

Models of flow through sponges must consider the sponge tissue

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ARISING FROM G. Falcucci et al. *Nature* <https://doi.org/10.1038/s41586-021-03658-1> (2021).

In their Article, Falcucci et al.¹ examined the hydrodynamics of the deep-sea glass sponge *Euplectella aspergillum* using a model of just the skeleton of the sponge. The authors present simulations showing flow lines and vortices crossing the sponge skeleton from the upstream to the downstream side of the tube in crossflow and conclude that the skeletal motifs give rise to internal recirculation patterns favouring the sponge's feeding and sexual reproduction. Unfortunately, in their model, Falcucci et al.¹ neglect the sponge's tissue that, with its complex labyrinth of feeding canals, forms a complete barrier with low permeability over the sponge wall^{2–5} (Fig. 1). The implication of this omission is that the flow simulations are not informative regarding the actual flow through and around live *E. aspergillum* and thus speculations about the effect of the flow patterns they observed on sponge biology (feeding, reproduction and hydrodynamic stress) are unfounded.

The Venus flower basket *E. aspergillum* is well known due to its beautiful lattice-work structure. The internal skeleton that underlies this structure is formed of glass, which persists long after the animal has died, and consequently many specimens are available in museums for study. Unlike other studies that focus on the mechanical properties of the skeleton⁶, Falcucci et al.¹ aimed to study the “fluid dynamic performance of the deep-sea glass sponge *E. aspergillum* in its actual living conditions, reproduced via in silico experiments.” Unfortunately, instead of using a model of a living sponge for their simulation, the authors omitted the sponge tissue and used only the highly porous bare skeleton.

The outside surface of any sponge is covered by tissue that in the case of hexactinellid sponges is formed by a syncytium^{2,3}. The surface of *Euplectella*, like other glass sponges, has 20–50 micrometre-sized openings (ostia)^{4,5} through which water is drawn into a complex maze of ever-narrowing canals that lead to submicrometre-sized slits between the collar microvilli where food particles are extracted^{2,7,8} (Fig. 1). The dimensions and flow resistance of the sponge aquiferous system have been measured and estimated for several species^{8–10}, including glass sponges⁷.

By omitting the sponge tissues in their simulations, Falcucci et al.¹ also neglect the role of the sponge's natural pumps (that is, the choanocytes) as the main driver of water flow through the sponge^{8,10}, and which in glass sponges can be arrested by electrical impulses¹¹ stopping all flow. The flow pattern in tube-like sponges is driven by the choanocyte pumps and is unidirectional, so that water is drawn from around the tube, through tiny canals in the body wall, and out through the upper common opening, the osculum (Fig. 2, Supplementary Video 1). Because of the low permeability of the tissue structure, it is highly unlikely that an imposed crossflow will change this pattern to that

suggested by the simulations of Falcucci et al.¹, with water flowing across the entire tube rather than exiting through the osculum. From the detailed descriptions of the tissues by Schulze^{4,5} (Fig. 1), there is no reason to believe that *E. aspergillum* has different flow patterns from other glass sponges. Flow patterns in a glass sponge can be demonstrated even in deep-sea situations using in situ flow visualization (for example, Supplementary Video 1).

The simulations of the flow patterns through the highly porous models of the bare skeleton of the sponge (P2, the “complete model” of Falcucci et al.¹) are physically robust and very interesting from an engineering point of view, but not informative about hydrodynamics of sponge feeding. A living sponge with intact tissue does not experience, for feeding, a flow pattern of jets of water entering through open pores and passing across the sponge wall into the cylinder (sponge atrium) as depicted by figure 4a or the right panels in Supplementary Video 1 of Falcucci et al.¹. This misunderstanding led the authors to incorrectly claim that the spiral outgrowths and a porous skeleton function to decrease drag and increase the water residence time, thereby giving the sponge an advantage in selective filter-feeding and increasing the chance of fertilization of eggs by sperm.

In their Article, the authors suggest that high-performance computational power allows the “study of realistically complex biological models.” However, a realistic representation of the flow through and around a living sponge must take into account the dimensions of the aquiferous system and therefore the low permeability of the sponge tissue. If technical limitations prevent the use of computational fluid dynamics (CFD) to model the flow within the realistic dimensions of the sponge aquiferous system^{12,13}, the sponge wall could be simulated as a porous medium with an estimated effective resistance to flow. In this respect, the solid models S1 and S2 of Falcucci et al.¹ are closer to reality. Such a simulation would also provide the pressure distribution on the outer surface of the sponge, serving as boundary condition for models aimed at investigating the effects of external flows on the pumping activity of the flagellated chambers⁷.

It is true, as the authors point out, that CFD is a powerful tool to study the complex patterns of flow in and around difficult-to-access specimens. A recent CFD study¹³ found that the choanocyte is the unit of the sponge pump with comparable flow rates from the choanocyte collar across a range of demosponge and glass sponge species (0.06×10^{-6} – 0.85×10^{-6} ml h⁻¹ per choanocyte). That work illustrates key features of the sponge pump, including the presence of a vane along the length of the flagellum, and a gasket joining the tips of each collar, causing the flow to enter the sponge collar

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Matters arising

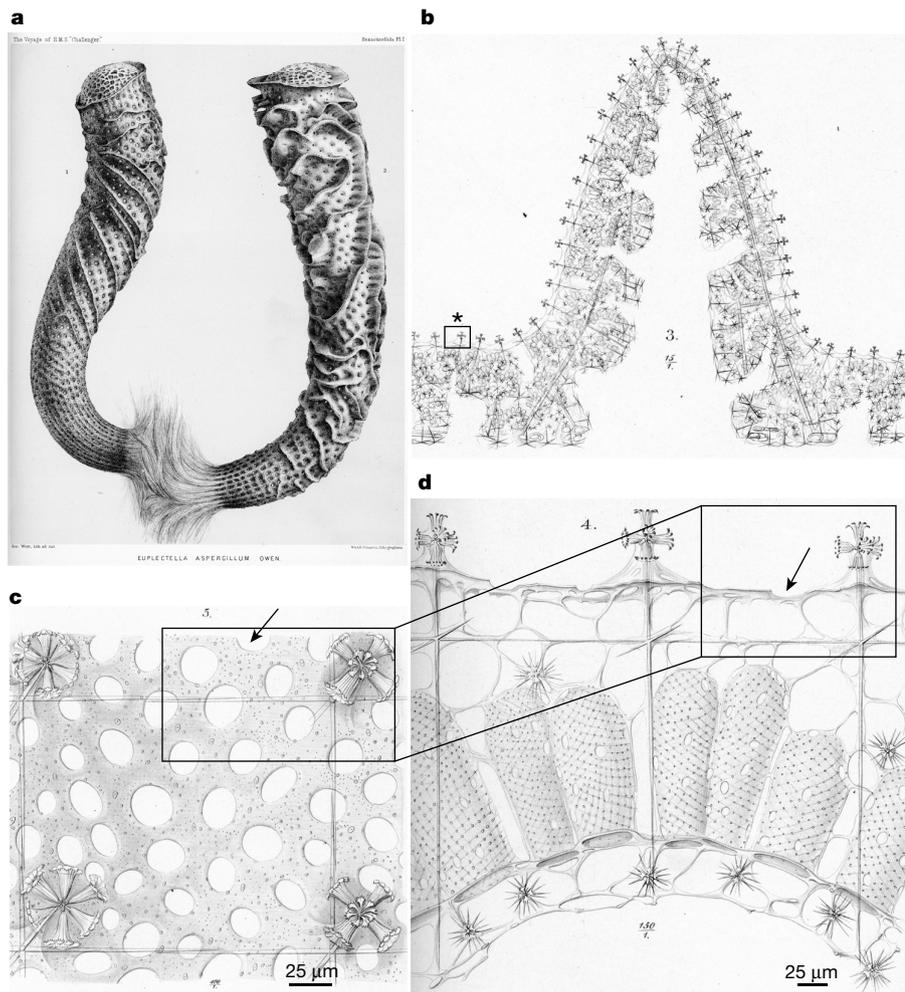


Fig. 1 | Drawings of the soft tissues of the glass sponge *Euplectella aspergillum* Owen. **a**, Two specimens with soft tissues preserved in alcohol. **b**, A section of the body wall at a ridge. **c**, External view of the outer membrane. **d**, Outer membrane and chambers in a section perpendicular to the surface. The asterisk in **b** indicates the region shown in **c**. The boxed regions in **b**, **c** indicate equivalent regions. The arrows indicate pores through which water enters the sponge. The drawings are from Schulze⁴, Challenger Expedition, plate IV, figures 4 and 5.

at its base at a speed of less than $25 \mu\text{m s}^{-1}$. That these features are conserved across the breadth of the phylum, and that the gross morphology appears unchanged for over 500 million years¹⁴ strongly suggests that the sponge pump is key to successful water transport, whether it is used for feeding or gas and nutrient exchange, regardless of the habitat.

A great range of skeletal structures underlie the tissues of the 9,000+ different sponge species¹⁵. The exact role that the intricate designs of internal skeletons have in allowing the sponges to take advantage of ambient currents is an ongoing question, especially for the deep-sea glass sponges. In conclusion, any future modelling of the interaction of sponges with flow must consider the whole animal and not only its bare skeleton.

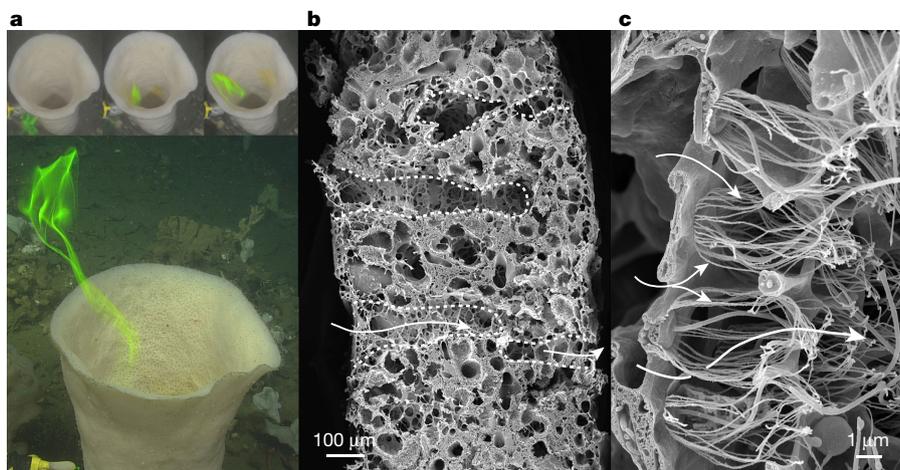


Fig. 2 | Natural flow through the glass sponges *Acanthascas* sp. and *Farrea occa*. **a**, Green dye (fluorescein) squirted near the sponge *Acanthascas* sp. moves across the wall and up out of the osculum. **b**, The body wall of the glass sponge *Farrea occa* after removal of the skeleton, seen by scanning electron microscopy. Incurrent and

excurrent canals are shown by the dashed lines and the arrows show the direction of water flow through the sponge. **c**, Section through a feeding chamber in *F. occa* showing the collar-flagella pumps in the tissue lining the chamber. The arrows show the direction of water flow through submicrometre-sized apertures.

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Additional information

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Reply to: Models of flow through sponges must consider the sponge tissue

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REPLYING TO S. P. Leys *Nature* <https://doi.org/10.1038/s41586-021-04380-8> (2022).

In their Comment¹, Leys et al. question the modelling choice of our original study² to focus on the skeletal motifs of *Euplectella aspergillum* may not be suited to gain insight into the hydrodynamics within the body cavity of the sponge and its surroundings, based on two main arguments: in living sponges, (1) the skeleton is embedded within soft tissues, which rely on canals and chambers of millimetre-to-submicrometre sizes, and (2) active pumping governs the water flows through the canals. Here we provide evidence that the above comments, although stimulating an interesting perspective for future studies, have marginal bearing on the conclusions drawn in our original paper—the level of detail of which is defined by the present state-of-the-art of modelling technology.

Our modelling choice—supported by the peer-review process—is not unique to our work, and it is informed by the classical description of *E. aspergillum* provided by Schulze (“We see in a well-preserved piece of the tube-wall that the circular apertures in the skeleton, [...] correspond also to circular apertures about 2 mm in diameter through the entire wall of the tube, by means of which the water surrounding the sponge communicates directly with that contained in its inner cavity”³).

Whether or not this framework is adequate to capture the hydrodynamics of a living sponge with an intact tissue is a reasonable question. Experimental endeavours in aquaria or in situ should be the cornerstone to build an improved understanding of the role of soft tissues in regulating the hydrodynamic regime around and inside *E. aspergillum*. In the absence of these experiments and on account of technological limitations that hinder computer modelling across widely different physical scales, one can draw some conclusion based on fluid mechanics research on the interaction between coherent fluid structures and porous media^{4–6}. Although not directly addressing the hydrodynamics of *E. aspergillum*, this literature provides evidence supporting that the flow physics associated with the skeletal motifs of this sponge should be robust to the presence of pores and canals from millimetre to submicrometre.

For example, experiments by Adhikari and Lim⁴ indicate that for Reynolds numbers above 1,000, a vortex ring has sufficient energy to pass through a porous screen, with minimal structural changes. These findings are confirmed in the comprehensive computational study by Cheng et al.⁵ on the interplay between the screen microstructure and Reynolds number, which further suggest that the transmission of vorticity through the screen is favoured by a higher porosity and a finer mesh. Experiments by Hrynuk et al.⁶ further justify this prediction, by demonstrating that at high Reynolds numbers (about 2,000),

a porous wall with a fine mesh is virtually transparent to an incoming vortex, whose downstream structure remains unaltered (Fig. 1). According to the above studies, coherent vortical structures propagate through porous walls in a surprising and somewhat counterintuitive manner, which supports our original modelling choice of focusing on the skeletal motifs of *E. aspergillum*.

In this vein, a promising approach to incorporate the porosity of the soft tissue within the present modelling technology is to homogenize the soft tissues through a permeable layer, thereby capturing the flow through an effective permeability coefficient. Such an approximation would constitute a first step to capture the complexity of soft tissues, preceding future research that could model bidirectional fluid–structure interactions, resulting into local deformation of the sponge.

The omission of canals in our computational model is not the only approximation that is being considered inadequate by Leys et al.¹: our model also neglects active pumping. Assessing the implications of such an approximation requires once again experiments in aquaria and in situ that could bring clarity on the actions of the choanocytes, aquaporins and submicrometric channels^{7,8}. Beyond practical challenges, the execution of these experiments calls for a fine level of control of the flow conditions, whereby it may be difficult to tease out active versus passive hydrodynamics from a mere flow visualization experiment. For example, Leys et al. offer as evidence of active pumping the flow through the osculum in another living sponge, different from *E. aspergillum* (figure 2 in ref. 1). Not surprisingly, an equivalent visualization is obtained by detailing the streaklines within the body cavity, from our simulations (Fig. 2). On the basis of the above, whether simulations ‘must’ or ‘should’ account for soft tissues is a matter of debate that can be resolved through constructive collaboration at the interface between mechanics and biology.

To study the fluid dynamics of *E. aspergillum*, we drew inspiration from the seminal studies by Vogel in the 1970s that have laid the foundations of the present understanding of how marine sponges take advantage of passive flow from ambient currents^{9,10}. In a pioneering experiment, Vogel and Bretz have shown that “the same unidirectional flow” measured in living sponges in controlled settings is also present in plastic models, which rely on passive ventilation and lack organic tissues and flagellated chambers¹⁰. In this respect, our work can be viewed as an extension of Vogel’s theory, informed by state-of-the-art computational fluid mechanics. Accounting for the difference in size of the models by Vogel and Bretz with respect to living sponges (about

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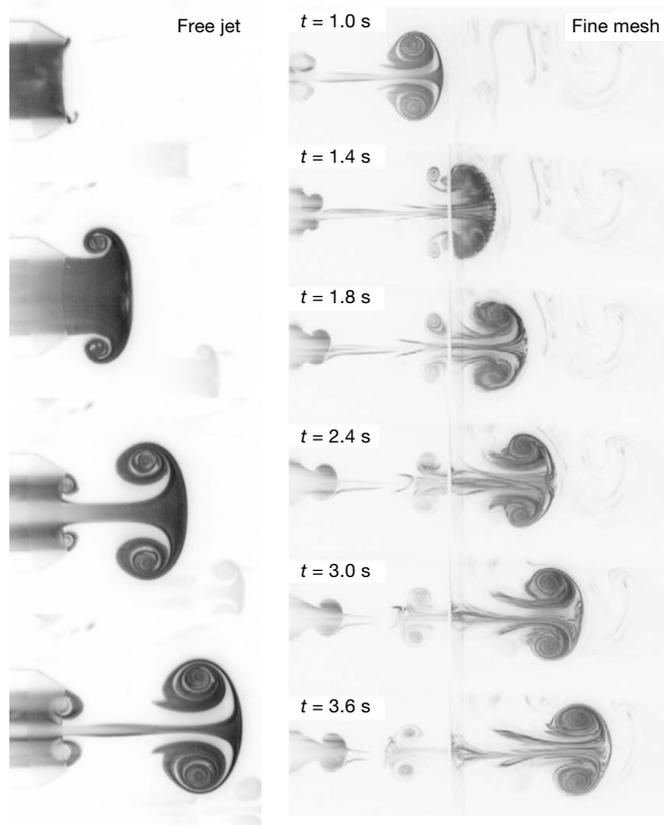


Fig. 1 | A porous wall with a fine mesh is virtually transparent to an incoming vortex. Free propagation of a vortex ring generated at a nozzle with a radius of about 1 cm travelling at about 10 cm s^{-1} versus the impact of the same vortex on a porous screen with a mesh of porosity about 65% and a wire radius of about 0.01 cm. For sufficiently large incoming currents, the presence of a fine array of channels in the organic tissues of *E. aspergillum* is unlikely to have a significant role on the flow patterns formed within and outside its body cavity. Figure reproduced from ref. ⁹, with the permission of AIP Publishing.

2 cm versus 10–30 cm), our simulations cover higher flow regimes, up to Reynolds numbers of 2,000.

Vogel's theory on the use of current-induced flow by marine sponges is widely accepted in the community, although its universality has been questioned by the authors of this Comment and others, see, for example, refs. ^{11,12}. For instance, Leys et al.¹² found that passive ventilation has a minor role at low ambient velocities, with certain glass sponges relying more on active water pumping. Yet, the high cost of active water pumping—which varies between species and habitats—might be better sustained by large sponges that live in nutrient-rich waters at low ambient currents. This cost is typically reduced by thin-walled sponges living in nutrient-poor waters at high ambient currents, like *E. aspergillum*, through passive ventilation, which is crucial for the survival of these organisms and provides a large proportion of the sponge's overall food intake¹². The classical work of Bidder¹³ points in this very same direction, indicating that fast and unchanging currents at great depths could be responsible for limited hydraulic evolution and efficiency of active pumping in glass sponges. As demonstrated by Vogel, the flow through live sponges is, in fact, often related to environmental currents, whereby increasing the speed of the ambient currents “increase[s] the rate at which water under natural conditions passes through” live sponges⁹. These studies support our understanding that passive ventilation is essential for the flow physics of *E. aspergillum*—underlying the evolution of its unique skeletal motifs as potentially regulating elements of the flow patterns within and outside its body cavity, as revealed in our original study².

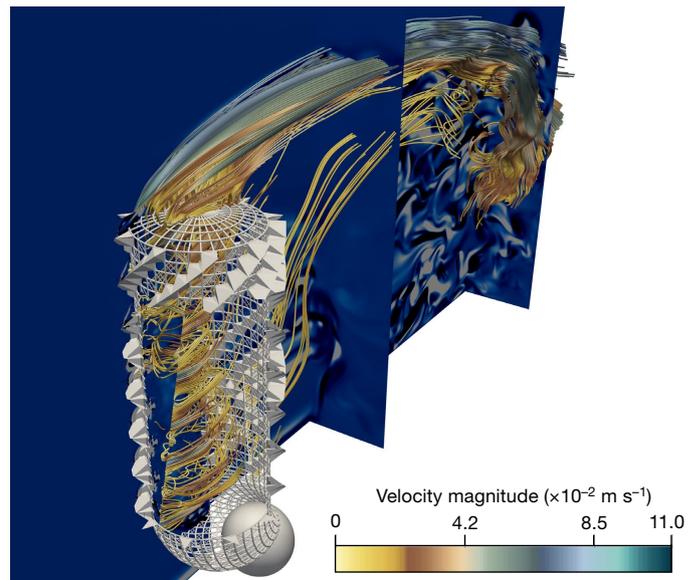


Fig. 2 | Detail of the flow streamlines exiting from the osculum of *E. aspergillum* complete model at a Reynolds number of 2,000. The plume is clearly visible. The flow out of the osculum is in qualitative agreement match with observations in the seminal studies by Vogel on plastic, mock-up sponges^{9,10}.

Leys et al. offer a potentially interesting perspective that might challenge the universality of Vogel's theory, especially in the case of larger sponges living in nutrient-rich waters and exposed to low and/or changing currents¹⁴. Should Vogel's theory be reconsidered? Perhaps, but such an endeavour cannot be undertaken without major advances in fluid and solid mechanics, like the one presented in our original Article. We may concur with Leys et al. that future computational modelling of sponges should consider the whole organism and not only its skeleton, with two caveats, though: (1) without some simplifying approximations, this is unviable on practical grounds, even with the most powerful current supercomputers, and (2) clear, experimentally based hypotheses shall be formulated to ensure better understanding of the biological mechanisms that are at present masked by incomplete empirical data.

Data availability

STL files for all of the models, raw data for the plots and scripts to reproduce the figures are available on GitHub at https://github.com/giacomofaluccci/Euplectella_HPC. Additional data that support the findings of this study are available from the corresponding author on request.

Code availability

All codes necessary to reproduce results in main paper are available on GitHub at https://github.com/giacomofaluccci/Euplectella_HPC.

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