Vortices rule the wake: structure and Reynolds’ scaling of animal-generated wakes

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Abstract

Swimming and flying animals propel themselves by generating forces against a fluid medium or, in other words, by transferring momentum to the fluid in time. Momentum transfer is always restricted to the propulsor and its vicinity. The induced velocity differences (shear) in the surrounding fluid cause rotation in the water which can be visualized and quantified using vorticity. At low Reynold’s number (Re), the elevated vorticity regions stay attached to the propulsor and decay almost instantly after the propulsion stops. At higher Re, the accelerated masses of water separate from the propulsor and form entities. At intermediate Re, intermediate phenomena are observed. Since vortices require a beginning and an end, the associated vortices show up as line vortices (almost straight) or horseshoe vortices (curved) both with a beginning and an end at a fixed plane or at the surface, or as rings. In a free fluid, rings appear to be the only way for a vortex to exist. These fluid mechanical principles can clearly be recognized in animal-generated wakes, although the interpretation at different Reynold’s numbers is sometimes counter-intuitive. Here, the manner in which the flow phenomena scale with Re in animal-generated wakes is illustrated with flow analysis examples from larval and adult copepods, barnacles, fish larvae, frogs, adult fish and birds.

1 Introduction

Movement is the most defining characteristic of animals. The term ‘animal’ is derived from the Greek word ‘anima’ meaning ‘movement’. Locomotion is one of the main movements of free-ranging animals. The diversity of locomotory styles is enormous in the animal kingdom [1]. Locomotion can in general be described as exerting forces against the surroundings aimed to move the animal in a certain direction. In the terrestrial world, this comes down to pushing or kicking against the ground and meanwhile keeping oneself up against gravity. Animals that live and move in fluids, e.g. water and air, have to exert forces against the fluid, which partly resists
and partly gives way to the motions. That characteristic of motion in a fluid gives great flexibility
to animals with aerial or aquatic locomotion but complicates formalization [2].

Aerial flyers, such as insects, birds and bats, spend most energy keeping themselves aloft and
only a relatively small part in moving forward. Aquatic animals, however, are hardly influenced
by gravity, because their body has (almost) the same density as the surrounding medium and
gravity forces are compensated by Archimedes forces [3]. Every movement in a fluid results in
fluid displacement or resistance and therefore involves a hydrodynamic force. The magnitude of
the force depends on the volume of fluid that is affected, on the density of the fluid and on the
viscosity of the fluid. Slow movement of an appendage in air may correspond with very small
forces due to the low viscosity and low density of the air. The same movement in water, however,
may correspond with considerable larger forces due to the 800 times higher density and almost
60 times higher viscosity.

According to Newton, force equals the product of mass and acceleration, and this equation
holds true in fluid media when we would neglect the role of viscosity. However, as we will see
later on, viscosity cannot be neglected because it plays a major role in the resistance to force and
in the dissipation of energy on the small scale, i.e. in small animals, and also in the boundary layer
of large animals [4].

Movement in a fluid medium induces acceleration of surrounding fluid. The effect is initially
confined to the direct surrounding of the moving structure and can develop in time during the
movement: the velocity of the structure may not be constant and the accelerated mass of water
may grow or become smaller in time. When we consider only inertial propulsive forces, the
hydrodynamic force based on Newton’s laws can be expressed formally as:

\[ F_i = (m \cdot a)_t = \frac{\partial (m v)}{\partial t} = \frac{\rho \cdot \partial (A \cdot L \cdot v)}{\partial t}, \]

where \( m \) is the mass, \( a \) is the acceleration, \( v \) is the velocity, \( \rho \) is the density of water, \( A \) is the
(cross sectional) area, \( L \) is the length and \( \rho \times A \times L = \text{density} \times \text{volume} = \text{mass} \).

For an object or animal propelling itself with a constant velocity through water, the average
propulsive force being the average rate of change of momentum can also be expressed as
the volume of water affected per unit of time multiplied by the velocity of the animal and the
density of water. The affected volume of water per unit of time depends on the volume of the
object and on its shape, and can be expressed as the product of the frontal area and the velocity
multiplied by a shape-dependent coefficient. The shape dependent coefficient depends on the
length of the object and can therefore be exchanged for another coefficient multiplied by the
object length. From this, the (average) propulsive force considering inertial forces only can be
expressed as:

\[ F_{\text{prop},i} = c \cdot \rho \cdot v^2 \cdot A \cdot L, \]

where \( c \) is a proportionality constant, \( \rho \) is the density of water, \( v \) is the velocity, \( A \) is the (cross-
sectional) area and \( L \) is the length.

When we consider only viscous forces, the resistive force arising from a motion through a fluid
is proportional not only to the velocity but also to the area exposed to the fluid and of course to
the viscosity itself. The hydrodynamic force due to viscosity can therefore be expressed as:

\[ F_v = c \cdot \mu \cdot v \cdot A, \]

where \( c \) is a proportionality constant, \( \mu \) is the dynamic viscosity of water, \( v \) is the velocity and \( A \) is the area.
The ratio of the inertial to the viscous forces was formalized by Osborne Reynolds [5] and is expressed below as the Reynolds’ number, which is the ratio of the density $\times$ the velocity $\times$ a characteristic dimension (length) $L$ and the dynamic viscosity:

$$\text{Re} = \frac{\rho \cdot v \cdot L}{\mu}.$$ 

This expression shows that in a fluid with a certain density and viscosity, the inertial forces become more important at relatively high velocities and/or large size, but at relatively small velocities and small sizes the viscous forces dominate. This trend is well recognized in locomotion in aquatic animals [6], and has severe ecological implications for those animals. At high Re, a reciprocal movement with somewhat different velocities for the different strokes may result in a higher momentum transfer in one direction compared to the other and therefore result in a net displacement of water for propulsion. At low Re with viscosity being dominant, a similar reciprocal movement cycle will only result in rowing the same amount of fluid forwards and subsequently backwards with no net displacement, and therefore such a movement does not make sense for propulsion.

In all cases of propulsion or other interaction with the fluid environment, forces have to be exerted against the fluid and momentum has to be transferred to be able to move. In all these cases, viscosity is present and plays a role, sometimes dominant, sometimes small, but always recognizable. At low Re, the dominance of viscosity over inertia has clear implications for the interaction process itself but also for the morphology and lifespan of the wake. On the other hand, at high Re, the influence of inertia sometimes seems overwhelming, but viscosity is hardly ever negligible when we want to understand the full interaction process. A survey of wake shapes and a discussion of the processes involved with increasing Reynolds numbers, mainly based on work in our laboratories, will illustrate this.

### 2 Shear forces dominate larval copepod wakes at Re $\approx 0.5$

Copepods are small water flea-like crustaceans that live in almost every fresh or marine water basin on the earth in numbers up to several hundreds per litre. They are a significant part of the aquatic food webs and questions on how they find their prey and how they themselves are detected by actively-hunting predators are directly linked to their range of influence and characteristics of their wake. Due to their small sizes (0.1–3 mm) and their low swimming velocities (0.1–10 mm/s), copepods live in Re regimes between 0.01 and about 300.

The wake characteristics of larval, juvenile and adult *Temora longicornis*, a copepod with an adult body length of about 1 mm and common in the North Sea, were mapped with digital particle image velocimetry (DPIV) [7–9]. Adults as well as juveniles were tethered to a thin glass pipette and submerged in particle-seeded seawater. The animals showed spontaneous swimming behaviour for feeding purposes, escape reaction were invoked by tapping lightly on the pipette. During escape swimming, *Temora* larvae or adults may swim 7–30 times faster compared to normal swimming for feeding purposes [7]. Median and frontal planes were illuminated with a thin laser sheet and the recorded particle images were processed to flow maps.

The flow map of a 0.4 mm long larva (sixth nauplius stage, see inset drawing Fig. 1a) shows a fully laminar converging flow in front of the animal, even when an escape reaction is elicited, as can be seen in Fig. 1a. The peak water velocity in this map is 7 mm/s, bringing the Re somewhere between 2 and 3 maximally. The maximum velocities are found just below the anterior
Figure 1: Flow patterns during (a) and 0.06 s after (b) escape response swimming of a 0.4 mm larval copepod (*Temora longicornis*) (N6 nauplius) in the sagittal plane. Animal in lateral view in centre of picture, anterior = left, ventral = down, black rod coming from upper right corner = tether. Vorticity displayed in colour, background/lowest levels (grey) removed for clarity.

side of the animal. The vorticity colour coding shows that the vorticity is highest just below the animal where the swimming appendages are located. The animal is exactly in the middle of a flow pattern that resembles the shape of an hourglass lying on its side. When the animal stops swimming, the flow pattern completely disappears within a tenth of a second. Figure 1b shows the flow pattern of the same nauplius 0.06 s after the animal has ceased to swim. The peak water velocity is about 10 times less compared to Fig. 1a, bringing the Re down to about 0.3, theoretically well in the viscous regime. There is no trace of free jets or shed water bodies in any of these two pictures that might have indicated the presence of inertia. Viscous forces are clearly prevailing.

The flow map of a 0.4 mm long juvenile (first copepodite stage, see inset drawing) during an escape response shows the increased ability of this more streamlined developmental stage to reach higher swimming velocities (Fig. 2a). The peak water velocities are now 21 mm/s, Re ≈ 8.5. The flow in front of the animal is convergent but the maximum flow velocities are found just behind and below the animal’s abdomen. The vorticity maxima are somewhat symmetrical above and below the area of max velocity. The whole flow pattern shows more resemblance to a cross section of a torus (or doughnut) with a small central opening than to an hourglass as in Fig. 1a. When the animal ceases to swim, the water keeps moving backwards for a few tenths of a second. Figure 2b shows the flow pattern 0.06 s after the copepodite stopped swimming. An area with elevated velocity is still very well recognizable although more diffuse compared to Fig. 2a, the velocity maxima are about 40% of the maxima during escape swimming. The vorticity maxima on either side of the jet are still well traceable but less then half in strength compared to Fig. 2a. The flow maps show resemblance to the central jet and the accompanying vortices of the cross section of a vortex ring [10–12], although not very well-defined. The Re numbers of the rings in Fig. 2a and b, based on ring diameter and maximum jet velocity, are 6.5 and 5.0, respectively, which is very low for a vortex ring to even exist. The accelerated water parcel or jet in the middle of the ring indicates that inertia is playing a role here, but the fast decay and the high rate of velocity diffusion (convection) show that viscosity is prominently present.
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Figure 2: Flow patterns during and after escape response swimming of a 0.4 mm juvenile copepod (Temora longicornis) (C1 copepodite) in the sagittal plane. Animal in lateral view, anterior = left, tether visible as black rod. Vorticity displayed in colour, background/lowest levels (grey) removed for clarity. (a) Flow velocity vectors and vorticity during the escape response. The flow map shows resemblance with a vortex ring: high velocity jet, rotational flow and vorticity maxima on either side. (b) Only 0.06 s after the animal has ceased to swim, the flow pattern is still recognizable but both velocity and vorticity have decreased to about 40% of the values in 2A or even lower. The jet as well as the vortices are much less defined but still recognizable.

3 Acorn barnacles use the best of both worlds at Re = 1–10

Acorn barnacles are common on intertidal and subtidal rocky shores almost all over the world and may reach densities of thousands per m². Acorn barnacles filter seawater for food particles with their extendable long biramous legs, called cirri. In (slow) external flow they often extend their filter perpendicular to the flow, but in standing water they actively beat their cirri to gather food particles [13]. The acorn barnacle Balanus crenatus is a common species on the Western European rocky shores. It has a maximum shell size of about 20 mm, the shell opening being maximally 8 mm. The cirri can be extended more than 10 mm by the bigger ones. When actively filtering the water for food, the animal beats its cirri about once per second. DPIV derived flow maps of the area around individual animals that lived attached to mussel shells [14] as well as close-ups revealed that the beat cycle has distinct stages that reflect the interaction processes of cirral filter and water: raking (1), paddling (2), shedding + retraction (3), harvesting (4) and extension (5).

During the raking phase (1), the extended filter is accelerated very fast in such a way that the surrounding water lags behind and is therefore filtered. This phase is illustrated in Fig. 3a, showing three consecutive images of the cirri at the start of the beat cycle, that have been assigned different colours, red, blue and green, respectively. The particle patterns in the left part of the image show flow that remained from the previous beat cycle. Comparison of particle displacement (a few groups of consecutive images of the same particles are indicated with yellow circles) with cirral displacement shows that the cirri move much faster than the (particles in the) water and therefore active filtration takes place. This is the raking phase where normally food particles are raked from the surrounding water. The water starts, however, to catch up with the cirri at the end of the raking phase, illustrated in Fig. 3b, and when the cirri decelerate just before retraction, the
velocity difference is almost zero. At that moment in the beat cycle, the filter resembles a paddle more than a filter, accelerating the water that it drags along. This is the paddling phase, moving the water that has just been filtered away from the animal.

By tracking single particles that passed through the filter, we calculated the exact velocity difference and thereby the local Reynolds number in time. The Re based on the cirri diameter (0.125 mm for the main cirri and much smaller for branching setae) increased from close to zero before the raking phase to 2.5 during most of the raking phase and then dropped down to again to about 0.2 during the paddling phase. When the Re is calculated based on the diameter of the whole filter ($\approx 8$ mm), $Re_{\text{filter}}$ is about 200 during the raking phase but only about 16 during the paddling phase. An additional parameter to indicate the function of the cirri in terms of filter or paddle is the leakiness [15], which is the relative amount of water passing through the filter, calculated from the velocity differences between filter and water, and the filter area. The leakiness of the cirral filter of the barnacle was close to 100% during the first part of the forward beat but dropped to 10% and less during the second half of the forward beat ending up at 0% at the end of the forward beat.

The water dragged along with the cirri during the paddling phase is shed from the filter when the filter retracts to be moved along the mouthparts to pick off the food particles (harvesting phase). This water shows up as a parcel of water with relatively high velocity (see Fig. 4a) in a broad flow that is ‘on average’ also accelerated by the beating action of the acorn barnacle. Vorticity is present along the whole band of accelerated water, but the highest values are found above and below the accelerated parcel of water (Fig. 4b).

The current generation mechanism of the acorn barnacle as well as the current itself show characteristics of inertial as well as viscous effects: due to inertia the water passes through the filter in the raking phase, due to viscosity the water catches up with the filter, due to inertia again
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Figure 4: Wake structure of an acorn barnacle (*Balanus crenatus*) during the first stage of its beating cycle. (a) The colour-coded velocity magnitude plot shows a broad jet of accelerated water resulting from the beating action of the barnacle. An area with significantly elevated velocity stands out, which is the water mantle of the cirri that has been shed from the cirri at the end of the previous cycle. (b) The vorticity is higher than background values almost all along the jet flow, but is most prominent next to the high velocity area.

the water is shed from the filter and again due to viscosity, the velocity gradients in the resulting flow pattern are rather shallow. Acorn barnacles use the best of both worlds when it suits them.

4 Fast decaying vortex wakes of juvenile fish at Re $\approx 10^2$

Juvenile and adult zebra danios (*Brachydanio rerio*) swim mainly in a burst-and-coast mode [16]. The larvae or juveniles live in Re regimes between 50 and 900, which is called the transitional regime, whereas adults usually live in the inertial regime (Re $> 1000$) [17]. In juveniles, a swimming bout mainly consists of one or a number of tail flicks followed by a coasting phase in which the body is kept straight. During this burst swimming activity, the fish produces a water disturbance which is quite impressive in terms of its own body length. Figure 5a shows the signature of a zebra fish larva (body length $\approx 4$ mm) resulting from one burst of swimming activity. The larva was initially standing still in fresh water seeded with small neutrally buoyant particles and illuminated with a 0.5 mm thick laser light sheet. The initial position of the larva (0.24 s before the flow pattern was recorded) and the direction of disappearance from the field of view are indicated. DPIV analysis of the signature shows a jet of water moving in a direction opposite to the direction of disappearance, accompanied by two counter-rotating vortices. The vortices are well visible with definite peaks (see colour coding in Fig. 5a). This pattern is characteristic for the cross section of a vortex ring. Only 0.4 s later, the pattern is still very well recognizable (Fig. 5b) but the peak velocities in the jet have halved, the vorticity maxima have been reduced to a third, and the vortices are much more diffuse compared to the previous recording.

Clearly, the zebra fish larva accelerates a mass of water backwards and thus relies on inertial forces for its propulsion. This water mass, however, is in strong viscous interaction with the surrounding water during the process of acceleration as well as after shedding, resulting in a vortex ring with a relatively small jet width and a relatively voluminous ring. Due to viscous shear and diffusion, the pattern deteriorates and spreads out within a short time and eventually disappears completely, indicating the ubiquitous and at this Reynolds number still emphatic character of viscosity.
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Figure 5: Horizontal cross section through the flow field resulting from a swimming burst of a juvenile zebra danio (Brachydanio rerio) \((L = 4\ \text{mm})\). The original position of the fish at \(t = 0\) and the direction of disappearance are indicated in the left panel with the dark outline (anterior = upper-left side) and the dark arrow. (a) Flowfield 0.24 s after the burst, showing a strong jet directing away from the fish and strong well defined vortices on either side. (b) At \(t = 0.64\ \text{s}\), the flow field has significantly decreased in strength and the distribution of velocity as well as vorticity has become more diffuse.

5 Frogs kick the most beautiful vortex rings at \(\text{Re} \approx 10^4\)

Frogs have a very distinct intermittent way of propelling themselves by forcefully stretching their legs in less than 0.1 s and meanwhile making their feet as large as possible to provide maximal thrust. Subsequently the legs are feathered for minimal drag during the gliding phase and finally the legs are retracted for the next kick [18]. Contrary to what has been assumed so far [1, 19], the feet do not interfere with one another during the kick and the legs do not clap together at the end of the stroke [20]. During active propulsion, each leg accelerates a mass of water that is dragged along by the webbed foot. At the end of the leg extension, the accelerated water mass is shed, and, due to viscous interaction with the surrounding fluid, forms a vortex ring. Figure 6a shows such a water mass just after it has left the foot of a green frog (Rana esculenta). Figure 6 is the result of a DPIV study of frog swimming and was recorded from a frog that was swimming in particle seeded water in a horizontal laser light sheet well below the surface [20, 21]. Together with the velocity vectors, the colour coding of velocity magnitude gives a good impression of the compactness of the area with significantly elevated velocity. On either side of the water parcel, the rotational flow of the vortex ring can be observed. Figure 6b shows the clearly defined vorticity maxima in this ring, with reasonably small cores compared to the jet diameter. The Reynolds number of the swimming frog as a whole as well as the moving feet based on foot size was in the order of magnitude of 10,000.

We also did some tests with clawed frogs (Xenopus laevis) swimming in similar conditions. These frogs were bigger in size and had larger webbed feet but moved somewhat slower, resulting in a similar magnitude Reynolds number. Due to the wider feet, the resulting vortex rings show a wider jet originating from the accelerated water mass (Fig. 7). The velocity distribution of the jet in the middle of the ring shows the theoretically expected maxima (Fig. 7a, red colour) next to
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Figure 6: A horizontal cross section of a vortex ring created by the kicking action of a frog’s leg. In the top panel, the velocity magnitude is displayed in colour coding, showing the high velocity jet core. The lower panel shows the vorticity in colour coding, revealing the vortex cores on either side of the jet.

Figure 7: Cross section of the vortex ring left behind by the kick of one leg of a clawed frog. (a) Colour coded velocity magnitude plot showing the high velocity jet core region with highest local velocities next to the vortices. (b) Vorticity colour coding in the same vortex ring wake, showing the well-defined vortex cores.

the vortices and a somewhat lower plateau in the middle (yellow–green). The vortex cores (areas of almost constant high vorticity) are very well defined and small compared to the jet diameter.

During the kick, the accelerated mass of water around the foot of the green frog as well as the clawed frog was well defined and hardly interacted with the surrounding water (for details, see [20]). The levels of shed vorticity during the stretch phase were minimal compared to the vortex
ring peaks. Clearly, inertia is the dominant force here and the effects of viscosity become only eminent after the accelerated water mass is shed and interacts freely with the surrounding fluid. The wake decays only moderately and the patterns as shown in Figs 6 and 7 are visible for 5–10 s after the actual kick, that is 50–100 times as long as it took to create the pattern. Elevated vorticity may be detectable in the water for an even longer period [22].

6 Big fish make whirl chains at \( \text{Re} = 10^4 - 10^6 \)

Most pelagic fish swim by undulating their body and tail. They create thrust by accelerating water backwards along the undulating body and add extra acceleration with the lateral motions of the tail. The exact role and contribution of body and tail fin are still not fully understood [1]. Quantitative studies of the wakes of undulating fish revealed quite a robust picture of the wake: A series of alternating vortex rings that are chained to one another, with a backwards directed jet waving through the rings [23–25]. This pattern confirmed theoretical expectations [1, 26–28]. The causality between the movement of body and tail and the vortex pattern can be interpreted in several ways (see also [23]).

A horizontal section through the vortex chain wake of a 0.12 m long mullet swimming at about 0.2 m/s (\( \text{Re} \approx 25,000 \)) is depicted in Fig. 8a. The individual vortices represent sections of the vertical sides of the (chained) vortex rings, which have opposite circulation at the opposite sides of the trail. This pattern is quite stereotypical and may persist for quite some time, e.g. for more than 10 s for the wakes of bigger fish. Aging of the wake, however, starts almost immediately, as is detectable in the levels of vorticity of the sectioned vortex rings in time. Figure 8b shows the same wake as in Fig. 8a but 0.32 s later. The vorticity levels in the oldest vortices are only 40% of the same vortices in the previous picture, indicating wake decay through viscous friction. This wake pattern shows typical characteristics of a high-\( \text{Re} \) number wake: accelerated water masses shed in the opposite direction as the swimming direction. The presence of viscosity is visible in the presence of the vortex rings and in the decay of the wake in time.

Not all fish propel themselves by body undulations. Quite a number of demersal fish swim with their pectoral fins. This can be in a ‘flight’ mode, with the fin moving up and down and creating...
backwards thrust through a lift mechanism. It may also be that the fish rows the fin backwards in a paddling mode, returning the fin to its original position with as little resistance as possible. The bluegill sunfish (Lepomis macrochirus) displays both methods to a certain extent [29], whereas angelfish (Pterophyllum eimekei) is a pure paddler [30]. In the paddling mode, one vortex ring is shed after each power stroke backwards, whereas in the flapping ‘flight’ mode, a pair of chained vortex rings are shed, similar to a section of the wake of an undulating fish [29]. So far, the decay and lifespan characteristics of such wakes have not been studied. The wake characteristics, however, show resemblance with the wakes of undulating fish, producing chained vortex rings and, to a certain extent, with the wakes of swimming frogs, showing single vortex rings.

7 Birds make rings and chains at $\text{Re} = 10^4 - 10^5$

Birds flap their wings to stay airborne during powered flight, or keep their wings spread and still during gliding flight. Visualizations of the wake of gliding kestrels, of doves and jackdaws in slow flapping flight, and of kestrels in normal flapping flight revealed the first quantitative impressions of the wake shapes and wake characteristics of flying birds [31–34]. The general wake pattern shows resemblance to the patterns found in insects although the aerodynamic mechanisms behind it may differ. Insects and birds both produce stacked vortex rings during hovering due to the momentum imparted to the air in a discontinuous way; during slow flight rows of separate vortex rings are produced [28, 35–38]. During normal forward flight, insects [35] and some birds shed rows of separate vortex rings, but fast-flying birds with slender wings are capable of producing downward directed momentum of variable strength continuously [38]. Actual quantitative information on levels of vorticity in the wake and on the wake geometry have only recently been revealed using DPIV at the thrush nightingale (Luscinia luscinia) flying in a wind tunnel [39]. These experiments showed separate large vortex rings during slow flight and a combination of large and small vortex rings during intermediate flight speeds. At relatively high flying speeds, separate rings are no longer observable but momentum and vorticity are continuously shed during the whole beat cycle, although the strength and direction may vary with the wingbeat phase [40, 41].

In search of the origin of bird wake patterns and of the aerodynamics governing the flow around a bird wing, the flow around a model of a swift (Apus apus) in a water tunnel has recently been mapped in Reynolds conditions comparable to fast gliding ($\text{Re} = 37,500$) [42]. This study revealed that the long hand wings produced high downwash levels through the presence of leading edge vortices (LEVs) (Fig. 9). The phenomenon of the LEV is well known from delta wing aircraft such as the Mirage and the Concorde [43–45] and also from insect flapping flight [34, 46]. The flow around bird wings, however, had so far mainly been treated according to classic airplane aerodynamics [47–49]. The presence of LEV flow on bird wings may therefore urge for reconsideration of bird wing aerodynamics. Flow phenomena such as the LEV may after all not only be restricted to gliding but may to a certain extent also be present during flapping flight, although this has not been confirmed experimentally yet.

8 Discussion and conclusion—vortex rings are everywhere?

Looking back along the Reynolds number scale, the presence and even prevalence of inertia in the wakes of birds, large fish and frogs is eminent. In all these cases, the influence of viscosity is well recognizable in the boundary layers where viscous shear causes fluid rotation showing
up as vorticity, vortices and vortex rings. In all cases of freely swimming or flying organisms that impart forces on the fluid causing part of that fluid to be accelerated, free or chained vortex rings were formed. The life span of these rings is longer at higher \( \text{Re} \) compared to lower \( \text{Re} \). In the Reynolds regimes between 1000 and about 50, the ‘transitional range’, we see the increasing influence of viscosity on the shape as well as the life span of the wake, as in the case of the zebra fish larva. Free vortex rings are created but their lifespan readily decreases with decreasing \( \text{Re} \). At Reynolds numbers below 1, free vortex rings cannot exist because viscous forces do not allow parcels of accelerated fluid to move freely. Almost immediately after a driving force stops, as in the case of the swimming tethered copepod larvae, the fluid stops moving.

This same phenomenon was observed during a DPIV study of artificially created vortex rings with initial \( \text{Re} \) between 600 and 30, calculated with the ring diameter as characteristic length (Stamhuis and Didderen, unpublished data). The rings were created by releasing an amount of water from a Perspex cylinder that was first partly dipped in the experimental vessel and then closed at the top before pulling it up again. The strength (read vorticity) of the resulting vortex ring and the peak velocity of the central jet were mapped from the particles displacing in the laser-illuminated plane. Most of the vortex rings lived more than long enough to cross the field of view of the camera and ended their life when crashing into the bottom of the vessel. In one case, however, the decay process towards complete disappearance was recorded. In all vortex rings, the peak velocity of the jet as well as the peak vorticity in the ring decayed according to an exponential decay function (Fig. 10a). This was also the case with the suddenly dying ring, in which case the jet velocity as well as the ring vorticity suddenly disappeared within a fraction of a second (Fig. 10b, arrow). The ring Reynolds number was around 7 at that moment.

In conclusion, for flow structures left behind by a self-propelled animal to exist and persist for some time, the flow regime needs to be inertial. The dominant flow structure in animal-generated wakes is the vortex ring, either as a single ring or multiple rings chained to ladder-like structures. Wake decay processes are mainly due to convection of momentum (in other words, viscous diffusion) and the decay processes can be described by exponential decay functions. In the transitional \( \text{Re} \) zone, the decay processes due to viscous diffusion can be mapped in the same way but higher damping coefficients will appear and the relation will be lost when approaching...
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Figure 10: Vortex ring jet velocity in time for two different ring Reynolds numbers (Re), from a DPIV study of artificial vortex rings created by releasing water from a tube into the experimental vessel. (a) Jet velocity resulting from a 10 mm tube at an initial Re = 146 showing the expected exponential decay after the ring has been created (t > 0). (b) Jet velocity resulting from a 3 mm tube at initial Re = 59 showing the same exponential decay until, at ring Re ≈ 7, the ring suddenly disappears (see arrow).

Re = 1. At Re numbers below unity, viscous dissipation absorbs all mechanical energy almost instantly.

The reason why the vortex ring is such an eminent structure in animal-generated wakes, almost regardless of the Re number, is more trivial than one would anticipate. Most animals move themselves through their environment by appendages that oscillate or bodies that undulate [50]. Although the resulting motion of the animals may seem steady, the actual momentum transfer is periodic resulting in most cases in separate parcels of accelerated fluid pushed away from the animal in a direction opposite to the desired direction of motion. As a consequence, stacks, series or chains of vortex rings can be observed. The exceptions to this rule are animals living in Re regimes close to or below unity. There, no separate accelerated bodies of fluid can be identified and shear forces are the main means of propulsion. It is therefore not surprising that probably the only really steady locomotory mode in the animal kingdom resulting from an actively moving organism is found in the low Re range: propulsion by flagellar rotation.

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