PERSPECTIVE

Oxygen, animals and aquatic bioturbation: An updated account

1 | INTRODUCTION

The modern biosphere owes its idiosyncratic expression to the activities of oxygen-metabolizing organisms, especially animals and eukaryotes (Butterfield, 2011). And with a permanently oxygenated atmosphere established during the ~2.4 Ga Great Oxidation Event (GOE), the stage was set for their early evolutionary debut. Curiously, however, eukaryotic organisms do not appear in the fossil record for another ~800 million years and animals for another billion years beyond that (Butterfield, 2015a). Since oxygen availability determines the activity of aerobic organisms, there is a long-standing view that, although free oxygen was certainly present through these extended intervals, it remained persistently below levels necessary to support multicellular animals (Nursall, 1959)—or if not animals per se, at least organ-grade bilaterians (Planavsky et al., 2014)—or if not bilaterians per se, at least the large carnivorous bilaterians capable of driving a major evolutionary radiation like the Cambrian explosion (Sperling et al., 2013). Such "permissive environment" causality provides an intuitively satisfying explanation for the delayed arrival of Phanerozoic-style ecosystems and is supported empirically by geochemical evidence for the expanding oxygenation of mid-late Neoproterozoic oceans (Cole et al., 2016; Hardisty et al., 2017; Och & Shields-Zhou, 2012).

Even so, there are problems with the oxygen-limitation hypothesis, not least the conspicuous monophyly of animals and eukaryotes (vs. the polyphyletic radiations expected of environmental threshold models), the curious absence of Proterozoic land plants (despite a seemingly optimal high pCO$_2$/low pO$_2$ Proterozoic atmosphere) and the fundamentally non-uniformitarian nature of the pre-metazoan biological pump (precluding any simple extrapolation of atmospheric composition from marine redox signatures) (Butterfield, 2009). Moreover, a wide range of extant animals are known to tolerate, even habitually occupy, conspicuously hypoxic environments (Childress & Seibel, 1998; Levin, 2003; Mills et al., 2014; Sperling, Knoll, & Girguis, 2015). In this light, there are clear grounds for considering an alternative, "permissive development" model, where the limiting factor in early animal evolution lies in the complex gene regulatory networks necessary to differentiate and integrate their constituent parts—with the emergent new ecologies driving biogeochemical and macroevolutionary perturbations "from the top down" (e.g., Butterfield, 2009, 2011, 2015b; Canfield & Farquhar, 2009; Erwin & Tweedt, 2012; Lenton, Boyle, Poulton, Shields-Zhou, & Butterfield, 2014).

To be sure, large multicellular aerobes consume more oxygen than their unicellular counterparts on a per capita basis, and they face obvious surface area to volume challenges in terms of diffusive gas exchange. At the same time, however, multicellularity and large

size introduce an entirely novel range of fluid-dynamic properties and ecophysiological opportunities to such organisms, not least an unparalleled capacity to circulate and swim through water. In this essay, I explore the role that aquatic propulsion has played in early animal evolution and its geobiological implications for marine oxygenation.

2 | THE UNICELLULAR TO MULTICELLULAR TRANSITION

The last eukaryotic common ancestor (LECA) was a flagellated amoeboid cell with an essentially full complement of modern eukaryotic features, including oxygen-metabolizing mitochondria (Koonin, 2010). Continuous recovery of diagnostically eukaryotic microfossils back to at least the late Palaeoproterozoic (>1,630 Ma) points to the uninterrupted presence of oxygenated shallow-water environments through this same interval (Butterfield, 2015a), consistent with contemporaneous redox geochemical signatures (Lyons, Reinhard, & Planavsky, 2014). Although neither of these proxies provides a quantitative measure of free oxygen, the physiology of unicellular eukaryotes presents a useful datum for assessing the environmental "permissibility" of evolving multicellular counterparts.

Unicellular organisms conduct their gas-exchange via simple transmembrane diffusion, afforded by their high surface area to volume ratios. Such facility, however, is progressively compromised as cells are joined together in three dimensions, leading, in principle, to a fundamental impasse in the evolution of multicellularity (Catling, Glein, Zahnle, & McKay, 2005). As oxygen demand outpaces diffusive delivery, the only obvious fix is to increase local concentration gradients—hence the attraction of atmospheric oxygen concentration being the first-order control on early animal evolution. What has been left out of these simple models, however, is the fact that eukaryotic cells are primitively flagellated and that the fluid flow—advection—generated by beating flagella/cilia fundamentally changes the nature of transmembrane gas exchange.

In fluid-dynamic terms, the degree to which the solute concentrations of a particular system are controlled by diffusion vs. advection is described by its (dimensionless) Péclet number: $Pe = UL/D$, where U is fluid velocity, L the relevant length-scale (size), and D the rate of diffusion. $Pe < 1$ indicates diffusion-dominated transport, vs. advection-dominated transport for $Pe > 1$ (Figure 1a). Velocity and length-scale are also the parameters that determine the nature of local fluid flow, quantified by the system's (similarly dimensionless) Reynolds number: $Re = UL/\nu$, where ν is the kinematic viscosity of the medium. $Re < 1$ indicates a predominance of viscous or frictional forces, vs.
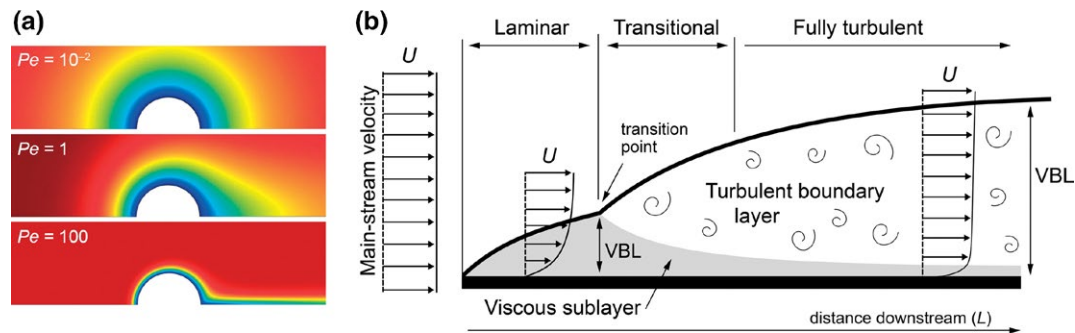
FIGURE 1 The effects of fluid flow and body size on diffusion gradients, turbulence and gas-exchange capacity (current flow from left to right). (a) Calculated concentration fields surrounding a body/cell exposed to differing flow at low-Reynolds numbers ($Re \ll 1$); the associated Péclet numbers (Pe) reflect the marked effect of fluid flow on diffusion gradients and advective exchange. Collective flagellar beating in multicellular eukaryotes is one means of generating such flow. Figure modified from Langlois et al. (2009), with permission of AME. (b) Schematic view of the velocity boundary layer (VBL) under higher Re conditions—illustrating the relationship between fluid velocity (U), length-scale (L) and turbulence on a smooth flat plate. Although the viscous sublayer (and associated diffusion boundary layer) initially thickens in the direction of flow, it collapses in the transition to turbulent conditions—entraining yet more water into the turbulently mixed VBL. For tethered or self-propelled cnidarian-grade animals, higher velocity and/or larger size dramatically enhance gas-exchange capacity. Figure redrawn from Hurd (2000)

inertia-dominated forces for $Re > 1$. Because the diffusivities (D) of molecules like O_2 and CO_2 are orders of magnitude smaller than the kinematic viscosity (ν) of water, even small increases in flow (and/or size) have a profoundly greater effect on Pe than Re. And because the collectivized activity of multiple flagellated cells increases both flow velocity (U) and organismal size (L), Péclet numbers rise precipitously in the transition from unicells to multicellular colonies (Short et al., 2006). In other words, localized concentration gradients can be dramatically enhanced by what might seem to be trivial levels of fluid flow (in terms of Re)—independently of absolute reservoir concentrations (Figure 1a). Simply by arranging themselves into colonies, flagellated cells gain access to fundamentally greater levels of gas exchange than would be possible in isolation. Far from being frustrated by low levels of oxygen, then, multicellularity presents a unique opportunity to escape the "tyranny of diffusion" (Goldstein, 2015; Roper, Dayel, Pepper, & Koehl, 2013; Solari, Kessler, & Goldstein, 2007). With a continuous 1,600+ million-year fossil record of unicellular aerobic eukaryotes, there has easily been more than enough free oxygen to support multicellular counterparts over this same interval.

3 | COLLECTIVE PROPULSION

Above a certain size, the rapid increase in solute transport per unit area in colonial flagellates levels off—at a diameter of around 50–100 μm in the case of volvocalean algae (Short et al., 2006). Even so, the collectivized flagellar activity of larger forms continues to advect the surface boundary layer, with Péclet numbers of several hundred easily keeping pace with the physiological requirements of (hollow) colonies of up to 50,000 cells. Flagella-induced flows at larger length-scales appear to be limited to metazoans and are particularly well developed in basal clades lacking differentiated respiratory or circulatory organ-systems. The ciliated epidermis of corals, for example, drives counter-rotating

vortices that extend outward two orders of magnitude further than the individual ciliary impellers, vigorously stirring boundary-layer water and substantially enhancing solute exchange (Pe ~500–6,000) (Shapiro et al., 2014). Such self-generated circulation can be essential for the viability of juveniles and other individuals trapped in low-Re, boundary-layer conditions.

Collectivized ciliary flow clearly needs to be factored into models of evolving multicellular eukaryotes, but on its own offers little respite from low-Reynolds numbers and the "tyranny of viscosity." Spherical Volvox colonies do not have an inertial coasting mode, and the surficial vortices produced by corals do not add up to anything more than broader fields of viscous laminar vortices: when these cilia stop beating, so does any associated motion. But there are ways of escaping such hydrodynamic constraints. Ciliary banding and dynamically tuned morphologies, for example, bring higher Re dynamics into play (Emlet, 1991; Gilpin, Prakash, & Prakash, 2017; Sleigh, 1989), particularly when accompanied by larger body size. By far, the most exotic application of cilia-based propulsion is found in ctenophores, where the assembly of exceptionally long cilia into macroscopic comb-plates and comb-rows allows decimetre-sized individuals to swim at speeds greater than 5 cm/s (Re ~6,000) (Matsumoto & Hamner, 1988; Tamm, 2014). With the transition between laminar and turbulent flow occurring at Reynolds numbers of ~2,000 (Vogel, 1981), these jelly-based animals have actively propelled themselves into a high-Pe system where diffusive boundary layers are compressed, turbulent boundary layers expanded, and gas exchange is dominated by advective mixing (Figure 1b).

A further range of fluid-dynamic properties emerge when collectivized ciliary/flagellar flows are contained within internal piping systems (LaBarbera, 1990; Sleigh, 1989; Vogel, 1981). All of the principal clades of cnidarians, for example, move fluids through cilia-lined gastrovascular canals and/or stolons, at speeds of up to a millimetre per second (Harmata et al., 2013; Parrin, Netherton, Bross, McFadden,

& Blackstone, 2010; Southward, 1955). In terms of raw propulsion, however, there is little to compete with the aquiferous system of sponges. In all but the simplest sponges, primary flow derives from the collectivized activity of flagellated choanocyte cells housed within individual choanocyte chambers—each of which is connected to a hydrodynamically tuned system of inhalant and exhalent canals (Larsen & Riisgård, 1994; Riisgård, Thomassen, Jakobsen, Weeks, & Larsen, 1993; Vogel, 1977). With a cubic millimetre of sponge choanoderm containing between 3,000 and 12,000 individual chambers (each containing 60–300 choanocytes), this massively parallel pumping apparatus can yield exhalent flow velocities of up to 25 cm/s (Leys et al., 2011), and correspondingly high throughput: up to 40 $m^3 m^{-2} day^{-1}$ reported from Jamaican reefs (Reiswig, 1974), and an extraordinary 108–250 $m^3 m^{-2} day^{-1}$ from hexactinellid reefs in the Straits of Georgia (Kahn, Yahel, Chu, Tunnicliffe, & Leys, 2015).

Ciliary pumps are also employed by a variety of suspension-feeding bilaterians, with those of mussels (epifaunal bivalves) and ascidians (epifaunal tunicates) approaching levels of performance similar to that of sponges (Petersen, 2007; Riisgård et al., 2011). Not surprisingly, all such pumps are scale-dependent, only working in larger multicellular organisms where the collective effects yield inertial jets of sufficient velocity to separate exhalent from inhalant water. Grünbaum, Eyre, and Fogelson (1998) estimate the critical transition to occur at a body size of around 200–300 μm, broadly equivalent to the ontogenetic shift from externally ciliated larvae to internally circulating juveniles/adults seen in many suspension-feeding groups. Large size is also a prerequisite for exploiting Bernoulli and associated traction flow phenomena (Leys et al., 2011; Riisgård et al., 1993; Vogel, 1977). Indeed, while individual cilia/flagella clearly serve as the primary impellers in all of these devices, the pumps themselves are a fundamentally more sophisticated thing (Riisgård & Larsen, 2001), only working in the context of the macroscopic, three-dimensional superstructures in which they are housed.

In the context of early animal evolution, the emergence of high Re/Pe fluid-dynamic properties from these constructional and scaling innovations will have introduced early sponge-grade forms to revolutionary new styles of both gas exchange and feeding (de Goeij et al., 2013; Mills & Canfield, 2016). Along with the pronounced hypoxia tolerance seen among modern sponges (e.g., Hoffmann, Larsen, Rapp, & Osinga, 2005; Hoffmann et al., 2008; Mills et al., 2014; Sperling et al., 2015), this capacity for quantitative pumping makes oxygen (or food) limitation an unlikely factor in the evolutionary first appearance of the clade. Rather, the challenge appears to lie in the design and assembly of the machine itself.

4 | MUSCLES AND SKELETON

Sponges and ctenophores are remarkable organisms, but they also mark limits of what can be moved by means of undulatory cilia and flagella. Fundamentally more sophisticated modes of propulsion are possible using linearly contractile muscle—from the viscous pulsatory swimming of cnidarian larvae ($Re < 100$) to copepod escape jumps at 20 cm/s (Re ~300), and the 1,000 cm/s swimming of sperm whales (Re ~300,000,000) (Nagata, Morandini, Colin, Migotto, & Costello, 2016; Vogel, 1981). The key to this functional versatility lies in the essentially limitless scalability of differentiated muscle tissue, combined with the myriad mechanical devices to which it can be attached. In the case of skeletal/striated muscle, the serially repeated sliding-filament motors/sarcomeres of an individual myofibril yield a mechanism in which both contraction speed and total travel scale with muscle length, while power scales with muscle mass (cross-sectional area).

The evolution of muscle and muscular propulsion will have faced numerous challenges, but elevated metabolic demand was not one of them. There is no measurable discontinuity between the mass-specific force output of cilia- and muscle-based motors (Marden, 2005), and mass-specific metabolic rate typically scales negatively (Kleiber's "law")—rarely more than isometrically—with body size (Glazier, 2006). In other words, larger multicellular organisms will almost always have a lower metabolic demand than an equivalent biomass of smaller or unicellular ones. Moreover, in its simplest cnidarian-grade form, muscle tissue is both epithelial and just a single cell thick, leaving every cell effectively in contact with gas-exchanging water. Under such conditions, the metabolic returns from muscular contraction can be particularly favourable. In xeniid soft corals, for example, rhythmic pulsation of cm-sized polyps is accompanied by order-of-magnitude increases in the photoendosymbiont productivity, a direct consequence of the increased turbulence and associated gas-exchange capacity (Kremien, Shavit, Mass, & Genin, 2013). Similar contractions in the upside-down jellyfish *Cassiopea* drive flows of up to 10 cm/s (Re ~450), with individual adults pumping up to 30 L an hour (Hamlet, Santhanakrishnan, & Miller, 2011; Santhanakrishnan, Dollinger, Hamlet, Colin, & Miller, 2012)—much of which passes through underlying sediments to entrain otherwise unavailable nutrients (Jantzen, Wild, Rasheed, El-Zibdah, & Richter, 2010). Muscular contraction is also the means by which almost all animals swim, opening up the pelagic realm to metazoan occupation.

Unlike ciliated cells, contractile muscle only works in the context of a corresponding skeleton, adding potential metabolic and constructional costs to the equation. Not all skeletons are equally expensive, however, and in the case of "jellyfish" (ctenophores and cnidarian medusae), the supporting structure is composed of mesoglea, a water-based material that delivers most of the fluid-dynamic advantages of large size at trivial cost. This "faking giant" strategy (Acuña, López-Urrutia, & Colin, 2011) yields Reynolds and Péclet numbers an order of magnitude higher than found in non-gelatinous organisms of similar carbon content, and mass-specific metabolic rates as much as two orders of magnitude lower than in non-gelatinous organisms of similar size (Pitt et al., 2013); it also accounts for the exceptionally high growth rates of jellyfish—via size-dependent increases in prey encounter—and the lowest known cost of transport in any animal (Gemmell et al., 2013). For medusae regularly encountering hypoxic conditions, the mesoglea is also used as a rechargeable oxygen reservoir (Thuesen et al., 2005).

The only construction material cheaper than mesoglea is water itself, and a variety of invertebrates incorporate environmental water

to form replaceable hydrostatic skeletons (Chapman, 1958). Among benthic cnidarians, both solitary actiniarians (sea anemones) and colonial pennatulatceans (sea pens/pansies) pump seawater into a semi-isolated gastrovascular cavity to serve as the fluid antagonist against which their variously oriented muscles can act. The range of emergent sizes, shapes and behaviours is enormous, even within single individuals, and carries important implications for metabolic gas exchange (Batham & Pantin, 1950). On exposure to hypoxic conditions, for example, the infaunal actiniarian *Haloclava producta* can increase its body volume by an order of magnitude, dramatically expanding, and thinning, its exposed surface area (Sassaman & Mangum, 1972). In combination with benthic tethering and ambient currents, such inflationary habits are accompanied by large increases in drag-induced *Re* and external gas exchange (Hurd, 2000; Koehl, 1984; Patterson & Sebens, 1989). By the same token, there are no obvious grounds for invoking oxygen limitation as an impediment to the early evolution of cnidarian-grade metazoans (Sperling et al., 2015): once oxygen levels were sufficient to sustain populations of unicellular eukaryotes, their assembly into larger sheet-like epithelia (>*L*) could only have enhanced gas-exchanging capacity (Figure 1b), particularly in the context of macroscopic movement (>*L* and >*U*) and an ability to control three-dimensional form.

5 | BILATERIAN PROPULSION AND CARNIVORY

Such surficial cnidarian-grade gas exchange is of course rapidly overwhelmed in the transition from two-dimensionally constructed cnidarians to three-dimensional bilaterians. Almost universally, this additional challenge has been met by the incorporation of an internal circulatory system linked to expanded external gas-exchanging organs, an anatomical upgrade fully within the developmental capacity of triploblastic bilaterians. Even so, Catling et al. (2005) have argued that the evolution of a closed pulsatory circulatory system would have been frustrated by a mechanical prerequisite for large body size—which would have been frustrated in turn by a prerequisite for elevated levels of atmospheric oxygen. As demonstrated above, however, there are no such size constraints in the case of sponge- or cnidarian-grade multicellularity, and there is no shortage of alternative means for driving internal circulation on smaller scales—from the (cilia-powered) gastrovascular and water-vascular systems of cnidarians/echinoderms to the (muscle-powered) vascular peristalsis of annelids, and the open blood-vascular systems of arthropods and molluscs (e.g., Harmata et al., 2013; Johansen & Vadas, 1967; Monahan-Earley, Dvorak, & Aird, 2013; Southward, 1955).

The evolution of bilaterian organ-systems clearly introduced a wealth of new physiological and ecological opportunities, but these did not come for free. Skeletons at this level become increasingly expensive, and the propulsion of larger three-dimensional bodies at higher velocities will ultimately require greater resources. Whether such developments are economically feasible depends not only on availability of oxygen and fuel, but also the efficiency with which they can be converted to pumping and propulsive devices. Useful analogies can be

found in more recent technological innovations. Steam engines, for example, revolutionized 18th-century industry not because of any new sources of fuel (or oxygen), but rather the dramatic increases in work output — most notably following Watts' addition of an external condenser to the pre-existing Newcomen engine. Paradoxically, it was this doubling of efficiency that drove the ever greater consumption and applications of coal through the 19th century (Jevons, 1865)—leading to the discovery of yet further efficiencies and novel technologies.

The question, then, is whether the timing of early bilaterian evolution was dictated by absolute levels of resources, or the anatomical and physiological sophistication necessary to exploit what was already there. If sufficient oxygen was available to support a cnidarian-grade ancestor, would there have been any additional energetic barriers to the evolution of respiration-enhancing organs or organ-systems along the bilaterian stem lineage? Certainly the diverse adaptions of bilaterians to hypoxia seen in modern oxygen minimum zones (OMZs) demonstrates the long-term potential of organ-grade animals to tolerate such conditions (e.g., Childress & Seibel, 1998; Levin, 2003; Seibel & Drazen, 2007; Sperling et al., 2015). Moreover, there is no obvious trend towards more simply constructed cnidarians, sponges or unicellular holozoans with increasing hypoxia (Parris, Ganesh, Edgcomb, Delong, & Stewart, 2014).

If oxygen availability presented no fundamental impediment to the evolution of bilaterians per se, then perhaps the critical step was their ability to engage in macro-carnivory (Norin & Clark, 2017; Sperling et al., 2013). A late Proterozoic rise in atmospheric oxygen may have provided the additional energy required for motile predators to successfully pursue prey, or become large enough to ingest whole prey, or to meet the elevated oxygen demand associated with whole-prey digestion. Predators, however, have never been fundamentally outpaced by their (co-evolving) prey, and there are obvious alternatives to gulping-type ingestion, including both preliminary comminution and external digestion. The oxygen loading effects of whole organism ingestion can also be addressed simply by increasing predator body size, a strategy that can add yet further advective gas-exchange capacity (see Verberk & Atkinson (2013) on the phenomenon of "polar gigantism").

Based on ecological distributions in modern OMZs, any suppression of early bilaterians to subcarnivorous grades of activity would seem to require atmospheric oxygen levels held perennially at or below levels consistent with "severe hypoxia" over the entire surface ocean (cf., Sperling et al., 2015). Whether or not this can be reconciled with evidence for widespread surface-water oxygenation through most of the Proterozoic (Lyons et al., 2014), or the fundamentally lower biological oxygen demand associated with less productive parts of these same oceans, or indeed with the challenge of maintaining atmospheric oxygen at perennially low levels once oxygenic photosynthesis was established (cf., Ward, Kirschvink, & Fischer, 2016), it is important to recognize the distinct fluid-dynamic properties of these two juxtaposed oxygen reservoirs (Liss & Duce, 1997; Wanninkhof & McGillis, 1999): whereas the low-viscosity atmosphere is continuously mixed, the fundamentally greater density and (dynamic) viscosity of seawater is accompanied by pronounced oxygen diffusion gradients. Significantly, the diffusion rate of oxygen in air is more than five orders of magnitude

greater than it is in water (Verberk, Bilton, Calosi, & Spicer, 2011). Taken together, the continuously oxygenated atmosphere and surface ocean will have presented an essentially inexhaustible redox buffer through all but the earliest Proterozoic, precluding the large-scale fluctuations commonly invoked to keep animal evolution at bay (e.g., Hardisty et al., 2017; Partin et al., 2013; Reinhard, Planavsky, Olson, Lyons, & Erwin, 2016). Certainly, the oxygenated surface layer of the ocean would be attenuated under less than modern levels of atmospheric oxygen, but it would still host vertically tiered aerobic communities on scales of centimetres, millimetres and micrometres (cf., Gladyshev, 1997; Hardy, 1997; Ploug, 2008). At the limit, it is simply a matter of tapping directly into the atmospheric reservoir and its five orders of magnitude more readily available oxygen. Air-breathing of course comes with its own challenges (Lefevre, Bayley, Mckenzie, & Craig, 2014; Verberk et al., 2011), but the only obvious impediment to its evolution since the GOE appears to have been the anatomical, behavioural and developmental capacity to use it.

6 | AQUATIC BIOTURBATION

Animals are large aerobic heterotrophic organisms, so it makes sense to view them as oxygen sinks (Catling et al., 2005; Nursall, 1959). But as swimmers, pumpers and tethered sources of drag (Hurd, 2000; Lassen et al., 2006), they also contribute importantly to environmental mixing. And as collectors, transformers and translocators of organic carbon, they fundamentally alter rates and styles of biological oxygen demand (Butterfield, 2011; Logan, Hayes, Hieshima, & Summons, 1995). All of these processes play a role in altering redox dynamics, from the physiology of individual organisms to large-scale ecosystem engineering and their reciprocal feedbacks on biological evolution. To this extent, the mixing and modification of water by aquatic animals mirror the effects of infaunal activity on soft sediments (e.g., Aller, 1982, 1994; Lohrer, Thrush, & Gibbs, 2004) and might reasonably be referred to as "aquatic bioturbation." By all appearances, the modern oceans are pervasively bioturbated.

Like its soft-sediment counterpart, the biological mixing of water is vertically tiered and, in its primitive benthic condition, tied to the sediment-water interface. Even so, the effects are substantial. At even modest levels of clearance (say, 0.1–1.0 $m^3 m^{-2} day^{-1}$; cf., Larsen & Riisgård, 1997), the filter-feeding benthos can process the volume equivalent of shelf seas (150 m average depth) in a matter of months or years. And with at least some sponges capable of extracting 85%–95% of small cells (<8 μm diameter) and 12% of dissolved organic carbon (DOC) in a single cycle (Yahel, Sharp, Marie, Häse, & Genin, 2003), this "sponge loop" alone constitutes a major sink in the marine carbon cycle—physically removing the same amount of DOC from seawater in 30 minutes as free-living bacteria remineralize in 30 days (de Goeij, van den Berg, van Oostveen, Epping, & van Duyl, 2008; de Goeij et al., 2013). At the same time, such volumetric extraction has the potential to radically transform physical environments and accompanying ecological structure. In the semi-restricted conditions of Florida Bay, for example, it is the suppression of cyanobacterial picoplankton by

sponges that maintains "normal" clear-water conditions—with the loss of this top-down control tipping the system into its stratified, dysaerobic, "alternate stable state" (Peterson, Chester, Jochem, & Fourqurean, 2006). Comparable engineering effects are seen in the regime shifts accompanying dreissenid mussels (Higgins & Vander Zanden, 2010), soft mussels (Petersen et al., 2008) and ascidians (Castilla, Lagos, & Cerda, 2004). In all of these instances, it is the impact of high-volume filtration on phytoplankton dynamics, light penetration and nutrient recycling that engineers the accompanying well-ventilated environments—setting the scene for further colonization and reinforcing feedbacks. On an evolutionary timescale, the selective extraction of cyanobacterial picoplankton by sponge-grade suspension feeders is likely to have driven the co-evolutionary radiation of larger export-prone eukaryotic phytoplankton (Butterfield, 2009, 2011; Lenton et al., 2014)—reflected in the dramatic expansion of eukaryotic biomarkers (e.g., Brocks et al., 2017) and mid-shelf oxygenation through the later Neoproterozoic.

Despite these benthic innovations, it was the further expansion of animals into the pelagic realm that revolutionized the impact of organism-ocean interactions. By shifting the focus of activity to the continuously aerated upper end of the water column, the entire ocean became susceptible to biological mixing, most obviously via the vortex trails and turbulent wakes produced by swimming animals (nekton). Since Re scales with both body size (L) and velocity (U), it is the relatively larger, faster and furthest swimming animals that generate most of this biological turbulence. Whales alone are responsible for a measurable fraction, with the additional inputs from fish, cephalopod molluscs and zooplankton prompting arguments that swimming animals may contribute as much kinetic energy to the modern oceans as the winds or tides (Dewar et al., 2006; Huntley & Zhou, 2004). Such estimates have been substantially deflated by the recognition of viscosity/friction effects at small (<1 mm), Kolmogorov length-scales (Prairie, Sutherland, Nickols, & Kaltenberg, 2012; Visser, 2007), but recent order-of-magnitude increases in the estimated biomass of mesopelagic fish (Irigoien et al., 2004) may reanimate the discussion.

Not all biological mixing derives from turbulence, however, and under more viscous circumstances, it is the frictional "dragging along" of material by a bioturbating organism that does most of the work. In an aqueous medium, this "drift" phenomenon is the principal means by which small (<L) and/or slow-swimming (<U) organisms contribute to mixing, particularly as they cross isopycnals or other stratification fronts (Darwin, 1953; Katija & Dabiri, 2009). Fluid drift is particularly sensitive to organism shape and can be magnified through coordinated swarming and schooling behaviour (Dabiri, 2010; Katija, 2015). Although difficult to quantify in global terms, the drift-based mixing contributed by various grades of marine "zooplankton" is undoubtedly substantial and represents a further type of ocean mixing that did not exist prior to the evolution of swimming animals.

In addition to mixing and stirring, pelagic metazoans have a major effect on the properties of seawater itself. Suspension-feeding forms, for example, systematically oxidize their habitat via the quantitative extraction of suspended biological oxygen demand. Pelagic tunicates, especially salps and appendicularians, play a key role in this process by combining muscle-based pumping/propulsion with a

sponge-like capacity to filter colloidal DOC (Flood, Deibel, & Morris, 1992; Harbison & Gilmer, 1976; Sutherland, Madin, & Stocker, 2010)—with cascading effects on light absorption, thermal stratification, water transparency and visual predation (cf., Caplanne & Laurion, 2008; Marshall, 2017). Actively swimming suspension feeders also control the production of positively buoyant, transparent exopolymer particles (TEP), and thus the formation of associated surface slicks, phytoplankton thin layers, and other impediments to vertical exchange (Calleja, Duarte, Prairie, Agustí, & Herndl, 2009; Durham, Kessler, & Stocker, 2009; Frew, 1997; Mari, Passow, Migon, Burd, & Legendre, 2017; Wurl, Stolle, Van Thuoc, The Thu, & Mari, 2016). More generally, uncontrolled TEP production can more than double the kinetic viscosity of seawater (ν)—with profound implications for Kolmogorov lengthscales, advective gas exchange and organismal ecology (Jenkinson & Sun, 2010; Seuront, Vincent, & Mitchell, 2006). By extension, the unscrubbed pre-metazoan oceans are likely to have been substantially more DOC/TEP-rich, oxygen-depleted and viscously challenging than their Phanerozoic counterparts.

7 | DIURNAL VERTICAL MIGRATION AND THE BIOLOGICAL PUMP

The modern ocean is ventilated by a combination of air–sea exchange, internal mixing and the vertical export of biological oxygen demand. In an inherently stratified ocean, the most significant contributor to biogenic mixing is the vertical movement of relatively large (>1 mm) swimmers as they intersect marine isopycnals (Dabiri, 2010; Katija & Dabiri, 2009; Wang & Ardekani, 2015). And by far the most significant such movement in the modern oceans is the diurnal vertical migration (DVM) practiced by a majority of marine zooplankton, especially copepods, euphausiids (krill) and gelatinous zooplankton

(jellyfish, pelagic tunicates, chaetognaths, pteropods)—which are followed in turn by fish, cephalopods and other higher-order predators (Figure 2). The primary motive for this daily commute to depth is visual predation, with primary consumers seeking refuge at depth during daylight hours and returning to the surface at night to feed (Bollens & Frost, 1991; Lampert, 1989; Ohman, 1990). Migratory amplitudes of DVM vary from a few tens or hundreds of metres for "jellyfish" (Haraldsson, Båmstedt, Tiselius, Titelman, & Aksnes, 2014; Kaartvedt, Klevjer, Torgersen, Sørnes, & Røstad, 2007) to mesopelagic depths (200–1,000 m) in the case of many salps, squid and fish (Gilly et al., 2006; Houssard et al., 2017; Solberg & Kaartvedt, 2017; Watanabe, Kubodera, Moku, & Kawaguchi, 2006; Wiebe, Madin, Haury, Harbison, & Philbin, 1979). Collectively, marine DVM is by far the largest coordinated movement of biomass on the planet— a continuous standing wave of pursued and pursuing animals extending across all but the highest latitude oceans (Wallace, Cottier, Brierley, & Tarling, 2013). Along with the higher frequency feeding dives of much larger, faster, turbulence-inducing whales (Aguilar Soto et al., 2008; Goldbogen et al., 2011; Roman et al., 2014), DVM is a first-order driver of diapycnal mixing in the modern oceans, particularly at depths below the reach of winds and tides (Dabiri, 2010; Dewar et al., 2006; Huntley & Zhou, 2004; Katija, 2015).

The daily migration of a major fraction of the marine biosphere to depth also has important implications for marine export. Rather than just gravitationally sinking, surface-generated productivity is actively collected and transported to depth by metazoan consumers, where it is off-loaded in the form of respiration, DOC secretion, faeces, exuviae and carcasses (Longhurst & Harrison, 1988; Steinberg & Landry, 2017). This muscle-powered pump systematically clears the upper water column of suspended organic carbon while concentrating it at depth. Indeed, the expression of modern OMZs is largely a consequence of DVM behaviour (Bianchi, Galbraith, Carozza, Mislan, & Stock, 2013),
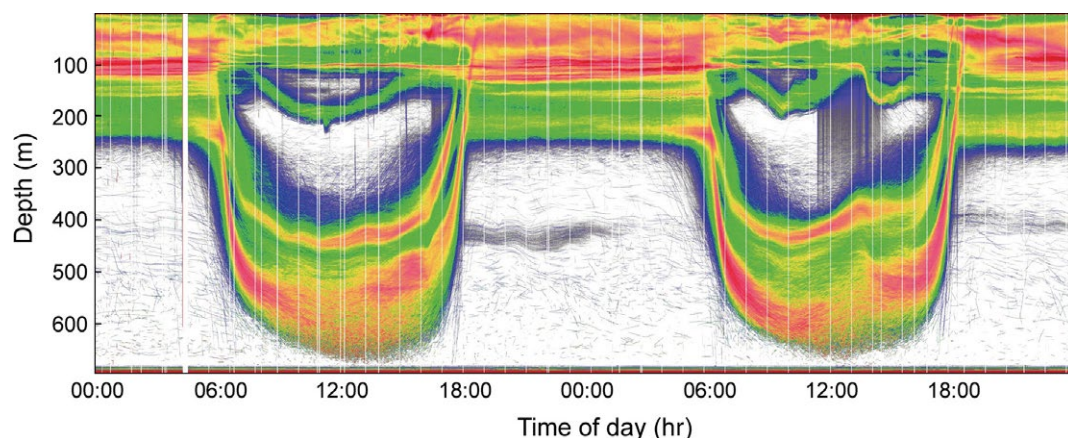

FIGURE 2 Diurnal vertical migration (DVM) in the Red Sea. Acoustic echograms from 15 to 16 November 2014 showing three distinct levels of DVM (colour scale indicates echo intensity: red high, blue low; the afternoon disruption on 16 November is a passing rain storm); the local oxygen minimum zone lies between 400 and 600 m, broadly coincident with maximum daytime depth (Klevjer, Torres, & Kaartvedt, 2012). A similar style of DVM occurs throughout most of the modern ocean, but did not exist prior to the evolution of muscular propulsion, visual predation and a swimming habit. Its full expression, and accompanying contributions to the biological pump, appeared in a stepwise, escalatory fashion through the course of the Phanerozoic. Figure courtesy of Stein Kaartvedt (Kaartvedt, Røstad, & Aksnes, 2017), with permission of *MEPS*

where the interplay between primary production and secondary consumption determines ambient light gradients—and thereby the depths at which visual predation can be effectively conducted (Aksnes et al., 2017; Norheim, Klevjer, & Aksnes, 2016). By parking their daytime activities just below this limit, migrating animals inevitably generate localized oxygen minima, both passively via their collective metabolic demands, but also through the active breakup of in-falling faecal pellets (coprohexy) by transient mesozooplankton (Giering et al., 2014; Iversen et al., 2017; Manno, Stowasser, Enderlein, Fielding, & Tarling, 2015; Wallace et al., 2013). In other words, DVM can both oxygenate surface water and intensify of deeper water OMZs independently of any increase in net export production or long-term carbon burial.

Even so, active transport by suspension-feeding zooplankton remains an important vector of net export in the modern oceans. In areas of the western Atlantic, for example, swarming salps can clear up to 74% of the surface ocean in the course of a night's feeding, before descending 600–800 m to spend the day (Madin et al., 2006). The release of faecal pellets at depth bypasses the most intense intervals of coprohexy and remineralization, adding substantially to their deep-water flux (Manno et al., 2015; Roullier et al., 2014). DVM accounts for up to 40% of exported carbon in the equatorial Pacific (Zhang & Dam, 1997), California Current (Stukel, Ohman, Benitez Nelson, & Landry, 2013) and Sargasso Sea (Steinberg et al., 2000). On longer time scales, the mesopelagic over-wintering behaviour of *Calanus finmarchicus*, a lipid-rich copepod, effectively doubles the deep-water flux of carbon in the North Atlantic (Jónasdóttir, Visser, Richardson, & Heath, 2015).

Because of the size-structured nature of pelagic food webs, a significant fraction of modern marine biomass is represented by higher-order consumers, most notably cephalopods, fish and aquatic mammals. Simply as localized concentrations of carbon and nutrients, these large motile organisms constitute a qualitatively distinct aspect of marine ecology and carbon/nutrient cycling, ultimately in the form of carcass falls (e.g., Henschke et al., 2013; Lebrato et al., 2013; Smith, Glover, Treude, Higgs, & Amon, 2015). It is their day-to-day habits, however, that play the larger part in material transport. In the oligotrophic North Pacific, some 50% of organic carbon at 400 m is represented by "fish-mediated export" (Davison, Checkley, Koslow, & Barlow, 2013), with faecal pellet production comparable to that of euphausiids or salps under high nutrient conditions (Saba & Steinberg, 2012). Given the systematic underestimation of larger nekton in the oceans (e.g., Irigoien et al., 2004; Longhurst & Harrison, 1988), and their pronounced feedback effects on primary production (e.g., Giering, Steigenberger, Achterberg, Sanders, & Mayor, 2012; Hernández-León, Fraga, & Ikeda, 2008; Roman et al., 2014), it is clear that modern biological pump is driven as much by metazoan consumers as it is by primary producers.

8 | PUMPING AND SWIMMING THROUGH TIME

Metazoans have not always been modern, so the biological mixing (and unmixing) dynamics of the modern ocean cannot be uniformly extrapolated to ancient systems. Prior to the appearance of animals, there was no active transport of surficial productivity at all, just an anoxia-/turbidity-/viscosity-inducing suspension of cyanobacteria and TEP. Gravitational sinking is likely to have been dominated by low-Re, Stokes' law dynamics (Butterfield, 2009; Logan et al., 1995; Vogel, 1981) (Figure 3a), with windblown dust the only obvious source of ballast (Droser, Tarhan, & Gehling, 2017; Keil, Neibauer, Biladeau, van der Elst, & Devol, 2016). In this light, the increasingly oxygenated geochemical signatures observed through the Neoproterozoic-Palaeozoic transition (e.g., Hardisty et al., 2017; Lyons et al., 2014; Och & Shields-Zhou, 2012; Planavsky et al., 2014; Reinhard et al., 2016; Sperling et al., 2013, 2015) may not so much be reflecting rising levels of atmospheric oxygen, as stepwise increases in the ability of animals to pump and swim through water.

If metazoan mixing plays a part in marine ventilation, then the process was initiated with the mid-late Neoproterozoic evolution of sponge-grade animals (Figure 3b) (Butterfield, 2009, 2011; Erwin & Tweedt, 2011; Lenton et al., 2014; Sperling, Pisani, & Peterson, 2007). Along with the immediate effects of sequestering local picoplankton and DOC, such processing will have introduced a major selective advantage to larger-celled eukaryotic phytoplankton—with cascading effects on light penetration, seawater viscosity, redox chemistry and organismal ecology (Meyer, Ridgwell, & Payne, 2016).

The subsequent Cambro–Ordovician migration of muscular animals into the pelagic realm dramatically expanded the reach of "aquatic bioturbation" to the whole of the surface ocean. As with its soft-sediment counterpart (cf., Seilacher & Pflüger, 1994; Tarhan & Droser, 2014), this would have been initiated by shallow "tiering" suspension/detritus feeders and the disruption of biofilm-like surface slicks at the air–sea (vs. the sea-sediment) interface—followed in turn by predator–prey co-evolution and low-level DVM (Figure 3c). The resulting, relatively shallow OMZs were widely occupied (and reinforced) by graptolitic zooplankton through much of the early Palaeozoic, a pelagic biota exhibiting little evidence of higher-order predation or evolutionary escalation, despite essentially modern levels of atmospheric oxygen from at least the middle Cambrian (Berry, Wilde, & Quinby-Hunt, 1978; Chen et al., 2015; Li et al., 2017), and the presence of large predatory invertebrates in the contemporaneous nekto-benthos (Klug et al., 2015). In the absence of any fundamental constraints on graptolite predation, the explanation for their evolutionary persistence presumably lies in more local, ecological circumstances, the most likely being their top-down engineering of hypoxic refugia via DVM (cf., Cooper, Rigby, Loydell, & Bates, 2012). As the first occurrence of an actively pumped redox gradient to appear in the open ocean, this graptolitic OMZ would have presented a significant barrier to would-be predators, at least in the unescalated context of the early Palaeozoic.

It is not until the Devonian that noticeably larger, faster swimming predators appear in the fossil record, undergoing a dramatic evolutionary radiation through the remainder of the period, broadly coincident with the disappearance of graptolites (Friedman & Sallan, 2012; Klug et al., 2010). Notably, this "Devonian Nekton Revolution" coincides with geochemical evidence for another major increase in marine oxygenation, offering an attractive bottom-up explanation
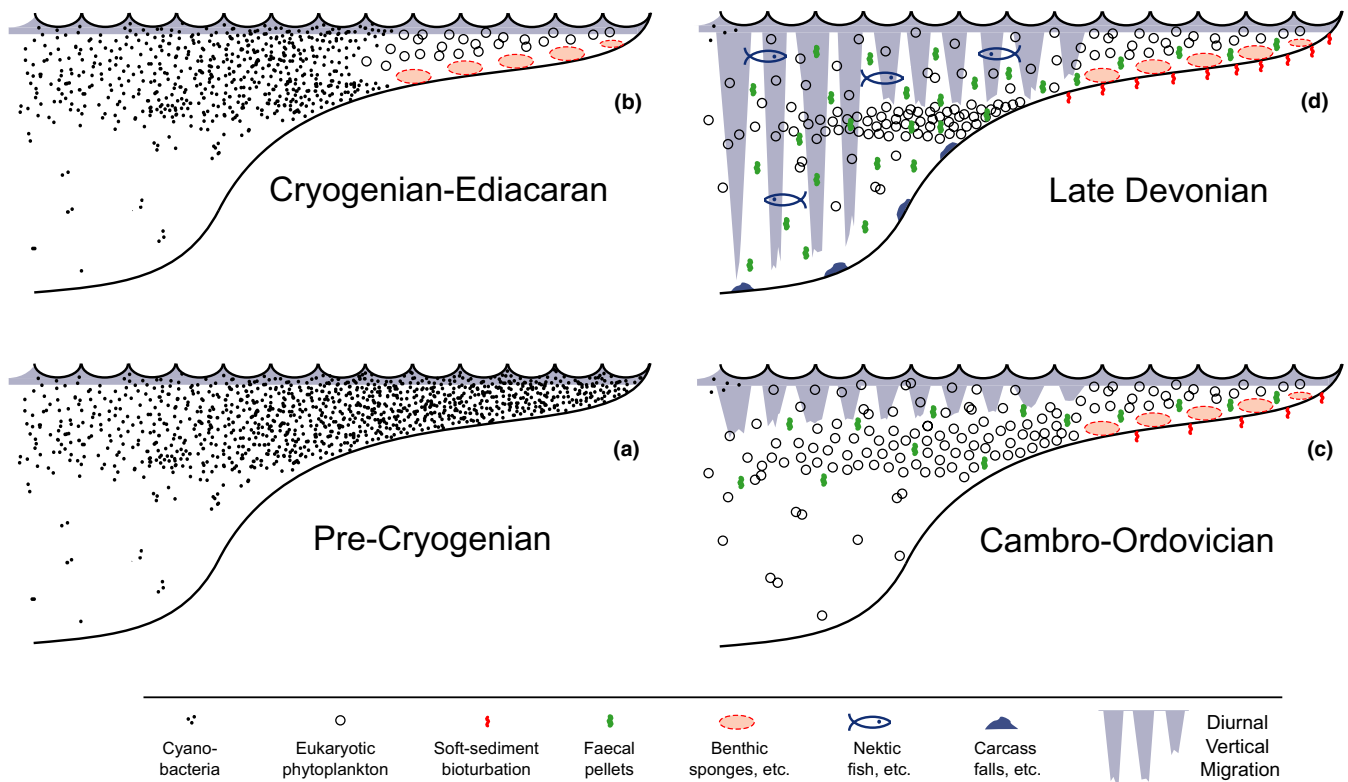
FIGURE 3 Co-evolution of animals and oceanic ventilation through the Neoproterozoic-Palaeozoic transition. (a) Pre-metazoan oceans dominated by cyanobacterial phytoplankton and accompanying redox stratification. (b) Benthic sponge-grade filter-feeding activity clears shallow marine shelf environments of turbidity-/viscosity-inducing cyanobacteria, dissolved organic carbon and transparent exopolymer particles—creating both the opportunity and selective pressures for a radiation of larger eukaryotic phytoplankton. (c) Early Palaeozoic expansion of metazoan filter feeding into the water column, with modest levels of muscle-based swimming and predation driving corresponding levels of diurnal vertical migration (DVM), surface-water oxygenation and oxygen minimum zone (OMZ) hypoxia. (d) Mid-Palaeozoic intensification of DVM, faecal pellet production, carcass falls and "aquatic bioturbation" leading to the increased depth and intensity of OMZs. The null hypothesis is that stepwise increases in marine ventilation through this interval occurred independently of atmospheric oxygen levels

for the seemingly belated radiation of large predatory fish, cephalopods, etc. (Dahl et al., 2010; Wallace et al., 2017). What's missing from this equation, however, is the conspicuously negative scaling of body size with mass-specific oxygen demand in most bilaterians (Catling et al., 2005; Glazier, 2006), as well as the unique abilities of large motile organisms to exploit and modify seemingly hostile environments. Insofar as large vertically migrating bilaterians are recognized as first-order agents of marine ventilation—and corresponding OMZ stagnation (Bianchi et al., 2013)—the causality of Devonian oxygenation is more likely to have run in the opposite direction: as predator–prey interactions escalated through the period, so too did the amplitude of contemporaneous DVM, its expansion of the oxygenated surface ocean, and associated deepening/compaction of OMZs (Figure 3d).

9 | CONCLUSIONS

All biological exchange ultimately depends on chemical diffusion, but it is the associated fluid-dynamic context that determines physiological and ecological properties (Agutter, Malone, & Wheatley, 2000). In the context of early animal evolution, it was the evolutionary assembly of increasingly sophisticated devices for manipulating fluids that revolutionized the biosphere. Collectivized flagellar beating was clearly the place to start, providing the stepping stone to higher-order divisions of labour and progressive release from the constraints of low-Re and low-Pe dynamics. In its wake came efficiencies of scale, the evolutionary discovery of muscular propulsion and stepwise application of emergent hydrodynamic properties. The sequential addition of larger faster visual predators to pelagic food webs will have forced most of the rest of the marine biosphere to correspondingly greater migratory depths through the Phanerozoic, progressively displacing OMZs and expanding the oxygenated epipelagic zone. The Cenozoic evolution of exceptionally energetic tuna fish and whales (Aguilar Soto et al., 2008; Goldbogen et al., 2011; Lowe, Brill, & Cousins, 2000) marks the current extent of this trajectory, but is no more an indication of rising atmospheric oxygen levels than the presence of hypoxia-adapted vampire squid and mysid shrimp in the accompanying OMZs (Childress & Seibel, 1998; Seibel & Drazen, 2007). All of these specialist modes of life are simply the end products of ecological escalation, ecosystem engineering and the deep evolutionary potential of tissue- and organ-grade

multicellularity. By extension, the geochemical redox signals for stepwise oxygenation of the Neoproterozoic, Cambrian and Devonian oceans may have more to do with stepwise innovations in biological pumping—specifically its cilia- and muscle-powered impellers—than any biologically significant shifts in atmospheric oxygen (Meyer et al., 2016).

So why did it take so long to get the metazoan show on the road? Once the challenge of supplying unicellular eukaryotes with oxygen had been met, all the rest might have been expected to fall rapidly into place. That this failed to occur reveals a more fundamental level of evolutionary control than mere permissive environments. The simplest explanation lies in the sheer complexity of the metazoan machine, not least the revolutionary invention of tissue-/organ-grade advection and propulsion. By all appearances, it just took a long time to evolve the myriad technologies and ecologies of crown-group animals from the LECA—roughly the same amount of time it took crown-group animals to build an energy efficient steam engine or begin the bioturbation of Mars.

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