1 Introduction

Echinoderms exhibit a plethora of morphological and behavioural adaptations to life in moving fluids. For example, the slot-like holes (lunules) that pass through the test in many sand dollars serve to reduce lift and thereby increase resistance to dislodgement (Telford, 1983), while at the same time drawing food-laden water up from the substrate (Alexander & Ghiold, 1980). Moreover, stalked crinoids bend the proximal-most part of the stalk and crown down-current, with the arms arranged into a fan in order to improve particle capture during suspension feeding (Macurda & Meyer, 1974; Baumiller, 2008). Laboratory experiments and field observations of living organisms enable us to better understand how extant echinoderms interact with fluid flows (e.g. Macurda & Meyer, 1974; Alexander & Ghiold, 1980; Telford, 1983; Messing et al., 1988; Baumiller et al., 1991; Loo et al., 1996; Thompson et al., 2005; Holtz & MacDonald, 2009; Cohen-Rengifo et al., 2018), but for fossil taxa, especially those lacking a modern analogue, methods of investigation are more limited. Flume studies have been used to explore the feeding and hydrodynamics of extinct echinoderms based on physical models of fossil organisms, both historically (e.g. Welch, 1978; Baumiller & Plotnick, 1989; Riddle, 1989; Parsley, 1990; Friedrich, 1993; Daley, 1996) and more recently (e.g. Huynh et al., 2015; Parsley, 2015). However, given the increasing availability of three-dimensional, digital models of fossil echinoderms (e.g. Rahman & Zamora, 2009; Zamora et al., 2012; Zamora & Smith, 2012; Waters et al., 2015; Briggs et al., 2017; Clark et al., 2017; Reich et al., 2017; Bauer et al., 2019; Rahman et al., 2019; Saulsbury & Zamora, 2019), virtual modelling approaches have great potential for analysing the paleobiology of extinct forms.

One of the most promising approaches for interrogating function and ecology in ancient organisms is computational fluid dynamics, or CFD. This is a tool for simulating flows of fluids, such as water or air. Computers solve the governing equations that describe fluid motions and their interactions with boundaries. In this way, fluid flows can be simulated for digital models of solid objects. Computational fluid dynamics is routinely used in engineering to analyse design and optimize performance for structures and machines. Furthermore, in the past ten to fifteen years, it has become increasingly important in paleontology (Rahman, 2017). Among the first to apply CFD to fossils were Rigby and Tabor (2006), who simulated water flow around digital models of graptolites. Shiino and colleagues subsequently applied the technique to brachiopods (Shiino et al., 2009; Shiino & Kuwazuru, 2010, 2011) and trilobites (Shiino et al., 2012, 2014). More recently, CFD has been used to study extinct vertebrates (Bourke et al., 2014, 2018; Kogan et al., 2015; Liu et al., 2015; Wroe et al., 2018; Dec, 2019; Gutarra et al., 2019; Troelsen et al., 2019), Ediacaran organisms (Rahman et al., 2015a; Darroch et al., 2017; Gibson et al., 2019), ammonoids (Hebdon et al., 2020) and fossil echinoderms (Rahman et al., 2015b, 2020; Dynowski et al., 2016; Waters et al., 2017).

In this Element, I introduce some basic principles of fluid dynamics and describe the key steps in a paleontological CFD study. I also discuss the applications of CFD to extinct echinoderms, highlighting recent work on cinctans (Rahman et al., 2015b), stalked crinoids (Dynowski et al., 2016) and blastoids (Waters et al., 2017). I end by considering possible future directions in this area, including new avenues of research that could improve our understanding of echinoderm paleobiology.

2 Fluid Dynamics

The discipline of fluid mechanics is the branch of physics that deals with fluids and the forces acting on them. It can be further subdivided into fluid statics and fluid dynamics, the latter of which is concerned with fluid flows and thus relevant for understanding the interaction between living organisms and moving fluids. Three conservation laws that must be satisfied in fluid dynamics are the conservation of mass, the conservation of momentum and the conservation of energy. Additionally, it is assumed that fluids can be treated as continuous substances (the continuum assumption), rather than being composed of discrete molecules. Applying these laws to the volume through which fluid will flow, by expressing them in terms of mathematical equations, allows us to calculate properties such as flow velocity and pressure as functions of space and time, thereby solving problems in fluid dynamics.

Water is treated as an incompressible Newtonian fluid, with density and viscosity assumed to be constant. The fluid velocity is zero at all solid boundaries (no-slip condition) and increases with distance from the boundary, giving a velocity gradient (the boundary layer). Where the viscous forces are relatively large, the fluid flows orderly in parallel layers, with little or no mixing (i.e. laminar flow). In contrast, where the inertial forces dominate, fluid flow is characterized by chaotic motion and the formation of unsteady vortices (i.e. turbulent flow). The dimensionless Reynolds number (Re) describes the ratio of inertial to viscous forces, and is defined as:

$$\mathrm{Re} = \frac{\rho U L}{\mu}$$

where ρ is the density of the fluid, U is the characteristic velocity, L is the characteristic dimension and μ is the dynamic viscosity of the fluid. For flow through closed conduits (e.g. pipes), the characteristic dimension is typically the diameter of the conduit, whereas for flow around objects, it is usually the width or length of the object. Low Re indicates the flow is mostly laminar, while high Re is indicative of predominantly turbulent flow; however, the critical Reynolds numbers over which flow transitions from laminar to turbulent will vary depending on the geometry. Flows with geometrically similar objects (i.e. scaled versions of the same shape in the same orientation) and the same Re are said to have dynamic similarity (assuming the Womersley number, which describes pulsatile flow frequency, is also constant), meaning the fluid flows will be identical.

Drag is the force that acts opposite to the relative motion of an object in fluid (i.e. parallel to the flow direction). It is dependent on the properties of the fluid and the geometry of the object. The dimensionless drag coefficient ($\mathrm{C_D}$) relates the drag force to the fluid density, velocity and object geometry, and is defined as:

$$\mathrm{C_D} = \frac{2F_D}{\rho U^2 A}$$

where F_D is the drag force exerted by the fluid, ρ is the density of the fluid, U is the characteristic velocity and A is the characteristic area (commonly the projected frontal area, wetted surface area or total surface area of the object). $\mathrm{C_D}$ can be used to compare the performance of different geometries at the same Re, assuming the boundary conditions are consistent.

Lift is the force that acts perpendicular to the flow direction. Similar to drag, it varies with the fluid properties and object geometry. The lift coefficient ($\mathrm{C_L}$) is defined as:

$$\mathrm{C_L} = \frac{2F_L}{\rho U^2 A}$$

where F_L is the lift force exerted by the fluid, ρ is the density of the fluid, U is the characteristic velocity and A is the characteristic area (typically the plan area).

The governing equations of fluid flow include the Navier–Stokes equations, which describe the motion of the fluid, and the continuity equation, which represents the conservation of mass. These equations can be simplified to make them easier to solve. Nevertheless, for all but the simplest problems, the equations must be solved numerically on a computer. This can be done by splitting up the flow domain into smaller cells, with the governing equations discretized and solved in each of these cells. This approach is termed *computational fluid dynamics*.

3 Steps in Computational Fluid Dynamics

Computational fluid dynamics dates back to the 1950s and 1960s, when the first computer simulations of fluid flows were undertaken (e.g. Evans & Harlow, 1957; Harlow & Welch, 1965; Hess & Smith, 1967). It has subsequently been used to address problems in a wide range of subjects, including paleontology (Rahman, 2017). In many cases, the same set of steps, outlined in this section, is followed.

The first step in a paleontological CFD study is to construct a digital model of the organism of interest. For an increasing number of extinct groups, three-dimensional virtual reconstructions of fossil specimens already exist. However, additional work to digitally correct taphonomic distortion and restore the original morphology of the organism (e.g. Lautenschlager, 2016) might be required. An alternative approach is to create digital models through box or NURBS modelling. This allows models to be constructed for taxa where complete, three-dimensionally preserved fossil specimens are not available, but is more subjective than tomographic or surface-based methods (Rahman & Lautenschlager, 2017).

In CFD simulations of flow around an organism, the computational domain surrounding the modelled organism must also be created. For three-dimensional models, this will typically consist of a cuboid or cylinder. The domain should be large enough to ensure full development of the flow around the model. A domain that extends three times the length of the model upstream, ten times the length of the model downstream and five times the size of the model in all other directions can be taken as a starting point. However, the optimal domain size will vary on a case-by-case basis, and sensitivity analyses should be undertaken to establish the most appropriate size (see later in this section).

Next, the domain is divided into a number of discrete cells (the mesh) (Figure 1A). The mesh is commonly made up of tetrahedral or hexahedral elements, with layers of prismatic elements at the fluid–solid interface to model the boundary layer. Increasing the number of mesh elements can improve the accuracy of the simulation, but will increase the memory requirements and computation time. Similar to the domain size, sensitivity analyses should be carried out to determine the optimal mesh size.

The material properties of the fluid, such as density and viscosity, must be specified. The flow model is then selected, which establishes the governing equations that will need to be solved in the simulation. The choice of model depends on the flow regime, which is indicated by the Reynolds number (see Section 2). Laminar flow can be described by the Navier–Stokes equations, but turbulent flows are more complex and so time-averaged equations of fluid

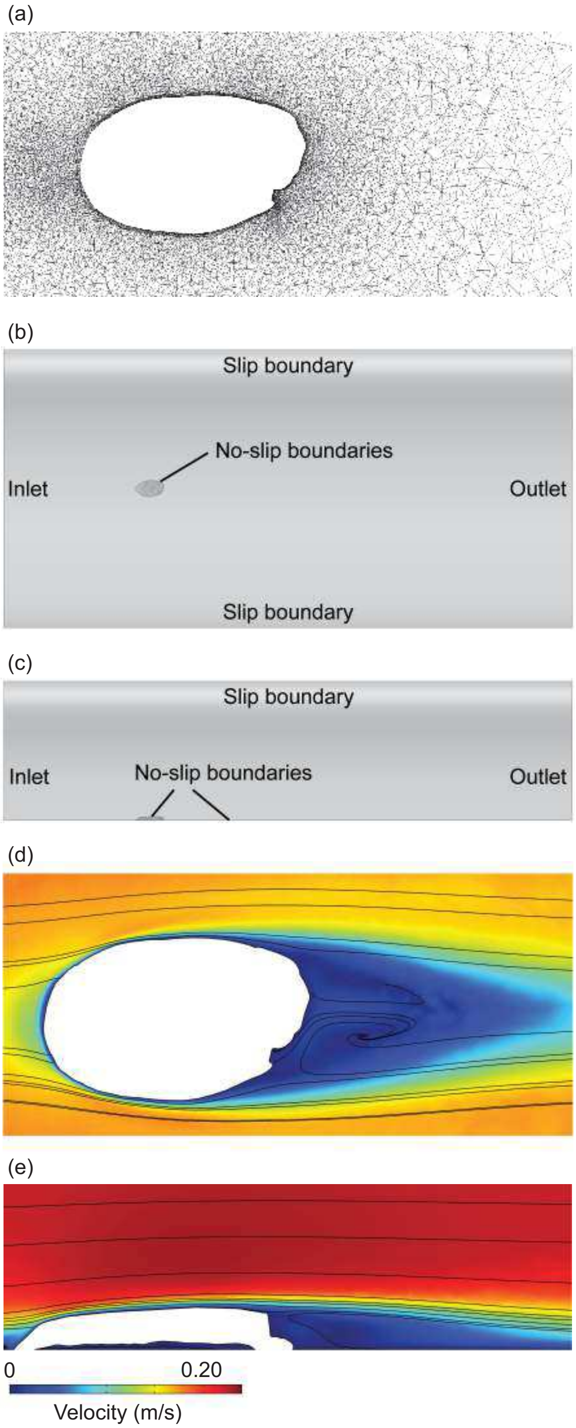

Figure 1 Steps in a paleontological CFD study. Simulation of water flow around a model of the cinctan *Protocinctus mansillaensis*. A: Two-dimensional plot

motion (the Reynolds-averaged Navier–Stokes, or RANS, equations) and a turbulence closure model are generally used. Various turbulence models exist, with the k-ε and shear stress transport (SST) models the most widely used in paleontological CFD analyses.

Following selection of the flow model, boundary conditions representing the flow variables are specified (Figures 1B, C). These include an inlet describing how flow enters the domain and an outlet that defines how it exits. Commonly, a velocity inlet and zero pressure outlet are used. For simulations of flow around a stationary organism, the inlet conditions will be informed by the current velocity, which can be inferred based on sedimentological characteristics (e.g. Stow et al., 2009) and/or direct measurements made in analogous modern environments (e.g. Emelyanov, 2005; Siedler et al., 2013). A no-slip boundary condition is often assigned to all solid surfaces (e.g. the model of the organism and the seafloor), meaning the fluid has zero velocity relative to the boundary. A slip boundary condition can be used for the remaining edges of the domain, allowing the flow to pass along these boundaries without friction.

When all of these steps have been completed, fluid flow is simulated by solving the discretized equations. This can be done using direct solvers, which are computationally expensive, or (more frequently) iterative solvers, which use less memory and can therefore reduce computation time. For steady flows, which do not vary temporally, a stationary solver is used to obtain a solution. However, for unsteady flows, where the flow properties change over time, a computationally much more expensive time-dependent solver must be used.

Computational fluid dynamics results are visualized and analysed in various ways. For example, plots of velocity magnitude supplemented with streamlines can be produced to study patterns of fluid flow around the modelled organism (Figures 1D, E). Furthermore, drag and lift forces and their coefficients (see Section 2) can be calculated to evaluate the forces exerted by the fluid on the organism. Testing the sensitivity of these results to simulation parameters, in particular the domain and mesh sizes, is a key part of the study. The size of the domain should be varied to determine the smallest possible domain that produces results matching theoretical expectations of flow development. Similarly,

Caption for Figure 1 (cont.)

(horizontal cross-section) of the mesh. B, C: Computational domain (top-down and side-on views, respectively) showing boundary conditions. D, E: Two-dimensional plots (horizontal and vertical cross-sections, respectively) of flow velocity with streamlines. Direction of ambient flow from left to right.

mesh independence must be established by undertaking simulations with different mesh sizes and identifying the coarsest mesh that did not substantially alter the results.

4 Examples in Echinoderm Paleobiology

Prior to CFD becoming part of the paleontologist’s toolkit, studies of the hydrodynamics of fossil echinoderms relied primarily on experiments in flume tanks. Crinoids were an initial focus of this work. Welch (1978) introduced life-size models of the Carboniferous camerate *Pterotocrinus* into a flume, performing experiments with models at three different orientations to the current. The results demonstrated that redirection of water flow to the filtration fan was strongest when the models were orientated with the fan perpendicular to the current direction and the ambulacral side downcurrent (Figure 2A), similar to the feeding posture of extant stalked crinoids. Building on this, Baumiller and Plotnick (1989) carried out experiments for models of *Pterotocrinus* with and without the wing-like tegminal appendages. This showed that the models with wing plates rotated into a position with the ambulacral side of the fan pointed downcurrent. Riddle (1989) placed fossil specimens and models of crinoid columns in a recirculating flow tank. He found that the models with helically twisted columns, as seen in some platycrinitids, deflected water strongly upwards (Figure 2B), towards where the filtration apparatus would have been located in the living animal. Baumiller (1990) conducted experiments using models of batocrinids with and without an anal tube. This revealed that the models with an anal tube reduced flow from the anus to the feeding appendages.

This experimental approach was also extended to other extinct echinoderm groups. Parsley (1990) studied flow around models of the diploporitan *Aristocystites*, orientated with the aboral end of the theca facing into the current. He was able to show that vortices were generated downcurrent of the oral end, transporting particles to the ambulacra. A similar pattern was documented for cinctans by Friedrich (1993), who found that the models orientated with the stele facing upcurrent created back eddies that brought particles towards the mouth and marginal grooves. Daley (1996) undertook flume experiments using a model of the solute *Coleicarpus sprinklei*, which revealed that turbulence was created around the single feeding appendage when the model was positioned close to the substrate. Huynh and colleagues (2015) investigated fluid flow in blastoid respiratory structures using a 72x scale model of part of the hydrospire of *Pentremites rusticus*. They observed that there was no mixing of water taken in through incurrent hydrospire pores within the associated hydrospire folds

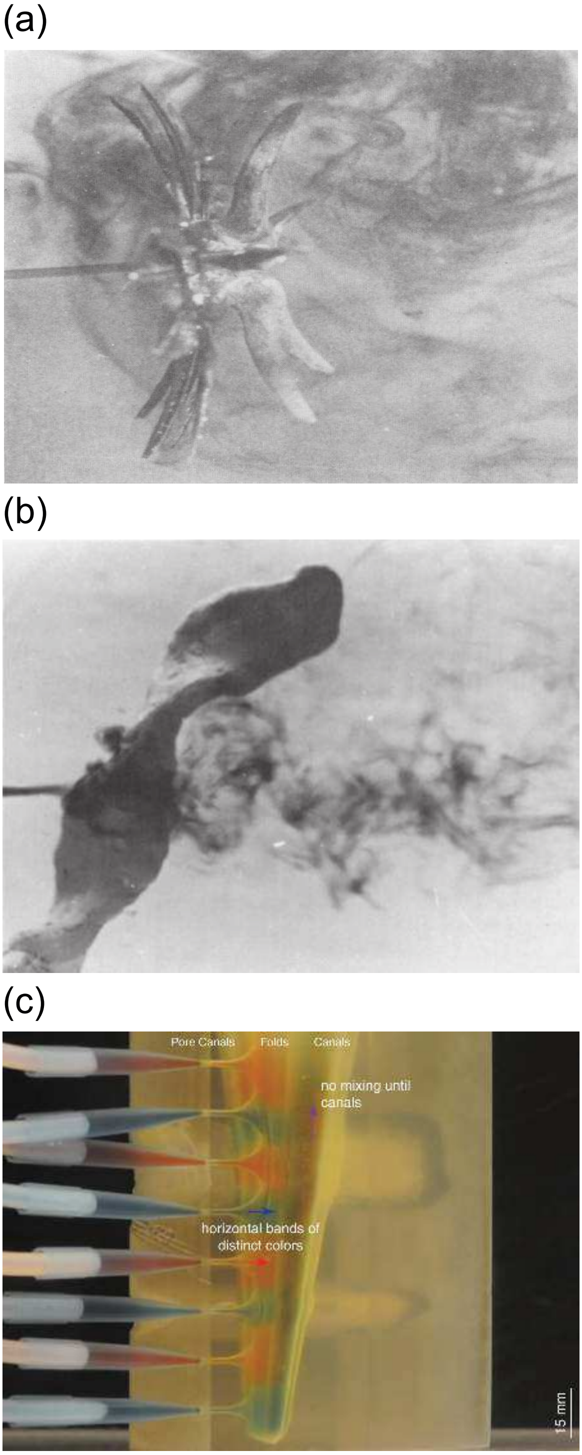

Figure 2 Flume experiments of fossil echinoderms. A: Water flow around a model of the crinoid *Pterotocrinus*. Modified from Welch (1978, fig. 3A),

(Figure 2C). Most recently, Parsley (2015) examined flow around models of the eocrinoids *Globoeocrinus*, *Guizhoueocrinus* and *Sinoeocrinus* in a flume tank. The results showed that the modelled brachioles were distally bent downcurrent by the flow, forming an open fan.

Computational fluid dynamics has considerable potential for expanding on this existing base of experimental work, enabling analyses of a wider range of model geometries and flow conditions. However, to date, only a few studies have applied the technique to fossil echinoderms. Rahman and colleagues (2015b) used the approach to explore the hydrodynamics of feeding in cinctans. Owing to their highly unusual body plan, which has no analogue among extant taxa, it is debated whether cinctans were passive suspension feeders (e.g. Parsley, 1999; David et al., 2000) or active filter feeders (e.g. Smith, 2005; Zamora & Smith, 2008). Computational fluid dynamics was used to test between these competing hypotheses. A digital model of the cinctan *Protocinctus mansillaensis*, created from an X-ray microtomography scan of the holotype (Rahman & Zamora, 2009), was placed in a virtual flume tank. Computer simulations of water flow were performed at inlet velocities of 0.05, 0.1 and 0.2 m/s, chosen to represent typical current velocities in the offshore environments inhabited by *Protocinctus* (Álvaro & Vennin, 1997). Models were positioned at different orientations and burial depths, and passive and active feeding scenarios were simulated by varying the boundary conditions at the main body openings. The results showed that in all cases the models positioned with the mouth downcurrent and the ventral swelling buried generated the least drag and lift, suggesting this position was optimal for enhancing stability. Moreover, in this orientation there was very little flow to the mouth and associated marginal groove in the simulations of passive feeding, demonstrating that such a feeding strategy would have been an ineffective way of obtaining nutrients. Conversely, there was strong flow to the mouth in the simulations of active feeding (Figure 3A), indicating that this was the most probable feeding mode and supporting previous interpretations of cinctans as pharyngeal filter feeders (e.g. Smith, 2005; Zamora & Smith, 2008).

Caption for Figure 2 (cont.)

reproduced with permission from Cambridge University Press. B: Water flow around a model of the column of the crinoid *Platycrinites*. Modified from Riddle (1989, fig. 1.3), reproduced with permission from Cambridge University Press. C: Water flow within a model of part of the hydrospire of the blastoid *Pentremites rusticus*. Modified from Huynh and colleagues (2015, fig. 4), reproduced under a CC BY-NC-SA 4.0 license.

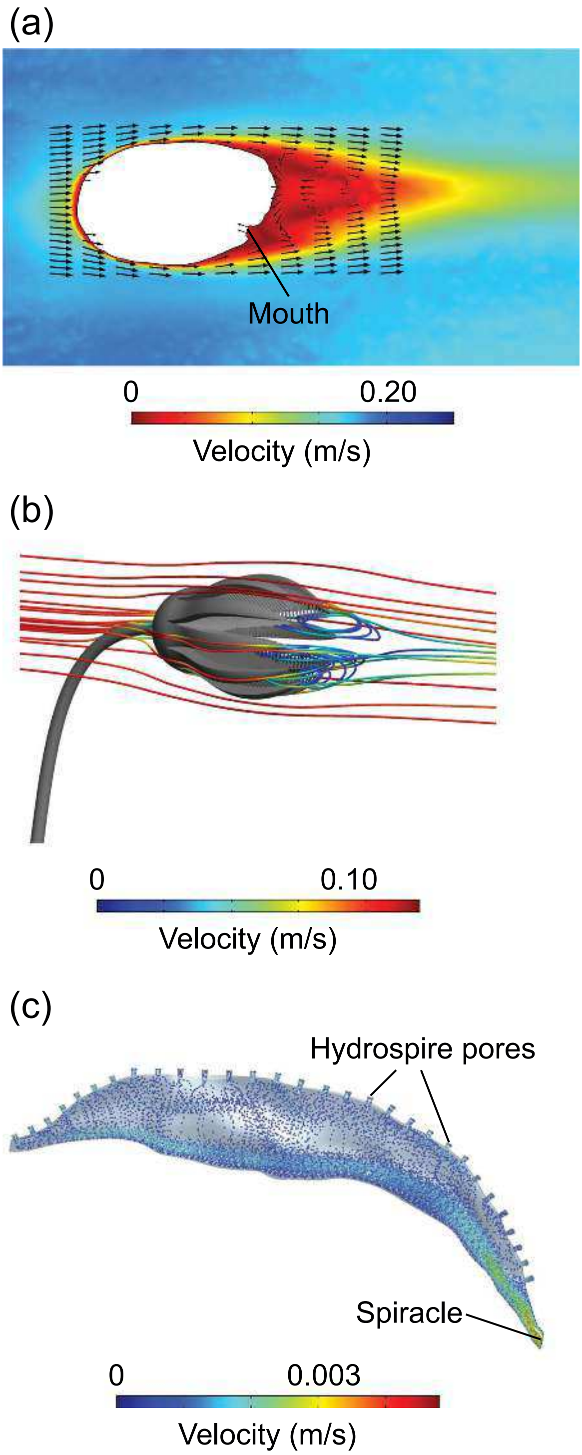

Figure 3 CFD analyses of fossil echinoderms. A: Two-dimensional plot (horizontal cross-section) of flow velocity with vectors from simulation of