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Fluid mixing by swimming organisms in the low-Reynolds-number limit

by Eric Kunze¹

ABSTRACT

Recent publications in the fluid physics literature have suggested that low-Reynolds-number swimming organisms might contribute significantly to ocean mixing. These papers have focussed on the mass transport due to fluid capture and disturbance by settling or swimming particles based on classical fluid mechanics flows but have neglected the role of molecular property diffusion. Scale-analysis of the property conservation equation finds that, while properties with low molecular diffusivities can have enhanced mixing for typical volume fractions in aggregations of migrating zooplankton, this mixing is still well below that due to internal-wave breaking so unlikely to be important in the ocean.

1. Introduction

Recent interest has been sparked into whether the motile ocean biosphere can contribute significantly to ocean mixing. Energetic arguments (Munk, 1966; Dewar *et al.*, 2006) suggest that up to 1 TW might be available while scale-analysis indicates that aggregations of swimming marine organisms ranging in size from O(1-cm) krill to O(1-m) cetaceans (Huntley and Zhou, 2004) might be able to generate high-Reynolds-number turbulent kinetic energy dissipation rates $\varepsilon \sim O(10^{-5} \text{ W kg}^{-1})$. Early observational support for such numbers (Kunze *et al.*, 2006) was not borne out by subsequent more extensive microstructure measurements which found that at least 90% of the time either (i) dissipation rates ε were not significantly higher during dawn and dusk migrations of acoustic backscattering layers (Rippeth *et al.*, 2007), (ii) dissipation rates were elevated in aggregations but two orders of magnitude below the predictions of Huntley and Zhou (Rousseau *et al.*, 2010; Lorke and Probst, 2010), or (iii) though dissipation rates were elevated, mixing efficiencies Γ were very low (Gregg and Horne, 2009).

Another line of research suggests that swimming or settling particles could induce significant mixing without generating turbulence by dragging captured fluid impelled by inertial or viscous forces behind them. These studies have invoked Darwin's (1953) drift flow as a starting point although this flow was shown to be ill-defined by Eames *et al.* (1994). Both idealized low- and high-Reynolds-number flows have been considered. Katija and

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Dabiri (2009) argued that mixing would be equally efficient for all particle sizes but viscous considerations (Dabiri, 2010; Thiffeault and Childress, 2010) suggest that lower-Reynolds-number (smaller) particles induce a great volume of mass transport relative to their size. Subramanian (2010) and Leshansky and Pismen (2010) argued that transport will be less efficient for swimmers, which have a force dipole, than for a sinking particle. These flows are of questionable applicability to understanding mixing induced by microscopic organisms. At high Reynolds numbers $Re = U\ell/\nu$ (large U or ℓ), viscous boundary layers will inject vorticity into the wake, inducing turbulent dissipation rates ε with high $Re = \varepsilon/(\nu N^2)$ based on the outer or Ozmidov scales for ℓ and U (Huntley and Zhou, 2004) and invalidating ideal flow theory. As already described, observational evidence provides little support for turbulence in the wake of swimming marine organisms. At low Reynolds numbers (small U or ℓ), one cannot neglect molecular property diffusion κ_c as has been done in the preceding work.

In this paper, we explore the influence of molecular diffusion for low-Reynolds-number mixing by motile particles using simple scaling arguments applied to the property conservation equations in the spirit of Melvin Stern's (1960) early salt-fingering work. It is shown that molecular diffusion short-circuits advective property transport.

2. Scaling analysis

The crudest scaling analysis one might invoke to infer an eddy diffusivity for a vertically migrating marine organisms is to assume that they transport roughly the equivalent of their body mass of fluid over distance L in transit time Δt

$$K \sim \frac{L^2}{\Delta t} R_{V1} R_{V2}$$

(Eckart, 1948) where R_{V1} is the volume fraction of organisms in an aggregation and R_{V2} the volume fraction of aggregations in the ocean. In the absence of molecular diffusion, this is a stirring rather than mixing argument. The appropriate lengthscale L is the distance traveled by the organisms because the captured fluid will be carried over this same distance. For typical migrating species with significant biomass ($\ell \sim 1$ cm), aggregations traverse $L \sim O(100$ m) twice a day ($\Delta t = 12$ h). For upper-bound volume fractions $R_{V1} \sim 10^{-3}$ and $R_{V2} \sim 10^{-1}$ characteristic of dense aggregations of 1-cm krill (Huntley and Zhou, 2004), this implies eddy diffusivities $K \sim 0.2 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$ within the aggregations, comparable to the eddy diffusivity due to internal-wave-driven turbulence in the pycnocline (Moum and Osborn, 1986; Gregg, 1987, 1989; Ledwell *et al.*, 1993). More typical volume fractions, particularly in the open ocean, are an order of magnitude smaller. However, this scaling neglects property exchange with neighboring fluid due to molecular diffusion which acts to short-circuit this advective property transport.

A particle moving under its own volition at speed U in a viscid fluid satisfies the viscous balance

$$0 = \nu \nabla^2 \zeta \tag{1}$$

with the boundary condition $w = U$ on the boundary of the particle (Kundu and Cohen, 2004), where $\vec{\zeta}$ is the vorticity vector. Solutions in the high-Reynolds-number (potential flow) and viscous low-Reynolds-number limits are well-known (e.g., Vogel, 1996). Here, we will be less concerned with exact solutions. What is relevant to the mixing problem is that, as fluid is drawn behind the particle, the accompanying shear U/ℓ will sharpen property gradients to scales where they are acted on by molecular diffusion κ (Eckhart, 1948; Taylor, 1953; Batchelor, 1959).

In general, conservation of a conservative fluid property, such as temperature, salinity or dissolved nutrients, can be expressed as

$$\frac{Dc}{Dt} = \frac{\partial c}{\partial t} + (\vec{v} \cdot \nabla)c = \kappa_c \nabla^2 c \quad (2)$$

(Stern, 1975). Making a Reynolds decomposition $\mathbf{v} = \mathbf{V} + \mathbf{v}'$ and $c = C + c'$, where we assume $\mathbf{V} = 0$, $C = C(z)$ and steady state, conservation of the perturbation can be expressed as a balance between advection $w'(x, y)$ acting on the mean gradient C_z and molecular diffusion of perturbations c' arising from this advection

$$w' C_z = \kappa_c \nabla^2 c' \Rightarrow w' C_z \sim \frac{\kappa_c c'}{\ell_c^2} \Rightarrow c' \sim \frac{C_z \ell_c^2}{\kappa_c} w', \quad (3)$$

which we have expressed in terms of cross-flow gradients $\partial/\partial r$, where ℓ_c will be the Batchelor lengthscale associated with property c at which molecular diffusion κ_c acts to damp out any smaller scales.

Now, consider a small particle of lengthscale ℓ_o in a fluid of kinematic molecular viscosity ν that is imparting vertical motion w' to the fluid either by self-propulsion or settling. The associated Reynolds number $Re = w'\ell/\nu$. The property lengthscale ℓ_c (3) and momentum lengthscale ℓ will not be the same for $\nu \neq \kappa_c$ (Batchelor, 1959). Neither need they be the same as the particle lengthscale ℓ_o because the viscous boundary layer that carries anomalous fluid may be thicker or thinner than the particle if Re is less than or greater than one, respectively.

The eddy diffusivity K is defined as

$$K = \frac{\langle w' c' \rangle}{C_z} R_V \sim \gamma \frac{w'^2 \ell_c^2}{\kappa_c} R_V \sim \gamma Re^2 \frac{\nu^2 \ell_c^2}{\kappa_c \ell^2} R_V, \quad (4)$$

where the scaling arises from multiplying (3) by w' , $\gamma < 1$ is the correlation between w' and c' , and $R_V < 1$ is the volume fraction occupied by the drift w' . This relation closely resembles the shear-dispersion horizontal diffusivity inferred by Young *et al.* (1982) for vertical shear U_z coupled with a vertical diffusivity. However, account has been made for the differing microscale lengthscales for momentum and properties here, as well as for the volume density R_V occupied by the moving particles. For schooling organisms, this should be further subdivided as $R_V = R_{V1} R_{V2}$ where R_{V1} is the volume fraction of organisms in aggregations and R_{V2} the volume fraction of aggregations in the water; both of these volume

fractions act to reduce the net diffusivity K . For most aggregations of marine organisms, $R_V \ll 1$ (Huntley and Zhou, 2004; see below).

From Batchelor (1959), provided $v > \kappa_c$, then $\ell_c^2/\ell^2 = \kappa_c/v$ so that (4) reduces to

$$K \sim \gamma v Re^2 R_V, \quad (5)$$

independent of lengthscales. An immediate consequence of (5) is that, for low Re , $K < v \sim O(10^{-6} \text{ m}^2 \text{ s}^{-1})$. This low-Reynolds-number approximation will be valid provided the flow doesn't become fully turbulent.

Oceanic measurements suggest that the transition to fully isotropic turbulence occurs for $Re \sim 200$ (Gargett *et al.*, 1984). Laboratory and numerical simulations of stationary homogeneous turbulence (e.g., Shih *et al.*, 2005) suggest that turbulence is fully isotropic with a maximum mixing efficiency $\Gamma = 0.2$ for $Re < 100$ and $\Gamma < 0.2$ for $Re > 100$. The apparent discrepancy between the ocean and laboratory/numerical results can be understood by recognizing that, for $Re > 100$, the laboratory and numerical domains were too small to include the Ozmidov or overturning scale $L_O = (\varepsilon/N^3)^{1/2}$ which contributes most of the downgradient flux in turbulence (Ramsden and Holloway, 1992; Sun *et al.*, 1996; D'Asaro and Lien, 2007). A similar argument was used by Visser (2007) to argue that high-Reynolds-number turbulence generated by swimming marine organisms on lengthscales less than the Ozmidov length [$\ell < L_O = (\varepsilon/N^3)^{1/2}$] would have reduced diffusivities $K = (\Gamma\varepsilon/N^2)(\ell/L_O)^{4/3}$ compared to the Osborn (1980) $K = (\Gamma\varepsilon/N^2)$; this appears to be borne out by observations in at least one instance (Gregg and Horne, 2009). For $Re < 100$, the laboratory and numerical studies appear to be robust and the likely reason for the discrepancy is that the low- Re ocean observations were nonstationary or nonhomogeneous.

As U and ℓ increase, so do Re and K (Fig. 1). In the strict low- Re limit ($Re < 1$) being considered here, $K < 10^{-10} \text{ m}^2 \text{ s}^{-1}$ within krill aggregations with volume fractions $R_V = 10^{-4}$. Huntley and Zhou (2004) summarize swimming speeds for aggregating marine organisms ranging from bacteria through copepods ($3 \times 10^{-3} \text{ m s}^{-1}$, $Re \sim 10$), krill (10^{-2} m , 10^{-2} m s^{-1} , $Re \sim 100$), mysids (small fish) and cetaceans (Table 1) as a function of wet body mass m . Assuming $m = \rho \ell^3$ and organism density ρ is comparable to water (10^3 kg m^{-3}), then for lengthscales ℓ ranging from 10^{-6} to 1 m , Huntley and Zhou's (2004) empirical relations imply cruising speeds $u_c = 3.23\ell^{0.83}$ ($Re_c = 1.16 \times 10^6\ell^{1.9}$) and escape speeds $u_e = 7.76\ell^{0.53}$ ($Re_e = 4.5 \times 10^6\ell^{1.53}$). These curves (Fig. 1) reveal that only organisms with lengthscales of bacteria, dinoflagellates and copepods qualify as low Reynolds number.

One can also assess the volume fraction R_V of aggregations more completely. For highly productive coastal waters, krill aggregations can reach volume fractions R_{V1} as high as 10^{-3} (10^3 individuals m^{-3} ; De Robertis, 2002; De Robertis *et al.*, 2003) but are usually an order of magnitude smaller. They are 1-2 orders of magnitude smaller still in the open ocean (Greenlaw, 1979). The maximum packing density relation in dense observed aggregations [(17) in Huntley and Zhou, 2004] can be re-expressed as a volume fraction $R_{V1} \sim 1.6 \times 10^{-4}\ell^{-0.6}$, reproducing the upper-bound krill aggregation values quoted above

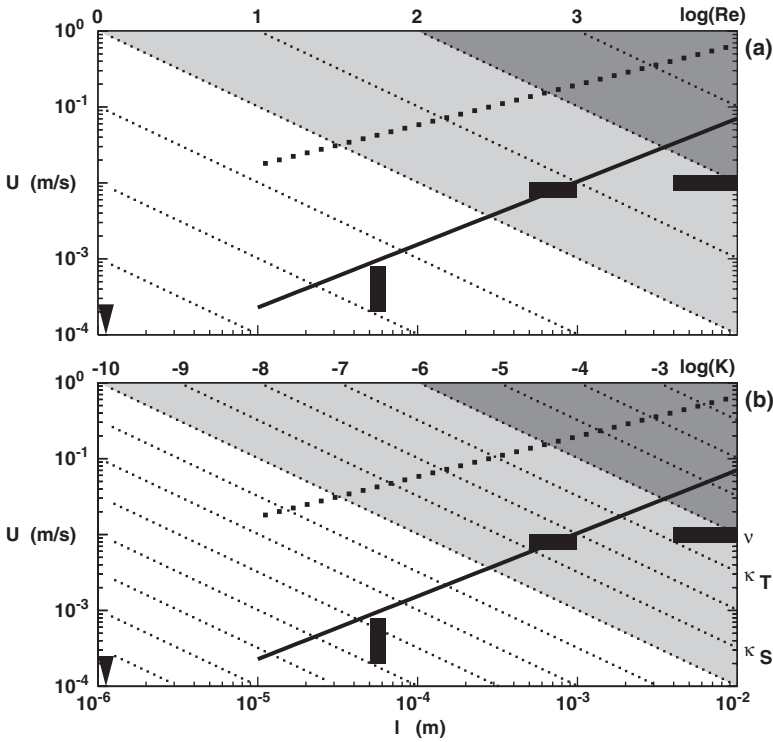


Figure 1. Contour plots of Reynolds number $Re = U \ell / \nu$ (upper panel) and property eddy diffusivity K_c as a function of particle size ℓ and velocity U in the low-Reynolds-number limit (5) assuming an upper bound volume fraction $R_V = 10^{-4}$ (based on upper bounds $R_{V1} = 10^{-3}$ for the volume fraction of organisms in aggregations and $R_{V2} = 0.1$ for the volume fraction of aggregations in the water, characterizing $\ell \sim 10^{-2}$ -m long krill) (lower panel). Reynolds numbers $Re > 1$ are shaded light gray, $Re > 100$ dark gray. The solid line corresponds to cruising speeds u_c of aggregating swimming marine organisms longer than 10^{-5} m ($10 \mu\text{m}$), the dotted line escape speeds u_e . The reader is referred to Huntley and Zhou (2004) for the data references and formulas used in these curves. Black shapes show the range in size and swimming speeds of low-Reynolds-number organisms: bacteria, dinoflagellates, copepods and krill, respectively. Note that bacteria swim at speeds $< 10^{-4} \text{ m s}^{-1}$.

but unrealistically approaching 1 for $Re < 10^{-2}$ ($\ell < 10^{-6}$ m) (Figs. 2a and 3a). We shall nevertheless use these upper-bound volume fractions throughout since we will show that even these overestimates are insufficient to induce mixing comparable to that due to internal-wave breaking in the stratified ocean. As the moving particle draws a line of anomalous fluid behind it, the decay time for molecular diffusion to eradicated property anomalies is ℓ^2 / κ_c . The decay lengthscale $\Delta z = u \ell^2 / \kappa_c$ falls below 1 mm for $Re < 1$ or particle size $\ell < 10^{-4}$ m (Fig. 2c and 3b). Combining R_{V1} with (5) gives diffusivities within aggregations

$$K_{c,e} = \nu(2.15 \times 10^8 \ell^3, 3.2 \times 10^9 \ell^{2.5}) \tag{6}$$

Table 1. Masses m , lengthscales ℓ and swimming speeds u for a range of schooling marine organisms (using common names) spanning $Re = 1$ (horizontal line) [adapted from Huntley and Zhou, 2004; Mitchell and Kogure, 2005; Ralston *et al.*, 2007 McHenry and Jed, 2003; Dabiri *et al.*, 2010; Bartol *et al.*, 2001; Anderson and Grosenbaugh, 2005].

organism	m (kg)	ℓ (m)	u (m/s)
bacteria	$(1 - 3) \times 10^{-14}$	$(1 - 3) \times 10^{-6}$	$(1 - 3) \times 10^{-5}$
dinoflagellates	10^{-10}	4×10^{-5}	$(1 - 5) \times 10^{-4}$
copepods	$(0.22 - 1.0) \times 10^{-6}$	$(6 - 10) \times 10^{-4}$	0.06
krill	$(0.1 - 2.0) \times 10^{-4}$	$(6 - 10) \times 10^{-3}$	0.05
jellyfish	$10^{-3} - 1$	$(1 - 10) \times 10^{-2}$	$(1 - 2) \times 10^{-2}$
anchovy/sardine	$(0.2 - 3.3) \times 10^{-2}$	$(1 - 3) \times 10^{-2}$	0.09–0.19
smelt	5×10^{-2}	4×10^{-2}	0.20
herring	0.3–0.4	7×10^{-2}	0.25
squid	0.01–1	0.02–0.1	0.1–0.6

(Fig. 2d) or

$$K_{c,e} = \nu(1.7 \times 10^{-2} Re_c^{1.7}, 6.3 \times 10^{-2} Re_e^{1.6}) \quad (7)$$

(Fig. 3c) which should be further reduced by the aggregation volume fraction R_{V2} to obtain bulk averages. For low Reynolds numbers ($Re < 1$) associated with microorganisms of lengthscale $\ell < 3 \times 10^{-4}$ m and swimming speeds $U < 5 \times 10^{-3}$ m s $^{-1}$, inferred eddy diffusivities within aggregations are smaller than the molecular diffusivity of heat (10^{-8} m 2 s $^{-1}$; Fig. 3c) and three orders of magnitude smaller than the mixing induced by to internal-wave breaking (Moum and Osborn, 1986; Gregg, 1987, 1989). For intermediate Reynolds numbers ($Re = 1 - 100$) associated with zooplankton such as copepods and krill [$\ell = (0.3 - 1) \times 10^{-2}$ m], inferred *nonturbulent* eddy diffusivities (10^{-8} – 10^{-6} m 2 s $^{-1}$) are less than molecular viscosity and more than an order magnitude below those due to internal-wave breaking. Biologically-generated *turbulent* mixing, which is outside the scope of this analysis, may play a role at these transitional Re ($\ell > 10^{-2}$ m) though turbulence has rarely been observed in connection with these size classes (Rippeth *et al.*, 2007; Lorke and Probst, 2010; Rousseau *et al.*, 2010).

3. Conclusions

Scale analysis based on the conservation equations for both momentum and property finds that, in contrast to recent suggestions in the fluid physics literature based on momentum conservation alone (Katija and Dabiri, 2009; Dabiri, 2010; Subramanian, 2010; Thiffeault

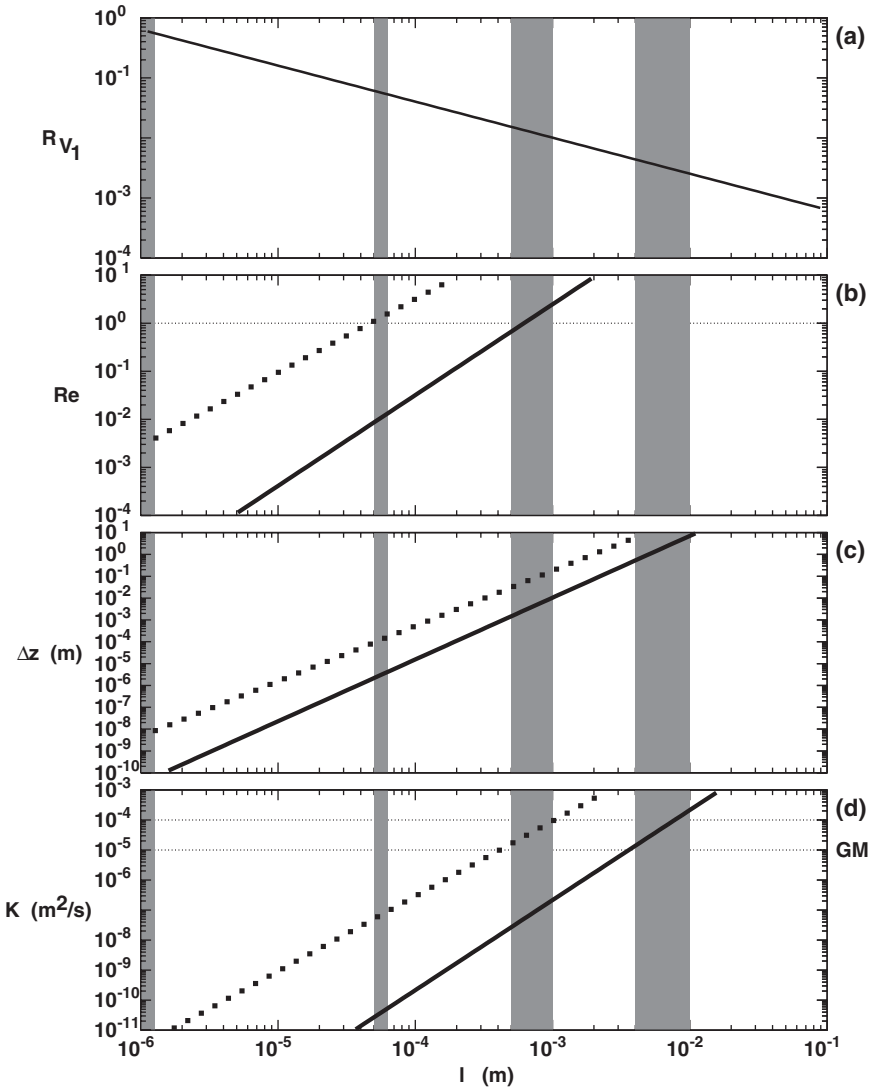


Figure 2. Volume fraction of organisms in aggregations R_{V1} (a), Reynolds number Re (b), along-path decay lengthscale $\Delta z = u\ell^2/\kappa$ (c) and eddy diffusivity K (d) as functions of lengthscale ℓ within dense aggregations of swimming marine organisms (assuming aggregations occupy all the water $R_{V2} = 1$). The solid curve corresponds to typical cruising speeds u_c , the dotted curve escape speed u_e in (b), (c) and (d). The horizontal line labelled GM in (d) corresponds to typical internal-wave-driven diffusivities in the ocean. The volume fraction R_{V1} (a) likely represents an upper bound by at least an order of magnitude compared to typical volume fractions, particularly in the open ocean. Average diffusivities K will be overestimated by the same amount as well as by the volume fraction of aggregates R_{V2} , i.e., at least another order of magnitude. Gray bars denote the size ranges of low-Reynolds-number bacteria, dinoflagellates, copepods and krill, respectively. The reader is referred to Huntley and Zhou (2004) for the data references and formulas used in these curves.

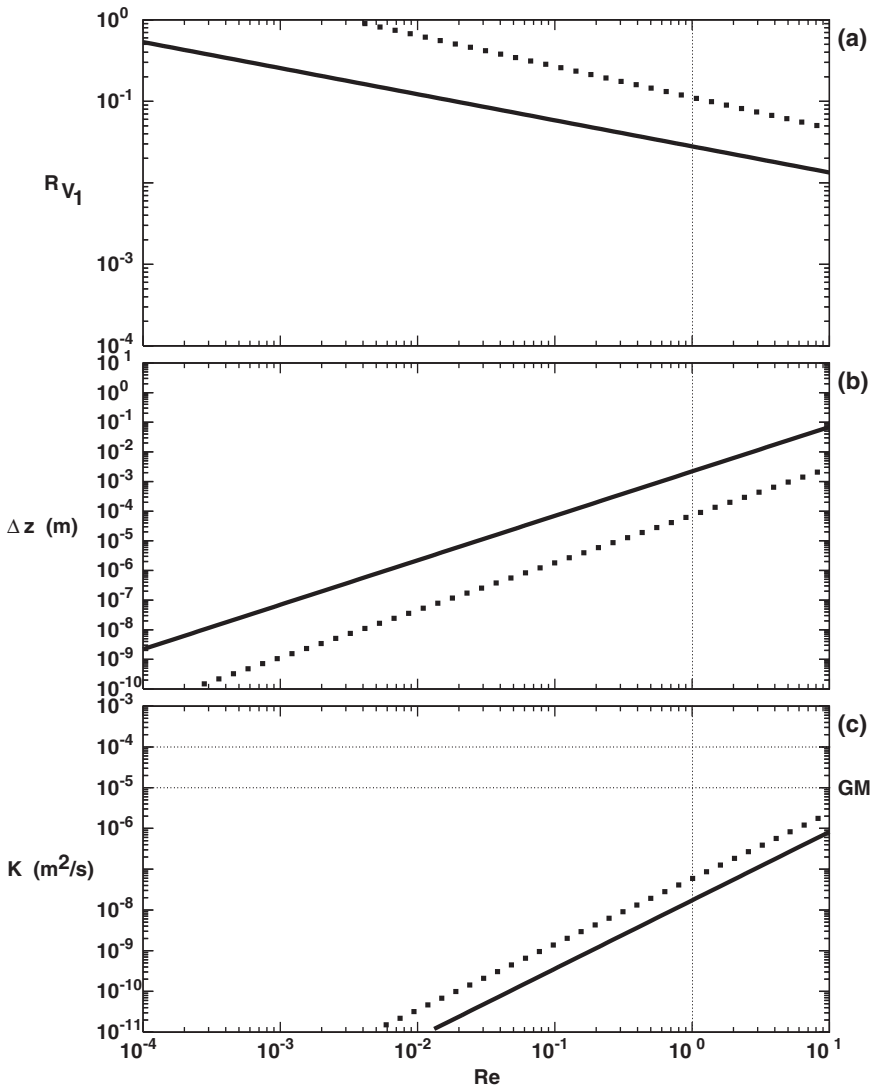


Figure 3. Volume fraction of organisms in aggregations R_{V1} (a), along-path decay lengthscale $\Delta z = u\ell^2/\kappa$ (b) and eddy diffusivity K (c) as a function of Reynolds number Re within dense aggregations of swimming marine organisms (assuming aggregations occupy all the water, i.e., $R_{V2} = 1$). Solid curves correspond to typical cruising speeds u_c , dotted curves escape speeds u_e . The volume fraction R_{V1} (a) represents an upper bound by at least an order of magnitude compared to typical volume fractions, particularly in the open ocean. The horizontal line labelled GM in (c) corresponds to typical internal-wave-driven diffusivities in the ocean. Even not taking into account the swarm volume fraction in the water R_{V2} , at low Reynolds number, induced diffusivities are below the molecular diffusivity of heat for both cruising and escape speeds. The reader is referred to Huntley and Zhou (2004) for the data references and formulas used in these curves.

and Childress, 2010; Leshansky and Pismen, 2010), swimming marine organisms will not contribute significant mixing ($K \geq 0.1 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$) at low Reynolds number. While viscosity enhances the fluid volume carried by a moving particle, shear dispersion associated with this flow is short-circuited by molecular property diffusion in the cross-flow direction. The volume fraction occupied by such aggregations $R_{V2} < 0.1$ is low, reducing the impact further. Previous observational work suggests that aggregations expected to generate high-Reynolds-number turbulent mixing (Huntley and Zhou, 2004) rarely do so (Rippeth *et al.*, 2007; Gregg and Horne, 2009; Lorke and Probst, 2010; Rousseau *et al.*, 2010).

For $Re < 1$, eddy diffusivities induced by swimming or settling particles are less than the molecular diffusion of heat and orders of magnitude less than that due to internal-wave breaking in the ocean, making contributions from low-Re swimming marine organisms or settling sediment negligible to ocean mixing overall. The bulk of the ocean's motile biomass, including bacteria, dinoflagellates, copepods and smaller euphausiids (krill), is in the low-Reynolds-number regime which is therefore unlikely to contribute to ocean mixing. Swimming marine organisms of higher Reynolds numbers, which include krill, squid and schooling fish species, may produce turbulent flows (Huntley and Zhou, 2004; Gregg and Horne, 2009), but observed turbulence levels appear to usually be well below predictions (Rippeth *et al.*, 2007; Lorke and Probst, 2010; Rousseau *et al.*, 2010) or to have low mixing efficiencies (Gregg and Horne, 2009). There may, of course, be regions of low internal-wave-driven mixing and high biomass where this mechanism is locally important. But as a mixing mechanism in the global ocean, stirring by swimming marine organisms does not appear to be significant. Aggregations of organisms swimming in a synchronized fashion may be more effective if they create motion on larger effective lengthscales, i.e., high Reynolds number. However, since the generation of turbulence and turbulent mixing comes at a considerable energetic cost to an organism, one might expect that species have evolved to minimize such losses.

These relations might be tested in the lab by dropping spheres of various sizes in a stratified water column and watching their effect on the spreading of a mid-depth layer of a dye. Preliminary experiments found little mixing by sinking spheres with $Re < 1$, consistent with the predictions given here.

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