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Modeling sinking rate of zooplankton carcasses: Effects of stratification and mixing

Georgiy Kirillin,a,* Hans-Peter Grossart,a,b and Kam W. Tangc

a Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany
b Potsdam University, Institute for Biochemistry and Biology, Potsdam, Germany
c Virginia Institute of Marine Science, College of William & Mary, Gloucester Point, Virginia

Abstract

Using the carcass sinking rate and density determined in laboratory for several freshwater zooplankton species, we developed a model of zooplankton carcass sinking as affected by turbulence and stratification. The model was subsequently used to estimate the residence time of zooplankton carcasses in the water column of Lake Stechlin, a typical temperate dimictic lake in northeastern Germany. The residence time varied among the different species and was strongly affected by thermal stratification. At the peak of summer stratification, the carcasses stayed up to 5 d in the 70 m-deep water column before reaching the lake bottom. Residence time was long enough that zooplankton carcasses could serve as an important matter and energy source for bacteria in the lake’s pelagic zone and hence have the potential to significantly affect aquatic carbon and nutrient cycling. The proposed model of sinking rates, based on physically sound relationships, can be easily applied to other passively sinking particles, and be integrated into large ecosystem models.

Zooplankton carcasses are commonly present in both marine and freshwater environments, and at times they comprise a high percentage of the plankton samples, implicating the occurrence of non-predatory mortality (reviewed in Tang et al. 2009). Examining individual zooplankters for vital signs is time consuming and impractical in large-scale field surveys, whereas the recently improved vital and mortal staining methods allow researchers to easily and quickly quantify zooplankton carcasses in the field (Elliott and Tang 2009; Bickel et al. 2009). Zooplankton can suffer non-predatory mortality due to injuries, starvation, disease, harmful algal blooms, or environmental stresses (Kimmerer and McKinnon 1990; Delgado and Alcaraz 1999; Bickel et al. 2011). Globally, it is estimated that marine adult copepods suffer 25–33% non-predatory mortality (Hirst and Kiørboe 2002). Non-predatory mortality is also common in lakes and reservoirs (McKee et al. 1997; Gries and Gu¨de 1999; Dubovskaya et al. 2003), especially near the end of the growing seasons, resulting in midsummer decline (Gries and Gu¨de 1999; Hülsmann and Weiler 2000; Hülsmann and Voigt 2002). For example, in Lake Constance, Gries and Gu¨de (1999) estimated that non-predatory mortality of Daphnia galeata accounts for 23% of its production. In Bugach reservoir, Siberia, Dubovskaya et al. (2003) estimated that non-predatory mortality accounts for an average of 30%, at times even 100%, of the total mortality of Daphnia sp.

Because zooplankton carcasses are very rich in labile organic constituents, they can be an important matter and energy source for microbes (Reinfelder et al. 1993; Bickel and Tang 2010). Both laboratory and field experiments have shown that zooplankton carcasses are quickly colonized by bacteria (Lee and Fisher 1992; Tang et al. 2006a), and the decomposition process can contribute to a substantial amount of bacterial production and enzymatic activities even in the surrounding water (Tang et al. 2006b, 2009). To understand to what extent zooplankton carcass carbon is recycled through the pelagic microbial loop, one needs to know the carcass residence time within the water column.

Information in the literature on zooplankton carcass sinking rates is scarce and equivocal. Several studies in coastal seas reported zooplankton carcasses in sediment traps, and the estimated carcass flux represents a major fraction of the carbon flux to the benthos (Sampei et al. 2009; Frangoulis et al. 2011). Gries and Gu¨de (1999) and Dubovskaya et al. (2003) observed in Lake Constance and Bugach reservoir, respectively, a close correspondence between high abundances of trap-collected Daphnia carcasses at depth and low pelagic population abundance. Together, these studies suggest a short residence time of zooplankton carcasses within the water column. On the contrary, zooplankton carcasses caught in shallow plankton net tows suggest that some carcasses may remain in the upper water column for an indefinite time (Bickel et al. 2009; Elliott and Tang 2011). A study in the Japan Sea even found an accumulation of copepod carcasses just below the thermocline, where the carcasses may remain for months (Terazaki and Wada 1988). These earlier observations provide only anecdotal information, as no direct measurements of carcass sinking rates were made.

Using a combination of experiments and modeling, Elliott et al. (2010) estimated that in a shallow estuarine environment, strong tidal energy and turbulence may greatly reduce carcass sinking rates and subject them to extended microbial actions within the water column. A simple model based on carcass decomposition and sinking rates further predicts that copepod carcasses may reach neutral buoyancy within the upper 300 m in the open ocean (Elliott et al. 2010), consistent with the observations in the Japan Sea (Terazaki and Wada 1988). The model also predicts that an ~1-mm copepod carcass would sink ~199 m d−1 in freshwater. A caveat to this prediction is that the model does not consider water column stratification.

*Corresponding author: kirillin@igb-berlin.de
and the highly variable mixing conditions in lakes, which may significantly lengthen carcass residence time within the water column. Strong thermal stratification in the summer often coincides with the growing season in dimictic lakes, when zooplankton abundances reach maximum. Carcass residence time may also vary among zooplankton types: Unlike the marine systems where copepods are the dominant zooplankton, cladocerans are highly abundant in lakes, and the very different body morphology and carapace structure among the zooplankton species may lead to different hydrodynamic characteristics, hence, sinking rate of their carcasses.

Located in northeastern Germany (53°10′N, 13°02′E), Lake Stechlin is a dimictic oligotrophic lake with low anthropogenic influence (Casper 1985). The lake serves as a reference lake for the European Water Framework Directive, and has been continuously studied for almost 50 yr. The lake has a maximum depth of 69.5 m and an area of 4.3 km². An earlier study showed that an average of 6% of the zooplankton in situ were dead in summer (Bickel et al. 2009). The goal of the present study was to construct a hydrodynamically realistic model for estimating in situ zooplankton carcass residence time in Lake Stechlin based on laboratory measurements of carcass sinking rate, in situ vertical temperature profile, and turbulence estimation from microstructure profiling. In order to evaluate the universality of the model, we tested the basic model parameterizations with temperature and turbulence data from Lake Arendsee (52°53′N, 11°28′E), which has similar morphometric characteristics: surface area 5.1 km², maximum depth 50 m (Halbfass 1896; Hupfer and Lewandowski 2005). Results were then discussed in the context of carcass carbon recycling and the effects on pelagic bacterial processes in Lake Stechlin. The model was further expanded to investigate other passively sinking particles, such as zooplankton fecal pellets.

Methods

In vitro carcass sinking rate—Sinking rate of zooplankton carcasses was measured in the laboratory in a 2-liter graduated cylinder filled with surface lake water that had been equilibrated to air temperature (21°C) to avoid convection. Live zooplankton collected from Lake Stechlin were killed by brief exposure to acid, and thereafter thoroughly rinsed with lake water (Tang et al. 2006b). Freshly killed zooplankton was gently released individually with a pipette into the cylinder, and sinking rate was measured as the time it took a carcass to sink 20 cm.

Sinking rate was measured for carcasses of each of the five dominant zooplankton groups: Daphnia cucullata, Diaphanosoma brachyurum, Eudiaptomus gracilis, cyclopoid copepod (6–8 carcasses each), and Ceriodaphnia sp. (3 carcasses). Some individuals of Daphnia cucullata opened up their carapace upon death, which may create a “parachute” effect; we therefore also measured the sinking rate of D. cucullata carcasses with open carapace.

Carcass density—Carcass density was measured by density gradient method. Freshwater and a saline solution (1 g mL⁻¹ NaCl) were mixed in different proportions in test tubes to create different fluid densities, and were then allowed to equilibrate to the room temperature before use. Freshly killed zooplankton were gently added to the test tubes, and the sinking pattern of the carcasses was observed. When carcasses remained at or near neutral buoyancy, carcass density was assumed to be equal to the ambient fluid density. Five to 10 carcasses were used for each zooplankton species to obtain an average carcass density.

Vertical temperature profiles—Vertical temperature profiles were measured at the deepest stations in Lake Stechlin and Lake Arendsee, using moored strings with temperature loggers (RBR-1050, Richard Branker Research). Lake Stechlin temperatures were measured during summer 2005 using 10 loggers distributed over the upper 30 m of the water column. Lake Arendsee temperatures were measured in 2010 using 15 loggers distributed over the upper 40 m. Temperature was measured at 10-s intervals in both cases. Typical summer profiles were derived by averaging temperature time series over the period from 01 June to 31 July of the corresponding year.

Turbulence estimation from microstructure profiling—In situ characteristics of turbulence were measured by a free-falling shear microstructure (MSS) profiler MSS-60 (Wassermeßtechnik Prandke) equipped with two airfoil velocity shear sensors for estimation of dissipation rate of the turbulence kinetic energy (ε), and a fast-response thermistor for estimation of temperature and density fields (Prandke 2005). The instrument was allowed to fall through the water column at a speed of 0.5 m s⁻¹, taking measurements at 1024 Hz. Ten profiles were taken in Lake Stechlin on 18 June 2008 at noon at an interval of 10 min to avoid previous mixing produced by the profiler itself. The upper 0–1.5 m was excluded because the sinking velocity of the profiler was not constant. The profiler was stopped 5 m above the lake bottom to avoid hitting the bottom. Another 10 profiles were taken on 21 June 2008 in Lake Arendsee using the same procedure. Subsequently, the dissipation rate ε was calculated from the measured velocity shear ∂U/∂z as (Hinze 1959):

\[ ε = \frac{15}{2} ν \left( \frac{\partial U}{\partial z} \right)^2 \left( \text{m}^2 \text{s}^{-3} \right) \]  

where \( ν \) (m² s⁻¹) is the kinematic viscosity of water (Lueck et al. 2002). The profiles of the vertical turbulent diffusion coefficient \( K_z \) were determined from \( ε \) by adopting the Kolmogorov–Prandtl hypothesis (Hinze 1959):

\[ K_z \sim L_T ε^{1/2} \]  

\[ ε \sim ε^{3/2} L_T^{-1} \]  

where \( ε \) is the kinetic energy of turbulent fluctuations, and \( L_T \) is the turbulent length scale. The latter was defined as:

\[ L_T = \begin{cases} \frac{C_k}{ε^{1/2}} & \text{at } ε^{1/2} N^{-3/2} ≥ \frac{C_k}{ε} \\ \frac{C_k}{ε^{1/2}} N^{-3/2} & \text{at } ε^{1/2} N^{-3/2} < \frac{C_k}{ε} \end{cases} \]
where \( z \) is the depth from the lake surface, \( \kappa = 0.4 \) is the von Karman constant, and \( N \) is the buoyancy frequency. Then, the final expression for the diffusion coefficient is:

\[
K_z = \begin{cases} 
C_1 \varepsilon^{1/3} z^{4/3} & \text{at } \varepsilon^{1/2} N^{-3/2} \geq \kappa z \\
C_2 \varepsilon N^{-2} & \text{at } \varepsilon^{1/2} N^{-3/2} < \kappa z
\end{cases}
\] (5)

with \( C_1 = \kappa^{4/3} \) and \( C_2 = 0.2 \) (Osborn 1980).

Eqs. 4–5 represent a combination of two turbulence models: “Law-of-the-wall” for the non-stratified surface boundary layer and the Ozmidov–Osborn model for the stratified interior. The latter has proven its validity for marine and lacustrine stratified environments but is not directly applicable to the lake mixed layer where \( N \approx 0 \). Therefore, the linear Law-of-the-wall length scale replaces the Ozmidov length scale in the vicinity of the lake surface as being smaller there and thereby limiting the size of the turbulent eddies. The mean profiles of the vertical diffusion coefficient were constructed by averaging over successive profiles and, subsequently, over 0.5-m depth intervals.

Results I: In vitro Zooplankton Carcass Sinking Rate and Carcass Density

The sinking rate remained nearly constant during a single trial, i.e., sinking rate within the first 10 cm was similar to that within 10–20 cm, demonstrating the steady-state regime of sinking. In vitro sinking rate varied greatly among species (Table 1). The shape of the carcass also had a clear effect: \( D. \ cucullata \) carcasses with open carapace sank at < 50% of the velocity as those with closed carapace. Carcass density varied interspecifically but differently from carcass sinking rate (Table 1). For example, \( E. \ gracilis \) carcass had a higher density than \( D. \ cucullata \), but its sinking rate was less.

Results II: Carcass Sinking Model

Flow regime of sinking zooplankton carcasses—Characteristics of sinking depend on the ratio of the inertial forces to viscous forces as expressed by Reynolds number \( Re \):

\[
Re = L u_s v^{-1}
\] (6)

where \( L \) (m) is the linear scale (particle diameter) and \( u_s \) (m s\(^{-1}\)) is the sinking rate. If \( Re < 1.0 \), the flow is laminar and the sinking rate is determined by the balance between the negative buoyancy of the particle and viscous forces:

\[
B \sim L^{-2} v u_s
\] (7)

where \( B = g \Delta \rho / \rho_w \) (m s\(^{-2}\)) is the particle’s buoyancy, \( g \) (m s\(^{-2}\)) is the gravity acceleration, \( \Delta \rho = (\rho_p - \rho_w) \) is the excess density, \( \rho_p \) is particle density, and \( \rho_w \) is density of surrounding water. For a spherical particle, Eq. 7 turns into the exact theoretical solution known as Stokes’ Law:

\[
U_s = \frac{1}{18} \frac{BL^2}{v}
\] (8)

For high sinking rate and/or large objects, \( U_s L \gg v \) and \( Re \gg 1 \), i.e., the flow around the falling object is unstable (turbulent). The negative buoyancy is balanced by the turbulent drag force, which is often parameterized as:

\[
B \sim L^{-1} C_D u_s^2
\] (9)

\( C_D \) is an empirical “drag coefficient” approaching a nearly constant value at very high \( Re \). Eqs. 7 and 9 can be combined by the interpolation formula:

\[
U_s = \frac{BL^2}{C_1 v + (C_D BL)^{1/2}}
\] (10)

with \( C_1 \) and \( C_D \) being empirical constants. At small \( L \) Eq. 10 turns into Eq. 7 and corresponds to the Stokes solution (Eq. 8) when \( C_1 = 18 \). At large \( L \) it corresponds to Eq. 9.

For estimation of the sinking flow regime using Eq. 6, we used sinking rates and densities measured in the laboratory. For initial parameterization, we used a value of 1 mm for \( L \) (hereafter \( L_1 \)), which is a good approximation for the species used in the experiment (Hutchinson 1967; Bottrell et al. 1976). To improve the parameterization, we further used the empirically measured \( B \) and \( u_s \) to reciprocally calculate \( L \) as the “equivalent spherical diameters” (ESDs) based on Eqs. 8 and 10. The ESD derived from Eq. 8 (hereafter \( L_{\text{stokes}} \)) represents the diameter of a spherical particle that sinks at the measured velocity in a nonturbulent regime. The ESD derived from the interpolation formula (Eq. 10) (hereafter \( L_{\text{int}} \)) indirectly accounts for a nonspherical particle shape by adopting the coefficient values \( C_1 = 24 \) and \( C_D = 0.75 \), which produce the best fit to experimental data on sinking of slightly nonspherical particles (Fergusson and Church 2004). The resistance drag produced by particles of irregular shape, like zooplankton carcasses, is larger than that produced by a sphere. Therefore, the particle length scales \( L_{\text{stokes}} \) and \( L_{\text{int}} \) estimated as ESDs from Eqs. 8 and 10, respectively, were 4–6 times smaller than the carcass sizes \( L_1 \) from the literature (Table 2). The corresponding “equivalent” Reynolds numbers \( Re_{\text{stokes}} \) and \( Re_{\text{int}} \) were significantly < 1, i.e., the sinking rates were small enough for spherical particles to sink in the laminar regime. \( Re \) based on maximum length scales \( L_1 \) was \( \sim 1 \) for all species such that the flow could deviate from a laminar one, although this deviation was not high. Batchelor (1967) showed that for Eq. 9 to be valid and to replace Eq. 8, the turbulent flow should be well

<table>
<thead>
<tr>
<th>Table 1. Zooplankton carcass sinking rates (m d(^{-1})) and carcass densities (kg m(^{-3})) (mean ± SD).</th>
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<tr>
<td><strong>Species</strong></td>
</tr>
<tr>
<td><strong>D. cucullata</strong> (open carapace)</td>
</tr>
<tr>
<td><strong>Sinking rate</strong></td>
</tr>
<tr>
<td><strong>Density</strong></td>
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developed with $Re > 10^3$. He also demonstrated, following Castleman (1926), that for practical purposes the laminar flow assumption is tolerably accurate for $Re = 1$. Under this condition, the corrections introduced by using Eq. 10 were small, as seen from comparison of the length scales and $Re$ provided by Eqs. 8 and 10 (Table 2). We assumed in the following analysis that the flow was viscous (nonturbulent) and adopted Eq. 8 in the following model.

**Temperature effects on carcass sinking rate**—Because water viscosity and density are affected by temperature, the sinking rates of zooplankton carcasses will vary within a thermally stratified water column. Dependence of viscosity on temperature can be approximated as (Sharqawy et al. 2010):

$$\nu(T) = \rho_w \left\{ 4.2844 \times 10^{-5} + \right.$$  
$$\left[ 0.157(T + 64.993)^2 - 91.296 \right]^{-1} \right\}$$ \hspace{1cm} (11)

The equation of state of Chen and Millero (1980) was adopted for calculation of freshwater density $\rho_w$ as a function of temperature. Temperature dependence of carcass density is unknown and is controlled, to a large extent, by the water content of the carcasses. We considered two extreme scenarios: In the first scenario the particle density $\rho_p$ is predominantly determined by the particle’s water content such that $\rho_p$ changes with temperature in the same manner as the environmental density $\rho_w$, and the excess density $\Delta \rho$ is temperature independent. In the second scenario the solid fraction constitutes the most of the particle’s weight such that $\rho_p$ is temperature independent, and $\Delta \rho$ changes with temperature as $d\Delta \rho / dT = -d\rho_p / dT$. The sinking rate derived from Eq. 8 showed only a slight difference between the two scenarios for the temperature range 0–30°C (cf. solid and dashed lines in Fig. 1). Only at temperature $> 30°C$ the second scenario gave a significant temperature-dependent increase in carcass sinking rate relative to the first scenario. Therefore, in the typical range of environmental temperature 0–30°C, temperature affected carcass sinking rate mainly via its effect on viscosity such that the sinking rate at 30°C was 2 times higher than that at 0°C. The typical summer water temperature in temperate lakes is 20–25°C at the surface and 4–5°C in the deep hypolimnion; hence, variations in viscosity should appreciably affect the rate at which a carcass sinks through the water column.

**Parameterization of the vertical temperature distribution**—Effects of vertical temperature distribution on carcass residence time in the lake water column can be estimated by putting temperature measurements into Eq. 11 and solving the equation $z(t) = z_0 + U_S(z, t) \times t$, where $t$ is time, $z$ is the distance from the lake surface, $z_0$ is the initial depth of a carcass, and $U_S$ is determined by Eq. 8. The vertical temperature distribution in the majority of temperate freshwater lakes follows a typical seasonal pattern: In spring and autumn, lakes are fully mixed vertically by convection, and the entire water column resides at temperature of maximum density (~ 4°C). In summer, the thermally homogeneous upper mixed layer (UML) extends from the lake surface to typically 5–10-m depth. The UML is bounded from below by the thermocline, which prevents heating of the lower water column. In winter, temperature increases from ~ 0°C at the surface to 4°C near the lake bottom. The summer-mean temperature profiles from Lake Stechlin and Lake Arendsee exhibited the same general characteristics of vertical temperature distribution (Fig. 2). We adopted the following approximation for this distribution:

$$T(z) = \begin{cases} 
T_{\text{UML}} & \text{at } z < Z_{\text{UML}} \\
T_B + (T_{\text{UML}} - T_B)e^{-z/4} & \text{at } z \geq Z_{\text{UML}} 
\end{cases}$$ \hspace{1cm} (12)

where $Z_{\text{UML}}$ and $T_{\text{UML}}$ are the UML’s thickness and temperature, respectively, and $T_B$ is the temperature at the

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**Table 2.** Zooplankton carcass length scales and Reynolds numbers. lit., from the literature.

<table>
<thead>
<tr>
<th>Species</th>
<th>$L_{\text{lit}}$ (µm, lit.)</th>
<th>$Re_{\text{lit}}$</th>
<th>$L_{\text{stokes}}$ (µm, Eq. 8)</th>
<th>$Re_{\text{stokes}}$</th>
<th>$L_{\text{int}}$ (µm, Eq. 10)</th>
<th>$Re_{\text{int}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Daphnia cucullata</em></td>
<td>1000</td>
<td>1.52</td>
<td>237</td>
<td>0.36</td>
<td>291</td>
<td>0.44</td>
</tr>
<tr>
<td><em>D. cucullata</em> (open carapace)</td>
<td>1000</td>
<td>0.73</td>
<td>149</td>
<td>0.09</td>
<td>178</td>
<td>0.11</td>
</tr>
<tr>
<td><em>Diaphanosoma brachyurum</em></td>
<td>1000</td>
<td>1.05</td>
<td>189</td>
<td>0.20</td>
<td>229</td>
<td>0.24</td>
</tr>
<tr>
<td><em>Eudiaptomus gracilis</em></td>
<td>1200</td>
<td>1.65</td>
<td>157</td>
<td>0.22</td>
<td>191</td>
<td>0.26</td>
</tr>
<tr>
<td>Cyclopoid copepod</td>
<td>1000</td>
<td>0.67</td>
<td>123</td>
<td>0.08</td>
<td>146</td>
<td>0.10</td>
</tr>
<tr>
<td><em>Ceriodaphnia</em> sp.</td>
<td>1000</td>
<td>0.98</td>
<td>173</td>
<td>0.17</td>
<td>208</td>
<td>0.20</td>
</tr>
</tbody>
</table>

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**Fig. 1.** Dependence of carcass sinking rate on temperature by means of viscosity (dashed lines) and by combined effect of viscosity and density difference (solid lines).
lake bottom. The same approximation describes the non-
stratified temperature distribution in spring and autumn by
assuming $Z_{UML}$ to be equal to the lake’s depth and
choosing an appropriate value for $T_{UML}$.

Turbulence effect—Turbulence effect on sinking rate is
described by the Peclet number ($Pe$):

$$Pe = \frac{U_S}{W_{rms}}$$

(13)

where $W_{rms}$ is the root mean square velocity of turbulent
fluctuations (cf. Eq. 3):

$$W_{rms} = e^{1/2} = (\varepsilon L_T)^{1/3}$$

(14)

At $Pe < 1$, the particle movement is strongly affected by the
turbulent fluctuations; otherwise, the kinetic energy of
sinking prevails and the effect of turbulence is minor. The
mixing conditions in our stratified lakes varied widely
throughout the water column (Fig. 3). $\varepsilon$ was $10^{-5}$ m$^2$ s$^{-3}$ in
the UML and the corresponding $Pe$ was $\ll 1$, indicating a
strong influence of turbulence on sinking carcasses. In the
strongly stratified meta- and hypolimnion, $\varepsilon$ decreased to
$10^{-9}$ m$^2$ s$^{-3}$; $Pe$ was $> 1$ and it decreased with depth in the
hypolimnion. For the slowest sinking carcasses ($D. cucullata$
with open carapace), $Pe$ decreased to $< 1$ at $\sim 40$ m. Consequently, the hypolimnion turbulence, which
was produced here by internal seiche currents, had kinetic
energy comparable to that of carcasses’ sinking. Turbulent
energy increased further closer to the bottom boundary layer, where additional mixing was produced by the bottom friction. The net effect of spatially variable turbulent motions on sinking particles is not straightforward. Turbulent fluctuations can, on the one hand, increase the residence time by supporting carcasses in the water column, and, on the other hand, accelerate sinking of carcasses by removing them quickly from highly turbulent regions. In order to introduce turbulence effect into the model, we adopted the following equation for particle trajectory in a spatially heterogeneous turbulence field (Hunter et al. 1993):

$$\frac{dZ}{dt} = -U_S + \frac{dK_Z}{dz} + R \times W_{rms}$$  \hspace{1cm} (15)

where $Z$ is the vertical coordinate of a single particle, $K_Z$ is the turbulent diffusivity, variable in the vertical direction, $R$ is a normally distributed random number with zero mean and variance of 1. $W_{rms}$ is the root-mean-square turbulent velocity for locally homogeneous turbulence, estimated as (Batchelor 1949):

$$W_{rms}^2 = 2K_Z dt^{-1}$$  \hspace{1cm} (16)

The vertical distribution of $K_Z$ was parameterized in a manner similar to that used for vertical temperature profile. The vertical profiles of $K_Z$ in both Lake Stechlin and Lake Arendsee were similar such that the diffusivity decreased quasi-exponentially with depth within the UML and increased in the same exponential manner in the hypolimnion. One remarkable difference was the mixing intensity in the metalimnion at ~ 10 m: $K_Z$ was at a minimum of ~ $10^{-5}$ m$^2$ s$^{-1}$ in Lake Stechlin, in contrast to a local maximum of $K_Z$ of ~ $10^{-3}$ m$^2$ s$^{-1}$ at the same depth in Lake Arendsee. This dissimilarity demonstrated strong effects of the internal seiche characteristics on the mixing in the metalimnion: Lake Arendsee had a larger surface area and regular shape, whereas Lake Stechlin had an indented shoreline, dividing the lake into several connected basins. As a result, internal seiche amplitudes at the thermocline were much higher in Lake Arendsee than in Lake Stechlin, and a higher mixing was produced by the internal wave breaking in the metalimnion of Lake Arendsee (G. Kirillin unpubl. data). In order to retain generality and to account for the features common for both lakes, we assumed a constant diffusivity of $5 \times 10^{-7}$ m$^2$ s$^{-1}$ in the metalimnion. Then, the vertical diffusivity distribution can be described as:

$$K_Z = \begin{cases} \frac{K_S}{(1 + \frac{z}{Z_{UML}})^2} & \text{at } z \leq Z_{UML} \\ \frac{K_M}{(H - z)(H - Z_M)} & \text{at } Z_{UML} < z \leq Z_M \\ \frac{K_M}{(H - z)(H - Z_M)} & \text{at } Z_M < z \leq H \end{cases}$$  \hspace{1cm} (17)

Based on visual inspection of the profiles, the boundaries of the UML and the metalimnion were set to $Z_{UML} = 9$ m, $Z_M = 18$ m, and the total depth of the water column $H$ was set to 70 m. Then, the values in Eq. 17 providing the best fit to the measured values based on log-linear regression were determined as (Fig. 4): $K_S = 10^{-2}$ m$^2$ s$^{-1}$, $K_M = 5 \times 10^{-7}$ m$^2$ s$^{-1}$, and $K_H = 10^{-4}$ m$^2$ s$^{-1}$.

**Carcass decomposition**—Given a long enough residence time in the water column, the density of the carcasses is subject to change due to microbial decomposition, which in turn is a complex and hardly determinable function of microbial community composition, characteristics of the carcass, and environmental variables, such as water temperature. Here, we described carcass decomposition based on an empirical function of temperature as suggested by Elliott et al. (2010):

$$\rho_p = \rho_{pi} - 3.78(1 - e^{-0.329T})[\ln(t) + 1.39]$$  \hspace{1cm} (18)

where $\rho_{pi}$ is the initial density of a carcass, and $t$ is time in hours ($t = 0$ at 0.25 h after death).

In summary, the final set of model equations looks as follows: Eq. 15 (with the random walk part determined by Eq. 16) represents the basic equation of the model, calculating an individual vertical track of a carcass across the water column. The diffusivity $K_Z$ for Eq. 15 is calculated from Eq. 17, and the sinking velocity $U_S$ is given by Eq. 8. In Eq. 8, the viscosity $\nu$ is given by Eq. 11 taking into account water temperature variations expressed by Eq. 12. The time-varied carcass buoyancy $B$ is calculated from the density $\rho_p$ using Eq. 18.

**Results III: Environmental Influences on Carcass Residence Time**

**Residence time of different species**—For a 70-m-deep, stratified water column, such as the deepest parts of Lake Stechlin and Lake Arendsee, the model predicted residence time for different species to vary between 1 and > 3 d (Fig. 5). *D. cucullata* with open carapace had the longest residence time of 3.6 d. The same species with closed carapace had the shortest residence time, slightly > 1 d.
Hence, depending on the carapace condition and the corresponding residence time, carcasses of *D. cucullata* would contribute to the water column carbon budget to different extents.

**Effects of environmental factors**—To estimate the effect of different factors—stratification (strat), microbial decomposition (decomp), and turbulence (turb)—on carcass residence time, the model was run in four different configurations:

- **Case 1**: With the sinking rate $U_S$ in Eq. 8 kept constant at the value determined in the lab;
- **Case 2**: With effects of temperature variations taken into account by means of temperature-dependent $B$ and $v$ in Eq. 8;
- **Case 3**: Additionally to the temperature effects on buoyancy and viscosity, with varying $B$ due to time- and temperature-dependent microbial decomposition as given by Eq. 18; and
- **Case 4**: With the turbulence model Eqs. 15–17 added to the Case 3 configuration. In this case, the mean residence time was estimated for each species by averaging > 100 model runs.

Case 1 corresponds to a homothermal lake at 21°C without turbulence. In this case, the sinking rate was constant and the residence time in a 70-m-deep water column was given simply by $70/U_S$, the latter value taken from Table 1. Carcasses of all species under consideration would settle to the lake bottom within approximately a day (Case 1 in Fig. 6a–f). *D. cucullata* carcasses would settle within 0.4 d (with closed carapace) to 1.4 d (with open carapace) (Fig. 6a,b). In a stratified water column (Fig. 6, Case 2), the modeled settling time increased rapidly in the metalimnion, where vertical temperature gradient was the strongest. Afterwards, carcasses sank at a rather constant rate within 20–70 m. The resulting residence time of carcasses in the water column roughly doubled when stratification was considered. The addition of microbial decomposition further reduced carcass densities, causing an increase in residence time by ~2.5 times against Case 1 (Fig. 6, Case 3). Consequently, the carcasses remained for up to 3.6 d in the water column.

Effects of turbulence on carcass residence time were noticeable only for *D. cucullata* with closed carapace (cf. Case 4 and Case 3 in Fig. 6). Compared to gradual sinking, the superimposed turbulent fluctuations produced a slightly shorter average carcass residence time in the upper half of the well-mixed epilimnion, and a longer residence time in the lower part (Fig. 7A). In the bulk of the water column, between 5 and 50 m, turbulence had no appreciable effect, in accordance with the high values of $Pe$ at these depths (cf. Fig. 3). Closer to the bottom, a higher background turbulence level caused higher average sinking rates (Fig. 7B), similar to the vicinity of the lake surface, such that the total carcass residence time remained practically unchanged. Although turbulence effect on the average carcass residence time was not strong, the trajectories of individual *D. cucullata* carcasses with closed carapace revealed a large scatter around the mean value: For the average residence time of 4 h in the UML, some carcasses stayed in the mixed layer for $\geq$ 20 h. The probability distribution of the residence time was noticeably asymmetric and was similar to theoretical Rayleigh or Weibull distributions, characteristic of direction-dependent data (Wilks 1995). Approximation of the probability distribution by the Weibull function showed that about 10% of the carcasses stayed in the epilimnion for twice as long as the average residence time, and about 1% stayed in the epilimnion for 4 times longer than the mean value (Fig. 8).

In general, the modeled residence time was about 3 times longer than laboratory estimations. The factors having the strongest effects were the high viscosity of the cold hypolimnion and microbial decomposition, which reduced the excess density of the carcasses.

**Seasonality**—The effects of seasonal variations in temperature were investigated by running the model with two additional vertical temperature profiles based on parameterization (Eq. 12): a homothermal “epilimnion” with temperature $T_{UML} = 4$°C down to the lake bottom ($Z_{UML} = 70$), which corresponds to the situation of spring and fall convective overturns, and a hypolimnion occupying the entire water column ($Z_{UML} = 0$) with inverse stratification $T_{UML} = 0$°C and $T_B = 4$°C, which mimics the winter situation in dimictic lakes. Seasonal variations in carcass residence time for the entire 70-m-deep water column were negligible (Table 3); the large part of the water column was occupied by the hypolimnion, where seasonal temperature variations were weak. The seasonal effects were most pronounced in the epilimnion (Table 4). In the upper 10 m of the water column, the difference in carcass residence time between winter and fall or spring was still small, since the dependence of viscosity on temperature was weak in the range 0–4°C. However, the carcass residence time in summer was almost 2 times shorter.
Despite the fact that carcasses spent less time in the upper part of the water column than in the hypolimnion, seasonal variations described here may still have important consequences for carbon and nutrient cycling, which proceeds faster in the warmer epilimnion. The results also imply that seasonality should play an important role in shallow polymictic lakes, where epilimnion extends to the lake bottom.

Extrapolation experiments: neutral buoyancy—As a carcass sinks through the stratified water column, it reduces its excess density due to microbial decomposition on the one hand, and due to increase in water density on the other hand. Theoretically, the carcass could achieve neutral buoyancy before it settles to the bottom so that decomposition would take place entirely in the water column. The residence time that a particle needs to stay in the water column to achieve neutral buoyancy ($t_{\text{MAX}}$) can be estimated by substitution of the zero excess density condition $\Delta \rho = 0$ in Eq. 18 such that:

$$t_{\text{MAX}} = \exp \left( \frac{\Delta \rho_i}{C_1} - C_2 \right)$$  \hspace{1cm} (19)

where $\Delta \rho_i = (\rho_{pi} - \rho_w)$ is the initial excess density of a carcass, $C_1 = 3.78 \left(1 - e^{-0.329T}\right)$, $C_2 = 1.39$. Sinking carcasses spend most of time in the quasi-homothermal regime.
Therefore, we substituted a constant hypolimnion temperature in the expression for $C_1$. With this assumption, the corresponding termination depth $Z_{\text{MAX}}$, at which carcasses would achieve neutral buoyancy, is determined from Eqs. 8 and 18 as:

$$Z_{\text{MAX}} = \frac{gL^2}{18\nu\rho_w} (\Delta\rho_i - C_1 \ln(t_{\text{MAX}}/3600) + C_2 - 1)t_{\text{MAX}}$$

(20)

where $t_{\text{MAX}}$ is time in seconds. That is, $t_{\text{MAX}}$ depends on the initial excess density and the environmental water temperature, and $Z_{\text{MAX}}$ depends additionally on the particle size. We adopted the value $L = 0.17$ mm in Eq. 20 that corresponds to the mean ESD of carcasses under investigation (Table 2). The excess densities measured in the laboratory were 44–90 kg m$^{-3}$, which, when substituted in Eq. 19, yielded a $t_{\text{MAX}}$ of several hundred days. Such a long residence time is unrealistic for the majority of lakes, which suggests the carcasses should unconditionally settle to the lake bottom. The excess density can, however, decrease with an increase in the environmental density $\rho_w$ due to an increase in ambient salt content or dissolved matter. Another factor able to significantly reduce the excess density is aggregation of carcasses, e.g., with algae (Grossart et al. 1998; Grossart and Simon 1998). For example, $t_{\text{MAX}}$ decreased nonlinearly with decreasing $D_{\text{ri}}$, and became comparable to the typical residence time at an excess density $<25$ kg m$^{-3}$ (Fig. 9). For $\Delta\rho_i = 20$ kg m$^{-3}$, microbial decomposition would completely eliminate the negative buoyancy within 2 d at 20°C, and within 8 d at 5°C. It is noteworthy that the sensitivity of $t_{\text{MAX}}$ to water temperature was especially high at low temperatures: An increase from 5 to 7°C resulted in a 2 times shorter $t_{\text{MAX}}$, whereas in the whole range 10–20°C, the temperature-driven changes were within 20% of the mean value (Fig. 9). Excess densities and the corresponding values of $t_{\text{MAX}}$ and $Z_{\text{MAX}}$ could additionally decrease if the high decomposition rates in the epilimnion due to higher temperatures would be taken into account through the variable coefficient $C_1$ in Eq. 19. In this sense, our numbers represent the upper bound estimations of the maximum residence time.

**Discussion**

Our model of particle trajectories contained original approximations of environmental factors, such as temperature and mixing intensity. For parameterization of the temperature profile below the homothermal epilimnion, we used an exponential function of depth, which is essentially
based on the self-similarity approach to the thermocline modeling. The latter has been effectively used for parameterization of boundary layer characteristics in the ocean, the atmosphere, and lakes (Kitaigorodskii and Miropolsky 1970; Fedorovich and Mironov 1995; Kirillin 2010). Several self-similarity functions have theoretical support from analytical solutions of the heat transport equation in special cases (Barenblatt 1978; Turner 1978). Our exponential function was a purely empirical profile, but had the advantage of being able to reproduce well both metalimnion and quasi-homothermal hypolimnion using the same exponential function. Testing with data from the two dimictic lakes, the parameterization proved its reliability. We therefore suggest that the parameterization of the temperature profile may be applied to any lakes with a well-defined hypolimnion, i.e., in di- or monomictic lakes with mean depths > 20 m. For shallow lakes with no distinct hypolimnion, application of polynomial (Zilitinkevich and Rumyantzev 1990) or linear-exponential parameterizations (Kirillin 2002) may be more appropriate. Alternatively, a three-layer model with different temperature profile parameterizations for meta- and hypolimnion can be constructed, applicable to both deep and shallow lakes.

Our parameterization of the turbulent diffusion coefficient assumed exponential decrease of the mixing intensity in the epilimnion, which is different from conveniently used piecewise-constant or linear approximations (Madsen 1977). Direct estimations of the turbulent dissipation rate from the two lakes provided a strong support to this parameterization and gave new insights into the turbulence characteristics of the surface layers of stratified lakes. Our results are also consistent with the direct turbulence measurements in the oceanic UML by Anis and Moum (1995), who found the same exponential decrease of the dissipation rate and referred to it as the wave-breaking effect on turbulence. Thus, our parameterization for the epilimnion turbulence can be easily extended to marine conditions.

The turbulence level in the metalimnion was the most uncertain parameter of the model, and it varied by 2–3 orders of magnitude depending on the intensity of seiche oscillations in the lake. Therefore, if processes in the metalimnion are of special concerns, additional observations may be required for proper parameterization of metalimnion mixing. For the class of dimictic lakes considered here, the metalimnion was thin compared to the depth of the entire water column, and the metalimnion turbulence level was low compared to the surface- and bottom-generated ones; therefore, adopting a constant $K_z$ value across the metalimnion appeared to be a reasonable approximation. The quasi-exponential increase of mixing intensity with depth across the hypolimnion was strongly supported by data from Lake Stechlin and Lake Arendsee. Up to now, information on the hypolimnion turbulence is very scarce. We hypothesized that the shape of the $K_z$ profile was produced by the breaking of internal waves, in the way similar to the exponentially decaying turbulence in the wave-affected epilimnion, which also supported the universality of the proposed approximation for all lakes with a well-defined hypolimnion. The quasi-universal profile of turbulence in stratified lakes obtained by direct microstructure measurements was an important outcome of the present study. The parameterization of the diffusion coefficient derived and applied in the model can be extended to other dimictic lakes, and integrated into transport models of particulate and dissolved matters.

Compared to other frequently studied marine snow materials, such as fecal pellets and phytoplankton aggregates, the contribution of zooplankton carcasses to the sinking fluxes remains unclear due to two “standard” practices in the research community: Zooplankton sampling often ignores the live or dead status of the animals such that researchers will have overlooked the presence of zooplankton carcasses in the field (Tang et al. 2009); and zooplankton in sediment trap samples are often treated as swimmers and excluded from flux estimation (Sampei et al.)

### Table 3. Model-predicted residence times for carcasses in a 70-m-deep water column in different seasons.

<table>
<thead>
<tr>
<th></th>
<th>Residence time (d)</th>
<th>Daphnia cucullata</th>
<th>D. cucullata (open carapace)</th>
<th>Cyclopoid copepod</th>
<th>Ceriodaphnia sp.</th>
<th>Diaphanosoma brachyurum</th>
<th>Eudiaptomus gracilis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>1.3</td>
<td>3.7</td>
<td>2.7</td>
<td>2.0</td>
<td>1.9</td>
<td>1.2</td>
<td></td>
</tr>
<tr>
<td>Fall and spring</td>
<td>1.3</td>
<td>3.7</td>
<td>2.7</td>
<td>1.9</td>
<td>1.9</td>
<td>1.2</td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>1.2</td>
<td>3.5</td>
<td>2.4</td>
<td>1.8</td>
<td>1.8</td>
<td>1.1</td>
<td></td>
</tr>
</tbody>
</table>

### Table 4. Model-predicted residence times for carcasses in a 10-m epilimnion in different seasons.

<table>
<thead>
<tr>
<th></th>
<th>Residence time (h)</th>
<th>Daphnia cucullata</th>
<th>D. cucullata (open carapace)</th>
<th>Cyclopoid copepod</th>
<th>Ceriodaphnia sp.</th>
<th>Diaphanosoma brachyurum</th>
<th>Eudiaptomus gracilis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>4.0</td>
<td>10.6</td>
<td>8.6</td>
<td>6.1</td>
<td>5.8</td>
<td>4.1</td>
<td></td>
</tr>
<tr>
<td>Fall and spring</td>
<td>3.9</td>
<td>10.5</td>
<td>8.4</td>
<td>6.0</td>
<td>5.7</td>
<td>3.9</td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>2.3</td>
<td>6.4</td>
<td>5.2</td>
<td>3.7</td>
<td>3.5</td>
<td>2.4</td>
<td></td>
</tr>
</tbody>
</table>
Nevertheless, evidence is accumulating for the fact that carcasses can make up a high percentage of the total zooplankton population in the water column (Bickel et al. 2009; Elliott and Tang 2011) and contribute to a substantial fraction of the total sinking fluxes (Sampei et al. 2009; Frangoulis et al. 2011). Two approaches have been used to estimate zooplankton carcass fluxes: The first is based on zooplankton carcass abundance in the upper water column and laboratory-measured carcass sinking rate (Elliott et al. 2010). The second approach, commonly used in sedimentation studies, directly measures the amount of zooplankton carcasses that have settled into the deep water (Sampei et al. 2009; Frangoulis et al. 2011). Combining the two approaches has not been attempted, but could prove useful for understanding the fate of zooplankton carcasses within the water column. For example, our model suggests that the largest reduction in carcass sinking rate happens within the thermocline, and when coupled with the high water temperature (relative to the bottom layer), microbial decomposition of the carcasses is expected to be highest there, which reduces the organic flux reaching the deep. However, the thermocline is a layer that is often poorly characterized in zooplankton sampling and sediment trap studies. Applying a physically sound model as the one described here may help link zooplankton carcass measurements in the surface waters and sediment trap measurements at depth, and provide insights into the processes that affect zooplankton carcass turnover in the water column.

Another interesting observation from our study was that the sinking rate of D. cucullata carcasses changed drastically due to their morphology (open vs. closed carapace). Sampei et al. (2009) reported that copepod carcasses can assume different postures depending on how they died—some had “collapsed” antennae, whereas others had their swimming legs extended out upon death. Based on our model results, one may hypothesize that even a subtle difference in carcass morphology could result in a large difference in sinking fluxes. Therefore, there is a need for not only an accurate quantification of zooplankton carcasses, but also an accurate description of carcass morphology.

We found that thermal stratification and decomposition had comparable effects such that both increased the carcass residence time in a stratified water column by up to ~ 40%. Thermal stratification affected sinking rates mostly via water viscosity, not excess density, which only slightly depended on temperature. However, the stratification effect on excess density may be stronger in the ocean. Assuming that initial excess densities of marine zooplankton are roughly the same as those of our species, the combined effect of increasing salinity and decreasing temperature across the water column could lead to indefinite retention of the carcasses within the water column, as previously hypothesized by Elliot et al. (2010). According to Fig. 9, if the excess density is reduced by salinity to 15 kg m$^{-3}$ or less, the carcasses would be retained within a layer of about 10 m thick. That is, a strong halocline would trap and prolong the exposure of zooplankton carcass to high microbial activity. Like other organic particles, zooplankton carcasses may potentially form agglomerates during their sinking that would reduce the sinking rates and increase the retention time in the water column (Grossart and Simon 1998). This effect was beyond the scope of the present modeling study, but deserves special attention in further research. Our model suggests that turbulence effects on carcass residence time were largely limited to the epilimnion. We did not consider such turbulence-related effects as resuspension, which could be important in shallow waters. The direct effects of turbulence in the UML may also differ from that achieved with a one-dimensional stochastic model, which does not take into account mixing by large coherent motions. Convective cells or Langmuir circulation at the lake surface, whose size achieves several meters, can potentially move the carcasses in a quasi-circular manner, affecting the residence time in the epilimnion. Additional field studies are needed to study the combined effects of these large coherent motions and turbulence on the residence time of zooplankton carcasses and other particles.

Our model also provides useful insights into climate change effects on the recycling of zooplankton carcass organic matter. For example, the hypolimnion temperatures in many temperate lakes have increased by 1–2 degrees during the last half century (Dokulil et al. 2006, Adrian et al. 2009). The future climate scenarios predict a rapid increase of hypolimnion temperature in the majority of dimictic lakes due to transition to warm monomictic conditions (Kirillin 2010). Based on our model results (Fig. 9), we predict that even with a slight warming of the hypolimnion, e.g., by 2°C, all carcasses with excess densities of ~ 20 kg m$^{-3}$ would be completely decomposed before reaching the lake bottom in water columns deeper than 20 m.

Another direction in which our model and results can be extended is the case of small particles with high excess density, such as fecal pellets. The reported excess density
Fig. 10. Mean trajectory of fecal pellets in the 5-m-thick turbulent epilimnion (solid line) and in a nonturbulent environment (dotted line).

for copepod fecal pellets is \( \sim 150 \text{ kg m}^{-3} \) (Feinberg and Dam 1998), which is 3 times higher than that for zooplankton carcasses. Consequently, environmental factors, such as temperature-driven variations in the water density and viscosity, affect their sinking rates to a much smaller degree than that of zooplankton carcasses. For the same typical vertical temperature distributions as considered here, fecal pellets sink at \( \sim 20-25 \text{ m d}^{-1} \) (decomposition not included), which is much slower than carcasses due to the small size of the pellets (about 100 \( \mu \text{m} \)). Microbial decomposition can additionally slow down the sinking. Due to the slow sinking rate, turbulence has a stronger effect on the residence time: in a 5-m-thick epilimnion, turbulent fluctuations would increase the residence time of fecal pellets from 6 to 8.5 h (Fig. 10). Taken into account that physical and biological decomposition could remove up to \( > 50\% \) of the labile fecal carbon content within hours (Urban-Rich 1999; Møller et al. 2003), the prolongation of residence time by turbulence can appreciably increase the recycling of fecal organic carbon in the epilimnion.

Our carcass sinking model is built on sound physical relationships. It shows that thermal stratification can significantly lengthen the residence time of zooplankton carcasses within the water column and hence increase their recycling by microbial activities. The model is universally applicable to any well-stratified lake or oceanic water column, can be easily applied to other passively sinking particles, and be integrated into larger ecosystem models.

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