REVIEW

Biogenic inputs to ocean mixing

Kakani Katija

Applied Ocean Physics and Engineering, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

kakani@whoi.edu

Summary

Recent studies have evoked heated debate about whether biologically generated (or biogenic) fluid disturbances affect mixing in the ocean. Estimates of biogenic inputs have shown that their contribution to ocean mixing is of the same order as winds and tides. Although these estimates are intriguing, further study using theoretical, numerical and experimental techniques is required to obtain conclusive evidence of biogenic mixing in the ocean. Biogenic ocean mixing is a complex problem that requires detailed understanding of: (1) marine organism behavior and characteristics (i.e. swimming dynamics, abundance and migratory behavior), (2) mechanisms utilized by swimming animals that have the ability to mix stratified fluids (i.e. turbulence and fluid drift) and (3) knowledge of the physical environment to isolate contributions of marine organisms from other sources of mixing. In addition to summarizing prior work addressing the points above, observations on the effect of animal swimming mode and body morphology on biogenic fluid transport will also be presented. It is argued that to inform the debate on whether biogenic mixing can contribute to ocean mixing, our studies should focus on diel vertical migrators that traverse stratified waters of the upper pycnocline. Based on our understanding of mixing mechanisms, body morphologies, swimming modes and body orientation, combined with our knowledge of vertically migrating populations of animals, it is likely that copepods, krill and some species of gelatinous zooplankton and fish have the potential to be strong sources of biogenic mixing.

Key words: biogenic mixing, biological fluids, ocean mixing.

The ocean mixing problem

The circulation of the oceans plays a major role in governing the world's climate because oceanic transport of heat is comparable to that of the atmosphere (Bryden and Imawaki, 2001). Ocean fluid dynamics are different from many classical fluid dynamics problems because of the vertical stratification (of salts and temperature) that inhibits fluid transport across surfaces of constant density, or isopycnals. The circulating currents of the oceans have to work against the vertical stratification in order to transport fluid. This circulation is maintained by external mixing processes whose identification and estimates of power input describe the ocean mixing problem (Linden, 1979; Barrett and Van Atta, 1990; Fernando, 1991; Ivey and Imberger, 1991; Ledwell et al., 1993). The importance of the ocean mixing problem to marine organisms is evident from our observations about biomass being distributed throughout the ocean's depths.

Ocean layers can be described by different fluid, nutrient and light properties, resulting in distinct assemblages of marine organisms at each layer (Fig. 1). The ocean layer between the sea surface and as deep as 200 m is known as the epipelagic (or euphotic) region. In this region, sufficient light is available for photosynthesis by phytoplankton. Phytoplankton are the base of the food webs in the ocean, and represent the largest proportion of biomass in the ocean (Sumich and Morrissey, 2004). For this reason, non-migrating zooplankton, pelagic fish and other organisms at higher trophic predatory levels spend substantial time in the epipelagic layer to feed.

The next layer in the ocean, the mesopelagic region, signals the start of the aphotic zone (indicated by a decrease in the light bar graph, Fig. 1), with a reduction in biomass. Many zooplankton and

pelagic organisms inhabit this region during daytime to evade predators (Sumich and Morrissey, 2004). Upon nightfall, large populations of these organisms begin their diel vertical migrations to feed at the surface (Stich and Lampert, 1981; Lampert, 1989). Many zooplankton species exhibit dramatic diel vertical migrations, moving anywhere between 100 to 500 m each way and, in some instances, crossing sharp pycnoclines (Wiebe et al., 1979).

Because of the lack of ambient light, organisms in the bathypelagic region utilize bioluminescence to communicate and detect other organisms. Although Fig. 1 shows a sharp decrease in biomass in this region, there are indications that this is contrary to observations of gelatinous zooplankton (B. H. Robison, personal communication). Upon reaching the ocean bottom, the biomass increases relative to the mid-ocean layers. This increase in biomass is due to the availability of food that settle from the surface and mid-ocean regions in the form of detritus, animal carcasses and dissolved nutrients (Rowe and Staresinic, 1979; Madin, 1982; Wilson et al., 2009).

There are many challenges associated with sustaining life throughout the depths of the ocean. For example, organisms living on the ocean bottom are largely separated from any sources of dissolved oxygen, nearly 4000 m away from the sea surface. Organisms in the upper ocean need to be sustained by food that has largely settled through the pycnocline to the abyssal plane. In addition, the pycnocline serves as a physical barrier between phytoplankton near the surface and nutrient-rich water below, thereby limiting primary production (Sumich and Morrissey, 2004). Therefore, in order to distribute necessary elements for sustaining marine life throughout the ocean's depths, rapid transport of dissolved oxygen and nutrient-rich fluid across the pycnocline and
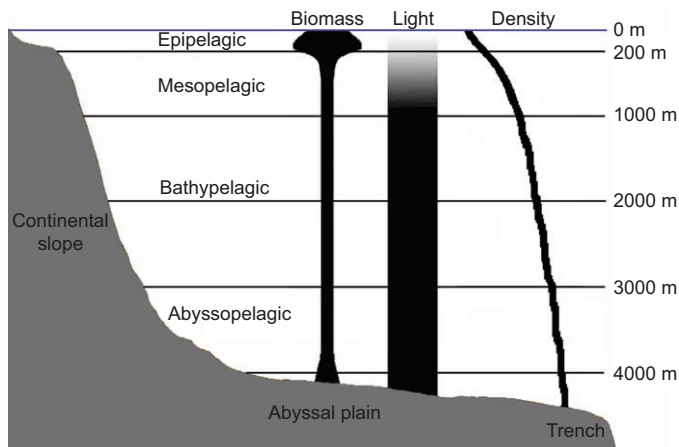
Fig. 1. Ocean layers have distinct characteristics that include biomass, light availability and fluid density (image adapted from J. Drazen; http://www.soest.hawaii.edu/oceanography/faculty/drazen/fishes.htm).

against the ocean's stratification is needed; oceanic circulation plays a major role in this fluid transport.

Oceanographers have spent much of the last five decades identifying mixing processes that can contribute to and account for the external work required to sustain oceanic circulation. These processes include, but are not limited to, surface heating and cooling, atmospheric forcing (i.e. surface winds), tidal mixing over rough topography, double-diffusive convection, and breaking internal waves in midwater generated by processes at the surface and at depth (Ivey and Nokes, 1989; Moum and Smyth, 2001; St Laurent and Garrett, 2002). Estimates of power required to sustain oceanic circulation (or the ocean mixing energy budget) vary between 2 and 3 TW (Munk and Wunsch, 1998; Wunsch and Ferrari, 2004; St Laurent and Simmons, 2006). Although the identification of these sources is an intriguing problem with a rich body of literature, these studies are outside the scope of this review and the author refers readers to other informative reviews on this topic (Fernando, 1991; Wunsch and Ferrari, 2004; Thorpe, 2004; Ferrari and Wunsch, 2009; Ferrari and Wunsch, 2010).

From satellite altimetry data, extensive ocean sampling and numerical modeling, it is clear that these physical processes impart large quantities of power to the ocean. However, the conversion of this power to mixing in the mid-ocean is poorly understood, and investigations of power input to ocean mixing from these sources have provided variable estimates of their contribution to the global ocean energy budget. For example, power that is injected at the sea surface by atmospheric forcing will experience substantial losses, where approximately 90% is dissipated as heat within the upper 100 m and only 10% actually contributes to ocean mixing (Ferrari and Wunsch, 2009). In light of these measurement uncertainties and our incomplete understanding of energy conversion processes in the ocean, it can be argued that processes contributing to ocean mixing have yet to be identified. A process that has the potential to impart substantial work to the ocean, and has been largely ignored by the oceanographic community, is biologically generated (or biogenic) mixing.

Estimates of biogenic inputs to ocean mixing

The potential input of marine organisms to the ocean mixing energy budget is not a new concept and was first proposed by oceanographer Walter Munk. Munk (Munk, 1966) noted that although turbulence is efficient at mixing a fluid (because of the energetic cascade from larger to smaller length scales), there might be far more efficient ways for biogenic mixing to contribute to ocean mixing besides turbulence. Nearly four decades later, Huntley and Zhou (Huntley and Zhou, 2004) estimated the fluid disturbance from schooling animals and compared it with physical mixing processes in the ocean. An estimate of the fluid disturbance (or turbulent kinetic energy dissipation rate, ε) by schooling animals can be found by assuming that the rate of turbulent energy production by the school (E_p, in units of $W\,kg^{-1}$) is approximately equal to the turbulent dissipation rate, and rewriting E_p as a function of the rate of energy expenditure to overcome drag (e_d), animal swimming efficiency (η) and number of animals (n) in the school:

$$E_p = \frac{e_d}{\eta} \frac{1}{\rho} \frac{n}{V} \, , \qquad (1)$$

where the volume (V) represents the volume inhabited by the school and ρ is the density of seawater. Using Eqn 1, Huntley and Zhou (Huntley and Zhou, 2004) estimated turbulent dissipation rates for schooling animals to be $10^{-5}\,W\,kg^{-1}$ across all schools regardless of animal size and composition. This analysis showed that dissipation rates of schooling animals are comparable to rates associated with major storms [winds at $20\,m\,s^{-1}$ correspond to $\varepsilon = 8.5 \times 10^{-6}\,W\,kg^{-1}$ (MacKenzie and Leggett, 1993)], potentially providing a source of fine-scale turbulent mixing in the ocean. To be sure, direct comparison of these quantities are tenuous as they represent fluid disturbances over different length scales, ranging from the surface area of the whole ocean (Munk, 1966) to the size of a swimming school (Huntley and Zhou, 2004).

Using three different approaches, a separate study estimated the biosphere input to ocean mixing (Dewar et al., 2006). Using the photosynthetic energy fixation rate to estimate the net primary production in the ocean as 62.7 TW, and assuming that 1% of net primary production is imparted to the aphotic ocean in the form of mechanical mixing, the net biosphere contributes approximately 1 TW to the ocean mixing budget (Dewar et al., 2006). This finding was confirmed by two other approaches in the same study, suggesting that biogenic mixing may be an important source of mixing in the ocean.

Although estimates of biogenic input to the ocean mixing energy budget are intriguing, without evidence to support these estimates, statements regarding the importance of biogenic mixing to ocean circulation are inconclusive. Biogenic ocean mixing is a complex problem that requires detailed understanding of: (1) marine organism behavior and characteristics (i.e. swimming dynamics, abundance and migratory behavior), (2) the mechanisms by which swimming animals have the ability to mix stratified fluids and (3) how processes in the physical environment will affect these two factors. It is the hope of the author to present the work in this field as complementary, elucidating complex processes that govern biogenic mixing. The following two sections discuss biogenic mixing mechanisms (mentioned in 2 above): turbulence generated by swimming marine organisms and fluid transport due to drift, a term that will be defined shortly. The next section will review recent studies that investigate the multiple body–fluid interactions in animal aggregations. Finally, a discussion on the future challenges for studying biogenic mixing will be presented.

Fluid mechanics terms and concepts

A common dimensionless quantity used in fluid mechanics is the Reynolds number (*Re*), formally defined as:

$$Re = \frac{UL}{\nu} , \qquad (2)$$

where *U* and *L* are the characteristic velocity and length scale, respectively, and ν is the kinematic viscosity of the fluid (with units of $m^2 s^{-1}$). For a swimming animal, *U* and *L* commonly correspond to average swimming speed and body length, and ν is defined by the properties of the fluid surrounding the animal. The Reynolds number measures the ratio of inertial forces to viscous forces in a fluid and, depending on its magnitude, quantifies the relative importance of inertial and viscous forcing for given flow conditions. As $Re \to \infty$, inertial forces are dominant, and the fluid regime is often referred to as the inertial or potential flow limit. As $Re \to 0$, viscous forces are dominant, and the fluid regime is the viscous or Stokes flow limit. Assuming that swimming velocity and fluid properties remain the same, smaller organisms will have a lower Reynolds number than larger organisms.

The Reynolds number can also be used to identify different flow regimes in the context of laminar (smooth) or turbulent (chaotic) flow. Laminar flow occurs at low Reynolds numbers whereas turbulent flow occurs at high Reynolds numbers. In turbulent flow, eddies, vortices and other flow instabilities are produced. The size and residence time of eddies produced in turbulence are often used to characterize length and time scales of the fluid, similar to length scales representing animal size. Interestingly, these turbulent eddy length and time scales have implications for mixing in the ocean.

Turbulence exists at all scales, from the swirling motion created by a tuna when chasing a bait ball to wake structures created by atmospheric flow interacting with a protruding mountain. Energy cascades from larger eddies to smaller eddies, where molecular mixing due to the effects of viscosity occurs at the smallest length scale, known as the Kolmogorov length scale (Tennekes and Lumley, 1972). Turbulent mixing is a three-stage process of fluid entrainment (spreading of turbulent region), dispersion (or stirring, separation or dispersal of fluid parcels) and diffusion (irreversibly reducing gradients of temperature or solute concentration), and each stage of turbulent mixing is quantified by a representative length and time scale (Eckart, 1948; Dimotakis, 2005; Thorpe, 2005). Turbulence is a mechanism largely responsible for mixing in the ocean.

Ocean turbulence quantities are commonly measured by using a suite of instruments: microstructure shear (or velocity gradient) probes, conductivity, temperature and depth profilers, and high-resolution thermistors. With these instruments, and applying assumptions to simplify measurements, quantities such as turbulent dissipation rate, mixing efficiency, buoyancy frequency and eddy diffusivity can be calculated. These turbulence quantities are often presented in the oceanographic literature to characterize the turbulence produced by a mixing process.

The dissipation rate (ε) represents the rate of loss of turbulent kinetic energy per unit mass through viscosity to heat. The dissipation rate is defined from the velocity gradients in the fluid such that:

$$\varepsilon = \frac{\nu}{2} \overline{\left(\frac{du_i}{dx_j} + \frac{du_j}{dx_i} \right) \left(\frac{du_i}{dx_j} + \frac{du_j}{dx_i} \right)} . \qquad (3)$$

Eqn 3 is written in tensor notation and the overbar indicates averaging. The quantities $u_{i,j}$ and $x_{i,j}$ represent the fluid velocity and position in the *i*th or *j*th direction, respectively (Tennekes and Lumley, 1972). Because of current technological limitations, assumptions of isotropic turbulence are often made. Isotropy occurs when a quantity, such as a velocity gradient, has the same value when measured in different directions. Small-scale structured turbulence is often assumed to be isotropic, in which case the dissipation rate in Eqn 3 simplifies to (Gregg and Horne, 2009):

$$\varepsilon \approx 7.5\nu \overline{\left(\frac{du}{dz} \right)}^2 . \qquad (4)$$

Using Eqn 4, the values of dissipation rate in the ocean have been found to range from $10^{-9}\,W\,kg^{-1}$ in the abyssal ocean to $10^{-1}\,W\,kg^{-1}$ in the surf zone.

In the ocean, mixing occurs when a process disrupts the density gradient in the fluid. The mixing efficiency Γ quantifies the ability of a mixing process to convert mechanical energy (*M*) to a change in the potential energy state (ΔPE) of the fluid. The mixing efficiency is defined as:

$$\Gamma = \frac{b}{M} \approx \frac{\Delta PE}{\Delta KE} , \qquad (5)$$

where the buoyancy flux (*b*) in the fluid is equivalent to the change in potential energy as denser fluid (colder, saline water) is lifted into less dense fluid (warm, fresh water) and *vice versa* (Tennekes and Lumley, 1972; Linden, 1979; Britter, 1985; Rehmann and Koseff, 2004). The mechanical energy (*M*) available to generate mixing by a specific process can be quantified by the change of kinetic energy in the fluid (ΔKE) induced by the mixing process.

A quantity that is used to describe the strength of stratification in the ocean is the buoyancy frequency *N*:

$$N = \sqrt{ -\frac{g}{\rho_0} \left(\frac{d\rho}{dz} \right) } , \qquad (6)$$

where **g** is the gravitational acceleration and ρ_0 is a reference density of the fluid (Thorpe, 2005). The mean buoyancy frequency in the ocean ranges between 10^{-2} and $10^{-4}\,s^{-1}$. Finally, eddy diffusivities (*K*) are used to provide a parameterization of turbulent fluxes due to viscosity, heat, salt and density (denoted by subscripts ν, *T*, s and ρ, respectively) (Thorpe, 2005). The vertical eddy diffusivity of mass or density (K_ρ) is:

$$K_\rho = \Gamma \frac{\varepsilon}{N^2} . \qquad (7)$$

These expressions, combined with the use of oceanographic measurement devices, allow for characterization of processes relevant to mixing.

Mixing *via* biogenic turbulence

The first known measurement of biogenic turbulence (to the author's knowledge) occurred accidentally during temperature and velocity gradient measurements aboard the submarine USS Dolphin in Monterey Bay, CA (Farmer et al., 1987). A velocity measurement probe mounted on the mast recorded changes in fluid velocity gradients in the vicinity of a school of fish. This observation was a matter of great concern because contamination of measured profiles by biological sources cannot be dismissed; anomalous structures observed in otherwise quiescent water may be due to aggregations of fish. These observations linking fish to variability in turbulent dissipation rates were noted by Huntley and Zhou much later (Huntley and Zhou, 2004). Two decades

later, elevated turbulent dissipation rates were measured during diel vertical migrations of schooling krill in Saanich Inlet. Saanich Inlet is a semi-enclosed fjord off the coast of British Columbia, Canada, and is an ideal study location for measuring biogenic turbulence due to high concentrations of schooling *Euphasia pacifica* or krill (up to 10^4 individuals m^{-3}). Resident krill populations have strong diel vertical migration behavior, which is largely dependent on weather and surface conditions (Kunze et al., 2006). Acoustic measurements of migrating krill show dense aggregations at 100 m depths during the day, and at dusk, the krill swim towards the surface, with the smallest individuals migrating before the largest (~2 cm long) individuals. Typical background dissipation rates before and after krill migrations in Saanich Inlet were found to be on the order of 10^{-9} W kg^{-1}; however, turbulence levels in the vicinity of krill were between 10^{-5} and 10^{-4} W kg^{-1}. Therefore, the turbulent dissipation rates associated with vertically migrating krill was thus 100 to 1000 times greater than rates associated with turbulent patches in the deep ocean, and are comparable to values of other mixing processes (Gregg, 1987). Based on their measurements, Kunze et al. (Kunze et al., 2006) concluded that during schooling, mixing scales increased beyond those associated with an individual animal. Therefore, by swimming in concert, vertically migrating krill are able to reduce viscous drag and enhance mixing at scales representative of the krill school.

These findings were later contested by Rippeth et al. (Rippeth et al., 2007) as not being representative of coastal seas. Measurements of turbulent dissipation rate in the coastal seas west of the United Kingdom yielded smaller dissipation rates, which may be attributed to much smaller aggregations of swimming krill than those reported in Saanich Inlet (Rippeth et al., 2007; Kunze et al., 2006). As a statistically significant enhancement of dissipation rates during periods of animal migration was not found in any of their data, Rippeth et al. (Rippeth et al., 2007) concluded that biogenic turbulence was not significant compared with physically induced turbulence in a location that was more representative of conditions in coastal seas. However, this finding was later contested because sampling was not conducted within the vertically migrating scattering layers to determine the species or sizes of organisms present (Kunze and Dower, 2007). In order to have appreciable biogenic mixing *via* turbulence, planktonic organisms large enough to generate significant turbulence need to be present. Unfortunately, in the region sampled, animals of this size range are rare, and therefore the lack of significant enhancement of turbulent mixing is not surprising (Kunze and Dower, 2007).

However, elevated levels of turbulence in the wake of a dense assemblage of swimming organisms does not necessarily imply that mixing is proportionally higher (Visser, 2007). The mixing efficiency (Γ, formal definition in Eqn 5) measures the ability of a mixing process to convert kinetic energy to a change in fluid potential energy (Thorpe, 2004), and is an accurate metric for fluid mixing, not dissipation rate (Visser, 2007). The efficiency of biogenic turbulence is limited not only by fluid stratification, but also by the size of eddies created by swimming organisms. For smaller, more abundant animals (i.e. phytoplankton and small zooplankton), the mixing efficiency achieved by the turbulent eddies they generate is on the order of 10^{-3}, nearly two orders of magnitude smaller than that of larger, but less abundant animals in the ocean [e.g. cetaceans (Visser, 2007)]. Therefore, because small swimming organisms make up the vast majority of biomass and they inject turbulent mechanical energy into the ocean with very small mixing efficiencies, it is unlikely that marine organisms are

important contributors to ocean circulation due to biogenic turbulence alone.

Simultaneous measurements of dissipation rate and mixing efficiency were independently conducted by Gregg and Horne (Gregg and Horne, 2009) during a study of horizontally moving schools of fish in Monterey Bay. Dissipation rates in aggregations were found to be 10–100 times the maximum dissipation rates outside aggregations; however, the mixing efficiency decreased 100-fold within the aggregation, resulting in essentially the same eddy diffusivity (K_ρ) inside and outside the school of fish (Gregg and Horne, 2009). Although these findings demonstrate that mixing within aggregations of fish is less efficient than mixing produced by background turbulence, a separate study of fish shoals moving horizontally in shallower water found that mixing efficiency did not differ between profiles with or without fish (Lorke and Probst, 2010). The conflicting conclusions from these studies illustrate the variability and challenges faced when characterizing biogenic mixing. It is clear that schools of swimming animals create measurable changes in fluid disturbances, and recent laboratory studies of schooling krill confirm this (Catton et al., 2011). However, in terms of generating mixing by disrupting stratification in the ocean, vertical migration behavior may result in more effective mixing than mostly horizontally swimming animals.

The occurrences of intense biogenic turbulence were often infrequent and difficult to predict in prior sampling studies (Kunze et al., 2006; Gregg and Horne, 2009; Lorke and Probst, 2010). A program to collect data over a 3 year period in Saanich Inlet and at an open ocean field site was later conducted to generate statistics on biogenic mixing (Rousseau et al., 2010). In the open ocean, the dissipation rates both inside and outside a non-migrating acoustic backscatter layer were not significantly different, although the precise biological composition of the layer was not determined. Measurements of elevated dissipation rates due to schooling krill at Saanich Inlet [which include results from Kunze et al. (Kunze et al., 2006)] were 10^{-6} W kg^{-1} on 73 of 376 profiles. Therefore, statistics based on six time series suggest that strong biogenic turbulence events [like those reported by Kunze et al. (Kunze et al., 2006)] occurred only 4% of the time. Although an occurrence of a mixing event is low, if biogenic turbulent bursts of the same intensity reported in Kunze et al. (Kunze et al., 2006) occur once every 1 to 12 months in the open ocean, they will produce average dissipation rates comparable to physical mixing processes in the ocean (Garrett, 1979; Gregg, 1987; Rousseau et al., 2010).

Transport *via* drift

A second, previously neglected mechanism of fluid transport by swimming animals was introduced to the biogenic mixing literature by Katija and Dabiri (Katija and Dabiri, 2009). Sir Charles Galton Darwin, the grandson of the 'On the Origin of Species' author, first described a mechanism of fluid mixing that does not require an object to generate rotational or shearing motion in the flow (Darwin, 1953). As a solid body travels through fluid, a portion of the surrounding fluid is set into motion by the body's pressure field and propagates along with the body (Fig. 2). The volume of fluid that 'drifts' with the solid object is proportional to the volume of the object itself, and depends only on the shape of the body and its orientation relative to the oncoming flow. In the case of a vertically stratified fluid such as the ocean, the induced fluid drift caused by vertical motion of a solid body will result in a concomitant change in the total potential energy of the fluid, because higher-density fluid is raised above lower-density fluid during upward body motion, and *vice versa* during downward body motion. The
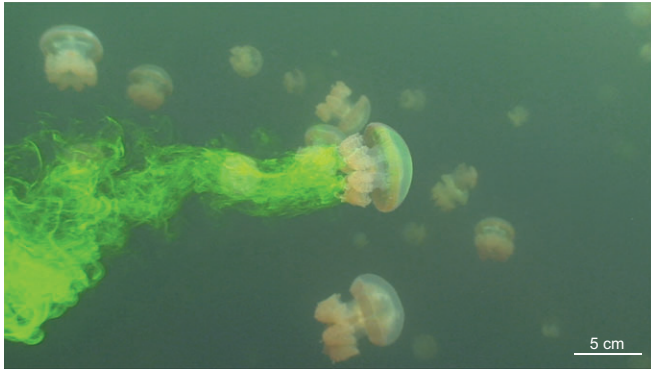
Fig. 2. Drift mechanism, illustrated by the interaction of fluorescein dye with *Mastigias* sp., a native jellyfish species in the stratified marine lakes of Palau. Image reproduced with permission from Katija and Dabiri (Katija and Dabiri, 2009).

resulting increased gradients between fluid masses of differing density will be susceptible to further stirring by ambient fluid motions and by interaction with neighboring solid bodies, ultimately leading to molecular mixing (Eckart, 1948; Eames and Bush, 1999). The efficiency of mixing by Darwin's mechanism is dependent on animal shape rather than fluid length scale and, unlike turbulent wake mixing, is enhanced by fluid viscosity (Eames, 2003; Katija and Dabiri, 2009). In the limit of Stokes flow, the induced fluid drift of a towed body becomes infinitely large [after the body moves an infinite distance (Eames et al., 2003)]. Therefore, unlike biogenic turbulence, drift provides a means for mixing that can be equally effective in small zooplankton and large mammals.

Experimental observations of drift

The first experimental observations of drift by swimming animals were conducted in the stratified marine lakes of Palau using a newly developed scuba-based laser velocimetry device (SCUVA) (Katija and Dabiri, 2008; Katija et al., 2011) to quantify biogenic mixing (Katija and Dabiri, 2009). Qualitative dye visualizations revealed that the drift mechanism occurred over a broad range of jellyfish sizes (Fig. 2). The mixing efficiency due to a single swimming jellyfish was measured by using Eqn 5 (Katija and Dabiri, 2009). The kinetic energy was evaluated from the velocity field data acquired from digital particle image velocimetry (DPIV) (Willert and Gharib, 1991; Videler et al., 2002; Katija and Dabiri, 2008). To determine the change in potential energy, the authors used planar laser induced fluorescence (Koochesfahani and Dimotakis, 1986; Dahm and Dimotakis, 1987; Ferrier et al., 1993; Crimaldi, 2008) to measure the jellyfish-induced displacement of an artificially created stratified layer in midwater. Katija and Dabiri (Katija and Dabiri, 2009) found the mixing efficiency induced by a swimming jellyfish to be 24±18%. Based on the fluid stratification imposed by the dye, these measurements show biogenic mixing in strongly stratified conditions, compared with the average conditions in the ocean (Kunze et al., 2006; Thorpe, 2005). Undoubtedly, measurements of mixing efficiency were conducted on time scales (after four swimming cycles) too short to determine whether flow completely restratifies (J. Moum, personal communication), a constraint in the field measurements. Measurements at longer time scales could be easily conducted under laboratory conditions.

A common criticism for biogenic mixing *via* drift is related to the perceived reversibility of fluid transport as animals migrate upwards and downwards daily. If a small animal (Re=1) transports fluid *via* drift during a diel migration, one might argue that the net transport of fluid is nearly zero because the animal returns to an initial position. This statement would be true (assuming animal swimming behavior and characteristics are repeated exactly throughout migration) if we ignore all other physical mixing processes in the ocean that may be active. For example, adjacent swimming animals may interact with stirred fluid drift, enhancing mixing rate. Stirring of fluid by migrating animals *via* drift would create gradients in the temperature or salinity fields, thereby providing conditions for diffusion to occur. If we define a diffusive time scale (t_{diff}) based on the thermal diffusivity of seawater (k_{T}) and characteristic length scale (L) of a swimmer:

$$t_{\mathrm{diff}} \sim \frac{1}{k_{\mathrm{T}}}\left(\frac{L}{2}\right)^2 , \qquad (8)$$

we find that the diffusive time scale is on the order of 10^4 s; this is less than the average time associated with a diel migration (~6 h, including time feeding at the surface). Therefore, by diffusion alone, the fluid transported by swimming animals *via* drift will irreversibly diffuse and mix with its surroundings before the end of the migration.

Katija and Dabiri (Katija and Dabiri, 2009) used simulations of a passively towed body (a body that moves by an applied external force) to illustrate the effects of fluid viscosity and body shape on drift. However, to understand the drift mechanism in the context of swimming animals, simulations of a passively towed body oversimplify the dynamics of swimmers. Another (also simplified) description of animal swimming dynamics is the self-propelled swimmer model (Chwang and Wu, 1975; Brennen and Winet, 1977), which is commonly used to describe flow fields generated by swimming microorganisms (at small Reynolds numbers). In the limit of steady motion, the self-propelled model swimmer generates no net force on the fluid because the contributions of time-averaged thrust and drag on the body offset (Taylor, 1951). A swimmer within this limit can be computationally described by a point-force dipole. Given these differences in the wake, the drift volume for the self-propelled model swimmer is substantially less than a passively towed body (Leshansky and Pismen, 2010; Subramanian, 2010). However, animal swimming is an unsteady process and animals move against an external force (gravity) during diel vertical migrations. These traits, among others, demonstrate that the self-propelled swimmer model alone cannot accurately describe animal swimming. Therefore, a passively towed body and a self-propelled swimmer model may provide limits of animal-induced drift for all swimming organisms.

Effect of morphology and swimming mode on drift

To understand how swimming mode and body morphology affect animal-induced fluid transport, the quantitative flow fields surrounding a swimming jellyfish, *Phylorhiza* sp., were analyzed using DPIV in the laboratory. Downstream from the bell, a protruding, passive structure (oral arms, Fig. 3A) serves to filter prey. This structure does not play a role in generating propulsion, but instead interacts with vortex rings in the animal's wake. Because of this interaction, the vortex ring created in its wake is deflected away from the body's rotational axis. The drift is clearly indicated by the region of flow directly behind the oral arms that is moving in the direction of the animal (Fig. 3A). Excising the oral
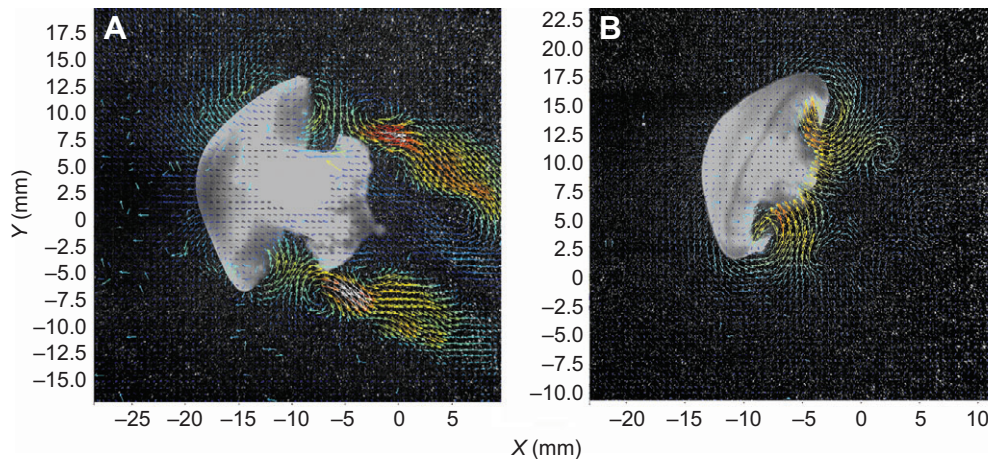
Fig. 3. Digital particle image velocimetry measurements of flow surrounding *Phylorhiza* sp. in the laboratory, exhibiting the effect of morphology on drift. (A) Velocity fields clearly indicate wake structures being redirected by the oral arms to reduce interaction with the drift volume (region behind the swimming animal, whose velocity vectors point in the same direction as travel). (B) After excising the oral arms, the drift volume is reduced.

arms produces a striking change in the wake (Fig. 3B), where the vortex rings now appear to be directed downstream, and a persistent drift volume is absent. Therefore, the deflection of the vortex ring by the oral arms serves to reduce the interaction of propulsive wake structures with the drift volume. In order for an animal to have a substantial drift effect, a morphology that prevents interaction of wake structures with the drift volume is necessary. Using the same argument, an animal's body orientation during swimming may also play a role if the resultant wake is directed away from the drift volume.

The swimming mode of an organism during migration will also affect fluid transport, as shown in simulations of copepod swimming (Fig. 4) (Jiang and Strickler, 2007). By numerically modeling steady feeding currents for different modes of observed copepod swimming behaviors (i.e. free-sinking, partial sinking, hovering, vertically swimming upwards and horizontally swimming backwards or forwards), the resulting fluid transport can be compared. In the case of a hovering copepod (Fig. 4A), the body is stationary and drift is absent; the wake generated by the moving appendages is able to stir a particle patch adjacent to the body. When the body moves, as in the case of partial sinking (sinking while beating cephalic appendages to offset terminal velocity) and unsteady swimming (Fig. 4B,C), drift is indicated by the streak of particles moving behind the body. In addition to drift, the combined contributions of body translation and appendage motion results in a wake that allows for continuous transport of fluid (a toroidal volume adjacent to the copepod). Therefore, for partial sinking and unsteadily swimming copepods, the resultant wake transports fluid on length scales of the swimming distance of the copepod. However, it is unclear whether transport by drift or the toroidal wake generated by moving appendages will dominate fluid transport for a copepod.

Estimates of drift in a linearly stratified flow

The estimates of biogenic mixing *via* drift in an unstratified fluid represent an upper bound on mixing. In the case of a stratified fluid, we would expect fluid transport to be limited to specific length and time scales, potentially reducing the contribution of drift to biogenic mixing. Using a first-order model to address fluid transport *via* drift in a stratified fluid ($N=10^{-2}\,s^{-1}$), no less than 60% of the drift volume in an unstratified fluid will mix and be permanently displaced by diffusion alone (Katija, 2010). Simulations of a self-propelled swimmer model showed changes in the fluid streamlines due to stratified conditions (Ardekani and Stocker, 2010) [similar formulation by List (List, 1971)]. In an

unstratified fluid, streamlines are open and the flow everywhere is moving in the direction opposite of the swimming body. However, in stratified conditions, the streamlines are closed. The fluid velocity induced by the swimmer model decays much faster in a stratified fluid than in an homogeneous fluid, effectively muting the mechanosensory signals that inform the presence of prey to predators and *vice versa* (Ardekani and Stocker, 2010). These findings suggest that, for a self-propelled swimmer at the Stokes flow limit, the consequence of buoyancy limits the vertical transport of fluid, which is consistent with the observations made by Katija (Katija, 2010) for a passively towed body in stratified flow.

Models for understanding multi-animal fluid transport

Measurements of single animal fluid transport should be considered as lower bounds for biogenic mixing. Drift volumes of neighboring animals in an aggregation may interact *via* their boundary layers to further enhance vertical transport, and by increasing the horizontal scale of vertically drifting fluid mass to the horizontal extent of the entire aggregation of animals. However, studies of fluid transport by a single animal cannot simply be superimposed to extrapolate the effect of an entire school of migrating swimmers. Extensive theoretical and experimental analyses are required to understand whole-population dynamics, and these approaches, particularly numerical, are currently being developed.

Adopting the viewpoint that drift may be more relevant to mixing than the scales of turbulence that swimming animals produce, Thiffeault and Childress (Thiffeault and Childress, 2010) modeled swimmers as cylinders and spheres moving in potential flow. From the model, they were able to determine the effective diffusivity (K) associated with a concentration of passive quantities such as heat, salt or nutrients. Simulations were initialized by placing a single particle at the origin and having randomly placed bodies (whose number were varied by n_V, the number of bodies per unit volume) move at constant speed U in random directions. As the bodies moved, the particle would be displaced each time a body was 'encountered'. From simulations of moving spherical and cylindrical bodies (Thiffeault and Childress, 2010), the effective diffusivity scaled with swimming speed, number density of swimmers and swimmer length scale (l, body radius) by:

$$K = \begin{cases} 1.19Un_Vl^3 & \text{cylinders;} \\ 0.266Un_Vl^4 & \text{spheres,} \end{cases} \qquad (9)$$
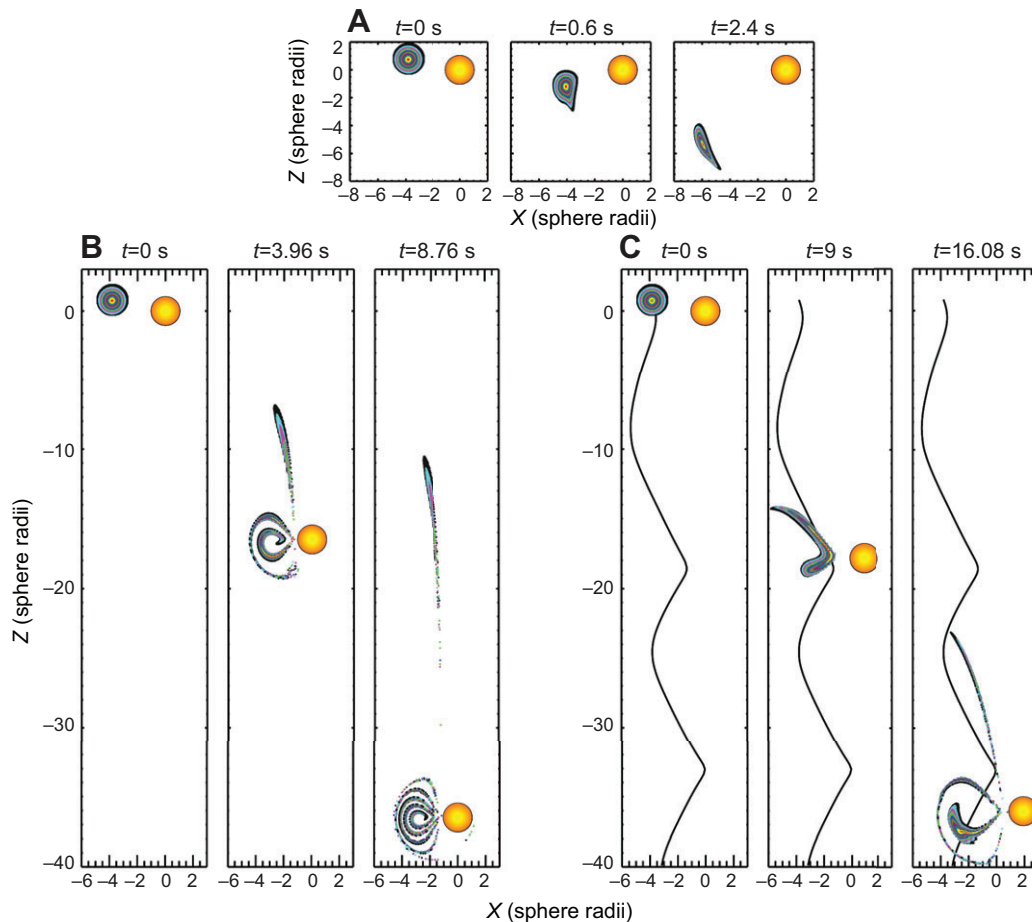
Fig. 4. Transport and stirring of a patch of particles by a swimming copepod exhibiting different swimming modes: (A) hovering, (B) partial sinking and (C) free-swimming with unsteady velocity. The yellow sphere corresponds to the copepod body, whose initial position is at the origin in the simulation. The multi-color region to the left of the copepod body indicates the particle patch. The black curve in C indicates the trajectory of the particle patch. Axes are in units of sphere radii. Time of each frame is indicated at the top of the frame. Image reproduced with permission from Jiang and Strickler (Jiang and Strickler, 2007).

where the constant for cylinders has units of m and the constant for spheres is dimensionless.

Using Eqn 9, and values of swimming speed, number density and size typical for krill schools, the simulations showed that during schooling, there can be considerable enhancement to molecular diffusion. The effective diffusivity associated with biomixing in Stokes flow is 200 times greater than that due to swimmers in potential flow under the same set of parameters (Lin et al., 2011). In Stokes flow, the largest contribution to particle displacement, and hence mixing, arises from random changes of swimming direction. These observations are similar in nature to the simulated particle patch stirring due to an unsteady downward swimmer, where chaotic mixing and stirring is apparent (Jiang and Strickler, 2007).

Aside from the parameters used to describe a krill school, these numerical studies incorporated little in terms of animal swimming behavior (Thiffeault and Childress, 2010; Lin et al., 2011). To estimate the effect of schooling animals on ocean mixing, investigations linking animal behavior during diel vertical migration are necessary. Research since Kunze et al. (Kunze et al., 2006) has measured biogenic turbulence in horizontally migrating schools of organisms, where mixing rates were found to be low. However, vertical migration across isopycnals may be necessary in order to generate mixing at length scales significantly larger than

individual animals. In a theoretical study of passive spheres moving in linearly stratified potential flow, as the number of bodies increased (and their relative position became more staggered), the vertical displacement of fluid parcels became much larger than individual body sizes (Dabiri, 2010). These simulations show that schooling animals during vertical migration through stratified fluid have the ability to generate mixing at scales larger than the individual animal.

Challenges for future investigations of biogenic mixing

Research in this field may require simultaneous bottom-up (small-scale, single-animal fluid dynamics to aggregations) and top-down (oceanographic measurements of mixing by schooling animals) approaches to elucidate processes involved in biogenic mixing. Biogenic ocean mixing is a complex problem that requires detailed understanding of several topics that include, but are not limited to, marine organism behavior, mixing mechanisms utilized by swimming organisms and the role of the physical environment. Given these substantial components, the challenges for predicting events of strong biogenic mixing are numerous and demanding.

Identifying potential biogenic mixers

It is clear from the studies presented in this review that the emphasis in our quest to understand biogenic mixing needs to be on biology.

It is insufficient to take multiple measurements of turbulence generated by a passing school of unidentified organisms to form conclusions about the global importance of biogenic mixing in the ocean. The biogenic mixing problem should be approached by first addressing what organisms have the potential to affect mixing in the ocean based on their behavior, population size and swimming mechanics. Since the work of Kunze et al. (Kunze et al., 2006) and Visser (Visser, 2007), this approach has been largely ignored.

The informative relationship between mixing efficiency and turbulence generation by swimming animals served to establish limits on the effectiveness single organisms have on mixing *via* turbulence (Visser, 2007). A swimming animal can generate turbulence at scales of the same order as their body size; smaller animals (residing in low-*Re*, viscous fluid regimes) are incapable of generating larger, more energetic eddies such as those produced by pelagic fish and whales. Although there are claims that schooling of small animals effectively increase the scales of turbulence to scales characterizing the school (Huntley and Zhou, 2004; Kunze et al., 2006; Dabiri, 2010), the mechanisms that would allow for this conversion is not well understood. However, with the identification of drift, a mixing mechanism that is applicable to any moving body regardless of size or shape, smaller animals can generate efficient mixing as well (Katija and Dabiri, 2009).

Although fluid drift provides a mechanism *via* which smaller swimming animals can efficiently mix a fluid, there are limitations to fluid transport that are due to animal swimming mode, morphology, energetics and fluid stratification (Ardekani and Stocker, 2010; Katija, 2010; Leshansky and Pismen, 2010; Subramanian, 2010). Jellyfish excision experiments showed that the presence of morphological structures can impede the interaction between the drift and propulsive wake structures, allowing for long-distance transport of fluid *via* drift. Comparison of copepod swimming modes revealed swimming modes where the self-propelled body also maintained fluid transport *via* drift (Jiang and Strickler, 2007). In addition to swimming modes and body morphology, body orientation during migration will also affect drift. Reports of krill orientation during vertical migration at dusk show that animals ascend obliquely (De Robertis et al., 2003), which may lead to enhanced drift when compared with swimming in line with an organism's longitudinal axis.

Finally, to inform the debate on whether biogenic mixing can efficiently mix the ocean, we should focus our studies on diel vertical migrators that traverse stratified waters of the upper pycnocline. As shown in the acoustic measurements of Kunze et al. (Kunze et al., 2006), krill travel approximately 100 m during vertical migrations in Saanich Inlet. Studies of some zooplankton species indicate that they undergo even more dramatic diel migrations, moving between 500 m and the surface daily (Wiebe et al., 1979). Diel vertical migrations are recognized and accepted as a global biological phenomenon and include plentiful and globally distributed krill, copepods and some species of gelatinous zooplankton and fish (Dewar et al., 2006). Therefore, based on our understanding of mixing mechanisms, body morphologies, swimming modes and body orientation, combined with our knowledge of vertically migrating populations of animals, we expect that copepods, krill and some species of gelatinous zooplankton and fish are potentially strong sources of biogenic mixing.

Scaling up from individual animals to aggregations

The concerted swimming of multiple animals, or schooling, may be more effective at producing large-scale mixing than that of a single individual. Turbulence in stratified flows decays with a characteristic time scale. In aggregations, turbulence will not have sufficient time to decay before being encountered by another organism, increasing turbulence time and length scales (Gregg and Horne, 2009). From inspection of turbulence alone, the dynamics of the mixing process change as the number of swimming animals is increased. To understand mixing generated by aggregations of swimming animals, it is insufficient to extrapolate single-animal results to the aggregation. However, by experimentally investigating single-organism dynamics and developing computational models and tools to investigate multi-organism dynamics, we can characterize important mixing parameters as a function of the organism and size of the aggregation. The recently developed statistical methods for analyzing multiple-animal interactions (Thiffeault and Childress, 2010; Lin et al., 2011) are a powerful tool, and by including animal behavior (i.e. biasing the motion of bodies in the vertical direction), hydrodynamics and population characteristics we can more adequately quantify mixing parameters. To be certain, we need to expand our computational capabilities beyond unstratified, potential or Stokes flow cases since most vertically migrating organisms reside in intermediary Reynolds number ranges (between potential and Stokes flow) in the stratified ocean.

Measuring biogenic inputs to ocean mixing

The identification of potential biogenic mixers is partly based on reported marine animals' abundance and migration distances gathered by indirect methods (Huntley and Zhou, 2004; Dewar et al., 2006). Indirect methods of field sampling include acoustic measurements (to locate populations of swimming animals in the water column) and net tows (which provide information on the identity of the migrating swimmers). However, powerful swimmers are able to evade nets and often these measurements do not adequately represent animal abundance in aggregations (Lawson, 2006). Therefore, oceanographers are employing additional methods (i.e. remotely operated vehicles, underwater cameras and scuba observations) to collect *in situ* data on animal packing density, body orientation, organism size and swimming behavior (Nicol and Brierley, 2010). The conditions (i.e. weather, surface temperatures, predator abundance, etc.) that are favorable to vertical migrations are poorly understood; this information is needed to better predict the occurrence of vertical migrations, which may correlate with strong biogenic mixing events.

Finally, biogenic mixing is challenging to measure because of the limitations posed by current oceanographic technologies. Measurements of physical characteristics in the ocean need to be conducted at temporal and spatial scales relevant to the mixing process. Without this capability, assumptions are often invoked that may not be appropriate for the mixing process. A common assumption made during measurements of oceanic mixing is that turbulence is isotropic and homogeneous. Recall that evoking this assumption only requires the measurement of the velocity gradient in one direction to fully characterize turbulent dissipation (Eqn 4). However, biogenic turbulence is produced locally (within the boundary layer and wake of each individual organism) and is therefore inhomogeneous (Lorke and Probst, 2010). If an invalid assumption is invoked in the determination of any turbulence parameter (i.e. dissipation), error will propagate to other quantities (i.e. mixing efficiency and diffusivity; Eqns 5 and 7), leading to large measurement uncertainties. Arguments such as these motivate the design and application of optical techniques [i.e. stereoscopic and holographic particle image velocimetry (Steinbuck et al., 2010;

Zarzecki and Diez, 2008)] that will provide non-invasive measurements of the full three-dimensional flow field induced by swimming aggregations.

Understanding the big picture: biogenic mixing and global climate

If global estimates of biogenic mixing in the ocean are indeed near 1 TW [as suggested in some of the biogenic mixing literature (Dewar et al., 2006; Katija and Dabiri, 2009)], then the inclusion of biogenic mixing to ocean and climate models is required to adequately represent global dynamics and inform the discussion on climate change. Accordingly, measurements of biogenic mixing must use similar metrics established in these computational models. Quantifying dissipation rate (ε) to characterize a mixing process is insufficient and a mixing efficiency should also be used (Visser, 2007). Measurements of microstructure velocity profiles and physical properties of the fluid (conductivity, temperature and salinity) are required to find the mixing efficiency (Γ, Eqn 5). Although measurements of mixing efficiency by a swimming organism have been conducted, with the result being comparable to other mixing processes (Rehmann and Koseff, 2004; Strang and Fernando, 2001; Linden and Redondo, 1991; Strang and Fernando, 2001; Katija and Dabiri, 2009), further observations are needed. The diffusivity (K_ρ, Eqn 7), another parameter that is often quantified in the oceanographic literature, has been approximated in numerical studies of biogenic mixing (Thiffeault and Childress, 2010; Lin et al., 2011), and experiments are needed to confirm these findings.

Because biogenic mixing may contribute to providing the nutrients to maintain or enhance biological productivity in nutrient-depleted regions of the ocean, researchers are currently looking into whether biogenic fertilization of feeding grounds occurs and how it may affect ocean chemistry (Nicol et al., 2010; Iriarte et al., 2011). Another area for future study [addressed briefly by Dewar et al. (Dewar et al., 2006)] is to understand the effect, if any, that overfishing has had on climate. From estimates of biomass and the total loss of metabolic requirements, overfishing of trophic levels 4 and 5 (i.e. whales, tuna and other pelagic fish) has led to the estimated loss of 32 GW of mixing power (Dewar et al., 2006). This energetic loss is comparable to twice removing the mixing generated in the ocean by the Hawaiian Islands (Egbert and Ray, 2000; Dewar et al., 2006). Although these estimates and concepts are intriguing, multidisciplinary teams of biologists, ecologists, oceanographers (both biological and physical) and engineers are needed to elucidate biogenic mixing in the ocean.

References

Ardekani, A. M. and Stocker, R. (2010). Stratlets: low Reynolds number point-force solutions in a stratified fluid. *Phys. Rev. Lett.* **105**, 084502.

Barrett, T. K. and Van Atta, C. W. (1990). Experiments on the inhibition of mixing in stably stratified decaying turbulence using laser Doppler anemometry and laser-induced fluorescence. *Phys. Fluids* **3**, 1321-1332.

Brennen, C. and Winet, H. (1977). Fluid mechanics of propulsion by cilia and flagella. *Ann. Rev. Fluid Mech.* **9**, 339-398.

Britter, R. E. (1985). Diffusion and decay in stably stratified turbulent flows. In *Turbulence and Diffusion in Stable Environments* (ed. J. C. R. Hunt), pp. 3-13. Oxford: Clarendon Press.

Bryden, H. L. and Imawaki, S. (2001). Ocean heat transport. In *Ocean Circulation and Climate: Observing and Modeling the Global Ocean* (ed. G. Siedler and J. Church), pp. 455-474. San Diego, CA: Academic Press.

Catton, K. B., Webster, D. R., Kawaguchi, S. and Yen, J. (2011). The hydrodynamic disturbances of two species of krill: implications for aggregation structure. *J. Exp. Biol.* **214**, 1845-1856.

Chwang, A. T. and Wu, T. Y. (1975). Hydromechanics of low Reynolds number flow. Part 2. Singularity method for Stokes flows. *J. Fluid Mech.* **67**, 787-815.

Crimaldi, J. P. (2008). Planar laser induced fluorescence in aqueous flows. *Exp. Fluids* **44**, 851-863.

Dabiri, J. O. (2010). Role of vertical migration in biogenic ocean mixing. *Geophys. Res. Lett.* **37**, L11602.

Dahm, W. J. A. and Dimotakis, P. E. (1987). Measurements of entrainment and mixing in turbulent jets. *AIAA J.* **25**, 1216-1223.

Darwin, C. (1953). Note on hydrodynamics. *Proc. Camb. Phil. Soc.* **49**, 342-354.

De Robertis, A., Schell, C. and Jaffe, J. S. (2003). Acoustic observations of the swimming behavior of the euphausiid *Euphausia pacifica*. *J. Mar. Sci.* **60**, 885-898.

Dewar, W. K., Bingham, R. J., Iverson, R. L., Nowacek, D. P., St Laurent, L. C. and Wiebe, P. H. (2006). Does the marine biosphere mix the ocean? *J. Mar. Res.* **64**, 541-561.

Dimotakis, P. E. (2005). Turbulent mixing. *Ann. Rev. Fluid Mech.* **37**, 329-356.

Eames, I. (2003). The concept of drift and its application to multiphase and multibody problems. *Proc. R. Soc. Lond. A* **361**, 2951-2965.

Eames, I. and Bush, J. W. M. (1999). Longitudinal dispersion of bodies fixed in a potential flow. *Proc. R. Soc. Lond. A* **455**, 3665-3686.

Eames, I., Gobby, D. and Dalziel, S. B. (2003). Fluid displacement by Stokes flow past a spherical droplet. *J. Fluid Mech.* **485**, 67-85.

Eckart, C. (1948). An analysis of the stirring and mixing processes in incompressible fluids. *J. Mar. Res.* **7**, 265-275.

Egbert, G. and Ray, R. (2000). Significant dissipation of tidal energy in the deep ocean inferred from satellite altimeter data. *Nature* **405**, 775-778.

Farmer, D. D., Crawford, G. B. and Osborn, T. R. (1987). Temperature and velocity microstructure caused by swimming fish. *Limnol. Oceanogr.* **32**, 978-983.

Fernando, H. J. S. (1991). Turbulent mixing in stratified fluids. *Ann. Rev. Fluid Mech.* **23**, 455-493.

Ferrari, R. and Wunsch, C. (2009). Ocean circulation kinetic energy: reservoirs, sources, and sinks. *Ann. Rev. Fluid Mech.* **41**, 253-282.

Ferrari, R. and Wunsch, C. (2010). The distribution of eddy kinetic and potential energies in the global ocean. *Tellus* **62**, 92-108.

Ferrier, A. J., Funk, D. R. and Roberts, P. J. W. (1993). Application of optical techniques to the study of plumes in stratified fluids. *Dyn. Atmos. Oceans* **20**, 155-183.

Garrett, C. (1979). Mixing in the ocean interior. *Dyn. Atmos. Oceans* **3**, 239-265.

Gregg, M. C. (1987). Diapycnal mixing in the thermocline. *J. Geophys. Res.* **92**, 5249-5286.

Gregg, M. C. and Horne, J. K. (2009). Turbulence, acoustic backscatter, and pelagic nekton in Monterey Bay. *J. Phys. Oceanogr.* **39**, 1097-1114.

Huntley, M. E. and Zhou, M. (2004). Influence of animals on turbulence in the sea. *Mar. Ecol. Prog. Ser.* **273**, 65-79.

Iriarte, J. L., Gonzalez, H. E. and Nahuelhual, L. (2011). Response to "Whales might also be an important component in Patagonian fjord ecosystems". *AMBIO* **40**, 106-107.

Ivey, G. N. and Imberger, J. (1991). On the nature of turbulence in a stratified fluid. Part I: the energetics of mixing. *J. Phys. Oceanogr.* **21**, 650-658.

Ivey, G. N. and Nokes, R. I. (1989). Vertical mixing due to the breaking of critical internal waves on sloping boundaries. *J. Fluid Mech.* **204**, 479-500.

Jiang, H. and Strickler, J. R. (2007). Copepod flow modes and modulation: a modeling study of the water currents produced by an unsteadily swimming copepod. *Philos. Trans. R. Soc. B* **362**, 1959-1971.

Katija, K. (2010). *Effects of In Situ Animal–Fluid Interactions on Transport and Mixing*. PhD thesis, California Institute of Technology.

Katija, K. and Dabiri, J. O. (2008). In situ field measurements of aquatic animal-fluid interactions using a self-contained underwater velocimetry apparatus (SCUVA). *Limnol. Oceanogr. Meth.* **6**, 162-171.

Katija, K. and Dabiri, J. O. (2009). A viscosity-enhanced mechanism for biogenic ocean mixing. *Nature* **460**, 624-626.

Katija, K., Colin, S. P., Costello, J. H. and Dabiri, J. O. (2011). Quantitatively measuring *in situ* flows using a self-contained velocimetry apparatus (SCUVA). *J. Vis. Exp.* **56**, e2615.

Koochesfahani, M. M. and Dimotakis, P. E. (1986). Mixing and chemical reactions in a turbulent liquid-mixing layer. *J. Fluid Mech.* **170**, 83-112.

Kunze, E. and Dower, J. F. (2007). Kunze and Dowers' response to Tom P. Rippeth et al. *Science*, available at www.sciencemag.org/content/313/5794/1768/reply#sci_el_10045.

Kunze, E., Dower, J. F., Beveridge, I., Dewey, R. and Bartlett, K. P. (2006). Observations of biologically generated turbulence in a coastal inlet. *Science* **313**, 1768-1770.

Lampert, W. (1989). The adaptive significance of diel vertical migration of zooplankton. *Funct. Ecol.* **3**, 21-27.

Lawson, G. L. (2006). *Distribution, Patchiness, and Behavior of Antarctic Zooplankton, Assessed Using Multi-frequency Acoustic Techniques*. PhD thesis, Massachusetts Institute of Technology and the Woods Hole Oceanographic Institution.

Ledwell, J. R., Watson, A. J. and Clifford, S. L. (1993). Evidence for slow mixing across the pycnocline from an open-ocean tracer-release experiment. *Nature* **364**, 701-703.

Leshansky, A. M. and Pismen, L. M. (2010). Do small swimmers mix the ocean? *Phys. Rev. E* **82**, 1-4.

Lin, Z., Thiffeault, J. L. and Childress, S. (2011). Stirring by squirmers. *J. Fluid. Mech.* **669**, 167-177.

Linden, P. F. (1979). Mixing in stratified fluids. *Geophys. Astrophys. Fluid Dyn.* **13**, 3-23.

Linden, P. F. and Redondo, J. M. (1991). Molecular mixing in Rayleigh-Taylor instability. Part I: global mixing. *Phys. Fluids* **3**, 1269-1277.

List, E. J. (1971). Laminar momentum jets in a stratified fluid. *J. Fluid Mech.* **45**, 561-574.

Lorke, A. and Probst, W. N. (2010). *In situ* measurements of turbulence in fish shoals. *Limnol. Oceanogr.* **55**, 354-364.

MacKenzie, B. and Leggett, W. (1993). Wind-based models for estimating the dissipation rates of turbulent energy in aquatic environments: empirical comparison. *Mar. Ecol. Prog. Ser.* **94**, 207-216.

Madin, L. P. (1982). Production, composition, and sedimentation of salp fecal pellets in oceanic waters. *Mar. Biol.* **67**, 39-45.

Moum, J. N. and Smyth, W. D. (2001). Upper ocean mixing processes. In *Encyclopedia of Ocean Sciences*, Vol. 6 (ed. S. A. Thorpe and K. K. Turekian), pp. 3093-3100. New York: Academic Press.

Munk, W. H. (1966). Abyssal recipes. *Deep Sea Res. Oceanogr. Abs.* **13**, 707-730.

Munk, W. H. and Wunsch, C. (1998). Abyssal recipes II: energetics of tidal and wind mixing. *Deep Sea Res. Part I* **45**, 1977-2010.

Nicol, S. and Brierley, A. S. (2010). Through a glass less darkly-new approaches for studying the distribution, abundance and biology of Euphausiids. *Deep Sea Res. Part II* **57**, 496-507.

Nicol, S., Bowie, A., Jarman, S., Lannuzel, D., Meiners, K. M. and van der Merwe, P. (2010). Southern Ocean iron fertilization by baleen whales and Antarctic krill. *Fish Fish.* **11**, 203-209.

Rehmann, C. R. and Koseff, J. R. (2004). Mean potential energy change in stratified grid turbulence. *Dyn. Atmos. Oceans* **37**, 271-294.

Rippeth, T. P., Gascoigne, J., Green, J. A. M., Inall, M. E., Palmer, M. R., Simpson, J. H. and Wiles, P. J. (2007). Turbulent dissipation of coastal seas. *Science*, available at www.sciencemag.org/content/313/5794/1768/reply#sci_el_10045.

Rousseau, S., Kunze, E., Dewey, R., Bartlett, K. and Dower, J. (2010). On turbulence production by swimming marine organisms in the open ocean and coastal waters. *J. Phys. Oceanogr.* **6**, 2107-2121.

Rowe, G. T. and Staresinic, N. (1979). Sources of organic matter to the deep-sea benthos. *Ambio Spec. Rep.* **6**, 19-23.

St Laurent, L. and Garrett, C. (2002). The role of internal tides in mixing the deep ocean. *J. Phys. Oceanogr.* **32**, 2882-2899.

St Laurent, L. and Simmons, H. (2006). Estimates of power consumed by mixing in the ocean interior. *J. Climate* **19**, 4877-4890.

Steinbuck, J. V., Roberts, P. L. D., Troy, C. D., Horner-Devine, A. R., Simonet, F., Uhlman, A. H., Jaffe, J. S., Monismith, S. G. and Franks, P. J. S. (2010). An autonomous open-ocean stereoscopic PIV profiler. *J. Atmos. Ocean. Tech.* **27**, 1362-1380.

Stich, H. and Lampert, W. (1981). Predator evasion as an explanation of diurnal vertical migration by zooplankton. *Nature* **293**, 396-398.

Strang, E. J. and Fernando, H. J. S. (2001). Entrainment and mixing in stratified shear flows. *J. Fluid Mech.* **428**, 349-386.

Subramanian, G. (2010). Viscosity-enhanced bio-mixing of the oceans. *Curr. Sci.* **98**, 1103-1108.

Sumich, J. L. and Morrissey, J. F. (2004). *Introduction to the Biology of Marine Life*. Sudbury: Jones and Bartlett Publishers.

Taylor, G. I. (1951). Analysis of the swimming of microscopic organisms. *Proc. R. Soc. Lond. A* **209**, 447-461.

Tennekes, H. and Lumley, J. L. (1972). *A First Course in Turbulence*. Cambridge, MA: MIT Press.

Thiffeault, J. L. and Childress, S. (2010). Stirring by swimming bodies. *Phys. Lett. A* **374**, 3487- 3490.

Thorpe, S. A. (2004). Recent developments in the study of ocean turbulence. *Annu. Rev. Earth Planet. Sci.* **32**, 91-109.

Thorpe, S. A. (2005). *The Turbulent Ocean.* Cambridge: Cambridge University Press.

Videler, J. J., Stamhuis, E. J., Müller, U. K. and van Duren, L. A. (2002). The scaling and structure of aquatic animal wakes. *Integr. Comp. Biol.* **42**, 988-996.

Visser, A. W. (2007). Biomixing of the oceans? *Science* **316**, 838-839.

Wiebe, P., Madin, L., Haury, L., Harbison, G. and Philbin, L. (1979). Diel vertical migration by *Salpa aspera* and its potential for large-scale particulate organic-matter transport to the deep-sea. *Mar. Biol.* **53**, 249-255.

Willert, C. E. and Gharib, M. (1991). Digital particle image velocimetry. *Exp. Fluids* **10**, 181-193.

Wilson, R. W., Millero, F. J., Taylor, J. R., Walsh, P. J., Christensen, V., Jennings, S. and Grosell, M. (2009). Contribution of fish to the marine inorganic carbon cycle. *Science* **323**, 359-362.

Wunsch, C. and Ferrari, R. (2004). Vertical mixing, energy and the general circulation of the oceans. *Ann. Rev. Fluid Mech.* **36**, 281-314.

Zarzecki, M. and Diez, F. J. (2008). High speed micro holographic PIV measurements of microorganisms. *ASME Conference Proc.* 2008 **48715**, 2029-2033.