

SHORT COMMUNICATION

Using a shell as a wing: pairing of dissimilar appendages in atlantiid heteropod swimming

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ABSTRACT

Atlantiid heteropods are zooplanktonic marine snails which have a calcium carbonate shell and single swimming fin. They actively swim to hunt prey and vertically migrate. Previous accounts of atlantiid heteropod swimming described these animals sculling with the swimming fin while the shell passively hung beneath the body. Here, we show, via high-speed stereophotogrammetric measurements of body, fin and shell kinematics, that the atlantiid heteropod *Atlanta selvagensis* actively flaps both the swimming fin and shell in a highly coordinated wing-like manner in order to swim in the intermediate Reynolds number regime ($Re=10-100$). The fin and shell kinematics indicate that atlantiid heteropods use unsteady hydrodynamic mechanisms such as clap-and-fling and delayed stall. Unique features of atlantiid heteropod swimming include the coordinated pairing of dissimilar appendages, use of the clap and fling mechanism twice during each stroke cycle, and the fin's extremely large stroke amplitude, which exceeds 180 deg.

KEY WORDS: Marine snail, Zooplankton, Locomotion, Clap-and-fling, Delayed stall

INTRODUCTION

Atlantiid heteropods are a family of holoplanktonic marine snails with a coiled shell composed of aragonite, a form of calcium carbonate that is sensitive to ocean acidification (Orr et al., 2005; Bednaršek et al., 2012; Wall-Palmer et al., 2016). Heteropods live in the upper 250 m of the ocean, display some diel vertical migration and have well-developed eyes for selectively preying on pteropods, copepods and other heteropods (Lalli and Gilmer, 1989; Wall-Palmer et al., 2018a,b). Heteropod visual capabilities likely allow them to avoid sampling nets, and thus their population densities have probably been underestimated from plankton hauls (McGowan and Fraundorf, 1966; Thiriot-Quévieux, 1973; Seapy, 1990; Wall-Palmer et al., 2016). Nonetheless, heteropods comprise a significant proportion of the shelled holoplanktonic gastropod population (e.g. thecosomatous pteropods and heteropods): up to 28% in one study off Baja California (McGowan and Fraundorf, 1966) and up to 69% in some locations in sub-polar climates in the past (Wall-Palmer et al., 2014). However, heteropods have rarely been studied, and little is known about their ecology or behavior (Lalli and Gilmer, 1989; Wall-Palmer et al., 2016).

Swimming is important for heteropod predation and diel vertical migration, but little is known about atlantiid heteropod swimming

behavior. Further, their negatively buoyant shells (into which they may fully retract) and pelagic lifestyle require an efficient use of energy. Heteropods have a modified foot used as a swimming fin which is held upward in the water column and allows them to normally swim at speeds of 2–3 cm s⁻¹ (Morton, 1964; Richter, 1973). Morton (1964) and Lalli and Gilmer (1989) describe atlantiid heteropods swimming by undulating their swimming fin 'like a single sculling blade' (Morton, 1964), and Land (1982) describes *Oxygyrus inflatus* flapping its swimming fin. Lalli and Gilmer (1989) further state that, compared with that of the larger shell-less heteropod species, atlantiid heteropod swimming is less efficient because they are hindered by their downward-hanging shell. They further describe the thin keel projecting outward from the shell's outer whorl as an adaptation to prevent the shell from excessively swinging back and forth beneath the body during swimming. In the current study, we show that the shell of the atlantiid heteropod *Atlanta selvagensis* does not passively hang downwards during swimming but that the animal flaps its shell as a second swimming appendage in synchrony with its swimming fin. The atlantiid heteropod's synchronized pairing of dissimilar body structures (i.e. the swimming fin and shell) for locomotion represents a unique and previously unknown type of adaptation.

MATERIALS AND METHODS

Two atlantiid heteropods (*Atlanta selvagensis*; De Vera and Seapy, 2006) were collected during a daytime cruise in September 2017 in a net tow offshore of Bermuda using a vertical tow from ~0 to 30 m depth using a 150 µm mesh size Reeve net with a specialized 20 l cod end. Zooplankton were kept in collected seawater and, on return to the laboratory at the Bermuda Institute of Ocean Sciences (BIOS), were visually identified under a stereomicroscope, transferred to filtered seawater and kept in a temperature-controlled chamber set at 21°C. Experiments were completed within 12 h of animal collection. A photogrammetry system composed of three synchronized high-speed Edgertronic cameras (Sanstreak Corp., San Jose, CA, USA) was used to measure the kinematics of the atlantiid heteropod freely swimming in a 30×30×30 mm³ glass aquarium. The cameras filmed at 600 Hz at a resolution of 1024×912 pixels and were equipped with 200 mm Nikon macro lenses with apertures set to f/32 to maximize the depth of field (approximately 12 mm). The cameras viewed the aquarium from three orthogonal perspectives. One monochrome camera with spatial resolution of 13.9 µm pixel⁻¹ viewed the aquarium from one tank side. Using mirrors, a second monochrome camera with spatial resolution of 17.2 µm pixel⁻¹ viewed the aquarium from the bottom, and a color camera with spatial resolution of 15.6 µm pixel⁻¹ viewed the aquarium from the other tank side. LED fiber optic illuminators (Dolan-Jenner Industries, Lawrence, MA, USA) provided collimated backlighting for each camera. The aquarium was filled with filtered seawater to a depth of 28 mm, and the field of view was at least 10 mm above the bottom of the tank such that only actively swimming heteropods appeared in the recordings. The camera system

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was calibrated using *Argus* software (Jackson et al., 2016) by recording and tracking the end points of a 9.6 mm calibration wand manually moved through the aquarium. The cameras were manually triggered when the heteropod swam into the field of view of multiple cameras, and a single in-focus recording of one of the heteropods was collected in this way. Heteropod kinematics were quantified in three dimensions by manually tracking eight points on the heteropod in this recorded sequence (483 ms) from two of the cameras.

RESULTS AND DISCUSSION

Fig. 1 shows a three-dimensional model of the heteropod with the tracked points labeled, including two points on the tentacle tips (*b* and *f*), one point on the body (*a*), two points on the shell edge (*d* and *e*), one point on the tip of the swimming fin (*c*), and points on the leading and trailing edges of the swimming fin (*g* and *h*). Global (*XYZ*) and body-based coordinate systems (*X'Y'Z'*) are defined. The heteropod has a body length $l_b=2.2$ mm (measured from the tip of the tentacles to the tip of the tail-like operculum), a shell diameter $d=1$ mm, swimming fin length $l_f=1.1$ mm (measured from point *a* to point *c*), fin surface area of 0.52 mm², shell surface area of 0.96 mm² (including the keel) and mean chord length $c=0.47$ mm (calculated as the surface area divided by the fin length). The animal beats its fin and shell synchronously at a frequency $f=9.1$ Hz and has a mean swimming speed $u=27$ mm s⁻¹. The animal thus inhabits an intermediate Reynolds number regime in which both viscous and inertial forces are important. We define a swimming Reynolds number $Re_s=ul_b/\nu$ and a chordwise Reynolds number $Re_c=2\phi l_f c/\nu$, where ϕ is the stroke amplitude of the appendage and ν is the kinematic viscosity of seawater at 21°C. The heteropod thus has $Re_s=59$ and $Re_c=33$.

As shown in Fig. 1B, θ is defined as the angle between the shell plane and fin plane on the animal's right side. The angles between the *X'Y'* plane and the heteropod's fin plane and shell plane are defined as ϕ_f and ϕ_s , respectively. It is important to note that, although the shell is rigid, the root that connects the shell and body is highly flexible and the animal is thus able to bend and twist the whole shell from the root. The fin is also highly flexible and may bend along its span and twist along its chord. Thus, as shown in Fig. 1C, α is defined as the angle of attack and β as the stroke plane angle. The stroke plane angle β is found for both the swimming fin and shell and is calculated as the angle between the *Y'* axis and the trajectory (i.e. stroke plane) of the fin or shell, respectively. The angle of attack α is defined as the angle between the stroke plane and the chord of the fin or shell, respectively. The advance

ratio $J=u/2\phi_{\max}f/l_b=0.35$, where ϕ_{\max} is the maximum stroke amplitude of the fin.

Fig. 2 shows a time sequence of images of one stroke cycle for a freely swimming heteropod. Fig. 3 shows the associated wing and body kinematics. Movies 1 and 2 show the associated high-speed video and an animation of heteropod swimming, respectively. The wingbeat cycle begins at $t'=0$, where the fin and shell lie parallel to each other on the animal's right side ($\theta\cong 0$ in Fig. 3B). The leading edges of the fin and shell separate as they rotate around their respective trailing edges to begin the power stroke, followed by separation of the trailing edges. The fin and shell then synchronously flap circumferentially around the body toward the animal's left side, with the fin and shell moving over and under the body, respectively. Fig. 3B shows the resulting increase in θ , and Fig. 3C shows that the fin moves at a higher angular velocity than the shell. By $t'=0.18$ in Fig. 2, the appendages are fully separated and the heteropod's speed has increased from 17.6 mm s⁻¹ to 25.1 mm s⁻¹ (Fig. 3B). The bottom camera view shows (at $t'=0.01$ – 0.35 in Fig. 2) that the animal actively reorients its shell as it flaps it beneath its body. As shown in Fig. 3D, the shell is rotated such that it has a leading edge and trailing edge with a positive angle of attack relative to the stroke plane, a pattern also seen in the swimming fin. At $t'=0.27$, the fin and shell are fully extended upwards and downwards, respectively (Figs 2 and 3B), and have reached their maximum angular velocities of 25.0 rad s⁻¹ and 16.3 rad s⁻¹, respectively (Fig. 3B). The animal also has achieved its maximum swimming speed of 53.1 mm s⁻¹ or 24.1 body lengths s⁻¹ (Fig. 3B). By $t'=0.35$, both the fin and shell are on the left side of the animal, the appendage motion has slowed, and the swimming speed has decreased to 44.2 mm s⁻¹ (Fig. 3B). At $t'=0.51$, the leading edges of the fin and shell closely approach each other on the heteropod's left side (Figs 2 and 3B). The shell and fin then rotate around their respective spans to become parallel, thus completing the power stroke and reaching the maximum value of $\theta=352.2$ deg. The result of this left-ward power stroke by both the fin and shell is that the heteropod's swimming trajectory moves forward and to the right (Fig. 3A).

The heteropod separates its fin and shell in the recovery stroke in the same way as in the power stroke. The fin and shell leading edges separate first, opening a V-shaped gap. The appendages then separate, with the fin again moving faster than the shell (Fig. 3C). As the heteropod begins to flap its appendages to the right side of its body, the animal's swimming trajectory changes direction to the left

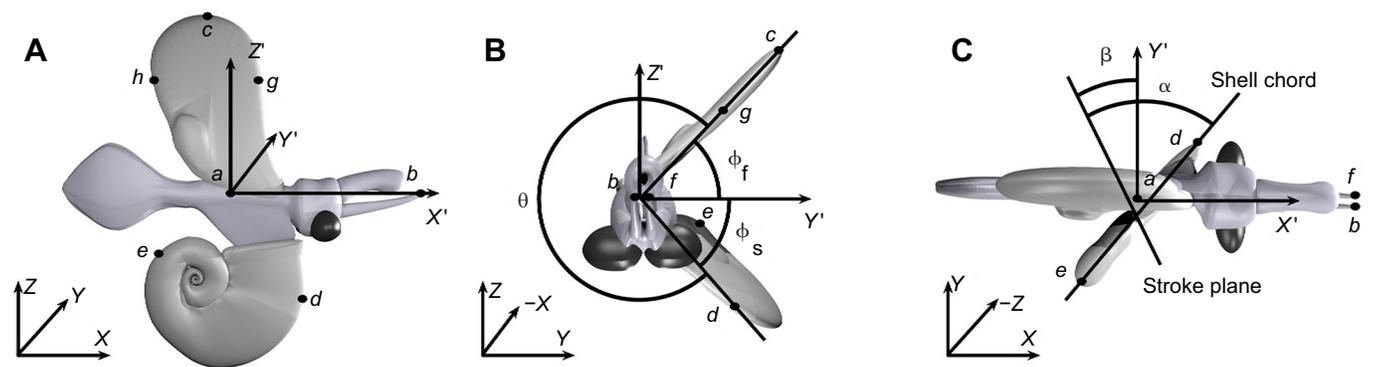


Fig. 1. Atlantiid heteropod morphology and coordinate systems. Schematic diagram of an atlantiid heteropod showing the global (*XYZ*) and body-centered (*X'Y'Z'*) coordinate systems, the locations of the tracked points (*a*–*h*), the definition of the angle between the fin plane and shell plane θ , the stroke plane angle β and the angle of attack α . The swimming fin and shell are positioned differently in each panel: (A) $\theta=180$ deg, $\alpha=0$ deg, (B) $\theta=270$ deg, $\alpha=0$ deg and (C) $\theta=180$ deg, $\alpha=45$ deg.

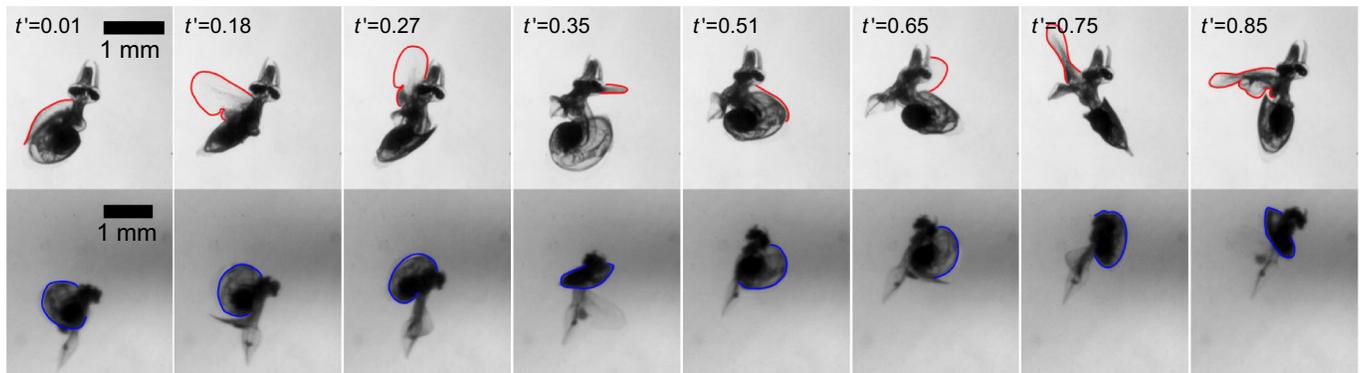


Fig. 2. Heteropod wing stroke. Sequence of synchronized images acquired from two perspectives illustrating one stroke cycle of heteropod swimming. The top row views the animal from the side, and the bottom row views the animal from the bottom. t' is time normalized by the stroke period (110 ms). The swimming fin and shell are outlined in red and blue, respectively.

(Fig. 3A). When swimming forward, the animal thus changes swimming direction laterally with each half-stroke, resulting in a sawtooth trajectory. By $t'=0.65$, the fin and shell have separated and are accelerating toward the animal's right side. Both the swimming speed and appendage angular speed increase as a result (Fig. 3B). At $t'=0.75$, the fin and shell are again fully outstretched (Figs 2 and 3C), and the animal reaches its maximum recovery stroke swimming speed (45.9 mm s^{-1}). Again, the fin has a larger angular velocity than the shell (16.5 rad s^{-1} versus 14.6 rad s^{-1}). As shown in Fig. 3C, the greater angular speed of the fin during both the power and recovery strokes reflects its greater stroke amplitude (222 deg) as compared with that of the shell (170 deg). By $t'=0.85$, the fin and shell are both on the animal's right side. The shell and fin again reorient over the recovery stroke ($t'=0.65\text{--}0.85$), this time in the opposite direction, such that they have positive angles of attack relative to the recovery stroke plane. By the end of the recovery stroke, the swimming speed again reaches a local minimum.

The kinematics of the fin and shell give insight into the hydrodynamics of atlantiid heteropod swimming. Further,

heteropod appendage kinematics are similar to the kinematics of other organisms swimming (e.g. pteropods) or flying (e.g. insects) at similar Re (Ellington, 1999; Sane and Dickinson, 2001; Chang and Yen, 2012; Adhikari et al., 2016; Murphy et al., 2016). These similarities include the use of high angles of attack, figure-eight appendage trajectories and the clap-and-fling mechanism. For example, in Fig. 3D, the shell is moved in a figure-eight motion relative to the body, thus providing lift and thrust on both power and recovery strokes. The fin and shell employ high angles of attack in both the power and recovery strokes. For example, the shell begins and concludes its power stroke with $\alpha=50$ deg and $\alpha=105$ deg, respectively. Leading edge vortices (LEVs) are thus probably developed and are important in generating the lift needed to counteract the heteropod's heavy shell. The heteropod is distinct from pteropods and insects in that, facilitated by its narrow body, it employs a clap-and-fling-type mechanism twice during each stroke cycle. On each side of the animal, the appendages closely approach each other (leading edges first) and then compress the fluid, probably causing a rearward jet that generates additional propulsive forces (Götz, 1987; Dickinson, 1996). The appendages then peel apart, likely creating enhanced LEVs on the fin and shell. Because of its large stroke amplitude and high stroke frequency, we speculate that the heteropod's flow signature consists of a linked chain of large vortex loops (Dickinson, 1996).

This is the first study to quantitatively report on atlantiid heteropod swimming kinematics. We show that swimming atlantiid heteropods actively coordinate shell and fin flapping. This finding contradicts earlier descriptions of atlantiid heteropod swimming in which the shell played only a stabilizing role (Morton, 1964; Richter, 1973; Lalli and Gilmer, 1989). Previous researchers may have misidentified the shell motion as being a result of the swimming fin motion instead of being a driver of propulsion. Many types of animals flap or reciprocate paired appendages such as wings, fins or parapodia to generate propulsive forces, but, to our knowledge, the synchronization of dissimilar propulsive appendages has not been seen before. Considered as propulsive appendages, the fin and shell have vastly different masses, geometries, surface areas and rigidities. These different characteristics lead to different appendage kinematics and affect the animal's swimming orientation. For example, the shell, though having a wall thickness of only 3–40 μm (Wall-Palmer et al., 2016), is nonetheless substantially heavier than the fin. The shell thus hangs downwards and flaps back and forth beneath the heteropod's body while the swimming fin is directed upwards. The heteropod is thus rotated 90 deg relative to the orientation of other flying

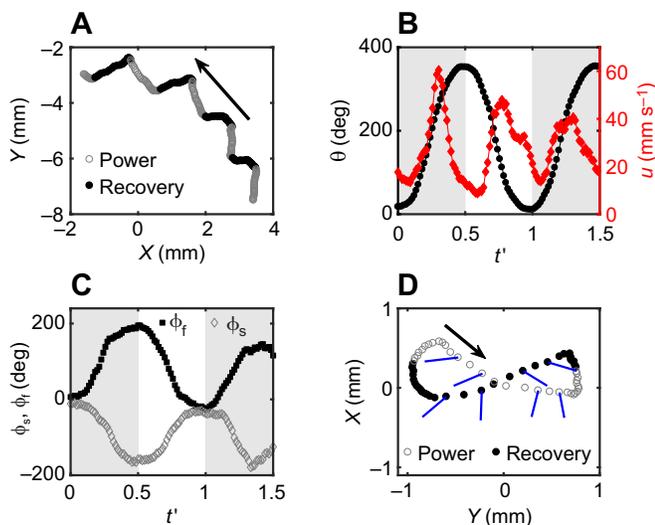


Fig. 3. Heteropod appendage and body kinematics. (A) Swimming trajectory in the horizontal plane. (B) Time series of swimming speed u and angle between fin and shell θ . (C) Time series of ϕ_f and ϕ_s , the angles between the $X'Y'$ plane and the fin and shell, respectively. (D) Trajectory of the shell leading edge in the global coordinate system through one stroke cycle. Blue lines indicate shell chord orientation. The leading edge coincides with the dot centers. In B and C, the power stroke period is shaded gray.

organisms and is therefore, in a sense, ‘flying sideways’. This unique downward-facing orientation facilitates prey detection because their eyes also look downwards. Differences in appendage mass and surface area also affect their kinematics. The less massive swimming fin exhibits a stroke amplitude of 222 deg while the shell, which is more massive and has a larger surface area, has a stroke amplitude of 170 deg. Heteropod shells are relatively thin and streamlined (Batten and Dumont, 1976; Lalli and Gilmer, 1989; Wall-Palmer et al., 2016) and thus may be particularly adapted to serve as lift-generating propulsive appendages. For example, the triangular spire of *Atlanta inclinata* is tilted to streamline the shell (Richter, 1988). Further the outer keel extending from the shell circumference enhances the propulsive appendage surface area without adding much mass or may serve as a flow control device to reduce drag (Rathakrishnan, 1999), a purpose which minute ornamentation on the shell spire surface of small heteropod species also may serve (Chamberlain and Westermann, 1976). In addition, some heteropod keels are composed of flexible conchiolin, and propulsor flexibility has been shown to increase thrust (Lauder et al., 2006). In sum, despite their differences, the fin and shell are remarkably coordinated and exhibit complex kinematics as evidenced by their use of unsteady hydrodynamic mechanisms such as a double clap-and-fling. The shell thus serves a dual role as a propulsive appendage and as protection from predators. Finally, stroke amplitudes for bilaterally symmetric swimming and flying organisms usually do not exceed 180 deg. Thus, the atlantiid heteropod’s swimming fin stroke amplitude of 222 deg may be the largest in the animal kingdom. The swimming of other atlantiid species with different shell shapes (e.g. *O. inflatus*), of the carinariid heteropods, which have a reduced shell, and of the pterotracheid heteropods, which have lost their shell, ought also to be investigated (Lalli and Gilmer, 1989), as should the swimming ability of heteropods with ocean acidification-induced shell damage.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: F.K., A.E.M., D.W.M.; Methodology: F.K., A.E.M., D.W.M.; Validation: F.K., A.E.M.; Formal analysis: F.K., A.E.M., D.W.M.; Investigation: F.K., A.E.M., D.W.M.; Resources: A.E.M., D.W.M.; Writing - original draft: F.K.; Writing - review & editing: F.K., A.E.M., D.W.M.; Visualization: F.K., D.D.; Supervision: D.W.M.; Project administration: D.W.M.; Funding acquisition: A.E.M., D.W.M.

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Supplementary information

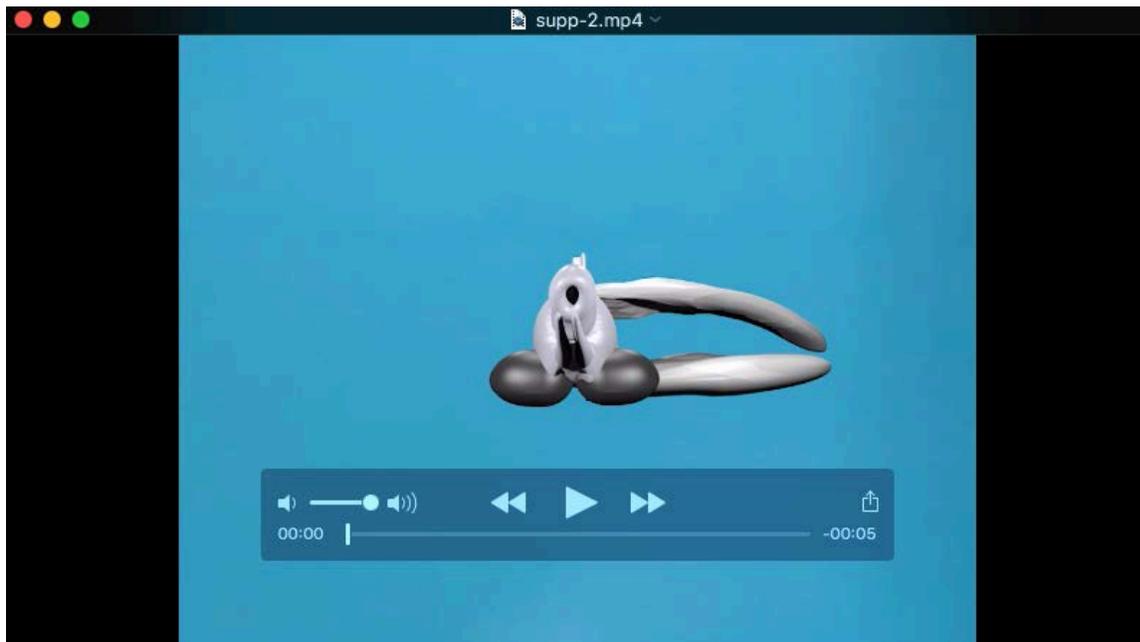
Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.192062.supplemental>

References

- Adhikari, D., Webster, D. R. and Yen, J. (2016). Portable tomographic PIV measurements of swimming shelled Antarctic pteropods. *Exp. Fluids* **57**, 180.
- Batten, R. L. and Dumont, M. P. (1976). Shell ultrastructure of the Atlantidae (Heteropoda, Mesogastropoda) *Oxygyrus* and *Protatlanta*, with comments on *Atlanta inclinata*. *Bull. Am. Museum Nat. Hist.* **157**, 263-310.
- Bednaršek, N., Turling, G. A., Bakker, D. C. E., Fielding, S., Jones, E. M., Venables, H. J., Ward, P., Kuzirian, A., Lézé, B., Feely, R. A. et al. (2012). Extensive dissolution of live pteropods in the Southern Ocean. *Nat. Geosci.* **5**, 881-885.
- Chamberlain, J. A. and Westermann, G. E. G. (1976). Hydrodynamic properties of cephalopod shell ornament. *Paleobiology* **2**, 316-331.
- Chang, Y. and Yen, J. (2012). Swimming in the intermediate reynolds range: kinematics of the pteropod *Limacina helicina*. *Integr. Comp. Biol.* **52**, 597-615.
- De Vera, A. and Seapy, R. R. (2006). *Atlanta selvagensis*, a new species of heteropod mollusc from the Northeastern Atlantic Ocean (Gastropoda: Carinarioidea). *Vieraea* **34**, 45-54.
- Dickinson, M. H. (1996). Unsteady mechanisms of force generation in aquatic and aerial locomotion. *Am. Zool.* **36**, 537-554.
- Ellington, C. P. (1999). The novel aerodynamics of insect flight: applications to micro-air vehicles. *J. Exp. Biol.* **202**, 3439-3448.
- Götz, K. G. (1987). Course-control, metabolism and wing interference during ultralong tethered flight in *Drosophila melanogaster*. *J. Exp. Biol.* **128**, 35-46.
- Jackson, B. E., Evangelista, D. J., Ray, D. D. and Hedrick, T. L. (2016). 3D for the people: multi-camera motion capture in the field with consumer-grade cameras and open source software. *Biol. Open* **5**, 1334-1342.
- Lalli, C. and Gilmer, R. (1989). *Pelagic Snails: The Biology of Holoplanktonic Gastropod Mollusks*. Stanford University Press.
- Land, M. F. (1982). Scanning eye movements in a heteropod mollusc. *J. Exp. Biol.* **96**, 427-430.
- Lauder, G. V., Madden, P. G. A., Mittal, R., Dong, H. and Bozkurtas, M. (2006). Locomotion with flexible propulsors: I. Experimental analysis of pectoral fin swimming in sunfish. *Bioinspir. Biomim.* **1**, 25-34.
- McGowan, J. A. and Fraundorf, V. J. (1966). The relationship between size of net used and estimates of Zooplankton diversity. *Limnol. Oceanogr.* **11**, 456-469.
- Morton, J. E. (1964). Locomotion. *Physiol. Mollusca* **1**, 383-423.
- Murphy, D. W., Adhikari, D., Webster, D. R. and Yen, J. (2016). Underwater flight by the planktonic sea butterfly. *J. Exp. Biol.* **219**, 535-543.
- Orr, J. C., Fabry, V. J., Aumont, O., Bopp, L., Doney, S. C., Feely, R. A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F. et al. (2005). Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* **437**, 681-686.
- Rathakrishnan, E. (1999). Effect of splitter plate on bluff body drag. *AIAA J.* **37**, 1125-1126.
- Richter, G. (1973). Zur Stammesgeschichte pelagischer Gastropoden. *Nat. Mus.* **103**, 265-275.
- Richter, G. (1988). Zur Kenntnis der Gattung *Atlanta*. IV: Die *Atlanta inclinata*—Gruppe (Prosobranchia: Heteropoda). *Arch. Molluskenk. Senckenb. Naturforsch. Ges.* **119**, 259-275.
- Sane, S. P. and Dickinson, M. H. (2001). The control of flight force by a flapping wing: lift and drag production. *J. Exp. Biol.* **2626**, 2607-2626.
- Seapy, R. R. (1990). Patterns of vertical distribution in epipelagic heteropod molluscs off Hawaii. *Mar. Ecol. Prog. Ser.* **60**, 235-246.
- Thiriou-Quievreux, C. (1973). Heteropoda. *Ocean. Mar. Biol. Ann. Rev.* **11**, 237-261.
- Wall-Palmer, D., Smart, C. W., Hart, M. B., Leng, M. J., Borghini, M., Manini, E., Aliani, S. and Conversi, A. (2014). Late Pleistocene pteropods, heteropods and planktonic foraminifera from the Caribbean Sea, Mediterranean Sea and Indian Ocean. *Micropaleontology* **60**, 557-578.
- Wall-Palmer, D., Smart, C. W., Kirby, R., Hart, M. B., Peijnenburg, K. T. C. A. and Janssen, A. W. (2016). A review of the ecology, palaeontology and distribution of atlantiid heteropods (Caenogastropoda: Pterotracheoidea: Atlantidae). *J. Molluscan Stud.* **82**, 221-234.
- Wall-Palmer, D., Metcalfe, B., Leng, M. J., Sloane, H. J., Ganssen, G., Vinayachandran, P. N. and Smart, C. W. (2018a). Vertical distribution and diurnal migration of atlantiid heteropods. *Mar. Ecol. Prog. Ser.* **587**, 1-15.
- Wall-Palmer, D., Burridge, A. K., Goetze, E., Stokvis, F. R., Janssen, A. W., Mekkes, L., Moreno-Alcántara, M., Bednaršek, N., Schiøtte, T., Sørensen, M. V. et al. (2018b). Biogeography and genetic diversity of the atlantiid heteropods. *Prog. Oceanogr.* **160**, 1-25.



Movie 1. High Speed Visualization of Heteropod Swimming. Synchronized movies from three orthogonal cameras of the atlantiid heteropod *Atlanta selvagensis* swimming. Movies acquired at 600 frames per second and played back at 25 frames per second.



Movie 2. Heteropod Swimming Animation. Animation of heteropod swimming created using realistic body and wing kinematics.