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

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In their accompanying Comment [1], Leys et al. question the modeling choice of our original study [2] 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 (i) the skeleton is embedded within soft tissues, which rely on canals and chambers of millimeter to submicron sizes, and (ii) active pumping governs the water flows through the canals. Here, we provide evidence that the above comments, while stimulating an interesting perspective for future studies, have marginal bearing on the conclusions drawn in our original paper—whose level of detail is defined by the present state-of-the-art of modeling technology.

Our modeling 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 endeavors 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 modeling 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 millimeter-to-submicron.

For example, experiments by Adhikari and Lim in [4] indicate that for Reynolds numbers above 1000, a vortex ring possesses 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 (Re) number, which further suggest that the transmission of vorticity through the screen is favored by a higher porosity and a finer mesh. Experiments by Hrynuk et al. [6] further justify this prediction, by demonstrating that at high Re (~2000), 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 modeling choice of focusing on the skeletal motifs of *E. aspergillum.*

[Figure 1]

In this vein, a promising approach to incorporate the porosity of the soft tissue within the present modeling 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 which 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 sub-micrometric channels [7, 8]. Beyond practical challenges, the execution of these experiments calls for fine level of control of flow conditions, whereby it may be difficult to tease out *active* versus *passive* hydrodynamics from a mere flow visualization experiments. For example, Leys et al. offer as evidence of active pumping the flow through the osculum in another living sponge, different from *E. aspergillum* (Fig. 2 in [1]). Not surprisingly, an equivalent visualization is obtained by detailing the streaklines within the body cavity, from our simulations (Fig. 2). Based on 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.

[Figure 2]

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 chambers [10]. 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 (~2cm versus 10-30cm), our simulations cover higher flow regimes, up to Re of 2000.

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, [11, 12]. For instance, Leys et al. [12] found that passive ventilation plays 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 intake [12]. The classical work of Bidder [13], also cited by Leys et al. in their Comment [1], 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 sponges [9]. 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 unveiled in our original study [2].

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 currents [14]. Should Vogel′s theory be reconsidered? Perhaps, but such an endeavor 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 modeling of sponges *should* consider the whole organism and not only its bare skeleton, with two caveats, though: (i) without some simplifying approximations, this is unviable on practical grounds, even with the most powerful current supercomputers, and (ii) clear, experimentally based hypotheses shall be formulated to ensure better understanding of biological mechanisms that are presently 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/giacomofalcucci/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/giacomofalcucci/Euplectella_HPC.

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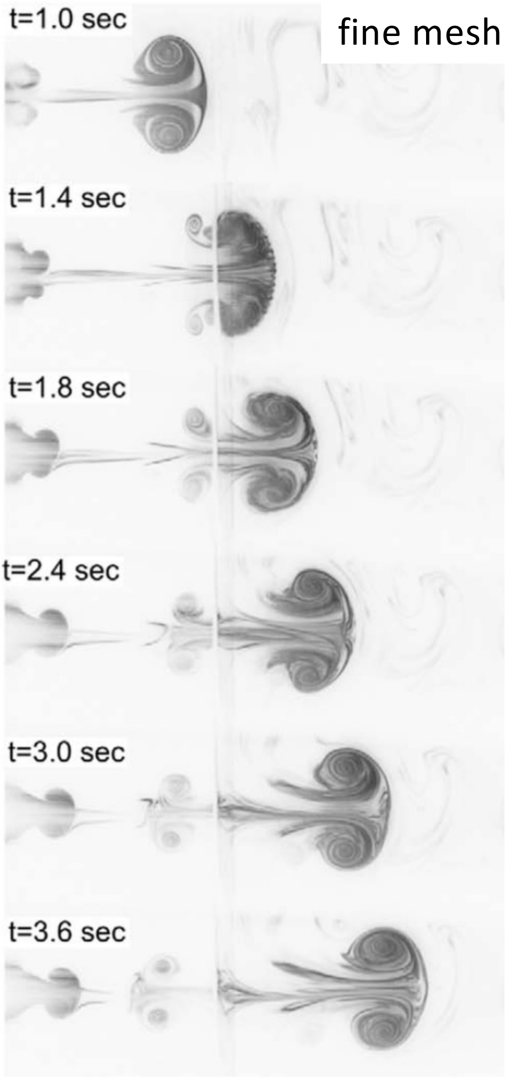
Figure Legends

Figure 1: Free propagation of a vortex ring generated at a nozzle of ~1 cm radius traveling at ~10 cm/s versus the impact of the same vortex on a porous screen with a mesh of porosity ~65% and wire radius of ~0.01 cm (courtesy of Hrynuk et al. [6]). For sufficiently large incoming currents, the presence of a fine array of channels in the organic tissues of *E. aspergillum* is unlikely to play a significant role on the flow patterns formed within and outside its body cavity.

Figure 2: Detail of the flow streamlines exiting from the osculum of *E. aspergillum* complete model at Re=2000. 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, mockup sponges [9, 10].


free jet


fine mesh
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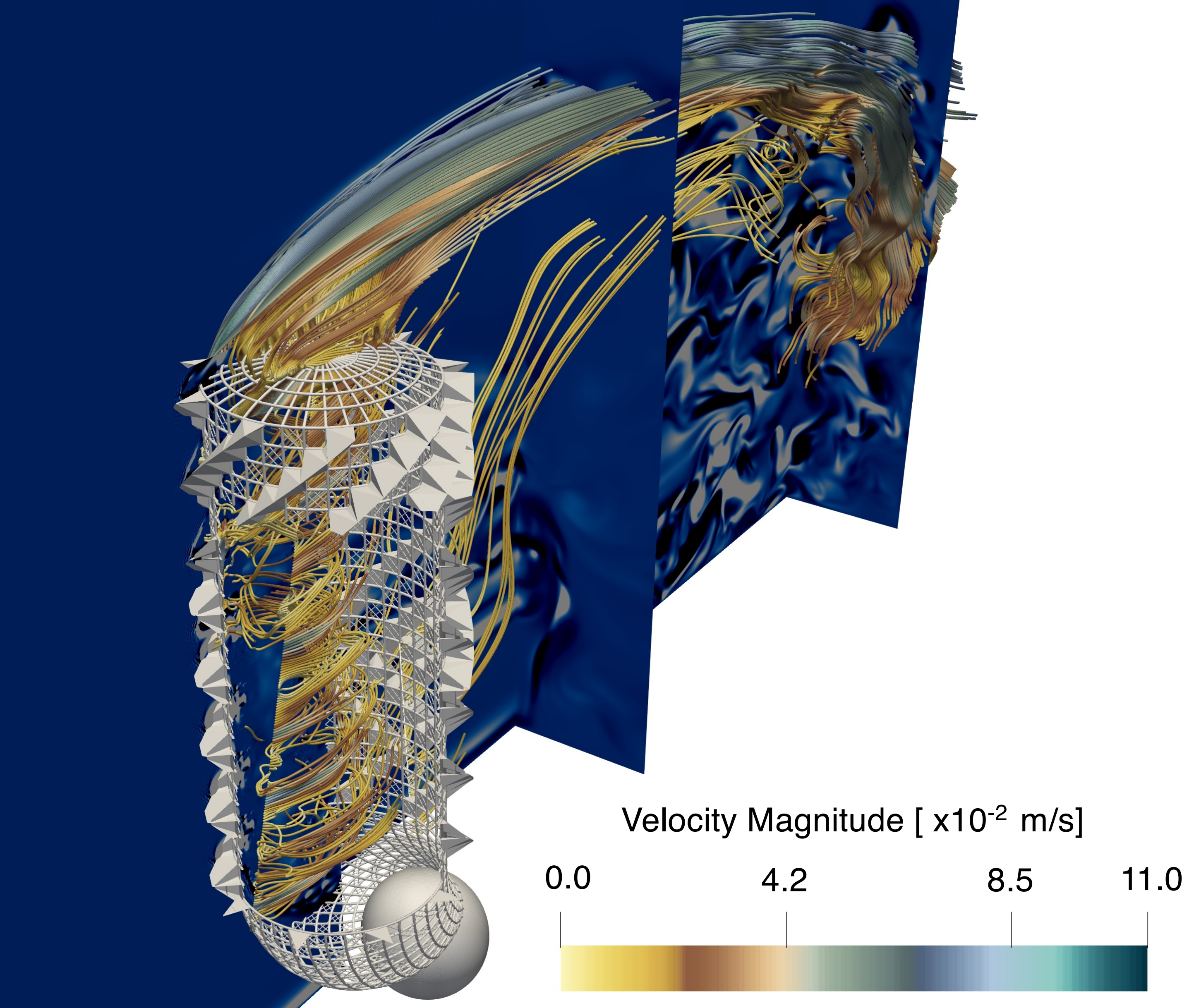
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8.5
11.0