

Size and structure of ‘footprints’ produced by *Daphnia*: impact of animal size and density gradients

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Abstract. Daphnids with higher density than the surrounding water body have to push water downwards to hold their position in the water column. This swimming current is mainly the result of the movement of the second antennae and only to a small extent due to the filter current. The water structures under the *Daphnia* are very variable depending on the swimming behavior. We focused on the hop and sink behavior, where the downward-pushed water masses form a wake which can be described as a mushroom-shaped vortex. The volume of this structure increases linearly with time. The wake volume is much larger than the zooplankton itself which can be important for the perceptibility by mechanically sensing carnivorous predators. In water with a density gradient of 10 kg m^{-4} the wake length W_L can be described by $W_L = 1.64 (\pm 0.096) \times L^{1.58 (\pm 0.14)}$ with the length of the *Daphnia* L in millimeters. The wake length, measured after 5 s, remained constant for gradients up to 1 kg m^{-4} . Above this value, the wake length declines in good agreement with the value expected from theory with $W_L = 10.66 (\pm 0.21) \times (dp/dz)^{-0.265 (\pm 0.010)}$. Since the intra- and inter-specific ‘communication’ (e.g. mate seeking, nutrient partition between phytoplankton and bacteria, predator avoidance) can be expected to be bound to the hydrodynamic properties of the wakes, different wake forms and sizes most likely have an important impact on the information sent out.

Introduction

As zooplankton move through the water, they create fluid mechanical signals as well as leaving chemical signals within their wakes (Strickler, 1977, 1985; Kerfoot *et al.*, 1980; Yen and Strickler, 1996). Depending on the species and their swimming pattern, the wakes can be a smooth, relatively uniform, velocity gradient (i.e. *Euchaeta rimana*; Yen and Strickler, 1996) or they can be a series of pulsed water masses (*Cyclops*; Kerfoot *et al.*, 1980). The implications of these mechanical and chemical signals, which can be seen as ‘footprints’ of the moving zooplankton, have been discussed in the light of predator avoidance (Fields and Yen, 1997), prey detection (Kerfoot, 1978; Kerfoot *et al.*, 1980; Gallagher, 1993) and mate recognition (Yen *et al.*, 1998). It is hypothesized (e.g. Strickler and Twombly, 1975) that different combinations of wake structure and embedded chemicals elicit different behavior patterns ranging from an escape reaction to an attack or mating response.

The wake is also important for its role in the distribution of regenerated nutrients within the pelagic zone. The regeneration of nutrients is a critical component controlling the production in oceans and lakes by providing up to 95% of the required nutrients to sustain the observed production (Dugdale and Goering, 1967; Eppley and Peterson, 1979; den Oude and Gulati, 1988; Wassmann, 1990; Poister *et al.*, 1994; Carr *et al.*, 1995). Since the nutrients released by zooplankton are constrained by the physical structures produced by the

zooplankton, the wakes produce a patchy distribution of nutrients which form microenvironments of high nutrient concentrations. There is a suggestion that the distribution of the nutrient (i.e. patch size and relative nutrient concentration) can affect species composition (Lehman and Scavia, 1982a,b; Rothhaupt and Güde, 1992). The data of Lehman and Scavia (1982) and Rothhaupt and Güde (1992) show that species with high K_M and V_{max} values (i.e. algae) take up relatively more nutrients when distributed in micropatches with higher nutrient concentration rather than in a well-mixed environment without micropatches. In contrast, bacteria, with low K_M and V_{max} values, are more successful in scavenging nutrients in environments having greater homogeneity in nutrient distribution. Thus, smaller patches with high nutrient concentrations would favor algal growth, whereas large patches with diluted nutrients would favor bacterial growth.

The magnitude and structure of the wake have profound implications on both the ability of organisms (potential prey and predators) to detect the signal and behave accordingly, and the size of the nutrient patch left by the animals, which has been shown to affect the outcome of the nutrient competition between algae and bacteria. Yet little is known about the size and structure of the zooplankton wakes or their potential ecological impact on the nutrient distribution in aquatic environments. Previous studies examining wake structure were performed using Schlieren optics (Strickler, 1977) with strong density gradients from 300 up to 1000 kg m⁻⁴ (Strickler, 1975, 1977; Yen and Strickler, 1996). However, natural density gradients are much smaller, typically as a result of temperature variations. For instance, within the thermocline, there is a density gradient of 2–3 kg m⁻⁴, corresponding to a temperature gradient of 15°C m⁻¹ (0.3°C per 2 cm). On smaller length scales (some millimeters), one can observe even larger temperature gradients which are due to turbulence (e.g. Imberger and Ivey, 1991). Smaller gradients are expected to give rise to larger fluid mechanical disturbances (wakes) than previously assumed. In this paper, we examined the impact of density gradients ranging from 0.1 up to 200 kg m⁻⁴ on the size and structure of wake formation behind zooplankton.

Method

Optical system

To measure the wake behind an individual zooplankton, Schlieren optics were used as described by Strickler (1977). We used a HeNe-laser (630 nm, Hughes Aircraft Company), a beam expander, and a collimator (Melles Griot) as a source of parallel light. Our filming vessel was 1.3 × 10 × 10 cm (130 ml). The light passing through the vessel was focused with a 135 mm Hasselblad lens. At the focal point, a glass edge was positioned in such a way that it formed a spatial filter which blocked all of the source light. However, any object entering the light pathway would refract the light, allowing it to miss the spatial filter [for a detailed description of the method, see Strickler (1977) and cited references] to be captured by a BW-video camera (Pulnix). Video tapes were analyzed on a TV screen with a 16- to 32-fold magnification in total.

Density gradients

Sodium chloride (NaCl) was used to create the density gradients. In contrast to previous studies which used dextran or highly polymerized substances (Strickler, 1975, 1977; Yen and Strickler, 1996), low concentrations (<0.2%) of NaCl alter the optical density of the fluid while minimally affecting the fluid viscosity (CRC Handbook of Chemistry and Physics, 1996). Gradients were made with a gradient mixer in the range of 0.2–200 kg m⁻⁴ (deionized water in the upper part of the chamber and 0.02–20 g NaCl l⁻¹ at the bottom). Using a simple diffusion model, we calculated that the gradients are stable (<5% deviation) for at least 20 h in the central 2 cm of the tank where our recordings were made. All our experiments were performed within 10 h after the beginning of filling the tank at a temperature of 21°C.

Zooplankton

We chose *Daphnia* as a model organism for our experiments since they survive salt concentrations ranging from distilled water to 40% of sea water concentration (Peters, 1987). Furthermore, *Daphnia* is a cornerstone species in most lakes (de Bernadi and Peters, 1987). *Daphnia pulicaria* (clone DISP-4 from S.Dodson, Madison, WI, USA) were grown in artificial lake water. Except for the determination of the size dependency of wake size, we selected female daphnids of 2.12 (± 0.38) mm length from the top of the head to the base of the spina. The length of the wakes was measured from the average position of the spina base during the hop and sink behavior of the *Daphnia* to the end of the wake.

Results

Swimming daphnids produced a downward current to compensate for the negative buoyancy. This water current is the combined result of the filter current, e.g. the current resulting from the movement of the filter legs, which should not be confused with the clearance rate or other terms of particle capture, and the left and right swimming currents produced by the movement of the two second antennae (Figure 1). However, this separation of the downward-directed current into three distinct ones was only occasionally visible due to technical reasons and therefore not included in our routine measurement. Swimming daphnids produced very different structures and it became problematic to classify and quantify the impact of the swimming behavior on the wake formation. Horizontally moving daphnids 'rode' on a 'water jet', whereas this 'jet' was not always clearly visible in sinking daphnids. However, the separation into three distinct currents was best visible for animals with only minor antennae currents, e.g. sinking daphnids. Larger antennae currents mask the smaller filter current.

One of the most outstanding behaviors of daphnids is the quasi stationary 'hop and sink' behavior (Gorski and Dodson, 1996). During this behavior, the *Daphnia* hops with only small jumps, pushing light water down and producing a water body of light water below the animal (Figure 2). The size of the water body can be measured and quantified. The volume of the water body V_w , approximated as an

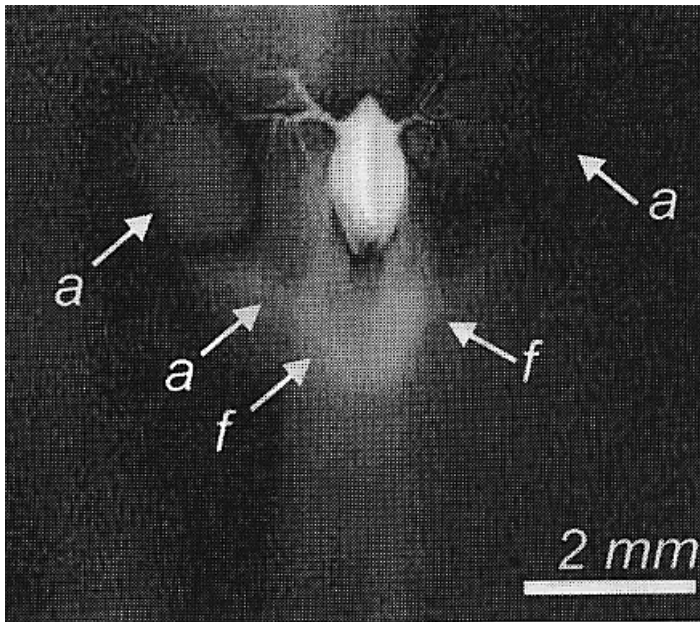


Fig. 1. Wake produced by a sinking *Daphnia* recorded with Schlieren optics. Note the antennae currents *a* and the filter current *f*. The last antennae movement was 1 s ago, thus the currents resulting from that movement are only weakly visible in the background. Density gradient: 10 kg m^{-4} .

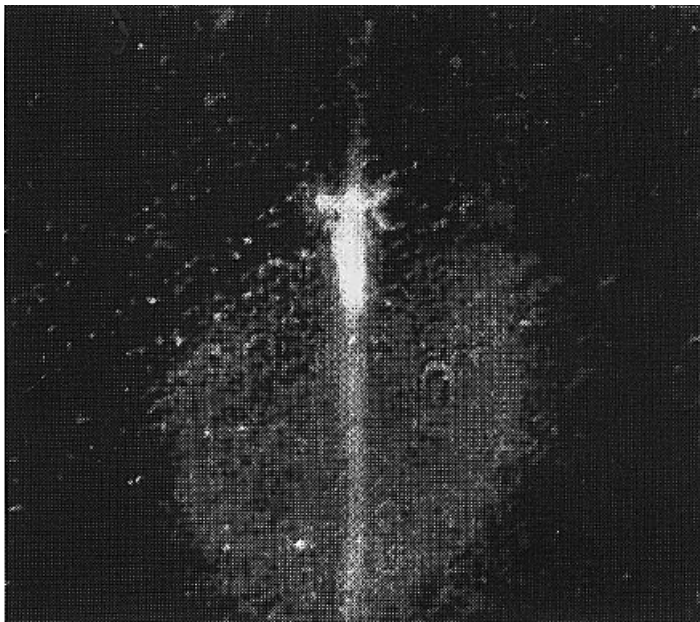


Fig. 2. Mushroom-shaped wake produced during the hop and sink behavior of the *Daphnia*. Length of the *Daphnia*: 2.1 mm. The diagonal stripes in the image result from a small contamination of the glass vessel.

ellipsoid $V_W = \pi \times W_w^2 \times W_L/6$ (W_w is wake width; W_L is wake length) increased linearly with time (Figure 3C). With increasing distance from the *Daphnia*, the downward motion of the water body is slowed down by viscosity and buoyancy effects (Figures 3A and 4). After ~ 5 s, the wake front stopped moving downward (Figure 3A), but now the wake extended in a horizontal direction (Figure 3B). After a while, depending on the gradient, the end of the water body was lifted up due to buoyancy and formed a ‘mushroom-shaped’ structure (Figure 2).

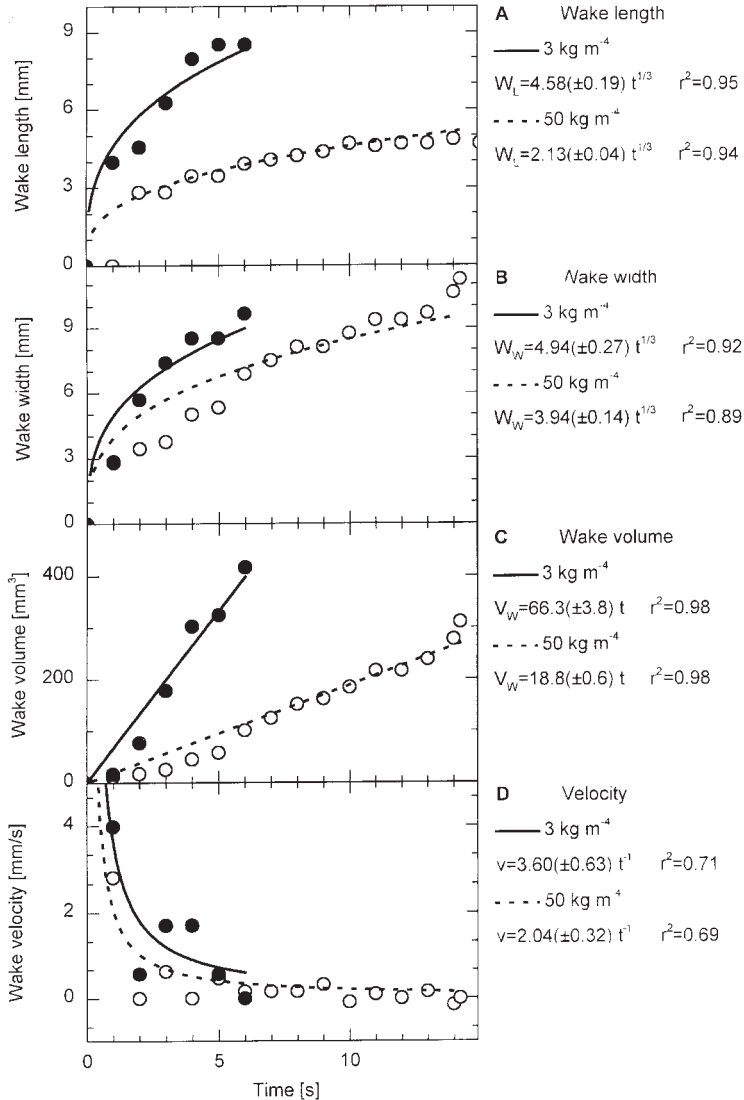


Fig. 3. Evolution of a wake at two different density gradients. **(A)** Evolution of the length of the wake measured vertically from the base of the spina to the end of the wake. **(B)** Horizontal width of the wake. **(C)** Wake volume calculated as an ellipsoid and linear fit. **(D)** Velocity of wake front and fitted equations: \pm SD in parentheses, t is time in seconds.

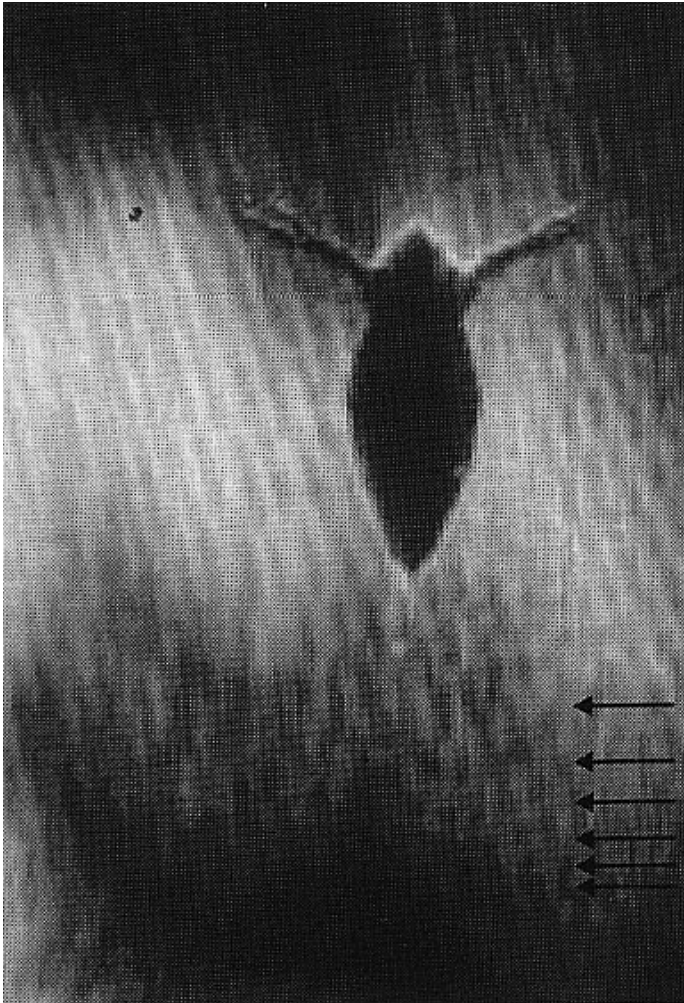


Fig. 4. *Daphnia* (length 1.9 mm) pushing water down during the hop and sink behavior. The wave fronts resulting from single antennae strokes can be seen as dark lines. Note the compression of the older water packages.

The shape and size of the released structures were functions of the size of the daphnids and the gradients in the water column. There was a clear correlation between the maximum length of the *Daphnia*, L (mm), and the length of the water body, W_L (mm). With a gradient of 10 kg m^{-4} , the wake length can be described by $W_L = 1.64 (\pm 0.096) \times L^{1.58 (\pm 0.14)} (\pm \text{SD}; N = 81, r^2 = 0.8728)$ (Figure 5).

The maximum length of wakes pushed down by daphnids showed a strong dependency of the density gradient at gradients $>1 \text{ kg m}^{-4}$. At gradients $<1 \text{ kg m}^{-4}$, the maximum length of the wake remained more or less constant (Figure 6). The volume of the water body increased 3.5 times faster with a gradient of

3 kg m⁻⁴ (length of the *Daphnia* 2.5 mm) than with a gradient of 50 kg m⁻⁴ (length of the *Daphnia* 2.03 mm; Figure 3C).

Discussion

High density gradients of 2 kg m⁻⁴ caused by temperature gradients of 15°C m⁻¹ on the length scale of millimeters to centimeters are not uncommon in nature, e.g.

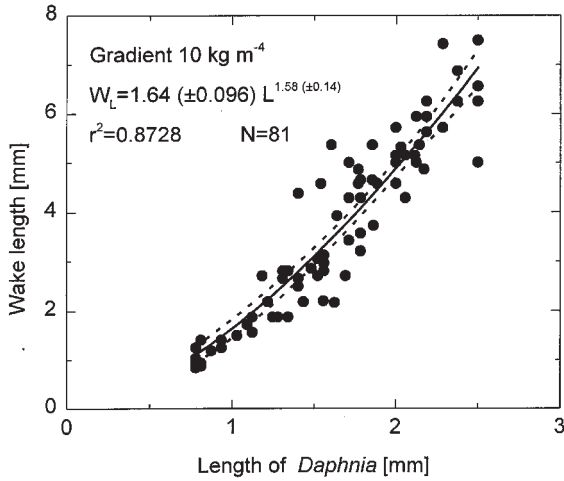


Fig. 5. Dependency of the wake size on *Daphnia* length in a density gradient of 10 kg m⁻⁴, measurements and fit.

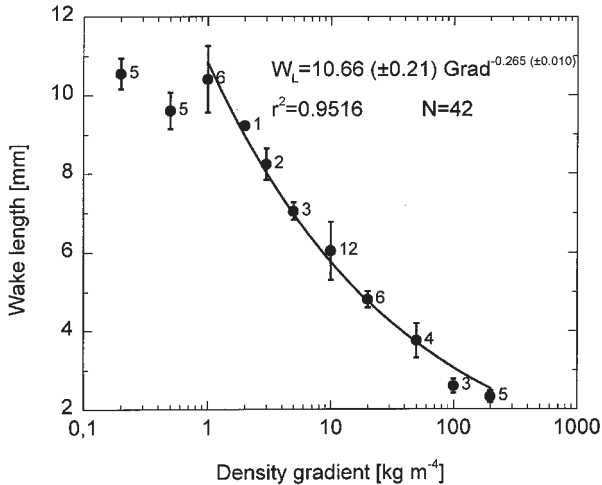


Fig. 6. Change in wake length with different density gradients. Length of the daphnids: 2.12 ± 0.38 mm. Numbers beside the points indicate the number of replicates, vertical lines the SD. The solid line represents the fitted curve according to $W_L = 10.66 (\pm 0.21) \times (dp/dz)^{-0.265 (\pm 0.010)}$ $N = 42$; $r^2 = 0.9516$.

the thermocline. Gradients of salinity and concentration of suspended particles can furthermore increase the density gradient. In regions where light and heavy water are mixed together, i.e. in estuaries, gradients can be much higher. In well-mixed water bodies (gradient $< 1 \text{ kg m}^{-4}$), the effect of density gradients on the released structures can be neglected, but it becomes important for the size and structure at gradients $> 3 \text{ kg m}^{-4}$. Knowledge about the effect of density gradients is important when interpreting the wakes formed by zooplankton measured with Schlieren optics (Strickler, 1975, 1977; Yen and Strickler, 1996).

The images obtained with Schlieren optics give some important information about the swimming mechanisms of zooplankton (Strickler, 1975, 1977; Yen and Strickler, 1996). In *Daphnia*, three currents were visible: one filtering current and two swimming currents. We were not able to determine from photographs whether these currents remain separate after being released or if they develop as distinct currents. This would have implications for the nutrient distribution within the wake (see below). With tethered daphnids, it has been shown that finer structures are incorporated in the filter current (Gries *et al.*, in preparation). Owing to the different technical set-up, these finer structures were not visible in this study.

Role of the filter current in swimming behavior of Daphnia

The role of the filter current in swimming behavior is not yet clear. Gorski and Dodson (1996) claimed in their provoking title that daphnids ‘avoid following Stokes’ law’ by settling 28% slower than predicted by Stokes’ law alone. One of the suggested mechanisms for this effect was the filter current. This would suggest an important impact of the filter current on the swimming behavior of the daphnids. However, in the images from the Schlieren optics, the filter current was occasionally visible and small, but the importance of the current in the swimming behavior cannot be judged from the image alone.

To check the effect of the filter current on the settling velocity, we assume a filter current of $Q = 3.6 \text{ ml h}^{-1}$, which is equivalent to $1 \text{ mm}^3 \text{ s}^{-1}$ (McMahon, 1965; McMahon and Rigler, 1965; Porter *et al.*, 1982). This flux is pressed through a carapace gap of $\sim 0.5 \text{ mm}$ width and 1 mm length (Porter *et al.*, 1982), or an area of $A = 0.5 \text{ mm}^2$. This yields a filter velocity of $v_F = Q/A = 2 \text{ mm s}^{-1}$. Gorski and Dodson (1996) report settling velocities of 2.14 or 2.64 mm s^{-1} at temperatures of 5 or 25°C , respectively. They try to match their measured values with those obtained by Stokes’ law, which is a result of the balance of friction and buoyancy forces expressed as:

$$6\pi\eta r\nu = (\rho_D - \rho)4/3\pi r^3 g \quad (1)$$

where ν is the settling velocity, r is the mean radius of the *Daphnia*, η is the (temperature-dependent) viscosity, ρ_D and ρ are the densities of the *Daphnia* and water, and g is the acceleration due to gravity.

Taking the values used by Gorski and Dodson (1996), i.e. $r = 0.75 \text{ mm}$, η (25°C) = $0.8904 \times 10^{-3} \text{ kg m}^{-3} \text{ s}^{-1}$ and $g = 9.81 \text{ m s}^{-2}$, this yields a density difference (possibly temperature dependent, which the authors do not take into

account) between *Daphnia* and water of about $\Delta\rho = \rho_D - \rho = 2 \text{ kg m}^{-3}$. Assuming this value to be constant over the whole range of temperature, Gorski and Dodson argue that the settling velocity of 2.14 and 2.64 mm s^{-1} cannot be explained fully by Stokes' law, which states that the velocity at 5°C must be lower than the one at 25°C by a factor of $\eta(25^\circ\text{C})/\eta(5^\circ\text{C}) = 0.585$. The observed decrease in velocity is by a factor of 0.813. This discrepancy between measurement and Stokes' law might be explained by the higher filter current at higher temperatures, or possibly less density difference between *Daphnia* and water at lower temperature, which pushes the *Daphnia* upward, or an increased resistance to sinking by for example changing the angle of the second antennae. In the following, we will show that the first assumption cannot entirely explain the decreased settling velocity.

The effect of the filter current can easily be included in the balance equation (1). The additional force due to the filter current is the change in momentum ($v_F \times dm$, where $dm = Q \times \rho \times dt$ is the amount of mass released in time dt); therefore, $F_F = v_F \times dm/dt = Q^2 \times \rho/A$ (assuming a constant filter current, not a pulsed one), yielding the slightly changed balance:

$$6\pi\eta r v = (\rho_D - \rho)4/3\pi r^3 g - Q^2\rho/A \quad (2)$$

Comparing the different terms inserting the values stated above, one recognizes that the Stokes' term is of magnitude $O(F_S) = 4 \times 10^{-8} \text{ N}$, the buoyancy term is of roughly the same magnitude, whereas the filter force gives a magnitude of $O(F_F) = 2 \times 10^{-9} \text{ N}$, or $\sim 5\%$. Therefore, the filter current can only account for a change in velocity of this size and cannot explain the discrepancy measured by Gorski and Dodson (1996). Assuming the dry weight (DW) M_{DW} of a 1.5-mm-long *Daphnia* within the range 8–25 μg DW (Geller and Müller, 1985), then one can calculate from equation (2) the filter current necessary to explain the measured change of velocities. In equation (2), the buoyancy term can be expressed in terms of the dry weight, $M_{\text{DW}} = M - \rho(4/3)\pi r^3 = (\rho_D - \rho)(4/3)\pi r^3$. This yields the expression:

$$Q = ((M_{\text{DW}}g - 6\pi\eta r v)A/\rho)^{0.5} \quad (3)$$

For a *Daphnia* of dry weight $M_{\text{DW}} = 8 \mu\text{g}$, this gives filter currents $Q(5^\circ\text{C}) = 4.1 \text{ mm}^3 \text{ s}^{-1}$ and $Q(25^\circ\text{C}) = 4.8 \text{ mm}^3 \text{ s}^{-1}$, respectively. The higher dry weight of $M_{\text{DW}} = 25 \mu\text{g}$ would be associated with filter currents of flux $Q(5^\circ\text{C}) = 10.1 \text{ mm}^3 \text{ s}^{-1}$ and $Q(25^\circ\text{C}) = 10.4 \text{ mm}^3 \text{ s}^{-1}$. These filter currents are not realistic, $Q = 1 \text{ mm}^3 \text{ s}^{-1}$ would be more appropriate, but results as already demonstrated in only a 5% effect on the settling velocity as described by Gorski and Dodson (1996).

Therefore, the filter current has some effect on the sinking rate, but cannot solely explain the discrepancy measured by Gorski and Dodson (1996), not even if the filter current is increased with temperature, but on the other hand, the filter current should not be completely neglected. Thus, other mechanisms reducing the settling velocity, like increasing the resistance due to body orientation or the second antennae, are more likely.

Without doubt, the movement of the second antennae is much more important for the swimming behavior than the filter current. This confirms the impressions obtained from Schlieren optics, which show only a weak effect of the filter current on the water displacement. For predators which sense their prey with hydro-mechanical receptors, the swimming current should be more important than the filter current. This hypothesis is supported by *Bosmina* which falls into akinesis when attacked by a copepod (Kerfoot, 1978). As a result, the hunting copepod fails to catch the *Bosmina* by losing the trace. When *Bosmina* starts swimming again too early, the copepod can sense it and is able to catch it (Kerfoot, 1978). This example demonstrates the effect of ‘noisy’ swimming on the predation risk.

As outlined above, the filtering current is $\sim 1 \text{ mm}^3 \text{ s}^{-1}$. The increase of the volume of the wake is of magnitude $20\text{--}75 \text{ mm}^3 \text{ s}^{-1}$ (Figure 3C). This is a further indication that the filter current is not of major importance for building up those structures visible with Schlieren optics. These structures are more likely produced by movement of the second antennae and the additional entrainment of surrounding fluid. The structure and behavior of the released water bodies will be discussed below.

Theoretical considerations

The dependence of the wake length, W_L , on the length, L , of the *Daphnia* as shown in Figure 5 can be interpreted as a dependence of the area of the second antennae related to body volume. Assuming a characteristic length, L_A , of the second antennae related to their area $A_A \sim L_A^2$, the volume flux generated by one beat of the antennae will be proportional to the third power of L_A , hence $V_W \sim L_A^3$. On the other hand, the volume of the wake is also proportional to this flux (which will be discussed later). Therefore, if the wake volume $V_W \sim W_L^3$ (we calculated the volume as an ellipsoid, see Results), we have a direct proportionality between the length of the wake and characteristic size of the second antennae, $L_A \sim W_L$. Hence, if one uses the relationship between wake length and length of *Daphnia* we found in our experiments ($W_L \sim L^{1.58} (\pm 0.14)$; Figure 5), we get $A_A \sim W_L^2 \sim L^{3.16} (\pm 0.28)$. This shows that the area of the second antennae is correlated with the volume L^3 of the *Daphnia*. This reasonable result, that the area is correlated with the volume, can be regarded as a weak, but independent proof of the values obtained with the Schlieren method.

For the discussion of the wake, we first focus on its development in time, the shape of the wake which is dependent on the ambient density gradient will be dealt with later on. The mushroom-shaped body we observed is characteristic for buoyant (or non-buoyant) jets and plumes (e.g. Fischer *et al.*, 1979). In our case, Reynolds number is low [assuming a characteristic velocity of 4 mm s^{-1} , a length scale of several millimeters ($L = 5 \text{ mm}$), the Reynolds number is about $Re = v \times L \times \rho/\eta = 22$ for a viscosity corresponding to 25°C] and thus the flow is laminar. We suggest, therefore, that the developed structure can be described as a vortex ring [see the examples in Batchelor (1967) plate 20], which is formed in viscous fluids by a local force (Voropayev *et al.*, 1991), here a short pulse of water pushed downward by the *Daphnia*. Another common example of such vortex rings can

be observed when drops of colored fluid are falling in a glass of water. The mathematical description of the development of vortex rings is cumbersome and we will give only some ideas which explain our experimental results.

During the formation of a vortex ring generated by a jet of fluid, entrainment of irrotational fluid occurs, which enlarges the volume of the wake significantly. The average fluid volume generated is of the order of $6 \text{ mm}^3 \text{ s}^{-1}$ (assumptions for this rough estimate: characteristic length of the antennae: 1 mm, characteristic area of the antennae: 1 mm^2 , 3 beats s^{-1} , two antennae, ignoring the pulsed character of the antennae current). After 10 s, the total volume should be $\sim 60 \text{ mm}^3$, but measurement of the wake shows a volume of 200 mm^3 or more (compare with Figure 3C), the exceeding fluid has been entrained during wake formation. The entrainment process results in an increase of volume linearly in time, and due to conservation of linear momentum (characterized by volume \times velocity) the velocity of the wake must be inversely proportional in time (Maxworthy, 1972; Shariff and Leonard, 1992). The experimental results resemble these features quite well, see the fit for the length, which must be proportional to the cubic root of time (Figure 3A), the fit for volume (Figure 3C) and velocity (Figure 3D) of the wake (velocities are calculated by differencing, which results in greater errors).

The vertical length of the wake, W_L , depends strongly on the density gradient (Figure 6). As long as the density gradient, and therefore buoyancy, is small, the wake can develop more freely, as observed also by particle tracing in the direct surrounding of planktivore filterers (Strickler, 1985; Gallager, 1993). With increasing buoyancy, the maximum length which can be reached after 5 s decreases. In a second phase of wake formation, we observed an asymptotic drift of the whole structure which is due to the buoyancy force lifting the structure after it reached its maximum distance in conjunction with a further increase in width. The relationship between the maximum distance W_L and the density gradient, or the buoyancy frequency defined by $N^2 = g/\rho \times \text{d}\rho/\text{d}z$, can be calculated with the help of dimensional analysis (for a more detailed analysis, see Fischer *et al.*, 1979). The physical process is determined by the volume flux Q generated by the *Daphnia*, the momentum flux $M = Q \times v$, where v is the velocity of the generated jet, and the buoyancy frequency N^2 . Together with the distance of the wake end from the *Daphnia*, W_L , dimensional analysis then gives two independent dimensionless parameters $\Pi_Q = W_L/l_Q$ and $\Pi_M = W_L/l_M$, where two characteristic length scales $l_Q = Q/M^{1/2}$ and $l_M = (M/N^2)^{1/4}$ are introduced. As long as buoyancy is weak, Π_M plays no role and we are left with a single dimensional parameter. Dimensional analysis then states that any physical process depending on a single dimensional parameter Π can be described by $\Pi = \text{const}$. In this case, this means that the maximum distance must be proportional to the length scale, $W_L \sim l_Q$. Since volume flux and velocity (or momentum) generated by the *Daphnia* are constant (or depend only on size, temperature, food concentration or constitution of the *Daphnia*), the maximum distance the wake can reach after a certain time is constant, as long as buoyancy is small. If the buoyancy effect becomes larger, Π_Q no longer plays any role and the same argument as above yields the dependence $W_L \sim (M/N^2)^{1/4}$. In Figure 6, this change from one state to the other can

easily be observed. As long as the density gradient is $\leq 1 \text{ kg m}^{-4}$, the maximum distance reached after 5 s is constant ($\sim 10 \text{ mm}$). When buoyancy prevails, the maximum distance decreases with $(N^2)^{-1/4}$, or equivalently with $(d\rho/dz)^{-1/4}$. An allometric fit of the data shown in Figure 6 (excluding the first two points where $d\rho/dz < 1 \text{ kg/m}^4$, which do not belong to the buoyancy-driven process) of the form $W_L = b \times (d\rho/dz)^c$ gives an exponent of $c = -0.265 (\pm 0.010)$, in excellent agreement with dimensional analysis.

Wakes as hydrodynamic signals

Now that we have given evidence that the observed structures are supported by theory, we turn to the potential implications of the wake formation on ecological processes. As has been shown, the increase in the wake volume is in the range of $20\text{--}75 \text{ mm}^3 \text{ s}^{-1}$, which is, even after a short time interval, much larger than the volume of the zooplankter itself (Figure 2). This large volume increases the probability of a mechanically orientating predator finding the zooplankter. To minimize the negative effect of the wakes as hydrodynamic ‘footprints’, it would be favorable to stay in areas where high gradients would allow only small patches. On the other hand, larger patches will persist for longer times and make the emitting zooplankton better traceable for the predator. Smaller patches would be favorable for zooplankton trying to attract a mate, since pheromone traces (postulated for copepods by Blades and Youngbluth, 1980) are most likely more stable in areas with high density gradients due to two reasons. First, the wakes will be smaller and thus the signal will be more concentrated, and second turbulence is reduced in areas with high density gradients. Observations from Gallager *et al.* (1997) showed that *Calanus* is aggregating in regions with high temperature gradients, while other species preferred water bodies with only small gradients. However, the reason why aggregation took place in these special regions still remains unclear.

Wakes and chemical communication

In contrast to the hydrodynamic signals which are generated by the second antennae, the filter current is likely more important for the chemical signals sent out. The released substances (i.e. pheromones, nutrients) are dissolved in the filter current since they are unlikely to be excreted through the thick cuticula of the carapace. Peters (1987), for instance, stated that the phosphorus excretion occurs most likely through the branchial sacs of the filter legs. Substances from the gut are also released into the filter current. It is not clear yet whether the filter current is mixed into the swimming current from the second antennae or if it remains as a more or less separate water body, but (turbulent) mixing is small due to low Reynolds number. On the other hand, the wake volume increase of $20\text{--}75 \text{ mm}^3 \text{ s}^{-1}$ can only be explained by an additional entrainment of surrounding fluid compared to the current of the second antennae. Also the filter current is somehow included in the wake, but it is unclear to what amount it is mixed with the fluid or stays in separate regions; this cannot be judged from our images.

Images of vortex rings (Voropayev *et al.*, 1991) demonstrate that the entrained fluid does not mix with the spiral-like shape. Since the currents from the strokes of the second antennae are pulsed, we suggest that such a vortex structure will not develop fully, but will be overlaid by the next water package, resulting in a number of stripes of entrained (ambient) and less dense water from the current from antennae and filter movement (which we could not distinguish) visible in Figure 4.

Thus, the nutrients and pheromones in the filter current are possibly not released into the whole wake structure, but are confined to its surface or 'outer shell'. This would have implications for the concentrations of these substances in the plume. For nutrients (i.e. phosphorus), it was shown that higher concentrations favor species with high K_M and V_{max} values (i.e. algae), compared to low concentrations where species with low K_M and V_{max} values (i.e. bacteria) take up more nutrients (Lehmann and Scavia, 1982; Rothhaupt and Güde, 1992). In environments with low density gradients, zooplankton will create large (diluted) nutrient patches, while in areas with strong gradients, the nutrient patches will be smaller, and therefore of higher concentration. The nutrient-enriched patches of the filter current in the wake, which is due to the low Reynolds number most likely separated from the antennae current and the entrained fluid during formation of the wake, of course will be mixed by molecular diffusion. Diffusive mixing occurs on time scales $T_d = l^2/\nu$, where l is a length scale and $\nu = 10^{-3} \text{ mm}^2 \text{ s}^{-1}$ is the diffusivity of dissolved substances in water. Taking the thickness of one of the stripes visible in Figure 4, $l = 0.1 \dots 0.2 \text{ mm}$, as characteristic length, the characteristic time for diffusive mixing will be around $T_d = 10 \dots 40 \text{ s}$. This must be compared to the time scale of nutrient uptake which is $T_u = [V_{max} \times C/(C + K_M)]^{-1}$, where C is a characteristic nutrient concentration. For instance, for phosphorus, the most important limiting nutrient in fresh water, C is likely in the range of $13 \mu\text{g P}$, and K_M and V_{max} of the order of $10 \mu\text{g P l}^{-1}$ and $3 \times 10^{-7} \mu\text{g P cell}^{-1} \text{ h}^{-1}$, respectively (Jørgensen, 1979). With an average cell density of $5 \times 10^{-6} \text{ cells l}^{-1}$, T_u is in the range of 1 h. This demonstrates that molecular diffusion is much more important for the vanishing of the nutrient patch than the uptake by organisms. However, it remains to be tested whether this patchiness has an impact on the uptake rates and/or the competition between algae and bacteria for P, as demonstrated by Lehman and Scavia (1982) and Rothhaupt and Güde (1992).

Conclusions

The shape and size of the wakes, which can be seen as 'footprints' produced by *Daphnia*, changed with density gradients and thus the results obtained with Schlieren optics cannot be extrapolated to nature without care. Even if the general scheme holds, there may be considerable differences in some of the details. Therefore, we recommend that more detailed measurements are made for gradients occurring naturally in lakes, reservoirs and the ocean in order to get more realistic results about wake size and structure.

As a rule, we found that patches are larger in environments with smaller gradients, but persist longer in the case of stronger gradients. It is likely that different

sizes of the wakes will have implications on the predator–prey and mate interaction, which could potentially explain preference and aggregation of zooplankton in certain density gradients. Furthermore, it is possible that different wake sizes have an impact on the competition between phytoplankton and bacteria for nutrients, and on mate-seeking behavior, since the signals, i.e. pheromones, are dispersed in the water column according to the physical structure of the wake.

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References

- Batchelor, G.K. (1967) *Introduction to Fluid Dynamics*. Cambridge University Press, Cambridge.
- Blades, P.I. and Youngbluth, M.J. (1980) Morphological, physiological and behavioral aspects of mating in calanoid copepods. In Kerfoot, W.C. (ed.), *Evolution and Ecology of Zooplankton Communities*. University Press of New England, pp. 39–51.
- CRC Handbook of Chemistry and Physics (1996) Viscosity of aqueous solutions. In Lide, D.R. and Frederiske, H.P.R. (eds), *CRC Handbook of Chemistry and Physics*. CRC Press, Boca Raton, FL, pp. 6–250.
- Carr, M.-E., Lewis, M.R. and Kelley, D. (1995) A physical estimate of new production in the equatorial Pacific along 150°W. *Limnol. Oceanogr.*, **40**, 138–147.
- de Bernadi, R. and Peters, R.H. (1987) *Why Daphnia?* In Peters, R.H. and de Bernadi, R. (eds), *Daphnia. Mem. Ist. Ital. Idrobiol.*, **45**, 1–9.
- den Oude, P.J. and Gulati, R.D. (1988) Phosphorus and nitrogen excretion rates of zooplankton from the eutrophic Loosdrecht lakes, with notes on other P sources for phytoplankton requirements. *Hydrobiologia*, **169**, 379–390.
- Dugdale, R.C. and Goering, J.J. (1967) Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnol. Oceanogr.*, **12**, 196–206.
- Eppley, R.W. and Peterson, B.J. (1979) Particulate organic matter flux and planktonic new production in the deep ocean. *Nature*, **282**, 677–680.
- Fields, D. and Yen, J. (1997) Implications of the feeding current structure of *Euchaeta rimana*, a carnivorous pelagic copepod, on the spatial orientation of their prey. *J. Plankton Res.*, **19**, 79–95.
- Fischer, H.B., Imberger, J., List, E.J., Koh, P.C.Y. and Brooks, N.H. (eds) (1979) *Mixing in Inland and Coastal Waters*. Academic Press, New York.
- Gallager, S.M. (1993) Hydrodynamic disturbances produced by small zooplankton: case study for veliger larva of a bivalve mollusc. *J. Plankton Res.*, **15**, 1277–1296.
- Gallager, S.M., Davis, C.S., Epstein, A.W., Solow, A. and Beardsley, R.C. (1997) High resolution observations of plankton spatial distributions correlated with hydrography in the Great South Channel, Georges Bank. *Deep-Sea Res. II*, **43**, 1627–1663.
- Geller, W. and Müller, H. (1985) Seasonal variability in the relationship between body length and individual dry weight as related to food abundance and clutch size in two coexisting *Daphnia* species. *J. Plankton Res.*, **7**, 1–18.
- Gorski, P.R. and Dodson, S.I. (1996) Free-swimming *Daphnia pulex* can avoid following Stokes' law. *Limnol. Oceanogr.*, **41**, 1815–1821.
- Gries, T., Liu, J. and Strickler, J.R. 'Footprints' in the water column: What is left behind? (Evidence for small scale patches caused by zooplankton). In preparation.
- Imberger, J. and Ivey, G.N. (1991) On the nature of turbulence in a stratified fluid. Part II: Application to lakes. *J. Phys. Oceanogr.*, **21**, 659–680.
- Jørgensen, S.E. (1979) *Handbook of Environmental Data and Ecological Parameters*. International Society for Ecological Modeling, Copenhagen.
- Kerfoot, W.C. (1978) Combat between predatory copepods and their prey: *Cyclops*, *Epischura* and *Bosmina*. *Limnol. Oceanogr.*, **23**, 1089–1102.
- Kerfoot, W.C., Kellogg, D.L. and Strickler, J.R. (1980) Visual observations of live zooplankters: evasion, escape and chemical defenses. In Kerfoot, W.C. (ed.), *Evolution and Ecology of Zooplankton Communities*. University Press of New England, pp. 10–27.

- Lehman, J.T. and Scavia, D. (1982a) Microscale nutrient patches produced by zooplankton. *Proc. Natl Acad. Sci. USA*, **79**, 5001–5005.
- Lehman, J.T. and Scavia, D. (1982b) Microscale patchiness of nutrients in plankton communities. *Science*, **216**, 729–730.
- Maxworthy, T. (1972) The structure and stability of vortex rings. *J. Fluid Mech.*, **51**, 15–32.
- McMahon, J.W. (1965) Some physical factors influencing the feeding behavior of *Daphnia magna* Straus. *Can. J. Fish. Aquat. Sci.*, **43**, 603–612.
- McMahon, J.W. and Rigler, F.H. (1965) Feeding rate of *Daphnia magna* Straus in different foods labeled with radioactive phosphorus. *Limnol. Oceanogr.*, **10**, 105–113.
- Peters, R.H. (1987) Metabolism in *Daphnia*. In Peters, R.H. and de Bernardi, R. (eds), *Daphnia. Mem. Ist. Ital. Idrobiol.*, **45**, 193–243.
- Poister, D., Armstrong, D.E. and Hurley, J.P. (1994) A 6-yr record of nutrient element sedimentation and recycling in three north temperate lakes. *Can. J. Fish. Aquat. Sci.*, **51**, 2457–2466.
- Porter, K.G., Gerritsen, J. and Orcutt, J.D. (1982) The effect of food concentration on swimming patterns, feeding behavior, ingestion, assimilation and respiration by *Daphnia*. *Limnol. Oceanogr.*, **27**, 935–949.
- Rothhaupt, K.-O. and Güde, H. (1992) The influence of spatial and temporal concentration gradients on the phosphate partitioning between different size fractions of plankton: Further evidence and possible causes. *Limnol. Oceanogr.*, **37**, 739–749.
- Shariff, K. and Leonard, A. (1992) Vortex rings. *Annu. Rev. Fluid Mech.* **24**, 235–279.
- Strickler, J.R. (1975) Intra- and interspecific flow around planktonic copepods: receptors. *Verh. Int. Ver. Limnol.*, **19**, 2951–2958.
- Strickler, J.R. (1977) Observation of swimming performance of planktonic copepods. *Limnol. Oceanogr.*, **22**, 165–169.
- Strickler, J.R. (1985) Feeding currents in calanoid copepods: two new hypotheses. In Laverack, M.S. (ed.), *Physiological Adaptations of Marine Animals. Symp. Soc. Exp. Biol.*, **39**, pp. 459–485.
- Strickler, J.R. and Twombly, S. (1975) Reynolds number, diapause and predatory copepods. *Verh. Int. Ver. Limnol.*, **19**, 2943–2950.
- Voropayev, S.I., Afanasyev, Y.D. and Filippov, I.A. (1991) Horizontal jets and vortex dipoles in a stratified fluid. *J. Fluid Mech.*, **227**, 543–566.
- Wassmann, P. (1990) Relationship between primary and export production in the boreal coastal zone of the North Atlantic. *Limnol. Oceanogr.*, **35**, 464–471.
- Yen, J. and Strickler, J.R. (1996) Advertisement and concealment in the plankton: what makes a copepod hydrodynamic conspicuous? *Invertebr. Biol.*, **115**, 191–205.
- Yen, J., Weissburg, M.J. and Doall, M.H. (1998) The fluid physics of signal perception by mate-tracking copepods. *Phil. Trans. R. Soc. Lond. B.*, **353**, 787–804.

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