



# Complementary Methods to Acquire the Kinematics of Swimming Snakes: A Basis to Design Bio-inspired Robots

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## Abstract

The vast diversity of morphologies, body size, and lifestyles of snakes represents an important source of information that can be used to derive bio-inspired robots through a biology-push and pull process. An understanding of the detailed kinematics of swimming snakes is a fundamental prerequisite to conceive and design bio-inspired aquatic snake robots. However, only limited information is available on the kinematics of swimming snake. Fast and accurate methods are needed to fill this knowledge gap. In the present paper, three existing methods were compared to test their capacity to characterize the kinematics of swimming snakes. (1) Marker tracking (Deftac), (2) Markerless pose estimation (DeepLabCut), and (3) Motion capture were considered. (4) We also designed and tested an automatic video processing method. All methods provided different albeit complementary data sets; they also involved different technical issues in terms of experimental conditions, snake manipulation, or processing resources. Marker tracking provided accurate data that can be used to calibrate other methods. Motion capture posed technical difficulties but can provide limited 3D data. Markerless pose estimation required deep learning (thus time) but was efficient to extract the data under various experimental conditions. Finally, automatic video processing was particularly efficient to extract a wide range of data useful for both biology and robotics but required a specific experimental setting.

**Keywords** Locomotion · Image processing · Motion capture · Kinematic analysis · Snake robot · Biomimicry · DeepLabCut

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## 1 Introduction

Both technology-pull and biology-push approaches depend on the availability of precise observations and measurements gathered on biological samples and living organisms [1]. Indeed, accurate data are needed to find technical solutions to engineering problems in natural systems (top-down approach) or to imagine possible engineering applications from the observation of the solutions retained by natural selection (bottom-up approach). These approaches are not mutually exclusive; instead, their combination represents an important source of creativeness for designers and biologists alike [2, 3]. Due to their prospective nature, biology-push approaches rely on a wide spectrum of observations to capture the diversity of morpho-functional options observable in living organisms [4]. However, carefully exploring the multiple solutions that species or individuals evolved to cope with biological challenges imposes logistic limitations, at least to collect high-quality data. Thus, fast albeit precise acquisition methods are needed to build exploratory data sets

allowing them to select relevant parameters and processes, and to identify potential applications.

In this study, we tackled these issues by focusing on one polyvalent locomotor mode: undulatory locomotion. This type of gait is based on the propagation of lateral undulations along the whole body, it enables both crawling and swimming [5]. It is one of the most versatile locomotor modes, efficient under many conditions [6]. This explains the growing interest in snake-inspired robots (snakebots) over the past decades [7, 8]. Snake robots provide examples of bio-inspired devices where conception and intended usage involve multiple approaches including feedback to biology [2, 9]. For example, the undulating aquatic snakebot Amphibot-II was designed using information about how the nervous system of lampreys coordinates the movements of successive body segments [2, 5]. This control is crucial to regulate the amplitude and frequency of undulations along the snakebot. In this broad context, the term “regulate” is vague, however; it may refer to the control of swimming speed (high speed presumably entails high energy demands), of swimming distance (low energy consumption required for long distances), or any compromise among desired characteristics for an autonomous robot, for example. Yet, physical and biological processes that underlie undulatory swimming remains poorly known [10]; a situation that hampers improvements in bioinspired engineering of undulatory swimming.

Anguilliform swimming has been mostly studied in elongated fish like eels or lampreys [11, 12]. One study notably revealed that this swimming mode is one of the most energy-saving types of swimming, roughly five times more efficient compared to other swimming modes based on caudal fin beats [6]. Snakes also rely on lateral undulations while swimming and hence are typical anguilliform swimmers [5]. Therefore, a better understanding of this swimming mode is promising to design autonomous aquatic and amphibious snakebots. A careful examination of the most relevant biological data that characterize the relationship between lateral undulations and swimming performance is essential to optimize biomimicry design [13]. In this context, a comparison of the swimming kinematics and performance of a wide range of snakes adapted to different degrees to an aquatic lifestyle appears promising. Surprisingly, however, studies on the kinematics of swimming in snakes are scant and involve very few species and individuals [5]. Considering

the immense diversity of snakes in terms of anatomy, body size, or lifestyle (nearly 4.000 snake species have been described to date; <http://www.reptile-database.org/db-info/SpeciesStat.html>), the paucity of biological data strongly restricts bio-inspired design [4]. For example, the lack of a fine understanding of the relationship between swimming kinematics and locomotor performance has prompted researchers to focus on the tail of snakebots, while the exact contribution of the tail in driving variation in the swimming performance of snakes remains largely unknown [14]. Gathering detailed swimming kinematics on a variety of snakes would thus be essential to help the design of snakebots and to address biological questions pertaining to the evolution of an aquatic lifestyle in snakes.

Various methods have been employed to characterize swimming in aquatic animals, including snakes (Table 1). They involve invasive and non-invasive investigations of anatomy and physiology, the quantification of swimming modes, swimming performance, and kinematics, and the tracking water put in motion by swimmers; consequently, the methods and metrics used differ drastically [15–17]. With respect to swimming speed and swimming kinematics, video recordings, occasionally coupled with accelerometry, have provided most of the information available [5, 18–20]. The displacement speed of the animal can be easily extracted from video, but detailed kinematic analyses require more complex investigations [5]. Data on the frequency and amplitude of undulations, the propagation of undulatory waves along the body, and thus how snakes actually propel themselves in the water thus remain scant. Important divergences between the ways snakes and fish (e.g. eels, lampreys), respectively, achieve anguilliform swimming precludes a direct comparison between these distant lineages. Visual measurement methods based on video analysis offer the possibility to rapidly investigate variations across species while reducing animal handling time and are thus widely used [5].

We selected and tested several video-based and motion-capture methods to study the kinematics of swimming snakes. Through this selection, we aimed to encompass different biological questions, as well as technical and logistical issues. A central objective was to compare the methods and their respective outcomes. The main contributions of the paper are listed below:

**Table 1** Non-exhaustive list of features considered in studies of swimming animals

Study	Invasive vs non-invasive	Measurement method	References
Anatomy	Invasive	Dissection	[16, 17]
Kinematics	Non-invasive	Accelerometers	[18]
		X-Rays/video fluoroscopy	[21]
		2D and 3D video analysis	[5, 19, 20]
		Timed by stopwatch (manual)	[22–24]

- (1) We developed a protocol to rapidly collect footages of swimming snakes to characterize swimming kinematics. We notably considered the complementarity of different methods. This protocol represents the first major contribution of the paper. We paid specific attention to DEFTAC, a method based on the tracking of well-identified markers that has been used to assess the accuracy of other methods. We also tested a markerless pose estimation (DeepLabCut), associated with video processing algorithms, and infrared motion capture based on reflective markers.
- (2) The development of a fast video processing algorithm called Software for the Analysis of Anguilliform Swimming (SAAS) to rapidly extract kinematic data from footages is the second strong contribution of this work. It allows us to analyze automatically whole snakes in motion, and thus to examine and compare a wide range of individuals and species.
- (3) We showed that selecting appropriate methods and experimental settings (protocol) and using the automatic analysis procedure (SAAS), building a database of the swimming kinematics of various snake species with contrasted ecology (e.g. terrestrial, aquatic, arboreal) can be achieved. This is essential for bio-inspiration projects in the robotics field, and for comparative evolutionary analyses in the field of evolutionary biology.

The remainder of this paper is organized as follows. Section 2 deals with the assessment of the selected methods used to analyze snake swimming kinematics. In Sect. 3, materials and methods are introduced to describe the protocol to obtain footages and the analytic approaches. In Sect. 4, experimental results obtained from various swimming sequences on a viperine snake (*Natrix maura*, a semi-aquatic species) are presented and examined. Finally, Sects. 5 and 6 are devoted to Discussion and Future Work, and Conclusion, respectively.

## 2 Snake Swimming Analysis Methods

The existence of a library of snake swimming kinematic data allowing to select relevant parameters and transfer of them to snake-like robots is critical for the design of snake drones. The lack of biological information has been identified as a major impediment to developing bio-inspired snakebots [25]. We compared/tested selected methods using the European

semi-aquatic viperine snake (*Natrix maura*). This semi-aquatic species is equally at home in the water and on land, and thus provides a suitable example of a polyvalent snake in terms of locomotion [26].

### 2.1 Manual Analysis

While manual measurements will not be used and compared in this study due to their inherent slowness, we take it into account as an established and reliable method (for further information, refer to Appendix 1).

### 2.2 Marker Tracking: DEFTAC (DEFormation TACHes) Software

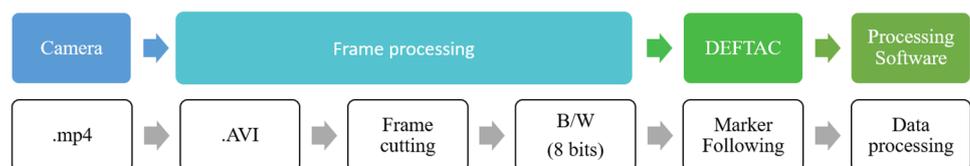
DEFTAC is a software designed to track markers positioned on the subject in motion, here a swimming snake. Natural variation in color pattern may offer a simple solution for markers, but in uniformly colored snakes landmarks may be painted (or glued) on the back of the snake. Usually, dots or circles (natural or artificial) are used. Each marker is manually identified and located on the image to allow the software to track it. The physical size of the marker, the lighting conditions and the resolution of the video directly influence the accuracy of successive positions [27]. The experimental setup and equipment used to videotape and monitor the snakes are described in Sect. 3 (Materials and Methods). In this study, we marked the snake with a white circular spot of 5 mm in diameter, positioned on the snake head (see Fig. 3). Figure 1 describes the successive steps to obtain the marker positions. Extracted data were finally processed using processing software (e.g. Excel or any other routine as RStudio, Matlab or Python) to obtain amplitudes, frequency, wavelength, wave speed (extracted from curves), and mean head speed (numerical derivation from position).

This robust method has been regularly applied [28–30], it provides high measurement accuracy (see Table 2). Note that the quality and technical specifications of the video camera and even more importantly the lenses directly influence the accuracy of the measurements.

### 2.3 Neural Network: DeepLabCut

DeepLabCut is a method to estimate successive positions of defined points in a plane or in a volume (volume is not used in this study) based on the training and subsequent

Fig. 1 Marker tracking protocol



deep learning of a neural network [31]. This method does not require the use of physical markers on the animal. The program is open source and easy to use thanks to its GUI interface. The execution of the program can be done on a GPU or on a CPU. We used a CPU (i3, 8 cores, 2.9 GHz, 32 Gb ram). The main steps necessary to extract the snake position are described in Fig. 2. Additional information can be found in the description of the routine [31]. First, training the network requires labelling a targeted part of the snake, i.e., manually defining specific points of the snake while it swims. In this study, 50 frames were extracted from each of the 3 videos selected. The ResNet network was trained on one specific and easily recognizable point: the head (see Fig. 2). The training was achieved after 50,000 iterations. Once the neural network is trained, the videos of the same individual under similar conditions can be analyzed. Extracted positions are analyzed through processing software (e.g. Excel or any other routine as RStudio, Matlab or Python) to obtain amplitudes, frequency, wavelength, wave speed (extracted from curves) and instantaneous speed (numerical derivation from position).

## 2.4 Motion Capture

Motion capture was used to track reflective markers (6.5 mm in diameter) placed on the dorsum at specific locations along the snake. A set of infrared cameras track the movements of each marker and record 3D positions with dedicated software (Qualisys). The results (marker X, Y, Z-coordinates) are post-processed with other programs (Excel, RStudio, Python or Matlab). The advantage of this method is to provide great accuracy of the position of the markers in a volume as a function of time (0.15–0.60 mm error). However, setting up the system is time-consuming, very small snakes cannot be fitted with markers, and the equipment is relatively expensive (compared to most video cameras). Moreover, as the markers in contact with the water are undetectable by the IR cameras only the movements of the head and of the neck of snakes swimming at the surface can be captured (other systems using shorter wavelengths can operate underwater, but they impose strong additional technical and logistical limitations). The 6.5 mm diameter markers are light (~0.5 g) and they can be fitted on snakes heavier than 100 g. This method may

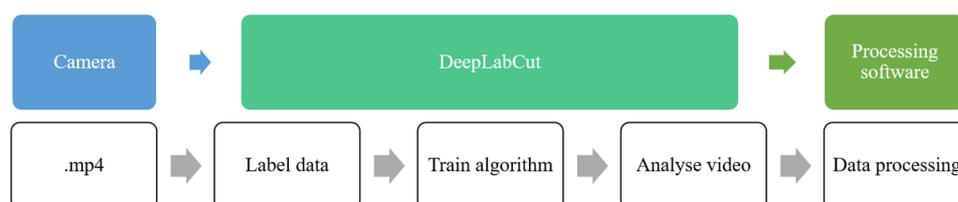
also influence snake swimming as the markers may generate undesirable drag. Finally, while this setup is easily employed under laboratory conditions, it is nearly impossible to use in the wild. Figure 3 details the steps to set up the motion capture and extract the marker positions. The data extraction is similar to the one used for the image processing algorithm (further details are provided in the next section).

## 2.5 Video Processing Algorithm: Software for the Analysis of Anguilliform Swimming (SAAS)

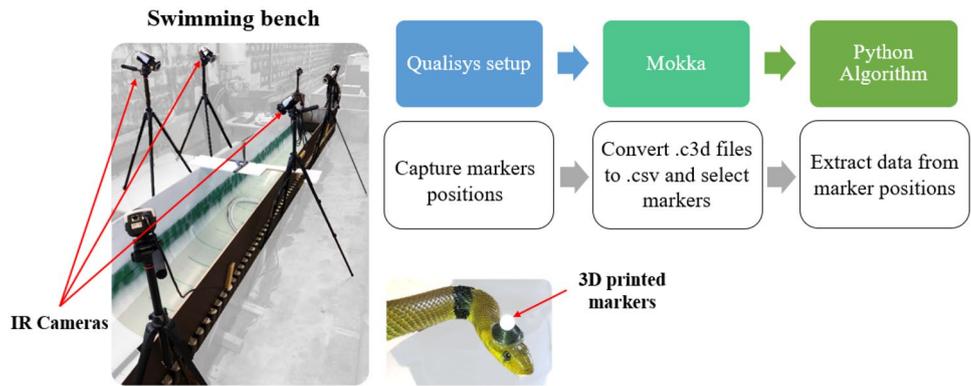
Video processing algorithms are essential to rapidly extract and analyze the swimming movements of the entire body of the snake (or eel, or other organism) and thus to generate large data sets required for comparisons [5]. The desired innovative characteristics of the tool are simplicity of use and automation of video processing. These features are important to promptly collect: undulation frequency, undulation amplitudes, longitudinal, transverse and resultant velocities along the body, wavelengths and wave velocities. SAAS is simple to implement and processes field data where laboratory equipment cannot be used. The use of SAAS requires limited animal handling (e.g., no need to fit and remove markers). Above all, the proposed method analyzes the whole snake body to extract all kinematics, unlike other methods in the literature. SAAS gives access to swimming cones, for instance (see Fig. 18). These data are relevant to both biology and robotics. A specific routine was developed under Python 3 using many libraries such as OpenCV. The processing steps are detailed in Fig. 4 and below.

- (1) Frame cutting. The first step is to format the videos to extract a skeleton of the snake and thus obtain the positions of the snake as a function of time. The rest of the processing is similar between video capture and motion capture. Each step is associated with a Python spreadsheet. The raw video is sequenced into  $n$  frames at regular time intervals (sequencing rate). These frames are stored in a folder; they are checked before the next step.
- (2) Binarization and contour. Images are scaled, cropped by the user and then processed by different filters to separate the snake from the background. Depending on the complexity of the image, it is possible to apply a

Fig. 2 DeepLabCut protocol

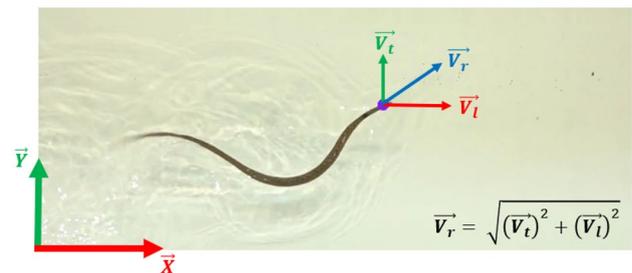


**Fig. 3** Motion Capture protocol using infrared cameras and reflective markers on snakes during swimming. The picture displays an Aesculapian snake (*Zamenis longissimus*)



low-pass filter. Note that each filter reduces the quality of the image and therefore the accuracy of the measurements. Selecting an appropriate threshold is thus important. The contour of the snake is determined after the binarization of the image.

- (3) Skeletonization and interpolation. From the outline, the midline of the snake is determined. However, from one image to another, the length (the number of points) of the midline can differ (e.g. in individuals with a fine-tipped tail tip). We performed a polynomial interpolation of degree 9 by iteration on each image (on each midline) to create a curve where the number of points is identical from one image to another (thereby ignoring variation generated by the tip of the tail).
- (4) Data extraction. From the videos, the procedure allows the extraction of data from the whole body of a snake and gives access to both qualitative data such as the swimming cone (see Fig. 17) and quantitative data (Table 2). The snake swimming speed is calculated along the x-axis of the trajectory using aligned or re-aligned swimming sequences. The swimming cone is obtained through the stacking of interpolations. This illustrates the amplitude and the general shape of the cumulative undulatory waves during a full swimming period. Amplitudes are determined in two steps. First, the local maxima and minima are calculated for each curve. We then perform a polynomial interpolation of degree 5 on each extremum. We calculate the average amplitude relative to the swimming direction of the snake. The oscillation period ( $T$ ) and oscillation frequency are determined for the snake head on each frame of the swimming sequence. The wavelength ( $\lambda$ ) of the snake over the entire swimming sequence is



**Fig. 5** Head speed:  $\vec{V}_t$  transversal head velocity,  $\vec{V}_l$  longitudinal head velocity,  $\vec{V}_r$  resulting head velocity

determined similarly. The wave velocity  $V_\lambda$  is determined from the wavelength and period  $T$  as:

$$V_\lambda = \frac{\lambda}{T} \tag{1}$$

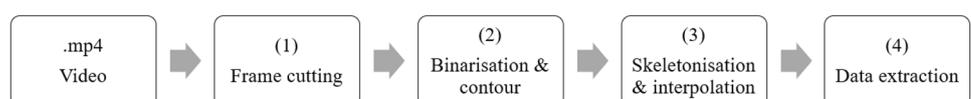
The calculation of the longitudinal, transverse and resultant velocities (see Fig. 5) ( $\vec{V}_l$ ,  $\vec{V}_t$ ,  $\vec{V}_r$ ) of the snake is performed by numerical derivation of the positions of each point  $j$  of each curve. These are therefore instantaneous velocities and accelerations at any point:

$$V_{lj} = \frac{x_{j+1} - x_{j-1}}{2T} \tag{2}$$

$$V_{tj} = \frac{y_{j+1} - y_{j-1}}{2T} \tag{3}$$

$$V_{rj} = \sqrt{V_{lj}^2 + V_{tj}^2} \tag{4}$$

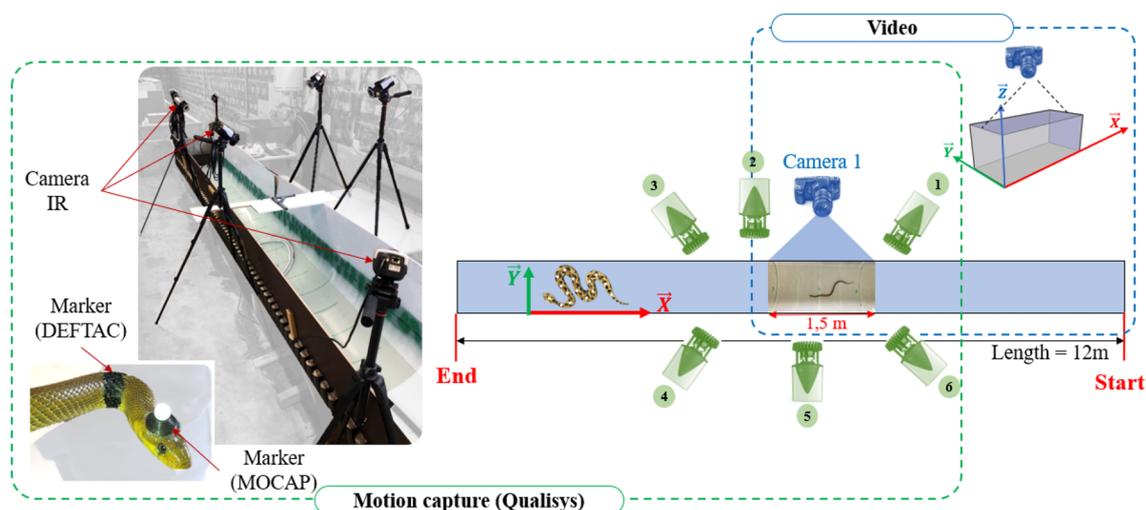
**Fig. 4** Video processing algorithm protocol



**Table 2** The main features of the data collected and several practical aspects are listed

Method	Software	Accessible data	Accuracy	Environment of use	Max sample size (arbitrary)
Marker tracking	DEFTAC	Frequency, wavelength, wave speed, mean longitudinal speed, mean transversal speed, mean resulting speed, amplitudes Data on a few specific points	$\sim 1/5$ pix = $\sim 1/100$ mm	Laboratory and natural conditions	$\sim 100$ snakes
Neural network	DeepLabCut	Frequency, wavelength, wave speed, mean longitudinal speed, mean transversal speed, mean resulting speed, amplitudes All along the snake body	$\sim 1/10$ mm	Laboratory and poorly in natural conditions	$\sim 1000$ snakes
Motion capture	Qualisys	Frequency, wavelength, wave speed, mean longitudinal speed, mean transversal speed, mean resulting speed, amplitudes All along the snake body	$\sim 1/2$ mm	Laboratory	$\sim 10$ snakes
Video processing algorithm	SAAS	Frequency, wavelength, wave speed, mean longitudinal speed, mean transversal speed, mean resulting speed, amplitudes All along the snake body	$\sim 3.92$ pix $\sim 1/10$ mm	Laboratory	$\sim 1000$ snakes

Each value is calculated from data obtained in this study



**Fig. 6** Swimming snake bench. Video and Motion capture were setup to analyze the same scene

## 2.6 Comparative Table of Measurement Methods

One important challenge of this work was to obtain data and observations that can be transferred from biology to robotics. Ultimately, we aim to implement and mimic locomotion parameters exhibited by living snakes into a bio-inspired snakebot assembled from multiple modules.

## 3 Materials and Methods

### 3.1 Materials

We studied anguilliform swimming patterns of snakes placed in a 12 m long semi-tubular raceway (Fig. 6). Two

different systems were positioned along the raceway: the video part (a) and the motion capture part (b). Snakes were thus examined successively by each system during each trial. The 12 m long raceway has a diameter of 50 cm and a water depth of 30 cm. The water temperature was adjusted between 18 and 25 degrees Celsius.

A video camera was positioned (Sony RX0-II, 1920 X 1080 pixels, 50 fps) in the section of the raceway. The camera covers a swimming field of 1.39 m. For motion capture, 6 infrared cameras were placed in the second section of the raceway. These cameras cover an area of 1.5 m in length and 40 cm in width. The same videos were analyzed and compared both manually using marker tracking software, by neural network routines (DeepLabCut), and the custom-made video processing algorithm SAAS.

We studied the swimming of wild semi-aquatic wild snakes (*Natrix maura*). The snake was captured nearby the forest of Chizé (West central, France) (permit number 261679862017, issued to XB by the DREAL). The individual was studied as follows:

- (1) Motion capture requires the detection of the markers out of the water. Thus a marker was placed on the head of the snake (*Natrix maura*). The swimming movement was recorded using motion capture.
- (2) The snake's neck was marked with a nontoxic black paint layer to form a 5-mm ring (See Fig. 6). The swimming movement was recorded using the video camera.

### 3.2 Protocol

The snake tested swam ten times across the 10 m raceway (Fig. 6). During each trial, the swimming snake was filmed with the video camera and recorded by motion capture. Position, velocity, amplitude, oscillation frequency and wavelength of snakehead were extracted and processed using the methods listed in Sect. 2. We tested other individuals belonging to other species (several wild and one captive snakes; see Appendix 2), but this paper focuses on the viperine snake.

The viperine snake and the other wild snakes tested were released at their exact place of capture rapidly after the tests (the captive snake was returned to its home). We did not notice any problem during the tests, all individuals were in good condition when released. The results are presented and discussed in the next sections.

## 4 Results

In the following section, snake swimming locomotion will be described according to the main methods presented above. The outcomes presented were selected keeping in mind specific requirements needed to design a bioinspired snake robot. The comparison of the methods was performed in terms of type, quality, and quantity of data, and considering the ease to use to extract and analyze snake swimming locomotion. Values provided by DEFTAC were used as a reference to assess measurement error.

### 4.1 Snake Swimming Characterization

The extracted head positions using the marker tracking method (DEFTAC depicted Figs. 7 and 8) enabled us to retrieve the following information: period of head oscillation  $T$ , head amplitude  $a$ , and wavelength  $\lambda$  with a manual curve reading.

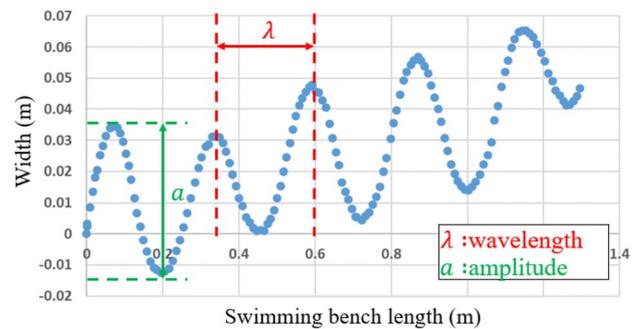


Fig. 7 Head positions extracted from marker tracking (DEFTAC, swim n°10)

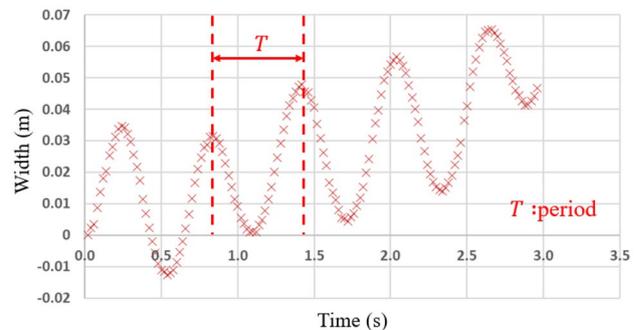


Fig. 8 Head amplitude in function of time extracted from marker tracking (DEFTAC, swim n°10)

The four methods used were compared in their ability to assess head oscillation frequency (Fig. 9), head movement amplitude (Fig. 10), and the resulting head velocity (Fig. 11). During all the trials, no evidence of exhaustion was observed. Frequency and velocity fluctuated but did not so drastically and did not decrease with successive trials. Moreover, head amplitude fluctuated and varied with the behavior of the snake but without exhibiting a clear temporal pattern. In general, the snake did not always swim in a straight line but swam diagonally, artificially increasing the amplitude of undulations.

Using DEFTAC as a reference, relative errors of the data generated by SAAS, MOCAP and DeepLabCut were evaluated (Figs. 12, 13 and 14). Head amplitude and frequency were manually extracted from curves. While the same swimming sequence was recorded both with MOCAP and video, the swimming sequence length analyzed varied across methods (Fig. 15). For instance, the swimming sequence duration recorded and analyzed with MOCAP was twice shorter than with DeepLabCut. Indeed, MOCAP suffered from the artefacts caused by surface water turbulence, thereby shortening usable sequences. These differences resulted in errors when comparing methods. Yet, regarding head speed, most errors

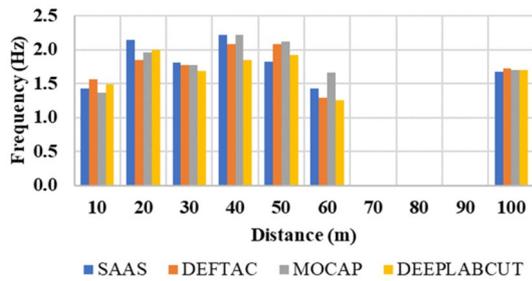


Fig. 9 Head frequency in function of the distance covered

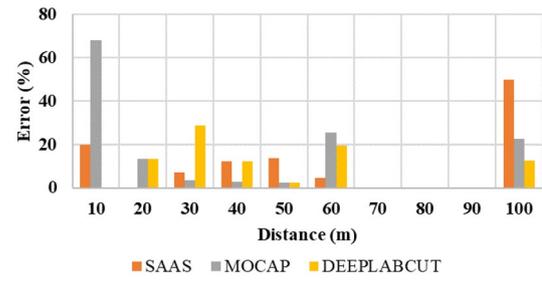


Fig. 13 Error of head amplitude in function of the distance covered (DEFTAC data are taken as reference)

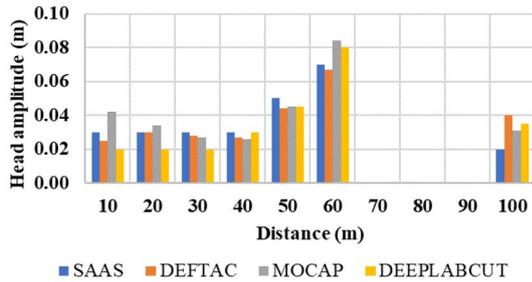


Fig. 10 Head amplitude in function of the distance covered

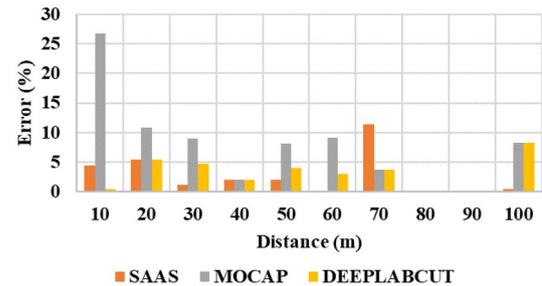


Fig. 14 Error in head resultant velocity in function of the distance covered (DEFTAC data are taken as reference)

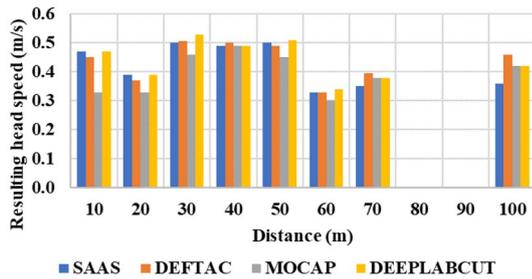


Fig. 11 Head resulting velocity in function of the distance covered

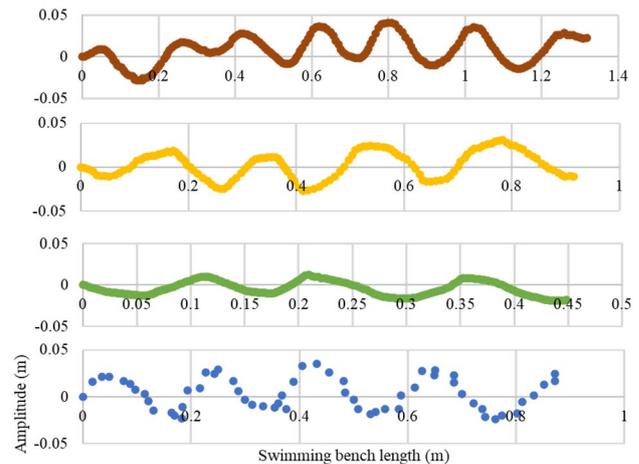


Fig. 15 *Natrix Maura*' swimming sequences (head amplitude in function of position) for each method. Blue: SAAS, green: MOCAP, yellow: DeepLabCut, brown: DEFTAC

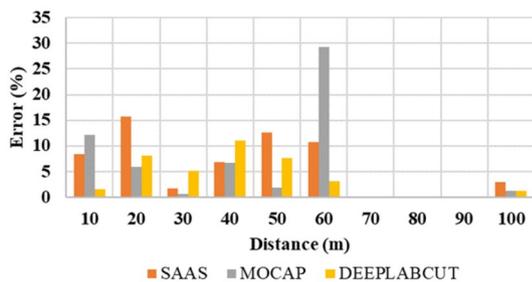
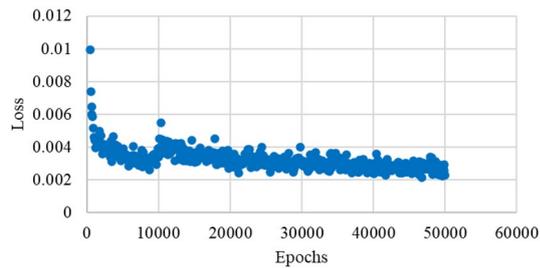


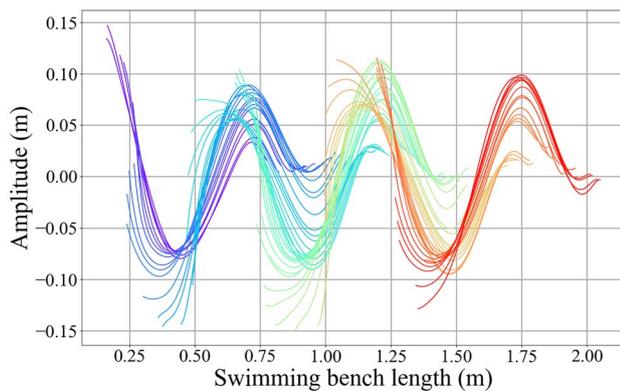
Fig. 12 Error in head frequency in function of the distance covered (DEFTAC data are taken as reference)

remained smaller than 10% of the estimates, for both SAAS (<5%), MOCAP (<10%), and DeepLabCut (<5%).

Data accuracy differed among methods. DeepLabCut relies on the number of iterations and labelled data used to train the model. In this study, 3 videos were labelled with 50 frames each and the model was trained for 7 days to achieve 50.000 iterations (Fig. 16). Regarding MOCAP, the accuracy



**Fig. 16** Loss (probability of uncertainty of a prediction) according to epochs. Loss rate is stabilizing from 10,000 to 50,000 epochs



**Fig. 17** Snake body positions during the 10th swimming sequence

was 0.6 mm according to initial calibration. DEFTAC, SAAS and DeepLabCut rely on experimental conditions.

All methods were able to track the head during a given swimming sequence. Obviously, the head cannot provide comprehensive information on the whole body of a swimming snake that is, however, essential to understand how the snake swims. Whole body locomotion was effectively processed using SAAS which generated large amounts of data, enabling us to characterize the kinematics of snakes with details. For example, this procedure generated clear swimming cones (Figs. 17, 18).

Such swimming cones differ among individuals and species. In practice, the cone presented in Fig. 18 takes the shape of an amphora. This shape is likely determined by the interactions between the snake's broad morphology, its skeleto-musculo-tendinous system, and other factors (maximal straight speed, snake's willingness...) [32]. For *Natrix maura*, the amplitudes of mid body and of the tip of the tail were higher compared to the cloacal region (limit between the body and the tail). The cone and the hydrodynamic implications are more complex than previously assumed, varying in a non-linear way along the snake's body. Understanding how all parts of the body interact with the surrounding fluid is essential to design a bio-inspired snake-like

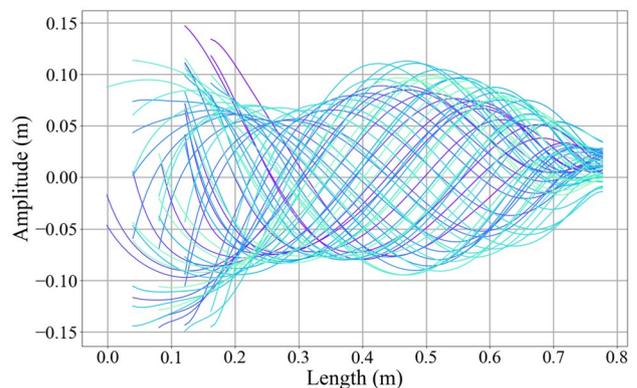
robot. Thus, comparing various swimming cones is essential to optimize the biomimetic design.

Extracting head motion was sometimes difficult, notably because this part of the snake displayed limited lateral movements compared to mid body for instance. In this case, SAAS was the most appropriate method to analyze the overall body.

## 4.2 Comparison of the Methods for the Acquisition of Experimental Data

The study of snake swimming locomotion was performed using four methods (as shown in Table 4). A quantitative and qualitative evaluation and comparison of the usefulness and relevance of these methods was performed for all snake swimming sequences we assessed. The objective was to improve the ability to gauge and sort the snake swimming kinematics collected using different methods. Sequences 1, 2, 3, 4, 5, 6 and 10 were used to compute relative errors (Fig. 19) of mean undulation frequency, mean head amplitude and mean wavelength. Sequences 1, 2, 3, 4, 5, 6 and 10 were used to compute relative errors for mean longitudinal head speed and mean resultant head speed (see Table 3). Following analysis of row data, sequences 7, 8 and 9 were discarded. In practice, MoCap method provided specific data, not easy to compare with those obtained with the other methods. Comparing methods and selecting the most appropriate could not be achieved in a standard way. Therefore, we partly relied on visual inspection of the outcomes.

The relative error values of the criteria used to compare methods were usually low. On one hand, the relative errors of criteria based on curve analysis (frequency, amplitude, and wavelength) were often higher compared to the relative errors of numerically computed criteria (longitudinal and resultant speed). Although curve analysis was sensitive, associated relative error values remain low.



**Fig. 18** Swimming cone extracted from Video processing algorithm with refocusing the middle of snake body at the neutral axis for the 10th swimming sequence

**Table 3** Relative errors obtained based on DEFTAC measurements for 10 swimming (100 m swim)

Mean criteria	Frequency (Hz)	Head amplitude (m)	Wave-length (m)	Longitudinal speed (m/s)	Resulting speed (m/s)
DEFTAC	1.77	0.0373	0.24	0.147	0.44

Mean amplitude was a parameter difficult to characterize because snake swimming direction varied during a swimming sequence. In another hand, Speed was numerically computed from one point to another in the course of a swimming sequence, and was relatively easily quantified. Relative errors calculated using SAAS were lower than those obtained with other methods, but the frequency of data acquisition was the lowest (see Fig. 15). Based on a comparison of criteria, SAAS was efficient and appropriate to analyze snake swimming characteristics. Experimental data were convergent for each criterion. This suggests that the methods used generated reliable results. Based on experimental data, it was not easy to identify the most suitable method. Qualitative criteria were thus considered, notably to take into account logistic aspects and intended outcomes.

### 4.3 Qualitative Comparison of the Methods

Qualitative issues are important to set up the most tractable system to collect the data, and thus to obtain pertinent data for biology and robotic (see Table 4). Since relative error values were similar (errors of mean resultant head speed for all methods < 10%), qualitative criteria can provide assistance for a user to select the appropriate method. Criteria were defined as follows: Handling level represents the number of times a snake was handled (e.g., biometric

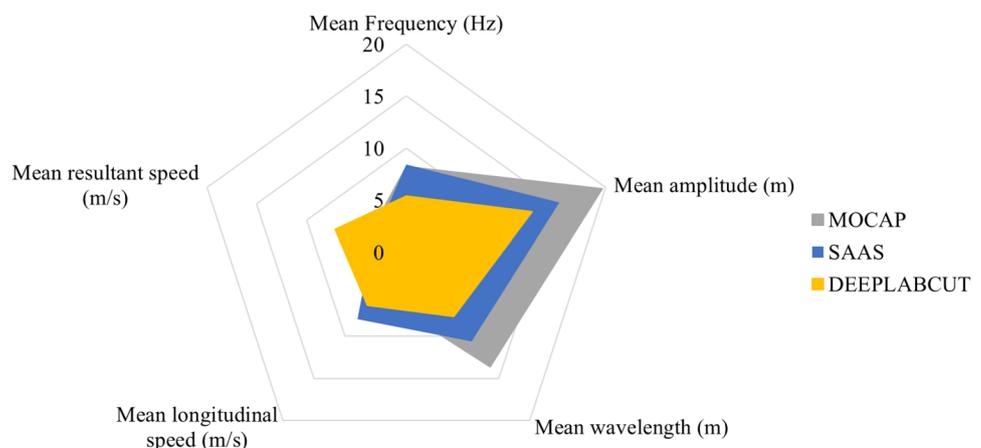
**Table 4** Qualitative results for the ease of use of each method

Criteria	Handling level	Settings	Data processing	Quality of results
DEFTAC	++	+++	+	++
DeepLabCut	++	+++	+++	++
MoCap	+	+	++	+
SAAS	+++	+++	+++	++

Handling level (+high handlings level, ++ moderate handlings, +++ minimal handlings), Settings (+ a lot, ++ many, +++ few), data processing (+ hard, ++ easy, +++ very easy), quality of results (+ data from head, ++ data from several positions along the body, +++ data from all along the body)

measurements, fitting markers). Stress increases with handling, and it may influence swimming performances. The second criterion was the logistical aspects of settings. In the field, and to a lesser extent in the laboratory, setting all the material can be a daunting challenge and time consuming. For instance, MOCAP requires many settings and adjustments due to the calibration of infrared cameras. Data processing is the third criterion. It represents the number of operations, and thus the amount of time necessary to extract the data. The last criterion concerns the quality of the outcomes. According to the complexity of the process scrutinized (analysis of many factors involved in the swimming kinematics of undulating animals), large data sets are desired to encompass the diversity of snake species (e.g., terrestrial, aquatic, amphibious, burrowing) along with individual variations (e.g., sex, age, condition). SAAS enabled extracting comprehensive and abundant data of the whole body. Depending on the number of markers, DEFTAC and DeepLabCut accurately assess several positions along the snake body. MoCap can hardly analyze the immersed part of the snake body and thus underwater markers which present a hard limit to this method.

**Fig. 19** Relative error (%) obtained based on DEFTAC measurements. Head frequency, head amplitude and mean head wavelength errors are measured on 7 swimming sequences. Mean longitudinal head speed and mean resulting head speed errors are measured on 8 swimming sequences



### 4.3.1 Marker Tracking: Deftac

Deftac generates measurements with excellent accuracy (1/100 mm), at least for biological and robotics perspectives. The protocol requires to use of natural markers or to place and remove multiple markers on the subject, and thus it necessitates repeated snake handling. When the snake is swimming underwater, the markers are subjected to diffraction, but using an underwater calibration this problem can be overcome. Processing time to extract the data from 10 successive swimming footages (full testing of a given snake requires 10 trials of 10 m each) was evaluated at about one hour. Velocity can be extracted easily, but kinematic data are limited to the tracked markers. This method is considered as a reference to obtain precise positions of the markers (3D), but the segments between markers are interpolated as straight lines. Therefore, this approach seems particularly adapted to calibration but not suitable to generate a large amount of whole-body swimming kinematics.

### 4.3.2 Neural Network: DeepLabCut

DeepLabCut can be used under laboratory and field conditions. DLC presents excellent accuracy (1/10 mm). However, this method requires a sufficient dataset for training the neural network, training sessions, and therefore it can be computationally demanding to test hundreds of individuals belonging to tens of species. In fact, processing time to train network and extract data is evaluated at about one hour for a set of 10 swimming footages. Indeed, the peculiarities of each snake species and strong interindividual variability mean that specific training might be needed for each snake. Different experimental (initial) conditions hardly allow analyzing various snake swimming (artificial vs natural lighting). This method can be used to analyze different movements of swimming snakes and thus might be suitable to characterize behavior more generally.

### 4.3.3 Motion Capture

Motion capture presents a good accuracy (1/2 mm) and importantly easily provides three-dimensional data. Although possible roles of the dorso-ventral component of the lateral undulation during anguilliform swimming are not yet understood, and thus not considered, this dimension should not be overlooked. However, this method requires a particularly complicated setup that cannot be easily deployed in the field. In addition, reflective markers must be placed (glued) on the snakes. Therefore, even if the processing time to extract data is evaluated at about one hour for 10 swimming footages, this method is not suitable for rapidly gathering large numbers of sequences of swimming snakes. In addition, the possible impact of the reflective markers

glued on the snakes has not been evaluated to date but may impact swimming kinematics through increased drag. When infrared is used, this method is operative only for individuals swimming at the water surface and only for the most anterior part of the snake. Tracking the whole snake is not possible because most of the body will remain underwater and the markers will be quickly lost by the system.

### 4.3.4 Video Processing Algorithm: SAAS

Video processing algorithm is an effective and particularly handy method to analyses the swimming movements of whole snakes. Position accuracy ( $\pm$  several mm along the midline of the snake) is judged sufficient for biological and robotics questions. The algorithm was designed for this specific study and it allows to rapidly extract key information to analyze swimming kinematics all along the snake body. A large data set with various species and many individuals can be automatically built. Processing time to extract data is evaluated at about one hour for 10 swimming footages. The SAAS is the only method capable of quickly generating swimming cones from swimming sequences. However, the quality of the footages is determinant. Using a well-designed raceway and appropriate lighting conditions is important to get much-contrasted images from which snakes can be separated from the background using filtering. Setting appropriate raceway and light conditions is a prerequisite to extract swimming kinematics in the field, and this may pose logistical difficulties.

## 5 Discussion and Future Work

This study shows that large numbers of the kinematics of swimming snakes can be collected and analyzed. Providing that authorizations to capture wild or captive animals have been issued, filming a wide range of swimming snakes in a standard way essentially relies on the use of a raceway fitted with an appropriate color background (e.g. matt white to limit reflection), lighting and well-positioned video cameras. Most individuals of (semi-) aquatic snakes will readily swim [23], but many terrestrial species and even arboreal snakes will provide high-quality data. For example, many terrestrial snakes have been spotted swimming at sea [33]. We successfully tested terrestrial snakes such as European whip snakes (*Hierophis viridiflavus*), vipers (*Vipera aspis*), grass snakes (*Natrix helvetica*), rattlesnakes (*Crotalus atrox*), and ball pythons (*Python regius*) (supplementary material, Appendix 2). Therefore, the major lack of kinematic data might be filled up, encompassing the extended diversity of snake life history traits, to facilitate and assist the development of bio-inspired snake robots. The main bottleneck lies in data processing (except for motion capture). The comparisons of

the methods we performed may help researchers to select or combine them, depending upon the question(s) addressed.

All methods have been compared using similar swimming sequences. However, for a given footage, some methods allowed us to analyze only part of the sequence. Most of the computed errors (i.e. measurement differences) arose from this bias.

The SAAS method we developed in this study is the most promising. Despite initial constraints to collect suitable videos, the extraction of kinematics was fast and efficient. It provides comprehensive information. For instance, curvatures displayed by the body of swimming snakes were sequenced and interpolated with circle arcs thanks to a video processing algorithm, offering possible guidance to control the motion of future robot [34, 35]. Swimming cones can be rapidly generated and analyzed. However, other approaches have some advantages. The combination of both DeepLab-Cut and video processing algorithm allows for analyzing swimming in fully controlled conditions (laboratory) but also using videos collected in a natural environment where the background was not uniform (unpublished data). This method might well be useful to extract information from various sources and to study poorly known species (or species not available in captivity). Our results open avenues to study various snake species swimming underwater, at the water surface or crawling on the ground. The outcome will provide basic data to address ecological and evolutionary questions. But they might be essential to robotic swimming snake applications. In the fields of robotics and biomimetics, a wide spectrum of kinematic patterns is needed to design a wide range of bio-inspired snake robot models [4, 36]. The versatility of lateral undulation, a locomotor mode efficient on land and in the water represents a major source of inspiration. Our results merely represent a first, albeit essential, step to better understand how snakes optimize swimming performances according to their morphology, body size and ecological constraints (e.g. travel distances). Further investigations are needed, however. Characterizing swimming undulations in a volume and not in a plane appears essential to truly understand the kinematics of snake swimming and to allow and efficient and biologically relevant transfer of kinematic data to robotics.

## 6 Conclusion

This paper presents four methods to study the kinematics of swimming snakes, how they were tested using living snakes and the outcomes of the comparison among them. A protocol was depicted to explain how three methods that are based on the use of marker tracking can be evaluated to characterize undulatory swimming in snakes. The

key contributions of this paper can be summarized as: (1) a practical and efficient protocol to assess snake swimming locomotion was developed. This protocol enables to rapidly collect abundant swimming kinematics. However, the quality and data type obtained depend on the method (and likely of the snake species) used. The combination of complementary methods is preferable to obtain a comprehensive dataset. Meanwhile, further investigations are needed to optimize calibration and minimize logistics. (2) SAAS software was designed to extract key kinematic information from video footages, and the main stages were described. Our results show that SAAS is efficient in automatically generating large and comprehensive data 2D sets. In the future, it should be extended to analyze 3D movements. SAAS can analyze the kinematics of the whole snake body in motion. (3) An approach is presented to extract a large amount of kinematics data that are essential in the fields of biomimicry and robotics.

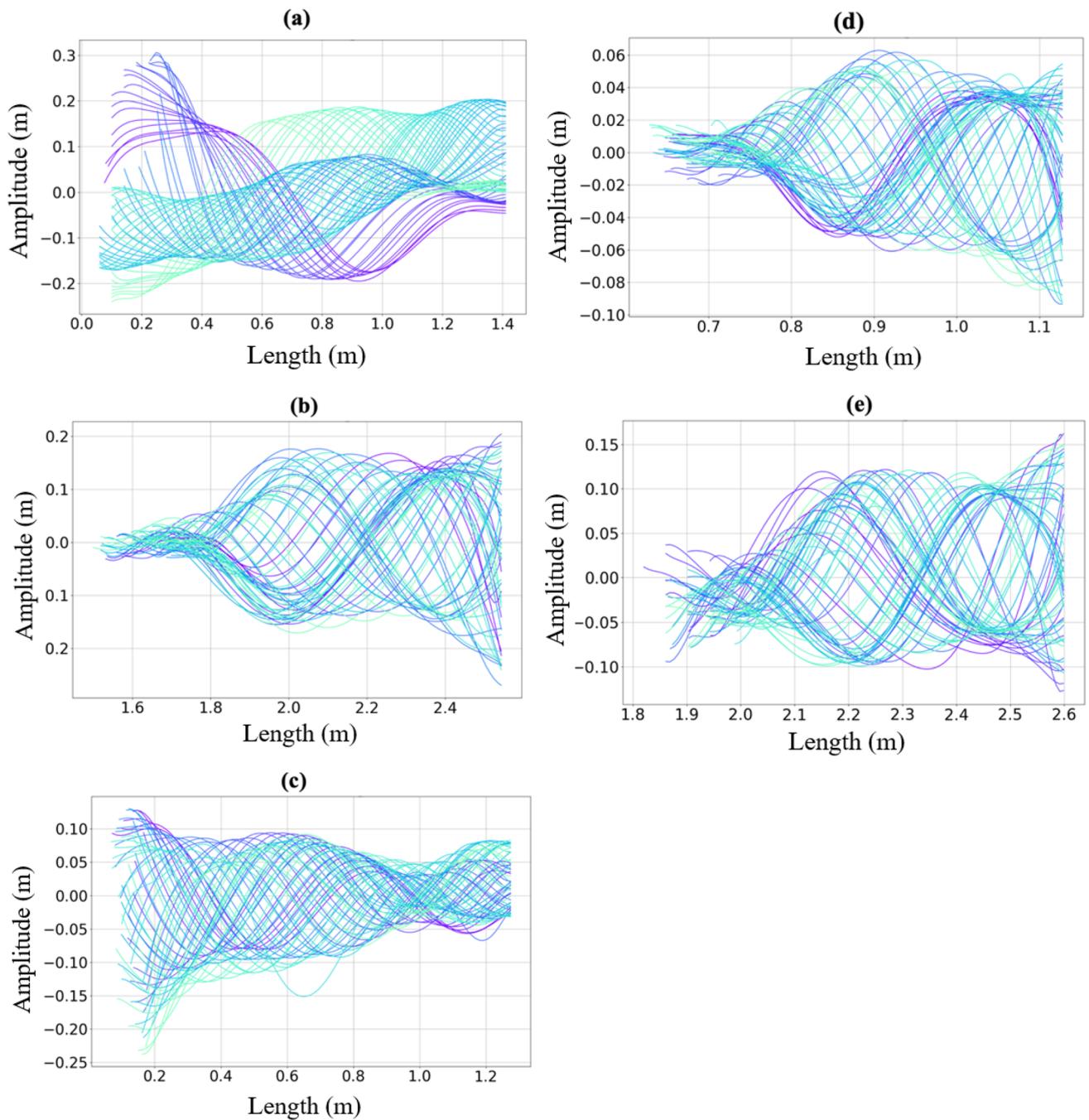
Overall, the protocol to assess kinematics through complementary methods will be used both to develop a bio-inspired swimming snake robot and for comparative analyses in evolutionary biology. Both disciplines can be mutually beneficial. Accurate characterization and transfer of anguilliform swimming motion from biological models (snakes) to the technological world enables better imitation of snake swimming. This represents a major source of inspiration for to design snake robots. In turn, snakebots will be considered as tools for biologists to answer biological issues, for example, to explore the impact of manipulating independently the amplitude and the frequency of undulations on swimming performances.

## Appendix 1: Manual Analysis

Manual measurements pertain to non-invasive methods; they have been employed to study snake swimming performances [23]. Swimming speed is measured using individuals placed in a raceway and filmed from above when moving along the track; time intervals in the function of the distance swam are used to calculate speed. This method has been successfully used both in the laboratory and in the field using various equipment [23]. But other key parameters such as the exact position of selected body segments, the amplitude and frequency of the undulations, are manually post-treated frame by frame to eventually extract mean frequency, mean amplitude, mean wavelength and mean wave speed [18]. Thus, except for swimming speed, the manual measurement approach is fastidious and limited to a few swimming sequences. It can hardly be employed to build a large set of comprehensive data sets of swimming kinematics.

## Appendix 2: Crude Swimming Cones

See Appendix Fig. 20.



**Fig. 20** Crude swimming cones extracted from Video processing algorithm. **a** *Crotalus atrox*, **b** *Python regius*, **c** *Hierophis viridiflavus*, **d** *Vipera aspis*, **e** *Natrix Helvetica*

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## Declarations

**Conflict of interest** On behalf of all authors, the corresponding author states that there is no conflict of interest.

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