17	1	
Chondrostoma nasus (L., 1758)	Common nase	2.08 ± 0.01	5	2.14
Cottus gobio (L., 1758)	Bullhead	3.72 ± 0.08	5	
Cyprinus carpio (L., 1758)	Common carp	3.25 ± 0.06		
Esox lucius (L., 1758)	Pike	3.20 ± 0.04	1	
Gasterosteus aculeatus (L., 1758)	Three-spined stickleback	2.86 ± 0.03		
Gobio gobio (L., 1758)	Gudgeon	2.96 ± 0.04	1	0.96
Gymnocephalus cernuus (L., 1758)	Ruffe	2.90 ± 0.08		
Lepomis gibbosus (L., 1758)	Pumpkinseed	2.63 ± 0.02	1	0.15
Leuciscus cephalus (L., 1758)	Chub	2.14 ± 0.05	1	0.80
Leuciscus leuciscus (L., 1758)	Common dace	2.35 ± 0.09	2	0.87
Leuciscus souffia souffia (Risso, 1827)	Blageon	2.40 ± 0.04	2	0.98
Perca fluviatilis (L., 1758)	European perch	2.84 ± 0.13	1	0.29
Phoxinus phoxinus (L., 1758)	Minnow	2.28 ± 0.11	1	0.42
Rhodeus sericeus (Pallas, 1776)	Bitterling	2.83 ± 0.05	1	
Rutilus rutilus (L., 1758)	Roach	2.73 ± 0.05	1	0.18
Salmo trutta fario (L., 1758)	Brown trout	2.16 ± 0.03	3	1.00
Sander lucioperca (L., 1758)	Pikeperch	3.10 ± 0.05		
Scardinius erythrophthalmus (L., 1758)	Rudd	2.68 ± 0.03	1	
Thymallus thymallus (L., 1758)	Grayling	2.49 ± 0.07	3	0.63
Tinca tinca (L., 1758)	Tench	2.39 ± 0.03	1	

* Lacking entries indicate data unavailability.

method in Sagnes 1995) and calculated (with Eq. (3)) values were good (n = 20, r^2 = 0.89)].

For comparisons of C_d values at different flow conditions and fish lengths, C_d values were plotted against Re_{Ls} so that differences in C_d values at a given Re_{Ls} were related to differences in body shape (note that, in the present experiment, theoretical irregularities occurring at $Re > 10^6$ in the C_d-Re relation [see Vogel 1994] were irrelevant as the maximum Re_{Ls} observed was $\sim 1.8 \times 10^5$). As expected, plots of C_d values against Re_{Ls} levelled at high Re_{Ls} (providing C_{dmin}). C_{dmin} of each individual was obtained from its C_d value at the highest Re_{Ls} (corresponding threshold value of that individual). At the species level, C_{dmin} of the different species were estimated as the mean of individual C_{dmin} values (n = 4).

A model II ANOVA was performed on individual C_{dmin} values to determine how similar these values were for specimens from the same species relative to variation among species.

2.4 Relating fish hydrodynamics to velocity use and morphology

We expected that relationships between fish hydrodynamics and velocities they use in their natural habitat would be biased for benthic species (i.e. *B. barbatula*, *B. barbus*, *C. gobio*, *G. gobio*, *A. nebulosus* and *T. tinca*). For these species, indeed, the values of preferred and used velocities are generally overestimated in the literature, because they live in a steep velocity gradient near the bottom, while velocity measurements in field are usually done away from the river bottom. Therefore, analyses including preferred and used velocities in natural habitats mainly focussed on pelagic species. Fish hydrodynamics and velocity use were related in two ways. First, C_{dmin} values of the different species were related to their velocity preferences. For each species, a velocity preference class (i.e. a velocity range in which field observations demonstrated the highest abundances for each species: Lamouroux et al. 1999a) was used; such classes were available for 22 of the 27 species studied (Table 1). The velocity preference of *T. thymallus* (Greenberg et al. 1996) was added to these data, but we failed to find reliable published velocity preferences for the four remaining species (see Table 1). Second, as C_{dmin} describes hydrodynamic abilities of fish at high Re_{Ls} conditions [i.e. at high velocities, see Eq. (2)], the C_{dmin} value of each species was plotted against a near-maximum velocity it uses in natural conditions. Given that the exact upper limit of the velocity niche cannot be obtained from preference curves, this near-maximum velocity was arbitrarily defined as the current velocity beyond which the preference coefficient (scaled to 1 for the preferred velocity) of a species (available for 15 species) drops below 0.2 ($U_{p<0.2}$, data from Pouilly 1994, see Table 1).

In contrast, although benthic species were not included in the analyses relating hydrodynamic potential and velocity use, they were used (jointly with pelagic species) to characterize the hydrodynamic potential of fish from morphometric characteristics. Thereby, we addressed the widest possible range of morphologies in the evaluation of C_{dmin} from fish morphometric features (i.e. we obtained a model as general as possible), and particular morphologies of benthic species (e.g. usual ventral flattening) were of interest in this general model. Therefore, for the 108 individuals, C_{dmin} was modelled using the 10 morphological variables and the first order interactions between all these variables, using a stepwise forward regression that included only significant independent variables. Similarly, fish dead drag was modelled using Re_{Ls}, the 10 morphological variables and the first order interactions between them. As stated above, morphological variables could have some optimal value (i.e. below- and above which C_{dmin} should increase). Therefore, the individual values of the 10 morphological variables were plotted against the individual C_{dmin} values, and a piecewise regression (using Systat© 10 package: Wilkinson et al. 1996) was used to detect a potential optimal value (i.e. a significant inflexion point of the plot). When a variable (x) presented a significant optimal value (a), it was used in the linear models as $|x–a|$.

To test the robustness of these C_{dmin} and drag models, their respective parameters were estimated using data from half of the individuals (n = 54, randomly chosen); these models were subsequently applied on the data from the 54 remaining individuals (independent data set).

3 Results

3.1 C_d-Re_{Ls} relations, velocity use and C_{dmin}

The variability of C_d values among all species and specimens was higher at low Re_{Ls} than at high Re_{Ls} (Fig. 2). All individual plots of C_d values against Re_{Ls} per species showed a similar pattern, and the variability of C_d values among the four specimens of each species (at a given Re_{Ls}) was very low (see Fig. 2b, c for four examples). At low or moderate Re_{Ls}, C_d values of a lotic species could either be higher (Fig. 2b) or lower (Fig. 2c) than those of a lentic species, and there was no relationship between C_d values and velocity preferences (lotic versus lentic). At higher Re_{Ls}, however, lotic species usually had lower C_d values (and therefore C_{dmin} values) than lentic species (see Fig. 2b, c for two examples).

The percentage of variance in individual C_{dmin} values due to variability between species was 88%, whereas the percentage of variance in these values due to variability within species was 12% (model II ANOVA, $d.f. = 26, 81$, $p < 0.001$). The mean species values of C_{dmin} ranged from 2.03×10^{-1} to 3.72×10^{-1} (Table 1). Species with the lowest values were *A. alburnus*, *C. nasus*, *L. cephalus*, *S. trutta fario* and *P. phoxinus*, while those with the highest values were *C. gobio*, *C. carpio*, *A. nebulosus*, *E. lucius* and *S. lucioperca*.

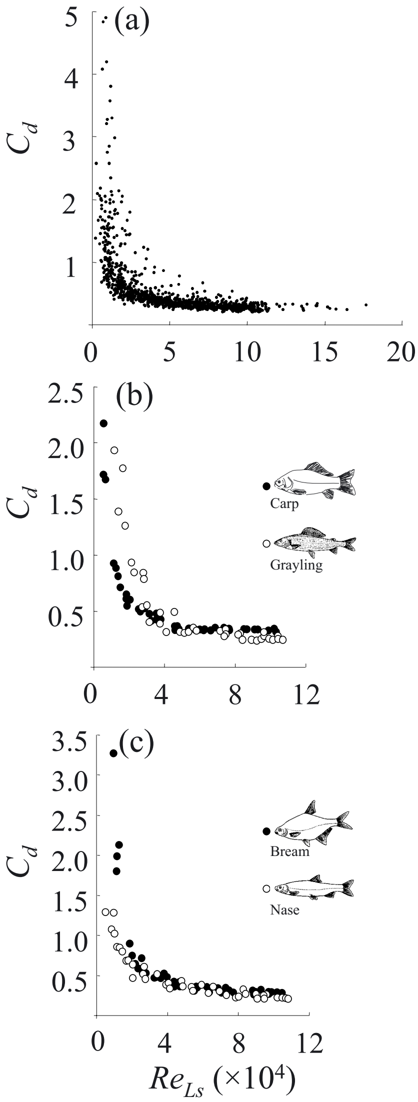

Fig. 2. Drag coefficient (C_d, dimensionless) against Reynolds number relative to standard length (Re_{Ls}, dimensionless) for 27 riverine fish species. (a) all studied specimens (4 individuals for each species), (b) carp (*C. carpio*, lentic species, black circles) and grayling (*T. thymallus*, lotic, open circles), (c) bream (*A. brama*, lentic, black circles) and nase (*C. nasus*, lotic, open circles).

Ignoring the benthic species (see Methods), the velocity preference of the remaining 17 pelagic species tended to reflect their hydrodynamic potential. Whereas pelagic species with high C_{dmin} values exclusively prefer low flow velocity habitats, species with a low C_{dmin} value either prefer low, intermediate or high velocity habitats (Fig. 3).

Excluding the benthic species (for the reasons stated before), the near-maximum velocity used by the pelagic species in their natural habitat ($U_{p<0.2}$, see methods) was negatively correlated to their C_{dmin} (Fig. 4).

3.2 Drag coefficient and morphology

Seven significant relationships between the individual values of C_{dmin} and the morphological variables were found. C_{dmin}

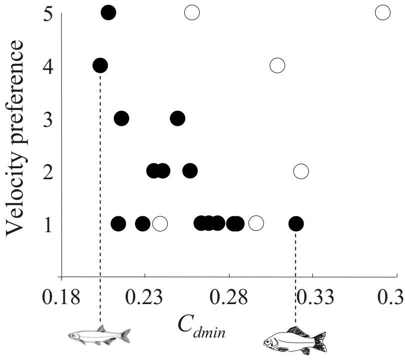

Fig. 3. Velocity preference (see Table 1) against minimum drag coefficient (C_{dmin}, see Table 1) for 23 riverine fish species (preferences were not available for the 4 remaining studied species). Black circles correspond to pelagic species, and open circles to benthic species (*B. barbatula*, *B. barbus*, *C. gobio*, *G. gobio*, *I. nebulosus* and *T. tinca*), for which the velocity preferences were biased (see text). Morphologies corresponding to a low (bleak) and a high (carp) value of C_{dmin} are indicated.

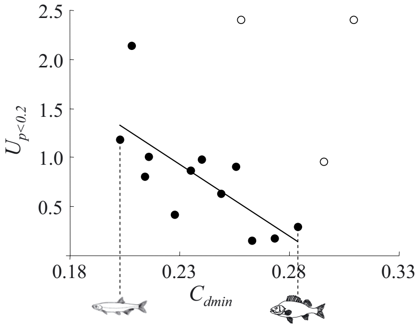

Fig. 4. Relationship between hydrodynamics (C_{dmin}, dimensionless) of 12 pelagic riverine fish species (black circles) and the near-maximum velocity they use in their natural habitat ($U_{p<0.2}$ in m s^{-1}, see methods). Regression parameters (±1SE in brackets): $U_{p<0.2} = +4.37(\pm 1.07) - 14.97(\pm 4.46)C_{dmin}$, $r^2 = 0.48$, $p = 7 \times 33 \times 10^{-3}$. Benthic species (open circles: *B. barbatula*, *B. barbus* and *G. gobio*) were not considered in the regression (see text). $U_{p<0.2}$ was not available for the remaining 12 species studied. Morphologies corresponding to a low (bleak) and a high (perch) value of C_{dmin} are indicated.

was positively correlated to L_{op}/L_S, W_{ma}/L_S and L_{ca}/L_S, ($r^2 = 0.31$, $p < 0.001$; $r^2 = 0.13$, $p < 0.001$; $r^2 = 0.03$, $p = 0.036$, respectively) and negatively correlated to L_{cp}/L_S ($r^2 = 0.07$, $p = 0.003$). There was an optimal value (i.e. at which C_{dmin} was the lowest, obtained from piecewise regression) for D_{ma}/L_S, L_{dma}/L_S and L_{pv}/L_S (0.201, 0.464 and 0.405, respectively).

Using stepwise forward regression, C_{dmin} could be estimated by linearly combining the previous morphological variables (±1 SE in brackets):

$$\begin{aligned} C_{dmin} = & -0.521(\pm 0.125) + 0.693(\pm 0.129)(L_{ca}/L_S) \\ & +0.430(\pm 0.090)(L_{op}/L_S) \\ & +0.569(\pm 0.123)(W_{ma}/L_S) \\ & +0.294(\pm 0.067)|(L_{dma}/L_S) - 0.464| \\ & -0.936(\pm 0.259)(W_{cp}/L_S) \end{aligned} \tag{4}$$

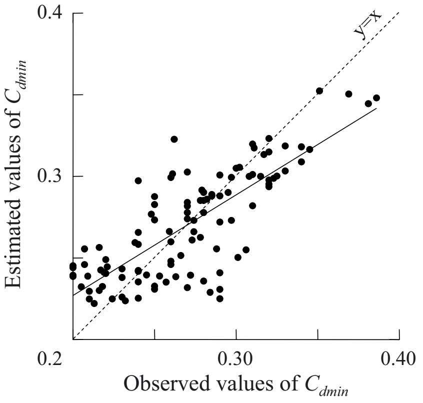

Fig. 5. Estimated (from Eq. (4), see text) versus observed values of C_{dmin} of 108 riverine fish individuals (27 species, four individuals per species). Regression parameters (±1SE in brackets): $y = 1.04 \times 10^{-1}(\pm 1.30 \times 10^{-2}) + 6.13 \times 10^{-1}(\pm 4.73 \times 10^{-2})x$, $r^2 = 0.61$, $p < 10^{-15}$.

$r^2 = 0.61$, $p < 10^{-15}$.

First order interactions between the morphological variables were not significant in the analysis. The C_{dmin} values estimated by this model correlated significantly with the observed values, although the estimated values were about 10% higher than the observed ones for low C_{dmin} values and about 10% lower for high C_{dmin} values (Fig. 5).

To test the robustness of this model, parameters of Eq. (4) were estimated using one half of the studied individuals and applied on the other half. The correlation between "blind" predictions and observations was good ($r^2 = 0.68$, $p < 10^{-13}$) but the slope (0.66 ± 0.06) of this relationship was, as in Fig. 5, smaller than one (i.e. slight over- and underestimations of low- and high C_{dmin} values, respectively).

3.3 Drag, Reynolds number and morphology

Modelling D as a function of Re_{Ls} required logarithmic transformations. The correlation between ln$D$ and lnRe_{Ls} was high ($r^2 = 0.86$, $p < 10^{-15}$). A stepwise forward regression of ln$D$ on lnRe_{Ls} and the morphometric variables of all the individuals studied showed that the integration of maximum body depth (D_{ma}) over L_S and maximum body width (W_{ma}) over L_S in the regression improved the explained variance from 86% to 94% (±1 SE in brackets):

$$\begin{aligned} lnD = & -20.250(\pm 0.130) + 1.345(\pm 0.011)(lnRe_{Ls}) \\ & +2.891(\pm 0.135)(D_{ma}/L_S) \\ & +4.691(\pm 0.312)(W_{ma}/L_S) \end{aligned} \tag{5}$$

$r^2 = 0.94$, $p < 10^{-15}$.

First order interactions between Re_{Ls} and the morphological variables were not significant in the analysis. The drag values estimated by this model correlated highly significantly with the observed values (Fig. 6).

To test the robustness of this model, parameters of Eq. (5) were estimated using one half of the studied individuals and applied on the other half. The correlation between "blind" predictions and observations ($r^2 = 0.94$, $p < 10^{-15}$) was better

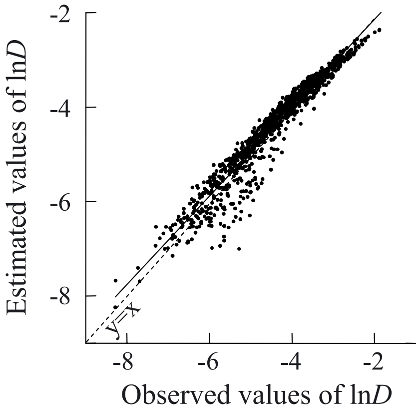

Fig. 6. Estimated (from Eq. (5), see text) versus observed values of drag (D, in N) for 108 riverine fish individuals (27 species, four individuals per species) at 10 hydraulic conditions (i.e. ten Re_{Ls}, see text) each. Regression parameters (±1 SE in brackets): $y = -2.79 \times 10^{-1}(\pm 3.38\times10^{-2})+9.36\times10^{-1}(\pm 7.43\times10^{-3})x$, $r^2 = 0.94$, $p < 10^{-15}$.

than for the C_{dmin}, and the slope (0.91 ± 0.01) of this relationship was near one.

4 Discussion

4.1 Validity of rigid body measurements

To assess relationships between morphology, hydrodynamic abilities and velocities fish use in their natural habitats requires the measurement and comparison of relevant components of swimming performance (e.g. drag) among fish varying in body shape and strategies of velocity use. To explicitly examine the link between body morphology and drag, hydrodynamic data were obtained on rigid bodies. It is well known that swimming behaviour would likely modify flow patterns around such bodies (Webb 1975; Blake 1983; Anderson et al. 2001; Schultz and Webb 2002). However, rigid-body measurements of drag could help to understand fish hydrodynamics during a typical phase of various swimming behaviours such as burst-and-coast swimming (where the fish body is kept motionless and straight during the coast phase, see Weihs 1980; Videler 1993) or, at a lesser extent, station holding (reduced body movements). For example, if the Reynolds number scaled to total length of the fish is >450, burst-and-coast swimming is ~ twice less costly than steady swimming at the same average speed (Videler and Weihs 1982; Fuiman and Batty 1997). Therefore, hydrodynamic optimisation (e.g. C_d minimisation) during the coasting phase should be of great benefit for fish and dead drag values can be used to evaluate this optimisation. During other swimming behaviours, fish movements can either increase (Blake 1983) or reduce (Gray 1936; Lang 1966) drag, the latter by delocating pressure forces from the body front to the rear through the creation of vortices. Moreover, other parameters such as skin surface condition (e.g. presence or absence of skin mucus) may reduce drag for live fish (Bernadsky et al. 1993; Sagnes et al. 2000).

Facing all these uncertainties, we asked ourselves if we produced meaningful results (i.e. was our simplification to measure drag on dead fish justified?). Three points support a "yes" as answer to this question. First, whatever the relationship between drag of dead and live fish, we searched for a comparable relative scale of C_d values depending on the general body shape of many fish species, using a large number of individuals and a repeatable method. Second, quantifying drag values for live swimming fish is also problematic and, depending on the theoretical approach, uncertainties remain (Schultz and Webb 2002). Published results (drag or C_d values) on live fish at a given Re_{Ls} are either comparable to (Gray 1957) or far below (Magnan 1930; Lang and Daybell 1963; Hughes and Kelly 1996) those obtained in this study. In contrast, the changes of C_d values over Re_{Ls} (Fig. 2) as well as the C_{dmin} (obtained for high Re_{Ls}, Table 1) of the species studied here corresponded well to results in comparable studies on other species (Webb 1970; Kokita and Mizota 2002). Third, the fact that lotic species have lower C_d values than lentic species at high Re_{Ls} (Figs. 2, 3, 4) suggested the adaptation of body shape to the use of different flow habitat types. Given that many of the species studied are not closely related (phylogenetically), they likely differ in many aspects other than body morphology. This scenario usually obscures cause-and-effect relationships. However, in this study, morphology alone allowed the prediction of fish drag, and C_{dmin} (irrespective of all other potential differences) allowed good predictions in terms of preferred velocities and maximum velocities fish use in their natural habitats. These observed trends provide evidence for their ecological importance, because they were observed despite variation of other characteristics across the species, and despite the fact that body shape is influenced by many factors other than water flow. Therefore, all these results made sense in the context of ecomorphology and hydrodynamic thinking, and the above points provided multiple and diverse support that the method employed produced meaningful results. As there are relationships between C_{dmin} and preferred velocities and maximum used velocities of various fish species, dead drag values seem to be of interest in ecomorphological studies dealing with fish velocity use. A future step should be to determine potential links between dead and live (i.e. swimming) drag values. This goal may be approached by combining morphological features with velocity and power consumption, which seem the best measures of swimming performance (Schultz and Webb 2002).

4.2 Velocity use and C_{dmin}

Species living in high current velocity conditions had a high hydrodynamic potential (i.e. low C_{dmin}). On the other hand, in low current velocities conditions, fish presence did clearly not depend on their hydrodynamic potential as lentic fish had a wide range of C_{dmin} values (Fig. 3). This result confirms results of Pettersson and Hendenström (2000), who found that fish with low-drag morphs (i.e. low C_{dmin} in the present study) use a broader range of velocities than fish with high-drag morphs. This pattern also confirms ideas expressed early in the 20th century, when increasing habitat harshness (e.g. increasing velocity) was seen as the cause for increasing similarity in the morphological adaptations (and other traits) of the species occurring in the habitat (Thienemann 1918; Hesse 1924).

The negative correlation between C_{dmin} and the maximum velocity fish use in their natural habitat (Fig. 4) is useful to understand the effects of velocity modifications on fish habitat use, and particularly to assess the effects of "exceptional" high discharge on fish communities. Considering also other factors such as shelter availability, C_{dmin} may help to predict whether a population or a community could withstand a discharge increase (e.g. an occasional one after hydroelectric peaking, or a permanent one after an increase of the minimum regulated discharge) of a given magnitude. It may also help in assessing limiting current velocities for a given species in fishways or in river sections fish have to cross to reach their spawning habitats.

At the community level, functional attributes can be used for comparing system-level properties among taxonomically distinct faunas (Bellwood et al. 2002). In this context, C_{dmin} could be used as a physical trait defining fish guilds, which would help to better understand the functional link between fish morphotypes (see below) and velocities they use in their natural habitats. Therefore, C_{dmin} could be a useful complementary tool in the use of "descriptive" guilds focusing on morphometrics (Miller 1984), ecological or dietary characteristics (Mathieson et al. 2000) or habitat use (Vadas and Orth 2000; Wolter and Bischoff 2001; Lamouroux and Souchon 2002).

The relationships between C_{dmin} and the velocities used by fish in their natural habitat can currently not be generalized to benthic species. For this purpose, the velocities really used by benthic species (e.g. mean velocities close to the substrate) have to be measured during field campaigns.

Finally, it should be interesting in future studies to consider the potential links between fish morphology (or hydrodynamics) and flow turbulence (or vorticity), which are important aspects of fish habitat (Liao 2007).

4.3 Drag coefficient and morphology

A functional link between fish morphology and habitat use was previously established by studying the hydrodynamic abilities of *T. thymallus* during its ontogeny (Sagnes et al. 1997; Sagnes et al. 2000). In that species, successive optimisations of C_d values (through morphological changes) in the context of preferred velocities were observed. Through the present study, it is possible to generalize such a link to different riverine species as their C_{dmin} (which influences the range of velocities they can use, or *vice versa*) was significantly related to their morphology.

Among all the morphological variables considered here, L_{dma}/L_S and W_{ma}/L_S played a main role in fish hydrodynamics, as they partly explained C_{dmin} values (Eq. (4)). This is not surprising as these morphological variables correspond to the relative shoulder position and a lateral index of body compression (streamlining index), respectively. Previous theoretical considerations of simple geometric body shapes (Hoerner 1965) and measurements on benthic macroinvertebrates (Statzner and Holm 1989) illustrated the importance of such morphometric variables in hydrodynamic studies, as these variables govern the position of flow separation along the body, and thus the drag. However, the optimal value of L_{dma}/L_S found here (0.464) was quite different from the theoretical one (i.e. ~0.3 as L_{dma}/L_S is the shoulder position). Unexpectedly, L_{pv}/L_S had also an optimal value (of 0.405). This may be explained by the "complex" shape of a fish (compared to simpler geometric bodies usually used in hydraulic studies), which could lead to numerous interactions between the morphological variables that are very difficult to parse.

Variables like D_{ma}/L_S [i.e. a dorso-ventral index of body compression, previously identified as a main morphological variable explaining critical swimming speed of young fish (Fisher et al. 2005)] and L_{wma}/L_S (i.e. the lateral relative shoulder position) were expected to be important for fish hydrodynamics, but they did not appear in the C_{dmin} models. However, the optimal value of D_{ma}/L_S found in the univariate analysis (C_{dmin} was lowest at $D_{ma}/L_S = 0.201$) was similar to the theoretically optimal value (i.e. 0.222 as D_{ma}/L_S is the inverse of the fineness ratio, for which the optimal value is 4.5, Blake 1983). In contrast, other variables (L_{op}/L_S, L_{ca}/L_S and W_{cp}/L_S) were unexpectedly related to C_{dmin} (Eq. (4)). There are no apparent reasons for the importance of L_{op}/L_S in fish hydrodynamics. However, L_{ca}/L_S corresponds to the relative location of minimum body depth of the fish, which may be important for posterior flow separation (caused by the caudal fin). Similarly, W_{cp}/L_S corresponds to a relative width of the caudal peduncle, which may partly control lateral flow separation at the rear part of the body.

Given that the C_{dmin} of riverine fish species was related to the velocities they use in their natural habitats and could be estimated from fish morphology, using fish body shape (in the range of morphometrics and Re_{Ls} studied here) should in principle enable the prediction of velocity use for many species on a world-wide scale.

4.4 Drag, Reynolds number and morphology

As expected, drag values largely depended on Re_{Ls}, which alone explained about 86% of the drag variability. Although the addition of the two indices of body compression D_{ma}/L_S and W_{ma}/L_S into the model explained only 8% more of the drag variability (Eq. (5)), an optimisation of body shape (i.e. to decrease drag) through these morphological variables should be important in extreme velocity conditions, and should provide relevant energy gains for fish. Modelling the drag force of fish using Re_{Ls} and morphometrics provides interesting perspectives for studies of fish energetics, especially as Eq. (5) achieves good predictions in the range of morphometrics and Re_{Ls} studied here. For example, the prediction of the drag experienced by station holding fish at known Re_{Ls} conditions should enable the classification of individuals of different species using the drag they face in given velocity conditions. Such a classification could enable comparisons of habitat use at a local scale for sympatric species, by quantifying the relative constraints experienced by the different species rather than describing velocities they use in a purely descriptive way. Thereby, it would be possible to couple this functional modelling of velocity use by fish with physical habitat modelling (see examples of coupling of biological and physical models in

Lamouroux et al. 1998, 1999b). However, to understand how fish swimming behaviour modifies the drag on a fish body (i.e. modifies the drag measured on a rigid body), ecomorphological studies such as the present one have to be complemented by the commonly used energetic approach, which considers complex relations between biomechanics and forces acting on fish (e.g. Hughes and Kelly 1996).

4.5 Phenotypic plasticity and trade-offs affecting shape

Given the well-known intraspecific phenotypic plasticity, are the functional relationships between species shape and velocity use illustrated here relevant? Within a species, habitat use can vary among individuals (Moyle and Baltz 1985) and body shape of individuals can be affected by the hydraulic conditions in the used habitat (Riddell and Leggett 1981; Köhler 1992; Pakkasmaa and Piironen 2001; Langerhans 2008). Moreover, morphological condition may not always determine biomechanical function and ecology (Losos 1990) and "*there are many reasons that a structure might not be optimal for a function that it serves*" (Koehl 1996, p. 528). Body shape is constrained by genetic, phylogenetic and developmental factors, which can limit the realized traits of fish, such as drag reduction, through multiple morphological adaptations. Therefore, drag is obviously not the only factor affecting body shape (and consequently the hydrodynamic potential) of fish. For example, fish body shape may be strongly altered during growth by changes in temperature, salinity or nutrient availability (Barlow 1961; Holliday 1969; Wimberger 1993; Loy, et al. 1996). Biotic interactions also determine fish shape, as a deeper body constitutes a morphological defense against gape-limited piscivores (Holopainen et al. 1997; Pettersson and Brönmark 1999; Pettersson and Hendenström 2000) and foraging behaviour partly governs body shape (Webb 1984). Therefore, any ecomorphological consideration has to address the potential phenotypic plasticity of fish (Robinson and Wilson 1994). However, the present results showed that intraspecific variations of C_{dmin}, depending on morphology, should be less important than interspecific ones. These results confirm previous observations showing that intraspecific morphological variations are usually less important than interspecific ones, even for species of the same genus exhibiting relatively similar body forms (see Guill et al. 2003).

Finally, reducing drag is obviously not the only adaptation to resist flow. Using Eq. (5) (with specific average body shape and length and estimating Re_{Ls} from specific values of $U_{p<0.2}$), it appeared that, despite their low C_{dmin} values, species able to inhabit high velocity habitats encountered higher drag forces (e.g. 8.5×10^{-2} N for *C. nasus*) than species occurring at lower velocity conditions (e.g. 2.9×10^{-3} N for *L. gibbosus*). Therefore, low C_{dmin} values of species living in high velocities should help to minimize drag in such hydraulic conditions, but these species should have complementary adaptations to resist high flow forces. For example, they may either increase their proportion of red muscles (Broughton et al. 1981; McGuigan et al. 2003), their relative propulsive area (Fisher et al. 2005) or adopt a morphology reducing lift (Denny 1994). Beyond drag, future studies should also consider lift forces, which could be of great importance in determining whether an organism will be dislodged, especially in the case of benthic organisms, and especially because morphological characteristics that reduce drag typically increase lift (Statzner and Holm 1989).

5 Conclusion

The hydrodynamic potential of riverine fish provides a key element to predict specific fish velocity preferences and persistence at harsh flow conditions. Generally, mechanistic studies assume that particular processes at the organismic level are important in governing the behaviour of a system at a larger level of organisation (population, community or ecosystem) (Koehl 1989; Reilly and Wainwright 1994). Hence, the effects of morphology on hydrodynamic performance can have important ecological consequences for the functional ecology of riverine fish at different scales. For example, the present results illustrated that streamlining may be a factor determining species persistence during floods in natural river reaches, or in canalised reaches lacking refuges from the current (Scarnecchia 1988), and that the conservation of various physical habitats at a local scale (allowing the spatial segregation of species) is essential for the fish biodiversity in rivers. In addition, intercontinental convergence of stream fish morphology along hydraulic gradients (Lamouroux et al. 2002) could be explained by the hydrodynamic abilities of fish. Finally, this study also provided information that could serve to improve and to expand (towards species with unknown habitat preferences) models predicting fish-habitat relationships by including the hydrodynamic potential of fish species (or their drag constraints) in future studies.

Acknowledgements. R. Morel and J.-Y. Champagne from the Fluid Mechanics and Acoustics Laboratory of INSA-Lyon provided the water flume. J.C. Boyer, J.M. Carrouge, C. Roblin, L. Kaci and C. Mottet designed and improved the hydrodynamic balance. G. Carrel provided fish drawings of Figs. 2 and 3. B. Milcendeau and an anonymous referee gave helpful comments on a previous version of the manuscript. This study was partly funded by the Programme Interdisciplinaire de Recherche "Environnement" (PIRE) "Modélisation de l'utilisation spatio-temporelle de l'habitat par les poissons" of the CNRS (France) and the "Programme Fédérateur Environnement" of the XI$^{\text{ème}}$ Contrat de plan Etat-Région Rhône-Alpes (France). All this help is gratefully acknowledged.

References

Anderson E.J., McGillis W.R., Grosenbaugh M.A., 2001, The boundary layer of swimming fish. J. Exp. Biol. 204, 81–102.

Atchley W.R., Gaskins C.T., Anderson D., 1976, Statistical properties of ratios. I- Empirical results. Syst. Zool. 25, 137–148.

Barlow G.W., 1961, Causes and significance of morphological variation in fishes. Syst. Zool. 10, 105–117.

Barrett D.S., Triantafyllou M.S., Yue D.K.P., Grosenbaugh M.A., Wolfgang M.J., 1999, Drag reduction in fish-like locomotion. J. Fluid Mech. 392, 183–212.

Bellwood D.R., Wainwright P.C., Fulton C.J., Hoey A., 2002, Assembly rules and functional groups at global biogeographical scales. Funct. Ecol. 16, 557–562.

Bernadsky G., Sar N., Rosenberg E., 1993, Drag reduction of fish skin mucus. Relationship to mode of swimming and size. J. Fish Biol. 42, 797–800.

Blake R.W., 1983, Fish locomotion. Cambridge University Press.

Boily P., Magnan P., 2002, Relationship between individual variation in morphological characters and swimming costs in brook charr (*Salvelinus fontinalis*) and yellow perch (*Perca flavescens*). J. Exp. Biol. 205, 1031–1036.

Boisclair D., Sirois P., 1993, Testing assumptions of fish bioenergetics models by direct estimation of growth, consumption, and activity rates. Trans. Am. Fish. Soc. 122, 784–796.

Borazjani I., Sotiropoulos F., 2008, Numerical investigation of the hydrodynamics of carangiform swimming in the transitional and inertial flow regimes. J. Exp. Biol. 211, 1541–1558.

Brinsmead J., Fox M.G., 2002, Morphological variation between lake- and stream-dwelling rock bass and pumpkinseed populations. J. Fish Biol. 61, 1619–1638.

Brönmark C., Pettersson L.B., 1994, Chemical cues from piscivores induce a change in morphology in crucian carp. Oikos 70, 396–402.

Broughton N.M., Goldspink G., Jones N.V., 1981, Histological differences in the lateral musculature of 0-group roach, *Rutilus rutilus* (L.) from different habitats. J. Fish Biol. 18, 117–122.

Charnov E.L., Berrigan D., 1991, Dimensionless numbers and the assembly rules for life histories. Phil. Trans. R. Soc. Lond. B. 332, 41–48.

Denny M.W., 1994, Extrem drag forces and the survival of wind- and water-swept organisms. J. Exp. Biol. 194, 97–115.

Fausch K.D., 1984, Profitable stream position for salmonids: relating specific growth rate to energy gain. Can. J. Fish. Aquat. Sci. 62, 441–451.

Fish F.E., Beneski J.T., Ketten D.R., 2007, Examination of the three-dimensional geometry of cetacean flukes using computed tomography scans: hydrodynamic implications. Anat. Rec. 290, 614–623.

Fisher R., Leis J.M., Clark D.L., Wilson S.K., 2005, Critical swimming speed of late-stage coral reef fish larvae: variation within species, among species and between locations. Mar. Biol. 147, 1201–1212.

Frith H.R., Blake R.W., 1995, The mechanical power output and hydromechanical efficiency of northern pike (*Esox lucius*) fast-starts. J. Exp. Biol. 198, 1863–1873.

Fuiman L.A., Batty R.S., 1997, What a drag it is getting cold: partitioning the physical and physiological effects of temperature on fish swimming. J. Exp. Biol. 200, 1745–1755.

Gatz A.J., 1979, Community organization in fishes as indicated by morphological features. Ecology 60, 711–718.

Gore J.A., Nestler J.M., 1988, Instream flow studies in perspective. Regul. Rivers Res. Manage. 5, 129–138.

Gray J., 1936, Studies in animal locomotion. VI. The propulsive powers of the dolphin. J. Exp. Biol. 13, 192–199.

Gray J., 1957, How fish swim. Scient. Am. 197, 48–54.

Greenberg, L., Svendsen P., Harby A., 1996, Availability of microhabitats and their use by brown trout (*Salmo trutta*) and grayling (*Thymallus thymallus*) in the river Vojmån, Sweden. Regul. Rivers Res. Manage. 12, 287–303.

Guill J.M., Hood C.S., Heins D.C., 2003, Body shape variation within and among three species of darters (Perciformes: Percidae). Ecol. Freshw. Fish 12, 134–140.

Hesse R., 1924, Tiergeographie auf Ökologischer Grundlage. Jena: Fisher.

Hoerner S.F., 1965, Résistance à l'Avancement dans les Fluides. Paris, Gauthier-Villars.

Holliday F.G.T., 1969, The effects of salinity on the eggs and larvae of teleosts. In: Hoar W.S., Randall D.J. (Eds.) Fish physiology, Vol. 1. New-York, Academic Press, pp. 293–311.

Holopainen I.J., Aho J., Vornanen M., Huuskonen H., 1997, Phenotypic plasticity and predator effects on morphology and physiology of crucian carp in nature and in the laboratory. J. Fish Biol. 50, 781–798.

Horwitz R.J., 1978, Temporal variability patterns and the distributional patterns of stream fishes. Ecol. Monogr. 48, 307–321.

Hubbs C.L., 1941, The relation of hydrological conditions to speciation in fishes. Symposium on Hydrobiology, Madison, Wisconsin Press, pp. 182–195.

Hughes N.F., Dill L.M., 1990, Position choice by drift-feeding salmonids: model and test for arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, Interior Alaska. Can. J. Fish. Aquat. Sci. 47, 2039–2048.

Hughes N.F., Kelly L.H., 1996, A hydrodynamic model for estimating the energetic cost of swimming maneuvers from a description of their geometry and dynamics. Can. J. Fish. Aquat. Sci. 53, 2484–2493.

Keddy P.A., 1992, Assembly and response rules: two goals for predictive community ecology. J. Veg. Sci. 3, 157–164.

Koehl M.A.R., 1989, Discussion: from individuals to populations. In: Roughgarden J., May R.M., Levin S.A. (Eds.) Perspectives in ecological theory. Princeton University Press, pp. 39–53.

Koehl M.A.R., 1996, When does morphology matter? Annu. Rev. Ecol. Syst. 27, 501–542.

Köhler C., 1992, Morphologische untersuchungen zur intraspezifischen Variabilität des Rotauges, *Rutilus rutilus* (L.), aus dem Rhein. Fischökologie 6, 43–67.

Kokita T., Mizota T., 2002, Male secondary sexual traits are hydrodynamic devices for enhancing swimming performance in a monogamous filefish *Paramonacanthus japonicus*. J. Ethol. 20, 35–42.

Lagergren R., Hellsten M., Stenson J.A.E., 1997, Increased drag, and thus lower speed: a cost for morphological defence in *Bosmina* (*Eubosmina*) (Crustacea: Cladocera). Funct. Ecol. 11, 484–488.

Lamouroux N., Capra H., Pouilly M., 1998, Predicting habitat suitability for lotic fish: linking statistical hydraulic models with multivariate habitat use models. Regul. Rivers Res. Manage. 14, 1–11.

Lamouroux N., Capra H., Pouilly M., Souchon Y., 1999a, Fish habitat preferences in large streams of southern France. Freshw. Biol. 42, 673–687.

Lamouroux N., Olivier J.-M., Persat H., Pouilly M., Souchon Y., Statzner B., 1999b, Predicting community characteristics from habitat conditions: fluvial fish and hydraulics. Freshw. Biol. 42, 275–299.

Lamouroux N., Poff N.L., Angermeier P.L., 2002, Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. Ecology 83, 1792–1807.

Lamouroux N., Souchon, Y., 2002, Simple predictions of instream habitat model outputs for fish habitat guilds in large streams. Freshw. Biol. 47, 1531–1542.

Lang T.G., 1966, Hydrodynamic analysis of cetacean performance. In: Norris K.S. (Ed.) Whales, dolphins and porpoises. Berkley, University of California Press, pp. 410–432.

Lang T.G., Daybell D.A., 1963, Porpoise performance tests in a seawater tank. Naval Ordinance Test Station Tech. Publ. 3063, 1–50.

Langerhans R.B., 2008, Predictability of phenotypic differentiation across flow regimes in fishes. Int. Comp. Biol. 48, 750–768.

Langerhans R.B., Layman C.A., Langerhans A.K., Dewitt T.J., 2003, Habitat-associated morphological divergence in two Neotropical fish species. Biol. J. Linn. Soc. 80, 689–698.

Liao J.C., 2007, A review of fish swimming mechanics and behaviour in altered flows. Phil. Trans. R. Soc. Lond. B 362, 1973–1993.

Losos J.B., 1990, The evolution of form and function: morphology and locomotor performance in west indian *Anolis* lizards. Evolution 44, 1189–1203.

Loy A., Cataudella S., Corti M., 1996, Shape changes during the growth of the sea bass, *Dicentrarchus labrax* (Teleostea: Perciformes), in relation to different rearing conditions. An application of thin-plate spline regression analysis. In: Marcus L.F., Corti M., Loy A., Naylor G., Slice D. (Eds.) Advances in morphometrics. New-York, Plenum Press, pp. 399–405.

Magnan A., 1930, Les caractéristiques géométriques et physiques des poissons. Ann. Sci. Nat. (10è sér.) 13, 355–489.

Mathieson S., Cattrijsse A., Costa M.J., Drake P., Elliott M., Gardner J., Marchand J., 2000, Fish assemblages of European tidal marshes: a comparison based on species, families and functional guilds. Mar. Ecol. Prog. Ser. 204, 225–242.

McCutchen C.W., 1977, Froude propulsive efficiency of a small fish, measured by wake visualisation. In: Pedley T.J. (Ed.) Scale effects in animal locomotion. London, Academic Press, pp. 339–363.

McGuigan K., Franklin C.E., Moritz C., Blows M.W., 2003, Adaptation of rainbow fish to lake and stream habitats. Evolution 57, 104–118.

McLaughlin R.L., Grant J.W.A., 1994, Morphological and behavioural differences among recently-emerged brook charr, *Salvelinus fontinalis*, foraging in slow- vs. fast-running water. Environ. Biol. Fishes 39, 289–300.

Miller G.L., 1984, Seasonal changes in morphological structuring in a guild of benthic stream fishes. Oecologia 63, 106–109.

Moyle P.B., Baltz D.M., 1985, Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determination. Trans. Am. Fish. Soc. 114, 695–704.

Nestler J.M., Milhous R.T., Layzer J.B., 1989, Instream habitat modeling techniques. In: Gore J.A., Petts G.E. (Eds.), Alternatives in regulated river management. Florida, CRC Press, pp. 295–315.

Oberdorff T., Hughes R.M., 1992, Modification of an index of biotic integrity based on fish assemblages to characterize rivers of the Seine basin, France. Hydrobiologia 228, 117–130.

Pakkasmaa S., Piironen J., 2001, Water velocity shapes juvenile salmonids. Evol. Ecol. 14, 721–730.

Palmer M.A., Poff N.L., 1997, The influence of environmental heterogeneity on patterns and processes in stream. J. N. Am. Benthol. Soc. 16, 169–173.

Persat H., Olivier J-.M., Pont D., 1994, Theoretical habitat templets, species traits, and species richness: fish in the Upper Rhône river and its floodplain. Freshw. Biol. 31, 439–454.

Pettersson L.B., Brönmark C., 1999, Energetic consequences of an inducible morphological defence in crucian carp. Oecologia 121, 12–18.

Pettersson L.B., Hedenstrom A., 2000, Energetics, cost reduction and functional consequences of fish morphology. Proc. R. Soc. Lond. B 267, 759–764.

Pouilly M., 1993, Habitat, écomorphologie et structure des peuplements de poissons dans trois petits cours d'eau tropicaux de Guinée. Rev. Hydrobiol. Trop. 26, 313–325.

Pouilly M., 1994, Relations entre l'habitat physique et les poissons des zones à cyprinidés rhéophiles dans trois cours d'eau du bassin rhodanien: vers une simulation de la capacité d'accueil pour les peuplements. PhD Thesis, Université Lyon I, France.

Power M.E., Sun A., Parker M., Dietrich W.E., Wootton J.T., 1995, Hydraulic food-chain models: an approach to the study of food-web dynamics in large rivers. Bioscience 45, 159–167.

Reilly S.M., Wainwright P.C., 1994, Conclusion: ecological morphology and the power of integration. In: Wainwright P.C., Reilly S.M., (Eds.), Ecological morphology: integrative organismal biology. University of Chicago Press, pp. 339–354.

Reiser D.W., Wesche T.A., Estes C., 1989, Status of instream flow legislation and practices. North America. Fisheries 14, 22–29.

Ricklefs R.E., Miles D.M., 1994, Ecological and evolutionary inferences from morphology: an ecological perspective. In: Wainwright P.C., Reilly S.M. (Eds.) Ecological morphology. integrative organismal biology. University of Chicago Press, pp. 13–41.

Riddell B.E., Leggett W.C., 1981, Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 38, 308–320.

Robinson B.W., Wilson D.S., 1994, Character release and displacement in fishes: a neglected literature. Am. Nat. 144, 596–627.

Robinson B.W., Wilson D.S., 1995, Experimentally induced morphological diversity in Trinidadian guppies (*Poecilia reticulata*). Copeia, 294–305.

Rosenfeld J.S., Boss S., 2001, Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. Can. J. Fish. Aquat. Sci. 58, 585–593.

Sagnes P., 1995, Un outil de prise de données sur une image numérisée et son utilité dans les études relatives aux poissons: exemple d'une application concrète en morphométrie. Bull. Fr. Pêche Piscic. 337/338/339, 131-137.

Sagnes P., 1998, Morphométrie, potentiel hydrodynamique et utilisation de l'habitat lotique par les poissons: une nouvelle approche écomorphologique. PhD Thesis, Université Lyon I, France.

Sagnes P., Champagne J.-Y., Morel R., 2000, Shifts in drag and swimming potential during grayling ontogenesis: relations with habitat use. J. Fish Biol. 57, 52–68.

Sagnes P., Gaudin P., Statzner B., 1997, Shifts in morphometrics and their relation to hydrodynamic potential and habitat use during grayling ontogenesis. J. Fish Biol. 50, 846–858.

Scarnecchia D.L., 1988, The importance of streamlining in influencing fish community structure in channelized and unchannelized reaches of a prairie stream. Regul. Rivers Res. Manage. 2, 155–166.

Schlosser I.J., 1982, Fish community structure and function along two habitat gradients in a headwater stream. Ecol. Monog. 52, 395–414.

Schultz W.W., Webb P.W., 2002, Power requirements of swimming: do new methods resolve old questions? Integr. Comp. Biol. 42, 1018–1025.

Statzner B., 1987, Ökologische Bedeutung der sohlennahen Strömungsgeschwindigheit für benthische Wirbellose in Fließgewässern. Habilitation Thesis. University of Karlsruhe, Germany.

Statzner B., Gore J.A., Resh V.H., 1988, Hydraulic stream ecology: observed patterns and potential applications. J. N. Am. Benthol. Soc. 7, 307–360.

Statzner B., Hildrew A.G., Resh V.H., 2001, Species traits and environmental constraints: entomological research and the history of ecological theory. Ann. Rev. Entomol. 46, 291–316.

Statzner B., Holm T.F., 1989, Morphological adaptation of shape to flow: microcurrents around lotic macroinvertebrates with known Reynolds numbers at quasi-natural flow conditions. Oecologia 78, 145–157.

Thienemann A., 1918, Lebensgemeinschaft und Lebensraum. Naturwissenschaftliche Wochenschrift Neue Folge 17, 281–290, 297–303.

Vadas R.L.J., Orth D.J., 2000, Habitat use of fish communities in a Virginia stream system. Env. Biol. Fish. 59, 253–269.

Videler J.J., 1993, Fish swimming. London, Chapman & Hall.

Videler J.J., Weihs D., 1982, Energetic advantages of burst-and-coast swimming of fish at high speeds. J. Exp. Biol. 97, 169–178.

Vogel S., 1994, Life in moving fluids. 2nd edn. Princeton University.

Wainwright P.C., 1996, Ecological explanation through functional morphology: the feeding biology of sunfishes. Ecology 77, 1336–1343.

Webb P.W., 1970, Some aspects of the energetics of swimming of fish with special reference to the cruising performance of rainbow trout. PhD Thesis, University of Bristol, England.

Webb P.W., 1975, Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Board Can. 190, 1–160.

Webb P.W., 1984, Body form, locomotion and foraging in aquatic vertebrates. Am. Zool. 24, 107–120.

Weihs D., 1980, Energetic significance of changes in swimming modes during growth of larval anchovy, *Engraulis mordax*. Fish. Bull. 77, 597–604.

Welch P.S., 1935, Limnology. New-York, McGraw-Hill Book Company.

Wikramanayake E.D., 1990, Ecomorphology and biogeography of a tropical stream fish assemblage: evolution of assemblage structure. Ecology 71, 1756–1764.

Wilkinson L., Blank G., Gruber C., 1996, Desktop Data Analysis with SYSTAT. Upper Saddle River, Prentice-Hall.

Wimberger P.H., 1993, Effects of vitamin C deficiency on body shape and skull osteology in *Geophagus brasiliensis*: implications for interpretations of morphological plasticity. Copeia 2, 343–351.

Wolter C., Bischoff A., 2001, Seasonal changes of fish diversity in the main channel of the large lowland River Oder. Regul. Rivers Res. Manage. 17, 595–608.

Yalin M.S., 1992, River mechanics. New-York, Pergamon Press.