Dancing *out-of-phase*

Coral tentacle stiffness evokes *out-of-phase* motion that improves mass transfer

Dror Malul, MSc student supervised by Prof. Uri Shavit (Technion) and Prof. Roi Holzman (TAU).

Introduction and research questions

Sessile marine organisms rely on the ambient flow for nutrient supply, waste removal and gas exchange. Many corals and sea-anemones have flexible tentacles that sway and bend under the torques applied by the waves and currents. Using high-speed videography, we recorded the motion of the tentacles of two coral and one sea-anemone species *in-situ* (Fig. 1 A) and in a standing wave laboratory tank. We visualized and quantified the flow around the tentacles using Particle Image Velocimetry (PIV), a non-intrusive flow measurement technique. In all the experiments, the tentacles exhibited an unintuitive motion: the velocity of the tentacle oscillated with the same frequency as the waves, but preceded the velocity of the water by around a $1/4$ of the wave period, generating an *out-of-phase* motion. One example of the *out-of-phase* motion of the tentacles of a *Dipsastraea favus* (Fig. 1 B,C) coral is given in Movie 1, where the white arrows indicate the instantaneous water velocity and the red arrow indicates the instantaneous horizontal tentacle velocity. When the movie slows down, it is possible to see that the tentacles change the direction of their velocity prior to the ambient water. This is also shown in Fig. 2, where the peaks of the tentacle velocity precede the peaks of the water velocity. These measurements ($N > 120$) led to three research questions: (1) is the *out-of-phase* motion general among tentacles and other tethered organisms and their appendages? (2) What are the

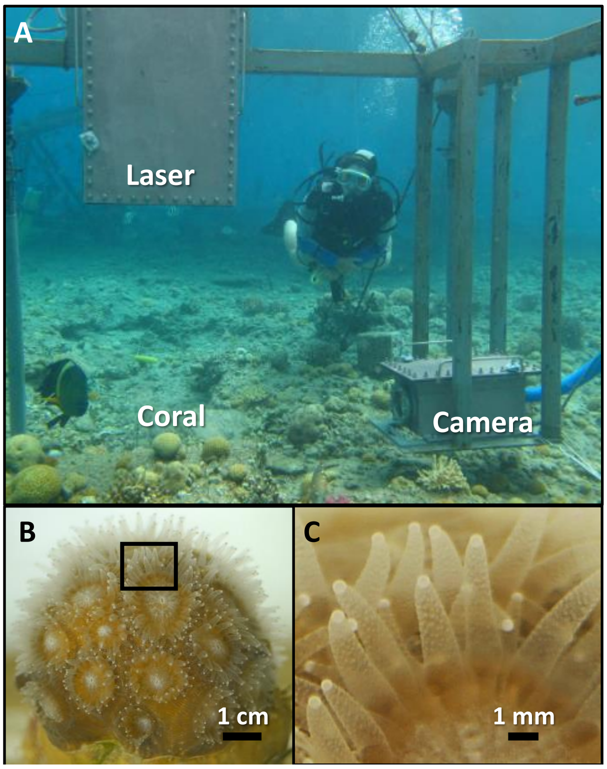

Fig. 1. Research animals and field apparatus. (A,B) A small colony (~5 cm diameter) of *Dipsasraea favus* coral with its tentacles extended. (C) Underwater PIV system deployed from the IUI pier.

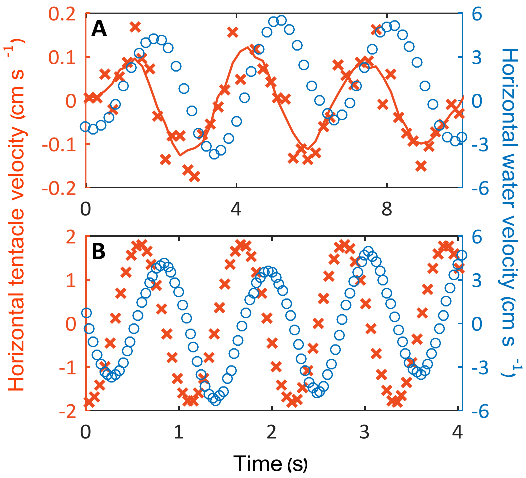

Fig. 2. *Out-of-phase* motion of *D. favus* tentacles in the field (A) and in the laboratory (B). The phase difference is the time between peak water (blue) and tentacle (orange) velocities. Line in (A) is a moving average of the tentacle velocity (span of 5).

mechanisms that generate this *out-of-phase* motion? (3) Is there a benefit to the coral, in terms of gas exchange with the water?

Results

Observing three species of Hexacorralia *in-situ* and in the laboratory, *out-of-phase* motion was apparent in every single measurement. To reach a generalized mechanistic understanding of this phenomenon, we fitted the laboratory measurements of the tentacles of *D. favus* coral (Fig. 1 B,C) with a dynamic model. The tentacle was represented as a torsional spring-damper system under hydrodynamic torques. An analytic examination of the model equation revealed that the *out-of-phase* motion is an emergent property of the elasticity of the tentacle hydroskeleton. Meaning that any elastic sessile organism or appendage that can be successfully modeled as an elasticity-dominated system is expected to move *out-of-phase*. The relative importance of the tentacle elastic properties in controlling the dynamics is exemplified using an order-of-magnitude analysis which compared the relative magnitude of the different torques acting on the tentacle in our measurements. This analysis revealed that the elastic torques that the tentacle exerts were in fact comparable in magnitude to the hydrodynamic torques applied on it by the water, and are the main contributor to the *out-of-phase* phenomenon.

To study the effect of the *out-of-phase* motion on the mass flux of gases between the tentacle and the water, we have conducted sets of numerical simulations. In each set we imposed a combination of tentacle and water velocity amplitudes, which covered the range of observed values. Each set consisted of five simulation, in which the phase difference varied between $-180°$ and $0°$. We solved the flow and mass transfer equations in each simulation, and obtained the time dependent water velocity field, and the oxygen concentration field in the vicinity of the tentacle. The *out-of-phase* motion affected the resulting velocity and concentration field substantially. In Movie 2, the velocity of the water and the tentacle are *in-phase* with one another (phase difference of $0°$), whereas in Movie 3 they are set to be $-90°$ *out-of-phase*. The colors in the movies indicate the concentration of oxygen (blue is zero and red is the ambient oxygen concentration) around the cross section of the tentacle which is marked by a white circle, and the arrows indicate the velocity field of the surrounding water. Fig. 3 shows snapshots of the resulting concentration fields generated due to *in-phase* (A) and *out-of-phase* (B) motion at a single snapshot during the simulation when both tentacles were at maximal speed. The difference in the concentration field between moving *out-of-phase* and *in-phase* results in a difference in the diffusive mass flux between the tentacle and the water. Using the solutions of the concentration fields and Fick's law we calculated the mass absorbed by a tentacle during one period of oscillation and learned that Moving *out-of-phase* enhanced the transfer of oxygen to the tentacle by up to 25%, compared with *in-phase* motion. Fig. 4 shows the mass of oxygen transferred to the tentacle per period as a function of the phase difference in one set of simulations where the water velocity amplitude was set to 3.3 $cm\ s^{-1}$, the tentacle velocity amplitude was set to 1.2 $cm\ s^{-1}$, and the phase difference was arterially varied to: $0°$, $-45°$, $-90°$, $-135°$ and $-180°$.

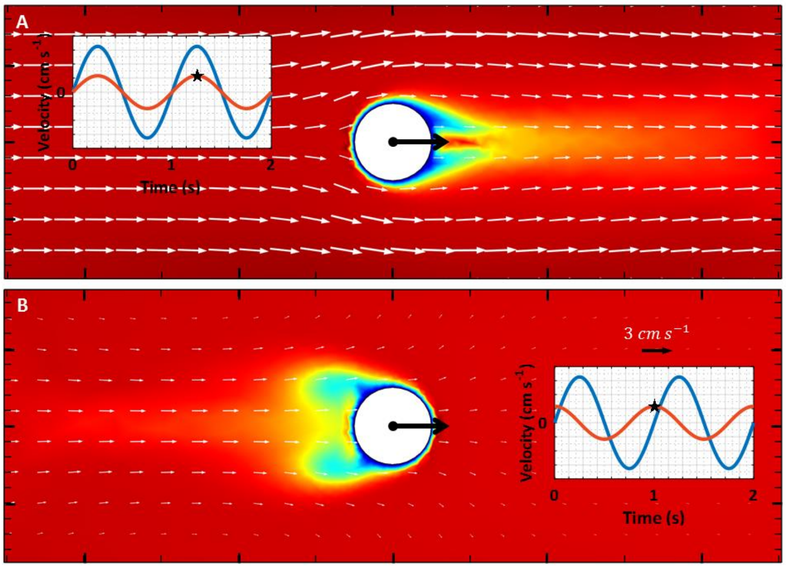

Fig. 3. A snapshot of the concentration field around a tentacle when moving *in-phase* (A) and *out-of-phase* (B). The concentration of oxygen as a tracer is represented by the colors ranging between 0 (blue) and 0.2 $mol\ m^{-3}$ (red), representative of ambient nightly surface oxygen concentration in the study site. In this snapshot, the two tentacles move at the same velocity (black arrows) and the water velocity (white arrows) is different due to out-of-phase motion. The insets show the velocities of the water (blue) and the tentacle (orange) in these two scenarios and the star in each inset indicates the time of the snapshot. The tentacle diameter is 0.5 mm. The black arrow in (B) serves as a scale for the white velocity field arrows.

The enhancement is caused by the increase in relative velocity, created by the *out-of-phase* motion. Fig. 4 B shows oxygen mass transfer as a function of the relative velocity in all the simulations conducted. The different symbols represent different combinations of water and tentacle velocity amplitudes, the colors and the sizes of the symbols indicate the phase difference (bigger symbols represent bigger phase difference value). Under ambient water velocities of $\sim 5\ cm\ s^{-1}$ the phase difference may enhance mass transfer by increasing the relative velocity. One example is a set indicated by a filled black diamond in which the phase difference increases the relative velocity from ~ 2 to $\sim 6\ cm\ s^{-1}$, and the mass transfer consequently enhanced by $\sim 25\%$.

We conclude that the phase difference is a general phenomenon caused by the elasticity of coral tentacles, which may substantially enhance gas exchange between the tentacle and the water. The enhancement is most pronounced when ambient velocities are lower than $\sim 5\ cm\ s^{-1}$, prevalent conditions in the reef, indicating that the elasticity of the tentacle hydroskeleton may represent an adaptive advantage to corals. We postulate that this phenomenon is general to flexible bodies and appendages residing in oscillatory flow, and driven by their elastic properties.

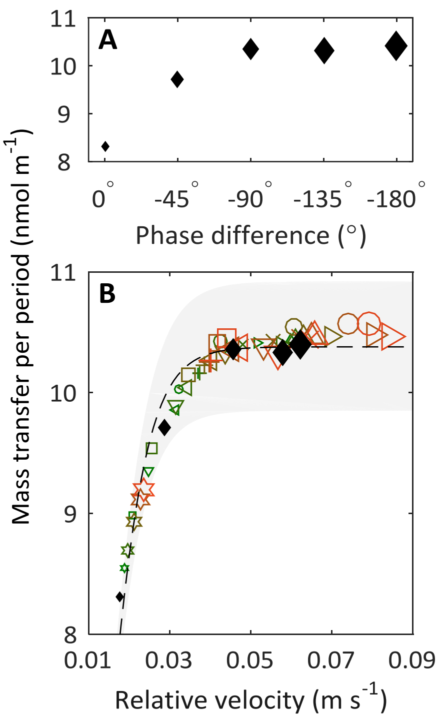

Fig. 4.The effect of *out-of-phase* motion in mass transfer. (A) Mass transfer per period as a function of the phase difference in one set of simulations. (B) Mass transfer as a function of relative velocity in all the simulations conducted.