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Feasibility of spectral-element modeling of wave propagation through the anatomy of marine mammals

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ABSTRACT:

This study introduces the first three-dimensional spectral-element method (SEM) simulation of ultrasonic wave propagation in the head of a bottlenose dolphin (*Tursiops truncatus*). Unlike traditional finite-element methods (FEM), which struggle with high-frequency simulations because of costly linear-system inversions and slower convergence, SEM offers exponential convergence and efficient parallel computation. Using computed tomography data, we developed a detailed hexahedral mesh capturing key anatomical features, such as acoustic fats and lower jaws. Our simulations of plane and spherical waves confirm SEM's effectiveness for ultrasonic time-domain modeling. This approach opens new avenues for marine-bioacoustic research, including echolocation, the biophysics of hearing and sound generation, and assessments of anthropogenic underwater noise. By overcoming FEM's limitations, SEM provides a powerful scalable tool to test hypotheses in dolphin bioacoustics, with significant implications for conservation and understanding marine-mammal auditory systems under increasing environmental challenges.

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I. INTRODUCTION

Numerical simulations of wave propagation in biological media have garnered significant attention in recent years, with a vast span of applications, ranging from medical physics (Bachmann and Tromp, 2020; Grimal *et al.*, 2004; Gu and Jing, 2015; van 't Wout *et al.*, 2015) to bioacoustics (Hejazi Nooghabi *et al.*, 2021; Wei *et al.*, 2024) and ecology (Castellazzi *et al.*, 2012). In prior work, some authors of this study highlighted the challenges of explaining the accuracy of auditory source localization by dolphins, particularly given their lack of pinnae. Gaining a better understanding of how elastic waves propagate through their bodies may help unravel some of the remaining mysteries of biosonar (Hejazi Nooghabi *et al.*, 2021; Nachtigall, 2016; Ali *et al.*, 2025).

Until recently, the feasibility of time-domain simulations through realistically complex biological structures remained uncertain. Advancements in computational power and a growing interest in biodiversity conservation have driven a greater focus on numerical methods. These methods are developed, adapted, or applied to study, for instance,

sound generation and propagation in animals, especially when experiments are not feasible (Feng *et al.*, 2019; Kazemi *et al.*, 2023). The leading numerical solvers in this context include the finite-element method (FEM) (Alnaes *et al.*, 2015; Arndt *et al.*, 2021; COMSOL Inc., 2024; Hecht, 2012), the boundary element method (BEM) (Bettcke and Scroggs, 2021; Haqshenas *et al.*, 2021), ray tracing (Porter and Bucker, 1987), and pseudo-spectral methods (Treeby *et al.*, 2014). Although each approach has specific strengths and weaknesses, performing wave-based simulations that account for fluid-elastic coupling, operate in the ultrasonic frequency range, and solve time-domain propagation have historically been highly impractical. This is where the spectral-element method (SEM) (Komatitsch and Tromp, 1999; Patera, 1984) stands out. SEM inherits from FEM the capability to handle complex geometries, but, unlike FEM, requires no linear-system inversion, which is a notoriously costly endeavor (Komatitsch *et al.*, 2000). In addition, compared to traditional FEM, SEM converges exponentially rather than with second-order accuracy, and as such it is particularly efficient for solving time-domain wave propagation problems. Well-known and widely used examples of SEM solvers are the commercial package SALVUS (Afanasyev

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et al., 2018) and its open-source counterpart SPECFEM (Komatitsch and Tromp, 2002a,b), used in this study. SPECFEM is FORTRAN-based, with no user interface, but is relatively simple to use and very efficiently parallelized. It was originally designed for use on large supercomputer clusters, where it still excels.

SPECFEM was originally developed by seismologists for global-scale seismology applications. In over two decades, it has been used successfully by geophysicists all over the world; its effectiveness has been largely proved at scales of (at least) a few km and in the infrasound frequency range. Scaling it to higher frequencies and shorter spatial scale lengths is, in theory, straightforward. However, the anatomy of marine mammals presents complexities not found in geological media. Reducing such intricate structures to discrete, numerical “meshes” turns out to be a non-trivial problem, to say the least. As a result and despite their potential, SPECFEM, and SEM in general, have not yet been applied to simulations of wave propagation in marine mammals. The literature on biological applications of SEM is, in fact, sparse [e.g., (Marty *et al.*, 2022a; Marty *et al.*, 2022b; Marty *et al.*, 2024)]. Perhaps the most significant challenge is that SEM inherently relies on hexahedral element meshes (see Ferroni, 2017) to understand the difficulties of applying SEM to non-hexahedral meshes. Unlike tetrahedral meshes, which can be generated algorithmically, e.g., via Delaunay triangulation, there is no automated tool to generate hexahedral meshes; such an algorithm is often referred to as the “Holy Grail” of mesh generation (Blacker, 2000). Potential users of SEM are cautioned that as the apocryphal rule of thumb states, they may spend around 80% of their time creating valid models and meshes before those can be fed to the SEM solver itself. On the other hand, other numerical methods such as traditional FEM, although easier to set up, often face scalability challenges as they require that linear systems be solved at each numerical iteration. Seismology applications of SEM suggest that mesh-related issues can be overcome, and we infer that SEM is potentially the most powerful available tool for addressing three-dimensional (3D) wave propagation in biological structures. This is particularly true for marine mammals, which have complex and yet to be fully explored auditory systems. Indeed, the need to model intrinsically complex shapes, to identify the contribution of different anatomical features, to place virtual sensors in otherwise inaccessible anatomical locations, and to estimate the effect of potentially harmful vibrations all emphasize the importance of efficient numerical simulations.

Several studies, mostly carried out by Chong Wei and his team, have addressed the problem of simulating sound propagation in marine mammals, especially in dolphins. Various hypotheses have been proposed to explain how dolphins receive and emit sound (Wei *et al.*, 2018a; Wei *et al.*, 2020), involving the roles of the melon (Zhang *et al.*, 2017), forehead shape (Wei *et al.*, 2022), and other anatomical structures (Song *et al.*, 2016; Wei *et al.*, 2016); the biosonar beam formation (Wei *et al.*, 2018b); and even biosonar-inspired metamaterials (Dong *et al.*, 2019). These studies relied mainly on two-dimensional (2D) models, which,

although they do contribute to advance our understanding of dolphin hearing and biosonar, do not capture its full complexity. The recent 3D FEM-based model of Wei *et al.* (2024) is very promising for overcoming this difficulty, but we submit that in the long run SEM might provide us with an equally or more efficient tool for 3D numerical modeling.

In this paper, we evaluate the feasibility of SEM-based simulations of 3D time-domain wave propagation in a real bottlenose dolphin head (*Tursiops truncatus*). We outline the challenges of using SEM for such simulations in animal tissues and anatomical structures, detailing the modeling process from input data derived from computed tomography (CT) scans, to geometry creation, mesh generation, and finally, wave propagation based on the SPECFEM3D module of SPECFEM.

II. THE SEM: GENERAL NOTIONS

All simulations in this study were conducted using the SPECFEM3D package (Komatitsch and Tromp, 1999; Komatitsch and Vilotte, 1998), a widely known and validated implementation of SEM. SEM (Patera, 1984) is a so-called high-order FEM, i.e., it uses high-order polynomial basis functions to approximate the numerical solution within each element of a discrete mesh. A brief overview of the method is presented here, intended to highlight the aspects of SEM that are most relevant to our application. For an accessible introduction to SEM, compared to other numerical methods, see Igel (2016, Chap. 7).

Consider the scalar potential $\varphi(\mathbf{x}, t)$ and a differential operator $\mathcal{L}$ describing the propagation of acoustic or elastic waves excited by a force f in lossless bounded acoustic and elastic domains Ω_a and Ω_e , respectively, with $\Omega_a \cup \Omega_e = \Omega$ as follows:

$$\mathcal{L}\varphi = f \quad \text{in } \Omega_{a,e}. \quad (1)$$

To solve Eq. (1), we first derive the weak form by multiplying the operator $\mathcal{L}$ by a test function $v \in V$ (a suitable function space) and integrate over the domain. The problem is then reformulated as finding $\varphi \in V$ such that

$$\int_{\Omega_{a,e}} v \mathcal{L}\varphi \, d\Omega_{a,e} = \int_{\Omega_{a,e}} v f \, d\Omega_{a,e}, \quad \forall v \in V. \quad (2)$$

The fluid-elastic coupled system in Eq. (2) can be expressed in matrix form (Marty *et al.*, 2024) as

$$\begin{bmatrix} \mathbf{M}_a \partial t^2 + \mathbf{K}_a & -\mathbf{C}_a \\ -\mathbf{C}_e \partial t^2 & \mathbf{M}_e \partial t^2 + \mathbf{K}_e \end{bmatrix} \begin{pmatrix} \varphi \\ \mathbf{u} \end{pmatrix} = \begin{pmatrix} \mathbf{F}_a \\ \mathbf{F}_e \end{pmatrix}, \quad (3)$$

where $\mathbf{u}(\mathbf{x}, t) = \rho^{-1} \nabla \varphi$ denotes the displacement of a moving particle, ρ the volumetric density, $\mathbf{M}_{a,e}$ the mass matrix, $\mathbf{K}_{a,e}$ the stiffness matrix, $\mathbf{C}_{a,e}$ the coupling matrix, and $\mathbf{F}_{a,e}$ is the source term expressed in the right-hand side of Eq. (2). The attractiveness of the SEM is that the global mass matrix is diagonal by construction, therefore solving the coupled fluid-elastic system, i.e., Eq. (3) can be

implemented with matrix-inversion-free time-domain solvers and implicit time-stepping schemes (e.g., Newmark).

A. Numerical parametrization of the solution

Within each discrete non-overlapping element, the solution φ is approximated by a high-order polynomial of degree N ,

$$\varphi(\mathbf{x}) = \sum_{i=0}^N \alpha_i \phi_i(\mathbf{x}). \quad (4)$$

The basis functions $\phi_i(\mathbf{x})$ are defined at the Gauss–Legendre–Lobatto (GLL) points within the element, and scaled by the nodal coefficients α_i . Namely,

$$\phi_i(\xi) = \prod_{\substack{j=0 \\ j \neq i}}^N \frac{\xi - \xi_j}{\xi_i - \xi_j}, \quad (5)$$

in which ξ represents a normalized coordinate within a standard reference element, which is typically the interval $[-1, 1]$.

B. Fluid-elastic coupling

When the medium to be modeled includes both fluid and solid regions, SPECIFEM implements the full elastic equation only in the solid elements and the more compact acoustic wave equation in the fluid ones. This reduces the computational cost of the simulation as the acoustic wave equation is less computationally expensive (scalar) than the elastic wave equation (vector) (Komatitsch *et al.*, 2000). At fluid-solid interfaces, boundary conditions are implemented explicitly, prescribing the continuity of pressure and normal stress.

III. FROM CT SCANS TO NUMERICAL SIMULATIONS

SPECIFEM requires that the medium to be modeled be projected onto a hexahedral mesh, and creating hexahedral meshes is notoriously complex and challenging. Successful simulations depend on each preceding step. To make sure that our results are fully reproducible and to facilitate future applications of our method, we next describe the entire procedure (summarized by Fig. 1) in some detail.

A. CT scans

To create a 3D model of the dolphin head, we used CT scans of a bottlenose dolphin (*Tursiops truncatus*) obtained from the Biology Department at the University of Padua. The resolution of the CT scan was $0.813 \times 0.813 \times 1.5$ mm. The head corresponds to an old individual with some missing teeth, as shown in Fig. 2(a). The CT scans were processed using 3D SLICER (Fedorov *et al.*, 2012), an open-source software for medical image processing and three-dimensional visualization. CT scans are commonly formatted as multiple DICOM files; each file is a 2D image

slice in which each pixel represents a voxel in 3D space. The intensity of each voxel corresponds to the Hounsfield unit (HU) value of each tissue (Brooks, 1977). We relied on HU values to differentiate between different types of tissues, such as bone, fat, and soft tissue. We employed 3D SLICER to identify and isolate the different types of tissues found in the dolphin through a process usually referred to as “segmentation.” This involved manually selecting the regions of interest and applying thresholding techniques (see Fig. 2). We segmented four types of tissue: bone, acoustic fat, melon, and soft tissue. The soft tissue is bounded externally by the skin [Fig. 2(b)] and internally by adjacent anatomical structures. Following segmentation, we exported each part in stereo-lithography (STL) format. STL is a widely used format for 3D printing and computer-aided design (CAD) applications. It represents the outer surface of a volume using a mesh of triangular facets.

B. Geometry manipulation

The resulting STL files were imported into BLENDER (Blender Foundation, 2022), where we performed some geometry modifications, such as smoothing sharp edges, removing all teeth and filling some internal canals within the skull, as well as some foramen holes. This helped simplify the subsequent meshing process. In fact, it would have been possible, in principle, to keep much of the details that we decided to smooth away. However, this would have implied a sharp decrease in the mesh size, with a corresponding increase in computational cost, which seemed unnecessary to our current feasibility study (conducted on relatively limited computational resources).

We next refined the mesh in MESH LAB (Cignoni *et al.*, 2008), removing any duplicate vertices, fixing non-manifold edges and other artifacts, occasionally left by BLENDER, that could cause problems in the subsequent process. This step can be implemented in PYTHON using PYMESH LAB (Muntoni and Cignoni, 2021), for all the files of interest at once. There are also multiple purchasable plug-ins in BLENDER intended to do this, but we have not explored them yet.

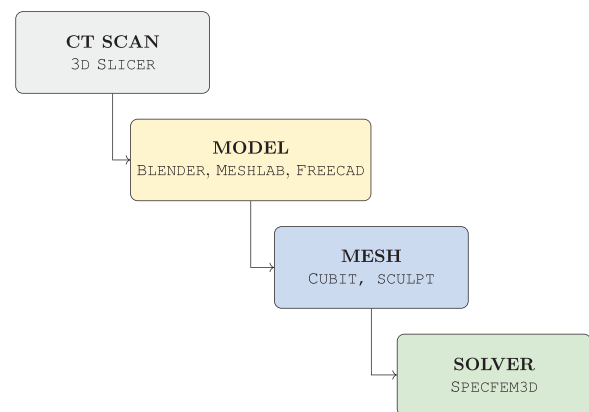


FIG. 1. Workflow. Software packages used at each step are specified in small fonts in the corresponding block.

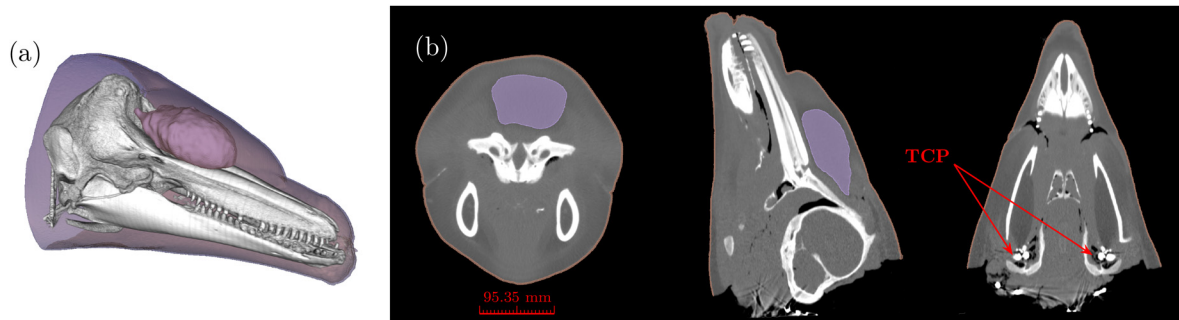


FIG. 2. Segmentation in 3Dy SLICER. (a) Original skull before segmentation. The melon and skin boundaries after segmentation. Some details from the original skull, such as the teeth, have been removed or smoothed to facilitate the meshing process. (b) The frontal (left), side (center), and bottom (right) views illustrate the segmentation processes for the skin (thin orange lines) and the melon (purple area). The TPC could be identified, although CT resolution was insufficient for detailed segmentation of its morphology.

Next, the resulting individual STL files were imported into FREECAD (Rieger *et al.*, 2024). A complete 3D model was constructed, including a water-filled rectangular box surrounding the dolphin head [Fig. 3(a)], with dimensions $0.42 \times 0.42 \times 0.86$ m. The model was designed to be large enough to capture the incoming signal well and small enough to minimize the computational cost of the simulation. The head was separated from the body before the CT scans were taken so some smoothing was needed at the back of the head. In SPECIFEM3D, outer surfaces must be aligned with the Cartesian plane for imposing non-reflecting boundary conditions. The back of the head was sculpted and sliced to align with the origin xy -plane, as shown in Fig. 3(a).

The imported STL files represent the outer surface mesh of a 3D volume. The next step consists of explicitly creating all interfaces between different domains, e.g., between soft and fat tissues, to ensure continuity of nodes when finally building the hexahedral mesh. The easiest way

to achieve this is via so-called “boolean operations,” i.e., subtracting, intersecting, and merging different objects that are in contact with each other. FREECAD provides simple but powerful tools for such operations. Specifically, we used the “boolean fragments” operation between objects that share surfaces, starting from the inner tissues and progressing to the outer ones. Boolean fragments create additional nodes when performing boolean operations, ensuring that meshes are conformal (Rieger *et al.*, 2024). BLENDER and MESHLAB can also perform boolean operations, but they do not incorporate boolean fragments, and the resulting meshes are not conformal.

Acoustic fats and jaws [see Figs. 3(c) and 3(d)] are enclosed within and in contact with the soft tissues. To properly honor such a complex structure, we first create an auxiliary object from the union of the acoustic fats and the jaws. This union was performed as a boolean fragment. We then subtract this auxiliary object from the fat tissues, which

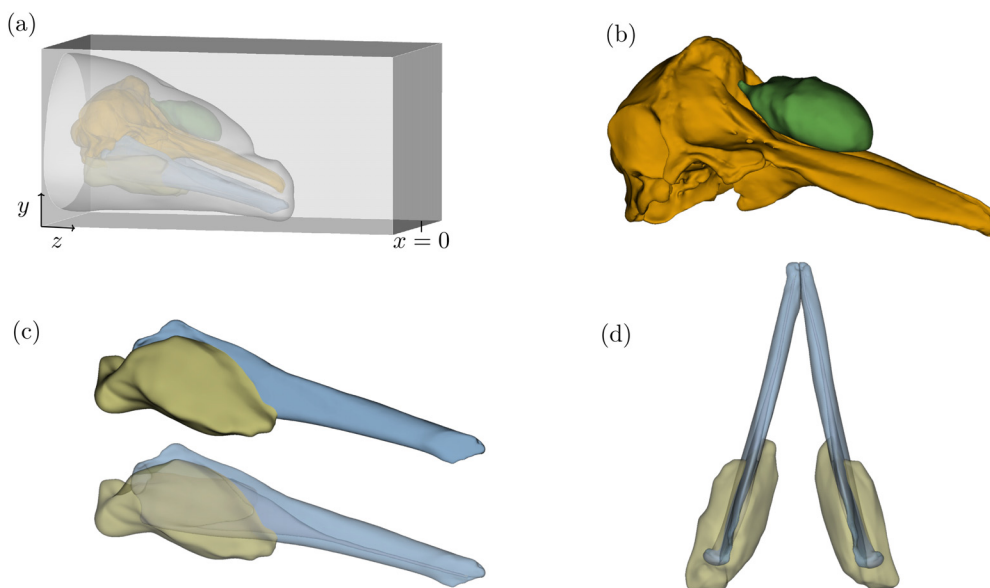


FIG. 3. Model geometry. (a) Complete model. The shaded box corresponds to the volume of water surrounding the dolphin head. Other anatomical features depicted are: the melon (green), skull (orange), lower jaws (light blue), and acoustic fats (light yellow). (b) Skull and melon geometry. (c) Side view, jaws and acoustic fats, opaque (top) and slightly transparent (bottom). (d) Top view, jaws and acoustic fats (slightly transparent). Transparency is necessary to visualize the bones that the fats partly enclose.

ensures explicit nodes at both boundaries. Creating the boundary surfaces for the skull and the melon [e.g., Fig. 3(b)] is simpler and can be done directly, without any further auxiliary object.

Last, the back of the head is aligned with the Cartesian plane xy . At the same position in z , we place the back side of the water volume. Care must be taken when performing the boolean subtraction between the soft tissues and the water volume at the back of the head as most algorithms do not handle coplanar faces well. To avoid issues, we slightly moved one object, the head in this case, a very small distance, e.g., 1 mm in the z direction. We then performed the subtraction and, finally, took away from the head the remaining 1 mm section.

C. Meshing process

This final model is imported into COREFORM CUBIT (Coreform LLC, 2024), a software for geometry manipulation and hexahedral mesh generation that is typically used in conjunction with SPECIFEM. Within CUBIT, the SCULPT tool was used to create a high-quality mesh of the dolphin head, as shown in Fig. 4. SCULPT employs an overlay-grid method, specifically an inside-out approach, for semi-automated hexahedral meshing. This method begins with a base Cartesian grid that encompasses the geometry and then carves, or sculpts, the geometric features from this grid to produce the final hexahedral mesh (Owen *et al.*, 2014), as shown in Fig. 4(a). Moreover, the results from the boolean fraction operations may leave some traces, as seen in Fig. 4(b). The fragmented geometry tells SCULPT explicitly where to mesh in such complex shapes. Figure 4(b) shows a small deformation in the outer part of the bone. This deformation, not present in the geometry, can be clearly seen as a line on the surface of the right jaw. This is an effect of SCULPT trying to create a conformal mesh for the acoustic fat and the jaw at the same time.

It should be noted that BLENDER, MESHLAB, and CUBIT each incorporate their own tools for cleaning and manipulating geometries through boolean operations, which are necessary for SCULPT to create complex meshes with mesh adaptivity. As previously mentioned, FREECAD was better suited to our needs because it ensures these operations produce a fragmented geometry mesh, i.e., a geometry where the intersections between objects have conformal surface meshes.

CUBIT allows us to define the material properties of each anatomical feature, assign faces to boundary conditions, and export the resulting mesh directly to SPECIFEM3D through PYTHON functions included in the package. Although simple to use, SCULPT can yield different results depending on the parameters used. For example, the present model was successfully meshed with SCULPT using a maximum cell size of 2.5 mm, but it may produce distorted elements if the cell size is decreased. This may seem counter-intuitive and is largely because of the nature of mesh sculpting and mesh adaptivity. At this stage, some trial and error is necessary to

determine the appropriate parameters. Most of these mesh-related problems can, in fact, be mitigated by drastically reducing the mesh size, for example, to 1 mm. However, this approach can lead to a significant increase in the number of elements. As a result, the computational cost scales polynomially with the inverse of the mesh size.

The mesh quality is evaluated according to the scaled Jacobian, which is based on the determinant of the Jacobian matrix (Knupp, 2001). SEM can accurately handle highly distorted mesh elements (Komatitsch, 2010; Maday and Rønquist, 1990), and although meshes with scaled Jacobian values above 0.5 are preferred, values above 0.2 are generally considered acceptable. However, achieving such values remains challenging when using semi-automated tools such as SCULPT. In our case, the average scaled Jacobian was 0.92, with a minimum value of 0.16, and only 11 elements had a scaled Jacobian below 0.2. Although these elements fall within the “poor quality” range, we considered them acceptable for the purposes of this feasibility study. At interfaces and/or particularly complex features, such as the skull, jaws, and acoustic fats [i.e., Figs. 4(b)–4(d)], mesh adaptivity was applied using one layer of SCULPT’s material-based adaptivity followed by two iterations of Laplacian smoothing (Owen, 2012). Additional parameters are specified in the Appendix. Using a computer with 24 cores, SCULPT took about 24 min to generate a mesh consisting of about 16×10^6 elements and consumed approximately 100 GB of RAM. The output mesh has a maximum element side size of 2.5 mm, by design, and a minimum element side size of 0.1 mm, automatically determined by SCULPT when applying adaptive meshing to capture small, complex features.

Finally, alternative methods and algorithms for automated hexahedral meshing could be taken into consideration. This is a critical step in using SEM as a wave propagation solver. For example, it is possible to generate hexahedral meshes from tetrahedral meshes (Gao *et al.*, 2025). However, the quality of the resulting meshes is generally poor (Baker, 2005). Improving such methods may alleviate the efforts required by hexahedral meshing for complex geometries.

D. Simulation setup

Our simulations were performed using with five GLL points in SPECIFEM3D, version 4.0.0, which supports direct visualization of models and simulations in PARAVIEW (Ahrens *et al.*, 2005) without requiring additional post-processing. The choice of five GLL points is documented in the literature as a good compromise between accuracy and cost (Komatitsch and Tromp, 1999; Seriani and Priolo, 1994). Each simulation was run on our local workstation consisting of one central processing unit (Intel Xeon Gold 5418Y, Intel Corporation, Santa Clara, CA) with 24 physical cores. The simulation used about 50 GB of RAM and lasted 400 h of runtime.

The mesh element size h is generally determined based on the number of GLL points and the minimum wavelength to be resolved $\lambda_{\min}$. The minimum wavelength size can be

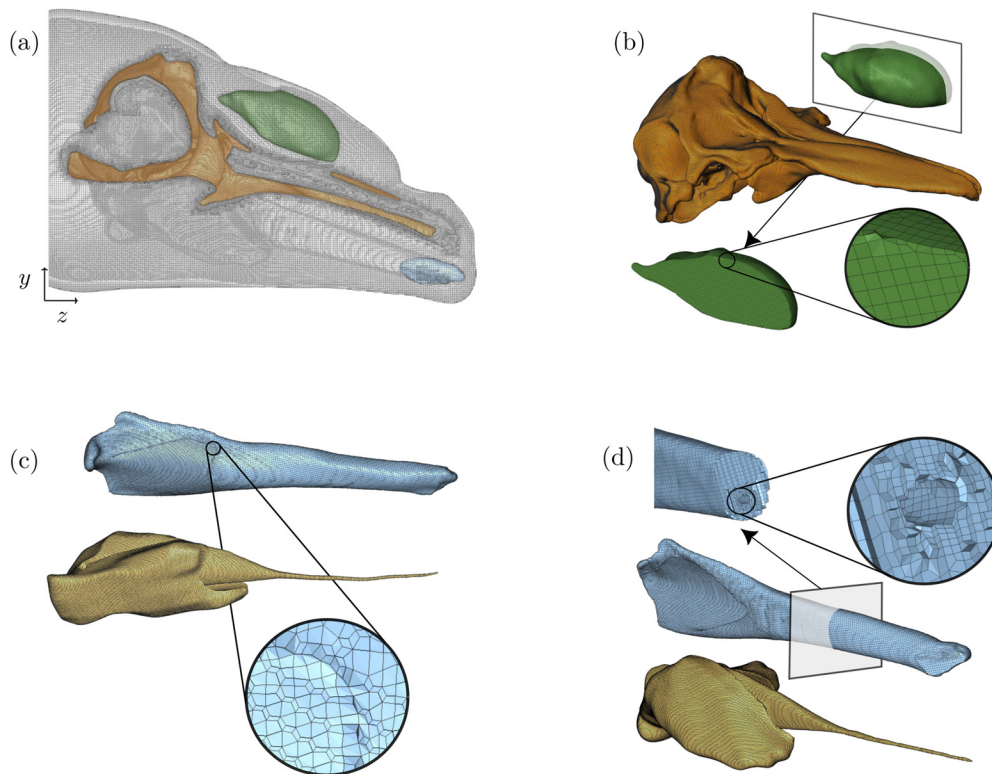


FIG. 4. (a) Transparent view of the mesh. A clipping plane along the median yz -plane at $x = 0$ was applied to reveal its internal structure. (b) Details of the skull and melon. Most elements are regular voxels, except near the interfaces, where they adapt to the geometry to form a conformal mesh as shown in the enlarged view outlined by a black circle. (c) Right side of the jaw and acoustic fats. The detail shows the conformal mesh between both tissues. (d) Left side of the jaw and acoustic fats. The interior bone cavity, filled with fat tissue and shown in detail, is a good example of mesh adaptivity.

calculated using the average distance between points $\lambda_{\min} = h \times \text{PPW} / (\text{NGLL} - 1)$. To control numerical dispersion, it is commonly recommended that a minimum of five (Komatitsch and Tromp, 1999) to six (Oliveira, 2018) points per wavelength be used, particularly for fourth-degree SEM, as used in this study. The corresponding values are summarized in Table I for each tissue. Our approach, however, was slightly different. Given the inherently complex nature of the geometry (characterized by very small features and delicate tissue structures) and the limitations in meshing such fine-scale details, we instead tailored the mesh size to accommodate these constraints while still ensuring a sufficiently high number of points per wavelength to preserve numerical accuracy. This allows us to better handle complex geometries but creates small elements that diminished the time step.

The time step Δt is determined by the Courant number C , the characteristic element size h , and the wave speed v . Both Δt and C are automatically calculated by SPEC-FEM3D and must satisfy $\Delta t < C \min(h/v)$ (Komatitsch and Vilotte, 1998). For this simulation, $\Delta t = 1.69 \times 10^{-9}$ s, and the total simulation time was $t = 0.7$ ms. Boundary conditions were defined using Clayton–Engquist absorbing boundary conditions (Komatitsch and Tromp, 1999), which minimize reflections at the mesh boundaries. Also known as “Stacey” boundary conditions, they are simple to implement in SPEC-FEM3D but may produce strong reflections at grazing angles. A tapered profile

was accordingly applied near each border [see Fig. 5(c)]. This profile gradually reduces the wave amplitude near the edges using a smooth Gaussian function, which helps to absorb outgoing waves and minimize artificial reflections.

SPEC-FEM3D supports GPU acceleration (Komatitsch, 2010), which could reduce the computation time by a factor of 5 to 10 per core; its scalability on large clusters is straightforward, and the simulations presented here could be completed within minutes on a typical “supercomputer.” However, not all features of SPEC-FEM3D are yet implemented on GPU; for instance, absorbing boundary conditions cannot yet be reliably prescribed via the perfectly matched-layer method.

TABLE I. Element size h , minimum wavelength $\lambda_{\min}$, elements per wavelength, and points per wavelength calculated using the average distance between points.

Tissue	h_{avg} (mm)	h_{max} (mm)	$\lambda_{\min}(v_p, v_s)$	EPW ^a	PPW ^b
Soft tissues	1.4	2.5	5.3	1.72	8.6
Skull	0.94	1.3	45.0	27.95	139.77
Melon	2.0	2.5	4.6	1.47	7.36
Acoustic fats	1.1	1.3	4.7	2.86	14.31
Jaws	0.87	2.5	45.0	14.54	72.68
Water	2.5	2.5	37.0	11.84	59.20

^aElements per wavelength (EPW).

^bPoints per wavelength (PPW).

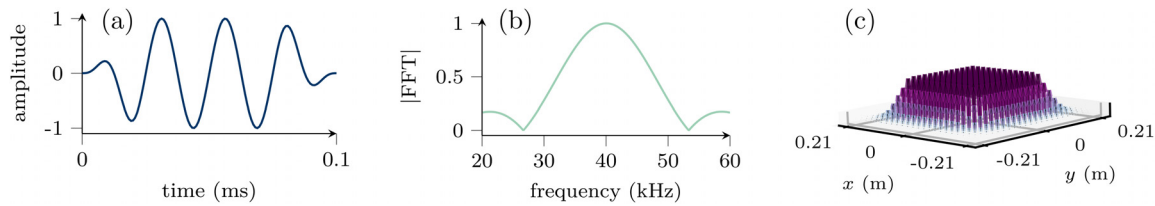


FIG. 5. (a) Source signal with four-cycles at 40 kHz. The waveform has been windowed with a Tukey window of length 0.1 ms. (b) Spectrum of the signal. The bandwidth of the first zeros (below 30 kHz and above 50 kHz) correspond to length of the window. (c) Tapered wave profile. The arrows colors and lengths illustrate the assigned force amplitudes of the signal and point in the $-z$ direction, toward the dolphin's head.

Through the rest of the present study, we shall discuss the results of two simulations: a plane wave incident on the head and a point source within the dolphin head. The first simulation consists on a plane wave source placed in front of the dolphin head, emitting four cycles with a fundamental frequency $f_0 = 40$ kHz, and Tukey-windowed as per Figs. 5(a) and 5(b). In practice, multiple point sources fired simultaneously along the z direction toward the dolphin head. Approaching the boundaries of the numerical domain, a Gaussian-shaped taper (decaying with decreasing distance from the boundary) was applied to the magnitude of point sources [Fig. 5(c)]. The resulting wavefield was recorded near the approximate locations of the left and right tympano-periotic complexes (TPCs). The TPC consists of the tympanic and periotic bones, which house the cochlea, vestibule, and semicircular canals, and are responsible for hearing and balance in dolphins (Cozzi *et al.*, 2017). Our CT scan data and mesh do not honor the extreme complexity of this area, but the simulations should describe fairly accurately vibrations at the end of the acoustic-fat area.

The second simulation involves a single point source inside the dolphin head. The source was placed near the location of the phonic lips, the anatomical origin of sound production in odontocetes (Cranford *et al.*, 2011). The source was defined as a force oriented along the z axis, varying in time as in Fig. 5(a).

E. Material properties

The density as well as shear and compressional velocities values of the dolphin head were derived from the CT scan described above, via the HU values. On the basis of HU values, we identified four different types of tissue and assigned a single set of average density and shear and compressional velocity to each, as per Table II. Other authors

TABLE II. Material properties of the dolphin head and surrounding medium, including the range of HUs, volumetric density ρ ($\text{kg} \cdot \text{m}^{-3}$), compressional wave velocity v_p ($\text{m} \cdot \text{s}^{-1}$), and shear wave velocity v_s ($\text{m} \cdot \text{s}^{-1}$).

Material	HU _{min}	HU _{max}	ρ	v_p	v_s
Soft tissue	−35	110	1013	1536	215
Acoustic fat	−115	−35	928	1390	186
Melon	−115	−35	884	1316	184
Bone	235	2030	2035	3400	1817
Water	<−2000		1028	1480	0

prefer to derive more complex 3D density-velocity maps directly from the HU values (Wei *et al.*, 2015); this could make a significant difference as the mechanic properties of some tissues (e.g., the melon) are known to vary, but it is not relevant to the feasibility of our general approach.

F. Model validation

SPECFEM3D has been validated in many earlier studies, including against analytical solutions (e.g., Komatitsch and Tromp, 1999, 2002a). We conduct here an additional test, to quantify numerical errors that might have been introduced by the specific complexities of the biological structures that characterize our model and the difficulty to honor them perfectly. We believe that most such errors will change “randomly” upon changing the locations of source and/or receiver. Accordingly, we base our test on the so-called reciprocity theorem (Aki and Richards, 1980). Consider the Green’s function $G = G(\mathbf{r}, t | \mathbf{r}_1, \tau)$ solution of $\mathcal{L}G = \delta(\mathbf{r} - \mathbf{r}_1)\delta(t - \tau)$, where the differential operator $\mathcal{L}$ describes as always the propagation of acoustic or elastic waves. For any pair of locations $\mathbf{r}_1, \mathbf{r}_2$, the reciprocity theorem states that

$$G(\mathbf{r}_1, t | \mathbf{r}_2, \tau) = G(\mathbf{r}_2, t | \mathbf{r}_1, \tau), \quad (6)$$

i.e., the physical quantity measured at point $\mathbf{r}_2$ at time τ because of an impulse source at $\mathbf{r}_1$ at time t is equal to that measured at $\mathbf{r}_1$ at time t because of an impulse source at $\mathbf{r}_2$ at τ . This reflects spatial symmetry: i.e., swapping the locations of source and receiver results in the same recorded signal.

We placed two sources on the (approximately) median plane of the dolphin head, parallel to one another and pointing in opposite directions as depicted in Fig. 6(a). Figure 6(b) shows the z -components of the velocity field generated by a point source at $\mathbf{r}_1$ and recorded at S_1 , compared with the velocity at S_2 from a source at $\mathbf{r}_2$. Their difference, which should be exactly zero according to theory, is four orders of magnitude (i.e., 40 dB) smaller than the computed signals themselves. This shows that most numerical errors have very small effects, certainly small enough for our current goals; it does not rule out numerical dispersion, whose effect should be about the same regardless of whether propagation is from $\mathbf{r}_1$ to $\mathbf{r}_2$ or vice versa. However, earlier literature (e.g., Komatitsch and Tromp, 1999, 2002a) has

addressed to what extent SPECFEM3D might be prone to numerical dispersion. In practice, we consider SPECFEM3D to be sufficiently accurate for our current goals.

IV. RESULTS

A. Incoming plane wave

We made wide use of the PARAVIEW software to visualize all our simulation results. Data from SPECFEM were imported directly into PARAVIEW as eXtensible Data Model and Format (XDMF) and associated Hierarchical Data Format (HDF5) files. Then, each STL file associated with a different anatomical feature (tissue type) was imported into PARAVIEW and the POINT DATASET INTERPOLATOR module was used to project the volume solution onto the outer surface of each feature. A slice along the median yz -plane at $x = 0$ shows the wave propagation toward and into the dolphin head in Figs. 7(a)–7(d). The color bar scale corresponds to the particle velocity v_z on the same plane. For illustration purposes, the amplitude in all 3D-displayed materials was increased uniformly to match that of the surrounding water.

The impedance mismatch between different tissues and water is clearly visible in Fig. 7(c), where the amplitude of the particle velocity is greater in the acoustic fats than in the jaws. Compared to the simple source signal that was injected into the model, the plane wave simulation in Figs. 7(b)–7(d) shows a very complex wavefield, dominated by the effects of the many sharp discontinuities characterizing the dolphin anatomy, including guided waves and reverberations. In Figs. 7(c) and 7(d), the high-frequency reflections observed near the skull are likely visual artifacts, as the cross-sectional view (2D slice) captures waves that have presumably been reflected in various directions near the dolphin's beak, giving the impression that the reflections are occurring at the skull. The frequency spectrum [Fig. 8(b)] of the recorded signal is largest around 40 kHz, and has its absolute maximum slightly below 40 kHz at the left ear, and slightly above at the right ear. Spectral amplitudes decay to zero approximately in the same way as those of the source signal [Fig. 5(b)], with the bandwidth between zeros corresponding to the length of the Tukey window. In Figs. 8(a) and 8(c), both pressure and particle velocity exhibit a slightly modulated source signal followed by a complex, high-amplitude reverberation pattern, consistent with the qualitative findings of Hejazi Nooghabi *et al.* (2021).

B. Outgoing point source

Figure 9 shows the wavefield originated by a point source at the approximate location of the phonic lips, responsible for generating dolphin clicks. We used the same synthetic signal shown in Fig. 5(a) for illustration purposes, although the frequency range of dolphin clicks is typically higher (around 120 kHz for *Tursiops truncatus*). Note that the outgoing wavefront propagates along the melon axis, which is consistent with its known role in directing biosonar emissions [Figs. 9(c) and 9(d)]. Figure 9(b) also shows the primary wave propagating at an angle above the head and slightly upward; the late wavelet propagating above the head in Fig. 9(d) appears to be a reflection of that, from the skull itself. This reflection may disappear or become less prominent if air is included in the model, which we have so far omitted. This is a non-trivial issue as air was largely absent from the CT scan.

The results of our relatively simple simulation show clearly that SEM is a powerful tool to capture the many complexities of wave propagation through the anatomy of marine mammals. In future work, and via a much more detailed analysis of numerical data, this can contribute to understanding the mechanisms underlying their auditory and biosonar systems.

V. DISCUSSION AND OUTLOOK

We demonstrated that the SEM can be used to successfully simulate 3D wave propagation through a bottlenose dolphin head. Ours was essentially a feasibility test, conducted on a relatively limited computational infrastructure but enough to infer that after migrating our code to a large high-performance cluster, we shall be able to model most of the complexities in the anatomy of real dolphins. Importantly, this study is the first instance of using SEM in this context and one of only relatively few attempts at modeling 3D time-domain wave propagation through anatomical structures (Bachmann and Tromp, 2020; Hejazi Nooghabi *et al.*, 2021; Marty *et al.*, 2024; Wei *et al.*, 2024; Ali *et al.*, 2025).

Features that were omitted in this study, but might turn out to play a significant role, include the dolphin's teeth and air sacs and ducts (Au, 1993; Dobbins, 2007). We also assumed homogeneous tissue properties within individual anatomical features, which may have a significant effect, e.g., on wave focusing/defocusing. The rationale for sticking to a simplified model is twofold: on the one hand, the specimen available to us was an old dolphin in relatively poor

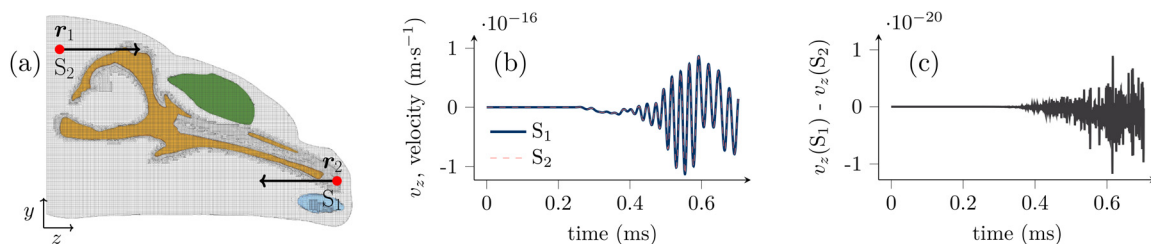


FIG. 6. Reciprocity theorem. (a) Location of the sources for the test, shown on a slice of the head mesh along the yz -plane at $x = 0$, (b) comparison of recorded signals. The recorded signal S_1 fired from r_1 is “equal” to the recorded signal S_2 fired from r_2 . (c) Absolute difference between the two recorded signals. The difference is four orders of magnitude smaller than the signals themselves.

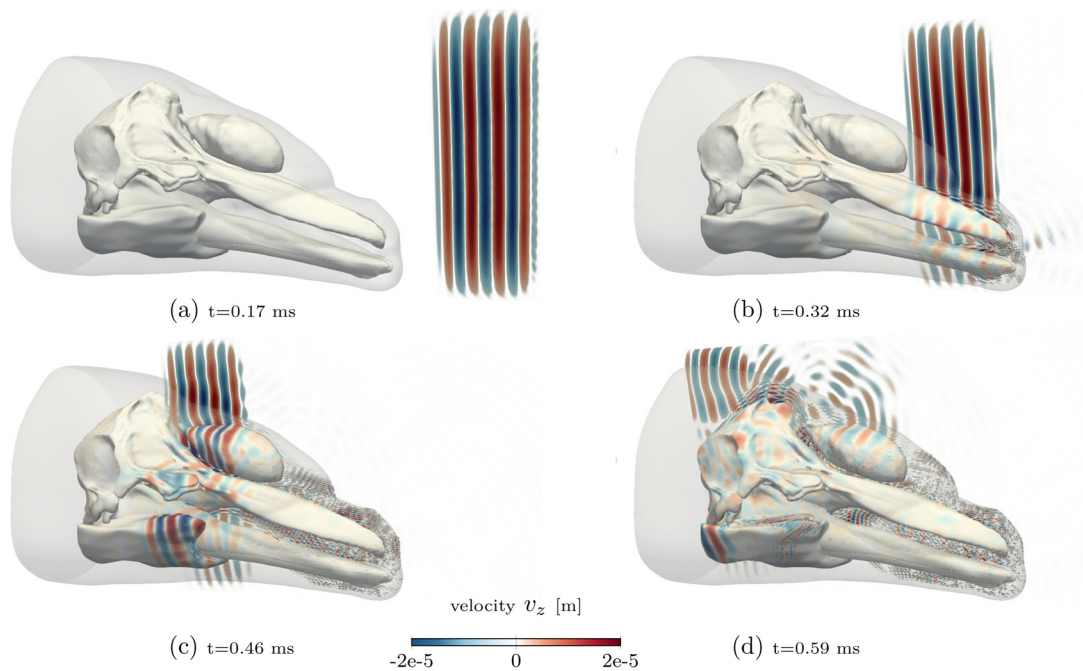


FIG. 7. A slice along the yz -plane at $x = 0$ is shown depicting the wavefront propagating in the fluid domain toward the dolphin head and through its different tissues at different times t . The color bar scale shows the amplitude of the z component of the particle velocity v_z . This value was projected onto the surface of each tissue to highlight the wave-propagation phenomenon. The scale across all 3D tissues was adjusted uniformly to enhance visualization.

condition; some teeth were missing, soft tissues around the beak were deformed, and the majority of the air spaces were missing in the CT scan. Accordingly, substantial reshaping and smoothing were required. On the other hand, the difficulty of hexahedral meshing is well known and grows with the complexity of the structures that are to be meshed. Semi-automated meshers like SCULPT alleviate this process, but still, prior to establishing an optimal mesh and a reliable protocol (described in much detail in Secs. III A–III C) to derive it, a significant iterative refinement process was required. The jaws and the acoustic fats, for instance, were particularly problematic.

As SCULPT can only deal with geometries that are conformal and fragmented at interfaces for external STL files and adaptive meshes, CUBIT often failed and crashed, as we fed it multiple trial versions of those features without providing information. We were surprised to find that FREECAD could succeed where all other “geometry tools” that we tested, such as BLENDER or MESHLAB, failed. Because these are all open-source packages, it is possible

that some plug-ins, of which we are not aware, exist to deal with such tasks. If that were the case, we would recommend to try and perform all necessary boolean operations directly in BLENDER without recurring to MESHLAB and/or FREECAD.

One relatively important issue with SCULPT is that the whole model needs to be meshed at once. Currently, SCULPT does not support meshing individual features separately; in our case, for instance, it would have been preferable to mesh the acoustic fats first, then the jaws, skull, soft tissues, and finally the water. In general, it would be easier to refine the mesh locally, only where it is needed (e.g., the TPC), before merging individual features in a single, large model.

SCULPT will always generate a mesh; however, depending on the input data, the mesh quality (measured by the scaled Jacobian) can become negative, rendering it unusable (Igel, 2016). Mesh quality can be significantly affected by very small adjustments in the input data. Even very minor smoothing of anatomical features can compromise it because of the iterative process of SCULPT; in particular, when trying to create the coarsest possible mesh according

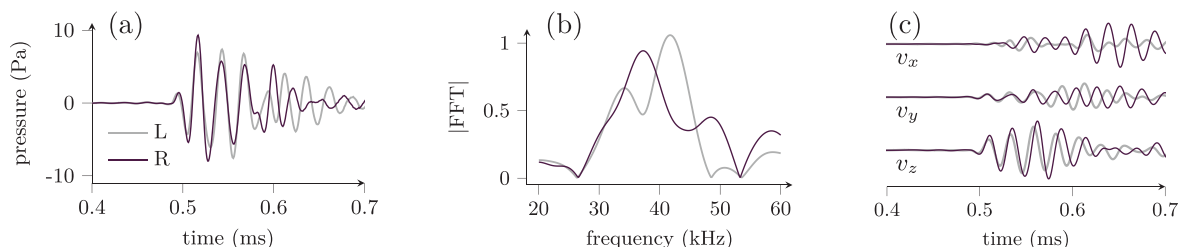


FIG. 8. Recorded signals near the TPC, at both left (L, in gray thick lines) and right (R, in violet thin lines) ears. (a) Pressure, (b) pressure spectrum, (c) each component of the particle velocity. The v_z component consists mainly of the direct signal with some reverberation. However, in the other components, the reverberations are more prominent.

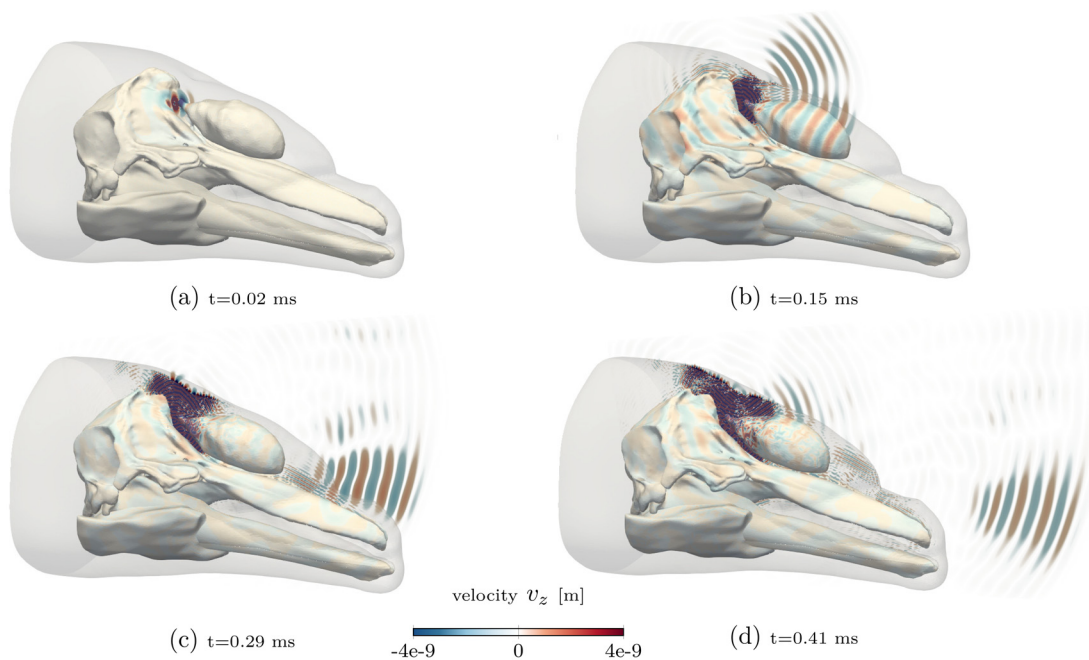


FIG. 9. Outgoing click propagation. The color scale is defined to be able to visualize the relative-low amplitude compressional wave propagating through water. This results in the saturation of vibration amplitude, within the head, in the immediate vicinity of the source. The scale shows the amplitude of the z component of the particle velocity v_z . This value was projected onto the surface of each tissue to highlight the wave-propagation phenomenon. The scale across all 3D tissues was adjusted uniformly to enhance visualization.

to the source-signal wavelength in a medium that includes, like ours, small ducts and sections. All this means that the user has to systematically and carefully check the output of SCULPT, which slows down the process. One advantage of the SEM, however, is its robustness in handling distorted meshes (Mada and Rønquist, 1990; Oliveira and Seriani, 2011). The number of points per wavelength in this study, as per Table I, ensure proper results and the reciprocity test shows the numerical noise to be low enough for this feasibility test. Moreover, dispersion errors can be substantially reduced by increasing the number of GLL points (Oliveira and Seriani, 2011) or decreasing further the size of the time step (Cohen, 2001), which significantly increases the computational cost. Performing such refinements is beyond what we can achieve with the computational resources currently available to us. Further research is needed, both to improve the mesh quality achievable with semi-automated tools and to assess how a small number of low-quality elements may impact overall solution accuracy.

SPECFEM3D assumes a Cartesian reference frame, and the boundaries of the simulation domain are aligned with its axes. This constraint arises from the nature of seismology simulations, which typically model only a portion of the domain (the earth), enclosed in a rectangular prism, with zero shear stress prescribed on (only) the upper surface (i.e., the earth's outer surface). Although this setup is well-suited for many geophysical applications, it imposes a fixed geometry on the domain boundaries. In contrast, other high-order numerical models mesh the outer surface as tightly as possible, sometimes following a smooth version of the external surface, namely a "convex hull" (Bériot and Modave, 2020,

Fig. 9). Adopting a similar approach could help reduce computational costs, but implementing it in SPECFEM3D may be challenging.

By assuming homogeneous, isotropic acoustic properties for all tissues independently, we also overlook known gradients in stiffness and lipid composition, for example, within the melon (Norris and Harvey, 1974). Future work may integrate 3D variations in material parameters as well as anisotropy, ideally based on empirical measurements. Likewise, attenuation (which SPECFEM3D can honor) will be incorporated in the model by taking into account viscoacoustic-viscoelastic coupling.

Finally, we implemented a point force directed parallel to the z axis at the approximate location of the phonic lips. This is not meant to be an accurate model of how echolocation clicks are actually generated but is a useful illustration of how a wave field generated at that location is affected by the surrounding anatomical structures. Figure 9 shows high-amplitude vibrations and multiple reverberations near the point source. Both effects might be strongly reduced once our model will account for air spaces with the dolphin head and for attenuation. Air spaces, particularly those located near the phonic lips, e.g., the nasal sacs (Cozzi *et al.*, 2017), might help to absorb these vibrations, preventing them to reach the skull. They may also enhance the amplitude of the outgoing signal (Au *et al.*, 2010; Wei *et al.*, 2018a). By incorporating attenuation, high-frequency reverberations will decrease faster in time than the fundamental frequency of the original signal.

The incorporation of all features discussed here, along with additional validation against independent numerical

solvers, is planned for a future stage, once we migrate our SPECIFEM3D workflow to a high-performance computing (HPC) infrastructure for large-scale simulations. This will also allow us to extend its use to a broader frequency range. Taking all this into account, we submit that the SEM may be the most powerful tool available to account for and analyze the effects of these and other complex features of marine mammal anatomy on hearing and wave propagation in biological tissues.

VI. CONCLUSIONS

We demonstrated that the SEM effectively simulates 3D wave propagation in marine mammals, using a detailed dolphin model built from CT scans. By leveraging STL files we simplified the meshing process, turning it into a practical 3D modeling task. We prepared the model carefully and used SCULPT for adaptive meshing to capture complex structures accurately. With SPECIFEM3D, we simulated both plane waves and point sources, unlocking the ability to further explore key issues like dolphin biosonar. This approach has wide-ranging applications: it could be used, e.g., to assess how anthropogenic noise affects marine life, recreate behavioral experiments for understanding image formation from sound in dolphins, and shed light on the biophysics of hearing and click generation in marine mammals. Our work shows the power of computational tools in marine biology, offering a clear path to study and protect marine mammals amid growing environmental pressures. Over the decades, several mechanisms, alternative or complementary to one another, have been suggested to explain, for instance, the sound transmission through the head (Norris and Harvey, 1974), the role of left-right asymmetry (Ryabov, 2023), the two-sonar source theory (Cranford *et al.*, 2011) and, in general, the mechanisms of sound reception and echolocation in different odontocetes species (Nachtigall, 2016; Ryabov, 2014; Wei *et al.*, 2018b; Wei *et al.*, 2016). We might be at the point where we can start testing all these theories efficiently.

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IT020)], University of Padua, under license from the Italian government, in the department's necropsy room. The head was severed and a CT scan was acquired during the necropsy. As the animal was not part of any experiment, no ethical permission was required. We thank Ksenia Orekhova and the Diagnostic framework to Assess and Predict the impact Of underwater Noise on marine species (DIAPHONIA) network for their constant feedback on the anatomy and hearing of dolphins. We are also grateful to Quentin Grimal for his ongoing involvement and valuable comments; Vadim Monteiller for assisting with the installation of the appropriate version of SPECIFEM; Daniel Peter for his earlier guidance; and Norbert Hofbauer for his helpful tips on using CUBIT.

AUTHOR DECLARATIONS

Conflict of Interest

The authors have no conflicts to disclose.

DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon reasonable request.

APPENDIX: MESHING COMMANDS

The detailed commands used for meshing with SCULPT are the following:

Command	Value	Detail
cores	24	Sets the number of cores for parallel computations to 24.
size	0.0025	Specifies the absolute cell size for the Cartesian grid as 0.0025.
box expand	0	Controls the bounding box expansion; 0 means no expansion.
csmooth	6	Sets the curve smoothing method to linear.
curve_opt_thresh	0.61	Sets the minimum metric threshold for curve optimization to 0.61.
smooth	3	Applies smoothing without surface projections.
max_opt_iters	80	Sets the maximum number of optimization iterations to 80.
max_pcol_iters	101	Sets the maximum number of parallel coloring iterations to 101.
pcol_threshold	0.3	Sets the parallel coloring threshold to 0.3.
defeature	1	Enables automatic defeaturing by filtering small features.
thicken_material	3 2 0.1 4 0.15 6 0.1	Expands materials 3, 4, and 6 (skull and acoustic fats) into surrounding cells with given parameters.
adapt_type	8	Sets the adaptive meshing type to material-based adaptation.
adapt_material	3 2 1 0.5 0 0 4 1 0.5 0 0 6 1 0.5 0 0	Specifies adaptive meshing parameters for materials 3, 4, and 6.

- Afanasyev, M., Boehm, C., van Driel, M., Krischer, L., and Fichtner, A. (2018). "Flexible high-performance multiphysics waveform modeling on unstructured spectral-element meshes," in *SEG Technical Program Expanded Abstracts 2018*, Anaheim, CA (Society of Exploration Geophysicists, Houston, TX), pp. 4035–4039.
- Ahrens, J., Geveci, B., and Law, C. (2005). "ParaView: An end-user tool for large-data visualization," in *Visualization Handbook*, edited by C. D. Hansen and C. R. Johnson (Elsevier, Amsterdam, the Netherlands), pp. 717–731.
- Aki, K., and Richards, P. G. (1980). *Quantitative Seismology. Theory and Methods* (Freeman, San Francisco, CA).
- Ali, F., García A. C., Hejazi Nooghabi, A., and Boschi, L. (2025). "Pseudo-spectral model of elastic-wave propagation through toothed-whale head anatomy, and implications for biosonar," *J. Acoust. Soc. Am.* **158**, 4348–4360.
- Alnaes, M., Blechta, J., Hake, J., Johansson, A., Kehlet, B., Logg, A., Richardson, C., Ring, J., Rognes, M. E., and Wells, G. N. (2015). "The FEniCS project version 1.5," *Archive Numer. Software* **3**(100), 9–23.
- Arndt, D., Bangerth, W., Davydov, D., Heister, T., Heltai, L., Kronbichler, M., Maier, M., Pelteret, J.-P., Turcksin, B., and Wells, D. (2021). "The DEAL.II finite element library: Design, features, and insights," *Comput. Math. Appl.* **81**, 407–422.
- Au, W. W. L. (1993). *The Sonar of Dolphins* (Springer, New York).
- Au, W. W. L., Houser, D. S., Finneran, J. J., Lee, W.-J., Talmadge, L. A., and Moore, P. W. (2010). "The acoustic field on the forehead of echolocating Atlantic bottlenose dolphins (*Tursiops truncatus*)," *J. Acoust. Soc. Am.* **128**(3), 1426–1434.
- Bachmann, E., and Tromp, J. (2020). "Source encoding for viscoacoustic ultrasound computed tomography," *J. Acoust. Soc. Am.* **147**(5), 3221–3235.
- Baker, T. J. (2005). "Mesh generation: Art or science?," *Prog. Aerosp. Sci.* **41**(1), 29–63.
- Bériot, H., and Modave, A. (2020). "An automatic perfectly matched layer for acoustic finite element simulations in convex domains of general shape," *Int. J. Numer. Methods Eng.* **122**(5), 1239–1261.
- Betcke, T., and Scroggs, M. W. (2021). "Bempp-cl: A fast PYTHON based just-in-time compiling boundary element library," *J. Open Source Software* **6**(59), 2879.
- Blackner, T. (2000). "Meeting the challenge for automated conformal hexahedral meshing," in *Proceedings of the 9th International Meshing Roundtable 11–19*.
- Blender Foundation (2022). "Blender (version 4.4.0) [computer program]," <https://www.blender.org/> (Last viewed June 25, 2025).
- Brooks, R. A. (1977). "A quantitative theory of the Hounsfield unit and its application to dual energy scanning," *J. Comput. Assist. Tomogr.* **1**(4), 487–493.
- Castellazzi, G., Krysl, P., Rojas, L., and Cranford, T. W. (2012). "Assessment of the effect of natural and anthropogenic aquatic noise on vaquita (*Phocoena sinuata*) through a numerical simulation," *Adv. Exp. Med. Biol.* **730**, 307–309.
- Cignoni, P., Callieri, M., Corsini, M., Dellepiane, M., Ganovelli, F., and Ranzuglia, G. (2008). "MESH LAB: An open-source mesh processing tool," <https://vcg.isti.cnr.it/Publications/2008/CCDGR08/MeshLabEGIT.final.pdf>, pp. 129–136 (Last viewed June 5, 2025).
- Cohen, G. (2001). *Higher-Order Numerical Methods for Transient Wave Equations* (Springer, Amsterdam, the Netherlands).
- COMSOL Inc. (2024). "COMSOL Multiphysics (version 6.0) [computer program]," <https://www.comsol.com/comsol-multiphysics> (Last viewed June 25, 2025).
- Coreform LLC (2024). "Coreform Cubit (version 2024.8) [computer program]," <http://coreform.com/coreform-cubit/> (Last viewed June 25, 2025).
- Cozzi, B., Huggenberger, S., and Oelschläger, H. (2017). "Head and senses," in *Anatomy of Dolphins* (Academic Press, San Diego, CA), pp. 133–196.
- Cranford, T. W., Elsberry, W. R., Van Bonn, W. G., Jeffress, J. A., Chaplin, M. S., Blackwood, D. J., Carder, D. A., Kamolnick, T., Todd, M. A., and Ridgway, S. H. (2011). "Observation and analysis of sonar signal generation in the bottlenose dolphin (*Tursiops truncatus*): Evidence for two sonar sources," *J. Exp. Mar. Biol. Ecol.* **407**(1), 81–96.
- Dobbins, P. (2007). "Dolphin sonar—modelling a new receiver concept," *Bioinspir. Biomim.* **2**(1), 19.
- Dong, E., Zhang, Y., Song, Z., Zhang, T., Cai, C., and Fang, N. X. (2019). "Physical modeling and validation of porpoises' directional emission via hybrid metamaterials," *Natl. Sci. Rev.* **6**(5), 921–928.
- Fedorov, A., Beichel, R., Kalpathy-Cramer, J., Finet, J., Fillion-Robin, J.-C., Pujol, S., Bauer, C., Jennings, D., Fennessy, F., Sonka, M., Buatti, J., Aylward, S., Miller, J. V., Pieper, S., and Kikinis, R. (2012). "3D Slicer as an image computing platform for the quantitative imaging network," *Magn. Reson. Imaging* **30**(9), 1323–1341.
- Feng, W., Zhang, Y., and Wei, C. (2019). "A biosonar model of finless porpoise (*Neophocaena phocaenoides*) for material composition discrimination of cylinders," *J. Acoust. Soc. Am.* **146**(2), 1362–1370.
- Ferroni, A. (2017). "Discontinuous Galerkin spectral element methods for the elastodynamics equation on hybrid hexahedral-tetrahedral grids," Ph.D. thesis, Politecnico Milano, Milan, Italy.
- Gao, J., Xiao, Z., Shen, S., Xu, C., Cai, J., and Xu, G. (2025). "Improved hexahedral mesh generation from quadrilateral surface meshes," *Comput. Struct.* **307**, 107620.
- Grimal, Q., Gama, B. A., Naili, S., Watzky, A., and Gillespie, J. W. (2004). "Finite element study of high-speed blunt impact on thorax: Linear elastic considerations," *Int. J. Impact Eng.* **30**(6), 665–683.
- Gu, J., and Jing, Y. (2015). "Modeling of wave propagation for medical ultrasound: A review," *IEEE Trans. Ultrason. Ferroelectr. Freq. Control* **62**(11), 1979–1992.
- Haqshenas, S. R., Gélât, P., van 't Wout, E., Betcke, T., and Saffari, N. (2021). "A fast full-wave solver for calculating ultrasound propagation in the body," *Ultrasonics* **110**, 106240.
- Hecht, F. (2012). "New development in freefem++," *J. Numer. Math.* **20**(3–4), 251–266.
- Hejazi Nooghabi, A., Grimal, Q., Herrel, A., Reinwald, M., and Boschi, L. (2021). "Contribution of bone-reverberated waves to sound localization of dolphins: A numerical model," *Acta Acust.* **5**, 3.
- Igel, H. (2016). *Computational Seismology: A Practical Introduction* (Oxford University Press, Oxford, UK).
- Kazemi, A., Kesba, M., and Provini, P. (2023). "Realistic three-dimensional avian vocal tract model demonstrates how shape affects sound filtering (*Passer domesticus*)," *J. R. Soc. Interface* **20**(198), 20220728.
- Knupp, P. M. (2001). "Algebraic mesh quality metrics," *SIAM J. Sci. Comput.* **23**(1), 193–218.
- Komatitsch, D. (2010). "Fluid–solid coupling on a cluster of GPU graphics cards for seismic wave propagation," *C. R. Méc.* **339**(2–3), 125–135.
- Komatitsch, D., Barnes, C., and Tromp, J. (2000). "Wave propagation near a fluid–solid interface: A spectral–element approach," *Geophysics* **65**(2), 623–631.
- Komatitsch, D., and Tromp, J. (1999). "Introduction to the spectral element method for three-dimensional seismic wave propagation," *Geophys. J. Int.* **139**(3), 806–822.
- Komatitsch, D., and Tromp, J. (2002a). "Spectral–element simulations of global seismic wave propagation—I. Validation," *Geophys. J. Int.* **149**(2), 390–412.
- Komatitsch, D., and Tromp, J. (2002b). "Spectral–element simulations of global seismic wave propagation—II. Three-dimensional models, oceans, rotation and self-gravitation," *Geophys. J. Int.* **150**(1), 303–318.
- Komatitsch, D., and Vilotte, J.-P. (1998). "The spectral element method: An efficient tool to simulate the seismic response of 2D and 3D geological structures," *Bull. Seismol. Soc. Am.* **88**(2), 368–392.
- Maday, Y., and Rønquist, E. M. (1990). "Optimal error analysis of spectral methods with emphasis on non-constant coefficients and deformed geometries," *Comput. Methods Appl. Mech. Eng.* **80**(1), 91–115.
- Marty, P., Boehm, C., and Fichtner, A. (2022a). "Elastic full-waveform inversion for transcranial ultrasound computed tomography using optimal transport," in *Proceedings of the 2022 IEEE International Ultrasonics Symposium (IUS)*, Venice, Italy (October 10–13), pp. 1–4.
- Marty, P., Boehm, C., Pavard, C., Rominger, M., and Fichtner, A. (2022b). "Full-waveform ultrasound modeling of soft tissue–bone interactions using conforming hexahedral meshes," in *Proceedings of Medical Imaging 2022: Physics of Medical Imaging*, SPIE, San Diego, CA (February 20–24), Vol. 12031, pp. 877–891.
- Marty, P., Boehm, C., van Driel, M., and Fichtner, A. (2024). "Transcranial ultrasound modeling using the spectral–element method," *J. Acoust. Soc. Am.* **156**(6), 3674–3693.
- Muntóni, A., and Cignoni, P. (2021). "PyMESH LAB 2023.12.post3: A PYTHON interface to MESH LAB [software]," <https://doi.org/10.5281/zenodo.4438750> (Last viewed June 25, 2025).
- Nachtigall, P. E. (2016). "Biosonar and sound localization in dolphins," in *Oxford Research Encyclopedia of Neuroscience*, <https://oxfordre.com/neuroscience/display/10.1093/acrefore/9780190264086.001.0001/acrefore-9780190264086-e-103> (Last viewed June 20, 2025).
- Norris, K. S., and Harvey, G. W. (1974). "Sound transmission in the porpoise head," *J. Acoust. Soc. Am.* **56**(2), 659–664.

- Oliveira, S. P. (2018). "Error analysis of Chebyshev spectral element methods for the acoustic wave equation in heterogeneous media," *J. Theor. Comput. Acoust.* **26**(3), 1850035.
- Oliveira, S. P., and Seriani, G. (2011). "Effect of element distortion on the numerical dispersion of spectral element methods," *Commun. Comput. Phys.* **9**(4), 937–958.
- Owen, S. J. (2012). "Parallel smoothing for grid-based methods," Technical Report SAND2012-6355C, Sandia National Laboratories, Albuquerque, NM.
- Owen, S. J., Staten, M. L., and Sorensen, M. C. (2014). "Parallel hexahedral meshing from volume fractions," *Eng. Comput.* **30**(3), 301–313.
- Patera, A. T. (1984). "A spectral element method for fluid dynamics: Laminar flow in a channel expansion," *J. Comput. Phys.* **54**(3), 468–488.
- Porter, M. B., and Bucker, H. P. (1987). "Gaussian beam tracing for computing ocean acoustic fields," *J. Acoust. Soc. Am.* **82**(4), 1349–1359.
- Rieger, J., Mayer, W., and van Havre, Y. (2024). "FreeCAD 1.0 – Free and open-source parametric 3D CAD modeler [computer program]," <https://www.freecad.org/> (Last viewed June 25, 2025).
- Ryabov, V. (2014). "Mechanisms of sound reception and conduction in the dolphin," *Biophysics*, **59**, 475–483.
- Ryabov, V. A. (2023). "The role of asymmetry of the left and right external ear of bottlenose dolphin (*Tursiops truncatus*) in the spatial localization of sound," *Acoust. Phys.* **69**(1), 119–131.
- Seriani, G., and Priolo, E. (1994). "Spectral element method for acoustic wave simulation in heterogeneous media," *Finite Elem. Anal. Des.* **16**(3), 337–348.
- Song, Z., Zhang, Y., Wei, C., and Wang, X. (2016). "Inducing rostrum interfacial waves by fluid-solid coupling in a Chinese river dolphin (*Lipotes vexillifer*)," *Phys. Rev. E* **93**(1), 012411.
- Treeby, B. E., Jaros, J., Rohrbach, D., and Cox, B. T. (2014). "Modelling elastic wave propagation using the k-wave MATLAB Toolbox," in *Proceedings of the 2014 IEEE International Ultrasonics Symposium*, Chicago, IL (September 3–6), pp. 146–149.
- van 't Wout, E., Gélât, P., Betcke, T., and Arridge, S. (2015). "A fast boundary element method for the scattering analysis of high-intensity focused ultrasound," *J. Acoust. Soc. Am.* **138**(5), 2726–2737.
- Wei, C., Au, W., and Ketten, D. (2020). "Modeling of the near to far acoustic fields of an echolocating bottlenose dolphin and harbor porpoise," *J. Acoust. Soc. Am.* **147**, 1790–1801.
- Wei, C., Au, W., Ketten, D., and Zhang, Y. (2018a). "Finite element simulation of broadband biosonar signal propagation in the near- and far-field of an echolocating Atlantic bottlenose dolphin (*Tursiops truncatus*)," *J. Acoust. Soc. Am.* **143**, 2611–2620.
- Wei, C., Au, W. W. L., Song, Z., and Zhang, Y. (2016). "The role of various structures in the head on the formation of the biosonar beam of the baiji (*Lipotes vexillifer*)," *J. Acoust. Soc. Am.* **139**(2), 875–880.
- Wei, C., Erbe, C., Smith, A. B., and Yang, W.-C. (2024). "Validated 3D finite-element model of the Risso's dolphin (*Grampus griseus*) head anatomy demonstrates gular sound reception and channelling through the mandibular fats," *Bioinspir. Biomim.* **19**(5), 056025.
- Wei, C., Gill, L. G., Erbe, C., Smith, A. B., and Yang, W.-C. (2022). "The distinctive forehead cleft of the Risso's dolphin (*Grampus griseus*) hardly affects biosonar beam formation," *Animals* **12**(24), 3472.
- Wei, C., Song, Z., Au, W. W. L., Zhang, Y., and Wang, D. (2018b). "A numerical evidence of biosonar beam formation of a neonate Yangtze finless porpoise (*Neophocaena asiaorientalis*)," *J. Theor. Comp. Acoust.* **26**, 1850009.
- Wei, C., Wang, Z., Song, Z., Wang, K., Wang, D., Au, W. W. L., and Zhang, Y. (2015). "Acoustic property reconstruction of a neonate Yangtze finless porpoise's (*Neophocaena asiaorientalis*) head based on CT imaging," *PLoS One* **10**(4), e0121442.
- Zhang, Y., Song, Z., Wang, X., Cao, W., and Au, W. (2017). "Directional acoustic wave manipulation by a porpoise via multiphase forehead structure," *Phys. Rev. Appl.* **8**, 064002.